Sustaining High Elevation Five-Needle Pines in the Southwestern United States: A Practical Management Perspective

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Abstract

High elevation five-needle pines are a group of related species which share various physical traits, ecological niches, and disturbance susceptibilities. Five-needle pines, commonly known as white pines, occur in highly vulnerable ecosystems and are often keystone species throughout their native range. Unfortunately, a series of threats are creating a unique set of challenges for white pine survival in the future. Climate change is increasing fire frequency and intensity as well as exposing many species to unprecedented heat and drought. As white pines are increasingly stressed by drought and increasing temperatures, they become more susceptible to heightened bark beetle activity. Additionally, the invasive pathogen responsible for the disease white pine blister rust continues to spread across white pine stands, causing cankers, decreased vigor, and high levels of mortality. Any of these stressors could be challenging to manage in isolation, but in synergy they paint a bleak future for white pines. Only by understanding how each of these threats effect white pine species' survival and dispersal can we sustainably manage these species in the future. The southwestern United States is experiencing climate change more strongly than many other parts of the country and is home to several white pines, including: southwestern white pine (*Pinus strobiformis* Engelm.), limber pine (*Pinus flexilis* James), Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.), and Great Basin bristlecone pine (*Pinus longaeva* Bailey). Additionally, this area is currently at the forefront for the spread of white pine blister rust infections making this area essential for early, informed, and proactive management.

Introduction

High elevation five-needle pines are a group of related tree species that commonly inhabit harsh environments and have low timber value, yet offer many ecological benefits for the ecosystems that they inhabit (Tomback et al. 2011). Where these species occur, they are commonly keystone species in vulnerable ecosystems (Gibson et al. 2008). Though five-needle pines, referred to as simply white pines throughout this paper, may represent a small portion of the overall forest cover in many areas, they are important ecological components in most coniferous forests in the West (Tomback and Achuff 2010). White pines contribute to snow capture, snowpack retention, and erosion control (Schoettle et al. 2014). Due to most white pines' ability to grow on dry rocky sites, they contribute to the overall ecological stability and biodiversity of high elevation stands (Conklin 2009). White pines commonly grow alongside more profitable timber species, yet they do not contribute high-value timber (Burns and Honkala 1990). Sadly, the lack of economic interest has resulted in minimal research into many white pine species that has only began to be remedied within the past fifteen years. White pines provide a variety of ecosystem services. For instance, they provide important habitat and mast resources for wildlife such as Clark's nutcrackers (*Nucifraga columbiana*, Corvidae), red squirrels (*Tamiasciurus hudsonicus*), and black bears (*Ursus americanus*), as well as a variety of rodents and insects (Schoettle and Négron 2001; Tomback et al. 2005; Mattson and Arundel 2013). At high elevations, wildlife relies heavily on the cover provided by white pines since few other tree species can survive the harsh climate conditions and high winds (Burns and Honkala 1990, Schoettle 2014). White pines are also important as pioneer species and for site protection after disturbance due to their ability to withstand undesirable conditions (Burns and

Honkala 1990). In fact, they are commonly the first species to re-colonize after large fires where newly-burned microclimates may be too harsh for other species (Schoettle 2014). Wildfires will continue to threaten millions of acres across the western United States, and white pine reforestation efforts will need to be included alongside efforts to maintain more profitable timber species in the interest of ecosystem health and diversity. In turn, white pines may act as nurse trees that facilitate the establishment of other late successional high elevation species (Donnegan and Rebertus 1999; Schoettle 2014).

In this paper, the focus is on four species of white pine that exist in the Four Corners region of the southwestern United States: southwestern white pine (*Pinus strobiformis* Engelm.), limber pine (*Pinus flexilis* James), Rocky Mountain bristlecone (*Pinus aristata* Engelm.), and Great Basin bristlecone (*Pinus longaeva* Bailey) (**Table 1**; Conklin 2009). The Four Corners region of the southwestern United States consists of Arizona, New Mexico, Utah, and Colorado, and is characterized by the Colorado Plateau as well as the Upper and Lower Colorado River Basins.

Table 1. White pines by common and scientific names in the Southwest

List of focal white pine species in the Four Corners region of the southwestern United States	
Common Name	**Scientific Name**
southwestern white pine	*Pinus strobiformis* Engelm.
limber pine	*Pinus flexilis* James
Rocky Mountain Bristlecone	*Pinus aristata* Engelm.
Great Basin Bristlecone	*Pinus longaeva* Bailey

Southwestern white pine and limber pine are closely related. A gradient of similar traits occurs where these species overlap, suggesting hybridization (Steinhoff et al. 1971; Benkman et al. 1984). Ongoing research suggests that the continued gene flow within the hybridization zone between these two species ultimately blurs the earlier defined ranges of each species (Menon et al 2018). Future understanding of the implications of the hybridization between southwestern white pine and limber pine may ultimately lead to novel management approaches for each species. Similarly, Rocky Mountain bristlecone and Great Basin bristlecone are closely related, and have only been classified as distinct species since 1970 (Bailey 1970).

Silvics and Associated Cover Types

Southwestern white pine

Southwestern white pine's native range extends across New Mexico and Arizona at mid to high elevation sites, though a significant portion of the range occurs in Mexico (**Figure 1**; Little 1975; Shirk et al. 2018). The elevation range for SWWP begins at 684m (2,244ft) and reaches to 3600m (11,811ft) above sea level (Looney and Waring 2012; Shirk et al. 2018). This pine is moderately shade tolerant and is generally a component of mixed stands, though pure stands have been documented (Sakulich and Taylor 2007; Looney and Waring 2012; Looney and Waring 2013). Southwestern white pine becomes dominant primarily in high elevation stands, though it can also occasionally occur in more riparian areas in

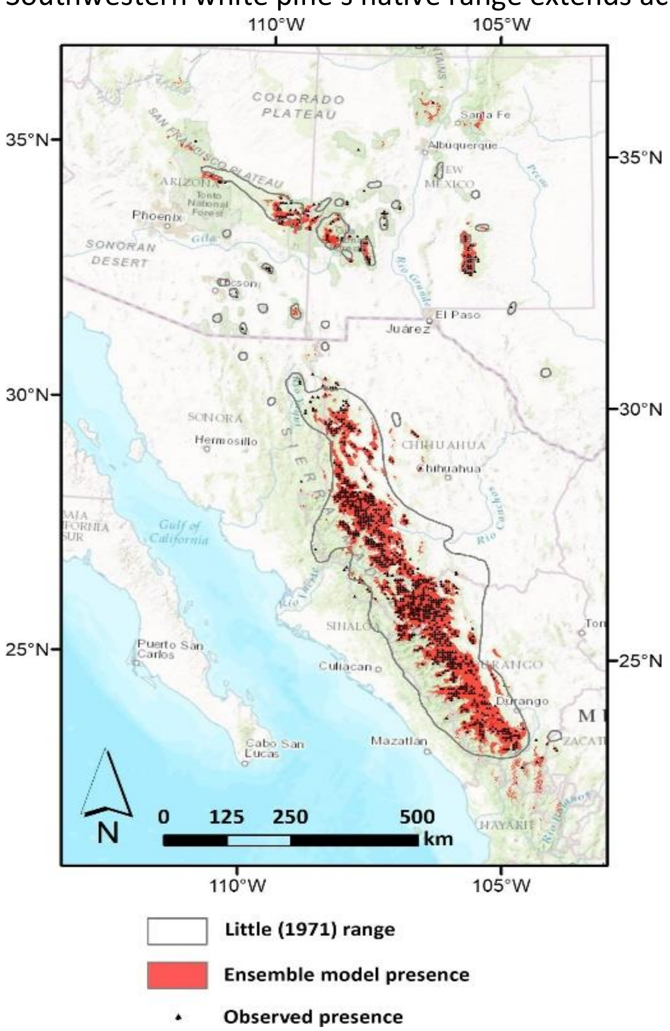

Figure 1. Southwestern white pine (*Pinus strobiformis* Engelm.) distribution map. Adapted from Shirk et al. 2018. This figure provides data from observations as well as modeled presence as compared established range maps provided by Little (1971).

south-central Arizona (Szaro and King 1990). This species can exist as a persistent long-lived species within mixed stands (Larson and Moir 1987). Southwestern white pine is a component of several Society of American Foresters' cover types, including types 206 (Engelmann Spruce-Subalpine fir), 210 (Interior Douglas-fir), 211 (white fir), 216 (blue spruce), 217 (Aspen), 219 (limber pine), and 237 (interior ponderosa pine) (Pavek 1993). Due to slow growth and frequently poor form, this species is rarely used for lumber production except when harvested in conjunction with mixed conifer (Burns and Honkala 1990). Seed production varies from year to year, and high-yield seed crops are critical for natural and artificial regeneration efforts (Depinte 2016).

Limber pine

Limber pine's native range extends from Alberta, Canada and southeastern British Columbia in the north, to California, Arizona, and New Mexico in the south (**Figure 2**; Burns and Honkala 1990). The elevation range extends from 2,850ft (870m) to 12,500ft (3,810m), with lower elevation sites existing primarily in the northern ranges (Burns and Honkala 1990). Limber pines are relatively shade intolerant and may be found in three main types of stands: monoculture, mixed-species, and invading (Rebertus 1991; Windmuller-Campione and Long 2016). Monoculture stands occur where the site is characterized by rocky soils and harsh dry conditions that allow for little outside competition (Schoettle 2014). Site characteristics in these stands ensure wide spacing and open growing space for individual trees that favor continued recruitment of young seedlings (Schoettle 2014). On milder sites limber pine functions as a generalist within mixed-species stands providing increased diversity, and may also act as an invader in stands where limber pine is not historically present (Windmuller-Campione and Long 2016). Limber pine is a component several Society of American Foresters' cover types, including types 206 (Engelmann Spruce-Subalpine fir), 208 (whitebark pine), 209 (bristlecone pine), 210 (Interior Douglas-fir),

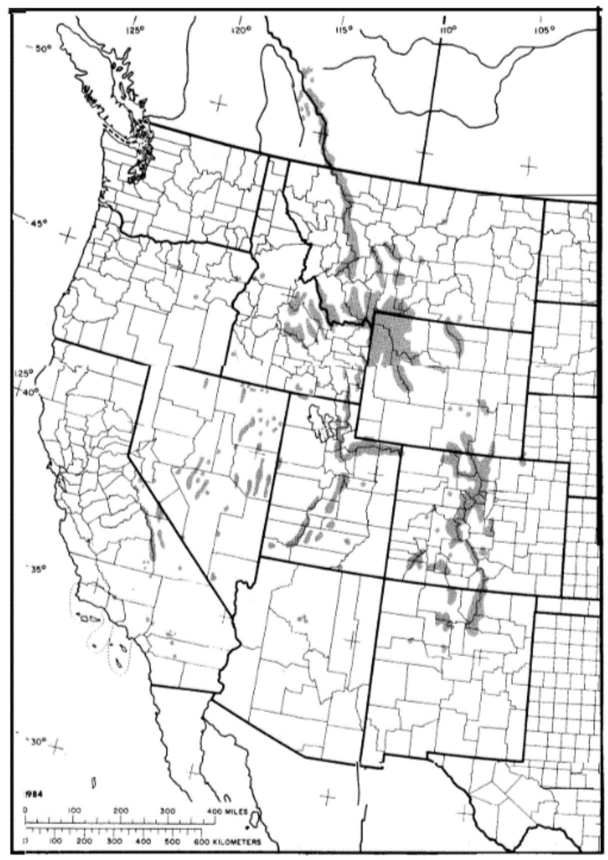

Figure 2. Limber pine (*Pinus Flexilis* James) distribution map. Adapted from Burns and Honkala 1990.

217 (Aspen), 218 (lodgepole pine), 220 (Rocky Mountain juniper), 237 (interior ponderosa pine), 239 (pinyon-juniper), 256 (California mixed subalpine) and is a dominant cover type in 219 (limber pine) (Burns and Honkala 1990; Johnson 2001). Limber pine is generally a small to medium sized, slow growing species (Burns and Honkala 1990). The wood is lightweight and mostly utilized in poles, ties, and other rough construction applications (Burns and Honkala 1990). However, slow growth and poor form make this species undesirable for more than incidental commercial timber harvest (Burns and Honkala 1990).

Rocky Mountain bristlecone

Rocky Mountain bristlecone pine occurs primarily in the state of Colorado, though small populations exist in Arizona and New Mexico (**Figure 3**; Fryer 2004b; Schoettle 2014). This species occurs from 7,000ft (2,100m) to 13,000ft (4,000m) in elevation, and has been recorded growing 130ft (40m) higher than the present treeline in response to climate change (Yamaguchi 1992). Rocky Mountain bristlecone acts as pioneer species after fires, is shade intolerant, and regenerates well on recently burned sites (Baker 1992; Schoettle 2014). Though not quite as long lived as Great Basin bristlecone, Rocky Mountain bristlecone

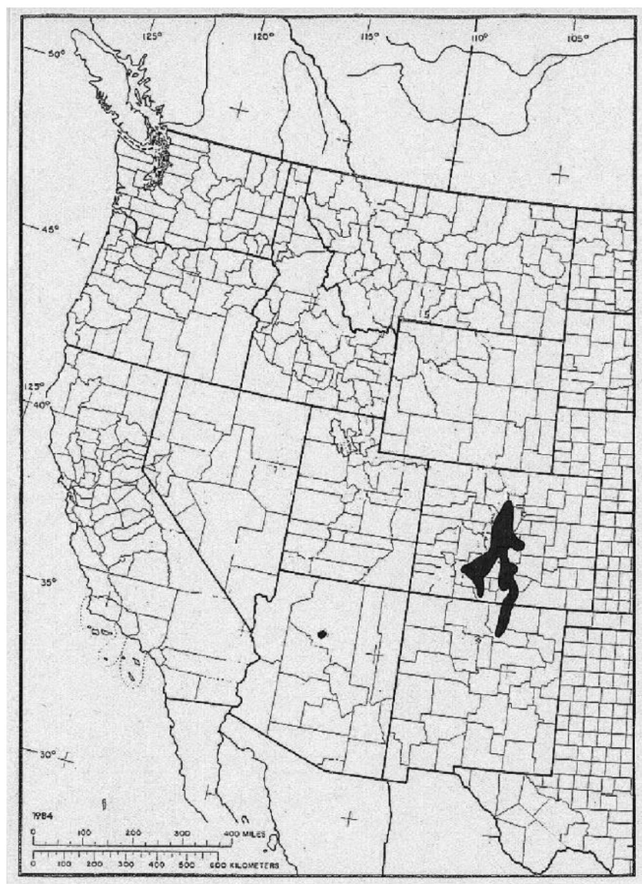

Figure 3. Rocky Mountain Bristlecone (*Pinus aristata* Engelm.) distribution map. Adapted from Burns and Honkala 1990.

pines are very long-lived species that can reach one to two thousand years, with a record estimated age of 2,500 years (Brunstein 1993). Part of this longevity is attributed to the slow growth and slow heart rot decay on the more extreme elevation sites, while lower elevation Rocky Mountain bristlecone pines have lower life expectancies due to higher risk of various mortality agents (Page and Gilbertson 1983). This species can occur as pure stands or can co-occur with other species in more mesic sites (Fryer 2004b). Rocky Mountain bristlecone pine is a component several Society of American Foresters' cover types, including types 206 (Engelmann Spruce-Subalpine fir), 209 (bristlecone pine), 210 (Interior Douglas-fir), 218 (lodgepole pine), and 219 (limber pine) (Fryer 2004b).

Great Basin bristlecone

Great Basin bristlecone pine's native range occurs in Southern California, Nevada, and Utah (**Figure 4**; Little 1971). It is a high elevation species that occurs from 7,200ft (2,200m) to 10,800ft (3,300m), and has been noted moving downward in elevation in the White Mountains in response to climate change (Fryer 2004a). Great Basin bristlecone is a widely known species for extreme longevity, and a specimen known as Methuselah is estimated to 4,765 years old (NPS 2015). At extreme elevations and site conditions, this species occurs in pure yet sparse stands and becomes a component of mixed conifer stands at lower elevations

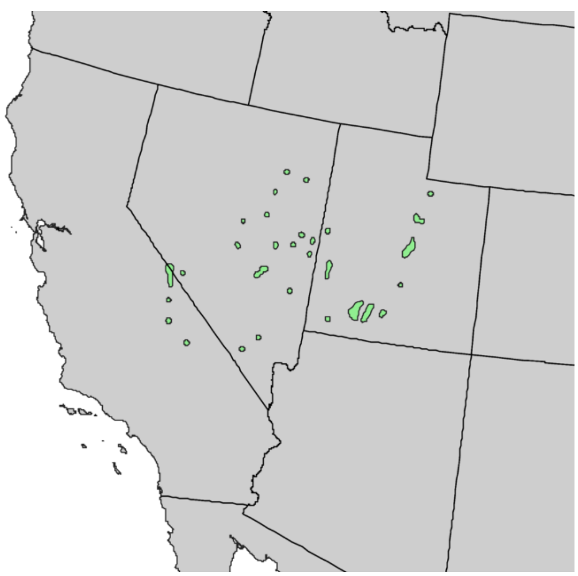

Figure 4. Great Basin bristlecone (*Pinus longaeva* Bailey) distribution map. Adapted from USGS Geosciences and Environmental Change Science Center: Digital Representations of Tree Species Range Maps from "Atlas of United States Trees" by Elbert L. Little, Jr. (and other publications)

(Hiebert and Hamrick 1984). Great Basin bristlecone naturally occurs in multi-aged stands where ancient individuals are a minority (Walker 1993). This species can occur in a variety of Society of American Foresters cover types, including 206 (Engelmann Spruce-Subalpine fir), 208 (whitebark pine), 209 (bristlecone pine), 210 (Interior Douglas-fir), 211 (white fir), 219 (limber pine), and 237 (interior ponderosa pine) (Fryer 2004a). It is important to note that Great Basin bristlecone does not co-occur with Rocky Mountain bristlecone, and the two species are separated by the Colorado-Green River drainage (Hawksworth and Bailey 1980). This species is highly drought tolerant due to thick, waxy needles and shallow branched root systems (Connor and Lanner 1991). Great Basin bristlecone pines are very shade intolerant, and act as both pioneer and climax species where the harshest conditions occur (Hawksworth and Bailey 1980).

Fire Ecology and Regeneration

Regeneration of many white pine species is facilitated by Clark's nutcracker (*Nucifraga columbiana*) caching over long distances. The nutcracker has a mutualistic relationship with limber pines, as well as other white pines, that provides the bird with nutritious seed and facilitates long range seed dispersal for the pine (Williams et al. 2017). This relationship plays an important role in post fire regeneration and recovery of limber pines in recently burned areas where local seed sources are unavailable (Coop and Schoettle 2008). Seeds can be dispersed over long distances, and are commonly cached in open sites such as burn scars (Coop and Schoettle 2009). This is critical since wind dissemination is poor due to seed mass and inadequately winged seeds (Looney and Waring 2013). Clark's nutcracker caching is likely significant component of long distance dispersal for southwestern white pine as well, and the behavior has been documented in the San Francisco Peaks of Arizona (Benkman et al. 1984;

Looney and Waring 2013). Where limber pine regenerates under closed canopies very young trees can be common, but pole sized trees are rare due to shade intolerance (Rebertus 1991). For this reason, openings and disturbances are critical to the spread and maintenance of limber pine.

Rocky Mountain bristlecone and Great Basin bristlecone produce small, winged seeds typical of wind dispersal, yet only Great Basin Bristlecone has been a documented food source for nutcrackers (Lanner 1988; Coop and Schoettle 2009). It is possible that Great Basin bristlecone seeds may play an important nutritional role when limber pines have reduced cone crops (Lanner 1988). Without the help of nutcrackers, Rocky Mountain bristlecone regeneration is common only within the edges of recently burned sites and adjacent to surviving seed trees (Coop and Schoettle 2009).

Historically, fire is a natural occurrence in many forest ecosystems, and white pine ecosystems are no exception. Though high elevation white pines on rocky, open sites are unlikely to face a significant threat from wildfire, many white pines occur as a component of mixed conifer stands that can be more fire prone (Schoettle 2014). Mixed stands in the Southwest can have a variety of fire regimes, ranging from infrequent high-severity fires to frequent low-severity fires (Battaglia and Shepperd 2007).

Young southwestern white pines and limber pines are thin barked and do not readily survive wildfires (Johnson 2001). As they reach maturity, these two species develop thicker bark which conveys greater resistance to wildfires (Looney and Waring 2013). Despite the high rate of mortality in wildfires, limber pine is frequently an early colonizer of burned areas due to its drought tolerance and long-range seed dispersal facilitated by Clark's nutcrackers (Johnson 2001). This results in a pattern of growth and stand development where limber pine dominates and persists on poor sites with long fire return intervals, and becomes an early colonizer after disturbance (Johnson 2001). Regeneration of southwestern white pine occurs most readily in stands with recent fire activity, bare mineral soils, low basal area, and with fewer ponderosa pine (*Pinus ponderosa*) (Goodrich and Waring 2016; Goodrich et al. 2018). This indicates that limber pines and southwestern white pines may both be highly beneficial species to plant or promote after fires where other species may have high seedling mortality.

Rocky Mountain bristlecone and Great Basin bristlecone also have thin bark which confers very little resistance to fires (Crane 1982; Fryer 2004a). However, there is little documentation on post-fire regeneration of these species, and further research will be needed (Fryer 2004a). Great Basin bristlecone pine largely occurs in very open stands where productivity is low which accounts for low fuel loading and infrequent and low severity fires (Bidartondo et al. 2001). However, little is known about the mortality and resilience of Great Basin bristlecone where it occurs alongside other conifers in more frequent fire regimes. For Rocky Mountain bristlecone, research has shown that it plays a critical role in early to mid, post-fire succession in high elevation sites (Baker 1992; Schoettle 2014). Establishment of young seedlings can be poor, and is not likely under closed canopies (Baker 1992). Young Rocky Mountain bristlecone seedlings do best in openings, recent burn scars, and on bare mineral soil and rarely germinate closer than 600ft (200m) from parent trees (Graves 1917; Baker 1992). Though more research is needed, it is likely that Great Basin bristlecone may respond similarly to limber pine and Rocky Mountain bristlecone and play important roles in post-fire early successional recovery

(Fryer 2004a). Though adapted to harsh sites, Great Basin bristlecone seedlings benefit from microsite shelter (Maher et al. 2015). Great Basin bristlecone seed production is consistent from year to year and continues even in ancient individuals, yet seedling establishment is rare (Fryer 2004a).

Primary Threats

The three primary threats facing white pines in the southwestern United States are climate change, mountain pine beetle (*Dendroctonus ponderosae Hopkins*, MPB), and white pine blister rust (*Cronartium ribicola*, WPBR). To manage for these species, we must understand how each species copes with biotic and abiotic stressors as well as the variability in adaptive traits that occurs within each species. An adaptive trait can be defined broadly as a genetically inherited characteristic that confers some level of advantage or increased fitness against a biotic or abiotic stressor (Dobzhansky 1956). These can occur throughout a species, or occur as local adaptions within populations (Bono et al. 2017). Such adaptations may come with a cost, known as a trade-off, where another adaptive trait is hindered and susceptibility to another stressor is increased (Bono et al. 2017). In conifers, adaptive traits include, but are not limited to: drought tolerance, cold hardiness, and insect and disease resistance.

Climate Change

The southwestern United States has always been known for its generally dry climate, seasonal monsoons and rugged landscapes. The Southwest is experiencing more elevated temperatures and depressed precipitation than many other parts of the country, and the effects of a changing climate are readily evident (**Figure 5**; Macdonald 2010). Under all current worldwide emissions projections, climate change models predict an even hotter southwestern United States with generally drier conditions and more extreme droughts and decreased snowpack (Figure 5; Seager et al. 2007). Although current and future policy shifts regarding climate change and greenhouse gas emissions will largely dictate the intensity of the coming changes, all tree species will be affected to some degree.

Climate change has already begun to alter plant communities, fire behavior, and water availability and in these already arid ecosystems (**Figure 5**; Macdonald, 2010). As rainfall patterns shift or decrease, the associated droughts are expected to trigger forest decline on an unprecedented scale (Choat et al. 2012). Unfortunately, drought-related stress is likely going to be a primary driver behind many species' range shifts due to changes in fitness and competition (Bickford et al. 2011; Shirk et al. 2018). Though much research has focused on mortality of adult trees, it is equally important to acknowledge the importance of drought on species regeneration patterns. Young trees are most sensitive to variations and extreme events, and lack of recruitment can have huge impacts on the long-term structure of a stand (Matías et al. 2014). It is nearly impossible to predict all the direct and indirect ways in which climate will redefine our forested landscapes, but ongoing research will help scientists and managers adapt to new challenges.

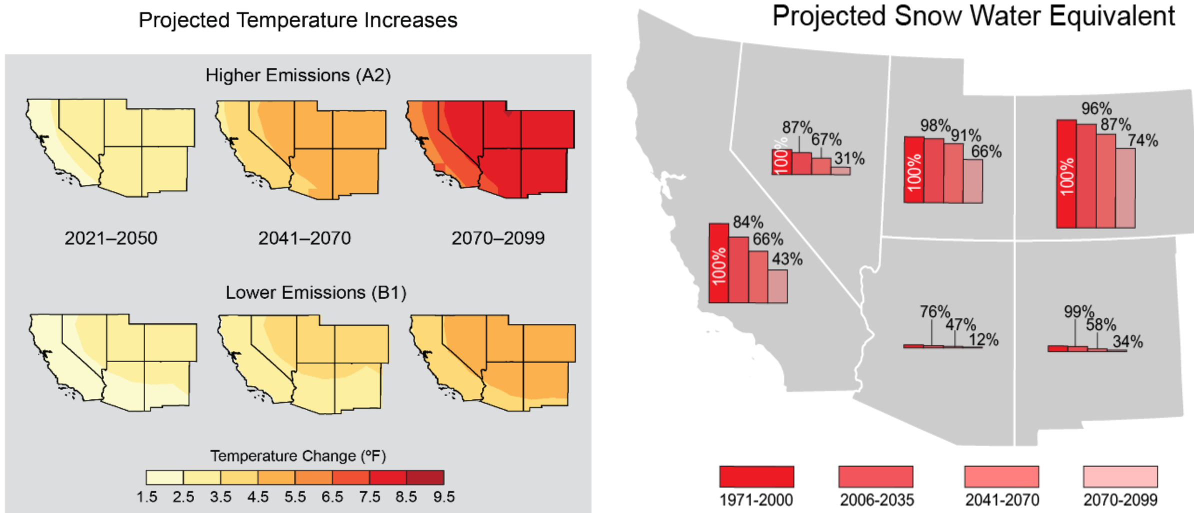

Figure 5. Left: High emission (A2) and low emission scenarios and their relative impact on future climate. Right: Snow Water Equivalent assuming high emissions (A2) scenario. Adapted from The National Climate Assessment. Chapter 20 Adapted from: Regional Climate Trends and Scenarios for the U.S. National Climate Assessment: Part 5. Climate of the Southwest U.S. NOAA Technical Report NESDIS 142-5

The most immediate and extreme effects are expected to occur at ecotones, where species already exist on the edge of their habitable range (Allen and Breshears 1998). This effect is expected to be more pronounced in arid and semi-arid regions such as the Southwest (Allen and Breshears 1998). Previous drought studies have shown that drought stress and drought resistance are natural barriers to lower elevation limits of conifer species (Barton and Teeri 1993). Understanding the adaptive traits that already occur at these extremes, and how those traits manifest within and between populations, is an important part of future research or management of climate-imperiled species. Not only are ecotone trees more likely to suffer from climate change, but they are also more likely to present genetic or phenotypic variation that allows them to live at the edge of their habitable zone. For instance, in a study focused on Scots pine (*Pinus sylvestris*), seedlings from the southernmost ranges exhibited lower drought stress and higher survival relative to seedlings from higher latitudes, which was attributed to higher carbon allocation into root biomass when compared to Scots pine seedlings from more northern provenances (Matías et al. 2014). Trees are faced with the direct effects of climate change such as drought stress, but may also face increased competition from neighboring species which were previously limited by harsh, freezing temperatures (Loehle 1998).

Climate modeling predictions for future habitability can provide insight into how forests might respond given various emissions scenarios. Under high emission scenario A2, the range of each of our focal white pines is expected to be significantly reduced by the year 2060. Southwestern white pine's range (**Figure 6**) is expected to contract within the U.S., limiting the species to high elevation sites in eastern Arizona and south-central New Mexico. Limber pine's range condenses sharply, and the prediction indicates a high likelihood of the species becoming extinct across many western states (**Figure 7**). Rocky Mountain bristlecone is likely to become limited to only marginal sites in Colorado and New Mexico (**Figure 8**). Great Basin bristlecone appears to become functionally extinct in the Four-Corners region, and only remains viable with California (**Figure 9**). However, climate models cannot fully account for adaptation, changes in competitive interactions between species, and other dynamic species reactions.

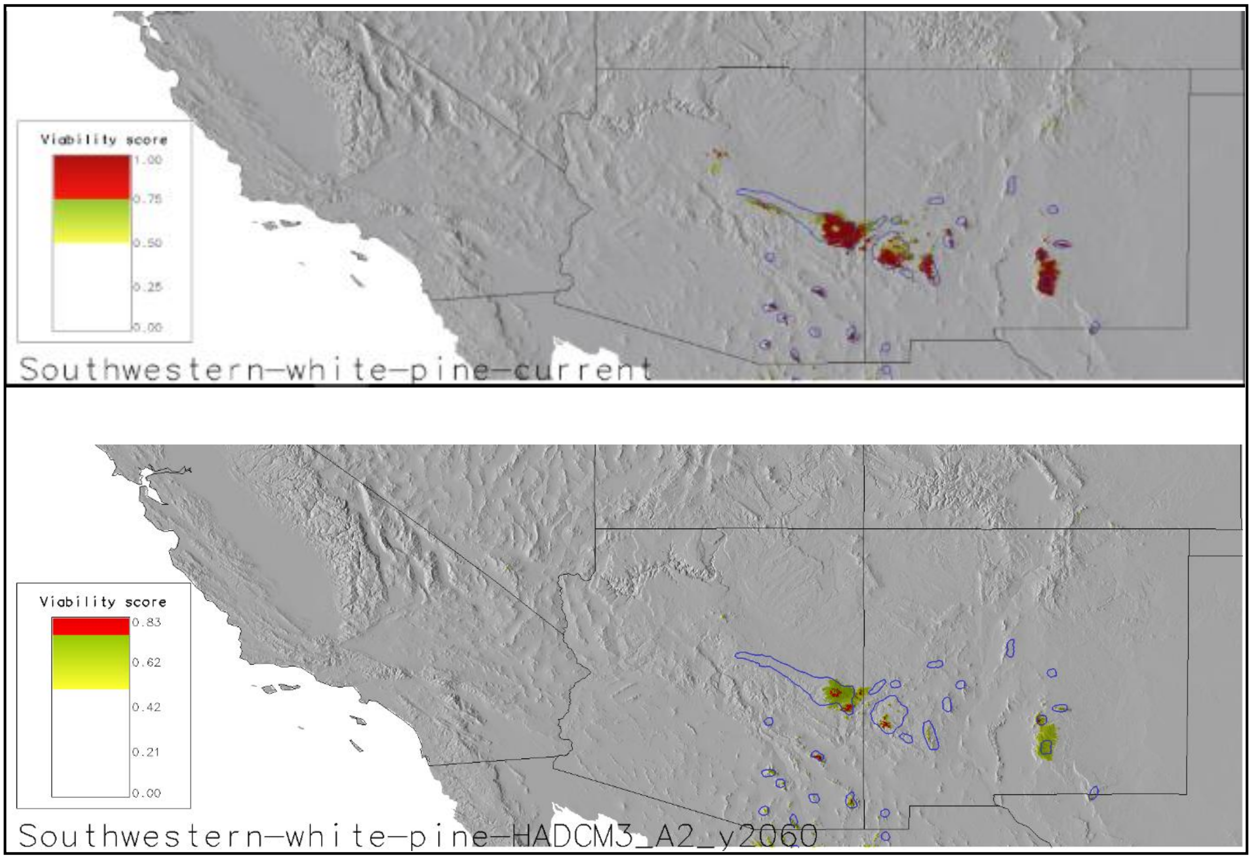

Figure 6. (Above) Southwestern white pine range within the United States: current (top) and projected range for the year 2060 (bottom) under the climate scenario A2. Blue lines represent established range maps from Little (1971). Red indicates high likelihood of species presence (high viability), while green and yellow represent reduced likelihood (low viability). Adapted from Nicholas Crookston, USFS, output model HADCM3 A2 (Hadley Center/World Data Center high emissions scenario). See also Rehfeldt et al. (2006) for detailed model descriptions.

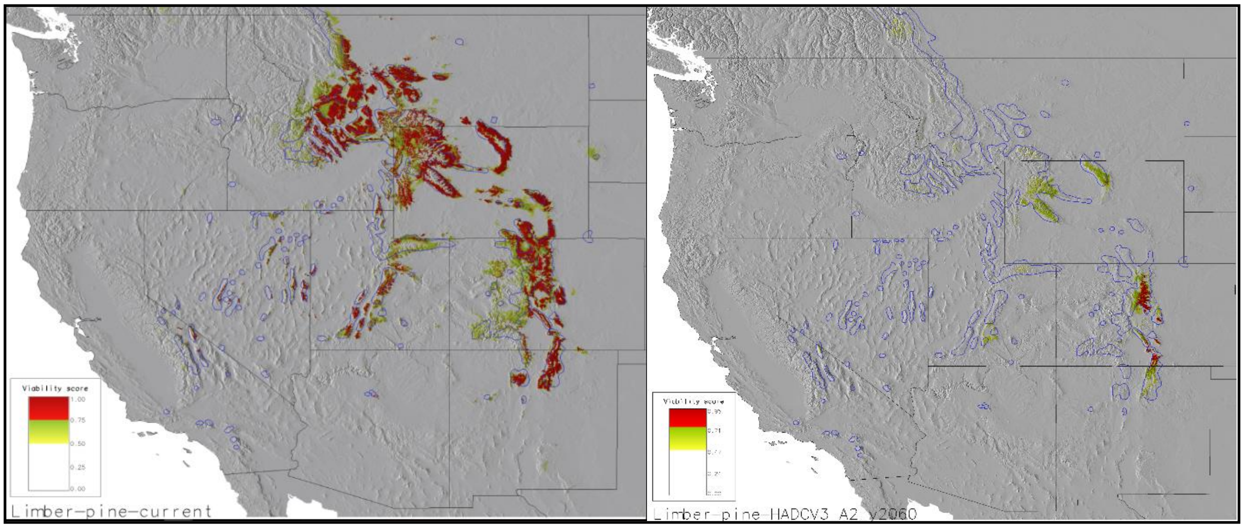

Figure 7. (Above) Limber white pine range within the United States: current (left) and projected range for the year 2060 (right) under the climate scenario A2. Blue lines represent established range maps from Little (1971). Red indicates high likelihood of species presence (high viability), while green and yellow represent reduced likelihood (low viability). Adapted from Nicholas Crookston, USFS, output model HADCM3 A2 (Hadley Center/World Data Center high emissions scenario). See also Rehfeldt et al. (2006) for detailed model descriptions.

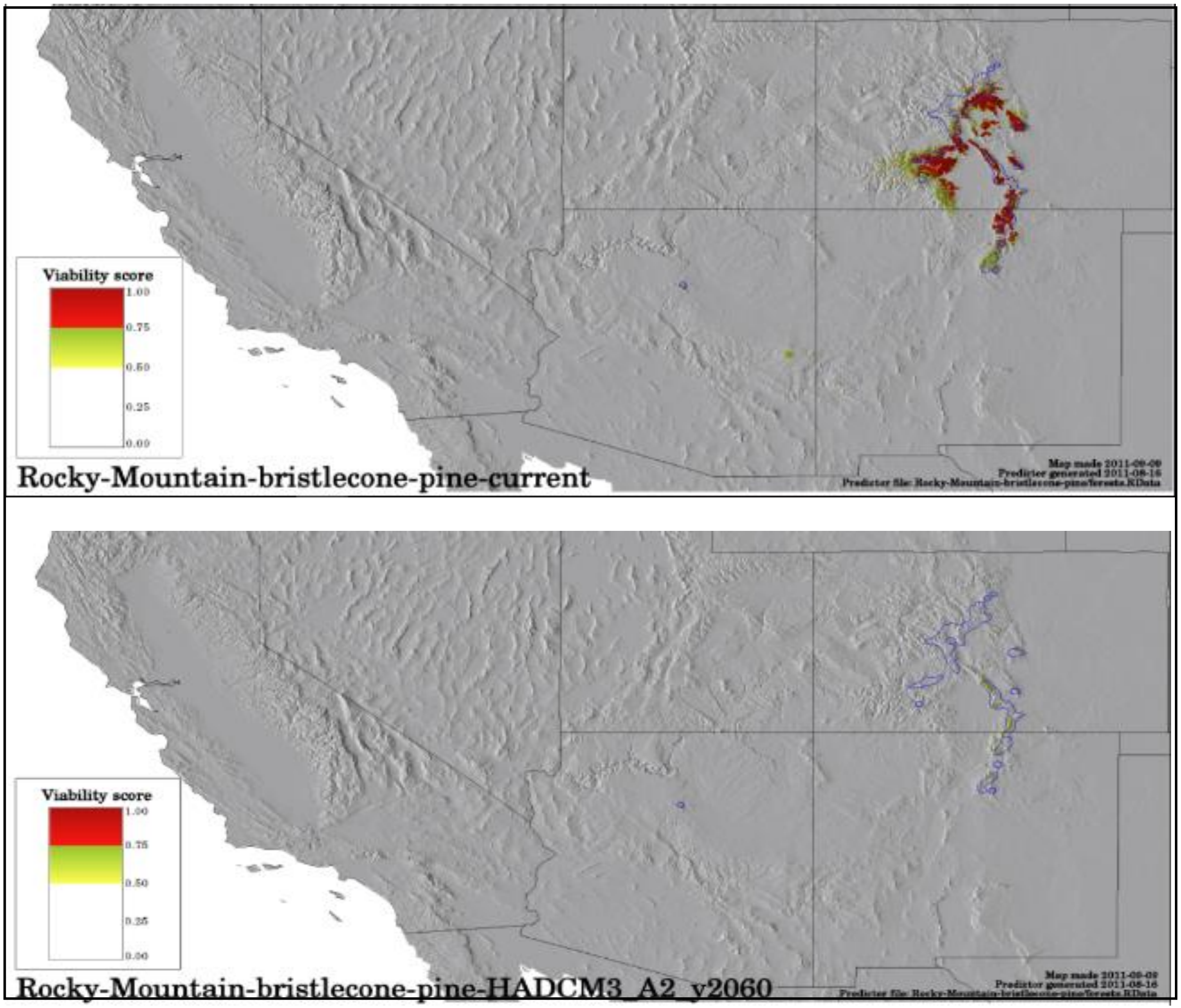

Figure 8. (Above) Rocky Mountain bristlecone pine range within the United States: current (top) and projected range for the year 2060 (bottom) under the climate scenario A2. Blue lines represent established range maps from Little (1971). Red indicates high likelihood of species presence (high viability), while green and yellow represent reduced likelihood (low viability). Adapted from Nicholas Crookston, USFS, output model HADCM3 A2 (Hadley Center/World Data Center high emissions scenario). See also Rehfeldt et al. (2006) for detailed model descriptions.

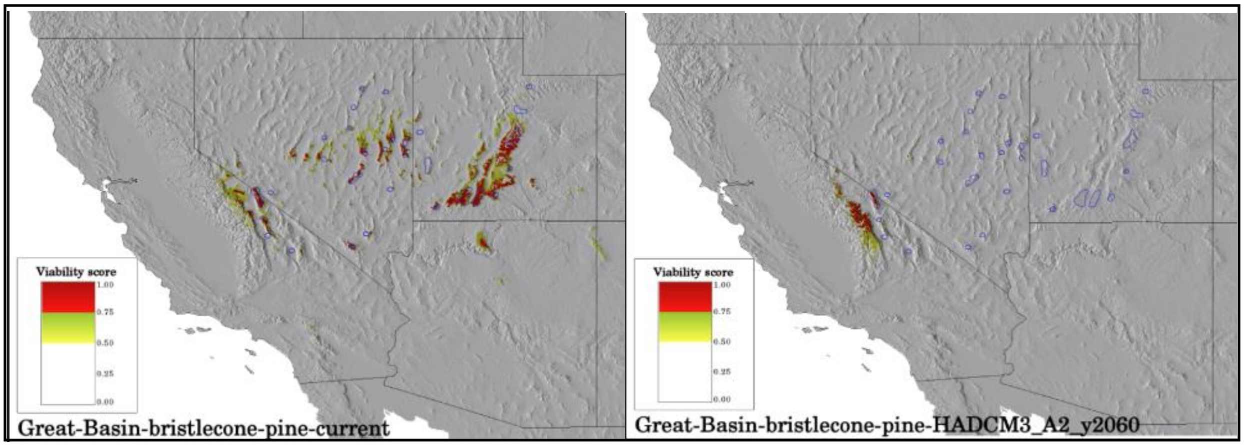

Figure 9. (Above) Great Basin bristlecone pine range within the United States: current (top) and projected range for the year 2060 (bottom) under the climate scenario A2. Blue lines represent established range maps from Little (1971). Red indicates high likelihood of species presence (high viability), while green and yellow represent reduced likelihood (low viability). Adapted from Nicholas Crookston, USFS, output model HADCM3 A2 (Hadley Center/World Data Center high emissions scenario). See also Rehfeldt et al. (2006) for detailed model descriptions.

Adaptive traits associated with drought tolerance

Drought tolerance traits are any adaptive trait which increases a tree's survival during prolonged drought. These can be a result of root and stem structure, carbon allocation, stomatal responses and other characteristics. Additionally, drought can trigger phenotypic changes or changes in carbon allocation that can aid in survival during periods of drought. For instance, study conducted on Scots pine (*Pinus sylvestris*) found that drought stressed trees exhibited shorter periods of wood formation and developed larger water conducting cells with thinner cell walls (Eilmann et al. 2011). Resource scarcity, whether from drought or competitive stress, may also reduce tree growth, making these trees less likely to recover from biotic and abiotic stressors (Kane and Kolb 2014). Wood properties are known to vary across tree species based on adaptive responses to their environments, and conifers have adapted to survive a wide variety of conditions including extremely cold, wet, arid, or hot environments

(Hacke 2015). Regardless of the extremes a given species of conifer experiences, they all share a similar hydrologic framework. In general, conifers maintain greater hydraulic safety margins, and their xylem structure is responsible for their high stress tolerance in relation to angiosperms making them better suited to arid sites (Choat et al. 2012; Hacke 2015).

Exact mechanisms of drought tolerance are poorly understood in most white pines. High elevation sites have thus far been mostly insulated from the effects of extreme drought, so it is hard to determine how each species will respond in the future (Miller et al. 2007). Southwestern white pine seedlings heavily allocate carbon to the formation of a taproot, which likely allows them to be more drought tolerant (Looney and Waring 2012).

Bark beetles

Another stressor to white pine survival is the increasing prevalence of native bark beetles due to climate change. The species of greatest concern is mountain pine beetle (*Dendroctonus ponderosae* Hopkins), which utilizes most pine species as hosts (Gibson et al. 2008; FHP 2011). Mountain pine beetle in the region infests limber pine (*Pinus flexilis* James), southwestern white pine (*Pinus strobiformis* Engelm.), ponderosa (*Pinus ponderosa*), lodgepole (*Pinus contorta*), whitebark (*Pinus albicaulis*), and Rocky Mountain bristlecone (*Pinus aristata* Engelm.) with lower success in Engelmann spruce (*Picea engelmannii*), blue spruce (*Picea pungens*), Douglas-fir (*Pseudotsuga menziesii*) and true firs during large outbreaks (Amman et al. 1990; FHP 2011).


Mountain pine beetle. Photo by USDA Forest Service.

Due in part to the beetle's range of host species, it is a prolific cause of pine mortality that outpaces all other insect pests (Gibson et al. 2008). An increase in outbreak severity across several host species can be tied to multiple effects of climate change, such as warmer winters, longer warm seasons, and increasing drought pressure (Gibson et al. 2008; Creeden et al. 2010). This results in greater pressure on host tree species than historically occurring outbreaks, and thereby imbalances the cycle in which both host and insect co-evolved (Creeden et al. 2010). Mountain pine beetle populations have reached levels greater than previously recorded, and have been increasing dramatically in white pine stands (Gibson et al. 2008). As outbreaks continue in the presence of milder winters and drought, it becomes increasingly likely that the only reprieve will occur as the populations of mature host trees dwindle (Gibson et al. 2008).

Adaptive traits associated with bark beetle defense

Several traits have been identified that allow a tree to defend against bark beetle attack. Conifers have a variety of defenses against bark beetle attacks, including resin, toxins, monoterpenes and autonecrosis (Boone et al. 2011). Resin provides a first line of defense, creating physical barriers to bark beetle entry (Raffa and Berryman 1983). Autonecrosis occurs at the site of invasion, which helps trap beetles within dead tissues, while toxic or inhibitory compounds are synthesized to prevent beetle advance (Raffa and Berryman 1983). However, some compounds, such as monoterpenes, have conflicting roles in bark beetle activity since they act as both attractants for beetles as well as a chemical defense (Seybold et al. 2006). Monoterpenes may dramatically increase following natural or manmade disturbances, thus increasing the risk for bark beetle invasion in recently thinned or otherwise damaged stands (Seybold et al. 2006). Beetle defenses require carbon allocation and sufficient resources to produce and maintain, therefore they are limited by tree vigor (Larsson et al. 1983). Since thinning projects designed to promote host vigor may also increase the risk of beetle aggregation, they should be considered carefully when bark beetle activity is present.

Though mountain pine beetle has a range of hosts under threat, there is some good news. Great basin bristlecone, *Pinus longaeva* Bailey, shows a high resistance to beetle attacks (Gray et al. 2015; Eidson et al. 2017). Bentz et al. (2016) discovered that Great basin bristlecone contains greater than eight times higher levels of monoterpenes and other defense compounds than adjacent stands of limber pine, which contributes to their success against beetle attacks.

White Pine Blister Rust

White pines in the southwestern United States are threatened by a lethal invasive pathogen *Cronartium ribicola*, that causes the disease white pine blister rust (Conklin 2009; Looney and Waring 2012). Except for Utah, the disease has reached every state with white pine populations (**Figure 10**). New Mexico has a large range of WPBR infections, including those found on the Lincoln, Gila, Cibola, and Santa Fe National Forests (Conklin et al. 2009). The disease has been in Colorado since 1998, and has been discovered in both the northern and southern portions of the state (**Figure 10**; Johnson and Jacobi 2000; Schoettle 2014). In Arizona, there are no reports of white pine blister rust on southwestern white pine populations on the Mogollon rim and the San Francisco Peaks near Flagstaff, AZ. However, the first reported case in Arizona occurred in Apache County near

White pine blister rust canker on a limber pine. USDA Forest Service, Anna Schoettle

Hawley Lake during April of 2009 (Fairweather and Geils 2011). Unfortunately, this disease is expected to continue to spread through white pine species and landscape scale management strategies offer little defense (Conklin 2009). The spores are wind disseminated, which facilitates the rusts expansion into new white pine stands (Hunt et al., 2010; Schwandt 2010). Since the southwest has a gradient of healthy, recently infested, and heavily infested stands, there is a unique window of opportunity to study the effects of this disease on each species. Increasing white pine blister rust mortality will reduce breeding populations across the landscape, creating a need for preemptive management activities, genetic resistance screening, and the protection of known resistant stock (Miller et al 2017). Such preemptive management has been found to be more successful than trying to restore ecosystems that are already experiencing collapse (Schoettle and Sniezko 2007). Ongoing research by government agencies and public universities continues to refine our understanding of white pine blister rust and its implications.

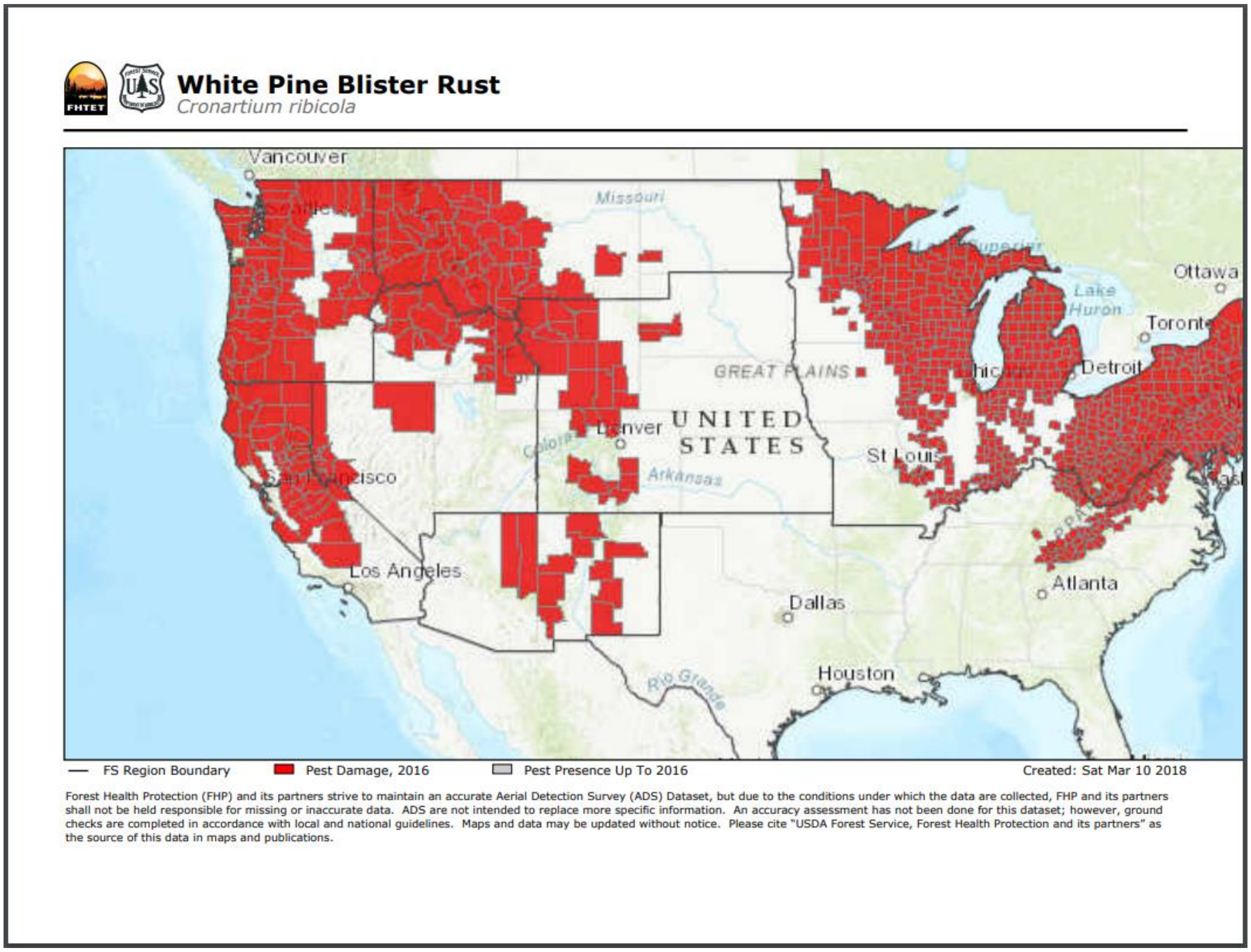

Figure 10. White Pine Blister Rust Damage. 2016. Adapted from: Forest Health and Protection: Forest Pest Conditions. Areas in red indicate known white pine blister rust (Cronartium ribicola) infected stands across all white pine species.

White pine blister rust mortality is a result of the symptomatic cankers which occur with the disease, creating wounds that eventually girdle stems and branches causing canopy dieback, branch flagging, and eventually whole tree mortality (Looney and Waring 2013). High levels of white pine blister rust infections can be devastating to populations of white pines, yet some silvicultural methods have been used with limited success (Hunt 2010). Unfortunately, the application of silvicultural or management practices alone is unlikely to sustain wild populations since treatments are not feasible to apply at a landscape scale (Conklin 2009). Abiotic site characteristics and tree age also have a direct effect on white pine blister rust resistance in western white pine (*Pinus monticola*), where older trees or trees subjected to shorter growing seasons have shown higher levels of resistance (Hunt 2005). Regardless, the effect of elevation on reducing infection rates must be put into perspective, as white pines in extreme elevation ranges are also slow growing and slow to reproduce (Smith et al. 2013). Similarly, a negative correlation appears between proportion of WPBR killed canopy and increasing elevation (Smith et al. 2013). Such a response may be a culmination of multiple factors, including climatic requirements of rust spore transmission, or the increased occurrence of bark beetles or drought stress at lower elevations (Smith et al. 2013).

Adaptive traits associated with white pine blister rust resistance

The most viable management option available is promoting genetic-based resistance to support wild populations (Kinloch 2003). More importantly, rust resistant genotypes and tree breeding programs may be the only path forward for preventing species' extinction (Sniezko and Koch 2017). Resistance to white pine blister rust can occur in two broad resistance categories: partial or major gene resistance (MGR). Partial resistance can occur through a variety of mechanisms which allow an infected tree to survive blister rust cankers, while major gene resistance imparts directly inherited immunity to stem infections (Sniezko et al. 2008). Partial resistance is thought to be a result of several overlapping genes and can include any method of surviving with, or recovering from, a rust infection that would otherwise prove fatal (McDonald et al. 2004; Sniezko et al. 2008). Major gene resistance is rare, though it occurs naturally in some white pines (Sniezko et al. 2008). In species where MGR is found, it is characterized by a single gene that offers complete resistance to the disease (Kinloch et al. 1999; Sniezko et al.

2008). Despite this, certain strains of white pine blister rust fungus have adapted a species-specific virulence, which allows the pathogen to overcome the mechanism of resistance conferred by MGR (Kinloch et al. 1999; Schoettle et al. 2014). In species where MGR mechanisms are overcome, partial resistance may be the only remaining defense. Major gene resistance, occurs in low frequencies in many species of white pine, including southwestern white pine and limber pine (**Table 2**; McDonald et al. 2004; Schoettle et al. 2014). Recent testing in the Southern Rocky Mountains yielded a 5% average, ranging from 0 to 13.9%, occurrence of major gene resistance in both healthy and diseased limber pine stands (Schoettle et al. 2014). Early trials on southwestern white pines were encouraging, as seedlings showed fewer infection sites than western white pine (*Pinus monticola*) and sugar pine (*Pinus lambertiana*), which were used as controls (Sniezko et al. 2011b). Regardless, high mortality rates are expected in infected southwestern white pine populations as additional testing has revealed very low levels of resistance (Sniezko et al. 2011b). No virulence to major gene resistance has been found in either southwestern white pine or limber pine, yet it would prudent to assume it can occur in the future since similar virulence has overcome major gene resistance in other white pine species (Schoettle et al. 2014). It should be noted that virulence is species-specific and does not cross white pine species, and additional rust adaptations must occur for new virulent strains to appear (Kinloch et al. 2004). As of this writing, it is unknown if Rocky Mountain bristlecone and Great Basin bristlecone have a major gene responsible for resistance (**Table 2**).

The introduction of white pine blister rust creates a powerful selection mechanism that favors pines with a genetic resistance to the disease (Vogan and Schoettle 2015). Since this pressure outweighs other selection pressures such as cold or drought tolerance, future populations of white pines may respond differently than previous generations to other stressors (Vogan and Schoettle 2015). In limber pine, Vogan and Schoettle (2015) found that there was a significant positive correlation with white pine blister rust resistant families and cold hardiness. The opposite was true with stomatal conductance, as resistant stock showed lower conductance than their blister rust susceptible counterparts (Vogan and Schoettle 2015). This study highlights an important uncertainly for managers, as artificially selecting for resistant stock may have unintended consequences that manifest in other adaptive traits. This phenomenon has been well documented in the literature as a trade-off, though it is still uncertain how critical the effects will be for white pine management.

Future work will need to establish the relative occurrence of genes which confer resistance, both partial and complete, if white pines are to continue to thrive across their native range. The possibility of virulence reinforces the need to maintain high levels of genetic variation in local populations, as well as the need to plant diverse resistant genotypes. It is expected that continued expansion of the pathogen responsible for white pine blister rust into Mexico will threaten large populations of southwestern white pines and other white pine species native to Mexico, creating greater need for international collaboration and research (Geils et al., 2010).

Table 2. This summarizes the susceptibility of high elevation five-needle pines to white pine blister rust by estimated resistance and initial identification of infection within each species. Resistance estimates account for both partial and major gene resistance pathways. (Schoettle 2007; Schoettle et al. 2011; Sniezko et al. 2011b; Looney and Waring 2012; Schoettle et al. 2012; Schoettle et al. 2014; Sniezko, personal communication, May 2018)

	Year First Recorded in Species	Estimated Resistance in Native Populations (%)	Evidence of Major Gene Resistance
Southwestern white pine	1970	<10 (Ongoing)	Yes
Limber Pine	1945	1 to 29	Yes
Great Basin bristlecone	NA	30 (early results)	Unknown
Rocky Mountain bristlecone	2003	17 to 60	Unknown

Species Recommendations

The planet is undergoing a period of unprecedented turbulence that will change every ecosystem in the coming centuries (Falk 2017). Proactive management and restoration work should be implemented to improve the natural level of resilience within a population or ecosystem.

Many recommendations for white pine sustainability and resilience are general, and can apply to multiple species (**Table 3**). Stand structure is a well-known driver of host vigor and insect and disease resistance. In white pines, there is evidence that vigorous nonresistant host trees of white pine blister rust have triple the canker growth of their less vigorous infected counterparts (Schoettle 2007). However, host vigor is a critical component of survival from bark beetle attacks, droughts, and other biotic and abiotic stressors (Björkman 2000; Hundsdorfer 2006). Additionally, any thinning activities completed to promote vigor will also open growing space for natural regeneration and reduce the risk of catastrophic stand-replacing wildfires. White pine blister rust damages white pines of all ages, though mortality is more rapid on younger trees due to more rapid canker girdling (Conklin 2004). Age class diversification and aggressive basal area reduction is a recommended course of action since it allows for the maintenance of mature trees and their associated ecosystem services while still promoting regeneration and population size for natural selection (Schoettle 2007; Goodrich et al. 2018). Natural selection can proceed rapidly under extreme pressures, and dramatic reductions in infected seedlings has been shown to occur in whitebark pine (Schoettle 2007). When parent stand mortality was less than 10%, only 0.9% of seedlings were canker free, yet when there was greater than 90% parent mortality, 44.4% of seedlings were canker free (Schoettle 2007). Further, when basal area is reduced in infected southwestern white pine stands through uneven aged or two aged management, both overstory and regeneration show significant decrease in infection rates (Goodrich et al. 2018). These results provide an encouraging look at how white pines may be sustained in the future despite low estimates of current resistance.

One of the most critical ways to increase future white pine survival is promoting larger white pine populations and genetic diversity in anticipation of a future decline. Most species of white pine had historically higher populations prior to fire suppression policies that dominated the 1900's (Schoettle 2007). Since white pine blister rust resistance is low across our native white pines, boosting population sizes through natural and artificial regeneration will facilitate natural selection. Artificial regeneration will be an extremely important management tool for maintaining white pines as white pine blister rust continues to advance, since it allows promotion of blister rust resistant families (Schoettle 2007). These resistant families are continually being identified through inoculation screening at the Dorena Research Center in Oregon, as well as at other Forest Service locations. However, there is a concern that white pine blister rust may become virulent to MGR, so incorporating seed stock with partial resistance may reduce likelihood of virulence evolving (Kinloch et al. 2004). Another important tool will be in the reintroduction of fire to fire-adapted landscapes, since white pines regenerate best in recently burned areas with exposed mineral soil (Schoettle 2007). If stands are currently diseased and there is a lack of data within a seed zone for resistant families, another option may require collecting and growing seed from apparently healthy white pines in infected stands (Schoettle 2007).

Table 3. General recommendations for white pine management by primary threat.

General Recommendations for White Pine Species		
White Pine Blister Rust	**Mountain Pine Beetle**	**Climate Change**
• Prioritize species retention during harvest to promote natural regeneration • Encourage age class diversity, high population levels, and recruitment of seedlings • Implement regeneration treatments in infected stands, targeting diseased trees with stem cankers • Outplant resistant seedlings at high densities in appropriate seed zones • Outplant additional bulk seedlings to facilitate natural selection and reduce the risk of WPBR virulence	• Thin stands to encourage tree vigor in all susceptible species except when local bark beetle activity is high • Monitor outbreaks to identify areas of concern	• Consult with regional geneticists to identify seed zones or species migration opportunities • Reference FVS climate models and projected species suitability maps to improve reforestation efforts • Consider the effects of microsites and aspect when planting seedlings
Preemptive seed collections and banking for reforestation after disturbance		

Specific recommendations for white pine blister rust mitigation in southwestern white pine have been established. Direct management through silviculture involves two-aged and uneven-aged management which maintains disease free overstory at a residual basal area of $9 - 10\ m^2 ha^{-1}$ (or approximately $39 - 44\ ft^2 ac.^{-1}$) (Goodrich et al. 2018). Basal area reductions will be most beneficial where rust hazard is low and natural regeneration is likely to promote natural selection pressure on families already on site (Goodrich et al. 2018). Artificial regeneration becomes more critical in high hazard sites and seedlings should be planted at high densities (~300 ha^{-1}, or ~740 $ac.^{-1}$) to account for white pine blister rust mortality (Goodrich et al. 2018). Additional considerations for natural regeneration in southwestern white pine include avoiding heavy duff, avoiding dense populations of Ponderosa pine (*Pinus ponderosa*), focusing efforts on north-facing slopes, and retaining canker-free saplings (Goodrich and Waring 2016).

Options and Opportunities for Forest Management Professionals.

Maximizing benefits with limited resources

One of the most cost-effective strategies for improving the chances of survival in white pines is the use of silviculture. Many objectives could be attained using traditional timber sales, timber stand improvement or precommercial thinning if the prescription stresses the need for protecting canker free seed sources. However, in many stands which are not already slated for management, there needs to be clear and open communication with forest managers and line officers to stress the need for keeping white pines as a component of our ecosystems regardless of economic value (Waring and Goodrich 2012).

Planting seedlings as a form of reforestation offers more flexibility in terms of species composition, knowledge of genetics, and site-specific planning. However, planting can be a costly project that does not always guarantee success. Prices for seedlings vary widely by species, age, and stock type, but have been reported for limber pine and southwestern white pine two-year-old bareroot stock at $0.62 per seedling and $0.59 per seedling respectively (Waring and Goodrich 2012). This can create a significant concern for government agencies, especially when considering landscape-scale restoration projects and restricted budgets. When this becomes a concern, there are systems in place that can allow proactive white pine management in conjunction with other objectives. On National Forests, requirements are set forth in the National Forest Management Act of 1976 that require restocking within five years after timber harvest (NFMA 1976). The act further states that “the management of the Nation's renewable resources is highly complex and the uses, demand for, and supply of the various resources are subject to change over time” (NFMA 1976). The Knutson-Vandenberg Act provides the framework for collecting funds from timber harvest specifically for reforestation efforts (KV 1930). Though traditionally, the funds have been used to promote valuable timber species, these funds can be leveraged to include reforestation with white pine species where the landscape and climate are favorable. Securing additional funding may require support from special interest groups, volunteers, and environmental organizations to support reforestation efforts on our public lands.

Conclusion

The future holds many unique and harrowing challenges that must be faced by land managers and silviculturists as our forests shift in composition due to a variety of causes. All species will face changing climatic conditions and changes in competitive ability that may help or hinder their success in each site. Though this paper looks primarily at a subset of the white pine group, every species will require thoughtful management in the future. White pines are especially susceptible since they are facing multiple threats at once. Climate change, increasing bark beetle pressure and white pine blister rust would each independently present novel challenges for white pines, but together they create a daunting challenge. Traits which may protect a tree from one threat, may hinder survival to another. Only by facing each challenge now do we hope to maintain the necessary genetic diversity to overcome these obstacles in the future. Some species, such as high elevation five-needle pines, are more vulnerable to changing climates, fire regimes and pests than others. These five-needle pine species in the interior southwest face a variety of threats including an increase in bark beetle activity, climate change, and white pine blister rust. These threats combine to create both a bleak outlook and a sense of urgency for land managers, scientists, and concerned citizens who wish to keep these species on our landscapes. Climate models paint a dire warning for us as habitat for these species are expected to dwindle, and genetic testing raises further concern for survivability as more and more stands become diseased with outbreaks of white pine blister rust.

As land managers, we must consider how each of these threats effects our local white pine communities and how we can best prepare these species for a turbulent future. Species shifts and local extinctions may be an inevitable part of the future of our forests, but we would be failing in our duties if we did not consider all available options for maintaining the ecological integrity of the forests that we manage. As we begin to see hotter and drier years, local die-offs, and other changes in our local plant communities, we must continue to look for opportunities to maintain ecological balance in the landscape. Partnerships such as the National Forest Foundation exist that can help support reforestation efforts through funding, volunteer work, and outreach. We must use the best science and the most up-to-date climate modeling to anticipate the best future sites for each species, but we must also remember that models cannot fully describe the intricacies of nature. We cannot become complacent and forgo opportunities to promote white pine regeneration even in areas where a climate model suggests a local extinction, or we may inadvertently guarantee that future.

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