

# Mountain Views

Chronicles of the Consortium for Integrated  
Climate Research in Western Mountains

CIRMOUNT



Informing the Mountain Research Community

---

Volume 13, Number 2 • December 2019



Sawtooth Ridge by Autumn Stock.

**Front Cover:** Great Basin Bristlecone Pine by Alli Fitzmorris. Painted for this issue of *Mountain Views*.

**Editor:** Connie Millar, USDA Forest Service, Pacific Southwest Research Station, Albany, California.

**Layout and Graphic Design:** Diane Delany, USDA Forest Service, Pacific Southwest Research Station, Albany, California.

**Back Cover:** Field Frames, Ice Worms and Gray-crowned Rosy Finches, Scott Hotaling.

Read about the contributing artists on page 78.

# Mountain Views

Chronicles of the Consortium for Integrated  
Climate Research in Western Mountains

CIRMOUNT

Volume 13, No. 2, December 2019

[www.fs.fed.us/psw/cirmount/](http://www.fs.fed.us/psw/cirmount/)

## Table of Contents

<b>Editor's Welcome</b>	Connie Millar	1
<b>Articles: High Elevation Pines and Climate</b>		
Taking the Long View and Acting Now—Prioritizing Management of High Elevation Five-Needle Pines	Anna Schoettle	2
The Importance of Whitebark Pine in Greater Yellowstone Treeline Communities and Potential Impacts of White Pine Blister Rust	Diana Tomback and Aaron Wagner	8
Whitebark and Foxtail Pines in the Sierra Nevada—Assessing Stand Structure and Condition	Jonathan Nesmith and Linda Mutch	17
Whitebark Pine Encroachment into Lower Elevation Sagebrush Grasslands in Southwest Montana, USA	Robert Keane and Sarah Flanary	22
Mountain Pine Beetle and Great Basin Bristlecone Pine: A Complicated Story	Barbara Bentz	28
Diversity and Function of Bacterial Endophytes Colonizing the Needles of Subalpine Conifers	Carolin Frank and Lara Kueppers	33
Best Friends Forever (reprinted from <i>The Wildlife Professional</i> )	Bob Keane and Sam Cushman	38
<b>Brevia</b>		
Long-Distance Dispersal, Ice Sheet Dynamics, and Mountaintop Isolation Underlie the Genetic Structure of Glacier Ice Worms	Scott Hotaling	42
<b>Interview</b>		
Malcolm Hughes		43



<b>Voices in the Wind</b>		48
<p>QUESTION: <i>What is the most (or one of the more) unusual phenomenon(a) you have witnessed in your mountain travels or field work? This could be atmospheric, terrestrial, aquatic, or anything ecologically or sociologically unusual. Tell us a little about it and how you reacted.</i></p>		
<p>Martha Apple, Jim Blanchard, Andy Bunn, David Charlet, Deb Finn, Lacey Hankin, Jeff Holmquist, Chrissy Howell, Jessica Lundquist, Greg Pederson, Sarah Stock, Scotty Strachan, Jane Van Gunst, Connie Woodhouse</p>		
<b>News and Events</b>		
Summary Report of IPCC Chapter on High Mountain Areas: “In the Mountains, Climate Change Is Disrupting Everything, From How Water Flows to When Plants Flower” (reprinted from <i>InsideClimateNews</i> )	Bob Berwyn	60
<i>MtnClim 2020</i> - September 14-18, 2020.		67
<i>PACLIM 2021</i> - February 7-10, 2021.		68
Second Conference on the Research and Management of High Elevation Five Needle Pines in Western North America		69
<b>Did You See It?</b>		
Great Basin Bristlecone Pine: A New Population, Dying Trees, and Prometheus Revisited	Connie Millar, David Charlet, and Scotty Strachan	70
<b>Contributing Artists</b>		78
Alli Fitzmorris		
Autumn Stock		
Bob Coats		
<b>Mountain Visions</b>		
Bob Coats		79
Autumn Stock		80
<b>Back Cover: Field Frames</b>	Scott Hotaling	



# EDITOR'S WELCOME

The spring 2019 issue of *Mountain Views Chronicle*, as you might recall, featured diversity and inclusivity in our science and resource community. This was a difficult issue for me to produce, and I know some authors also struggled with their contributions. The subsequent responses I received from readers were overwhelming in their support, and I thank everyone who wrote. In that many comments were more personal than I feel comfortable to share, I want all the authors of that issue to know that their pieces were welcome and had impact.

With this issue I greedily took up some of my favorite (= easy) topics and people to highlight. The main section features high-elevation five-needled pines—their biology, environmental problems, and management options. I am pleased to include articles by many of the main players in the field. I interviewed one of our CIRMOUNT founders and my long-time hero, Malcolm Hughes. I know everyone will find wisdom in Malcolm's words. Always looking for the unusual in my mountain travels, I asked colleagues for the *Voices in the Wind* section to describe a most (or one of the more) unusual phenomenon they have witnessed in the wilds. I hope you enjoy reading these as much as I did. Maybe this will pique your memory to recall your own wild mountain adventures.

The art that bookends this issue especially thrills me to show off. Alli Fitzmorris, who has joined several of our GLORIA (alpine plant monitoring) field surveys, painted the bristlecone pine on our cover especially for this issue, to honor the focus on high-elevation pines. Artist and high-school sophomore, Autumn Stock, shares several of her remarkable paintings of Sierra mountain highlands, as well as a mountain lion view that accompanies her mother, Sarah Stock's, response to my *Voices* question. And I include another mountain poem by our colleague, Bob Coats, whose work I cannot read enough of.

One of the reasons to choose some of my favorite topics for this issue is because that is how I want to end my role as Editor for *Mountain Views*. This autumn 2019 issue is the last that Diane Delany and I will produce. Almost fourteen ago, Henry Diaz

decided that any science consortium as active as CIRMOUNT needed a communication forum, and he launched *Mountain Views Newsletter*, with me as co-editor. After I took over and as the years went by, we expanded to “more than a newsletter”, and I started to include in *Mountain Views Chronicle* (MVC) other kinds of articles in addition to technical science pieces. My vision, as for the MtnClim Conferences, has been to focus on “serious science in an informal context.” For the latter in MVC, I opted to include sections with first-person familiarity, and also mountain art created by members of our community. With these, I hoped to engage MVC as a means to keep our community together and in touch between conferences and meetings where we meet in person, recognizing that informal communication often benefits our science as well as warms our souls. I hope this concept has worked for you.

What next for MVC? One of the reasons for Diane and me to step aside is to allow new (and younger) colleagues to take MVC—or a subsequent version—to different places. It is time for others to guide this effort. We have no expectation that the format we used (page layout style) should continue. Maybe an interactive forum is more useful, or blogging, or any of the other social media opportunities that still elude me, would work. We have had some show of interest from colleagues for coordinating, but need a team to work together. Anyone with interest to participate, even in brainstorming a future for this effort, please write me (cmillar@fs.fed.us).

Diane and I join in sending our thanks to everyone with whom we've worked on MVC over the years, and of course, to the readers, without whom there would be no reason for it.

As the first big winter storms descend on my Mono Lake home near the western edge of the Great Basin, I send you all warmest thoughts for the holidays ahead.

--*Connie Millar*

USDA Forest Service, Pacific  
Southwest Research Station  
Albany, California, USA  
cmillar@fs.fed.us



# ARTICLES

## Taking the Long View and Acting Now— Prioritizing Management of High Elevation Five-Needle Pines

Anna Schoettle

*USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado*



**Anna Schoettle** is a research ecophysiologicalist whose work focuses on understanding responses of high elevation pines to stressors such as climate change and invasive pathogens and developing management strategies to maintain resilience.

Some of the most vulnerable ecosystems include subalpine forests where growing space declines with elevation and species distributions are defined by distinct climatic gradients and biotic interactions. Climate change is projected to be rapid and heightened in these habitats, highlighting the importance of genetic diversity and adaptive capacity of plant species that occupy them (Millar et al. 2007). The North American high elevation five-needle white pines (Fig. 1) define the forest-alpine ecotone in many mountain systems and provide watershed protection and wildlife habitat. They are also being challenged



**Figure 1.** The high elevation five-needle pines. Clockwise from the upper left: Whitebark pine (*Pinus albicaulis*), Rocky Mountain bristlecone pine (*P. aristata*), Great Basin bristlecone pine (*P. longaeva*), Foxtail pine (*P. balfouriana*, photo: Wikipedia), Limber pine (*P. flexilis*, photo: CT Holtz).

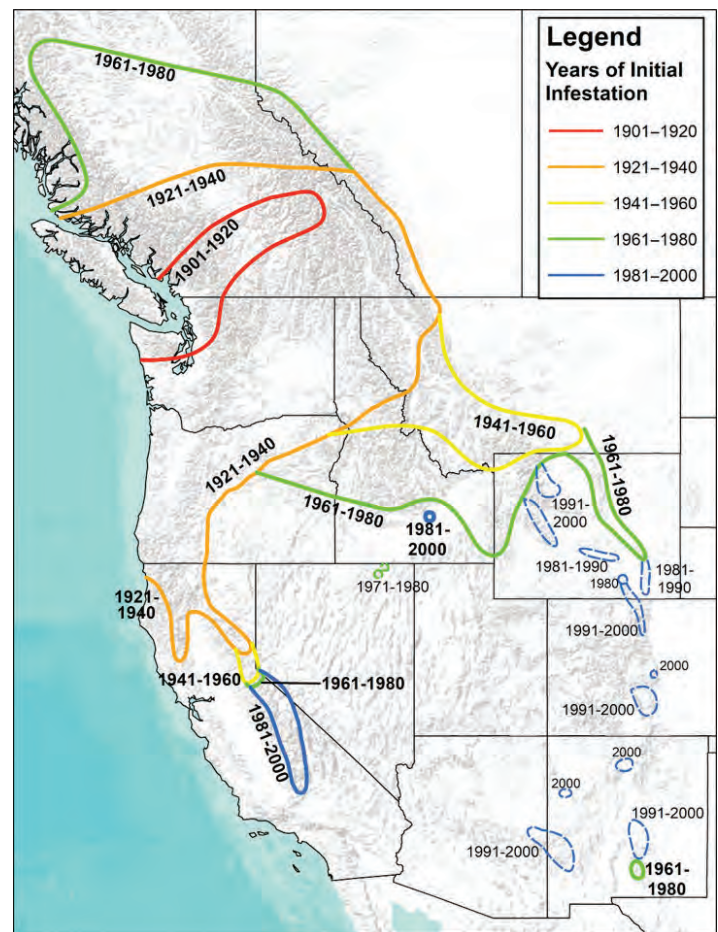




**Figure 2.** *Cronartium ribicola* fruiting on a limber pine branch and the bole of a Rocky Mountain bristlecone pine tree.

be an invasive fungal pathogen, *Cronartium ribicola*, that was introduced to North America in the early 1900s and causes the lethal disease white pine blister rust (WPBR) on five-needle white pines (subgenus *Strobus*; Fig. 2). All the high elevation five-needle white pines of North America are susceptible to *C. ribicola*. The disease spread rapidly through host ranges in the moist forests of the northwest and east and continues to spread, though more slowly, into the drier habitats of the southern Rockies, Great Basin and southwest. WPBR has killed many five-needle white pines in the north although it wasn't detected in Colorado until the late 1990s, and has yet to be found on trees in Utah or most of Great Basin (Fig. 3). As the pathogen continues to spread, and the disease intensifies, the populations currently less affected may too follow the same trajectory as those to the north if effective management intervention is not pursued.

How do we prioritize limited management resources across these remote and harsh landscapes for the greatest benefit to the five-needle pine species and likelihood of sustaining or restoring ecosystem services into the future? Traditionally, management is focused in the crisis areas, those that have the highest mortality or impact. However, if only crisis areas receive attention, the currently healthy five-needle pine ecosystems will progressively degrade as the pathogen continues to spread. Also, the crisis-centric management approach neglects that management options are often not equally effective under different forest conditions and successful restoration is less likely in severely impacted areas. Thus, to manage the high elevation white pine species for future persistence and health, one needs to look beyond the crisis areas and across the full spectrum of ecological conditions. Therefore, both Proactive and Restoration Strategies have been



**Figure 3.** Progression of white pine blister rust on western North American pine hosts. Dashed blue lines indicate finer date resolution within the 20 years of 1981-2000. (From Jacobi et al. 2018; used with permission from HSJ Kearns.)

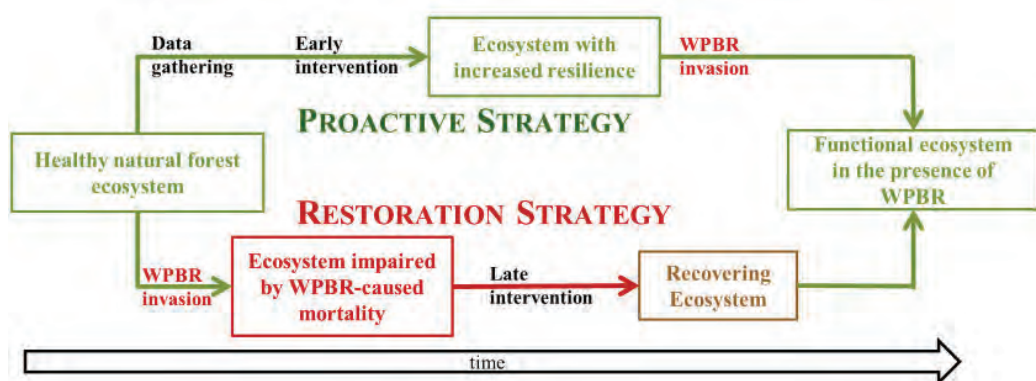


developed for the high elevation five needle pines (Fig. 4). Both have the same long-term management goal of sustaining, restoring and promoting self-sustaining pine populations in the presence of WPBR and other stresses to support ecosystems processes and services into the future (e.g. Schoettle and Sniezko 2007, Keane and Schoettle 2011, Keane et al. 2012, Schoettle et al. 2019a). The opportunities and timing of interventions to achieve this goal are, however, different. The Proactive Strategy approach focuses on augmenting natural processes in healthy pine populations to increase forest resilience to mitigate WPBR impacts upon invasion such that ecosystem function and services are sustained throughout the naturalization process of the rust. The approach of the Restoration Strategy is to restore the already impacted populations and impaired ecosystems to re-establish natural processes and ecosystem services.

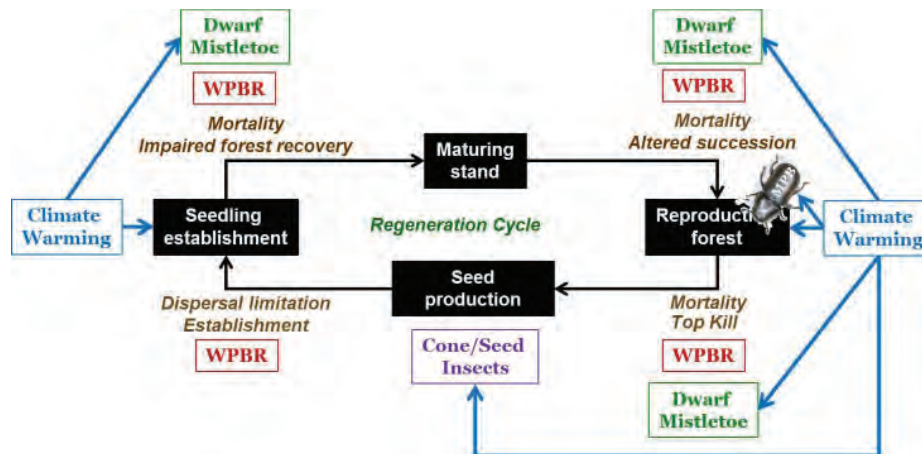
Fortunately, the five-needle pines have some genetic resistance to *C. ribicola* even though they lack a shared evolutionary history with the pathogen. Although the frequency of resistance is very low, it provides the genetic variation on the landscape on which natural selection can operate. Because deployment strategies for increasing the frequency of genetic resistance in natural forests (as opposed to plantation forests) using regeneration management were not well developed, the regeneration for resilience (R4R) framework was advanced to provide a decision structure to prioritize limited resources and utilize natural and artificial regeneration management to offer the best likelihood of success in positioning stands and landscapes to support multi-generational self-sustaining pine populations in the presence of WPBR (Schoettle et al 2019a). The objectives include (1) increasing pine population size to offset WPBR-caused mortality, (2) increasing the frequency of genetic disease resistance traits in pine populations in habitats that enable their expression and durability to reduce future mortality and facilitate population sustainability and recovery, and (3) maintaining pine genetic diversity, adaptive capacity, and population connectivity.

The complexity of natural ecosystems makes mitigating disease impacts more difficult than in managed forests. Sustaining natural forest resilience in the presence of an invasive species requires maintenance of the host population's recovery and adaptive capacity on a landscape spatial and multi-generational temporal scale. Regeneration management, whether it be planting genetically resistant seedling stock, maintaining and augmenting the size of host species populations, or generating a diverse mosaic of stand ages across a landscape, can foster forest adaptation and mitigate impacts caused by invasive species such as *C. ribicola*. Natural regeneration offsets mortality and is therefore a stabilizing force in forests. Regeneration also provides the individuals and genetic combinations to support the dynamic natural selection for genetic resistance and other traits important for long-term adaptation in a changing climate.

Positioning forests for accelerated adaptation to new conditions while sustaining viable population sizes will promote resilience (Schoettle and Sniezko 2007, Keane and Schoettle 2011). Therefore, the management approach must incorporate a long-term and evolutionary perspective which also incorporates adaptation to climate change. Unfortunately for the high-elevation five-needle pines, generation time is very long, and the stressors directly affect all nodes of the regeneration cycle (Fig. 5). The high elevation five-needle pines are tolerant of stresses under which they have evolved but are not well equipped for rapid adaptation to novel stresses such as those imposed by the introduction of *C. ribicola* in a changing climate. Reducing the effect of disease on survival and fecundity by increasing heritable disease resistance is essential to sustaining many of these populations and ecosystems services. Many trials are underway to discern geographic patterns of genetic WPBR resistance to identify parent trees for seed collections and populations for protection. Ultimately, an increase in the frequencies of resistance in populations over the landscape will help establish a new equilibrium from which pine species and associated ecosystems will have the best opportunity to exist and function in the presence of the permanent residence of *C. ribicola*.



**Figure 4.** A schematic of pathways for facilitating sustainable natural forest ecosystems in the presence of a nonnative invasive species.



**Figure 5.** High elevation five-needle pine regeneration cycle and damage agents (from Schoettle et al. 2019b). White pine blister rust (WPBR) affects the regeneration cycle at all points (brown text), while mountain pine beetle (MPB) only impacts larger mature trees, and cone and seed insects only impact seed production. Dwarf mistletoe can infect trees of all ages. Climate change may directly impact insect populations and seedling establishment and tree growth and may indirectly affect other interactions within the cycle.

Ecological condition and context determine the likelihood of success of management interventions to mitigate impacts of WPBR. In populations heavily impacted by WPBR, the remaining seed trees are too few to support natural regeneration even with management intervention. Likewise, rust pressure can be so high that it will overcome the expression of WPBR-resistance, reducing the efficacy of artificial regeneration with resistant stock as well. Management has a low probability of successfully rebuilding a population under these conditions; triaging these areas in favor of managing areas with less rust pressure may be a better investment. In threatened but currently healthy populations, interventions to increase natural resistance can help increase population size while early planting of seedling stock with disease resistance traits will enable them to begin to mature and offset mortality of the reproductive overstory trees as the disease intensifies over time. The R4R framework encourages looking beyond the crisis areas for other opportunities to conserve the species and prevent population extirpation.

These interventions entail integrating genetic resistance information into an ecological context to prioritize and inform regeneration interventions to restore and sustain healthy landscapes. The R4R decision framework helps guide when, where, and how to utilize regeneration to increase forest resistance and resilience to invasive nonnative pests and pathogens in natural forests. The R4R framework for WPBR integrates science-based information on (1) current forest health condition, (2) genetic resistance to WPBR, (3) WPBR risk and hazard, and (4) host population dynamics to prioritize when and where interventions will have the greatest likelihood of success in sustaining high elevation forests in the presence of

WPBR (Schoettle et al. 2019a). It highlights opportunities across stand conditions and discourages management in areas where management has a low probability of success. The framework has been applied in the development of the Proactive Limber Pine Conservation Strategy in the Greater Rocky Mountain National Park Area (Schoettle et al. 2015, 2019b) and prioritizing treatments for a Restoration Strategy for whitebark pine in a pilot area within the Crown of the Continent Ecosystem (Jenkins et al. 2019).

Rocky Mountain National Park (RMNP) is at the infection front for *C. ribicola* in Northern Colorado and the park has a responsibility to prevent ecosystem impairment. The Proactive Limber Pine Conservation Strategy for the Greater Rocky Mountain National Park Area is an outcome of a partnership between RMNP and the USDA Forest Service. The Strategy focuses on timing specific monitoring and interventions efforts to inform management to sustain healthy limber pine populations and ecosystems during invasion and naturalization of WPBR, thereby putting limber pine on a trajectory that does not lead to ecosystem impairment in the future (Schoettle et al. 2015, 2019b, Cleaver et al. 2017). During this collaboration, a high frequency of complete resistance to WPBR in limber pine populations in RMNP and surrounding areas was discovered revealing a unique feature of this area's ecology (Schoettle et al. 2014). That we have this information and the other site-based genetic and disturbance ecology information before the limber pine populations have been invaded by WPBR is unique. This situation justified developing a conservation strategy specific to the greater RMNP area.

The major focal areas for management activities are (1) Promote ex situ and in situ conservation—continue and expand efforts to collect and archive limber pine genetic diversity through seed collections and protect limber pine trees from mountain pine beetle, WPBR, and fire to minimize mortality when and where land designations and management objectives permit; (2) Increase population size and sustain genetic diversity—increase the number of limber pine trees on the landscape through planting or seeding, or both, immediately to offset future mortality and to sustain viable self-sustaining populations; (3) Locate treatments to maintain durability of complete WPBR resistance—minimize selective pressure on the rust by planting trees with a range of susceptibilities only in low-WPBR-risk areas to reduce the probability of the proliferation of genotypes virulent to the complete resistance in limber pine; (4) Discover, develop, and deploy local quantitative WPBR-resistant sources—research quantitative (polygenic) WPBR resistance types in limber pine in the greater RMNP area and establish a clone bank of these genotypes (which can be protected from fire and other stresses) to provide seed for future plantings and (5) Monitor pines and rust—monitor for limber pine health, early detection of WPBR, and WPBR virulence. The Proactive Conservation Strategy was adopted by the Park in 2015 and has served as a model for ongoing proactive conservation efforts for Rocky Mountain bristlecone pine, Great Basin bristlecone pine, as well as southwestern white pine, and can be applied to other healthy portions of the distribution of limber pine and for those for foxtail pine and whitebark pine also.

The R4R framework has also been applied to the very heavily impacted area of the Crown of the Continent Ecosystem (CCE - northern Montana, southern British Columbia and Alberta; <https://www.crownmanagers.org/five-needle-pine-working-group>). The decision space is constrained by high impacts, but the landscape can still be stratified by forest condition and context to allocate treatment resources to have the highest likelihood of restoring whitebark pine within the CCE. It is well documented that five-needle pine forests in the CCE have declined significantly due to a combination of biotic and abiotic stressors. The High Five Working Group of the Crown Managers Partnership was formed to prioritize and advance collective efforts to effectively monitor, conserve, and restore five-needle pines across the complex jurisdictional boundaries of the CCE. The working group developed a proof of concept methodology for whitebark pine restoration within a US portion of the CCE. Future applications will cover the full CCE including both whitebark and limber pine. The strategy integrates existing data sources, expert opinion and modeling within a GIS platform. Areas were first identified where whitebark pine is capable of existing on the landscape and then rated related to (1) their conservation value as defined as those areas currently providing

ecosystem services or capable of providing ecosystem services, and then (2) the threats/stressors that have reduced, or are likely to reduce, conservation value were identified and quantified. Restoration actions were then prioritized based on the likelihood of successfully benefitting whitebark pine under each of the stressor's levels such that areas where stressors negatively impacted the potential success of the treatments were assigned a lower priority using an adaptation of the R4R framework. Finally, all factors were integrated, and priority core areas are defined for focused restoration in the future. The outcome of this effort is a draft methodology to identify priority areas for restoration within the CCE and for the National Whitebark Pine Restoration Strategy within the USA and can serve as a model for restoration strategies for other areas impacted by WPBR including the northern distributions of whitebark, limber and foxtail pines.

Timely management approaches that incorporate both ecological context and an evolutionary perspective increase the likelihood of successfully sustaining high-mountain pine ecosystems into the future. The R4R framework highlights opportunity for increasing the resilience of both WPBR-threatened and impacted high elevation five-needle pines ecosystems across western North America. In healthy but threatened ecosystems, acting now will increase forest resilience to position the ecosystems to develop fewer impacts, and need less restoration, in the future and the R4R framework encourages managers not to wait until the ecosystems are impaired to begin managing for increased resilience. In impacted systems, R4R recommended prioritizing management in locations that have the greatest likelihood of successfully restoring function and to look for opportunities beyond the heavily impacted areas that often attract most of the attention but have a poor prognosis. Spreading treatments over a diversity of current stand conditions and WPBR hazards will increase the likelihood that some populations avoid extirpation and sustain the species. When prioritizing limited resources, context is critical. Accepting that some habitats may not support sustainable populations in the future even with intervention is essential for making good treatment investment decisions. The future of the high elevation five-needle pine ecosystems may depend on it.

### Acknowledgements

I thank and recognize that this work has been enriched by collaborations and discussions with Kelly Burns, Mike Antolin, Stu Field, Richard Snieszko, Jeff Connor, Christy Cleaver, Melissa Jenkins, Linh Hoang, Sabine Mellman-Brown, Katie Renwick, Angelia Kegley, Bill Jacobi, Kristen Waring, Betsy Goodrich, Holly Kearns, John Schwandt, Christine Holtz, Sparkle Malone, John Guyon, Gregg DeNitto, Gretchen Baker, Brian Verhulst and many others.



## References

- Cleaver C.M., Burns K.S., and Schoettle A.W. 2017. Limber Pine and White Pine Blister Rust Monitoring and Assessment Guide for Rocky Mountain National Park. Final Report prepared by Rocky Mountain Research Station for Rocky Mountain National Park. Inter-Agency Agreement 15-IA-11221633-157. 28p. <https://www.fs.usda.gov/treearch/pubs/56244>
- Jacobi W.R., Kearns H.S.J., Cleaver C.M., Goodrich B.A., and Burns K.S. 2018. Epidemiology of white pine blister rust on limber pine in Colorado and Wyoming. *Forest Pathology DOI: 10.1111/efp.12465*
- Jenkins M.B., Schoettle A.W., Hoang L., Incashola T., LaFleur D., Mellman- Brown S., Renwick K., Sissons R., Keane R., Meyer E., Lozeau J., et al. In press. Project Summary – Crown of the Continent Ecosystem Whitebark Pine Restoration Strategy 2019 Pilot. Will be available at <https://www.crownmanagers.org/five-needle-pine-working-group>
- Keane R.E and Schoettle A.W. 2011. Strategies, tools, and challenges for sustaining and restoring high elevation five-needle white pine forests in western North America. In: *The Future of High-Elevation, Five-Needle White Pines in Western North America: Proceedings of the High Five Symposium*. 28-30 June 2010, Missoula, MT. Edited by R.E. Keane, D.F. Tomback, M.P. Murray, C.M. Smith. USDA For. Serv. Proc. RMRS-P-63. pp 276-294.
- Keane R.E., Tomback D.F., Aubry C., Bower A., Campbell E., Jenkins M., Manning M., McKinney S., Murray M., Perkins D., Reinhart D., Ryan C., Schoettle A.W., and Smith C.M. 2012. A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). USDA For. Serv. Gen Tech Rep RMRS-GTR-279. 108 p.
- Millar C.I, Stephenson N.L, and Stephens S.L. 2007. Climate change and forests of the future: Managing in the face of uncertainty. *Ecol Appl* 17:2145–2151.
- Schoettle A.W., Burns K.S., Cleaver C.M., and Connor J.J. 2019b. Proactive Limber Pine Conservation Strategy for the Greater Rocky Mountain National Park Area. General Technical Report RMRS-GTR-379. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 81 p. [https://www.fs.fed.us/rm/pubs\\_series/rmrs/gtr/rmrs\\_gtr379.pdf](https://www.fs.fed.us/rm/pubs_series/rmrs/gtr/rmrs_gtr379.pdf)
- Schoettle A.W., Cleaver C.M., Burns K.S., and Connor J.J. 2015. Limber pine conservation strategy for Rocky Mountain National Park. On file as an active management guide at Rocky Mountain National Park.
- Schoettle A.W., Jacobi W.R., Waring K.M, and Burns K.S. 2019a. Regeneration for Resilience Framework to support regeneration decisions for species with populations at risk of extirpation by white pine blister rust. *New Forests* 50: 89–114. <https://doi.org/10.1007/s11056018-9679-8>
- Schoettle A.W., Klutsch J.G., and Sniezko R.A. 2012. Integrating regeneration, genetic resistance and timing of intervention for the long-term sustainability of ecosystems challenged by non-native pests—A novel proactive approach. In: *Disease and Insect Resistance in Forest Trees: Proceedings of the 4th International Workshop on the Genetics of Host-Parasite Interactions in Forestry*. August 2011, Eugene OR. Techn coords. Sniezko, R.A., A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J.M. Alexander, and S.J. Frankel. USDA For. Serv. Gen Tech Rep PSW-GTR-240. Pp. 112-123.
- Schoettle A.W. and Sniezko R.A. 2007. Proactive intervention to sustain high elevation pine ecosystems threatened by white pine blister rust. *Journal of Forest Research* 12:327-336.
- Schoettle A.W., Sniezko R.A., Kegley A., and Burns K.S. 2014. White pine blister rust resistance in limber pine: Evidence for a major gene. *Phytopathology* 104:163-173.

## The Importance of Whitebark Pine in Greater Yellowstone Treeline Communities and Potential Impacts of White Pine Blister Rust

Diana Tomback and Aaron Wagner  
*Department of Integrative Biology*  
*University of Colorado Denver, Denver, Colorado*



**Diana Tomback** is Professor of Integrative Biology with expertise in the evolution, ecology, and population biology of bird-dispersed pines and their corvid dispersers and in the conservation and restoration of five-needle white pines in western North America.

**Aaron Wagner** recently completed his M.S. in the Tomback Lab, where he also served as research assistant. He now works in the corporate sector as a data manager.

### Abstract (Wagner, Tomback, Resler and Paning 2018)

Temperate zone treeline communities provide important ecosystem services, such as snow retention, soil stabilization, and wildlife habitat. In the northern Rocky Mountains of the U.S. and Canada, whitebark pine (*Pinus albicaulis*) is a functionally important species in treeline communities, especially on arid aspects with poor soils. The introduced fungal pathogen *Cronartium ribicola*, which causes white pine blister rust, has led to extensive whitebark pine mortality nearly rangewide. Although whitebark pine is distributed widely throughout the Greater Yellowstone Ecosystem (GYE), its treeline communities are largely unstudied. We examined four treeline communities within the GYE, both east and west of the Continental Divide, to assess structure and composition, prevalence and functional role, the relationship between composition and mesoclimate, and blister rust infection incidence. We found that (1) whitebark pine frequently serves as the majority overall, solitary, and leeward tree island conifer, (2) the prevalence of different tree species in the windward position in tree islands, and thus their potential as tree island initiators, may be predicted from their relative abundance as solitary trees, and (3) white pine blister rust infection incidence ranged from 0.6% to 18.0% across study areas and, in many communities, poses a threat to treeline structure and ecosystem services provision. Increasing blister rust resistance in nearby subalpine whitebark pine communities through seedling planting or direct seeding projects should eventually result in higher levels of blister rust resistance in whitebark pine in treeline communities.

### Treeline Studies

The Tomback Forest Ecology Laboratory, University of Colorado Denver, focuses on the ecology, population biology, and conservation of whitebark pine (*Pinus albicaulis*) and related high elevation five-needle white pines. For more than a decade, we have collaborated with Lynn Resler, Department of Geography, Virginia Tech, and with George Malanson, Department of Geography, University of Iowa, to examine the ecological role of whitebark pine, a stress-tolerant conifer (e.g., McCune 1988) in treeline communities of the U.S. and Canadian Rocky Mountains. We asked how whitebark pine decline from the invasive pathogen *Cronartium ribicola*, which causes white pine blister rust, might potentially impact the composition and ecological function of Rocky Mountain treeline communities, especially east of the Continental Divide. The work, supported primarily by NSF and the U.S. Forest Service, has spanned the latitudinal distribution of whitebark pine from Willmore Wilderness Park, Alberta, Canada to the southern Wind River Range, WY, USA. Key papers from this work include Pyatt et al. (2016), Resler and Tomback (2008), Resler et al. (2014), Smith-McKenna et al. (2013, 2014), Tomback and Resler (2007), and Tomback et al. (2016a, 2016b).

Funding for the work reported here was provided by the U.S. Forest Service (Shoshone National Forest, FS-CS-11011100-029) to DFT, and a University of Wyoming and U.S. Department of Interior, National Park Service Award (award ID 1002614E-VATECH) to LMR.

## Summary

The structure and composition of treeline communities in some geographic regions of western North America are not well known. In the Greater Yellowstone Ecosystem (GYE), subalpine conifers include whitebark pine, Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*). Previous studies from the Beartooth Plateau in the northeastern GYE indicate that all four conifers form krummholz treeline communities east of the Continental Divide but vary in relative abundance (Tomback et al. 2016a). In the Line Creek Plateau Research Natural Area (RNA), Custer Gallatin and Shoshone National Forests, whitebark pine was the most frequent windward conifer in tree islands, providing protection through facilitation interactions for species established in its lee (Tomback et al. 2016b, Resler et al. 2014). Information about the structure and composition of treeline communities in most other regions of the GYE is lacking.

Facilitation, defined as a positive interaction between an individual of the same or different species of plant or between a protective (“nurse”) object and a plant (e.g., Callaway 2002), often shapes plant community spatial structure in stressful environments (Bertness et al. 1994, Lortie et al. 2004, Brooker et al. 2008). At treeline, solitary trees may establish leeward of protective objects, such as rocks or plants, or in topographic depressions, which facilitate seed and seedling survival (Fig. 1; Hättenschwiler and Smith 1999, Resler 2006, Pansing et al. 2017). Once established, these trees ameliorate wind (Alftine

and Malanson 2004, Resler et al. 2001), reduce solar radiation exposure (Germino et al. 2006), decrease soil temperature variation (Pyatt et al. 2016), and improve water availability (Callaway 1998) in leeward microsites. Tree islands form when the initiator facilitates the establishment of conifers in its lee (Marr 1977).

Whitebark pine functions as an important subalpine and treeline conifer and tree island initiator in the Rocky Mountains of the U.S. and Canada (Tomback et al. 2014, 2016a). Moderately shade-intolerant and slow-growing, whitebark pine is out-competed by faster-growing conifers on productive sites (Arno and Hoff 1990). However, a comparatively high water-use efficiency and carbon gain relative to other treeline conifers, hardy seedlings, and efficient seed dispersal allow it to tolerate arid, windy conditions and poor soils (Bansal et al. 2011, Tomback et al. 2016b, Pyatt et al. 2016). Whitebark pine relies on Clark’s nutcracker (*Nucifraga columbiana*) for seed dispersal. In late summer and fall, nutcrackers bury caches of ripe pine seeds for future retrieval throughout the montane landscape, as far as ~30 km from parent trees, often in recently burned and high elevation terrain, including treeline and tundra (Tomback 1982, 1986, Hutchins and Lanner 1982, Lorenz and Sullivan 2009). Unretrieved seeds may germinate following snowmelt or rain, leading to regeneration. Moreover, nutcrackers often cache seeds near nurse objects, which improves seedling survival at treeline (Tomback 1978, Resler et al. 2005, Resler and Tomback 2008, Pansing et al. 2017).



**Figure 1.** Facilitation at treeline. Whitebark pine (*Pinus albicaulis*) established in the lee of a rock on Tibbs Butte, Shoshone National Forest, Wyoming. Photo: E.R. Pansing.

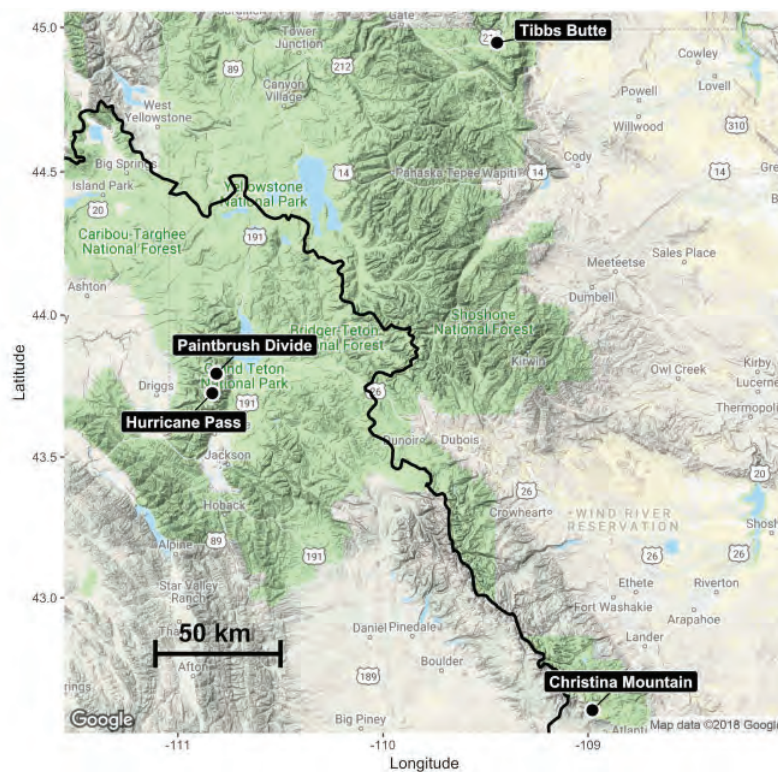


Throughout much of whitebark pine's range, the disease white pine blister rust—resulting from infection by the exotic fungal pathogen, *Cronartium ribicola*—has caused extensive mortality (McDonald et al. 2001, Tomback and Achuff 2010, Schwandt et al. 2010). Blister rust can kill whitebark pine at all life stages and reduce cone production by damaging tree canopies (McDonald et al. 2001). Due to significant declines in many regions from white pine blister rust and other threats, whitebark pine is a candidate for listing under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2011) and listed in Canada under the Species at Risk Act (Government of Canada 2012). Because establishment of whitebark pine at treeline depends on seed dispersal from subalpine communities, and the ecological function of whitebark pine at treeline depends on the occurrence of healthy trees, white pine blister rust may limit the development of treeline communities in some areas. In the GYE, subalpine whitebark pine blister rust incidences ranged from 20% to 30% (GYWPMWG 2017). A treeline survey at Line Creek Plateau RNA estimated blister rust infection incidence at 19.2% (Smith-McKenna et al. 2013).

In this study, we examined four treeline communities both east and west of the Continental Divide within the GYE. Our objectives were as follows: (1) describe community structure and composition, (2) assess the ecological role of whitebark

pine (solitary, leeward, initiator), (3) explore the relationship between solitary conifer abundance and tree island initiation, (4) examine nurse object associations with solitary tree and tree island initiator establishment, (5) determine how differences in mesoclimate among the study areas might account for variation in community structure and composition, and (6) evaluate the incidence of white pine blister rust and the potential benefit of restoration.

We performed community composition and climatic assessments for four treeline communities in the GYE (Fig. 2). The Paintbrush Divide study area, Grand Teton National Park, is at the upper end of Paintbrush Canyon. Hurricane Pass, also in Grand Teton National Park, is proximal to the terminal moraine of the Schoolroom Glacier. The Tibbs Butte study area, Shoshone National Forest, is 3.7 km southeast of the Beartooth Pass summit. Christina Mountain, Shoshone National Forest, is near the southernmost end of the Wind River Range. Both study areas in Grand Teton National Park are west of the Continental Divide and Tibbs Butte and Christina Mountain are east of the Continental Divide. In July 2014 and 2015, we established 225 m<sup>2</sup> assessment plots at each study area as follows: Paintbrush Divide (n = 20, circular: r = 8.46 m), Hurricane Pass (n = 20, circular: r = 8.46 m), Tibbs Butte (n = 12, square: 15 x 15 m), and Christina Mountain (n = 30, square: 15 m x 15 m). We generated



**Figure 2.** Study area geographic locations. The geographic location of study areas within the GYE. The black line traces the Continental Divide. Map base courtesy of Google Maps.

random points for plot placement using ArcGIS (Paintbrush Divide and Hurricane Pass) (ESRI 2012) or the *splancs* package in R (R Core Team 2017, Rowlingson and Diggle 2017).

For each plot, we classified conifers by tree island membership (i.e., solitary tree or tree island component), ecological role (i.e., tree island initiator, leeward tree island conifer, or solitary tree), and species. We defined a ‘tree island’ as two or more contiguous conifers with spatially overlapping foliage. The windward conifer of each tree island was designated as the initiator if integrated within the tree island (i.e., not a separate, younger tree), and all other trees categorized as leeward. To determine prevailing wind direction, we examined the flagged branches of conifers within the plot or in the immediate vicinity. Trees spatially isolated from other conifers (i.e., having canopies that did not overlap with any other conifers) were classified as solitary. Following the methods of Resler and Tomback (2008), we characterized multi-stem growth forms of whitebark pine as a single individual. We also categorized tree island initiators and solitary conifers based on windward nurse object type (i.e., rocks, topographic depressions, and woody plants). We defined ‘nurse objects’ as potentially protective objects or microtopography directly windward of solitary trees or tree island initiators. We designated conifers with the apparent absence of a nurse object (or no protective microtopography) as ‘unprotected’. Finally, we evaluated each whitebark pine for blister rust infection by thoroughly examining stems and canopies. The criteria for classifying a stem as infected were at least one active canker, or three of five symptoms from the following list: 1) inactive canker, 2) stem swelling, 3) branch flagging (i.e., dead foliage), 4) rodent gnawing, and 5) oozing sap (e.g., Burns et al. 2008).

To assess mesoclimate, we obtained 30 years (1985 – 2015) of mean daily temperature and precipitation data using open-source Precipitation Elevation Regressions on Independent Slopes Model (PRISM) information (PRISM Climate Group 2015). For each study area and year, we retained only the growing season data, which we defined as the temporal period between mean daily air temperatures of  $>5$  °C for  $>5$  consecutive days and

mean daily air temperatures of  $<5$  °C for  $>5$  consecutive days (e.g., Körner and Paulsen 2004).

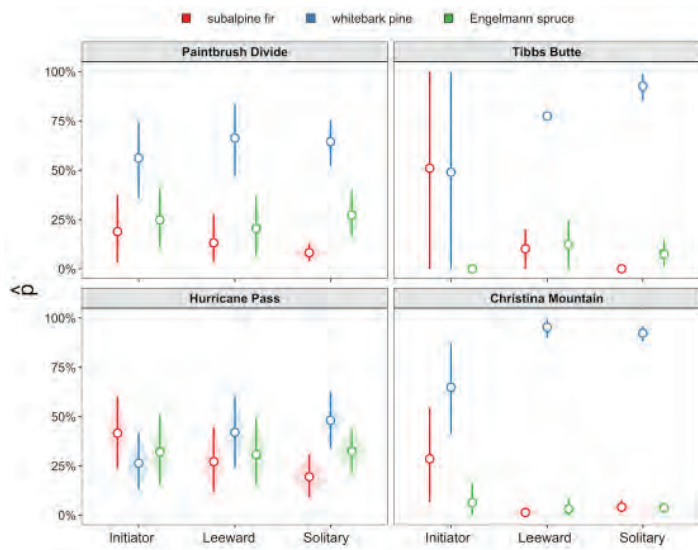
For data analysis, we considered the plot to be the sampling unit and converted raw counts to raw relative abundances for all assessment plots. We conducted all statistical analyses using R (version 3.4.2; R Core Team 2017). For each study area, we bootstrapped the per-plot relative abundance data—that is, we sampled randomly with replacement over the size of the sample (e.g., 20 plots on Paintbrush Divide) and calculated the mean for each of 5000 iterations. This process generated a sampling distribution of mean relative abundances for each variable of interest. We then calculated the mean of each sampling distribution to identify the percent relative abundance parameter estimate (*p hat*). We used the 2.5% and 97.5% quantiles of each sampling distribution to determine the lower and upper boundary, respectively, of the 95% confidence interval (CI; Calmettes et al. 2012). We also bootstrapped the PRISM growing season data (5000 iterations) to generate sampling distributions for mean growing season length, temperature, and precipitation. We calculated the mean of each sampling distribution to estimate the average growing season length (*L hat*), temperature (*T hat*) and precipitation (*P hat*) for each study area. Finally, we estimated the 95% CI by calculating the 2.5% and 97.5% quantiles of each sampling distribution as the lower and upper boundary.

We found that there were more solitary conifers relative to tree island conifers at both study areas east of the Continental Divide, Tibbs Butte and Christina Mountain. At those two locations, solitary conifers comprised 95.5% (95% CI: 88.0%, 100.0%) and 74.5% (95% CI: 61.5%, 85.9%), respectively, of all conifers assessed. We did not detect any differences in the relative abundance of solitary conifers and tree island conifers at the study areas located west of the Continental Divide, Paintbrush Divide and Hurricane Pass. Species comprising the treeline communities at all four study areas included whitebark pine, Engelmann spruce, and subalpine fir. The relative abundance of whitebark pine was significantly greater than that of Engelmann spruce and subalpine fir at three of four study areas: Paintbrush Divide, Tibbs Butte, and Christina Mountain (Table 1).

**Table 1 Tomback & Wagner**

Study Area	$\hat{p}$ whitebark pine (95% CI)	$\hat{p}$ subalpine fir (95% CI)	$\hat{p}$ Engelmann spruce (95% CI)
Paintbrush Divide	57.9% (43.8%, 70.3%)	14.4% (7.2%, 22.8%)	27.7% (17.4%, 39.5%)
Hurricane Pass	42.0% (30.4%, 54.4%)	25.4% (17.1%, 34.1%)	32.6% (23.3%, 43.1%)
Tibbs Butte	91.3% (84.3%, 97.5%)	1.1% (0.0%, 3.1%)	7.6% (1.4%, 15.0%)
Christina Mountain	90.3% (85.6%, 94.5%)	6.5% (2.8%, 10.9%)	3.2% (1.5%, 5.2%)

**Table 1.** Overall community composition parameter estimates. Parameter estimates and CIs for species relative abundance by study area.

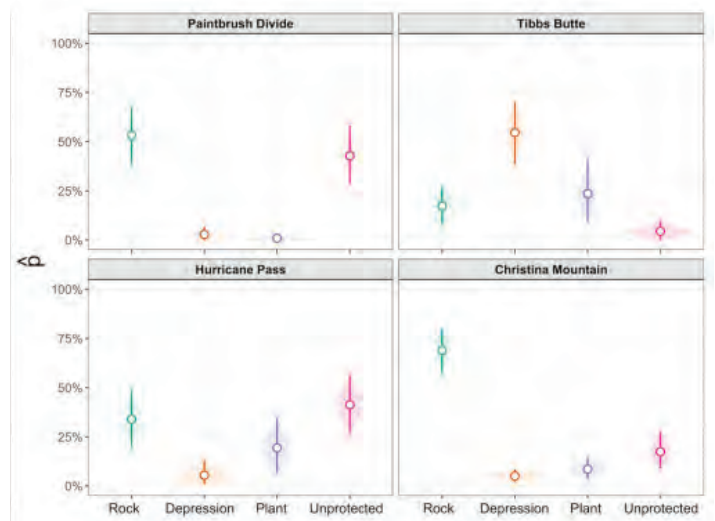


**Figure 3.** Parameter estimates for community composition by ecological role. Conifer species relative abundance by ecological role. Shaded centers delineate sampling distributions, circles indicate parameter estimates, and vertical lines delineate 95% CIs.

Our analysis of community composition by ecological role revealed that whitebark pine was the most abundant solitary and leeward conifer at three of the four study areas: Paintbrush Divide, Tibbs Butte, and Christina Mountain (Fig. 3). At those locations respectively, whitebark pine comprised 64.5% (95% CI: 52.1%, 75.3%), 92.6% (95% CI: 85.2%, 98.8%), and 92.3% (95% CI: 88.2%, 96.1%) of all solitary conifers; it comprised 66.3% (95% CI: 46.8%, 83.4%), 77.5% (95% CI: 75.0%, 80.0%), and 95.4% (95% CI: 89.7%, 99.5%) of all leeward conifers. At Hurricane Pass, we did not observe a majority solitary or leeward conifer species.

Our analysis did not reveal any species as a majority tree island initiator at any study area. We found that whitebark pine's relative abundance as a tree island initiator did not differ from its relative abundance as a solitary tree at any study area with the exception of Hurricane Pass. There, subalpine fir served as tree island initiator more than expected given its relative abundance as a solitary tree.

Nurse objects varied in relative abundance by type—rocks, topographic depressions, woody plants, and no nurse object (i.e., unprotected)—across study areas. West of the Continental Divide, the relative abundance of unprotected solitary or tree island conifers was never less than that of any other nurse object type (Fig. 4). East of the Continental Divide, however, the relative abundance of unprotected solitary conifers and tree island initiators was always less than that of rocks and woody plants, and only exceeded that of topographic depressions at Christina Mountain.



**Figure 4.** Parameter estimates for nurse object facilitation. Nurse object relative abundances. Shaded curves delineate sampling distributions, circles indicate parameter estimates, and vertical lines delineate 95% CIs.

The mean white pine blister rust infection incidence was highest for the two study areas west of the Continental Divide: 18.0% (95% CI: 9.8%, 27.4%) at Paintbrush Divide and 14.4% (95% CI: 6.2%, 23.9%) at Hurricane Pass. The infection incidence for the two study areas east of the Divide were 0.6% (95% CI: 0.0%, 1.8%) at Tibbs Butte, and 2.0% (95% CI: 0.5%, 3.8%) at Christina Mountain.

From 1985 to 2015, mean growing season lengths varied by study area, ranging from 115 days (95% CI: 107 days, 123 days) at Tibbs Butte to 136 days (95% CI: 129 days, 143 days) at Christina Mountain (Table 2). Estimates for mean growing season temperature (1985 to 2015) ranged from 8.7 °C (95% CI: 8.3 °C, 9.2 °C) at Tibbs Butte to 9.9 °C (95% CI: 9.5 °C, 10.3 °C) at Paintbrush Divide. For mean growing season precipitation from 1985 to 2015, estimates ranged from 19.2 cm (95% CI: 16.3 cm, 22.1 cm) for Tibbs Butte to 28.1 cm (95% CI: 23.5 cm, 33.0 cm) for Hurricane Pass. Study areas west of the Continental Divide had higher mean growing season precipitation estimates relative to study areas east of the Continental Divide.

In general, we found that whitebark pine is locally abundant, regionally common, and frequently serves as the majority conifer in the GYE treeline communities we sampled. Our results also show that solitary whitebark pine define much of the treeline community structure and composition east of the Continental Divide. The general abundance of whitebark pine at treeline within the GYE is consistent with studies conducted across the Central and Northern Rocky Mountains, which establish it as a prevalent treeline conifer (e.g., Tomback et al. 2014, 2016a).



Table 2 Tomback &amp; Wagner

Study Area	$\bar{L}$ (95% CI)	$\bar{T}$ (95% CI)	$\bar{P}$ (95% CI)
Paintbrush Divide	136 days (129 days, 142 days)	9.9 °C (9.5 °C, 10.3 °C)	27.6 cm (23.8 cm, 31.5 cm)
Hurricane Pass	128 days (120 days, 136 days)	9.0 °C (8.5 °C, 9.4 °C)	28.1 cm (23.4 cm, 33.0 cm)
Tibbs Butte	115 days (107 days, 123 days)	8.7 °C (8.3 °C, 9.2 °C)	19.2 cm (16.3 cm, 22.1 cm)
Christina Mountain	136 days (129 days, 143 days)	9.1 °C (8.7 °C, 9.5 °C)	19.4 cm (16.3 cm, 22.5 cm)

**Table 2.** Mesoclimate parameter estimates. Parameter estimates and CIs for mean annual growing season length ( $L_{hat}$ ), mean daily growing season temperature ( $T_{hat}$ ), and mean annual growing season precipitation ( $P_{hat}$ ) from 1985 through 2015, by study area.

Whitebark pine's high relative abundance compared to other treeline species east of the Continental Divide underscores its ability to survive harsh conditions. Continental climates that shape these treeline landscapes impose greater annual temperature variation (White et al. 1997), aridity (Manabe and Broccoli 1990), and downslope winds (Griggs 1938) relative to climates with maritime influence. Complex, and mostly downslope, winds also highlight the importance of "directed" upslope nutcracker seed dispersal. Other treeline conifers depend on wind for seed dispersal from subalpine to treeline, which has a higher element of chance, particularly with respect to seeds ending up in treeline "safe sites" (Malanson et al. 2007).

Our results revealed that the relative abundance of solitary trees by species was similar to the relative abundance of tree island initiators by species at three of four study areas. This finding is consistent with a meta-analysis by Tomback et al. (2016a), which showed the abundance of solitary whitebark pine and subalpine fir predicted their tree island initiator abundance across the Central and Northern Rocky Mountains. Further, Pyatt et al. (2016) measured biophysical conditions leeward of treeline conifers and found that species-specific differences in protection were not strongly evident. Tree island initiation appears to be related to the relative abundance of solitary trees at a landscape-scale and not necessarily better microclimate amelioration. By this logic, it follows that whitebark pine's importance in community structure and composition is likely abundance-based (i.e., more opportunities to facilitate tree island development). Understanding the processes leading to whitebark pine's high abundance clarifies its dominant role in community structure and composition.

Differences in the facilitation of solitary trees and tree island initiators by windward nurse object type may reflect variation in microsite availability and/or mesoclimatic conditions among study areas. For the former, the availability of some microsites may reflect surface roughness elements (e.g., rocks) or the result of fine-scale geomorphic processes (e.g., topographic depressions). When examining solitary tree and tree island

initiator facilitation by nurse object type, we in fact found differences that may be based on community location relative to the Continental Divide. At Tibbs Butte and Christina Mountain, which are both east of the Divide, the relative abundance of solitary conifers and tree island initiators in unprotected microsites was lower than that of protected microsites (i.e., topographic depressions at Tibbs Butte and rocks at Christina Mountain). Conversely, our results from the communities west of the Continental Divide show that the relative abundance of solitary trees and tree island initiators in unprotected microsites was never lower than any other nurse object type. The occurrence of relatively fewer trees in unprotected microsites relative to protected microsites east of the Continental Divide may reflect the harsher continental climate and represent evidence of establishment limitations in continental climates where nurse object protection may be essential for recruitment.

This is the first study to specifically assess and consider the ramifications of blister rust infection in treeline communities across the GYE. Our results revealed that treeline white pine blister rust infection ranged from 0.6% to 18.0% and was highest west of the Continental Divide (14.4% to 18.0%) relative to sites east of the Continental Divide (0.6 to 2.0%). Several studies at larger geographic scales have demonstrated an increase in blister rust infection levels along a continental east to west gradient (Keane et al. 1994, Smith et al. 2008), and suggest that climates with a maritime influence (i.e., moderate temperatures and high relative humidity) may be more favorable for spore transmission (e.g., Van Arsdel 1972, McDonald and Hoff 2001). Our finding that white pine blister rust was highest west of the Continental Divide supports those results.

Given that whitebark pine was the most abundant conifer in three of our four treeline study areas and comprised between 42.0% to 91.3% of the total trees per plot across all study areas, the spread of *C. ribicola* has the potential to significantly reduce overall conifer abundance at treeline and thereby alter community structure and composition. This disturbance to the

GYE's extensive treeline whitebark pine population could disrupt the ecosystem services that treeline conifers provide, including substrate stabilization against erosion, snow retention, and regulation of downstream flows as a result of reduced whitebark pine occurrence, and resulting effects on snow retention and snowmelt (Geddes et al. 2005, Tomback et al. 2016a).

Management actions that increase the number of trees resistant to white pine blister rust in subalpine whitebark pine communities near treeline communities should eventually lead to higher numbers of resistant whitebark pine at treeline. Planting seedlings or sowing seeds from parent trees with confirmed resistance to white pine blister rust is one of the major strategies for reversing the rapid decline in whitebark pine populations (Tomback and Achuff 2010, Schwandt et al. 2010, Keane et al. 2012). Restoration work directly at treeline, however, would greatly reduce the time between treeline community decline and treeline community recovery, and thus recovery of ecosystem services. The relatively high incidence of blister rust in the two treeline study areas west of the Continental Divide, Paintbrush Divide and Hurricane Pass, suggest the need for timely management intervention.

## References

- Alftine, K. J., and G. P. Malanson. 2004. Directional positive feedback and pattern at an alpine tree line. *Journal of Vegetation Science* 15, 3, doi:10.1658/1100-9233(2004)015[0003:DPFAPA] 2.0.CO;2.
- Arno, S. F., and R. J. Hoff. 1989. *Silvics of whitebark pine (Pinus albicaulis)*; U.S. Department of Agriculture, Forest Service, Intermountain Research Station: Ogden, UT.
- Bansal, S., K. Reinhardt, and M. J. Germino. 2011. Linking carbon balance to establishment patterns: comparison of whitebark pine and Engelmann spruce seedlings along an herb cover exposure gradient at treeline. *Plant Ecology* 212: 219–228, doi:10.1007/s11258-010-9816-8.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* 9: 191–193, doi:10.1016/0169-5347(94)90088-4.
- Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, et al. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96: 18–34, doi:10.1111/j.1365-2745.2007.01295.x.
- Burns, K. S., A. W. Schoettle, W. R. Jacobi, and M. F. Mahalovich. 2008. Options for the management of white pine blister rust in the Rocky Mountain Region; U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: Ft. Collins, CO.
- Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the Northern Rocky Mountains, USA. *Oikos* 82: 561, doi:10.2307/3546376.
- Callaway, R. M. 2002. The detection of neighbors by plants. *Trends in Ecology & Evolution* 17: 104–105, doi:10.1016/S0169-5347(01)02438-7.
- Calmettes, G., G. B. Drummond, and S. L. Vowler. 2012. Making do with what we have: use your bootstraps. *The Journal of Physiology* 590: 3403–3406, doi:10.1113/jphysiol.2012.239376.
- ESRI. 2012. ArcGIS: Environmental Systems Research Institute: Redlands, CA., USA.
- Geddes, C. A., D. G. Brown, and D. B. Fagre, D. B. 2005. Topography and vegetation as predictors of snow water equivalent across the alpine treeline ecotone at Lee Ridge, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research* 37: 197–205, doi:10.1657/1523-0430(2005)037[0197:TAVAPO]2.0.CO;2.
- Germino, M. J., W. K. Smith, and A. C. Resor. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology* 162: 157–168.
- Government of Canada. 2012. Order amending Schedule 1 to the Species at Risk Act. *Canada Gazette, Part II. Vol. 146. No. 14, SOR/2012–113*. Available online: [http://www.sararegistry.gc.ca/virtual\\_sara/files/orders/g2-14614i\\_e.pdf](http://www.sararegistry.gc.ca/virtual_sara/files/orders/g2-14614i_e.pdf) (accessed on 20 June 2012).
- Greater Yellowstone Whitebark Pine Monitoring Working Group. 2017. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2016 annual report. Natural Resource Report NPS/GRYN/NRR—2017/1453. National Park Service, Fort Collins, Colorado.
- Griggs, R. F. 1938. Timberlines in the Northern Rocky Mountains. *Ecology* 19: 548–564, doi:10.2307/1930935.
- Hättenschwiler, S., and W. K. Smith. 1999. Seedling occurrence in alpine treeline conifers: a case study from the central Rocky Mountains, USA. *Acta Oecologica* 20: 219–224, doi:10.1016/S1146-609X(99)80034-4.
- Hutchins, H. E., and R. M. Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia* 55: 192–201, doi:10.1007/BF00384487.
- Keane, R. E., P. Morgan, and J. Menakis. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. *Northwest Science* 68: 213–229.

- Keane, R. E., D. F. Tomback, C. A. Aubry, A. D. Bower, E. M. Campbell, C.L. Cripps, M. B. Jenkins, M. F. Mahalovich, M. Manning, S. T. McKinney, M. P. Murray, D. L. Perkins, D. P. Reinhart, C. Ryan, A. W. Schoettle, C. M. Smith. 2012. A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*): General Technical Report RMRS-GTR-279, USDA Forest Service, Fort Collins, Colorado, USA.
- Körner, C., and J. A. Paulsen, J.A. 2004. World-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31: 713–732, doi:10.1111/j.1365-2699.2003.01043.x.
- Lorenz, T. J., and K. A. Sullivan. 2009. Seasonal differences in space use by Clark's Nutcrackers in the Cascade Range. *The Condor* 111: 326–340, doi:10.1525/cond.2009.080070.
- Lortie, C. J., R. W. Brooker, P. Choler, Z. Kikvidze, R. Michalet, F. I. Pugnaire, and R. M. Callaway. 2004. Rethinking plant community theory. *Oikos* 107: 433–438, doi:10.1111/j.0030-1299.2004.13250.x.
- Malanson, G. P., D. R. Butler, D. B. Fagre, S. J. Walsh, D. F. Tomback, L. D. Daniels, L. M. Resler, W. K. Smith, D. J. Weiss, D. L. Peterson, A. G. Bunn, C. A. Hiemstra, D. Liptzin, P. S. Bourgeron, Z. Shen, C. I. Millar. 2007. Alpine treeline of Western North America: Linking organism-to-landscape dynamics. *Physical Geography* 28: 378–396, doi:10.2747/0272-3646.28.5.378.
- Manabe, S., and A. J. Broccoli. 1990. Mountains and arid climates of middle latitudes. *Science* 247: 192–195, doi:10.1126/science.247.4939.192.
- Marr, J. W. 1977. The development and movement of tree islands near the upper limit of tree growth in the Southern Rocky Mountains. *Ecology* 58: 1159–1164, doi:10.2307/1936937.
- McCune, B. 1988. Ecological diversity in North American pines. *American Journal of Botany* 75: 353–368, doi:10.1002/j.1537-2197.1988.tb13450.x.
- McDonald, G. I., and R. J. Hoff. 2001. Blister rust: An introduced plague. In *Whitebark Pine Communities: Ecology and Restoration*; Tomback, D. F., Arno, S. F., Keane, R. E., Eds.; Island Press: Washington, D.C., USA; pp. 193–220.
- McDonald, G. I.; Hoff, R. J. Blister rust: An introduced plague. In *Whitebark Pine Communities: Ecology and Restoration*; Tomback, D. F., Arno, S. F., Keane, R. E., Eds.; Island Press: Washington, D.C., USA, 2001; pp. 193–220.
- Pansing, E. R., D. F. Tomback, M. B. Wunder, J. P. French, and A. C. Wagner. 2017. Microsite and elevation zone effects on seed pilferage, germination, and seedling survival during early whitebark pine recruitment. *Ecology and Evolution* 7: 9027–9040, doi:10.1002/ece3.3421.
- Pyatt, J. C., D. F. Tomback, S. C. Blakeslee, M. B. Wunder, L. M. Resler, L. A. Boggs, and H. Beveney. 2016. The importance of conifers for facilitation at treeline: Comparing biophysical characteristics of leeward microsites in whitebark pine communities. *Arctic, Antarctic, and Alpine Research* 48: 427–444. DOI: <http://dx.doi.org/10.165/AAAR.0015-055>. Online appendices DOI: <http://dx.doi.org/10.165/AAAR.0015-055a>.
- R Core Team. 2017. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria.
- Resler, L., D. Butler, G. Malanson. 2005. Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. *Physical Geography* 26: 112–125, doi:10.2747/0272-3646.26.2.112.
- Resler, L. M. 2006. Geomorphic controls of spatial pattern and process at alpine treeline. *The Professional Geographer* 58: 124–138, doi:10.1111/j.1467-9272.2006.00520.x.
- Resler, L. M., and D. F. Tomback. 2008. Blister rust prevalence in krummholz whitebark pine: Implications for treeline dynamics. *Arctic, Antarctic, and Alpine Research* 40: 161–170.
- Resler, L. M., Y. Shao, D. F. Tomback, and G. P. Malanson. 2014. Predicting functional role and occurrence of whitebark pine (*Pinus albicaulis*) at alpine treeline: Model accuracy and variable importance. *Annals of the Association of American Geographers* 104: 703–722. DOI: <http://dx.doi.org/10.1080/00045608.2014.910072>.
- Rowlingson, B. D., and P. Diggle. 2017. *Splancs: Spatial and Space-Time Point Pattern Analysis*. R package version 2.01-40 <https://CRAN.R-project.org/package=splancs/> (accessed on 16 April 2017).
- Schwandt, J. W., I. B. Lockman, J. T. Kliejunas, and J. A. Muir. 2010. Current health issues and management strategies for white pines in the western United States and Canada: Current health and management strategies. *Forest Pathology* 40: 226–250, doi:10.1111/j.1439-0329.2010.00656.x.
- Smith, C. M., B. Wilson, S. Rasheed, R. C. Walker, T. Carolin, and B. Shepherd. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. *Canadian Journal of Forest Research* 38: 982–995, doi:10.1139/X07-182.
- Smith-McKenna, E. K., L. M. Resler, D. F. Tomback, H. Zhang, and G. P. Malanson. 2013. Topographic influences on the distribution of white pine blister rust in *Pinus albicaulis* treeline communities. *Écoscience* 20: 215–229.

- Smith-McKenna, E. K., G. P. Malanson, L. M. Resler, L. W. Carstensen, S. P. Prisley, and D. F. Tomback. 2014. Cascading effects of feedbacks, disease, and climate change on alpine treeline dynamics. *Environmental Modelling and Software* 62:85-96.
- Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. *Living Bird* 16: 123-161.
- Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: a mutualism hypothesis. *The Journal of Animal Ecology* 51: 451, doi:10.2307/3976.
- Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. *Madroño* 33: 100-110.
- Tomback, D. F., and L. M. Resler. 2007. Invasive pathogens at treeline: consequences for treeline dynamics. Invited contribution for special section on alpine treeline. *Physical Geography* 28: 397-418.
- Tomback, D. F., and P. Achuff. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines: Blister rust and western forest biodiversity. *Forest Pathology* 40: 186-225, doi:10.1111/j.1439-0329.2010.00655.x.
- Tomback, D. F., K. G. Chipman, L. M. Resler, E. K. Smith-McKenna, and C. M. Smith. 2014. Relative abundance and functional role of whitebark pine at treeline in the Northern Rocky Mountains. *Arctic, Antarctic, and Alpine Research* 46: 407-418, doi:10.1657/1938-4246-46.2.407.
- Tomback, D. F., L. M. Resler, R. E. Keane, E. R. Pansing, A. J. Andrade, and A. C. Wagner. 2016a. Community structure, biodiversity, and ecosystem services in treeline whitebark pine communities: potential impacts from a non-native pathogen. *Forests* 7: doi:10.3390/f7010021
- Tomback, D. F., S. C. Blakeslee, A. C. Wagner, M. B. Wunder, L. M. Resler, J. C. Pyatt, S. Diaz. 2016b. Whitebark pine facilitation at treeline: Potential interactions for disruption by an invasive pathogen. *Ecology and Evolution*. <http://onlinelibrary.wiley.com/doi/10.1002/ece3.2198/full>
- U.S. Fish and Wildlife Service. 2011. Endangered and threatened wildlife and plants; 12-month finding on a petition to list *Pinus albicaulis* as Endangered or Threatened with critical habitat. *Federal Register* 76: 42631-42654.
- Van Arsdel, E. 1972. Environment in relation to white pine blister rust infection. Biology of rust resistance in forest trees: 1969 August 17-24; Moscow, ID. Misc. Publ. no. 1221. Washington, DC: U.S. Department of Agriculture, Forest Service: 479-493. Proceedings of a NATO-IUFRO advanced study institute, pp. 479-493.
- Wagner, A.C., Tomback, D.F., Resler, L.M., and Pansing, E.R. 2018. Whitebark pine prevalence and ecological function in treeline communities of the Greater Yellowstone Ecosystem, U.S.A.: Potential disruption by white pine blister rust. *Forests* 9: 635; doi:10.3390/f9100635 [www.mdpi.com/journal/forests](http://www.mdpi.com/journal/forests)
- White, M. A., P. E. Thornton, and S. W. Running. 1997. A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Biogeochemical Cycles* 11: 217-234, doi:10.1029/97GB00330.



## Whitebark and Foxtail Pines in the Sierra Nevada— Assessing Stand Structure and Condition

Jonathan Nesmith and Linda Mutch

*Sierra Nevada Network Inventory and Monitoring Network,  
Sequoia and Kings Canyon National Parks, Three Rivers, California*



**Jonathan Nesmith** is a forest ecologist with interests in understanding interactions among montane forest structure, condition, and disturbance agents including insects and disease, fire, and climate change.



**Linda Mutch** is a science communication specialist whose interests include fire ecology and forest dynamics, as well as facilitating communication among scientists, land managers, and broader audiences.

*This article was adapted from Sierra Nevada Network  
Publication Brief:*

<https://irma.nps.gov/DataStore/DownloadFile/620119>

### Importance

Whitebark pine (*Pinus albicaulis*) and foxtail pine (*P. balfouriana*) grow at high elevations in rugged, rocky terrain with harsh weather and short growing seasons. The seeds from these trees provide food for birds and mammals, their canopies provide shade that helps slow snowmelt, and their branches and trunks provide structure important for wildlife habitat.

In most of their range, which extends from the Sierra Nevada to the North Cascades and Rocky Mountains, whitebark pines have declined dramatically in response to multiple factors, including infection from the non-native white pine blister rust (*Cronartium ribicola*) and outbreaks of mountain pine beetle (*Dendroctonus ponderosae*). In the southern Sierra Nevada, both whitebark pine and foxtail pine have remained healthy, as these stressors have been rare. However, increasing white pine blister rust and mountain pine beetle occurrence coupled with climate change impacts, may cause future declines.

The Sierra Nevada Network Inventory & Monitoring Program participates in a collaborative monitoring project that tracks change in high-elevation white pines in several Pacific West

Region national parks. Sierra Nevada white pines include whitebark, foxtail, limber (*P. flexilis*), western white (*P. monticola*), and sugar (*P. lambertiana*) pines. Here we summarize whitebark pine and foxtail pine stand structure and condition in Sequoia, Kings Canyon, and Yosemite national parks, based on an initial assessment of monitoring data collected between 2012 and 2017 and published in a special issue of *Forests: Ecology and Restoration of Whitebark Pine* (Nesmith et al. 2019).

### Key Findings

- High elevation white pines are relatively healthy in the Sierran national parks compared to other parts of their range.
- White pine blister rust infection rates in whitebark and foxtail pine were low in both parks. For whitebark pine, well below 1% of trees were infected, or about one tree per hectare in Yosemite and Sequoia & Kings Canyon.
- In Yosemite, the infections were all found in one plot, scattered across 12 different whitebark pine trees. New infections were recently found in additional plots in 2019.
- In Kings Canyon, fewer trees had disease symptoms, but they were more widely scattered across several different plots.
- Foxtail pine occurs only in Sequoia & Kings Canyon and showed no symptoms of white pine blister rust.

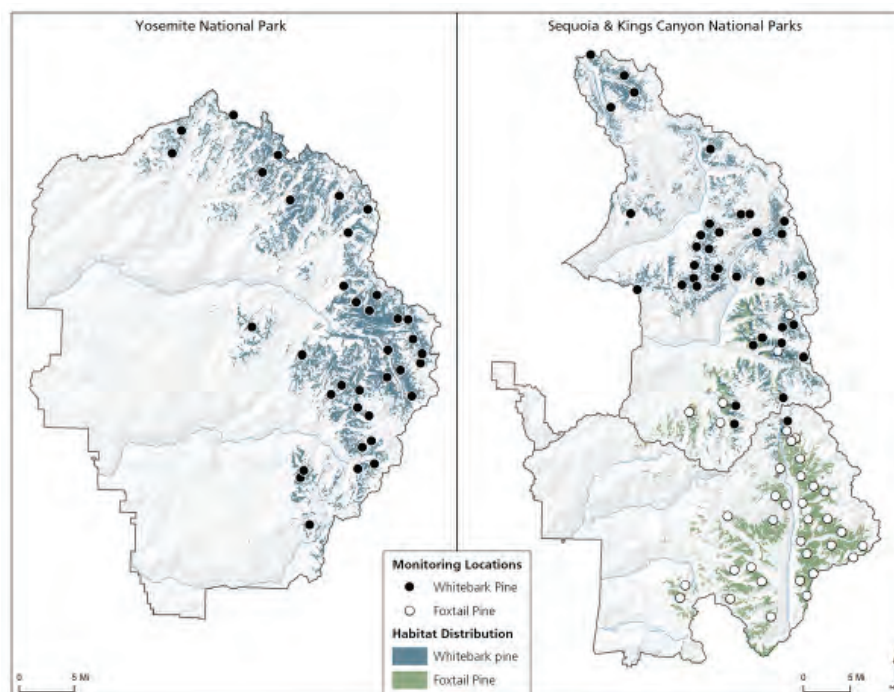


Whitebark pines in the Southern Sierra Nevada

- Mountain pine beetle activity was rare in these subalpine forests. Beetle activity was recorded in 1.0% of whitebark pine and 0.1% of foxtail pine in Sequoia and Kings Canyon and <0.1% of whitebark pine in Yosemite.
- Although these pine populations are still relatively healthy, our recent observations of white pine blister rust and mountain pine beetle at high elevations may portend future declines.

## Methods

We collected long-term monitoring data between 2012 and 2017 in Sequoia & Kings Canyon and Yosemite national parks. Detailed methods are available in the monitoring protocol developed for multiple Pacific West Region national parks (McKinney et al. 2012). We selected random plot locations using an equal probability, spatially-balanced approach, and based



**Figure 1.** Distribution of whitebark pine and foxtail pine populations and monitoring plots in Sierra Nevada Network parks. Maps by: Alex Eddy (NPS).

sample frames on the distribution of whitebark pine and foxtail pine identified in park vegetation maps (Fig. 1). The sample design allows inference to the entire area of the parks where these species occur.

Field crews documented whitebark pine and foxtail pine tree characteristics and the presence/absence of factors influencing mortality:

- diameter at breast height (DBH)
- height
- cone counts
- level of canopy kill
- live seedling counts and height class assignment
- tree status (live, recently dead, dead)
- assessment of mortality cause
- blister rust cankers (bole and canopy)
- number of blister rust indicators (pitching, rodent chew marks)
- mountain pine beetle indicators (pitch tubes, frass, or J-shaped galleries)
- dwarf mistletoe infection
- growth form (for whitebark pine)

Field crews measured 7899 whitebark pine, 1112 foxtail pine, and 6085 other trees. Table 1 summarizes the number of live and dead trees recorded in plots for each park.

Park-Species	No. of plots	No. of live trees	No. of dead trees
YOSE - PIAL	35	7866 (48% PIAL)	181 (15% PIAL)
SEKI - PIAL	31	5038 (71% PIAL)	125 (66% PIAL)
SEKI - PIBA	33	2192 (49% PIBA)	191 (50% PIBA)

**Table 1.** Summary of the number of plots, live trees, and dead trees for whitebark pine (PIAL) populations in Yosemite (YOSE) and Sequoia and Kings Canyon (SEKI) and the foxtail pine (PIBA) populations in SEKI. The tree number totals include all tree species in the plots.

### What Did We Learn?

This study provides a baseline for quantifying status and trend in high elevation white pine forests related to: tree species composition and structure; incidence of white pine blister rust and level of crown mortality; incidence of bark beetles; tree species birth, death, and growth rates; and cone production.

### Species Composition and Structure

Stand structure for whitebark pine was variable and reflects the multiple habitats and growth forms of this species. Figure 2 illustrates the krummholz form that can occur in harsh growing conditions near treeline. Whitebark pine can occur in pure stands as a single species as well as in mixed forests with other species, such as lodgepole pine (*P. contorta*), and mountain hemlock (*Tsuga mertensiana*). Foxtail pine stand structure was less variable and it tended to occur at lower stem densities but higher basal area than whitebark pine (Fig. 3). Foxtail pine co-occurred most often with whitebark pine and lodgepole pine.

Whitebark pine average stem densities were: 431 trees/ha in Yosemite and 442 trees/ha in Sequoia & Kings Canyon, with greater variability in Yosemite. Foxtail pine average stem density was 130 trees/ha.



**Figure 2.** Low, shrubby krummholz growth form of whitebark pine, Yosemite National Park. Whitebark pine growing as krummholz was much more common in Yosemite than in Sequoia & Kings Canyon. NPS photo: 2017 forest crew.





**Figure 3.** Foxtail pine stand in Sequoia National Park. NPS photo: Roxanne Kessler.

### White Pine Blister Rust and Crown Mortality

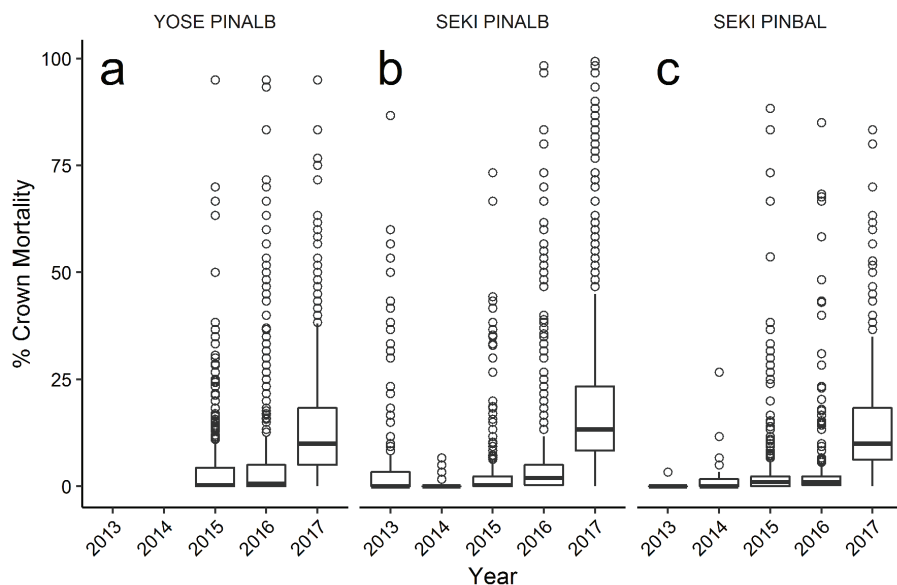
White pine blister rust was rare in whitebark pine in both Yosemite and Sequoia & Kings Canyon, with an average infection rate of 0.1%. Only one plot was infected in Yosemite—12 out of 251 live trees within that plot showed signs of infection. This plot had the highest overall whitebark pine basal area in Yosemite, with relatively low basal area for other species. Fewer whitebark pine (6) were infected in Sequoia &

Kings Canyon, but they were more spatially dispersed, occurring over four plots in Kings Canyon National Park. We found no symptoms of white pine blister rust on foxtail pine within the monitoring plots, though we observed one infected whitebark pine within a foxtail plot in Kings Canyon National Park.

Whitebark pine generally appeared to be in good health and had low levels (8.2%) of crown mortality in Yosemite as well as Sequoia & Kings Canyon. The average proportion of crown mortality in live whitebark pine increased with DBH and was significantly higher in 2017 for Yosemite compared to other years (Fig. 4a), and in 2016 and 2017 for Sequoia and Kings Canyon (Fig. 4b). Much of this crown damage was due to environmental factors including wind and ice damage, as well as limited damage from biological agents like brown felt blight and insects. For foxtail pine, average crown mortality was low, averaging 6%. Crown mortality increased with DBH, and was higher in 2017 compared with 2013-2016. (Fig. 4c).

### Bark Beetles

Mountain pine beetle activity was rare, averaging less than five attacked trees per hectare and representing less than one percent of all white pines. In contrast, lower elevation forests in the Sierra Nevada have experienced dramatic mortality driven by the recent severe drought and associated mountain pine beetle outbreak. We observed successful attacks primarily on whitebark pine and lodgepole pine, often limited to single trees or very small clumps.



**Figure 4.** Individual tree percent crown mortality by year in (a) Yosemite whitebark pine sample frame (YOSE PINALB), (b) Sequoia & Kings Canyon whitebark pine sample frame (SEKI PINALB), and (c) Sequoia and Kings Canyon foxtail pine sample frame (SEKI PINBAL).



In addition, whitebark pine has experienced significant mortality from bark beetles in other parts of its range, including other areas of the Sierra Nevada.

### **Cone Production**

The proportion of cone-bearing trees was quite different across species: roughly 25% of whitebark pine trees had female cones (23% and 28% in Yosemite and Sequoia & Kings Canyon, respectively), compared to 69% for foxtail pines. The proportion of cone-bearing trees increased with tree size and decreased with crown mortality across all sample frames. While these results generally agree with previous research in other areas, one study reported a much larger percentage of cone-bearing whitebark pine in Lake Tahoe area further north (80%). This may be a reflection of asynchronous mast years, as whitebark cone production is believed to be somewhat periodic with large cone crops generally occurring every three to five years, depending on specific location.

### **Demography—Tree Birth, Death, Growth Rates**

As this is the first complete cycle of monitoring high-elevation pine plots, we cannot yet report birth, mortality, or growth rates, but have recorded existing dead trees and seedling recruitment at plot establishment. Environmental factors appear to be the driving factor of tree mortality, however, as most of the snags where we were able to assign a cause of death were attributed to

environmental or physical causes. Standing dead basal area was low in general, indicating extensive mortality has not occurred in these areas in recent history. Seedling recruitment was low but variable for whitebark pine and was consistently low for foxtail pine. Low seedling densities for foxtail pine in the southern Sierra Nevada do not appear uncommon, and other research indicates populations have been stable for the last 1,000 years.

### **Conclusion**

Managers face multiple challenges related to conservation of white pines, including a rapidly changing climate, existing widespread degradation of white pine ecosystems, and potential conflicts between restoration activities and wilderness policy. These data provide a solid baseline for assessing current status and evaluating future change in subalpine forests of the southern Sierra Nevada. As this long-term monitoring plot network is re-sampled its value and utility will continue to grow and help both current and future land managers ensure the persistence of these iconic species.

### **Reference**

Nesmith, J., Wright, M., Jules, E., and McKinney, S. 2019. Whitebark and foxtail pine in Yosemite, Sequoia, and Kings Canyon National Parks: Initial assessment of stand structure and condition. *Forests* 35: 1-24.

## Whitebark Pine Encroachment into Lower Elevation Sagebrush Grasslands in Southwest Montana, USA

Robert Keane and Sarah Flanary

USDA Forest Service, Rocky Mountain Research Station,  
Missoula Fire Sciences Laboratory, Missoula, Montana



**Robert Keane** is a research ecologist investigating the ecology and restoration of whitebark pine. Bob combines observational approaches with ecological simulation models to explore landscape, fire, and climate dynamics.



**Sarah Flanary** works as a biological science technician in the fire, smoke, and fuel program area.

### Introduction

The collective impacts of fire exclusion policies, mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks, and white pine blister rust (*Cronartium ribicola* J.C. Fisch) infections have resulted in a rapid decline of whitebark pine (*Pinus albicaulis* Engelm.) forests in western North America over the last several decades (Arno 1986, Kendall and Keane 2001, Goeking and Izlar 2018). Especially distressing are the projected declines in these iconic forests because of future changes in climate (Warwell et al. 2007, Chang et al. 2014). Future warmer and drier climates could result in increases in the frequency of wildland fire (Flannigan et al. 2009, Abatzoglou and Williams 2016, Schoennagel et al. 2017) and mountain pine beetle outbreaks (Carroll et al. 2003, Wong and Daniels 2016), but it is also speculated that it will also increase white pine blister rust infections (Landguth et al. 2017, Wyka et al. 2018). However, more alarming is that many statistical modeling studies have shown significant reduction in the biophysical conditions that define suitable whitebark pine habitat over the next century (Warwell et al. 2007, Chang et al. 2014). Historically, whitebark pine forests composed about 10-15% of the upper subalpine zone of the northern Rocky Mountains (Arno and Weaver 1990) with around 48% of that in wilderness landscapes, but future projections for these iconic forests suggest that they may inhabit as little as 0.5-7.0% by 2070-2100 (Hansen and Phillips 2015).

In general, there are modes of response to climate change for most tree species in western North America: modification, contraction, and expansion (synonymous with encroachment in

this study; Keane et al. 2018). A species may increase or decrease in productivity or abundance *in situ* within its current range due to climate change (Ashton 2010; *modification*). The species could also potentially decline in parts of its range where conditions change enough to become inhospitable to that species (Allen et al. 2010; *contraction*). And last, the species could migrate to new areas that are now more conducive for establishment and growth (Johnstone and Chapin 2003; *expansion*). In reality, many tree species may respond to future climates via all three modes. Conventional wisdom and statistical modeling have predicted that whitebark pine will probably contract in range over the next century with warmer, drier climates, but may perhaps expand into high elevation timberline environments (Koteen 2002, Warwell et al. 2007, Chang et al. 2014). However, expert opinion and empirical analyses rarely address the complex feedbacks and interactions between climate, biophysical environment, disturbance, and the tree species. The challenge then is to determine the validity of these predictions by measuring early responses of whitebark pine to changing climates. We feel that field detection of migration patterns of tree species into new environments may provide potential information on the impacts of climate change on species response and validate existing empirical and simulation modeling study results.

The objective of this case study was to document the encroachment (local expansion of species into new habitats) of whitebark pine (Fig. 1) into both lower elevation sagebrush grassland areas and upper elevation subalpine meadows that were



**Figure 1.** Examples of whitebark pine trees encroaching into sagebrush grasslands for the three sites in this study. a) Photo from Morrison site. Edge of mature seed source stand showing whitebark pine encroachment into sagebrush landscape b) Photo from Morrison site. Mature cone bearing whitebark pine interspersed on sagebrush habitat c) Photo from potential site in southwestern Montana. Downward encroachment of whitebark pine into open sagebrush d) Photo from Morrison site. Seedling and sapling sized whitebark pine mixing in with sagebrush. All photos by Sarah Flanary.

directly adjacent to mature, cone-bearing whitebark pine stands, which might provide seeds for dispersal into the two non-forest settings. We sampled seedling, sapling, and mature tree densities by species on three study sites in southwestern Montana, USA where we found evidence of encroachment either into the upper subalpine meadow or lower sagebrush grasslands. This limited field assessment only documents whitebark pine encroachment into the two non-forest areas, but we speculate on possible reasons as to why this encroachment occurred.

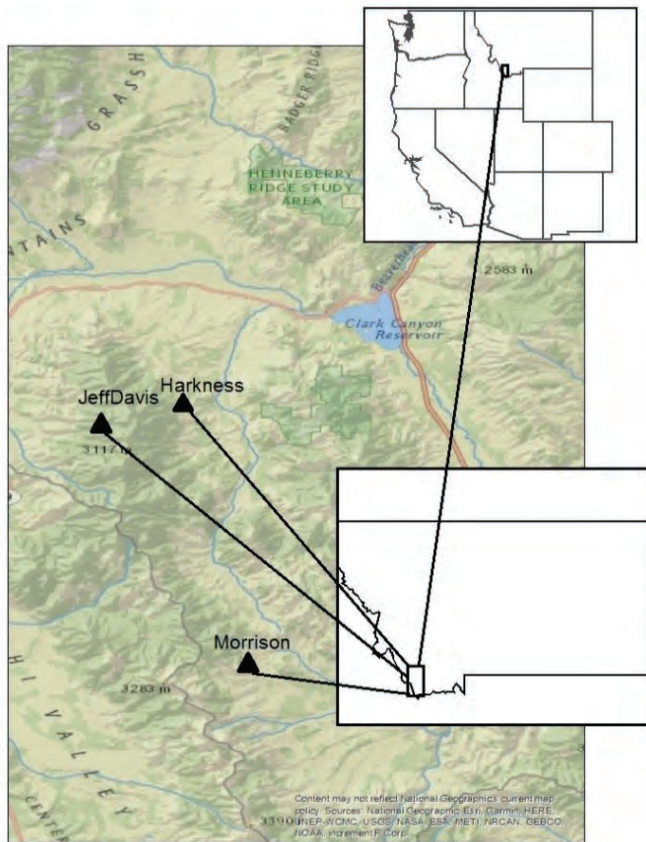
## Methods

The Tendoy and Beaverhead mountain ranges of southwestern Montana USA served as the study area in this project (Fig. 2). Lower elevational lands within this area contain mountain big sagebrush (*Artemisia tridentata* ssp. *Vasseyana* Rydb.) grasslands

intermixed with dry Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and lodgepole pine (*Pinus contorta* Douglas) forests (Pfister et al. 1977, Larson 2009), while the upper elevation lands contain subalpine meadows and grasslands with forest patches of whitebark pine, limber pine (*Pinus flexilis* James), subalpine fir (*Abies lasiocarpa* (Hook) Nutt.), Engelmann spruce (*Picea engelmannii* (Parry) Engelm.), lodgepole pine, and Douglas-fir. Mountain big sagebrush lands had a mean pre-settlement fire interval between 25 to 40 years, but fire suppression, elimination of Native American burning, and livestock grazing in these areas have decreased the fire frequencies and increased the amount of dense-canopy mountain big sagebrush.

Sites in this study were chosen opportunistically by driving and hiking throughout the study area and finding those areas that displayed possible whitebark pine encroachment either uphill into





**Figure 2.** Locations of the three sites sampled in this field study in the southwest Montana, USA study area: a) Harkness, b) Jeff Davis, and c) Morrison sites.

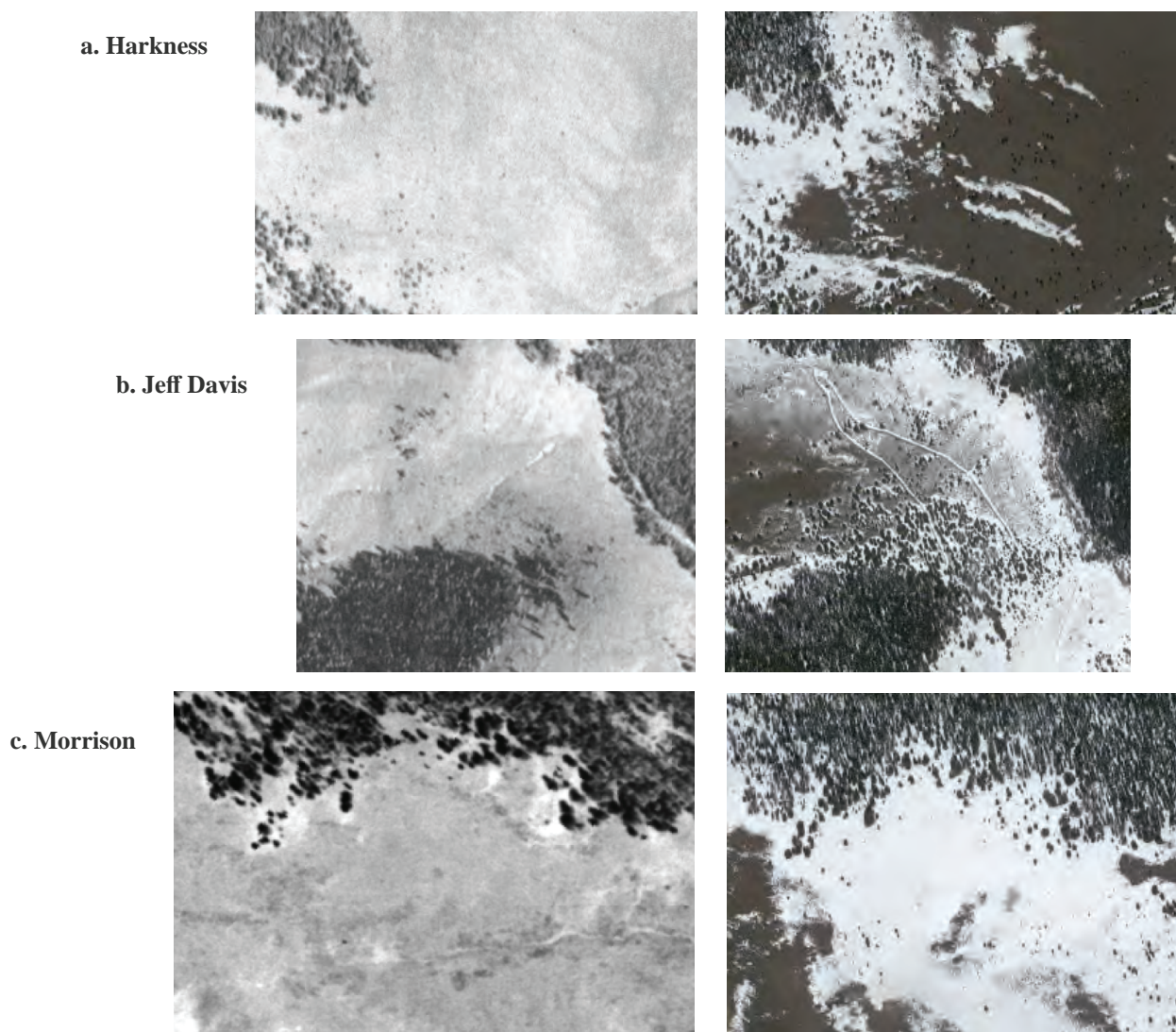
subalpine grasslands or downhill into sagebrush grasslands. We also used aerial survey imagery from the 1950's and compared it to current aerial products for provide further confirmation of encroachment (Fig. 3). At each sampling site, we established plots in the mature seed source stands to quantify seed source trees. At the lower and upper edge of the seed source stand, we also installed one 100 m belt transect running downhill into the sagebrush grassland and uphill into the subalpine meadow. Each belt transect was 100 meters wide and at least 100 meters long following the shape of the stand. Within these belt transects, we tallied and measured diameter, height, and age of all whitebark pine trees (seedlings, saplings, and mature trees).

## Results

In this limited case study, we found whitebark pine encroachment into non-forested areas only occurred downslope into the drier, warmer sagebrush grasslands rather than upslope into the cooler, moister subalpine meadows. This finding suggests that conventional wisdom and the findings of some statistical

modeling studies may be incorrect in their future projections within our study area. We found that not only were substantial amounts of whitebark pine regenerating downslope in the sagebrush grasslands, but the sampled individual trees were healthy and thriving as evidenced by the large height growth increments, pitch exudations from growth cracks at branch origins near the bole, and large diameters in the young trees. Some of the young trees were producing numerous cones at an early age (<50 yr), which is in contrast to the first cone production ages of 60 years documented by Arno and Hoff (1990). Moreover, we found that this encroachment occurred over the last 100 years and did not occur as a pulse but rather as a gradual increase as evidenced by the wide span in ages (Fig. 4). We did not observe any subalpine fir or Engelmann spruce encroachment into either the sagebrush grasslands or the subalpine meadows. We also found abundant non-serotinous lodgepole pine and Douglas-fir seed source stands adjacent or near (<500 m) the sagebrush grassland belt transects on all three sites but found few of these tree species within the belt transects (we found five Douglas-fir trees within the Harkness sagebrush grassland belt transect). The only tree species successfully populating and thriving in the sampled sagebrush grasslands was whitebark pine. While we did not sample additional sites because of time and funding issues, we are sure there are other sites in this expansive area where whitebark pine encroachment is occurring. We also observed many areas in the study region where whitebark pine forests bordered sagebrush grasslands and there was no detectable encroachment. Moreover, we failed to detect this phenomenon outside of southwest Montana.

The explanation for this limited downward migration of whitebark pine remains a mystery. We speculate that the lack of fire in the southwestern Montana sagebrush grasslands over the fire exclusion era, perhaps since 1860 (Heyerdahl et al. 2006), has allowed whitebark pine to expand its range downward in elevation, as has been documented by Arno et al. (1993) for the Bitterroot Valley in Montana, but this doesn't explain why other tree species in the area failed to migrate into the non-forested areas. Whitebark pine seeds are dispersed by a bird, the Clark's nutcracker (Tomback 1998), which can disperse seeds great distances (>10 km) allowing whitebark pine a dispersal advantage over wind-dispersed species. However, 90 years is more than sufficient to allow wind to disperse seeds of whitebark pine's competitors into sagebrush grasslands. Still more compelling is that few studies have identified sagebrush grasslands as reliable or common nutcracker caching habitat or suitable whitebark pine regeneration environments. Sagebrush has been known to facilitate some pines (Callaway et al. 1996), and many whitebark pine sites have a sagebrush component (Arno 2001), but this encroachment facilitation has never been



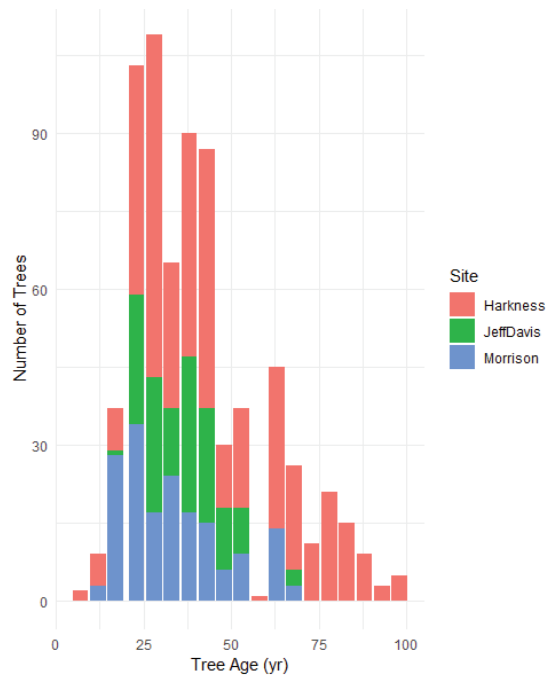
**Figure 3.** Aerial photographs showing each of the sampled sites in this study, showing both upper and lower forest margins for the three sampling sites: a) Harkness, b) Jeff Davis, and c) Morrison. Photos on left were taken between 1953-1954 while photos on right are a 2018 visual of the same spot. Encroachment is evident in the 2018 visual. Data available from the U.S. Geological Society, USGS Aerial Single Frame Archive at [earthexplorer.usgs.gov](http://earthexplorer.usgs.gov)

documented in whitebark pine communities. Mycorrhizae may also play a role in the regeneration of whitebark pine in this arid area by allowing access to more soil water (Lonergan et al. 2013), but many of the other tree species in the area often share the same beneficial mycorrhizae (Mohatt et al. 2008).

Results from this limited case study of three sites in western Montana USA indicate that we still have an incomplete understanding of what will drive tree regeneration and growth dynamics into our uncertain future. We can anticipate possible responses of tree species such as whitebark pine to a warming climate, but it will always be difficult to determine the primary

change agents or factors that influence future species populations because of the complex interactions among changes in disturbance, climate, vegetation, and land management. Further investigation is needed in other areas within whitebark pine's range to determine if our measured trend is widespread and if other species follow this same expansion downward in elevation (Harsch and Hille Ris Lambers 2014). Caution should be used when applying climate change projections into land management decisions by fully recognizing the uncertainty of future climate projections and the great complexity of forested ecosystems. This case study serves as evidence of that uncertainty in climate change vegetation response projections.





**Figure 4.** Count data and field estimated ages for sapling (<10 cm DBH) and mature (>10 cm DBH) whitebark pine trees sampled on the lower sagebrush grassland belt transects in the potential encroachment areas across all sites.

## References

- Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences* 113:11770-11775.
- Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, and E. T. Hogg. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660-684.
- Arno, S. A. 2001. Community types and natural disturbance processes. Pages 74-89 in D. F. Tomback, S. A. Arno, and R. E. Keane, editors. *Whitebark pine communities: ecology and restoration*. Island Press, Washington, DC USA.
- Arno, S. F. 1986. Whitebark pine cone crops—a diminishing source of wildlife food? *Western Journal of Applied Forestry* 1:92-94.
- Arno, S. F., and T. Weaver. 1990. Whitebark pine community types and their patterns on the landscape. General technical report INT (USA).
- Ashton, I. W. 2010. Observed and projected ecological response to climate change in the Rocky Mountains and Upper Columbia Basin: A synthesis of current scientific literature.
- Callaway, R. M., E. H. DeLucia, D. Moore, R. Nowak, and W. H. Schlesinger. 1996. Competition and Facilitation: Contrasting Effects of *Artemisia tridentata* on Desert vs. Montane Pines. *Ecology* 77:2130-2141.
- Carroll, A. L., S. W. Taylor, J. Régnière, and L. Safranyik. 2003. Effect of climate change on range expansion by the mountain pine beetle in British Columbia. In Pages 223-232 in TL Shore et al. (eds) *Mountain Pine Beetle Symposium: Challenges and Solutions*, Oct. 30-31, 2003. Kelowna BC. Natural Resources Canada, Information Report BC-X-399, Victoria.
- Chang, T., A. J. Hansen, and N. Piekielek. 2014. Patterns and variability of projected bioclimatic habitat for *Pinus albicaulis* in the Greater Yellowstone Area. *PLoS One* 9:e111669.
- Flannigan, M. D., M. A. Krawchuk, W. J. de Groot, B. M. Wotton, and L. M. Gowman. 2009. Implications of changing climate for global wildland fire. *International Journal of Wildland Fire* 18:483-507.
- Goeking, S. A., and D. K. Izlar. 2018. *Pinus albicaulis* Engelm. (Whitebark Pine) in mixed-species stands throughout its US range: broad-scale indicators of extent and recent decline. *Forests* 9:131.
- Hansen, A. J., and L. B. Phillips. 2015. Which tree species and biome types are most vulnerable to climate change in the US Northern Rocky Mountains? *Forest Ecology and Management* 338:68-83.
- Harsch, M. A., and J. Hille Ris Lambers. 2014. Species distributions shift downward across western North America. *Global Change Biology*:n/a-n/a.
- Heyerdahl, E. K., R. F. Miller, and R. A. Parsons. 2006. History of fire and Douglas-fir establishment in a savanna and sagebrush-grassland mosaic, southwestern Montana, USA. *Forest Ecology and Management* 230:107-118.
- Johnstone, J. F., and F. S. Chapin. 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology* 9:1401-1409.
- Keane, R. E., M. F. Mahalovich, B. L. Bollenbacher, M. E. Manning, R. A. Loehman, T. B. Jain, L. M. Holsinger, and A. J. Larson. 2018. Effects of climate change on forest vegetation in the Northern Rockies. Pages 59-95 *Climate Change and Rocky Mountain Ecosystems*. Springer.
- Kendall, K. C., and R. E. Keane. 2001. Whitebark pine decline: infection, mortality, and population trends. *Whitebark pine communities: ecology and restoration*. Edited by DF Tomback, SF Arno, and RE Keane. Island Press, Washington, DC:221-242.
- Koteen, L. 2002. Climate change, whitebark pine, and grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife responses to climate change: North American case studies*. Edited by SH Schneider and TL Root. Island Press, Washington, DC:343-414.



- Landguth E. L.; Holden, Z. A. M., M. F.; Cushman, S. A. 2017. Using landscape genetics simulations for planting blister rust resistant whitebark pine in the US northern Rocky Mountains. *Frontiers in Genetics* 8.
- Larson, E. R. 2009. Status and dynamics of whitebark pine (*Pinus albicaulis* Engelm.) forests in southwest Montana, central Idaho, and Oregon, USA. University of Minnesota.
- Lonergan, E. R., C. L. Cripps, and C. M. Smith. 2013. Influence of site conditions, shelter objects, and ectomycorrhizal inoculation on the early survival of whitebark pine seedlings planted in Waterton Lakes National Park. *Forest Science* 60:603-612.
- Mohatt, K. R., C. L. Cripps, and M. Lavin. 2008. Ectomycorrhizal fungi of whitebark pine (a tree in peril) revealed by sporocarps and molecular analysis of mycorrhizae from treeline forests in the Greater Yellowstone Ecosystem. *Botany* 86:14-25.
- Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest habitat types of Montana. USDA Forest Service, Intermountain Forest and Range Experiment Station Gen. Tech. Rep. INT-GTR-34. 174p.
- Schoennagel, T., J. K. Balch, H. Brenkert-Smith, P. E. Dennison, B. J. Harvey, M. A. Krawchuk, N. Mietkiewicz, P. Morgan, M. A. Moritz, and R. Rasker. 2017. Adapt to more wildfire in western North American forests as climate changes. *Proceedings of the National Academy of Sciences* 114:4582-4590.
- Tomback, D. F. 1998. Clark's nutcracker (*Nucifraga columbiana*). *The Birds of North America* 331:1-23.
- Warwell, M. V., G. E. Rehfeldt, and N. Crookston. 2007. Modeling contemporary climate profiles of whitebark pine (*Pinus albicaulis*) and predicting responses to global warming. Pages 139-142 in *Proceedings of the Conference Whitebark Pine: A Pacific Coast Perspective*. Citeseer.
- Wong, C. M., and L. D. Daniels. 2016. Novel forest decline triggered by multiple interactions among climate, an introduced pathogen and bark beetles. *Global Change Biology*:n/a-n/a.
- Wyka, S. A., I. A. Munck, N. J. Brazee, and K. D. Broders. 2018. Response of eastern white pine and associated foliar, blister rust, canker and root rot pathogens to climate change. *Forest Ecology and Management* 423:18-26.

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

Barbara J. Bentz

USDA Forest Service, Rocky Mountain Research Station, Logan, Utah



**Barbara Bentz** is a research entomologist focused on understanding temperature response and adaptations of bark beetles and associated communities for increased understanding of population outbreaks in a changing climate.

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

### Background

GB bristlecone pine is a keystone species that typically grows on abiotically stressed sites at high elevations in the Great Basin. It has the longest lifespan of any non-clonal organism world-wide, and the oldest recorded living tree, Methuselah, is estimated

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

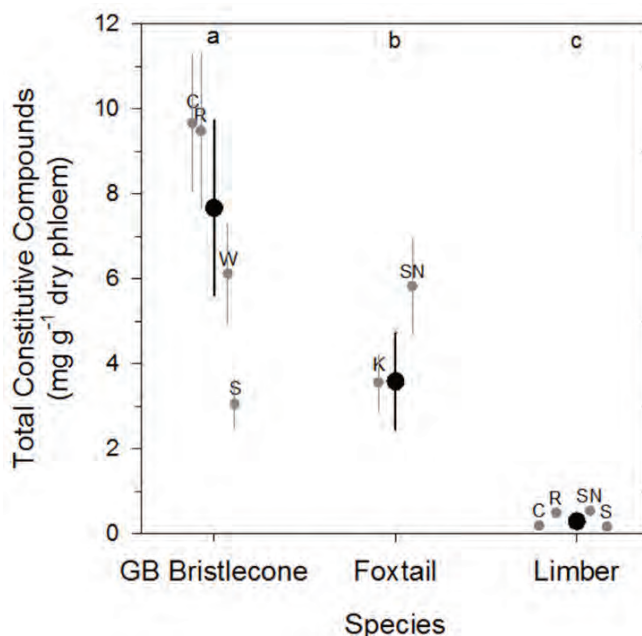


**Figure 1.** MPB-caused limber pine mortality in mixed limber and GB bristlecone pine stands in the Pequop Mountains, NV. Photo, Matt Hansen, 2014.

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

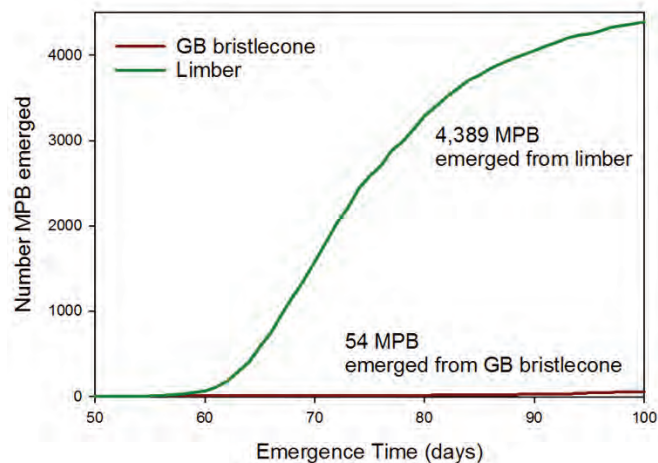
These observations suggested that GB bristlecone in particular, but also foxtail pine, have a level of resistance against, and are not preferred hosts of MPB, relative to limber pine. Tree resistance to bark beetles is a function of traits that have evolved to decrease behavioral preferences for oviposition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

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



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

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



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



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

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

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

### Potential Factors Influencing the GB Bristlecone Pine and MPB Relationship

*Long-term evolutionary relationship* Long-term contact and evolutionary history between specific plant and herbivorous insect species are expected to increase plant allocation to secondary metabolic defenses (Herms & Mattson, 1992). Some bark beetle species, including MPB, have evolved counter-adaptations to tolerate and even benefit from tree defense allocations. MPB has evolved to use terpene defense compounds as synergists in aggregation pheromones that facilitate mass attacks on trees (Franceschi et al. 2005). This ‘Red Queen arms-race’ between MPB and *Pinus* has undoubtedly been battled

throughout evolutionary time. Extant tree species within *Pinus* and beetle species within *Dendroctonus* both have Eastern Eurasia as the likely center of origin (Eckert and Hall 2006, Godefroid et al. 2019). For *Pinus*, inter-continental migrations between Eurasia and North America, through the Beringia Land Bridge, were concentrated in the late Cretaceous and Tertiary (Eckert and Hall 2006). The first inter-continental vicariance event for *Dendroctonus*, also across the Beringia Land Bridge, is estimated to have occurred later, during the early Miocene (Godefroid et al. 2019). Community reorganization and diversification during the Quaternary followed in both *Pinus* (Millar 1998, Godbout et al. 2008) and *Dendroctonus* (Godefroid et al. 2019). The *Pinus* subsection Balfourianae, which includes GB bristlecone and foxtail pine, were concentrated in Great Basin, western US refugia during the early Tertiary with population expansions and shrinkages during glacial and interglacial waves of the Quaternary (Wells 1983, Millar 1998). Downward GB bristlecone pine movement during the last full glacial, to as low as 1900 m elevation, likely occurred prior to a retreat upward to the sky island mountain ranges inhabited today. Glacial patterns within the western US that influenced GB bristlecone pine also played a role in *Dendroctonus* diversification, which is ongoing. MPB is considered to be in the early stages of speciation wherein infertile F<sub>1</sub> offspring are produced when populations from either side of the Great Basin are mated (Bracewell et al. 2017, Dowe et al. 2017). Although glacial and interglacial range shifts may have decoupled GB bristlecone pine and its insect predators, the long-lived and non-senescent GB bristlecone pine likely retained evolutionary signals of past selection (Hamrick 1979).

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

### New Developments

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

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

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

### Acknowledgements

The thoughts and ideas expressed here are based on observations and discussions with multiple collaborators including Sharon Hood, Justin Runyon, Karen Mock, Jim Vandygriff, Matt Hansen, Erika Eidson and David Soderberg.

### References

- Amman G.D. 1982. Characteristics of mountain pine beetles reared in four pine hosts. *Environmental Entomology* 11: 590-593.
- Armbruster W.S., J.J. Howard, T.P. Clausen, E.M. Debevec, J.C. Loquvam, M. Matsuki, B. Cerendolo, and F. Anel. 1997. Do biochemical exaptations link evolution of plant defense and pollination systems? Historical hypotheses and experimental tests with *Dalechampia* vines. *American Naturalist* 149: 461-484.
- Bentz B.J., S. Hood, E.M. Hansen, J.C. Vandygriff, and K.E. Mock. 2017. Defense traits in the long-lived Great Basin bristlecone pine and resistance to the native herbivore mountain pine beetle. *New Phytologist* 213:611-624.
- Bracewell R.R., B.J. Bentz, B.T. Sullivan, and J.M. Good. 2017. Rapid neo-sex chromosome evolution and incipient speciation in a major forest pest. *Nature Communications* 8:1593.
- Coley P.D., J.P. Bryant, and F.S. Chapin. 1985. Resource availability and plant antiherbivore defense. *Science* 230: 895-899.
- Dowle E., R. Bracewell, M. Pfrender, B. Bentz, K. Mock, and G. Ragland. 2017. Reproductive isolation and environmental adaptation shape the phylogeography of mountain pine beetle (*Dendroctonus ponderosae*). *Molecular Ecology* 26:6071-6084.
- Eckert A.J. and B.D. Hall. 2006. Phylogeny, historical biogeography, and patterns of diversification for *Pinus* (Pinaceae): Phylogenetic tests of fossil-based hypotheses. *Molecular Phylogenetics and Evolution* 40: 166-182.
- Eidson E.L., K.E. Mock, and B.J. Bentz. 2018. Low offspring survival in mountain pine beetle infesting the resistant Great Basin bristlecone pine supports the preference-performance hypothesis. *PLoS ONE* 13(5):e0196732, <https://doi.org/10.1371/journal.pone.0196732>.
- Esch E.D., D.W. Langor, and J.R. Spence. 2016. Gallery success, brood production, and condition of mountain pine beetles (Coleoptera: Curculionidae) reared in whitebark and lodgepole pine from Alberta, Canada. *Canadian Journal of Forest Research* 46:557-63.
- Franceschi V.R., P. Krokene, E. Christiansen, and T. Krekling. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* 167: 353-376.
- Furniss R.L. and V.M. Carolin. 1977. *Western Forest Insects*. USDA Forest Service, Misc. Pub. No 1339.

- Godbout J., A. Fazekas, C.H. Newton, F.C. Yeh, and J. Bousquet. 2008. Glacial vicariance in the Pacific Northwest: evidence from a lodgepole pine mitochondrial DNA minisatellite for multiple genetically distinct and widely separated refugia. *Molecular Ecology* 17: 2463-2475.
- Godefroid M., A.S. Meseguer, L. Saunè, G. Genson, J-C. Streito, J-P. Rossi, A.Z. Riveròn, F. Mayer, A. Cruaud, J-Y. Rasplus. 2019. Restriction-site associated DNA markers provide new insights into the evolutionary history of the bark beetle genus *Dendroctonus*, *Molecular Phylogenetics and Evolution* 139 <https://doi.org/10.1016/j.ympev.2019.106528>
- Hamrick J.L. 1979. Genetic variation and longevity. In: Solbrig OT, Jain S, Johnson GB, Raven PH, eds. *Topics in plant population biology*. London, UK: Macmillan Education UK, 84–113.
- Herms D.A. and W.J. Mattson. 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* 67: 283-335.
- Hood S. and A. Sala. 2015. Ponderosa pine resin defenses and growth: metrics matter. *Tree Physiology* 35:1223-1235.
- Jaenike J. 1978. On optimal oviposition behavior in phytophagous insects. *Theoretical Population Biology*. 14:350-356.
- LaMarche V.C. 1969. Environment in relation to age of bristlecone pines. *Ecology* 50:53-59.
- Langor D.W. 1998. Host effects on the phenology, development, and mortality of field populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *The Canadian Entomologist* 121:149-57.
- Millar C.I. 1998. Early evolution of pines. In DM Richardson (ed) *Ecology and biogeography of Pinus*. Pp 69-91.
- Rosenberger D.W., B.H. Aukema, and R.C. Venette. 2017. Cold tolerance of mountain pine beetle among novel eastern pines: A potential for trade-offs in an invaded range? *Forest Ecology and Management* 400:28-37.
- Wood S.L. 1982. *The Bark and Ambrosia Beetles of North and Central America (Coleoptera; Scolytidae)*, a Taxonomic Monograph. *Great Basin Naturalist Memoirs*, Num. 6.



## Diversity and Function of Bacterial Endophytes Colonizing the Needles of Subalpine Conifers

A. Carolin Frank<sup>1</sup> and Lara Kueppers<sup>2</sup>

<sup>1</sup>*School of Natural Sciences, University of California, Merced, California*

<sup>2</sup>*Energy and Resources Group, University of California, Berkeley, California*



**Carolin Frank** is Associate Professor of Environmental Sciences, with interests in forest tree microbiomes, including roles of nitrogen fixation, bacteria and fungi, genomics, and ecosystem implications.



**Lara Kueppers** is Assistant Professor in the Energy and Resources Group, and Faculty Scientist at Berkeley Lab. Lara's research focuses on ecological responses and feedbacks to climate change to advance understanding of climate-ecosystem interactions in forests and agroecosystems.

### Summary

Over the past five years, we have studied the diversity and function of bacteria that colonize the inside and surface of conifer needles, with a particular emphasis on subalpine species. We have found that bacteria inside needles fix atmospheric nitrogen (N) at low rates. While the amount of N fixed is probably too low to matter for forest N budgets, it may nevertheless provide a significant source of N for subalpine conifers growing in N limited soil. Though the bacterial species or communities responsible for needle N-fixation are still unknown, a group of N-fixing bacteria called acetic acid bacteria tend to be the most common inhabitants of conifer needles, potentially reflecting an evolutionary relationship and significant association. In two recent studies aimed at better understanding the drivers of variation in the conifer needle microbiome, we found that different species of subalpine conifers host slightly different bacterial communities in their foliage, but that the main driver of variation in the leaf microbiota is forest site.

### Overview

Eukaryotic life originated as a symbiosis between a bacterium and an archaeon, and continued to evolve in a sea of microbes. Consequently, all animals and plants depend in some way on interactions with microbes that became integrated in host biology from the beginning. In the past decade, our ability to study complex microbial communities in various systems—from our own gut flora to the roots of agricultural crops—has been

revolutionized by cheaper and more efficient DNA sequencing technology that allows us to characterize microbes that cannot be grown in the laboratory.

In addition to the visible and well-studied associations between plants and microbes like mycorrhizal fungi and root nodulating nitrogen-fixing bacteria, all plants have microbiomes—diverse, complex communities of bacteria and fungi that colonize all parts of healthy plants, both above- and belowground, inside and out, from roots to reproductive organs (Turner et al. 2013). The plant microbiome mediates many important plant traits, including acquisition of limiting nutrients, protection against pests and pathogens, and abiotic stress tolerance (Friesen et al., 2011). Members of the plant microbiome can also stimulate plant growth through the production or modulation of plant hormones. Interestingly, recent research on the rhizosphere and root microbiome has demonstrated that plants can actively recruit helper microbes in response to stress (Castrillo et al. 2017).

Research on the microbes that colonize conifer needles was pioneered by George Carroll, who studied fungal needle endophytes in various species of trees growing in Northern California and the Pacific Northwest. Carroll suggested that fungal endophytes may contribute heterogeneity in defense chemicals, allowing long-lived trees to resist disease over centuries to millennia; unlike the host tree, the short life cycle of fungi should allow them to respond on ecological timescales to

short-cycle pathogens and pests (Carroll 1988). Recent research on the microbiome of various animals and plants supports a similar idea—that microbiomes bring flexibility and variability to a host’s genetic makeup that allows it to respond to variable environments (Cordovez et al. 2019).

Our research on the leaf bacteria in subalpine conifers was originally motivated by the harsh conditions that these trees tolerate near treeline, including low temperatures, desiccating winds, and low soil moisture and nutrient content, and the possibility that microbes help alleviate some of this stress. For example, conifers may meet some of their demand for N via N-fixing bacteria in their foliage (Moyes et al. 2016). Only bacteria and archaea have the enzyme nitrogenase that reduces atmospheric dinitrogen to ammonia. Nitrogen fixation in association with plants has been intensively studied in legumes, which host large amounts of N-fixing bacteria in root nodules, and to lesser degree in other plants, where bacterial sometimes fix N inside leaf or root tissue as endophytes, or in the rhizosphere (root surface) or leaf surface (phyllosphere).

We began researching N-fixation in conifers after finding that the needles of limber pine (*Pinus flexilis*) and Engelmann spruce (*Picea engelmannii*) growing at Niwot Ridge were colonized by acetic acid bacteria (family Acetobacteraceae in the class Alphaproteobacteria) related to known endophytic N-fixing species (Carrell and Frank 2014; Fig. 1). This work was also inspired by earlier findings by Christopher Chanway, who had isolated N-fixing bacteria from lodgepole pine, and subsequently showed that lodgepole pine seedlings inoculated with such bacteria acquired more atmospheric N than control plants grown from sterile seeds (Chanway 2011).

To characterize bacteria inside needles, we rely on DNA sequencing. The reason for this is that most bacteria in the environment are not culturable; common estimates of the percent of bacterial species from a given environment that can be grown in the lab range from 1-5%. We extract total DNA from the needles, and use primers for the RNA gene encoding a part of the bacterial ribosome called 16S to amplify bacterial sequences, which we then sequence on a next-generation sequencing



**Figure 1.** Top: Limber pine at treeline at Niwot Ridge, CO, where we started our conifer microbiome research. Bottom: The Acetylene Reduction Assay to test for nitrogenase activity in limber pine foliage.

instrument capable of producing tens- to hundreds of thousands of sequences for every sample. This allows us to characterize the majority of bacterial species present in our samples by matching them to sequences in databases. We typically find a few hundred species of bacteria inside needles, but the community is usually dominated by a few strains that together make up the majority of the community (Carrell and Frank 2014, Carrell et al. 2016).

After finding that acetic acid bacteria dominate the bacterial communities inside limber pine and Engelmann spruce needles, we tested if nitrogenase, the enzyme responsible for N-fixation, was active in surface-sterilized twigs from limber pine. The motivation for the research was two-fold; first, we were hoping to contribute to a better understanding of how conifers acquire their N, something that is not fully understood (Högberg et al. 2017). Second, research over many decades suggests that there are unknown sources of N in old growth forest ecosystems—there is more N in foliage, litter, and soil than there should be given known sources of N—a mystery sometimes referred to the forest ‘N gap’ (Binkley et al. 2000, Bormann et al. 2002).

To test if nitrogen is fixed in conifer foliage we used the acetylene reduction assay (ARA), an indirect method that takes advantage of the nitrogenase enzyme’s ability to reduce triple bonded substrates (Hardy et al. 1968; Fig 1.). Nitrogenase reduces acetylene gas to ethylene, and build-up of ethylene after incubation with acetylene measures nitrogenase activity. Since ethylene happens to be a plant hormone, it is important to use no-acetylene controls when using this assay on plants. Using the ARA, we showed that there is low but significant nitrogenase activity in the foliage of adult limber pine trees (Moyes et al. 2016). This result was supported by another experiment where we exposed twigs to  $^{15}\text{N}$ , the radioisotope of N, and subsequently saw the needles light up in a position emission tomography (PET).  $^{15}\text{N}$  has a half-life of a little under ten minutes, and we were fortunate enough to collaborate with physicists at the Lawrence Berkeley National Lab who have a cyclotron for making  $^{15}\text{N}$  and a PET scanner on site. More recently, we have confirmed our result using labelling with the stable isotope of nitrogen,  $^{15}\text{N}$  (Quiroz et al. in prep).

Around the same time that we published our result that nitrogenase is active in conifer foliage, another group published similar data for black cottonwood (*Populus trichocarpa*), demonstrating that diverse trees can use an atmospheric source to meet some of their demand for N (Doty et al. 2016). Although the rates of fixation we measured in conifer foliage is probably too low to explain the N gap (Moyes et al. 2016), widespread N-fixation in forest vegetation, including both deciduous and

evergreen trees, might collectively explain the source of N to forest ecosystems.

What other beneficial traits, besides N-fixation does the microbiome bring to their conifer host? In another study, we characterized the bacterial communities in roots and shoots of one-year-old limber pine seedlings from a warming experiment at Niwot Ridge, CO. We found that unlike adult trees at the same site, which were dominated by acetic acid bacteria, the seedlings hosted different microbial communities dominated by a few Betaproteobacterial species in the family Oxalobacteraceae (Carper et al. 2018). The species found inside seedlings were identical or closely related to strains previously isolated from the skin of amphibians, where they protect their host against fungal infection by producing secondary metabolites with antifungal activity. Their function in seedlings still needs to be confirmed, but it is possible that microbiomes protect young trees against fungal infection. In the same study, we also found that watering, but not warming, altered the microbial communities in seedling roots and shoots, suggesting that the seedling microbiome varies with environmental conditions in addition to host factors (Carper et al. 2018).

In other forest trees, both host species and geographic site have been found to influence the microbial communities present in and on leaves (Laforest-Lapointe et al. 2016). After finding that both limber pine and Engelmann spruce growing at Niwot Ridge, CO were dominated by acetic bacteria, we wondered if subalpine conifers always associate with these bacteria, and we decided to investigate limber pine and lodgepole pine (*Pinus contorta*) at two sites; Niwot Ridge and a site in the Eastern Sierra Nevada. We were surprised to find that the trees in the two sites hosted very similar bacterial communities, dominated by identical acetic acid bacterial sequences (Carrell et al. 2016). This pattern was difficult to explain given what we know about plant microbiomes, and it became clear to us that in order to better understand the processes governing assembly of bacterial communities in conifer needles, we needed to include more sites and species in our studies. We also needed to characterize the leaf communities over time and at different spatial scales, ranging from within the canopy of a single tree to across a tree species’ distribution.

In one of these studies, we characterized endophytic communities of bacteria in the foliage of twelve species of conifers growing in the same site at the Miracle Mile, a hotspot of conifer diversity in California’s Russian Wilderness. The conifer species sampled spanned three families (Pinaceae, Cupressaceae, and Taxaceae) and hosted significantly different needle endophyte communities. We found that host plant taxonomic identity explained roughly



30% of the variation in endophytic community composition across trees, and that associations between conifer species and bacterial taxa was non-random (Quiroz et al in prep). This could mean that conifers have co-diversified with their foliar microbiomes over time, or alternatively, that more closely related plant species have similar selectivity for specific microbes.

In another study, we took a biogeographical approach to examining the factors that structure subalpine needle microbial communities. We were interested in the influence of forest site on the microbiome inside and on needles, and whether it may be stronger than the effect of host species identity. Continuing the focus on limber pine, we sampled foliage from this species at 16 sites across its native range, which extends from New Mexico to Canada and from California to South Dakota. Most of our sites were in the Colorado Rockies, but we also included sites in California, Oregon, Nevada, Montana, South Dakota, New Mexico, and Wyoming. At each site, we sampled ten limber pine trees, along with ten individuals of any co-occurring conifer species. These differed by site, but included lodgepole pine, ponderosa pine (*Pinus ponderosa*), bristlecone pine (*Pinus longaeva*), Engelmann spruce, white spruce (*Picea glauca*), Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and subalpine fir (*Abies lasiocarpa*). Our results showed that forest site explained ca. 20% of the variation in the communities, whereas host species explained less than 5% (Carper et al, in prep). Interestingly, we found that needle age (we sampled young and old needle cohorts from the pines) was a significant driver of leaf microbiome variation, with the largest impact in bristlecone pine, which has the record among conifers for needle longevity. It is possible that the change in leaf chemistry, wax, and other characteristics are more important than host species identity in shaping the leaf microbiota.

To better understand why forest site was the strongest driver of needle microbiome variation, we tested the hypothesis that there is a ‘distance-decay’ relationship for leaf communities, such that similarity between samples decreases with distance, which would be expected with limited dispersal of microbes between forest site. That was not the case—geographic distance was not significantly correlated with microbial community dissimilarity. However, climatic variables such as temperature, precipitation, and vapor pressure deficit were, suggesting that local climate is an important driver of variation. It was not, however, the whole story. Different forests sites have their own signature foliar microbiome such that trees growing in a site share a similar microbiome regardless of species, and climate variables only explain some of that. Another possibility is that the ‘metacommunity’ of microbes that are available to colonize needles differ among forest sites. However, these local communities are also linked via dispersal—many of our so

called ‘sequence variants’—identical sequences separated at the strain level—were found in and on needles all over the limber pine range. This was particularly true of the acetic acid bacteria, which again dominated the needle communities in most, but not all sites. The widespread strains in our dataset are similar to bacteria sampled from the atmosphere, which makes us think that the atmosphere is the vector for leaf colonization from a variety of sources including other plants, soil, dust, and rain. We recently started a study to examine the temporal variation of leaf microbiomes at smaller spatial scales, and we are sampling the microbes in the air to better understand how canopy microbiomes are dispersed.

Although acetic acid bacteria were the most common bacteria in our leaf communities in most forest sites across the limber pine range, other bacterial families like Burkholderiaceae, Enterobacteriaceae, Pseudomonadaceae dominated at some sites, in particular ‘outlier’ sites in California and South Dakota. It is difficult to say, based only on the 16S rRNA gene that we sequenced so far, what these bacteria do, and whether they perform important functions for the host tree. However, we are in the process of sequencing so called ‘shotgun metagenomes’, where rather than sequencing a taxonomic marker gene, entire genomes from a bacterial community are sequenced without culturing bacteria first, allowing identification of a wide range of bacterial gene functions. We hope that this approach will identify the elusive N-fixing microbes in limber pine needles (Moyes et al. 2016), as well as new and interesting functions in the canopy microbiome. Stay tuned!

## References

- Binkley, D., Yowhan, Son., and Valentine, D.W. 2000. Do forests receive occult inputs of nitrogen? *Ecosystems* 3: 321–331.
- Bormann, B.T., Keller, C.K., Wang, D., and Bormann, H. 2002. Lessons from the sandbox: Is unexplained nitrogen real? *Ecosystems* 5: 727–733.
- Carper, D.L., Carrell, A.A., Kueppers, L.M., and Frank, A.C. 2018. Bacterial endophyte communities in *Pinus flexilis* are structured by host age, tissue type, and environmental factors. *Plant Soil* 428: 335–352.
- Carrell, A.A., and Frank, A.C. 2014. *Pinus flexilis* and *Picea engelmannii* share a simple and consistent needle endophyte microbiota with a potential role in nitrogen fixation. *Front. Microbiol.* 5.
- Carrell, A.A., Carper, D.L., and Frank, A.C. 2016. Subalpine conifers in different geographical locations host highly similar foliar bacterial endophyte communities. *FEMS Microbiol. Ecol.* 92.

- Carroll, G. 1988. Fungal endophytes in stems and leaves: from latent pathogen to mutualistic symbiont. *Ecology* 69: 2–9.
- Castrillo, G., Teixeira, P.J.P.L., Paredes, S.H., Law, T.F., de Lorenzo, L., Feltcher, M.E., Finkel, O.M., Breakfield, N.W., Mieczkowski, P., Jones, C.D., et al. 2017. Root microbiota drive direct integration of phosphate stress and immunity. *Nature* 543: 513–518.
- Chanway, C.P. 2011. Can lodgepole pine provide its own nitrogen? *Branchlines* 22: 8–9.
- Cordovez, V., Dini-Andreote, F., Carrión, V.J., and Raaijmakers, J.M. 2019. Ecology and evolution of plant microbiomes. *Annu. Rev. Microbiol.* 73: 69–88.
- Doty, S.L., Sher, A.W., Fleck, N.D., Khorasani, M., Bumgarner, R.E., Khan, Z., Ko, A.W.K., Kim, S.-H., and DeLuca, T.H. 2016. Variable nitrogen fixation in wild *Populus*. *PLOS ONE* 11: e0155979.
- Friesen, M.L., Porter, S.S., Stark, S.C., von Wettberg, E.J., Sachs, J.L., and Martinez-Romero, E. 2011. Microbially mediated plant functional traits. *Annu. Rev. Ecol. Evol. Syst.* 42:23–46.
- Hardy, R.W., Holsten, R.D., Jackson, E.K., and Burns, R.C. 1968. The acetylene-ethylene assay for n(2) fixation: laboratory and field evaluation. *Plant Physiol* 43: 1185–1207.
- Högberg, P., Näsholm, T., Franklin, O., and Högberg, M.N. 2017. Tamm Review: On the nature of the nitrogen limitation to plant growth in Fennoscandian boreal forests. *For. Ecol. Manag.* 403: 161–185.
- Laforest-Lapointe, I., Messier, C., and Kembel, S.W. 2016. Host species identity, site and time drive temperate tree phyllosphere bacterial community structure. *Microbiome* 4, 27.
- Moyes, A.B., Kueppers, L.M., Pett-Ridge, J., Carper, D.L., Vandehey, N., O’Neil, J., and Frank, A.C. 2016. Evidence for foliar endophytic nitrogen fixation in a widely distributed subalpine conifer. *New Phytol.* 210: 657–668.
- Turner, T.R., James, E.K., and Poole, P.S. 2013. The plant microbiome. *Genome Biol.* 14: 209.





## RESEARCH AND PRACTICE

This article was originally published in *The Wildlife Professional*, Vol.12.5. Reprinted with permission from The Wildlife Society, Bethesda, Md. 20814. Learn more about The Wildlife Society at [wildlife.org](http://wildlife.org).

## Best Friends Forever

### THE WHITEBARK PINE AND CLARK'S NUTCRACKER

By Robert E. Keane and Samuel A. Cushman

▼ The whitebark pine comprises 10 to 15 percent of total forest cover in the lower timberline areas of the Northern Rocky Mountains.

It's late fall in the high mountains of western North America and the whitebark pine (*Pinus albicaulis*) forests are alive with activity. Birds and mammals are feasting on the pine's copious amounts of large seeds. When the cones ripen, the competition for the fatty, nutritious seeds — which contain “more energy than chocolate per unit of weight” according to the Cornell Laboratory of Ornithology — is a sight to see.



Credit: Marshal Hedin/Flickr

▲ The Clark's nutcracker has a mutualistic relationship with the whitebark pine, acting as the tree's main seed dispersal mechanism.

Among the important wildlife species that consume the seeds is the iconic grizzly bear (*Ursus arctos*). Highly dependent on the pine seeds, the grizzly population in the Greater Yellowstone Ecosystem thrives when the cone crop is good. Local management agencies even conduct extensive annual cone survey transects to measure the crop size and adjust their grizzly bear management plans based on the size of the crop.

While the grizzly bear may be the largest species that covets the seeds, over 110 species of animals compete for them in many parts of the tree's range. That's why scientists often describe whitebark pine forests as “keystone” or “foundation” ecosystems in these high mountain settings. If the tree is lost, so too is an important food source for many wildlife species.

Sadly, whitebark pine trees are dying at astounding rates across the species' range, and the seed crops from this keystone ecosystem are dwindling rapidly (Keane et al. 2012). The decline is so bad that the pine is a candidate species under the federal Endangered Species Act; however, it's currently precluded from listing due to administrative backlogs.





One bird in particular, the Clark's nutcracker (*Nucifraga columbiana*), functions as the main dispersal vector for whitebark pine seeds. It's a story of a unique mutualistic relationship that is in trouble.

### Whitebark pine characteristics

Whitebark pine is a five-needled pine that is distributed from timberline to lower subalpine regions in the northern and central Rocky Mountains, Cascade Range and in portions of the Sierra Nevada range in the United States and Canada (Keane et al. 2012). It's unique among pines because it's not used for commercial timber or pulp. The tree's value lies in its seed crop.

Over its range, the whitebark pine typically occupies about 8 to 12 percent of the landscape, ranging from the upper subalpine to timberline regions of these mountain ranges. In most upper subalpine settings, this shade-intolerant species is eventually replaced over centuries by a suite of shade-tolerant competitors, namely subalpine fir (*Abies lasiocarpa*), spruce (*Picea engelmannii*) and, in some places, mountain hemlock (*Tsuga mertensiana*). However, in lower timberline areas, whitebark pine is typically the dominant tree species. This lack of competition creates the idyllic open stands often enjoyed by high-elevation hikers and bird enthusiasts.

Whitebark pine typically produces a good cone crop every three to five years. The highly visible cones are bright purple and arranged upwards at the end of branches. The seeds are large and wingless, with no vestige of a wing. Curiously, the cones rarely open; and even if they did, the round seeds would drop directly below the crown and be eaten quickly by rodents. All of these distinctive characteristics allow the Clark's nutcracker to easily find the cones and harvest the seeds from them.

### Clark's nutcracker

The Clark's nutcracker is an extremely intelligent bird in the corvid family, a relative of jays and crows. Smaller than a crow and slightly larger than a jay, Clark's nutcrackers range across much of the mountainous western United States and southwestern Canada and are highly dependent on several five-needle pine species for food, including whitebark pine, limber pine (*Pinus flexilis*) and southwestern white pine (*Pinus strobiformis*).

As the only mechanism for whitebark pine seed dispersal, the Clark's nutcracker has several



Credit: Robert Keane/USFS

adaptations that promote its mutualism with the pine, including unique behavior, physiology and anatomy optimized for foraging on the pine seeds. It's the only bird that has a hole under its tongue leading to a sublingual pouch where it can carry a large number of seeds, often over 50. The bird's heavy, hooked bill is also well-suited for prying seeds out of cones.

▲ The Clark's nutcracker's heavy, hooked bill helps it excavate seeds from the cones of the whitebark pine.

But of all the bird's adaptations, the most impressive is its high level of intelligence as demonstrated by a very strong spatial memory. After collecting a pouchful of seeds, nutcrackers fly across vast landscapes and select distinctive places to store their seeds. The bird typically buries one to 15 seeds in a "cache," which is about one to two centimeters deep. A typical Clark's nutcracker will make 10,000 to 20,000 caches annually and recovers between 50 to 80 percent of the seeds, depending on the size of the cone crop and the energy needs of the bird. This leaves a large portion of cached seeds free to germinate and create the whitebark pine forests of tomorrow.

While the birds store seeds across the entire landscape, they especially like to create their caches in open areas, typically burned areas that have a rich pattern of landmarks so they can recognize the location of the cache. They do not rely on magnetic fields or solar angles to find their caches. Rather, they use spatial pattern recognition, keying in on logs, rocks, and other spatial features to produce a mental map.



▼ Fire creates pattern-rich, competition-free conditions that favor caching by the Clark's nutcracker and subsequent whitebark pine regeneration and growth.

Typically they disperse the pine seeds within a 10 to 20 kilometer range, but observations of flights up to hundreds of miles long have been recorded (Lorenz et al. 2009). These dispersal distances are several orders of magnitude greater than the distances that wind can disperse the seed of the pine's competitors and gives the whitebark pine a strong competitive advantage in recolonizing patches where disturbance, primarily wildfires, have opened the canopy. The sheltered microsites — especially near logs, snags and rocks — provides protection for the trees to regenerate by providing shelter from snow creep that can uproot seedlings.



Credit: TK

### A triangle of interactions

Ecologists have found an interesting relationship triangle between wildfire, which creates openings; the Clark's nutcracker, which disperses the seeds; and the whitebark pine, which provides the seeds. Fire creates pattern-rich, competition-free conditions suitable for both nutcracker caching and subsequent whitebark pine regeneration and growth. Fire also reduces competition by killing shade-tolerant tree species, thereby creating open-canopy conditions suitable for whitebark pine growth. The birds concentrate caching in burned areas because of the rich spatial pattern left after fire (Keane 2012).

The whitebark pine has a complex fire ecology. Most forests dominated by the tree experience a mixture of three types of fire regimes: high-severity stand replacement fires, mixed-severity fires and non-lethal surface fires. Fire-return intervals vary by topography, landscape conditions and local climate and range between 80 and 500 or more years.

Lightning causes nearly all fires in high-elevation forests, usually during major seasonal droughts that occur in the driest part of the summer and early fall. Stand-replacement fires tend to be large in size and often kill more than 90 percent of the trees, creating large openings that are not readily seeded via wind dispersal from distant seed sources such as the subalpine fir and Engelmann spruce.

Whitebark pine seeds easily reach the centers of these burns, however, thanks to the Clark's nutcracker. In mixed severity fires — which often produce a heterogeneous mosaic of canopy openings — nutcrackers place most of the cache within 0.5 to 1 kilometer from the seed source. Mixed severity burn patches from 20 to 40 hectares are optimal for nutcracker seeding because the birds prefer to place their caches within 1 to 3 kilometers of the seed source (Keane 2012).

Non-lethal surface fires maintain whitebark pine dominance by killing the shade-tolerant subalpine fir and Engelmann spruce understory. The pine survives fire better than these major competitor tree species because it has thicker bark, deeper roots and sparse crowns.

### Whitebark pine decline

Complex interactions — worsened by the lack of fire and climate change — have decimated many populations of whitebark pine across its range. The



decline is occurring at varying rates across many areas in the northern U.S. Rocky Mountains, causing more than 80 percent of the trees to die off in some areas (Kendall and Keane, 2001).

White pine blister rust (*Cronartium ribicola*) — a non-native pathogen accidentally introduced to North America in 1910 from Eurasia — is rapidly becoming the greatest threat to whitebark pine that is escalating with a warming climate. The trees have little natural resistance to the rust — less than 1 percent — and since 1960, it has invaded most of the species' range, often resulting in catastrophic die-offs.

Multiple federal agencies, including the U.S. Forest Service and National Park Service, are working to mitigate the disease by identifying and breeding genetic variants that are resistant to blister rust, and then strategically planting them to increase native resistance levels and create resilient whitebark pine forests. Researchers also are pursuing new approaches in landscape genetics and simulation modeling to develop management solutions that increase resistance (Keane et al. 2017).

These restoration efforts are confounded by another complex interaction between the mountain pine beetle (*Dendroctonus ponderosae*) and whitebark pine. Scientists thought the trees' cold habitat would slow the rate of larval development and reduce the rate of the beetle's spread because periodic cold snaps killed nearly all larvae in large expanses of the trees' habitat. But instead, the conditions produced low levels of the insects in most whitebark pine communities.

This dynamic has changed dramatically in the last few decades, coinciding with rapid warming of mountain ecosystems in western states. As the climate has warmed, mountain pine beetle populations have increased to outbreak levels in montane ecosystems, particularly those dominated by lodgepole pine (*Pinus contorta*), which has caused waves of dispersing beetles to move upslope into whitebark pine communities. The warming temperatures



Credit: Robert Keane/USFS

also have increased the susceptibility of whitebark pine ecosystems to the mountain pine beetle, accelerating the rate of larva development and greatly decreasing the frequency of die-offs from extreme cold snaps. As a result, the beetles have invaded extensive portions of the whitebark pine range, killing many of the trees.

Fire exclusion is also a threat to the whitebark pine. Without wildfire, the trees are replaced by shade-tolerant competitors in many areas of the upper subalpine. In the western U.S., federal and state agencies have followed an aggressive fire suppression policy focused on extinguishing all wildfires since the early part of the 20<sup>th</sup> century. This management strategy has resulted in a large change in fire regimes over the last 80 to 100 years, with much lower levels and frequencies of fire in most locations.

However, since the early 2000s, the area burned by wildfires in many parts of the whitebark pine's range has expanded greatly, likely driven by a combination of recent climate warming and the accumulation of atypical fuel loads from 100 years of fire exclusion. The increase in the number of fires may have reduced the negative impacts of fire exclusion on whitebark pine, but it also caused great concern about the future of the trees. Wildfires also kill rust-resistant whitebark pine, further facilitating the decline of the trees.

▲ A USFS biologist demonstrates how to cage whitebark pine cones near Cody, Wyo., to protect them from squirrel and nutcracker predation.



When the local abundance of whitebark pine falls, scientists also have observed a threshold effect. Instead of acting as seed dispersers, nutcrackers become seed predators, consuming nearly all cached seeds, creating a negative feedback loop of population dynamics that could wipe out local whitebark pine populations (McKinney et al. 2009).

### What is being done?

The USFS, NPS, Bureau of Land Management, and several government agencies in Canada are conducting restoration activities across the range of whitebark pine in the U.S. and Canada with great success. Rust resistance levels in planted whitebark seedlings are often greater than 40 percent, and many of the areas that were burned in wildfires are now being planted with this resistant stock. Some agencies, primarily USFS, are using prescribed fire and mechanical cuttings in areas that are successional advanced to the shade tolerant competitors.

But there is so much more to be done. Efforts are currently underway to create a local strategies and corresponding cross-agency programs for restoring whitebark pine across its range. While these efforts are laudable, the extent of the restoration needs to expand if we are to retain whitebark pine forests

on the landscape. A range-wide strategy published in 2012 includes regional and project-level strategies for conserving this precious tree species; and currently, the U.S. and Canadian land management agencies are in the process of developing a comprehensive multi-national restoration plan for public lands (Keane et al, 2012).

It may take a century to see the results of current restoration efforts; but hope is that the high mountain whitebark pine forests of North America will once again be alive with activity, ensuring the pine and the bird remain best friends forever. ■



**Robert E. Keane, PhD**, is a research forest ecologist with the U.S. Forest Service Rocky Mountain Research Station.



**Samuel A. Cushman, PhD**, is a research ecologist with the U.S. Forest Service Rocky Mountain Research Station.

# BREVIA

## Long-Distance Dispersal, Ice Sheet Dynamics and Mountaintop Isolation Underlie the Genetic Structure of Glacier Ice Worms

Scott Hotaling

School of Biological Sciences

Washington State University, Pullman, Washington



**Scott Hotaling** is a postdoctoral researcher whose work centers around understanding what lives where in cold places, how they've adapted to those environments, and their future given a rapidly warming climate and receding cryosphere.

*Hotaling, S., Shain, D.H., Lang, S.A., Bagley, R.K., Tronstad, L.M., Weisrock, D.W., and Kelley, J.L. 2019. Long-distance dispersal, ice sheet dynamics and mountaintop isolation underlie the genetic structure of glacier ice worms. Proceedings of the Royal Society B, 286(1905), p.20190983. <https://doi.org/10.1098/rspb.2019.0983>*

Despite constant near-freezing temperatures, extreme levels of ultraviolet radiation, and a lack of free water, glaciers and perennial snowfields still support diverse biological communities. These communities are generally dominated by microbes but in rare cases, glacier-obligate macroinvertebrates have also evolved to survive (and thrive!) in a world of ice. Perhaps the best-known glacier invertebrate is the North American ice worm (*Mesenchytraeus solifugus*), a thread-like, heavily pigmented annelid that inhabits coastal glaciers from Oregon to Alaska.

When present, ice worms are far from rare. Rather, they often cover the glacier surface at densities in excess of 100 per m<sup>2</sup>. This abundant, easy-to-catch resource provides a boon for alpine foraging birds in a landscape generally devoid of prey. Previous studies identified a complex biogeographic history for

ice worms, with evidence for genetic isolation, unexpectedly close relationships among geographically disjunct lineages, and contemporary migration across large (e.g., greater than 1500 km) areas of unsuitable habitat.

In this study, we used high-resolution population genomic data to generate the most comprehensive investigation of ice worm biogeography to date. We found clear support for divergence between populations along the Pacific Coast and the inland flanks of the Coast Mountains that was likely precipitated by episodic ice sheet expansion and contraction during the Pleistocene. We also found clear, genetic support for extreme long-distance dispersal of ice worms from Alaska to Vancouver Island. The most plausible explanation for this pattern is passive movement of ice worms on, or perhaps inside of, migrating birds (see back cover, Field Frames). Our results shed new light on mountain glacier biology and highlight the power of genomic data for disentangling complex biogeographic patterns, including the detection of long-distance dispersal in an enigmatic organisms.



Abundant ice worms on the Noisy Creek Glacier, North Cascades National Park, USA, May, 2017. Photo, Jon Riedel.



# INTERVIEW

**Dr. Malcolm Hughes** is Regents' Professor at the Laboratory of Tree-Ring Research (LTRR), University of Arizona in Tucson, where he has worked since coming to the US from his homeland in the UK in 1986. He is a Fellow of the American Geophysical Union and of the American Association for the Advancement of Science. At UA, Malcolm served as Director of the LTRR from 1986 to 1999, during which time the Laboratory recovered greatly in size and international influence, serving as the flagship dendrochronology institution for a rapidly growing discipline. Malcolm is a well-known and pioneering leader in our mountain-science world—a founding father and key energizer of CIRMOUNT— but that is only a small aspect of his influential role in the international climate-science community. His work in the late 1990s with Ray Bradley and Michael Mann led to publication of seminal papers during the awakening years of the global climate crisis. In these works, Malcolm and colleagues used multiple proxies to compile a global climate reconstruction for the past 1,000 years, which famously became known as the “hockey-stick graph,” used in multiple IPCC and other assessments subsequently. Malcolm’s studies over the decades blazed the trail for tree-ring research as the field blossomed under his research leadership. He continues this work at present in collaboration with Andy Bunn and Matt Salzer to improve the spatial and temporal resolution of response of high-elevation Great Basin bristlecone pines to past climate. I first met Malcolm at a PACLIM workshop on Santa Catalina Island, CA, in 1997, and he has been a hero and mentor—as well as close friend—ever since. I deeply admire Malcolm’s strength as a scientist, leader, and teacher, and I am inspired by his wisdom, conviction, and courage, and always delight in his wonderful sense of humor. *–Editor*

## MALCOLM HUGHES



**Connie:** A long and brilliant career such as yours has clearly had many phases as you tackled changing questions, interests, and topics over time. Can you highlight how the path of your career has played out in this way across the decades?

**Malcolm:** Such a kindly phrased first question! Good fortune saw me arrive at university when traditional subject categories were being challenged, albeit fairly gently by modern standards. In early 1960s Britain, studying both Botany and Zoology at undergraduate level was considered either adventurous or a bit dodgy. Whichever it was, that initial preparation served me well for my graduate work. My Ph.D. supervisor, John Philipson, was a pioneer in ecosystem energetics and was focusing on a local woodland ecosystem. That was my introduction to quantitative forest ecology and to multidisciplinary, international collaboration through the International Biological Program (IBP). A post-doc fellowship on an IBP project in Denmark followed, again quantifying Net Primary Production in a temperate

forest. Then in 1969 I met my first mountain environment, the windswept Pennines of northern England, in a “rescue ecology” project on algae (mainly blue-green algae, a.k.a. cyanobacteria) in a soon to be submerged mountain valley.

My generalist bent served me well in my first faculty position in Liverpool (1971), where we set about building an integrated biology undergraduate curriculum, one of the earlier of its kind. Undergraduate research projects were central, so urban ecology, especially pollution and trace element cycling in the historical heart of the Industrial Revolution, was a good source of topics. At the same time I came across the work of the late Hal Fritts on climate, tree growth and tree rings and visited the Tucson lab in 1973. Encouraged and inspired, I started my five-decade apprenticeship in dendrochronology and was lured away from



Malcolm at Liverpool lab, early 1980's.



“pure” ecology. These were the early days of building world-wide tree-ring networks for climate reconstruction and then of integrating them with other natural (for example ice-cores, varves, corals) and documentary archives. For my part, with colleagues, I checked if dendroclimatology would work in the British Isles, with our native oaks. It did. Then, in the mid-1970s, back to the mountains, in this case the Scottish Highlands, and a network of Scots pine chronologies. Comparison with some of the longest meteorological records in the world (for example at the capital of Scotland, Edinburgh), revealed a temporally very stable July-August temperature signal in this network back to the 18th Century, especially in maximum latewood density (MXD). This was a springboard for using conifer MXD to reconstruct summer temperature where the instrumental record was much shorter, for example, in the Western Himalaya, as a contribution to the nascent global tree-ring network. It also furthered my transition from old, round mountains to young, rugged ranges.

Working to promote international cooperation and data sharing brought me opportunities, not least my move to Arizona in 1986. The generous collaboration of Tom Swetnam and Lisa Graumlich introduced me to the ancient trees of the Sierra Nevada, especially giant sequoia. Don Graybill and Gary Funkhouser taught me about bristlecone pine in the mountains of the Great Basin and its margins. It is remarkable that there are many thousands of living trees of these species whose lives started long before the Common Era, and in the case of bristlecone pine, thousands of relict snags and logs covering most of the Holocene scattered in high, cold, dry places. Each of these species presents its own challenges to those of us intent on extracting some quantifiable signal of past climate from its thousands of annual rings. Neither is a prime candidate for the multivariate statistical approaches to climate signal identification and extraction that are often used in tree-ring based climate reconstructions. Giant sequoia rings don't care much unless summer soil moisture goes below a rather severe threshold. Bristlecone pine live in places that are both dry and cold, with needles retained for decades as well as some of them living at high enough elevation for indirect CO<sub>2</sub> fertilization to be a possibility. How to get a useful record of past climate from such tree rings? These are the puzzles for which I have sought answers over the past 30 years, with great colleagues such as Peter Brown and Ramzi Touchan (giant sequoia), Matt Salzer, Andy Bunn and Gary Funkhouser (bristlecone pine).

The vision of continental and global networks of dendroclimatic records glimpsed by Hal Fritts in the early 1970s and worked on by many in the following twenty years took substance with the emergence of high-resolution paleoclimatology in the 1990s. My contributions of primary data were from Western Europe, Russia, China and the American West. My good fortune linked

me with climatologists such as Henry Diaz (an old CIRMOUNT hand), Ray Bradley, and Mike Mann. From all these years of effort by so many muddy-booted field scientists in scattered and seemingly unconnected places, hemispheric-scale patterns of physically-plausible climate variability emerged on interannual to century time scales. Amazing! Our “product” – annual maps of, for example, temperature, for several centuries over all or a large part of the Northern Hemisphere, represented boxfuls of climate hypotheses ready for testing, made possible by the great gift of dendrochronology, namely, robust chronology good to the calendar year.

Fritts wove his fabric of dendroclimatology with a warp of statistics and a weft of plant ecophysiology. As high-resolution paleoclimatology has matured in recent decades and made greater claims and undergone closer inspection, the wiser his approach seems to be. To look to the Earth's near future, we need to understand mechanisms, not only associations. Fritts started collaboration with Eugene Vaganov and his team in Siberia on process-modeling of tree-ring formation and this has informed my work since the mid-1980s. What I believe has been a mutually illuminating synergy arose between the research traditions of the former Soviet block and the West and continues to this day. Newly practicable techniques are enabling the determination of parameters on a process-observational basis for models like Vaganov's. So, in recent years, in collaboration with Kiyomi Morino and Peter Brown, I have gone back to biology through the study of the phenology of xylogenesis, mainly at flux tower sites in the mountains of the West from Arizona to Wyoming. That's the next chapter!

**Connie:** Growing up, attending university, and having early-career jobs in the UK, what prompted you to come “across the Pond” to the US and to stay and make this your personal and academic home? Was this intentional or were you following the best job opportunities?

**Malcolm:** There was pull, namely a unique opportunity to join and direct the Laboratory of Tree-Ring Research at the UA in 1986, and the chance to live in the Sonoran Desert with views of the ‘Sky Island’ mountain ranges. Then there was a push. Early 1980s Britain was difficult for science and for higher education.

**Connie:** You have been deeply involved with, and instrumental in, developing core climate science at international to local scales. What aspect of this work has been most exciting to you and why?

**Malcolm:** Two intertwining threads have given me great satisfaction. The first was playing a part in the realization of Hal Fritts' vision of a global dendroclimatology and high-resolution



Coring giant sequoia, early 1990's.

paleoclimatology. The 1998 Mann, Bradley, Hughes Nature paper (MBH98) came from a project aimed at reconstructing hemispheric spatiotemporal patterns of climate and in this case we were able to cover the past six centuries, mainly using tree-ring series. The unusual pattern of late-20th century warming stood out against recent centuries and correlation analyses saw only increased atmospheric carbon dioxide as driving this.

The second thread started with our 1999 GRL paper (MBH99), where we explored the possibilities and hazards of pushing back to 1000 C.E. with then-available records. It turned out that a set of bristlecone pine tree-ring width chronologies formed an important predictor of temperature for the first centuries of the millennium. Current understanding was that their growth spurt over the prior 150 years might be the result of indirect fertilization by increased atmospheric CO<sub>2</sub>, rather than of increasing temperatures, bringing into question the possibility of objective calibration. As I mentioned above, sorting out this puzzle has kept a group of us busy since ~1999, leading to some exciting and intriguing results in papers by Salzer et al. (Climate Dynamics, 2013) and Bunn et al. (GRL, 2018). In my view, these results indicate that, in MBH99, we were overly cautious in using these materials as temperature archives. I am proud to have been involved in the careful, step-by-step investigation that has shown that the right bristlecone records can provide good temperature proxies on multi-year to century time scales.

**Connie:** In this context (global-change science leadership) you also got the brunt of some of the most vicious climate denial attacks. Can you tell us a bit about that episode in your career, and what philosophy you took in addressing those challenges? Any advice or lessons learned you would share with us?

**Malcolm:** It's a little disturbing to get a letter from the Chairs of two major committees of the US House of Representatives asking for very extensive professional records, as well as posing a series of questions about the science, all to be answered within a few days. Along with a few colleagues, I got such a letter in June 2005. It was the first major incident in a history of accusations, questions, inquiries, and also litigation concerning very broad public records requests. This continued through, at least, 2018. There was a major flare-up of official inquiries and internet mob behavior in 2010 after the theft and selective release of many thousands of emails from the Climate Research Unit at the University of East Anglia in the U.K. In dealing with this, family, friends and colleagues have been vital. I am very grateful to my university, in particular my department head, Dean, and President, for making a major commitment to maintaining academic freedom. To honor their support, I have worked to keep a strong focus on honest science.

As for lessons? You do not need to stand alone. We have learned a great deal in the past decade about how to defend science and scientists from special interests and/or the forces of unreason. Lawyer up (organize yourself) right now! Look up the Climate Science Legal Defense Fund (<https://www.csldf.org/>), or PEER if you are a government scientist (<https://www.peer.org/>) and read their materials and guidelines. These bodies can link you to others who may have similarly been targets, as well as giving very practical guidance and active help. After that, find out your employer's policies on scientific integrity and what structures they have for such situations. It is possible that your immediate supervisor may not really know the institution's actual policies, so check in to published policies yourself and reach out to organizations like CSLDF and PEER.

**Connie:** During your years as Director of the Laboratory of Tree Ring Research, the lab expanded and grew in many important dimensions. I think the skills of being a successful executive (e.g., Lab Director) compared to a successful scientist are somewhat different. Can you speak to these roles in your career, and how you balanced both so successfully?

**Malcolm:** I'm really not sure I did, but all the evidence suggests that the number one skill in both arenas is showing up at the right time and asking the right questions. Particularly in a university setting I felt the term 'Director' wasn't very descriptive of the actual job to be done. Given that faculty and other PIs

are effectively independent academic entrepreneurs, some combination of leadership through vision and the model of a sheepdog herding a preternaturally smart flock in a more or less agreed direction works better, in my mind.

**Connie:** Given the disheartening lack of political will to address global climate change in time to avoid dangerous outcomes, more and more discussion is arising in regard to what are terrifying but potentially unavoidable prospects. That is, of using atmospheric-intervention methods, such as converting methane to carbon dioxide, removing carbon dioxide from the atmosphere and storing below-ground, and deflecting solar radiation from the Earth with shields. What are your thoughts on these methods, and their uses?

**Malcolm:** Here I answer as a citizen with some science background, but no specifically applicable expertise. It's increasingly clear that drastic solutions are very likely to be called for. At the same time care must be taken to avoid serious unintended consequences, as have already been suggested for deflecting solar radiation and for ocean fertilization schemes. Substantially reducing greenhouse gas emissions by root-and-

branch decarbonization of the economy and promoting all benign means of carbon sequestration (land use, soil and peat conservation, industrial carbon capture, etc.) are where we must start.

I think early consideration should be given to actions that can be taken by large nation-states or groups of countries (for maximum impact on the carbon cycle), within their existing governance structures and traditions and on their own territory (for the quickest response). These would be good places to start, soon.

**Connie:** Any last words of wisdom to share with incoming scientists to our field, as well as for your other peers?

**Malcolm:** No wisdom, just amazement. Expect to see the way we think of our Earth and our species' possibilities total transformed at an accelerating rate. My generation started in science before plate tectonics, the five kingdoms of the living world, civilian remote sensing, ubiquitous cheap computer capability, geospatial technology, and any but the sketchiest concepts of the Earth System. That was less than one lifetime ago. Be ready for an exciting ride!



Malcolm near Wengen, Switzerland.



# VOICES IN THE WIND

In this section, I query members of the CIRMOUNT community for their perspectives on a topic of interest. — Editor

**Question:** What is the most (or one of the more) unusual phenomenon(a) you have witnessed in your mountain travels or field work? This could be atmospheric, terrestrial, aquatic, or anything ecologically, or sociologically unusual. Tell us a little about it and how you reacted.



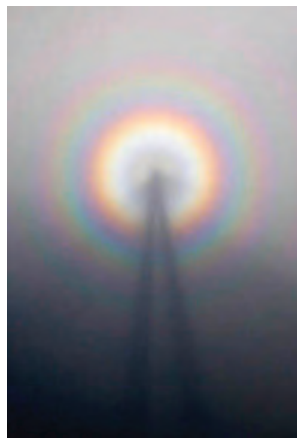
**Jeff Holmquist** is a Research Scientist, Institute of the Environment and Sustainability, White Mountain Research Center, University of California, Los Angeles, Bishop, California

A few last crunches of gravel underfoot, and there was finally no more earth above us. Jutta and I stood seemingly alone on the summit in the misty dawn. But we were very much not alone.

became dark and oppressive, a fierce, bitter wind whisked among the boulders. . . . A strange shape loomed up, receded, came charging at me! Without hesitation I whipped out the revolver and fired three times at the figure. When it still came on I turned and hared down the path, reaching Glen Derry in a time that I have never bettered.” (Jutta and I stared down our antagonists with revolvers holstered).



We had risen early in an effort to avoid untoward weather and to have the peak to ourselves. The horizontal miles and vertical feet had magically melted away as they always do when traveling in the hills. We had started our climb with headlamps, then squinted our way through wisps of mist in the half-light, and finally reached the summit simultaneously with the sun. But when we turned away from that first bright light, we were met with two impossibly large, humanoid apparitions, their heads surrounded by rainbow-like rings of light. Their legs were incredibly long, but indistinct, and their torsos, heads, and arms moved unpredictably and with a vertigo-inducing disregard for our depth perception. We had encountered two Brocken spectres.



Brocken spectres (*Brockengespenst*) were formally described by Johann Silberschlag in 1780. A spectre is the typically towering shadow of a person cast upon clouds or mist—when conditions are just right—at the bearing opposite to that of the observer to the sun. The head is also often surrounded by a “glory:” the rainbow-like rings that we observed. A glory is created by uniformly-sized water droplets that refract and backscatter sunlight. The unpredictable spectre motions result from three-dimensional movements of the water droplets in the mist or clouds against which the shadows have been cast. Sightings are usually at sunrise or sunset.

These infrequently observed creatures have been startling people for centuries, no doubt millennia. Brian Dunning cites the poet James Hogg (1791): “It was . . . at least thirty feet high . . . and very near me. I was actually struck powerless with astonishment and terror.” Dunning also quotes naturalist and mountaineer Alexander Teknion, who described the strangest experience of his life in *The Scots* magazine in 1958. “One afternoon, just as I reached the summit cairn of Ben Macho, mist swirled across the Lairing Guru and enveloped the mountain. The atmosphere



Brocken spectres are a relatively rare sight but have been observed sufficiently frequently to spawn scary local legends notably in the vicinity of The Brocken, a peak in the Harz Mountains of Germany. The figures have been known variously as simply “the Spectre,” “the Grey Man of Ben Macho,” or the “Brocken Witch.” But they are also more generously called “Buddha’s Light” in China and “God Shadows” in several regions, both of which are far happier thoughts.



Minutes later, the bighorns exploded again, and this time they were literally running for their lives. Their pursuer, golden brown, powerful, and larger than life, filled my field of view and my senses. The pursuit by predator of prey unfolded before me as the mountain lion closed in on three of the bighorns. In a strange twist of events, the bighorns unexpectedly turned and launched back in the same direction they’d come, in the direction of the lion. Surprised, the lion’s agility gave way to awkwardness as it struggled to reverse momentum and direction. After a fraction of a second lost, it quickly resumed the chase. In the next moment a large boulder split the trajectory of the three bighorns, and the smallest one went left while the other two went right. The small bighorn made a desperate leap over the boulder toward the others. The lion followed, soared over the boulder and they both disappeared from view.

I slowly dropped to the ground in disbelief. I just witnessed what every wildlife biologist dreams of seeing: nature in its most raw and primal form. I slowly rose and positioned myself back in front of the scope. A minute later, I saw the lion emerge from behind the boulder carrying the freshly killed lamb in its mouth, lumbering toward the cover of a nearby willow thicket. And there it disappeared from view. I memorized the location of the kill and the hiding spot before taking my eyes from the scope.



**Sarah Stock** is Wildlife Ecologist, Yosemite National Park, El Portal, California

Looking through my spotting scope at the slope across the lake, I counted 14 bighorn sheep. I quickly counted again, yes, 14. Same group that others have reported recently on Mount Lewis. I was not accustomed to seeing bighorns so close and so low in the trees. The bighorns

foraged in the meadows among the old abandoned mines and whitebark pines on the northwestern flank of Mount Lewis along Yosemite’s eastern boundary.

Not taking my eyes from the eye piece, I zoomed in more closely from 10x to 30x magnification and scrutinized each bighorn, classifying individuals as lambs, yearlings, or adult ewes. Suddenly the pastoral scene in my scope changed from tranquil to turmoil as the bighorns scattered across the slope. Seeing them flee, I exclaimed out loud. Just as suddenly, they came back together and resumed their foraging. Following my intuition, and acting on years of experience observing wildlife, I studied the sheep more intently, wondering what had caused their alarm.

Mountain lion predation is one of the biggest threats to recovering the endangered Sierra Nevada bighorn sheep. Guided by the California Department of Fish and Wildlife Bighorn Sheep Recovery Plan, the goal is to boost the herd’s long-term persistence by increasing bighorn numbers and genetic diversity. While the threat of disease from contact with domestic sheep remains the biggest threat to bighorn sheep, the main causes



On the Prowl by Autumn Stock.



of natural mortality include avalanches, winter starvation, and predation by mountain lions. Biologists remain vigilant to population fluctuations by monitoring the herds carefully with ground observations and GPS collars. The recovery plan goal for delisting the bighorns from their endangered status is 305 adult and yearling females. Recovering an endangered species requires decades of hard work, millions of dollars, and the readjustment of complex relationships among landowners, agencies, biologists, and tax payers. Every individual animal counts.

I found myself in a daze of conflicting emotions: elation over seeing one of the most incredible phenomena of my life, juxtaposed by the hard management reality of losing a lamb and witnessing the group size shrink from 14 to 13 bighorns. The next morning, the bighorn group was gone, except for the ewe that lost her lamb. She stood by herself for hours, looking across at the site where her lamb was killed. Eventually, she wandered away and we saw her later that afternoon on the top of Mount Lewis. Meanwhile, we never saw evidence of the mountain lion again, except for its incremental progress on the lamb carcass beneath the willow thicket.



Ewe that lost her lamb



**Deb Finn** is Assistant Professor, Department of Biology, University of Missouri, Springfield, Missouri

For the very first landscape-scale study that I designed on my own as a Masters student, I was aiming to figure out how predictable patterns of biological turnover were along steep stream gradients in the high Rocky Mountains. I poured over

1:24,000 USGS paper topo maps, looking for replicate streams in the greater Rocky Mountain National Park area that had similar physical gradients (e.g. headwaters at same elevation, similar patterns of increasing stream size with decreasing elevation), with accessible sites to sample along those gradients. When I had

a number of potential candidates I went out with my nets, tape measures, and flow meter to field-check them.

I was really on a roll after scouting three of the potential streams from alpine headwaters down along the elevational gradient well into the thick lodgepole pine zone. Those first three fit my plan perfectly. I felt like a true independent scientist, and I dreamed about how impactful my future publication would be. On the fourth stream, I scouted the headwaters first: all good. Then I drove down to a lower access point to check out the larger stream reaches below treeline. When I arrived, I was confused. Streamflow had decreased to less than half of what I had measured just 1-2 river km upstream. WTH?? This must be caused by something that I had not yet learned about in Fluvial Geomorphology class, and I had to figure out what it was. I ended up walking the whole stream and was utterly flabbergasted to come to a point where the stream ‘branched’... but in the wrong direction. One branch was moving a substantial amount of water in a channel embedded into the side a hillslope. The other followed the natural stream channel, where my maps said it should be. This was my first real-world experience of a major artificial streamflow diversion. My reaction at age 25 was a combination of shock and dread, and the location deep within a National Forest was unsettling, like something from a horror movie.

Decades have passed since my first experience of witnessing the seemingly stealthy, stolen flow from a natural river into a weird ‘inverse tributary’ running unnaturally along the side of a hill. I learned not long after that >50,000 such flow diversion points exist in the state of Colorado alone. And the diversions are necessary to meet human water demand. No big deal, right? I am no longer the least bit flabbergasted by these or indeed much of any of the weird stuff that we humans do. Totally jaded. But that shock from my first experience stumbling across a diversion point was so deep-seated that it remains part of my psyche to this day.



**Andy Bunn** is Professor, Huxley College of the Environment, Western Washington University, Bellingham, Washington

I saw the photograph in the Times and recognized it immediately. It’s the most beautiful and remotest treeline site I’ve visited in the American West. “What on earth is the Times doing all the way up

there?” I thought. The headline brought me up short: “Hikers Find Mystery Skeleton on Remote Mountain in California.” In the summer of 2001 I was working on my PhD dissertation under



the Lisa Graumlich (along with Connie Millar, one of the great matriarchs of CIRMOUNT). My project, in a broad sense, was to investigate the dynamics of the alpine treeline ecotone over the late Holocene. The site in the picture is nestled in between Mt Williamson, Mt Versteeg, and Mt Tyndall. It is adjacent to a glorious remnant alpine treeline described in a landmark paper in Ecology by Lloyd and Graumlich (1997). Getting to this area is not trivial. It involves a hike starting in the sagebrush of the Owens Valley and ascending six thousand feet to Shepherd Pass and then traversing above treeline, off trail, for several more miles. When every campsite is booked, every permit for the high country is filled, and horse and mule trains clog the trails, climbing Shepherd Pass is wide open. Even in August at the high point of the hiking season, my crew and I set up camp for seven days of fieldwork and saw not another soul. At least not right away.

About five days in, I remember it was about that long because we still had food but were starting to eye each other suspiciously at mealtimes, we saw two people picking their way across the granite. It took them the better part of an hour to reach where we were working on the slopes of Mt Tyndall. I anticipated the arrival of the alarmingly fit ultralight trail runners that one encounters even in the wildest places but a septuagenarian and an octogenarian carrying full backpacks were not what I expected. This couple was delightful. They had the thickest Boston accents I had heard since leaving that city when I was 19 years old. It was an incongruous sound to hear at 12,000 feet in the Sierra and they explained that their accents were sticking with them despite having spent their adult lives in the west. They spent the summers exploring the high country of the Sierra and Inyo mountains and from where they were now it was clear that they'd been at this game for a while. They camped near us, not too close, and kept to themselves. As we got ready for work in the morning and they got ready to head out, we shared a cup of coffee and I picked their brains about other places with remnant wood that they might have seen. I couldn't stop myself from warning them that the way they were going (off trail and steep) was treacherous hiking. They were unconcerned and explained that they planned to be out in the high country as long as they could. And that if one of them fell or was injured their plan was wrap their partner up warmly and stay with them until the end. Not to go for help, not to do anything to save them, but sit and have a good death. It was the most remarkable and frank end-of life conversation I'd ever had—and I grew up in a family with a mother who worked in hospice and a father in oncology. The idea of a good death was something we discussed at the dinner table the way other families talked about the Red Sox.

Their devotion to each other and commitment to living the way they wanted was quiet and sincere. I hadn't thought about that

couple, whose names I can't remember, for at least a decade until I saw that picture and read the story. I have nothing to suggest that the skeleton found near there has anything to do with that couple. Accidents can happen to the firm and infirm and that environment is unforgiving. However, as I've aged and lost friends and family to the ravages of disease and age, I'm struck by the dignity and fortitude of that couple. They are almost certainly gone by now. I hope that they enjoyed every ounce of health and well-being that they had coming and I want nothing more than to live my life the way they did.



Photo: TIMES



**Martha Apple** is Professor, Department of Biological Sciences, Montana Tech, Butte, Montana

This seems like it would be easy to answer, but for me it was not. So, I went on a bike ride to try to jar some ideas loose and as I was riding my trusty green mountain bike up past an apple tree, I saw a flock of magpies and started wondering about how they can stay outside all winter. Which reminded me of these unusual phenomena:

1) Hummingbirds. It is quite the thing to be sitting on top of a mountain at 9,000 to 10,000 feet, which is pretty high but not super high by Montana standards, and have a hummingbird come buzzing by you en route to some destination. The hummingbirds look like they are travelling and using the mountain tops as transportation routes. I've seen them a little further downslope and there they do not seem to be travelling but are flying around on short trips between flowers and trees. It happens so quickly that my reaction is mostly just to notice them.



Atop 9801 ft. Mt. Keokirk where a hummingbird flew by.



In the Cairngorm Mountains of Scotland



2) Blue butterflies. Up on the alpine tundra in Montana, I set down my blue backpack and my camera. Soon a little crowd of small blue butterflies landed on their surfaces so I got out my phone and photographed them. I thought they would leave but they just stayed there for a good while. They may have landed on the backpack because it was blue, but I don't think that is the whole story because they also landed on my camera. Maybe there was some mineral such as salt that they sought and found!

we were so far north that it wouldn't get dark until the wee hours, there aren't any bears, and thunderstorms are a rarity. So, we stayed out and kept working until well into the evening and still made it back to town before dark.

5) Patterned Ground. It is endlessly amazing to me that entire mountainsides can have striped patterns and that other areas can have polygonal patterns. I was first aware of this when I visited Goat Flat in the Pintler Mountains of Montana but had it on the back burner until hiking up to Siyeh Pass at Glacier National Park, reached the top of the pass, turned to look, and Voila! A hillside of stripes! My students and I then proceeded to sample plant and microbial distribution with microhabitat and have since expanded our efforts to include the installation of an array of soil temperature sensors to look at differences in soil temperature with position on the patterned ground at Goat Flat.



Castle Geyser at Yellowstone

3) Geysers. These are not in the mountains per se, but it is so great to venture a trip to nearby Yellowstone National Park and walk around to see the geysers and other thermal features.

4) Latitude and Topography. When I was over in the Cairngorm Mountains of Scotland for the RAPT (Researching Alpine Plant Traits) project, it was late in the afternoon and a colleague suggested that we just stay on the hill and continue with our

field work. I must have looked worried but then realized that coming from Montana, you usually have to come down from the mountain since it will get dark, animals such as bears will come out, and thunderstorms can brew late in the day. But in Scotland,



Goat Flat Patterned Ground





**David Charlet** is Professor, Department of Biological Science, College of Southern Nevada, Henderson, Nevada

On 14 August 1989, I was spending my third month in the wilderness working on the floras of the Warner Mountains (California) and Jarbidge Mountains (Nevada). I

was now at the end of my first week, camping at 8200 ft near the meadows below the headwaters of Slide Creek in the Warner Mountains. I was already long accustomed to camping alone in a wilderness setting, and I had not taken any kind of mind-altering substances, including alcohol. I was so astonished by what I saw that I did not write it down that day, but at the end of the next day, sitting on the same rock, I tried to tell the tale. Here is what I wrote:

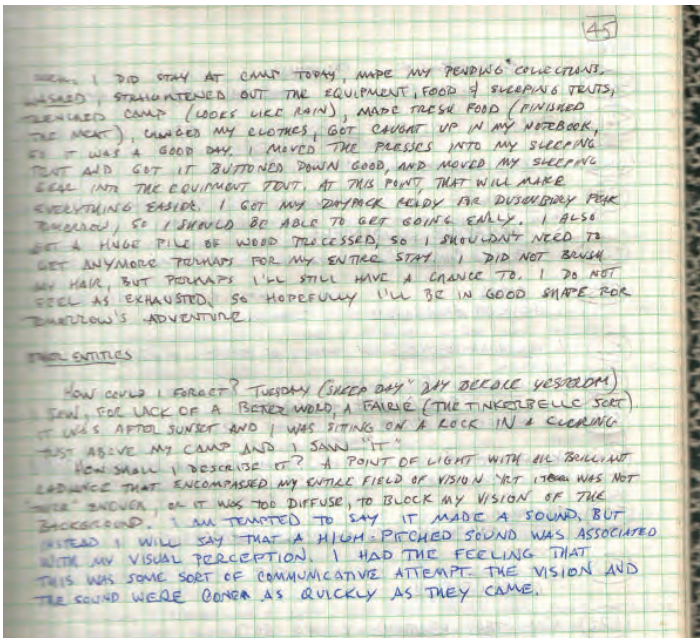
I saw, for lack of a better word, a Faerie (the Tinkerbelle sort). It was after sunset and I was sitting on a rock in a clearing just above my camp and I saw "it." How shall I describe it? A point of light with a brilliant radiance that encompassed my entire field of vision, yet it was not "thick" enough, or it was too diffuse, to block my vision of the background. I am tempted to say it made a sound, but instead I will say that a high-pitched sound was associated with my visual perception. I had the feeling that this was some sort of communicative attempt. The vision and the sound were over as quickly as they came.



**Jane Van Gunst** is a Nongame Biologist, Nevada Department of Wildlife, Winnemucca, Nevada

I've been doing fieldwork throughout the seasons in the Great Basin for almost longer than I can remember. It's a landscape of change, beauty, and, sometimes, of oddity and novelty. My most unique "natural-event"

experience happened in the Monitor Range of central Nevada when I was a field technician for U.S. Geological Survey working on sagebrush and pinyon-juniper woodland birds. Late summer there brings frequent small storms with lightning, rain, hail... the usual! Often these storms look threatening but dissipate as the afternoon wears on. My field partner and I were finishing up a vegetation plot and, very wrongly, counted on the storm's eventual disappearance. First, some thunder...no problem, we kept working. Then, a bit of lightning...seemed pretty far off, we just had a few points left, so we persevered. Then, the rain turned into large hail and, suddenly, the storm was right over us. A quick crack of lightning and we turned around to watch a pinyon pine thirty meters from us start smoking! I have yet to be that scared in the field. We dropped everything and sprinted for the truck in the midst of the hailstorm, looking back toward the smoking tree. Thankfully, the heavy rain and hail eventually put out the small fire and ten minutes later, the sun was starting to shine. Another Great Basin day!



Storm over the Jarbidge Mountains

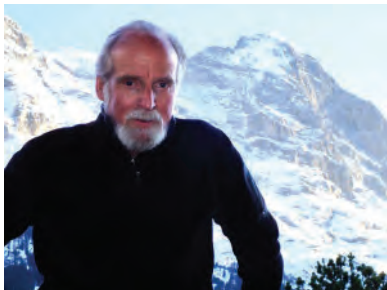




**Connie Woodhouse** is Professor, School of Geography and Development, University of Arizona, Tucson, Arizona

I've done much of my dendro-chronological fieldwork in western Colorado in mid-August, when any lingering mosquitos have disappeared. We have been extremely lucky with the weather over the past decades, and getting caught in bad weather

has been rare. An example of that luck was an evening in June (2003) when we arrived at a potential *Pinus edulis* (pinyon pine) sampling site near Slickrock, Colorado, just in time to set up camp and make dinner. As we were setting up, we noticed big, dark gray convective clouds developing quickly. As a few drops of rain fell with some rumbles of thunder, we hastily finished dinner and packed away equipment, ready for a deluge. From our mesa-top location, we could see lightening and sheets of rain falling not too far in the distance to the east, then to the south, ...the west, ... the north, but not on us! We just enjoyed the amazing lightening show (and a rainbow!) over the course of the next few hours. The next day, we sampled at the Slickrock site (the oldest tree dated to 1490) and headed to our next site in Disappointment Valley, just 13 miles away as the crow flies. There we found evidence of intense sheet flooding and erosion from the storm we had watched the evening before (and more good pinyon pines to sample!).



**Jim Blanchard** is retired Director of the Outdoor Pursuits Program at the University of Oregon, Eugene, Oregon.

In about 1957 (I may be off by a year) I was on our boat, a sea-going lifeboat that had been

converted for use as a small cabin cruiser, on the Columbia River near Portland, Oregon. It was a sunny summer day, and I was with my parents and sister. I was below decks, in the cabin with my dad, working on the perpetually cranky engine. My mother was at the tiller, and my disabled sister was nearby, in her chair.

Suddenly we heard my mother screaming loudly for my dad. Mom was always "excitable" but I recall thinking that something terrible had happened. My dad, as I learned later, had thought that my sister had fallen overboard, given how anxious my mom sounded. I recall him bounding up the few stairs and

bonking his head on the hatch frame, which left him bleeding and later resulted in a good sized lump on his head. I was close behind him. Despite our fears we found my sister sitting in her usual place, but my mother was pointing frantically at the sky—high and to the east, i.e. more or less directly up the river. In the sky were five small white points of light, all in a line, moving slowly and making a gradual turn to the right. She said that when she first saw the lights they were almost directly overhead, moving east in a straight line, before they began their slow turn to the right.

After a few minutes we heard the distinctive sound of the Air National Guard F-89 Scorpions taking off from the nearby airbase at what is now PDX. We knew they were Scorpions as they were, at the time, the most efficient machines yet invented for turning jet fuel into noise, and their sound was unlike that of other types of jet fighters. The two Scorpions gained elevation in several long circles. At first we weren't sure whether this was a practice flight or if they were scrambled in response to the lights in the sky. That question was resolved when they headed straight toward the last light in the line, which at this point was about 40 degrees from the horizon and from our perspective more or less in line with Mt. Hood. That's when things became really spooky. As Scorpions approached the last light in the line they shot off to the southeast, one at a time, starting with the first one in line. Their apparent acceleration and speed was astonishing, and within seconds all of the dots had disappeared from sight. We then watched the Scorpions slowly descend and eventually disappear over the south shore of the river as they landed at the air base.

Unfortunately, we didn't get any pictures as my dad was busy on the rudder, my mom was too excited to hold or aim a camera, even if she'd had one, and I apparently didn't have my trusty old Brownie with me. So, I have no pictures to add a bit of credibility. We later stopped for lunch and swimming on one of the islands, and I recall my folks talking to another couple who watched the incident from their camp on the beach.

We expected to learn about what we'd seen once we returned home and had access to the news. Instead, I recall my folks' great frustration at the nearly complete lack of news coverage, and at the denial by the Air National Guard of ever having been involved in such an incident. I recall hearing some time later that the objects had been visible on radar, but I have no idea whether or not that information was credible.

On several occasions since the advent of the internet I've tried searching on Google, but have found no news accounts or other references to this event, despite the fact that many people must have witnessed it. The 50s were known for frequent "UFO" sightings in Oregon, and I recall that before our experience my folks routinely discounted them as being hoaxes or misinterpretations of natural phenomena. After the event they were much more open to the possibility that some of these

sightings were credible and worth investigating. I recall a friend of my dad, a meteorologist, suggesting that what we saw might have been reflections off the interface between two layers of the atmosphere, and that the approach of the jets might have induced distortions or ripples in the interface surface. Who knows! Whatever it was that we saw it certainly had an impact on us, and still gives me chills...



The Blanchard's family boat.

the truck to try to part the sea of wings as I inched forward behind him. We crawled through the cloud of fluttering orange wings once more, seeing that the road cleared ahead. We continued on our way in silent disbelief of what we had witnessed, wondering why that specific spot was their stopping ground of choice. They were gone when we returned back down the road several hours later—only a few lingering individuals fluttered from puddle to puddle to remind us that they were ever there.



**Lacey Hankin** is a doctoral student in the Department of Natural Resources and Environmental Sciences, University of Nevada, Reno, Nevada

*Unexpected Roadblock* We slowly crested the hill on the rocky forest road that was meant to take us to our next set of forest mortality plots. Up ahead, against the background

of red-phase pines, the road looked like it was breathing under a blanket of black. Not wanting to run something over, we inched up to the edge of the black sea and hopped out of the truck to take a look. Only then did we realize that the strange blanket over the road was thousands and thousands of butterflies. Our steps prompted a silent eruption of vibrant orange wings fluttering around us. The air filled with movement and color in every direction. We stood there in the middle of the road being enveloped by delicate wings, not wanting the moment to end. Slowly, the butterflies grew accustomed to our presence and settled back down on the road. Our steps back to the truck prompted several small clouds of flight, but we seemingly weren't so threatening anymore. We still had miles to go to access our sites, but were faced with this unexpected road block. Since I was driving, I sent my field partner on foot out in front of



**Jessica Lundquist** is Professor, Department of Civil and Environmental Engineering, University of Washington, Seattle, Washington

I have a number of things that are near and dear to my heart (as "coolest thing in the field I've seen") but I'm not sure how unusual any of them are:

- a) Sedges in Tuolumne that grow in the shape of a heart (I just love those);
- b) Supersonic aircraft that illegally practice in the canyons around Tuolumne—you feel the rush of wind in the canyon and then you hear the noise (I don't love those, but they stand out);
- c) A bear that almost stepped on me while I was backpacking and sleeping under the stars;
- d) How the Dana River runs white after a major thunderstorm (from the white glacial till wash out on the road);
- e) A pika in Lyell Canyon who had better food options than any other pika I've ever seen (they're always up on rocky slopes and not down by the river in Lyell Canyon). The pika kept biting off giant stalks of lupine and then dashing off to hide



them somewhere and then coming back for another giant flower—it felt like that pika was getting ready to sell flowers at a farmer's market...

- f) Just seeing a pine martin and a wolverine (I only ever saw each once, on separate occasions);
- g) The bath-tub ring of dead baby lodgepole pines in Tuolumne Meadows after the rain falling on snow and freezing in 2017—the ice turned the pine needles all brown in a perfect bath-tub ring;
- h) The total solar eclipse, which I watched with my family (like many people), and I was just awe-struck;
- i) Lava in Hawaii flowing into the ocean and making giant billows of steam, best watched after dark—just one of the most awesome things in the world;
- j) The tale of two forests lava tubes made from fallen conifers near Mt. St. Helens (the coolest thing to crawl through!).



**Chrissy Howell** is Program Manager for the Ecosystem Function and Health Program, USDA Forest Service, Pacific Southwest Research Station, Albany, California

I had mostly finished up with the day's field work in the mountains of south central New Mexico and was hiking over a ridge to get back to my truck. It was a

beautiful November day, the elk were bugling across the ridges and the clouds were building as the sky turned gray. I knew there was the potential for snow, but that wasn't unexpected at 8,000'. I was only two miles from my truck and prepared for weather extremes. Snow started to fall lightly, then heavier as I trekked up the ridge. It got very quiet, the ambient noise muffled by the snow, and the elk quieting down. Suddenly there was a crash of thunder and lightning and a more violent downpour of ... snow. I was experiencing my first bout of "thunder snow", but at that point in my life, and having mostly lived in California, I didn't

even know that was a phenomenon. I was particularly alarmed because I was carrying a Yagi antenna as part of a radio telemetry project and at that moment it seemed like it had the potential to become a glorified lightning rod. I raced back to the truck by traversing around the ridge instead of going over it to avoid the high point of the ridge and the chance of a lightning strike. Once I was safely back in the truck I enjoyed the beauty of the storm—lightning strikes cloaked in low hanging snow clouds that flashed purple in the stormy light with the snow muffling the thunder booms. (Although, in retrospect I should have ditched the antenna before I ran back to the truck).



**Scotty Strachan**, Director, Nevada Climate-ecohydrology Assessment Network, University of Nevada, Reno

*Naked Ben & the Cow Shower*

It's kinda like standing on a downtown corner: spend enough time in the field, and you'll see a lot of crazy

things. Sometimes, those crazy things happen to you, but those stories aren't nearly as interesting as the ones that happen to others. Certainly not as much fun to tell, in any case.

It was a somewhat chilly week in June when Scotty (Strachan) and Ben (Trustman) drove across the Great Basin on the Loneliest Road™ out to the Snake Range in eastern Nevada to help build a weather station and get some general maintenance done on the NevCAN systems. Scotty had made the trip so many times that he'd lost count, while Ben was coming out to see the science observatory for the first time. As each successive mountain range was passed on the journey from Reno, Ben was increasingly reminded that civilization as he knew it was being left far behind. At Scotty's insistence, the two paused at the Austin Chamber of Commerce so that a commemorative Lincoln Highway coffee mug could be scored. This somewhat unusual pit stop was enough to start Ben's brain wondering about what else was likely to happen on the trip.

After a couple of work days on Scotty's climate monitoring sites high in the mountains, the pair descended to the valley floor to prepare for the next project: constructing the final station in the network. The rest of the crew was to arrive the next morning, and the hard labor would begin in earnest. Before diving into what was certain to be a stretch of lake-sediment dust and concrete, Scotty and Ben decided that a good washing was in order first.





“Let’s hit the Cow Shower before we set up camp,” Scotty suggested as they reached the bottom of the Pole Canyon switchbacks.

“Cow Shower?” Ben asked, wondering if this was some sort of joke.

Scotty stated affirmatively, “Cow Shower. It’s real. Not what you think though, it’s just a capped spring system that’s a great place to wash up.”

“Well, I guess that’s not a bad idea,” Ben acquiesced, “we had better hurry though, the sun’s almost down.”

The two pulled up to the managed wetland and spring head just as the sun was dropping. Scotty slapped the big Ford 1-ton into park and turned to Ben. “You had better take the first shift, that way you’ll at least have some sunlight and not freeze.” Even in June, the high valleys of the central Great Basin can get pretty chilly in the evenings, especially if there is a little wind. Scotty’s habit of wearing shorts even in the dead of winter was well-established, so Ben didn’t argue.

“Fine. Just give me about 10 minutes and it’ll be your turn.” Ben hopped out with his travel bag in hand, but suddenly stopped short. “Wait a second, what about them?” He gestured at the group of black cattle obliviously mowing the grass 100 meters away.

Scotty replied, “The cows? Just ignore them. They’re not looking for handouts.”

Scotty seemed pretty sure of himself, so Ben went about his business while Scotty wandered off to explore the area. A series of shouts was soon heard coming from the general direction of the truck and the Cow Shower, but Scotty figured it was just

the chilly water waking Ben up. After 10 minutes or so, Scotty headed back to the spring to take his turn. Upon arrival, he found a somewhat amusing scene. Ben was standing on one side of the spring cap in his skivvies with about 20 head of cattle mere feet away on the other side, appearing very interested in the human’s activities.

“Wait a second, Mr. Man,” Scotty called as he walked up. “You weren’t supposed to put on a show or anything!”

“I didn’t do anything but wash up! I tried to shoo them away, but that didn’t help,” Ben protested, edging towards the safety of the vehicle. The cows’ large lolling eyeballs followed him, and they slowly shifted their hooves to maintain proximity as Ben grabbed his shoes and managed to get his shirt on.

“Well, it’s not getting any warmer, I had better get this over with,” Scotty remarked as he picked up his own travel bag and sat down on the concrete cap. “I suppose they’re going to start staring at me now. I swear, cows can have the most vacant expression I’ve ever seen!”

It turned out that even though Scotty was certainly whiter than Ben, and had slightly more facial hair, that didn’t impress the cattle. As Ben moved around the far side of the truck to take his own exploratory hike, the herd shuffled clear of the meadow and started after him. “Hey! Leave me alone!” Ben called as he increased his pace.

“Have fun! I’ll make it fast,” Scotty called after him before dunking his head under the frigid flow, happy that the creatures were distracted. The faster walk of the pursued field assistant did not deter the cows. In fact, it only increased their desire to catch up. The ones in back thought they were being left behind, so they broke into a trot that only increased the herd’s momentum.





Soon the dirt road was obscured in a cloud of dust. Scotty had a difficult time staying focused on washing, as the scene only became more comical as Ben made a run for the nearest juniper tree. Fortunately, he reached the safety of the low branches before his admiring fans swarmed him (presumably for autographs), and Scotty was able to return to his task unsuccessfully suppressing laughter. After a few minutes, the chilly portion was over and Scotty was sufficiently re-clothed to check up on Ben's status. At last check, the small grove of trees had been surrounded by the floppy-eared domesticated ungulates. Scotty was relieved to find that Ben was rapidly approaching from a slightly different direction, apparently unmolested.

"I gave them the slip! Can you believe they had me surrounded in that tree over there?" Ben was looking a bit frazzled by the experience.

"What, were you wearing purple Calvin Kleins or something?" Scotty could not resist the opportunity to hassle his new field partner.

Ben was ready. "Clearly they followed me rather than you!" He wasn't about to look bad on his first trip to the field sites. "There was a minute there that I thought they were going to go all stampede mode on me."

Scotty couldn't blame him for immediately hopping into the truck and shutting the door. "Well, I suppose you made an impression. Come on, let's go set up camp."

Later, after the pair had finished dinner and retired to their tents, Scotty called to Ben. "Now don't wander off too far if you need to use the facilities in the middle of the night. We're only about a mile away from your new buddies."

"Yeah yeah, very funny." Ben still sounded perturbed at his narrow escape.

Scotty let the night air settle as the breeze dropped and the stars slowly brightened. There was the occasional rustle as Ben turned the pages of the book he was reading by headlamp. All seemed peaceful and back to normal. There was still one more thing to do, however.

"Mooooooooooooo!" Scotty called, as Ben shut off his lamp. Eerie silence, then surprised laughter. Apparently it was going to be a great trip after all.



**Greg Pederson** is a research ecologist with the Northern Rocky Mountain Science Center, US Geological Survey, Bozeman, Montana

Hands down the strangest thing I have ever come across while in remote field locations is biological and sociological in nature for sure. It's a mammal that's fairly ubiquitously distributed globally, though within its distribution it often clusters in extremely high

density colonies with complex social interactions and hierarchies. In mountainous regions of the world, this mammal tends to be found in relatively lower densities than elsewhere (along coasts and major riverways), and it tends to exhibit some very strange habits related to feeding, mating, and shelter. This particular species tends to feed in packs (or herds), though they've been observed feeding alone at times. Its diet is quite diverse, feeding on both plants and animals it's clearly an omnivore, though in the mountain areas of the world a high number of this species often tend to eat a dried carrion of sorts, usually consisting of both plant and animal remains and often emitting rather pungent odors. They also expend large amounts of energy constructing and transporting temporary shelters. It's not entirely clear why

they do this apart from the obvious protection from the elements the rather flimsy structures provide. Though it's thought to also be related somehow to this species complex courting and mating rituals, the latter of which is rarely observed outside of the shelter. Another strange thing about this mammal is that most individuals never appear completely comfortable with the surrounding environment, though their defenses are usually more than adequate, in addition to the fact that they also tend to bury their feces and occasionally try hiding their excrement under rocks or logs. And, in mountainous regions this relatively

hairless mammal has often been observed with much higher densities and percent coverage of hair follicles than in other parts of its distribution (e.g. along coasts and lakes). I suspect this may be an adaptation to the colder mountain environment, and have something to do with the occasional misidentification of members of this species by less astute field observers as possibly being a "Sasquatch".

Yes, I have met the strange and unusual while working in the field, and it is us.





# NEWS and EVENTS

## Intergovernmental Panel on Climate Change (IPCC) Report on High Mountain Areas

Many in CIRMOUNT will recall our interest over the years to focus national and international science assessment efforts on mountain regions specifically. A significant step toward recognition of the unique processes and significant consequences of climate change in mountain regions was the decision by the Intergovernmental Panel on Climate Change (IPCC) to prepare a special report that includes assessment of impacts to mountains. This Special Report on the Oceans and Cryosphere in a Changing Climate (SROCC) was posted in late September 2019 (<https://report.ipcc.ch/srocc/>). The SROCC includes a report (Chapter 2) on High Mountain Areas. Thanks to several of our CIRMOUNT colleagues who were significant contributors to the chapter. I had the opportunity to meet environmental journalist Bob Berwyn this summer, whose summary report of the IPCC mountain chapter for *InsideClimateNews* I thought would be of interest to our community. —*Editor*

Reprinted with permission from *InsideClimateNews*: <https://insideclimatenews.org/news/07102019/mountain-climate-change-disruption-glaciers-water-ecosystems-agriculture-plants-food>

### In the Mountains, Climate Change Is Disrupting Everything, From How Water Flows to When Plants Flower

*The melting of glaciers and loss of snow has a cascading effect for ecosystems, agriculture and billions of people downstream*

By Bob Berwyn, *InsideClimate News*  
Oct 7, 2019

LEADVILLE, Colorado — With ominous orange-gray smoke clouds seething on the western horizon, it's easy to understand how Colorado's highest city and other mountain communities are directly threatened by global warming.

Mountain snowpack is shrinking and melting earlier in the spring. Warmer and longer summers dry out vegetation and increase the threat of wildfires in western mountain forests, where the fire season has lengthened by at least a month since 1979.

The growing wildfire risk is just part of an accelerating cycle of global warming impacts in the world's mountain regions, according to a new Intergovernmental Panel on Climate Change report that includes a section focused on mountains for the first time in more than 20 years.

"Snow cover duration has declined in nearly all regions, especially at lower elevations, on average by five days per decade," the mountain chapter of the IPCC report says. On average across Western North America, the European Alps and High Mountain Asia, temperatures are warming by 0.54 degrees Fahrenheit per decade.

That's melting glaciers and changing mountain river flows, disrupting plants and wildlife, and increasing the risk of extreme rockslides, avalanches and mountain floods caused by rain falling on snow.

Taken together, global warming impacts represent an existential threat to millions of people in the Andes, the Himalaya, the European Alps, and the U.S. Mountain West including Alaska, said Heidi Steltzer, a biologist at Fort Lewis College in Durango, Colorado, and a lead author of the mountain chapter.

"Shrinking glaciers and snow harm Indigenous Peoples and rural communities greatly. Concern, commitment and action on climate change should not depend on which places, species or people are impacted. Instead, they should be motivated by compassion," Steltzer said.

### Will Water Reliability Break Down?

In Crested Butte, about 100 miles southwest of Leadville, hydrologist and physicist Rosemary Carroll studies how disruptions to the water cycle will affect local ranchers and ski areas, as well as drinking and agricultural water supplies hundreds of miles away.

The IPCC assessment found that global warming will change the timing and amount of runoff, "affecting water storage and delivery infrastructure around the world," a finding backed by research focusing on the West.

A 2016 study in six Western mountain ranges showed rising temperatures will shift the snow accumulation zone and runoff timing enough to have significant impacts on water cycles. And some towns in the Rockies and Sierra Nevada are at risk from dangerous flash floods as global warming brings rain, rather than snow, to some mountain regions.

Carroll pointed out her living room window to a craggy ridgeline where she measures how water from melted snow trickles through rocks and meadows down to the East River, on to the Gunnison River and finally into the mighty Colorado.

"The new normal is that the snowpack is melting earlier and we have earlier runoff, and that's a fact. There's going to be less water for a given snowpack," she said. Even in average snowfall years, global warming is reducing the amount of available water for irrigation and storage, she said.



*The Colorado River has faced water shortages in recent years. The seven states that rely on the river's water for communities and agriculture reached a new water-sharing agreement this year to reduce their use to try to stave off future shortages. Credit: Justin Sullivan/Getty Images*

Her research for the University of Nevada's Desert Research Institute and the U.S. Department of Energy will help communities adapt as global warming disrupts flows from mountain streams. Around Crested Butte, the ski industry and local ranchers will feel the changes first.

But addressing those impacts isn't as easy as just throwing a new report on the table. Translating science into action requires working with stakeholders from the start.

"Ranchers know what's happening, they know that things are shifting, but they're afraid the policy will shift in a way that they will carry the burden of the change. Since they have most of the water, they fear they will have to give up the most, and that it won't be equitable," she said.

The states that get their water from the Colorado River are already restructuring water-sharing agreements to stave off shortages and trying to develop new storage plans to account for extreme wet and dry years.

## Goodbye to Glaciers

Global warming will change nearly every mountain ecosystem, starting with the very visible meltdown of glaciers.

In the European Alps, some glaciers retreated by as much 410 feet last year — imagine the Empire State Building shrinking by a third. Globally, the world's glaciers have lost 9 trillion tons of ice since 1961, raising sea level by about 1 inch, according to the European Space Agency.

As glaciers melt, they create a series of risks: newly formed meltwater lakes can burst through their banks, flooding towns and farms below. And as the ice dwindles, that will significantly change the timing and amount of water available for hydropower production and agriculture.

Along with disrupting ecosystems and downstream communities that rely on glacier meltwater, global warming in the mountains will cause emotional and cultural loss as cherished landscapes vanish. In Switzerland, people recently held a memorial service for the disappearing Pizol Glacier as a way of dealing with that grief, a sometimes overlooked component of climate resilience.



*In September 2019, people in Switzerland marked the disappearance of the Pizol Glacier. Credit: Fabrice Coffrini/AFP/Getty Images*

The physical threats are real and growing, said Swiss glaciologist Matthias Huss.

If greenhouse gas emissions peak in the next few years and then start to decline, glaciers in the European Alps will lose two-thirds of their current ice. With continued high emissions, the glaciers will all but vanish, with only 5 percent of the current ice remaining, Huss and colleagues found in recent study.



"An increase in rockfall events, and flooding from glacier lakes, also due to more extreme weather events, is likely," Huss said. "I think European countries are prepared, and they have the financial means to adapt. It will be much more difficult for developing countries to adapt to the challenges in mountain regions."

Extreme storms that destroy forests and damage roads and railroad lines could also become more frequent in the world's mountains, although climate models aren't yet localized enough to project such changes accurately, the IPCC assessment concluded.

It won't be cheap to redesign and rebuild water infrastructure, Huss said. In some snow-dependent communities, the meltdown will also drive wrenching cultural and economic changes. But "one could also see this as a chance for major development toward a more sustainable way to live on our planet," he said.

### **Adapting Food Crops In East African Highlands**

That's what University of Colorado researcher Tsegay Wolde-Georgis was thinking when he led a project in the early 2000s to cultivate apple trees around Atebe, in the dry highlands of Ethiopia where he grew up.

Diversifying local food supplies will help make the region more resilient to global warming, he said. The new IPCC assessment affirms that global warming is driving dangerous changes in mountain environments that threaten food supplies. But along with warnings, the world needs action, he said.

"Everything is getting more extreme, and there is seasonal confusion," he said. But there is enough scientific and traditional knowledge to find on-the-ground projects and do them, he said.

For the apple orchard, he adapted a traditional permaculture technique, using water-filled clay pots to efficiently irrigate the young trees. At the same time, residents enhanced the water-holding capacity of deforested hillsides by building terraces and planting vegetation.

Such regenerative agriculture is crucial for food security in developing countries, said Wolde-Georgis, who works with the Consortium for Capacity Building, part of the University of Colorado's Institute of Alpine and Arctic Research.



*Farms in Colorado's North Fork Valley also rely on snow melt. That snow melt has been diminishing. Credit: Jutta Strohmaier*

After decades of academic research and projects, he radiates the kind of practical wisdom that can help shape resilience to global warming. His eyes gleam as he recalls the look on a local priest's face during the first apple harvest.

"It was the first time in his life he tasted an apple. When we plant apples, it's mitigation [of the climate impact], but at the same time, we are solving problems. We have to find something that's doable on the ground," he said. In four years, the farmers planted 1,400 apple trees.

At the same time, communities worked to restore watersheds by building terraces and replanting clear-cut hillsides. Wolde-Georgis said the work was successful. Streams that had been dry by the end of December now hold water through the end of May.

On a larger scale, Wolde-Georgis helps build physical and information infrastructure to boost resilience, including new roads and railroads to help transport food when climate extremes cause crop failures.

Ethiopia and other developing countries also need more institutional science-based infrastructure to inform good governance across jurisdictional boundaries, he said. To meet the challenges ahead requires working in an atmosphere of trust and a spirit of collaboration, he said.

### Timing Is Off: Disrupting Plant Cycles in the Rockies

At the Rocky Mountain Biological Lab in Gothic, Colorado, David Inouye's cabin near a patch of shimmering gold aspens is marked by wisps of chimney smoke. For nearly 50 years, he's been recording plant and animal activity while other observers tally snowfall and snowmelt data day by day — a scientific deep dive into time and space.

Compared to the 1970s, spring is coming earlier. There is more winter rain, and summers are longer and drier. It all adds up to disruption for mountain ecosystems, where most plants only have a few weeks to bloom. And the plants are tightly linked with pollinating insects in a delicately timed cycle.



*"As the climate changes, we're tending to get less snow and warmer and earlier springs. A paradoxical consequence is that we're getting more frost damage," said David Inouye, professor emeritus at the University of Maryland and principal investigator at the Rocky Mountain Biological Laboratory. Credit: Jutta Strohmaier*

"The ecology of this altitude is driven largely by how much snow we get in the winter and when that snow melts," Inouye said. "As the climate changes, we're tending to get less snow and warmer and earlier springs. A paradoxical consequence is that we're getting more frost damage," he said. The effects ripple through the ecosystem as global warming disrupts plants and seed production, which, in turn, means less food for small mammals and birds.

Graceful yellow glacier lilies are blooming 17 days earlier than they did in the 1970s, but migrating hummingbirds that depend on the flower nectar aren't keeping up. By the time they arrive, many of the plants have withered away, and if current trends continue, in two decades the hummingbirds will miss the first flowers entirely. Ecosystems could collapse as global warming continues to decouple complex ecological relationships, showing why global warming is a threat to biodiversity.

Another study documented how earlier spring snowmelt makes mountain daisies bloom earlier, when they are more susceptible to frost. The research showed how the frost damage reduces the amount of nectar for a species of butterfly that depends on that particular flower for feeding during the egg-laying season.

"If they don't get nectar, they can't make eggs, and the population declines," Inouye said.

## Tipping Points

The research at the Rocky Mountain Biological Lab helps connect the dots in complex ecosystems and how global warming can make them unravel, said lab Executive Director Ian Billick.

"What people don't realize is that we're changing multiple things at the same time. People don't realize how drastically things are going to change," he said. Massive disturbance events linked with global warming like the early 2000s bark beetle outbreak that killed trees across millions of acres will happen again and again. Multiple stressors are driving mountain ecosystems past tipping points, leading to fundamental change, he said.

"Our agricultural productivity depends on these ecosystems functioning in a highly integrated way, so it's like if you throw a screwdriver in the middle of an engine, the whole thing falls apart, and I think it's like with ag, where these finely tuned things are going to fall apart."

The IPCC report represents only the tiny tip of a "massive global change iceberg," said Steltzer, the Colorado biologist and lead author of the mountain chapter.

"Nine-tenths is what we haven't seen, measured and documented. We know things are changing for which we have no peer-reviewed scientific articles, and things are changing too fast to keep up," she said. "There's no reason to wait to act. We know enough."



*"Policy-makers ask for data to show how bad it is. ... Instead, they could ask how do we preserve the benefits of nature for each of us and all of us," said Heidi Steltzer, a biologist at Fort Lewis College in Durango, Colorado, and a lead author of the IPCC report's mountain chapter. Credit: Jutta Strohmaier*



Just this past winter, both Europe and parts of the Rockies experienced unprecedented avalanche cycles after record snowfalls, surprising scientists as well as public safety managers charged with keeping mountain roads open. Recently, mosquitoes that carry West Nile Virus have been appearing in the high mountains but remain largely untracked, along with other invasive species. And there are likely scores of other ecological cycles being disrupted that haven't been studied at all, Inouye said.

The IPCC assessment also concluded that forest fires are likely to increase in mountain areas where summers become warmer and drier. "Coastal ranges of California, the Blue Mountains of Australia, Mt. Kenya, and mountains on the fringes of the Mediterranean Sea, already subject to frequent fire episodes, would be severely affected," the assessment said.

A 2019 study showed that the fivefold increase in the extent of California's wildfires since the 1970s was "very likely driven by drying of fuels promoted by human-induced warming."

"Snow is decreasing, temperatures are warming, and mountains are changing in ways I never expected I'd live to see," Steltzer said. "Policy-makers ask for data to show how bad it is. ... Instead, they could ask how do we preserve the benefits of nature for each of us and all of us."

## ***MtnClim 2020* Early Announcement**

Hold the date for *MtnClim 2020*  
September 14-18, 2020 at the Rocky Mountain Biological Lab, Gothic, Colorado

The MtnClim research conferences are sponsored by the Consortium for Integrated Climate Research in Western Mountains (CIRMOUNT) and dedicated to mountain climate sciences and effects of climate variability on ecosystems, natural resources, and conservation in western North American mountains. MtnClim conferences feature invited and contributed talks, poster sessions, field trips, and working-group sessions. Post-conference workshops address topics of interest for further discussion. Mtnclim conferences convene every two years. *MtnClim 2020* will be held September 14-18, 2020 at the Rocky Mountain Biological Lab in Gothic, Colorado.

Contact Andy Bunn (WWU, [bunna@wwu.edu](mailto:bunna@wwu.edu)) or  
Scotty Strachan (UNR, [strachan@unr.edu](mailto:strachan@unr.edu)) for more information.



Photo: Jeff Wyneken

## ***PACLIM 2021 Early Announcement***

Hold the date for PACLIM 2021  
Feb 7-10, 2021 at Asilomar Conference Grounds, Pacific Grove, California

For information contact Michelle Goman (SSU, [goman@sonoma.edu](mailto:goman@sonoma.edu))  
or Scott Mensing (UNR, [smensing@unr.edu](mailto:smensing@unr.edu))



Photo: Michelle Goman





The Second Conference on the  
Research and Management of  
High Elevation Five Needle Pines  
in Western North America

Hosted By The Whitebark Pine Ecosystem Foundation

**We invite you to participate in the H5II Conference  
in Missoula MT, September 15-17, 2020.**

Call for Special Sessions is open November 1, 2019-January 1, 2020

Call for Workshops and Attached Meetings is open November 1, 2019– February 1, 2020

Call for Abstracts for Presentations will open February 1– May 1, 2020

Visit [www.highfivepines.org](http://www.highfivepines.org) for submission details

Join us in this unique opportunity to reach over 250 scientists, outdoor enthusiasts, and management professionals gathered to share new information on high-elevation, five-needle pine ecosystems.

The three-day conference will include over 150 speakers, a field trip to a nearby high-elevation whitebark pine restoration site, and opportunities for networking with resource professionals.



WHITEBARK PINE  
ECOSYSTEM FOUNDATION

# DID YOU SEE IT?

## Great Basin Bristlecone Pine: A New Population, Dying Trees, and Prometheus Revisited

Constance Millar

USDA Forest Service, Pacific Southwest Research Station, Albany, California

David Charlet<sup>1</sup> and Scotty Strachan<sup>2</sup>

<sup>1</sup>Department of Biological Science, College of Southern Nevada, Henderson, Nevada

<sup>2</sup>Department of Geography, University of Nevada, Reno, Nevada

From basin to range to basin to range, one of my greatest joys is to walk into yet another forest of Great Basin bristlecone pines (*Pinus longaeva*). Ancient trees with iconic twists and colors earned from millennial-long exposure to Great Basin aridity, juveniles with erect stance and covered like armadillos from tip to toe with dense deep green foliage, they are in all forms breathtaking. You have been lucky if you have experienced these pines on the plateau of the White Mountains in California, but that is only a hint of the costumes they wear, postures they take, and stages on which they dance. My bread-and-butter research species is limber pine (*P. flexilis*), companion to bristlecone pine in many locations. I mostly spare the borer into bristlecone pine stems, leaving me to behold these trees in their unblemished beauty. Here I share a few bristlecone pine updates from my recent field seasons.

### A New Bristlecone Pine Population: Rawhide Mountain, Hot Creek Range, Nevada

In early June 2019 my Great Basin (GB) buddies, Scotty Strachan and David Charlet, and I were headed east from Tonopah, NV toward the Hot Creek Range. I love traveling with these two, not just for their companionship and endless ideas that emerge when we travel together, but because they are fearless drivers. In Nevada, one never expects a road sign or a map to show the routes and always expects major washouts – and that is when conditions are good. When traveling alone my style is to drive as far toward the mountains as I feel comfortable, at best achieving the crease that marks the juncture of basin and range, and to start walking. With Scotty and David, however, I abandon my Jeep at that point and jump in with them for access that brings us to launch by foot high on the slopes.

The road was one of the nastier kinds as Scotty navigated toward the base of Rawhide Mountain (2795 m) near the southern end of the long Hot Creek Range. Bristlecone pines are known to grow in the range only in one area, 65 km distant, at the remote

north end on the slopes of Morey Peak (3123 m) and adjacent ridges (Charlet 1996, in press). Continuing a long-term study to analyze GB bristlecone pine growth on marginal, low-elevation sites, Scotty had long eyed Rawhide Mountain on Google Earth as likely to support bristlecone pine at a geographical distribution edge. I was hoping for a stand of limber pine (very likely), and, given a few talus patches on the slopes, to indulge my fanatic search to extend the range of American pika (*Ochotona princeps*).

Amid the typical maze of ancient mining roads, we parked at 2460 m near the southwest ridge of the peak, and headed up through single leaf pinyon woodlands (*Pinus monophylla*; Fig. 1) and along the rocky ridge toward the summit. Mining debris that seemed to have been abandoned in mid-action was strewn along the ridge, but our attention was soon diverted as we encountered the first limber pines (Fig. 2), growing at 2690 m along the northwest slope below the south summit (the two summits of Rawhide Mountain compete for being the high points). From here northward it was pine heaven! Bristlecone pines of all ages mixed with limber pines soon appeared (Fig. 3) and we got busy scoping their condition and extent (Fig. 4). Although in this dry rocky



Figure 1. David starts toward the summit in pinyon pine woodlands.





**Figure 2.** Scotty encounters the first limber pine.



**Figure 4.** Scotty inspecting a bristlecone pine.

environment, the pines of both species were relatively scattered, reproduction of both was present, and young trees were healthy (see, however, about mature tree health below). Pines occurred mostly on the northwest slopes, extending from the summit ridge to about 2600 m, and also on southeast slopes below the south summit (Fig 5). Although the species co-occurred, limber pine dominated on soils of rhyolitic origin whereas bristlecone pine dominated on carbonate substrates (Fig. 6). Pinyon pines co-occurred throughout all but the rockiest sites, as did little-leaved mountain mahogany (*Cercocarpus ledifolius* var. *intricatus*). Altogether, the limber/bristlecone pine stands covered at least 50 ha.

As far as we know this stand has not previously been mapped or described in the botanical literature. Good sleuthing, Scotty!

P.S. For the record, I found no evidence of pikas at Rawhide Mountain.

### Dead and Dying Bristlecone Pines

As is well known to the CIRMOUNT community, recent decades of extreme warmth and droughts, intercepted by extreme wet

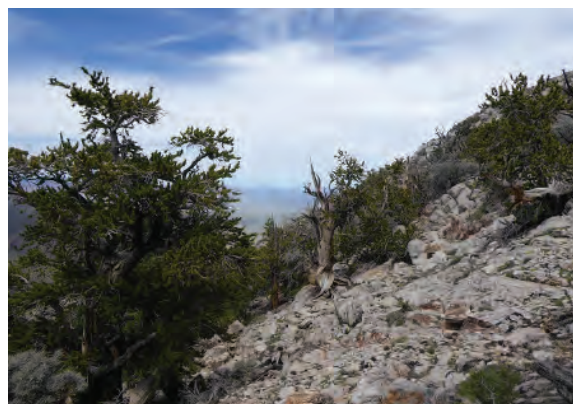
years, have catalyzed stress-induced forest mortality in many conifer species throughout the West. This has occurred directly from physical effects and indirectly through cascading biotic impacts involving insects and disease. The massive mortality that ensued makes us, forest ecologists, edgy about who, what, and where will be the next victims. Despite disturbance agents lurking in the shadows of bristlecone pines (white pine blister rust and various bark beetles) that have caused high mortality on co-occurring species, Great Basin bristlecone pines have



**Figure 5a, b.** Diverse forms and spiral grain of old bristlecone pines.



**Figure 3.** Bristlecone pines along the northwest slopes of Rawhide Mountain. The only stand of bristlecone pine known previously in the range is on Morey Peak, the black, fortress-like mountain in the far upper-right background.



**Figure 6.** Bristlecone pines growing on carbonate soils.



remained remarkably free from impact—so far. Dying or recently dead trees are rarely observed, and then are usually solitary and highly scattered. An incisive research program lead by Barbara Bentz (US Forest Service, Rocky Mountain Research Station; see her article on page 28) revealed unique mechanisms through which GB bristlecone pine appears to resist attack—or at least escape mortality—from mountain pine beetle (*Dendroctonus ponderosae*), the most common bark beetle to affect GB high-elevation forests. For the time being, we all sighed in relief, thinking that bristlecone pine had reprieve from future bark beetle epidemics.

Thus it was disturbing in recent years to encounter stands of bristlecone pine in three separate regions of Nevada with dying and recently dead trees. I describe these in order of the trips where I observed them.

*Silver Peak, Silver Peak Range, NV* After whooping it up with the festivities of the 2017 Jim Butler Days and the final Memorial Day Parade (Fig. 7) in Tonopah, NV, our band of Scotty Strachan and family, my husband, Jeff, and I headed toward the remote Silver Peak Range, south and west of Tonopah. In particular our destination was Silver Peak (2854 m), the second-highest point in the Silver Peak Range. The entire range, and in particular Silver Peak, is extremely dry, lying in the triple rain-shadow created by the mighty southern Sierra Nevada, the high plateau of the White Mountains, and the bulk of the Silver Peak Range to the west of our destination.

Bristlecone pines were already known from the slopes of this peak (Charlet 1996), and Scotty and I had overlapping reasons to visit them. Scotty, as at Rawhide, was interested in the low-elevation, dry, and isolated context in his quest to unravel the long-term responses of bristlecone pine to these seemingly marginal conditions. I had been exploring the range the year

before for evidence of pikas, which I really thought would be in the range, given its proximity to the White Mountains (lots of pikas) and abundant high-quality talus habitat. I had surveyed Piper Peak (high point of the range at 2881 m; no pikas), and then Red Mountain (2727 m; no pikas). From the summit of the latter I could see Silver Peak to the south, as well as the stands of bristlecone pine on its slopes. I was surprised to see, through binoculars, what looked to be recently dead trees. I assumed that these were limber pines, a common associate of bristlecone and a ready host for mountain pine beetle, although that species had not been documented from the range.

So it was we made our way in early June 2017 to a flat saddle below the summit ridge of Silver Peak, where we set up a glorious camp (Fig. 8). The next day we hiked the summit ridge and explored the small bristlecone pine stand (Fig. 9). Pines



**Figure 8.** Connie at camp on the saddle below Silver Peak, looking southwest to the White Mtns and Sierra Nevada.



**Figure 9.** Bristlecone pine near the Silver Peak ridge crest; Red Mountain to the north.



**Figure 7.** Jim Butler Days Parade, Tonopah, NV



occur primarily on the steep and cliff-bordered east slopes (Fig. 10) but slop over the crest to the west as well. Scotty plunged down one canyon and I took the other. We emerged with the same observations: Lots of well-preserved ancient bristlecone pine deadwood; highly scattered ancient live trees, primarily on northward aspects; and ravine bases with corridors of younger mature trees extending down to about 2490 m. The latter context is where we found most of the recent mortality (Fig. 11). The cause was not obvious to us, and we observed no trees that were in the process of dying (which might have been diagnostic). Importantly we found no limber pines on Silver Peak, but the bristlecone pines were growing amid dense pinyon forests.

P.P.S. No pika evidence on Silver Peak either...

*Rawhide Mountain, Hot Creek Range, NV* During the same trip in 2019 that I describe above, Scotty, David, and I also observed recently dead and dying bristlecone pines in the Rawhide Mountain population (Fig. 12). They were not abundant, mostly young-mature, and occurred primarily near the low edge of the stands on the northwest slopes, ~2600 m. The pattern there looked like bark beetle (galleries) to us. In this stand the bristlecone pine are mixed, as I mentioned, with limber pine, including those that appeared to have been killed by bark beetles, as well as pinyon pines.

*Telescope Peak, Panamint Range, CA* In early July 2019 I visited the Panamint Range, CA, which, like the Silver Peak Range, is extremely dry, lying in a triple rainshadow, in this case, of the Sierra Nevada and the Coso-Argus Ranges. Telescope Peak is famous for its record-breaking escarpment, which descends from Telescope Peak's summit elevation of 3368 m to Badwater Basin in Death Valley National Park at -85 m, a drop of 3453 m. An extensive population of bristlecone and limber pines is known to

occur on the slopes of Telescope Peak and subsummit slopes to the south. Once again the paired goal of searching for pikas as well as visiting the pines brought me to this range.

Telescope Peak is easily approached from the north, along a well-used foot trail (!) that contours lesser summits and then traverses the long narrow range crest to the saddle north of the



**Figure 11a, b.** Recently dead bristlecone pines in ravine bases of the east slope canyons, Silver Peak.



**Figure 10.** A handful of bristlecone pines growing on the rocky knob, low center. Trees in the foreground are single leaf pinyon pine.



**Figure 12.** Recently dead bristlecone pines in the Rawhide Mountain stand.



main peak. Limber pines (Fig. 13) appear on the ridge about 3 km from the trailhead, and it soon became apparent that they were experiencing similar mortality (I assumed from mountain pine beetle) as are/were many Great Basin limber pine stands I have observed in the past decade (Fig. 14).

Continuing south, limber pine becomes more abundant and, near Telescope Peak, bristlecone pine starts to mix in and then becomes dominant. What I didn't expect was the massive extent of recently dead and dying bristlecone pines on Telescope Peak (Fig. 15). The affected trees were mature ages, from small stems to ancient old-growth individuals. The mortality event seemed to concentrate in stands on northeast and east aspects whereas the equally abundant bristlecone pine forests on the northwest and west slopes appeared relatively healthy. Although many of the affected bristlecone were in monotypic stands, affected limber pines were near and in some cases admixed, and pinyon pine woodlands were present with bristlecone pine in the mid- and lower elevations.

I described the situation at Telescope Peak, and the other bristlecone pine stands with recent mortality, to Barbara Bentz as soon as I returned home. She made a trip to Telescope Peak soon after. You can read Barbara's thoughts about this situation in her



**Figure 13.** First limber pines along the trail to Telescope Peak (in the background).



**Figure 14.** Dead and dying limber pines along the trail.

**Figure 15a, b, c.** Dead and dying bristlecone pines on the northeast slopes of Telescope Peak.

article (page 28) and how this presents a new twist in the matrix of apparent resistance of bristlecone pine to bark beetle mortality. Barbara is planning to pursue this with new bristlecone pine research, and I hope to participate from the sidelines. If drought and warmth of these range-margin stands are involved, or even just geographic proximity could put other stands at risk, then the matriarchs and patriarchs of the great bristlecone pine groves of the White Mountains, on lands administered by the Inyo National Forest (INF; Ancient Bristlecone Pine Forest), could be next to succumb. The INF should consider preparing for action if



early detection and swift attention could forestall advance of an epidemic such as has occurred (and continues) at Telescope Peak.

P.P.P.S. Again, no evidence for pikas in the Panamint Range...

## Prometheus Revisited

The Methuselah Tree in the White Mountains, CA is famously known to tree aficionados as the oldest living non-clonal tree in the world, at ~4852 yrs old in 2019 (a live tree in the White Mountains with over 5000 rings has been rumored but unpublished). In the shadows of the Methuselah story is the equally well known, if infamous, Prometheus—or Currey—Tree, of the Snake Range, eastern NV.

In the mid-20th century, at a time when scientists were seeking long-lived trees among western high-elevation conifer forests to advance the young science of dendrochronology, bristlecone pines of the White Mountains were emerging as exceptional for their great ages. Bristlecone pines in other parts of the range were old but none was found that reached the ages of the White Mountain trees. That is, not until Donald Currey, then a University of North Carolina graduate student in geomorphology, started to work in the Snake Range. Interested in reconstructing glacial history, bristlecone pines situated on moraines of the Wheeler Peak cirque might serve as useful chronometers. So the litany goes, Currey was unable to successfully core an especially large living bristlecone pine, and gained permission from then-land-administrator US Forest Service to have the tree cut. It was sawn down, and sections removed. Currey counted the rings from multiple slabs, estimating the remaining number of rings to the missing pith. He determined the tree to have been at least 4,900 years old when standing, the oldest known living bristlecone pine. He published his findings in a short article for the journal *Ecology* (Currey 1965).

There is much more to the story, detailed by one author in his account of the effort to establish Great Basin National Park (Lambert 1991). I have long been fascinated by the Prometheus Tree. What is the nature of the stand that contains it? What scientific value came of the tree? What was the role of the US Forest Service? Where are the slabs now? Why is it called Prometheus?

I have visited the Snake Range annually since 2009 for various reasons, routinely to change temperature loggers in limber pine forests. I've also explored many of the bristlecone pine stands (Fig. 16), including the photo-shoot-perfect grove in the Wheeler cirque, near Currey's site. Perhaps because I had extra time this year, or perhaps I was piqued by the fact that Scotty has visited

the Prometheus Tree “many times” and I hadn't; for whatever reason, I determined 2019 was the year I would find it.

In his 1965 paper, Currey described the general location of WPN 114 (his sample number for Prometheus), and in August 2019, my husband Jeff and I set off across the Wheeler rock glacier to search for Prometheus. The stand is perched on a lateral moraine near treeline with the Wheeler Peak cirque cliffs in the backdrop. Many iconic old bristlecone pines, all healthy (I was happy to note) compose the small stand (Fig. 17). It didn't take long to find the carcass, weathered grey sections scattered like bones amid the living forest (Fig. 18). A forester by training, I was surprised at my emotional reaction—I'm not sure what I expected, probably a clean cut, one stump, and I hadn't anticipated the fact that the tree would be in such dramatic context. We spent several hours in the grove, admiring the live trees as well as ancient dead stems (Fig. 19), and running across other evidence of Currey's work.



Figure 16. Bristlecone pines on the slopes of Mt. Washington, Snake Range, NV.



Figure 17. Bristlecone pines in the stand with Prometheus.



**Figure 18.** Connie with Prometheus's remains. Photo: J. Wyneken.

Since that visit, I have thought a lot about how we conduct our science, and how standards for what is acceptable change over time. It is safe to say, I feel quite certain, that permission to cut an ancient bristlecone pine would not be granted today, whether the lands were administered by the National Park Service land (as this area is now) or US Forest Service. I recognize—and applaud—that ethical standards have matured. Of the many uses to which wild species were subjected for human use in the mid-20th century, including medical testing, bioassays for bomb impacts, and many aspects of environmental research, practices have changed as our respect for non-human life increased.

The Zeitgeist of science conditions what we consider appropriate and how we act. While I am still shocked to read (if the Lambert 1991 account is credible) that the local US Forest Service District Ranger (DR) approved Currey's request to cut WPN-114, and the Forest Supervisor concurred, I am also interested that the local agency reaction was so strong against cutting the tree. The Superintendent of then-Lehman Caves National Monument attempted to stop the cutting. And, as the story is told, the chainsaw man, ordered by the DR to cut the tree, refused to follow orders once he saw the Prometheus tree, and left the scene. The next day the DR himself headed a crew to cut the tree, sharing the chainsaw with apparently reluctant staff. Amid the finger-wagging toward those actions, I have to ask myself: what am I doing with my science practices (and otherwise) today that will be shocking by ethical standards of tomorrow?

What bothers me almost as much as the ancient tree having been cut is that so little scientific analysis came of it. Once cut and hauled off, I hoped that the Prometheus sections had been scoured for ecological and geological insight. I couldn't believe that Currey's 1965 paper was all there was to it. The findings of that paper were few: he counted the rings, proclaimed that old bristlecone pines exist in the eastern Great Basin, and made a few lame comments about neoglacial conditions (most I disagree with). No cross-dating, no ring-width measurements, no climate reconstructions, no geomorphic assessments.

I was thrilled to find Matt Salzer and Chris Baisan's more recent poster wherein they detail their successful cross-dating of the Prometheus slabs (Salzer and Baisan 2013). The new analyses allowed Matt and Chris to estimate that Prometheus was at least 5,000 yrs old when cut in 1964, and that no other bristlecone pines, living or dead, are known to have reached this age. The slabs from Prometheus are archived at the Laboratory of Tree Ring Research, University of Arizona, Tucson (I haven't been able to track down a section reportedly once on display at the Nevada Hotel in Ely, NV).

Finally, as to the name Prometheus, it is still not clear to me the connection of that bristlecone pine with the mythical creature. Lambert (1991) explains, "The tree was one we park advocates in the late 1950s had named Prometheus—for the ancient Greek who brought fire and the arts into human culture, then had been punished for transgressions by being chained to a mountain and repeatedly eaten by vultures, each time restoring himself only to be eaten again."



## References

Charlet, D.A. 1996. Atlas of Nevada conifers: A phytogeographic reference. University of Nevada Press. Greatly expanded 2nd edition in preparation.

Currey, D.R. 1965. An ancient bristlecone pine stand in eastern Nevada. *Ecology* 46: 564-566.

Lambert, D. 1991. *Great Basin Drama: The Story of a National Park*. Roberts Rinehart Publishers.

Salzer, M. and C. Baisan, C. 2013. Dendrochronology of the “Currey Tree”. In: *Second American Dendrochronology Conference*, University of Arizona, Tucson, United States, May 13-17, 2013.

*Except as noted, all photos by the lead author.*



**Figure 19.** Bristlecone pine at treeline in the Prometheus stand.



# CONTRIBUTING ARTISTS



**Alli Fitzmorris** tells me this about her path to being a scientific illustrator: “As a little girl, I wished that I could travel back in time and become a naturalist. I dreamed of discovering strange creatures and exotic plants while trekking through unexplored jungles and over unmapped peaks. I would draw them and name them and then send my journals back home so everyone could see what I saw, so everyone could see how beautiful and wild the world is. How lucky I am to have discovered the field of scientific illustration! My childhood wishes have been fulfilled: I can share all the amazing and wonderful things I see with the rest of the world, and strive to impart the awe I feel in nature with my artwork.” Follow her work @fitzalli



**Autumn Stock** is an artist living in Yosemite Valley. She enjoys watercolor and pen-and-ink drawing and is inspired by her mountain home. Autumn is a sophomore at Mariposa High School.



**Bob Coats** is a research hydrologist with the UC Davis Tahoe Environmental Research Center. He has been studying climatic, hydrologic, and ecological processes in the Lake Tahoe Basin—and writing poetry—for more than 40 years. His poems have appeared in *Orion*, *Zone 3*, *Windfall*, *The Acorn*, the Pudding House anthology, *Fresh Water: Poems from the Rivers, Lakes and Streams*, and in his book *The Harsh Green World*, published by Sugartown Publishing.



Stormy Pywiack by Autumn Stock

# MOUNTAIN VISIONS

## What to Do on August 26<sup>th</sup>

Go to Rock Lake, Plumas country.  
Before sunrise, stand  
on the slate ledge that juts the lake.  
Look to the western shore,  
watch sunlight creep down  
the red bank of schist.

Now turn east, look up  
to the canyon rim  
where Jacob's ladders converge  
at a dark hemlock  
silhouetted  
against the bright sky.

In the moment before the sun  
crests the wall  
the entire tree--bole,  
branches, foliage--  
will flash  
into silver filigree.

Then the orb's leading edge  
will clear the jagged ridge, shooting  
gold deep into liquid indigo  
warming your face  
flooding you  
with light.

—Robert Coats  
August 1995





Tower Peak by Autumn Stock



# FIELD FRAMES

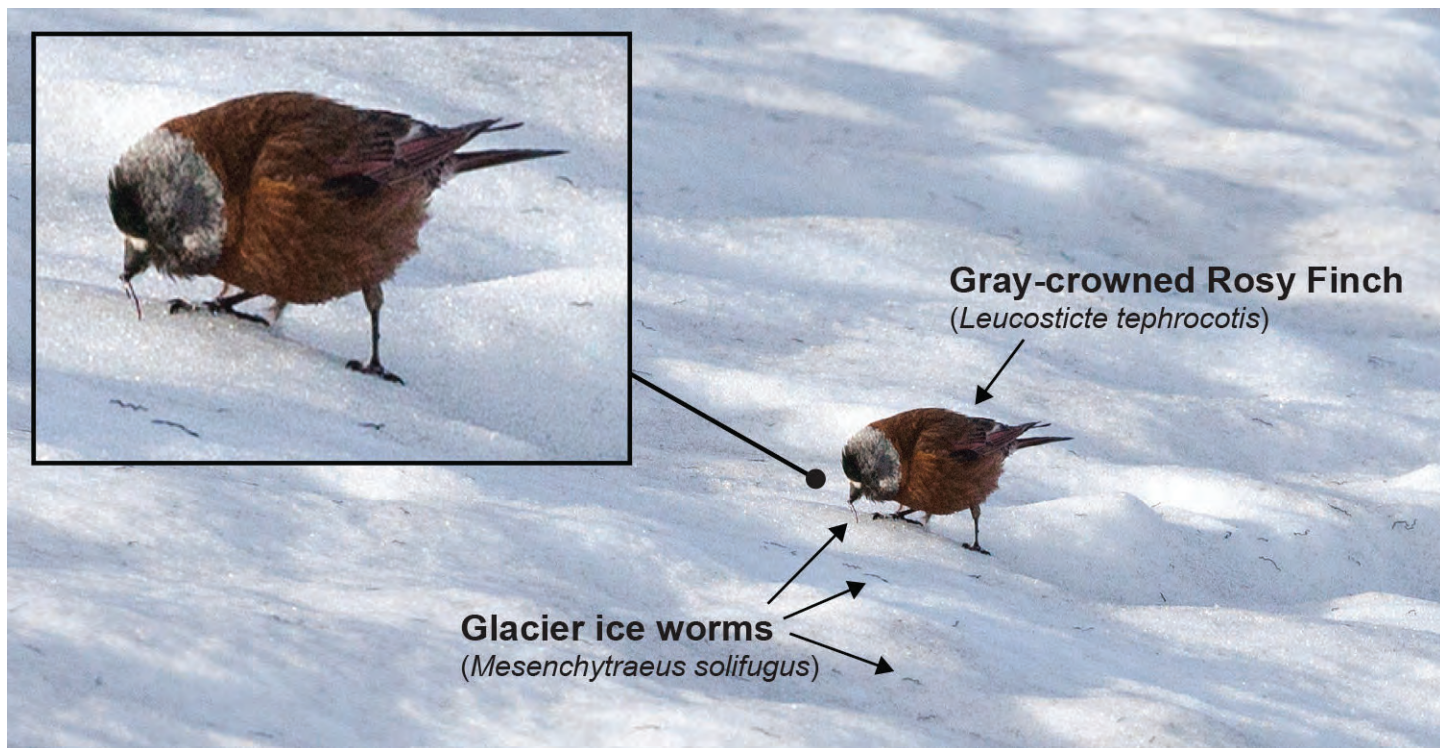


Photo: Scott Hotaling

*A Gray-crowned rosy finch (Leucosticte tephrocotis), the highest-elevation nesting bird in North America, feeds on abundant ice worms (Mesenchytraeus solifugus) on the Paradise Glacier of Mount Rainier, Washington, USA, in June 2019. Ice worms appear to be a key food resource for rosy finches during their nesting period and reciprocally provide a means of passive dispersal of ice worms across their range (see Hotaling et al., 2019, Brevia, this issue, page 43).*



**Scott Hotaling**  
Washington State University  
Pullman, Washington