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Why this special issue is focused on the high elevation five-needle white pines

Across the higher mountains of the western United States and Canada and in northern Mexico, there are six species of pines informally referred to by researchers and managers as the "high elevation five-needle white pines" (e.g., Tomback et al., 2011; Keane et al., 2011; H5II High Elevation Five Needle Pine Research Conference (highfivepines.org). These pines are related at the subgenus level (Family Pinaceae, Genus *Pinus*, Subgenus *Strobus*) but classified within two different taxonomic pine sections, reflecting their different evolutionary affinities: Section *Quinquefoliae*—whitebark (*Pinus albicaulis* Engelm.), limber (*Pinus flexilis* James), southwestern white (*Pinus strobiformis* Engelm.); and Section *Parrya*—foxtail (*Pinus balfouriana* Balf.), Rocky Mountain bristlecone (*Pinus aristata* Engelm.), and Great Basin bristlecone (*Pinus longaeva* D.K. Bailey) (Gernandt et al., 2005; Hao et al., 2015). The species in *Quinquefoliae* and *Parrya* are characterized by needles in fascicles of five—thus "five-needle" pines (Fig. 1).

The ranges of the high elevation five-needle white pines vary from localized or regional within a mountain range or complex of ranges to cordillera-wide: Three pines have localized or regional distributions within the U.S. (e.g., the bristlecone pines, foxtail pine), one pine is widely distributed across the southwestern U.S. and northern Mexico (southwestern white pine), and two pines are widely-distributed within the higher mountains of the western U.S. and Canada (whitebark and limber pine) (see maps in: Tomback and Achuff, 2010; Tomback et al., 2011; Schoettle et al., 2022, In this issue).

This special issue of *Forest Ecology and Management*, "*Ecology and Restoration of High Elevation Five-Needle White Pines*," features two overview papers plus the invited plenary and keynote presentations from "H5II: The Second Conference on the Research and Management of High Elevation Five Needle Pines in Western North America," held virtually October 2–5, 2021 (H5II High Elevation Five Needle Pine Research Conference (highfivepines.org) and attended by more than 274 students, researchers, and managers from across the U.S. and Canadian ranges of these species. Organized and sponsored by the Whitebark Pine Ecosystem Foundation (whitebarkfound.org), this conference included more than 100 presentations on the ecology, conservation, restoration, and management of the six pine species.

Why are international conferences such as H5II devoted to the high elevation five-needle white pines? These pines are generally of limited timber value and thus historically of lower management priority. However, in the last 30 years, we have come to recognize the important ecosystem services and ecological roles (i.e., as foundation and keystone species) that they provide with respect to watershed and avalanche protection, preventing soil erosion, facilitation of community development after disturbance, and ecosystem structure and function (Tomback et al., 2001; Ellison et al., 2005; Tomback and Achuff, 2010; Tomback et al., 2011; Degrassi et al., 2019; Schoettle et al., 2022, In this issue). The pines also provide high elevation wildlife habitat and shelter, and their seeds are important wildlife food resources across their high mountain distributions (Arno, 1986; Tomback and Kendall, 2001; Tomback et al., 2011).

The high elevation five-needle white pine commonalities also include their elevational distribution, general ecology, and the burgeoning threats that imperil their future survival (Goeking and Windmuller-Campione, 2021, In this issue). All these pines are susceptible to white pine blister rust (WPBR), an introduced, often fatal disease caused by the fungal pathogen *Cronartium ribicola* J.C. Fisch. that has spread widely across the range of its five-needle pine hosts (Schwandt et al., 2010; Schoettle et al., 2022, In this issue; Sniezko and Liu, 2022, In this issue). Furthermore, all pines experienced losses during the recent mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks (Gibson et al., 2008; Bentz et al., 2022, In this issue). All are threatened by altered fire regimes, drought, and distributional shifts resulting from a changing climate (Tomback et al., 2001, 2011; Tomback and Achuff, 2010 and references therein; Schwandt et al., 2010; Schoettle et al., 2022, In this issue). Whitebark pine, which has rapidly declined throughout much of its range, is currently listed as Endangered in Canada under the Species at Risk Act (SARA) (Whitebark Pine (Pinus albicaulis) - Species search - Species at risk registry (Canada.ca); it was recently proposed for threatened status under the U. S. Endangered Species Act (U.S. Fish and Wildlife Service, 2020). Limber pine has been proposed for listing as an endangered species under the Species at Risk Act in Canada (COSEWIC Assessment and Status Report on the Limber Pine Pinus flexilis in Canada - 2014 - Canada.ca), and foxtail pine has been assessed for *The IUCN Red List of Threatened Species* in 2011, and is listed as Near Threatened (Farjon, 2013). Several other high elevation five-needle white pines, especially limber pine, are declining in parts of their U.S. range and warrant management intervention.

With respect to ecology, the high elevation five-needle white pines vary from moderately to highly shade-intolerant, which diminishes their competitiveness in successional forest communities and results in dependence on disturbance for regeneration (Tomback and Achuff, 2010; Tomback et al., 2011). Their mode of seed dispersal varies, with two pines—whitebark and limber—highly dependent Clark's nutcracker (*Nucifraga columbiana* Wilson), a bird that transports seeds over long distances and stores them in small caches across the montane landscape (Tomback, 1982). The other pines depend on a mix of wind-dissemination, nutcrackers, jays, and small mammals, which also cache seeds, for seed dispersal (Tomback et al., 2011). The seed dispersal mode strongly influences gene flow and population structure (e.g., Tomback and Linhart, 1990). All the pines are well-adapted to poor soils

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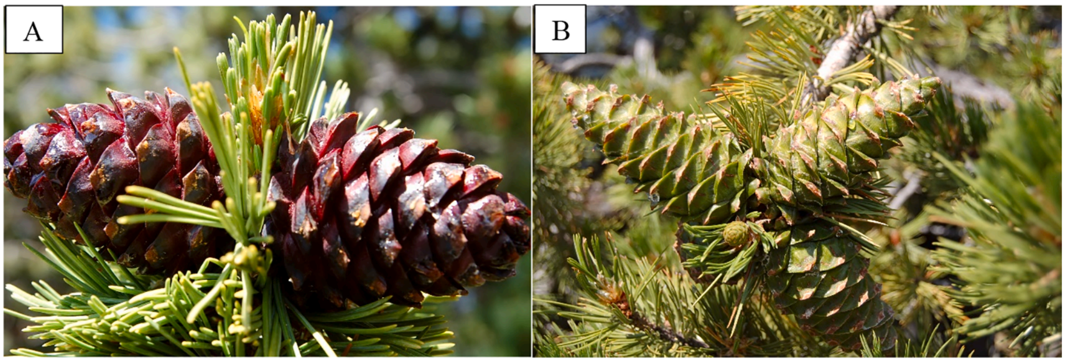

Fig. 1. Cones and five-needle fascicles of (A) whitebark pine (*Pinus albicaulis*) and (B) limber pine (*Pinus flexilis*), two of the six high elevation five-needle white pines. Photo credit: D.F. Tomback.

and exposed, droughty sites, enabling them to inhabit windswept slopes of upper forest limits, where they grow slowly with sculpted canopies and twisted stems. Whitebark, limber, and Rocky Mountain bristlecone pine form treeline krummholz (mat-like growth forms at treeline) communities; but foxtail, southwestern white pine, and Great Basin bristlecone pine usually maintain upright forms up to their elevational limits (Tomback and Achuff, 2010; Schoettle et al., 2022, In this issue).

Given the rapid loss of whitebark pine across much of its range, as well as declines in other high elevation five-needle white pines, for the past 25 years U.S. and Canadian forest scientists and managers have been developing techniques and tools to restore several of these species, but more information is required. For example, characterizing the frequency and distribution of genetic resistance to WPBR within populations of these pines and determining whether resistance is both durable and stable provide essential information to restore populations currently impacted by WPBR and to build resilience to *C. ribicola* in relatively healthy populations. The identification of sufficient numbers of genetically resistant trees is critical to providing seed sources with sufficient genetic diversity to use for restoration. Resistance to WPBR has been examined to varying degrees in all six of the high elevation five-needle white pines, and the species differ in the type, frequency, and effectiveness of resistance present, with implications for restoration approaches (see Sniezko and Liu, 2022, In this issue). Additional research is needed to refine our knowledge of adaptive genotypes within these pines to implement assisted migration under a changing climate and ensure the long-term success of restoration plantings.

Among the high elevation five-needle white pines, whitebark pine has been the most studied in relation to WPBR resistance, with the latest contribution a series of common garden trials (see Cartwright et al., 2022, In this issue). However, with genome sequencing of whitebark pine and Great Basin bristlecone pine underway, there will be great opportunity for landscape genomics-related studies to elucidate adaptive variation in both species (Sniezko and Liu, 2022, In this issue).

Additional treatment and management actions help maintain viable five-needle white pine populations in response to other threats (Keane et al, 2021, In this issue; Schoettle et al, 2022, In this issue; Tomback et al, 2022, In this issue). Range-wide programs including inventory, mapping, planning, seed collection, nursery infrastructure development and practice, education, and research in general provide the critical information, tools, and materials required for effective restoration or management at regional and local scales for these pines. Landscape-level restoration treatments, for example, can be designed for the different high elevation five-needle white pine species to mimic the community effects of wildland fire and other disturbances by creating open stands for manual seedling planting, direct seeding, and nutcracker caching. Stand level treatments, such as combining silvicultural cuttings and prescribed fires in both healthy and declining forests, can be designed to meet local stand objectives. The most important stand-level treatment is the planting of rust-resistant five-needle white pine seedlings in burned or otherwise open areas in order to build resilient populations. Also, certain proactive tree-level actions can be used to protect known rust-resistant pine trees from fire and mountain pine beetles in both treated and untreated stands. Sufficient knowledge exists to implement effective restoration programs, but the impacts of climate change will require developing new approaches to mitigate these effects, such as using appropriate adaptive genotypes in targeted planting sites.

The papers in this special issue, *Ecology and Restoration of High Elevation Five-Needle White Pines*, address in detail many of the topics that we described above. Below, we categorize and list the contributions:

(1) Health status and management. Goeking and Windmuller-Campione (2021, In this issue) describe the U.S. range-wide health status of all the high elevation five-needle white pines, and Bentz et al. (2022, In this issue) describe mortality factors in the enigmatic Great Basin bristlecone pine.

(2) Management practices. Tomback et al. (2022, In this issue), an invited Tamm review, present an overview of key current and best management practices for restoring whitebark pine; Keane et al. (2021, In this issue) describe how high elevation five-needle white pine management and restoration practices can incorporate mitigation for climate change and other disturbances, and Schoettle et al. (2022, In this issue) indicate how differences in the genetics and frequency of rust resistance and adaptive potential among the high elevation five-needle white pines entail different management approaches and limitations.

(3) Climate change. Hansen et al. (2021, In this issue) compare the climate sensitivity of young vs. mature whitebark pine in the Greater Yellowstone.

(4) White pine blister rust resistance screening. Sniezko and Liu (2022, In this issue) describe the results of blister rust resistance studies in the high elevation five-needle white pines, some considerations for use of resistance, and how biotechnology could speed up the search for resistant genotypes; and, Cartwright et al. (2022, In this issue) report the outcome of common garden field trials in British Columbia screening for resistance and adaptability in whitebark pine using seedlots from much of the range of the species.

(5) Restoration planning. Tomback and Sprague (2022, In this issue) describe the conceptual basis of the National Whitebark Pine Restoration Plan, its assembly, and proposed implementation, and how the process can be a model for devising restoration plans for other high elevation five-needle white pines. Jenkins et al. (2022, In this issue) describe the complex process of assembling a trans-boundary, multi-jurisdictional plan to restore whitebark pine in the Crown of the continent ecosystem.

We hope that these papers collectively serve to (1) inform managers and researchers of the precarious status of the high elevation five-needle white pines, (2) provide key information on restoration treatments and conservation actions, and (3) communicate the urgent need to plan and implement management and restoration projects to build resilience into populations of all the high elevation five-needle white pines. We also hope that the papers serve as an impetus for innovation and the application of technology in the near future to devise more efficient and effective management approaches. For several of these white pines, current losses are already having cascading effects on local and regional biodiversity and ecosystem services.

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