ENHANCING IDENTIFICATION OF WHITEBARK AND LIMBER PINES: A LITERATURE REVIEW FOR IMPROVING FOREST MANAGEMENT

by

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ABSTRACT

Whitebark pine (*Pinus albicaulis* Engelm.) and limber pine (*Pinus flexilis* E. James.) are two high-elevation, five-needle pine species with overlapping ranges and numerous morphological similarities. Distinguishing these two species is challenging, but the recent listing of whitebark pine under the Endangered Species Act in 2022 emphasizes the importance of accurate identification. Therefore, I conducted a narrative literature review of identification methods and their effectiveness in distinguishing whitebark pine from limber pine. My review aims to synthesize existing literature concerning whitebark pine and limber pine identification to recommend identification methods for future researchers and discuss management implications. My literature review used search terms and research questions to identify studies. After study identification and screening, I included 16 studies in my review. I found multiple methods to distinguish whitebark pine from limber pine, including visual identification, elevational threshold, needle morphology, and genetic testing.

Visual identification can be effective when seed and pollen cones are present. However, seeds and pollen cones are not always present or visible. Using needle morphology for identification is not recommended due to the limited research on this technique. When limber pine and whitebark pine co-occur, whitebark pine typically occupies higher elevation, moister sites. Considering this, an elevational threshold is another method that has been applied, with researchers assuming non-cone-bearing five-needle pines found below 2,440 m are limber pine, while those found above are whitebark pine. However, numerous studies suggest that whitebark and limber pine are found above and below these elevations. Finally, genetic testing represents a new identification method that is both effective and affordable for future researchers and natural resource managers. I conclude that genetic testing is the most reliable way to identify each species and should be used to identify non-cone-bearing trees in areas of range overlap. The suggested identification methods will help managers determine where restoration and protection are needed most and are cost-effective.

CHAPTER ONE

INTRODUCTION

Ecosystem Services

Ecosystem services encompass a multitude of benefits derived from healthy, natural systems, which are essential to human survival (food, fiber, climate regulation, air purification, crop pollination) or enhance our quality of life (aesthetics, recreation) (Kremen 2005). Scientists, policy-makers, and land managers increasingly acknowledge the contributions of healthy ecosystems to human well-being and are working to develop the necessary tools and knowledge for effective management (Binder et al. 2017). Forest vegetation absorbs atmospheric carbon dioxide globally, reducing global warming potential (Krieger 2001). Forests provide numerous ecosystem services to humans, but timber production is one of the most apparent. However, not all forested areas are suitable for timber harvesting.

Tree Lines

Generally, trees cannot grow in regions where the mean temperature of the warmest month is below 10 °C (Jarvis et al. 1989). Tees exhibit short, crooked growth at their elevational limit, a form known as *Krummholz* (Jarvis et al. 1989). The transition from tall, upright forests to dwarf shrubby vegetation is often abrupt, creating a distinct tree line (Jarvis et al. 1989). High elevation is a relative concept, and tree lines around the world vary in elevation; however, they are all characterized by having a similar mean July temperature of about 10-13 °C (Richardson et al. 2004, Cogbill & White 1991, Daubenmire 1954). Additionally, many tree species that form the tree line are slow growing with long lifespans (Körner 1989). Their slow and stunted growth

form contributes to their unsuitability for timber production, although these species can offer other valuable ecosystem services. High-elevation five-needle pine forests located at subalpine and tree lines cover a great portion of western North America (Arno & Hoff 1989). They support high biodiversity and unique landscape structures that provide ecosystem services such as watershed protection, soil erosion reduction, wildlife food, habitat provision, and recreational and aesthetic values (Keane et al. 2022). Therefore, the management of forests situated at high elevations near the tree line might prioritize the ecological significance of the forest over timber production.

High-Elevation Five-Needle Pines

High-elevation five-needle pines are six white pine species belonging to the Family Pinaceae, Genus *Pinus,* and subgenus *Strobus,* which share similar ecology and morphology (Tomback et al. 2011). The six species of high-elevation, five-needle white pine in the U.S. are whitebark pine (*Pinus albicaulis* Engelm.), limber pine (*Pinus flexilis* James.), Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.), Great Basin bristlecone pine (*Pinus longaeva* D.K Bailey), foxtail pine (*Pinus balfouriana* Grev. & Balf.), and southwestern white pine (*Pinus strobiformis* Engelm.). These species are relatively shade intolerant and compete poorly on productive sites but can form more dominant stands in harsh environments (Goeking & Windmuller-Campione 2021, Hankin & Bisbing 2021). When found in these inhospitable environments, five-needle white pines act as foundational and keystone species that contribute to biodiversity. However, it is evident that many high-elevation five-needle pines in western North America are declining because of complex interactions across multiple disturbance factors (Keane et al. 2011).

Foundation and Keystone Species

Biodiversity refers to the variety of species, described in terms of the number of species, genotypes, or ecosystems, the evenness of their distribution, the differences in their functional traits, and their interactions (Hooper et al. 2005). Exotic and non-native species and the reduction or loss of species populations can alter or diminish biodiversity (Tomback & Achuff 2010). Reductions in species populations are important because species do not contribute equally to biodiversity. Keystone species strongly influence community diversity through their interactions, the strength of which is disproportionate to their abundance (Soulé et al. 2003). Foundational species are highly interactive and similar to keystone species but are often extremely abundant or ecologically dominant (Soulé et al. 2003). Foundational species influence community stability or ecosystem functions (Ellison et al. 2005). Trees are more likely to be foundational species in forested ecosystems because their functional and physiological characteristics define forest structure and alter microclimates, while their biomass and chemical makeup contribute to ecosystem processes (Ellison et al. 2005). Many white pines serve as a foundation or keystone species (Tomback & Achuff 2010), and as foundation species, they shape community structure and alter tree line microclimates (Windmuller-Campione & Long 2016). As keystone species, they serve as an important food source for many animal species, influence snow dynamics and the timing of run-off, and provide wildlife habitat (Windmuller-Campione & Long 2016). Losing these keystone and foundational species could reduce biodiversity and alter species interactions (Schoettle et al. 2022).

Whitebark Pine and Limber Pine

Whitebark and limber pine are important high-elevation species sharing extensive, overlapping ranges across western North America (Figure 1) (Ulrich et al. 2023). However, they have different elevational distribution limits, with whitebark pine found at elevations ranging from 1,600 to 3,660 m (Arno and Hoff 1989) and limber pine between 870 and 3,810 m (Steele 1990). Whitebark pine is considered a specialist species, while limber pine is considered a generalist (Arno & Hoff 1989, Hankin & Bisbing 2021, Tomback et al. 2011). When co-occurring, whitebark pine is typically found at higher elevation moister sites (Tomback et al. 2011). Despite their distributional differences, whitebark and limber pine share similar needle and bark morphological features, making it difficult to differentiate them unless mature seed cones are visible (Alongi et al. 2019, Ulrich et al. 2023). They also have similar growth habits and dispersal methods for large, wingless seeds (Ulrich et al. 2023). The similarities of each species pose a challenge for visual identification when cones are not present. The status of each species is important to managers because there are many threats facing both species. It is also important to note that whitebark pine is listed as threatened under the U.S. Endangered Species Act.

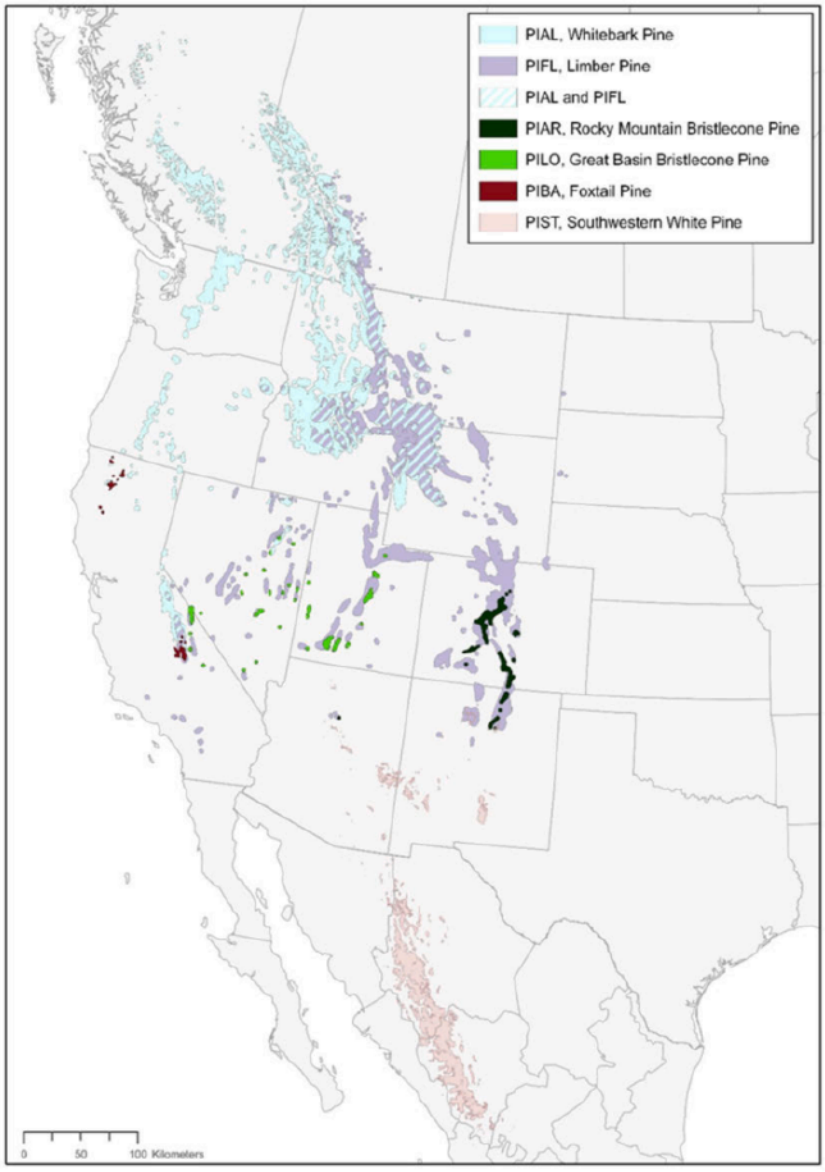

Figure 1. Distribution of high-elevation five-needle white pines in western North America. Map from Schoettle et al. (2022).

Threats to Five-Needle Pines

High-elevation five-needle pine forests face threats from mountain pine beetle (*Dendroctonus ponderosae* Hopkins.), white pine blister rust (*Cronartium ribicola* J.S Fisch.), climate change, and altered fire regimes (COSEWIC 2014, Windmuller-Campione & Long

2016). Fifty-one percent of all standing whitebark trees have died throughout their U.S. range, with half of this mortality occurring in the last two decades (Goeking & Izlar 2018). The high mortality rates have caused great concern among natural resource managers (Goeking & Windmuller-Campione 2021). Limber pine is also declining due to white pine blister rust, mountain pine beetle, and other stressors throughout its Canadian range (Shepard et al. 2025). Additionally, the historical exclusion of wildfires by humans has eliminated a crucial disturbance factor necessary for whitebark pine to establish and gain a competitive advantage over faster-growing, less fire-resistant species like subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (Keane 2001).

Status of Whitebark Pine and Limber Pine

In light of these threats, the U.S. Fish and Wildlife Service (USFWS) listed whitebark pine as a threatened species under the Endangered Species Act of 1973 (ESA). In Canada, the Committee on the Status of Endangered Wildlife designated the whitebark pine as endangered in 2012 under the Canadian Species at Risk Act. In Alberta, limber is Endangered under the Wildlife Act (COSEWIC 2014). Although limber pine does not share the same endangered status as whitebark pine in the U.S., identifying and monitoring each species remains important due to their similar ecology and shared habitats.

Endangered Species Act

Under the ESA, a species qualifies for listing if it meets the definition of an endangered species (in danger of extinction throughout all or a significant portion of its range) or a threatened species (likely to become endangered in the foreseeable future across all or a

significant portion of its range) (USFWS 2022). When the USFWS lists a species under the ESA, it must designate the species' critical habitat to the maximum extent that is prudent and determinable. In the case of whitebark pine, USFWS officials determined that it meets the definition of a threatened species and concluded that designating critical habitat is not advisable (USFWS 2022). The USFWS did not designate critical habitat because habitat loss does not threaten the species' survival; mortality from white pine blister rust is the primary threat (USFWS 2022). They also finalized a rule based on section 4(d) of the ESA that outlines essential conservation measures for the species. This rule prohibits importing or exporting, commercial delivery/shipping, selling, removing, or damaging whitebark pine under federal jurisdiction, as well as violating state laws regarding species protection or trespass (USFWS 2022). This approach continues to allow essential forest management, restoration, and research activities needed for whitebark pine conservation (USFWS 2022).

The Importance of Whitebark Pine to Grizzly Bears

The grizzly bear (*Ursus arctos horribilis* L.), classified as threatened in the lower 48 states, typically feeds on whitebark pine seeds during spring and fall (Kendall 1983). When available within their home range, grizzly bears in the Greater Yellowstone Ecosystem direct their feeding activities towards foods with high gross energy content that could be efficiently foraged, such as whitebark pine seeds (Gunther et al. 2014). Limber pine is not a fall food source for grizzly bears in the Greater Yellowstone area and U.S. Rocky Mountains (McCutchen 1996), and research indicates that limber pine does not serve as a food source for grizzly bears in these areas when whitebark pine is present (Kendall 1983, Mace & Jonkel 1986, Aune & Kasworm 1989). In 2007, the USFWS service established a distinct population segment (DPS) of the grizzly bear for

the GYE and surrounding area and removed the GYE DPS from the List of Threatened & Endangered Wildlife (72 FR 14866). However, three lawsuits challenged this decision. In the Montana case, the plaintiff claimed that the USFWS did not adequately consider how global warming and other factors would affect whitebark pine nuts (75 FR 14496). The Montana district court agreed with this claim and relisted the grizzly bear in the GYE (75 FR 14496). The reversal of the delisting of grizzly bears in the GYE indicates that the well-being of grizzly bears partially depends on the availability of whitebark pine seeds in certain areas. If this important fall food source is diminished, grizzly bears may need to travel farther in the spring and fall in search of food, increasing the likelihood of human interactions (Costello et al. 2014).

Additional Importance of Whitebark Pine

There are also additional consequences associated with the decline of whitebark pine. The decline of whitebark pine will increase the homogenization of subalpine landscapes, diminishing their ecological and structural diversity (Tomback et al. 2001). In the absence of whitebark pine, forests at high elevations will shrink, and the forest composition may likely shift to subalpine fir, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), or mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) (Tomback et al. 2001, Tomback & Achuff 2010, Schwandt et al. 2010). Although specialist species may currently outcompete generalist species in some areas, changes in climate and disturbance regimes will favor generalist species that are more tolerant to changing conditions (Hankin & Bisbing 2021). A reduction in whitebark pine will make forests more vulnerable to large, stand-replacing fires, insects and diseases, ultimately leading to declines in both landscape structural and compositional diversity (Tomback et al. 2001). Losses and declines of specialist tree species like whitebark pine would be consequential for high-

elevation forests that rely on a few species to fulfill critical ecosystem roles (Hankin & Bisbing 2021). These consequences highlight the need to accurately identify each species to facilitate restoration, which is especially important for federal natural resource managers.

Monitoring and Identification

Recognizing the importance of whitebark pine, cataloging current whitebark pine and limber pine stands is essential for identifying the best areas for conservation and restoration efforts. Moreover, accurately identifying trees that lack seed cones is essential for field sampling, particularly in creating species distribution models that help assess the sensitivity of whitebark pine to climate change (Alongi et al. 2019). Evaluating the status of whitebark pine and implementing conservation strategies depends on their inventory, monitoring, and mapping (USFWS 2022). Long-term monitoring plots are important for tracking and understanding gradual changes due to treatments, natural disturbances, and climate change effects on whitebark pine habitats (USFWS 2021). The listing of whitebark pine as an endangered species has increased the urgency for monitoring and conservation efforts. However, accurate monitoring is challenging because whitebark pine closely resembles limber pine, and their geographic ranges are highly overlapping. Although whitebark and limber pine are quite similar visually, distinguishing between them is crucial for several reasons. Monitoring both species depends on distinguishing them, as does developing accurate species distribution models and conservation strategies. Because they hold different conservation statuses in the U.S. and Canada, this influences how the managers in each country approach their management.

Several monitoring efforts have been concerned with white pine blister rust in the Greater Yellowstone Ecosystem (GYE) (Greater Yellowstone Whitebark Pine Monitoring Working

Group 2011, Shanahan et al. 2022). Studies have also recommended methods for surveying and monitoring whitebark pine for blister rust infection and damage (Tomback et al. 2005, Greater Yellowstone Whitebark Pine Monitoring Working Group 2011). Accurate monitoring cannot occur without the precise identification of both limber pine and whitebark pine, and there are several approaches to identification. A number of papers have used visual identification to distinguish the two species (Greater Yellowstone Whitebark Pine Monitoring Working Group 2011, Shanahan et al. 2022, Tomback et al. 2005), while others have used needle morphology (Resler & Tomback 2008) and elevation threshold (Alongi et al. 2019). Additionally, Alongi et al. (2019) have developed a genetic tool to distinguish whitebark pine and limber pine, which several other studies have also used (Hansen et al. 2012, Mantgen et al. 2023, Williams et al. 2024). However, no single source has compiled and reviewed all identification methods for distinguishing whitebark pine and limber pine. Thus, a review of the identification methods for whitebark pine and limber pine is necessary to assess the effectiveness of each approach and serve as a resource for researchers and managers.

Study Objectives

Therefore, my study's objectives are to critically review the current body of scientific literature on whitebark pine and limber pine identification to determine methods of identification, assess their effectiveness, and provide recommendations to future researchers and land managers. To critically assess this knowledge, I conducted a narrative literature review on current identification techniques identified in the literature. I hypothesize that reviewing the literature on whitebark pine and limber pine identification will help to enhance their

identification and improve forest management. My goal was to develop a resource for land managers and future researchers to increase identification accuracy.

Distribution

Whitebark pine's range extends from approximately 36º N latitude in the southern Sierra Nevada Range to around 55º N in the northern coastal ranges of Canada (Tomback & Sprague 2022). In the Rocky Mountains, it spans from about 42º N in the southern Greater Yellowstone to about 54º N latitude in Canada. Whitebark pine is a stress-tolerant species, and slow growth and long lifespans are typical of these species (McCune 1988). This stress tolerance, however, restricts its elevation and competitive abilities (Tomback et al. 2016). Whitebark pine is grouped into two relatively distinct distributions. The coastal distribution follows the British Columbia Coast Ranges, Cascade Range, and Sierra Nevada, while the Rocky Mountain Distribution extends from Alberta to Wyoming (Figure 1). Limber pine, like whitebark pine, has a broad distribution, but it occurs at lower elevations and inhabits more arid regions, which include the southern Sierra Nevada, southern California, the Southwest, the Great Basin, and southern Rocky Mountains (Figure 1) (Keane et al. 2010).

Habitat

Whitebark pine is most prevalent on dry exposures in moist mountain ranges, but in semiarid ranges, it prefers cool exposures and moist sites (Arno & Hoff 1989). These sites are characterized by short summers and a cool growing season with a mean annual precipitation of 61 to 183 cm (Arno & Hoff 1989). Whitebark pine abundance decreases as annual drought, precipitation, and humidity increase (Keane et al. 2010). Most whitebark pine stands grow on

weakly developed soils and are most abundant on warm aspects and ridgetops with direct exposure to sun and wind (Schoettle et al. 2022). Whitebark pine is less commonly found on north-facing slopes, preferred by sub-alpine fir, Engelmann spruce, mountain hemlock, or subalpine larch (*Larix lyallii* Parlatore) (Arno & Hoff 1989). Whitebark pine is a major and minor component of timberline communities, depending on its location within its range and the site characteristics (Arno & Hoff 1989). On warm, moist, and productive sites, whitebark pine is a poor competitor (Keane et al. 2010, Peet 1978, Tomback et al. 2016). Whitebark pine develops early in succession at these sites, but its overall basal area declines over time (Tomback & Achuff 2010, Keane et al. 2010). As forest succession progresses, the cover and abundance of whitebark pine typically decrease over time, and its cone production capacity diminishes under dense, subalpine fir canopies (Mattson & Reinhart 1990, Keane 2001). Whitebark pine becomes more dominant as sites become colder and dryer, with poorer soils (Tomback et al. 2016). Whitebark pine grows with other high mountain conifers, or pure whitebark pine stands, most common in relatively dry mountain ranges (Arno & Hoff 1989).

Limber pine may be the first species to establish after a stand-replacing disturbance but is outcompeted by shade-tolerant conifers like Engelmann spruce and subalpine fir over time (Keane et al. 2010). This competition results in limber pine only being a minor component of spruce-fir forests (Windmuller-Campione & Long 2016). Limber pine tolerates highly xeric environments like steep slopes, shallow rocky soils, and windy, arid sites (Keane et al. 2010, Peet 1978), where it can form climax communities (Windmuller-Campione & Long 2016). Unlike whitebark pine, limber pine can occupy harsh sites at all elevations (Tomback et al. 2010). At tree line, limber pine can also form Krummholz stands (Tomback et al. 2010).

Reproduction

Whitebark pine is monoecious, and the female strobili (also called seed cones) develop at the top of upper crown branches, and the male strobili (also called pollen cones) develop throughout the crown on the current year's growth (Arno & Hoff 1989). The ripe male strobili are a distinctive carmine color (Figure 2), and pollen is released when the tree flowers in July (Arno & Hoff 1989, Alongi et al. 2020). The seed cones are ripe by September of the following year. The crop size varies; large yields occasionally occur along with small crops and instances of crop failure between. Several factors restrict reproduction, including white pine blister rust, fire exclusion, bark beetles, animals, and fungal diseases (Fryer 2002). The large wingless seeds are found within a dense ovoid cone 4-8 cm long with tightly overlapping woody scales (Figure 2) (Alongi et al. 2020). An unusual feature of whitebark pine seed cones is that they remain closed (indehiscent) after ripening rather than releasing their seeds (Arno & Hoff 1989). Cones receive heavy predation from Clark's nutcracker (*Nucifraga columbiana* Wilson) and squirrels, who harvest the ripening cones in August, September, and October (Arno & Hoff 1989). Few to no cones remain after this predation.



Figure 2. Limber pine (left column) and whitebark pine (right column) seed cones (top row), and pollen cones (bottom row). Photo from Alongi et al. (2019).

Limber pine is also monoecious, with male and female strobili borne separately on the same tree (Steele 1990). Like whitebark pine and most other pines, male strobili are found in the lower crown, with female strobili forming on apical branches in the upper crown (Steele 1990). Male pollen cones are typically yellow to pale red (Figure 2) (Alongi et al. 2019, Alongi et al. 2020, Arno & Hoff 1989). Female cones can be green, red, or purple and mature to brown (Figure 2) (Steele 1990). Female cones are 7-15 cm long with woody scales, and cones often persist on the tree and beneath it (Alongi et al. 2020).

Because whitebark pine and limber pine seeds are wingless, their unique reproductive strategy depends on their association with Clark's nutcracker for seed dispersal (Steele 1990).

Each year, the nutcracker harvests and caches seeds from late summer to early fall (Tomback 1982). They can cache seeds up to 23 km from the seed source to caching areas (Steele 1990). Nutcrackers can carry as many as 125 seeds at a time and usually cache one to five seeds at a depth of 2 to 3 cm (Steele 1990). Whitebark and limber pine seeds are an important food source for Clark's nutcracker, although they do not recover all of their caches and seeds within (Arno & Hoff 1989). These unrecovered caches facilitate the regeneration and spread of whitebark and limber pine (Arno & Hoff 1989). Seedling regeneration from caches is the primary recruitment means for whitebark and limber pine (Feldman 1991). Other mammals, such as red squirrels (*Sciurus vulgaris* Erxleben), can also transport and cache seeds (Arno & Hoff 1989). In areas where whitebark and limber pine co-occur, nutcrackers will harvest whitebark pine seeds first, then move on to limber pine seeds (Tomback et al. 2010).

Growth Form

There is little commercial value for either of these species, but they are highly important to the ecology of high-mountain ecosystems of the Western U.S. (Tomback et al. 2011). Both whitebark pine and limber pine tend to fork, crook, and produce twisted gain, which limits their commercial value (Rockwell 1911). Depending on its growing site, whitebark pine can attain a small to moderately large size (12-18 m) after 250 or more years (Arno & Hoff 1989, Lackschewitz 1991). At higher elevations, where the species is most abundant, it frequently forms a shorter tree with a multi-stemmed trunk and an open, irregular crown of wide-spreading branches (Lackschewitz 1991). At the upper limits of its elevational range, whitebark pine forms as shrublike trees called Krummholz. Due to its location on the landscape, slow regeneration, and form, it is mostly unsuitable for timber production (Arno and Hoff 1989).

Limber pine is also slow-growing and long-lived and achieves small to medium size, with it rarely growing over 15 m in height (Johnson 2001, Steele 1990). It generally has an irregular form with a distinctive branching pattern (Steele 1990). Limber pine typically grows in a cluster of two to five individuals, with their stems growing near, touching, or fused (Feldman 1991). At high elevations, it can form as Krummholz stands (Johnson 2001). The similarities between whitebark pine and limber pine growth form make it difficult to distinguish the two species based on vegetative characteristics alone (Williams et al. 2024).

Special Uses

Whitebark pine seeds are highly nutritious and are a principal year-round food source for Clark's nutcrackers and red squirrels (Arno & Hoff 1989). Other species, such as seed-eating birds, small mammals, black bears (*Ursus americanus* Pallas), and grizzly bears, rely on whitebark pine and limber pine seeds as a food source (Arno & Hoff 1989, Kendall 1981, Steele 1990). Additional uses of whitebark pine include nesting sites for cavity-nesting birds in large, hollow, standing dead trees and roosting and feeding sites for blue grouse (*Dendragapus obscurus* Say). Lastly, whitebark and limber pine provide hiding and thermal cover for mammals where few trees grow (Arno & Hoff 1989, Steele 1990).

Species Threats

White Pine Blister Rust

Whitebark and limber pine are declining throughout their ranges due to many compounding threats, which include white pine blister rust, mountain pine beetle (*Dendroctonus ponderosae)*, climate change, wildland fire exclusion, and fir encroachment (Gibson et al. 2008).

Blister rust and mountain pine beetle are the principal reasons for population losses in whitebark pine (Tomback & Achuff 2010). White pine blister rust (WPBR) is a fungal disease of five-needle pines caused by the nonnative pathogen *Cronartium ribicola* (USFWS 2022). It has become established throughout most of the ranges of all five needle pines (Gibson et al. 2008). The fungus is causing a rise in the loss of whitebark and limber pine in the northern and central Rocky Mountains. White pine blister rust has a complex life cycle. It does not spread from tree to tree but alternates between primary hosts (five-needle pines) and alternate hosts (Hoff et al. 2001). Alternate hosts for blister rust in North America are often woody shrubs in the genus *Ribes* (gooseberries and currants). Infection of white pine by blister rust requires a cool, moisture-saturated environment (Schwandt et al. 2010). White pine blister rust attacks seedlings, saplings, and mature trees, damaging stems and cone-bearing branches, which restricts nutrient flow (USFWS 2022). The cutoff of nutrients quickly girdles young trees and cone-bearing branches on mature trees, which may kill branches or the entire tree (Burns et al. 2023). This pathogen contributes to the increased losses of whitebark and limber pine in the northern and central Rocky Mountains by its ability to decrease seed production (Gibson et al. 2008). The fungus has caused up to 90% mortality of whitebark pine stands across its range, especially in more mesic areas like the Cascade Mountains, northern Idaho, and western Montana (McDonald & Hoff 2001). Recent monitoring in the GYE revealed blister rust infection rates in whitebark pine ranging from 20% to 30% (Shanahan et al. 2016).

Mountain Pine Beetle

The native mountain pine beetle is another source of whitebark pine and limber pine mortality. All five-needle pines are suitable hosts for mountain pine beetle (Gibson et al. 2008).

Beetles attack host trees and enter the inner bark where they lay their eggs. The larvae then feed on the phloem of the tree. Beetles disproportionately kill larger trees because their larvae require a thick inner bark layer to inhabit them (Arno & Hoff 1989). Two years are usually needed to complete larvae development into an adult at higher elevations and more northern latitudes. The larvae are relatively cold hardy, but extremely cold winter temperatures can kill the developing brood (Gibson et al. 2008). Warmer than normal temperatures increase the susceptibility of whitebark pine and limber pine to beetles through drought stress and increased survival of beetles (Gibson et al. 2008). Recently, outbreaks have occurred during periods of warmer-than-average temperatures and drought (Gibson et al. 2008). Additionally, beetles have expanded their range into more northern latitudes and higher elevations, partly attributed to climate change (Gibson et al. 2008). Beetles may interact with WPBR to exacerbate the poor health of limber pine and whitebark pine (Burns et al. 2023).

Altered Fire Regimes

Another threat to both species is the reduction in the frequency and size of fires (Keane et al. 2010). Whitebark pine is well adapted to mixed severity and high severity fire effects, which have historically been important for the maintenance of whitebark pine ecosystems (USFWS 2022). Fire can expose bare mineral ground and reduce forest canopy cover, providing optimal growing sites for whitebark pine. Whitebark pine seedlings are extremely hardy and more tolerant of exposed sites and drought than the seedlings of other species, such as Englemann spruce and subalpine fir (Tomback et al. 2001). Fire exclusion policies in the U.S. and Canada have resulted in longer fire return intervals, contributing to the successional replacement of high-elevation five-needle white pines growing on productive sites (Keane et al. 2010). The

combination of white pine blister rust and other stressors hinders the regeneration of whitebark pine stands after disturbances like fire and mountain pine beetle activity outbreaks (USFWS 2022). Both species will likely face a substantial decline in reproductive adults in the future. This decline in reproductive trees will decrease the establishment of new seedlings, and new trees will not be able to replace old ones due to the species' lengthy generation time (USFWS 2022).

Climate Change

Last, climate change is a threat to both species that interacts with other stressors. Temperature and precipitation regimes are very likely to shift during the 21st century (Christensen et al. 2007), which could have negative effects on whitebark and limber pine. Climate change may lead to more frequent, longer-lasting, and more intense droughts and heat stress, which could alter the composition and structure of forests in many regions (Allen et al. 2010). Mountain pine beetles have historically been associated with whitebark pine (Brunelle et al. 2008), but the nature of outbreaks is changing, possibly due to climate change (Raffa et al. 2008). Large-scale beetle outbreaks have occurred in the U.S. Rocky Mountains and western Canada (Schwandt et al. 2010). Since WPBR requires a cool and moist environment, changes in the timing and duration of warmth and moisture could significantly influence the epidemiology of WPBR (Schwandt et al. 2010). Whitebark pine has a geographically limited habitat and delayed and low reproduction dependent on dispersal by Clark's nutcracker (Tomback & Achuff 2010). Widespread infection by WPBR, and population decline due to mountain pine beetle and climate change could exacerbate each of these factors (Tomback & Achuff 2010). Climate change has the potential to worsen WPBR and mountain pine beetle outbreaks as well as increase

wildfires above historic levels, reducing suitable high-elevation five-needle pine habitats (Keane et al. 2022).

Interaction of Threats

All these threats interact in different ways and contribute to the decline of whitebark pine populations (Tomback & Achuff 2010). Population decline can start with a mountain pine beetle outbreak or an infestation of blister rust, which kills cone-bearing branches, seedlings, or young trees (Tomback & Achuff 2010). Beetle outbreaks and infestations can be exacerbated by advanced succession or fire suppression (Tomback & Achuff 2010). Climatic changes can affect the reproduction and distribution of whitebark pine, mountain pine beetle, and WPBR (Tomback & Achuff 2010). The numerous threats to whitebark pine and limber pine highlight the need for proper identification and monitoring.

CHAPTER TWO

METHODS

I conducted a thorough search of the literature to find relevant studies for my literature review. My primary search engines included the MSU library database, Web of Science, and Google Scholar, which I used to locate peer-reviewed studies. My search strategy involved using specific search terms and research questions to identify relevant studies. I also found additional papers from the literature cited sections in other relevant peer-reviewed papers. The search terms I used included: 1) identifying whitebark and limber pine, 2) monitoring whitebark pine, 3) distinguishing between whitebark pine and limber pine, 4) ecology of whitebark pine and limber

pine, and 5) assessing threats to whitebark pine. The research questions I used to guide my search were: 1) Did the paper employ a specific method for identification? 2) Did it detail the identification protocol in the methods? 3) Did the paper assess the accuracy of the identification method? And 4) Did the paper compare one of the detailed identification approaches?

I excluded studies that did not address at least one of these questions. Papers included were those accessible through the MSU library and published in peer-reviewed journals. However, I made a few exceptions to the peer-review requirement for dissertations, papers from symposium proceedings, and U.S. Forest Service protocols. I based my inclusion or exclusion of papers on these selection criteria by reviewing titles and abstracts. After study identification and screening, I included 16 studies in my review (Figure 4). Due to the differences in topics and research methods, I provided a qualitative analysis of the literature. I summarized the selected papers using a narrative synthesis, extracting relevant information by asking: 1) What should I capture from the research? 2) What outcomes are important to address the topic? And 3) What is the quality of the research, including potential limitations?

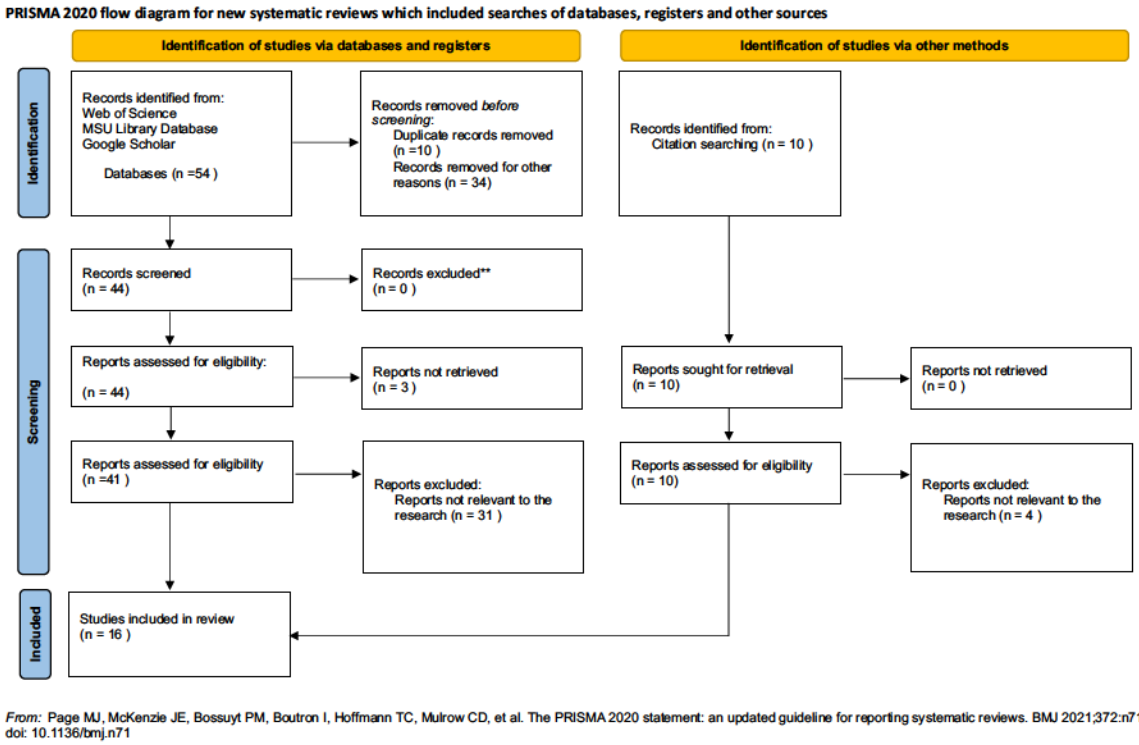

Figure 3. Preferred Reporting Items for Systematic reviews and Meta-Analyses flow diagram, which visually outlines my study selection process, from identifying potential studies to including those that met my inclusion criteria.

CHAPTER THREE

RESULTS

Studies Using Visual Identification

Whitebark and limber pine identification has been approached in several different ways. I found four studies addressing visual identification, and determined there were mixed results and different field protocols. Tomback et al. (2005) developed a series of methods for assessing the

occurrence and severity of blister rust in whitebark pine communities and for tracking blister rust's impacts over time. They formulated these techniques based on an analysis of 10 surveys on blister incidence across various regions where whitebark pine is found. Their study recommended that at least one field crew member should be able to identify forest tree species, particularly whitebark pine. Where whitebark and limber pine co-occur, one crew member must be able to identify the morphological differences between the seed and pollen cones of each species (Tomback et al. 2005). The methods of Tomback et al. (2005) have also been widely used by other studies (Shepherd et al. 2025, Burns et al. 2011, Greater Yellowstone Whitebark Pine Monitoring Working Group 2011).

Another study that has a detailed identification protocol is the Greater Yellowstone Whitebark Pine Monitoring Working Group (2011). This study was initiated with the help of the Greater Yellowstone Coordinating Committee (GYCC), the National Park Service (NPS) Inventory and Monitoring Division (Greater Yellowstone Network), and several other agencies to create a collaborative, long-term monitoring program to track and document the health status of whitebark pine across the GYE (Greater Yellowstone Whitebark Pine Monitoring Working Group 2011). This alliance helped form the Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG), which has representatives from the NPS, U.S. Forest Service, U.S. Geological Survey, Bureau of Land Management, and Montana State University. The Greater Yellowstone Network has led this multiagency whitebark pine monitoring program on NPS and U.S. Forest Service lands since 2004. Being a cross-jurisdictional program, the GYWPMWG developed a protocol between 2004 and 2007 for monitoring the health status of the whitebark pine population in the GYE. After peer review, the *Interagency Whitebark Pine*

Monitoring Protocol for the Greater Yellowstone Ecosystem was approved in 2007 and updated in 2011 (Greater Yellowstone Whitebark Pine Monitoring Working Group 2011). Their methods are largely drawn from the efforts of the Whitebark Pine Ecosystem Foundation (Tomback et al. 2005).

The objectives of the GYE interagency whitebark pine monitoring program are to answer two questions that will help land managers understand and take action to protect the health of whitebark pine in the GYE. These questions are: 1) Is white pine blister rust increasing in the GYE? and 2) Is the resulting mortality of whitebark pine sufficient to warrant consideration of management intervention, such as active protection and/or restoration? The target population is all whitebark pine in the GYE, and the sampling units are whitebark pine-dominated stands of approximately 2.5 ha or larger. The GYWPMWG uses visual identification of whitebark pine and limber pine, and they have implemented specific identification protocols to help improve their accuracy. First, field crews conduct monitoring in the summer, between June and September, and they also have specific personnel requirements and training. The protocol also includes directing crew members to use seed cones if available, as they are the most reliable way to distinguish between whitebark and limber pine. If absent, pollen cones can aid in identification. Additionally, they select an alternate plot if the crew cannot identify each tree with 100% certainty. The monitoring protocol established by the GYWPMGW has also influenced the study design of several other peer-reviewed papers (Cleaver et al. 2015, Shanahan et al. 2022).

Shanahan et al. (2022) evaluated and monitored the long-term health trajectory of five-needle pines in 2013, 2014, 2016, and 2017 on Wyoming Bureau of Land Management (BLM) lands within the GYE. They followed the Interagency Whitebark Pine Monitoring Protocol

methods for the GYE (Greater Yellowstone Whitebark Pine Monitoring Working Group 2011) to assess the health of five-needle pine on lands managed by the Wyoming BLM. Their study does not specify the extent to which they adhered to this protocol, but their results suggest they did not follow the identification protocol from GYWPMWG, which requires using pinecones when available and relocating the plot if they cannot confidently identify each tree. Instead of relocating plots, Shanahan et al. (2022) recorded trees they could not identify as unknown five-needle pine. This study demonstrates the consequences of not using a specific identification protocol, as they recorded 83% of trees as unknown during the 2013-2014 monitoring period. Consequently, this limitation forces researchers to make assumptions about five-needle pines rather than distinguishing between limber pine and whitebark pine specifically.

Alongi et al. (2019) developed an economic identification tool to distinguish non-cone-bearing limber pine and whitebark pine. They aimed to identify which chloroplast loci that would best distinguish whitebark pine and limber pine. They collected chloroplast DNA barcode sequences from limber and whitebark pine trees, which they identified by their attached seed cones. Additionally, they used the color of pollen cones as a secondary visual identification marker. Their analyses revealed multiple DNA-sequence differences between limber and whitebark pine in the matK and the psbA-trnH spacer. After completing genetic testing, they concluded that their initial visual identification of limber and whitebark pine agreed with the genetic testing results.

Studies Using an Elevation Threshold

Alongi et al. (2019) genetically distinguished whitebark pine and limber pine needles as described above. Before genetic testing, researchers visually identified five-needle pines using

seed and pollen cones. If five-needle pines lacked seed or pollen cones, they assumed trees below 2,440 m were limber pines, while those above this elevation were whitebark pines. Based on current species distribution models, whitebark pine rarely establishes in the warmer, drier environments of the lower tree line, where limber pine is abundant in the GYE (Chang et al. 2014). However, they found this rule of thumb problematic because limber pines often exceeded the elevation threshold while whitebark pine occasionally fell below the threshold.

Studies That Contradict the Elevation Threshold Method

In 2014, Chang et al. studied the patterns and variability of projected bioclimatic habitat for whitebark pine in the Greater Yellowstone area. They presented a bioclimate niche model for whitebark pine based on historical climate observations and field sampling of whitebark pine presence and absence. Their findings reveal that persistent whitebark pine patches could shift to cooler sites at higher elevations. The authors also discuss that physiologically, no upper elevation limit appears to restrict whitebark pine in the Greater Yellowstone Area. They suggest that competitive exclusion by late seral species, which include subalpine fir, lodgepole pine (*Pinus contorta* Dougl.), and Engelmann spruce, likely influences the lower tree line limits for whitebark pine. Paleoecological pollen records indicate competitor migration during the Early Holocene (9000–5000 yr B.P.), a period with warmer and drier climate conditions (Whitlock et al. 2003, Whitlock 1993). Extended growing seasons will likely facilitate the invasion of competitors and shift whitebark communities farther upslope.

Buermeyer et al. (2016) conducted a case study on whitebark pine in the Greater Yellowstone Ecosystem. They researched how climate change could affect whitebark pine at the landscape level and examined its implications for conservation efforts. They suggest that drier

conditions may benefit whitebark pine due to its superior drought tolerance, enhancing its competitive edge over rivals like subalpine fir. Their conclusion suggests that in more open sites, where little competition from other species exists, whitebark pine may establish at elevations ranging from 1,950 m to 2,103 m.

Ulrich et al. (2023) examined the functional traits that underlie specialist-generalist strategies in whitebark pine and limber pine. The researchers compared the physiological and morphological traits of 5-year-old, greenhouse-grown whitebark pine and limber pine. Their findings indicate that limber pine's resource use traits, both acquisitive and conservative, support its generalist strategy and enable it to thrive at a broader range of elevations compared to whitebark pine. Limber pine displayed superior resource acquisition traits, such as high light tolerance, enhanced biomass dedicated to photosynthetic tissue, and elevated carbon and water uptake. Moreover, limber pine possessed more conservative resource utilization characteristics, including improved resistance to physical stress (shorter stature, larger stem and branch diameters, and higher diameter-to-length ratios of branches and stems), as well as drought tolerance and avoidance, compared to whitebark pine.

Studies Using Needle Morphology

In their study of blister rust prevalence in Krummholz whitebark pine in the northern Rocky Mountains of Montana, Resler and Tomback (2008) differentiated whitebark and limber pine using needle morphology. Although they did not specify an identification protocol, they noted that they employed the dichotomous key from the Flora of North America North of Mexico (Kral 1993). The key describes limber pine needles as 1-1.5 mm long, pliant, dark green, with stomatal bands that appear less conspicuous on the abaxial surface than on the adaxial

surface. The stomatal bands on the adaxial surface are pale and strong with finely serrulate margins. The needles of whitebark pine are 1-1.5 mm long, deep yellow-green, with a lesser intensity on the abaxial surface. Stomata noticeably whiten the adaxial surface of the needles. One can distinguish whitebark pine from other five-needle pine species by examining the stomata on the abaxial and adaxial sides of the needles.

Studies Using Genetic Testing

Alongi et al. (2019) successfully identified an economically feasible method to distinguish whitebark pine from limber pine. They identified chloroplast loci that vary in DNA sequences between limber pine, whitebark pine, and their close relatives. The selected regions included the matK coding area, the psbA-trnH spacer, the trnG intron, the trnT-trnF region, and the trnD-trnT region with the chloroplast matK and psbA-trnH regions as the best genetic barcodes for differentiating limber pine from whitebark pine (Figure 3) (Alongi et al. 2019). They found that forest ecologists, paleoecologists, and managers interested in genetically differentiating the two types of pine can do so with limited research funding and basic technical skills. Their estimated cost for analyzing 200 needle samples, the minimum order quantity of items needed for analysis, was $1,184.69 (Alongi et al. 2019). This cost included DNA extraction and PCR kit, PCR primers, restriction endonuclease analysis, and 40 hours of undergraduate student labor ($15/h) (Alongi et al. 2019). Several other studies have used this approach (Hansen et al. 2012, Mantgem et al. 2023, Williams et al. 2024).

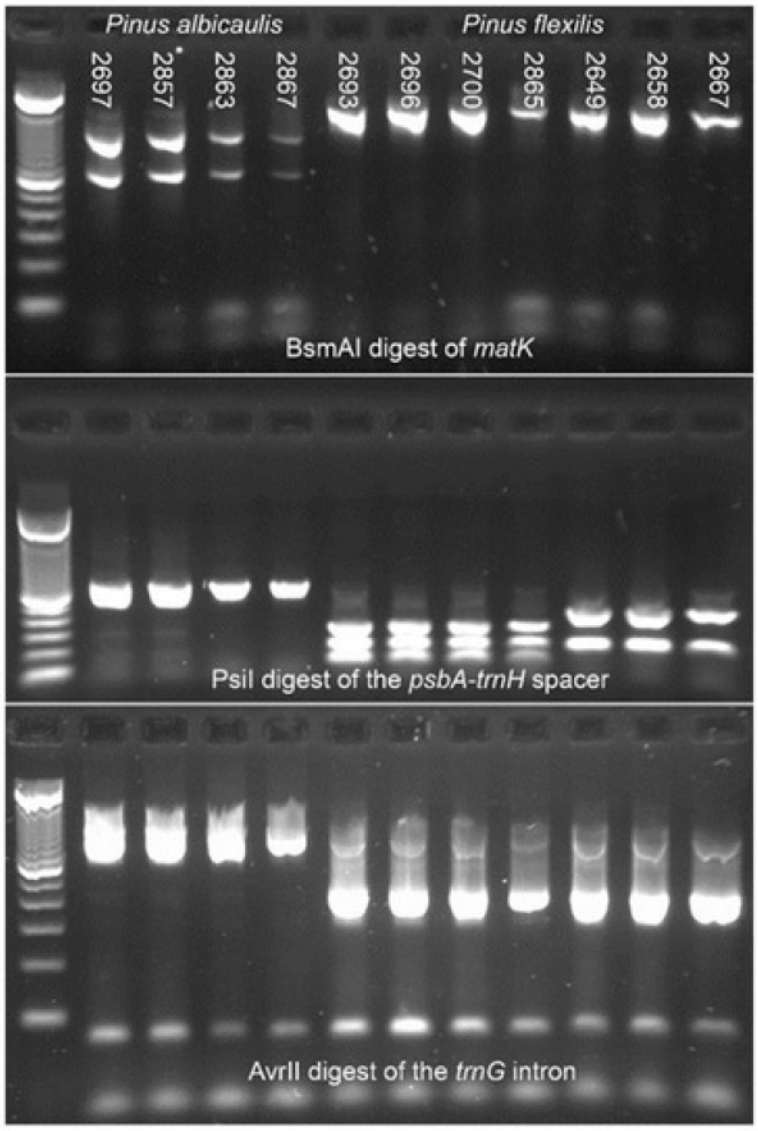

Figure 4. Restriction enzyme digests of whitebark pine (2697 to 2867) and limber pine (2693 to 2667) PCR amplicons. Photo from Alongi et al. (2019).

Williams et al. (2024) investigated how accurately U.S. Forest Service Forest Inventory and Analysis (FIA) field crews identified whitebark pine and limber pine. The methods used by the FIA crews for identification are unknown. Researchers compared visual identifications of FIA crews to genetically identified needle samples using the DNA sequence method developed

by Alongi et al. (2019). Field crews accurately identified 100% of samples from outside regions where the species' ranges overlap. In regions of range overlap, 83% of identifications were correct. The identification accuracy among trees surveyed (large trees, saplings, and seedlings) was 89%, 88%, and 78%, respectively (Williams et al. 2024). Breaking down accuracy by species, field-identified samples were correct 60% of the time for limber pine and over 99% for whitebark pine. Virtually all individuals identified as whitebark pine were genetically confirmed to be whitebark pine, although nearly 40% of individuals identified as limber pine were whitebark pine. The identification accuracy for seedlings was lower because more than half of the seedlings identified as limber pine were whitebark pine, and the field crew correctly identified only 73% of whitebark pine seedlings.

Factors affecting identification accuracy included crew experience, the presence of large limber or whitebark pines (≥ 32.3-cm diameter) in the plot, elevation, the Julian day of sample collection, and habitat type. Researchers categorized the likelihood of misidentification into three types of variables: observer-related, tree-related, and site-level variables.

Analysis of observer-related variables indicated that crew leader experience was an important predictor of identification accuracy. Researchers struggled to test whether accuracy increased as individual crew leaders gained experience due to low sample sizes from the crew leaders. Despite this low sample size, crew leader experience and cumulative accuracy were highly correlated ($p < 0.001$, Spearman rank correlation).

Researchers also assessed how the presence of cones influenced identification accuracy using two tree-related variables: tree size class and Julian Day, which are associated with the likelihood of cone presence. They accomplished this by comparing accuracy rates among size

classes and tested for relationships between accuracy and Julian Day. Their results did not find a correlation between size class and accuracy. However, they found that Julian Day was an important predictor of identification accuracy in their model. Their model revealed that the likelihood of correct identification was low before mid-July and peaked from mid-August through late September, after which it declined.

Finally, large trees of either species recorded by field crews were the most important site-level predictors of identification accuracy. Identification accuracy for samples was >99% for whitebark pines compared to limber pine (66%). Overall, their findings suggest that whitebark pine has likely been under-reported, while limber pine has been over-reported in areas where their ranges overlap.

Mantgem et al. (2023) studied growth, drought response, and climate-associated genomic structure in whitebark pine in the Sierra Nevada of California. They analyzed growth patterns using population genomic diversity and structure from a sample of 327 trees. The researchers took several precautions to prevent misidentification of whitebark pine. First, they focused sampling on large trees that exhibited visual identification characteristics, such as male and female cones, and relied on experienced field crews. Second, they tested a subset of needle samples using genetic analysis (Alongi et al. 2019). Genetic analysis confirmed that researchers accurately identified all samples as whitebark pine.

Hansen et al. (2012) examined how climate warming affects the sensitivity of whitebark pine by considering the climate tolerance of juveniles. They investigated whether juvenile-sized whitebark pines fared better in warmer and drier areas compared to larger trees. This research was based on the idea that competitive exclusion may take several years to decades to influence

the distribution of regenerating whitebark pine. They used genetic testing (Alongi et al. 2019) to confirm visual identifications of all non-cone-bearing five-needle pines. Researchers found that trees with smaller diameters did not outnumber those at lower elevations. These results suggest that competitive exclusion may not be the primary factor limiting whitebark pine distribution at lower elevations. Additionally, smaller trees displayed slightly less tolerance to warm, dry conditions than larger-diameter trees. The climate tolerance displayed by juvenile trees indicated that the whitebark pine regeneration zone has shifted to higher elevations in recent years, correlating with warming trends observed in the GYE.

CHAPTER FOUR

DISCUSSION

Results from my literature review suggest that visual identification using seed and pollen cones can be an effective approach to identification. Genetic testing is also an effective method, and more studies continue to adopt this approach. Furthermore, an explicit identification protocol for field crews could also help improve identification accuracy. Additionally, my results suggest that using an elevation threshold is not well-supported by research. The literature on using needle morphology for identification is also lacking.

Visual Identification

The most common method to identify whitebark and limber pine is visual identification using seed and pollen cones. When pollen or seed cones are present, their differences in color, morphology, and persistence provide a reliable way to identify each species (Williams et al.

2024). However, seed and pollen cones are not always present. These slow-growing species can take 20-40 years to produce cones and 60-80 years to produce large cone crops (Williams et al. 2024). Therefore, cones may not be visible or present in younger stands. Cones may be absent due to branch dieback caused by white pine blister rust (Cleaver et al. 2015, Tomback & Achuff 2010) and seed predation (Lorenz & Shoal 2008). Additionally, seed crop production in whitebark pine is erratic, with large seed crops produced at irregular intervals with smaller crops or crop failures in between (Arno & Hoff 1989)

The monitoring protocols detailed in the Greater Yellowstone Whitebark Pine Monitoring Working Group (2011) and Tomback et al. (2005) can be beneficial in guiding other researchers' methods; however, there will always be some errors when it comes to visual identification. These errors may be due to the cones of limber pine persisting longer than whitebark pinecones. Whitebark pine seed cones typically mature from mid-August to mid-September (Arno & Hoff 1989). After maturity, Clark's nutcrackers and other agents quickly remove them, often leaving little to no traces of the cones behind. When crews find both pine species in the same area, they are more likely to observe signs of limber pine, which may lead them to mistakenly identify other five-needle pines in the area as limber pine (Williams et al. 2024). Moreover, greater accuracy in identification aligns with the period when mature pollen and seed cones of whitebark pine are most likely present (Williams et al. 2024).

Forest Service Inventory and Analysis data are widely used datasets, but genetic analysis of whitebark and limber pine samples indicates that misidentification rates exceed the data quality standards set by the U.S. Forest Service FIA protocol (Williams et al. 2024). The U.S Forest Service FIA protocol aims to correctly identify species at least 95% of the time for large

trees and saplings and at least 85% for seedlings (USDA 2010). The FIA misidentification rates reported by Williams et al. (2024) did not meet these standards. While these rates stem from visual measurements taken by FIA field crews, they probably also reflect the error rates associated with the visual identification of whitebark, and limber pines conducted by other trained monitoring teams.

Elevation Threshold

Using an elevation threshold to identify non-cone-bearing five-needle pines is easy to apply in the field, but it may not always hold true. Alongi et al. (2019) found that limber pine often occurred above 2,440 m. These results suggest that limber pine has a higher elevational range than 2,440 m. Additionally, climate change is predicted to alter the geographic distribution of plant species, including where plants can establish from seed (Moyes et al. 2013). To add to this, Moyes et al. (2013) found that seasonal moisture stress and elevated soil surface temperatures hinder the establishment of limber pine seeds across a wide elevation range and ongoing climate change is predicted to intensify this effect. The limit of seedling establishment could affect the elevational range of limber pine, and they may expand into higher elevations. Furthermore, Ulrich et al. (2023) found that limber pine's resource uses traits support its generalist strategy and enable it to thrive at a broader range of elevations than whitebark pine. These results indicate that limber pine can grow at elevations above 2,440 m.

In addition to limber pine being found above 2,440 m, whitebark pine may be found below 2,440 m. Other studies suggest the elevational cutoff is due to whitebark pine being competitively excluded by different species at lower elevations (Buermeyer et al. 2016, Chang et

al. 2014). Open sites also favor the development of whitebark pine at lower elevations, from 1,950 to 2,103 m, such as in northeastern Nevada (Critchfield & Allenbaugh 1969). Drier conditions benefit certain habitats for whitebark pine within the GYE by enhancing its ability to compete against species like subalpine fir, owing to its greater drought resilience (Buermeyer et al. 2016). This drought resilience may indicate that in more open areas, where competition from other species is minimal, whitebark pine could establish at elevations between 1,950 m and 2,103 m. Therefore, the elevation threshold is unreliable for identifying non-cone-bearing five-needle pines.

Needle Morphology

Another field identification method is needle morphology. However, this was not a well-researched method, and only one study used this technique (Resler and Tomback 2008). Researchers did not detail methods for this identification technique besides referencing the dichotomous key they used, so replicating this method in another study would be difficult. Additionally, another study suggested that this method requires specialized equipment and knowledge (Williams et al. 2024). Lastly, there is no known research on the effectiveness of this technique, so it is difficult to assess its efficacy or recommend its use in future research.

Genetic Testing

Genetic testing is a relatively new (2019) technique to identify whitebark and limber pine (Alongi et al. 2019), with only three additional studies having used it. Research so far indicates that it is effective and easy to apply. Additionally, the studies that have used genetic testing also

help confirm visual identification since the initial identification is usually visual. Moreover, genetic testing may reveal that whitebark pine is more prevalent at elevations below 2,440 m than previously believed (Alongi et al. 2020). These findings could guide future research and lead to studies that more accurately model species distribution (Alongi et al. 2020). Improved accuracy could help estimate how climate change will influence species geographic ranges and climatic tolerances, which is vital for these ecologically significant pine species (Alongi et al. 2019, 2020).

Recommended Identification Approaches

Based on the findings of this literature review, future researchers should consider these approaches to species identification accuracy in the field. First, they should establish an explicit visual identification protocol for the field crew. This protocol must include training requirements for the crew and guidelines for identifying trees using seed and pollen cones. Field sampling should also be conducted when trees are most likely to have seed and pollen cones (mid-July to late September), as identification accuracy was correlated to Julian Day (Williams et al. 2024). Additionally, they should adjust the plot location if the crew cannot identify cone-bearing trees with 100% confidence. All non-cone-bearing trees should undergo genetic testing in areas of range overlap. Genetic testing is quite affordable, with current laboratory expenses averaging around $20 per sample, excluding additional costs and time for collection, cataloging, and shipping (Williams et al. 2024). This genetic testing tool will enhance data quality for field-based monitoring programs and improve the accuracy of models and maps related to seedling niches and climate change projections. These elements all depend on field-based observations for

calibration and validation. Genetic testing will also be beneficial for federal land managers to inform their decision-making for management and restoration activities.

Implications for Managers

Restoring whitebark pine is essential for high-elevation ecosystems, and many species rely on it for survival (Tomback et al. 2001). Increased restoration activities are necessary to protect and improve existing whitebark pine populations and offer suitable chances for regeneration (Schwandt, 2006). However, a significant challenge to restoration is the cost and determining who will be responsible for it (Tomback et al. 2001). Whitebark pine, a non-commercial tree species, currently faces limited federal funding, which is likely to continue (USFWS 2021). The overall expense of restoration can vary based on the number of proposed projects and the logistics involved. Restoration could be very costly, considering the vast areas affected by white pine blister rust (Tomback et al. 2001). Because of budget priorities, limited access, policy constraints, and prior losses, restoration of every population is impossible (Tomback & Achuff 2010). Critical information for restoration planning is obtained from surveying and monitoring (Tomback et al. 2005). The constraints on restoration reinforce the importance of accurate identification to understand where restoration is needed most and maximize the use of limited funds (USFWS 2021).

Numerous management actions support the sustainability and restoration of white pines and control white pine blister rust (Schwandt et al. 2010). These include 1) conserving the genetic resistance to white pine blister rust, 2) reducing the risk of adverse impact to stands already infected, 3) restoring and maintaining white pines where blister rust is causing impacts, and 4)

assessing and monitoring the health, and management of white pine (Schwandt et al. 2010). Distinguishing whitebark pine and limber pine is important for these management actions to be the most effective.

Conclusions

Researchers can reliably identify cone-bearing whitebark pine and limber pine in the field. Some studies that employ visual identification implement explicit identification protocols that can improve accuracy. However, seed and pollen cones are not always present, so this method cannot always be relied upon. Some degree of error will always remain because of the nature of visual identification. Another method, using an elevational threshold to identify non-cone-bearing trees, is unreliable because studies show that both limber pine and whitebark pine can grow above or below this threshold (Alongi et al. 2019, Buermeyer et al. 2016, Chang et al. 2014, Critchfield & Allenbaugh 1969, Moyes et al. 2013, Ulrich et al. 2023). Similarly, due to its limited research use, needle morphology does not provide a reliable identification method. In contrast, genetic testing proves effective for identifying non-cone-bearing five-needle pines where whitebark pine and limber pine overlap in their ranges. Combining visual identification using seed and pollen cones with genetic testing can enhance identification accuracy. Future researchers and land planners should use this combination of identification methods. These methods will enhance the data accuracy of research, which is crucial for land managers who must determine where to implement restoration on a limited budget.

REFERENCES CITED

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, et al. 2010. "A Global Overview of Drought and Heat-Induced Tree Mortality Reveals Emerging Climate Change Risks for Forests." Forest Ecology and Management, Adaptation of Forests and Forest Management to Changing Climate, 259 (4): 660–84. https://doi.org/10.1016/j.foreco.2009.09.001.

Alongi, F., A.J. Hansen, D. Laufenberg, R.E. Keane, K. Legg, and M. Lavin. 2019. "An Economical Approach to Distinguish Genetically Needles of Limber from Whitebark Pine." Forests 10 (12): 1060. https://doi.org/10.3390/f10121060.

Alongi, F., A. J. Hansen, D. Laufenberg, R.E. Keane, K. Legg, and M. Lavin. 2020. "Using Genetics to Distinguish Limber from Whitebark Pine."

Arno, S. F., and R. J. Hoff. 1989. "Silvics of Whitebark Pine (Pinus Albicaulis)." Gen. Tech. Rep. INT-GTR-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p. 253. https://doi.org/10.2737/INT-GTR-253.

Aune, K, and W. Kasworm. 1989. Final report East Front grizzly studies. Montana Department of Fish, Wildlife and Parks, Helena. 332 pp. https://doi.org/10.5962/bhl.title.109744

Binder, S., R. G. Haight, S. Polasky, T. Warziniack, M. H. Mockrin, R.L. Deal, and G. Arthaud. 2017. "Assessment and Valuation of Forest Ecosystem Services: State of the Science Review." Gen. Tech. Rep. NRS-170. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 47 p. 170:1–47. https://doi.org/10.2737/NRS-GTR-170.

Brunelle, A., G. E Rehfeldt, B. Bentz, A.S Munson. 2008: Holocene records of Dendroctonus bark beetles in high elevation pine forests of Idaho and Montana, USA. For. Ecol. Manage. 255, 836–846. https://doi.org/10.1016/j.foreco.2007.10.008

Buermeyer, K., D.P. Reinhart, K. Legg, V. Kelly. Case study: Whitebark Pine in GYE. In *Climate Change in Wildlands: Pioneering Approaches to Science and Management in the Rocky Mountains and Appalachians*; Hansen, A.J., Theobald, D.M., Oliff, T., Monihan, W., Eds.; Island Press: Washington, DC, USA, 2016; pp. 304–326.

Burns, K., Blodgett, J., Jackson, M., Howell, B., Jacobi, W., Schoettle, A., et al. (2011). "Monitoring limber pine health in the Rocky Mountains and North Dakota," in *Proceedings of the future of high-elevation, five-needle white pines in Western North America: High five symposium*, *proceedings RMRS-P-63*, eds R. E. Keane, D. F. Tomback, M. P. Murray, and C. M. Smith (Fort Collins, CO: U.S. Department of Agriculture Forest Service), 47–50.

Burns, K. S., W. T. Tinkham, K. A. Leddy, A.W. Schoettle, W.R. Jacobi, and J. E. Stewart. 2023. "Interactions between White Pine Blister Rust, Bark Beetles, and Climate over Time Indicate Vulnerabilities to Limber Pine Health." Frontiers in Forests and Global Change 6 (April):1149456. https://doi.org/10.3389/ffgc.2023.1149456.

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

Christensen J., Hewitson B., Busuioc A., (2007). Regional climate projections. In Climate Change 2007: the physical science basis. Contribution of Working group 1 to the fourth assessment report of the Intergovernmental Panel on Climate Change. University Press, Cambridge. IPCC 2007.

Cleaver, C.M., W. R. Jacobi, K.S. Burns, and R. E. Means. 2015. "Limber Pine in the Central and Southern Rocky Mountains: Stand Conditions and Interactions with Blister Rust, Mistletoe, and Bark Beetles." Forest Ecology and Management 358 (December):139–53. https://doi.org/10.1016/j.foreco.2015.09.010.

COSEWIC. 2014. COSEWIC assesesment and status report on the Limber Pine Pinus flexilis in Canada. Assessment and Status report, Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON. Available from https://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Limber%20Pine_2014_e.pdf

Costello, C., F. Manen, M. Haroldson, M. Ebinger, S. Cain, K. Gunther, D. Bjornlie. (2014). Influence of whitebark pine decline on fall habitat use and movements of grizzly bears in the Greater Yellowstone Ecosystem. Ecology and Evolution. 4. 10.1002/ece3.1082.

Cogbill, C. & P. White. (1991). The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian Mountain chain. Vegetatio. 94. 153-175. 10.1007/BF00032629.

Critchfield, W.B., and G.L. Allenbaugh. "The Distribution of Pinaceae in and Near Northern Nevada." *Madroño* 20, no. 1 (1969): 12–26. http://www.jstor.org/stable/41423333.

Daubenmire, R.F. (1954). Alpine Timberlines in the Americas and Their Interpretation. *Butler University Botanical Studies, 11,* 14.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B. and Webster, J.R. (2005), Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment, 3: 479-486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2

Endangered and Threatened Wildlife and Plants; Reinstatement of Protections for the Grizzly Bear in the Greater Yellowstone Ecosystem in Compliance With Court Order." 2010. Federal Register. March 26, 2010. https://www.federalregister.gov/documents/2010/03/26/2010-6802/endangered-and-threatened-wildlife-and-plants-reinstatement-of-protections-for-the-grizzly-bear-in.

"Endangered and Threatened Wildlife and Plants; Removing the Greater Yellowstone Ecosystem Population of Grizzly Bears From the Federal List of Endangered and Threatened Wildlife." 2017. Federal Register. June 30, 2017. https://www.federalregister.gov/documents/2017/06/30/2017-13160/endangered-and-threatened-wildlife-and-plants-removing-the-greater-yellowstone-ecosystem-population.

Feldman, R. 1991. Growth form and reproductive output inlimber pine: the cost of mutualism. Thesis. University ofColorado, Denver, Colorado, USA.

Fryer, J. L. 2002. Pinus albicaulis. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available:

https://www.fs.usda.gov/database/feis/plants/tree/pinalb/all.html [2025, March 29 2024, December 20].

Gibson, K., Skov, K., Kegley, S., Jorgensen, C., Smith, S., Witcosky, J., 2008. Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges. US Department of Agriculture Forest Service, Northern Region, Missoula, Montana. R1-08-020, 1-32.

Goeking, S.A., and D.K. Izlar. 2018. "Pinus Albicaulis Engelm. (Whitebark Pine) in Mixed-Species Stands throughout Its US Range: Broad-Scale Indicators of Extent and Recent Decline." Forests 9 (3): 131. https://doi.org/10.3390/f9030131.

Goeking, S.A., and M. A. Windmuller-Campione. 2021. "Comparative Species Assessments of Five-Needle Pines throughout the Western United States." Forest Ecology and Management 496 (September):119438. https://doi.org/10.1016/j.foreco.2021.119438.

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

Gunther, K. A., Shoemaker, R. R., Frey, K. L., Haroldson, M. A., Cain, S. L., van Manen, F. T., & Fortin, J. K. (2014). Dietary breadth of grizzly bears in the Greater Yellowstone Ecosystem. *Ursus*, *25*(1), 61–73. http://www.jstor.org/stable/24643797

Hankin, L.E. and Bisbing, S.M. (2021), Let it snow? Spring snowpack and microsite characterize the regeneration niche of high-elevation pines. J Biogeogr, 48: 2068-2084. https://doi.org/10.1111/jbi.14136

Hansen, A.J.; East, A.; Keane, R.E.; Lavin, M.; Legg, K.; Holden, Z.; Toney, C.; Alongi, F. 2021. Is whitebark pine less sensitive to climate warming when climate tolerances of juveniles are considered? Forest Ecology and Management. 493: 19221.

Hooper, D.U., F.S., III, Chapin, J.J Ewel, A. Hector, P. Inchausti, S. Lavorel, J.H Lawton, D.M Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A.J Symstad, J. Vandermeer, D.A Wardle. (2005), Effects of Biodiversity on Ecosystem Functioning: A Consus of Current Knowledge. Ecological Monographs, 75: 3-35. https://doi.org/10.1890/04-0922

Hoff, R. J., D. E. Ferguson, G. I. McDonald, R.E. Keane. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust [Chapter 17]. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: Ecology and restoration. Washington, D.C.: Island Press. p. 346-366.

Jarvis, P. G., Grace, J., Hutchings, N., Monteith, J. L., Shuttleworth, W. J., Fowler, D., Corlett, J., & Thomas, J. (1989). Tree Lines [and Discussion]. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *324*(1223), 233–245. http://www.jstor.org/stable/2990181.

Johnson, K.A. 2001. Pinus flexilis. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: https://www.fs.usda.gov/database/feis/plants/tree/pinfle/all.html [2025, March 7].

Keane, R. E. 2001. Successional dynamics: Modeling an anthropogenic threat. In Whitebark Pine Communities, Ecology and Restoration, edited by D. F. Tomback, S.F. Arno, and R. E. Keane, 159–92. Washington, DC: Island Press.

Keane, R.E., K. C. Ryan, T. T. Veblen, C. D. Allen, J. Logan, and B. Hawkes. 2002. "Cascading Effects of Fire Exclusion in the Rocky Mountain Ecosystems: A Literature Review." General Technical Report. RMRS-GTR-91. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 24 p. https://doi.org/10.2737/RMRS-GTR-91.

Keane, R.E., and R. A. Parsons. 2010. "Restoring Whitebark Pine Forests of the Northern Rocky Mountains, USA." Ecological Restoration. 28(1): 56-70., 56–70. https://doi.org/10.3368/er.28.1.56.

Keane, R.E., Tomback, D.F., Murray, M.P., Smith, C.M., 2011. The future of high-elevation, five-needle white pines in Western North America. In: Proceedings of the High Five Symposium. US Department of Agriculture, Forest Service.

Keane, R. E., A.W. Schoettle, and D. F. Tomback. 2022. "Effective Actions for Managing Resilient High Elevation Five-Needle White Pine Forests in Western North America at Multiple Scales under Changing Climates." Forest Ecology and Management 505 (February):119939. https://doi.org/10.1016/j.foreco.2021.119939.

Kendall, K. C. (1983). Use of Pine Nuts by Grizzly and Black Bears in the Yellowstone Area. *Bears: Their Biology and Management*, *5*, 166–173. https://doi.org/10.2307/3872534

Körner, C. (1998). A Re-Assessment of High Elevation Treeline Positions and Their Explanation. Oecologia. 115. 445-459. 10.1007/s004420050540.

Kral, R., 1993: Pinus. In Flora of North America EditorialCommittee, 1993, Flora of North America North of Mexico, Vol.2. New York and Oxford: Oxford University Press

Kremen, C. 2005. "Managing Ecosystem Services: What Do We Need to Know about Their Ecology?" Ecology Letters 8 (5): 468–79. https://doi.org/10.1111/j.1461-0248.2005.00751.x.

Krieger, D. (2001). Economic Value of Forest Ecosystem Services: A Review. The Wilderness Society. 1615.

Lackschewitz, K. 1991. Vascular plants of west-central Montana--identification guidebook. Gen. Tech. Rep. INT-227. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 648 p.

Lorenz, T.J., C. Aubry, and R. Shoal. 2008. "A Review of the Literature on Seed Fate in Whitebark Pine and the Life History Traits of Clark's Nutcracker and Pine Squirrels." PNW-GTR-742. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/PNW-GTR-742.

Mace, R. D., & Jonkel, C. J. (1986). Local Food Habits of the Grizzly Bear in Montana. *Bears: Their Biology and Management*, *6*, 105–110. https://doi.org/10.2307/3872813.

Mantgem, P., E. Milano, J. Dudney, J. Nesmith, A. Vandergast, H. Zald. (2023). Growth, drought response, and climate-associated genomic structure in whitebark pine in the Sierra Nevada of California. Ecology and Evolution. 13. 10.1002/ece3.10072.

Mattson, D.J. and Reinhart D.P. 1990. whitebark pine on the Mount Washburn Massif, Yellowstone National Park. IN Schmidt WC and MacDonald K (comps), Whitebark pine ecosystems:: ecology and management of a high mountain resource. Proceedings of a symposium, March 29-13, 1989, Bozeman, MT, USA. USDA Forest Service General Technical Report INT-270: 106-117.

McCutchen, H. E. (1996) "Limber pine and bears," Great Basin Naturalist: Vol. 56 : No. 1 , Article 12. Available at: https://scholarsarchive.byu.edu/gbn/vol56/iss1/12

McCune, B. 1988. "Ecological Diversity in North American." American Journal of Botany 75 (3): 353–68. https://doi.org/10.1002/j.1537-2197.1988.tb13450.x.

Moyes, A.B., C. Castanha, M. J. Germino, and L. M. Kueppers. 2013. "Warming and the Dependence of Limber Pine (Pinus Flexilis) Establishment on Summer Soil Moisture within and above Its Current Elevation Range." Oecologia 171 (1): 271–82. https://doi.org/10.1007/s00442-012-2410-0.

Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. BMJ 2021;372:n71. doi: 10.1136/bmj.n71

Peet, R.K. 1978. "Latitudinal Variation in Southern Rocky Mountain Forests." Journal of Biogeography 5 (3): 275–89. https://doi.org/10.2307/3038041.

Raffa, K. F., B.H Aukema, B.J Bentz, A.L Carroll, J.A Hicke, M.G Turner, W.H Romme. 2008: Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517. [Online]. doi: 10.1641/B580607

Resler, L. M., and D. F. Tomback. 2008. "Blister Rust Prevalence in Krummholz Whitebark Pine: Implications for Treeline Dynamics, Northern Rocky Mountains, Montana, U.S.A." Arctic, Antarctic, and Alpine Research 40 (1): 161–70. https://doi.org/10.1657/1523-0430(06-116)[RESLER]2.0.CO;2.

Richardson, A.D., X. Lee, and A.J. Friedland. 2004. "Microclimatology of Treeline Spruce–Fir Forests in Mountains of the Northeastern United States." *Agricultural and Forest Meteorology* 125 (1): 53–66. https://doi.org/10.1016/j.agrformet.2004.03.006.

Rockwell, F. I. 1911. The white pines of Montana and Idaho—their distribution, quality, and uses. Forestry Quarterly 9: 219-231.

Schoettle, A. W., K.S. Burns, S.T. McKinney, J. Krakowski, K.M. Waring, D.F. Tomback, and M. Davenport. 2022. "Integrating Forest Health Conditions and Species Adaptive Capacities to Infer Future Trajectories of the High Elevation Five-Needle White Pines." Forest Ecology and Management. 521: 120389. 521:120389. https://doi.org/10.1016/j.foreco.2022.120389.

Schwandt, J.W. 2006. Whitebark pine in peril: a case for restoration. U.S. Department of Agriculture, Forest Service, Northern Region (Region 1), Forest Health Protection, Missoula, MT. R1-06-28. 20 pp.

Schwandt, J. W., I.B. Lockman, J.T Kliejunas, J.A Mulir. 2010: Current health issues and management strategies for white pines in the western United States and Canada. Forest Pathology 40, 226–250

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

Shanahan, E., K. Irvine, K. Legg, S. Wilmoth, R. Daley, and J. Jackson. 2022. "Monitoring Five-Needle Pine on Bureau of Land Management Lands in Wyoming: Summary Report for

2013, 2014, 2016, 2017—Republished." National Park Service. https://doi.org/10.36967/nrr-2293294.

Shepherd, B., J. Krakowski, R. Moody, I. Reid, M.P Murray, N. Stafl, R. Sissons, G. Alger, J. Park, C. McLellan, C.J. Schwarz, and C.M. Smith. 2025. Climate dominates geographic influences on whitebark pine and limber pine trends and landscape patterns in Canada. *Canadian Journal of Forest Research*. **55**: 1-19. https://doi.org/10.1139/cjfr-2024-0114

Soulé, M.E., Estes, J.A., Berger, J. and Del Rio, C.M. (2003), Ecological Effectiveness: Conservation Goals for Interactive Species. Conservation Biology, 17: 1238-1250. https://doi.org/10.1046/j.1523-1739.2003.01599.x

Steele, R. 1990. Pinus flexilis James. In Silvics of North America, Vol. 1: Conifers, Burns, R.M., and H.B. Honkala (tech. coords.). USDA For. Serv., Agri. Handbk. 654, Washington, DC. Available online at www.na.fs.fed.us/pubs/silvics_manual/Volume_1/pinus/flexilis.htm

Tomback, D.F, Sprague, E., 2022. The National Whitebark Pine Restoration Plan: Restoration model for the high elevation five-needle white pines, Forest Ecology and Management, Volume 521, 120204, ISSN 0378-1127, https://doi.org/10.1016/j.foreco.2022.120204.

Tomback, Diana F. 1982. "Dispersal of Whitebark Pine Seeds by Clark's Nutcracker: A Mutualism Hypothesis." Journal of Animal Ecology 51 (2): 451–67. https://doi.org/10.2307/3976.

Tomback, D.F., Arno, S.F., Keane, R.E. 2001. The compelling case for management intervention. In: Tomback, D.F.; Arno, S.F.; Keane, R.E., eds. Whitebark pine communities: Ecology and restoration. Washington, DC: Island Press: 3-25.

Tomback, D.F., R. E. Keane, W. W. McCaughey, and C. Smith. 2005. "Whitebark Pine Ecosystem Foundation Methods for Surveying and Monitoring Whitebark Pine for Blister Rust Infection and Damage." March 2005 https://www.researchgate.net/publication/265233145_Whitebark_Pine_Ecosystem_Foundation_Methods_for_Surveying_and_Monitoring_Whitebark_Pine_for_Blister_Rust_Infection_and_Damage.

Tomback, D. F., and P. Achuff. 2010. "Blister Rust and Western Forest Biodiversity: Ecology, Values and Outlook for White Pines." Forest Pathology 40 (3–4): 186–225. https://doi.org/10.1111/j.1439-0329.2010.00655.x.

Tomback, D.F., Achuff, P., Schoettle, A.W., Schwandt, J.W., Mastrogiuseppe, R.J., 2011. The magnificent high-elevation five-needle white pines: Ecological roles and future outlook. Keane Robert E Tomback Diana F Murray Michael P Smith Cyndi M Eds Future High-Elev. Five-Needle White Pines West. N. Am. Proc. High Five Symp. 28–30 June 2010 Missoula MT Proc. RMRS-P-63 Fort Collins CO US Dep. Agric. For. Serv. Rocky Mt. Res. Stn., vol. 63, pp. 2–28.

Tomback, D.F., L. M. Resler, R. E. Keane, E. R. Pansing, A.J. Andrade, and A. C. Wagner. 2016. "Community Structure, Biodiversity, and Ecosystem Services in Treeline Whitebark Pine Communities: Potential Impacts from a Non-Native Pathogen." Forests 7 (1): 21. https://doi.org/10.3390/f7010021.

Ulrich, D. E., C. Wasteneys, S. Hoy-Skubik, and F. Alongi. 2023. "Functional Traits Underlie Specialist-Generalist Strategies in Whitebark Pine and Limber Pine." *Forest Ecology and Management* 542 (August):121113. https://doi.org/10.1016/j.foreco.2023.121113.

USDA. 2010. *Interior West Forest Inventory and Analysis Forest Survey P2 Field Procedures*, 370, *Ver. 4.0.* Washington, DC: USDA Forest Service.

US Fish and Wildlife Service. 2022. "Endangered and Threatened Wildlife and Plants; Threatened Species Status with Section 4 (d) Rule for Whitebark Pine (Pinus albicaulis)." Federal Register 87: 76882–76917

US Fish and Wildlife Service. 2021. Whitebark pine SSA. Species Status Assessment Reports. WYFO Cheyenne Wyoming

Whitlock C, Shafer SL, Marlon J (2003) The role of climate and vegetation change in shaping past and future fire regimes in the Northwestern US and the implications for ecosystem management. Forest Ecology and Management 178: 5–21.

Whitlock C (1993) Postglacial vegetation and climate of Grand Teton and southern Yellowstone national parks. Ecological Monographs: 173–198.

Williams, S.R, J. E. Steed, J. Morrone, S.A. Goeking, M. Lavin, E.K. Dodson, and R.E. Simons. 2024. "Accuracy of Whitebark Pine and Limber Pine Identification by Forest Inventory and Analysis Field Crews." Forest Science, September, fxae027. https://doi.org/10.1093/forsci/fxae027.

Windmuller-Campione, M. A., and J. N. Long. 2016. "Limber Pine (Pinus Flexilis James), a Flexible Generalist of Forest Communities in the Intermountain West." PLOS ONE 11 (8): e0160324. https://doi.org/10.1371/journal.pone.0160324.