Species Status Assessment Report for the Whitebark Pine, *Pinus albicaulis*

Prepared by the Wyoming Ecological Services Field Office
U.S. Fish and Wildlife Service, Cheyenne, Wyoming
December 2021, version 1.3

Photo Credit: Shawn McKinney (RMRS)

This document was prepared by the Whitebark Pine SSA Team, including Amber Aguilera, Sarah Backsen, Thomas Brumbelow, Tara Callaway, Alexandra Kasdin, Douglas Keinath, Erin Knoll, James Lindstrom, Elizabeth McKeag, Karen Newlon, Amy Nicholas, Julie Reeves, Genevieve Skora, Lisa Solberg Schwab, Ben Solvesky, and Sean Sweeney.

Valuable peer and partner reviews of a draft of this document were provided by Peter L. Achuff, Robert E. Keane, Kristin Legg, Mary Frances Mahalovich, Cyndi Smith, Richard A. Sniezko, Diana F. Tomback, the Bureau of Land Management, the Idaho Department of Fish and Game, the Idaho Department of Lands, the National Park Service, the United States Forest Service and the Washington DNR Natural Heritage Program.

EXECUTIVE SUMMARY

This report summarizes the results of a species status assessment (SSA) that the U.S. Fish and Wildlife Service (Service) completed for the whitebark pine (*Pinus albicaulis*). Whitebark pine is a slow-growing, long-lived tree, with trees on the landscape documented at 500 to over 1,000 years old. Whitebark pine occurs at high elevations across western North America and is considered a keystone and foundation species; whitebark pine stabilizes soils, regulates runoff, slows the progression of snowmelt, and provides nutritious seeds for numerous species of wildlife. This SSA report summarizes the current and future condition of whitebark pine to assess the species' overall viability now and into the future. For the purposes of this SSA, we define viability as the ability of the whitebark pine to sustain populations in the wild into the future.

To assess whitebark pine's current and future status, we used the three conservation biology principles of resiliency, redundancy, and representation (together, the 3Rs). Specifically, we identified the species' ecological requirements at the individual, population, and species levels, and described the stressors and other factors influencing the species' viability. Whitebark pine needs multiple, resilient populations distributed across its range in a variety of ecological settings to persist into the future and to avoid extinction.

For our analyses, we divided the species' range into 15 analysis units. Our analysis of the current condition of whitebark pine found that the species is being impacted by four main stressors: altered fire regimes, white pine blister rust, mountain pine beetle, and climate change. These stressors already occur in widespread areas, decreasing resiliency in all 15 analysis units. This reduction in resiliency is rangewide, however, the Canadian, U.S., and Northern Rockies analysis units are likely being most heavily impacted.

We evaluated trends and predicted the future viability of the whitebark pine by forecasting the conditions of the 15 analysis units under three potential future scenarios. Our future scenarios varied based on the four key stressors mentioned above (severe wildfire, the non-native pathogen white pine blister rust, the native mountain pine beetle, and climate change) and the potential

impacts of conservation efforts. The four key stressors are known to be operating at a rangewide scale and affecting whitebark pine population dynamics. Due to the longevity and long generation time of the species, our projections of impacts go out 180 years, which corresponds to approximately three generations of whitebark pine.

The projected future conditions of each analysis unit varied depending on the forecasted scenario, but we predict that the resiliency of all of the analysis units will be reduced from current conditions. Based on historical trends, there is widespread agreement among whitebark pine experts that all key stressors are likely to continue to impact whitebark pine at levels above current conditions in the future. However, the degree and pace of impacts from these stressors depends on uncertain future levels of increase in wildfire and mountain pine beetle predation due to climate change, the level of genetic resistance to white pine blister rust, and conservation efforts. Therefore, our future scenarios were designed to encompass the full range of plausible future conditions.

Overall, we predict that whitebark pine will continue to decline in levels of resiliency, redundancy, and representation within one to three generations. We acknowledge that our assessment is a prediction and may not accurately forecast future events. However, we used the best available science for our analyses and acknowledged any key assumptions and uncertainties throughout this SSA report.

Table of Contents

List of Figures

List of Tables

CHAPTER 1. INTRODUCTION AND ANAYLYTICAL FRAMEWORK

BACKGROUND

This report summarizes the results of a species status assessment (SSA) conducted for whitebark pine (*Pinus albicaulis*). Whitebark pine is a wide-ranging conifer found at high elevations across the western U.S. and Canada. The SSA is intended to be an in-depth review of the species' biology and threats, an evaluation of its biological status, and an assessment of the resources and conditions needed to maintain populations over time (i.e., viability). The intent is for the SSA report to be easily updated as new information becomes available and to support all functions of the Endangered Species Program, from candidate assessment to listing to consultations to recovery. As such, the SSA Report will be a living document upon which other documents such as listing rules, recovery plans, and 5-year reviews would be based if the species warrants listing under the Endangered Species Act (Act). There is a voluminous body of scientific information and literature related to whitebark pine, however, we note that the SSA is not intended to be an exhaustive review of everything related to this well-studied species, but rather the SSA focuses on those aspects of whitebark pine that are most relevant to understanding the species' current status and predicted viability into the future at a rangewide scale.

This SSA Report for whitebark pine is intended to provide the biological support for the U.S. Fish and Wildlife Service's (Service's) forthcoming decision on whether or not whitebark pine warrants protection under the Act. Importantly, the SSA Report does not result in a decision by the Service on whether whitebark pine should be listed as a threatened or endangered species under the Act. Instead, this SSA Report provides a review of the relevant and available information strictly related to the biological status of whitebark pine. The listing decision will be made by the Service after reviewing this document and all relevant laws, regulations, and policies, and the results of a decision will be announced in the Federal Register.

The SSA assesses the ability of whitebark pine to maintain populations over time (i.e., viability). To assess whitebark pine viability, we used the three conservation biology principles of resiliency, representation, and redundancy (or the “3Rs”). These principles are generally described later in this chapter. In Chapter 2, we outline the needs of whitebark pine at the individual, population, and species levels. In Chapter 3 we examine the biology of four primary stressors affecting whitebark pine at the rangewide level. In Chapter 4 we summarize the current condition of whitebark pine in terms of the four main rangewide stressors (and beneficial factors) that are influencing its viability. In Chapter 5 using the baseline conditions established in Chapter 4 and the predictions for future risk and beneficial factors, we project the likely future condition of whitebark pine.

PREVIOUS FEDERAL ACTIONS

We were petitioned to list whitebark pine under the Act on February 5, 1991, by the Great Bear Foundation of Missoula, Montana. The petition stated whitebark pine was rapidly declining due to impacts from mountain pine beetles, white pine blister rust, and fire suppression. After reviewing the petition, we found that the petitioner had not presented substantial information indicating that listing whitebark pine may be warranted. We published this finding in the Federal Register on January 27, 1994 (59 FR 3824).

On December 9, 2008, we received a petition dated December 8, 2008, from the Natural Resources Defense Council (NRDC) requesting that we list whitebark pine as endangered throughout its range and designate critical habitat under the Act. The petition clearly identified itself as such and included the requisite identification information for the petitioner, as required by 50 CFR 424.14(a). Included in this petition was supporting information regarding the species’ natural history, biology, taxonomy, lifecycle, distribution, and reasons for decline. The NRDC reiterated the threats from the 1991 petition, and included climate change and successional replacement as additional threats to whitebark pine. In a January 13, 2009, letter to NRDC, we responded that we had reviewed the information presented in the petition and determined that issuing an emergency regulation temporarily listing the species under section 4(b)(7) of the Act was not warranted. We also stated that we could not address the petition promptly because of staff and budget limitations. We indicated that we would process a 90-day petition finding as quickly as possible.

On December 23, 2009, we received NRDC's December 11, 2009, notice of intent to sue over our failure to respond to the petition to list whitebark pine and designate critical habitat. We responded in a letter dated January 12, 2010, indicating that other preceding listing actions had priority, but that we expected to complete the 90-day finding during the 2010 Fiscal Year. On February 24, 2010, we received a formal complaint from NRDC for our failure to comply with issuing a 90-day finding on the petition. On May 7, 2010, we responded in writing to the formal complaint and provided answers to their claims and allegations. We completed a 90-day finding on the petition, which was published in the Federal Register on July 20, 2010 (75 FR 42033). In that finding we determined that the petition presented substantial information such that listing whitebark pine may be warranted, and announced that we would be conducting a status review of the species. We opened a 60-day information collection period to allow all interested parties an opportunity to provide information on the status of whitebark pine (75 FR 42033, July 20, 2010), and received 20 letters from the public.

We published a 12-month finding in the Federal Register on July 19, 2011 following a review of all available scientific and commercial information (76 FR 42631). In that finding, we found that listing whitebark pine as threatened or endangered was warranted. However, at that time listing whitebark pine was precluded by higher priority actions to amend the Lists of Endangered and Threatened Wildlife and Plants and whitebark pine was added to our candidate species lists. Therefore, whitebark pine became a candidate for listing under the Act, and it remained a candidate until December 2, 2020, when we proposed a rule to list the species as Threatened (85 FR 77408) with a 4(d) rule.

ANALYTICAL FRAMEWORK

To assess the viability of whitebark pine, we used the SSA Framework to apply the conservation biology principles of resiliency, representation, and redundancy (henceforth, 3Rs) (Service 2016a, entire). For the purposes of this assessment, we define viability as the ability to sustain populations in the wild over time; to do this, a species must have a sufficient number and distribution of healthy populations to withstand changes in its biological (*e.g.*, novel diseases, predators) and physical (*e.g.,* climate change) environment, environmental stochasticity (*e.g.,* wet or dry, warm or cold years), and catastrophes (*e.g.,* severe and prolonged droughts). Viability is not a single state—viable or not viable; rather, there are degrees of viability—less to more viable or low to high viability. Generally speaking, the more resiliency, representation, and redundancy a species has, the more protected it is against the vagaries of the environment, the more it can tolerate stressors (one or more factors that may be acting on the species or its habitat, causing a negative effect), the better able it is to adapt to future changes, and thus, the more viable it is. The 3Rs framework, wherein we assess the health, number, and distribution of whitebark pine populations relative to the frequency and magnitude of environmental stochasticity and catastrophic events across its range of adaptive diversity, is useful for describing a species' degree of viability through time. For the purposes of this assessment, we define each of the 3Rs using the SSA Framework (Service 2016a, entire), as follows.

Resiliency

Resiliency is the ability to sustain populations in the face of environmental variation and transient perturbations. Environmental variation includes normal year-to-year variation in rainfall and temperatures, as well as unseasonal weather events. Perturbations are stochastic events such as fire, flooding, and storms. Simply stated, resiliency is having the means to recover from "bad years" and disturbances. To be resilient, a species must have healthy populations; that is, populations that are able to sustain themselves through good and bad years. The healthier the populations and the greater number of healthy populations, the more resiliency a species possesses. For many species, resiliency is also affected by the degree of connectivity among populations and the diversity of ecological niches occupied. Connectivity among populations increases the genetic health of individuals (heterozygosity) within a population and bolsters a population's ability to recover from disturbances via rescue effect (immigration). Diversity of climate niches improves a species' resiliency by guarding against disturbances and perturbations affecting all populations similarly (*i.e*., decreases the chance of all populations experiencing bad years simultaneously or to the same extent).

Representation

Species-level representation is the ability of a species to adapt to near and long-term changes in the environment; it is the evolutionary capacity or flexibility of a species. Representation is the range of variation found in a species, and this variation–called adaptive diversity–is the source of species' adaptive capabilities. Representation can, therefore, be measured through the breadth of adaptive diversity of the species. The greater the adaptive diversity, the more responsive and adaptable the species will be over time, and thus, the more viable the species is. Maintaining adaptive diversity includes conserving both the ecological diversity and genetic diversity of a species. By maintaining these two sources of adaptive diversity across a species' range, the responsiveness and adaptability of a species over time is preserved. Ecological diversity is the physiological, ecological, and behavioral variation exhibited by a species across its range. Genetic diversity is the number and frequency of unique alleles within and among populations.

Redundancy

Species-level redundancy is the ability of a species to withstand catastrophic events. Redundancy protects species against the unpredictable and highly consequential events for which adaptation is unlikely. In short, it is about spreading the risk. Redundancy is best achieved by having multiple populations widely distributed across the species' range. Having multiple populations reduces the likelihood that all populations are affected simultaneously, while having widely distributed populations reduces the likelihood of populations possessing similar vulnerabilities to a catastrophic event. Given sufficient redundancy, single or multiple catastrophic events are unlikely to cause the extinction of a species. Thus, the greater redundancy a species has, the more viable it will be. Furthermore, the more populations and the more diverse or widespread that these populations are, the more likely it is that the adaptive diversity of the species will be preserved. Having multiple populations distributed across the range of the species, will help preserve the breadth of adaptive diversity, and hence, the evolutionary flexibility of the species.

CHAPTER 2. WHITEBARK PINE ECOLOGY

In this chapter, we provide basic biological information about whitebark pine, including its physical environment and distribution, taxonomic history and relationships, morphological description, and reproductive and other life history traits. We then outline the needs of whitebark pine at the individual, population, and species levels. This is not an exhaustive review of the species' natural history; rather, it provides the ecological basis for the SSA analyses conducted in this report.

RANGE AND DISTRIBUTION

Whitebark pine has persisted in high-elevation sites in western North America for the past 8,000 years (McCaughey and Schmidt 2001, p. 32). Whitebark pine has a broad range both latitudinally (occurring from a southern extent of approximately 36° north in California to 55° north latitude in British Columbia, Canada) and longitudinally (occurring from approximately 128° in British Columbia, Canada to an eastern extent of 108° west in Wyoming). For this SSA we developed an updated whitebark pine range map based on the best available occurrence and distribution data (Figure 1). This range map is at a coarse scale but encompasses the known distribution of species occurrences.

Whitebark pine typically occurs on cold and windy high-elevation or high-latitude sites in western North America, although it also occurs in scattered areas of the warm and dry Great Basin. As a result, many stands are geographically isolated (Arno and Hoff 1989, p. 1; Keane *et al.* 2012, p. 3). The distribution of whitebark pine includes coastal and Rocky Mountain ranges that are connected by scattered populations in northeastern Washington and southeastern British Columbia (Arno and Hoff 1990, p. 268; Keane *et al.* 2012, p. 3). The coastal distribution of whitebark pine extends from the Bulkley Mountains in northwestern British Columbia to the northeastern Olympic Mountains and Cascade Range of Washington and Oregon, to the Kern River of the Sierra Nevada Range of east-central California (Arno and Hoff 1990, p. 268). Isolated stands of whitebark pine are known from the Blue and Wallowa Mountains in northeastern Oregon and the subalpine zone of mountains in northeastern California, south-central Oregon, and northern Nevada (Arno and Hoff 1990, p. 268; Keane *et al.* 2012, p. 3). The Rocky Mountain distribution of whitebark pine ranges from northern British Columbia and Alberta to Idaho, Montana, Wyoming, and Nevada (Arno and Hoff 1990, p. 268; Keane *et al.* 2012, p. 3), with extensive stands occurring in the Yellowstone ecosystem (McCaughey and Schmidt 2001, p. 33). The Wind River Range in Wyoming is the eastern most distribution of the species (Arno and Hoff 1990, p. 268; McCaughey and Schmidt 2001, p. 33) (Figure 1).

In general, the upper elevational limits of whitebark pine decrease with increasing latitude throughout its range (McCaughey and Schmidt 2001, p. 33). The elevational limit of the species ranges from approximately 900 meters (m) (2,950 feet (ft)) at its northern limit in British Columbia up to 3,660 m (12,000 ft) in the Sierra Nevada (McCaughey and Schmidt 2001, p. 33). Whitebark pine is typically found growing at subalpine treeline or with other high-mountain conifers just below the treeline and subalpine zone (Arno and Hoff 1990, p. 270; McCaughey and Schmidt 2001, p. 33). In the Rocky Mountains, common associated tree species include *P. contorta* var. *latifolia* (lodgepole pine), *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (subalpine fir), and *Tsuga mertensiana* (mountain hemlock). Common associated tree species are similar in the Sierra Nevada and Blue and Cascade Mountains, except lodgepole pine is present as *P. contorta var. murrayana* (Sierra-Cascade lodgepole pine), mountain hemlock is absent from the Blue Mountains (Arno and Hoff 1990, p. 270; McCaughey and Schmidt 2001, pp. 33–34), and Engelmann spruce and subalpine fir are absent in the Sierra Nevada.

Rangewide, whitebark pine occurs on an estimated 32,616,422 hectares (ha) (80,596,935 acres (ac)) in western North America (Figure 1). Roughly 70 percent of the species' range occurs in the United States, with the remaining 30 percent of its range occurring in British Columbia and Alberta, Canada (Service 2018). In Canada, the majority of the species' distribution occurs on federal or provincial Crown lands (COSEWIC 2010, p.12). In the United States, approximately 88 percent of land where the species occurs is federally owned or managed (Figure 2). The majority is located on U.S. Forest Service (USFS) lands (approximately 74 percent, or 17,391,455 ha (42,975,220 ac)). The bulk of the remaining acreage is located on National Park

Service (NPS) lands (approximately 10 percent, or 2,275,746 ha (5,623,490 ac)). Small amounts of whitebark pine also can be found on Bureau of Land Management lands (approximately 4 percent, or 1,002,152 ha (2,476,371 ac)). The remaining 12 percent of the range is under non-Federal ownership, on State, private, and Tribal lands. In the United States, 29 percent of the range is designated as wilderness under the Wilderness Act of 1964 (16 U.S.C. 1131 1136) (Figure 3). This designation limits management options and conservation efforts in those areas to some degree (see appendix A).

Figure 1 Whitebark pine range.

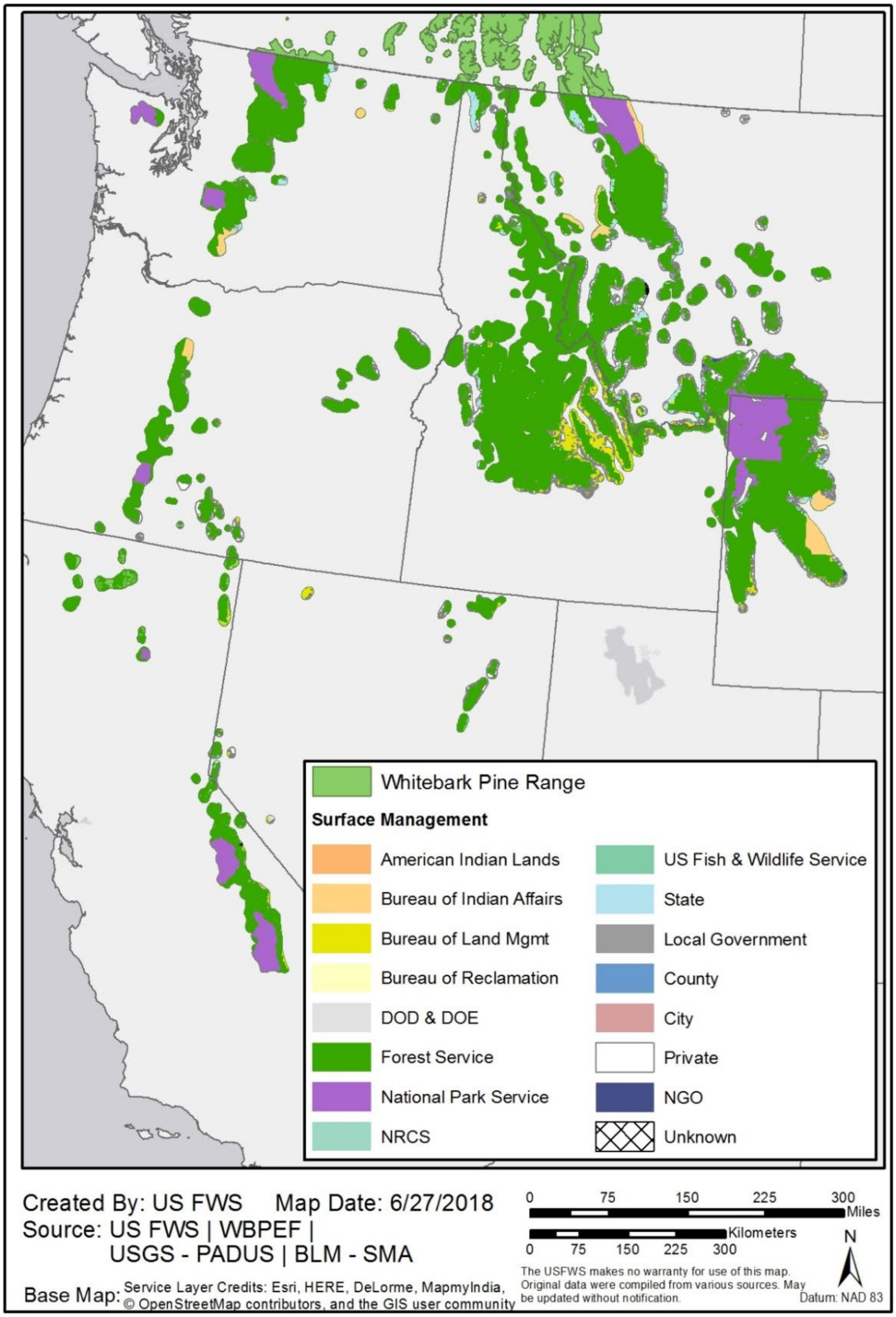

Figure 2 Surface management of whitebark pine range in the U.S.

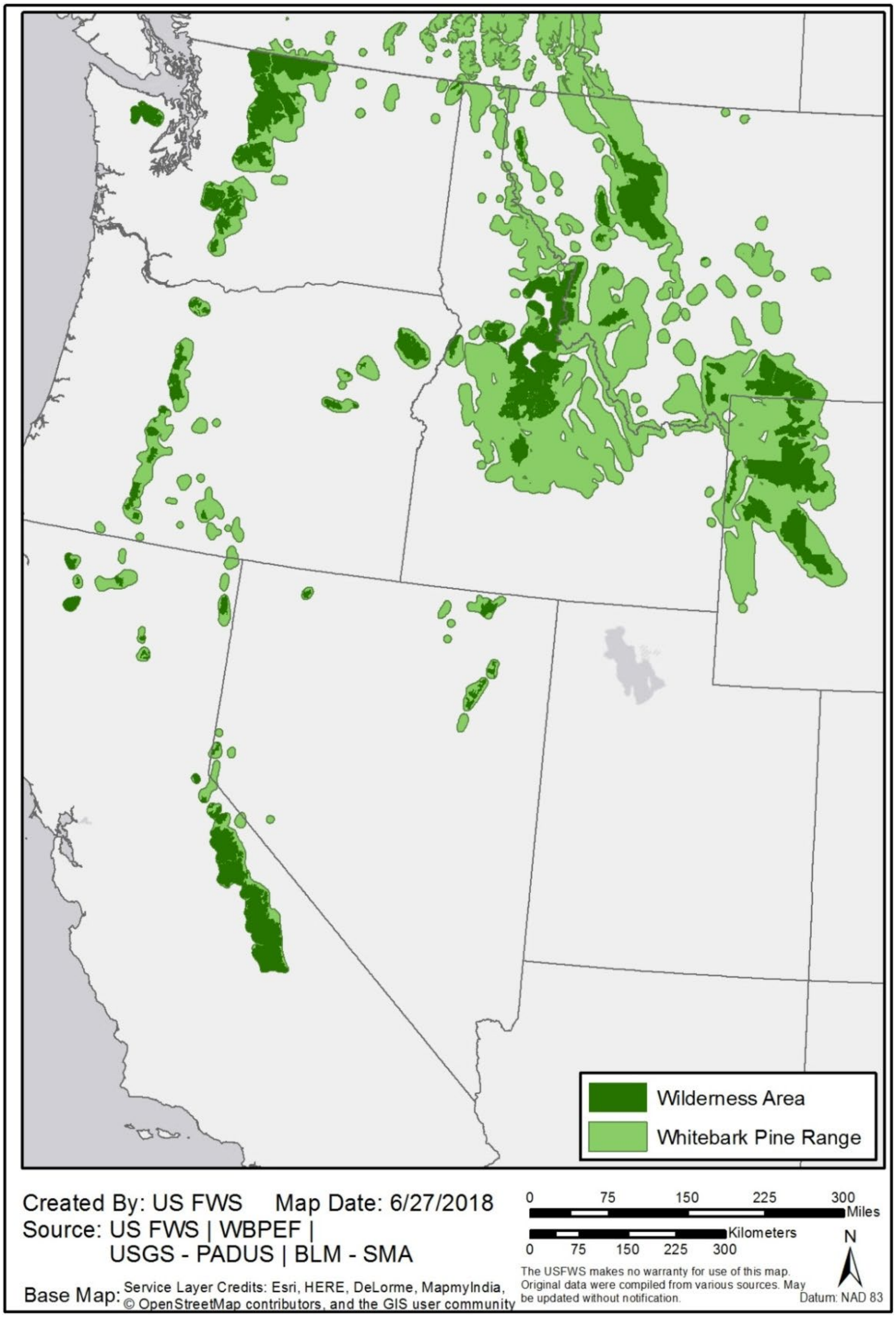

Figure 3 Areas of whitebark pine range designated as wilderness in the U.S.

WHITEBARK PINE TAXONOMY

Whitebark pine (*Pinus albicaulis* Engelm) is a five-needle conifer species placed in the genus *Pinus*, subgenus *Strobus,* which also includes other five-needle white pines (Tomback and Achuff 2010, p. 188). This subgenus *Strobus* is further divided into two sections (*Strobus* and *Parrya*), and under section *Strobus,* into two subsections (*Cembrae* and *Strobi*). The traditional taxonomic classifications place whitebark pine in the subsection *Cembrae* with four other Eurasian stone pines (Critchfield and Little 1966, p. 5; Lanner 1990, p. 19). No taxonomic subspecies or varieties of whitebark pine are recognized (COSEWIC 2010, p. 6). Based on this taxonomic classification information, we recognize whitebark pine as a valid species.

WHITEBARK PINE LIFE HISTORY AND SPECIES DESCRIPTION

There are four stages in the life cycle of the whitebark pine: seed, seedling, sapling, and mature trees (i.e., reproductive adults) (see Figure 4). Seeds are produced in female cones and once on the ground may take two years or more (up to 11 years) to germinate. Germinated seeds become seedlings that are between 8 and 10 centimeters (cm) (3 to 4 inches (in)) tall with a 13 to18 cm (5 to 7 in.) taproot with 7 to 9 cotyledons (embryonic first leaves) (Arno and Hoff 1990, p. 272). Whitebark pine seedlings may persist for multiple years, depending on growing conditions, until reaching the sapling stage of the life cycle. Whitebark pine saplings persist for few to many years, depending on growing conditions, until they produce male and female cones. Mature reproductive whitebark pines contain both female and male cones (i.e., monoecious reproduction), and can survive on the landscape for hundreds of years.

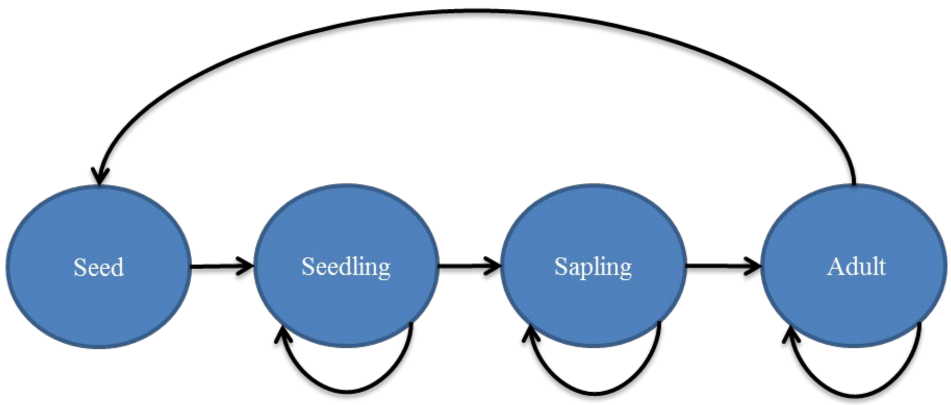

Figure 4 Whitebark pine life cycle

Whitebark pine is the only stone pine (so-called for their stone-like seeds) in North America of the five species worldwide (McCaughey and Schmidt 2001, p. 30). Characteristics of stone pines include five needles per cluster, indehiscent seed cones (scales remain essentially closed at maturity) that stay on the tree, and wingless seeds that are held in place by the cone's scales and not dislodged by the wind. Because whitebark pine seeds are not wind disseminated, primary seed dispersal occurs almost exclusively by Clark's nutcrackers (*Nucifraga columbiana*) in the avian family Corvidae (whose members include ravens, crows, and jays) (Lanner 1996, p. 7; Schwandt 2006, p. 2). Consequently, Clark's nutcrackers facilitate whitebark pine regeneration and influence its distribution and population structure through their seed caching activities (Tomback *et al.* 1990, p. 118).

Whitebark pine may occur as a climax species, or an early to seral mid-successional stage codominant associated with other tree species. Although it occasionally occurs in pure or nearly pure stands at high elevations, it more typically occurs in stands of mixed species in a variety of forest community types. Whitebark pine is typically 5 to 20 m (16 to 66 ft) tall with a rounded or irregularly spreading crown shape. On higher density conifer sites, whitebark pine tends to grow as tall, single-stemmed trees, whereas on open, more exposed sites, it tends to have multiple stems (McCaughey and Tomback 2001, pp. 113–114). Above tree line, it grows in a krummholz form (stunted, shrub-like growth) (Arno and Hoff 1989, p. 6). Production of male and female cones in mature trees will begin sometime from June to September depending on environment

(McCaughey and Tomback 2001, p. 106; Sala *et al.* 2012, p. 190). Female cones take 2 years to fully develop (Weaver 2001, p. 64). Its characteristic dark brown to purple seed cones are 5 to 8 cm (2 to 3 in.) long and grow in clusters of 2 to 4 cones at the outer ends of upper branches (Hosie 1969, p. 42).

Whitebark pine is considered a keystone and foundation species in western North America where it increases biodiversity and contributes to critical ecosystem functions (Tomback *et al.* 2001a, pp. 7– 8; Tomback and Achuff 2010, p. 205; Tomback *et al*. 2011). As a pioneer or early successional species, it may be the first conifer to become established after disturbance, subsequently stabilizing soils and regulating runoff (Tomback *et al.* 2001a, pp. 10–11). At higher elevations, snow drifts around whitebark pine trees, thereby increasing soil moisture, modifying soil temperatures, and holding soil moisture later into the season (Farnes 1990, p. 303). These higher elevation trees also shade, protect, and slow the progression of snowmelt, essentially reducing spring flooding at lower elevations. Whitebark pine also provides nutritious seeds for a number of birds and mammals (Tomback *et al.* 2001a, pp. 8, 10).

INDIVIDUAL-LEVEL ECOLOGY

In general, whitebark pine has similar requirements to other tree species. That is, all four life stages require adequate amounts of sunlight, water, and soil for survival and reproduction (mature trees only). Whitebark pine is a hardy conifer that tolerates poor soils, steep slopes, and windy exposures and is found at alpine tree line and subalpine elevations throughout its range (Tomback *et al*. 2001a, pp. 6, 27). Whitebark pine is slow-growing and shows an intermediate level of shade tolerance and can be outcompeted and replaced by more shade-tolerant trees in the absence of disturbances like fire (Arno and Hoff 1989, p. 6). The amount of sunlight exposure to a given individual can be determined by its location on a slope (Agee 1993), being located in an opening created by fire, clear-cut (Arno 2001, p. 84; Arno and Hoff 1989, p. 4), or avalanche (Environment Canada 2010, p. 70), or whether it is being shaded through competition with other species (Environment Canada, 2010 p. 70, Tomback *et al*. 2016, p.2). Whitebark pine grows under a wide range of annual precipitation amounts, from about 51 to over 254 cm (20 to 100 in.)

per year and is considered relatively drought tolerant (Arno and Hoff 1989, p. 7; Farnes 1990, p. 303). Whitebark pine likely needs two or more consecutive years of adequate and consistent soil moisture to allow for sustained growth of reproductive individuals and resulting nut production (Farnes *et al*. 1990, p. 303). Precipitation and winter temperatures affect phenotypic variation within the species (Aitken *et al*. 2008, p. 103), and the species has adapted to closing stomata (leaf pores used in gas exchange) during periods of drought (Keane *et al*. 2017b, p. 31). There are a variety of soil types that support whitebark pine (Arno and Hoff 1989, p. 2; Weaver 2001, pp 47–48; Keane *et al*. 2012, p. 3). These soil types are generally described as well-drained soils that are poorly developed, coarse, rocky, and shallow over bedrock (COSEWIC 2010, p. 10). Additionally, soils that support whitebark pine contain nitrogen-fixing microbes that are restricted by low soil temperatures and high acidity (Arno and Hoff 1989, p.2). Essential biotic soil factors include a variety of ectomycorrhizal fungi that whitebark pine, like other pines, requires for survival, growth, and reproduction (Mohatt *et al*. 2008, p. 15). While many thousands of these fungi have been described in association with other trees and woody shrubs, only between 32 and 50 species of ectomycorrhizae have been described in association with whitebark pine (COSEWIC 2010, p. 17; Cripps and Antibus 2011, p. 40; Mohatt *et al*. 2008, p. 14).

Regarding the portions of the whitebark pine's life cycle, each stage has specific resource and/or circumstances required for an individual to complete that life stage. Table 1 provides a summary of each of these resources and/or circumstances that are required for each life stage.

Table 1 The ecological requisites for survival by life stage. As mentioned above all life stages require adequate amount of sunlight, water, soil, and ectomycorrhizal fungi for survival, and in the case of mature trees, for reproduction.

Life stage	Specific resource and/or circumstances needed for individual to complete life stage	Resource function
Seed	Clark's nutcracker caching behavior in suitable habitat	Dispersal
	Lack of seed predators	Habitat
	Cold stratification and scarification to initiate germination	Habitat
	Ground fires or other disturbance (e.g., avalanches) to reduce surface fuel load and competition	Habitat & Nutrition
Seedling	Open space on forest floor and low to moderate shading	Habitat
Sapling	Open space on forest floor and low to moderate shading	Habitat
Mature Tree	Dispersal of seeds by Clark's nutcracker	Reproduction & Dispersal
	Two summers of suitable temperatures and precipitation for pollinated cones to mature	Reproduction
	Nitrogen and phosphorus adequate to restore values after being depleted in masting year	Nutrition
	Open forest canopy, low to moderate shading	Habitat

Seed life stage:

Seeds of whitebark pine are typically cached by seed predators such as the Clark's nutcracker. Seeds not retrieved by Clark's nutcrackers or other seed predators are subsequently available for germination (McCaughey and Tomback 2001, p. 111). Delayed seed germination results in the formation of a seed bank in the soil where seeds can remain dormant for several years presumably until conditions favorable to germination arise (Tomback *et al*. 2001b, pp. 2596–2597). In years with low seed production, most seeds are predated and, therefore, unavailable for germination (McKinney and Tomback 2007, p. 1049; Lorenz *et al.* 2008, p. 4). A single nutcracker can cache up to an estimated 98,000 whitebark pine seeds during good seed crop years (Hutchins and Lanner 1982, p. 196). Clark's nutcrackers typically bury seeds within a few kilometers of the parent tree, however travel distances over 30 kilometers (km) (19 miles (mi)) away have been documented (Lorenz *et al* 2011, p. 242). Cache sites have been found to occur on forest floors, tree canopies, above treeline, in rocky outcrops, cliffs, meadow edges, clear-cuts, and burned areas (Tomback *et al.* 1990, p. 120; Lorenz *et al*. 2011, p. 244-245). Although it remains unclear how cache sites are selected, Clark's nutcrackers appear to use a wide range of sites that are not limited to just clearings or burned areas. Whitebark pine seed predators are numerous and include more than 20 species of vertebrates including Clark's nutcrackers, pine squirrels (*Tamiasciurus spp.*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), Steller's jay (*Cyanocitta stelleri*), and pine grosbeak (*Pinicola enucleator*) (Lorenz *et al.* 2008, p. 3). Seed predation plays a major role in whitebark pine population dynamics, as seed predators largely determine the fate of seeds. However, whitebark pine has coevolved with seed predators and has several adaptations, like masting (regional synchrony of mass production of seeds), that has allowed the species to persist despite heavy seed predation (Lorenz *et al.* 2008, pp. 3–4).

Whitebark pine seeds can be classified based on their age and contribution to the seed bank (i.e., first year seed and second year seeds as in Tomback and Pansing 2018, pp. 5−6), assuming that first year seeds have lower germination success than second year seeds. For the purposes of this analysis, we assume that all seeds have the same needs, regardless of their age. Germination success is affected by climate (Keane *et al*. 2017b, p. 55) and seeds require some sort of cold stratification (45 to 60 days) and/or scarification (60 days plus clipping) to germinate (McCaughey and Tomback 2001, p. 112).

Seedling life stage:

The seedling stage of whitebark pine can be described as germinated individuals that are between 8 and 10 cm (3 to 4 in.) tall with a 13 to18 cm (5 to 7 in.) taproot and 7 to 9 cotyledons (embryonic first leaves) (Arno and Hoff 1990, p. 272). First year seedlings are those recently germinated with no mature foliage and have not experienced a winter. Whitebark pine seedlings are generally between 1 and 29 years of age and, on average, are1.37 m (4.5 ft), which is the height assessed at diameter at breast height (dbh)) (Tomback and Pansing 2018, p. 6). Whitebark pine seedlings have highly variable survival rates; seedlings originating from nutcracker caches ranged from 56 percent survival over the first year to 25 percent survival by the fourth year (Tomback 1982, p. 451). First year seedlings are also different than other seedlings because the rate of survival substantially decreases after the first year (Tomback and Pansing 2018, p. 6). However, for the purposes of this analysis, we combine all seedlings because we assume that they share the same individual needs.

Whitebark pine seed germination often occurs in years with higher levels of March-April precipitation, 1 to 3 years after the seeds are cached by Clark's nutcracker (Tomback et al. 2001b, p. 2597). Although germination has been associated with fire disturbance, germination may occur in undisturbed sites (Moody 2006, p. 39) and in areas that experience mountain pine beetle mortality (Larson and Kipfmueller 2010, p. 482). Higher whitebark pine seedling density has been correlated with higher densities of nearby mature healthy whitebark pine, the presence of intermediate amounts of vegetation cover, and lower solar radiation (Leirfallom *et al.* 2015, p. 1603). Although whitebark pine seedling density has been correlated with wetter warmer sites, sapling density has been found to be greater on colder sites, suggesting that recruitment from seedling to sapling is higher on colder sites (Larson and Kipfmueller 2010, p. 484).

.

Sapling life stage:

Saplings are non-reproductive trees greater than 1.37 m (4.5 ft) in height; for whitebark pine, the average age of reproductive maturity is 29 to 40 years of age (Tomback and Pansing 2018, p. 7).

Whitebark pine saplings compete with a wide assemblage of other tree species within the subalpine forest, though at treeline are mostly affected by climactic conditions. Individuals in this life stage are also frequently shaded by intra- and interspecific competitor tree species. Therefore, in addition to the four general needs for all life stages, the sapling life stage requires open space and low to moderate canopy cover.

Mature tree life stage:

Some whitebark pine individuals are capable of producing limited amounts of seed cones at 20–30 years of age, although large cone crops usually are not produced until 60–80 years (Krugman and Jenkinson 1974, as cited in McCaughey and Tomback 2001, p. 109), with average earliest first cone production at 40 years (Tomback and Pansing 2018, p. 7). Therefore, the generation time of whitebark pine is approximately 40 to 60 years (Tomback and Pansing 2018, p. 7; COSEWIC 2010, p. v). Mature whitebark pine trees require two summers of suitable temperatures and precipitation for fertilized cones to mature (Rapp *et al*. 2013, p. 2). During years with high seed production, typically once every three to five years, hypothetically seed consumers are satiated, resulting in excess seeds that escape predation (Lorenz *et al.* 2008, pp. 3–4). Years with high seed production (mast years) typically occur once every three to five years, however that time interval can vary by geographic location and health condition of the stand (McCaughey and Tomback 2001, p. 110). After such a masting year, each individual whitebark pine is depleted of nitrogen and phosphorus and so those nutrients must be replaced during the three to five years between masting events (Sala *et al*. 2012, p. 195).

While whitebark pine is almost exclusively dependent upon Clark's nutcracker for seed dispersal, the reverse is not true as Clark's nutcracker will forage on seeds from numerous species of trees. The frequency of nutcracker occurrence and probability of seed dispersal from a whitebark pine forest is strongly associated with the number of available cones. The number of cones produced is dependent on stand condition and tree abundance (Barringer et al. 2012, p.7). A threshold of 1,000 cones per ha (2.47 ac) may be needed for a high likelihood of seed dispersal by nutcrackers, and this level of cone production occurs in forests with a live basal area (the total stem cross-sectional area (sq m) per area (hectare) greater than 5 square meters per ha

(McKinney *et al.* 2009, p. 603). For an adult Clark's nutcracker to survive a subalpine winter (accounting for those seeds consumed by rodents and those fed to juvenile nutcrackers), it would need to cache seeds from 767 to 2,130 cones (McKinney *et al.* 2009, p. 605). Clark's nutcrackers are able to assess cone crops, and if there are insufficient seeds to cache, they will emigrate in order to survive (McKinney *et al.* 2009, p. 599). Other seed predators such as Steller's jays, deer mice, and chipmunks provide limited dispersal of whitebark pine seeds (McCaughey and Tomback 2001, p. 111).

Like the other life stages, the mature tree life stage of whitebark pine is moderately shade-tolerant and therefore high-quality habitat is often characterized by a more open canopy (Maloney 2014, p. 268) or lower competition with other overstory trees. Whitebark pine is a slow-growing, long-lived tree with a life span between 500 years and 1,000 years (Arno and Hoff 1989, pp. 5–6; Perkins and Swetnam 1996, p. 2123), provided it is located in an area with lower competition, such as a more open canopy with low litter depth and high rock cover (Maloney 2014, p. 268). Therefore, in addition to the four general needs for all life stages, mature whitebark pine trees require a more open canopy, dispersal of seeds by Clark's nutcracker, two summers of suitable temperatures and precipitation for pollinated cones to mature, and nitrogen and phosphorus adequate to restore values after being depleted in masting year.

POPULATION-LEVEL ECOLOGY

Populations are typically defined by the potential for genetic exchange among their members, to the exclusion of members of other populations (in the absence of immigration or emigration). For whitebark pine, genetic exchange is limited by the dispersal distance of pollen, which is carried by wind, and the seed caching behavior of Clark's nutcracker (Lorenz *et al.* 2011, p. 242; Keane *et al.* 2017b, pp. 39–40). Both pollen dispersal and Clark's nutcracker seed dispersal can occur at a scale of few to many kilometers (e.g., up to 30 km in the case of Clark's nutcracker seed dispersal).

To survive and maintain resiliency, a population's recruitment must equal or exceed its mortality over the long term. Whitebark pine is a long-lived species that exhibits masting, where years of high seed production are synchronized within a population approximately every three to five years (McCaughey and Tomback 2001, p. 110). This masting strategy is an adaption to heavy seed predation; during masting years seed consumers are satiated, resulting in excess seeds that escape predation (Lorenz *et al.* 2008, pp. 3–4). Whitebark pine populations need a certain density of reproductive individuals to produce sufficient pollen clouds that facilitate the synchronization of masting, and thus increased probability of regeneration (Rapp *et al*. 2013, p. 1345). Whitebark pine populations also need a certain density of reproductive individuals to attract Clark's nutcrackers, which are almost exclusively the seed dispersal mechanism for whitebark pines (McKinney *et al.* 2009, p. 603).

In the absence of stressors, each individual tree has many opportunities over its lifespan of potentially 1,000 or more years to reproduce. For this long-lived species, successful regeneration of populations (establishment of new trees to replace mortality) at any given moment, or recruitment of any given cohort of seedlings, appears to be less critical to population resiliency than survival of mature trees capable of producing young. Successful recruitment of young trees becomes increasingly critical as mature trees are eliminated by catastrophic events (such as severe wildfire) or environmental conditions (such as climate change). If all trees in a population manage to replace themselves during their lifetime, on average, the population will persist. Where this average rate is exceeded, the population will grow, but repeated failures of individuals replacing themselves, or catastrophic losses, can lead to population declines or losses.

Our whitebark pine analysis units (as described further below in Chapter 4) include many stands spread across large areas. Many of the stands in these larger analysis units are contiguous or comparatively close together and likely maintain genetic interchange. Other stands, or groups of stands, are more isolated and probably function as independent populations, such as the stands in Nevada.

Stands of whitebark pine that are many kilometers (km) from other stands of the same species likely operate as independent populations, from the perspective of demographics and genetics. Typically, however, populations consist of many stands spread across a landscape. We are not aware of any effort to formally define discrete whitebark pine populations beyond genetic investigations that have documented high genetic diversity and little geographic structure across the range of the species. Instead, whitebark pine distribution is typically described, and the species is managed, on the basis of jurisdictional boundaries (e.g., National Forests, State and Provincial boundaries, etc.). We lack adequate data on distribution and genetic exchange to precisely map or describe functional populations at a rangewide scale. Instead, for the purposes of analysis, we discuss resiliency of whitebark pine on the basis of “analysis units” (see Chapter 4: Analysis Units).

In summary, whitebark pine populations need sufficient density and abundance of reproductive individuals to facilitate masting and attract Clark’s nutcrackers, to achieve adequate recruitment and maintain resiliency to stochastic events. Since biological populations are challenging to define for this species, we use the concept of analysis units instead.

SPECIES-LEVEL ECOLOGY

In this section, we describe the ecological requirements at the species-level in terms of the 3Rs. These requirements allow the whitebark pine to maintain self-sustaining populations over a biologically meaningful timeframe, i.e., needed for viability. The species' range (Figure 8, map of whole range, broken by ecoregions) spans half a continent and includes 15 analysis units (as described in Chapter 4), each composed of many populations. The species-level ecological requirements are discussed below and summarized in Table 2.

Resiliency

Resiliency is the ability of a species to respond to and recover from disturbances and perturbations. Disturbances include stochastic events such as fires and avalanches; perturbations include normal year-to-year variation in temperature and precipitation. To have high resiliency, a species must have healthy populations capable of sustaining themselves through good and bad years. As discussed in Population-Level Ecology above, resiliency is positively related to population size and growth rate and may be influenced by connectivity among populations. For the whitebark pine, it needs to have multiple, highly resilient populations within each analysis unit that are capable of withstanding stochastic events.

Redundancy

Redundancy, or the ability of a species to withstand catastrophic events, is measured by the number and resilience of populations, their distribution, and their connectivity. These factors spread the risk to the species as a whole. Having many highly resilient populations that are distributed spatially yet connected genetically helps to preserve the breadth of adaptive diversity of the species.

Representation

Representation, or the ability of a species to adapt to long-term changes in the environment, is measured by environmental or ecological variation and genetic variation. It is the evolutionary potential of a species. To have high representation, populations of a species must have high diversity in terms of geographic location, ecological settings, genetic identity, and/or niche fulfillment as well as morphological and genetic variation.

Summary

At the species-level, for long-term viability, whitebark pine requires multiple (redundancy), self-sustaining populations (resiliency) distributed across the landscape (representation) to maintain the ecological and genetic diversity of the species. Understanding the 3Rs at the species level will help to apply what is known about the current condition of the species and make predictions about what the future condition will be.

Table 2 Summary of species-level needs for the viability of whitebark pine.

3Rs	Need	Function of Need
Resiliency	Large enough populations to cross-pollinate and have masting events	Maintain genetic variability and allow for regeneration of populations, respond to and recover from disturbances and perturbations
Redundancy	Connectivity among populations	Pollen and seed movement are dispersal mechanisms that aid in genetic diversity
	Multiple, connected, resilient populations across the species' range	Improves viability of the species by spreading risk associated with catastrophic events
Representation	Maintain ecological diversity in terms of elevation, latitude, and climate	Preserves diversity and provides for adaptability in the face of changing environments
	Maintain genetic diversity within populations	
	Maintain morphological diversity	
	Maintain phenological diversity	

CHAPTER 3: FACTORS AFFECTING WHITEBARK PINE

We have focused our analysis of whitebark pine viability on four main stressors: altered fire regimes, white pine blister rust (a disease caused by an introduced fungus), mountain pine beetle, and climate change. We chose to focus on these four stressors for our analysis because, according to the best available data, these stressors are the leading factors attributed to the decline of whitebark pine (Keane and Arno 1993, p. 44; Tomback *et al*. 2001a, p. 13; COSEWIC 2010, p. 24; Tomback and Achuff 2010, p. 186; Keane *et al*. 2012, p. 1; Mahalovich 2013, p. 2; Mahalovich and Stritch, 2013, entire; Smith *et al*. 2013, p. 90; GYWPMWG 2016, p. v; Jules *et al*. 2016, p. 144; Perkins *et al*. 2016, p. xi; Shanahan *et al*. 2016, p. 1; Shepherd *et al*. 2018, p. 138). We acknowledge that our risk factor analysis is not a thorough evaluation of all stressors affecting the species and its habitat; there are numerous other mortality factors that operate on whitebark pine at more local scales (see Appendix B), affecting individuals or local areas; however, these factors are likely not driving population dynamics of whitebark pine on a rangewide scale, or at the species level. Below we describe each of these four main stressors listed above and our rationale and available evidence of how they may be affecting whitebark pine.

ALTERED FIRE REGIMES

Fire is one of the most important landscape-level disturbance processes within many forested systems (Agee 1993, p. 259; Morgan and Murray 2001, p. 289; Spurr and Barnes 1980, p. 422), and is relevant to whitebark pine both as a stressor that causes mortality of seedlings and adult trees and as a mechanism that may affect forest succession (Arno 2001, p. 82; Shoal *et al.* 2008, p. 20; Keane and Parsons 2010, p. 57). Although whitebark pine is fire-adapted, there is uncertainty surrounding the specifics of these adaptations, including the species' susceptibility to damage from fires of differing intensity, the role of low-severity fire, and how fire suppression interacts with fire return intervals to affect forest succession across the range of whitebark pine.

When considering the role of fire in whitebark pine ecosystems, it is critical to consider the potential effects that differing fire intensities have on fire severity and, consequentially, how differing severities may affect the species. Fire intensity is a term that describes the energy released from the combustion of organic matter; fire severity describes the effects that the fire's intensity has on the ecosystem (Keeley 2009, p. 117-118). Fire resistance is the ability of mature trees to withstand surface fire, and different tree species have different functional traits that affect their ability to resist surface fires of differing intensities (Stevens *et al.* 2020, p. 945). Higher intensity fires often result in higher severity fire effects, and lower intensity fires often result in lower severity fire effects, but the latter is not necessarily always the case. In systems where the vegetation is not well-adapted to resist and survive lower intensity fire, such fires can result in more severe fire effects.

Forest systems where most trees survive fires are termed "low-severity" fire regimes, whereas systems dominated by fire effects where most trees are killed by fires are termed "high-severity" fire regimes. High-severity fires, sometimes referred to as stand replacement fires or crown fires (Agee 1993, p. 16), are typically high intensity and restart the process of forest succession. Complex, fine-scaled interactions between slope, aspect, and elevation that result in fine-grained mosaics of low- and high-severity fire effects are termed mixed-severity fires (Fulé et *al*. 2003, p. 466). Although mixed-severity fire is somewhat difficult to define, a relative constant in mixed-severity fire regimes is the spatial patterning and presence of many small patches of high-severity fire effects, with few large patches of high-severity fire effects (Perry *et al*. 2011, p. 715).

At larger spatial scales, landform, climate, and vegetation are the primary drivers of fire regimes; at the stand-scale, fire intensity is driven by terrain, weather, and fuel (Cochrane and Ryan 2009, p. 26). Fires burning in areas with little topography, under cooler and wetter conditions, and with lower fuel loads often result in smaller and lower intensity fires while fires burning on steep slopes, under warmer and drier conditions, and with higher fuel loads tend to result in larger and higher intensity fires, although the relationship is complex. Higher-intensity forest fires are generally less frequent, because it takes longer time intervals to build the large fuel accumulations necessary to promote these types of fires (Agee 1993, p. 258).

Fire regimes in whitebark pine systems are often characterized as being of mixed severity (Arno *et al*. 2000, p. 226; Arno 2001, p. 83, Campbell and Antos 2003, p. 393; Larson *et al*. 2009, p. 283). However, some whitebark pine systems are dominated by high-severity fire effects (Romme 1982, p. 208, Campbell and Antos 2003, p. 393). Low-severity surface fires may also occur in whitebark pine stands, particularly at higher elevations (Barrett 1994, p. 73). Clark's nutcracker ecology provides further insight into the typical fire regime in whitebark pine ecosystems. The Clark's nutcracker serves as the main dispersal agent for whitebark pine, caching seeds in open, disturbed sites, such as areas that recently experienced high-severity fire. Wildfire can expose mineral soils and reduce forest canopy closure, providing optimal growing conditions for whitebark pine seedlings (Tomback *et al*. 2001a, p. 13). Clark's nutcrackers have been found dispersing seeds farther than the wind-dispersed seeds of other conifers, allowing for the establishment of whitebark pine seedlings in the interior of large patches of high severity fire effects and over broad geographic areas (McCaughey *et al*. 1985, Tomback *et al*. 1990, 1993 in Keane and Parsons 2010, p. 58). Whitebark pine's mutualistic relationship with Clark's nutcracker seems to demonstrate the tree's adaptation to high- and mixed-severity fire regimes.

In addition to this evidence supporting the importance of and adaptation to high- and mixed-severity fire, some experts also conclude that low-intensity surface fires that result in low-severity fire effects are an important ecosystem process in some whitebark pine systems, since low-severity fire can remove small-diameter trees, reduce fuel loads, and allow mature whitebark pine trees to maintain site dominance or co-dominance (Arno 2001, p. 82; Keane and Parsons 2010, p. 57; Flanagan *et al.* 1998, p. 307). However, whitebark pine's ability to resist and survive low-intensity fire is still somewhat uncertain. Some experts have hypothesized that whitebark pine exhibits phenotypic characteristics (i.e., thicker bark, thinner crown, and a deeper root system) that incur resistance to low-intensity fires better than many of its competitors (Arno and Hoff 1990 in Keane and Parsons 2010, p. 58). The proportion of whitebark pine systems where low-severity fire effects from low-intensity fires are common remains unknown, as we are not aware of any studies quantifying the proportion of the range where fire-scarred whitebark pine is a common stand component.

Although some experts have suggested that whitebark pine is phenotypically adapted to survive low-intensity fire, Stevens *et al.* (2020, p. 948) found that whitebark pine had relatively thin bark compared to other conifer species and, based on a systematic ranking of numerous traits associated with fire resistance in western conifers, whitebark pine was found to have one of the lowest fire resistance scores of the 29 conifers examined in the study. Others have also observed that whitebark pine trees can be sensitive to bole (main steam of the tree) scorching, resulting in cambium injury or death, even from low-intensity fire (Hood *et al*. 2008, p. 66). Keane *et al.* (2020, p. 7) noted several recent reports of prescribed fire and low-intensity fire killing whitebark pine trees, despite pre-fire site preparation activities implemented to reduce or modify surface and ladder fuels and protect the residual whitebark pine trees. Keane and Parsons (2010, p. 63) studied the effects of seven different fuel treatment combinations on whitebark pine at five treatment sites in Montana and Idaho and found that whitebark pine mortality from low-intensity fire was comparable to subalpine fir under all treatment combinations. As a result, empirical evidence shows that low-intensity fire in whitebark pine can result in higher-severity fire effects. In summary, although it is clear that whitebark pine individuals are capable of surviving some low-intensity fire, based on the presence of multiple fire scars in some areas, the biotic and abiotic (i.e., terrain, weather, and fuel) conditions under which the species is most likely to survive such fires remain largely unknown.

Determining if periodic fire is necessary to maintain ecosystem integrity in whitebark pine systems may be as important as understanding the conditions under which whitebark pine trees are most likely to survive fire. Experts have suggested that, without periodic low-severity fire in some subalpine forests where whitebark pine co-occurs with subalpine fir and Engelmann spruce, successional pathways can lead to climax communities dominated by these shade-tolerant conifers and the loss of whitebark pine (Arno 1980, p. 460; Arno 2001, p. 82; Keane *et al*. 2017a, p. 3; Keane and Parsons 2010, p. 57; Flanagan *et al*. 1998, p. 307). It has further been suggested that, in these whitebark pine systems, fire suppression policies over the past 90 years have resulted in whitebark pine declines due to succession to subalpine fir and Engelmann spruce (Arno 1980, p. 460; Arno 2001, p. 82; Keane *et al*. 2017a, p. 3; Keane and Parsons 2010, p. 57; Flanagan *et al*. 1998, p. 307). This is supported by the presence of multiple fire scars in whitebark pine trees at some locations, which shows they are capable of surviving repeated low-intensity fires and maintaining dominance or co-dominance in stands for long-periods of time when these fires are occurring periodically (Morgan and Bunting 1990, p.167, Barrett 1994, p. 73). Additional support for the successional theory is based on documented densification of subalpine fir and Engelmann spruce in stands where whitebark pine was once prevalent (Hartwell *et al*. 1997, p. 15; Arno *et al*. 1993 in Keane *et al*. 1994, p. 225; Flanagan *et al*. 1998, p. 307). However, in these studies, the authors noted that the densification of and succession to subalpine fir and Engelmann spruce co-occurred with whitebark pine mortality caused by bark beetle outbreaks and/or blister rust; therefore, disentangling the effects of blister rust- and bark beetle-mortality on succession from the effects of fire suppression in these studies is difficult.

The idea that fire suppression in some whitebark systems has resulted in tree densification and loss of whitebark pine has been a predominant hypothesis in the whitebark pine literature (Arno 1980, p. 460; Arno 2001, p. 82; Keane *et al*. 2017a, p. 3; Keane and Parsons 2010, p. 57; Flanagan *et al*. 1998, p. 307). However, other recent research has challenged these assumptions. For example, Larson and Kipfmueller (2012, p. 204) suggested there is uncertainty in the effects of fire suppression on whitebark pine and a relative lack of data supporting the hypothesis. Larson and Kipfmueller (2012, p. 204) noted that age structure data in their study showed that many of the small subalpine fir trees occurring below the whitebark pine, trees that visually appeared to be young saplings, were more than 100 years of age, suggesting that size class data should not be used as a surrogate for tree age or to determine the rate of succession. Campbell and Antos (2003, p. 395) also noted that successional patterns in whitebark pine forests are more complex than others have reported, finding that subalpine fir readily established after fire in their British Columbia study areas, and although subalpine fir density was increasing in older whitebark pine stands with relatively open canopies, they estimated that succession to subalpine fir would take more than 500 years. Campbell and Antos (2003, p. 395) reported that whitebark pine in their study area was stress-tolerant (able to persist under conditions that restrict production), was capable of surviving long periods of suppressed growth, and was able to release upon reaching the main canopy after more than 150 years of low growth rates. The results of these studies indicate that the loss of whitebark pine due to succession to subalpine fir and Engelmann spruce in some areas may be an extremely slow process and that whitebark pine may be more shade-tolerant and resilient to suppression than previously suggested.

The broad range of fire return intervals in whitebark pine ecosystems further complicates theories that fire suppression has caused succession in whitebark pine systems. Fire history studies in whitebark pine forests have identified fire return intervals ranging from 33 years (Morgan and Bunting 1990, p. 167) to greater than 400 years (Campbell and Antos 2003, p. 393). Several authors have noted that mean fire return intervals in subalpine forests that include whitebark pine can be much longer than contemporary fire suppression policies (Dolanc *et al*. 2013, p. 270; Meyer and North 2019, p. 73; Sibold *et al*. 2006, p. 631). Over an 80-year period, Dolanc *et al.* (2013, p. 270) documented an increase in the number of small diameter trees, including whitebark pine, in subalpine forests of the central Sierra Nevada. However, Dolanc *et al*. (2013, p. 272) attributed the densification of small trees in their study areas to climate warming, which they suggested may be moderating extreme temperatures and reducing snowpack, thereby providing better growing conditions for small trees. Dolanc *et al*. (2013, p. 271) did not attribute the observed densification of small trees to fire suppression, because fire suppression policies have only been in effect for 75 to 100 years, which was a relatively short period of time compared to the fire return intervals of subalpine forests in their study areas (Dolanc *et al.* 2013, p. 270). Moreover, despite the presence of late successional species in the whitebark pine stands, Larson *et al.* (2009, p. 294) found that the time since the last widespread fire and stand age structure in two of the three whitebark pine stands in their study area were within the historical fire return interval for the sites. Thus, although fire suppression undoubtedly impacts whitebark pine stands, it is unclear under what conditions fire suppression begins to negatively affect whitebark pine populations and the rate at which succession occurs in those populations.

Despite adaptations that allow whitebark pine to recolonize areas that experience high-severity fire effects, the ability of whitebark pine to regenerate and reestablish following high-severity fire has been disrupted by white pine blister rust in many areas. This novel stressor makes the species more vulnerable to the impacts of fire (see Chapter 4: Analysis of Current Conditions). Blister rust has killed many mature whitebark pine trees, effectively reducing or eliminating whitebark pine seed sources. The presence of blister rust also reduces whitebark pine seedling survival, which significantly reduces the species' ability to regenerate in fire-created openings that are typically ideal for seedling establishment.

In general, wildfire characteristics are expected to shift with future climate changes. Substantial increases in fire season length, number of fires, area burned, and intensity are predicted (reviews in Keane *et al*. 2017b, pp. 34–35, and Westerling 2016, pp. 1–2). In contrast, some models, like Keyser and Westerling (2017), predict a static or lessened degree of high severity fire, due in part to biota adaptations to the changes in fire behavior and an eventual reduction in fuels and fire breaks created from an initial spate of high-severity fires (Keyser and Westerling 2017, p. 4; Parks *et a*l. 2016 p. 5). However, these models assume the vegetation will exhibit concomitant changes in composition and fuel loading with the trajectory of climate change. Changes in vegetation composition, including the ability of whitebark pine to colonize new locations, are limited by long-lived, slow-evolving organisms (such as whitebark pine) and simultaneously occurring human impacts on ecosystem processes (Parks *et al*. 2016 p. 5). In addition, the projections of Keyser and Westerling (2017, p. 6) are based on a limited record of fire severity data, leading to less confidence in the projections that suggest a constant rate of high-severity fire in the future.

In summary, wildfire has been an important ecosystem process in maintaining whitebark pine on the landscape throughout the species' evolutionary history. Whitebark pine is well-adapted to mixed- and high-severity fire effects. In many areas, mixed- and high-severity fire have historically been conducive to the maintenance of whitebark pine ecosystems at the landscape scale. However, the broader role that low-severity fire plays across the range of the species remains uncertain. Many experts have suggested that low-severity fire is a necessary ecosystem process in areas where succession is occurring because of fire suppression, while others have found that whitebark pine may be less susceptible to succession than conventionally thought. In addition, whitebark pine may be less resistant to low-intensity fire than previously thought. Regardless, the loss of whitebark pine to low-intensity fire would primarily affect individuals at the stand scale and be unlikely to affect the species' broader distribution and viability. Mixed- and high-severity fires create open areas that whitebark pine may colonize via seed dispersal facilitated by Clark's nutcracker, though this colonization depends on the availability of nearby seed sources. However, these historical dynamics with fire have likely been altered due to the compounding effects of white pine blister rust and mountain pine beetles. Also, in general, wildfire characteristics are expected to shift with future climate changes. Substantial increases in fire season length, number of fires, area burned, and intensity are predicted (reviews in Keane et al. 2017b, pp. 34–35, and Westerling 2016, pp. 1–2). Thus, although there is variation in the degree to which specific stands have been affected, over the range of whitebark pine, the widespread incidence of poor stand health and reduced reproductive capacity from disease and predation, coupled with changes in fire regimes due to climate change, has compromised and will continue to compromise regeneration of whitebark pine in many cases (Tomback et al. 2008, p. 20; Leirfallom et al. 2015, p. 1601). These factors increase the likelihood of negative effects to whitebark pine populations from fire, especially from high-severity fires that can cause widespread tree mortality.

WHITE PINE BLISTER RUST

White pine blister rust is a fungal disease of five-needle pines caused by a nonnative pathogen, *Cronartium ribicola* (Geils *et al*. 2010, p. 153). The fungus was inadvertently introduced at a single point in western North America around 1910 near Vancouver, British Columbia from eastern white pine nursery stock imported from Europe (McDonald and Hoff 2001, p. 198; Brar *et al*. 2015, p. 10). White pine blister rust initially spread rapidly through coastal and montane environments, which have environmental conditions more conducive to spread of infection, reaching western white pines in Idaho by 1923, northwestern Montana by 1927, and southern Oregon by 1929 (McDonald and Hoff 2001, p.199). Over the last several decades, it has also spread through continental and treeline environments throughout western North America and to the northern edge of whitebark pine (Geils *et al.* 2010, p. 163; Tomback *et al*. 2016, p.11). It was first observed in whitebark pine in the Coast Mountains of British Columbia in 1926, and by 1936 it was observed in whitebark pine on Mt. Hood, Oregon, which was the first documented case in whitebark pine in the United States (Childs *et al*. 1938, p. 139; Mielke 1943, p. 103). It was soon thereafter documented at additional sites in Washington and Idaho (Childs *et al*. 1938, p. 139). White pine blister rust's rate and intensity of spread is influenced by microclimate and other factors (described below). Therefore, the incidence of white pine blister rust at stand, landscape, and regional scales varies due to time since introduction and presence of suitable primary and alternate hosts for its development. It continues to spread into areas originally considered less suitable for infection, such as the Sierra Nevada Mountains, and it has become a serious threat, causing severe population losses to several species of western pines, including whitebark pine, *P. monticola* (western white pine), and *P. lambertiana* Dougl. (sugar pine) (Schwandt *et al*. 2010, pp. 226–230). Its current known geographic distribution in western North America includes all U.S. States and British Columbia and Alberta, Canada (See Table 6, Figure 10). The highest incidence of white pine blister rust infection is in the northern U.S. and southern Canadian Rocky Mountains.

The white pine blister rust fungus has a complex life cycle: It does not spread directly from one tree to another, but alternates between primary hosts (i.e., five-needle pines) and alternate hosts. Alternate hosts in western North America are typically woody shrubs in the genus *Ribes* (gooseberries and currants) but also may include herbaceous species of the genus *Pedicularis* (lousewort) and the genus *Castilleja* (paintbrush) (McDonald and Hoff 2001, p. 193; McDonald *et al.* 2006, p. 73).

Ribes is widespread in North America and, while most species are susceptible to white pine blister rust infection, they vary in their susceptibility and capability to support inoculum (spores) that are infective to white pines, depending on factors such as habitat, topographic location, timing, and environment (Zambino 2010, pp. 265–268). A widescale Federal program to eradicate *Ribes* from the landscape was conducted from the 1920s to the 1960s. However, due to the abundance of *Ribes* shrubs, longevity of *Ribes* seed in the soil, and other factors, white pine blister rust continued to spread, and pathologists realized that eradication of *Ribes* was ineffective in controlling white pine blister rust. White pine blister rust is now pervasive in high-elevation five-needle pines within most of the western United States (McDonald and Hoff 2001, p. 201).

White pine blister rust progresses through five spore stages to complete each generation: two spore stages occur on five-needled pines (*Pinus* spp.), and three stages occur on an alternate host (Figure 5). The five fungal spore stages require specific temperature and moisture conditions for production, germination, and dissemination. The spreading of spores depends on the distribution of hosts, the microclimate, and the different genotypes of white pine blister rust and hosts (McDonald and Hoff 2001, pp. 193, 202). Local meteorological conditions also may be important factors in infection success, infection periodicity, and disease intensity (Jacobi *et al.* 2010, p. 41).

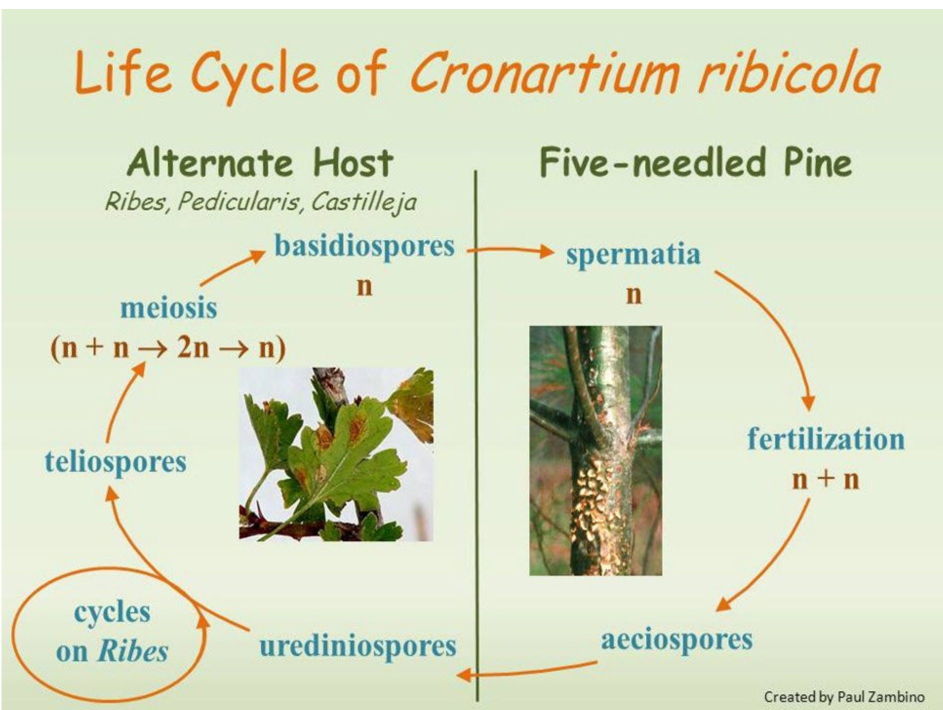

Figure 5 Life cycle of white pine blister rust

White pine blister rust spores enter through openings in the needle surface, or stomates, and move into the twigs, branches, and tree bole (main stem of the tree), causing swelling and cankers to form. White pine blister rust attacks whitebark pine seedlings, saplings, and mature trees, damaging stems and cone-bearing branches and restricting nutrient flows; it eventually girdles branches and boles, leading to the death of branches or the entire tree (Tomback *et al.* 2001a, p. 15, McDonald and Hoff 2001, p. 195). White pine blister rust can kill small trees within 3 years, and even one canker can be lethal (Hoff and Hagle 1990, p. 187). While some infected mature trees can continue to live for decades (Wong and Daniels 2017, p. 1935), their cone-bearing branches typically die first, thereby eliminating the seed source required for reproduction (Geils *et al*. 2010, p. 156). In addition, the inner sapwood moisture decreases, making trees prone to desiccation and secondary attacks by insects (Six and Adams 2007, p. 351). Death to upper branches results in reduced photosynthetic capacity weakening the tree, lower or no cone production, and a reduced likelihood that seeds will be dispersed by Clark's nutcrackers (McKinney and Tomback 2007, p. 1049). Similar to a total loss of cone production, even when cone production is low there could be a loss of regeneration for two reasons: (1) Clark's nutcrackers abandon sites with low seed production or (2) the proportion of seeds taken by predators becomes so high that few seeds remain for regeneration (McKinney and Tomback 2007, pp.1049–1051).

Each year that an infected tree lives, the white pine blister rust fungus infecting it continues to produce spores, thereby perpetuating and intensifying the disease. A wave event, or massive spreading, of new white pine blister rust infections into new areas or intensification from a cumulative buildup in already-infected stands occurs where alternate hosts are abundant and when late summer weather is favorable to spore production and dispersal and subsequent infection of pine needles (McDonald and Hoff 2001, p. 199). Depending on a number of factors, including climate and topography, wave events can be localized, where white pine blister rust is spread and intensified only in the immediate area, or widespread, where white pine blister rust travels to new areas hundreds of miles from the source (Frank *et al.* 2008, p. 664; Mahalovich 2013, p. 6.; Smith-Mckenna *et al.* 2013, p. 225). Spores can be produced on pines for many years, and appropriate conditions need to occur only occasionally for white pine blister rust to spread and intensify (Zambino 2010, p. 265). The frequency of wave years depends on various factors, including elevation, geographical region, topography, wind patterns, temperature, and genetic variation in the rust (Kendall and Keane 2001, pp. 222–223); it appears to occur on a ten-year cycle in the Inland Northwest (Idaho, western Montana, western Wyoming) (Schwandt *et al*. 2013b, p. 3).

Because its abundance is influenced by weather and host populations, white pine blister rust also is affected by climate change. If conditions become moister, white pine blister rust will likely increase; conversely, where conditions become both warmer and drier, it may spread more slowly. Because host infection occurs through the stomates, whatever affects the stomates affects infection rates (Kliejunas *et al.* 2009, pp. 19–20). Stomates close in drought conditions and open more readily in moist conditions. In general, weather conditions favorable to the intensification of white pine blister rust occur more often in climates with coastal influences than in dry continental climates (Kendall and Keane 2001, p. 223). White pine blister rust now infects whitebark pine populations throughout all of its range (See Current conditions: white pine blister rust). The incidence of white pine blister rust is highest in the Rocky Mountains of northwestern Montana and northern Idaho, the Olympic and western Cascade Ranges of the United States, the southern Canadian Rocky Mountains, and British Columbia Coastal Mountains (Schwandt *et al.* 2010, p. 228; Tomback *et al.* 2001a, p. 15).

Genetic Investigations of White Pine Blister Rust Resistance and Virulence

Although some areas of the species' range may have been impacted by white pine blister rust for 90 years or more, for whitebark pine that timeframe equates to only 1.5 generations (Mahalovich 2013, p. 17), which means the species has had a limited time to adapt to or develop resistance to white pine blister rust. However, rust resistance has been documented on the landscape and in seeds, indicating that there is some level of heritable resistance to white pine blister rust (Hoff *et al*. 2001, p. 350; Mahalovich *et al*. 2006, p. 95; Mahalovich 2015). Genetic research and development of white pine blister rust resistance may offer the best long-term prospect for control (Kinloch, Jr. 2003, p. 1045); however, understanding of the dynamics of resistance to white pine blister rust, as well as its virulence and evolution, is incomplete (Schwandt *et al*.

2010, p. 241; Richardson *et al*. 2010, p. 321). A number of whitebark pine rust-resistance trials, in which seedlings are grown under varying conditions from seeds produced from rust-resistant parents, have produced progeny seedlings with a range of resistance levels from 0 percent to 64 percent (Mahalovich 2013, Table 3, p. 33). Testing continues on seedlings and parent trees from throughout the species range, primarily from Idaho, Montana, Nevada, Washington, and Wyoming (Mahalovich 2015; Sniezko 2015). In the northwestern United States, whitebark pine rust-resistance trial results have indicated a trend of increasing resistance levels from southern Oregon north to Mount Rainier in Washington (Sniezko 2011, pers. comm.). Recent provenance trials and progeny tests in Oregon, Washington, and British Columbia have shown the potential to significantly improve understanding of the adaptive capacity of whitebark pine to both white pine blister rust and climate change (Sniezko 2018). In the inland western United States, white pine blister rust resistance levels increase from the southern portion of the Greater Yellowstone Ecosystem northwest to Idaho (Mahalovich 2015). Some of the highest levels of white pine blister rust resistance occur in the Pacific coastal portion of the range and in northwestern Montana (Mahalovich 2013, p. 8; Sniezko and Kegley 2015). In some populations and geographic areas there is moderate frequency and level of resistance, while in others the frequency of resistance appears to be much lower (Sniezko 2018). Active research and management to identify and use genetic resistance to white pine blister rust offers the best potential for successful long-term reforestation or restoration (Sniezko 2014, pers. comm; Kegley *et al*. 2012, p. 315).

The frequencies, levels, and heritability of resistance identified to date are very encouraging. However, trees that are rust resistant today only have known resistance to the current white pine blister rust strain. There is some possibility that hybridization between different white pine blister rust populations could result in genetic variation in virulence, creating a new assortment of genes and behaviors (McDonald and Hoff 2001, p. 210). The potential for development of new white pine blister rust strains between eastern and western North America with greater virulence, fitness, and aggressiveness is currently unknown (Schwandt *et al*. 2010, p. 241), although gene flow appears to be precluded between western and eastern strains, due to the absence of white pine hosts in the central North American prairies (Brar *et al*. 2015, p. 8, 11).

While western North American populations of white pine blister rust have low genetic diversity and differentiation overall (Richardson *et al*. 2010, p. 316; Brar *et al*. 2015, p. 6), rust genotypes with specific virulence to major resistance genes currently exist in local populations of several other species of white pines at high frequencies (Kinloch, Jr. 2003, p. 1044). The introduction of new strains of white pine blister rust, and reintroduction of strains that have since mutated, from goods imported from abroad also poses a serious danger to genetic selection and breeding programs. In Asia, white pine blister rust exists with different alternate host affinities and also may contain additional genes with wider virulence (Kinloch, Jr. 2003, pp. 1044, 1046).

Management and Restoration Efforts

Most current management and research focuses on producing and planting white pines (including whitebark) with genetic resistance to white pine blister rust, but also includes natural regeneration and silvicultural treatments, such as appropriate site selection and preparation, pruning, and thinning (Zeglen *et al.* 2010, p. 347). Genetic management of white pine blister rust is actively conducted for several five-needle white pine species breeding programs (Sniezko 2016, Mahalovich 2015, Mahalovich 2010, Shelly 2016) including the USFS resistance screening programs for whitebark pine. High-elevation pines such as whitebark pine also present management challenges to restoration due to remoteness, difficulty of access, a perception that some whitebark pine restoration activities conflict with wilderness values, and variable implementations of wilderness management within and amongst Federal land management agencies (management considerations regarding wilderness are discussed in more detail under Appendix A) (Schwandt *et al.* 2010, p. 242). Furthermore, the vast scale at which planting rust-resistant trees would need to occur, long timeframes in which restoration efficacy could be assessed, and limited funding and resources, will make it challenging to restore whitebark pine throughout its range. Although current planting efforts may be sufficient to restore whitebark pine at some local levels, the current rates appear to be insufficient to restore whitebark pine on a scale large enough to ensure its continued viability.

Model Predictions

Several models have been developed to predict residence times of white pine blister rust infection and long-term persistence of whitebark pine. Ettl and Cottone (2004, pp. 36–47) developed a spatial stage-based model to examine whitebark pine persistence in the presence of heavy white pine blister rust infections in Mt. Rainier National Park. They predicted that the median time to quasi extinction (population of less than 100 individuals) would be 148 years, which represents approximately two to three generations of whitebark pine. A recent modeling effort by Hatala *et al*. (2011) is the first known study of the rate of white pine blister rust progression and residence time in whitebark pine. Their analysis compares four possible white pine blister rust dynamic infection models in whitebark pine at the ecosystem scale (Greater Yellowstone Ecosystem) and predicts that on average, whitebark pine trees live with white pine blister rust infection for approximately 20 years before succumbing to the disease. Their model also predicted that, within all their study sites, an average of 90 percent of the trees would be infected with white pine blister rust by the year 2013, while two other models calculated a 90 percent infection level within sites by the years 2026 and 2033. These results predict white pine blister rust will continue to spread within whitebark pine, and within 10-20 years almost all whitebark pine trees will be impacted. Notably, model results from Field *et al*. (2012, p. 180) show it is possible for high-elevation white pine populations to tolerate moderate levels of white pine blister rust infection as long as seedling recruitment is maintained and stands are not simultaneously suppressed by other competing tree species or mortality (i.e., mountain pine beetle). Based on these modeling results, we conclude that, in addition to white pine blister rust presence across the entire range of whitebark pine, white pine blister rust infection likely will continue to increase and intensify within individual sites, ultimately resulting in stands that are no longer viable and potentially facing extirpation in the absence of restoration.

MOUNTAIN PINE BEETLE

Whitebark pine trees are fed upon by a variety of insects; however, none has had a more widespread impact than the native mountain pine beetle (*Dendroctonus ponderosae* Hopkins). The mountain pine beetle is recognized as one of the principal sources of whitebark pine mortality (Raffa and Berryman 1987, p. 234; Arno and Hoff 1989, p. 7). Mountain pine beetles feed on whitebark pine and other western conifers and to successfully reproduce the beetles must kill host trees (Logan and Powell 2001, p. 162; Logan *et al.* 2010, p. 895). Upon locating a suitable host (i.e., large diameter tree with sufficient resources for brood production success), adult female mountain pine beetles emit pheromones that attract adult males and other adult females to the host tree. This attractant pheromone initiates a synchronized mass attack for the purpose of overcoming the host tree's defenses to mountain pine beetle predation. Once a tree has been fully colonized, the beetles produce an anti-aggregation pheromone that signals to incoming beetles to pass on to nearby unoccupied trees. Almost all host trees, even stressed individuals, will mount a physiological defense against these mass attacks. However, given a sufficient number of beetles, even a healthy tree's defensive mechanisms can be exhausted (Raffa and Berryman 1987, p. 239). Following the pheromone-mediated mass attack, male and female mountain pine beetles mate in the phloem (living vascular tissue) under the bark of the host tree. Females subsequently excavate vertical galleries where they lay eggs. Larvae hatched from these eggs feed on the phloem, pupate, and emerge as adults to initiate new mass attacks of nearby suitable trees (Gibson *et al.* 2008, p. 3). Mountain pine beetle development is strongly linked to temperature. The entire mountain pine beetle life cycle (from egg to adult) can take between 1 and 2 years depending on ambient temperatures. Warmer temperatures promote a more rapid development that facilitates a 1-year, or univoltine, life cycle (Amman *et al.* 1997, p. 4; Gibson *et al*. 2008, p. 3).

Beetle activity in the phloem mechanically girdles the host tree, disrupting nutrient and water transport and ultimately killing it. Additionally, mountain pine beetles carry symbiotic blue stain fungi on their mouthparts, which are introduced into the host tree upon feeding. These fungi also inhibit water transport and further assist in killing the host tree (Raffa and Berryman 1987, p. 239; Keane *et al.* 2012, p. 27).

Mountain pine beetles are considered an important component of natural forest disturbance regimes (Raffa *et al*. 2008, p. 502; Bentz *et al.* 2010, p. 602). At endemic, or more typical, levels, mountain pine beetles remove relatively small numbers of trees, changing stand structure and species composition in localized areas. However, when conditions are favorable (abundant hosts and favorable climate), mountain pine beetle populations can erupt to epidemic levels and create stand-replacing events that may kill 80 to 95 percent of suitable host trees (Berryman 1986 as cited in Keane *et al.* 2012, p. 26). Such outbreaks are episodic, can have a magnitude of impact on the structure of western forests greater than wildfire (the other major component of natural forest disturbance), and are often the primary renewal source for mature stands of western pines (Hicke *et al*. 2006, p. 1; Raffa *et al*. 2008, pp. 502–503; Six *et al.* 2014, p. 104). Mountain pine beetle outbreaks typically subside only when the supply of suitable host trees has been exhausted or winter temperatures are sufficiently low to kill larvae and adults (Gibson *et al.* 2008, p. 2).

The range of mountain pine beetle completely overlaps with the range of whitebark pine, and mountain pine beetle epidemics affecting whitebark pine have occurred throughout recorded history (Keane *et al.* 2012, p. 26). Recent outbreaks occurred in the 1930s, 1940s, and 1970s, and numerous ghost forests of dead whitebark pine still dot the landscape as a result (Arno and Hoff 1989, p. 7; Perkins and Swetnam, 1996, p. 2129, Ward *et al*. 2006, p. 8). The most recent epidemic began in the late 1990s and, although the levels of mortality from this epidemic have since subsided considerably, mountain pine beetles continue to be a measurable source of mortality for whitebark pine (Macfarlane *et al*. 2013, pg. 434; Mahalovich 2013, p. 21; Shelly 2014, pp.1–2).

Despite recorded historical impacts to the species, whitebark pine has not been considered an important host of mountain pine beetle in the past. Unlike the lower elevation sites occupied by mountain pine beetle's primary hosts, lodgepole pine and *Pinus ponderosa* (ponderosa pine), the high-elevation sites occupied by whitebark pine typically have been climatically inhospitable to mountain pine beetle (Logan and Powell 2001, p. 161). At the low temperatures typical of high-elevation sites, mountain pine beetles mostly experience a 2-year (bivoltine) life cycle, which is not favorable to epidemic outbreaks (i.e., eruptive population growth). Warmer temperatures promote a 1-year life cycle, which facilitates population growth and the synchronized mass attacks important in overcoming host tree defenses and result in epidemic level outbreaks (Logan and Powell 2001, p. 167).

However, unlike previous epidemics, the most recent mountain pine beetle outbreak has had a significant rangewide impact on whitebark pine (e.g., Figure 5) (Logan *et al.* 2003, p. 130; Logan *et al.* 2010, p. 898; MacFarlane *et al*. 2013, p. 434). The reported mortality rates of mostly mature trees (i.e., large-diameter trees) have been as high as 96 percent or more in stands across the range (Gibson *et al.* 2008, p. 9; Kegley *et al.* 2011, p. 87). In 2007 alone, whitebark pine trees on almost 202,342 ha (500,000 ac) were impacted (4 percent of the range). By 2009, an estimated 809,371 ha (2,000,000 ac) were impacted (16 percent of the range) (Service 2010). The USFS estimates that over 5.8 million individual whitebark pines were killed by mountain pine beetle between 1999 and 2015 on over 401,448 ha (992,000 ac) in portions of western Montana and northern Idaho (Shelly 2016). The USFS also estimates 5.7 million trees were killed on over 404,686 ha (1,000,000 ac) from 2000-2015 in portions of Idaho, Wyoming, and Nevada (USFS 2016). It is important to note, however, that all of the above mortality estimates are largely derived from the USFS's annual aerial detection surveys. While considered valuable as a rapid assessment technique, these surveys are known to significantly underestimate tree mortality because: (1) not all forested lands are flown over regularly; (2) wilderness areas are seldom flown over; and (3) an individual year's survey does not represent a cumulative mortality estimate (Macfarlane *et al.* 2013, p. 423). Therefore, whitebark pine mortality during the most recent epidemic is likely higher than the values being reported.

Figure 6 Greater Yellowstone Area in 2009 during the peak of the most recent mountain pine beetle outbreak. Photo credit J. Pargiter.

Warmer, shorter winter seasons caused by climate change have provided favorable conditions necessary for the most recent, unprecedented mountain pine beetle epidemic in high-elevation communities across the western United States and Canada (Logan and Powell 2001, p. 167; Logan *et al.* 2003, p. 130; Raffa *et al*. 2008, p. 511). Warming trends have resulted in not only intensified mountain pine beetle activity in high-elevation whitebark pine forests, but have resulted in mountain pine beetle range expansion into more northern latitudes and higher elevations (Logan and Powell 2003, p. 131; Carroll *et al.* 2003 in Gibson *et al*. 2008, p. 4; Raffa *et al.* 2008, p. 503; Logan *et al.* 2010, p. 895; Sidder *et al*. 2016, p. 9). Winter temperatures are now warm enough for winter survival of all mountain pine beetle life stages and for maintenance of the 1-year life cycle that promotes epidemic mountain pine beetle population levels (Bentz and Schen-Langenheim 2007, p. 47; Logan *et al.* 2010, p. 896; Buotte *et al.* 2016, pp. 2515–2516; Buotte *et al*. 2017, p. 136). Along with warmer winter conditions, summers have become drier, with droughts occurring through much of the range of whitebark pine (Bentz *et al.* 2010, p.

605). Mountain pine beetles frequently target drought-stressed trees, which are more vulnerable to attack; drought-stressed trees are less able to mount an effective defense even against less-dense mass attacks by mountain pine beetles (Bentz *et al.* 2010, p. 605). Given ongoing and predicted environmental effects from climate change, we expect mountain pine beetles will continue to expand into higher elevation habitats and that epidemics will continue within the range of whitebark pine (Buotte *et al*. 2016, p. 2516; Sidder *et al*. 2016, p. 9). Recent research predicts that future climate suitability will decrease, maintain, and increase epidemic mountain pine beetle epidemics in the Cascade, Northern Rockies, and Greater Yellowstone Ecosystem regions, respectively (Buotte *et al*. 2017, pp. 137–138).

There is some evidence that mountain pine beetles also may preferentially attack whitebark pine trees infected with and weakened by white pine blister rust (Six and Adams 2007, p. 351; Bockino and Tinker 2012, p. 38); however, this may not always be the case (Six et al. 2018, p. 7). In the Greater Yellowstone Ecosystem, whitebark pine trees that were selected as hosts by mountain pine beetle exhibited significantly greater white pine blister rust severity than trees not selected by mountain pine beetle (Bockino and Tinker 2012, p. 31). The mountain pine beetle's preference for trees infected with white pine blister rust increases the susceptibility of whitebark pine to mountain pine beetle-caused mortality, further increasing stress and potentially reducing resilience to disturbance in stands with already substantial health problems (Bockino and Tinker 2012, p. 38).

Recent research has found that whitebark pine trees that survived a mountain pine beetle outbreak had narrower tree rings, and therefore slower growth rates, than whitebark pine trees that were killed by mountain pine beetles (Kichas *et al.* 2020, p 6; Six *et al*. 2021, p. 19). Whitebark pine trees that survive mountain pine beetle outbreaks have been shown to have greater genetic diversity than trees too small to be killed by mountain pine beetles (Six et al. 2021, p. 9) and there is evidence of a genetic basis for resistance to mountain pine beetle attack, with mountain pine beetles selecting some whitebark pine genotypes for attack over other genotypes, even during outbreaks (Six et al. 2018, p. 7). Whitebark pine trees that survived an outbreak also have larger resin ducts (resin production and resin storage structures) and greater resin duct area than trees that die in an outbreak (Kichas et al. 2020, p. 9). Resin is a primary defense pine trees have against bark beetle attack. When a bark beetle attacks a tree, resin ducts in the tree are severed, filling the attack site with resin, displacing, smothering, or entrapping the bark beetle. Increased resin production may be a trade-off to tree growth, with slower growing trees instead investing limited resources in resin production (Kichas *et al.* 2020, p. 9; Six *et al*. 2021, p. 17). Although tree vigor is often used as an indicator of resistance to bark beetles in some conifer species, tree vigor does not appear to be an indicator of resistance to mountain pine beetle in whitebark pine, suggesting that thinning treatments may not enhance whitebark pine's defenses to bark beetles (Six et al. 2021, p. 19).

Recent monitoring data indicates this most recent epidemic is waning across the majority of the west (Hayes 2013, pp. 3, 41, 42, 54; Alberta Whitebark and Limber Pine Recovery Team 2014, p. 18; Bower 2014, p. 2; Shelly 2014, pp. 1–2). For example, in Montana and Idaho, the estimated number of dead whitebark pine increased sharply in the early 2000s, peaked in 2008, and has declined significantly since then (Figure 6).

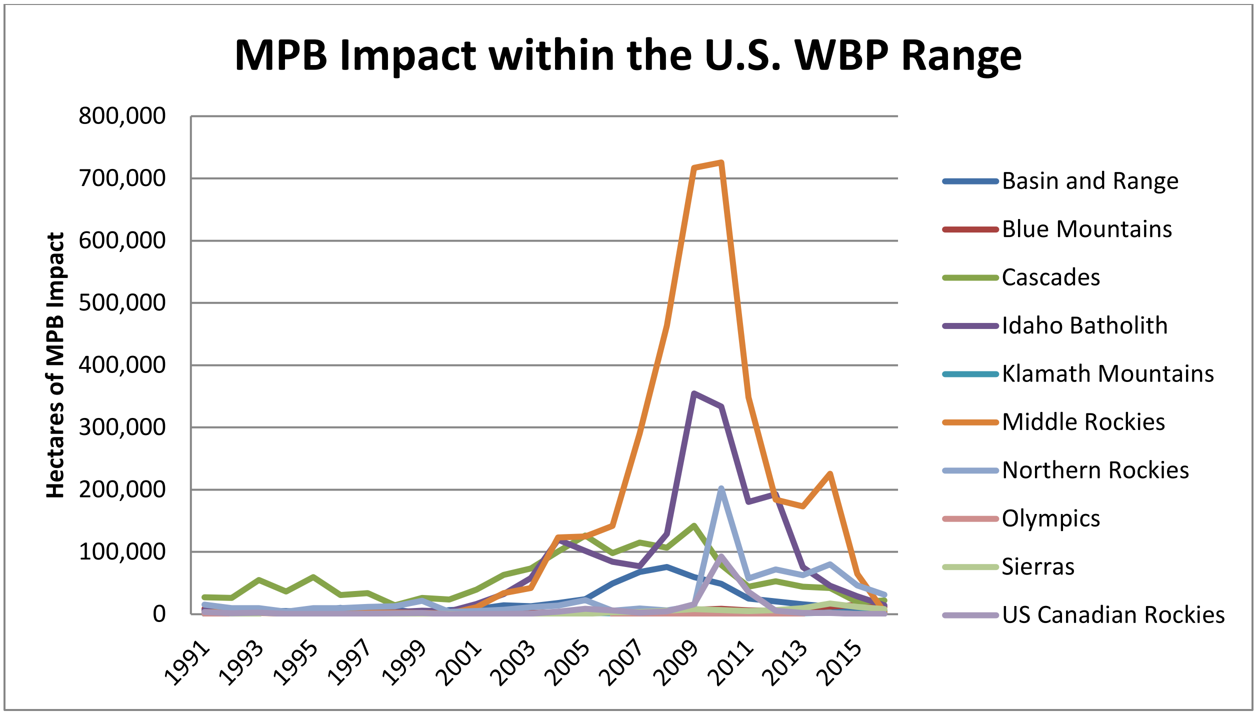

Figure 7 Annual estimated hectares of whitebark (and limber pine) impacted by mountain pine beetle (MPB) from 1991 to 2016, in the U.S. portion of the whitebark pine range. Estimates are derived from USFS aerial detection surveys. Data indicate this epidemic began approximately in year 2000 and declined by 2016. Because of the difficulty distinguishing whitebark and limber pine from the air, this estimate includes what is considered a relatively small portion of limber pine.

In 2012, aerial detection surveys showed that the area of forested stands in western Montana with mountain pine beetle-caused mortality was lower (9,052 ha) (22,369 ac) than in 2011 (30,460 ha) (75,269 ac) and 2010 (77,421 ha) (191,312 ac) (Hayes 2013, pp. 3, 39, 41, 42, 54). This observed mortality included high-elevation five needle pine trees, which includes whitebark pine and small amounts of limber pine (*Pinus flexilis*) (Hayes 2013, pp. 3, 39, 41, 42, 54). Aerial detection surveys were also conducted in 2013 and 2014 over all forested areas with whitebark pine and other conifers in Oregon and Washington (Bower 2014, p. 2). In 2013, 2,384 ha (5,891 ac) were affected by mountain pine beetle, but in 2014, less area was affected (1,687 ha (4,170 ac)) (Bower 2014, p. 2). Overall, mortality of whitebark pine due to mountain pine beetle has declined in Montana, Oregon, and Washington (Hayes 2013, p. 3; Bower 2014, p. 2; Jules *et al*. 2020, p. 134). Currently, mountain pine beetle population levels are very low in the southwest part of Alberta, and most infestations are outside of the range of whitebark pine (Alberta Whitebark and Limber Pine Recovery Team 2014, p. 18). However, we have no data from previous years for comparison. It is estimated that fewer than 5,000 whitebark pine trees have been killed by mountain pine beetle in Alberta during the current outbreak (Alberta Whitebark and Limber Pine Recovery Team 2014, p. 18). As part of the Government of Alberta's mountain pine beetle management program, any whitebark pine detected attacked by mountain pine beetle is felled and burned.

This reduction in beetle-caused mortality over a majority of the range is expected. Significant numbers of whitebark pine have already been killed, leaving less food (i.e., live relatively large diameter, older trees) available for mountain pine beetles to continue reproducing at epidemic levels (Amman *et al*. 1997, p. 5). Although mortality from mountain pine beetle will continue in localized areas at lower endemic levels, given the extensive mortality from the most recent epidemic, a 'back-to-back,' or immediate sequential epidemic is unlikely to occur (Mahalovich 2013, p. 20). However, despite the reduction of epidemic levels of mountain pine beetle-caused mortality rangewide, we expect that mountain pine beetle will remain a threat to whitebark pine because of the epidemic's cyclic nature. We also anticipate that ongoing warming trends will continue to allow expansion of beetle populations into previously unhospitable areas and will provide environmental conditions favorable for future beetle outbreaks (Buotte *et al*. 2016, p. 2516; Sidder *et al*. 2016, p. 9).

Current management and research continue to explore methods to control mountain pine beetle, mainly with the use of the pesticide Carbaryl, the anti-aggregation pheromone called Verbenone, and six- and seven-carbon alcohols and aldehydes known as green leaf volatiles (e.g., Gillette *et al*. 2014, p. 1023, Eglitis 2015). Both methods can be effective for limited time periods (Progar 2007, p. 108). However, use of either control method can be prohibitively expensive and challenging given the scale of mountain pine beetle outbreaks (i.e., millions of acres) and the inaccessibility of much of whitebark pine habitat. Currently, these methods are mostly being suggested for use in targeted protection of high-value trees (e.g., individuals resistant to white pine blister rust, stands in recreational areas) rather than as a large-scale restoration tool (Keane *et al.* 2012, p. 83). Therefore, these control methods are not currently sufficient to protect the species as a whole from mountain pine beetle predation.

CLIMATE CHANGE

Our analyses under the Act include consideration of ongoing and projected changes in climate. The terms "climate" and "climate change" are defined by the Intergovernmental Panel on Climate Change (IPCC). The term "climate" refers to the mean and variability of different types of weather conditions over time, with 30 years being a typical period for such measurements, although shorter or longer periods also may be used (IPCC 2014, pp. 119–120). The term "climate change" thus refers to a change in the mean or variability of one or more measures of climate (e.g., temperature or precipitation) that persists for an extended period, typically decades or longer, whether the change is due to natural variability, human activity, or both (IPCC 2014, p. 120). Various types of changes in climate can have direct or indirect effects on species. These effects may be positive, neutral, or negative and they may change over time, depending on the species and other relevant considerations, such as the effects of interactions of climate with other variables (e.g., habitat fragmentation) (IPCC 2014, pp. 6-7;10–14). In our analyses, we use our expert judgment to weigh relevant information, including uncertainty, in our consideration of various aspects of climate change.

The National Fish, Wildlife and Plants Climate Adaptation Strategy (National Fish, Wildlife and Plants Climate Adaptation Partnership [NFWPCAP] 2012, pp. 28–30) provides observed and projected ecological changes from the effects of climate change on forests. Changes in precipitation can result in longer fire seasons, altered fire regimes, changes in biomass growth and accumulation (e.g., fuels), and exacerbate both wetter and drier conditions. Increasing temperatures are predicted to increase forest pest damage; increase fire frequency, size, and intensity; lengthen the growing season; and increase drought stress. The increases in drought conditions can result in increased fire frequency and intensity, decreased productivity, and increased tree mortality. Therefore, the consequences of climate change, if current projections are realized, are likely to exacerbate the existing primary threats to whitebark pine, and climate change has been of high interest to forest managers. However, the question of how climate change will directly or indirectly impact any species is complex and researchers have taken several approaches to gain a better understanding of how climate change will impact whitebark pine.

The USFS recently ranked the vulnerability of tree species based on a number of risk factors including: (1) extent of distribution; (2) reproductive capacity; (3) habitat affinity; (4) genetic variation; and (5) threats from insects and diseases. These five risk factors were averaged to calculate an overall regional climate change vulnerability score for numerous tree species including whitebark pine. Based on this analysis, whitebark pine was given the highest average vulnerability score among the 36 native tree species included in the analysis (Devine *et al.* 2012, p. 34, Halofsky *et al*. 2018a, 2018b). This analysis did not include spatially explicit predictions about future habitat, but instead the objective was to identify traits which might make a species particularly vulnerable to rapidly changing climates. Similarly, in an assessment of 20 western tree species Mathys *et al*. (2016, p. 9) found that whitebark pine was one of the most vulnerable species to climate change.

Habitat loss is anticipated to occur across the whitebark pine range, with current habitats becoming unsuitable for the species as a result of both direct and indirect impacts from climate change (Bartlein *et al*. 1997, p. 788; Hamann and Wang 2006, p. 2783; Hansen and Phillips 2015, p. 74; Schrag *et al.* 2007, p. 8; Warwell *et al.* 2007, p. 2; Aitken *et al*. 2008, p. 103; Loehman *et al.* 2011, pp. 185-187; Rice *et al*. 2012, p. 31; Chang *et al.* 2014, p. 10; Mathys *et al*. 2016, pp. 6-7, 9). Researchers have hypothesized that there will be significant habitat loss as (1) temperatures become so warm that they exceed the thermal tolerance of whitebark pine and the species is unable to survive, (2) warmer temperatures favor other species of conifer that currently cannot compete with whitebark pine in cold high-elevation habitats, and (3) climate change alters the frequency and intensity of disturbances (e.g., fire, disease) to such an extent that whitebark cannot persist.

Given the anticipated loss of suitable habitat, whitebark pine persistence could be dependent on several factors including the species' ability to either migrate to new suitable habitats, or adapt to changing conditions (Aitken *et al*. 2008, p. 95). Historical (paleoecological) evidence indicates that plant species have generally responded to past climate change through migration, and that adaptation to changing climate conditions is less likely to occur (Bradshaw and McNeilly 1991, p. 12; Huntley 1991, p. 19). Adaptation to a change in habitat conditions as a result of a changing climate could be unlikely for whitebark pine, given its very long generation time of approximately 60 years (Bradshaw and McNeilly 1991, p. 10). However, despite whitebark pine’s long generation time, the species has been shown to have a comparatively high level of genetic diversity, the result being a better ability to adapt to changes over the long term (Mahalovich and Hipkins 2011, p. 128) (i.e., representation). Additionally, whitebark pine has one of the largest latitudinal ranges of any of the other five-needle white pines in North America, which suggests the species may be able to tolerate a relatively wide range of temperatures and precipitation (Tomback and Achuff 2010, pp. 187–188).

The rate of latitudinal plant migration during past warming and cooling events is estimated to have been on the order of 100 m (328 ft) per year (Aitken *et al.* 2008, p. 96). Given the current and anticipated rates of global climate change, migration rates will potentially need to be substantially higher than those measured in historical pollen records to sustain the species over time. A migration rate of at least a magnitude higher (1,000 m (3,280 ft)) per year is estimated to be necessary in order for tree species to be capable of tracking suitable habitats under projected warming trends (Malcolm *et al.* 2002, entire). Latitudinal migration rates on this scale may significantly exceed the migration abilities of many plant species, including whitebark pine (Malcolm *et al.* 2002, pp. 844–845; McKenney *et al.* 2007, p. 941).

Whitebark pine may have an advantage in its ability to migrate given that its seeds are dispersed by Clark's nutcracker. As mentioned above, Clark's nutcrackers can disperse seeds farther than the wind-dispersed seeds of other conifers (McCaughey *et al.* 1985, Tomback *et al.* 1990, 1993 in Keane and Parsons 2010, p. 58). However, despite the advantages of seed dispersal by Clark’s nutcracker, the migration of whitebark pine to the north may be impeded by the disease white pine blister rust, which is currently present even at the northern range limits of whitebark pine (Smith *et al*. 2008, Figure 1, p. 984; Tomback *et al*. 2016, p.14).

Whitebark pine is typically the first species to establish on cold, exposed high-elevation sites, thus the species could potentially migrate higher in elevation to more suitable habitats. Shifts in the optimum elevation for many high-elevation plant species have already been documented under current warming trends (Lenoir *et al.* 2008, p. 1770). Elevational migration as a refuge from temperature increase has limits, because eventually, suitable habitat may not be present even on mountaintops due to continuing temperature increases and resulting conditions that favor whitebark pine competitors like subalpine fir and Engelmann spruce, or mountain hemlock. Expansion above current treeline may also indirectly affect the biodiversity and ecosystem services of alpine communities in multiple ways (Greenwood and Jump 2014, p. 835). Additionally, the presence of white pine blister rust even at treeline, an area previously thought too cold and dry to support white pine blister rust, further limits the potential for high-elevation habitats to provide refuge for whitebark pine (Smith-Mckenna *et al.* 2013, p. 224; Tomback *et al.* 2014, p. 416).

Further complicating the capacity of whitebark pine to persist is the potential for climate change to directly impact Clark's nutcracker populations. Birds are particularly susceptible to the effects of climate change on a global scale (Bellard et al. 2012, p. 371). While the best available information based on the American Breeding Bird Survey indicates that overall abundance of Clark's nutcracker currently appears relatively stable (Rosenberg et al. 2016, p. 108), future population changes derived from the effects of warming temperatures throughout the range of Clark's nutcracker are possible, if not likely. Though specific research on the effects of climate change to Clark's nutcracker is scarce, western forest birds, including Clark's nutcrackers, are considered highly vulnerable to climate change (Bateman et al. 2020, p. 7). Should climate change negatively impact Clark's nutcracker populations under future warming scenarios, the additive effect would likely exacerbate the decline of whitebark pine in the future by disrupting the mutualistic relationship between the two species (Ray et al. 2020, p. 20).

Numerous models indicate climate change will significantly decrease the probability of rangewide persistence of whitebark pine. Projections from an empirically based bioclimatic model for whitebark pine showed a rangewide distribution decline of 70 percent and an average elevation loss of 333 m (1,093 ft) for the decade beginning in 2030 (Warwell *et al.* 2007, p. 2). At the end of the century, less than 3 percent of currently suitable habitat is expected to remain (Warwell *et al.* 2007, p. 2). Similarly, climate envelope modeling on whitebark pine distribution in British Columbia estimated a potential decrease of 70 percent of currently suitable habitat by the year 2055 (Hamann and Wang 2006, p. 2783). The area occupied by whitebark pine in the Greater Yellowstone Ecosystem also is predicted to be significantly reduced with increasing temperature under various climate change scenarios (Schrag *et al.* 2007, p. 6). Whitebark pine is predicted to be nearly extirpated under a scenario of warming only and warming with a concomitant increase in precipitation (Schrag *et al.* 2007, p. 7). Climate envelope modeling by the USFS using the A2 scenario (global average surface warming of +6.1 °F (+3.4 °C)) projects that by 2090, a temperature increase of 9.1 °F (5.1 °C) would cause whitebark pine suitable climate to contract to the highest elevation areas in the northern Shoshone National Forest and Greater Yellowstone Ecosystem or whitebark pine to be extirpated from these areas (Rice *et al.* 2012, p. 31). Using a model to assess climate change and wildfire patterns on whitebark pine in Glacier National Park, Loehman *et al.* 2011 (pp. 185–187) also project a decline in whitebark pine. The decline was an indirect result of climate change-altered distributions of competing tree species and an increased frequency and size of wildfires. Under all nine climate models and two emissions scenarios examined by Chang *et al.* 2014 (p. 10), the distribution of whitebark pine suitable habitat also declined, with only small, fragmented islands of habitat remaining. The above studies all suggest that the area currently occupied by whitebark pine will be severely reduced in the future.

We recognize, however, that there are many limitations to such modeling techniques, specifically for whitebark pine. For example, climate envelope models use current environmental conditions in the distribution of the species' range to determine whether similar environmental conditions will be available in the future given predicted climate change. Whitebark pine, however, is a very long-lived species, and current environmental conditions may not closely resemble environmental conditions present when the trees currently on the landscape were established (Keane 2001c, pers. comm.). Additionally, these models also describe current environmental variables in averages taken over large areas. Whitebark pine may experience very different environmental conditions even over a small range as individuals can be separated by thousands of meters (Keane 2011c, pers. comm.).

A more comprehensive modeling effort was recently undertaken with the above considerations in mind (Keane *et al.* 2017b, entire). Using a spatially explicit, ecological process model, Keane *et al.* (2017) examined scenarios where levels of climate change, management approaches (thinning, planting, prescribed burning), and degrees of fire exclusion were varied. Response variables included whitebark pine basal area and the proportion of the landscape dominated by whitebark pine given the different scenarios explored. The results indicate that whitebark pine will decline, regardless of any potential negative climate change impacts, as a result of disease and predation (Keane *et al*. 2017b, pp. 165, 168). However, results also indicate that timely management intervention (i.e., planting potentially rust-resistant seedlings and targeted, proactive restoration treatments) will benefit the species such that it could persist on the landscape, although at lower levels, in the future.

Generally, there is a high degree of uncertainty inherent in any predictions of species responses to a variety of climate change scenarios. This is particularly true for whitebark pine given it is very long lived, has a widespread distribution, has complex interactions with other competitor tree species, relies on Clark's nutcracker for both distribution and regeneration, and has significant threats present from disease, predation, and fire. In other words, the level of uncertainty is multiplied because one must consider the potential impacts of climate change not only on whitebark pine's ability to tolerate changes in temperature and precipitation, but also the uncertain impacts of climate change on the complex ecosystem it inhabits (i.e., tree competitors, Clark's nutcracker and other seed predators, white pine blister rust, mountain pine beetle, and fire). Although research results are not definitive concerning specifics of anticipated direct and indirect impacts from climate change, without active management, the projected impacts from climate change will likely contribute substantially to the ongoing decline of whitebark pine (Hamann and Wang 2006, p. 2783; Schrag *et al.* 2007, p. 8; Warwell *et al*. 2007, p. 2; Aitken *et al.* 2008, p. 103; Loehman *et al.* 2011, pp. 185–187; Rice *et al.* 2012, p. 31; Chang *et al.* 2014, p. 10; Keane *et al.* 2017b, entire).

In summary, the pace of predicted climate change will likely outpace many plant species' abilities to respond to the concomitant habitat changes. Whitebark pine is potentially particularly vulnerable to warming temperatures because it is adapted to cool, high-elevation habitats. Therefore, current and anticipated warming is expected to make its current habitat unsuitable for whitebark pine, either directly or indirectly as conditions become more favorable to whitebark pine competitors, such as subalpine fir or mountain hemlock. The rate of migration needed to respond to predicted climate change will be substantial (Malcolm *et al.* 2002, pp. 844–845; McKenney *et al.* 2007, p. 941). The ability of whitebark pine to migrate to more favorable areas at a pace sufficient to survive the projected effects of climate change is unknown. We also do not know the degree to which Clark's nutcracker could facilitate this migration. In addition, the presence of significant white pine blister rust infection in the northern range of whitebark pine could serve as a barrier to effective northward migration. Whitebark pine currently inhabits high elevations, so there is little remaining habitat for the species to migrate to higher elevations in response to warmer temperatures. Adaptation in response to a rapidly warming climate could also be unlikely as whitebark pine is a long-lived species with a long generation time. Climate models suggest that climate change is expected to act directly and indirectly to significantly decrease the probability of rangewide persistence in whitebark pine within the next 100 years. This time interval is less than two generations for this long-lived species. In addition, projected climate change is a significant threat to whitebark pine, because the impacts of climate change interact with other stressors such as mountain pine beetle epidemics and wildfire, resulting in habitat loss and population decline.

CHAPTER 4: ANALYSIS OF CURRENT CONDITIONS

In this chapter, we summarize the current condition of whitebark pine in terms of the main stressors that are influencing its viability. The following influence diagram (Figure 7) illustrates how certain stressors (mountain pine beetle, white pine blister rust, and high severity wildfire) predominantly impact whitebark pine negatively by affecting seed source and survival, two essential components of population resiliency. Experts predict that climate change may exacerbate the impacts of mountain pine beetle and high severity wildfire on whitebark pine in the future, while the potential effects of climate change on white pine blister rust are not as clear.

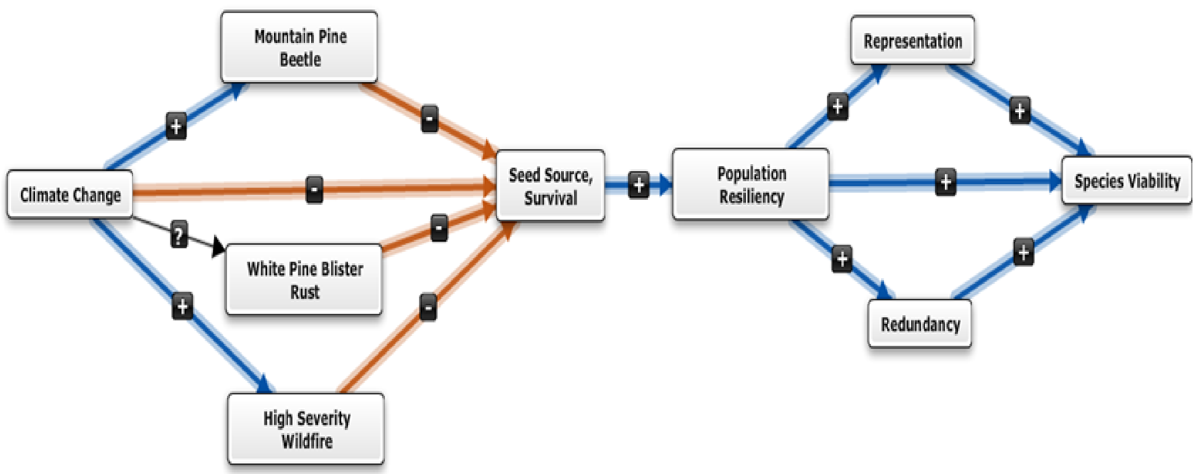

Figure 8 Influence diagram illustrating the influence of certain stressors on whitebark pine viability.

ANAYLYSIS UNITS

As described above (Chapter 2: Range and Distribution) whitebark pine has an extensive range that covers many millions of hectares in western North America. To allow meaningful assessment of viability, we broke the range into fifteen smaller analysis units (AUs) (Figure 8). We based analysis units primarily on ecoregions identified in the Environmental Protection Agency Level III Ecoregions data set (https://www.epa.gov/eco-research/ecoregions). Ecoregions identify areas of general similarity in ecosystems, as well as topographic and environmental variables. Ecoregions are designed to serve as a spatial framework for research, assessment, management, and monitoring. We then modified analysis units based on comments from whitebark pine experts. We further divided analysis units in the United States from those in Canada to reflect differences in management and legal status. All analyses in this SSA were limited to the whitebark pine range within each of the 15 designated analysis units. As mentioned above, the whitebark pine range is depicted at a coarse scale, however, it encompasses all known occurrences and distribution of whitebark pine (Table 3). We note that not all analysis units are equal in size; they encompass varying proportions of the species' range, ranging from the Middle Rockies AU (27.6 percent of the range) to the Olympics AU (0.4 percent of the range) (Table 3).

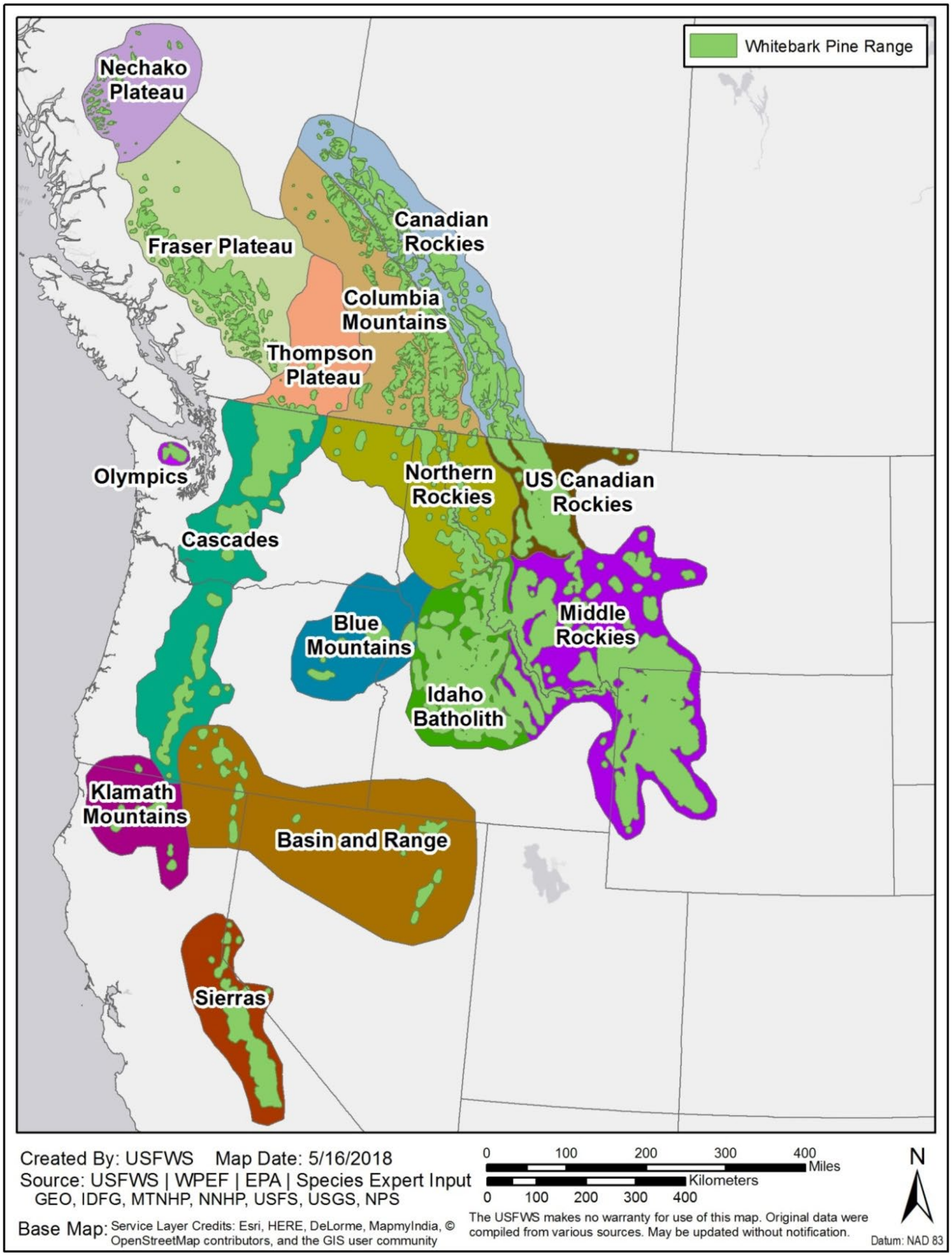

Figure 9 Whitebark pine Analysis Units

Table 3 Whitebark pine range in each analysis unit

Analysis Unit	Hectares of WBP range within each AU	Percent of total WBP range within the each AU
Middle Rockies	9,008,418	27.6 percent
Idaho Batholith	4,621,881	14.2 percent
Canadian Rockies	3,660,161	11.2 percent
Cascades	2,906,758	8.9 percent
Columbia Mountains	2,849,789	8.7 percent
US Canadian Rockies	2,153,185	6.6 percent
Fraser Plateau	2,122,498	6.5 percent
Northern Rockies	1,704,834	5.2 percent
Sierras	1,292,333	4.0 percent
Basin and Range	827,089	2.5 percent
Blue Mountains	554,865	1.7 percent
Klamath Mountains	334,950	1.0 percent
Nechako Plateau	266,078	0.8 percent
Thompson Plateau	194,264	0.6 percent
Olympics	119,319	0.4 percent
TOTAL	32,616,422	

Whitebark pine's viability is a function of its resiliency (the ability of populations to withstand periodic disturbance and environmental stochasticity), redundancy (the duplication and distribution of populations across the species' range) and representation (the genetic, morphological, and ecological diversity within a species). At the species level, whitebark pine needs multiple, connected, resilient populations in a breadth of ecological settings across its range to be viable. In this chapter, we first discuss the current status of factors affecting the resiliency of each Analysis Unit. Then, we evaluate what the species as a whole has in terms of representation and redundancy.

RESILIENCY: CURRENT CONDITION

Current Condition: Fire

To assess the current impact of wildfire on whitebark pine, we examined burn data collected from 1984 to 2016 (Monitoring Trends in Burn Severity [MTBS] https://www.mtbs.gov; GeoMac, https://www.geomac.gov/; Canadian Forest Service, http://cwfis.cfs.nrcan.gc.ca/ha/nfdb). Although we collected information on all fires, our analysis focuses on areas of high burn severity that could potentially negatively impact the species. However, the high burn severity data only covers the U.S. portion of the range (MTBS https://www.mtbs.gov). It should be noted that the range maps used for this analysis also include potential whitebark pine habitat that may or may not currently be occupied by whitebark pine. In instances where high severity fires have burned in potential habitat totally or predominantly occupied by competing tree species (e.g., subalpine fir), a desirable outcome for whitebark pine would be realized. However, because there is a widespread lack of fine-scale presence/absence data for whitebark pine throughout its potential range, at this time we assume that all mapped habitat is in fact occupied by whitebark pine.

The 33-year time period covered by this dataset provides the most comprehensive information for burns across all analysis units in the whitebark pine range; data collected before this period was likely more incomplete and opportunistic. For analysis units within the United States, we were able to differentiate between low/moderate or high severity fires. Unfortunately, finer-scale fire severity data is not available for the Olympics or any of the analysis units in Canada. This differentiation is important because low and moderate severity fires primarily affect individuals at the stand scale and are unlikely to affect the species' broader distribution. In contrast, high severity fires can be detrimental and kill all life stages of whitebark pine. Although high-severity fires may also create ideal openings for seed caching, facilitate seedling establishment, and reduce competitive pressures; we view the immediate large-scale loss of mature whitebark pine trees, the corresponding loss of seed sources, and potential reduction of genetic diversity as the predominant effects of high-severity fire.

Between 1984 and 2016, 3,107,852 ha of whitebark pine range burned in a fire, which represents 13 percent of the species' range. Specifically, over this same time period, between 0.08 percent and 42.64 percent of each analysis unit burned (Table 4). As little as 215 ha burned in the Nechako Plateau, while 1,970,615 ha burned in the Idaho Batholith analysis unit alone. In general, the Canadian analysis units experienced less fire than those in the United States (Table 4 and Figure 9). While the majority of fires in analysis units within the United States were classified as low to moderate severity, the Idaho Batholith AU saw 24 percent of their burned ha affected by high severity, detrimental fires. Overall, a minimum of 1,273,583 ha of whitebark pine habitat burned in high severity fires between 1984 and 2016, equating to approximately 5 percent of the species' range within the United States. We cannot determine the total proportion of the species' range affected by high severity wildfires because of the lack of finer-scale data from Canada. There have been several severe fire seasons since 2016; however, given the large range of whitebark pine, these additional localized fires do not substantially change our overall understanding of the extent of the species' range that has been affected by fire. As of October 2021, data from MTBS is only available through 2019. In 2017, 2018, and 2019, an additional 648,510 ha burned in whitebark range in the United States, which represents an additional 3 percent of whitebark pine range. Between 2016 and 2019, an additional 0.8 percent of whitebark pine range within the United States (or 471,105 acres (191,459 ha)) burned at high severity. Thus, between 1984 and 2019, at least 16 percent of habitat within the range of whitebark pine has burned in a fire, and less than 6 percent of whitebark pine range within the United States has burned at high severity.

Table 4 Burn data from 1984-2016 for whitebark pine (WBP) analysis units (AUs).

Analysis Unit	Total hectares of WBP range within AU	Total ha of WBP Range Burned 1984-2016	Percent of WBP range burned within AU	Percent of WBP range with high severity burn
Middle Rockies	9,008,418	1,317,220	14.62 percent	4.30 percent
Idaho Batholith	4,621,881	1,970,615	42.64 percent	10.10 percent
Canadian Rockies	3,660,161	105,413	2.88 percent	--
Cascades	2,906,758	488,527	16.81 percent	4.90 percent
Columbia Mountain	2,849,789	63,561	2.23 percent	--
US Canadian Rockies	2,153,185	516,966	24.01 percent	8.00 percent
Fraser Plateau	2,122,498	58,540	2.76 percent	--
Northern Rockies	1,704,834	152,622	8.95 percent	2.20 percent
Sierras	1,292,333	89,546	6.93 percent	0.70 percent
Basin and Range	827,089	112,588	13.61 percent	2.1 percent
Blue Mountains	554,865	149,532	26.95 percent	6.30 percent
Klamath Mountains	334,950	42,738	12.76 percent	2.60 percent
Nechako Plateau	266,078	215	0.08 percent	--
Thompson Plateau	194,264	8,924	4.59 percent	--
Olympics	119,319	1,460	1.22 percent	--

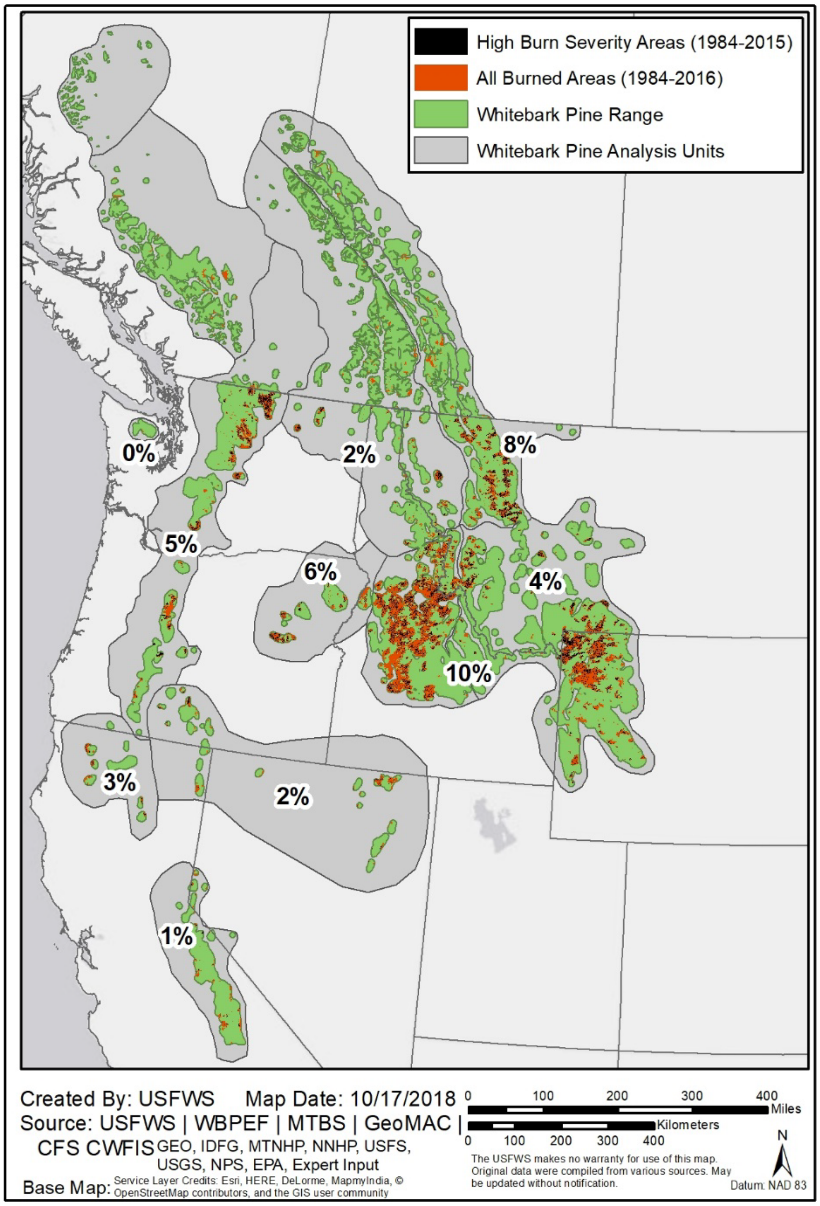

Figure 10 Areas burned within whitebark pine's range from 1984-2016. Areas in orange have burned at least once in the last 33 years. Areas in black indicate only high burn severity fires. Overall, approximately 16 percent of whitebark pine's range burned during this time period. Percentages shown on this map are areas of high burn within each analysis unit. Approximately 5 percent of the range within the United States was impacted by high severity fire (data unavailable for Canada).

Current Condition: White Pine Blister Rust

Researchers have used various sampling methods to assess the effects of white pine blister rust on whitebark pine and the amounts of infection present; therefore, exact comparisons between studies are not possible. While white pine blister rust occurs throughout all of whitebark pine range, not all trees are infected and infection rates vary widely. Furthermore, it can be difficult to detect white pine blister rust, especially if cankers occur on gnarled canopy branches where infections may remain undetected (Rochefort 2008, p. 294). We do not have historical information available regarding the percent of the range that may have been lost due to this stressor following its initial introduction into various areas of the range, with the estimated first introduction to western North America in 1910 (See Chapter 3, White pine blister rust). However, more recent, targeted research has indicated a substantial impact of this stressor and despite slight differences in sampling methods, general trends can be identified from the published literature (Schwandt *et al*. 2010, p. 228). Trends strongly indicate that white pine blister rust infections have increased in intensity over time and are now prevalent even in trees living in cold, dry areas formerly considered less susceptible (Tomback and Resler 2007, p. 399; Smith-Mckenna *et al*. 2013, p. 224), such as the Greater Yellowstone Ecosystem (Middle Rockies AU) (Table 5).

Table 5 Percentage of live trees with white pine blister rust infection on plots/transects from recent surveys (adapted from Schwandt 2006, Table 1, p. 5)

GEOGRAPHIC REGION – NUMBER OF REPORTS (CITATION)	ANALYSIS UNIT(S)	RANGE OF INFECTION (percent)	MEAN (percent)
British Columbia (rangewide) (Campbell and Antos 2000)	Nechako, Fraser, and Thompson Plateaus, Columbia Mountains	0-100	50.0
British Columbia (rangewide) (Zeglen 2002)	Nechako, Fraser, and Thompson Plateaus, Columbia Mountains	11-52.5	38.0
Northern Rocky Mountains (United States and Canada) (Smith *et al*. 2008)	Canadian Rockies, U.S. Canadian Rockies	0-100	43.6
Selkirk Mountains, northern Idaho – 5 stands (Kegley *et al*. 2004)	Northern Rockies	57-81	70.0
Colville National Forest, northeast Washington – 2 reports (Ward *et al*. 2006)	Northern Rockies	23-44	41.4
Greater Yellowstone Ecosystem (GYWPMWG 2006)	Middle Rockies	0-100	25.0
Intermountain West (Idaho, Nevada, Wyoming, California (Smith and Hoffman 2000)	Idaho Batholith, Blue Mountains, Basin and Range, Middle Rockies, Sierras, Klamath Mountains	0-100	35.0
Blue Mountains, northeast Oregon (Ward *et al*. 2006)	Blue Mountains	0-100	64.0

Coast Range, Olympic Mountains, Washington – 2 reports (Ward *et al*. 2006)	Olympics, Cascades	4-49	19.0
Western Cascades, Washington and Oregon – 6 reports (Ward *et al*. 2006)	Olympics, Cascades	0-100	32.3
Eastern Cascades, Washington and Oregon – 13 reports (Ward *et al*. 2006)	Cascades, Northern Rockies	0-90	32.3
Coastal Mountains, southwest Oregon (Goheen *et al*. 2002)	Cascades	0-100	52.0
California, Statewide (Maloney and Dunlap 2006)	Sierras, Klamath Mountains	0-71	11.7
Northern Divide Ecosystem, western Montana (Fiedler and McKinney 2014)	Northern Rockies, Middle Rockies, U.S. Canadian Rockies	--	92.0
Greater Yellowstone Ecosystem (Fiedler and McKinney 2014)	Middle Rockies	--	62.0
Mount Rainier and North Cascades NPS Complex, Washington (Rochefort 2008)	Cascades	0-70	22.0
North Cascades NPS Complex, Washington (Rochefort *et al*. 2018)	Cascades	--	51.0
Mount Rainier National Park, Washington (Rochefort *et al*. 2018)	Cascades	--	38.0

While numerous studies have reported the incidence of white pine blister rust on whitebark pine and subsequent mortality, until relatively recently few have reported on rates of change. Long-term monitoring of whitebark pine and white pine blister rust incidence was not explicitly conducted until recent decades, thereby limiting the capacity to determine rates of spread and intensification since the arrival of the rust. In western Montana, mortality rates from white pine blister rust averaged 2.1 percent per year from 1971 to 1991 (Keane and Arno 1993, p. 45). In northern Idaho, 51 percent of live whitebark pine were uninfected in 1995 (Schwandt *et al.* 2013a, p. 10), but over the following 17 years (1995 to 2012), white pine blister rust infection increased by 4.3 percent per year and mortality increased from 12 percent to 60 percent, with white pine blister rust causing 90 percent of the recorded mortality. This level of mortality exceeded the amount of new ingrowth, or trees that grew to be taller than 6 inches, indicating that whitebark pine are experiencing a measurable decline in northern Idaho (Schwandt *et al.* 2013a, pp. 1, 14). In the northern Cascades, progressive blister rust infection increased from 32 to 51 percent (North Cascades National Park Service Complex) and from 38 to 44 percent (Mount Rainier National Park) over the survey period from 2004 to 2016 (Rochefort *et al*. 2018, Table S1). In the Bob Marshall Wilderness Complex in Montana, over the last 20 years mortality increased from 35 to 80 percent with more than 60 percent of that mortality attributed to blister rust (Retzlaff *et al*. 2016). In parts of the Greater Yellowstone Ecosystem, surveys indicate that the proportion of infected whitebark pine (greater than 1.4 meters tall) has remained relatively static at an estimated 14 to 26 percent over the survey period from 2004 to 2015 (Shanahan *et al*. 2014, pp. 11, 13, 16; Shanahan *et al.* 2017, pp. 9–11, 17). This apparently static infection rate likely reflects a combination of several factors including (1) some individual whitebark pine show genetic resistance to white pine blister rust and (2) prevailing environmental conditions have not been favorable for the intensification of white pine blister rust in the areas surveyed (Shanahan *et al*. 2014, p. 12). However, as stated previously, favorable conditions need to occur only occasionally for white pine blister rust to eventually spread and intensify (Zambino 2010, p. 265). This fact is important to note, given that white pine blister rust maintains a significant presence in the area with 81 percent (2004-2007) and 86 percent (2008-2011) of the transects surveyed containing the pathogen (Shanahan *et al.* 2014, p. 11). In addition, by the end of the 2015 monitoring period, 63 percent of white pine blister rust infections occurred on the bole of infected trees (Shanahan *et al*. 2017, p. 17). This is more of a concern than infection in the canopy because bole infection compromises the longevity and reproduction of those trees (Shanahan *et al.* 2014, pp. vii, 18).

Additional information on infection trends has been reported for Canada. In the Canadian Rockies, stands surveyed in 2003 and 2004 had an overall infection level of 42 percent and 18 percent mortality. These were remeasured in 2009 and found to have increased to 52 percent infection and 28 percent mortality (Smith *et al*. 2010, p. 67; Smith *et al*. 2013, p. 90). Of the eight plots that were surveyed three times, the proportion of infected whitebark pine was 43 percent (1996), 70 percent (2003) and 78 percent (2009) while mortality increased from 26 percent to 65 percent (Smith *et al*. 2013, p. 90). A similar study in the same area determined that infection levels increased 1.5 percent per year from 2003 to 2014, while mortality levels increased 0.8 percent per year (Shepherd *et al*. 2018, p. 6). This information indicates both infection rates and mortality increased substantially in the Canadian Rockies within the last two decades. Infection and mortality from white pine blister rust were present in all stands, with the highest levels occurring in the southern portions of the study area. The high mortality and infection levels, high crown kill, and reduced regeneration potential in the southern portion of this study area suggests that long-term persistence of whitebark pine is unlikely (Smith *et al*. 2008, p. 982).

Importantly, whitebark pine infected with white pine blister rust has increased in all regions of the Canadian Rockies, where it ranged from 7 to 70 percent in 2003–2004 to 13 to 83 percent in 2009 (COSEWIC 2010, p. viii and Table 4, p. 19). Further, based on current mortality rates (including all mortality factors), the estimated whitebark pine population decline within 100 years is 78 percent in the Canadian Rockies, 97 percent in Waterton Lakes National Park, and 57 percent for all of Canada (COSEWIC 2010, p. viii and Table 4, p. 19). Based on the above studies showing rates of change in the United States and Canada as well as the plethora of infection percentage data, we conclude that white pine blister rust infection has continued spreading and intensifying rangewide. This trend has resulted in reduced seed production and increased mortality.

We assessed the current impact of white pine blister rust on whitebark pine by evaluating data from a whitebark pine white pine blister rust estimate modeled dataset developed by the USFS in 2011 for the United States. This modeled dataset is based on white pine blister rust infection information from the WLIS database (Whitebark and Limber pine Information System) combined with environmental variables from Daymet data (Daily Surface Weather and

Climatological Summaries, https://daymet.ornl.gov/). Canadian white pine blister rust data was derived from a combination of survey data from Parks Canada and empirical literature.

We used this data to estimate the percent of whitebark pine range infected within each analysis unit. This represents the most comprehensive collection of data on white pine blister rust infection levels to date. Every analysis unit within whitebark pine's range is currently affected by the disease. The average white pine blister rust infection level of whitebark pine range within each analysis unit ranges between 2 percent and 74 percent, with 12 of the 15 analysis units having an average infection level over 20 percent, and five of the analysis units have average infection levels above 40 percent (Table 6). Average infection levels are lowest in the southern analysis units (Klamath Mountains, Basin and Range, and Sierras) and then sharply increase moving north into the latitudes of the Rocky Mountains and Cascades (Figure 10).

Table 6 White pine blister rust infection levels by analysis unit.

Analysis Unit (AU)	Total hectares of WBP range within AU	Estimated hectares infected	Percent of WBP Range infected within each AU
Middle Rockies	9,008,418	2,039,141	22.64 percent
Idaho Batholith	4,621,881	1,039,282	22.49 percent
Canadian Rockies	3,660,161	1,556,666	42.53 percent
Cascades	2,906,758	1,211,160	41.67 percent
Columbia Mountains	2,849,789	1,360,974	47.76 percent
US Canadian Rockies	2,153,185	1,592,076	73.94 percent
Fraser Plateau	2,122,498	636,749	30.00 percent
Northern Rockies	1,704,834	1,059,692	62.16 percent
Sierras	1,292,333	29,144	2.26 percent
Basin and Range	827,089	148,558	17.96 percent
Blue Mountains	554,865	214,987	38.75 percent
Klamath Mountains	334,950	50,862	15.18 percent
Nechako Plateau	266,078	79,823	30.00 percent
Thompson Plateau	194,264	58,279	30.00 percent
Olympics	119,319	32,957	27.62 percent

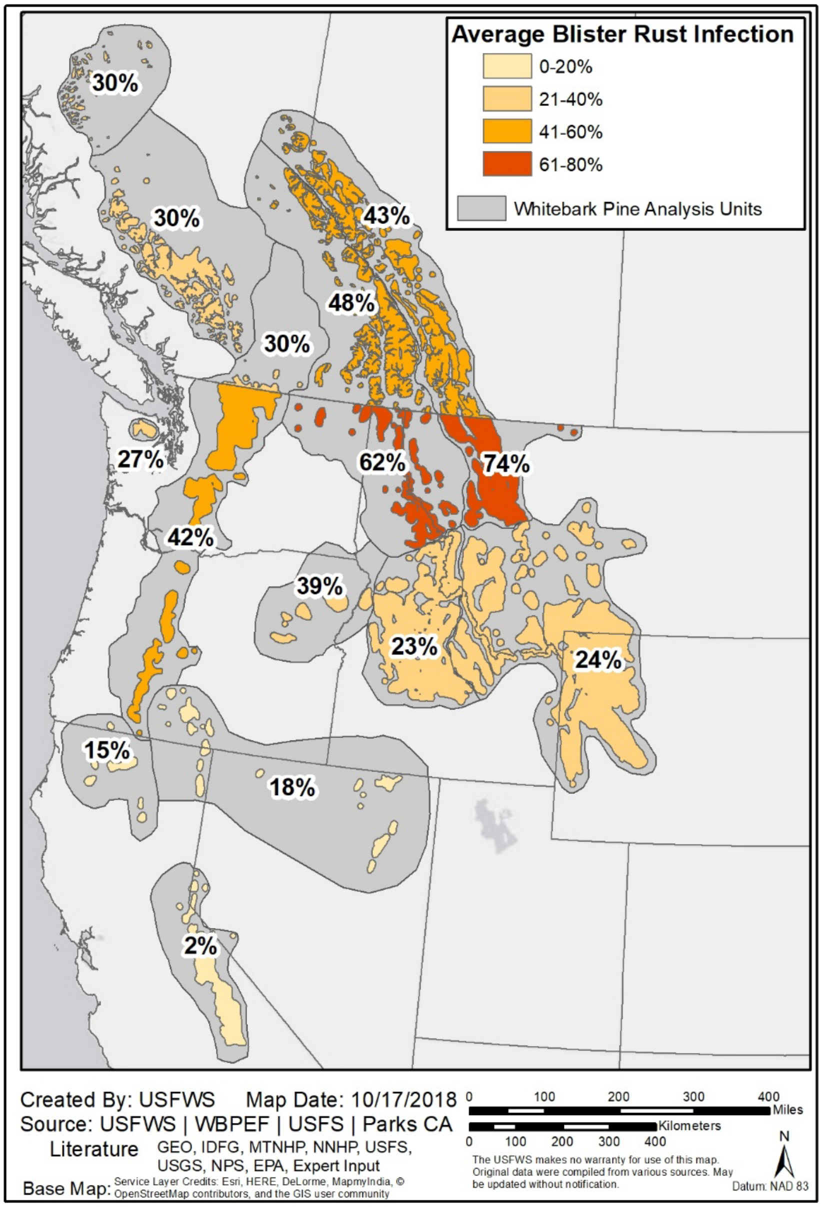

Figure 11 Average white pine blister rust infection level for each analysis unit.

Current Condition: Mountain Pine Beetle

We assessed the current impact of mountain pine beetle on whitebark pine by aggregating Aerial Detection Survey (ADS, United States) and Aerial Overview Survey (AOS, Canada) data from 1991-2016 across the range (ADS, https://foresthealth.fs.usda.gov; AOS, https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/foresthealth). As mentioned above (Chapter 2: Range and Distribution), the whitebark pine range is mapped at a coarse scale but encompasses the known distribution of species occurrence. Thus, aerial surveys are not appropriate for estimating the number of individual whitebark pine trees killed by mountain pine beetles within the whitebark pine range. However, they are very useful for determining a minimum number of hectares within the whitebark pine range that have been impacted by mountain pine beetle over time (i.e., recorded areas of beetle kill during surveys) (See Figure 6 above). Since mountain pine beetles only attack mature trees, the effects of mountain pine beetle attacks observed during aerial surveys can be interpreted as the loss of seed-producing mature trees. From 1991-2016, 5,919,276 ha of whitebark pine have been impacted by mountain pine beetle, resulting in at least 18 percent of the species' range being negatively impacted (Table 7). Similar to white pine blister rust infection, the more southern analysis units are currently less impacted by mountain pine beetle than their more northern counterparts (Figure 11). On the west coast, the Cascades, Thompson Plateau, and Fraser Plateau analysis units have had at least 25 percent of the range impacted by mountain pine beetle. Whitebark pine stands in these analysis units have seen severe reductions in reproduction and regeneration.

Table 7 Estimated hectares of whitebark pine range impacted by mountain pine beetle (MPB) in the most recent epidemic (2000-2016).

Analysis Unit (AU)	Total hectares of WBP range within AU	Hectares of WBP range impacted	Percent of WBP range impacted within each AU
Middle Rockies	9,008,418	1,990,990	22.10 percent
Idaho Batholith	4,621,881	972,358	21.04 percent
Canadian Rockies	3,660,161	341,345	9.33 percent
Cascades	2,906,758	640,851	22.05 percent
Columbia Mountains	2,849,789	309,662	10.87 percent
US Canadian Rockies	2,153,185	144,747	6.72 percent
Fraser Plateau	2,122,498	532,180	25.07 percent
Northern Rockies	1,704,834	342,764	20.11 percent
Sierras	1,292,333	66,338	5.13 percent
Basin and Range	827,089	179,645	21.72 percent
Blue Mountains	554,865	57,450	10.35 percent
Klamath Mountains	334,950	23,436	7.00 percent
Nechako Plateau	266,078	31,778	11.94 percent
Thompson Plateau	194,264	61,117	31.46 percent
Olympics	119,319	538	0 percent

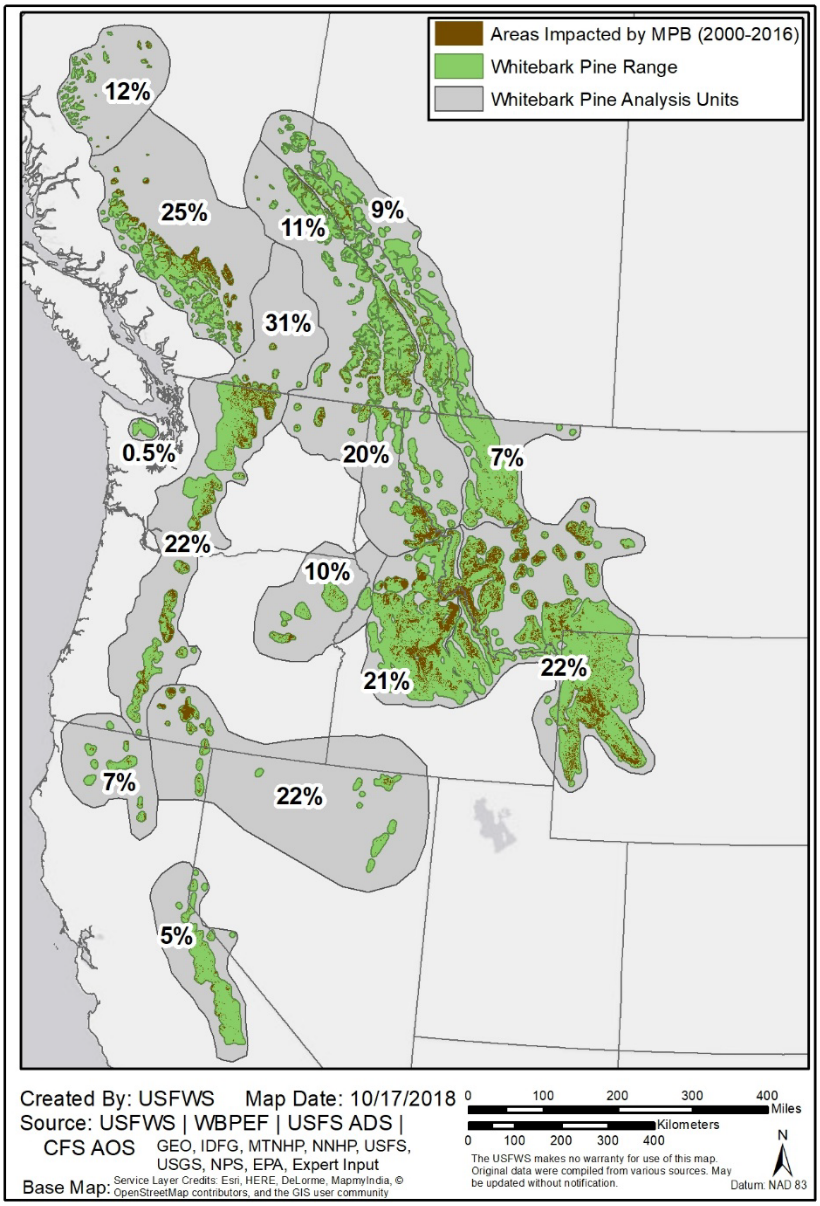

Figure 12 Areas impacted by the most recent mountain pine beetle (MPB) epidemic (2000-2016) within the whitebark pine range.

While regeneration has occurred following historical mountain pine beetle epidemics like those of the 1930s, 1940s, and 1970s, the current best available science indicates whitebark pine recovery following the most recent epidemic has been hindered due to the following factors: (1) the nearly ubiquitous presence and intensification of white pine blister rust and altered fire regimes resulting from climate change; and (4) successional replacement of whitebark pine by competitors as a result of all the above stressors combined. As a result, millions of large, cone bearing whitebark pine have been removed from vast areas of the landscape since the 1990s. In areas hardest hit by the recent epidemic, only the smaller trees not targeted by the mountain pine beetle remain for regeneration and replacement of whitebark pine stands. Unfortunately, in large portions of the range, these remaining smaller trees are subjected to white pine blister rust. Although white pine blister rust is not selective and infects all age and size classes of whitebark pine, seedlings suffer mortality more quickly (Hoff and Hagle 1990, p. 187) and some data has shown that seedlings may also be more vulnerable to white pine blister rust infection (Mahalovich 2013, p. 14; Shanahan *et al*. 2016, p. 10). Thus, in the current environment, seedlings are not susceptible to mountain pine beetle mortality but are still susceptible to white pine blister rust.

REPRESENTATION: CURRENT CONDITION

Here we discuss various factors contributing to the current levels of representation, or adaptive capability, of whitebark pine at the species level. As discussed above, representation is the range of variation found in a species, which may include ecological, genetic, morphological, and phenological diversity.

Ecological settings

Whitebark pine historically was a dominant species in upper subalpine habitats in the western United States and Canada. Whitebark pine can be found in a number of ecological settings throughout its range, mainly depending on elevation, latitude, and climate of an area. At lower to mid-slope elevations, whitebark pine is part of mixed-conifer forests typically dominated by Douglas fir and lodgepole pine, respectively. At upper-slope elevations and near treeline, krummholz whitebark pine is part of alpine plant communities (Billings 1951; Arno and Hoff 1990, p. 270). A recent analysis of rangewide data from the USFS national forest inventory (FIA) suggests that only 15 percent of the sampled areas with whitebark pine occurred in whitebark pine-dominant forest types, while the majority of whitebark pine was found predominantly within lodgepole, Englemann spruce/subalpine fir, and subalpine fir forest types (Goeking and Izlar 2018, p. 5).

Whitebark pine can occur as a climax species in cold, dry climates where there are few other species hardy enough to compete. Whitebark pine can occur as a co-climax species in less cold, less dry climates, a major seral species in warmer and wetter climates usually as a result of periodic fires, and can occur as a minor seral species in the warmest and wettest portions of its range in lower subalpine habitats, also as a result of periodic fires (see Figure 12).

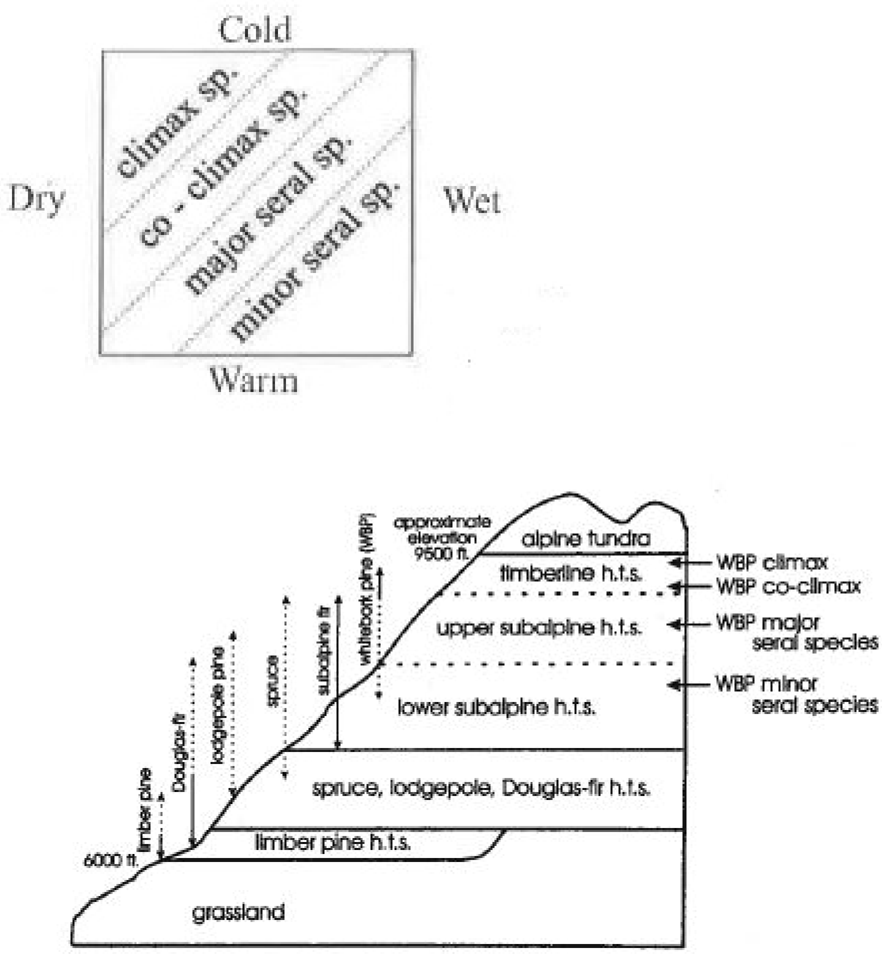

Figure 13 Successional status of whitebark pine based on moisture and temperature gradients and general elevational distribution of whitebark pine. Taken from Arno 2001, pp. 76–79 Figure 4-1 and 4-2.

Genetic diversity

Genetic diversity within a species provides the foundation for adaptation to new and changing environments. Whitebark pine has high genetic diversity relative to other conifer tree species (i.e., high representation in terms of genetic variation), with poor genetic differentiation among zones, and similar levels of diversity to other highly geographically distributed tree species in North America based on isozyme and cpDNA analysis (Mahalovich and Hipkins 2011, p. 126). Like other wind-pollinated species, whitebark pine has general random mating, and a high number of migrants (Mahalovich and Hipkins 2011, p. 129), which leads to a high value of within-population variation (Keane *et al*. 2012, p. 13). The high levels of genetic diversity within the species may be impacted through bottleneck events caused by mortality resulting from white pine blister rust, mountain pine beetle, or fires.

Whitebark pine has higher rates of inbreeding than most other wind-pollinated conifers, likely due to the close proximity of mature trees arising from clumps of seeds of related individuals or even from the same cone, suggesting that population genetic structure is driven by seed dispersal of Clark's nutcracker (Keane *et al*. 2012, p 14). Mitochondrial markers indicate that the eastern California and Nevada populations are genetically distinct from the other zones in Idaho, Montana, eastern Washington, and Wyoming (Mahalovich and Hipkins 2011, p. 125).

Morphological diversity

Whitebark pine exhibits a range of morphologies, from tall, single-stemmed trees to shrub-like krummholz forms. Older trees in open forests have diffuse, flat-topped crowns, but have narrower crowns in closed forests. Tree height typically ranges between 12-18 m (40-60 ft) at maturity, though the low shrub and krummholz form are less than 1 m (3 ft) tall (Billings 1951; Flora of North America 2021; Lackschewitz 1991) Multi-stemmed trees are also common, either from branching at the base or germination of several seeds at once (Linhart and Tomback 1985, p. 108; Weaver 2001, p. 63). The krummholz form is typical at treeline, and results from seeds germinated in leeward rock microsites or in tree islands (Tomback *et al*. 2016, p. 2).

Phenological diversity

Whitebark pine exhibits a seasonal niche with most growth occurring in the spring, followed by fruiting in summer and fall, and finally a period of inactivity during the winter. Based on a tree's genetic makeup, position latitudinally, longitudinally, and altitudinally, requirements for resources and tolerance to stress affect the timing of the seasonal patterns (Weaver 2001, p. 52). At treeline, the growing season is shorter than other portions of the whitebark pine's range, and wind-scoured snow allows soil to freeze thereby lowering root temperature and postponing spring-season bud break (Weaver 2001, p. 55). Pollination typically occurs from low to high elevation and at different times than other Pinus species (Weaver 2001, p. 64).

REDUNDANCY: CURRENT CONDITION

As discussed above, redundancy is the ability of a species to withstand catastrophic events, and is best achieved by having multiple populations widely distributed across the species' range. Whitebark pine is widely distributed, and thus this species inherently has higher levels of redundancy than many other species. Rangewide, whitebark pine occurs on an estimated 32,616,422 ha (80,596,935 ac) in western North America. Whitebark pine has a broad range both latitudinally (occurring from approximately 36° in south California to 55° north latitude in BC, Canada) and longitudinally (occurring from approximately 128° in BC, Canada to 108° east in Wyoming). The species currently occupies all 15 Analysis Units, spanning a variety of ecoregions. However, as a result of the rangewide reduction in resiliency due to the stressors discussed above, there has been a concomitant loss in species redundancy, as many areas become less able to contribute to the ability to withstand catastrophic events.

CURRENT CONDITION: SUMMARY AND INTERACTION OF FACTORS

Rangewide data from USFS FIA surveys indicate that 51 percent of all standing whitebark pine trees in the U.S. are now dead, with over half of that amount occurring approximately in the last two decades alone (Goeking and Izlar 2018, p. 7). Similarly, in all but the smallest size-classes (dbh less than 17.7 cm), dead whitebark pine trees now outnumber live ones and mortality has exceeded gross growth (volume). This large-scale reduction of live cone-producing trees has led to pervasive conditions in most AUs that fall below the estimated basal area threshold (5 m^2 ha^{-1}) that has been determined to provide a minimum number of cones to attract and retain Clark's nutcrackers during seed dispersal periods (McKinney *et al*. 2009, p. 605; Goeking and Izlar 2018, p. 12). Although causal agents of increased whitebark pine decline may be attributed variously to the stressors identified in this SSA, Wong and Daniels (2017, pp. 1939) have shown that multiple stressors, including drought, can act simultaneously to kill individual whitebark pine trees, and these synergistic effects have increased mortality rates 12-fold since the introduction of white pine blister rust.

High severity wildfires, white pine blister rust, and mountain pine beetle all act on portions of whitebark pine's range, killing individuals and limiting reproduction and regeneration (Figure 14). Interactions between these factors have further exacerbated the species' decline and have reduced its resiliency. For example, many whitebark pine stands that would otherwise have the ability to regenerate following mountain pine beetle attacks have succumbed to white pine blister rust infections. In addition to killing enormous amounts of mature trees, white pine blister rust may disproportionately kill more seedlings, limiting regeneration when infection follows mountain pine beetle attack (Mahalovich 2013, p. 14; Shanahan *et al*. 2016, p. 10, Tomback *et al*. 1995, p. 662). Conversely, trees weakened from infection or drought stress may be more susceptible to beetle-induced mortality (from both mountain pine beetle and secondary ips beetles (*Ips spp*.) (Wong and Daniels 2017, pp. 1938-1939; Dooley and Six 2015, p. 9). In whitebark pine stands that have experienced high rates of mortality, any remaining seed sources become limited, and the role of Clark's nutcrackers likely will shift from seed disperser to seed predator as they consume most of the available seeds. High-severity fires also exert greater impacts to stands that have high rates of white pine blister rust and mountain pine beetle-induced mortality by killing any remaining putatively rust-resistant trees. This reduction in resiliency is rangewide, occurring across all analysis units, with the Canadian, US, and Northern Rockies likely the most impacted.

Because the current mountain pine beetle epidemic is subsiding (see Chapter 4, Current Condition: Mountain Pine Beetle), we do expect impacts from synergistic interactions between mountain pine beetle and white pine blister rust to be measurably reduced. Importantly for the persistence of the species, reproductive individuals that show genetic resistance to white pine blister rust now have a higher probability of survival and reproduction in the absence of significant mountain pine beetle mortality. However, the number of genetically resistant individuals in some populations on the landscape may be low. At this time, there is no known way to control, reduce or eliminate either stressor, particularly at the landscape scale needed to effectively conserve this species. Thus, we expect both disease and predation to continue to impact whitebark pine. The subsidence of the most recent mountain pine beetle epidemic, however, means mortality from mountain pine beetle will play a smaller role in the near future. While the species is still wide ranging and therefore has inherently higher levels of representation and redundancy than many species, reductions to resiliency across the range are reducing the species' adaptive capacity and ability to withstand catastrophic events.

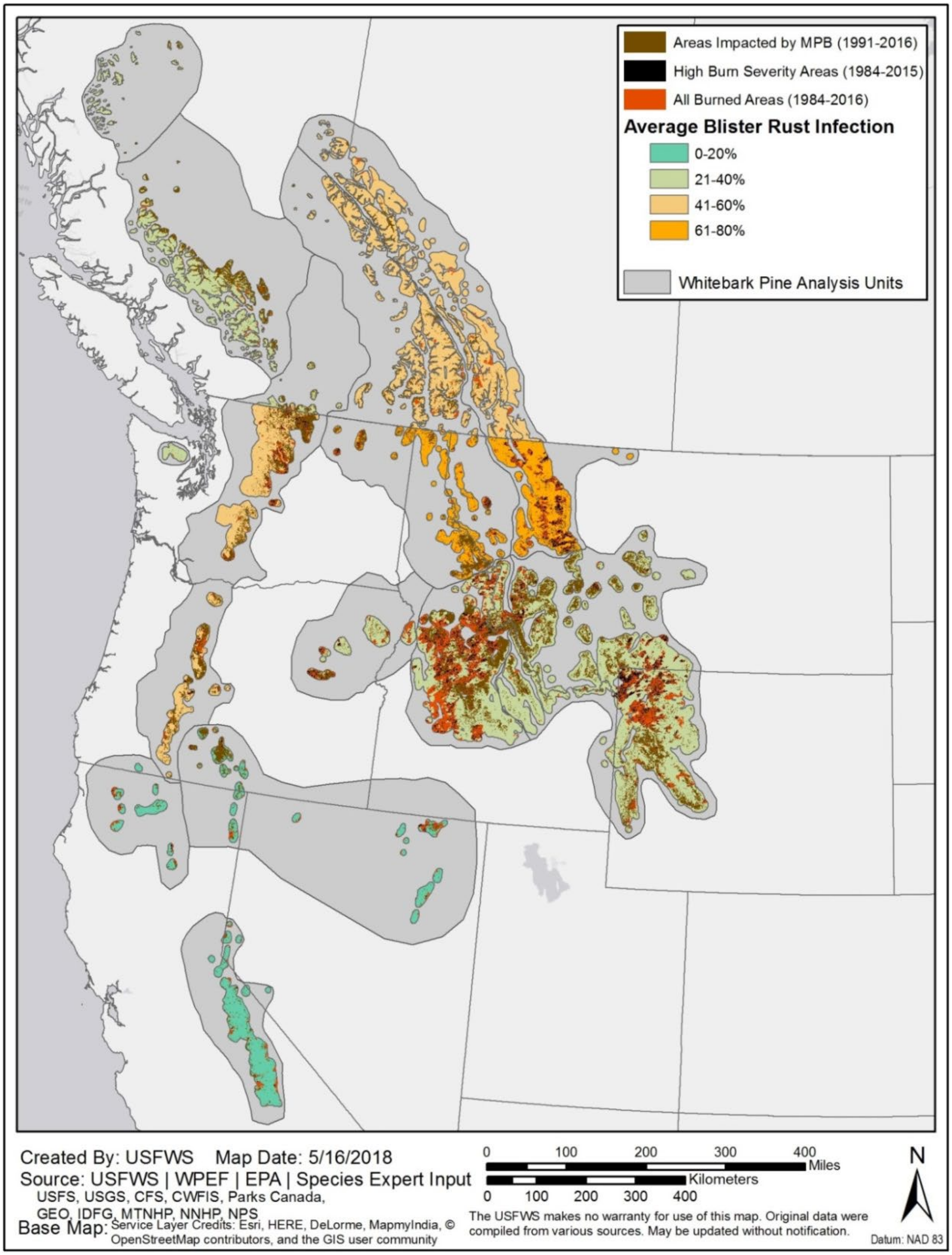

Figure 14 Areas of whitebark pine range currently affected by one, two, or three of the main stressors impacting the species viability: high severity wildfires, white pine blister rust, and mountain pine beetle.

CHAPTER 5: ANALYSIS OF FUTURE CONDITION

In this chapter, we predict the future condition of whitebark pine under three scenarios capturing a range of potential changes in the key stressors discussed above (Chapters 3-4) as well as potential benefits of conservation efforts. This analysis of future condition will help us predict how the viability of whitebark pine may change in the future.

PREDICTING FUTURE CONDITION

There is uncertainty in how each of the main stressors may impact whitebark pine into the future. There is also potential for conservation efforts to influence the future condition of the species. Therefore, to estimate impacts from the four main stressors (i.e., altered fire regimes, mountain pine beetle, white pine blister rust, and climate change), we projected impacts out to 180 years, or three generations, for each of three potential scenarios described below. These projections are forecasts of well-documented trends derived from empirical data on all four main stressors discussed in Chapter 4 (climate change, mountain pine beetle, white pine blister rust, and wildfire), including long-term geospatial data sets for severe wildfire (1984-2015) and mountain pine beetle (2000-2016). Climate change is understood to impact whitebark pine principally through its effect on the magnitude of the other three key stressors, and was therefore included in these projections as an indirect impact to whitebark pine resilience by modifying the rate of change in the other stressors. Similarly, potential levels of current and future conservation efforts were also included indirectly in these projections by varying rate of change of those stressors for which conservation could potentially have an effect (i.e., if conservation efforts were enacted, the magnitude of the stressors would be decreased in the future relative to when conservation is not enacted).

Due to the longevity and long generation time of the species, our projections of impacts go out 180 years, which corresponds to approximately three generations of whitebark pine. Whitebark pine trees are capable of producing seed cones at 20–30 years of age, with average first cone production at 40 years (Tomback and Pansing 2018, p. 7), although large cone crops usually are not produced until 60–80 years (Krugman and Jenkinson 1974, as cited in McCaughey and Tomback 2001, p. 109), Therefore, the generation time of whitebark pine is approximately 40 to 60 years (Tomback and Pansing 2018, p. 7; COSEWIC 2010, p. v).

There is inherent uncertainty in any prediction of future conditions. However, based on historical trends, there is widespread agreement among whitebark pine experts that all key stressors are likely to continue to impact whitebark pine at levels above current conditions in the future. The exact magnitude of effects from each stressor in the future is uncertain, which translates to uncertainty in predictions of whitebark pine viability in the future, and that uncertainty increases the farther those predictions are carried into the future. We identified specific areas of uncertainty which could lead to overestimates (species viability appears better than it actually is) or underestimates (species viability appears worse than it actually is) of viability (Table 8). However, despite these uncertainties, it is important to highlight that our projections are based on long-term geospatial data sets and a large body of empirical data, and the scenarios chosen encompass the full range of conditions that could plausibly occur.

Table 8 Effect of uncertainty regarding (a) severe wildfire, (b) white pine blister rust, and (c) mountain pine beetle on our analysis of species viability.

a) Stressor: Severe Wildfire			
Analysis	**Areas of Uncertainty**	**Potential effect on viability analysis**	**Supporting information**
Wildfire severity trends	Geospatial data set • Smaller fires are not included in the data • MTBS (Monitoring Trends in Burn Severity) high severity data only available on U.S. side of range • Therefore, there could be more high severity fires than shown in our analysis.	overestimate	MTBS https://www.mtbs.gov
	Level of increase in severe wildfire • Climate change models predict wildfire severity will increase, but the magnitude is unknown • Therefore, wildfire severity could increase by more or less than we predicted.	over- or underestimate	Westerling 2016, entire; Keane *et al*. 2017b, p. 18
	Population response to increase in severe wildfire • Dependent on available nearby seed source and presence of Clark's nutcrackers • Seed source dependent on MPB epidemics, presence of BR, and frequency and spatial distribution of severe fires. • Severe wildfire may eliminate rust-resistant individuals/seed sources in stands with high mortality. • Therefore, there may be more or less ability for WBP to regenerate after a fire than we predicted.	over- or underestimate	Keane *et al*. 2017b, p. 35; Keane *et al*. 2012, p. 68; Logan *et al*. 2010, p. 895; Gibson *et al*. 2008, p. 10
	Human activities • Level of wildfire due to fire suppression activities • Therefore, there could be more or less wildfire than we predicted depending on how much fire suppression is carried out.	over- or underestimate	USFS 2000, p.1; Keane *et al*. 2012, p. 68

<table>
<tr><th colspan="4">b) Stressor: White Pine Blister Rust</th></tr>
<tr><th>Analysis</th><th>Areas of Uncertainty</th><th>Potential effect on viability analysis</th><th>Supporting information</th></tr>
<tr><td rowspan="3">Changes in White pine blister rust infection</td><td>Geospatial data set
US side of data set is dated. It was created by USFS and published in 2011
Model estimate based off of WLIS (which is on the ground survey data) and environmental variable data from Daymet.
Entry of survey point data into WLIS database is voluntary; more points would improve accuracy. However, it aligns well with occurrence and severity reported in literature.
Data set was extrapolated out to our updated range.
Coarse scale average and does not reflect local conditions.
Therefore, there could be more white pine blister rust on the landscape than reflected in the data.</td><td>overestimate</td><td>USDA Forest Service, 2011, https://www.fs.usda.gov/detailfull/r1/landmanagement/gis/?cid=fsp5_030924&width=full; Parks Canada 2015; Smith et al., 2013, entire; other literature</td></tr>
<tr><td>Level of increase in BR
Rates of spread and intensification due to climate change. Moist, warm conditions promote spread and intensification. Hotter drier conditions slow spread and intensification.
Changes in alternate host (e.g., Ribes) due to climate change
Potential for changes in white pine blister rust virulence.
Therefore, white pine blister rust could increase more rapidly or more slowly than we predicted.</td><td>over- or underestimate</td><td>Schwandt et al. 2010; Keane et al. 2017b, p. 18</td></tr>
<tr><td>Population response to increase
Natural level of WBP genetic resistance and response to natural selection.
Loss of BR resistant trees to mountain pine beetle.
Loss of BR resistant individuals to increase in severe wildfire.</td><td>overestimate</td><td>Keane et al. 2017b, p. 35</td></tr>
</table>

	• Therefore, there could be fewer white pine blister rust-resistant trees on the landscape than we predicted, because they have been lost to other stressors.		
	Human activities • Level and effectiveness of restoration efforts (i.e., active cultivation and planting of genetically resistant individuals). • Therefore, there could be more or less restoration efforts, and those efforts could be more or less effective than we predicted.	over- or underestimate	

c) Stressor: Mountain Pine Beetle predation			
Analysis	**Areas of Uncertainty**	**Potential effect on viability analysis**	**Supporting information**
Changes in severity of future MPB epidemics	Geospatial data set • Not all forested lands are surveyed regularly • Wilderness areas are flown over less frequently • An individual year's survey does not represent a cumulative mortality estimate • Not specific to WBP trees, data was clipped to our updated range • Coarse scale average and does not reflect local conditions • Therefore, there could be more areas impacted by MPB than shown in the data.	overestimate	USFS ADS https://foresthealth.fs.usda.gov; British Columbia Ministry of Forests AOS https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health
	Level of increase in MPB • Climate change models predict impact of MPB epidemics will increase, but the magnitude is unknown • Therefore, impacts from MPB epidemics could increase more or less than we predicted.	over- or underestimate	Keane *et al*. 2017b, p. 18; Buotte *et al*. 2017, pp. 137–138; Sidder *et al*. 2016, p. 13.
	Population response to increase • Dependent on level of natural regeneration following epidemics • Level of natural regeneration following epidemics given presence of BR • Level of impact to individuals genetically resistant to BR • Therefore, there could be more or less regeneration after future MPB epidemics than we predicted.	over- or underestimate	Keane *et al*. 2017b, p. 18
	Human activities • Level of funding for conservation efforts that mitigate impacts from MPB • Therefore, there could be more or less future conservation efforts than we predicted.	over- or underestimate	Gibson *et al*. 2008, p. 15

DEVELOPMENT OF FUTURE SCENARIOS

For our analysis of whitebark pine's future condition, we constructed three future scenarios focused on changes in stressors and levels of conservation efforts (Table 9). These scenarios are meant to account for uncertainty by covering a breadth of future conditions that could plausibly occur within the whitebark pine range. As mentioned above (see Range and Distribution), whitebark pine has a broad range both latitudinally (occurring from approximately 36° in south California to 55° north latitude in BC, Canada) and longitudinally (occurring from approximately 128° in BC, Canada to 108° east in Wyoming) and occurs on an estimated 32,616,422 ha (80,596,935 ac). Given its extensive distribution, current impacts from stressors and levels of conservation efforts are highly variable across the range. Because of the difficulty identifying an average rangewide magnitude of key stressors, we analyzed current and future conditions of whitebark pine by analysis unit under varying scenarios to assess a range of possible conditions. Our analysis examined area of impact for all stressors to abate variation and limitations within the data, and to have a comparable analysis across all stressors. All scenarios may not be equally likely, but all are plausible given the range of values presented for each stressor in the best available scientific information.

Scenarios constructed include variation in:

1) The presence of white pine blister rust. Given historical trends, we assume in all scenarios that white pine blister rust will continue to spread and intensify throughout the range of whitebark pine. There is no information to suggest that the rate of spread or prevalence of white pine blister rust will decrease in the future. The incidence of white pine blister rust at stand, landscape, and regional scales varies due to time since introduction and environmental suitability for its development. It continues to spread into areas originally considered less suitable for persistence, and it has become a serious threat. In our future scenarios, we varied the future rate of white pine blister rust spread between one and four percent annually based on values presented in the literature (e.g., Schwandt *et al*. 2013a; Smith *et al* 2013). The percentage of genetically resistant individuals and the effectiveness and scale of management efforts to collect, propagate,

and plant genetically resistant individuals are key areas of uncertainty. Therefore, we varied the level of genetic resistance between a lower value of 10 percent and higher value of 40 percent based on a range of values presented in the literature (e.g., Mahalovich 2013, p. 33). We considered the higher 40 percent value to include both the presence of some level of natural resistance and planting of resistant individuals.

2) The frequency of high severity wildfire. Given current trends and predictions for future changes in the climate, we assume in all scenarios that the frequency of stand replacing wildfire will increase although the magnitude of that increase is uncertain (Keane *et al*. 2017b, p. 18; Westerling 2016, entire; Littell *et al*. 2010, entire). Because of that uncertainty, we choose what are likely conservative values of a 5 or 10 percent increase in severe wildfire above current annual levels (between 1984 and 2016).

3) The magnitude of future mountain pine beetle impacts. Given warming trends, we assume in all scenarios that mountain pine beetle epidemics will continue to impact whitebark pine in the future. There is no information to suggest that mountain pine beetle epidemics will decrease in magnitude or frequency in the future. In our future scenarios, we predicted a new mountain pine beetle epidemic would occur every 60 years, as that is the minimum time it would likely take for individual trees to achieve stem diameters large enough to facilitate successful mountain pine beetle brood production that is required to reach epidemic levels.

Scenario 1

Scenario 1 can be considered a continuation of current trends. Impacts from high severity fires and mountain pine beetle continue at current levels (Table 4 and 7, respectively). White pine blister rust begins at the current estimated proportion of the range infected (Table 6) and spreads at 1 percent per year with 10 percent genetic resistance. In this scenario, we assume any impacts from recent conservation activities and impacts from climate change are captured in the current condition values (See Table 4, 6, 7) that form the baseline of this scenario.

Scenario 2

In Scenario 2, high severity wildfires are increased by 5 percent over current trends. The spread of white pine blister rust continues at a relatively low annual rate (1 percent per year) and the level of genetic resistance to white pine blister rust is relatively high at 40 percent. We considered this higher level of genetic resistance could include both natural resistance and an increased resistance due to some level of conservation efforts (i.e., restoration or actively planting known genetically resistant trees). Mountain pine beetle epidemics continue to occur at 60-year intervals, but with 20 percent recruitment between epidemics.

Scenario 3

In Scenario 3, high severity wildfires are increased by 10 percent over current trends. The spread of white pine blister rust increases (4 percent per year) and only 10 percent of individuals on the landscape have genetic resistance to white pine blister rust. Mountain pine beetle epidemics continue to occur at 60-year intervals, but impacts increase by 10 percent and there is no recruitment between epidemics.

Table 9 Future scenarios focused on changes in stressors (i.e., high severity wildfires, white pine blister rust, mountain pine beetle, and indirect impacts from climate change). In these scenarios, genetic resistance includes both natural resistance and increased resistance due to conservation efforts (e.g., planting of trees resistant to white pine blister rust).

Stressor	Scenario 1 (Continuation of current trends)	Scenario 2	Scenario 3
Severe Fire	Loss of whitebark pine from high severity fires continue at rates observed from 1984-2015 (data only available for U.S portion of the range)	Increased from current trend by 5 percent due to climate change	Increased from current trend by 10 percent due to climate change
White pine blister rust	1 percent per yr spread 10 percent genetic resistance	1 percent per yr spread 40 percent genetic resistance	4 percent per yr spread 10 percent genetic resistance
Mountain Pine beetle	Severity of most recent epidemic repeats every 60 years. No recruitment.	Severity of most recent epidemic repeats every 60 years. 20 percent recruitment.	Severity of most recent epidemic + 10 percent repeats every 60 years. No recruitment.

RESULTS OF FUTURE CONDITION ANALYSIS

Confidence in future projections inherently decreases as the length of time forecast increases. For this long lived species, we forecast each scenario out to 180 years, or three generations, and present that information below. However, we will focus our discussion of viability largely on the 60-year (1 generation) timeframe where our confidence is greatest.

Results projected out to 180 years or three generations:

Under Scenario 1, loss of whitebark pine from high severity wildfire in the U.S. range increases more than 6-fold. The average white pine blister rust infection rate rangewide more than doubles and the average impact from mountain pine beetle triples (Table 10). Under Scenario 2, loss of whitebark pine from severe wildfire in the U.S. increased by 10-fold. The average rangewide white pine blister rust infection rate almost doubles. The average impact from mountain pine beetle decreases almost by half. Under Scenario 3, loss from severe wildfire in the U.S. increases by more than 12-fold. The average rangewide white pine blister rust infection rate increases almost 3-fold. The average impact from mountain pine beetle increases by 4-fold. In Figures 14-16 (Scenarios 1-3, respectively) we display these results spatially.

Table 10 Projected rangewide impact of stressors within 3 generations or 180 years under Scenario 1, 2, and 3.

	Stressor	Current	60 years	120 years	180 years
Scenario 1	Severe Fire	5 percent	15 percent	24 percent	31 percent
	White Pine Blister Rust	34 percent	61 percent	76 percent	84 percent
	Mountain Pine Beetle	17 percent	31 percent	43 percent	52 percent
Scenario 2	Severe Fire	5 percent	24 percent	38 percent	50 percent
	White Pine Blister Rust	34 percent	52 percent	62 percent	67 percent
	Mountain Pine Beetle	17 percent	15 percent	12 percent	10 percent
Scenario 3	Severe Fire	5 percent	32 percent	51 percent	64 percent
	White Pine Blister Rust	34 percent	88 percent	93 percent	93 percent
	Mountain Pine Beetle	17 percent	40 percent	56 percent	67 percent

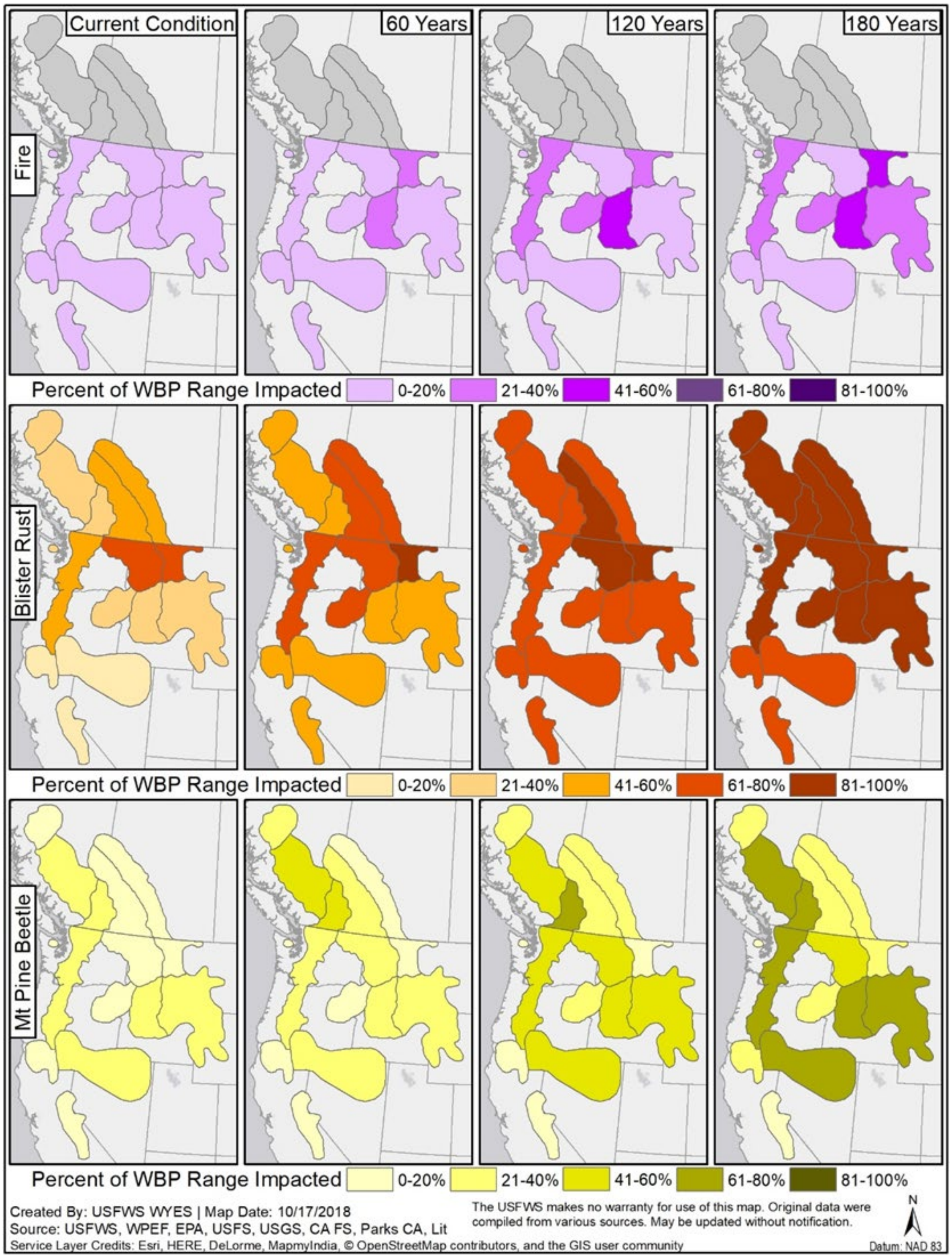

Figure 15 Percentage of the whitebark pine range impacted by severe fire, white pine blister rust, and mountain pine beetle in each analysis unit under Future Scenario 1. (No high severity wildfire data is available for the Canada portion of the range)

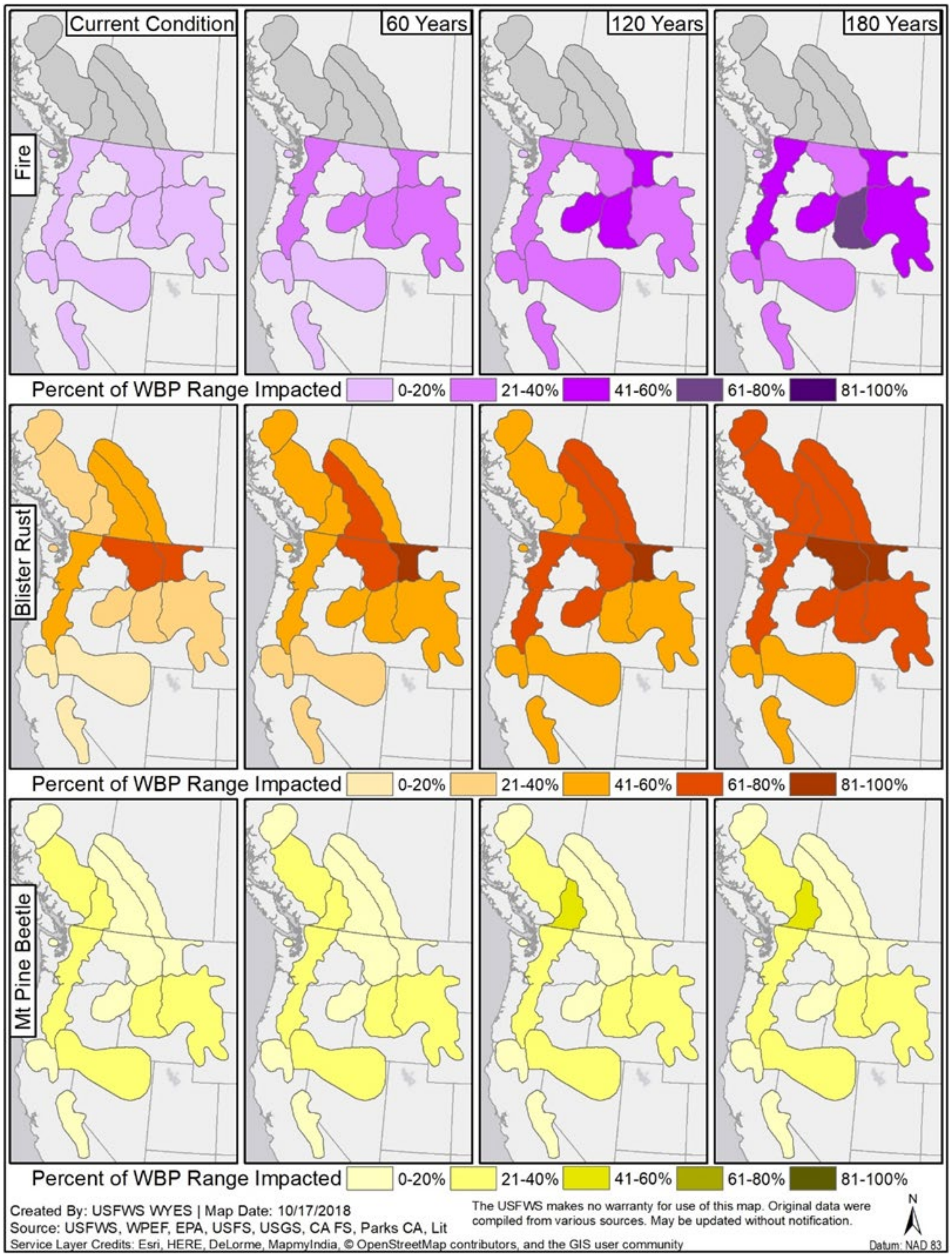

Figure 16 Percentage of the whitebark pine range impacted by severe wildfire, white pine blister rust, and mountain pine beetle in each analysis unit under Future Scenario 2. (No high severity wildfire data is available for the Canada portion of the range)

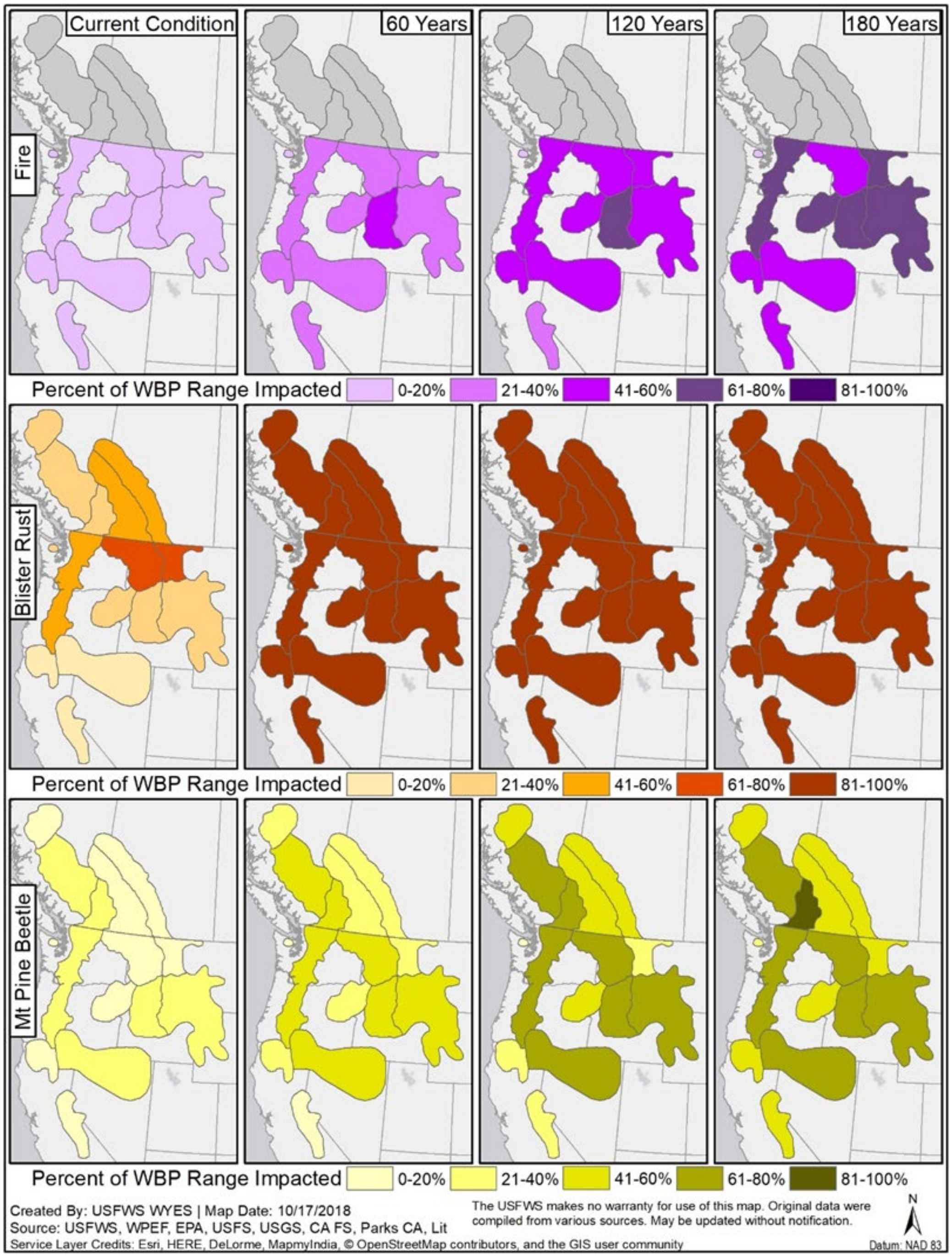

Figure 17 Percentage of the whitebark pine range impacted by severe wildfire, white pine blister rust, and mountain pine beetle in each analysis unit under Future Scenario 3. (No high severity wildfire data is available for the Canada portion of the range)

Results at the AU scale projected out to 60 years or 1 generation:

Severe Wildfire Results

Currently, none of the 10 AUs in the U.S. portion of the range (where data on severe fire is available) have experienced loss of whitebark pine from severe wildfire of over 10 percent. However, if levels of severe wildfire continue at their current rate (Scenario 1), approximately 15 percent of the U.S. whitebark pine range is estimated to be lost within the next 60 years in the absence of other stressors (Table 11).

Levels of severe wildfire are expected to increase in the future due to climate change. If severe wildfire increases by 5 percent (Scenario 2), 24 percent of the U.S. whitebark pine range will be lost in 60 years. If severe wildfire increases by 10 percent (Scenario 3), 32 percent of the U.S. whitebark pine range will be lost in 60 years. The Idaho Batholith and U.S. Canadian Rockies AUs (comprising 21 percent of the estimated U.S. range) have been most impacted by severe wildfire since 1984. If current trends continue, in the next 60 years loss of whitebark pine range in the Idaho Batholith and U.S. Canadian Rockies AUs will be 27 percent and 22 percent, respectively. The remaining eight AUs within the U.S. will experience less than 20 percent loss from severe wildfire if current trends continue. If severe wildfire increases by 5 percent (Scenario 2), five of ten AUs will experience greater than 20 percent loss from severe wildfire. If severe wildfire increases by 10 percent (Scenario 3), nine of ten AUs will experience greater than 20 percent loss from severe wildfire. Four of ten AUs (Idaho Batholith, Cascades, U.S. Canadian Rockies, and Blue Mountains; comprising 34 percent of the range) will experience greater than 30 percent loss from severe wildfire.

A continuation of current trends in high severity fires would not likely severely negatively impact whitebark pine resiliency, redundancy, or representation in the absence of other threats, as newly burned areas can potentially provide a seedbed for whitebark pine if stands of healthy cone-producing whitebark pine are nearby resulting in some level of regeneration.

Therefore, if current trends continue or increase by 5 to 10 percent, the relatively small projected increase in severe wildfire under scenarios 2 and 3, high severity fires alone (in the absence of other threats) would not likely severely negatively impact whitebark pine.

Table 11 High severity fire projected out to 60 years under Scenarios 1, 2, and 3 across the U.S. portion of the range of WBP; * denotes Canada portion of the range where we do not have data on high severity fire.

Analysis Unit	Percent of total WBP range within each AU	Percent of AU impacted under Scenario 1	Percent of AU impacted under Scenario 2	Percent of AU impacted under Scenario 3
Middle Rockies	27.6 percent	12 percent	21 percent	30 percent
Idaho Batholith	14.2 percent	27 percent	35 percent	43 percent
Canadian Rockies	11.2 percent	*	*	*
Cascades	8.9 percent	14 percent	23 percent	31 percent
Columbia Mountains	8.7 percent	*	*	*
US Canadian Rockies	6.6 percent	22 percent	30 percent	38 percent
Fraser Plateau	6.5 percent	*	*	*
Northern Rockies	5.2 percent	6 percent	16 percent	25 percent
Sierras	4.0 percent	2 percent	12 percent	21 percent
Basin and Range	2.5 percent	6 percent	15 percent	24 percent
Blue Mountains	1.7 percent	18 percent	26 percent	34 percent
Klamath Mountains	1.0 percent	8 percent	17 percent	26 percent
Nechako Plateau	0.8 percent	*	*	*
Thompson Plateau	0.6 percent	*	*	*
Olympics	0.4 percent	0 percent	0 percent	0 percent
US range		15 percent	24 percent	32 percent

White Pine Blister Rust Results

Currently, only three of 15 AUs (Basin and Range, Klamath Mountains, and Sierras; comprising 8 percent of the range) have an estimated white pine blister rust infection rate below 20 percent. If levels of white pine blister rust infection continue at their current rate of expansion (Scenario 1), approximately 61 percent of the range will be infected within the next 60 years (Table 12). All 15 AUs will have an average estimated white pine blister rust infection rate of greater than 40 percent (across 100 percent of the range). Six of the 15 analysis units (Blue Mountains, Cascades, Canadian Rockies, Columbia Mountains, Northern Rockies, U.S. Canadian Rockies; comprising 42 percent of the range) are projected to have white pine blister rust infection rates in the range of 61-80 percent.

If the rate of white pine blister rust spread is relatively slow and genetic resistance is relatively high (Scenario 2), approximately 52 percent of the range will be infected within the next 60 years. Fourteen of the 15 AUs will still have an average estimated white pine blister rust of greater than 40 percent (comprising 96 percent of the range). Three of the 15 AUs (Columbia Mountains, U.S. Canadian Rockies, Northern Rockies; comprising 21 percent of the range) are projected to have white pine blister rust infection rate in the 61-80 percent range.

If the rate of white pine blister rust spread is relatively high and genetic resistance is relatively low (Scenario 3), approximately 88 percent of the range will be infected within the next 60 years. All 15 AUs will have infections rates above 80 percent.

Table 12 White pine blister rust projected out to 60 years under Scenarios 1, 2, and 3 across the range of WBP

Analysis Unit	Percent of total WBP range within each AU	Percent of AU impacted under Scenario 1	Percent of AU impacted under Scenario 2	Percent of AU impacted under Scenario 3
Middle Rockies	27.6 percent	54 percent	44 percent	86 percent
Idaho Batholith	14.2 percent	54 percent	44 percent	86 percent
Canadian Rockies	11.2 percent	66 percent	58 percent	90 percent
Cascades	8.9 percent	65 percent	58 percent	90 percent
Columbia Mountains	8.7 percent	69 percent	62 percent	91 percent
US Canadian Rockies	6.6 percent	85 percent	81 percent	95 percent
Fraser Plateau	6.5 percent	59 percent	49 percent	88 percent
Northern Rockies	5.2 percent	78 percent	72 percent	93 percent
Sierras	4.0 percent	42 percent	29 percent	83 percent
Basin and Range	2.5 percent	51 percent	40 percent	85 percent
Blue Mountains	1.7 percent	64 percent	55 percent	89 percent
Klamath Mountains	1.0 percent	50 percent	38 percent	85 percent
Nechako Plateau	0.8 percent	59 percent	49 percent	88 percent
Thompson Plateau	0.6 percent	59 percent	49 percent	88 percent
Olympics	0.4 percent	57 percent	47 percent	87 percent
Rangewide		61 percent	52 percent	88 percent

Mountain Pine Beetle Results

Currently, a minimum of 17 percent of the whitebark pine range has been impacted by mountain pine beetle, with the majority of that mortality occurring in the most recent epidemic. If the severity of the most recent epidemic were to repeat every 60 years and there is no recruitment (Scenario 1), an estimated 31 percent of the range will be impacted by mountain pine beetle within 60 years in the absence of other stressors (Table 13). Seven of the 15 AUs (Middle

Rockies, Idaho Batholith, Cascades, Fraser Plateau, Northern Rockies, Basin and Range, Thompson Plateau; comprising 51 percent of the range) will experience an estimated mortality of greater than 30 percent.

If the severity of the most recent epidemic repeats every 60 years, but there is 20 percent recruitment between epidemics (Scenario 2), an estimated 15 percent of the range will be impacted by mountain pine beetle within 60 years. Eight of the 15 AUs (Canadian Rockies, Columbia Mountains, U.S. Canadian Rockies, Sierras, Blue Mountains, Klamath Mountains, Nechako Plateau, Olympics; comprising 34 percent of the range) will experience a negligible impact, with the remaining AUs experiencing between 20-39 percent impact.

If the severity of the most recent epidemic increases by 10 percent, and repeats every 60 years, but with no recruitment (Scenario 3), approximately 40 percent of the range will be impacted within 60 years. Seven of 15 AUs (Middle Rockies, Idaho Batholith, Cascades, Fraser Plateau, Northern Rockies, Basin and Range Thompson Plateau; comprising 66 percent of the range) will experience greater than 60 percent impact.

Table 13 Mountain pine beetle impacts projected out to 60 years under Scenarios 1, 2, and 3 across the range of WBP

Analysis Unit	Percent of total WBP range within each AU	Percent of AU impacted under Scenario 1	Percent of AU impacted under Scenario 2	Percent of AU impacted under Scenario 3
Middle Rockies	27.60 percent	39 percent	24 percent	47 percent
Idaho Batholith	14.20 percent	38 percent	22 percent	46 percent
Canadian Rockies	11.20 percent	18 percent	0 percent	27 percent
Cascades	8.90 percent	39 percent	24 percent	47 percent
Columbia Mountains	8.70 percent	21 percent	3 percent	29 percent
US Canadian Rockies	6.60 percent	13 percent	0 percent	22 percent
Fraser Plateau	6.50 percent	44 percent	29 percent	51 percent
Northern Rockies	5.20 percent	36 percent	20 percent	44 percent
Sierras	4.00 percent	10 percent	0 percent	19 percent
Basin and Range	2.50 percent	39 percent	23 percent	47 percent
Blue Mountains	1.70 percent	20 percent	2 percent	29 percent
Klamath Mountains	1.00 percent	14 percent	0 percent	23 percent
Nechako Plateau	0.80 percent	22 percent	5 percent	31 percent
Thompson Plateau	0.60 percent	53 percent	39 percent	60 percent
Olympics	0.40 percent	1 percent	0 percent	11 percent
Rangewide		31 percent	15 percent	40 percent

Synergistic and cumulative interactions between four key stressors

Although not specifically analyzed in our projections, the best available science indicates that there are strong synergistic and cumulative interactions between the four key stressors (mountain pine beetle, white pine blister rust, severe fire, and climate change), which will increase negative impacts to whitebark pine under all three scenarios. Therefore, our assessment of the future effects of each individual stressor on whitebark pine may be underestimating the total impact of these combined stressors on the species' overall viability.

Climate change and the interaction with other stressors

In addition to direct habitat loss (see Chapter 3, Climate Change), whitebark pine is expected to experience decreases in population size due to synergistic interactions as a result of climate change and other threat factors including altered fire regimes, disease, and predation (Devine *et al*. 2012, p. 55; Loehman *et al*. 2011, p.187). Whitebark pine has evolved with fire, and is therefore well-adapted to the fire regimes under which it evolved (see Altered Fire Regimes above). However, environmental changes resulting from climate change are expected to alter fire regimes resulting in decreased fire return intervals and increased pace and scale of high severity fire effects. More frequent and larger stand-replacing fires will likely negatively impact whitebark pine resiliency by reducing the probability of regeneration in many areas given the widespread incidence of poor stand health and limited seed source as a result of white pine blister rust and mountain pine beetle predation (Tomback *et al.* 2008, p. 20; Leirfallom *et al*. 2015, p. 1601). This could convert whitebark pine stands to other vegetation types (Westerling *et al*. 2006, p. 943; Leirfallom *et al.* 2015, p. 1605).

Whitebark pine also evolved with the aggressive, native mountain pine beetle. However, the life cycle of the mountain pine beetle is temperature dependent, and warming trends have resulted in unprecedented mountain pine beetle epidemics throughout the range of whitebark pine (Logan *et al.* 2003, p. 130; Logan *et al.* 2010, p. 896). At epidemic levels, mountain pine beetle outbreaks become stand-replacing events, killing 80 to 95 percent of suitable host trees, and in many parts of the whitebark pine range, those levels of mortality have already been exceeded (Gibson *et al.* 2008, p. 10; Kegley *et al.* 2011, p. 87). Even populations of whitebark pine once considered to occur outside the typical range of mountain pine beetles s have been severely impacted; mountain pine beetles have moved into areas previously climatically inhospitable for epidemic-level mountain pine beetle population growth (Carroll *et al*. 2003 in Gibson *et al.* 2008, p. 4; Raffa *et al.* 2008, p. 503; Logan *et al.* 2010, p. 895). As discussed in Chapter 3, recent monitoring data indicates that the current mountain pine beetle epidemic and associated mortality is waning rangewide. However, given ongoing and predicted environmental changes resulting from global climate change, we expect the expansion of habitat favorable to mountain pine beetle (and mountain pine beetle epidemics) due to higher temperatures and drought stress in the future (Buotte *et al*. 2016, p. 1).

As identified in Chapter 3, fire historically played an integral role in shaping the evolution of whitebark pine. However, climate change has resulted in an increase in extent and frequency of high severity wildfire effects. We expect that changing fire regimes will continue to affect the species. Whitebark pine can regenerate, even following stand-replacing burns, if a seed source is available. However, widespread predation and disease currently impacting whitebark pine are limiting available seed sources, reducing the probability of regeneration following increasing wildfire episodes, and reducing the ability of seedlings to survive (Leirfallom *et al.* 2015, pp. 1603–1605).

The pace of predicted climate change will outpace many plant species' abilities to respond to the concomitant habitat changes. Whitebark pine is potentially vulnerable to warming temperatures because it is adapted to cool, high-elevation habitats. Therefore, current and anticipated warming is expected to make its current habitat unsuitable for whitebark pine, either directly or indirectly as conditions become more favorable to whitebark pine competitors, such as subalpine fir or mountain hemlock. The rate of migration needed to respond to predicted climate change will be significant (Malcolm *et al.* 2002, pp. 844–845; McKenney *et al.* 2007, p. 941). It is not known whether whitebark pine is capable of migrating at a pace sufficient to move to areas that are more favorable to survival as a result of climate change. It is also not known the degree to which Clark's nutcracker could facilitate this migration. In addition, the presence of significant white pine blister rust infection in the northern range of whitebark pine could serve as a barrier to effective northward migration. In summary, the impacts of climate change interact with other stressors such as mountain pine beetle epidemics and wildfire, resulting in habitat loss and population decline.

The Interaction of Fire with other Stressors

High-severity fires can have negative consequences for whitebark pine. Large increases in the frequency and extent of high severity wildfire have been documented and are particularly pronounced in forests of the Northern Rockies, which account for 60 percent of documented increases in large fires (Westerling *et al*. 2006, pp. 941, 943). Much of the increase has been independent of past management activities and, thus, appears to be a direct result of warming trends in the last several decades (Westerling *et al*. 2006, p. 943). Large, high-severity wildfires burned within the whitebark pine overall range in central Idaho in 2007, 2010, 2012, and 2013 (USFS 2016). In Montana, natural regeneration of whitebark pine following stand replacement fires of over 100 ha (247 ac) was sparse when nearby seed sources were limited due to disease and mountain pine beetle damage and mortality (Leirfallom *et al*. 2015, p. 1603).

Mountain Pine Beetle interaction with White Pine Blister Rust

As stated above, mountain pine beetle is a native herbivore that has been an important component of natural forest disturbance throughout recorded history. At endemic levels the mountain pine beetle removes relatively small numbers of trees, changing stand structure and species composition in localized areas. At epidemic levels mountain pine beetle can create stand-replacing events, killing almost all the large diameter, reproductive pines at landscape scales. "Ghost forests" of dead whitebark pine demonstrate that the species experienced mountain pine beetle epidemics in the 1930s, 1940s, and 1970s, yet significant regeneration and recovery of some whitebark pine stands followed these events. The current best available science, however, indicates whitebark pine recovery following the most recent epidemic has been hindered due to the nearly ubiquitous presence and intensification of white pine blister rust.

As expected, during the most recent epidemic, mountain pine beetles preferentially attacked and killed large diameter trees. As a result, since the 1990s many millions of large, cone bearing whitebark pine have been removed from vast areas of the landscape. Currently, in areas hardest hit by the mountain pine beetle, only the smaller trees not targeted by the mountain pine beetle are left for regeneration and replacement of whitebark pine stands. However, studies have observed significant seedling and sapling recruitment following mountain pine beetle outbreaks

(Larson and Kipfmueller 2010, p. 482). Unfortunately, in large portions of the range, these remaining smaller trees are subjected to white pine blister rust. Although white pine blister rust is not selective and infects all age and size classes of whitebark pine, seedlings have been shown to be more vulnerable to white pine blister rust infection and mortality (Mahalovich 2013, p. 14; Tomback *et al*. 1995, p. 662). Thus, in the current environment, the seedlings and saplings that escaped mountain pine beetle mortality are still susceptible to white pine blister rust, and the possibility of natural regeneration following mountain pine beetle epidemics is likely decreased in many areas.

Importantly, the latest mountain pine beetle epidemic and white pine blister rust have impacted the probability of whitebark pine regeneration because both have resulted in severely decreased seed cone production. Whitebark pine rely almost exclusively on Clark’s nutcrackers for seed dispersal, however, in years when seed production is low, the bird becomes essentially a seed predator, leaving few seeds left available for germination (Barringer *et al*. 2012, p.8; McKinney and Tomback 2007, p.1045; McKinney *et al.* 2009, p. 598). Clark’s nutcrackers also are able to assess cone crops, and will abandon sites with low seed production, which reduces the probability of whitebark pine regeneration in areas with widespread mortality from the most recent mountain pine beetle epidemic. Of concern, recent research has shown that Clark's nutcracker exhibited no breeding in years following low cone production, which could result in population-level declines of the bird in the future given areas of widespread whitebark pine mortality from the mountain pine beetle and other sources like white pine blister rust (Schaming 2015, pp. 15–16). Additionally, a reduction in the density of cone producing whitebark pine can disrupt masting patterns and reduce seed cone maturity, further exacerbating impacts from other seed-reducing stressors (Rapp *et al*. 2013, pp 1348–1349). Eventually, the proportion of seeds taken by seed predators becomes too high to allow regeneration.

The USFS, NPS, BLM, and other researchers have several long-term monitoring projects with baseline data that can be compared to information being gathered on whitebark pine health and regeneration following this most recent mountain pine beetle epidemic (See Conservation Measures Planned or Implemented). Monitoring results, however, are limited and in early stages given that the epidemic has just recently begun to subside. On 42 whitebark pine stands in Idaho, Montana, and Wyoming, following significant mountain pine beetle mortality, white pine blister rust infection levels on whitebark pine regeneration (trees less than 5 inches in diameter) ranged from 0 to 81 percent (Kegley *et al*. 2011, pp. 88–89). Regeneration of other tree species, predominantly subalpine fir, outnumbered whitebark pine in 69 percent of areas, and it was estimated that 57 percent of the stands surveyed would likely convert from whitebark pine to other stand types without active restoration (Kegley *et al*. 2011, p. 92). Preliminary data collected following mountain pine beetle epidemics in parts of Idaho, Wyoming, and Montana, show substantial whitebark pine mortality and a predominance of subalpine fir regeneration (Schotzko *et al*. 2012). In the National Parks within the Pacific West Region, white pine blister rust was found to be common in all parks except Kings Canyon and Sequoia National Parks in the Sierra Nevada, while mountain pine beetle was present at low levels at all parks (Jules *et al*., 2020, p. 134).

Most remaining high-elevation whitebark pine stands in the U.S. Intermountain West that are climax communities have little regeneration (Kendall and Keane 2001, p. 228). In contrast, new and advanced whitebark pine regeneration was documented on the majority of plots in southwestern Montana and eastern Oregon, indicating that the Wallowa and Pioneer Mountains sites seem to be more vigorous and to be regenerating better than sites farther north in the Rockies (Larson 2007, pp. 16–18). However, there is much whitebark pine site variability and the regeneration on some of these sites was preceded by a particularly large cone crop in 2006. In addition, as seedlings grow, their increased foliage surface area becomes a larger target for infection by white pine blister rust spores (Tomback *et al*. 1995, p. 662). Therefore, despite observed regeneration, the level of effective regeneration (i.e., seedlings that will actually reach a reproductive age) is questionable given the high incidence of white pine blister rust currently on the landscape. We conclude that whitebark pine regeneration will generally be less successful in the future than it has been in the past.

There is no known way to control, reduce, or eliminate either mountain pine beetle or white pine blister rust at this time, particularly at the landscape scale needed to effectively conserve this species. Thus, we expect both disease and mountain pine beetle predation to continue to impact the resiliency of whitebark pine. The subsidence of the most recent mountain pine beetle epidemic, however, means mountain pine beetle predation will play a smaller role in the near future.

Summary of Future Conditions Analysis

Based our analyses above, whitebark pine viability has declined over time, and continuation of current trends and synergistic and cumulative interactions between wildfire, white pine blister rust, mountain pine beetle and climate change will continue to result in actual or functional loss of populations. We recognize that our projections of each of the stressors are based on averages of the best available data applied across very large areas of the range (i.e., at the analysis unit scale). We acknowledge that there may be significant differences and a large degree of variation when examining stressors at smaller landscape or stand scales. For example, as mentioned above (See Chapter 3: White pine blister rust) the spreading of white pine blister rust spores depends on the distribution of hosts, the microclimate, and the different genotypes of white pine blister rust and hosts (McDonald and Hoff 2001, pp. 193, 202). Local meteorological conditions also may be important factors in infection success, infection periodicity, and disease intensity (Jacobi *et al*. 2010, p. 41). In other words, some areas may have higher or lower rates of white pine blister rust spread than the 1 to 4 percent spread per year (reported in the literature) that we have applied broadly at the analysis unit scale in our 3 scenarios. We also recognize that as a result of the highly heterogeneous ecological settings of this widespread species (e.g., difference in topography, elevation, weather, and climate) and geographic variation in levels of genetic resistance to blister rust, trajectories for rates of whitebark pine decline will likely vary for each analysis unit.

However, despite the limitations inherent in our future condition analysis, we have relied on the best available science to examine the status of whitebark pine at a rangewide scale. We also note that our results are generally consistent with other modeling efforts we are aware of; all of which project continued decline of whitebark pine (e.g., Angeli and McGowan, in prep.; Keane *et al*. 2017b; Hatala *et al*. 2011; Warwell *et al* 2007). In summary, the abundance of whitebark pine is projected to decline over time under all three scenarios we considered. In these scenarios, the rate of decline appeared to be most sensitive to the rate of white pine blister rust spread, the presence of genetically resistant individuals (whether natural or due to conservation efforts) and the level of regeneration.

SPECIES VIABILITY

We have considered what whitebark pine needs for viability (Chapter 2) and have evaluated the species' current condition in relation to those needs (Chapter 4). We also forecast how the species' condition may change in the future under three different scenarios (Chapter 5). In this section, we synthesize the results from our future condition analyses and discuss the potential consequences for the future viability of whitebark pine. We assess the viability of the species by evaluating the ability of the species to maintain a sufficient number and distribution of healthy populations to withstand environmental stochasticity (resiliency), catastrophes (redundancy), and changes in its environment (representation) into the future.

Resiliency

Resiliency is the ability of populations to tolerate natural, annual variation (stochasticity) in their environment and to recover from periodic disturbance.

Our predictions of future conditions varied under our three future condition scenarios, but under all scenarios, we predict all Analysis Units will have a reduced level of resiliency in the future. This reduction in resiliency will be the result of continued increase in white pine blister rust infection, synergistic and cumulative interactions between white pine blister rust and other stressors, and the resulting loss of seed source and subsequently lower regeneration. White pine blister rust is currently ubiquitous across the range, and under all three future condition scenarios it is expected to expand significantly. Under the three scenarios, within one generation, 52-88 percent of the range will be infected, and within three generations 67-93 percent of the range will be infected. These combined impacts will reduce the ability of whitebark pine stands to regenerate following disturbances, such as fire and mountain pine beetle outbreaks.

Redundancy

Redundancy is the ability of a species to withstand catastrophic events. Redundancy is measured by the duplication and distribution of populations across the range of the species.

Whitebark pine remains widely distributed across the spatial extent and ecological settings of its historical range. However, populations are likely becoming more fragmented and isolated due to increased mortality and functional extirpation as a result of white pine blister rust, the most recent mountain pine beetle epidemic, and altered fire regimes. Under all three future scenarios, we predict redundancy will decline. That decline will be most pronounced in the northern two-thirds of the whitebark pine range where white pine blister rust infection rates are predicted to be highest. As fewer populations persist and the spatial extent and connectivity of the species declines, the species' ability to withstand catastrophic events and changes in its environment is likely to be greatly reduced.

Representation

Representation is the ability of a species to adapt to changing physical (climate, habitat) and biological (diseases, predators) conditions. It can be thought of as the 'adaptability' of the species.

A species' representation is measured by looking at the genetic, morphological, behavioral, and ecological diversity within and among populations across its range. The more representation, or diversity, a species has, the more likely it is to persist in changing environments. Whitebark pine still occupies its historical range and all of the varied habitats within it. However, in all three future scenarios we predict whitebark pine representation will likely decrease. This reduction in representation will be the result of continued increase in white pine blister rust infection and associated mortality, synergistic and cumulative interactions between white pine blister rust and other stressors and the resulting loss of seed source.

Appendix A: Management and Restoration

RESTORATION PLANS

Due to the broad distribution of whitebark pine in the United States, management of this species falls under numerous jurisdictions that encompass a spectrum of local and regional ecological, climatic, and management conditions and needs. Several management and restoration plans have been developed for specific regions or jurisdictions to address the task of conserving and restoring this widespread, long-lived species. Some plans overlap in their respective regions of concern, and can often be duplicative in their guidance. Conversely, some areas within the range of whitebark pine do not have a specific management plan for whitebark pine (e.g., central Idaho). Within the United States, management actions in these areas without a species-specific management plan would generally follow established forest or vegetation management plans developed under the National Forest Management Act of 1976 or other similar policies (e.g., National Forest land management plans, National Park Service vegetation management plans).

Additionally, many organizations, States, agencies, Tribes, and local entities have begun to implement local conservation and restoration programs for whitebark pine, including conservation on private lands, State Forest Action Plans, and other small-scale restoration projects. While these programs may provide some localized benefits to the species, they do not currently provide a reduction of the influence of stressors at the species-scale across the 32-million hectare range of the species. Moreover, the primary stressors have continued to spread and are predicted to increase in prevalence in the future. Specifically, white pine blister rust is already ubiquitous rangewide, and there is currently no effective method to reverse it on a meaningful scale.

The following are some of the most prominent guidance documents published or in development to-date, including some of the recent accomplishments achieved utilizing these plans (accomplishments prior to those outlined here can be found in the 2016 Whitebark Pine Candidate Notice of Review).

National Whitebark Pine Restoration Plan (in development; anticipated completion in 2022

A comprehensive and consensus-based strategic restoration plan is currently being developed to address the significant logistical and financial constraints inherent to whitebark pine restoration activities. This collaborative effort is being led by the U.S. Forest Service, the Whitebark Pine Ecosystem Foundation, and American Forests, with participation and input solicited from all vested agencies, non-governmental organizations, tribes, and individuals. This plan will designate priority core areas within broader administrative units (e.g., National Forests, National Parks, etc.), to comprise of 20-30 percent of the total whitebark pine distribution within each unit. Specific restoration protocols will then be developed for each priority core area, allowing for flexibility to accommodate specific physical conditions, resource needs and constraints inherent to each. Implementation costs will be assessed for these protocols so that budgetary and planning concerns can be sufficiently addressed prior to implementation of the plan. Also included will be strategies for monitoring and adaptive management, as well as a comprehensive GIS database that will support spatial and non-spatial data in a publicly available format. A national kick-off summit was held in November 2017 in Missoula, MT, that brought together managers and other participants from the U.S. Forest Service, National Park Service, Bureau of Land Management, U.S. Fish and Wildlife Service, tribal governments, and NGOs to begin the formal planning process. A draft plan is anticipated to be completed in the fall of 2019.

Climate Change Vulnerability and Adaptation in the Northern Rocky Mountains (2018)

This comprehensive document was developed by the Northern Rockies Adaptation Partnership to identify climate change issues, develop solutions to minimize the effects of climate change, and facilitate ecosystem change in response to warmer climates in the Northern Rockies region of the U.S. The response to current and predicted climate change of whitebark pine and the stressors that act upon it are presented, highlighting the perilous outlook of the species and the inherent challenges of protecting and restoring what currently remains on the landscape. It also offers the primary adaptive tactics, restoration potential, and management recommendations in general terms, largely building upon specific strategies developed in species and region-specific plans identified below.

U.S. Forest Service Restoring Whitebark Pine Ecosystems in the Face of Climate Change (2017)

This is a companion document for the earlier-published (2012) Range-wide Strategy for Whitebark Pine (Strategy) outlined below, which did not address climate change effects on whitebark pine communities and restoration strategies. This document utilizes the same concepts described in the Strategy, and applies those concepts to modeled future climate-impacted scenarios. Guidelines for developing adaptation strategies for restoration were developed from a comprehensive literature review, as well as a spatially explicit, ecological process model that simulated future climate change, management, and fire behavior and treatment scenarios. Strategies developed in this document are intended to be implemented at fine scales (e.g., stand-level) of management.

Guidelines and Best Practices for Managing Fire in Whitebark Pine Stands in the Crown of the Continent (Final Draft 2017)

This guide is a product of the Crown of the Continent Ecosystem (CCE) High Five Working Group, an international consortium of Federal, state, and provincial government agencies, tribal and First Nations, industry, and non-profit interests. It details strategies and techniques for managing both prescribed fire and wildfire to support restoration of whitebark pine within the CCE. This is intended to be a precursor to and supportive of the eventual development of a full restoration plan for all five-needle pines in the CCE. A rangewide version of these guidelines will likely be published in 2019 (Keane, in review).

Conservation and Management of Whitebark Pine Ecosystems on Bureau of Land Management Lands in the Western United States (2016)

This reference is adapted and developed from the Range-wide Strategy (2012), the Whitebark Pine Strategy for the Greater Yellowstone Area (2011), and the USFS Pacific Northwest Region Strategy (2008) (all described below), and provides general guidance for whitebark pine restoration on Bureau of Land Management (BLM) administered lands. This plan acknowledges and accounts for the uniqueness of whitebark pine communities that occur on BLM lands, which often occur on the periphery of major core areas, on the margins of the species' range, at lower elevations, and in isolated stands.

In 2016, the BLM identified 51 "plus" trees amongst four states, while multiple districts in Montana and Wyoming began cone, pollen, and scion collections, established new permanent monitoring plots, and initiated new and completed existing inventories that were initiated prior to the publication of this plan. In 2017, approximately 100 ac in Wyoming were treated to reduce competition and fire severity, while a three-year effort to plant over 7500 seedlings on 20 ac in the Dillon district was completed. Verbenone is applied annually to all "plus" trees in the Missoula district, and on 300-plus ac in the Dillon district. "Plus" trees have also been identified on the BLM-managed Hunt Mountain Area of Critical Environmental Concern on in eastern Oregon, though cone collections have not yet taken place.

Adaptive Action Plan, Whitebark Pine in the Greater Yellowstone Area (rev. 2015)

This document is an extension of and based on the Whitebark Pine Strategy for the Greater Yellowstone Area (2011) (outlined below). By addressing recent developments of the understanding of whitebark pine systems, it provides an up-to-date plan to address ongoing conservation efforts in the Greater Yellowstone Area (GYA). It also provides updated target areas (with maps) most suited for restoration, and includes more current and detailed discussion on the impacts of climate change.

Annual monitoring efforts, begun in 2004, continue on Federal lands throughout the GYA. Cone collections yielded 70-140 bushels from across the entire region in 2016, while pollen and scion collections were conducted in Yellowstone and Grand Teton National Parks, as well as the Caribou-Targhee and Custer-Gallatin National Forests. Verbenone has been used extensively throughout the GYA, while Carbaryl was utilized only on the Shoshone and Custer-Gallatin National Forests. The Bridger-Teton National Forest manually treated 188 ac of whitebark pine habitat. Approximately 80,000 seedlings were planted on National Forest lands in the GYA in 2016 and 2017, including 40,000 alone in 2017 planted to rehabilitate the Burroughs Creek Fire on the Shoshone National Forest.

Crater Lake National Park Whitebark Pine Conservation Plan (2014)

This document presents a formalized strategy for conserving whitebark pine in Crater Lake National Park. It describes the current status and associated research and monitoring of whitebark pine in the Park, while providing management goals and objectives to guide conservation and restoration efforts. Some of these goals include facilitating adaption to climate change, adaptive management strategies, specifying roles of those tasked with managing the program, as well as engaging the public through education and outreach.

In addition to annual monitoring at long-term and restoration planting sites, nine new "plus" trees were identified and utilized for cone collection in 2016, with five previously identified "plus" trees also targeted for collection. Approximately 482 seedlings were planted in the Park in 2016 as well. Verbenone was applied on 192 trees, an increase from the preceding two years.

U.S. Forest Service Range-wide Restoration Strategy for Whitebark Pine (2012)

This reference document provides a top-down, multi-scale approach for prioritizing, designing, implementing, and assessing whitebark pine restoration strategies across its range in the U.S. and Canada. The goal of this guide is to promote inter- and intra-agency coordination to improve efficiency of whitebark pine restoration activities. Four main principles are applied to each spatial scale under consideration: (1) promote white pine blister rust resistance; (2) conserve genetic diversity; (3) save seed sources; and (4) employ restoration treatments. Strategic plans are presented for broad-scale strategies, and real-world examples are provided for finer scale situations (e.g., tree or stand level). As this plan encompasses the entire range of whitebark pine and is utilized by multiple agencies, recent accomplishments conducted using this guidance are too numerous to detail here.

Whitebark Pine Strategy for the Greater Yellowstone Area (2011)

Prepared by the Whitebark Pine Subcommittee of the Greater Yellowstone Coordinating Committee, a collaborative partnership of Federal, state, university and non-profit representatives, this living document provides guidance to "…promote the persistence of whitebark pine over time and space in the Greater Yellowstone Area." The primary goals of this strategy are to (1) assess the current conditions of whitebark pine in the GYA; (2) define criteria to identify priority areas; (3) identify techniques and guidelines to protect and restore whitebark pine; and (4) facilitate communication and distribution of information. An initial three-year action plan is provided to guide protection and restoration activities throughout the GYA, and gives examples of various tools and techniques available to achieve identified actions. Recent accomplishments under this strategy are provided above under the Adaptive Action Plan describe above.

Whitebark Pine Restoration Strategy for the Pacific Northwest Region 2009-2013 (2008)

This plan was developed to address whitebark restoration on USFS administered lands in Washington and Oregon (USFS Region 6). Its stated goal is to "restore and conserve a network of viable populations of whitebark pine and associated species across the Pacific Northwest." Five priority actions are identified as part of a five year restoration plan, including (1) restoration of whitebark pine habitats affected by the primary stressors; (2) collect seeds from across the region and place them in long-term storage; (3) increase the levels of genetic resistance to white pine blister rust through various means; (4) evaluate stands with unknown parameters; and (5) work within and between agencies to enhance understanding of the cumulative impact of primary stressors under current and future conditions. This document also presents results of a comprehensive assessment of the status of whitebark pine on USFS lands in Region 6, which provides the basis for proposed restoration actions.

An updated revision of this plan is currently in development, but management activities in Region 6 have continued to follow the guidance of this version. Nearly all of the National Forests in Region 6 collected cones in 2016, from five trees on the Deschutes National Forest to 87 trees on the Fremont-Winema National Forest. The Fremont-Winema National Forest also manually treated 665 ac of whitebark pine habitat to reduce competition and improve fuel loadings, and established two baseline transects in a recently completed timber harvest unit to monitor the response of whitebark pine trees left on site. Verbenone was applied to "plus" trees on the Malheur and Umatilla National Forests, which were the only forests to not collect cones in 2016. The Deschutes National Forest also installed eight interpretive trail signs that included information on whitebark pine ecology, and hosted a television series that highlighted whitebark pine conservation in the area.

Flathead Indian Reservation Forest Management Plan (2000)

This plan includes specific recommendations for management of the 110,000 ac of whitebark pine forests on the Flathead Indian Reservation, Montana. It highlights the significant cultural importance of whitebark pine to the Salish Tribes, who used the seeds as a vital food source, as well as myriad wildlife uses. It also documents the decline of the species due to fire exclusion policies and white pine blister rust, and suggests it may disappear altogether from some areas within the reservation if active management is not implemented. To this end, this plan proposes the following activities to address the threats facing whitebark pine: (1) map the extent of whitebark pine; (2) reintroduce periodic fire to whitebark pine habitats with target return intervals of 35 to 50 years; (3) protect rust-resistant individuals from timber harvest whenever possible.

Recently, the Confederated Salish and Kootenai Tribes have begun collecting cones from two healthy stands of whitebark pine, and have begun an active search for additional "plus" trees on tribal lands. The Tribes also operate their own tree nursery where they grow some of their own whitebark pine seedling stock, which are continually outplanted as warranted. A study is under way that aims to reconstruct historic fire patterns in whitebark pine habitat by analyzing fire scars on living and dead whitebark pines. Plans are also being made to establish a high-elevation whitebark pine seed orchard. Traditional knowledge of whitebark pine ecosystems is being passed on through youth educational programs, and by including youth in restoration activities.

RESTORATION STRATEGIES

Most current management focuses on producing whitebark pine with inherited (genetic) resistance to white pine blister rust, as well as protecting rust-resistant trees from wildfire and increasing resistance and resilience of whitebark pine stands to stand-replacing wildfire. Additional research investigates natural regeneration and silvicultural treatments, such as appropriate site selection and preparation, pruning, and thinning in order to protect high-value genetic resources, increase reproduction, reduce white pine blister rust damage, and increase stand volume (Zeglen *et al*. 2010, p. 361). Conservation measures for whitebark pine can generally be categorized as either protection (of existing healthy trees and stands) or restoration (of damaged, unhealthy, or extirpated trees and stands). Inventory, monitoring, and mapping of whitebark pine stands are critical for assessing the current status and implementing conservation strategies. Each of these strategies is described in more detail below.

Protection

Protection measures are usually employed at the individual tree level to guard critical sources of rust-resistant genotypes (i.e., "plus" trees) from the threats of white pine blister rust, mountain pine beetles, seed predation, and wildfire. While no measures are known to protect against white pine blister rust infection, infected branches (flagging) can be pruned from the tree to delay or prevent further infection or mortality of the tree. High-value trees can be protected from mountain pine beetle attack by application of insecticides or anti-aggregation pheromones. Carbaryl is a highly effective insecticide that is sometimes used for this purpose, but requires either locations with vehicle access, or pack animals to access more difficult to reach locations. Verbenone is a commonly used anti-aggregation pheromone that can offer short-term effectiveness for preventing mass beetle attacks on and around high-value trees, and has multiple delivery methods for both tree and stand level applications. However, its effectiveness can be overwhelmed during extreme epidemics (Progar 2005, p. 1405; Progar *et al.* 2013, pp. 224–225). Cones slated for collection from "plus" trees are routinely protected from seed predation by red squirrels and Clark's nutcrackers by wrapping cone bundles in wire mesh (hardware cloth) cages early in the growing season. These must be installed by certified tree climbers, or if feasible, by a boom and bucket truck, and thus this activity can be costly and time-consuming, yet it remains highly effective and the only proven method to protect valuable natural sources of rust-resistant seed. Protecting individual trees from wildfire involves removal of ladder fuels from a specified distance around the tree (daylighting). In the past, attempts to protect individual trees by wrapping them in fire shelter material proved ineffective (Keane and Parsons 2010, p. 5, Keane *et al*. 2012, p. 81).

Due to the inherent challenges involved in utilizing carbaryl insecticide, it has only been used on a limited number of occasions in the past two years to protect "plus" trees on the Custer-Gallatin and Shoshone National Forests. However, verbenone has been used much more extensively by the USFS, BLM, and NPS due to its relative ease of use and ability to be deployed in wilderness areas (if allowed by local management guidelines). Most "plus" trees are treated with verbenone to protect the important cone crops from loss to mountain pine beetles.

Restoration

Restoration strategies are multi-faceted but employed consistently throughout whitebark pine's range and across most management agencies. These strategies are broadly defined by two actions: propagation, screening, and planting of seedlings from genetically rust-resistant parent trees; and fuel reduction treatments designed to reduce fire severity in whitebark pine stands

Propagation, Screening and Planting

Ensuring future generations of whitebark pine are genetically resistant to white pine blister rust is the most critical action for achieving long-term recovery of this species (Mahalovich and Dickerson 2004, p. 181; Perkins *et al*. 2016, p. 31). Genetic management of white pine blister rust is actively conducted for whitebark pine, including the USFS white pine blister rust resistance screening programs (Mahalovich 2016; Sniezko and Koch 2017). Seeds and pollen sourced from "plus" trees (those with presumed (i.e., phenotypic) rust resistance) or "elite" trees (those with proven (i.e., genotypic) rust resistance) are used for screening and selective breeding for white pine blister rust resistance (not immunity), molecular genetics studies, assessing levels of inbreeding, growing compatible rootstock for grafting in seed orchards, clone banking and gene conservation, and identifying genetic macro-refugium (Mahalovich 2016, Perkins *et al*. 2016, p. 30, Sniezko and Koch 2017). In the inland west, 1334 plus trees have been identified to-date, although approximately 20 percent of these have been lost due to the deleterious effects of mountain pine beetle and catastrophic wildfires (Mahalovich 2017); efforts are continuing rangewide to identify additional rust-resistant seed sources. In 2016, the BLM identified 51 additional "plus" trees across four states, while Crater Lake National Park identified 9 new "plus" trees.

Eventually, the long-term goal is to establish whitebark pine seed orchards in situ across the spectrum of whitebark pine habitat to provide reliable and accessible sources of genetically resistant seed (Mahalovich 2017). Scions (e.g., living branches) taken from trees with proven genetic resistance to white pine blister rust are grafted onto established root stocks, enabling them to develop the capability to produce cones much sooner than the time required for outplanted seedlings to reach reproductive maturity (approximately 60 years). Four seed orchards have recently been established or are currently being developed in whitebark pine habitat representing distinct breeding zones, with current overall establishment level at approximately 60 percent (Mahalovich 2017). These seed orchards are located on the Custer-Gallatin, Helena-Lewis and Clark, and Lolo National Forests in Montana, and the Nez Perce-Clearwater National Forest in Idaho, with another proposed by the Salish Kootenai Tribe on the Flathead Indian Reservation in Montana. Another seed orchard is in the early stages of development at the Dorena Genetic Resource Center in western Oregon, while another has been established at the Coeur d'Alene Nursery to develop full-sibling crosses to monitor changes in behavior of white pine blister rust. Once established, these orchards will reduce the need for more costly and time-intensive field-based cone collections, and provide a reliable and validated source of genetically resistant seed stock.

Seeds from cone collections in the northwest (WA, OR) are now stored at the USDA National Center for Genetic Resources Preservation in Fort Collins, CO for long-term ex situ gene conservation (Sniezko and Kegley 2017, p. 4). Seven separate white pine blister rust screening trials are occurring at the USFS Coeur d'Alene Nursery in Idaho using over 100,000 seedlings (Mahalovich 2016; Mahalovich 2017). Progeny from 1225 parent trees on public and Tribal lands in Oregon and Washington are currently being screened for white pine blister rust resistance at the Dorena Genetic Resource Center, with early results suggesting over 30 percent of the sources may have levels of resistance to be useful for restoration. Some of the parent trees have already succumbed to wildfire and/or mountain pine beetle, however, prompting an effort in 2018 to collect seed from at least 100 new "plus" trees in Oregon and Washington.

Overall, since 1988, 2,682 ha (6,628 ac) have been planted with rust resistant seedlings among three USFS Regions (Mahalovich 2016); about half of those have occurred since 2006 in USFS

Region 1 alone. Seedlings are often planted in recently burned areas, simulating the natural regeneration strategy for whitebark pine. Efforts range from relatively small planting projects, such as the 900 seedlings planted at a burned site on the Colville National Forest in Washington in 2017, to much larger projects, such as the 40,000 seedlings planted on the Shoshone National Forest in Wyoming in 2017. The Idaho Panhandle National Forest, in partnership with the Friends of Scotchman Peak, directly sowed whitebark pine seeds in a recently burned area within the proposed Scotchman Peak Wilderness in 2017, while the Custer-Gallatin National Forest conducted a similar project in the same year, to be followed by five years of annual monitoring. Over 22,000 seedlings derived from rust-resistant parents have been planted throughout Glacier National Park since 2002, while 482 seedlings were planted in Crater Lake National Park in 2016 alone. The BLM also plants seedlings on the limited areas of whitebark pine habitat within the agency's jurisdiction. Most recently, in 2017, the Dillon, MT field office completed a 3-year project to plant 7,500 seedlings across 20 ac of whitebark pine habitat.

Recent research has also provided insights into appropriate situations for planting whitebark pine. These researchers suggest that managers should consider planting whitebark pine directly beneath adult trees that have been killed by mountain pine beetle, since it is likely that these areas represent Clark's nutcracker caching sites (Larson and Kipfumeller 2010; Lorenz *et al.* 2011; Schaming and Sutherland 2020). Managers may also consider planting whitebark pine trees in recently burned areas or in areas where there are fewer seeds for Clark's nutcrackers (Maier 2012).

Fuel Reduction Treatments

Silvicultural practices, such as thinning, are frequently employed to treat existing stands of whitebark pine to modify surface and ladder fuels and improve their chances of surviving fire. Most thinning treatments are designed to mimic non-lethal mixed-severity fire (Keane and Arno 2001, p. 383), reduce or eliminate competition from other conifer species such as subalpine fir (*Abies lasiocarpa*), and to increase regeneration space for potentially rust-resistant seedlings. Approaches include creating openings wherein all trees except healthy whitebark pines are cut within a 1-5 ac opening to provide open growing space for whitebark pine regeneration and existing whitebark pine trees (Keane and Arno 2001, p. 382; Keane and Parsons 2010, p. 9); thinning of all non-whitebark pine trees below a certain diameter (Chew 1990); and fuel enhancement treatments where other competing trees are directionally felled to modify fire behavior and reduce fire intensity (Keane and Arno 2001, p. 388; Keane and Parsons 2010, p. 9). Reducing tree density within whitebark pine stands may result in increased vigor (e.g., growth rate) of remaining sapling to mature-class trees (Keane, Gray, and Dickinson 2007, pp. 7–8; Retzlaff *et al*. 2018, p. 11); however, counterintuitively, increased whitebark pine vigor may not impart increased resistance to mountain pine beetle, as some evidence suggests that mountain pine beetles select faster growing trees for attack (Six et al. 2021, p. 18). In addition to or in place of treating fuels within whitebark stands, managers should consider conducting fuel reduction treatments in non-whitebark pine stands adjacent to whitebark pine, thereby reducing the intensity of fire as it moves from the adjacent stand into the whitebark pine stand.

In 2016, over 14,000 ac of whitebark pine habitat in non-wilderness areas were manually treated on most National Forests throughout USFS Region 1. In 2017, the Service provided candidate conservation funds to the Idaho Panhandle National Forest to begin thinning an initial portion of 577 targeted ac of dense, late-successional whitebark pine habitat. The Service has provided funding for similar thinning projects in the past on other National Forests in Idaho, including the Boise, Sawtooth, and Caribou-Targhee National Forests. The application of prescribed fire in whitebark pine stands has also often been advocated for restoration purposes to reduce surface and ladder fuels and to reduce stand density and increase residual tree vigor (Arno 2001, p. 83, Perkins *et al*. 2016, p. 40). However, recent research has found that whitebark pine does not exhibit phenotypic traits known to impart fire resistance in other conifer species (Stevens et al. 2020, p. 950) and prescribed fire can result in significant whitebark pine mortality and not achieve desired restoration outcomes (Keane and Parsons 2010, p. 65), depending on the circumstances. Researchers continue to build their understanding the role of prescribed burns in the management and recovery of whitebark pine; however, since we do not believe mortality from prescribed burns would present species-level effect, these recent research findings do not substantially alter our understanding of the primary threats to the species and whitebark pine viability.

Proactive Intervention

As described above, most restoration approaches target stands that have already experienced high impacts from the primary stressors. However, in stands where white pine blister rust has yet to take a strong hold, proactive management may offer a means to prepare and protect existing healthy stands from impending impacts of white pine blister rust. This approach is premised on the concept of actively facilitating evolutionary change in whitebark pine to improve its resiliency on the landscape in the persistent presence of white pine blister rust (Schoettle and Sniezko 2007, p. 328). Strategies to prepare healthy stands of whitebark pine include managing stand composition, diversifying age class structures, increasing tree vigor, and promoting natural regeneration and introducing rust-resistant stock onto the landscape in existing healthy stands, utilizing some of the techniques described above (Schoettle and Sniezko 2007, p. 329). Healthy stands of whitebark pine are more responsive to management actions, thereby increasing the available management options in a proactive approach (Keane and Schoettle 2011, p. 286). This proactive approach has been implemented recently in the southern Rocky Mountains within the range of other high-elevation 5-needled pines that are also susceptible to white pine blister rust (Keane and Schoettle 2011, p. 287). More recently, a framework has been developed to help guide implementation of this strategy in remaining healthy stands of whitebark pine, particularly in the southern and southwestern portions of its range (Schoettle *et al.* 2018, entire). As whitebark pine has declined precipitously throughout much of its range, it will be important to implement proactive intervention in remaining healthy stands to retain the resiliency of the species.

INVENTORY, MAPPING, AND MONITORING

Inventory of existing whitebark pine stands is crucial for determining where to most effectively direct conservation and restoration efforts. In the past, forest inventories were generally focused in lower-elevation commercial stands that rarely included whitebark pine. The USFS Forest Inventory and Analysis (FIA) system is designed to be applied across the entire range of forestlands under Federal management, using a widely spaced, systematic grid-pattern for inventory plot locations. This coarse method can underrepresent whitebark pine that often is distributed along ridge and mountain tops in small, fragmented stands (Zack 2016 pers. comm.). Furthermore, large, inaccessible areas, such as the Frank Church-River of No Return Wilderness in Idaho, are logistically challenging to obtain accurate and up-to-date inventory data for whitebark pine. As a result, comparatively few stand-level data are available in some portions of whitebark pine's range, as it relates to overall stand and tree health, post-wildfire survivorship, and current levels of white pine blister rust. Conversely, other more accessible or charismatic areas (e.g., non-roadless lands, National Parks) have received much greater attention and resources leading to a more comprehensive understanding of the status of whitebark pine in these areas.

Mapping of whitebark pine occurrences is also an important aspect of the inventory process, particularly in light of the species' decline and outright loss in some areas of its historic range. In the past, broad-scale mapping efforts were conducted with myriad agency standards and objectives, leading to range maps that were either inaccurate or generally ambiguous. Modern modeling efforts have attempted to refine range maps based on site potential for supporting whitebark pine, but often lack ground-truthed data in some areas to corroborate or refine the modeled results. In 2014, Parks Canada completed a reassessment of whitebark pine's entire range based on current available information and expert feedback, leading to a much-improved understanding of whitebark pine's range (WPEF 2014). However, much work remains to continue to refine and develop range maps at finer scales across the entire range. Accurate and up-to-date maps depicting forest-, stand-, and tree-level characteristics throughout whitebark pine's range will be crucial for identifying and developing core areas for high-impact restoration efforts.

Monitoring whitebark pine can entail multiple objectives. Nearly all "plus" and other important individual trees are monitored with each visit for overall health and vigor, cone production, encroachment from competing tree species, and response to restoration treatments. Post-fire monitoring is also important for understanding the response of whitebark pine to increased fire frequencies and severity throughout its range. Additionally, monitoring annual survivorship of plantings can help guide adaptive restoration strategies by helping to refine out-planting techniques, identify superior parentage of seedling stock, and ensure stocking level goals are met. Permanent, long-term monitoring plots are also necessary to document and understand gradual changes in response to treatments, natural disturbances, and climate change effects in whitebark pine habitats. However, long-term monitoring success can be hampered when plots are subjected to the stressors acting on live whitebark pine. For example, 8 percent of the monitoring transects in the Greater Yellowstone Area have been affected directly in some way by wildfire, and over 250 marked whitebark pine trees have been lost as a result of high severity fires (Shanahan *et al*. 2017 pp. ix, 17).

The BLM has recently prioritized inventories and assessments of all whitebark pine on their lands, primarily in Idaho, Montana, and Wyoming. In addition to expanding inventories into new areas, permanent plots have been established in these states as well, including in the Axolotl Wilderness Study Area in the Dillon (MT) district, Grandmother Mountain Wilderness Study Area in Idaho. In many western National Parks, annual and rotating monitoring plots are assessed each year as part of long-term vegetation monitoring plans, as well as individual “plus” tree and outplanting monitoring. The Sequoia-Kings Canyon, Yosemite, Crater Lake, and Lassen Volcanic National Parks conducted first re-visits in 2015 of permanent plots established in 2012 under the Pacific West Region five-needle pine protocol (McKinney *et al*. 2012). In the GYA, monitoring of over 5000 tagged trees has been ongoing since 2004 with three re-visits already conducted, and a fourth slated for 2019, following an established protocol (GYWPMWG 2011). Similarly, permanent whitebark pine plots were established in North Cascades and Mount Rainier National Parks in 2004 to document the status and trends of whitebark pine health (Rochefort *et al*. 2018 p. 2) Permanent whitebark pine monitoring plots have also been established throughout numerous National Forests, to supplement previously established long-term forest inventory plots. In 2016, the Helena-Lewis and Clark National Forest established stake row plots to monitor seedling survival in the Forest’s first operational planting effort.

CHALLENGES TO RESTORATION

Wilderness

A separate, important challenge to actively restoring whitebark pine is the fact that a significant portion of its range in the U.S. lies within designated and de facto wilderness areas (Service 2011, p. 1). Currently, the Wilderness Act of 1964 (16 U.S.C. 1131 1136) generally does not allow for many direct restoration activities to occur in designated or recommended wilderness areas (GYCC 2015, p. 6). However, section 4(c) of the Wilderness Act (the minimum requirement tool) may be utilized to accomplish certain management objectives such as prescribed fire, planting seedlings or application of verbenone, while still maintaining the wilderness character (GYCC 2015, p. 6; GYCC 2011, p. 14; NPS 2018; USFS 2018). How the Wilderness Act is implemented can vary between agencies, regions, or even between species. For example, USFS wilderness directives do not specifically prohibit vegetation treatments as long as the actions are properly analyzed and approved at a local or regional level (USFS 2018). The Aldo Leopold Wilderness Research Institute has also developed a framework to analyze the effects of ecological intervention in wilderness areas, which may provide a consistent and unified approach to actively restoring whitebark pine in wilderness areas in the future (USFS 2018). In addition, other wilderness designations, such as recommended, proposed, or wilderness study areas, are usually managed in the same manner as designated wilderness (NPS 2018).

The Wilderness Act states that wilderness should be managed to preserve its natural conditions and yet remain untrammeled by man, thus presenting a fundamental debate as to whether restoring whitebark pine in wilderness areas detracts from or enhances the wilderness character, and whether human intervention to restore potentially trammeled whitebark pine forests is a legally and socially acceptable pursuit. The effect of the non-native white pine blister rust has indirectly led to unnatural (i.e., trammeled) conditions in whitebark pine habitat, and though restoration activities in wilderness areas may lead to short-term trammeling effects, the long-term payoff may be a return of the system to a more naturalized state (McCool and Freimund 2001, p. 277). In short, management actions undertaken to restore whitebark pine in wilderness areas may impact the perceived untrammeled condition of an area, yet the alternative of doing nothing may lead to an eventual degradation of the inherent naturalness by allowing the continued decline and potential loss of a keystone species due the effects of an introduced pathogen, which may owe at least some responsibility to the actions of humankind. While the Wilderness Act allows for some "minimal actions" to address certain management needs, it does not directly acknowledge the impacts of white pine blister rust, mountain pine beetle epidemics, or climate change (Service 2016b, p. 32). It is evident that continued debate and collaborative decision-making will be required to address this complex issue.

Limited Access

In concert with the wilderness issue, the remote and challenging terrain in which whitebark pine frequently exists presents numerous logistical challenges for accessing sites for restoration. In non-wilderness roadless areas, much effort and/or costs may be required to transport equipment, seedlings, and personnel to work sites, whether by foot, livestock, or aerial means. Seasonal access to many sites is likely to be brief due to abbreviated snow-free conditions at high elevations, which often coincides with summer wildfire seasons. As the level of accessibility to whitebark pine stands decreases, so does the number of available restoration options (Keane *et al*. 2012, p. 89), meaning fewer options to restore impacted stands in more difficult-to-access sites.

Threatened and Endangered Species

Restoration activities for whitebark pine may conflict with recovery plans for other currently endangered or threatened species whose critical habitats may at times include whitebark pine habitat. In some cases, restoring whitebark pine may prove beneficial in the long-term, but the restoration actions themselves may present short-term impacts. For example, although grizzly bears (*Ursus arctos horribilis*) rely on whitebark pine as a food source in many parts of its range, restoration activities and the associated human presence during these may negatively impact individual bears, even if the long-term goal is improving an important component of their habitat. In 2017, the Service issued a Biological Opinion to the Idaho Panhandle National Forest for a large-scale whitebark pine restoration project that was determined to "likely adversely affect" grizzly bears in the area via the use of chainsaws, helicopters, and prescribed fire, along with the prolonged presence of humans in the work area. It was determined that although the project may have short-term adverse effects on some bears, it would provide long-term beneficial effects and would not jeopardize the continued existence of grizzly bears.

In other cases, restoration may directly conflict with the needs of species such as Canada lynx (*Lynx canadensis*). Subalpine fir is a principal component of Canada lynx habitat, yet is the primary competing species to whitebark pine that is often targeted for removal in mechanical thinning and prescribed fire treatments. Critical habitat for Canada lynx overlaps with the range of whitebark pine in many areas throughout the Northern Rockies, U.S. Canadian Rockies, Middle Rockies, and a small portion of the Cascades analysis units. Other federally listed threatened and endangered species that could potentially conflict with whitebark pine restoration include endangered woodland caribou (*Rangifer tarandus caribou*) and its critical habitat; endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierra*) and its critical habitat; endangered Sierra Nevada and mountain yellow-legged frogs (*Rana muscosa, R. sierrae*) and their critical habitats; non-recovered distinct population segments of endangered gray wolf (*Canis lupus*); threatened bull trout (*Salvelinus confluentus*) and Little Kern golden trout (*Oncorhynchus aguabonita whitei*) and their critical habitats; threatened Yosemite toad (*Anaxyrus canorus*) and its critical habitat; threatened northern Idaho ground squirrel (*Urocitellus brunneus*); threatened northern spotted owl (*Strix occidentalis caurina*) and its critical habitat; and the proposed threatened North American wolverine (*Gulo gulo luscus*). Additional state-listed threatened, endangered, or other species of concern could also present obstacles.

Funding

As a non-commercial tree species, Federal funding for whitebark pine restoration has been and may continue to be limited (Keane *et al*. 2012, p. 89). Appropriated funds account for a significant portion of restoration funds, and are available through various programs, including Vegetation and Watershed Management, Wildlife and Fisheries Habitat Management, Wildland Fire and Fuels Management, and others (Kittler 2017). However, agencies must compete for these pots of money that are made available to all or many natural resource management programs and species, not just whitebark pine, leading to highly variable and unpredictable funding opportunities from Federal coffers (NPS 2018). Another major source of restoration dollars from appropriated funds comes from the USFS Forest Health Protection (FHP) Whitebark Pine Restoration Program, initiated in 2006, which offers a suite of cost-share grants (Man 2017). This program has funded numerous activities rangewide, including development of strategic plans, gene conservation, health surveys, silvicultural treatments, cone collections, seedling plantings, and public outreach efforts (Service 2016b, p. 38).

Limited funding has been made available through reforestation partnerships with a number of NGOs, including American Forests, National Forests Foundation, and the Arbor Day Foundation, chiefly focused on purchasing and planting of seedlings (Kittler 2017). The Whitebark Pine Ecosystem Foundation (WPEF) has established a restoration fund to match funding provided from the USFS through solicited donations and membership dues. Most recently in 2017, these funds were used to plant 1000 seedlings in Glacier National Park, and to plant whitebark pine seeds for a pilot project on the Custer-Gallatin National Forests (WPEF 2017). The WPEF also provides annual $1000 scholarships for student research in whitebark pine.

For both the USFS and BLM, stewardship contracting is a growing, albeit small, source of funding on resource rich forests, accounting for approximately 3 percent of total whitebark pine restoration funds (Kittler 2017). Stewardship contracting allows for the value of timber or other products removed to offset the costs of services, or for retention of timber receipts (i.e., revenue) when the product value exceeds the costs of services to be applied to projects in other areas (Kittler 2017). As a candidate species, whitebark pine projects are also eligible for federal Interagency Special Status Sensitive Species (ISSSSP) funding; $89,000 from this fund were expended in USFS Region 6 in 2017 (Kittler 2017).

The Greater Yellowstone Coordinating Committee (GYCC) provides annual funding for restoration activities in the Greater Yellowstone Area (GYA), particularly focusing on the development and planting of rust-resistant seedlings (Service 2016b, p. 38). From 2005-2011, 12 percent of the GYCC’s funds went towards whitebark pine restoration (Kittler 2017). Funding for NPS restoration programs outside of the GYA may come from park entrance fees or other recreation fee programs, individual park-associated foundation funds, or base program funds. However, these types of funds are allocated to multiple uses, and thus are cannot be relied upon for consistent annual allocations (Beck and Holm 2014, p. 72). The Service has also provided limited funding for individual projects through Candidate Conservation and Section 6 funds, primarily in Idaho (Table A1).

Section 7 Consultations (TAILS inquiries)

- 5,064 consultations
- 326 CPAs
- 13 contaminant activities

Table A1. USFWS Funded Grants (ECOS)

Year	State	Type	Partner	Title	Amount
2018	WA	Sect 6		Conservation status ranking for whitebark pine	$19,007
2017	ID	Sect 6	IDFG	Water howellia monitoring and other plant conservation efforts	$120,975
2017	ID	CC	USFS - IPNF	Treasured Landscapes – Whitebark Pine daylighting	$10,000
2016	ID	CC	USFS - Boise	Boise NF whitebark pine restoration database development	$10,000
2015	ID	Sect 6	IDFG	Milkweed Guide and other Plant Conservation Efforts	$153,942
2015	ID	Sect 6	IDFG	Fuel Treatment Effects on Whitebark Pine	$32,225
2015	ID	CC	USFS - Boise	Cascade Whitebark Pine Restoration	$20,000
2014	NV	Sect 6		Survey and assessment of high-priority plant conservation targets in Nevada	$45,112
2014	ID	CC	USFS - Sawtooth	Ketchum Whitebark Pine Enhancement Project	$25,000
2013	ID	CC	USFS – Caribou-Targhee	Centennial Mtns Whitebark Pine Release	$23,000

2013	ID	CC	USFS – Caribou-Targhee	SCA Whitebark Pine Survey	$25,000
2012	ID	Sect 6	IDFG	Assessment of Whitebark Pine and Other Rare Plants	$94,987

Appendix A References

Arno, S.F. 2001. Community Types and Natural Disturbance Processes. In Tomback, D.F., Arno, S.F., and Keane, R.E. (eds.) Whitebark Pine Communities (pp. 74-88). Washington, D.C.: Island Press.

Beck, J.S. and G.W. Holm. 2014. Whitebark Pine Conservation Plan. Crater Lake National Park, Crater Lake, Oregon.

Chew, J. D. 1990. Timber management and target stands in the whitebark pine zone. Pages 310-314 In Schmidt, W. C., McDonald, K. J. (compilers). Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. Gen. Tec. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Greater Yellowstone Coordinating Committee (GYCC). 2015. Adaptive Action Plan: Whitebark Pine in the Greater Yellowstone Area.

Greater Yellowstone Coordinating Committee (GYCC). 2011. Whitebark pine strategy for the Greater Yellowstone Area. 41p.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2011. Interagency Whitebark Pine Monitoring Protocol for the Greater Yellowstone Ecosystem, Version 1.1. Greater Yellowstone Coordinating Committee, Bozeman, MT.

Keane, R.E. 2019 [in review]. Managing wildfire for whitebark pine ecosystem restoration in western North America.

Keane, R.E., and Arno, S.F. 2001. Restoration Concepts and Techniques. In Tomback, D.F., Arno, S.F., and Keane, R.E. (eds.) Whitebark Pine Communities (pp. 367–400). Washington, D.C.: Island Press.

Keane, R.E. and R.A. Parsons. 2010. Restoring whitebark pine forests of the Northern Rocky Mountains, USA. Ecological Restoration 28:56–70.

Keane, R.E., Gray, K.L. and Dickinson, L.J., 2007. Whitebark pine diameter growth response to removal of competition. Res. Note RMRS-RN-32. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 9 p.

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: Keane, R.E., Tomback, D.F., Murray, M.P., and Smith, C.M. eds. 2011. 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. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 pp.

Keane, R.E.; Tomback, D.F.; Aubry, C.A.; Bower, A.D.; Campbell, E.M.; Cripps, C.L.; Jenkins, M.B.; Mahalovich, M.F.; Manning, M.; McKinney, S.T.; Murray, M.P.; Perkins, D.L.; Reinhart, D.P.; Ryan, C.; Schoettle, A.W.; Smith, C.M. 2012. A range-wide restoration strategy for whitebark pine (Pinus albicaulis). Gen. Tech. Rep. RMRS-GTR-279. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 108 p.

Kittler, B. 2017. “Funding the Restoration of Whitebark Pine.” National Whitebark Pine Restoration Plan Summit, November 7, 2017, Missoula, MT.

Larson, E.R. and K.F. Kipfmueller. 2010. Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. Canadian Journal of Forest Research 40:476-487.

Mahalovich, M.F. 2016. Inland west whitebark pine genetic restoration program CY15. White paper. 6 p.

Mahalovich, M.F. 2017. "Inland West Whitebark Pine Genetic Restoration Program." National Whitebark Pine Restoration Plan Summit, November 7, 2017, Missoula, MT.

Mahalovich, M.F. and Dickerson, G.A., 2004. Whitebark pine genetic restoration program for the Intermountain West (United States). Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance. Proc RMRS-P-32, USDA Forest Service Rocky Mountain Research Station, Ft. Collins, CO, pp. 181-187.

Maier, M. 2012. Clark's nutcracker seed harvest patterns in Glacier National Park and a novel method for monitoring whitebark pine cones. M.S. Thesis. Utah State Univeristy. Logan, UT. 68 p.

Man, G. 2017. "U.S. Forest Service Funding Needs and Opportunities." National Whitebark Pine Restoration Plan Summit, November 7, 2017, Missoula, MT.

McCool, S.F. and W.A. Freimund. 2001. Threatened Landscapes and Fragile Experiences: Conflict in Whitebark Pine Restoration. In Tomback, D.F., Arno, S.F., and Keane, R.E. (eds.) Whitebark Pine Communities (pp. 263–284). Washington, D.C.: Island Press.

McKinney, S. T., T. Rodhouse, L. Chow, A. Chung-MacCoubrey, G. Dicus, L. Garrett, K. Irvine, S. Mohren, D. Odion, D. Sarr, and L. A. Starcevich. 2012. Monitoring white pine (Pinus albicaulis, P. balfouriana, P. flexilis) community dynamics in the Pacific West Region - Klamath, Sierra Nevada, and Upper Columbia Basin Networks: Narrative version 1.0. Natural Resource Report NPS/PWR/NRR—2012/532. National Park Service, Fort Collins, Colorado.

National Park Service (NPS). 2018. SSA Partner comments.

Perkins, D.L., Means, R.E, and Cochrane, A.C. 2016. Conservation and management of whitebark pine ecosystems on Bureau of Land Management lands in the western United States. Technical Reference 6711-1. Bureau of Land Management, Denver, CO. 93 p.

Progar, R.A. 2005. Five-year operational trial of verbenone to deter mountain pine beetle (*Dendroctonus ponderosae*; Coleoptera: Scolytidae) attack of lodgepole pine (*Pinus contorta*). Environmental Entomology, 34(6): 1402–1407.

Progar, R. A., Blackford, D. C., Cluck, D. R., Costello, S., Dunning, L. B., Eager, T., ... & Rinella, M. J. 2013. Population densities and tree diameter effects associated with verbenone treatments to reduce mountain pine beetle-caused mortality of lodgepole pine. Journal of Economic Entomology, 106(1), 221–228.

Retzlaff, M.L., R.E. Keane, D.L. Affleck, and S.M. Hood. 2018. Growth response of whitebark pine (*Pinus albicaulis* Engelm) regeneration to thinning and prescribed burn treatments. Forests: 9, 311; http://dx.doi.org/10.3390/f9060311.

Rochefort, R.M., Howlin, S., Jeroue, L., Boetsch, J.R., and Grace, L.P. 2018. Whitebark Pine in the Northern Cascades: Tracking the effects of blister rust on population health in North Cascades National Park Service Complex and Mount Rainier National Park. Forests, 9(5), 244.

Schaming TD, Sutherland CS. 2020. Landscape- and local-scale habitat influences on occurrence and detection probability of Clark's nutcrackers: Implications for conservation. PLOS ONE 15(5): e0233726.

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., Jacobi, W.R., Waring, K.M., and Burns, K.S. 2018. Regeneration for resilience framework to support regeneration decisions for species with populations at risk of extirpation by white pine blister rust. New Forests, 1-26.

Service (U.S. Fish and Wildlife Service). 2011. Whitebark pine on Federal lands. Excel table. January 14, 2011. 1 p.

Service (U.S. Fish and Wildlife Service). 2016b. U.S. Fish and Wildlife Service Species Assessment and Listing Priority Assignment Form for Whitebark Pine. May 16, 2016. 57 pp.

Shanahan, E., K. Legg, and R. Daley. 2017. Status of whitebark pine in the Greater Yellowstone Ecosystem: A step-trend analysis with comparisons from 2004 to 2015. Natural Resource Report NPS/GRYN/NRR—2017/1445. National Park Service, Fort Collins, Colorado.

Six, D.L., A. Trowbridge, M. Howe, D. Perkins, E. Berglund, P. Brown, J.A. Hicke, and G. Balasubramanian. 2021. Growth, Chemistry, and Genetic Profiles of Whitebark Pine Forests Affected by Climate-Driven Mountain Pine Beetle Outbreaks. Frontiers in Forests and Global Change 4:1-22.

Sniezko, R., and Kegley, A. 2017. *F&WS Candidate Notice of Renewal (CNOR) for Calendar Year 2016 – WHITEBARK PINE Update.* U.S. Department of Agriculture, Forest Service, Region 6 (Pacific Northwest) – Dorena Genetic Resource Center. White paper. 11 p.

Stevens, J.T., Kling, M.M., Schwilk, D.W., Varner, J.M. and Kane, J.M., 2020. Biogeography of fire regimes in western US conifer forests: A trait-based approach. *Global Ecology and Biogeography*, *29*(5), pp.944-955.U.S. Forest Service (USFS). 2018. SSA Partner comments.

Whitebark Pine Ecosystem Foundation (WPEF). *2014*. Whitebark pine and limber pine range maps. Available online from http://whitebarkfound.org.

Whitebark Pine Ecosystem Foundation (WPEF). 2017. 2017 Restoration Projects Funded by WPEF. Accessed online February 4, 2018 at http://whitebarkfound.org/2017-restoration-projects-funded-by-wpef/.

Zack, A, Silviculturist (retired), U.S. Forest Service, Idaho Panhandle National Forest. Verbal exchange. (September 16, 2016).

Zeglen, S., J. Pronos, and H. Merler. 2010. Silvicultural management of white pines in western North America. Forest Pathology 40:3–4, 347–368.

Appendix B. A summary of threats assessment (taken from Table 2 in Environment and Climate Change Canada 2017).

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
1	Residential & commercial development	Negligible	Negligible (<1 percent)	Extreme (71-100 percent)	High (Continuing)	blank
1.2	Commercial & industrial areas	Negligible	Negligible (<1 percent)	Extreme (71-100 percent)	High (Continuing)	Primary concern is loss of habitat and trees to due to construction of ridge-top communication towers.
1.3	Tourism & recreation areas	Negligible	Negligible (<1 percent)	Moderate (11-30 percent)	High (Continuing)	All existing ski areas in range, plus new developments and expansions. Includes heli- or cat-ski operations, and backcountry ski cabins.

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
2	Agriculture & aquaculture	Negligible	Negligible (<1 percent)	Slight (1-10 percent)	High (Continuing)	blank
2.3	Livestock farming & ranching	Negligible	Negligible (<1 percent)	Slight (1-10 percent)	High (Continuing)	This impact applies to trampling of regenerating (rather than mature) trees. Soil disturbance and compaction caused by livestock trampling may destroy microsites for cached seeds, interrupt drainage, limit tree rooting, and damage seedlings. Any trampling damage of young seedlings would be because of overuse caused by the time and duration of grazing and poor distribution. Additional concerns related to ranching include similar potential impacts of feral horses. Heavy grazing in Whitebark Pine habitats characterized by grassy fine fuels can substantially reduce natural fire occurrence (Murray *et al*. 1998).

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
3	Energy production & mining	Negligible	Negligible (<1 percent)	Extreme (71-100 percent)	High (Continuing)	blank
3.1 (AB)	Oil & gas drilling	Negligible	Negligible (<1 percent)	Extreme (71-100 percent)	High (Continuing)	Alberta: Potential to increase in the next 10 years. The Province has also developed industrial setback guidelines to be employed in such developments (Government of Alberta 2012b).
3.1 (BC)	Oil & gas drilling	Negligible	Negligible (<1 percent)	Extreme (71-100 percent)	Moderate (Possibly in the short term, < 10 yrs/3 gen)	British Columbia: Limited potential, most likely drilling in Whitebark Pine range limited to coalbed methane in the Elk Valley and Sacred Headwaters.

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
3.2 (AB)	Mining & quarrying	Negligible	Negligible (<1 percent)	Extreme (71-100 percent)	Moderate (Possibly in the short term, < 10 yrs/3 gen)	Alberta: Most Alberta mines are below Whitebark Pine range. Potential to expand into range of Whitebark Pine.
3.2 (BC)	Mining & quarrying	Negligible	Negligible (<1 percent)	Extreme (71-100 percent)	High (Continuing)	British Columbia: At least 10 mines currently operate in Whitebark Pine habitat. Mining exploration and proposed mine development is ongoing.
3.3	Renewable energy	Negligible	Negligible (<1 percent)	Serious (31-70 percent)	Low (Possibly in the long term, >10 yrs/3 gen)	Wind farm potential to be developed within Whitebark Pine range in the future.

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
4	Transportation & service corridors	Negligible	Negligible (<1 percent)	Extreme (71-100 percent)	High (Continuing)	blank
4.1	Roads & railroads	Negligible	Negligible (<1 percent)	Extreme (71-100 percent)	High (Continuing)	Roads are relevant to commercial and industrial development, not just public transportation. Depending on the size of development the road size and impacts may vary.
4.2	Utility & service lines	Negligible	Negligible (<1 percent)	Moderate (11-30 percent)	High (Continuing)	Construction and maintenance of power lines. Powerline right-of-ways may create beneficial scenarios for seedling planting where trees can be pruned to acceptable heights.
5	Biological resource use	Low	Small (1-10 percent)	Extreme (71-100 percent)	High (Continuing)	blank

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
5.2	Gathering terrestrial plants	Unknown	Unknown	Unknown	Unknown	Limited First Nations traditional use known.
5.3 (AB)	Logging & wood harvesting	Negligible	Negligible (<1 percent)	Extreme (71-100 percent)	High (Continuing)	Alberta: In Alberta, timber companies in the C5 Forest Management Unit (a management unit occurring from north of Waterton Lakes National Park to just south of Kananaskis Country) may not destroy Whitebark Pine unless unavoidable and written consent from the Environment and Sustainable Resource Development (ESRD) is obtained (Government of Alberta 2019). The Province has also developed industrial setback guidelines to be more broadly applied (Government of Alberta 2012b).

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
5.3 (BC)	Logging & wood harvesting	Low	Small (1-10 percent)	Extreme (71-100 percent)	High (Continuing)	British Columbia: Incidental harvest. There has been notable harvesting in mixed Whitebark Pine forests of Kootenays, Omineca, and possibly in the Coast Range; a net loss due to timber harvesting activities is occurring on the landscape. There are active attempts to voluntarily reduce harvest, but no regulatory mechanisms. Harvest of Whitebark Pine is not well tracked as records often group it with other species or ignore it. Stands that contain Whitebark Pine prior to harvest are not routinely replanted with Whitebark Pine thus silviculture approaches create a system that excludes regeneration opportunities and increases competition by planting faster-growing species. Some timber companies have incorporated Whitebark Pine into Sustainable Forest Management Plans (SFMP).

#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
6	Human intrusions & disturbance	Negligible	Negligible (<1 percent)	Slight (1-10 percent)	High (Continuing)	blank
6.1	Recreational activities	Negligible	Negligible (<1 percent)	Slight (1-10 percent)	High (Continuing)	ATVs, snowmobiles, backcountry lodges, backcountry visitors on trails (ground compression, climbing on trees, trail clearing), increased access from logging road networks, burning for campfires, bike trail construction; impacts of horses used by recreationists and/or picketed at campsites.
7	Natural system modifications	Medium - Low	Restricted (11-30 percent)	Serious - Moderate (11-70 percent)	High (Continuing)	blank

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
7.1	Fire & fire suppression	Medium - Low	Restricted (11-30 percent)	Serious - Moderate (11-70 percent)	High (Continuing)	Trees can be destroyed by severe forest fires, and depending on site-specific factors, trees stressed by fire may be more susceptible to Mountain Pine Beetle. Fire suppression may facilitate successional replacement by other tree species and reduce abundance of suitable regeneration sites. Mixed severity fires may create regeneration sites and retain mature trees. Fire requirements for recruitment are variable across the range and need to be considered within local contexts.
7.3	Other ecosystem modifications	Negligible	Negligible (<1 percent)	Serious (31-70 percent)	High (Continuing)	Potential decrease of Clark's Nutcracker populations due to decline of Whitebark Pine and thereby reduced seed dispersal of remaining Whitebark Pine. Alternative food sources for Clark's Nutcracker may play a large role in population stabilization, but these species occur at

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
						varying abundance across the range of Whitebark Pine. Main alternative species in Canada documented so far are Limber Pine, Ponderosa Pine and Douglas-fir. Limber Pine is COSEWIC-assessed as endangered and faces similar recovery challenges as Whitebark Pine.
8	Invasive & other problematic species & genes	Very High	Pervasive (71-100 percent)	Extreme (71-100 percent)	High (Continuing)	blank
8.1	Invasive non-native/alien species	Very High	Pervasive (71-100 percent)	Extreme (71-100 percent)	High (Continuing)	White Pine Blister Rust found throughout the Canadian range. Smith *et al*. (2013) found increases of 35 percent infection and 39 percent mortality from 1996 to 2009. Study was along

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
						Rocky Mountains from McBride to Waterton Lakes National Park.
8.2	Problematic native species	Low	Small (1-10 percent)	Serious (31-70 percent)	High (Continuing)	There are several unknowns regarding the future impacts of Mountain Pine Beetle. The epidemic is over through much of Whitebark Pine's range, but endemic native beetle populations may still kill some stressed (particularly weakened, rust-infected trees. Based on a 3 generation time to maximum of 100 years and estimating beetle epidemics at 30 year intervals, severity was rated serious. Bark Beetles were identified as being a potentially significant cause of mortality in stressed trees and on sites with high solar radiation (Wong 2012). Pine Leaf Adelgid (Pineus pinifoliae) also kills and damages Whitebark Pine in areas where it co-occurs with White or Engelmann Spruce. There are also a variety of

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
						other native insects and pathogens that may reduce tree vigor (increasing susceptibility to other stressors) or kill trees outright (S. Haeussler pers. comm. 2013). Scope of current impact is small, but this could increase in the future if a subsequent epidemic outbreak occurs. Impacts of future outbreaks may be exacerbated owing to (a) ongoing loss of Whitebark Pine, and (b) an increase in the amount of monotypic stands of susceptible pine plantations on the landscape.
9	Pollution	Negligible	Negligible (<1 percent)	Unknown	Unknown	blank
9.2	Industrial & military effluents	Negligible	Negligible (<1 percent)	Unknown	Unknown	Industry specific: may include leaking pipe lines, gas flaring, spills, blow out, tailings sites and

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	**Threat description**	**Impact[e]**	**Scope[f]**	**Severity[g]**	**Timing[h]**	**Comments**
						ponds, avalanche control artillery along mountain passes.
9.5	Air-borne pollutants	Negligible	Negligible (<1 percent)	Unknown	Unknown	Difficult to determine. Some areas may have high-elevation impacts.
11	Climate change & severe weather	High	Pervasive - Large (31-100 percent)	Serious (31-70 percent)	High (Continuing)	blank
11.1	Habitat shifting & alteration	High - Medium	Pervasive - Large (31-100 percent)	Serious - Moderate (11-70 percent)	High (Continuing)	Shifts in climatically suitable habitat to more northerly latitudes and higher elevations are anticipated (Hamann and Wang 2006, Hamann and Aitken 2013). There are knowledge gaps regarding the degree to which Whitebark Pine morphological or physiological plasticity can

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
						permit adaptation to climate change in situ. The ability of Whitebark Pine to migrate/establish in newly suitable climates is projected to be slower than the predicted rate of change.
11.2	Droughts	High	Large (31-70 percent)	Serious (31-70 percent)	High (Continuing)	It is speculated that there will be increased drought potential in the eastern part of the range in Crowsnest Pass (D. Sauchyn pers. comm. 2013); however, the driest regions of B.C. range such as Chilcotin and portions of Cariboo also likely susceptible. Drought stress may also exacerbate other threats such as insect and fire impacts.
11.3	Temperature extremes	High - Low	Large - Restricted (11-70 percent)	Serious - Slight (1-70 percent)	High (Continuing)	Temperature extremes have potential effects on seed viability and may cause direct death due to changes in natural cold stratification. Temperature

Table 2. IUCN[d] threats summary for Whitebark Pine in Canada.						
#	Threat description	Impact[e]	Scope[f]	Severity[g]	Timing[h]	Comments
						extremes may also exacerbate other stressors such as insects and fire. There is uncertainty about the response of subalpine and treeline forest ecosystems to increased temperatures; they may create higher stress on some sites making them better suited to Whitebark Pine recruitment; however they may create conditions on some sites that either limit all tree species recruitment or result in suitable conditions for more competitive species.
11.4	Storms & flooding	Unknown	Unknown	Unknown	High (Continuing)	Storms and flooding cause increased blowdown and mechanical damage.

d Classification of Threats adopted from IUCN-CMP, Salafsky *et al*. (2008).

e Impact – The degree to which a species is observed, inferred, or suspected to be directly or indirectly threatened in the area of interest. The impact of each threat is based on Severity and Scope rating and considers only present and future threats. Threat impact reflects a reduction of a species population or decline/degradation of the area of an ecosystem. The median rate of population reduction or area decline for each combination of scope and severity corresponds to the following classes of threat impact: Very High (75 percent declines), High (40 percent), Medium (15 percent), and Low (3 percent). Unknown: used when impact cannot be determined (e.g., if values for either scope or severity are unknown); Not Calculated: impact not calculated as threat is outside the assessment timeframe (e.g., timing is insignificant/negligible or low as threat is only considered to be in the past); Negligible: when scope or severity is negligible; Not a Threat: when severity is scored as neutral or potential benefit.

f Scope – Proportion of the species that can reasonably be expected to be affected by the threat within 10 years. Usually measured as a proportion of the species' population in the area of interest. (Pervasive = 71–100 percent; Large = 31–70 percent; Restricted = 11–30 percent; Small = 1–10 percent; Negligible < 1 percent).

g Severity – Within the scope, the level of damage to the species from the threat that can reasonably be expected to be affected by the threat within a 10-year or three-generation timeframe. Usually measured as the degree of reduction of the species' population. (Extreme = 71–100 percent; Serious = 31–70 percent; Moderate = 11–30 percent; Slight = 1–10 percent; Negligible < 1 percent; Neutral or Potential Benefit ≥ 0 percent).

h Timing – High = continuing; Moderate = only in the future (could happen in the short term [< 10 years or 3 generations]) or now suspended (could come back in the short term); Low = only in the future (could happen in the long term) or now suspended (could come back in the long term); Insignificant/Negligible = only in the past and unlikely to return, or no direct effect but limiting.

LITERATURE CITED

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press. Washington, D.C. 493 pp.

Aitken, S.N., S. Yeaman, J.A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1:95–111.

Alberta Whitebark and Limber Pine Recovery Team. 2014. Alberta Whitebark Pine Recovery Plan 2013-2018. Alberta Environment and Sustainable Resource Development, Alberta Species at Risk Recovery Plan No. 34. Edmonton, AB. 63 pp.

Amman, G.D., M.D. McGregor, and R.E. Dolph, Jr. 1997. Mountain pine beetle. USDA Forest Service. Forest Insect & Disease Leaflet 2. Available online at: http://www.fs.fed.us/r6/nr/fid/fidls/fidl-2.pdf. 12 pp.

Angeli, N. and C. McGowan. In prep. Status assessment model for a long-lived species, the Whitebark Pine. Alabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences, Auburn University, Auburn, Alabama 36849-5418, USA. 55 pp.

Arno, S.F. 1980. Forest fire history in the northern Rockies. Journal of Forestry 78:460–465.

Arno, S. F. 1986. Whitebark pine cone crops-a diminishing source of wildlife food? Western Journal of Applied Forestry 1(3):92–94.

Arno, S.F. 2001. Community types and natural disturbance processes. Pages 74–88, Chapter 4 In Tomback, D.F., S.F. Arno, and R.E. Keane (eds.). Whitebark Pine Communities:Ecology and Restoration. Island Press. Washington, D.C. 440 pp.

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. General Technical Report INT–253. January 1989. 11 pp.

Arno, S.F. and R.J. Hoff. 1990. Pinus albicaulis Engelm. Whitebark pine. Pages 268–279 In Burns, R.M. and B.H. Honkala (tech. coords.). Silvics of North America. USDA Forest Service, Agriculture Handbook 654. Washington, D.C. 675 pp.

Arno, S.F., Parsons, D.J. and Keane, R.E., 2000. Mixed-severity fire regimes in the northern Rocky Mountains: consequences of fire exclusion and options for the future. In *Wilderness science in a time of change conference* (Vol. 5, pp. 225-232). US Department of Agriculture, Forest Service, Rocky Mountain Research Station Ogden, UT.

Aubry, C., D. Goheen, R. Shoal, T. Ohlson, T. Lorenz, A. Bower, C. Mehmel, and R. Sniezko (compilers). 2008. Whitebark pine restoration strategy for the Pacific Northwest Region 2009–2013. USDA Forest Service, Pacific Northwest Region. Olympia, Washington. 90 pp.

Barrett, S.W. 1994. Fire regimes on andesitic mountain terrain in northeastern Yellowstone-National-Park, Wyoming. International Journal of Wildland Fire 4:65-76.

Barringer L.E., D.F. Tomback, M.B. Wunder, and S.T. McKinney. 2012. Whitebark Pine Stand Condition, Tree Abundance, and Cone Production as Predictors of Visitation by Clark's Nutcracker. PLoS ONE 7: 1–5 e37663. doi:10.1371/journal.pone.0037663

Bartlein, P. J.; Whitlock, C.; Shafer, S. L. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology. 11: 782–792.

Bateman, B.L., C. Wilsey, L. Taylor, J. Wu, G.S. LeBaron, and G. Langham. 2020. North American birds require mitigation and adaptation to reduce vulnerability to climate change. *Conservation Science and Practice*, *2*(8), 18 pp.

Beck, J., and G. Holm. 2013. *Draft Crater Lake National Park Whitebark Pine Conservation Plan*. Crater Lake, OR: Crater Lake National Park.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of Climate Change on the Future of Biodiversity. *Ecology letters*, *15*(4), 365-377.

Bentz, B.J. and G. Schen-Langenheim. 2007. The mountain pine beetle and whitebark pine waltz: has the music changed? Pages 43–50 In Proceedings of the Conference Whitebark Pine: A Pacific Coast Perspective. USDA Forest Service, Rocky Mountain Research Station. Logan, Utah.

Bentz, B.J., J. Régnière, C.J. Fettig, E.M. Hansen, J.L. Hayes, J.A. Hicke, R.G. Kelsey, J.F. Negrón, and S.J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60:602–613.

Berryman, A. A. 1986. Forest Insects Principles and Practices of Population Management. Plenum Press, New York. 279 pp.

Billings WD. 1951. Vegetational zonation in the Great Basin of western North America, pp. 101–122. In Compt. Rend, du Colloque sur les Bases Ecologique de la Regeneration de la Vegetation des Zones Arides. IUBS, Paris.

Bockino, N.K., and D.B. Tinker. 2012. Interactions of white pine blister rust and mountain pine beetle in whitebark pine ecosystems in the southern Greater Yellowstone Area. Natural Areas Journal 32:31–40.

Bower, A. 2014. 2013-2014 Annual Progress Report. Whitebark pine Restoration Program, Pacific Northwest Region. 59 pp.

Bradshaw, A.D. and T. McNielly. 1991. Evolutionary response to global climatic change. Annals of Botany 67:5–14.

Brar, S., Tsui, C. K., Dhillon, B., Bergeron, M. J., Joly, D. L., Zambino, P. J., El-Kassaby, Y.A., and Hamelin, R. C. 2015. Colonization history, host distribution, anthropogenic influence and landscape features shape populations of white pine blister rust, an invasive alien tree pathogen.PloS one 10(5). 16 pp.

Buotte, P.C., Hicke, J.A., Preisler, H.K., Abatzoglou, J.T., Raffa, K.F., Logan, J.A., 2016. Climate influences on whitebark pine mortality from mountain pine beetle in the Greater Yellowstone Ecosystem. Ecol. Appl. 26, 2507–2524.

Buotte, P.C., J. A. Hicke, H.K. Preisler, J.T. Abatzoglou, K. F. Raffa, and J. A. Logan. 2017. Recent and future climate suitability for whitebark pine mortality from mountain pine beetles varies across the western US. Forest Ecology and Management 399:132–142.

Campbell, E. M. and J. A. Antos. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canada Journal of Forest Restoration 30: 1051–1059.

Campbell, E.M. and J.A. Antos. 2003. Postfire succession in *Pinus albicaulis - Abies lasiocarpa* forests of southern British Columbia. Canadian Journal of Botany 81:383-397.

Carroll, A.L., S.W. Taylor, J. Regniere, and L. Safranyik. 2003. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. Pages 223–232 In Shore, T.L., J.E. Brooks, and J.E. Stone (eds.). Proceedings of the Symposium on Mountain Pine Beetle Symposium: Challenges and Solutions. Oct. 30–31, 2003, Kelowna, British Columbia. Information Report BC–X–399. National Resources Canada, Canadian Forest Service, and the Pacific Forestry Centre. Victoria, British Columbia.

Chang T, Hansen AJ, Piekielek N. 2014. Patterns and Variability of Projected Bioclimatic Habitat for Pinus albicaulis in the Greater Yellowstone Area. PLoS ONE 9(11): e111669. doi:10.1371/journal.pone.0111669.

Chew, J. D. 1990. Timber management and target stands in the whitebark pine zone. Pages 310–314 In Schmidt, W. C., McDonald, K. J. (compilers). Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. Gen. Tec. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Childs, T.W., Bedwell, J.L., and Englerth, G.H. 1938. Blister rust infection on Pinus albicaulis in the northwest. Plant Disease Reporter 22:139–140. U.S. Department of Agriculture, Bureau of Plant Industry.

Cochrane, M.A., and K.C. Ryan, K.C. 2009. Fire and fire ecology: Concepts and principles. In Tropical fire ecology (pp. 25-62). Springer, Berlin, Heidelberg.

Cohen, J. 2008. The wildland-urban interaface fire problem: A consequence of the fire exclusion paradigm. Forest History Today. Fall: 20–26.

Confederated Salish and Kootenai Tribes. 2000. Flathead Indian reservation forest management plan: an ecological approach to tribal forest management. Final Environmental Impact Statement. Pablo, MT.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2010. COSEWIC assessment and status report on the whitebark pine Pinus albicaulis in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Canada. Available online at: http://www.sararegistry.gc.ca/status/status_e.cfm. x + 44 pp.

Cripps, C.L. and R. Antibus. 2011. Native ectomycorrhizal fungi of limber and whitebark pine: Necessary for forest sustainability? In *The future of high-elevation, five-needle white pines* *in western North America.* Proceedings of the High Five Symposium. June 28–30, 2010, Missoula, MT. R. E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith, eds., 37–44. Fort Collins, CO:US Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Critchfield, W.B. and E.L. Little, Jr. 1966. Geographic Distribution of the Pines of the World. U.S.D.A. For. Serv. Misc. Public. 991, Washington, D.C.

Devine, W.; Aubry, C.; Bower, A.; Miller, J.; Maggiulli Ahr, N. 2012. Climate change and forest trees in the Pacific Northwest: a vulnerability assessment and recommended actions for national forests. Olympia, WA: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 102 pp.

Dolanc, C.R., J.H. Thorne, and H.D. Safford. 2013. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. Global Ecology and Biogeography 22:264-276.

Dooley, E.M. and D. Six. 2015. Severe White Pine Blister Rust Infection in Whitebark Pine Alters Mountain Pine Beetle (Coleoptera: Curculionidae) Attack Density, Emergence Rate, and Body Size. Ecosystem and Conservation Sciences Faculty Publications. 60. http://scholarworks.umt.edu/decs_pubs/60

Eglitis, A. 2015. Protection of whitebark pines on the Fremont-Winema NF with the bark beetle anti-aggregant pheromone verbenone. USDA, USFS, Central Oregon Service Center for Insects and Diseases, Bend, OR.

Environment Canada. 2010. Consultation on amending the list of species under the species at risk act: terrestrial species. Environment Canada, Canadian Wildlife Service. Ottawa, Ontario. 76 pp.

Environment and Climate Change Canada. 2017. Recovery Strategy for the Whitebark Pine (Pinus albicaulis) in Canada [Proposed]. Species at Risk Act Recovery Strategy Series. Environment and Climate Change Canada, Ottawa. viii + 54 pp.

Ettl, G.J. and N. Cottone. 2004. Whitebark pine (Pinus albicaulis) in Mt. Rainier National Park, Washington, USA. Pages 36–47 In Akçakaya, M. Burgman, O. Kindvall, C.C. Wood, P. Sjögren-Gulve, J.S. Hatfield, and M.A. McCarthy (eds.). Species Conservation and Management Case Studies. Oxford University Press. Oxford, United Kingdom.

Farnes, P.E. 1990. SNOTEL and snow course data: describing the hydrology of whitebark pine ecosystems. Pages 302–304 In Schmidt, W.C. and K.J. McDonald (compilers). Proceedings-Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource. 1989 March 29–31. Boseman, Montana. General Technical Report INT–270. Ogden, Utah. USDA Forest Service, Intermountain Research Station. 386 pp.

Fiedler, C. E. and S. T. McKinney. 2014. Forest Structure, Health, and Mortality in Two Rocky Mountain Whitebark Pine Ecosystems: Implications for Restoration. Natural Areas Journal 34(3):290–299.

Field, S. G., A. W. Schoettle, J. G. Klutsch, S. J. Tavener, and M.F. Antolin. 2012. Demographic projection of high-elevation white pines infected with white pine blister rust: a nonlinear disease model. Ecological Application: 22(1): 166–183.

Flanagan, P.T., P. Morgan, and R.L. Everett. 1998. Snag Recruitment in subalpine forests. Northwest Science 72:303–309.

Flora of North America. 2021. Pinus albicaulis. Accessed from http://floranorthamerica.org/Pinus_albicaulis on October 8, 2021.

Frank, K. L., B.W. Wells, L.S. Kallstein, and H. W. Thistle, Jr. 2008. Synoptic climatology of the long-distance dispersal of white pine blister rust II. Combination of surface and upper-level conditions. International Journal of Biometerol 52:653–666.

Fulé, P.Z., J.E. Crouse, T.A. Heinlein, M.M. Moore, W.W. Covington, and G. Verkamp. 2003. Mixed-severity fire regime in a high-elevation forest of Grand Canyon, Arizona, USA. Landscape Ecology 18:465-486.

Geils, B.W., K.E. Hummer, and R.S. Hunt. 2010. White pines, Ribes, and blister rust: a review and synthesis. Forest Pathology 40:147–185.

Gibson, K., K. Skov, S. Kegley, C. Jorgensen, S. Smith, and J. Witcosky. 2008. Mountain pine beetle impacts in high-elevation five-needled pines: current trends and challenges. USDA Forest Service. Forest Health Protection. R1–08–020. September 2008. Missoula, Montana. 32 pp.

Gillette, N.E., S.J. Kegley, S.L. Costello, S.R. Mori, J.N. Webster, C.J. Mehmel, and D. L. Wood. 2014. Efficacy of verbenone and green leaf volatiles for protecting whitebark and limber pines from attack by mountain pine beetle (Coleoptera: Curculionidae: Scolytinae). Environmental Entomology 43:1019–1026.

Global Climate Change Impacts in the United States. 2009. A state of the knowledge report from the U.S. Global Change Research Program. Karl, T.R., J.M. Melillo, and T.C. Peterson (eds.). Cambridge University Press. New York, New York. 188 pp.

Goeking, S.A., and D.K. Izlar. 2018. *Pinus albicaulis* Engelm. (whitebark pine) in the mixed-species stands throughout its US range: Broad-scale indicators of extent and recent decline. Forests 9(131), 16 pp.

Goheen, E.M., D.J. Goheen, K, Marshall, R.S. Danchok, J.A. Petrick, and D.E. White. 2002. The status of whitebark pine along the Pacific Crest National Scenic Trail on the Umpqua National Forest. General Technical Report - Pacific Northwest Research Station, USDA Forest Service. No.PNW-GTR-530 pp.19

Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee. 2011. *Whitebark Pine Strategy for the Greater Yellowstone Area.* 41 pp.

Greater Yellowstone Coordinating Committee (GYCC). 2015. Adaptive Action Plan: Whitebark Pine in the Greater Yellowstone Area.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2006. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2005 annual report. In: C.C. Schwartz, M.A. Haroldson, and K. West, (eds.), Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team, 2005, pp. 73-80.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2015. Monitoring Whitebark Pine in the Greater Yellowstone Ecosystem 2014 Annual Report. Natural Resource Data Series NPS/GRYN/NRDS—2015/796. 26.pp.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2016. Monitoring Whitebark Pine in the Greater Yellowstone Ecosystem 2015 Annual Report. Natural Resource Report NPS/GRYN/NRR—2016/1146. 26.pp.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2017. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2017 annual report. Pages 128–130 In van Manen F. T., M.A. Haroldson, and B. E. Karabensh (eds.). Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team, 2017. U.S. Geological Survey, Bozeman, Montana. U.S.A.

Greater Yellowstone. 2015. *Adaptive Action Plan, Whitebark Pine in the Greater Yellowstone Area.*

Greenwood, S. and A.S. Jump. 2014. Consequences of treeline shifts for the diversity and function of high altitude ecosystems. *Arctic, Antarctic, and Alpine Research*, *46*(4), pp.829-840.

Halofsky, Jessica E.; Peterson, David L.; Dante-Wood, S. Karen; Hoang, Linh; Ho, Joanne J.; Joyce, Linda A., eds. 2018a. Climate change vulnerability and adaptation in the Northern Rocky Mountains - Part 1. Chapter 6. Effects of climate change on forest vegetation. Gen. Tech. Rep. RMRS-GTR-374. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 1–273.

Halofsky, Jessica E.; Peterson, David L.; Ho, Joanne J.; Little, Natalie, J.; Joyce, Linda A., eds. 2018b. Climate change vulnerability and adaptation in the Intermountain Region [Part 1]. Gen. Tech. Rep. RMRS-GTR-375. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 112–164.

Hamann, A. and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2773–2786.

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(0): 68-83.

Hartwell, M.G., P. Alaback. and S.F. Arno. 2000. Comparing historic and modern forests on the Bitterroot Front. *In* The Bitterroot Ecosystem Management Research Project: What We Have Learned. Symp. Proc. USDA Forest Service, Rocky Mountain Research Station pp. 11-16.

Hartwell, M.G., P. Alaback. and S.F. Arno. 2000. Comparing historic and modern forests on the Bitterroot Front. *In* The Bitterroot Ecosystem Management Research Project: What

We Have Learned. Symp. Proc. USDA Forest Service, Rocky Mountain Research Station pp. 11-16.

Hatala, J.A., M.C. Dietze, R.L. Crabtree, K. Kendall, D. Six, and P.R. Moorcroft. 2011. An ecosystem-scale model for the spread of a host-specific forest pathogen in the Greater Yellowstone Ecosystem. Ecological Applications.

Hayes,C., M.Casey, G. DeNitto, J. Egan, M. Jackson, B. Lockman, S. Sontag, B. Steed, N. Studevant, A. Gannon, and R. Silverstein. 2013. Montana Forest Insect and Disease Conditions and Program Highlights – 2012. USDA. Forest Service, 63 pp.

Hicke, J.A., J.A. Logan, J. Powell, and D.S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (Dendroctonus ponderosae) outbreaks in the western United States. Journal of Geophysical Research 111:G02019:1–12.

Hoff, R. and Hagle, S., 1990. Diseases of whitebark pine with special emphasis on white pine blister rust. In: Schmidt, W.C., and K.J. McDonald (compilers). Proceedings--Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT. General Technical Report INT-270. 179-190 pp.

Hoff, R.J., D.E. Ferguson, G.I. McDonald, and R.E. Keane. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust. Pages 346–366, Chapter 17 In Tomback, D.F., S.F. Arno, and R.E. Keane (eds.). Whitebark Pine Communities: Ecology and Restoration. Island Press. Washington, D.C. 440 pp.

Hood, S. M., Cluck, D. R., Smith, S. L., & Ryan, K. C. 2008. Using bark char codes to predict post-fire cambium mortality. Fire Ecology, 4(1), 57–73.

Hosie, R.C. 1969. Native Trees of Canada. Can. Forest Service. Queen's Printer for Canada. Ottawa. 380 pp.

Hudson, L.E. and E. Karnaugh. 2010. Whitebark pine restoration under way at Crater Lake. Preemptive strike against blister rust based on disease-resistant seedlings. Park Science 27(2):68–69.

Huntley, B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for plant communities. Annals of Botany 67:15–22.

Hutchins, H.E. and R.M. Lanner. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192–201.

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: synthesis report. Report adopted at IPCC Plenary XXVII, Valencia, Spain, 12–17 November,2007. 104 pp.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Jacobi, W., B. Goodrich, H.S.J. Kearns, K. Burns, and B. Geils. 2010. Can micro-scale meteorological conditions predict the impact of white pine blister rust in Colorado and Wyoming? Presentation and abstract In High-Five Symposium: the Future of High-Elevation Five-Needle White Pines in Western North America. Missoula, Montana. June 28–30, 2010.

Jules, E.S. et al. 2016. The relative contributions of disease and insects in the decline of a long-lived tree: a stochastic demographic model of whitebark pine (Pinus albicaulis). Forest Ecology and Management 381: 144–156.

Jules, E.S., P.J. van Mantgem, B.G. Iberle, J.C.B. Nesmith, and R.M. Rochefort. 2020. Whitebark pine in the National Parks of the Pacific states: An assessment of population vulnerability. Northwest Science 94(2): 129-141.

Keane, R.E. 2001a. Can the fire-dependent whitebark pine be saved? Fire Management Today 61:3, 17–20.

Keane, R.E. 2001b. Successional dynamics: modeling an anthropogenic threat. Pages 159–192, Chapter 9 In Tomback, D.F., S.F. Arno, and R.E. Keane (eds.). Whitebark Pine Communities: Ecology and Restoration. Island Press. Washington, D.C. 440 pp.

Keane and Arno 2001. Keane, R.E., and Arno, S.F. 2001. Restoration Concepts and Techniques. In Tomback, D.F., Arno, S.F., and Keane, R.E. (eds.) Whitebark Pine Communities (pp. 367–400). Washington, D.C.: Island Press.

Keane, R. F. and S. F. Arno. 1993. Rapid decline of whitebark pine in western Montana: Evidence from 20-year measurements. Western Journal of Applied Forestry 8(2): 44–47.

Keane, B., A. Bower, and S. Hood. 2020. A burning paradox: Whitebark is easy to kill but also dependent on fire. Nutcracker Notes. 38:7-8.

Keane, R.E. and R.A. Parsons. 2010. Restoring whitebark pine forests of the Northern Rocky Mountains, USA. Ecological Restoration 28:56–70.

Keane, R.E., P. Morgan, and J.P. 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., Gray, K.L. and Dickinson, L.J., 2007. Whitebark pine diameter growth response to removal of competition. Res. Note RMRS-RN-32. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 9 p.

Keane, Robert E.; Tomback, D.F.; Aubry, C.A.; Bower, A.D.; Campbell, E.M.; Cripps, C.L.; Jenkins, M.B.; Mahalovich, M.F.; Manning, M.; McKinney, S.T.; Murray, M.P.; Perkins, D.L.; Reinhart, D.P.; Ryan, C.; Schoettle, A.W.; Smith, C.M. 2012. A range-wide restoration strategy for whitebark pine (Pinus albicaulis). Gen. Tech. Rep. RMRS-GTR-279. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 108 pp.

Keane, R. E., D. Quinn, J. Cochrane. 2017a. Guidelines and Best Practices for Managing Fire in Whitebark Pine Stands in the Crown of the Continent. General Technical Report RMRS–GTR–XXX . U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 26 pp.

Keane, R. E., L. M. Holsinger, M.F. Mahalovich, and D. F. Tomback. 2017b. Restoring Whitebark Pine Ecosystems in the Face of Climate Change. Gen. Tech. Rep. RMRS-GTR-361. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 123 pp.

Keeley, J.E. 2009. Fire intensity, fire severity, and burn severity: a brief review and suggested usage. International Journal of Wildland Fire. 18:116-126.

Kegley, S.; Schwandt, J. W.; Gibson, K. 2004. Forest health assessment of whitebark pine in selected stands in the Selkirk Mountains of Northern Idaho. USDA Forest Service, Northern Region Forest Health Protection, FHP Report 04-5. 8 pp.

Kegley, S., J. Schwandt, K. Gibson, and D. Perkins. 2011. Health of whitebark pine forests after mountain pine beetle outbreaks. USDA Forest Service Proceedings RMRS-P-63.

Kegley, A., R. A. Sniezko, R. Danchok, and D. P. Savin. 2012. Blister Rust Resistance Among 19 Families of Whitebark Pine, Pinus albicaulis, From Oregon and Washington – Early Results From an Artificial Inoculation Trial. Proceedings of the 4th International Workshop on Genetics of Host-Parasite Interactions in Forestry. General Technical Report PSW-GTR-240.

Kendall, K.C. and R.E. Keane. 2001. Whitebark pine decline: infection, mortality, and population trends. Pages 221–242, Chapter 11 In Tomback, D.F., S.F. Arno, and R.E. Keane (eds.). Whitebark Pine Communities: Ecology and Restoration. Island Press. Washington, D.C. 440 pp.

Keyser, A., and Westerling, A.L. 2017. Climate drives inter-annual variability in probability of high severity fire occurrence in the western United States. Environmental Research Letters, 12: 1–9.

Kichas, N.E., S.M. Hood, G.T. Pederson, R.G. Everett and D.B. McWethy. 2020. Whitebark pine (Pinus albicaulis) growth and defense in response to mountain pine beetle outbreaks. Forest Ecology and Management 457:1-13.

King, J.N., A. David, D. Noshad, and J. Smith. 2010. A review of genetic approaches to the management of blister rust in white pines. Forest Pathology 40:292–313.

Kinloch, Jr., B.B. 2003. White pine blister rust in North America: past and prognosis.Phytopathology 93:1044–1047.

Kipfmueller, K.F. and W.L. Baker. 2000. A fire history of subalpine forests in south-eastern Wyoming, USA. Journal of Biogeography. 27:71-85.

Kittler, B. 2017. “Funding the Restoration of Whitebark Pine.” National Whitebark Pine Restoration Plan Summit, November 7, 2017, Missoula, MT.

Kliejunas, J.T., B.W. Geils, J.M. Glaeser, E.M. Goheen, P. Hennon, M.-S. Kim, H. Kope, J. Stone, R. Sturrock, and S.J. Frankel. 2009. Review of literature on climate change and forest diseases of western North America. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW–GTW–225. 54 pp.

Lackschewitz, K., 1991. Vascular plants of west-central Montana: identification guide book. US Department of Agriculture, Forest Service, Intermountain Research Station. Gen. Tec. Rpt. INT-277. May 1991. 650 pp.

Lanner, R.M. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. Pages 14–24 in W.C. Schmidt and K.J. McDonald (compilers). Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. USDA Forest Service. Gen. Tech. Rpt. INT-270. June 1990. 386 pp.

Lanner, R.M. 1996. Made for Each Other: A Symbiosis of Birds and Pines. Oxford University Press. New York, NY. 155 pp.

Larson, E.R. 2007. Whitebark pine regeneration in southwest Montana and eastern Oregon.Nutcracker Notes 13:16–18.

Larson, E.R. 2009. Status and dynamics of whitebark pine (Pinus albicaulis Engelm.) forests in southwest Montana, central Idaho, and Oregon, U.S.A. Ph.D. dissertation. University of Minnesota. Twin Cities, Minnesota. 176 pp.

Larson, E.R. and K.F. Kipfmueller. 2010. Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. Canadian Journal of Forest Research 40:476-487.

Larson, E.R. and K.F. Kipfmueller. 2012. Ecological disaster or the limits of observation? Reconciling modern declines with the long-term dynamics of whitebark pine communities. Geography Compass 6:189-214.

Larson, E.R., S.L. Van De Gevel, and H.D. Grissino-Mayer. 2009. Variability in fire regimes of high-elevation whitebark pine communities, western Montana, USA. Ecoscience 16:282-298.

Leirfallom *et al*. 2015. The effects of seed source health on whitebark pine (*Pinus albicaulis*) regeneration density after wildfire. Canadian Journal of Forest Research 45: 1597–1606.

Lenoir, J., J.C. Gégout, P.A. Marquet, P. de Ruffray, and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771.

Linhart, Y.B. and D.F. Tomback. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. Oecologia 67: 107–110.

Liston, A., W. A. Robinson, D. Pinero, and E. R. Alvarez-Buylla.1999. Phylogenetics of *Pinus* (Pinaceae) Based on Nuclear Ribosomal DNA Internal Transcribed Spacer Region Sequences. Molecular Phylogenetics and Evolution 11(1): 95–109.

Littell, J.S., Oneil, E.E., McKenzie, D., Hicke, J.A., Lutz, J.A., Norheim, R.A. and Elsner, M.M., 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. Climatic change, 102(1), pp.129-158.

Loehman, R. A., A. Corrow, and R. E. Keane. 2011. Modeling Climate Changes and Wildfire Interactions: Effects on Whitebark Pine (Pinus albicaulis) and Implications for Restoration, Glacier National Park, Montana, USA. USDA Forest Service Proceedings RMRS-P-63.
.
Logan, J.A. and J.A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidate. American Entomologist 47: 160–172.

Logan, J.S., J. Regniere, and J.A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1:130–137.

Logan, J.A., W.W. MacFarlane, and L. Willcox. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecological Applications 20:895–902.

Lorenz, T.J., C. Aubry, and R. Shoal. 2008. A review of the literature on seed fate in whitebark pine and the life history traits of Clark's nutcracker and pine squirrels. USDA Forest Service, Pacific Northwest Research Station. Portland, Oregon. General Technical Report PNW–GTR–742. April 2008. 62 pp.

Lorenz, T.J., K.A. Sullivan, A.V. Bakian, and C.A. Aubry. 2011. Cache-Site Selection in Clark's Nutcracker (*Nucifraga columbiana*). The Auk 128: 237–247.

MacFarlane, W. W., J.A. Logan, and W. R. Kern. 2013. An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. Ecological Application 23(2): 421–437.

Mahalovich, M.F. 2010. U.S.A. inland northwestern western white pine breeding and restoration program: history, current and future directions. Proceedings of the third Western White Pine Management Conference, Vernon, British Columbia.

Mahalovich, M.F. 2013. Grizzly bears and whitebark pine in the greater yellowstone ecosystem. future status of whitebark pine: blister rust resistance, mountain pine beetle and climate change. USDA Forest Service. 2470 RRM-NR-WP-13-01.

Mahalovich, M.F. 2015. Inland West Whitebark Pine Genetic Restoration Program CY14. White paper. 5 pp.

Mahalovich, M.F. 2016. Inland west whitebark pine genetic restoration program CY15. White paper. 6 pp.

Mahalovich, M.F. 2017. "Inland West Whitebark Pine Genetic Restoration Program." National Whitebark Pine Restoration Plan Summit, November 7, 2017, Missoula, MT.

Mahalovich, M. F. and V. D. Hipkins. 2011. Molecular Genetic Variation in Whitebark Pine (Pinus albicaulis Engelm.) in the Inland West. USDA Forest Service Proceedings RMRS-P-63.

Mahalovich, M. and Stritch, L. 2013. Pinus albicaulis. The IUCN Red List of Threatened Species 2013: e.T39049A2885918. http://dx.doi.org/10.2305/IUCN.UK.2013p1.RLTS.T39049A2885918.en

Mahalovich, M.F., K.E. Burr, and D.L. Foushee. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: planting strategies for restoration. USDA Forest Service Proceedings RMRS–P–43.

Maier, M. 2012. Clark's nutcracker seed harvest patterns in Glacier National Park and a novel method for monitoring whitebark pine cones. M.S. Thesis. Utah State Univeristy. Logan, UT. 68 pp.

Malcolm, J.R., A. Markham, R.P. Neilson, and M. Garaci. 2002. Estimated migration rates under scenarios of global climate change. Journal of Biogeography 29:835–849.

Maloney, P.E. 2014. The multivariate underpinnings of recruitment for three Pinus species in montane forests of the Sierra Nevada, USA. Plant Ecology 215: 261–274.

Maloney, P. and D. Dunlap. 2006. White pine blister rust and whitebark pine ecosystems in California. pp. 106–107. In Proceedings of the Conference Whitebark Pine: A Pacific Coast Perspective USDA Forest Service R6-NR-FHP-2007-01.

Man, G. 2017. "U.S. Forest Service Funding Needs and Opportunities." National Whitebark Pine Restoration Plan Summit, November 7, 2017, Missoula, MT.

Mathys, A.S., N.C. Coops, and R.H. Waring. 2016. An ecoregion assessment of projected tree species vulnerabilities in western North America through the 21st century. Global Change Biology 23(2):920-932.

McCaughey *et al*. 1985. Proceedings-Conifer Tree Seed in the Inland Mountain West Symposium. USDA Forest Service. 14 pp.

McCaughey, W.W. and W.C. Schmidt. 2001. Taxonomy, distribution, and history. Pages 29–40, Chapter 2 In Tomback, D.F., S.F. Arno, and R.E. Keane (eds.). Whitebark Pine Communities: Ecology and Restoration. Island Press. Washington, D.C. 440 pp.

McCaughey, W.W. and D.F. Tomback. 2001. The natural regeneration process. Pages 105–120, Chapter 6 In Tomback, D.F., S.F. Arno, and R.E. Keane (eds.). Whitebark Pine Communities: Ecology and Restoration. Island Press. Washington, D.C. 440 pp.

McCool, S.F. and W.A. Freimund. 2001. Threatened Landscapes and Fragile Experiences: Conflict in Whitebark Pine Restoration. In Tomback, D.F., Arno, S.F., and Keane, R.E. (eds.) Whitebark Pine Communities (pp. 263–284). Washington, D.C.: Island Press.

McDonald, G.I. and R.J. Hoff. 2001. Blister rust: an introduced plague. Pages 193–220, Chapter 10 In Tomback, D.F., S.F. Arno, and R.E. Keane (eds.). Whitebark Pine Communities: Ecology and Restoration. Island Press. Washington, D.C. 440 pp.

McDonald, G.I., B.A. Richardson, P.J. Zambino, N.B. Klopfenstein, and M.-S. Kim. 2006. Pedicularis and Castilleja are natural hosts of Cronartium ribicola in North America: a first report. Forest Pathology 36:73–82.

McKenney, D.W., J.H. Pedlar, K. Lawrence, K. Campbell, and M.F. Hutchinson. 2007.Potential impacts of climate change on the distribution of North American trees. Bioscience 57:939–948.

McKinney, S.T. and D. Tomback. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research 27:1044–1057.

McKinney, W.T., C.E. Fiedler, and D.F. Tomback. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications 19:597–607.

McKinney, S. T., T. Rodhouse, L. Chow, A. Chung-MacCoubrey, G. Dicus, L. Garrett, K. Irvine, S. Mohren, D. Odion, D. Sarr, and L. A. Starcevich. 2012. Monitoring white pine (Pinus albicaulis, P. balfouriana, P. flexilis) community dynamics in the Pacific West Region - Klamath, Sierra Nevada, and Upper Columbia Basin Networks: Narrative version 1.0. Natural Resource Report NPS/PWR/NRR—2012/532. National Park Service, Fort Collins, Colorado.

Meyer, M. and M. North. 2019. Natural range of variation of red fir and subalpine forests in the Sierra Nevada bioregion. General Technical Report PSW-GTR-263. Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station, 263.

Mielke, J. L. 1943 White pine blister rust in western North America. Yale University School of Forestry Bulletin 52, New Haven, Connecticut.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species—a literature review. USDA Forest Service. Pacific Northwest Forest and Range Experimental Station, General Technical Report PNW-87.

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(1):14–25.

Moody, R.J. 2006. Post fire regeneration and survival of whitebark pine (*Pinus albicaulis* Engelm.) Thesis. University of British Columbia. 106 pages.

Morgan, P. and S.C. Bunting. 1990. Fire effects in whitebark pine forests. *In*: Schmidt, W. C. and K.J. McDonald (eds) Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource, 29–31 March 1989, Bozeman, MT. Ogden, UT: U.S. Department of Agriculture, Forest Service, General Technical Report GTR-INT-270, Intermountain Forest and Range Research Station, pp. 166–170.

Morgan, P. and M.P. Murray. 2001. Landscape ecology and isolation: implications for conservation of whitebark pine. 2001. Pages 289–309, Chapter 14 In Tomback, D.F., S.F. Arno, and R.E. Keane (eds.). Whitebark Pine Communities: Ecology and Restoration. Island Press. Washington, D.C. 440 pp.

National Fish, Wildlife and Plants Climate Adaptation Partnership. 2012. National Fish, Wildlife and Plants Climate Adaptation Strategy, Association of Fish and Wildlife Agencies, Council on Environmental Quality, Great Lakes Indian Fish and Wildlife Commission, National Oceanic and Atmospheric Administration, and U.S. Fish and Wildlife Service. Washington, DC. 112 pp.

NatureServe. 2010. NatureServe conservation status. Available online at: http://www.natureserve.org/explorer/ranking.htm. Accessed February 5, 2011. 7 pp.

NatureServe. 2011. Pinus albicaulis Available online at: http://explorer.natureserve.org/servlet/NatureServe?searchName=pinus+albicaulis. Accessed January 11, 2011. 9 pp.

Parks, S. A., Miller, C., Abatzoglou, J. T., Holsinger, L. M., Parisien, M. A., & Dobrowski, S. Z. 2016. How will climate change affect wildland fire severity in the western US? Environmental Research Letters, 11: 1–10.

Parks Canada. 2015. Survey Plot Data [Data File]. Jasper, AB: Parks Canada. Provided by Brenda Shepherd.

Perkins, D.L., Means, R.E, and Cochrane, A.C. 2016. Conservation and management of whitebark pine ecosystems on Bureau of Land Management lands in the western United States. Technical Reference 6711-1. Bureau of Land Management, Denver, CO. 93 pp.

Perkins, D.L. and T.W. 1996. A dendroecological assessment of whitebark pin in the Sawtooth-Salmon River region, Idaho. Canadian Journal of Forestry Research 26: 2123–2133.

Perry, D.A., P.F. Hessburg, C.N. Skinner, T.A. Spies, S.L. Stephens, A.H. Taylor, J.F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. Forest Ecology and Management 262:703-717.

Progar, R.A. 2007. Verbenone suppression of mountain pine beetle in lodgepole pine at the Sawtooth National Recreation Area in Central Idaho. USDA Forest Service R6-NR-FHP-2007-01. 1 p.

Raffa, K.F. and A.A. Berryman. 1987. Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? The American Naturalist 129:234–262.

Raffa, K.F., B.H. Aukema, B.J. Bentz, A.L. Carroll, J.A. Hicke, M.G. Turner, and W.H. Romme. 2008. Disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58:501–517.

Rapp, J.M., J.B. McIntire, and E.E. Crone. 2013. Sex allocation, pollen limitation and masting in whitebark pine. Journal of Ecology 101: 1345–1352

Ray, C., R.M. Rochefort, J.I. Ransom, J.C. Nesmith, S.A. Haultain, T.D. Schaming, J.R. Boetsch, M.L. Holmgren, R.L. Wilkerson, and R.B. Siegel. 2020. Assessing trends and vulnerabilities in the mutualism between whitebark pine (Pinus albicaulis) and Clark's nutcracker (Nucifraga columbiana) in national parks of the Sierra-Cascade region. *PloS one*, *15*(10), p.e0227161. 25 pp.

Resler, L.M. and D.F. Tomback. 2008. Blister rust prevalence in krummholz whitebark pine: implications for treeline dynamics, Northern Rocky Mountains, Montana, U.S.A. Arctic, Antarctic, and Alpine Research 40:161–170.

Retzlaff, M.L., S.B. Leirfallom, and R.E. Keane. 2016. A 20-year reassessment of the health and status of whitebark pine forests in the Bob Marshall Wilderness Complex, Montana, USA. Res. Note RMRS-RN-73. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 10 p.

Retzlaff, M.L., R.E. Keane, D.L. Affleck, and S.M. Hood. 2018. Growth response of whitebark pine (*Pinus albicaulis* Engelm) regeneration to thinning and prescribed burn treatments. Forests: 9, 311; http://dx.doi.org/10.3390/f9060311.

Rice, Janine; Tredennick, Andrew; Joyce, Linda A. 2012. Climate change on the Shoshone National Forest, Wyoming: a synthesis of past climate, climate projections, and ecosystem implications. Gen. Tech. Rep. RMRS-GTR-264. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 60 pp.

Richardson, B.A., A.K.M. Ekramoddoulah, J.-J. Liu, M.-S. Kim, and N.B. Klopfenstein. 2010. Current and future molecular approaches to investigate the white pine blister rust pathosystem. Forest Pathology 40:314–331.

Rochefort, R.M. 2008. The influence of white pine blister rust (*Cronartium ribicola*) on whitebark pine (Pinus albicaulis) in Mount Rainer National Park and North Cascades National Park Service Complex, Washington. Natural Areas Journal 28:290–298.

Rochefort, R.M.; Howlin, S.; Jeroue, L.; Boetsch, J.R.; Grace, L.P. 2018. Whitebark Pine in the Northern Cascades: Tracking the Effects of Blister Rust on Population Health in North Cascades National Park Service Complex and Mount Rainier National Park. Forests 9: 244.

Romme, W. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. The UW National Park. Ecological Monographs 52:199-221.

Rosenberg, K.V., J.A. Kennedy, R. Dettmers, R.P. Ford, D. Reynolds, J.D. Alexander, C.J. Beardmore, P.J. Blancher, R.E. Bogart, G.S. Butcher, A.F. Camfield, A. Couturier, D.W. Demarest, W.E. Easton, J.J. Giocomo, R.H. Keller, A.E. Mini, A.O. Panjabi, D.N. Pashley, T.D. Rich, J.M. Ruth, H. Stabins, and T. Will. 2016. Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee. 119 pp.

Sala, A., K. Hopping, E.J. B. McIntire, S. Delzon, E. E. Crone. 2012. Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. New Phytologisst 196 (1): 189–199.

Schaming T.D. 2015. Population-Wide Failure to Breed in the Clark's Nutcracker (Nucifraga columbiana). PLoS ONE 10(5): e0123917. https://doi.org/10.1371/journal.pone.0123917

Schaming TD, Sutherland CS. 2020. Landscape- and local-scale habitat influences on occurrence and detection probability of Clark's nutcrackers: Implications for conservation. PLOS ONE 15(5): e0233726.

Schotzko K., S. Cook, C. Jorgensen, S. Kegley, J. Schwandt, L. Lazarus, and J. Hoffman. 2012. Whitebark Pine Stand Conditions after Mountain Pine Beetle Outbreaks in Idaho, Wyoming and Montana. Poster presentation, Forest Health Monitoring.

Schwandt, J.W. 2006. Whitebark pine in peril: a case for restoration. United States Department of Agriculture. Forest Service Report R1–06–28. August 2006. Available online at: http://www.fs.fed.us/r1-r4/spf/fhp/publications. 20 pp.

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. Forest Pathology 40:226–250.

Schwandt, J.W., H. S.J. Kearns, J. W. Byler. 2013a. Impacts of White Pine Blister Rust and Competition on Natural Whitebark Pine Regeneration in Northern Idaho 1995–2012. Forest Health Protection, Report Number 13-09.

Schwandt, J.W., H. Kearns, and J. Byler. 2013b. White Pine Blister Rust General Ecology and Management. USDA Forest Service, Forest Health Protection. Available online at: https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5415080.pdf. Accessed October 31, 2018. 25 pp.

Schrag, A.M., A.G. Bunn, and L.J. Graumlich. 2007. Influence of bioclimatic variables on treeline conifer distribution in the Greater Yellowstone Ecosystem: implications for species of conservation concern. Journal of Biogeography. doi:10.1111/j.13652699.2007.01815.x.

Service (U.S. Fish and Wildlife Service). 2010. USDA Forest Service aerial detection mountain pine beetle survey results overlayed on whitebark pine distribution.

Service (U.S. Fish and Wildlife Service). 2016a. USFWS Species Status Assessment Framework: an integrated analytical framework for conservation. Version 3.4 dated August 2016.

Service (U.S. Fish and Wildlife Service). 2018. WBP range map.

Shanahan, E., K. Legg, R. Daley, K. M. Irvine, D. Roberts, and A. Litt. 2014. Status of Whitebark Pine in the Greater Yellowstone Ecosystem A Step-trend Analysis Comparing 2004-2007 to 2008-2011. Natural Resource Technical Report NPS/GRYN/NRTR—2014/917

Shanahan, E., K. Legg, and R. Daley. 2017. Status of whitebark pine in the Greater Yellowstone Ecosystem: A step-trend analysis with comparisons from 2004 to 2015. Natural Resource Report NPS/GRYN/NRR—2017/1445. National Park Service, Fort Collins, Colorado.

Shanahan, E., K. M. Irvine, D. Thoma, S. Wilmoth, A. Ray, K. Legg, and H. Shovic. 2016. Whitebark pine mortality related to white pine blister rust, mountain pine beetle outbreak, and water availability. Ecosphere 7(12): e01610. 10.1002/ecs2.1610

Shelly 2016. USFS Region 1 data request response for WBP 2015 CNOR. 5 pp.

Shelly 2014. USFS Region 1 data request response for WBP 2014 CNOR. 3 pp

Shepherd, B., Jones, B., Sissons, R., Cochrane, J., Park, J., Smith, C. M., and Stafl, N. 2018. Ten years of monitoring illustrates a cascade of effects of white pine blister rust and focuses whitebark pine restoration in the Canadian Rocky and Columbia Mountains. Forests, 9(3), 138. 18 pp.

Shoal, R., T. Ohlson, and C. Aubry. 2008. Land managers guide to whitebark pine restoration in the Pacific Northwest Region 2009-2013. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 37 pp.

Sibold, J.S., T.T. Veblen, and M.E. González. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. Journal of Biogeography 33:631-647.

Sidder, A.M.,S.Kumar, M. Laituir, and J. S. Sibold. 2016. Using spatiotemporal correlative niche models for evaluating the effects of climate change on mountain pine beetle. Ecosphere, 7(7).

Six, D. and J. Adams. 2007. White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scolytinae). Entomology Science 42:345–353.

Six, D.L., E. Biber, and E. Long. 2014.Management for mountain pine beetle outbreak suppression: does relevant science support current policy? Forests (5): 103-133.

Six, D.L., C. Vergobbi, and M. Cutter. 2018. Are survivors different? Genetic-based selection of trees by mountain pine beetle during a climate change-driven outbreak in a high-elevation pine forest. Frontiers in Plant Science 9:1-13.

Six, D.L., A. Trowbridge, M. Howe, D. Perkins, E. Berglund, P. Brown, J.A. Hicke, and G. Balasubramanian. 2021. Growth, Chemistry, and Genetic Profiles of Whitebark Pine Forests Affected by Climate-Driven Mountain Pine Beetle Outbreaks. Frontiers in Forests and Global Change 4:1-22.

Smith and Hoffman. 2000. Status of white pine blister rust in the Intermountain West. Western North American Naturalist 60(2), Article 6.

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.

Smith, C.M., B. Shepherd, C. Gillies, and J. Stuart-Smith. 2010. Re-measurement of whitebark pine infection and mortality in the Canadian Rockies. High-Five Symposium: The Future of High Elevation Five-Needle White Pines in Western North America, Presentation and Abstract (p. 67). University of Montana, Missoula, Montana.

Smith, C. M., B. Shepard, C. Gillies, and J. Stuart-Smith. 2013. Changes in blister rust infection and mortality in whitebark pine over time. Canadian Journal of Forest Research 43:90–96.

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. Ecoscience 20 (3): 215–229.

Sniezko, R.A. 2018. Whitebark pine SSA peer review comment.

Sniezko, R.A.; Kegley, A. 2015. Report on results of Interior West (Region 1) whitebark pine seedlots evaluated in two screening trials at Dorena Genetic Resource Center. Report R6-DGRC-2015-02. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 11 pp.

Sniezko, R.A., Koch, J., 2017. Breeding trees resistant to insects and diseases: putting theory into application. Biological Invasions, 19(11), pp. 3377-3400.

Sniezko, R.A.; Hill, J.; Savin, D.P.; Mutch, R.; Sticha, J.; Kegley, A.; Beck, J. 2016. Genetic variation in needle traits of *Pinus albicaulis* seedling families: within- population variation at Crater Lake National Park. In: Schoettle, A.W.; Sniezko, R.A.; Kliejunas, J.T., eds. Genetics of five-needle pines, rusts of forest trees, and strobusphere: proceedings of the IUFRO joint conference. RMRS-P-xxx. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Sniezko, R., and Kegley, A. 2017. *F&WS Candidate Notice of Renewal (CNOR) for Calendar Year 2016 – WHITEBARK PINE Update.* U.S. Department of Agriculture, Forest Service, Region 6 (Pacific Northwest) – Dorena Genetic Resource Center. White paper. 11 pp.

Spurr, S.H. and B.V. Barnes. 1980. Forest ecology (third edition). John Wiley and Sons, Inc. New York, NY. 687 pp.

Stevens, J.T., Kling, M.M., Schwilk, D.W., Varner, J.M. and Kane, J.M., 2020. Biogeography of fire regimes in western US conifer forests: A trait-based approach. *Global Ecology and Biogeography*, *29*(5), pp.944-955.

Syring, J., A. Willyard, R. Cronn, and A. Liston. 2005. Evolutionary relationships among Pinus (Pinaceae) subsections inferred from multiple low-copy nuclear loci. American Journal of Botany 92:2086–2100.

Syring, J., Farrell, K., Businský, R., Cronn, R., and Liston, A. 2007. Widespread genealogical nonmonophyly in species of *Pinus* subgenus Strobus. *Syst. Biol.* 56, 163–181

Tomback, D. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. Journal of Animal Ecology 51:451–467.

Tomback, D.F. and P. Achuff. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology 40:186–225.

Tomback, D.F. and E.R. Pansing. 2018. Effects of climate change and climate-altered fire regimes on whitebark pine populations. Joint Fire Science Project 16-2-01-13. 16pp.

Tomback, D.F. and L.M. Resler. 2007. Invasive pathogens at alpine treeline: consequences for treeline dynamics. Physical Geography 28:397–418.

Tomback, D. F., L.M. Resler, R. E. Keane, E.R. Pansing, A. J. Andrade, and A. C. Wagner. 2016. Community structure, biodiversity, and ecosystem services intreeline whitebark pine communities: potential impacts from a non-native pathogen. Forests7(21):1–22.

Tomback, D.F., L.A. Hoffmann and S.K. Sund. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. Pages 118–129 in W.C. Schmidt and K.J. McDonald (compilers). Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. USDA Forest Service. Gen. Tech. Rpt. INT-270. June 1990. 386 pp.

Tomback, D.F., J.K. Clary, J. Koehler, R.J. Hoff, and S.F. Arno. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance Burn of northern Idaho. Conservation Biology 9:654–664.

Tomback, D.F., Arno, S.F., and R.E. Keane. 2001a. The compelling case for management intervention. Pages 4–25 In Tomback, D.F., S.F. Arno, and R.E. Keane (eds.). Whitebark Pine Communities: Ecology and Restoration. Island Press. Washington, D.C. 440 pp.

Tomback, D.F., Anderies, A.J., Carsey, K.S., Powell, M.L., and S. Mellmann-Brown. 2001b. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology 82: 2587–2600.

Tomback, D.F., S. Wirt, W.W. McCaughey, and R.E. Keane. 2008. Preliminary pattern of investigation of the magnitude and time-frame of post-fire whitebark pine regeneration within selected areas in the Bob Marshall Wilderness Area and adjacent lands. Final Report 2008. JVA 03-JV-11222022-251. Unpublished data.

Tomback, Diana F., Peter Achuff, Anna W. Schoettle, John W. Schwandt, and Ron J. Mastrogiuseppe. 2011. The magnificent high-elevation five-needle white pines: ecological roles and future outlook. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. 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. Proceedings RMRS-P-63. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, vol. 63, pp. 2-28.

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(2):407–418.

Tomback, D. F. and E. R. Pansing. 2018. Effects of climate change and climate-altered fire regimes on whitebark pine populations. Joint Fire Science Program, JFSP Program ID: 16-2-01-13, available at firescience.gov.

USDA Forest Service 2000. An agency strategy for fire management. A report from the National Mangement Review Team. 27 pp.

USDA Forest Service 2011. White bark pine blister rust infection estimate.

USDA Forest Service. Forest Health Protection. 2016. Intermountain Region. Response to Candidate Notice of Review for Whitebark Pine. 7 pp.

Ward, K., R. Shoal, and C. Aubry. 2006. Whitebark pine in Washington and Oregon: a synthesis of current studies and historical data. USDA Forest Service, Pacific Northwest Region. February 2006.

Warwell, M.V., Rehfeldt, G.E., and Crookston, N.L. 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. USDA Forest Service R6–NR–FHP-2007–01.

Weaver 2001. Whitebark pine and its environment. Pages 41–73, Chapter 3. In Tomback, D.F., S.F. Arno, and R.E. Keane (eds.). Whitebark Pine Communities: Ecology and Restoration. Island Press. Washington, D.C. 440 pp.

Westerling, A.L., H.G. Hidalgo, D.R. Cayan, and T.W. Swetnam. 2006. Warming and earlier spring increase in western U.S. forest wildfire activity. Science 313:940–943.

Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Phil. Trans. R. Soc. B, 371(1696).

Wilson, B. 2007. Status of the whitebark pine (Pinus albicaulis) in Alberta. Alberta Sustainable Resource Development. Edmonton, Alberta, Canada. Publication No. T/151. 26 pp.

Whitebark Pine Ecosystem Foundation (WPEF). 2014. Whitebark pine and limber pine range maps. Available online from http://whitebarkfound.org.

Whitebark Pine Ecosystem Foundation (WPEF). 2017. 2017 Restoration Projects Funded by WPEF. Accessed online February 4, 2018 at http://whitebarkfound.org/2017-restoration-projects-funded-by-wpef/.

Wong, C.M., and L.D. Daniels. 2017. Novel forest decline triggered by multiple interactions among climate, an introduced pathogen and bark beetles. Global Change Biology 23(5):1926-1941.

Zambino, P.J. 2010. Biology and pathology of Ribes and their implications for management of white pine blister rust. Forest Pathology 40:264–291.

Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. Can. J. For. Res. 32(7): 1265–1274. doi:10.1139/x02-049.

Zeglen, S., J. Pronos, and H. Merler. 2010. Silvicultural management of white pines in western North America. Forest Pathology 40:347–368.

PERSONAL COMMUNICATIONS

Achuff, P. L., Scientist Emeritus, Parks Canada, in Waterton Lakes National Park, Waterton Park, Alberta. Telephone interview. (November 15, 2010).

Arnett, J., Rare Plant Botanist, Washington Natural Heritage Program, in Olympia, Washington.Telephone interview. (January 19, 2011).

Aubry, C., Area Genetist, U.S. Forest Service, in Olympia, Washington. Telephone interview. (January 5, 2011).

Keane, R., Research Ecologist, USDA Forest Service, Rocky Mountain Research Station, in Missoula, Montana. (April 7, 2011)a.

Keane, R., Research Ecologist, USDA Forest Service, Rocky Mountain Research Station, in Missoula, Montana. (April 27, 2011)c.

Reinhart, D., Resource Specialist, U.S. National Park Service, in Yellowstone National Park, Montana. Telephone interview. (July 1, 2010).

Reinhart, D., Resource Specialist, U.S. National Park Service, in Yellowstone National Park, Montana. Email exchange. (February 15, 2011).

Sniezko, R., Center Geneticists, USDA Forest Service, Dorena Genetic Resource Center, in Cottage Grove, Oregon. Telephone interview. (February 8, 2011).

Sniezko, R., Center Geneticists, USDA Forest Service, Dorena Genetic Resource Center, in Cottage Grove, Oregon. Telephone interview. (XX, 2014).

Schwandt, J., Plant Pathologist and Whitebark Coordinator, USDA Forest Service, Forest Health Protection, in Coeur d'Alene, Idaho. Telephone interview. (April 7, 2011).

Zack, A, Silviculturist (retired), U.S. Forest Service, Idaho Panhandle National Forest. Verbal exchange. (September 16, 2016).