Conserving the high elevation five-needle pines under climate change and other threats in North America

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A PROFESSIONAL PAPER SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE MASTER OF FORESTRY DEGREE
Northern Arizona University
November 2020

Abstract

Maintaining pine species in forests of North America is an important concern for land managers and other stakeholders. A key set of species are the "high-five," a group of five-needle pine species residing at high elevations. The species in this group are limber pine (*Pinus flexilis*), whitebark pine (*Pinus albicaulis*), foxtail pine (*Pinus balfouriana*), southwestern white pine (*Pinus strobiformis*), Rocky Mountain bristlecone pine (*Pinus aristata*), and Great Basin bristlecone pine (*Pinus longaeva*). These species are ecologically important because they reduce erosion, stabilize snowpack, protect downstream flow, provide shelter, and act as a reliable food source for multiple animal species, such as Clark's nutcracker. Unfortunately, they face multiple threats, which are expected to get worse with climate change. The objective of this review was to (1) review the silvics and ecology of each of the high-five species, (2) discuss threats to the high-five, (3) synthesize land management strategies to aid their conservation, and (4) discuss challenges, research needs, and limitations to conserving these species.

Threats of climate change, white pine blister rust and mountain pine beetle are increasing. The high-five are especially vulnerable to these threats, especially when faced with multiple stressors. Various silvicultural methods are key towards maintaining the health of forest stands: planting, assisted migration, silvicultural treatments, and burning. Planting or assisted migration using genetically superior seedlings gives the species a head start in regeneration, along with stronger defenses against white pine blister rust and higher drought tolerance. Silvicultural treatments and burning are two silvicultural techniques to reduce competition and promote the focal species. Land managers are currently using these four techniques in some locations in order to reach management objectives, but shifting to a conservation perspective is needed. Further research on predicting species range shifts and how species will respond to increased drought, temperatures, and fire is needed in order to make conservation methods effective. Use of these silvicultural methods for a conservation objective depends mostly on the species, site, and overall land management objectives, which are discussed in further detail. Comprehensive management plans that are feasible and can be monitored need to be implemented to aid in species conservation. More research is needed to assess range shifts accurately, and determine how growth and regeneration will be affected by climate change. Without action to conserve the high-five, we risk habitat and population loss, along with the ecosystem services these species provide.

Introduction

Conserving forests of western North America, especially those at higher elevations, is important for the ecological and cultural benefits they provide. High-elevation forests have disproportionately large effects on their environment, because they regulate snowmelt and water quality for ecosystems down below (Tomback et al. 2011 and sources within). Climate change, coupled with decades of fire suppression, the spread of the introduced disease white pine blister rust (WPBR), and mountain pine beetle (MPB, *Dendroctonus ponderosae*) attacks, are threatening the high elevation five-needle pine species, collectively known as the "high-five" (Tomback et al. 2011). This group includes limber pine (*Pinus flexilis*), whitebark pine (*P. albicaulis*), southwestern white pine (*P. strobiformis*), foxtail pine (*P. balfouriana*), Rocky Mountain bristlecone pine (*P. aristata,* hereafter RM bristlecone pine), and Great Basin bristlecone pine (*P. longaeva,* hereafter GB bristlecone pine) (Tomback et al. 2011). These species are taxonomically classified in the genus *Pinus* and the subgenus *Strobus* (Tomback et al. 2011). Southwestern white pine, whitebark pine, and limber pine are considered white pines, while foxtail pine, RM bristlecone pine, and GB bristlecone pine are considered foxtail pines (Tomback et al. 2011). The high-five, although not known for their commercial timber value, have high ecological importance in montane ecosystems as habitat and a food source for animals, regulators of springtime snowmelt, food and medicinal uses by Native Americans, and other ecosystem processes (Tomback et al. 2011, Shirk et al. 2018, Jackson et al. 2019). However, these species face increasing threats, especially those that are related to climate change. Climate change is a natural phenomenon, but has been accelerated by human activities since the industrial revolution (National Climate Assessment "Southwest," Cho 2017).

Figure 1. The high-five pine species. Top left: whitebark pine. Credit: Kristen Waring. Top right: limber pine. Credit: nfs.unl.edu. Center left: foxtail pine. Credit: Janet Fryer. Center right: RM bristlecone pine. Credit: Anthony Mendoza. Bottom left: GB bristlecone pine. Credit: David Rasch. Bottom right: southwestern white pine. Credit: Kristen Waring.

Climate change, mostly caused by anthropogenic factors, is disrupting ecosystem services and threatening species survival (Mooney et al. 2009). The Intergovernmental Panel on Climate Change (IPCC) (2018) predicts global average temperature increases of about 1.2ºC (2.2ºF) since pre-industrial levels by 2030 to 2052. Subalpine and southwestern forests are some of the most sensitive ecosystems to climate change (Diffenbaugh et al. 2008, Malone et al. 2018). Climate change is also altering the timing, frequency, intensity, and spatial extent of fires, which in turn, alters forest structure (Pansing et al. 2020). Regional tree mortality in the western U.S. can be attributed to higher temperatures (Allen et al. 2010), increasing wildfires (Stephens et al. 2014), drought stress (Allen et al. 2015), bark beetle outbreaks (Bentz et al. 2009), and invasive species (Shepherd et al. 2018). These threats are likely to change the structure, function, and composition of high elevation forests and become more prevalent as climate change progresses (Loehman et al. 2011, Allen et al. 2015, Jackson et al. 2019, Nesmith et al. 2019). Another prominent threat to five-needle white pines is white pine blister rust (WPBR), caused by the introduced fungus *Cronartium ribicola* (Maloney et al. 2016, Wagner et al. 2018, Jackson et al. 2019). It can be lethal to all five needle pines at all ages, reducing their reproductive potential (Fins et al. 2002, Wagner et al. 2018, Schoettle et al. 2019). Another serious damaging agent is MPB (Eidson et al. 2017). Its main hosts are Rocky Mountain lodgepole pine (*Pinus contorta,* hereafter lodgepole pine) and ponderosa pine (*Pinus ponderosa*), but it is known to attack most pine species. Notably, MPB has never been documented to attack GB bristlecone pine (Eidson et al. 2017). Warmer temperatures and drought provide preferable conditions for MPB, foreshadowing that this threat will become worse with climate change (Thoma et al. 2019).

Native pines are expected to migrate to northward latitudes and higher elevations as a result of warming temperatures (Zhu and Woodall 2011, SWWP: Shirk et al. 2018). Treeline, the upward-most edge of a habitat where trees are capable of growing, may move upward in elevation by as much as 2300 ft by the year 2100 (Kullman and Oberg 2009, Smithers et al. 2018). In fact, Smithers et al. (2018) showed potential for treeline advance currently occurring in the Great Basin mountain range by between 16 and 82 ft (time span not stated). Other areas with rapidly growing tree species are colonizing above treeline at even faster rates (Smithers et al. 2018). However, only some species will be able to keep up with this rapid rate of migration (Roberts and Hamann 2016).

It is important to conserve the high-five species because of the numerous ecosystem services they provide. The main threats to these species, namely climate change, WPBR, and MPB, have the potential to severely decrease their populations. By understanding management options, land managers can take the best course of action to conserve these species for future generations. This paper will (1) review what we know about each species, (2) discuss the three main threats (climate change, WPBR, and MPB) and (3) synthesize across species to find common management strategies for conservation.

Silvics and Ecological Importance

All six of the high-five species have great ecological importance (Tomback 2011 and sources within). All of these species, except for SWWP, are able to thrive on harsh sites up to the treeline. They reduce erosion, stabilize snowpack, protect downstream flow, provide shelter, and act as a reliable food source for multiple animal species (Tomback 2011, Looney and Waring 2013, Jackson et al. 2019). Five-needle pines are considered keystone species in upper subalpine and treeline forests, meaning they have disproportionately large effects in the environments where they dominate (Jackson et al. 2019). While the high-five are not known for their commercial timber value, they are held in high regard for their ecosystem services. This makes their conservation critical for forest ecosystems and the persistence of animal species.

Limber Pine

Range

Limber pine inhabits a wide range of locations, including the southern Sierra Nevada, the southwestern U.S., the southern Rocky Mountains, and multiple Great Basin mountain ranges (Figure 2, Tomback et al. 2011), occupying montane and subalpine forests (Peters and Visscher 2019). The species extends from northern New Mexico up to Canada, and from the western U.S. to North Dakota (Figure 2, Peters and Visscher 2019, Tomback et al. 2020). Limber pine is found on a broad range of elevations, occurring at 5,950-10,850ft in the central Rocky Mountains, and as great as 2,657-12,500ft overall (Table 1, Schoettle and Rochelle 2000, Sindewald et al. 2020). It inhabits both xeric (low moisture) and mesic (moderate moisture) sites, but is often outcompeted on mesic sites (Coop and Schoettle 2010, Webster and Johnson 2016). It is considered a habitat generalist, occurring with 22 different overstory species around its range (Windmueller-Campione and Long 2016). It can occur at upper and lower treeline across North American forests, but only dominates on harsh, rocky, and xeric sites due to its low competitive ability (Windmueller-Campione and Long 2016 and sources within). Limber pine is also tolerant of cold sites (Johnson 2001). Douglas-fir (*Pseudotsuga menziesii*) and quaking aspen (*Populus tremuloides*) are the only species that can occur within limber pine forests across all of its elevation gradient, but other species that commonly occur in limber pine communities are ponderosa pine, Rocky Mountain juniper (*Juniperus scopulorum*), white fir (*Abies concolor*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (Windmueller-Campione and Long 2016).

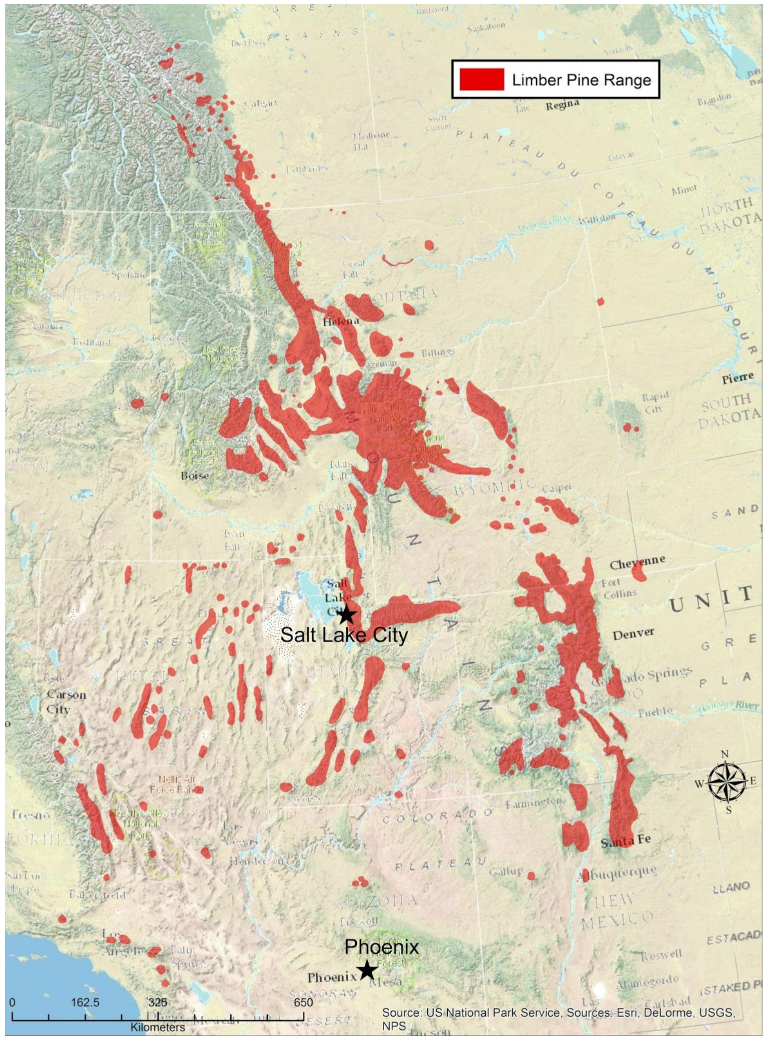

Figure 2. Limber pine's range throughout the U.S. and Canada. Source: U.S. National Park Service (2014).

<u>Seeds and Regeneration</u>

Limber pine has large, nearly wingless seeds, which are harvested and cached by Clark's nutcracker (*Nucifraga columbiana*) and other birds (Table 1, Lanner and Vander Wall 1980, Tomback et al. 2005, Peters and Visscher 2019, Sindewald et al. 2020). One nutcracker can cache up to 30,000 seeds per hectare per season, retrieving about 80% of the seeds cached (Lanner and Vander Wall 1980, Schoettle and Rochelle 2000). That leaves the remaining 20% to be eaten by rodents or to germinate (Lanner and Vander Wall 1980, Schoettle and Rochelle

2000). Seeds that are left on the surface are more likely to be washed away or consumed by animals (Nyland et al. 2016). Some seeds are dispersed by gravity, falling to the forest floor when the cones open (Tomback et al. 2005, Webster and Johnson 2016). However, seeds that are dispersed by gravity lie on top of the forest floor, leaving them more vulnerable to being washed away by precipitation and more likely to be consumed by animals (Nyland et al. 2016 and sources within). Furthermore, limber pine is considered a keystone species in Rocky Mountain National Park (RMNP) because its nutrient-rich seeds are an essential food source for wildlife (Sindewald et al. 2020).

Limber pine seedlings are drought tolerant (Table 1), although they survive better with higher moisture (Sindewald et al. 2020). Dawe et al. (2020) speculates that fire promotes limber pine regeneration, given that Clark's nutcracker prefers to cache seeds in open areas. However, Dawe et al. (2020) found 124 limber pine seedling clusters in unburned plots, and only 6 clusters around the same age on burned plots, concluding that extensive wildfire does not enhance limber pine's regeneration abilities on the northern extent of its range. Although limber pine is known for regenerating quickly after fire, extensive and severe wildfires limit immediate-post fire regeneration of limber pine (Dawe et al. 2020). Disease in general is likely to reduce limber pine's regeneration abilities in its northern habitats (Peters and Visscher 2019).

Fire

Fire regimes in mixed-conifer forests where limber pine occurs are hard to define because they are not well studied (Coop and Schoettle 2010), and because limber pine occurs in many locations and with a variety of species. Limber pine is known for having a relatively low fire tolerance (Table 1, Johnson 2001 and sources within), and being able to quickly colonize a burned area (Coop and Schoettle 2010). However, more research is needed on the fire regimes of pure limber pine stands, as well as regeneration response to fire.

Importance

This species may become more important to subalpine communities in the future due to its lower sensitivity to warmer temperatures (Kueppers et al. 2017), supporting ecosystem processes in these communities. Limber pine is an important foundation species in the alpine treeline ecotone, where it is difficult for trees to initiate (Sindewald et al. 2020). It is considered a keystone species in Rocky Mountain National Park for its large, nutritious seeds, which provide a food source for wildlife (Sindewald et al. 2020 and sources within). Limber pine may also contribute to snowpack retention at treeline, but more research is needed to understand how it specifically affects treeline communities (Sinewald et al. 2020 and sources within).

Threats

Limber pine has a wide distribution, but its status is not nearly as steady. Threats to limber pine include climate change, WPBR, and MPB (Table 2, Schoettle 2004, Schoettle et al. 2008, Cleaver et al. 2017, Long et al. 2018, Liu et al. 2020). WPBR is spreading through limber pine populations (Cleaver et al. 2017, Jacobi et al. 2018). The disease affects 88% of limber pine stands in Alberta (Dawe et al. 2020), and causes 40% mortality in many places (Smith et al. 2013). In addition, WPBR is altering limber pine dominance by killing the top of the tree, reducing its reproductive potential (Jacobi et al. 2018 and sources within). Stands with heavy WPBR infections may not regenerate (McKinney and Tomback 2007). About 50% of limber pine seedlings in RMNP are declining or dead (Cleaver et al. 2015). MPB is another lethal agent to limber pine, although not as substantial as WPBR (Jacobi et al. 2018). Limber pine is listed as *Least Concern* on the IUCN red list (Table 1, IUCN 2020), a *Species of Concern* in Rocky

Mountain National Park, and *Endangered* in Alberta, Canada (Cleaver et al. 2017, Visscher 2019, Dawe et al. 2020, Sindewald et al. 2020). Luckily, a conservation plan has been implemented for limber pine in Alberta (Alberta Whitebark and Limber Pine Recovery Team, 2014).

Table 1. IUCN status, fire tolerance, seed type, and elevation for each of the high-five species.

	IUCN Status[1,3]	Fire tolerance	Seed type[1]	Elevation
Limber pine	Least concern	Low[1]	Large and wingless	2,657-12,500 ft[1,10]
Whitebark pine	Endangered	Intermediate[1,12]	Large and wingless	3,600-12,100 ft[1]
Southwestern white pine	Least concern	High[5,6]	Large and wingless	5,900-12,175 ft[1,3,6]
Foxtail pine	Near threatened	High[1]	Small and winged	6,900-12,00 ft[1]
RM bristlecone pine	Least concern	Intermediate[1]	Small and winged	6,760-13,000 ft[1,4,10]
GB bristlecone pine	Least concern	Low[1,11]	Small and winged	7,000-12,000 ft[1]

Sources: FEIS database[1], Tomback et al. 2011[2], Shirk et al. 2018[3], Landscapeplants[4], L&W 2012[5], L&W 2013[6], Samano and Tomback 2003b[7], Zeglen et al. 2010[8], Schoettle and Rochelle 2000[9], Smithers et al. 2017[10], Burton et al. 2020[11], Keane et al. 2017a[12], IUCN 2020[13].

Whitebark Pine

<u>Range</u>

Whitebark pine inhabits upper subalpine forests to the top of the treeline, and extends further north than other white pine species (Tomback et al. 2011, Wagner et al. 2018). It is distributed from the Sierra Nevada in California, to Wyoming and Montana, to western Canada (Figure 3, Nesmith et al. 2019), and can tolerate poor seedbeds (lack of adequate nutrients or moisture) and harsh sites (Arno and Hoff 1989, Wagner et al. 2018). The elevation and species it occurs vary by region. It occurs between 3,600-12,100 ft in elevation, the lowest on Mt. Hood in Oregon, and the highest in the Sierra Nevada (Table 1, Fryer 2002 and sources within). Depending on the elevation, whitebark pine is typically found in communities with subalpine fir (*Abies lasiocarpa*), coastal and Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* and *Pseudotsuga menziesii* var. *glauca*), Engelmann spruce, lodgepole pine, lodgepole shore pine (*Pinus contorta* var. *contorta*), Sierra Nevada lodgepole pine (*Pinus contorta* var. *murrayana*), alpine larch (*Larix lyallii*), common juniper (*Juniperus communis*), limber pine, western hemlock (*Tsuga heterophylla*), Washoe pine (*Pinus washoensis*), white fir, and Jeffrey pine (*Pinus jeffreyi*) (Fryer 2002 and sources within). It occurs in pure stands at treeline, and forms krummholz communities on harsh sites (Fryer 2002 and sources within). Krummholz refers to the area between treeline and open alpine vegetation, where harsh conditions force trees to resort to a shrub-like form (Holtmeier 1981).

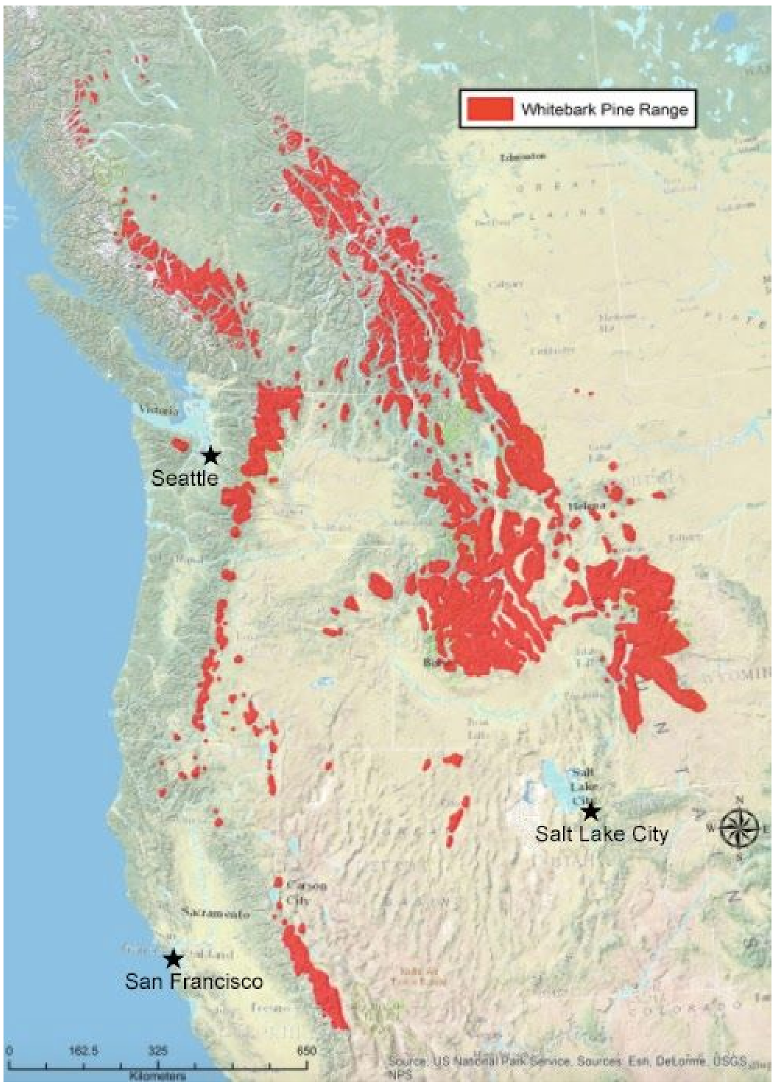

Figure 3. Whitebark pine's range throughout the U.S. and Canada. Source: U.S. National Park Service (2014).

Seeds and regeneration

Substantial cone crops only occur every 3-5 years in whitebark pine (Scott and McCaughey 2006). Whitebark pine seeds are large and nearly wingless, relying completely on Clark's nutcracker and rodents for dispersal (Table 1, Fryer 2002 and sources within). The cones are indehiscent, meaning they do not open when they are ripe. Therefore, nutcrackers must pry the cone scales open in order to retrieve the seeds (Fryer 2002 and sources within). Nutcrackers cache the seeds underground, where the seeds overwinter (Scott and McCaughey 2006). The seeds remain dormant for up to 3 years until spring conditions are moist enough (Scott and McCaughey 2006). Whitebark pine regeneration has been shown to occur in clumps, with stems fused or separate at the base (Weaver and Jacobs 1989 and sources within). This can be caused by nutcrackers and rodents caching seeds causing separate trees to grow together, or by single trees producing multiple stems (Weaver and Jacobs 1989 and sources within). Whitebark pine does not have strong apical dominance compared to other pines. In Weaver and Jacobs (1989) study, the majority of whitebark pine seedlings (58%) grown in a greenhouse had three main stems, while the majority of lodgepole pine seedlings (90%) only had one main stem.

Figure 2. Example of a whitebark pine in a krummholz community. Note the compacted, shrub-like structure. Credit: Kristen Waring.

Fire

Whitebark pine is drought and fire tolerant (Table 1, Keane et al. 2017a). Mature trees are able to survive low and sometimes moderate severity fires (Fryer 2002 and sources within). Seed caching by Clark's nutcracker makes whitebark pine regenerate quickly after fire (Fryer 2002 and sources within, Keane and Parsons 2010). In the northern portions of whitebark pine's range, regeneration events are stimulated by high-severity fires (Retzlaff et al. 2018). Its fire regimes vary between frequencies and severities depending on the location (Fryer 2002 and sources within, Retzlaff et al. 2018). Whitebark pine is considered a pioneer species, as one of the first species to germinate following fires (Retzlaff et al. 2018). However, fire exclusion over the past century has led to more shade-tolerant species outcompeting whitebark pine, contributing to its decline (Retzlaff et al. 2018). Managers will need to implement silvicultural treatments, including prescribed fire, in order to encourage whitebark pine to return to the landscape (Retzlaff et al. 2018).

Importance

Whitebark pine, like the rest of the high-five, is considered to be a keystone species for its multitude of ecosystem benefits and its strong role in structuring upper treeline communities (Keane et al. 2017a, Thoma et al. 2019). It provides soil stability, aids in community development after fire, delays snowmelt, and provides food to grizzly bears, Clark's nutcracker, and more (Maher et al. 2018, Nesmith et al. 2019).

Threats

Climate change is expected to alter the growth, mortality, and recruitment of whitebark pine (Maher et al. 2018). By 2030, about 70% of whitebark pine's habitat in the U.S. and Canada is expected to be eliminated (Warwell and Shaw 2017). Management for whitebark pine will need to be adaptive in order to be successful. Luckily, whitebark pine has been shown to be adaptive to drought, especially trees from low precipitation climates (Warwell and Shaw 2017). Whitebark pine is also very vulnerable to WPBR and MPB (Table 2, Keane et al. 2017a, Shepherd et al. 2018). Whitebark pine mortality is over 90% due to the combined forces of WPBR and MPB in certain areas (Pansing and Tomback 2019).

Since whitebark pine is an abundant conifer at treeline, WPBR has the potential to severely affect treeline communities. WPBR weakens the tree, predisposing it to MPB attacks. Whitebark pine is listed as a candidate for listing under the Endangered Species Act in the U.S., *Endangered* on the IUCN's red list (IUCN 2020), and *Endangered* under Canada's Species at Risk Act, making its conservation even more critical (COSEWIC 2010, Keane et al. 2017b). If no action is taken to conserve whitebark pine, its populations will steadily decline (Keane et al. 2017a).

Southwestern White Pine

<u>Range</u>

SWWP has not been studied as extensively as other North American five-needle pines (Bower et al. 2011). SWWP's native range spreads from Mexico to Arizona, New Mexico, Colorado, and Texas (Figure 4, Tomback et al. 2011, Looney and Waring 2013, Shirk et al. 2018). It is found at elevations of 5,900-12,175 ft (Pavek 1993 and sources within). SWWP is typically found in mixed-conifer forests comprised of Douglas-fir, ponderosa pine, quaking aspen, white fir, subalpine fir, blue spruce (*Picea pungens*), and Engelmann spruce (Looney and Waring 2013). SWWP often hybridizes with limber pine in New Mexico and Arizona, making it difficult to distinguish (Looney and Waring 2012 Menon et al. 2018), but location of the species is sometimes used to classify it as either southwestern white pine or limber pine (Looney and Waring 2013). This hybridization may help SWWP migrate northward due to the adaptive alleles of limber pine (Menon et al. 2019). SWWP also hybridizes with Mexican white pine or ayacahuite pine (*Pinus ayacahuite*) at the southern end of its range (Moreno-Letelier and and Pinero 2009). Eastern populations of SWWP have less genetic variation and are more genetically similar to Mexican white pine than western SWWP populations (Moreno-Letelier and Pinero 2009). The shade tolerance of SWWP is intermediate, acting as a shade-tolerant in ponderosa pine forests and a shade-intolerant in forests dominated by shade-tolerants (Table 1, Looney and Waring 2012), setting it apart from the rest of the high-five.

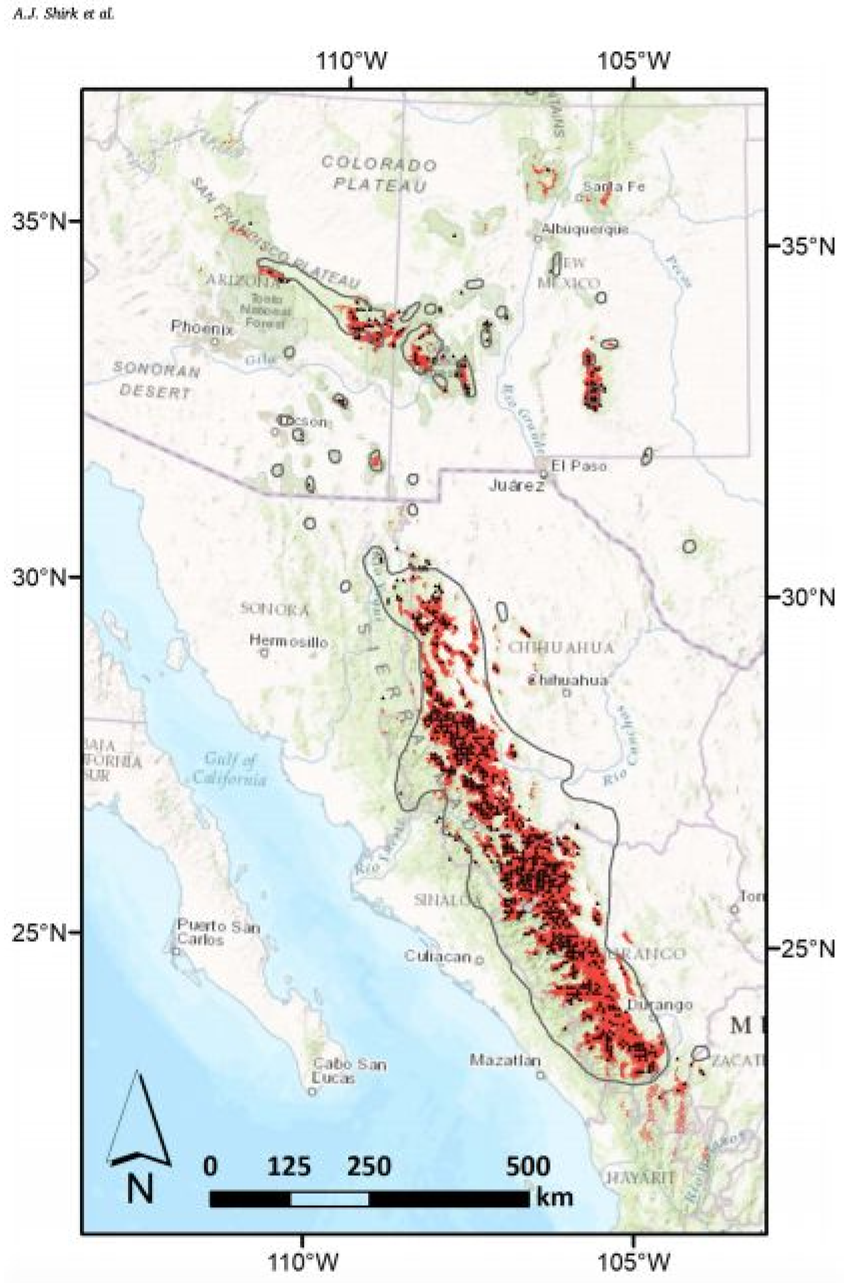

Figure 4. Range of SWWP according to Shirk et al. (2018). The black line shows SWWP's range as of 1971, recorded by E.L. Little. The red shows the presence of SWWP according to a model produced by Shirk et al. (2018), and the black points show a field observed presence of SWWP.

<u>*Seeds and regeneration*</u>

SWWP seeds are large and relatively wingless, limiting their dispersal by wind (Table 1, Looney and Waring 2013). Although SWWP has lower seed production compared to the other

Pinus species, the seedlings are comparatively more shade tolerant and browse resistant, increasing their survival rates (Looney and Waring 2013). Little research is available on SWWP's seed dispersal methods, but studies suggest that Clark's nutcracker (Samano and Tomback 2003a, Lorenz et al. 2008), nocturnal rodents (Tomback et al. 2011), and jays (Samano and Tomback 2003a, Bhagabati and Horvath 2006) aid in SWWP seed dispersal (Looney and Waring 2013). SWWP is faster growing than the other high-five pines (Schoettle et al. 2019), although its seedlings can be relatively slow growing, depending on management techniques applied and available light (Goodrich and Waring 2017).

<u>Fire</u>

Mature SWWP with thick bark is resistant to low- to moderate-intensity fires (Dieterich 1983, Looney and Waring 2013). Besides its bark, SWWP does not have any fire adaptations, such as sprouting or post-fire seed germination (Pavek 1993 and sources within). Historic fire regimes of mixed-conifer forests supporting SWWP range from frequent, low-severity surface fires, some evidence of mixed-severity burns, and a few studies reporting high severity fires (Looney and Waring 2013 and sources within, Yocom-Kent et al. 2017). According to multiple studies, the average fire return interval for mixed-conifer SWWP forests in Texas and Arizona were between 4.7-22 years (Pavek 1993 and sources within).

<u>Importance</u>

SWWP communities provide food for wildlife, promote soil stability, influence nutrient cycling, and aid in forest succession (Looney and Waring 2013 and sources within). SWWP provides habitat for many species including Mexican spotted owl, northern goshawk, and Sacramento Mountain salamander (Pavek 1993 and sources within).

Threats

The main threats to SWWP are climate change (Shirk et al. 2018) and WPBR (Table 2, Goodrich et al. 2018a), although it is also vulnerable to MPB, dwarf mistletoe, and other diseases (Looney et al. 2015). WPBR infection in SWWP was first detected in 2004, and has spread steadily since (Looney et al. 2015). Looney et al. (2015) found that widespread tree mortality due to recent infections of WPBR is not an imminent threat in Arizona and New Mexico. Due to warming temperatures, SWWP's range is expected to shift dramatically by 2080 (Shirk et al. 2018). Although SWWP can survive longer in the understory than the other high-five species, it is more susceptible to drought than Douglas-fir and ponderosa pine (Barton and Teeri 1993). SWWP can be killed by MPB, but its overall risk is relatively low (Gibson et al. 2008). SWWP is listed between *Least Concern* and *Secure* throughout its range (Table 1, IUCN 2020). More research is needed in order to determine the effects of increased drought and temperatures on SWWP (Bucholz et al. 2020).

Foxtail Pine

Range

Foxtail pine is endemic to California (Tomback et al. 2011). There are two distinct populations: one in the Klamath Mountains and one in the southern Sierra Nevada (Figure 5, Eckert et al. 2008). Southern foxtail pine occurs at elevations of 8,900-12,000ft, and northern foxtail pine occurs at 6,900-8,200ft (Table 1, Hickman 1993). It is a foundational species in subalpine and treeline forests (Nesmith et al. 2019). Dendrochronological research on foxtail pine has provided important insight into paleoclimate (Nesmith et al. 2019). This species is commonly found in pure stands, but also occurs with red fir (*Abies magnifica*), Jeffrey pine, lodgepole pine, whitebark pine, mountain hemlock (*Tsuga mertensiana*), and western white pine

(*Pinus monticola*) (Eckert and Sawyer 2002, Tomback et al. 2011 and sources within). It is tolerant of harsh sites and prolonged drought, but is shade-intolerant (Table 1, Tomback et al. 2011). Foxtail pine is less researched than the other high-five species, but is still important regarding ecosystem processes. To clarify how little research there is on foxtail pine, when "foxtail pine" or "Pinus balfouriana" is searched as a topic in the Web of Science database, only 29 results are returned.

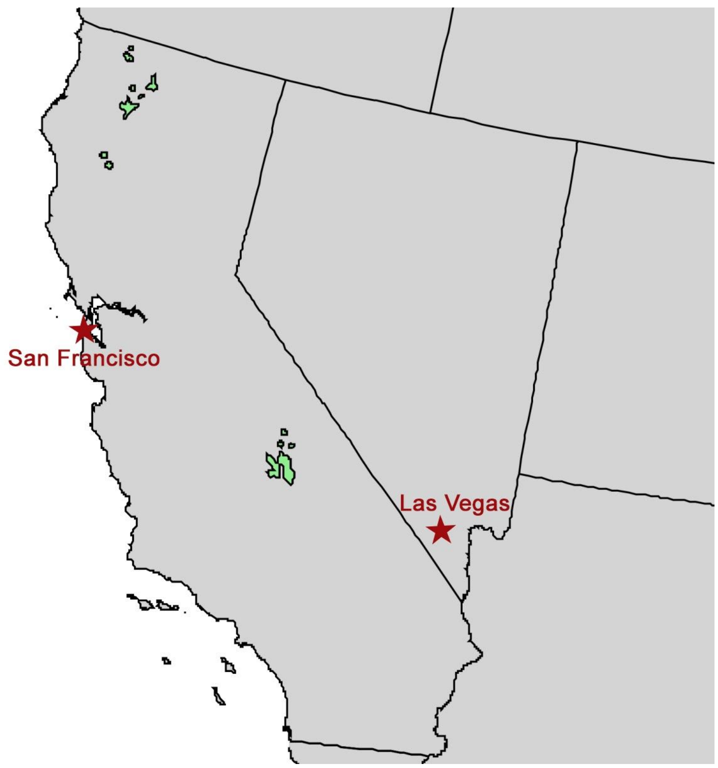

Figure 5. Natural range of foxtail pine. There are two populations, one in the north (Klamath mountains) and one in the south (Sierra Nevada). Source: American Conifer Society (1993).

Seeds and regeneration

Foxtail pine has small, winged seeds dispersed by wind, and speculated to also be dispersed by Clark's nutcracker (Table 1, Tomback et al. 2011). A reduction in grazing has been shown to benefit foxtail pine regeneration (Vankat 1970). More research is needed on foxtail pine's seed dispersal methods and regeneration dynamics.

Fire

Foxtail pine recolonizes quickly after fire (Tomback et al. 2011). Its large-diameter bole, thick bark, and large-diameter branches are similar to those of ponderosa pine, a highly fire-adapted species (Arno 1988, Rourke MD 1988). There is limited information on the fire regimes of foxtail pine communities.

Importance

Foxtail pine, similar to other high-five species, is ecologically important because it provides habitat and food for animals, regulates snow melt, and provides soil stability (Nesmith et al. 2019). It can occur in pure stands, making it essential habitat for certain species (Nesmith et al. 2019).

Threats

In foxtail pine's case, growth does not decline as elevation increases due to declining temperatures. In other words, habitats at treeline are favorable for foxtail pine seedlings, and they are not affected much by the change in temperature (Lloyd 1997, Lloyd 1998). However, they are vulnerable to WPBR, dwarf mistletoe, and *Lophodermium durilabrum* (Table 2, Miller 1965, 1968, 1969). WPBR infections in foxtail pine are much lower in Sequoia and Kings Canyon National Parks than other areas of limber pine's range for unknown reasons (Nesmith et al. 2019, Dudney et al. 2020), suggesting that these might be ideal areas of refugia for foxtail pine. Foxtail pine, especially its northern populations, have low genetic diversity, which make it more vulnerable to infections (Oline et al. 2000). Foxtail pine is listed as *Near Threatened* on the IUCN Red List (Table 1, Sniezko et al. 2017, IUCN 2020).

Rocky Mountain Bristlecone Pine

Range

RM bristlecone pine has a narrow range confined to the southern Rocky Mountains between elevations of 6,760 and 13,100 ft. (Table 1, Figure 6, Tomback et al. 2011, Malone et al. 2018). It is found on xeric sites with limited competition, but is often replaced by faster growing species on mesic sites (Coop and Schoettle 2010). It is known to be one of the longest living organisms (Smithers et al. 2018) and has the lowest genetic diversity of the high-five species (Malone et al. 2018). It is slow growing, drought tolerant (Table 1), and can live upwards of 2,400 years (Coop and Schoettle 2010, Tomback et al. 2011).

Throughout its range, RM bristlecone pine is mostly found in pure stands or with limber pine, but also associates with ponderosa pine, Gambel oak (*Quercus gambelii*), Engelmann spruce (*Picea engelmannii*), subalpine fir (corkbark fir, *Abies lasiocarpa* var. *arizonica*), and southwestern white pine (Tomback et al. 2011 and sources within). It also occurs in pure stands, and occurs all the way up to treeline (Fryer 2004a and sources within).

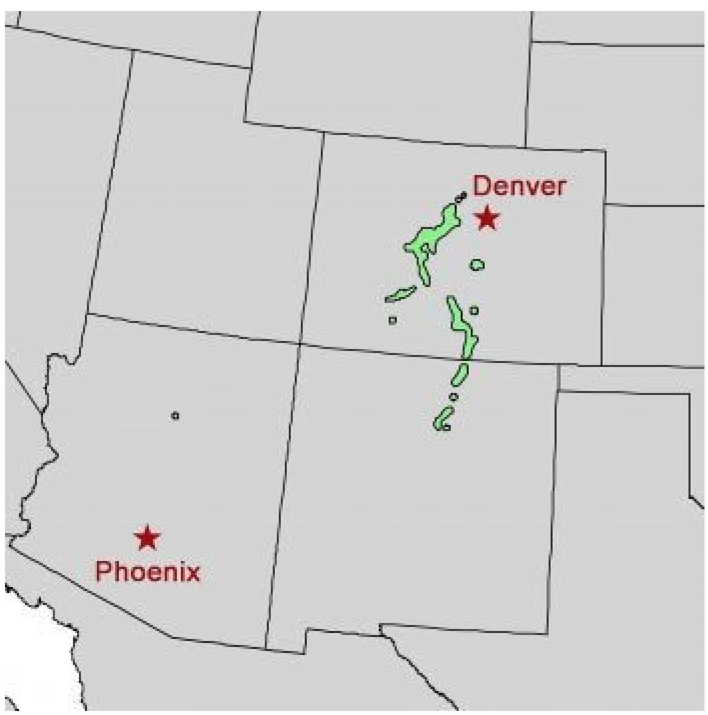

Figure 6. Natural range of Rocky Mountain bristlecone pine. Source: American Conifer Society (1993).

Seeds and regeneration

RM bristlecone pine seeds are small and winged, allowing for wind dispersal (Table 1, Woodmansee 1977). There have been some observations of Clark's nutcracker dispersing RM bristlecone pine seeds (Vander Wall and Balda 1977). More research is needed to determine the seed banking and seedling establishment conditions for RM bristlecone pine (Fryer 2004a and sources within).

Fire

RM bristlecone pine's regenerative response to fire is uncertain. Some studies report it as a primary pioneer after fire (Baker 1992), while other studies report continuous regeneration without fire (Cocke et al. 2005, Schoettle 2008). Data suggests that fire return intervals for bristlecone pine forests vary (<20-500+ years) (Fryer 2004a and sources within, Coop and Schoettle 2010). It has an intermediate fire tolerance (Table 1, Krebs 1972), and regenerates slowly after fire (Tomback et al. 2011). Similar to other species, the ideal use of fire in RM bristlecone pine stands is to prevent mature trees from burning while creating bare mineral soil (Fryer 2004a and sources within).

Importance

RM bristlecone pine occurs in pure stands at treeline, providing habitat for species at high elevations (Fryer 2004a and sources within). RM bristlecone pine communities provide habitat for big game animals such as elk, and seeds provide a food source for red squirrels and Clark's nutcracker (Fryer 2004a and sources within). Additional research is needed to determine habitat uses of RM bristlecone pine communities (Fryer 2004a and sources within). Furthermore, RM bristlecone's long lifespan makes it useful for dendrochronological research (Fryer 2004a and source within).

Threats

Like the rest of the high-five, it is particularly vulnerable to climate change, especially because of its endemic status (Table 2, Malone et al. 2018). Unfortunately, RM bristlecone pine's suitable habitat range as a whole is modeled to contract by 74% by the year 2090, but the range in the San Francisco Peaks area in northern Arizona is expected to increase (Malone et al. 2018). RM bristlecone pine, like other high-five species, is threatened by WPBR, warming temperatures, changing precipitation patterns, and "altered disturbance regimes that stem from climate change" (Schoettle and Coop 2017). Multiple studies suggest that RM bristlecone pine is not as susceptible to WPBR as other North American five-needle pines (Fryer 2004a and source within). However, even with this resistance, RM bristlecone pine is still vulnerable to the disease, and infections are always fatal (Hoff 1992). RM bristlecone pine is listed as *Least Concern* by the IUCN (IUCN 2020).

Great Basin Bristlecone Pine

Range

GB bristlecone pine inhabits the Great Basin mountain ranges in California, Nevada, and Utah (Figure 7, Tomback et al. 2011, Smithers et al. 2018). It grows on the most arid sites of all the five-needle white pines in North America (Tomback and Achuff 2010), between 7,200-12,000 ft in elevation (Table 1, Fryer 2004b and sources within). It is the longest living non-clonal species, and is found mostly in pure stands (Tomback et al. 2011, Burton et al. 2020). GB bristlecone pine also occurs with singleleaf pinyon (*Pinus monophylla*), limber pine, Engelmann spruce, and whitebark pine (Tomback et al. 2011 and sources within).

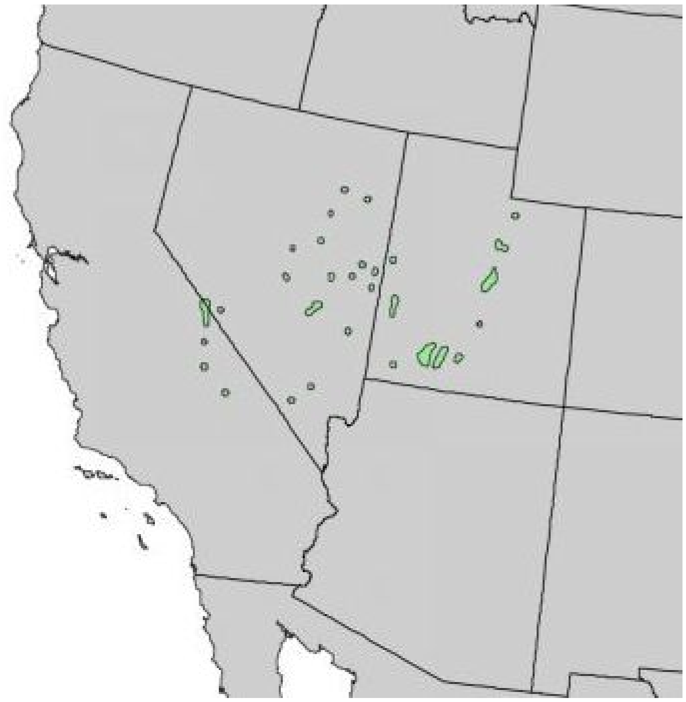

Figure 7. Natural range of Great Basin bristlecone pine. Source: American Conifer Society (1993).

Seeds and regeneration

GB bristlecone pine, like the other foxtail pines, has small, winged seeds that are primarily dispersed by the wind (Table 1, Tomback et al. 2011 and sources within). Jays (Lanner et al. 1984), Clark's nutcracker, and Palmer's chipmunk (*Neotamias palmeri*), may also be important to seed caching and regeneration of GB bristlecone pine (Burton et al. 2020). This is especially important after wildfires, as natural regeneration after a disturbance is slow (Burton et al. 2020).

Fire

GB bristlecone pines have relatively thin bark, contributing to its low fire tolerance (Table 1, Fryer 2004b and sources within). At high-elevation sites dominated by this species, fire is fairly infrequent, and when it does occur, is low severity (Fryer 2004b and sources within). In mid-elevation GB bristlecone pine communities, fire is more frequent and mixed-severity (Fryer

2004b and sources within). There is a lack of studies on fire history in the lower subalpine/montane forests of the Great Basin (Fryer 2004b and sources within), but research focused on this could provide insight into historical fire regimes.

Importance

GB bristlecone pine-limber pine communities and pure GB bristlecone pine stands at treeline provide habitat and a food source for birds and small mammals (Lanner 1985, Lewington and Parker 1999). Since this species is so long lived, the longest individuals living over 4000 years (LaMarche and Mooney 1972), it has provided important climatic information through dendrochronology (Fryer 2004b and sources within). The species has made many contributions to science, such as allowing the carbon-14 dating technique to be accurately calibrated (Fryer 2004b and sources within).

Threats

Luckily, GB bristlecone pine is not as threatened by WPBR (Tomback et al. 2011) or MPB (Table 2, Bentz et al. 2016, Eidson et al. 2017) as the other high-five species. However, only a few GB bristlecone pine trees replace mature trees over centuries, making it difficult for the species to migrate, and thus adapt (Burton et al. 2020). However, their long lifespan makes low regeneration events sufficient to sustain the species (Burton et al. 2020). GB bristlecone pine is currently listed as *Least Concern* by the IUCN (IUCN 2020).

Threats to the High-Five

White pine blister rust, MPB, and warmer temperatures due to climate change project an uncertain future for the high-five (Tomback et al. 2011, Dudney et al. 2020). These threats are likely to change the structure, function, and composition of high elevation forests (Jackson et al.

2019), challenging survival of each of the high-five species. The conservation status of the high-five and other white pine species is variable, depending on the source, location, and scale (Table 1). For example, whitebark pine is listed as *Endangered* by the International Union for Conservation of Nature (IUCN 2020), *Species of concern* by the Washington State US Fish and Wildlife Service, and *Endangered* by the Alberta: Wildlife Act (Tomback et al. 2011). Variability in status across scales and between sources complicates conservation.

Climate Change

A major threat to the high-five species as a whole is climate change. Wide-scale tree mortality in the western U.S. can be attributed to higher temperatures, drought stress, and beetle outbreaks (Tomback et al. 2011), which are all related to a changing climate. The Intergovernmental Panel on Climate Change (IPCC) (2018) predicts global average temperature increases between 1.1^{o} and 6.4^{o}C by the year 2100, relative to the end of the 20th century. Climate change is also altering the timing, frequency, intensity, and spatial extent of fires, which in turn, alters forest structure (Pansing et al. 2020).

Warming temperatures are expected to push native pines toward northward latitudes and higher elevations (Zhu and Woodall 2011, Kueppers et al. 2017 and sources within). However, this is not always the case. Whitebark pine has been reported encroaching downslope into sagebrush grasslands, and producing cones at a younger age (~50 years) than previously found (Flanary and Keane 2019). This supports the implication that migration of tree species will not purely be northward and upward, and will lean more towards finding areas of refugia (see below for further discussion of refugia).

Species are expected to respond to climate change in different ways, such as altering their bud burst timing, leaf morphology and physiology, and chemical defenses (Maguire et al. 2018 and sources within, Bucholz et al. 2020). These changes may have positive or negative effects on the plant itself (Bucholz et al. 2020). Stimulating natural regeneration by creating light openings or reducing competing vegetation, or restoring populations with artificial planting may be necessary in order to conserve the high-five under changing climatic conditions, (Goodrich and Waring 2017). Natural or artificial regeneration will be essential for the conservation of whitebark pine (Keane 2018) and tree species in general.

One of the most effective ways to sustain forests under climate change is by assessing genetic variation in traits that may be important in surviving in future conditions. Identifying and planting seedlings with these superior genetics is likely to help conserve tree species (Bower et al. 2011).

White pine blister rust

One of the most prominent threats to five-needle white pines is WPBR, caused by the fungus *Cronartium ribicola* (Figures 2 and 8, Maloney et al. 2016, Jackson et al. 2019). The pathogen was introduced to the U.S. around 1900 and alternates hosts between five needle pines and *Ribes spp.* through spores (Tomback et al. 2011, Shirk et al. 2018, Jackson et al. 2019, Schoettle et al. 2019). WPBR infects trees by entering the stomata of needles, and spreading through branches and eventually the main stem, killing tissues as it progresses (Geils et al. 2010 and sources within). WPBR can be lethal to all five needle pines at all ages, reducing the reproductive potential of mature trees (Fins et al. 2002, Schoettle et al. 2019). Furthermore, WPBR is more likely to be lethal in small trees (Tainter and Baker 1996, Kearns and Jacobi 2007, Schoettle et al. 2011). WPBR has not spread to the Great Basin, and GB bristlecone pine remains the only species of the high-five that has yet to be affected (Figure 94, Hoff et al. 1980, Tomback et al. 2011, Burton et al. 2020).

Figure 8. SWWP seedlings infected with WPBR. Credit: Kristen Waring.

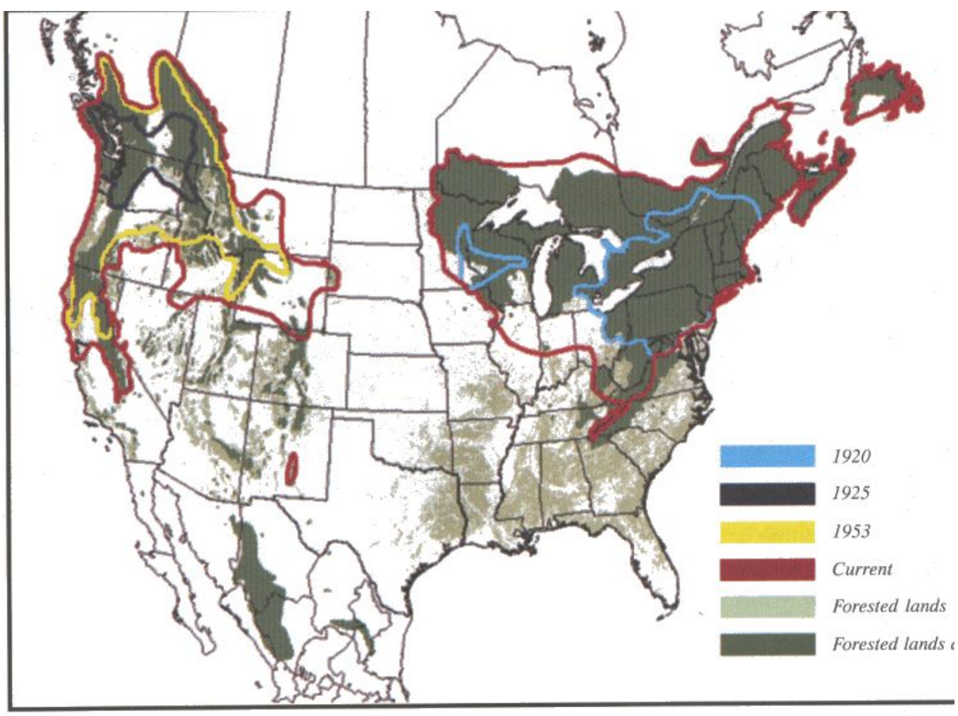

Figure 9. Expansion of WPBR from 1920 to present (as of 2015). Source: The Nature Conservancy. Available from
https://www.americanforests.org/blog/trees-and-pests-a-different-pathway/

Eliminating *Ribes* spp. from WPBR-infected white pine populations and injecting white pines with antibiotics were attempted to remove WPBR in the mid 1900's, but without much success (Fins et al. 2002). Effective defensive strategies against WPBR for the high-five include silvicultural treatments such as thinning and prescribed burning to encourage regeneration, and planting rust resistant individuals (Fins et al. 2002, Zeglen et al. 2010, Goodrich et al. 2018a). Sometimes, WPBR kills the top of large trees, limiting their reproductive potential by killing the part of the tree that produces cones (Scott and McCaughey 2006, Pansing and Tomback 2019, Thoma et al. 2019).

Mountain pine beetle

Another lethal threat to the high-five is MPB (*Dendroctonus ponderosae*). MPB (*Dendroctonus ponderosae*) attacks and feeds on pines as part of its life cycle, eventually killing the tree. Adults emerge from hosts in the mid-summer and mass attack new hosts. They bore through the bark of the tree, mate, and adult females proceed to lay their eggs in cavities of the phloem (Eidson et al. 2017 and sources within). The larvae feed and spread, cutting off the flow of nutrients and water within the tree (Tomback et al. 2011). Larvae remain in the host tree for one to three seasons, eventually killing their host. Once adults, they emerge to find a new host (Eidson et al. 2017). Pines are at higher risk of MPB infections if already stressed by WPBR, drought, or other factors (Cartwright 2018, Jackson et al. 2019). Warmer temperatures and drought provide preferable conditions for MPB, foreshadowing that this threat will become worse with climate change (Bentz et al. 2016, Thoma et al. 2019), especially in the western U.S (Eskelon and Monelon 2018).

Fire suppression and behavior

Wildfire is a key component of ecosystem processes. It influences stand structure and stimulates regeneration for some species (Nyland et al. 2016). For the high-five, lack of fire leads to successional replacement due to their shade intolerance (Tomback et al. 2011). Fire suppression efforts began in the late 19th century, and became very successful by the early mid 20th century (Arno and Allison-Bunnell 2002). However, this has led to altered fire regimes, which in turn, alters forest structure (Tomback et al. 2011 Stoddard et al. 2018. For example, limber pine is expanding its range into lower elevations, likely due to reduced fire frequency (Gruell 1983). Since fire frequency and severity are expected to get worse with climate change, forest structure of high-elevation communities can be expected to change as well (Buechling and Baker 2004).

Combined factors

Changing climate, successional replacement from years of fire suppression, altered fire regimes, WPBR, and MPB are exerting heavy tolls on the high-five (Tomback et al. 2011 and sources within). This is especially true for whitebark pine populations, since it is already nearly endangered (Keane et al. 2017a, Cartwright 2018, Long et al. 2018). Unfortunately, whitebark pine's decline is expected to continue with climate change, making restoration efforts especially crucial at this point (Keane et al. 2017a, Maher et al. 2018, Flanary and Keane 2019). Whitebark pine is especially vulnerable to WPBR, and when combined with a MPB attack, often kills the individual (Wagner et al. 2018, Jackson et al. 2019). There are some areas where whitebark pine mortality is over 90% due to the combined forces of WPBR and MPB (Pansing and Tomback 2019).

Given the literature, it is possible for the combined forces of climate change, wildfire, WPBR, and MPB to cause other high-five species to eventually become as threatened as whitebark pine. Conservation of these species through management can attempt to restore dwindling populations, but it is also a useful tool to make sure that species do not become endangered in the first place.

Management Implications for the High-Five

Various efforts are in motion to conserve and restore several white pine species at national and regional scales (Alfaro et al. 2014, Dudney et al. 2020). International efforts would be helpful as well, since some species ranges occur across multiple countries (Figure 2, 3, 4). The main strategies of restoration efforts include "protecting and maintaining genetic diversity, documenting current conditions and trends, protecting known rust-resistant seed sources, and using forest management practices to improve forest health" (Dundey et al. 2020 and sources within). Some of the restoration tools mentioned by Dudney et al. (2020), specifically planting WPBR-resistant seedlings, using MPB anti-aggregation pheromones to prevent attacks, and prescribed burning are included in this review.

Management frameworks

The Proactive Strategy is a framework used to collect data in order to design an effective management plan to increase ecosystem resiliency to WPBR or MPB outbreaks (Schoettle et al. 2011). This strategy can be applied to any high-five ecosystem that has yet to be infected or is within the early stages of an infection (Schoettle and Sniezko 2007, Schoettle et al. 2011). The Northern Colorado Limber Pine Conservation Program implemented the Proactive Strategy as a method to conserve limber pine in Rocky Mountain National Park and the results led to an in-depth and feasible management plan (Schoettle et al. 2011). The Proactive Strategy in this sense had five objectives:

> "(1) provide protection to limber pine from MPB so immediate seed collections can be made for WPBR resistance tests, genetic conservation, and research; (2) screen seedlings for WPBR resistance to determine the frequency of resistance across the landscape among populations and to identify resistant parent trees for future seed collections; (3) estimate population differentiation along the elevation gradient to refine seeds transfer guidelines; (4) survey forest health, biotic damage incidence and advanced regeneration to project persistence of these populations after MPB invasion; and (5) prepare management plans for northern Colorado" (Schoettle et al. 2011).

Certain measurements, such as estimating WPBR resistance frequency across a landscape, can only be taken from a healthy stand, giving proactive management its value (Schoettle et al. 2011). WPBR resistance assessments can only be taken from a healthy stand because the disease has not yet affected ecological processes of the stand (Schoettle et al. 2011). WPBR kills susceptible trees, skewing resistance estimates performed later because susceptible trees would no longer be included in the assessment. Future conifer populations are sustained by individuals with genetic resistance for WPBR, therefore WPBR is able to select individuals with resistance via the process of evolution. Shifting management to a proactive perspective can promote forests' adaptive capabilities and resilience to disturbances (Schoettle et al. 2011).

The regeneration for resilience (R4R) framework is a tool used to make critical regeneration decisions for populations impacted by WPBR infection (Schoettle et al. 2019). Prioritizing areas that have the highest chance of success in the presence of WPBR is the first step in applying this framework. Intervention options within high-five ecosystems become further focused around regeneration when the host species have a natural genetic resistance to WPBR. These strategies include (1) stimulating natural regeneration, either by increasing available light or decreasing competing vegetation, (2) planting seedlings or seed, and (3) planting seedlings or seeds from other populations with known resistance to WPBR (Schoettle et al. 2019). The goal is to increase the population and its resistance before WPBR can impact the reproduction of mature trees. Planting may be necessary to sustain certain populations (Schoettle et al. 2019). By being proactive with management, or focusing efforts on stands that have a high chance of survival, the resistance and resilience of high-five pines to WPBR will be sustained. The prevalence of WPBR is expected to get worse, especially in the western U.S. (Eskelon and Monelon 2018), making this framework time sensitive.

"A range-wide restoration strategy for whitebark pine (Pinus albicaulis)" (Keane et al. 2012) is a management framework specific to whitebark pine conservation. It proposes an in-depth restoration strategy across whitebark pine's range, and also details the ecology, importance, and status of whitebark pine (Keane et al. 2012). The broad principles that need to be addressed when restoring whitebark pine are promoting WPBR resistance, conserving genetic diversity, saving seed sources, and employing restoration treatments (Keane et al. 2012 and sources within). These principles are meant to be used in conjunction with possible actions at various spatial scales. The possible actions according to Keane et al. (2012) are: assess condition, plan activities (treatments), reduce disturbance impacts, gather seeds, grow seedlings, protect seed sources, implement treatments, plant seedlings, monitor activities, and conduct research (especially when identifying WPBR-resistant parent trees). "A range-wide restoration strategy for whitebark pine" is an excellent example of a detailed management plan that can be applied at different scales. Other species could benefit from such detailed restoration strategies. However, plans are only useful if they are actually implemented.

The Forest Inventory and Strategic Plan (FIA) implemented by the U.S. Forest Service is a strategic plan developed to keep an updated and comprehensive inventory of forest and rangelands within the U.S (USFS 2020). The FIA program collects data on where forests exist, who owns them, health conditions, and much more. This information is useful for evaluating wildlife habitat, assessing management practices, and supporting decision making (USFS 2020). While the program is effective for monitoring forests in general, how do we know if it is sufficient for conserving the high-five? The last strategic plan was updated in 2007, and there may need to be updates due to climate change and local range shifts of species. While the FIA program is sufficient for monitoring the overall status of forests, it is not a sufficient conservation plan for the high-five specifically.

Table 2. Threats, management options, ideal management strategies, and limitations to management for each of the high-five species.

Species	Main threats	Management options for conservation	Ideal management techniques	Limitations and research needs
Limber pine	• Climate change • WPBR • MPB	• Planting • Assisted migration • Stimulate natural regeneration • Silvicultural treatments	• Planting • Assisted migration with WPBR and drought resistant seedlings • Prune branches infected with WPBR of high value trees • Reduce competition via thinning • Create openings	• Need accurate modeling of range shifts • Fire regimes of limber pine communities • Genetics regarding climate adaptations and WPBR resistance • Refugia locations
Whitebark pine	• Climate change • WPBR • MPB	• Planting • Assisted migration • Stimulate natural regeneration • Silvicultural treatments	• Planting • Assisted migration with WPBR and drought resistant seedlings • Prune branches infected with WPBR of high value trees • Reduce competition via thinning or burning	• Need accurate modeling of range shifts • How climate change will affect regeneration • Genetics regarding climate adaptations and WPBR resistance • Refugia locations
SWWP	• Climate change • WPBR • MPB	• Planting • Assisted migration • Stimulate natural regeneration • Silvicultural treatments	• Planting • Assisted migration with WPBR and drought resistant seedlings • Prune branches infected with WPBR of high value trees • Reduce competition via thinning or burning • Reduce fuels	• Need accurate modeling of range shifts • Effects of increased drought and temperatures on SWWP • Seed dispersal methods • Genetics regarding climate adaptations and WPBR resistance • Refugia locations
Foxtail pine	• Climate change • WPBR • Dwarf	• Planting • Assisted migration • Stimulate	• Planting • Assisted migration with WPBR and drought resistant seedlings	• Need accurate modeling of range shifts • Fire regimes of foxtail pine communities

	mistletoe ● *Lophodermium durilabrum*	natural regeneration ● Silvicultural treatments	● Prune branches infected with WPBR of high value trees ● Reduce competition via thinning or burning ● Fire to stimulate regeneration	● Genetics regarding climate adaptations and WPBR resistance
RM bristlecone pine	● Climate change ● WPBR	● Planting ● Assisted migration ● Stimulate natural regeneration ● Silvicultural treatments	● Planting ● Assisted migration with WPBR and drought resistant seedlings ● Prune branches infected with WPBR of high value trees ● Reduce competition via thinning or burning	● Need accurate modeling of range shifts ● Post-fire response ● Genetics regarding climate adaptations and WPBR resistance ● Refugia locations
GB bristlecone pine	● Climate change	● Planting ● Assisted migration ● Stimulate natural regeneration	● Planting ● Assisted migration ● Prune branches infected with WPBR of high value trees	● Need accurate modeling of range shifts ● Historical fire regimes ● Genetics regarding climate adaptations and WPBR resistance ● Refugia locations

WPBR = White pine blister rust, MPB = mountain pine beetle.

Genetics and genetic resistance

Climate change is likely to surpass species ability to adapt, leading to mortality at the receding edge of species ranges (Davis and Shaw 2001). The incidence of extreme events (fire, flooding, late frosts, extensive droughts) will make natural selection less efficient, because selection pressures are contrasting (Alfaro et al. 2014 and sources within). Climate change is likely to have severe effects on forest ecosystems if they lose their adaptive advantage (Whitham et al. 2006).

Current forest genetic resources are “the result of natural geological, ecological, and genetic processes” (Alfaro et al. 2014), which have led to adaptations to the surrounding environment, including local disturbances (Alberto et al. 2013). Therefore, genetics play a significant role in tree survival (Alfaro et al. 2014). Trees that are resistant to WPBR, for example, are much more likely to survive an epidemic of WPBR (Geils et al. 2010 and sources within). Likewise, trees that are resistant to drought are much more likely to survive one. The ideal seedling would be fast growing, resistant to drought, WPBR, and MPB. Not only would the tree be aesthetic and a strong competitor, but it would also have strong defenses. Scientists recognized that planting seedlings with superior genetics improves their survival, and thus is more time and cost effective than planting regular seedlings (Kinloch et al. 1999).

According to multiple sources, planting seedlings with resistance to WPBR is one of the major strategies for keeping a stand healthy (Figure 10, Schoettle and Sniezko 2007, Tomback 2010, Schwandt 2010, Schoettle et al. 2011, Keane et al. 2012, Wagner et al. 2018). In order for a population to sustain itself where WPBR is present, there needs to be the genetics for WPBR resistance and healthy regeneration (Schoettle and Sniezko 2007). Luckily, all of the high-five species have at least one strategy for resisting WPBR, but the frequency of trees with these genetics are low (Hoff et al. 1980, Schoettle et al. 2011).

There are two types of genetic resistance to WPBR in pine trees. Major disease resistance (MDR) is one gene that improves tree resistance to WPBR (Sniezko et al. 2019). The other type of resistance is called quantitative disease resistance (QDR), which is conferred by multiple genes (Sniezko et al. 2019). Therefore, trees with both the MDR and QDR genes have the most resistance to WPBR (Sniezko et al. 2019). Genetic resistance is important because it allows trees to live with WPBR and still be able to produce cones and seed. However, WPBR can evolve virulence to both the MDR and QDR genes, which is a major concern for land managers (Sniezko et al. 2019).

Natural and artificial regeneration

Regeneration, the growth of new seedlings, is important because it supports ecosystem processes, including timber and non-timber related products (Chazdon and Guariguata 2016). There are two types of regeneration, natural and artificial or assisted (Chazdon and Guariguata 2016). Natural regeneration is the process of germination without human intervention (Chazdon and Guariguata 2016). It can also be "viewed as a gradual process of recovery of the structure, function, and composition of the pre-disturbance ecosystem" (Chazdon and Guariguata 2016).

Planting is a commonly used method for improving the stocking, altering the species composition, restoring degraded stands, or proactively increasing genetic resilience of a stand (Table 2, Schoettle et al. 2011). Planting can also be used to give a species a competitive advantage by giving it a head start after a disturbance. In other words, faster growing species will dominate during succession, so by planting seedlings that are a few years old, they have a competitive advantage over other vegetation that will colonize (Nyland et al. 2016). Another advantage of planting over natural regeneration is that the species, arrangement of trees, and genetics can be selected. Therefore, planting is often preferred in high value stands, so that managers can choose the species, place the seedlings so that they have the right amount of growing space, and choose genetically superior trees (Nyland et al. 2016).

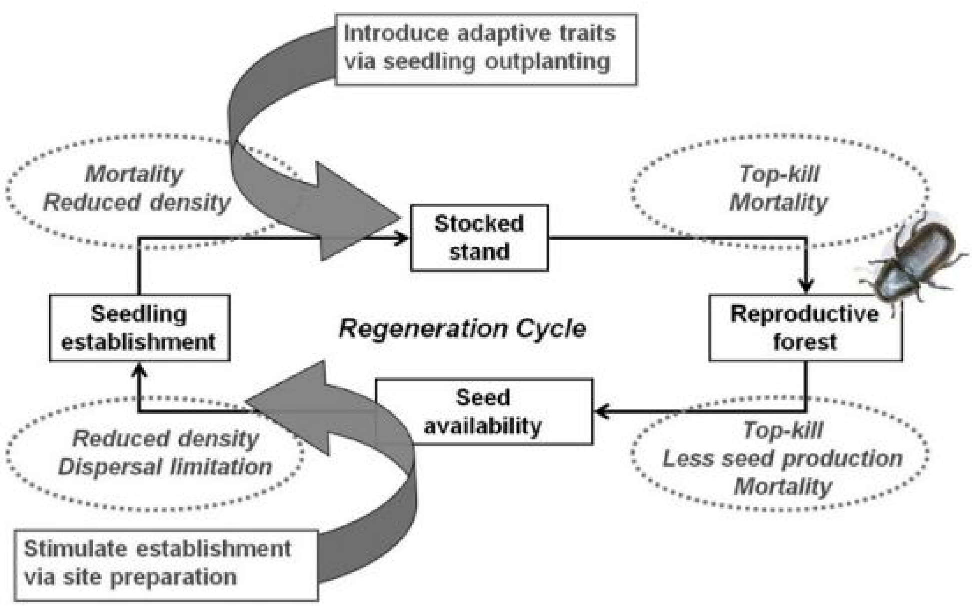

Figure 10. "Flow diagram of the forest regeneration cycle and the points of interaction with WPBR and management interventions. White pine blister rust can cause impacts at all stages (ovals) and the mountain pine beetle preferentially kills larger trees. Broad arrows depict intervention options for increasing rust resistance and population resiliency." Source: Schoettle et al. 2011, redrawn from Schoettle et al. 2009, redrawn from Schoettle and Sniezko 2007.

Artificial regeneration does have its drawbacks, however. It takes years to grow seedlings that will be ready to be transplanted out in the field. Planting seedlings is difficult, time consuming work, especially when foresting a large area. There might not be enough seed in storage, and planting costs can be high. However, if reasonably priced seedlings with resistance to WPBR and adaptations to their environment can be achieved, planting is a reliable strategy of conserving and promoting species (Waring and Goodrich 2012).

Scott and McCaughey (2006) developed several conditions that should be included in prescriptions when outplanting whitebark pine seedlings, in order to increase survival rates. These conditions are: (1) reduce overstory competition to increase light, except for newly planted seedlings, whose microclimates are improved with shade, (2) reduce understory vegetation to reduce competition for soil moisture, (3) avoid planting in swales (bottom of hills) or frost pockets to increase chances of survival, (4) plant where there is some protection from heavy snow, (5) do not crowd planted trees, (6) plant when there is sufficient soil moisture, such as in the summer or fall, and (7) "plant large, hardy seedlings with good root development."

Artificial regeneration will support SWWP conservation and migration to higher elevations, and may become crucial to the species survival in the long term (Bucholz et al. 2020). SWWP seedlings are also more likely to survive in optimal planting spots, i.e., northern aspect sites, mesic sites, and low amounts of litter and duff (Goodrich and Waring 2017). Planting SWWP seedlings with a source of shade and protection reduces their water loss potential and gives them an advantage in surviving during drought (Goodrich and Waring 2017). Studies similar to that of Bucholz et al. (2020) for the rest of the high-five species would be extremely useful in determining species responses to drought, and the conditions for planted seedlings to have the best chance of survival. Soil moisture is critical to seedling physiology and survival, and seedling survival is critical to migration of tree species (Moyes et al. 2013).

Planting WPBR resistant seedlings is the most effective strategy for maintaining whitebark pine populations where WPBR is present (Table 2, Thoma et al. 2019) until natural regeneration can form populations with sufficient resistance (Wagner et al. 2018, Pansing and Tomback 2019). Specifically, if planting targets include areas outside the temperature and humidity range identified as ideal for infection, the probability of infection may be temporarily reduced, thus buying time for growth to cone-producing age (Thoma et al. 2019). However, planting seedlings is time consuming, work intensive, and logistically complex. Not only that, developing nurseries, collecting seed, and growing seedlings are all major investments. Pansing and Tomback (2019) propose direct seeding for whitebark pine restoration. This method is cheaper, more efficient, and can be applied to remote areas. Out of 372 seed caches created by Pansing et al. (2017) in 2012, 184 caches had at least one seedling germinate in 2013 or 2014, and by 2018, there was a 37% survival rate. The predicted survival rate for one or more seedlings in a cache after five years was about 27% in subalpine forest and 57% in treeline. The authors estimated annual survival rates produced via modeling are between 57-99%, suggesting that direct seeding could be a viable option for restoring whitebark pine communities (Pansing and Tomback 2019). In addition, seedlings have better survival rates when planted next to a nurse object, such as a stump or rock (Peters and Visscher 2019). Planting whitebark pine seedlings may play a critical role in keeping this species on the landscape (Keane et al. 2017a). Due to the slow growing nature of the species, however, it will take at least 100 years before restoration efforts begin to boost whitebark pine populations resistance to WPBR (Keane et al. 2017a).

Maher et al. (2018) found that neither prescribed fire nor thinning altered whitebark pine recruitment rates. The authors stated that this conclusion could be due to different factors: restoration treatments do not increase recruitment rates, that seed sources were not sufficient, or "that climatic conditions were not suitable for regeneration during the study period" (Maher et al. 2018). Maher et al. (2018) speculates that this could be a result from dramatically reduced cone crops due to WPBR, or human land use (grazing). These treatments do support recruitment in other mixed-conifer species, however. Therefore, the success of silvicultural treatments used to restore whitebark pine forests relies heavily on site conditions and treatment type, and cannot be expected to work everywhere. In order to achieve desired whitebark pine regeneration, planting rust-resistant seedlings is necessary (Maher et al. 2018).

Limber pine seedlings should be planted next to an object to protect them from the elements (Cleaver et al. 2017). In existing limber pine stands, the ideal spot for planting has some overstory cover, is near rocks or dead trees but not competing vegetation, and in a site with higher soil moisture (Cleaver et al. 2017). In stands that will regenerate naturally, cone-producing trees should be retained (Cleaver et al. 2017).

Fortunately, tree seed lots of the high elevation white pine species have been collected since 2008 and are stored at the National Laboratory for Genetic Resources Preservation (NCGRP) in Fort Collins, Colorado, which will be a valued resource if the species continue to decline and artificial planting or direct seeding is necessary (GRIN-Global 2016, Sniezko 2017).

After planting or seeding has been implemented, it is important to monitor the seedlings at least once per year to make sure they are established and thriving properly. If mortality occurs to a degree higher than expected, it is important to address the issue sooner rather than later.

Assisted migration and projecting range shifts

The environmental niche of species is expected to shift outside their current ranges with climate change (Aitken et al. 2008). One of the greatest challenges to conservation is predicting species range shifts (Malone et al. 2018), but predicting range shifts is essential towards making artificial replanting and assisted migration successful. If research on range shifts is not developed or reliable enough, then implementing assisted migration could be a waste of time, money, and effort. Therefore, studying projected range shifts and inhabitable areas of species would be worthwhile to further their conservation.

Many whitebark pine seedlings do not survive after planting, making assisted migration a challenge for this species (Cripps et al. 2018 and sources within). Unfortunately, we know little about why whitebark pine does not respond to silvicultural treatments as well as other species.

While tree species are generally expected to shift their ranges upward and northward due to warming temperatures, that is only sometimes the case (Roberts and Hamann 2016). Each species' range shifts are variable depending on seed source, topography, and climate in each area (Roberts and Hamann 2016). Coupled with assisted migration is identifying areas of refugia, which are locations that support isolated populations of a species.

Refugia

Identifying areas of refugia will be an essential component of implementing assisted migration (Cartwright 2018). Refugia with cooler or moister microclimates is preferred in order to contrast with regional warming and drying (Cartwright 2018). This will help prevent additional disturbances such as drought and fire from further stressing the forest (Cartwright 2018). More refugia can be expected at higher elevations, concave areas, shaded areas, riparian areas, areas where soil is less compacted, and areas with lower forest density (Cartwright 2018).

Species in inland Canada and the northern parts of the U.S. will have to migrate further to reach refugia than species near the coast or in the southern U.S. (Roberts and Hamann 2016).

Low elevation ravines provide climate refugia for limber pine, at least in the Great Basin, given their cooler and wetter nature (Millar et al. 2018). These areas can help conserve limber pine during warmer and dryer periods, enforcing the need for their protection (Millar et al. 2018).

Pruning

Pruning branches that have a notable WPBR infection can possibly save the tree from death, although this method is expensive and should only be used when economically feasible (Zeglen et al. 2010). Attempting to restore heavily diseased stands, however, may not be the best use of resources given that new seedlings will face high mortality due to the pressure from WPBR. In order to conserve species, it is more efficient to pool resources to prevent healthy stands from declining in the first place (Schoettle et al. 2019a). Preventative and sanitation pruning has been shown to be effective in reducing crown mortality in limber pine stands highly susceptible to WPBR (Jacobi et al 2017, Schoettle et al. 2019a), and it may be effective with other species.

There are two specific types of pruning. Prevention pruning removes the branches on the lower third of the tree, where most infections occur on western white pine, eastern white pine, and sugar pine (Burns et al. 2008). However, limber pine, RM bristlecone pine, and SWWP are equally as likely to be infected at any spot on the crown, so prevention pruning is not effective for these species (Burns et al. 2008). The other type of pruning is sanitation pruning, which is the removal of cankers or infected branches. More research is needed on how pruning affects trees in specific areas such as cool, moist climates.

Thinning and intermediate treatments to reduce competition

Intermediate treatments are those that "reduce density in a stand and favor the trees that best serve a landowners objectives" (Nyland et al. 2016). One of these treatments is thinning. Some of the goals of thinning are to reduce fire risk, promote regeneration, and promote growth of desirable trees (Nyland et al. 2016). Thinning, the process of removing undesirable trees from a stand in order to reach management objectives, is an effective tool to stimulate growth of the desired trees (Table 2, Stoddard et al. 2015, Nyland et al. 2016, Goodrich et al. 2018a and sources within). There are multiple methods of thinning, which result in different stand structures. A thin from below is the removal of small, understory trees, mainly to reduce fire hazard or because they have undesirable form. A thin from above removes overstory trees, which may be lumber grade, in order to stimulate growth of the understory. Another thinning method that would be applicable to conservation is a thin across all age classes, where trees that are undesirable are removed and trees that are desirable are left, regardless of age or size. This method would be especially useful in regards to conservation, because the focal species could be left and the trees that do not need conservation assistance (at least in the area of treatment) could be removed. Thinning is often used in conjunction with prescribed fire to quickly and effectively remove understory fuels and small trees (Nyland et al. 2016). However, thinning or other intermediate treatments should be used with caution in areas of light WPBR infection, because the increased light to the understory can increase the amount of *Ribes* individuals (Goodrich et al. 2018a and sources within).

In regards to SWWP in particular, it faces heavy interspecific competition from other species, namely Douglas-fir, Engelmann spruce, and white fir (Looney and Waring 2012). Thinning its competitors and removing overstory trees besides SWWP is likely an effective strategy of encouraging SWWP release and new growth (Looney and Waring 2012), and this strategy is likely to be effective on other species. When SWWP stands are infected with WPBR, trees with stem cankers should be removed, but sapling-sized trees can remain if they are not infected by WPBR (Goodrich et al. 2018a).

Regeneration methods

Certain silvicultural strategies are used in order to increase regeneration and meet restoration objectives. These strategies are in four broad groups: even-aged methods, uneven-aged methods, the two-aged (or leave-tree) method, and irregular silviculture methods (Nyland et al. 2016). Even-aged methods involve maintaining a stand with one age-class or cohort relative to the rotation length (the length of time between harvests) (Nyland et al. 2016). Trees are harvested at once, and then after site preparation, planted at once (except with a seed-tree cut, where a few overstory trees are left in order to regenerate the site naturally). This is a widely used method when the objective is timber harvesting, because is it efficient, trees can be planted at the optimal distance, and the whole stand can be harvested all at once (Nyland et al. 2016).

Uneven-aged methods of regeneration involve maintaining stands with multiple cohorts. These methods include single-tree selection, group selection, and a hybrid between the two (modified single-tree selection) (Nyland et al. 2016). In a single-tree selection, "regeneration openings cover an area equivalent to the crown spread of a single mature tree" (Nyland et al. 2016). These small canopy gaps create spaces of light for understory trees, but eventually become more shaded in. Seedling growth may diminish due to increased shade towards the end of the cutting cycle, and the shade-intolerant individuals often die (Nyland et al. 2016). Single-tree selection increases vertical diversity of a stand (Nyland et al. 2016).

Group selection harvests trees growing next to each other to create small openings, leading to a mosaic of different age classes across the stand (Nyland et al. 2016). This method is more suitable when trying to regenerate shade-intolerant or shade-intermediate species (Nyland et al. 2016). In group selection, trees within groups may also be taken out to promote growth of the residual trees. This method is used to create horizontal diversity, which provides desirable habitat for certain species while also maintaining fuel breaks between groups. A hybrid between single-tree and group selection, also known as modified single-tree selection, is used when using one method across the entire stand does not reach optimal results (Nyland et al. 2016). An example of this would be when previous entries have led to a more homogenous stand structure, and the goal is to restore heterogeneity (Nyland et al. 2016).

The two-aged method is where foresters remove a considerable amount of trees while retaining some of the mature trees, allowing for widespread regeneration (Nyland et al. 2016). This method is beneficial for aesthetic reasons, and provides more vertical diversity than an even-aged regeneration method (Nyland et al. 2016).

Irregular silviculture methods involve partial cuttings of mature trees to stimulate regeneration without consideration to temporal or spatial differences of age classes (Nyland et al. 2016). In other words, continuous forest cover is maintained, but there is an irregular horizontal and vertical structure. It should still retain ecological processes while corresponding with economic interests, but with less guidelines on how harvesting should be implemented (Nyland et al. 2016).

Not every regeneration method was discussed herein, but the importance of outlining the major strategies was to highlight the fact that managing for regeneration is a complex, well thought-out process. Multiple strategies are available for regenerating a stand, and the method chosen should be selected based on the current conditions of a stand, species composition, and management objectives. For the high-five, SWWP would do well under each regeneration method (depending on the site) given its intermediate shade tolerance. The rest of the high-five are shade intolerant, so two-aged or even-aged management would be best to stimulate growth of these species because they allow the most light to the forest floor. However, two-aged or even-aged management is not common in stands where the goal is restoration, so these species may need bigger openings to survive under uneven-aged or irregular silviculture methods.

Prescribed fire

Prescribed fire is the method of lighting surface fuels on fire in order to reduce woody material, to prevent catastrophic wildfires, to control pests and diseases, and more (Nyland et al. 2016).Using prescribed fire on stands infected with WPBR is an effective way to promote healthier stands in general (Table 2), although if used to promote regeneration, needs to be used with caution. Certain species do not regenerate well after fire in certain locations, such as limber pine in the northern extent of its range (Dawe et al. 2020).

Using fire as a tool to reduce competition and using it to stimulate regeneration are two different strategies. While fire may stimulate regeneration for one species, it may not affect another species, just consume established regeneration. Fire can reduce competition, but can also remove trees that have genetic resistance to WPBR, limiting successful regeneration where WPBR is present (Keane et al. 2017a). Prescribed burning must be used with caution and close monitoring to ensure it does not engulf desirable trees.

Prescribed burning as a method of preparing sites can be used by removing fuels from the forest floor (Nyland et al. 2016). It is important to prepare a site before natural or artificial regeneration occurs in situations where (1) conditions are preferable for less desirable species,

(2) preferred species need specific environmental conditions to regenerate, or (3) unfavorable vegetation or soil conditions limit growth of new trees (Nyland et al. 2016). Prescribed burns for site prep can be used widely across a stand (broadcast burn), in narrow strips (strip treatments) or certain spots (spot treatments) (Nyland et al. 2016). This method is quicker and cheaper than alternate forms of site preparation, such as mechanical methods or chemical applications (Nyland et al. 2016).

Integrated management

Given the threats that the high-five face, it is essential to address these threats and adopt management strategies that will help the species overcome them. Common management goals for the high-five include maintaining resistance to WPBR and MPB and maintaining the relationship between Clark's nutcracker and the species that depend on it (whitebark pine: Keane et al. 2017a, Long et al. 2018). It is important to keep in mind that there is no one solution that will be effective for all six high-elevation five-needle pine species at all sites (Keane et al. 2017a). It is important to consider the silvics of the species and characteristics of the site in order to determine what restoration strategy will be most effective in the long run.

The best strategy for conservation depends on the species in question, the site, and the prominent threats to the species. The first step in conserving the high-five is determining the focal species and establishing management objectives. In regards to conservation, stimulating regeneration, releasing trees that are already established, and expanding a species range are likely going to be the main objectives. The second step is to analyze and gather information on the site where management will occur. Things to take note of include the species present, pests or pathogens present, and the physiognomy of the site. Management objectives should be site-specific; the objective to reduce WPBR infection in SWWP stands would not be applicable if WPBR is not present. Proactive management to prevent WPBR would be a better objective in this case. Being proactive in maintaining healthy stands or preventing infection are worthwhile, especially in the long run.

The next step is determining the silvicultural strategy or strategies that would be effective to achieve management objectives. If the objective is to boost a population, planting, assisted migration, and burning (for certain species) would be efficient methods. If the objective is to reduce competition in order to stimulate growth of the focal species, silvicultural treatments, burning, or a combination of the two can be used, but only if the species is known to respond to it. If the objective is to reduce MPB infestations or prevent them in the first place, MPB anti-aggregation pheromones can be effective (Byers 1995). Of course, this guideline is flexible, and the actual strategies used would depend on a variety of factors.

After the focal species, management objectives, and features of the site have been established, a management plan is needed in order to determine exactly how the silvicultural strategies will be implemented in order to reach the management objectives. This is where budgeting and a monitoring plan should come in as well. Management plans are only effective if they are actually implemented and maintained, which is only possible if the money and resources are available. A monitoring plan would ensure that management objectives are being reached and progress is being made. Species conservation efforts must extend into the future, otherwise their populations will eventually fall into decline again.

Research limitations

Research is lacking in many areas when it comes to the high-five. By conducting more studies, land managers will have a better idea on how to conserve them. The main gap in research is accurate and reliable projections of how each species range will shift in the next few decades under climate change (Table 2). This is difficult to achieve because modeling depends on the greenhouse gas emissions scenario used, data of current species range, and how other factors will affect range shifts. Therefore, even though models are a useful tool to make predictions, they are not 100% accurate when facing a wide range of variables and uncertainty. However, it is still important to make scientific predictions on how species ranges will shift in order to make the best possible effort in conserving them.

There is a large gap of research on how insects and pathogens will respond to climate change. As conifer ranges shift, it is likely that insect ranges will shift as well in order to keep up with their hosts (Pureswaran et al. 2018). More studies are needed on how susceptibility of trees and environmental factors will affect the spread and persistence of WPBR, similar to Dudney et al. (2020).

What can land managers do to conserve the high-five? Different species in varying climates and stressors will have different reactions to climate change, WPBR, and MPB. The main thing that managers can do to help conserve species is assisted migration or planting (Table 2). This ensures that more individuals are replenishing populations, and if done properly, drought tolerant and WPBR resistant individuals may have an advantage in surviving. In regards to maintaining healthy individuals, silvicultural treatments are key (Table 2).

What happens if we do not take any action to conserve the high-five?

If no action is taken to conserve the high-five, they may become vulnerable or threatened, and fewer individuals will make it more difficult to conserve populations in the future. The high-five provide a variety of ecosystem services, which would be compromised if high-five populations continue to decline (Ellison et al. 2005). Ecosystem services are invaluable, therefore restoration may be worth the cost (Costanza et al. 2014). The reduction in whitebark pine or limber pine communities reduces Clark's nutcrackers primary food source (Lanner and Vander Wall 1980, Fryer 2002 and sources within). Without any restorative action, whitebark pine will continue to steadily decline over the next hundred years (Keane et al. 2017a), eventually becoming endangered and possibly extinct. Whitebark pine, foxtail pine, RM bristlecone pine, and GB bristlecone pine can occur in pure stands (GB bristlecone: Lanner 1985, foxtail: Eckert and Sawyer 2002, whitebark: Fryer 2002 and sources within, RM bristlecone: Fryer 2004a and sources within), so reductions in their populations could be catastrophic for the species that depend on them.

Ethics of Conservation

There are certain ethical considerations when managing for the high-five. First, management actions should be sustainable. Actions such as logging or burning will disturb the landscape, but would be unethical if they degraded the landscape. Second, cultural values should be taken into consideration when managing species. Native Americans who rely on forests for their livelihoods may be at a disadvantage if management actions are implemented. For example, indigenous people rely on the inner bark of pine trees as a source of food, so by removing trees from the landscape, their food source may be compromised. Certain forested areas, species, or ecosystems may have high cultural significance to indigenous peoples, warranting special considerations to management actions. In like manner, adjacent landowners should be informed of any management activities, and how they may be affected should be taken into consideration. For example, the high-five regulate snowmelt, so if logging occurred on top of a mountain, it could affect the watersheds below. Furthermore, all management activities need to comply with the National Environmental Policy Act (NEPA). This ensures that all actions are legal and will not degrade the environment. Professional ethics also need to be taken into account when managing for the high-five. Professional ethics is the concept of standards that are set and expected to be maintained within a professional career. For example, a land manager who does not act or behave like a professional reduces their credibility by doing so. Without professionalism, management decisions may be questioned.

Accelerated climate change, fire suppression, and WPBR can all be attributed to humans. In other words, the factors that are leading to the decline of the high-five are human caused. Therefore, we have the responsibility to take conservation into our own hands. If we do nothing, the loss of high-five species will be partially our fault, and some ecosystems may never recover. Ecosystems may decline due to natural factors, but humans have been a major influence on their status.

On the flip side, it is possible that high-five populations could decline due to our actions. If this happens, we have an even bigger responsibility for the species status. There is much uncertainty when it comes to managing forests under a changing climate and increased stressors, but we know that if no action is taken, it is likely that the high-five will decline (Ellison et al. 2005).

Conclusion

The high-five play crucial roles in montane ecosystems as habitat and a food source for animals, regulating springtime snowmelt, providing soil stability, and multiple food and medicinal uses by Native Americans (Tomback et al. 2011, Shirk et al. 2018, Jackson et al. 2019). The high-five aid in succession and provide shade for other species. Unfortunately, these species are threatened by climate change, WPBR, and MPB, as well as other minor threats specific to species and locations (such as dwarf mistletoe).

In order to conserve the high-five, adaptive, well-informed management is needed. Planting and assisted migration are two strategies we can use to boost populations, make them more resilient to changing temperatures, and improve their genetic resistance to drought and WPBR. Thinning and burning are two silvicultural strategies that can be used to reduce competition in a stand, and for some species, promote regeneration. By reducing stress on an individual, their resistance to other stressors is improved. More research is needed on range shifts under climate change, how altered fire regimes will affect the high-five, and how environmental effects will affect susceptibility to WPBR. By gaining an understanding of these areas, we are better equipped to make effective management strategies to conserve the high-five.

Currently, land managers are already starting to adopt conservation strategies, and more emphasis is being put on the influential effects of climate change. The need for assisted migration, planting, and silvicultural treatments have been recognized. Luckily, plenty of seed of whitebark and foxtail pine has been stored in order to facilitate regeneration of these species (Sniezko et al. 2017), and they are the ones most threatened (IUCN 2020). SWWP seeds (Goodrich et al. 2018b), limber pine seeds, and RM bristlecone pine seeds (Schoettle and Coop 2017) have also been stored. However, we can do better. With cooperation between federal, state, and private organizations, we can accomplish restoration goals across the country, increasing the likelihood that species will be able to survive under a changing climate. It is essential to monitor populations of the high-five species and make sure they can survive under climate change, coupled with increasing threats of WPBR, MPB, and other stressors. If we risk losing a species, or even a large amount of individuals, we reduce losing an important contributor to wildlife habitat and key ecosystem processes. The further populations decline, the more difficult it will be to conserve species for future generations. If we do not do anything to conserve the high-five, we are at risk of losing species permanently, which will have devastating effects on forest ecosystems.

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Acknowledgments

Special thanks to Dr. Kristen Waring, Dr. Tom Kolb, and Dr. Pete Fulé for their thoughtful and constructive feedback. Thank you to the Northern Arizona University School of Forestry for my undergraduate and graduate education and experiences.