forests

Review

Complex Challenges of Maintaining Whitebark Pine in Greater Yellowstone under Climate Change: A Call for Innovative Research, Management, and Policy Approaches

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Abstract: Climate suitability is projected to decline for many subalpine species, raising questions about managing species under a deteriorating climate. Whitebark pine (WBP) (*Pinus albicaulis*) in the Greater Yellowstone Ecosystem (GYE) crystalizes the challenges that natural resource managers of many high mountain ecosystems will likely face in the coming decades. We review the system of interactions among climate, competitors, fire, bark beetles, white pine blister rust (*Cronartium ribicola*), and seed dispersers that make WBP especially vulnerable to climate change. A well-formulated interagency management strategy has been developed for WBP, but it has only been implemented across <1% of the species GYE range. The challenges of complex climate effects and land allocation constraints on WBP management raises questions regarding the efficacy of restoration efforts for WBP in GYE. We evaluate six ecological mechanisms by which WBP may remain viable under climate change: climate microrefugia, climate tolerances, release from competition, favorable fire regimes, seed production prior to beetle-induced mortality, and blister-rust resistant trees. These mechanisms suggest that WBP viability may be higher than previously expected under climate change. Additional research is warranted on these mechanisms, which may provide a basis for increased management effectiveness. This review is used as a basis for deriving recommendations for other subalpine species threatened by climate change.

Keywords: climate change; whitebark pine; resource management; policy; Greater Yellowstone Ecosystem

1. Introduction

Impending climate warming is perceived as a major threat to the many species that are adapted to subalpine habitats [1–3]. Upper subalpine and tree-line species have a number of traits that make them challenging to manage under climate change. These species are especially vulnerable to climate change because many mountain ranges have decreasing area at higher elevations and upslope movement of suitable climates often results in range loss or "mountain-top extinctions" [4]. Potential change in climate suitability for these species has high uncertainty due to the narrow distributions of these species, small sample sizes, and technical difficulties in modeling climate at the fine spatial scales relevant to these species [5,6]. The ecology of these species is typically less studied and less understood than commercially valuable species and management experience is often limited. Within the U.S., the ranges of these species are often within restricted federal lands such as Proposed or Designated Wilderness and Wilderness Study Areas (hereafter termed wilderness) where management is constrained by law and policy [7]. Finally, similar to other species, these projected changes in climate suitability for tree-line species are often much larger in spatial scales (e.g., sub continental) than the scales of management jurisdictions, necessitating interagency collaboration [8].

Resource managers of locations where a species is projected to undergo declining climate suitability face difficult decisions as to appropriate management strategies. Agency policy often promotes retention of viable populations of native species [9,10]. Yet, ecological theory would suggest that species are unlikely to persist in areas that are outside of the species' climate tolerances [11]. New perspectives on research, policy, and management are needed to maintain the viability of many subalpine species under climate change. To illustrate these perspectives, we have selected an iconic high-elevation tree species in one of the most iconic areas in the United States.

Whitebark pine (WBP) (*Pinus albicaulis*) crystalizes the complex challenges that natural resource managers will likely face for many subalpine species in the coming decades [12]. WBP is a member of the montane and subalpine forest community in western North America and is considered a keystone species for the unique ecosystem services it provides including facilitating increased forest cover, enhanced persistence of snowpack and runoff, and providing seeds that are an important food for threatened Grizzly bear (*Ursus arctos*) and many other wildlife species [13–15]. Because of these benefits, there is concern over the forest die-off that is underway. WBP is declining throughout its range because of the combined effects of mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, fire exclusion management policies, and the introduced disease white pine blister rust (causal agent *Cronartium ribicola*) [13]. In addition to these current threats, climate suitability is projected to decline over much of the species current range [16–18].

The Greater Yellowstone Ecosystem (GYE) in the U.S. Northern Rocky Mountains has a cold continental climate and supports extensive stands of WBP in the subalpine zone [19], and WBP individuals in the sub canopy of forests in the montane zone. Some 53% of the aerial extent of WBP in the U.S. is located in the GYE [20,21]. The GYE WPB population has been particularly hard hit in recent years with over 95% mortality of cone bearing trees [22,23] in some areas due to factors related to warming climate [24]. Beyond the current forest die-off, scientists are projecting that the area of suitable habitat for WBP in GYE will decline dramatically in the coming century under changing climate [25–28]. Consequently the U.S. Fish and Wildlife Service listed WBP on its U.S. Candidate species list [29]. An interagency committee was formed in 2000 (called the Whitebark Pine Subcommittee of the Greater Yellowstone Coordinating Committee, or GYCC WBP Subcommittee) and has begun implementing a strategy for WBP management in the GYE [30]. The potential effectiveness of this strategy under climate change has not been evaluated.

Assessing the risk of climate change to population viability of WBP in the GYE and the potential effectiveness of management is difficult because the species is influenced by a complex array of interacting ecological factors [13]. These include the direct effect of climate on WBP and the indirect effects of climate on competing tree species, fire regimes, mountain pine beetles, and white pine blister rust, all of which interact and limit WBP viability. In this paper we synthesize current knowledge on the complex interactions that impact WBP in the GYE and summarize current management approaches taken by federal land managers as coordinated by the GYCC WBP Subcommittee. We then evaluate evidence regarding new perspectives on the complex WBP system that may allow opportunities for WBP persistence in the face of climate change. We conclude by offering recommendations for research, policy, and management to increase likelihood of persistence of WBP in the GYE. Although the ethical implications of some management options have been discussed elsewhere for example, see discussions of assisted migration in [31,32], our goal here is not to debate philosophical views on active management under climate change, but to present management recommendations that might make sense if active management of WBP were an agreed upon goal. This synthesis of a well-studied species that is currently responding to climate change is relevant to the many other subalpine species around the world that are likely to face similar threats in coming decades. Thus, we end with recommendations for research, climate-informed management, ecological forecasting, re-evaluation of policy, and interagency collaboration that may improve the viability of other subalpine species vulnerable to climate change.

2. Complex Interactions that Limit WBP under Climate Change

Research on WBP in the past decade provides a basis for a conceptual model of the complex interactions by which future climate change may directly and indirectly influence the demography of WBP (Figure 1). The population growth rate of any species is a consequence of vital rates in each life-history stage. Climate change influences WBP viability through its direct effects on establishment, growth, survival, reproduction, and dispersal and through its indirect effects on biotic interactions and disturbance.

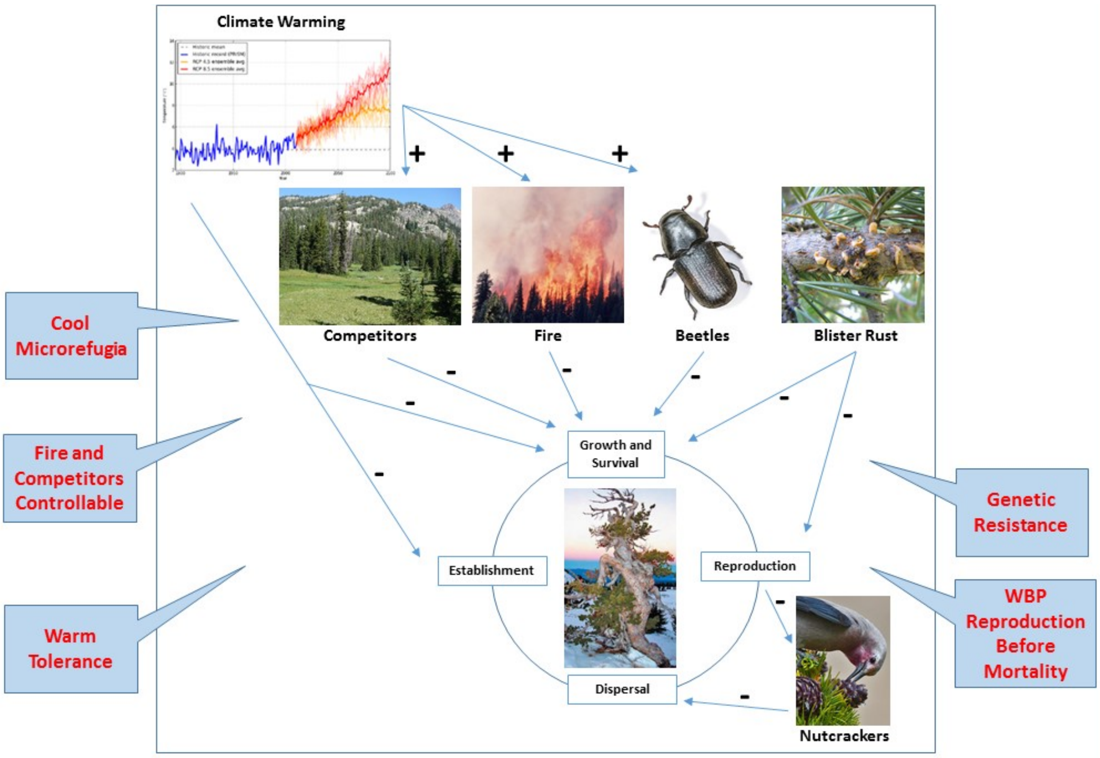

Figure 1. (Inner box) Conceptual model of the projected direct and indirect effects of climate warming on WBP demography based on the current literature. Positive and negative signs denote the nature of the effect. Climate warming reduces whitebark pine (WBP) establishment, growth, and survival directly by exceeding WBP physiological tolerances and indirectly by favoring competing vegetation, severe fire, and mountain pine beetles. White pine blister rust negatively influences WBP growth, survival, and reproduction. However, the influence of climate change on white pine blister rust in the Greater Yellowstone Ecosystem (GYE) is not currently understood. (Outer Box) Ecological mechanisms that may allow WBP to remain viable in GYE in the face of projected climate warming and related threats (red text in call-out boxes). Picture and figure credits from left to right and top to bottom are: Tony Chang, Andrew Hansen, Yellowstone National Park Photo Archive, Colleen Kimmett, Grav Skeldon, Louisa Willcox, Karen Rentz.

2.1. Climate Suitability

Climate suitability is an important determinant of the distribution of many tree species, hence the climate characteristics of where a species is found is often used to infer climate tolerances and potential effects of future climate change [33,34]. The subalpine locations where WBP is present in the GYE are characterized by low maximum July temperatures, low summer minimum temperatures, and deep April snowpack [25,26]. Climatically-suitable habitats for WBP are projected to decrease substantially by the end of the century across the species range [17,18,35] and within the GYE [25,26]. As a result, WBP was ranked as most vulnerable to climate change based on climate suitability among eight conifer species in the Northern Rockies [36]. Based on the most recent climate projections, mean annual temperatures across the GYE are projected to rise 3–7 °C above the 100-year historical mean by the end of the century and snowpack in the subalpine zone is projected to decrease by 20%–30% [26]. The area within the GYE where climate is projected to be suitable for WBP in reproductive size classes (>20-cm diameter at breast height or DBH) by 2100 was 82% less than at present under a moderate warming scenario (RCP 4.5) and 97% less under a higher warming scenario (RCP 8.5) by 2100 [26].

2.2. Competition

In addition to its physiological tolerances to climate, the performance of WBP in the GYE is structured by competition with lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). At the highest elevations, climates are mostly unsuitable for competitors, allowing WBP to persist in pure stands [24,37,38]. At lower elevations in the montane zone, the other conifer species typically grow faster than WBP, and by mid to late seral stages, there is reduced growth, reproduction, and survival of WBP through competition [38]. Under future climate scenarios in the GYE, climate suitability for all the conifer species is projected to shift upslope [39]. Locations where WBP is currently dominant are projected to increase in climate suitability for Douglas-fir, lodgepole pine, subalpine fir, and Engelmann spruce [39]. The highest elevations in the GYE, which are now not occupied by trees are projected to be suitable in climate for subalpine fir as well as WBP. Thus, the effects of competition on WBP may increase under future climates.

2.3. Fire

Nearly all effects of competition on WBP are mediated by wildland fire. Severe fire kills all species of montane and subalpine trees, including WBP [13]. WBP regenerates well in burned areas and is among the tree species that initially colonize these open sites and persist in them for decades until outcompeted by other conifer species [40]. WBP's higher resistance to fire [41] delays succession under mixed-severity fire regimes through the preferential removal of competitors such as subalpine fir and Engelmann spruce by fire [24].

Over much of the WBP range, humans have excluded fire in the past several decades resulting in shifts to greater dominance of later seral stages, to the detriment of WBP [13]. In the West Big Hole Range of Idaho and Montana, for example, Murray *et al.* [42] found that nearly half of all stands have shifted to later seral stages since 1753, possibly due to fire exclusion. The fire regime within the montane zone of the GYE is characterized by infrequent, high-severity fires [28]. This has likely favored WBP in the decades following severe fires because its seed is bird dispersed allowing great dispersal distances [43]. There is no evidence, however, that fire exclusion activities have altered the fire return interval within this zone in the GYE [44].

Climate change is expected to affect fire regimes throughout the range of WBP and, in turn, WBP dynamics [45]. In western Montana, increasing frequency of severe fires is projected to reduce the abundance of WBP, but not as much as its competitors e.g., [46]. In the GYE, fire is projected to increase in both frequency and size [47], which probably will result in increases of WBP mortality rates as well as competing species. A simulation modeling study by Clark *et al.* [48] in the montane zone of the GYE projected substantial reductions in lodgepole pine and Douglas-fir stand age and basal area under changing climate and increased fire severity. Such studies have not been done in the subalpine zone, where WBP is most dominant. The potential effects of frequent severe fire on WBP relative to competing species are not known. However, it is likely that stand size and stand age for all conifer species will be much reduced.

2.4. Mountain Pine Beetle

Mountain pine beetle is a native species that has periodically irrupted in western forests in the past and caused significant mortality to western pine species [49]. During most of the past century, mountain pine beetles have typically been at endemic levels in WBP ecosystems, causing little host mortality because of inhospitable cold temperatures [50,51]. While periodic outbreaks have occurred during warm periods in the past, 1730s, 1819, 1887, 1930's, and 1970s [52], these outbreaks were typically short-lived. In the GYE, cold winter temperatures have limited the severity of outbreaks in WBP forests due to negative impacts on beetle development [50]. The current outbreak, which is more severe than any in recorded history, is thought to be the result of favorable forest conditions, perhaps resulting from fire exclusion [22], as well as shortened mountain pine beetle generation times linked to recent above-average temperatures [50,53].

Mountain pine beetles are cambial feeders, which along with associated fungi typically kill their host in order to complete their life cycle. Time of development is variable and is driven largely by temperature [54]. In WBP systems, development can take up to two years because of prolonged cold temperatures. Recent milder winters and warmer summers have allowed beetles to complete an entire life cycle in one year or less, rapidly increasing the rate of population growth and the severity of the outbreak [50]. The current decline of WBP in the GYE is largely due to the abnormally severe mountain pine beetle outbreak. During 1999–2007, some 95% of WBP stands had adult mortality levels exceeding 50% [23]. Future projections show increased climate suitability for mountain pine beetle in the WBP zone of the GYE in the coming century, provided there are sufficient living host trees [53,55].

2.5. White Pine Blister Rust

White pine blister rust is an invasive pathogen native to Asia and introduced to North America *circa* 1910. Since initial invasion, it has followed a typical pattern of slow establishment leading to exponential growth, and now endemic persistence [56]. For decades, the pathogen has attacked white pine populations in waves but the recent spike in blister rust infection as well as high mortality rates of WBP of all ages are unprecedented [57]. The fungus is now found across almost the entire distribution of WBP, with highest levels in the north western Rocky Mountains, likely due to cool, moist climate conditions favored by the pathogen [24].

The multiple stage, five spore life cycle of white pine blister rust alternates between WBP and mainly *Ribes* species [56]. This advantageous life cycle allows for genetic diversity, short and long distance dispersal, longevity, and annual amplification [56]. WBP is susceptible to infection by *C. ribicola* at any life stage. Infection of the needles occurs first, with the fungus then spreading to branches and stems, girdling and eventually killing the tree. The pathogen is most destructive when infecting mature individuals as it cuts off and kills the upper, cone-producing canopy.

Within the past few decades blister rust infection rates have increased dramatically within much of the range of WBP. During a 17-year study monitoring blister rust infection in northern Idaho, over 75% of originally uninfected WBP became infected [57]. The GYE has seen lower infection rates, mainly 20%–30% [58]. A model of blister rust prevalence based on data from 1968 to 2008, however, projected that blister rust infection and subsequent mortality will be widespread across the GYE over the next 20 years [59].

2.6. Seed Predation and Dispersal

WBP seeds are dispersed by a species of bird, the Clark's nutcracker (*Nucifraga columbiana*) [60]. The birds store WBP seeds as a food source in caches that can be up to 32 km from the parent tree [61]. Some of the cached seeds germinate and the result is a relatively rapid dispersal of WBP [61,62]. Thus, WBP is able to colonize patches opened by fires, avalanches, and other disturbances relatively rapidly and establish new populations [13]. Although species other than Clark's nutcracker harvest and store WBP seeds in middens, uneaten seeds seldom become established because the microhabitats of the middens do not provide suitable conditions [63]. Whether WBP seeds are lost to predators or are dispersed by nutcrackers is governed by various interacting relationships. In years of low cone production, most seeds are consumed by predators [63]. In areas of high WBP mortality or in years of small WBP cone production, the crop may be too small for nutcrackers to find adequate food and they relocate to more productive areas [64]. Additionally, trees stressed by competition, beetles, blister rust or unfavorable climates are less capable of producing the large seed crops that are required to swamp seed predators and allow for WBP establishment. Consequently, WBP populations under climate change may be on the path to extinction long before the last individual dies because of the lack of dispersal and regeneration due to abandonment by nutcrackers [13] in high mortality areas.

In total, the conceptual model of the WBP in GYE (Figure 1) suggests the potential for continued population declines under future climate change. Little of the current range is projected to remain suitable in climate for WBP populations based on statistical models. Effects of climate warming on competitors, fire regimes and mountain pine beetle populations, especially in the presence of white pine blister rust, are expected to further reduce WBP vital rates. Nonlinear effects of WBP abundance on seed dispersal by nutcrackers could cause threshold declines in dispersal and reproduction as the population size decreases. Alternatively, increases in fire would lead to more open areas suitable for WBP regeneration and thereby favor future population viability [12], if adequate adult trees survive the fires and provide seed sources.

3. Current Management Approach and Status

In recognition of the many cross-boundary issues in the GYE, federal agencies in the region collaborate to manage WBP forests via the GYCC WBP Subcommittee. The subcommittee formed to "work together to help ensure the long-term viability and function of whitebark pine in the Greater Yellowstone Area" [30]. The subcommittee initially focused on mapping and monitoring WBP across the GYE. Substantial mortality of WBP was observed by 2004 leading the subcommittee to address the need for management of the species, culminating in the publication of the *Whitebark Pine Strategy for the Greater Yellowstone Area* [30].

The Strategy is organized around four goals and specific treatments are identified for each goal [65].

- Monitoring. The goal is to quantify the status and trends in WBP condition and use results to guide management. This goal is achieved by monitoring WBP survival, reproduction, and mortality agents.
- Protection. The goal is to prevent or minimize damage to existing trees and stands from insects, disease, and fire. Strategies to realize this goal include protecting genetically disease resistant trees, cone-producing trees, and trees exhibiting blister rust resistance through use of anti-aggregation pheromones (verbenone), insecticides (carbaryl), and pruning. Additionally, blister rust resistant trees and stands are protected from wildland fire.
- Restoration. The goal is to restore WBP stands by replanting or by creating conditions that favor natural regeneration and dominance of WBP. Methods include planting blister-rust resistant seedlings, creating openings conducive to the natural regeneration of WBP, and removing competing vegetation.

- Tree Improvement. The goal is to identify and propagate genotypes that have resistance or tolerance to adverse factors such as drought and white pine blister rust. This is realized by collecting seeds from WBP trees having potential resistance to white pine blister rust, propagating the seeds in nurseries, testing for blister rust resistance, and using seeds from trees that show resistance to populate a seed orchard to produce resistant seedlings for planting.

The Strategy was not formulated in the context of projected climate change because of a lack of climate science information at the time. Rather, the Strategy stated, "As scaled regional models or more detailed predictive mapping become available, this information will be incorporated into the annual work plan and future revisions of the Whitebark Pine Strategy" [30].

The potential for applying management treatments across the GYE varies with federal agency and land allocation type. The majority of WBP distribution in the GYE (68%) lies in wilderness (Table 1) where the enabling legislation or current policy dissuades active management. Twenty three percent of the WBP range in the GYE is within Inventoried Roadless Areas, where lack of mechanized access constrains management feasibility [66]. Only 8% is within multiple use lands where active management is permitted and logistically feasible.

Table 1. Aerial distribution of WBP in GYE by federal land allocation type. Not shown is the 0.21% of the WBP distribution that is on tribal and other land allocation types.

Land Allocation Type	Agency	Legal Direction/Management Philosophy	Proportion of GYE WBP Aerial Extent
Multiple Use	National Forest Service; Bureau of Land Management	Multiple use while maintaining ecological integrity	8.09%
Non-wilderness	National Park Service	Preserve unimpaired natural resources for the enjoyment, education, and inspiration of this and future generations.	0.14%
Wilderness (Designated, Proposed, Recommended, Study Area)	National Forest Service; Bureau of Land Management; National Park Service; U.S. Fish and Wildlife Service	Maintain natural and untrammeled conditions	68.18%
Inventoried Roadless Area	National Forest Service	Roads and timber harvest prohibited. Forest health treatments allowed.	23.38%

The distribution of WBP management activities coordinated by the GYCC WBP Subcommittee to date reflects these land allocation constraints. While research and monitoring plots are well distributed across land allocation types (Table 2), the majority of protection and restoration treatments were done on multiple use lands, with intermediate levels of treatment in roadless areas and very low levels of treatment in wilderness. Importantly, the estimated minimum area treated to date (*ca.* 2227 ha) is much less than 1% of the WBP aerial extent in GYE.

In summary, while considerable progress has been made in WBP management in the GYE, the scale and scope of the effort is likely inadequate considering current WBP mortality levels and future climate projections. Federal agencies have been collaborating for some 15 years and the interagency working group has prepared a comprehensive strategy document, deployed research and monitoring efforts, developed a genetically-improved seedling program, and implemented protection and restoration activities. This implementation, however, has been done on a small proportion of the GYE WBP range. Moreover, the GYE WBP Strategy, while using the best available science at the time, was not developed in the context of the projected direct and indirect effects of climate change on WBP viability. The projected loss of climate suitability over most of the GYE and potential exacerbation of the effects of bark beetles, competition, and fire under climate change are likely to substantially reduce WBP viability in GYE. Thus, the potential long-term effectiveness of the GYE WBP Strategy as currently applied is unknown.

Table 2. Estimated minimal extent of monitoring and management treatments for WBP for federal lands in the GYE by land allocation type as coordinated by the GYCC WBP Subcommittee. Data are estimates provided by the GYCC WBP Subcommittee with most of the U.S. Forest Service data compiled from the Forest Service Activity Tracking System (FACTS) in September 2015. Research/monitoring plots are described in [67].

Management Activity	Land Allocation Type		
	Multiple Use	Wilderness [1]	Inventoried Roadless Areas
Research/monitoring	101 plots	105 plots	83 plots
Reforestation monitoring	700 ha total	0 ha	351 ha
Protection from mountain pine beetle	688 trees and 890 ha annually	398 trees and 34 ha annually	76 trees and 157 ha annually
Planting seeds/seedlings	302 ha total	4 ha total	351 ha total
Mechanical pruning/thinning	428 ha total	0 ha total	8 ha total
Targeted fire suppression	0 ha total	0 ha total	0 ha total
Wildland/prescribed fire use	53 ha total	0 ha total	0 ha total
Seed collection	166 bushels total	20 bushels total	101 bushels total

[1] Designated, Proposed, Recommended, or Study Area.

4. New Perspectives on WBP Dynamics under Climate Change

If the abundance of large cone-producing WBP has declined dramatically in the GYE over the past decade and climate suitability is projected to deteriorate in the future, does this portend the extinction of WBP in the GYE and render efforts at management futile? It is currently unknown what rates of establishment, growth, reproduction, survival and dispersal are necessary for a minimum viable population of WBP in the GYE. Our increasing understanding of the complex WBP system, however, focuses attention on existing and new perspectives on mechanisms by which the species may persist in the GYE under future conditions, probably in younger age classes and smaller population sizes (Figure 1). Improved knowledge about these potential mechanisms of persistence may improve management effectiveness. In this section we identify and evaluate six key mechanisms that may allow WBP population persistence (Table 3).

Table 3. Ecological mechanisms that may favor WBP population persistence under climate warming. Weight of evidence is based on current knowledge from the literature. Research needs and management implications are discussed in Sections 5 and 6.

Limiting Factors	Mechanism	Weight of Evidence (Citations)	Research Needs	Management Implications (Citations)
Climate change	WBP persistence in microrefugia	Strong [68–72]	Finer resolution modeling to identify microrefugia and monitoring of WBP performance	Remove competing species in cold/wet settings; protect from mountain pine beetles in cold/dry settings; protect microrefugia from severe fire [71,73]
Climate tolerances	Fundamental temperature niche broader than currently perceived	Moderate [71,74–76]	Physiological studies of temperature, precipitation limits	Remove competing species to reduce competitive exclusion of WBP in warmer settings [12,13,24,30,65,77]
Competing tree species	Release from competition improves WBP viability	Strong [40,78,79]	Species/age specific competitive effects on WBP	

Table 3. *Cont.*

Limiting Factors	Mechanism	Weight of Evidence (Citations)	Research Needs	Management Implications (Citations)
Fire	Enhanced moderate severity fire favors WBP	Weak [77,80]	Projections of fire severity in WBP habitat; WBP sensitivity to fire	Protect rust-resistant trees, especially those whose seeds are being harvested; allow more wildland fire use fires during moderate years; [12,13,48,65,81]
Mountain Pine Beetle	Medium sized WBP [1] resist beetles and reproduce	Strong [82–85], Figure 4	Rates of reproduction and survival of medium sized WBP[1] relative to minimum population size	Remove competing vegetation and perhaps thin existing WBP to increase vigor of reproducing trees [12,13,65,86]
White Pine Blister Rust	Natural and artificial selection allows persistence	Well known [87,88]	Long term monitoring of rust resistance	Plant rust-resistant seedlings; protect known rust-resistant individuals from MPB and fire [89,90]

[1] 18–25 cm diameter at breast height.

4.1. Microrefugia

Projected loss of climate suitability for WBP may fail to adequately consider variation in microclimate. "Microrefugia" are defined as localized landscape settings that support suitable climate conditions amidst unfavorable regional climate [91]. Evidence for species survival in microrefugia in the Holocene suggests that microrefugia might allow cold-adapted species to persist under future climate warming [92]. Under this mechanism, localized landscape settings in the GYE could remain climatically-suitable and serve as microrefugia for WBP persistence under future warming.

Microrefugia may be missed by bioclimate envelope analyses if the resolution of the climate projection is coarser than the climatic factors that influence spatial patterning of the organism [93]. Fine scale variation in aspect, slope, elevational extremes, topographic shading, and cold air or water drainage may influence plant distributions [5]. For example, consideration of cold-air pooling and projected climate warming resulted in 6 °C differences in modeled temperature between nearby locations in the Cascade Mountains [68]. Analyses of the effects of spatial resolution on projected climate suitability found that coarse scale models (e.g., >4 km) predicted loss of climate suitability while fine-scale models (e.g., ~90 m) projected persistence for some species [70,93]. Simply put, the finer resolution models were able to identify meaningful climatic variability in mountainous terrain that could not be resolved by the coarse scale models. In the case of WBP in GYE, the 800-m resolution used by Chang *et al.* [26], while state of the art for climate projection, may be too coarse to accurately model a narrowly distributed species like WBP by missing small areas of locally suitable habitat.

We speculate that two types of landscape positions may serve as microrefugia for GYE populations of WBP. The first are locations with relatively cool and wet conditions where temperatures may stay within the tolerances of WBP and mortality due to mountain pine beetle may be lower. Mortality of WBP from mountain pine beetle in GYE was found to be positively associated with mean minimum temperature [73] and with climate water deficit, a measure of aridity [72]. The effect of aridity was especially strong for larger WBP trees. Increases of 75 mm in climate water deficit were associated with a 20% increase in mortality rates for trees >20 cm DBH. Similar results were obtained for WBP in eastern California [71]. High elevation depressions, north-facing slopes, and medium to fine-textured soils with higher water holding capacity are areas in the GYE [72] that may possibly maintain relatively cool temperatures and higher water availability and serve as microrefugia for WBP.

In the absence of mortality from mountain pine beetles, colder and drier landscape positions represent potential microrefugia where climate conditions could remain suitable for WBP but be too harsh for competing tree species or for white pine blister rust. At upper tree line, WBP is able to establish and survive in more exposed sites than subalpine fir or Engelmann spruce, presumably because of its: phenotypic traits to increase stress tolerance (e.g., higher soluble sugar concentrations, lower specific leaf area) and improve carbon balance (e.g., greater water use efficiency, lower respiration) [69]; higher photosynthetic tolerance for the frequent frost and bright sunlight [94]; and tolerance of wind-induced drought [95]. Such microrefugia are most likely found in wind-swept, high elevation sites where WBP currently forms the upper tree line. These drier and cooler sites are also less favorable for white pine blister rust attack on WBP [96].

4.2. Temperature Niche

Bioclimate envelope modeling only identifies the climate conditions where a species is present today and uses this to predict where it will be under climate change [34]. To the extent that competition with other conifer species restricts the presence of WBP in warmer settings in the GYE, the species may be able to tolerate warmer and drier conditions than where it is currently distributed and thus be better able to persist under warming climate than projected by bioclimate envelope models.

The upper temperature tolerances of WBP are not well known. The single study done in the GYE [76] suggested that WBP can tolerate warmer conditions than those where it currently is found. In laboratory experiments under well-watered conditions, optimal photosynthesis of WBP occurred at 20 °C with upper and lower limits of 0 °C and 35 °C. Root growth and germination ranged from 10–45 °C to 10–40 °C, respectively. Currently, only about 5% of WBP trees are growing where temperatures are near the optimum for photosynthesis identified by Jacobs and Weaver [76]. Thus, mean summer temperatures where WBP currently occur in GYE may be lower than the physiologically limiting temperatures for the species, at least when adequate moisture is available. In support, studies elsewhere in the range of WBP found that the species increased in growth rate with increasing minimum temperature [71] and increased in density and basal area in response to warmer, wetter conditions [74].

A recent paleoecological reconstruction in GYE [75] also suggests that the fundamental niche of WBP is broader than its current realized niche. WBP was most abundant (as evidenced by pollen) at a time prior to about 7500 years ago with the warmest summers and lowest effective moisture of the past 15,000 years, albeit colder winters. In the mid-late Holocene, WBP declined as summer temperatures decreased, winter temperatures and precipitation increased, and lodgepole pine increased. This persistence of WBP in the GYE since the last glacial maximum suggests that the species can tolerate a much wider range of climatic variation than its current distribution would suggest, particularly under lower levels of competition from other tree species. A caveat of this study, however, is that pollen of WBP cannot be separated from the closely related limber pine (*P. flexilis*) that tolerates much warmer conditions than WBP and the presence of limber pine in GYE during the Holocene is poorly known [75].

4.3. Release from Competition

If the distribution and abundance of WBP are influenced by competition, then ecological theory would suggest that reducing competition may increase vital rates such as establishment, growth, survival, and reproduction. This release can be initiated by humans (e.g., thinning, harvesting) or by disturbances (e.g., fire, disease).

It is well established that WBP is often limited by competition at lower elevations within it range. A study in British Columbia found that WBP was inhibited early in post-fire succession by lodgepole pine and later in succession by subalpine fir and Engelmann spruce [40]. In lower elevations in western Montana, WBP and subalpine fir individuals are found further apart than expected if the trees were distributed randomly, implying competition, whereas at high elevations, the two are found closer together [78]. The most direct evidence comes from experimental removal of competitors. Among 45 WBP trees aged 51–395 years released from competition, 31 trees exhibited a significant increase in growth rate in the first five years post-thinning, with a mean increase in radial growth of 64% [79] (Figure 2). This increase was higher for trees in stands with high tree density before thinning.

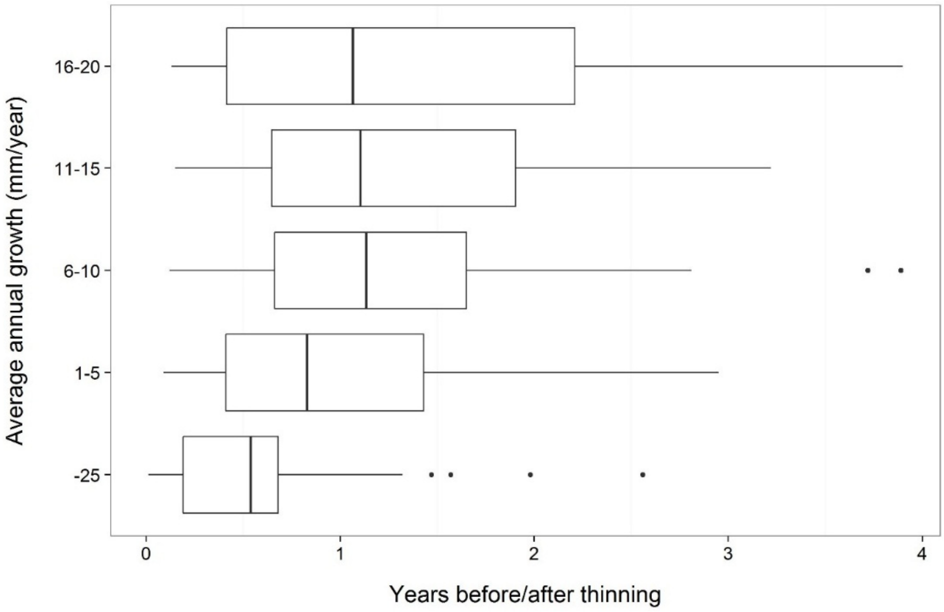

Figure 2. Average annual growth of WBP before and after thinning of competitors. Data from Keane *et al.* [79].

Competition is thought to play a more important role at lower elevations of WBP's range, as abiotic conditions are favorable for both WBP and its competitors [38]. At higher elevations, climate is less favorable for competitors, whose absence releases WBP from competition [24,37,38]. Consistent with these predictions, the elevational distributions of tree species in GYE illustrates that the prevalence of species potentially competing with WBP is reduced at higher elevations (Figure 3).

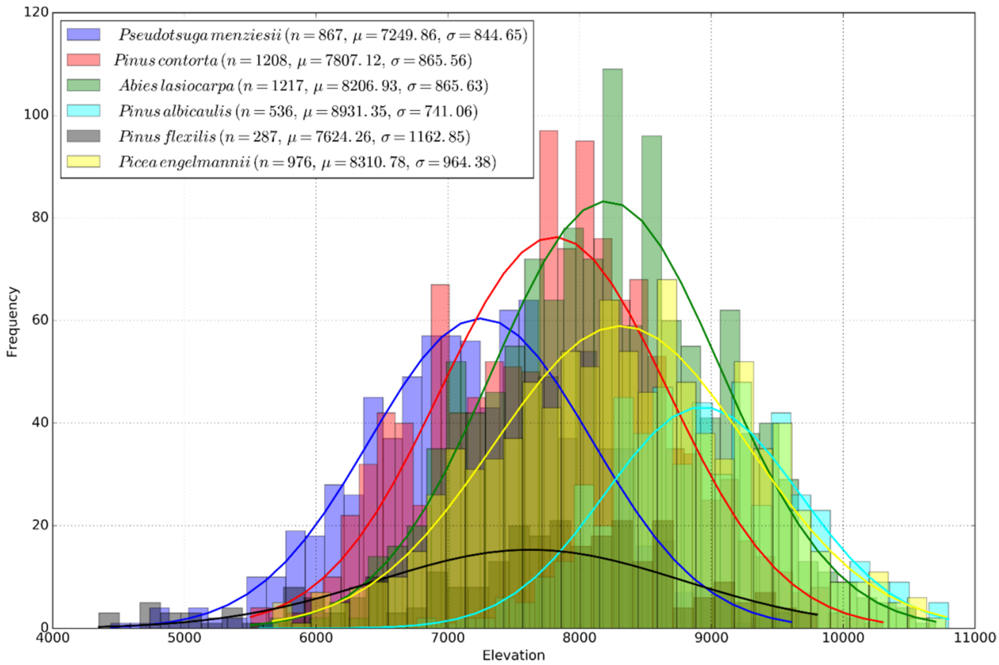

Figure 3. Frequency of occurrence of the major conifer species along the elevational gradient in the GYE as derived from Forest Inventory and Analysis data [20,21].

4.4. Shifting Fire Regime

The influence of fire on WBP varies with fire severity. Mixed-severity fire may benefit established WBP trees by killing competitors while severe fire often kills WBP along with its competitors. WBP may benefit by release from competition if climate change increases mixed-severity fire in the subalpine zone.

WBP is generally assumed to be more tolerant of fire than its competitors [97,98]. Following moderate-severity fire, Barmore *et al.* [80] found a 35% mortality rate of mature WBP, but much higher rates in Engelmann spruce (47%) and subalpine fir (59%). In contrast, experiments with prescribed fire found little difference in fire-caused mortality between WBP and subalpine fir [77], suggesting that WBP fire tolerance may be highly dependent on stand structure.

As is the case for western forests in general, climate warming is expected to increase fire frequency in the GYE. Based on the statistical relationship between past climate and fire, Westerling *et al.* [47] projected for mid-century that fire rotation will be reduced to <30 years from the historical 100–300 years for montane forests in the GYE using a statistical approach. A study that additionally included feedbacks from vegetation to fire projected a decrease in fire rotation of 16%–76% from the modeled historic period on the Yellowstone Plateau [48]. Neither study reported changes in fire severity, however. It is plausible that light fuel loads in upper subalpine environments and in previously burned areas will limit fire severity in subalpine settings under a warming climate to the benefit of WBP. But current knowledge does not allow strong inference on the potential influence of climate-induced shifts in fire regimes on WBP viability in the GYE.

4.5. Mountain Pine Beetle Escape

In well-studied pine species such as lodgepole pine, resistance to mountain pine beetle attack is known to be highest in vigorously growing individuals which are able to shunt more energy into defense tactics [99–102]. Because vigor often declines with age and size, resistance to beetles is often lower in larger, older trees. If similar patterns hold for WBP, some individuals may reach the age of reproduction and produce cones before reaching a size class where they become highly susceptible to mountain pine beetles.

Several studies across the range of WBP and in the GYE have found mortality rates due to bark beetles increase with tree age and size [82–85]. The increasing susceptibility to mountain pine beetles with increasing WBP tree size and age is likely related to the tree's reduced capacity to mobilize carbohydrates for defense as it matures [103].

One of the authors of this paper (K. Legg) has been working with the Greater Yellowstone Whitebark Pine Monitoring Working Group [67] and provided unpublished data indicating that some of the small and medium sized WBP trees survive mountain pine beetle attacks at higher rates than larger trees and are capable of producing cones. During 2004–2007, live WBP trees (>1.4 m tall) (n = 4742) were tagged within 176 transects distributed across the GYE. These transects were selected using a probabilistic, two-stage cluster design where whitebark pine stands were the primary sample units and 10 × 50-m transects were the secondary sample units [104]. Tagged trees were visited at least twice from 2011 to 2014 to measure survival and whether the trees were bearing cones in addition to other variables such as presence of blister rust and mountain pine beetle indicators. We tallied survival rates by diameter class and evidence of cone bearing among trees alive at the end of 2014. By the end of the resample period, 30% of the trees were dead, with survival rates declining in larger size classes; mortality rates exceeded 50% in trees >20 cm DBH (Figure 4). The percentage of live trees in the resample period that showed evidence of cone bearing was low for the smallest DBH class (2%), moderate for the 10–18 cm DBH class (34%), and was substantially higher for larger diameter classes (82%). These results suggest that survival rates of WBP under beetle attack decline with increasing size while proportion of individuals that are cone bearing increases. Thus, intermediate size classes have moderate rates of both survival and cone bearing. This study did not quantify total cone production, which is known to increase with diameter and canopy volume [97]. McKinney *et al.* [105] estimated that a threshold level of ~1000 cones/ha is needed for a high likelihood of seed dispersal by nutcrackers, and that this level of cone production can be met by forests with live WBP basal area > 5.0 m^2/ha. Additional research is needed to determine if reproduction by mid-sized WBP trees is sufficient to allow population persistence during beetle outbreaks that lead to high mortality of larger individuals.

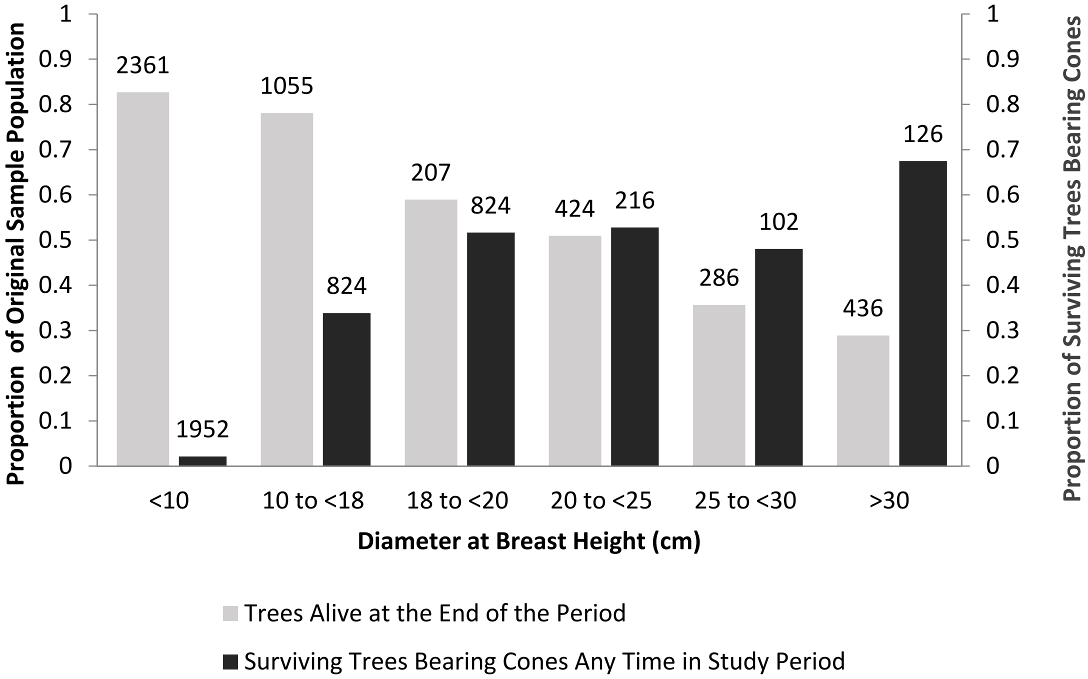

Figure 4. Results for a sample of whitebark pine trees that were living in the 2004–2007 study initiation period and monitored through a 2012–2014 resample period. Rates of tree survival during the study period are shown by the gray bars and the left Y axis. Sample size in each diameter class is displayed above the gray bars. Potential reproduction as indicated by evidence of cone bearing (cones, conelets, or cone scars present) for trees alive at the end of the period is shown by the black bars and the right Y axis. Sample size in each diameter class is shown above the black bars. Data from the Greater Yellowstone Whitebark Pine Monitoring Working Group [106].

4.6. White Pine Blister Rust Resistance

Genetic resistance to white pine blister rust and natural selection processes could potentially counter rising infection rates and offer an opportunity for increased potential for species persistence. Some individual WBP typically survive blister rust attacks and this resistance or tolerance to infection is thought to be genetically determined [89]. Trees monitored in Mount Rainier National Park, for example, have shown a promising long-term resistance to blister rust, surviving infection periods for decades [88]. Moreover, in seedling trials, survival rates for rust-exposed individuals after four years averaged from 7.7% to 17.1%, with some related individuals showing a 30% to 68.5% survival rate [88]. This purported durable resistance has important implications for species viability; rust resistance may spread through the WBP under natural selection. In support, WBP typically have high regeneration rates in stands attacked by blister rust and differential mortality of regenerating seedlings appears to favor those that are rust resistant [87].

Genetic resistance also provides the basis for artificial selection for genetic resistance through planting of genetically resistant WBP seedlings. Genetically resistant parent trees are now being utilized in the collection and screening of genetically resistant stock [87]. Rearing genetically resistant WBP seedlings provides a basis for planting WBP in locations where natural regeneration is low [107]. Thus, both natural and artificial selection may increase resistance to white pine blister rust across the GYE WBP population.

In sum, these six mechanisms and supporting evidence suggest that WBP distribution, survival, and reproduction may be higher than previously expected under the direct and indirect effects of climate change.

5. Research, Management, and Policy Needs

Progress to date on WBP ecology and management and the new perspective on the WBP system reviewed above provide a basis for developing a comprehensive climate adaptation program for WBP in the GYE. The Climate-Smart Conservation framework [108] is being widely embraced by U.S. federal land managers as a conceptual framework for integrating research and management to sustain natural resources under climate change. The approach assesses what species and places are vulnerable to climate change, identifies and evaluates adaptation options, and implements the options in an adaptive management [109] fashion where management effectiveness is monitored and results used to modify adaptation options to best meet objectives. We next examine the research, management, and policy needs for a comprehensive climate adaptation program for WBP in the GYE.

5.1. Research Needs

The specific research suggested by each of the ecological mechanisms reviewed above is described below and summarized in Table 3.

Analysis is needed of the areal extent of the two types of potential microrefugia described above under future climate scenarios. The problem involves how to downscale climate with adequate accuracy to the spatial resolution that is appropriate to capture actual WBP microrefugia in the GYE. Some fine-scale climate phenomena are difficult to model across complex landscapes [5] and weather station data in GYE may be too sparse to validate fine-scale projections. If downscaling climate below the 800-m scale currently used, perhaps to 90 m or 30 m, proves feasible, then the topographic effects on microclimate and soil water balance could be analyzed. Future climate scenarios could then be downscaled to these finer resolutions and used as a basis for bioclimate envelope modeling to more accurately determine the aerial extent and locations of potential suitable habitat for WBP.

The tolerances of WBP to warmer and drier conditions need to be better understood. Greenhouse and field experiments could be used to better determine the physiological tolerances of WBP establishment, growth rates, and survival rates to temperature, precipitation, and water balance. The findings on those tolerances could be validated through management experiments where WBP seedlings are planted across gradients in habitat conditions and survival and growth monitored.

Managers are capable of controlling the strong effects of competing species on WBP. Doing so in select locations could allow WBP to have a higher chance for viability. Experiments involving thinning, prescribed fire, and allowing wildfire under prescribed conditions are underway and expansion of these experiments could be used to refine understanding of the upper level of competition that still allows WBP adequate vigor to tolerate warmer temperatures and resist pests. Again, this could be done in the context of adaptive management where the treatments are monitored to determine the requirements for WBP growth, survival, and reproduction.

The role of fire in influencing WBP survival relative to competing species is not adequately understood, nor is the possible change in fire severity in subalpine habitats under projected climate change. Prescribed burning trials could be done to better determine levels of fire severity that allow WBP to survive but kills competing species. More dendrochronological paleo-fire studies of WBP would be insightful, including those that reconstruct past fire activity and post-fire vegetation dynamics. Interactions among competing tree species, fire severity, and fuel loads under projected climate change can perhaps best be estimated with spatially-explicit mechanistic models such as Fire-BGCv2 [46] or LPJ-GUESS [110]. These models simulate establishment, growth, reproduction, and mortality of individuals within species as a function of climate, soils, and disturbance. Applications of these models across gradients in elevation, climate, and soils could help to identify geomorphic settings where projected future fire regimes are more favorable to WBP.

With regards to the currently devastating effects of mountain pine beetle, more research is needed on the relationships between WBP tree age, vigor, age of reproduction, susceptibility to mountain pine beetle attack, and levels of reproduction required to allow for WBP persistence under future climates. A combination of field observation of WBP age of reproduction, vigor, and mortality and spatially explicit population viability modeling [111] may be the best means of addressing these knowledge gaps. Such analyses will need to consider nonlinear relationships among climate, WBP, beetles, and seed dispersers. Pest management is included in the GYCC Whitebark Pine Strategy, largely aimed at protecting important individual trees such as those with high reproductive potential and genetic resistance to blister rust or stands within climate refugia [30]. Research on feasibility and effectiveness of pesticide treatments could improve understanding of the spatial scales at which such treatments could be applied.

Finally, mortality due to white pine blister rust can potentially be controlled by planting genetically resistant stock. Longer term studies of rust resistance would reduce uncertainty on this strategy. Analysis to determine the locations where the planted seedlings are most likely to survive under projected future climate conditions would also be informative.

5.2. Management and Policy Recommendations

5.2.1. Spatial Distribution of Treatments

Given the progress in developing strategic objectives and management treatments by the GYCC WBP Subcommittee [30], the key challenge to management involves how to distribute these treatments across the GYE landscape to be most effective under climate change. The challenge involves both where to place treatments and how large an area needs to be treated to meet goals related to WBP persistence and ecosystem function. Projected climate change will likely alter the strength of the interactions of the WBP system depicted in Figure 1 and the magnitude of change in strength will vary spatially across the biophysical gradients of the GYE. Thus, there is an opportunity to place management treatments so as to be most effective relative to climate suitability for WBP, competing tree species, mountain pine beetles, and fire regimes. We suggest a "screening" approach to placing treatments in the landscape that is based on changing climate suitability for these elements of the WBP system.

The first order screen is based on climate suitability for WBP. Hansen and Phillips [36] suggested that climate suitability is an appropriate starting point for climate adaptation planning because knowledge of climate suitability is a critical filter for deciding where to use management actions to protect, restore, or establish species populations under climate change. Plants seldom have viable populations where climate is outside of their tolerances. Bioclimate envelope modeling does not consider the many factors in addition to climate suitability that may influence actual species distributions such as soil type and texture, water balance, and changes in disturbance regimes, competitors and pests. Managers can manipulate many of these other factors, however, but cannot manipulate climate over large landscapes. Thus, climate suitability is a critical first filter for prioritizing management approaches.

We recognize three climate suitability zones [36]. "Core habitats" are locations where populations are currently present and habitat is projected to remain suitable in the future. "Future habitats" are currently unsuitable in climate but are projected to become suitable in the future. "Deteriorating habitats" are those that are currently suitable but are projected to become unsuitable. The distribution of these three zones in the GYE based on the analyses of Chang *et al.* [26] is depicted in Figure 5. As discussed above, those analyses should be revised after improved understanding of the climate tolerances of WBP and the distribution of microrefugia across the GYE become available. Nonetheless, the maps based on the current analyses are useful for illustrating the approach.

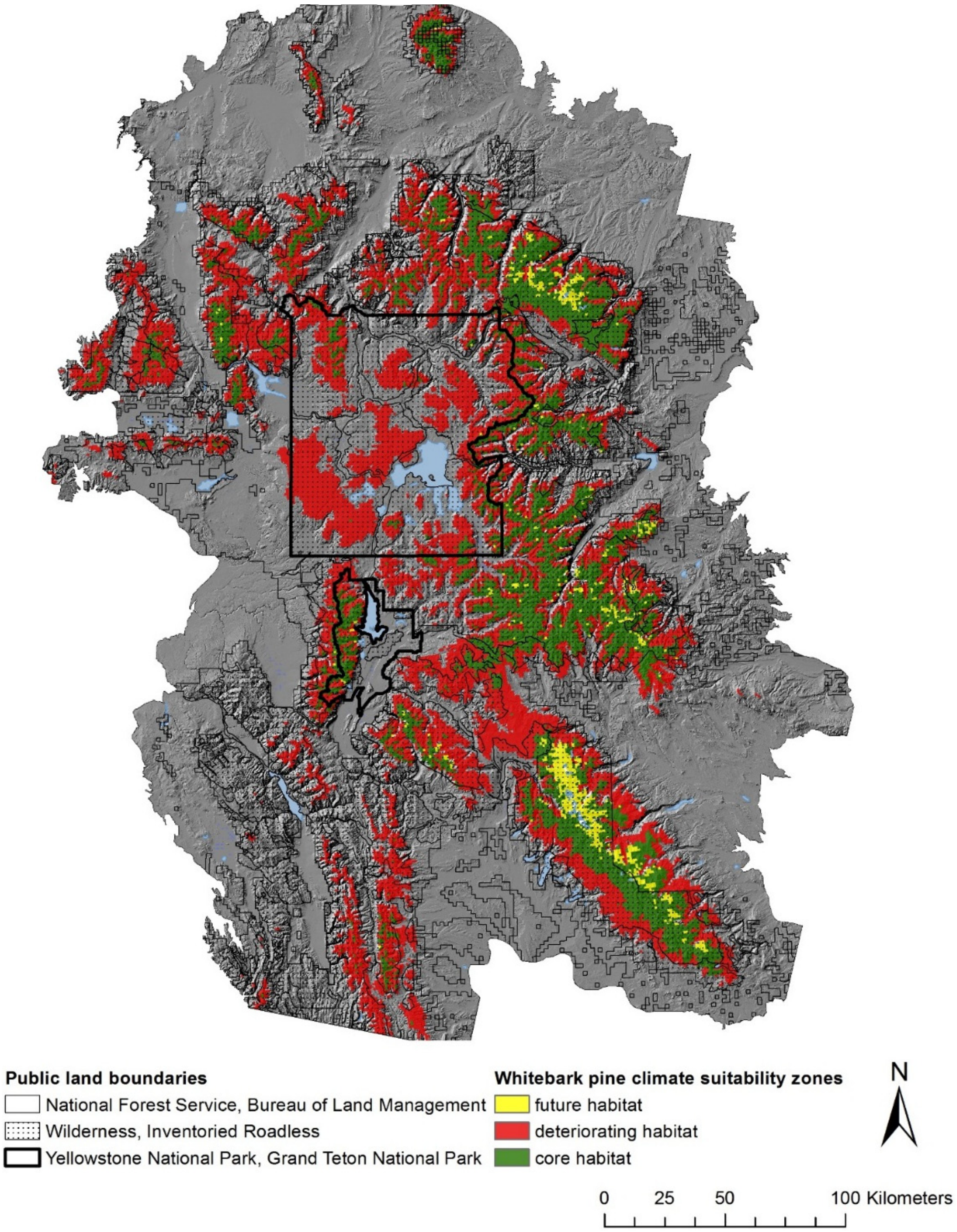

Figure 5. Distribution of projected deteriorating, core, and future habitat for WBP in the GYE under a moderate warming scenario for the period 2040–2070. These habitat projections are based on climate data from the CESM1-CAM5 global circulation model for the AR5 RCP 4.5 scenario [112]. WBP climate suitability is from [26]. Habitat types are defined in the text.

Core habitats for WBP in the GYE are largely in the current upper subalpine zone and represent 34% of the current WBP range (under the mid-range CESM1-CAM5 GCM for 2040–2070 for RCP 4.5). These habitats are of most ecological importance because populations within them have the highest chance of remaining viable in the future, given that climate is projected to remain suitable within them. The primary goal in these locations could be to maintain population viability (Table 4).

Additional goals include maximizing seed dispersal into adjacent future suitable habitats and obtaining blister rust-resistant seeds for growing and planting seedlings. Key management strategies in these settings include preventing stand-replacing fires that could kill large numbers of adult WBP, using prescribed fire, thinning, and pruning to reduce inter and intra specific competition, especially for early reproductive WBP individuals that are more resistant to mountain pine beetle, and use of insecticides to protect key older reproductive individuals. Particular focus could be placed on biophysical settings that may be microrefugia for WBP.

Table 4. A framework for managing WBP in the GYE based on projected future climate suitability.

Habitat Type	Goals	Objectives	Strategies
Core	Maintain currently viable populations	Reduce probability of stand replacing disturbances	Exclude stand replacing fires
		Maximize tree vigor to enhance survival and reproduction	Use prescribed fire and thinning to reduce competition
		Minimize beetle populations	Apply insecticides to reduce mortality due to beetles
	Maximize seed dispersal to future habitats	Maximize tree vigor to enhance survival and reproduction	Use prescribed fire and thinning to promote WBP cone production to swamp predation and maintain dispersers
	Produce seedlings for planting in future habitats	Grow rust-resistant and warm-tolerant stock	Collect seed from rust-resistant and/or warm tolerant WBP trees and rear in nurseries
Deteriorating	Retain WBP population functions as long as possible	Same objectives as in core habitat as resources allow	Same strategies as in core habitat as resources allow
Future	Encourage establishment of WBP	Create suitable sites for seedling establishment	Use prescribed fire and mechanical treatment to create suitable openings
		Establish new stands from nursery stock	Plant rust-resistant and/or warm tolerant WBP trees and rear in nurseries
	Encourage development of viable populations	Same objectives as in core habitat as resources allow	Same strategies as in core habitat as resources allow
All	Improve knowledge and management effectiveness	Refine management effectiveness	Research, monitoring, adaptive management

Most of the current range of WBP in GYE (66%) is projected to become deteriorating habitat by 2100. The goal in these habitats could be to maintain WBP population ecological functions as long as possible while populations build in future habitats. The strategies described above for core habitats could be used in deteriorating habitats as resources allow. Stands that are adjacent or connected to core or future habitats could be prioritized for treatments, in order to maximize the potential of natural colonization of areas which will be suitable for WBP in the future.

Future habitats for WBP in GYE are mostly alpine locations that are not currently forested (4% of the area of the current range). These areas represent opportunities for the species to expand to new locations under climate change. Management strategies to encourage such expansions include promoting high levels of seed immigration and or planting blister-rust resistant seedlings. The future habitats in the GYE are close to existing WBP stands (see Figure 5), thus the substantial ecological and philosophical issues associated with assisted migration [31,32] are less of a concern here. Planting experiments could be done to determine if soils are suitable for WBP in these locations and if seedlings sheltered from desiccating winds (which are not considered in the species distribution modeling) can survive and grow in these locations. As temperature warms in these locations in the coming decades, sheltering may become less necessary. As these seedlings grow to sizes that are susceptible to mountain pine beetle attack, pest management could be used to reduce attack rates.

The locations of these treatments within each WBP climate suitability zone could be further refined based on screens relating to climate suitability for competing species e.g., [39], mountain pine beetles e.g., [73], and fire [113]. For example, thinning treatments would be most effective if focused on locations of increased suitability for competing tree species. Chemical treatments to protect WBP from mountain pine beetles may be most needed and effective in locations of intermediate beetle climate suitability where beetles are likely to be present but possibly at manageable densities. Fire protection strategies, such as reduction of ladder fuels, would be most needed in locations of increased suitability for stand-replacing fires.

As an example, we illustrate how just two climate suitability screens, WBP climate suitability zone and future fire risk, could be used to prioritize treatments (Table 5). Although these future climate suitability screens could be useful to prioritize general locations for different treatments, we recognize that implementation of specific treatments within these general areas will come down to site-specific decisions by managers acting at the stand or watershed level. Core habitats have the highest chance of maintaining viable WBP populations in the future, so all management options would be appropriate. The highest priorities would be focused on protecting existing stands from mountain pine beetle, promoting regeneration and establishment of WBP seedlings, and promoting wildland fire use to protect existing stands from high-severity fires and promote WBP cone production. Deteriorating habitats represent the majority of WBP in GYE, so the management options in these areas would be focused on maintaining WBP ecological functions as long as possible to allow for natural colonization of adjacent core and future habitats. The highest priority might be to allow wildland fire to promote landscape heterogeneity in areas where the risk of high-severity fire killing existing trees is low. Planting and protection from mountain pine beetle might be beneficial where future fire risk is low but not appropriate where high future fire risk decreases the likelihood of success. Future habitats represent opportunities for expansion of WBP into new locations, most of which are currently unforested, alpine areas. The primary goal in these habitats would be to promote natural colonization and the use of wildland fire in both low and high future fire risk categories to reduce fuels and promote conditions favorable to WBP establishment. In low future fire risk areas, where seedling survival is more likely, protection of newly established WBP from mountain pine beetle would be a priority.

The potential effectiveness of alternative landscape-scale management scenarios can perhaps best be evaluated by simulating them with mechanistic forest ecosystem models such as those mentioned above see [46,48]. The results of the mechanistic models can then be input into population viability models to evaluate likelihood of population persistence under each of the landscape management scenarios as a guide to the aerial extent of treatments necessary to meet population viability goals.

5.2.2. Adaptive Management

The high level of uncertainty on potential future climate and the direct and indirect effects on WBP viability necessitates that adaptive management be a central feature of a revised GYCC WBP Strategy. This involves three components: placing treatments across biophysical gradients; expanding monitoring efforts to gauge WBP response to these treatments; and using mechanistic and population viability models to project potential long-term outcome of the treatments.

Above, we suggested an approach for designing landscape-scale management scenarios based on current knowledge (Section 5.2.1). Under an adaptive management approach, the treatments could additionally be placed across gradients in climate, topography, and soils that span the edges of the climate suitability zones described above. The outcomes of these treatments would provide improved knowledge of the interactions of WBP, competing species, mountain pine beetles, and white pine blister rust as mediated by climate, topography, and soils. This knowledge can then be used to increasingly place treatments in the landscape settings where they are likely to be most effective.

Table 5. An example of placing treatments in the landscape based on future climate suitability for WBP and future fire risk. MPB refers to mountain pine beetle.

Climate Zone	Future Fire Risk	Treatment and Priority: 1-High, 2-Moderate, 3-Low, 4-not Appropriate				
		Planting	**Thinning**	**MPB Protection**	**Prescribed Fire**	**Wildland Fire Use**
Core	Low	1-plant to regenerate WBP stands following mortality from MPB or blister rust	2-reduce competition to increase vigor	1-protect rust-resistant individuals from MPB mortality	3-reduce competition to increase vigor	1-reduce fuels, increase vigor, and create landscape heterogeneity
	High	1-plant favorable burned areas with rust-resistant seedlings	2-reduce canopy and surface fuels to lower potential fire-caused mortality	1-protect rust-resistant individuals from MPB mortality	3-use prescribed fire to reduce competition and fuel loads	1-reduce fuels, increase vigor, and create landscape heterogeneity
Deteriorating	Low	3-plant rust-resistant seedlings to keep the species in historical lands to monitor for success	4-benefits will be minimal	3-protect rust-resistant individuals	3-reduce competition for rust-resistant individuals	2-promote landscape heterogeneity
	High	4-seedlings have a high risk of being burned	3-may promote growth of rust-resistant individuals	4-existing trees have a high risk of being killed by fire	3-reduce canopy and surface fuels to protect rust-resistant individuals	3-reduce fuels and promote landscape heterogeneity
Future	Low	3-plant burns with rust-resistant seedlings	4-most high elevation stands competition free	2-protect rust-resistant individuals	3-lower fuels to reduce fire risk to rust-resistant individuals	2-Promote landscape hetereogeneity and reduce fuels
	High	3-plant to ensure future competitive advantage and mimic nutcracker dispersal	4-most high elevation stands competition free	3-Protect rust-resistant individuals	4-probably won't need additional fire	2-promote landscape heterogeneity, reduce fuels

The current monitoring program by the Greater Yellowstone Whitebark Pine Monitoring Working Group [67] was designed to detect trends in WBP demography under the influence of beetles, blister rust, and fire. The Forest Service conducts short-term monitoring post treatments. Either of these efforts could be supplemented to measure WBP response to management by adding monitoring plots at the locations where treatments are implemented and measure beyond shorter-term efforts underway. Metrics for effectiveness monitoring include WBP survival, growth, cone production, regeneration, beetle and blister rust prevalence, and the demography of competing species.

Given the slow growth rates of WBP, the success of treatments in increasing WBP viability will not be known for decades. Simulation modeling provides a means of projecting potential long-term outcomes of the treatments. As the adaptive management approach proceeds, results from the monitoring studies can be used to iteratively improve the parameterization of the models and reduce uncertainty in the long-term projections.

Through this combination of imposing treatments, monitoring short-term response, and simulating long-term outcomes, the management strategy can be revised to be increasingly effective.

5.2.3. Policy Evaluation for Restricted Federal Land Allocations

Active management of WBP in the GYE to date has focused on multiple-use federal lands, which comprise only 8% of the WBP stands (Table 1). This focuses attention on the need for re-evaluation of the legal and philosophical interpretations that currently constrain active management in restrictive federal lands.

The Wilderness Act of 1964 is considered among the most restrictive of U.S. natural resource laws. Thus debate on active management for climate adaptation centers on wilderness. Long and Biber [114] reviewed both legal interpretation on the question and federal agency policy. They concluded, "The vast majority of potential management actions for climate change adaptation, both active and passive, are possible under the Wilderness Act, provided that the right procedural steps are followed and the right substantive analyses are produced. Active management, even management that uses tools that are generally prohibited under the Act, is permissible if it can be shown to be necessary to achieve conservation purposes and if its impacts on other wilderness values are minimized." Moreover, they cite federal agency policies and actions consistent with the conclusion above.

Philosophical views on active management in wilderness among both agency personnel and the public are varied. On the one hand, Stephenson and Millar [115] make a case that the Wilderness Act was written before there was widespread understanding that human activities could alter the state of the biosphere and consequently the act leads to a duality that will require tradeoffs. The duality is between "untrammeled quality" and "historical fidelity (primeval and natural character)". They suggest in a global change world, retaining "primeval and natural character" will require increasing management intervention (trammeling). Alternatively, some national park managers are wary of their management actions doing more harm than good and advocate a "natural regulation" approach whenever possible [116]. For a rebuttal to this view, see Stephenson [117].

Regarding public views, a survey of visitors to Sequoia and Kings Canyon National Parks [118] found little support for strategies to make forests less vulnerable to climate change such as introducing new genetic material more resistant to drought or disease. Respondents showed mild to moderate support for management actions intended to restore natural conditions such as removing non-native species and reintroducing missing native species. A recent survey of residents in the three states surrounding the GYE found that respondents strongly supported active management for protection and restoration of WBP both on all federal public lands and within designated Wilderness Areas [119]. We agree with Stephenson and Millar [115] that climate adaptation planning "will require a broader engagement of wilderness stewards, policy makers, and the public to assess the implications of climatic changes for wilderness values and policy."

Such engagement is increasingly crucial in the case of WBP in the GYE given that its current distribution lies largely in restricted federal lands and this is projected to be increasingly the case for habitat suitability under climate change (see also [7]).

6. Prognosis

The WBP is at the center of a complex web of interactions involving climate, competition, fire, and pests. Science is increasingly unravelling the one-way interactions within the WBP system, but the interactive effects and feedbacks within the system remain elusive. The population trajectory of adult WBP over the past decade in the GYE, however, is cause for alarm and speaks to the need for increased research and management. The majority of reproductive WBP trees in the ecosystem have died since 2000. Much of the vast subalpine forest across the GYE is covered with the grey cast of dead trees. The loss of ecosystem services associated with this die-off has not yet been quantified, but is certainly substantial. Climate warming, the ultimate factor driving the mortality, is projected to accelerate in the coming century and further favor competing species, pests, and severe fires that kill WBP.

This situation begs the question of if the WBP population in the GYE will remain viable in the coming century or will it be lost as climate change progresses. New perspectives on the complex WBP system have identified ecological mechanisms by which WBP may remain viable, particularly if aided by well-crafted management treatments. In the passages above we summarized the research questions and landscape-scale management approaches that show promise for better understanding and more effectively managing WBP across the GYE.

Our compilation of area treated to date by federal managers (Table 2), however, makes a strong case that the effort taken by the managers in the GYE is too little to be significant relative to the scale of the problem. Less than 1% of the aerial distribution of WBP has been treated by active management for protection and restoration. Above, we describe a landscape-scale adaptive management approach that has promise of meaningfully tackling the issue. Substantially more resources are required to enact this approach and treatments will need to be done much more widely across the GYE landscape to meaningfully influence the viability of WBP here and the ecosystem services they provide.

We hope that this paper further stimulates the conversation among federal managers in the GYE and at higher levels within agencies and the legislative branch on policy and commitment relative to managing the WBP and other natural resources under climate change. Beyond issues of funding and capacity, the discussion necessarily involves the question of appropriate levels of active management on restricted federal lands such as wilderness where many sensitive subalpine species are disproportionately located.

The challenges of WBP in GYE are typical of those for many species across the U.S. and globally. Other subalpine tree species showing direct and indirect responses to climate change include limber pine in the Rocky Mountains [120], red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) in the Appalachians [121], and Alaska yellowcedar (*Chamaecyparis nootkatensis*) in Southeast Alaska [122]. Within the European Alps, average range reductions of 44%–50% were projected for 150 high mountain plant species by 2100 and complete range loss was projected for 6%–8% of these species [6]. Many plants in mountains in the humid tropics are also sensitive to climate change because the relatively stable environment has led to narrow climate tolerances which are projected to be exceeded under projected climate change [123]. Other studies showing high vulnerability of subalpine species and montane ecosystems to climate change include [1–3,18,36,39,124–128].

The recommendations for WBP are likely relevant to many of these other vulnerable subalpine species. These include:

- Research to better understand the direct and indirect effects of climate change and mechanisms that may allow the species to remain viable under changing climate, especially if aided by management;
- Development of management strategies that are spatially and temporally organized in the context of future climate suitability for the target species and the organisms that influence that species;

- Adaptive management where treatments are arrayed across key biophysical gradients and monitored to quantify effectiveness and tailor future management to biophysical conditions;
- Use of demographic and mechanistic models to project treatments forward in time.
- Re-evaluation of legal and policy constraints regarding active management in high elevation locations; and
- Interagency collaboration to allow unified management approaches across the larger spatial scales relevant to managing these species under climate change.

Beyond improving viability of these subalpine species, application of these recommendations will provide a basis for managing the large number of tree and other plant species at lower elevations as climate change begins to exceed their limits of tolerance.

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