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Integrating forest health conditions and species adaptive capacities to infer future trajectories of the high elevation five-needle white pines

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ABSTRACT

Tree mortality rates have been increasing globally with mountainous regions experiencing higher temperatures and impacts from the expansion and intensification of pests and invasion by non-native agents. Western North American high-elevation forests exemplify these trends, and they often include one or more species of five-needle white pines (High-5 hereafter). These species share many characteristics critical to defining the structure and function of many subalpine forests. The main threats to High-5 populations include the non-native pathogen *Cronartium ribicola*, which causes the disease white pine blister rust, climate-driven drought stress, episodic and high mortality from mountain pine beetle (*Dendroctonus ponderosae*), and wildfires of increasing frequency, size, and intensity. The six High-5 species occurring in western North America (whitebark pine, *Pinus albicaulis*; limber pine, *P. flexilis*; southwestern white pine, *P. strobiformis*; Rocky Mountain bristlecone pine, *P. aristata*; Great Basin bristlecone pine, *P. longaeva*; and foxtail pine, *P. balfouriana*) differ in their health status and threat level. The convergence of threats impacting the rapidly declining species could portend future declines in the species and populations currently less impacted by recent disturbances. Differences in the innate adaptive capacities of the species affect their population trajectories under these novel combinations of stressors. We evaluate the status and outlook for each species and address the following questions: (1) Is the environment changing too fast and the intensity of stressors too great for the species to adapt and recover? (2) Do the species have the heritable traits necessary to sustain fitness under *C. ribicola* and climatic stresses? (3) Are other mortality factors increasing to the degree that they reduce the populations further and delay or preclude adaptation and population recovery? (4) Can the species escape the stressors through migration? Insights related to these questions provide guidance for forest management to facilitate adaptation and increase the resilience of these species into the future.

1. Introduction

Tree mortality is increasing at a rapid rate globally because of novel disturbance conditions (Adams et al., 2009; Allen et al., 2010). Mountainous regions, including many forest communities of western North America (Gergel et al., 2017), are facing seasonal warming rates that are greater than the global land average (Rangwala and Miller, 2012). High-elevation forests and alpine treelines in many western mountain ranges are often defined by the presence of high-elevation five-needle white pines (hereafter referred to as “High-5” species). The High-5 may have a disproportionally large effect on ecosystem functioning and biodiversity relative to their abundance (i.e., serving as keystone species) and they

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Abbreviations: High-5, High elevation five-needle white pines; WPBR, white pine blister rust; MPB, mountain pine beetle; RM bristlecone pine, Rocky Mountain bristlecone pine; GB bristlecone pine, Great Basin bristlecone pine; SW white pine, southwestern white pine.

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often define ecosystem structure and functional dynamics (i.e., serving as foundation species) (Paine, 1995; Tomback et al., 2001b; Tomback and Achuff, 2010). The loss of keystone and foundation species could destabilize ecosystems through loss of biodiversity and changing species interactions (Ellison et al., 2005).

The High-5 species occurring in western North America are whitebark pine (*Pinus albicaulis* Engelm.), limber pine (*P. flexilis* James), southwestern white pine (*P. strobiformis* Engelm.; SW white pine), Rocky Mountain bristlecone pine (*P. aristata* Engelm.; RM bristlecone pine), Great Basin bristlecone pine (*P. longaeva* D.K. Bailey; GB bristlecone pine), and foxtail pine (*P. balfouriana* Grev. & Balf.) (Fig. 1). The High-5 were classified by McCune (1988) as stress-tolerators, though they are now confronted with a new combination of stressors. Tree mortality in High-5 forests over the past decades is primarily attributed to the non-native pathogen *Cronartium ribicola* Fisch. which causes the often-lethal disease white pine blister rust (WPBR) and climate-driven increases in drought stress, intensity and extent of mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) outbreaks, and wildfire size, frequency, and severity (Tomback and Achuff, 2010; Keane and Schoettle, 2011; Keane et al., 2017; Parks and Abatzoglou, 2020). WPBR is viewed here as a "novel stressor," given that the High-5 were first exposed to the pathogen in the early 1900s and some populations have still not been exposed. The unprecedented geographic scale and intensity of the recent MPB outbreaks, driven by rising temperatures, are similarly considered a novel stress in some environments, although the insect is native and outbreaks have been documented historically (e.g., Brunelle et al. 2008; Logan et al., 2010). We consider recent changes in fire regimes throughout western North America and climate change itself as novel stressors, as well as the interactions among these conditions.

The estimated percentage of standing whitebark pine trees in the U.S. that are dead has increased from 12% in 1999 to 43% in 2009 and 54% as of 2020 (Goeking and Windmuller-Campione, 2021). Overall, whitebark pine stands have more dead than live trees for all but the smallest diameter class, although this varies regionally (Goeking and Izlar, 2018). Limber pine is showing similar but lagging trends in mortality in the U.S. compared to whitebark pine; mortality increased from 8% to 34% to 42% in 1999, 2009, and 2019, respectively (Goeking and Windmuller-Campione, 2021). Whitebark pine is listed as endangered nationally in Canada (Government of Canada, 2012) and limber pine is proposed for endangered listing under the Canadian Species at Risk Act (COSEWIC, 2014). In December 2020, whitebark pine was proposed for listing as Threatened under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service, 2020). Mortality of the four other High-5 species in

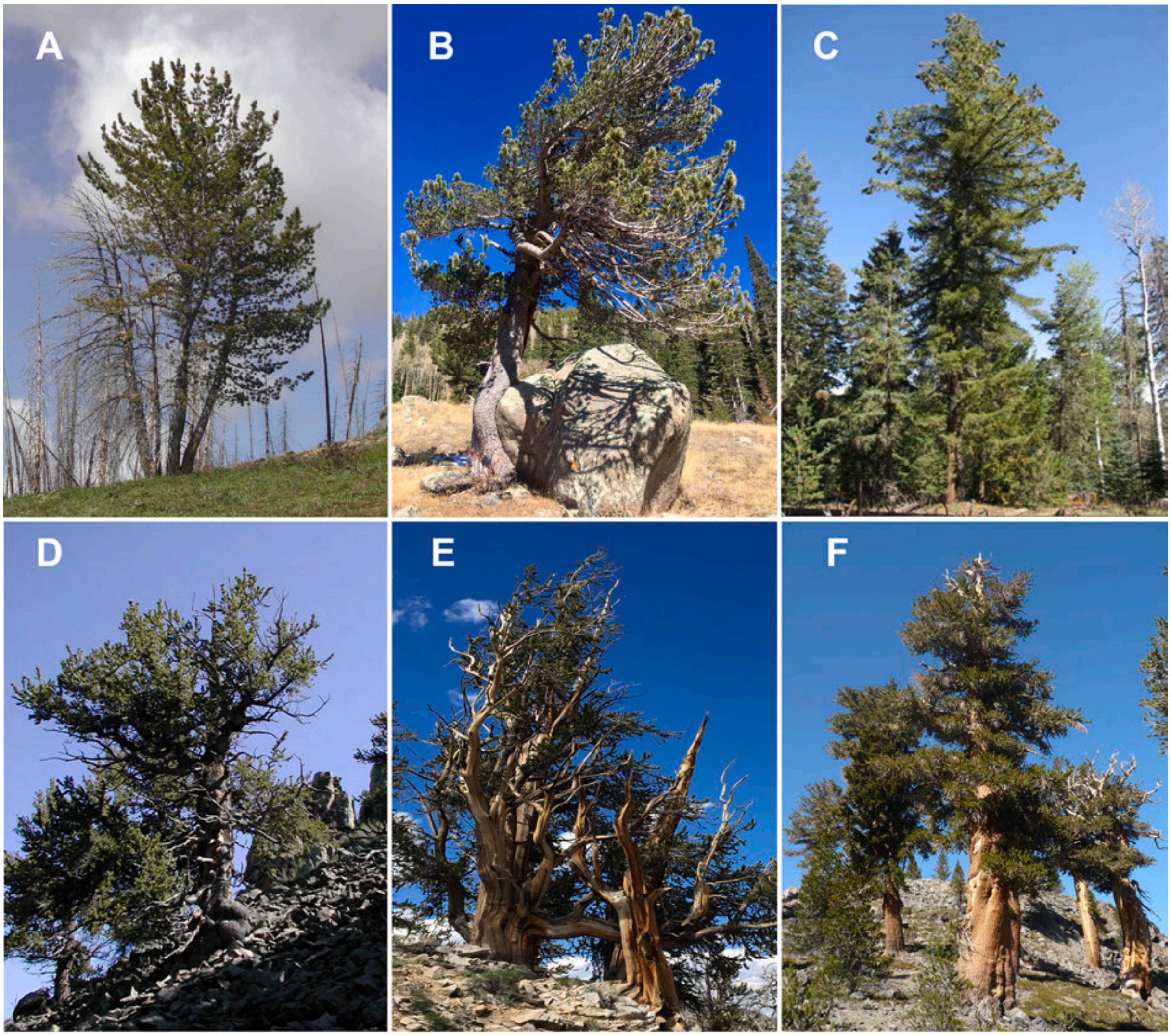

Fig. 1. Collage of photos of the High-5 species. A) whitebark pine (*Pinus albicaulis*); B) limber pine (*P. flexilis*); C) southwestern white pine (*P. strobiformis*); D) Rocky Mountain bristlecone pine (*P. aristata*); E) Great Basin bristlecone pine (*P. longaeva*); F) foxtail pine (*P. balfouriana*). Photo credits: A, D, E: A.W. Schoettle; B: C.T. Holtz; C: K.M. Waring; F: S.T. McKinney.

the U.S. averages about 18% each (Goeking and Windmuller-Campione, 2021) and will likely rise with greater exposure to stressors and disturbances.

High mortality of the High-5 has consequences not only for the viability of these pine populations but also for the resilience of many high mountain ecosystems. These species provide important ecosystem services that contribute to ecosystem resilience, but these services become compromised by high mortality levels. Most of the High-5 can grow in harsh habitats where other trees cannot, thereby providing critical slope stabilization and watershed protection in high mountain areas (Tomback and Achuff, 2010; Tomback et al., 2011). The High-5 species also add roughness to otherwise barren slopes which contributes to snow capture and retention and slows snowmelt dynamics which is increasingly important for timely water delivery as the climate continues to change (Hock et al., 2019). The species also play important roles in forest recovery as they tend to be early colonizers (albeit sometimes at low density) following disturbance (Donnegan and Rebertus 1999). Over time they can mitigate environmental conditions on exposed sites to facilitate the establishment of other plant species (Baumeister and Callaway, 2006; Resler and Tomback, 2008). The High-5 also provide wildlife habitat and, in several species, highly nutritious seeds relative to sympatric conifers which are a food source for many species of birds, insects, rodents, and bears (Tomback and Achuff, 2010).

Biological diversity and ecosystem function are receiving more attention as forests are impacted by novel stressors at rates that may exceed their adaptive capacity (Brasier, 2008; Carroll et al., 2014; Jacobs et al., 2015; Stanturf, 2015). Forest decline is especially likely in the slow-growing long-lived High-5 species as they face the novel stressor *C. ribicola* in the presence of compounding climate and forest health challenges. Climate envelope models developed under climate change scenarios, with no accounting for other disturbances or adaptation, show extensive contractions in suitable habitat for the High-5 (e.g., Crookston, 2012). To assess whether the High-5 species will adapt to the novel combination of conditions and persist into the future, we address several questions: (1) Is the biotic and abiotic environment changing too fast and the intensity of the stress too great for the species to adapt and recover? (2) Do the species have the heritable traits necessary to sustain fitness under WPBR and climatic stresses? (3) Are other mortality factors increasing to the degree that they reduce the populations further and delay or preclude adaptation and population recovery? (4) Alternatively, can the species escape the stressors through migration? Insights related to these questions can help provide direction for forest management to facilitate adaptation and increase the resilience of these species into the future (Millar et al., 2007; Schoettle and Sniezko, 2007; Desprez-Loustau et al., 2016).

Past reviews of the High-5 provide valuable ecological information on the species (e.g., Tomback et al., 2001b; Tomback and Achuff, 2010; Tomback et al., 2011) and management tactics (e.g., Keane and Schoettle, 2011; Keane et al., 2012; Alberta Whitebark and Limber Pine Recovery Team, 2014; Schoettle et al., 2019a; Alberta Environment and Parks, 2021; Keane et al., 2021; Tomback et al., 2022). Here we focus on evaluating the adaptive capacity and future trajectory of each of the High-5 species. We review the biotic and abiotic stressors that impact or threaten the High-5 and discuss specific components of High-5 vulnerability and adaptive resilience within the framework of evolutionary rescue and contemporary evolution (Gomulkiewicz and Holt, 1995; Bell and Gonzalez, 2009, 2011; Bell, 2013; Hendry et al., 2011; Carlson et al., 2014). Finally, we integrate the current and future expected forest health conditions with species-specific traits to infer a trajectory for each High-5 species. We explore conservation and management approaches that might improve the outcome for each species.

2. The High Elevation Five-Needle Pines (High-5)

Table 1

Taxonomic classification of the North American five-needle pines (according to Jin et al., 2021). The six High-5 species are listed in bold with their four-letter acronyms.

- Genus *Pinus*
  - Subgenus *Strobus*
    - Section *Quinquefoliae*
      - Subsection *Strobus*
        - **Limber pine, *P. flexilis* James (PIFL)**
        - **Southwestern white pine, *P. strobiformis* Engelm. (PIST)**
        - **Whitebark pine, *P. albicaulis* Engelm. (PIAL)**
        - Mexican white pine, *P. ayacahuite* Ehrenb. ex Schltdl.
        - Chiapas white pine, *P. chiapensis* (Martínez) Andresen
        - Sugar pine, *P. lambertiana* Dougl.
        - Western white pine, *P. monticola* Dougl. ex D. Don
        - Eastern white pine, *P. strobus* L.
    - Section *Parrya* Mayr
      - Subsection *Balfourianae*
        - **Rocky Mountain bristlecone pine, *P. aristata* Engelm. (PIAR)**
        - **Foxtail pine, *P. balfouriana* Grev. & Balf. (PIBA)**
        - **Great Basin bristlecone pine, *P. longaeva* D.K. Bailey (PILO)**

The High-5 comprise a subset of a unique group of related species in the subgenus *Strobus* (Table 1). They occur across the high mountains of western North America (Fig. 2). Whitebark pine, limber pine, and SW white pine have broad geographic distributions. Whitebark pine has the most widespread distribution—from 37° to 56° N latitude and from 107° to 128° W longitude (McCaughey and Schmidt 2001; Fig. 2). Throughout its range, whitebark pine inhabits the upper subalpine and treeline zones (Arno and Hoff, 1990; 1,370–3,660 m above sea level [asl] range-wide). It occurs as the only tree species on some of the coldest and driest sites at treeline and as a seral species in some regions on less harsh lower elevation sites more favorable for its shade-tolerant competitors (Arno and Weaver, 1990; Tomback et al. 2016). It commonly coexists with nine tree species range-wide including limber pine and foxtail pine (Tomback and Achuff, 2010). The habitats that support whitebark pine are cool and water availability is strongly driven by snow and early summer moisture with lower precipitation in July and August (Fig. 3).

Limber pine has a broad western distribution and elevational range (Fig. 2). In northern Colorado, it grows below the lower treeline in the shortgrass steppe (1600 m), defines the alpine treeline on dry aspects (3300 m), and occupies sites at all elevations in between (Schoettle and Rochelle, 2000). It also grows along a wide elevational range in the Great Basin (1830–3540 m) (Hankin and Bisbing, 2021; Windmuller-Campione and Long, 2016). Limber pine coexists with 15 tree species across its range including each of the five other High-5 species (Tomback and Achuff, 2010). The environments that support limber pine are diverse and tend to be warmer in the summer and have lower precipitation year-round than those supporting whitebark pine (Fig. 3).

In the 1970s geneticists reported hybridization in Arizona between limber pine and SW white pine (Steinhoff and Andresen, 1971). Recently, the broad hybrid zone across the U.S. portion of the SW white pine's range has been confirmed using genomic tools (Moreno-Letelier & Piñero, 2009; Menon et al., 2018). For this discussion, we will refer to the U.S. and Mexican distributions as SW white pine, although ongoing research may lead to changes in the taxonomy (Fig. 2). SW white pine is an important component of the mixed-conifer forests upslope from pure ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) (2130–3050 m elevation but is more commonly found between 2290 m and 2750 m) (Looney and Waring, 2013). It does not reach treeline elevations. In the U.S., its distribution is fragmented among the southwestern sky islands, and it coexists with eight tree species, including limber pine and RM bristlecone pine (Tomback and Achuff, 2010; Looney and Waring, 2013). The signal of the North American Monsoon is strong in U.S. habitats of SW white pine; precipitation minimums occur in April through June and maximums in July through September (Fig. 3).

The final three High-5 species (RM bristlecone pine, GB bristlecone pine, and foxtail pine) are in Subsection *Balfourianae* Engelm within the foxtail section (Parrya) of the subgenus *Strobus* (Table 1). RM

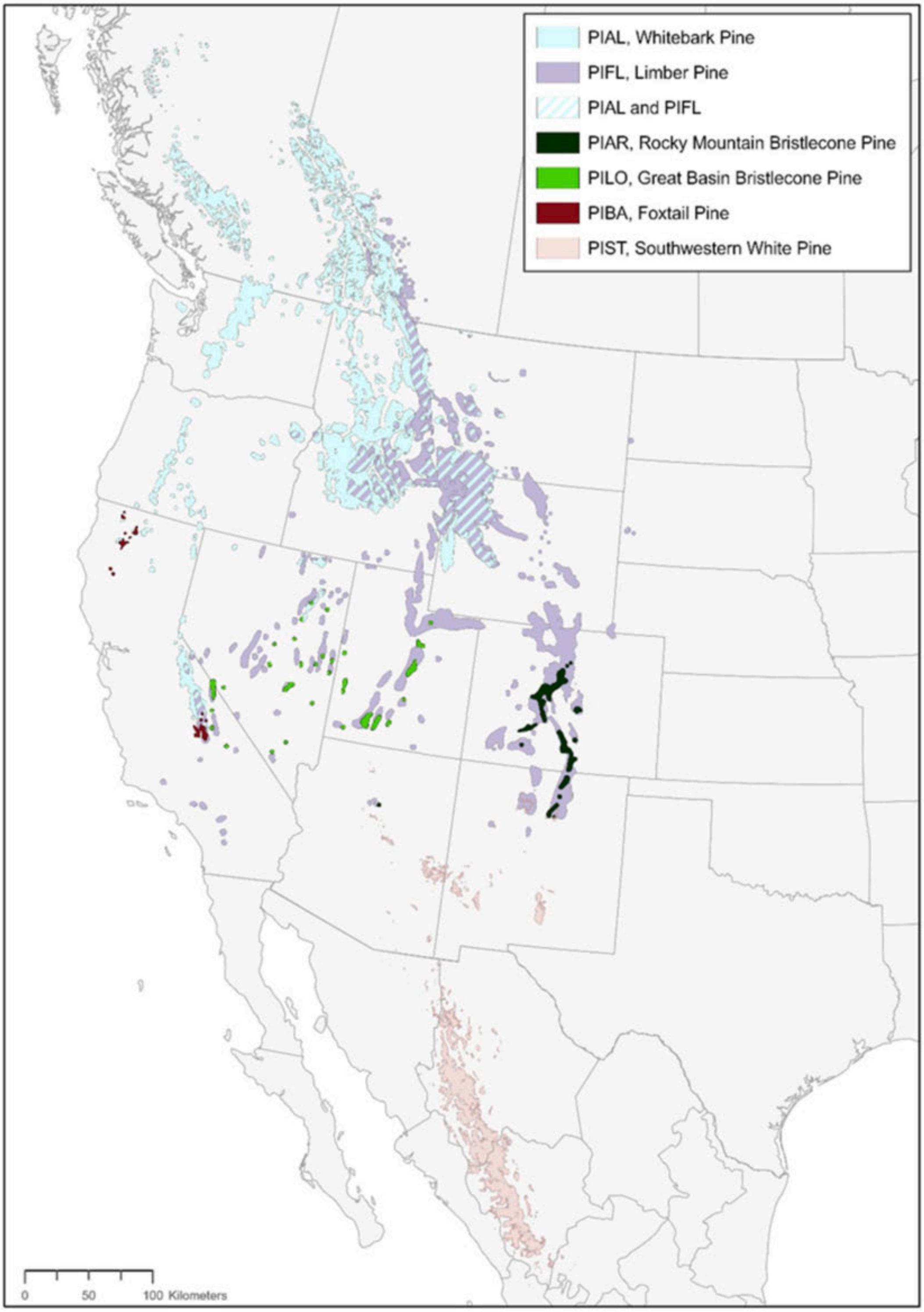

Fig. 2. Distribution of the High-5 species in western North America. Sources for the distributions are Whitebark Pine Ecosystem Foundation (2014) for whitebark pine and limber pine, Little (1971) for Rocky Mountain bristlecone pine, foxtail pine, Great Basin bristlecone pine, and an adaptation from Shirk et al. (2018) for southwestern white pine.

bristlecone, foxtail, and GB bristlecone pines are all long-lived approaching age 2500, 3000, and 5000 years, respectively (Currey, 1965; Ferguson, 1968; Brunstein and Yamaguchi, 1992; Maloney, 2011b; Scuderi, 1993). RM bristlecone pine and GB bristlecone pine were distinguished as separate species in 1970 (Bailey, 1970) with no overlap in their distributions (Fig. 2); before that time both species were called *P. aristata*. The core distribution for RM bristlecone pine is in central Colorado; its distribution extends into New Mexico with a disjunct population in northern Arizona. RM bristlecone pine grows from 2500 to 3670 m elevation in extensive forests, small stands, and as isolated trees on rocky outcrops. In some locations, it forms spreading krummholz mats above treeline (Barrick and Schoettle, 1996; Shiels and Sanford, 2001). RM bristlecone pine coexists with 12 tree species including SW white pine and limber pine (Tomback and Achuff, 2010).

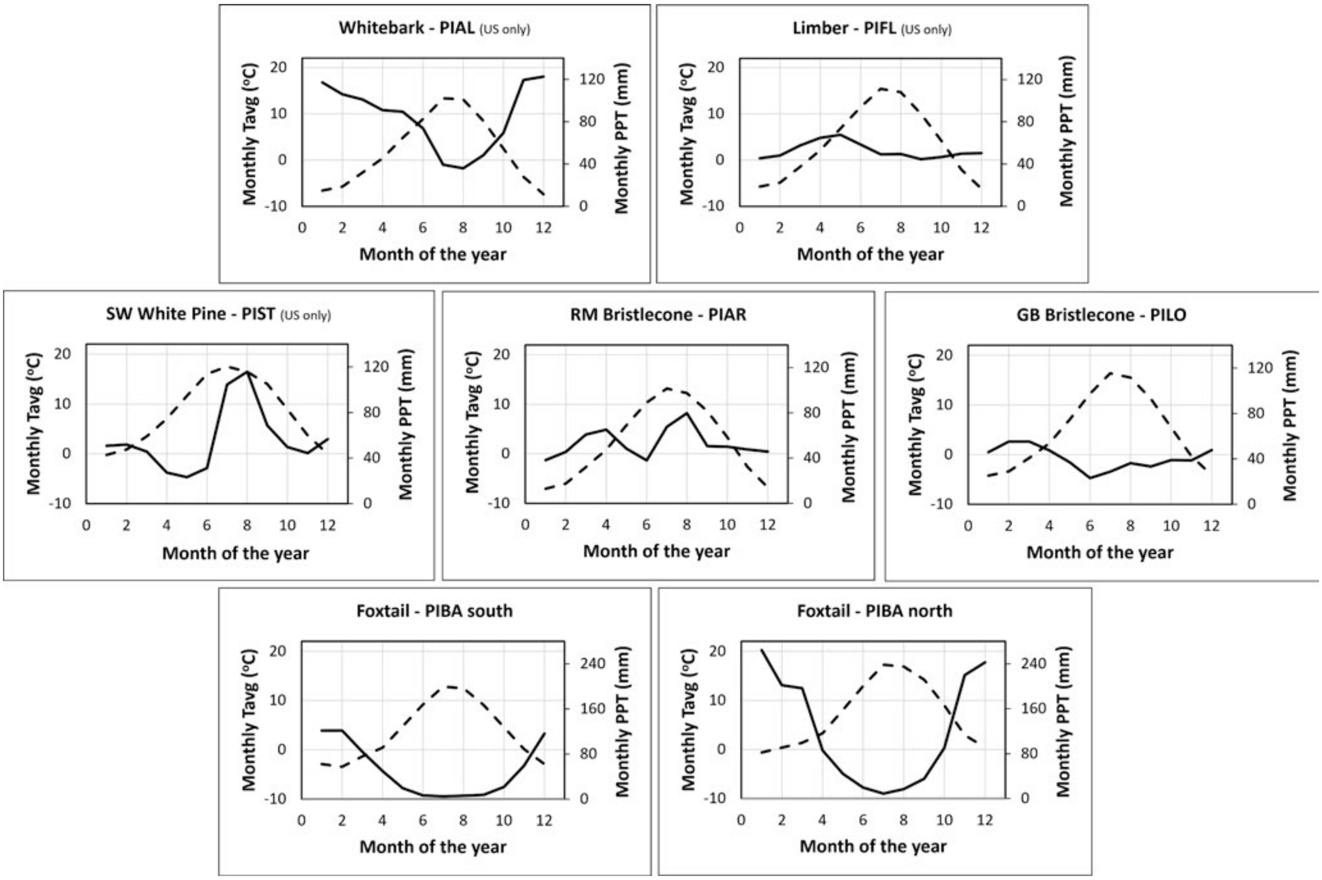

Fig. 3. Climate diagrams for the High-5 species. Modeled monthly average mean temperature (dashed line) and precipitation (solid line) from 1981 to 2010 using ClimateNA (Wang et al., 2016) for plots in USDA Forest Service Forest Inventory and Analysis (FIA), Maloney (2011b), and Eckert (2006). Note that the scale for the precipitation axis of the foxtail pine plots is twice that of the other plots.

Like SW white pine, RM bristlecone pine habitats have precipitation minimums in June and peaks in July and August because of the monsoon, though rainfall is lower, and late summer precipitation tends to be less reliable year-to-year (Fig. 3). GB bristlecone pine grows on isolated mountain ranges and sky islands in Utah, Nevada, and the White Mountains of eastern California. Its elevation range is 1700–3400 m (Bailey, 1970) and it coexists with 13 associated tree species including whitebark pine and limber pine (Tomback and Achuff, 2010). GB bristlecone pine habitats are warmer and drier than those of RM bristlecone pine, with only a weak pattern of late-summer precipitation and less late winter snow than environments supporting whitebark pine or limber pine (Fig. 3) (Liu and Biondi, 2020; Hankin and Bisbing, 2021).

Foxtail pine has the most restricted distribution of the High-5 species. The distribution is disjunct with one portion in the Klamath Range in northern California (1500–2750 m elevation) and the other 500 km south in the southern Sierra Nevada (2300–3500 m) (Fig. 2). The two populations are fundamentally different in structure, composition, and diversity (Eckert, 2006). In the north, foxtail pine is the dominant tree on isolated peaks but often occurs in mixed subalpine forest communities that can include whitebark pine (Eckert and Sawyer, 2002). In the south, foxtail pine usually forms extensive low-diversity stands where it can co-occur with whitebark pine, limber pine, and other species (Eckert and Sawyer, 2002; Nesmith et al., 2019). The two populations have been considered subspecies (Mastrogiuseppe and Mastrogiuseppe, 1980), although they show little genetic divergence (Oline et al., 2000). The climate is warmer and wetter for the northern habitats than for those in the south (Fig. 3) (Maloney, 2011b).

3. Contemporary Evolution

Species or populations have three options when faced with a novel stressor: they can adapt to the new environment over time in place, avoid the stressor through migration, or go extinct (Aitken et al., 2008). Adaptation is the process by which a population becomes fitted to its environment through natural selection acting upon heritable variation over generations; the new population exhibits greater fitness in the new environment relative to the population first exposed to the stress. Evolutionary rescue is the process by which a population escapes extinction and persists due to adaptation (Gomulkiewicz and Holt, 1995; Carlson et al., 2014). If that process of adaptation occurs over a short period (~200 yrs.), it is called contemporary evolution (Hendry et al., 2011).

Three phases of contemporary evolution, as they affect population size in response to a novel stressor, have been defined (Fig. 4) (Gomulkiewicz and Holt, 1995; Carlson et al., 2014). Because natural selection is a demographic process (i.e., occurring at a population level), the challenge facing a population under intense selection is maintaining a viable population size. In this process, less adapted individuals are selected against, and the frequency of the adaptive traits conveying fitness increase over time with successive generations. If the selection pressure (i.e., rate of mortality) is too rapid for the population growth rate to offset, the population size can drop below a demographic and possibly a genetic threshold from which it may not recover (phase 2, Fig. 4) (Gilpin and Soulé, 1986). While at this population minimum, or low effective population size, the population is at risk of extirpation from stochastic mortality factors that can further reduce population size jeopardizing recovery (Gilpin and Soulé, 1986; Gomulkiewicz and Holt,

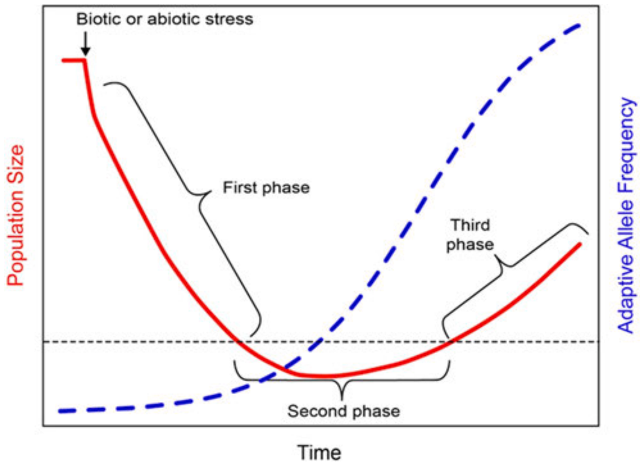

Fig. 4. Conceptual representation of the three phases of adaptation to a novel stressor as they affect population abundance and adaptive allele frequency. During the first phase, less adapted individuals are selected against by the change in the biotic or abiotic environment, leading to mortality and population decline (red line). In the second phase, population growth offsets mortality stabilizing the population at a low size. For the duration of the time the population is at the minimum (red line below the dashed black line), the population is at high risk for extirpation by stochastic mortality factors. Sexual reproduction provides individuals with new combinations of adaptive genes on which selection can continue to act, resulting in an increase in the allele frequency of these genes and associated adapted phenotypes in the population (dashed blue line). If extirpation is avoided, the population enters the third phase when less adapted individuals are increasingly rare, and establishment of adapted individuals dominates; the population is recovering and continues to adapt to the stress by an increase in the adaptive allele frequency that increases fitness under the new environment. The figure was adapted with permission from Carlson et al. (2014). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1995; Bell, 2013; Carlson et al., 2014). For the High-5, the additive mortality from increased pest pressures (e.g., MPB) and altered fire regimes threaten High-5 population viability during the process of adapting to the primary stressors of WPBR and climate-driven drought. The outcome of selection by WPBR and other compounding stressors has been observed and modeled for the High-5 (Tomback and Kendall, 2001; Barringer et al., 2012; Field et al., 2012).

Adaptation that occurs within the time frame of contemporary evolution (~200 yrs.) (hereafter referred to as "rapid adaptation"), is most likely to occur under conditions where environmental change is gradual, initial population size is large, generation time is short, and genetic variation within populations is high (Aitken et al., 2008; Bell and Gonzalez, 2009). Unfortunately for the High-5, the environmental change imposed by the introduction of *C. ribicola* and climate change is rapid, especially in some regions (Keane et al., 2017). In general, the life-history strategies of the High-5 lead to tolerance and perseverance (longevity), rather than turnover, to sustain populations. Most High-5 trees begin to produce large cone crops only after a century (Lanner and Connor, 2001; Tomback and Achuff, 2010). Seedling recruitment is slow in the harsh high-elevation habitats (e.g., Tomback et al., 1990; Tomback et al., 2001a; Coop and Schoettle, 2009). Long-lived, stress-tolerant species, such as the High-5, are tolerant of historical conditions but are not well equipped for rapid adaptation to novel stressors.

Conserving genetic diversity during rapid adaptation protects a population's evolutionary potential (Kardos et al., 2021). This may be important for the High-5 given the potentially strong selection from a changing climate and increasing disease pressure (Kim et al., 2003; Bower et al., 2011). In general, genetic diversity for the High-5 species is at or below the mean levels for other widespread western North American conifers (Bower et al., 2011). Whitebark, limber, and GB bristlecone pine have moderate levels of genetic diversity, foxtail and SW white pine have less genetic diversity, and RM bristlecone pine has very low diversity (Schoettle et al., 2012b; Bower et al., 2011). Typical of long-lived trees, most of the genotypic diversity in the High-5 occurs within populations rather than among populations (Liston et al., 1999). Foxtail and GB bristlecone pine contain signatures of more continuous and widespread distributions in past epochs even though the current populations are isolated from one another (Hiebert and Hamrick, 1983; Oline et al., 2000; Lee et al., 2002). Furthermore, inbreeding levels for populations of whitebark, limber, and foxtail pine are higher than many other pine species (Krakowski et al., 2003; Bower and Aitken, 2007; Bower et al., 2011). All these species exhibit some evidence of seed dispersal by Clark's nutcracker (*Nucifraga columbiana* Wilson), either as an obligate (whitebark pine) or facultative (all others) disperser. Clark's nutcrackers cache clusters of seeds, frequently related as half to full siblings, that may then germinate and grow into multi-stemmed tree clusters (Furnier et al., 1987; Carsey and Tomback, 1994; Rogers et al., 1999). Clumped multi-stem growth forms can be one genotype, or related genets (Tomback and Linhart, 1990), and may be prone to within-clump pollination.

Although genotypic diversity patterns often reflect historical geographic refugia and zones of secondary mixing and genetic drift associated with recolonization after the latest glacial retreat (Bower and Aitken, 2006; Hiebert and Hamrick, 1983; Jørgensen et al., 2002; Lee et al., 2002; Mitton et al., 2000; Oline et al., 2000; Richardson et al., 2002; Schoettle et al., 2012b), adaptive traits such as budburst date, growth amount and rate, water use efficiency, and cold hardiness that have been under selection for many generations respond to latitudinal, longitudinal, elevational, as well as local environmental variation (Mahalovich et al., 2006; Bower and Aitken, 2008; Bower and Aitken, 2008; Borgman et al., 2015; Eckert et al., 2016; Gass, 2016; Goodrich et al., 2018; Warwell and Shaw, 2018; Bucholz et al., 2020). While traits that confer resistance to WPBR are adaptive in that they increase fitness in the presence of *C. ribicola*, the origins of these traits and their selective value before WPBR invasion (i.e., in naïve populations) are unknown, thwarting our ability to predict their distributions. The baseline frequency of WPBR resistance traits varies among and within the High-5 for reasons not yet understood (Kinloch and Dupper, 2002; Schoettle et al., 2014; Vogan and Schoettle, 2015, 2016), although this may determine the trajectory of the High-5 species as they are challenged by *C. ribicola* (King et al., 2010; Schoettle et al., 2012a; Landguth et al., 2017). High-5 populations invaded by *C. ribicola* have been under selection for less than a century and any associations between WPBR resistance traits and environmental gradients related to WPBR selection pressure may only now be developing.

The High-5 vary in their current exposure to stressors, tolerances to stressors, adaptive capacity, and migration potential to avoid stressors. Informed by concepts of evolutionary rescue, here we evaluate the vulnerability of each High-5 species, infer the outlook for each species, and provide guidance to focus management attention on critical ecological processes (Lawler, 2009; Hellmann and Pfrender, 2011; Hendry et al., 2011; Carlson et al., 2014; Thurman et al., 2022).

4. Stressors and High-5 Responses

4.1. White pine blister rust (WPBR)

WPBR is the greatest threat to the long-term viability of the High-5 populations. The fungal pathogen that causes WPBR, *C. ribicola*, was first introduced into western North America near Vancouver, Canada, in the early 1900s (Geils et al., 2010) and continues to spread (Blodgett and Sullivan, 2004; Vogler and Charlet, 2004; Vogler et al., 2017b; Burns and Schoettle, 2018; Dudney et al., 2020). All North American five-needle white pine species are susceptible to WPBR (Hoff et al., 1980; Schoettle et al., 2014, 2022; Vogler et al., 2006). WPBR was first reported on whitebark pine in 1926, limber pine in 1945, northern population of foxtail pine in 1967, SW white pine in 1990, and RM bristlecone pine in 2004 with most infections thought to be 10–15 years old at the time of first detection (McDonald and Hoff, 2001; Blodgett and Sullivan, 2004). Only two foxtail pine trees in the southern population have been found with WPBR (Kliejunas and Dunlap, 2007; Nesmith et al., 2019; Dudney et al., 2020). GB bristlecone pine is the only North American five-needle white pine that has no confirmed instances of WPBR in its natural habitat, but controlled inoculation studies confirm it is susceptible to the disease (Hoff et al., 1980; Schoettle et al., 2022; Vogler et al., 2006). There are populations of each High-5 species that are not yet infected, and the current WPBR infection fronts for the High-5 on the continental scale are in southern California, the southern Rocky Mountains, the southwestern U.S., the Great Basin, and northern British Columbia and Alberta (see Fig. 5).

WPBR can kill trees of all ages (Fig. 6) (Geils et al., 2010). Once infected, small trees can be killed within a few years; therefore, natural selection against susceptible young trees is rapid (Schoettle and Sniezko, 2007). Larger trees can take decades to succumb to WPBR; however, disease-caused branch mortality can reduce cone production long before killing the tree, thereby curtailing its contribution to key components of

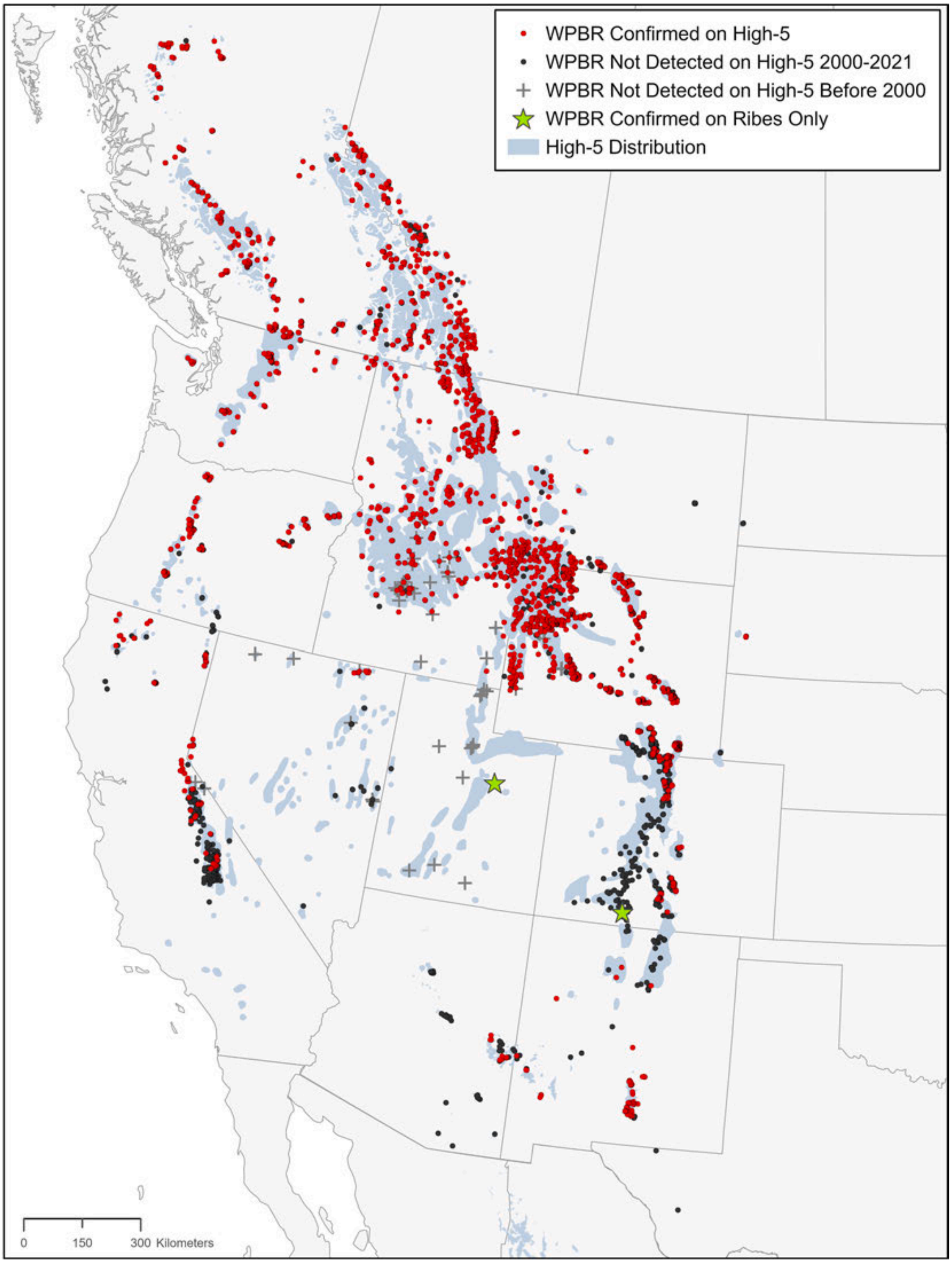

Fig. 5. Distribution of white pine blister rust (WPBR) on the High-5 species in western North America as of 2021. Red dots indicate locations where *C. ribicola* has been detected on High-5 species, black dots where *C. ribicola* has not been detected on High-5 species (since 2000), and green stars are where *C. ribicola* has been confirmed on the alternate host *Ribes inerme* but has not been detected on nearby five-needle pines hosts. Gray crosses indicate areas where rust was not detected before 2000 and more recent data is unavailable. The distribution of the High-5 is displayed in gray (see Fig. 2 for data sources). See Supplemental Material for data sources and field methods. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

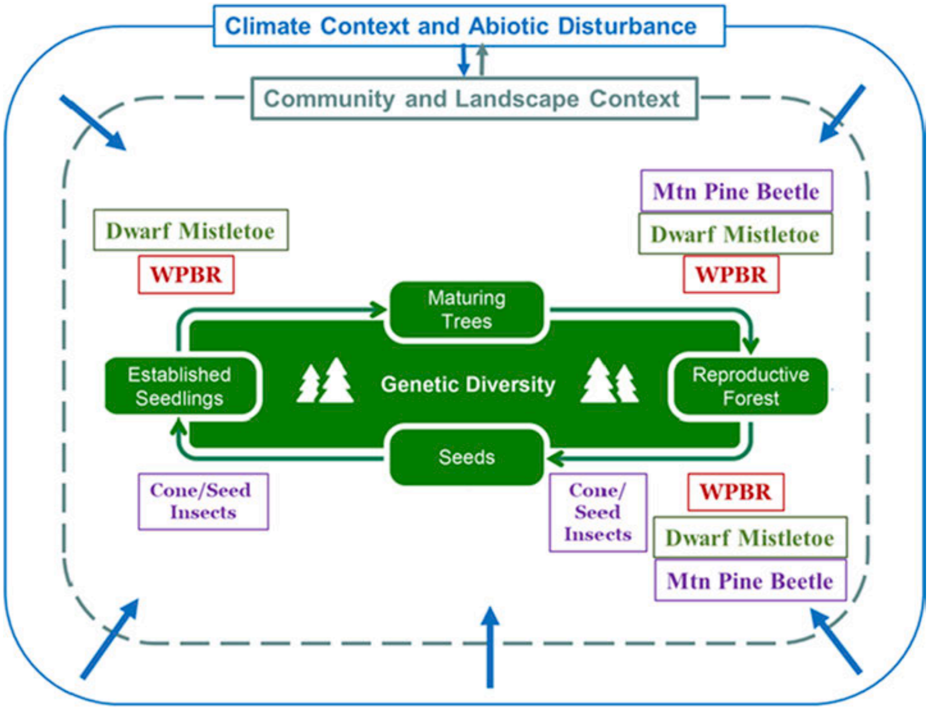

Fig. 6. Biotic and abiotic stressors affecting the High-5 life cycle. Genetic diversity and High-5 generation time (i.e., time for one revolution of the life stages – green inner portion of the diagram) are foundations for population viability. Specific biotic stressors may affect only one life-history stage of the High-5 while others impact all age or size cohorts; they can cause mortality directly or as predisposing or inciting factors to other stressors that cause mortality. The community and landscape context can affect the prevalence of a stressor. For example, lower elevation forests can serve as sources of *C. ribicola* inoculum for infections in higher elevation forests (Maloney, 2000; Newcomb, 2003), mountain pine beetle populations can build up in non-High-5 hosts and increase the risk of attack to nearby High-5 species (Bentz et al., 2022), or wildfire can spread from other forest types into High-5 forests (Higuera et al., 2021). Climate affects every aspect of the ecosystem and its components, directly or through the community and landscape context (or both, e.g., through competitive interactions and susceptibility to pest and pathogen interactions). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

evolutionary rescue (e.g., population size and population growth rate) well before tree death (McDonald and Hoff, 2001; McKinney and Tomback, 2007).

Cronartium ribicola requires two host groups to complete its life cycle – five-needle white pines and alternate hosts, which in North America are typically species of *Ribes* (currants and gooseberries) and can also include *Pedicularis* (louseworts) or *Castilleja* (paintbrushes) (McDonald and Hoff, 2001; McDonald et al., 2006; Zambino et al., 2007). There is no tree-to-tree transmission of *C. ribicola* (Schwandt et al., 2010); only *C. ribicola* basidiospores produced on the leaves of an alternate host can cause new infections on a pine host. Basidiospores are thin-walled and wind-dispersed over short distances (i.e., a few hundred meters) to infect pine needles (Zambino, 2010). Aeciospores, produced on pines, are thicker-walled and can disperse farther by the wind to infect leaves of the alternate hosts (Frank et al., 2008). Generally, aeciospores are produced and dispersed in early summer and basidiospores in later summer to early fall (Mielke, 1943; Geils et al., 2010), although production and dissemination of both spore types can occur at other times during the growing season in some habitats (Vogler and Charlet, 2004; Smith et al., 2000; Hunt and Jensen, 2000).

Cronartium ribicola infections are perennial on susceptible pine hosts and accumulate over the life of the tree, though some may become inactive on live branches or lost on killed branches (Hungerford, 1977; Geils et al., 2010). The fungus enters the pine needle through the stomata and grows into the twig, branch, and bole of the tree leading to branch death, stem girdling, and tree mortality (Mielke, 1943). A single infection can lead to severe disease and mortality, however, the greater the number of infections that develop into cankers on a tree, the greater the probability of a canker reaching the main stem and leading to tree mortality (Slipp, 1953). In contrast, infections on alternate hosts are seasonal and *C. ribicola* colonization is restricted to the leaves such that infections are shed with leaf abscission in the fall (Mielke, 1943).

Each of the five spore stages of the *C. ribicola* life cycle (two on the pine and three on the alternate hosts) requires a different combination of temperature and moisture conditions for a period of hours to weeks for their formation and dispersal (see Table S1 in Jacobi et al., 2018a). When the appropriate cool and moist climatic conditions occur at the right times of year in the presence of the pathogen and hosts, “wave years” of high infection on pines can happen (McDonald and Hoff, 2001). The frequency of wave years and the number of resultant infections on the pines contributes to the selection pressure of WPBR on pines. Wave years can occur annually in some areas (e.g., the northern U.S. Rocky Mountains) where new infections occur each year, while in other areas they are less frequent and infections accumulate on trees more slowly (e.g., the southern Rocky Mountains) (Jacobi et al., 2018a).

Specific climatic conditions have been correlated with disease presence and severity on the High-5 (e.g., Dunlap, 2012; Maloney et al., 2012; Smith-McKenna et al., 2013; Cleaver et al., 2015; Thoma et al., 2019; Dudney et al., 2020) and in some cases have been used to map projections of WPBR risk and hazard across landscapes (e.g., Geils et al., 1999; Kearns et al., 2014). In addition to climatic factors, density and proximity of *Ribes* can contribute to WPBR risk (Kearns et al., 2014) and some *Ribes* spp. are better hosts, and therefore more influential, than others (Van Arsdel and Geils, 2004). The magnitude of the contribution of the other alternate hosts to WPBR in High-5 populations is not fully understood (Richardson et al., 2007; Mulvey and Hansen, 2011).

The durable aeciospores formed on the pines are likely to be the life stage responsible for founding new disjunct infection centers, such as those in southern New Mexico on SW white pine and in southern Colorado on RM bristlecone pine and limber pine (Blodgett and Sullivan, 2004; Burns, 2006; Frank et al., 2008). There have also been apparently failed founder events in central Utah and southern Colorado. *Ribes* infected with *C. ribicola* were observed in those locations, but no infected pines were later found; environmental conditions may not have been conducive to basidiospore infection of the pines in that year (see the stars in Fig. 5; Vogler et al., 2017a; Burns, pers. comm.). At local scales, upslope dispersal of basidiospores from lower elevations is suspected to have been the source of inoculum for infection of High-5 species in some high-elevation areas (Newcomb, 2003; Mulvey and Hansen, 2011).

Because *C. ribicola* is still spreading, it cannot be assumed that the realized niche of *C. ribicola* is fully occupied and defined by the current distribution in North America. Analyses of WPBR risk project that suitable habitat exists beyond its current distribution (Geils et al., 1999; Howell et al., 2006; Kearns et al., 2014). The absence of disease near forests infected with WPBR does not necessarily imply that the trees or species there are less susceptible to the pathogen. Some of these habitats may currently be “climate escapes” for WPBR (Van Arsdel, 1972). They may remain disease-free until (1) sufficient time elapses to allow the rust to spread, (2) *C. ribicola* strains evolve to overcome climatic or genetic barriers to colonization, or (3) climate or landscape conditions change and become more suitable for disease (or a combination thereof).

There are many points of intersection between climate, pathogen, and hosts, where a change in the environment can increase or decrease the frequency of wave years or the likelihood of disease (Hennon et al., 2020; Sturrock et al, 2011; Kolb et al., 2016). The current understanding of the WPBR–five-needle pine pathosystem provides clues as to how disease incidence or severity may be affected by a changing climate. Intervals of cool, moist conditions are needed for *C. ribicola* infection (Geils et al., 2010); therefore, a warmer, drier future may be expected to reduce the prevalence of conditions conducive to the spread of *C. ribicola* (Sturrock et al., 2011). However, this may not always be the case as warming may increase WPBR severity in moist habitats. For example, WPBR canker expansion rate on susceptible pines is greater on more vigorous trees and for trees on sites with longer growing seasons (Kearns et al., 2009). It would follow, therefore, that climate warming in high-elevation environments that are temperature-limited with ample water may extend the growing season and increase tree growth (e.g., Salzer et al., 2009; Bunn et al., 2018) causing trees to become more vulnerable to faster WPBR disease progression.

Numerous surveys have revealed a pattern of greater WPBR prevalence at mid-elevation sites compared to higher elevation sites within a pine host’s distribution early in the invasion process (e.g., Mielke, 1943; Burns, 2006; Smith and Hoffman, 2000; Kearns and Jacobi, 2007; Maloney, 2011a). This pattern further suggests a role of growing season length in the distribution of WPBR (Shepherd et al., 2018, Thoma et al., 2019) and therefore the potential for climate warming at higher elevations to facilitate WPBR spread uphill (Dudney et al., 2021). Likewise, seasonal climate warming in lower elevation water-limited ecosystems may reduce infections in pines because of stomatal closure caused by lower moisture availability or increased vapor pressure deficit (e.g., Pataki et al., 2000; Eamus et al., 2013; Thoma et al., 2019).

Topography creates microsite conditions that add spatial complexity to disease patterns. For example, krummholz mats above the alpine treeline can have a greater number of WPBR cankers than nearby solo trees or erect trees below the treeline (Resler and Tomback, 2008; Smith-Mckenna et al., 2013). A single exposure of 12–24 h of suitable weather can result in tree infections (Hirt, 1942), so an increase in short-term climate variability and rare climatic events, at any scale, may influence the frequency of wave years and disease dynamics.

The response of WPBR to changes in climate may also be influenced by plant community composition and disturbances at the landscape scale (Fig. 6). The risk of WPBR and its spread is greater in areas where pine hosts are close to alternate hosts (e.g., Newcomb, 2003; Kearns and Jacobi, 2007). The phenological matching of spore production on one host and the receptivity of the other host to infection is essential for disease development (see Mulvey and Hansen, 2011). Climate change may affect their respective habitats differently thereby altering the degree of phenological synchrony, or lack thereof, causing an increase or decrease in *C. ribicola* infection of either host (or both) (Maloney, 2011a). In addition, *Ribes* can proliferate within burned areas (e.g., Coop and Schoettle, 2009; Coop et al., 2010; Zambino, 2010); therefore, a climate change-driven increase in fire frequency and extent may indirectly increase WPBR risk and pressure on nearby High-5 forests. Likewise, increases in *Ribes* cover following subalpine forest mortality by spruce beetle (*Dendroctonus rufipennis* Kirby) may also increase WPBR risk to nearby five-needle pines (Carter et al., 2022). These are just a few simplified examples of possible climate-WPBR interactions. Climatic conditions interact with many components of the complex WPBR-five-needle pine pathosystem suggesting that the effects of a changing climate will not be easily predicted. The response may be context-dependent, where disease pressure may increase in some habitats and decrease in others, as expected for other diseases caused by rust fungi (Helfer, 2013).

Although the North American white pines did not historically coevolve with *C. ribicola*, and all the High-5 are highly susceptible, heritable (genetic) resistance to WPBR is present in each species providing an evolutionary pathway to adaptation to WPBR (King et al., 2010). There are two classes of genetic resistance to WPBR that differ in their genetic bases (1) major gene resistance, also called R gene resistance, qualitative resistance, or complete resistance, and (2) quantitative resistance, also called partial resistance or polygenic resistance (Kinloch, 2003; Sniezko and Liu, 2022). Although major gene resistance and quantitative disease resistance are often studied separately, genomic studies suggest that they should be considered as extremes along a continuum (e.g., Weiss et al., 2020) and may share phenotypes (Liu et al., 2021). Resistance to infection or disease development that can develop with tree age, called ontogenetic resistance, can allow older trees to remain free of disease symptoms, yet their young progeny may be highly susceptible to WPBR (King et al., 2010). Because the High-5 have resistance traits, albeit at low frequencies, the traits are available for selection to act on; the High-5 do not, at least initially, need to rely on the uncertain and very rare occurrence of de novo mutation as the source of resistance traits to WPBR.

The major gene resistance immunity response conferred by a dominant resistance gene (R gene) curtails disease progression in infected trees. R genes to *C. ribicola* are present in sugar pine (Cr1), western white pine (Cr2), SW white pine (Cr3), and limber pine (Cr4) (Kinloch and Dupper, 2002; Schoettle et al., 2014). Emerging genomic research suggests that Cr3 and Cr4 may be the same or similar R gene in SW white pine and limber pine (Liu et al., 2020, 2021), which may be explained by the historical natural hybridization of the two pine species (Menon et al., 2018). Because an R gene prevents disease development after infection (Kinloch and Dupper, 2002; Schoettle et al., 2014), they increase the fitness of the host in the presence of *C. ribicola*. Therefore, natural selection for the R gene resistance trait in forest stands can be rapid if rust pressure is high (Kinloch and Comstock, 1981). However, since the resistance is controlled by a single gene, a mutation in the rust can overcome the resistance response (Kinloch et al., 2004). Virulent *C. ribicola* races, vcr1 and vcr2, have evolved to overcome major gene resistance in sugar pine and western white pine, respectively (Kinloch and Dupper, 2002). Virulent rust strain(s) to Cr3 and Cr4 in SW white pine and limber pine have not yet been reported.

Quantitative resistance suppresses but generally does not prevent disease (King et al., 2010), though it may in some cases (Liu et al., 2021). Because several physiological mechanisms contribute to suppressing *C. ribicola*, quantitative resistance appears to be inherited via multiple genes (i.e., polygenic). Individuals show a continuum of susceptibility, theoretically depending on which and how many genes they have inherited that contribute to resistant phenotypes (King et al., 2010). The complex genetic basis of quantitative resistance traits makes them less likely to be overcome by the pathogen, so they are considered more durable than major gene resistance (Sniezko et al., 2020). However, the effectiveness of some quantitative resistance traits can be reduced by high *C. ribicola* infection (King et al., 2010; Jacobi et al., 2018b); therefore, quantitative resistance may be less durable under conditions of high WPBR pressure. Likewise, the growing environment can also tip the balance between fungal growth and tree defenses (Hunt, 2004, 2005; Parmesan, 2006; Zeglen et al., 2010; Maloney, 2011a; Hennon et al., 2020). The inconsistent expression of some quantitative resistance traits in seedling families among testing sites suggests that there may be a gene-by-environment interaction for these traits (Hunt, 2004; Sniezko et al., 2011). Consequently, phenotypic responses to climatic changes may alter the expression of resistance and the susceptibility of trees to disease (Stenlid and Oliva, 2016).

4.2. *Climate change-driven drought*

As the climate continues to get warmer and drier, its effects on the ecological interactions and processes that influence the High-5 can be expected to be context-dependent (Keane et al., 2017). Warming during periods of low water availability will increase the likelihood of water stress; while warming during periods with ample water availability may increase tree growth and extend the growing season. Climate change effects on precipitation patterns are harder to predict than temperature increases, especially in complex terrain (Hock et al., 2019). However, even if precipitation remains unchanged, rising temperatures amplify evaporative demand which can lead to drought stress in trees (Ficklin and Novick, 2017; Grossiord et al., 2020). Resulting heat-induced drought stress is already causing increased mortality in subalpine forests (Stephenson, 1990; Allen et al., 2010, 2015; Millar et al., 2012; Elliott et al., 2020). However, at the alpine treeline, as mentioned in the previous section, climate warming may lengthen the growing season and cause increased radial growth in some High-5 populations if ample water is available (Bunn et al., 2018). Salzer et al. (2009) identified a sharp elevational threshold where the positive correlations between temperature and radial growth reverse and become negative at short distances below upper treeline. For example, Bunn et al. (2018) found that in the White Mountains (California) growth of GB bristlecone pine is limited by temperature in habitats where the seasonal mean temperature is $<$ 7.5 ˚C, while tree growth in habitats with warmer seasonal mean temperature is limited by moisture. Consequently, climate warming is likely to shift a greater proportion of the subalpine and treeline ecosystems from temperature-limited to water-limited, thereby increasing the risk of drought stress that can hinder growth and seedling establishment (Moyes et al., 2013, 2015; Bunn et al., 2018). Adaptation, or lack thereof, to prolonged drought and climate extremes will influence the future distributions of the High-5.

4.3. Stressors that can compromise High-5 adaptation to white pine blister rust and drought

4.3.1. Mountain pine beetle (MPB)

Recent MPB outbreaks have caused large-scale mortality in North American five-needle pines (Fig. S1 in Supplemental Material). Historically, MPB has been a natural disturbance agent that contributes to the overall health of western forests, including those with High-5 species (e.g., Logan et al., 2010). However, current outbreaks are occurring in habitats where they previously have not or were limited in extent or duration (Cudmore et al., 2010; Logan et al., 2010; Raffa et al., 2013; Jactel et al., 2020; Lehmann et al., 2020). While MPB is native to North America, it is now behaving as a novel stressor in some High-5 populations; for example, some whitebark pine populations exhibit many characteristics of a naïve host thereby showing little evidence of past co-evolution with MPB (Raffa et al., 2017). Increasing minimum winter temperatures in the past decades have led to higher survival of over-wintering broods in some high-elevation and high-latitude forests (Logan et al., 2010). The range expansion has also increased the risk of attack in some High-5 habitats that are not suitable for brood development from beetle sources outside of the stand (Bentz et al., 2022).

MPB alone have not threatened the persistence of High-5 species; however, in combination with WPBR, this additive mortality factor can significantly affect the adaptive capacity and survival of High-5 populations. MPB generally attack and kill only trees that are larger than 15.2 cm at breast height (Logan et al., 2010) (Fig. 6). For the slow-growing High-5, mature cone-bearing trees lost to MPB can take a century or more to replace, thereby reducing the reproductive capacity of the population during that time. Trees stressed by drought, disease, or other insects can be particularly susceptible to attack by MPB (see Kolb et al., 2016; Larson and Kipfmueller, 2012; note the exception for severe disease reported by Dooley and Six, 2015; Cardinal et al., 2022). Under epidemic conditions, however, MPB is less discriminating; it attacks and kills healthy trees (Gibson et al., 2008), including those that have genetic resistance to WPBR (e.g., Shepherd et al., 2018). Mortality by WPBR of newly established trees slows forest recovery after a MPB epidemic. However, the shift to a younger forest following MPB-caused mortality may accelerate selection by WPBR for resistance but will only benefit High-5 populations if the number of individuals remaining and their genetic composition can support continued persistence (Schoettle and Sniezko, 2007; Larson, 2011).

Ecological context, including the climatic conditions, landscape mosaic of forest types and size classes, stand densities, and relative abundance of host species in mixed-species stands sets the stage for High-5 exposure to MPB (see Bentz et al., 2010; Millar et al., 2012; Anderegg et al., 2015). There are, however, fundamental differences among High-5 species in their constitutive chemical defense capabilities to defend against MPB (Bentz et al., 2022). Limber pine and whitebark pine have low levels of defenses, RM bristlecone pine and SW white pine have moderate defense levels, though they can be overwhelmed during epidemics, and foxtail pine and GB bristlecone pine have the highest levels of constitutive chemical defenses; GB bristlecone pine is the least susceptible High-5 species to MPB (Bentz et al., 2017; Bentz et al., 2022).

4.3.2. Fire

Although the impact of climate change varies with latitude, elevation, ecoregion, and local topography, increasing temperature and altered hydrology are driving increases in fire size, frequency, and severity across western North America (Westerling, 2016; McKenzie and Littell, 2017; Halofsky et al., 2020), with implications for the High-5 pines. These large-scale mortality events can delay or disrupt adaptation to WPBR or drought (or both) by reducing population size and recovery capabilities and directly killing trees with desirable traits.

The increasing area burned and severity of fires have been documented for the Pacific Northwest (Cansler and McKenzie, 2014; Westerling, 2016; Halofsky et al., 2020), Sierra Nevada and Cascade Ranges (Miller et al., 2009), northern and central Rocky Mountains (Westerling, 2016; Higuera et al., 2021) and the southwestern U.S. (Westerling, 2016). These changing regimes have most strongly affected lower elevation forests, which experience warmer temperatures and declining moisture (e.g., Gergel et al., 2017). Subalpine elevations are also experiencing rapid changes in fire regimes, the product of increasingly severe fire seasons resulting from low snowpack and aridity, expressed as an upward trend in vapor pressure deficit (Davis et al., 2019; Higuera et al., 2021). Several of the High-5 pines are early successional pioneers in seral communities, whereby they require the “right amount” of fire given that these stands exhibit declining basal area caused by fire suppression but risk extirpation from too much fire (Arno and Hoff, 1990; Keane, 2018; Keane et al., 2021).

Pines, including the bristlecones and foxtail, that inhabit arid high-elevation sites with little understory vegetation and low fuel loads have historically been less vulnerable to fire in general. However, climate warming projections coupled with fuel measurements suggest that denser, drier lower-elevation forests, especially under extreme conditions including high winds, will carry fire upslope, placing these High-5 species at greater risk for population losses (e.g., Gray and Jenkins, 2017). A comparatively recent fire history, however, indicates that the recent large fires of the high-elevation forests of Madrean and Mogollon Plateau sky islands, which include SW white pine, are within the historical range of variability (Margolis et al., 2011).

Historically, the cool, moist climate of subalpine forests limited fire occurrence to centuries-long return intervals, but this is rapidly changing (Halofsky et al., 2020; Higuera et al., 2021). Climate change is increasing fire severity and shortening fire return intervals for subalpine elevations across the west. For example, for the southern Rocky Mountains Higuera et al. (2021) describe five extreme fire seasons since the year 2000, which account for 99% of subalpine forests burned since 1984; the 2020 fires accounted for 72% of the burned subalpine area alone. These same subalpine forests are home to patchy distributions of RM bristlecone pine and limber pine, with the latter species occurring from lower to upper treeline (Fig. 2) (Schoettle and Rochelle, 2000). Similarly, fires in subalpine forests in the northern Rocky Mountains, Sierra Nevada, and Cascades, and southwest are experiencing increasing fire severity and area burned (e.g., Westerling, 2016; Gergel et al., 2017; Halofsky et al., 2020, Higuera et al., 2021; Keane et al., 2021). The combination of decreasing fire return intervals and larger and more severe fires in higher elevation High-5 forests may create conditions outside the range of historical variability with implications for both recovery and long-term persistence (e.g., Coop and Schoettle, 2011; Pansing et al., 2020).

Increasing soil temperatures, declining soil moisture, and increasing vapor pressure deficit are not only altering fire regimes but impeding recovery of burned forests. For example, in the northern Rocky Mountains, recovery in whitebark pine has been impeded by a combination of increasingly unfavorable conditions for seed germination and seedling survival and extensive seed source mortality from WPBR and MPB (e.g., Leirfallom et al., 2015; Stevens-Rumann et al., 2018; Hansen et al., 2021). These combined effects are currently impacting other High-5 species, where regional damage and mortality to cone-bearing trees from WPBR or MPB (or both) are high such as in limber pine and across the fire-prone SW white pine forests in the southern Rocky Mountains. Seed sources will increasingly become limiting as WPBR spreads and intensifies and with future MPB outbreaks.

Other effects of changing fire regimes include the increasing occurrence of reburns, which between 1984 and 2016 impacted nearly 10% of the western forested landscape (Buma et al., 2020). Reburns are occurring more frequently, but their effects depend on their return intervals relative to fuel accumulation and conifer regeneration (Prichard et al., 2017). For example, reburns were more likely in areas that burned 10 to 20 years prior than 5 years prior (Buma et al., 2020). Major challenges to the High-5 pines are “immaturity risk” (Keeley et al., 1999), which refers to the potential immaturity of seed sources as previously burned areas are reburned, and the related challenge of “interval squeeze,” which suggests that slower rates of seedling recruitment, growth, and survival under increasingly unfavorable conditions and more frequent fire could alter communities or shift them to other community types (Enright et al., 2015). The High-5 pines are generally vulnerable to these effects, because of their delayed maturity.

4.3.3. *Other interactions, insects, pathogens*

Climate stress can predispose the pines to be more vulnerable to native insects, and insects and diseases can predispose the pines to be more vulnerable to climate impacts (Parmesan, 2006; Sturrock et al., 2011; Weed et al., 2013; Hennon et al., 2020). In droughted environments, it has been suggested that *Ips woodi* Thatcher may be switching roles from a secondary to a primary pest causing direct limber pine mortality (Witcosky, 2017). Twig beetles (*Pityophthorus* spp. and *Pityogenes* spp.) attack smaller diameter trees or smaller diameter branches in the crowns of larger trees and can also lead to tree mortality. For example, 51% of limber pines classified as declining or dying in the Rocky Mountains had evidence of twig beetle attack (Burns et al., 2011). Cone and seed insects can cause significant loss of seed in SW white pine range-wide (DePinte et al., 2020; Leal-Sáenz et al., 2021), limber pine and RM bristlecone pine in the southern Rocky Mountains (Schoettle and Negron, 2001; Williams et al., 2020; Schoettle, unpublished data), whitebark pine in the U.S. (Kegley et al., 2001b), and GB bristlecone pine in the Great Basin (Barber, 2013).

Dwarf mistletoe species (*Arceuthobium* spp.) are semiparasitic plants that photosynthesize but siphon water and mineral nutrients from the host plant. They amplify the impacts of drought stress on trees such that High-5 trees infested with dwarf mistletoe use more water and experience greater water stress and mortality than uninfected trees, regardless of the drought tolerance of the pine (Robinson and Geils, 2006; Glatzel and Geils, 2009; Zweifel et al., 2012; Kolb et al., 2016). Each High-5 species is host to at least one dwarf mistletoe species (*Arceuthobium* spp.) (Table S1 in Supplemental Material). The distribution of dwarf mistletoe is patchy in the U.S. and Mexico and less of a forest health issue for the High-5 in Canada (Table S2 in Supplemental Material). The occurrence of dwarf mistletoe is more restricted at higher elevations than their hosts (Hawksworth et al., 2002) suggesting that range expansion may ensue with climate warming. Because dwarf mistletoe intensifies drought stress in its pine host, it can also be an inciting factor for MPB and other bark beetle attacks (Scott and Mathiasen, 2012; Klutsch and Erbilgin, 2018).

In combination with WPBR, other mortality factors that are episodic (e.g., MPB, drought), unpredictable (e.g., fire, climate extremes), and persistent (e.g., dwarf mistletoe, twig beetles, seed and cone insects) can reduce High-5 species fecundity or increase mortality (or both) and influence the risk of population extirpation (Fig. 6) (see Gomulkiewicz and Holt, 1995; Kimmel et al., 2022). Climate change adds further interactions, risks, and uncertainty. Native pests and pathogens that historically were relatively unimportant, may become more important as stressors under the changing climate (Hennon et al. 2020). These additive mortality agents, or stochastic mortality factors as described by Carlson et al. (2014), increase the risk of population extirpation during adaptation to other stressors.

5. Current Condition, Adaptive Capacity, Migration Potential, and Outlook for each High-5 species

Whether each High-5 species can adapt to WPBR and climate-driven drought will depend on exposure and specific rates of mortality induced by these primary stressors, the frequency of heritable traits that increase survival under exposure to these stressors, the population’s ability to regenerate to offset mortality of maladapted individuals, and the confounding effects of other coincident mortality and stressor agents to which they are exposed (Fig. 6). In theory, if the cost of selection is too high, populations will be extirpated (Haldane, 1957).

5.1. *Whitebark pine*

5.1.1. *Primary stressors of whitebark pine*

WPBR is a leading cause of whitebark pine mortality (Tomback et al., 2011; Shanahan et al., 2016; U.S. Fish and Wildlife Service, 2018) and the greatest threat to long-term viability of the species (Goeking et al., 2019). A strong positive relationship exists between WPBR incidence and latitude at a range-wide level (Fig. 7). Incidence of WPBR and whitebark pine tree mortality are highest in the northern U.S. Rocky Mountains and adjacent regions in Canada, exceeding 90% in some stands (Kendall and Keane 2001; Keane et al., 2012; Smith et al., 2013b; Fiedler and McKinney, 2014; Goeking and Izlar, 2018). Incidence of WPBR and tree mortality are lowest in the southern part of whitebark pine’s range, where, for example, incidence ranges between 0% and 2% in the southern Sierra Nevada (Nesmith et al., 2019; Dudney et al., 2020). This broad geographic relationship may be due to transmission dynamics and climate, reflecting the time–space relationship of spore transmission from introduction points as well as climate suitability. Within the broad trend of increasing WPBR infection incidence with increasing latitude, incidence can be highly variable at finer spatial levels (i.e., among sites within regions, Fig. 7), influenced by local environmental conditions.

Water availability is believed to determine the southern latitudinal extent of whitebark pine throughout its range and its lower elevational limit in some locations (Tomback et al., 2001b). Drought conditions are associated with low germination and seedling survival rates in whitebark pine (McCaughey, 1990). Whitebark pine is a snowpack-dependent species (Tomback et al., 2011) and, therefore, observed and predicted changes to snowpack from climate warming will have negative effects on population viability. For example, whitebark pine regeneration density in the arid Great Basin increases with increasing spring snowpack (Hankin and Bisbing, 2021). The proportion of precipitation in the form of snow is expected to decrease while the proportion in the form of rain is expected to increase in the western U.S. (Moore et al., 2017), and this would further impact the regeneration niche of whitebark pine

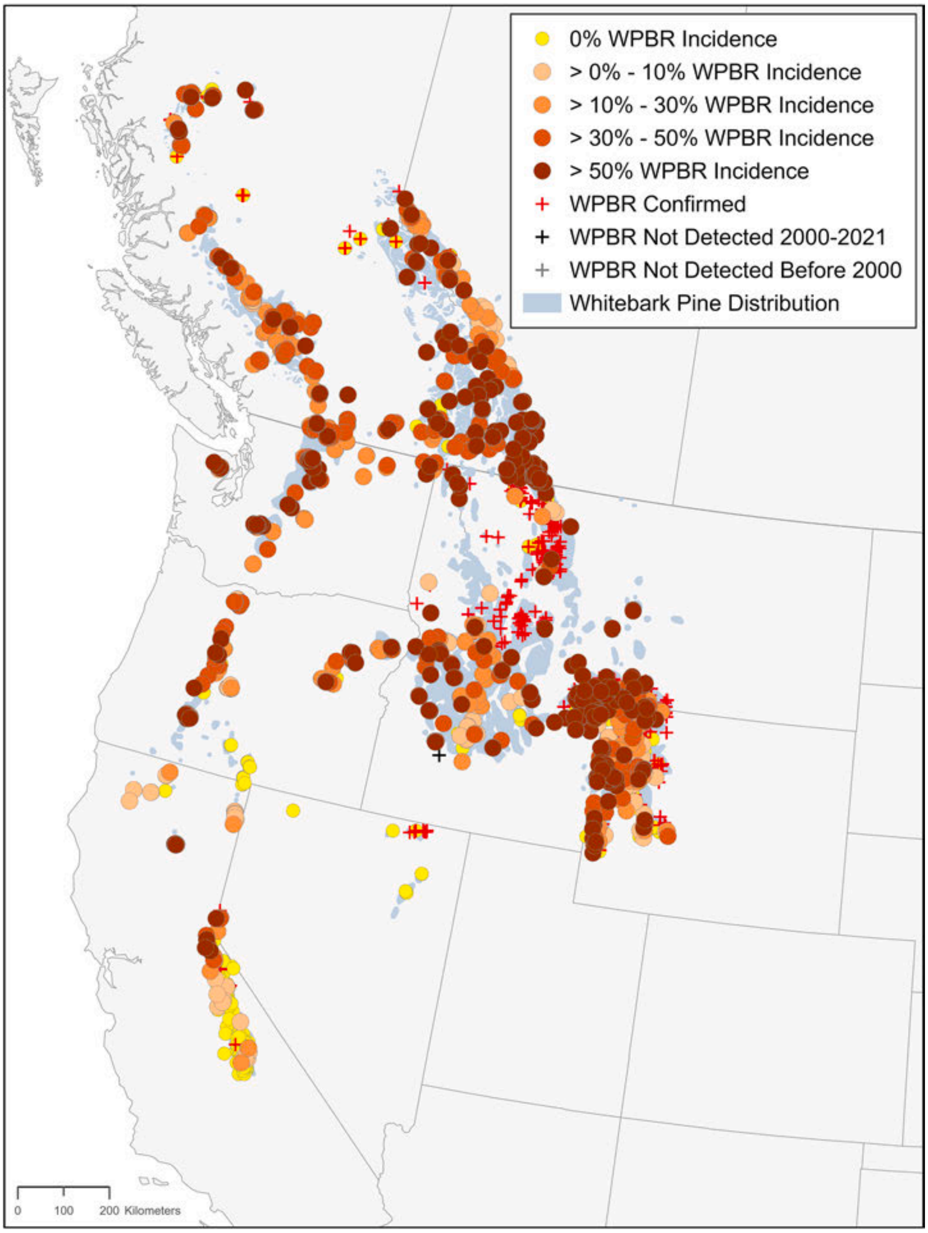

Fig. 7. The incidence of white pine blister rust (WPBR) on whitebark pine (PIAL) in western North America as of 2021. WPBR incidence was calculated for trees above a height of 1.3 m as the number of live infected trees divided by the total number of live five-needle pine trees, times 100. All depicted WPBR incidence data are from field plots. Red crosses indicate areas where rust is present, but incidence data are unavailable. Black crosses indicate areas where WPBR has not been detected in whitebark pine in recent surveys (since 2000), but plot data are not available. Gray crosses indicate areas where WPBR was not detected in whitebark pine before 2000 and no current data are available. The distribution of whitebark pine is displayed in gray (see Fig. 2 for data source). See Supplemental Material for data sources and field methods. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Hankin and Bisbing, 2021). Furthermore, young age classes of whitebark pine are less tolerant of heat and drought than older trees, and the regeneration niche is estimated to have shifted upward in elevation in recent decades in some regions (Hansen et al., 2021).

Higher whitebark pine mortality from MPB infestation has been attributed in part to drought stress in Montana and Wyoming (Shanahan et al., 2016), and whitebark pine trees in California that experienced multi-year drought later succumbed to MPB attack (Millar et al., 2012). Within-region variability in drought is linked to heterogeneous topographic and soil conditions, leading to spatial heterogeneity in whitebark pine mortality from MPB (Cartwright, 2018). In the southern Sierra Nevada, climate warming associated with drought has moved the expanded WPBR distribution to higher elevations and into the whitebark pine zone, potentially increasing future incidence of WPBR in whitebark pine (Dudney et al., 2021). Drought coupled with increasing temperatures has also been linked to greater wildfire severity and tree mortality in the western U.S. (Crockett and Westerling, 2018) (see Section 4.3.2).

5.1.2. *Adaptive capacity of whitebark pine*

Overall, whitebark pine is doing poorly with estimates of more standing dead than live trees are reported throughout its U.S. range (Goeking and Izlar, 2018). However, heritable resistance to WPBR has been confirmed for whitebark pine in controlled screening trials (e.g., Mahalovich et al., 2006; Sniezko et al., 2014), which in part explains differential survival among whitebark pine trees in stands heavily impacted by WPBR. Surviving whitebark pine trees from high-mortality stands have a much greater probability of having a higher heritable resistance level than trees from low-mortality stands (Hoff et al., 1994) as a result of selection by WPBR in natural populations. For example, in high mortality stands, resistance frequencies have been estimated from about 25% (Sniezko et al., 2007) to nearly 50% (Mahalovich et al., 2006), with natural background levels (i.e., pre-WPBR) believed to have been very low (~1%) (Hoff et al., 2001).

Whitebark pine is drought tolerant relative to most sympatric conifer species (Tomback et al., 2001b), but early seedling survival depends on moisture availability. Evidence is emerging that drought tolerance varies over the landscape at fine scales and has a genetic basis (e.g., Lind et al., 2017). Pollen evidence demonstrates that whitebark pine south of the glacial maximum has occupied most of its current range for tens of thousands of years, suggesting that the species is capable of withstanding varied climatic conditions, including drought, that are different from current conditions. For example, whitebark pine was at a higher relative abundance in Wyoming during the warmer climatic period 10,000 years ago (Iglesias et al., 2015). However, the contemporary rate of climate warming is greater than in the past, which could affect the potential for adaptation. A genetic basis for slower growth exists in some conifer species, and slower growing trees may be more drought-tolerant (Moran et al., 2017; Six et al., 2021).

Resistance gene frequencies and population sizes need to increase over time for whitebark pine populations to become adapted to the novel environment. Given that whitebark pine is dependent on Clark's nutcracker for seed dispersal (e.g., Tomback, 1982), demographic factors could constrain population adaptation and recovery. If Clark's nutcrackers do not remove seeds from whitebark pine's indehiscent cones and cache them in a suitable location, whitebark pine does not regenerate. This relationship is not only elegant but also successful across the millennia. Clark's nutcrackers cache whitebark pine seeds in recently disturbed sites, effectively providing whitebark pine an advantage in colonizing early successional habitats over long distances from source trees (greater than 30 km, Tomback et al., 2001a; Lorenz et al., 2011)—much farther than wind-dispersed species (Tomback et al., 1990). However, the dramatic declines in some whitebark pine populations and reduced cone production means fewer seeds for Clark's nutcrackers to disperse.

Although Clark's nutcrackers are coevolved with whitebark pine, they are also adapted to harvest and cache other conifer seeds, which sustains the mutualism (Tomback and Linhart, 1990). Clark's nutcrackers are less likely to forage in whitebark pine communities where seed rewards are low (McKinney and Tomback, 2007; McKinney et al., 2009; Barringer et al., 2012). Live whitebark pine basal area strongly correlates with seed cone density (McKinney et al., 2009), so cone abundance and energy reward are likely the environmental cues Clark's nutcrackers use to determine whether they will visit and remain in whitebark pine stands through the period of seed dispersal (late summer and fall) (McLane et al., 2017). High mortality stands have low seed production, and seeds can often be entirely consumed by American red squirrel (*Tamiasciurus hudsonicus*) and Clark's nutcrackers (McKinney and Tomback, 2007; McKinney et al., 2009; McKinney and Fiedler, 2010). This is problematic because seeds from surviving trees are most likely to have genes that confer resistance to WPBR (McKinney and Tomback, 2007). Without Clark's nutcracker seed dispersal and seedling establishment, not only is regeneration limited but resistant alleles will not increase in subsequent generations.

5.1.3. *Migration potential of whitebark pine*

The seed dispersal and caching behavior of Clark's nutcrackers and the pine's ability to establish and grow on recently disturbed harsh sites suggest that whitebark pine possesses the ability to colonize areas beyond its current range. Further, Clark's nutcrackers cache whitebark pine seeds in other forest types and whitebark pine seedlings establish in sites currently unoccupied by mature whitebark pine (Goeking and Izlar, 2018), as well as above treeline and below forests containing mature whitebark pine (Tomback, 1978; Lorenz et al., 2011; Tomback et al., 2016).

There is evidence of whitebark pine range shifts over longer time periods, including colonization of previously unoccupied regions. For example, whitebark pine was absent in the northern Cascades during the Pleistocene but was colonized from two separate geographic and genetically distinct regions during the early Holocene (Richardson et al., 2002). Late Pleistocene to early Holocene postglacial colonization from established whitebark pine regions is believed to have occurred in at least three regions in western North America where distinct groupings of genomic variants occur today (Richardson et al., 2002). Richardson et al. (2002) conclude that whitebark pine distribution has been closely tied to climate change and associated glacial advance and retreat, which have led to changes in the species' range facilitated by Clark's nutcracker seed dispersal.

Empirical evidence also suggests that whitebark pine can establish and grow in sites beyond its current range limits. Seeds planted as far as 800 km northwest of the observed northern boundary of whitebark pine's extent germinated, grew, and survived for at least three years (McLane and Aitken, 2012). Survival of seedlings was directly related to seed mass and warmer summers, and negatively related to later snowmelt dates (McLane and Aitken, 2012). The latter finding is notable because seedling survival within the current range is positively associated with spring snowpack, which may indicate that beyond the current northern range boundary, whitebark pine seedling survival may be more limited by the amount of time exposed to sunlight (i.e., not buried in the snowpack) than in more southern areas where it currently exists. However, the missing link here is Clark's nutcracker, which does not occur consistently at the current northern limits of whitebark pine, let alone farther north, because of limited dependable whitebark pine seed production and lack of alternative seed resources (Keane et al., 2017; Clason et al., 2020). The northern limits of Douglas-fir (*Pseudotsuga menziesii*), a seed source that Clark's nutcracker also uses, coincide with the northern limits of whitebark pine (Keane et al., 2017). If whitebark pine cone production increases at the northern limits and Douglas-fir moves northward with climate warming, Clark's nutcracker potentially may enable a northward shift in whitebark pine's range as well.

Results from climate and species distribution modeling also suggest that whitebark pine could expand beyond its current range limits. At the southern extreme of whitebark pine's range, modeling results indicate whitebark pine could migrate farther south into higher-elevation habitats in the southern Sierra Nevada (Moore et al., 2017).

5.1.4. *Outlook for whitebark pine*

The conditions for evolutionary rescue do not portend a bright outlook for whitebark pine. Individuals and populations are negatively affected by both abiotic and biotic stressors. Population sizes have been reduced throughout much of the range because most individuals are highly susceptible to WPBR. Genetic variation among populations is moderate relative to other conifers; however, within-population variation is high and polygenic heritable resistance to WPBR exists, offering some hope for adaptation with management. In addition to the basic conditions for evolutionary rescue, whitebark pine has other ecological constraints, namely reliance on Clark's nutcracker for seed dispersal, nutcracker sensitivity to cone densities that are inversely related to tree mortality, and high rates of seed predation. Whitebark pine is a long-lived species and individuals are slow to mature; therefore, individuals must withstand exposure to stress for decades before reproduction. Finally, whitebark pine populations that have declined from WPBR-caused mortality are at risk of extirpation from MPB outbreaks and large and severe wildfires. These additive mortality factors are strongly associated with climate warming and drying and therefore more likely to continue to threaten whitebark pine population viability over time.

The biogeographic history of whitebark pine demonstrates that the species can adapt and overcome environmental change. The mutualism with Clark's nutcracker has allowed whitebark pine to colonize new areas following major climatic events over long time periods and establish on disturbed sites in contemporary times. However, the rate and severity of stress-induced decline make it doubtful that many populations will adapt and recover via evolutionary rescue without forest management (i.e., restoration) to increase frequencies of WPBR-resistant genotypes and assist in the recovery of whitebark pine to ensure long-term population viability.

5.2. Limber pine

5.2.1. Primary stressors of limber pine

The incidence of WPBR is unevenly distributed across limber pine's extensive range (Fig. 8). This disease is a primary stressor in some areas of the Rocky Mountains, newly spreading and intensifying in other areas, and currently low or absent in the drier portions of limber pine's distribution (see Fig. 8) (Jacobi et al., 2018a). Incidence of WPBR in live limber pine in Canada increased overall from 33% to 43% between 2003 and 2004 and 2009, exceeding 50% on average by 2019 (B. Shepherd, unpubl. data) continuing to put some populations at risk for extirpation. In southwestern Montana, Wyoming, and northern Colorado, 73% of stands have been invaded by *C. ribicola* with an average WPBR incidence of 26%, an increase of 6% over 8–9 years (Cleaver et al., 2015). In the more recently invaded landscape in southern Colorado, WPBR incidence averaged 14% and ranged from 0% in the drier habitats to 56% in the

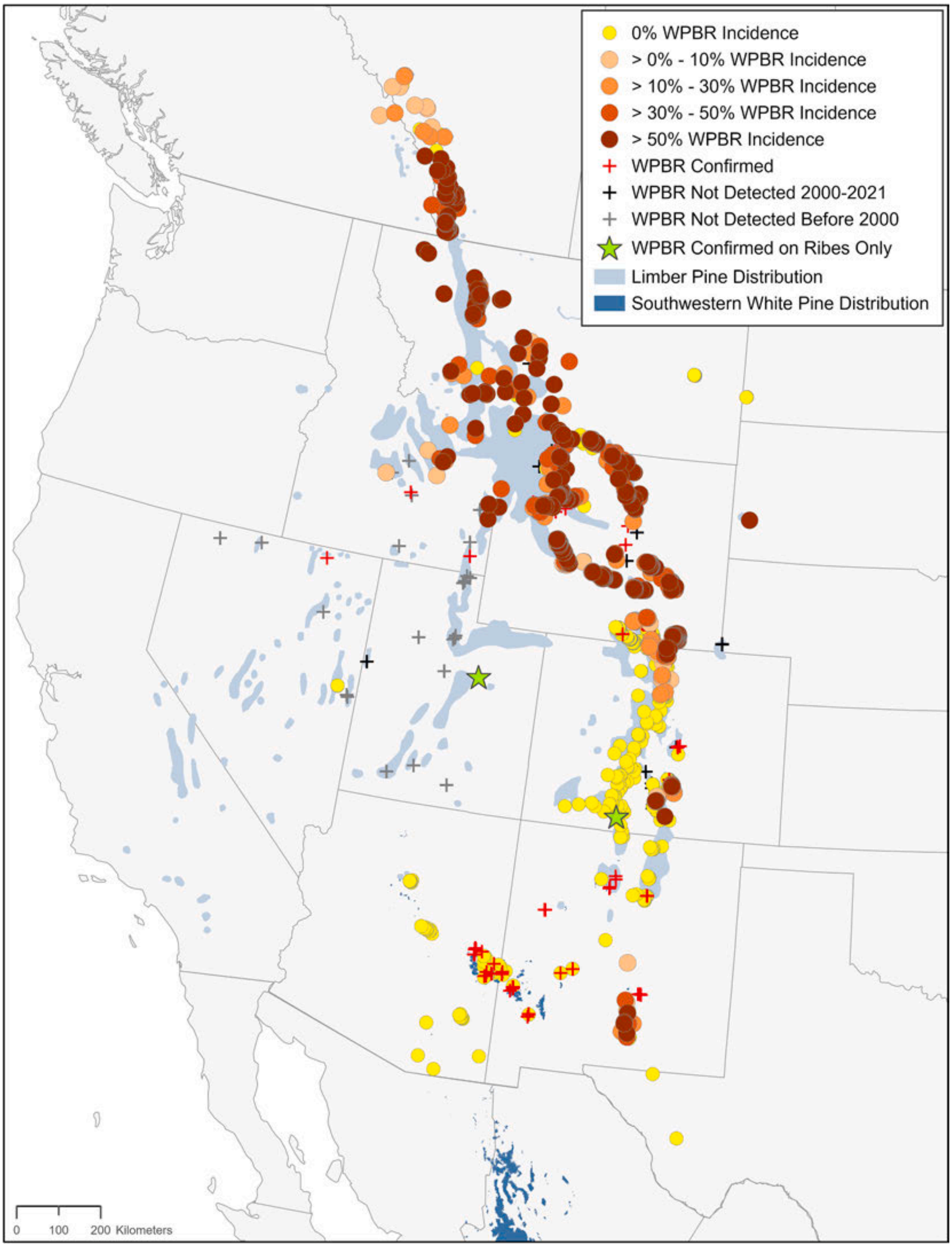

Fig. 8. The incidence of white pine blister rust (WPBR) on limber pine (PIFL) and southwestern white pine (PIST) in western North America as of 2021. Symbols and incidence are as described in Fig. 7 shown here for limber pine and southwestern white pine. Limber pine distribution is in light blue and southwestern white pine is in darker blue (see Fig. 2 for distribution sources). Limber and southwestern white pine are known to hybridize along the Colorado and New Mexico border and southward into the Colorado Plateau, so precise pine species assignments in the plots were not possible. WPBR has not been found in the southwestern white pine distribution in Mexico or on limber pine in California (Maloney, 2011a; plot locations are not available). See Supplemental Material for data sources and field methods. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

more mesic areas (Burns, 2006). Risk analysis modeling using climate variables projects that 41–53% of limber pine habitat is at risk for WPBR in Colorado and 61–79% is at risk in Wyoming (Kearns et al., 2014). Recent spread in this area is consistent with these projections (Burns and Schoettle, 2018; Schoettle et al., 2018a). Limber pine, along with whitebark pine, is infected in a localized area of northeastern Nevada (Vogler and Charlet, 2004; Vogler et al., 2017b), but WPBR has not yet been found on limber pine in California, Oregon, or Utah (Maloney, 2011a; Dunlap, 2012); *C. ribicola* has been identified only on *Ribes* in Utah (Vogler et al., 2017a). Aridity and mismatched phenologies among the pine, alternate hosts, and pathogen may contribute to this distribution (Smith et al., 2000; Vogler and Charlet, 2004; Vogler et al., 2017b), but whether these limitations will be affected by climate change is not known. Populations of limber pine are in different stages of the adaptation process across its distribution (see Fig. 4). In southern Alberta, WPBR has likely challenged most of the limber pine populations (Smith et al., 2013a), and they may be approaching the population minimum of the natural selection curve (phase 2 in Fig. 4). Many of these populations were lost in the Kenow Fire in 2017 (Buunk, 2021). In other areas, WPBR selection has not begun on limber pine (see Fig. 8).

Climate change-driven drought will be a key stressor across the range of limber pine and especially in the drier portions of the distribution. Drought-caused mortality of mature limber pine trees is associated with long-term cumulative, rather than short-term acute, climate stress in the Rocky Mountain eastern front of Alberta, the southwestern U.S., and the Sierra Nevada (Millar et al., 2007; Kane and Kolb, 2014; Smith et al., 2015; Millar et al., 2015). Recent mortality of limber pine by drought has been substantial but often lower than for other less tolerant co-occurring species in some areas (Kane et al., 2014). Accordingly, community composition and competitive interactions are likely to shift due to climate change alone; these shifts may be to limber pine's advantage, increasing its role in some western forests in the future if WPBR remains rare (Windmuller-Campione and Long, 2016; Kueppers et al., 2017). In contrast, in the Greater Yellowstone Ecosystem, limber pine growth is correlated with both cool-season and warm-season precipitation as well as with snowpack, suggesting that limber pine in this area is more vulnerable than co-occurring lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) to the predicted decline in snowpack and increase in drought conditions (Dye et al., 2022).

5.2.2. *Adaptive capacity of limber pine*

Limber pine has genetic resistance to WPBR and drought tolerance traits, so there is potential for adaptation to each stressor. However, although limber pine has both heritable major gene resistance and quantitative resistance to WPBR, the frequency of the more durable quantitative resistance appears to be very low (Stephan, 1986; Bingham, 1972; Hoff et al., 1980; Schoettle et al., 2014; Jacobi et al., 2018b; Schoettle et al., 2022). The frequency of quantitative resistance traits may be too low in limber pine to sustain viable populations when under high natural selection pressures without active management.

Major gene resistance to WPBR in the southern Rocky Mountains is present at a higher frequency in limber pine populations, even those that have not yet been invaded by *C. ribicola*, than the R genes in other white pine species (Schoettle et al., 2014). The same R gene (called Cr4) as found in limber pine in the southern Rocky Mountains has also been detected in Alberta, albeit at a lower frequency (Sniezko et al., 2016; Liu et al., 2020). The R gene appears rare in other portions of the range (Schoettle et al., unpubl. data). Why the northern Colorado and southern Wyoming area is a hot spot for Cr4 is not understood (Schoettle et al., 2014; Vogan and Schoettle, 2015, 2016; Holtz and Schoettle, 2018). A genetic marker for the Cr4 resistance allele is under development to accelerate the detection of trees with resistance and to distinguish major gene resistance and quantitative resistance (Liu et al., 2016, 2019, 2020, 2021). This technology will enable tracking of the resistance allele frequency in populations in real-time as natural selection proceeds under pressure from WPBR and to assess the impacts of other disturbances (e.g., MPB) on that trajectory. A virulent *C. ribicola* strain, vcr4, that can overcome this resistance in limber pine has not yet been reported, so its spread dynamics and, therefore, the utility of Cr4 to limber pine's future, is uncertain.

Limber pine has many traits that confer drought tolerance. Evidence suggests that they are heritable and vary geographically (e.g., Pataki et al., 2000; Fischer et al., 2002; Adams and Kolb, 2004, 2005; Letts et al., 2009; Borgman et al., 2015; Lazarus et al., 2018; Liu and Biondi, 2020). Limber pine has a strong stomatal response to vapor pressure deficit (VPD), which limits water loss under highly evaporative conditions and thereby conserves hydraulic function (Pataki et al., 2000; Letts et al., 2009; Reinhardt et al., 2011, 2015; Fischer et al., 2002; Liu and Biondi, 2020). At upper elevational range edges, climate warming is shifting limber pine's growth from temperature-limited to water-limited (Adams and Kolb, 2004, 2005). Limber pine can grow in some grassland habitats because its deep tap root can access groundwater thereby decoupling its water supply from local precipitation patterns (Roberts et al., 2004). Because of the species' drought tolerance, the rate of population decline in response to drought stress (phase 1 in Fig. 4) may be less than that for other High-5 species. Cr4 and drought tolerance are mildly correlated, so as the frequency of Cr4 increases in a population, it may have greater drought tolerance than pre-invasion limber pine populations (Vogan and Schoettle, 2015, 2016). A higher frequency of Cr4 could occur through natural selection in the field or artificial selection and planting by management. This may be one instance where adaptation to drought and WPBR may work in concert.

Unlike some other early seral species, seedling establishment by limber pine is slow after disturbance. Individuals accumulate over decades, generating an uneven age structure (Brown and Schoettle, 2008; Cleaver et al., 2016; Windmuller-Campione and Long, 2016; Goeking and Windmuller-Campione, 2021). Fire has played a historical role in the metapopulation dynamics of limber pine (Webster and Johnson, 2000). Post-fire colonization can vary across the landscape with successful establishment within decades after fire in some areas and only sparse establishment in others (Coop and Schoettle, 2009, 2011; Dawe et al., 2020; Kilpatrick and Biondi, 2020), suggesting that the seedbed and lack of competition are not the only factors contributing to seedling establishment. A clear relationship between fire and regeneration for limber pine is not apparent at its northern range limit (Peters and Visscher, 2019; Dawe et al., 2020). Sparce canopy cover and nurse objects can help seedling establishment under harsh conditions (Coop and Schoettle, 2009; Casper et al., 2016; Dawe et al., 2020; Hankin and Bisbing, 2021); with climate warming these conditions may be increasingly important. Distance to a seed source and soil substrate also play a role in regeneration densities (Coop and Schoettle, 2009; Smithers, 2017), though high seed availability is not always a good predictor of regeneration success (Peters and Visscher, 2019). Under low selection pressures, limber pine regeneration may be sufficient to support population growth and offset mortality.

Both adaptation to WPBR and climate warming may be slowed or derailed by high mortality of limber pine caused by MPB and other stressors (see Section 4.3). Early reports of limber pine as a preferred MPB host (Langor et al., 1990) are consistent with the recent studies of low constitutive chemical defenses (Bentz et al., 2022) and observed high MPB-caused mortality in 75% of limber pine plots in the U.S. Rocky Mountains (Cleaver et al., 2015). MPB and wildfire have already killed known WPBR-resistant limber pine trees in the field (Buunk, 2021; Schoettle, pers. comm.) and are projected to continue to threaten these forests in the future (Gibson et al., 2008; Parks and Abatzoglou, 2020; Higuera et al., 2021). Dwarf mistletoe is a serious forest health concern for limber pine in the southern portion of its distribution. Until the recent MPB epidemic, limber pine dwarf mistletoe (*Arceuthobium cyanocarpum* (A. Nelson ex Rydb.) A. Nelson) was the second most damaging agent of limber pine behind WPBR in the central and southern Rocky Mountains (Cleaver et al., 2015; Kearns and Jacobi, 2007; Taylor and Mathiasen, 2002). Twig beetles and cone and seed insects are common in limber pine in the southern Rocky Mountains (Schoettle and Negron, 2001; Burns, 2006; Williams et al., 2020) and their expected responses to climate warming are uncertain (Jactel et al., 2019).

5.2.3. Migration potential of limber pine

Limber pine has a high migration potential to escape climate warming because of long-distance seed dispersal by Clark's nutcracker beyond its current range but within the extant range of Clark's nutcracker. Broad ecological and mycorrhizal tolerances enable recent and projected seedling establishment above the current treeline in the Great Basin (Millar et al., 2015; Smithers et al., 2018; Smithers and North, 2020; Shemesh et al., 2020) and southern Rocky Mountains (Kueppers et al., 2017; Jabis et al., 2020). Limited summer precipitation is a significant constraint to the elevational advancement of limber pine seedlings above the current alpine treeline (Moyes et al., 2013, 2015). In addition, only a modest portion of limber pine's distribution is at treeline, so advances above this ecotone may not offset habitat loss at lower elevations.

Limber pine also escapes climate warming by finding refuge in ravines with cold air drainage in the Great Basin (Millar et al., 2018). However, these cool, moist habitats often contain *Ribes* spp. (Charlet, 2020) and consequently may have conditions conducive to *C. ribicola* infection if the pathogen continues to spread. Drier and warmer sites with less *C. ribicola* spore production can provide refuge from WPBR pressure but may be subject to increased warming and drought stress in a changing climate. Avoiding both climate stress and WPBR pressure through migration will require tradeoffs, and increased resilience may be possible only in areas where the pressure from one stressor is low.

5.2.4. Outlook for limber pine

Limber pine is a generalist and has broad tolerances to abiotic stressors but is highly susceptible to biotic stressors. The proportion of dead limber pine lags that observed in whitebark pine by approximately a decade, suggesting that limber pine populations may be following a similar trajectory (Goeking and Windmuller-Campione, 2021), especially in the areas impacted by both WPBR (see Fig. 8) and MPB (see Fig. S1 in Supplemental Material). This does not bode well for limber pine. While the adaptive capacity of limber pine, in general, may be reasonably high compared to some of the other High-5, especially concerning drought tolerance, the compounding effects of the apparently low frequency of quantitative resistance to WPBR and high susceptibility to MPB will slow adaptation to WPBR in areas with high rust and MPB pressure.

If further research continues to reveal that the baseline frequency of quantitative resistance to WPBR is low range-wide and a virulent strain of *C. ribicola* to Cr4 major gene resistance evolves and becomes common, the outlook for limber pine in areas with high WPBR pressure is poor.

In areas with lower rust pressure, for example, the Great Basin and southern Rocky Mountains, the outlook for limber pine is more positive, although proactive management may be needed to supplement populations with WPBR resistance. Regeneration may be able to offset a slower rate of WPBR-caused mortality, however, the selection will not yield adapted populations if the frequency of WPBR resistance in the population is very low (Schoettle et al., 2012a; Schoettle et al., 2019b). The combination of WPBR and MPB will still pose a challenge to these populations. In areas where WPBR is very low or absent, limber pine may fare better under the direct effects of climate change than co-occurring conifers (Kane and Kolb, 2014; Windmuller-Campione and Long, 2016).

5.3. Southwestern (SW) white pine

5.3.1. Primary stressors of SW white pine

Currently, SW white pine forest health is in good condition. WPBR was first noted in SW white pine in the Sacramento Mountains of south-central New Mexico in 1990, with an initial infection date of ~ 1975 (Hawksworth, 1990). It continued to spread across New Mexico and into Arizona, where it was first identified in 2009; infections were dated to between 1988 and 1995 (Conklin et al., 2009; Fairweather and Geils, 2011) (Fig. 8). The current known distribution of WPBR in Arizona is limited to the east-central parts of the state, and it is not known to occur yet in Mexico (Looney et al., 2015).

Early season drought is a prominent feature of SW white pine habitats in the U.S. (see Fig. 3). Depending on the North American Monsoon, drought conditions can persist into the fall. Studies of drought response of SW white pine in forests in the U.S. are complicated by the likelihood of including both SW white pine and hybrid SW white pine - limber pine individuals (Menon et al., 2018; Peach, 2021). Indications are that SW white pine has moderate drought tolerance but is less tolerant than limber pine (Waring, pers. comm.). In the state of Durango, Mexico, drought was found to positively influence earlywood growth of SW white pine, but generally, radial growth was found to be insensitive to climate variables due to its moist ecological niche (Acosta-Hernández et al., 2020). The increase in the variation in the monsoon under climate change suggests that SW white pine may be increasingly exposed to prolonged drought in the future.

5.3.2. Adaptive capacity of SW white pine

SW white pine has genetic resistance to WPBR and exhibits drought tolerance traits, so there is potential for adaptation to each stressor within its current range. SW white pine has both heritable major gene resistance and quantitative resistance to WPBR (Kinloch and Dupper, 2002; Johnson and Sniezko, 2021). While more research is needed, the first estimates of the baseline frequency of quantitative resistance are at modest levels (~10%): higher than whitebark, limber, and foxtail pines and lower than the bristlecone pines (Johnson and Sniezko, 2021). Durability trials have been established in Arizona and New Mexico to monitor long-term resistance and infection rates in the field and an orchard of grafted scion from trees with known major gene resistance (Wilhelmi et al., 2022). Although there is relatively high resistance to an introduced pathogen, most trees are highly susceptible and high mortality is expected as WPBR continues to spread.

SW white pine is adapted to moister sites than some of the other High-5 species. Climate projections for the southwestern U.S. indicate a more arid future, which would be likely to challenge the long-term survival of mature SW white pine trees, reproductive capacity, and seedling establishment success. SW white pine has heritable drought tolerance traits and plasticity to acclimate to warm and dry conditions, which improve water use efficiency and survival (DaBell, 2017; Bucholz et al., 2020). Traits differ among populations; Goodrich et al. (2018) found that families with taller seedlings, which typically originated from southern sources, succumbed to drought faster than populations with shorter seedlings, which also aligns with the hybridization gradient (increasing proportion of SW white pine ancestry moving south (Menon et al., 2018)). Drought response variation among sites suggests SW white pine growth is more water-limited at lower, drier sites than those at higher elevations (Adams and Kolb, 2005).

SW white pine is intermediate in shade tolerance and regenerates readily in the absence of disturbance and following partial harvesting (Jones, 1974; Looney and Waring, 2012; Goodrich et al., 2018). Height growth is reduced under heavy shade ($>\sim 30\ m^2\ ha^{-1}$ overstory basal area) (Goodrich and Waring, 2017). The fastest height growth occurs following silvicultural treatments leading to two-aged structures; overstory densities of 9–10 $m^2\ ha^{-1}$ have been recommended to achieve similar structures while also meeting restoration objectives (Goodrich and Waring, 2017; Goodrich et al., 2018). In Mexico, overstory cover along gap edges promotes higher regeneration densities than open conditions within gaps (Maciel-Nájera et al., 2020).

Studies identifying preferred field regeneration sites for natural regeneration or planting are lacking. Under field conditions, shaded microsites on north-facing aspects with low levels of duff and litter best promote survival and growth of natural SW white pine seedlings

(Goodrich and Waring, 2017; Bucholz et al., 2020). Limited studies to assess planting survival in post-fire areas in the mixed conifer forest type are underway, but additional research is needed to evaluate performance following planting. An experimental field planting in Nebraska found high survival and steady, fast height growth rates of SW white pine relative to limber pine grown in the same study (van Haverbeke, 1983).

Several common biotic factors (other than WPBR) challenge SW white pine's adaptive capacity: competition, MPB, animal damage, and dwarf mistletoes (primarily *Arceuthobium apachecum* but including *A. blumeri*, particularly in Mexico). These factors may be spatially variable and localized. For example, at three sites in northern Arizona, MPB was the most common cause, and significant predictor, of mortality for SW white pine, but long-term competition was the best predictor of mortality in analyses of past tree growth patterns (Kane et al., 2014; Kane and Kolb, 2014). Looney et al. (2015) surveyed SW white pine damaging agents across 59 sites in Arizona and New Mexico and found generally healthy SW white pine populations but localized animal damage (including girdling by black bears (*Ursus americanus* Pallas, 1780) in some areas) and dwarf mistletoe were the most common biotic damaging agents (Looney et al., 2015). Dwarf mistletoe is a common damaging agent that is not evenly distributed across the range but can cause local mortality in highly infected stands (Mathiasen, 1979). Cone and seed insects can also have severe impacts on seed availability, with up to 80% infestation rates (and high variation between years and across sites), and may restrict natural regeneration (DePinte et al., 2020; Leal-Sáenz et al., 2021). Under climate warming, each of these stressors may increase.

Among the potentially intensifying abiotic stressors, wildfires have already become larger and more severe in the U.S. southwest, and this trend is likely to continue (Mueller et al., 2020). Looney et al. (2015) found fire to be the most common abiotic damaging agent of SW white pine across Arizona and New Mexico. Large, stand-replacing fires threaten entire populations of SW white pine, which often occur on isolated sky islands in the southwestern U.S.; such fires have already killed individuals with known major gene resistance to WPBR (Waring and Wilhelmi, 2022).

5.3.3. *Migration potential of SW white pine*

Dispersal of SW white pine seeds is not limited to a single agent, but a comprehensive study has not been completed across the range. Morphologically, cones and seeds of SW white pine increase in size and weight along a gradient from north to south (Benkman et al., 1984; Leal-Sáenz et al., 2020; Tomback et al., 2011). Animal dispersers vary geographically for SW white pine as seed size increases (Steinhoff and Andresen, 1971; Samano and Tomback, 2003; Tomback et al. 2011) and may be the most diverse of all the High-5 pines. but include Clark's nutcracker and red squirrel in the northern part of the range (Benkman et al., 1984) and other species (e.g., Mexican jay [*Aphelocoma wollweberi*], Steller's jay [*Cyanocitta stelleri*], or *Sciurus* species) farther south (Tomback et al., 2011). Gravity and wind may be the most important agents of dispersal. SW white pine cones open simultaneously both within and between trees, a strategy that may help saturate seed predators (Benkman et al., 1984) and aid other dispersal mechanisms. While SW white pine is occasionally observed in clusters, especially at more northern latitudes where it is dispersed by Clark's nutcracker (Samano and Tomback, 2003), it is more often found as a single stem elsewhere (Goodrich, 2015) and no genetic spatial autocorrelation has been found between individuals growing on the same site (Quiñones-Pérez et al., 2014).

Climate envelope modeling suggests that habitat conditions for SW white pine may become unsuitable across much of the southern range in Mexico, while areas of stability were identified across the entire range and areas of expansion predicted primarily in the northern extent (Shirk et al., 2018). Ongoing research aims to include genetic resistance to WPBR and adaptive traits along with statistical distributions of dispersal distances (i.e., dispersal kernels) into a more robust future distribution model (Waring et al., 2022). Results from a common garden trial across an elevational gradient in northern Arizona indicate that abrupt long-distance movement of populations from south to north is unlikely to be successful due to increased variation in fall and spring frost events that result in seedling mortality (Bucholz et al., 2020). Adaptive introgression between limber pine and SW white pine may lead to novel genotypes and higher genetic diversity, potentially resulting in greater adaptive capacity in hybrid populations (Menon et al., 2020).

5.3.4. *Outlook for SW white pine*

Compared with other High-5 species, SW white pine may have a higher probability of adapting and persisting in the landscape. Mortality events will occur, however, caused by WPBR, high- or moderate-severity fire, drought, and the interactions between damaging agents, with the potential to remove entire populations rapidly. However, relatively high levels of genetic resistance to WPBR are being reported (Johnson and Sniezko, 2021) and additional resistant trees are being identified, including in Mexican source populations (Waring et al., 2022). Drought adaptive capacity also appears promising, as evidenced in the plasticity of traits and potentially tolerant hybrids. Regeneration in the absence of fire is robust (Goodrich et al., 2018) and field planting trials to monitor WPBR resistance durability and survival of different source populations are underway (Wilhelmi et al., 2022). A broader understanding of managing the mixed-conifer forests under climate change is needed given species interactions and the potential for novel mixtures under climate change (Yanahan and Moore, 2019). Engaging managers across the range to participate in developing adaptive management strategies that meet forest goals and objectives while addressing climate adaptation and damaging agents in the mixed-conifer forest type of the southwestern U.S. and Mexico is a critical next step for SW white pine.

5.4. *Rocky Mountain (RM) bristlecone pine*

5.4.1. *Primary stressors of RM bristlecone pine*

RM bristlecone pine forests are healthy with only localized and low levels of insect and disease damage (Burns, 2006; Schoettle and Coop, 2017; Bentz et al., 2021). Currently, WPBR has not yet spread to overlap with most of the distribution of RM bristlecone pine (Fig. 5 and Fig. 9). Infected RM bristlecone pines have only been found in one disjunction WPBR infection center in the Sangre de Cristo Mountains of southern Colorado (Fig. 9) (Blodgett and Sullivan, 2004; Burns, 2006). At this early stage of invasion, the diseased RM bristlecone pine trees are predominantly in moist, riparian areas, where *Ribes* is common, and conditions are conducive to *C. ribicola* spore production. Infections are less common on the upland drier slopes (Burns, 2006). Within the same upland plots, cankers are well-developed on infected limber pine trees but absent or nearly absent on RM bristlecone pine suggesting that, under similar exposure to *C. ribicola*, RM bristlecone pine may be harder to infect, may be slower to develop disease symptoms, or may have more cryptic disease symptoms (or a combination thereof) than limber pine (Burns, 2006; Schoettle et al., 2011; Schoettle and Coop 2017). All three of these phenotypes may reflect differences in genetic resistance to WPBR between the species, but it is still too early in the invasion at this site to be confident that *C. ribicola* has challenged all the trees. RM bristlecone pine is susceptible to WPBR, and the disease is expected to continue to spread through much of the five-needle pine habitat in Colorado (Howell et al., 2006; Kearns et al., 2014), making WPBR a primary threat to the species.

In recent decades, the severity of droughts in the southern Rocky Mountains and southwestern U.S. has increased (Allen et al., 2010). Drought impacts are evident in the radial growth patterns of RM bristlecone pine (Tintor and Woodhouse, 2021) and may also be contributing to the substantial recent crown and branch dieback in individuals observed across much of the species' range (Schoettle and Coop, 2017). At lower elevations, recent branch tip damage, likely caused by twig

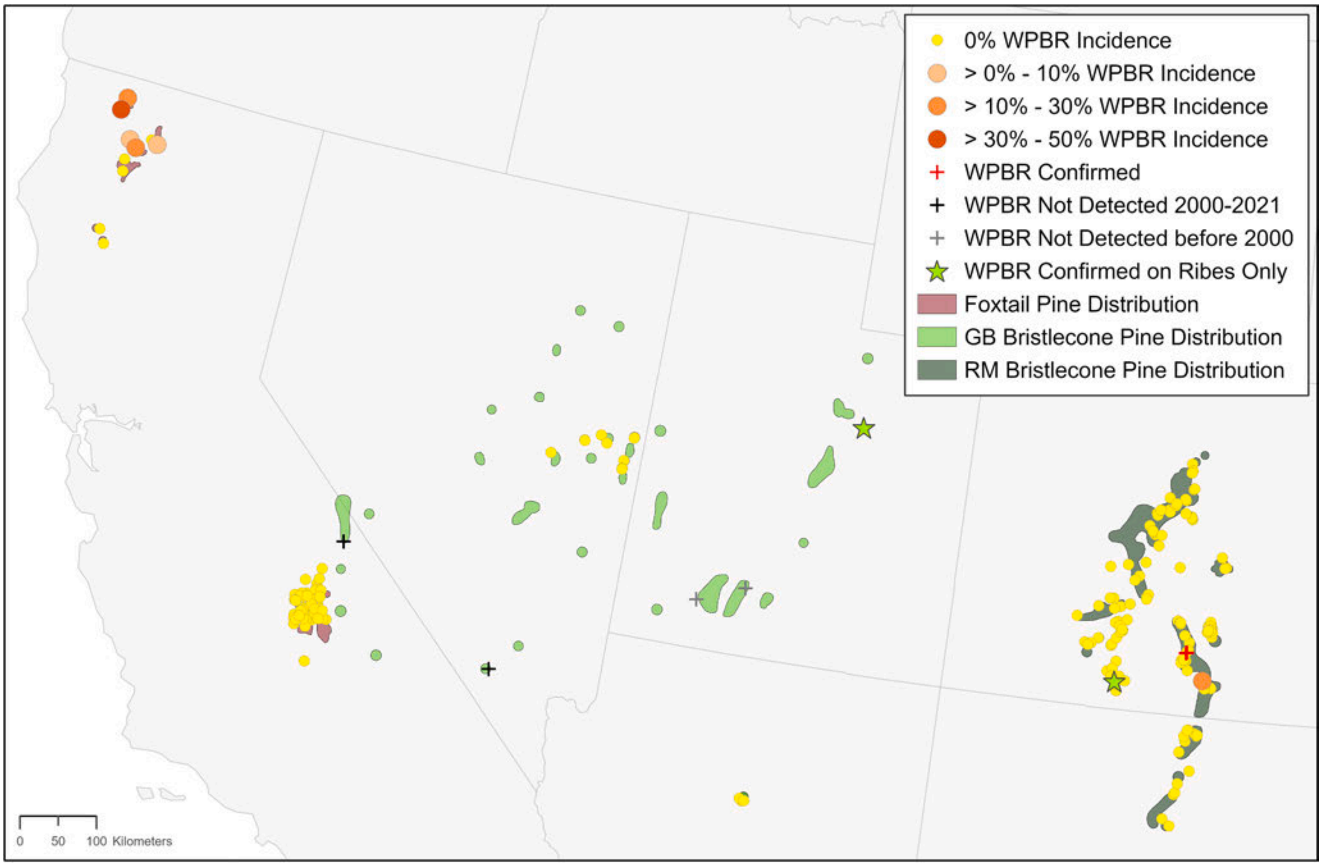

Fig. 9. The incidence of white pine blister rust (WPBR) on Rocky Mountain bristlecone (PIAR), Great Basin bristlecone (PILO), and foxtail (PIBA) pines in western North America as of 2021. Symbols and incidence are as described in Fig. 7 shown here for Rocky Mountain bristlecone (dark green polygons), foxtail pine (maroon polygons), and Great Basin bristlecone pine (light green polygons) (see Fig. 2 for distribution sources). Two WPBR-infected foxtail pine trees in the southern Sierra Nevada were recently found (Dudney et al., 2020) but coordinates were not available. WPBR infections have not been found on Great Basin bristlecone pine in its native habitat. See Supplemental Material for data sources and field methods. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

beetles (*Pityophthorus*, *Pityogenes*, or *Pityoborus* spp., or a combination thereof), may be linked to recent drought (Schoettle and Coop, 2017). Species distribution models predict that RM bristlecone pine's current climatic niche may almost entirely vanish from the Rocky Mountain region by 2090 (Crookston, 2012), but models of the sub-populations associated with distinct genetic lineages present a slightly more positive forecast (Malone et al., 2018). Drought is already a feature of RM bristlecone's environment, and the forecasted increase in climate variability may further intensify drought as a primary stressor.

5.4.2. *Adaptive capacity of RM bristlecone pine*

RM bristlecone pine has genetic resistance to WPBR and some drought tolerance traits, so there is potential for adaptation to both stressors. Early studies of WPBR resistance in RM bristlecone pine indicated that it was among the most resistant of the North American five-needle pines (Hoff et al., 1980; Stephan, 2004). Consistent with these studies, more recent work has shown that RM bristlecone pine has higher frequencies of heritable quantitative resistance than limber pine (Schoettle et al., 2011; Schoettle et al., 2022), and the species does not appear to have major gene resistance (Vogler et al., 2006). The greater resistance to infection by *C. ribicola* in RM bristlecone compared to limber pine in controlled screening trials (Schoettle et al., 2011; Schoettle et al., 2022) may contribute to the differences in WPBR incidence in the forest communities where they both reside (Burns, 2006, Schoettle and Coop, 2017). As observed for quantitative resistance in other white pines, there is some experimental evidence and field observations (see Section 5.4.1) that indicate resistance in RM bristlecone pine may be lower under higher disease pressure (Burns, 2006; Jacobi et al., 2018b).

RM bristlecone pine's long lifespan suggests that the species tolerates climate variability, although drought tolerance traits have not been characterized. The root-to-shoot ratio of RM bristlecone pine seedlings is lower than limber pine's, suggesting only moderate drought tolerance (Borgman et al., 2014). Its northern range limit coincides with the extent of the North American Monsoon, suggesting that seedling establishment may require late summer precipitation (Schoettle, 2004).

Large-scale disturbance can contribute to pulses of RM bristlecone pine recruitment (Baker, 1992; Coop and Schoettle, 2009), yet smaller establishment events regularly occur within stands and generate mixed-age bristlecone pine stands over time (Brown and Schoettle, 2008). The rate of seedling recruitment is very low, often taking many decades to accumulate a cohort of established seedlings (Coop and Schoettle, 2009), and then many more years for trees to reach reproductive maturity. At the stand scale, seedling density is positively related to the magnitude of cone production (Schoettle and Coop, 2017). Cone production is greater in more open stands and on colder sites (Schoettle and Coop, 2017) suggesting a sensitivity of RM bristlecone pine reproduction to a warming climate. Seedling density is also positively correlated with growing season precipitation, further suggesting a regeneration niche that requires dependable summer moisture and thus may also be affected by climate variability (Schoettle and Coop, 2017). A lack of regeneration in some stands indicates that older trees can persist in suboptimal environments that are currently outside the conditions suitable for seedling establishment. Cone and seed insects are common on lower elevation (<3300 m) trees and are scarcer on trees growing at higher elevations (Schoettle, unpubl. data). Cone harvesting and caching by squirrels before cone opening and seed release is also common on some sites (Schoettle, pers. observation). The size class distribution for the species shows the pattern typical of healthy self-replacing populations (Goeking and Windmuller-Campione, 2021), but the generation time is so long that it may not support rapid adaptation.

RM bristlecone pine's very low genetic diversity (Schoettle et al., 2012b), does not position it well for sustaining evolutionary potential after populations undergo rapid natural selection. Variation in neutral genetic markers that correlate with site temperature and precipitation suggests local adaptation (Schoettle et al., 2012b) but functional genomic and common garden studies are lacking. Mortality caused by WPBR and direct and indirect effects of a changing climate may lead to reduced overall genetic diversity through loss of rare alleles (see Kim et al., 2003).

Wildland fires occur in RM bristlecone habitats (see Baker, 1992; Brown and Schoettle, 2008; Coop and Schoettle, 2011), and are expected to increase in the high elevations of the southern Rocky Mountains (Higuera et al., 2021). This species has moderate constitutive defenses to MPB attack (Bentz et al., 2021). During the recent epidemic, MPB was less common in southern portions of RM bristlecone pine's distribution compared to farther north, where the beetle populations were far greater due to the proximity to extensive forests of other susceptible pine hosts (Bentz et al., 2021). Significant dwarf mistletoe infestation was not detected in survey plots in Colorado (Schoettle and Coop, 2017), but high infestation is common in the disjunct population of RM bristlecone pine in Arizona, where it has contributed to high tree mortality during periods of elevated drought stress (Scott and Mathiasen, 2012). In general, RM bristlecone may have fewer additive mortality factors that could compromise the adaptation trajectory to WPBR or drought than some of the other High-5 species.

5.4.3. Migration potential of RM bristlecone pine

The small-winged seeds of RM bristlecone pine are primarily wind-dispersed, but dispersal by Clark's nutcracker also occurs and may contribute to long-distance colonization events (Torick et al., 1996). Patterns of genetic variation in this species suggest that gene flow is restricted between mountain-top populations, which may limit migration of genes or genotypes to new suitable habitats as the climate continues to change (Schoettle et al., 2012b). The species form krummholz in alpine habitats, and evidence of recent (since 1965) seedling establishment at one study site represents the highest advance of treeline for this species in at least 1200 years (Carrara and McGeehin, 2015). More research is needed to better understand RM bristlecone pine's capacity for forest migration into alpine habitats range wide.

5.4.4. Outlook for RM bristlecone pine

RM bristlecone pine is relatively tolerant of both the abiotic and the biotic stressors that challenge it. It has drought tolerance, moderate levels of quantitative resistance to WPBR, and some constitutive defenses to MPB. However, the species' very low standing genetic variation reduces its adaptive potential to rapidly changing conditions (Schoettle et al., 2012b). In combination with its very slow regeneration dynamic, the species' evolutionary potential is low if mortality increases from WPBR, climate variation, or other factors (or combinations thereof). The habitats that RM bristlecone pine occupies are currently under low pressure from WPBR with modest impacts from other stressors, but WPBR has only recently begun to overlap with its distribution and is likely to continue to spread (Howell et al., 2006; Kearns et al., 2014). The trajectory for RM bristlecone is unclear. Proactive management, before populations decline, to increase the abundance of younger cohorts with more diverse genetic combinations will improve RM bristlecone pine's adaptive capacity (Schoettle and Coop, 2017; Schoettle et al., 2012a; Schoettle et al., 2012b; Schoettle et al., 2019b).

5.5. Great Basin (GB) bristlecone pine

5.5.1. Primary stressors of GB bristlecone pine

Currently, GB bristlecone pine forests are in good condition. GB bristlecone pine has not yet been found to be infected with WPBR in its native habitat (Fig. 9), although it is susceptible to the disease under controlled conditions (Schoettle et al., 2022; Vogler et al., 2006). WPBR on other five-needle pine species are just beyond GB bristlecone pine's range in California and Nevada (Vogler and Charlet, 2004; Maloney 2011a; Vogler et al., 2017b) and on *Ribes* within its range in Utah (Vogler et al., 2017a) (Fig. 9). Alternate hosts for WPBR (*Ribes* spp. and *Castilleja* spp.) are common in GB bristlecone pine stands and the lower-elevation habitats (Fryer, 2004; Charlet, 2020). The most recent thorough monitoring of GB bristlecone pine populations for WPBR was in 1997 (Smith and Hoffman, 2000). In 2004, 12 more plots were inspected for WPBR in eastern Nevada and Utah (J. Guyon, unpubl. data) and 5 plots in 2004–2006 in the far western portion of the distribution (Maloney, 2011a). More field surveys are needed to provide greater confidence in the current infection status of GB bristlecone pine.

The arid climate of the Great Basin may inhibit spore production and the effective transmission of *C. ribicola* to GB bristlecone pine. However, the recent expansion of the WPBR infection front into other arid habitats (Burns, 2006; Shanahan et al., 2016; Dudney et al., 2020, 2021) suggests that climate change may be altering the environment to be more suitable for the pathogen (Dudney et al., 2021) or that *C. ribicola* may be evolving greater drought tolerance to overcome limitations to colonization (or both). Sporulation of *C. ribicola* on limber pine and whitebark pine in the Great Basin in the fall (Smith et al., 2000; Vogler et al., 2017b) rather than during the spring and early summer suggests that a current phenological mismatch among *C. ribicola* and High-5 and alternate hosts may contribute to the low levels of the disease in the Great Basin. How climate change may affect the epidemiology of the disease in the Great Basin is yet to be determined. Because WPBR is caused by a non-native pathogen, the implications of its spread could be devastating to the already small, fragmented populations of GB bristlecone pine; it is prudent to prepare for WPBR to be a primary stressor that may play a role in GB bristlecone pine's future condition.

The current GB bristlecone pine distribution is a relic of a more extensive distribution in the Great Basin during the Late Pleistocene when precipitation was greater, and temperatures were cooler (Wells, 1983). As the climate has warmed and become drier since the last glacial retreat, the lower-elevation habitats have become unsuitable, and GB bristlecone pine is now restricted to a narrow elevation band that defines treeline on the mountain tops (Charlet, 2020). Moisture availability and timing define the lower elevational limits of GB bristlecone pine (Bunn et al., 2018). With recent warming, there has been a shift at the higher elevations toward an increase in moisture sensitivity of radial growth in GB bristlecone pines that were formerly limited by temperature, suggesting that these populations may be increasingly vulnerable to drought (Salzer et al., 2009, 2014; Tran et al., 2017; Bunn et al., 2018). Likewise, GB bristlecone pine phenology is sensitive to growing season conditions (Hallman and Arnott, 2015). Growth sensitivity is mediated by snow cover duration in the spring (Ziaco et al., 2016) and moisture from monsoonal rainstorms in late summer (Ziaco and Biondi, 2018).

5.5.2. Adaptive capacity of GB bristlecone pine

WPBR has not been found on GB bristlecone pine in its native habitat, but resistance screening trials demonstrate that the species is susceptible to WPBR and has some resistance that is expressed under controlled conditions (Hoff et al., 1980; Stephan, 2004). These early studies combined seed sources of both RM and GB bristlecone pine, but they suggest that the tested sources have greater survival than the other North American five-needle pines that were tested together. More recent assessments demonstrate the presence of heritable quantitative resistance traits and the likely absence of major gene resistance (Kinloch and Dupper, 2002; Schoettle et al., 2022; Vogler et al., 2006). That these traits were detected with a small number of seedling families (10 families) from randomly selected seed trees from disease-free stands suggests that the resistance traits may be common in the sampled populations and will respond to the selection pressure of *C. ribicola* (Schoettle et al., 2022). These trials have identified the first GB bristlecone pine trees with WPBR resistance which can be used for seed collections for seedling culture and proactive plantings. Further rust resistance screening studies are ongoing with more families to improve trait frequency estimates (Schoettle et al., 2022). Range-wide testing of families and populations has not been started, although the low level of genetic differentiation among populations for this species (Bower et al., 2011) supports optimism that the resistance found thus far in part of the range may be representative of the species. Given GB bristlecone pine's longevity, the older trees may express ontogenetic resistance and survive in the presence of *C. ribicola*; however, their progeny may be fully susceptible and therefore not contribute to adaptation to WPBR. Although baseline WPBR resistance is present in the few naïve populations that have been tested, most of the individuals within each population are still highly susceptible (Schoettle et al., 2022; Vogler et al., 2006). Consequently, adaptation to WPBR will be needed to sustain healthy populations if WPBR spreads in the Great Basin.

The episodic recruitment pattern for GB bristlecone pine will limit its potential for sustaining viable populations under strong selection pressures. The last pulse of successful GB bristlecone pine seedling establishment occurred between 1955 and 1978 and was correlated with cumulative climatic factors rather than single-year conditions (Millar et al., 2015). Increased precipitation over several years, with summer monsoonal rains being more important than snowpack, is positively correlated with the natural regeneration pulse (Barber, 2013; Millar et al., 2015; Smithers and North, 2020). In a secondary role, greater growing-season minimum temperature also correlates with increased regeneration; the significance of maximum growing season temperature to regeneration differed between studies (Barber, 2013; Millar et al., 2015). This suggests that while GB bristlecone pine has drought tolerance traits (Beasley and Klemmedson, 1976; Liu and Biondi, 2020), they may be insufficient in the younger age classes to permit frequent successful regeneration in these harsh environments. These findings also suggest that if precipitation is reduced in the future, regeneration may be even less common. The infrequent regeneration and recruitment events for GB bristlecone pine are evident in the flat age-class structure for the species range-wide (Goeking and Windmuller-Campione, 2021). This structure, as opposed to the classic "reverse-J" size-class structure that is more common for most of the other High-5, indicates that GB bristlecone pine populations are sustained by tree longevity rather than turnover; it is the latter process that is required for rapid adaptation.

Stand-replacing fires are infrequent within high-elevation subalpine ecosystems of the Great Basin, but fuel loads can accumulate to enable surface fire spread (Kilpatrick and Biondi, 2020). Climate warming has lowered foliar moisture levels, especially in lower elevation forests, increasing the risk of ignitions and the uphill fire spread to treeline forests of the Great Basin (Gray and Jenkins, 2017). Natural recolonization of an extirpated population on an isolated sky island may be difficult due to the distance between populations and limited seed dispersal. Two studies have addressed post-fire regeneration dynamics in the Great Basin, one 4 years (Burton et al., 2020) and the other 12–13 years post-fire (Kilpatrick and Biondi, 2020). Post-fire seedbed conditions are suitable for GB bristlecone pine under modern climate conditions but do not generate recruitment densities above those in unburned areas (Kilpatrick and Biondi, 2020). Seed availability to colonize new distant areas, such as burned area interiors, is low due to the distance limitations of wind-dispersed seed (Burton et al., 2020, Kilpatrick and Biondi, 2020). No studies have addressed the suitability of the seedbed following small disturbances for natural regeneration of GB bristlecone pine.

Unlike most of the other High-5 species, GB bristlecone pine is not a suitable host for MPB though trees can be attacked if large beetle populations erupt in nearby forests-types that support brood development (Gray et al., 2015; Bentz et al., 2016; Bentz et al., 2022). Dwarf mistletoe can cause additional mortality under drought conditions; quantitative assessments are lacking. Cone and seed insects can cause dramatic decreases in seed availability, but their effects on recruitment are unclear (Barber, 2013).

5.5.3. *Migration potential of GB bristlecone pine*

Smithers et al. (2018) found little recent GB bristlecone pine seedling establishment above the alpine treeline in contrast to limber pine in the Great Basin. The difference may be due in part to the more effective dispersal of limber pine seeds by Clark's nutcracker compared to the predominantly wind-dispersed seeds of GB bristlecone pine. GB bristlecone pine establishment was also largely restricted to sites associated with adult GB bristlecone pine trees compared to the more random distribution of limber pine seedlings (Smithers et al., 2018). This may reflect not only seed availability but also a greater dependence of GB bristlecone pine than limber pine on habitats with suitable mycorrhizae above treeline (Bidartondo et al., 2001; Shemesh et al., 2020). Early establishment of limber pine above the current treeline may, over time, provide suitable habitat to facilitate the subsequent migration of GB bristlecone pine (Shemesh et al., 2020; Smithers and North, 2020). Great Basin treelines have historically been dynamic and are lower than expected from the current climate, highlighting GB bristlecone pine's slow migration (Bruening et al., 2017).

5.5.4. *Outlook for GB bristlecone pine*

GB bristlecone pine is tolerant of the abiotic stresses and has low to moderate susceptibility to the biotic stressors. The aridity of its habitat likely limits its exposure to WPBR and may keep rust pressure low, even if the pathogen spreads in the Great Basin. Relatively high baseline frequencies of resistance to WPBR have been observed in one portion of its distribution, and range-wide testing is needed. The greatest obstacle to rapid adaptation in this species is its low and sporadic seedling establishment success, which may be further diminished if growing season precipitation decreases under climate change. The proliferation of any selected traits will be restricted by low recruitment suggesting that the species has a low capacity for rapid adaptation. Fortunately, it may also experience the lowest selection pressures from the biotic stressors of the High-5 species, unless they are intensified by a changing climate. The unknown range-wide baseline frequency of WPBR resistance, future epidemiology of WPBR, and future climate in the Great Basin limits our ability to project GB bristlecone pine's future. If pressure by WPBR and MPB continues to be low, GB bristlecone pine may continue to be at low risk of population extirpation, although the effects of climate warming may narrow the species' elevational distribution. GB bristlecone pine is an excellent candidate for proactive intervention to diversify the age-class structure to increase its adaptive capacity before WPBR and climate change cause increased mortality (Schoettle and Sniezko, 2007; Keane and Schoettle, 2011; Schoettle et al., 2019b; Keane et al., 2021).

5.6. *Foxtail pine*

5.6.1. *Primary stressors of foxtail pine*

Foxtail pine forests are currently in good condition. WPBR incidence varies from 0 to 32% (Fig. 9) among the isolated sky islands in the north and as of 2009 no mature tree mortality could be attributed to WPBR (Maloney, 2011a). Only two trees have been found with the disease in the southern population (Kliejunas and Dunlap, 2007; Nesmith et al., 2019). The latitudinal trend in WPBR incidence is likely to be due to the distance from the points of introduction of *C. ribicola* in southern Canada and climatic differences; the wetter northern habitats are more suitable for the disease (Maloney, 2011b). In addition, alternate hosts for *C. ribicola* are rare in subalpine stands in the southern Sierra Nevada, so wind-driven transport of spores from lower elevations is required for foxtail pine infection (Maloney, 2011a). The pathogen has recently spread into the subalpine whitebark pine forests in the southern Sierra Nevada (Dudney et al., 2020). The similarity of the risk factors for WPBR for whitebark pine and foxtail pine habitats (Dunlap, 2012) suggests that foxtail pine may be increasingly exposed to *C. ribicola* in the future. As stated, for the other threatened, but not yet heavily impacted, High-5 species (i.e., both bristlecone pines species, see Sections 5.4 and 5.5), the implications of the spread of the non-native pathogen to the southern Sierra Nevada foxtail pine populations could be significant. It is prudent to consider WPBR as a primary stressor that will play a role in foxtail pine's future condition.

Higher temperatures and associated changes to the water balance are significant determinants of seedling recruitment and radial growth of foxtail pine at treeline (Lloyd 1997; Lloyd and Graumlich, 1997). The impacts of reduced or seasonally shifting precipitation patterns on foxtail pine will be dependent, in part, on soil substrate effects on water availability (Eckert and Sawyer, 2002) and interactions with other pests and pathogens. Low levels of drought-induced mortality of foxtail pine (~2%) were observed in the southern populations before 2009 (Maloney, 2011a). MPB is more active in the north but is not currently severely impacting foxtail pine populations, and twig beetle and seed and cone insect activity is greater in the south (Maloney, 2011a, 2011b). Some populations in the north are also infested with dwarf mistletoe (Mathiasen and Daugherty, 2001). Wildland fire, however, is more common in the south and could become an increased threat under climate warming; currently, there is little evidence of fire in the northern distribution (Eckert, 2006).

5.6.2. *Adaptive capacity of foxtail pine*

Foxtail pine is highly susceptible to WPBR. The species appears to lack major gene resistance (Kinloch and Dupper, 2002; Vogler et al., 2006) and the frequency of quantitative resistance is very low (Hoff et al., 1980; Stephan, 1986; Sniezko and Liu, 2022). Foxtail pine has drought-tolerant traits (Eckert et al., 2016). Water use efficiency differed among foxtail pine families, and several patterns were documented that are consistent with drought tolerance as a fitness-related trait under natural selection (Eckert et al., 2016), and therefore available for further selection throughout the species' range. Foxtail pine has higher constitutive defenses to MPB than most of the other High-5, and MPB currently does not impose a high additive mortality risk for foxtail pine (Bentz et al., 2017, 2022).

The demographic structure of foxtail pine populations in the south and north differs. The cooler, drier climate of the habitats that support the southern populations are dominated by older trees with low regeneration resulting in a flat size-class distribution (Maloney, 2011b; Nesmith et al., 2019), like that of GB bristlecone pine (Goeking and Windmuller-Campione, 2021) (see Section 5.5). These populations are currently stable due to historically low mortality of older trees (Lloyd, 1997). Therefore, tree longevity (up to ~ 3000 yrs.) is integral to the persistence of the southern populations. Another consequence of low regeneration densities in these southern forests is the low production of individuals with new genetic combinations on which natural selection can act. Furthermore, recruitment is correlated with winter snowpack (Lloyd, 1997), suggesting sensitivity to shifting precipitation patterns that may develop under climate change (Hajek and Knapp, 2022). Regeneration is positively correlated with foxtail pine density and cone production (Maloney, 2011b; Nesmith et al., 2019). Foxtail pine cone production is high in the southern Sierra Nevada, but seed losses by cone and seed insects can be substantial (Maloney, 2011b).

The size-class distribution for populations in the warmer, mesic northern areas is typical of other forest species in being skewed toward the younger age classes. The youngest cohort (<40 yrs. old) accounts for 34% to 69% of the trees, yet long-lived trees (1500 yrs.) are still common (Eckert, 2006; Maloney, 2011b). Regeneration is evident throughout the northern distribution and frequent disturbances do not appear to be important in promoting regeneration (Eckert, 2006). The higher regeneration densities in the north suggest greater overall adaptive capacity and resilience compared to the southern populations (Eckert, 2006).

5.6.3. *Migration potential of foxtail pine*

Seed dispersal, while primarily wind-driven for foxtail pine, can occur via Clark's nutcracker (Maloney, 2011b; Nesmith et al., 2019). Foxtail pine seedlings grow well above treeline in the southern Sierra Nevada, presumably because of seed dispersal by Clark's nutcracker (Lloyd, 1998). With the concentration of genetic diversity within stands in the south (Oline et al., 2000), nutcracker-facilitated seed dispersal has the potential to provide genetically diverse founding individuals to new habitats. In the northern foxtail pine distributions, long-distance seed movement is limited among the mountain top populations, but downslope range expansion is evident (Eckert and Eckert, 2007).

5.6.4. *Outlook for foxtail pine*

Foxtail pine is tolerant of abiotic stresses and some biotic stressors but it is highly susceptible to WPBR. The early indications that the frequency of resistance to WPBR is very low in this species make it highly vulnerable to the continued spread of the disease. Differences in the regeneration dynamic between the north and the south populations suggest that the consequences of WPBR-caused mortality may differ. The northern populations are isolated from one another on sky islands and consequently are at greater risk for extirpation should WPBR continue to increase in prevalence, yet the greater regeneration capacity may offset some mortality. The rust pressure has been very low in the southern Sierra Nevada populations but may increase if WPBR continues to spread into the higher elevation forests (Dudney et al., 2020, 2021). Upon an increase in WPBR pressure in the southern Sierra Nevada, the species' natural regeneration rate may be too low to offset mortality, resulting in future population declines. Any increase in cone and seed insect impacts may further reduce natural regeneration densities and thereby put the populations at additional risk for decline. Foxtail pine is a good candidate for proactive intervention to increase the frequency of genetic resistance to WPBR in the populations before they are challenged and decline to reduce the impact and risk to population sustainability in the future (Schoettle and Sniezko, 2007).

6. Discussion

Applying an evolutionary perspective to evaluate the trajectory for each of the High-5 has revealed differences among the species that can help focus research and management attention on the critical vulnerabilities of each species (Table 2). Estimating trajectories involved two steps: a review of the biotic and abiotic stressors that threaten each of the High-5, and specific components of population vulnerability, resilience, and adaptive capacity. This review and analysis provides a view of each species' status and condition within the construct of evolutionary rescue and contemporary evolution (Gomulkiewicz and Holt, 1995; Bell and Gonzalez, 2011; Hendry et al., 2011; Carlson et al., 2014).

The strong selection pressure of WPBR alone is formidable, and adaptation to WPBR is imperative to sustain or restore future self-sustaining viable High-5 populations as the pathogen continues to spread. This challenge is further complicated by pressure from other mortality factors, most notably drought, MPB, and wildfire that are at risk of increasing in a warming climate. These compounding stressors and resultant forest health conditions have led to conservation status decisions in Canada and potentially in the U.S. to address the decline of whitebark pine and limber pine (Government of Canada, 2012; COSEWIC, 2014; U.S. Fish and Wildlife Service, 2020). While most High-5 populations are likely to be exposed to lower WPBR pressure than those in the central and northern Rocky Mountains and northern coastal regions due to different climatic conditions, *C. ribicola* is spreading into more arid regions. How the pathogen and disease will be affected by a changing climate is not well understood at this time. Climate or

Table 2

Summary of some key components of adaptive capacity for the High-5 species. Estimated ratings are relative among these species and based on the best available, but incomplete, knowledge. Ratings do not include consideration for the current or projected exposure to or impact by WPBR or climate change.

High-5 Pine Species	Primary Stressors		Additive Stressor	Regeneration Potential	Genetic Diversity
	WPBR susceptibility[1]	Drought sensitivity	Mountain pine beetle Susceptibility		
Whitebark	High	High	Very High	Moderate[3]	Moderate
Limber	Very High[2]	Low	Very High	Moderate[3]	Moderate
SW white	High[2]	Moderate	Moderate	High	Moderate
RM bristlecone	Moderate	Moderate	Low	Low	Very Low
GB bristlecone	Moderate[2]	Moderate	Very Low	Very Low	Moderate
Foxtail - N	Very High[2]	Moderate	Low	High	Low
Foxtail - S	Very High[2]	Moderate	Low	Very Low	Low

[1] Based on estimated baseline frequencies of quantitative resistance to WPBR in naïve populations (e.g., low WPBR resistance frequency leads to a rating of high WPBR susceptibility).

[2] Estimated on limited data; range-wide information is lacking.

[3] Currently reduced by WPBR mortality in some populations.

disturbance changes may make conditions greater or less suitable for *C. ribicola* infection or WPBR disease development (or both) (see Section 4.1). Likewise, *C. ribicola* is also evolving in North America and has already developed greater virulence to overcome some resistance traits in pine hosts and may overcome some climatic barriers that may be currently restricting spread or intensification. Past efforts to reduce exposure to WPBR failed (see Maloy, 1997; Kinloch, 2003; Geils et al., 2010); *C. ribicola* is now a permanent resident of North America.

The theory of evolutionary rescue and contemporary evolution suggest that rapid adaptation to novel stressors is greater when traits that confer fitness are available for natural selection, populations are large and have high growth rates to offset mortality, and stochastic mortality factors are low. Consequently, the broad management objectives to improve the adaptive capacity of each High-5 species to promote self-sustaining High-5 populations include (1) increasing the frequency of individuals with adaptive traits that confer greater fitness in populations (i.e., WPBR resistance and drought tolerance traits), (2) increasing the size of populations, and thereby the genetic combinations, for natural selection and to offset mortality of less adapted individuals, and (3) managing the other additive mortality factors directly or at the landscape scale to reduce their impacts (Fig. S2 in Supplemental Material).

Management options to achieve these objectives will depend, in part, on the condition of the populations to be treated (Fig. S2 in Supplemental Material) (Schoettle and Sniezko, 2007; Keane and Schoettle, 2011; Schoettle et al., 2019b; Jenkins et al., 2022; Tomback et al., 2022). For example, if the populations have experienced high mortality from WPBR, low seed available or seed dispersal (or both) may limit the natural regeneration response to silvicultural treatments. In these situations, planting with seed lots that have WPBR resistance, and other desirable traits (i.e., drought tolerance) if available, will offer a higher likelihood of success in increasing population size and adaptive potential of the population. Both natural regeneration and planting may be options for populations that have not yet experienced high mortality but are threatened. These proactive treatments in threatened populations can help diversity the age class structure and provide more individuals with new genetic combinations for selection to act. Selection for WPBR resistance, and drought tolerance, is often faster in younger trees, therefore providing an overabundance of young trees on the landscape will allow for an accelerated rate of natural selection and an increase in the number of trees with desired traits in the emerging forest (Schoettle and Sniezko, 2007). If this is done proactively, the cohort will be established before, and selection will proceed during, the period when selection pressures increase. This will reduce the window of time between mortality of the original overstory and maturation of the new adapted cohort when the population would have low seed availability and recovery capacity to other disturbances.

For natural selection to proceed and yield an adapted future population, the traits need to be present in the original populations or seed source. Knowing the frequency of WPBR resistance and identifying trees with heritable WPBR resistance is critical for inferring the species trajectory and for making management decisions (Schoettle et al., 2019b). Likewise, protecting WPBR resistant trees and population from mortality by MPB, fire, other insects and disease, or from damage by other forest management (e.g., fuels treatment) applies to all the High-5 species.

The analysis presented here highlights the vulnerabilities of each High-5 species and reveals opportunities to further tailor management for each species to improve future trajectories. For example, whitebark pine and limber pine in the northern U.S. and Canadian portions of their distributions have experienced high mortality from WPBR and MPB (see Sections 5.1 and 5.2). The severity of the declines makes it unlikely that many of these populations will adapt and recover via evolutionary rescue without forest management intervention. In the U.S., restoration strategies and techniques have been developed for whitebark pine (e.g., Greater Yellowstone Co-ordinating Committee, 2011; Aubry et al., 2008; Burns et al., 2008; Keane et al., 2012; Keane et al., 2017, 2021; Keane, 2018; Perkins et al., 2016; Jenkins et al., 2022; Tomback et al., 2022; Tomback and Sprague, 2022). Canada has management strategies for whitebark pine and also for limber pine (e.g., Government of Alberta, 2022; Alberta Environment and Parks, 2021; Krakowski and Gutsell, 2022; Krakowski, 2018). Both countries have WPBR resistance screening programs, planting projects, seed orchards, and other conservation projects for whitebark pine (Mahalovich and Dickerson, 2004; Sniezko et al., 2011; Krakowski and Gutsell, 2022); Canada's activities also include parallel programs for limber pine including an extensive WPBR resistance screening program (Krakowski and Gutsell, 2022).

Whitebark pine and limber pine populations further south are experiencing less WPBR pressure and are candidates for proactive information gathering and intervention (Figs. 7 and 8; Fig. S2 in Supplemental Material). Conservation strategies have been developed for whitebark pine in California (Interagency Conservation Strategy Team. 2020) and for limber pine in the southern Rocky Mountains (Burns et al., 2008; Schoettle et al., 2019a). Currently, there is no range-wide conservation or restoration program for limber pine in the U.S. However, progress has been made in the southern Rocky Mountains in screening limber pine families for WPBR resistance, establishing field durability trials and a clone bank of resistant genotypes, monitoring for WPBR spread, characterizing WPBR epidemiology in the region, and developing a seed archive for genetic conservation (e.g., Cleaver et al., 2015, 2017; Jacobi et al., 2018a; Kearns et al., 2014; Schoettle et al., 2014, 2022; Burns, 2006; Schoettle et al., 2011; Schoettle et al., 2018b; Schoettle et al., 2019a). Planting projects and protection of WPBR-resistant seed trees from MPB are ongoing in individual jurisdictions. A key limitation to projecting limber pine's population trajectories and implementing treatments in the U.S. is the paucity of data on the frequency of quantitative resistance to WPBR; early indications suggest the baseline frequencies are very low (e.g., Schoettle et al., 2022). Focus on identifying limber pine individuals and populations with quantitative resistance to WPBR range-wide, in currently impacted and healthy populations is needed to support restoration and proactive management.

Both GB bristlecone pine and the southern population of foxtail pine share the vulnerability of reliance on tree longevity for population persistence rather than robust regeneration and individual turnover (see Sections 5.5 and 5.6). If WPBR pressure and climate-caused drought increase in their habitats, they are restricted in their ability to offset increases in mortality with new individuals, an essential process for adaptation in the face of stressors that reduce tree life spans. Research is needed to determine how management can increase natural seedling establishment in these species to increase population size and age-class diversity. Until then, proactive planting of seedlings is an immediate means of increasing the number of individuals in the younger age classes on the landscape (Fig. S2 in Supplemental Material). Because the limited available data suggest that resistance to WPBR may be very low in foxtail pine, planting with stock supplemented with WPBR resistance would be an effective means to increase adaptive capacity. Though foxtail pine has more defenses to MPB than most of the other High-5 (Bentz et al., 2017), protection of foxtail pine trees that have genetic resistance to WPBR from MPB attack would help preserve these valuable individuals. However, the efficacy of anti-aggregate pheromones to protect foxtail pine from MPB has not been evaluated. Initial studies of GB bristlecone pine populations in one portion of its distribution indicate that it has modest levels of WPBR resistance, although range-wide testing is needed. Planting seedlings from bulked lots or select lots with resistant seed sources will help diversify the species' age-class structure and improve the outlook for this species. If pressure by WPBR and MPB continues to be low, GB bristlecone pine may continue to be at low risk of population extirpation, although the effects of climate warming may narrow the species' distribution to the higher elevations.

RM bristlecone pine's greatest vulnerability is its very low standing genetic variation (Table 2; see Section 5.4). Selective mortality by WPBR and drought stress and population loss from wildfire or MPB, or all factors interacting, could further reduce the genetic diversity of RM bristlecone pine and compromise its adaptive potential. The species has modest levels of WPBR resistance and WPBR has only recently spread to overlap with the distribution of RM bristlecone pine. Creating small forest openings to facilitate natural regeneration or planting with bulked seed lots from dispersed seed sources will increase adaptive potential through increased local genetic diversity. These are examples of how understanding strengths and limitations in the adaptive potential of each High-5 species can provide management intervention pathways to improve the outlook for the High-5 species.

Gaps in our knowledge and uncertainty about future conditions limit the precision of the predicted High-5 trajectories. The effects of climate change on WPBR are uncertain and likely to vary at local scales (see Section 4.1). In the past two decades, there has been progress in describing the pattern of WPBR on the landscape and correlating that pattern with climatic conditions and other variables (e.g., Cleaver et al., 2015; Dunlap, 2012; Jacobi et al., 2018a; Kearns and Jacobi, 2007; Maloney, 2011a; Smith-Mckenna et al., 2013; Thoma et al., 2019). Short duration episodes of conducive climatic conditions can increase local infection rates even if average conditions over weeks or months are unsuitable. To improve our ability to predict population trajectories, we need to expand our understanding of the mechanistic interactions responsible for the observed patterns of stressors and their interactions in a changing climate. This will require more experimentation and process modeling to define and explore causal relationships. Empirical information from the field of both hosts, the pathogen, other stressors, and environmental conditions, while essential, are not enough to decipher underlying processes in these complex and dynamic systems.

Cronartium ribicola is also evolving in North America, and at a faster rate than the hosts because of its short generation time. Virulence has already evolved in *C. ribicola* to overcome major gene resistance in two five-needle pine species (Kinloch and Comstock, 1981; Kinloch et al., 2004). The challenge for managers is to package and deploy resistance genes in ways that will reduce the likelihood of rust variants evolving with wide virulence (Kinloch, 2003). Hybrids of *C. ribicola* and the native comandra blister rust (*Cronartium comandrae* Peak) have been confirmed on limber pine and lodgepole pine; their contribution to the evolution of the pathogen(s) and the epidemiology of WPBR is not currently known (Joly et al., 2006). Also unknown is whether *C. ribicola* in western North America has evolved tolerances to drier habitats as it has spread south from its areas of introduction in the northwest. The research defining the environmental conditions required for *C. ribicola* spore production and host infection was conducted over 60 years ago primarily with *C. ribicola* sources from eastern North America (see Table S1 in Jacobi et al., 2018a). Eastern *C. ribicola* populations have greater genetic diversity than those in the west, possibly due to the greater number of initial introductions in the east and longer residence in North America (Hamelin et al., 2000; Brar et al., 2015). Studies of the environmental requirements for current *C. ribicola* populations at the more arid infection fronts in the west may indicate adaptation and help explain the recent spread events in these habitats.

Some ecological relationships and population dynamics of each High-5 species that are important to adaptive capacity are not well characterized, such as regeneration requirements, phenology, fecundity, stress tolerances and physiological plasticity, population connectivity, and competitive interactions. Resistance phenotypes to WPBR and defenses to MPB are being studied (see Sections 4.1 and 4.3.1) but much more work is needed for all the High-5 species. Also, understanding how the physiological condition of the High-5 affects not only infection but also WPBR disease development and resistance expression will be important as trees face the challenges of a changing climate. Information on the molecular basis for the resistance traits, how they are distributed among populations and habitats, and their durability and stability is needed. Molecular methods can help to track adaptation to WPBR (i.e., changes in gene frequencies), and possibly adaptation to other stressors, and to monitor the genetic diversity of surviving populations to assess continued evolutionary potential.

Although there is still much to learn about the High-5 and the WPBR pathosystem, it is clear that many High-5 populations are declining, and others are threatened. Given how slowly these species grow and mature, we cannot wait to have all the answers before moving forward with management interventions. Experimental research can proceed in parallel with adaptive management projects. Collaborative production of knowledge by engaged researchers, managers, non-government organizations, and the public working together can accelerate learning and feedback to improve management treatments (e.g., McKelvey et al., 2021).

The co-production learning approach builds community and the necessary shared investment and commitment to the future of the High-5 species among partners. A major challenge to management at the regional or range-wide scale is coordinating conservation and restoration across different federal, state or provincial, private, and tribal jurisdictions with different missions and procedures (Keane et al., 2021; Jenkins et al., 2022; Tomback and Sprague, 2022). Furthermore, SW white pine, whitebark pine, and limber pine distributions cross international borders. The remote locations and consequently the cost of accessing and implementing treatments in some High-5 ecosystems, especially in the Canadian Rocky Mountains, is another major challenge. Administrative access to conduct management in protected areas with special designations such as Wilderness Areas in the U.S. presents added complexity (see Landres, 2010). Societal support for interventions in the traditionally unmanaged High-5 ecosystems is needed to meet these and other challenges (Meldrum et al., 2011, 2013; Bond et al., 2011; Naughton et al., 2019).

7. Conclusions

Whether a High-5 population thrives, declines, or is extirpated in a new environment is the outcome of the dynamics among demographics, stochastic events, and adaptive evolution. The impact of WPBR and climate change-driven drought on each High-5 species depends on the degree of exposure and mortality rates induced by these primary stressors, the frequency of heritable traits that increase survival, the population's ability to recover, and the demographic effects of other contemporary stressors. The High-5 differ in response to these factors (see Table 2). Some species are sensitive to abiotic stress and highly susceptible to biotic stressors (whitebark pine), others are more tolerant of abiotic stressors and highly susceptible to biotic stressors (limber pine), and others have mixed sensitivities (SW white pine, foxtail pine, GB bristlecone pine, RM bristlecone pine). The species also differ in evolutionary history thus genetic variation and life history strategies, which together affect the adaptive capacity of populations being challenged by novel conditions. A greater understanding of the interrelationships among these factors reveals management opportunities that can potentially increase adaptive capacity for each High-5 species.

Although WPBR may appear to impact populations slowly, taking a decade or longer to kill a mature High-5 tree, it will take at least a century for that mature tree to be replaced. Likewise, because the High-5 and *C. ribicola* share virtually no evolutionary history, more than half of High-5 trees are susceptible to WPBR even in the most resistant naïve populations, and a far greater proportion in the others. The rate of mortality will vary geographically, but as the pathogen continues to spread and evolve, only a few High-5 populations will likely escape this disease over time. There are still many gaps in our knowledge of the adaptive capacity of the High-5, and the future climate and biotic selection pressures are uncertain. However, this synthesis of the current state of the knowledge highlights potential species-specific vulnerabilities in their capacities for rapid adaptation in general and specifically to WPBR and climate-driven drought. Research and forest management can help overcome these vulnerabilities to increase each species' adaptive capacity and population resilience as they face these stressors. The outlook for each of the species can be improved through timely restoration treatments and proactive management activities.

CRediT authorship contribution statement

Anna W. Schoettle: Conceptualization, Writing – original draft, Writing – review & editing. **Kelly S. Burns:** Data curation, Writing – original draft, Writing – review & editing. **Shawn T. McKinney:** Writing – original draft, Writing – review & editing. **Jodie Krakowski:** Writing – original draft, Writing – review & editing. **Kristen M. Waring:** Writing – original draft, Writing – review & editing. **Diana F. Tomback:** Writing – original draft, Writing – review & editing. **Marianne Davenport:** Data curation, Visualization, Writing – review & editing.

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Appendix A. Supplementary Material

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