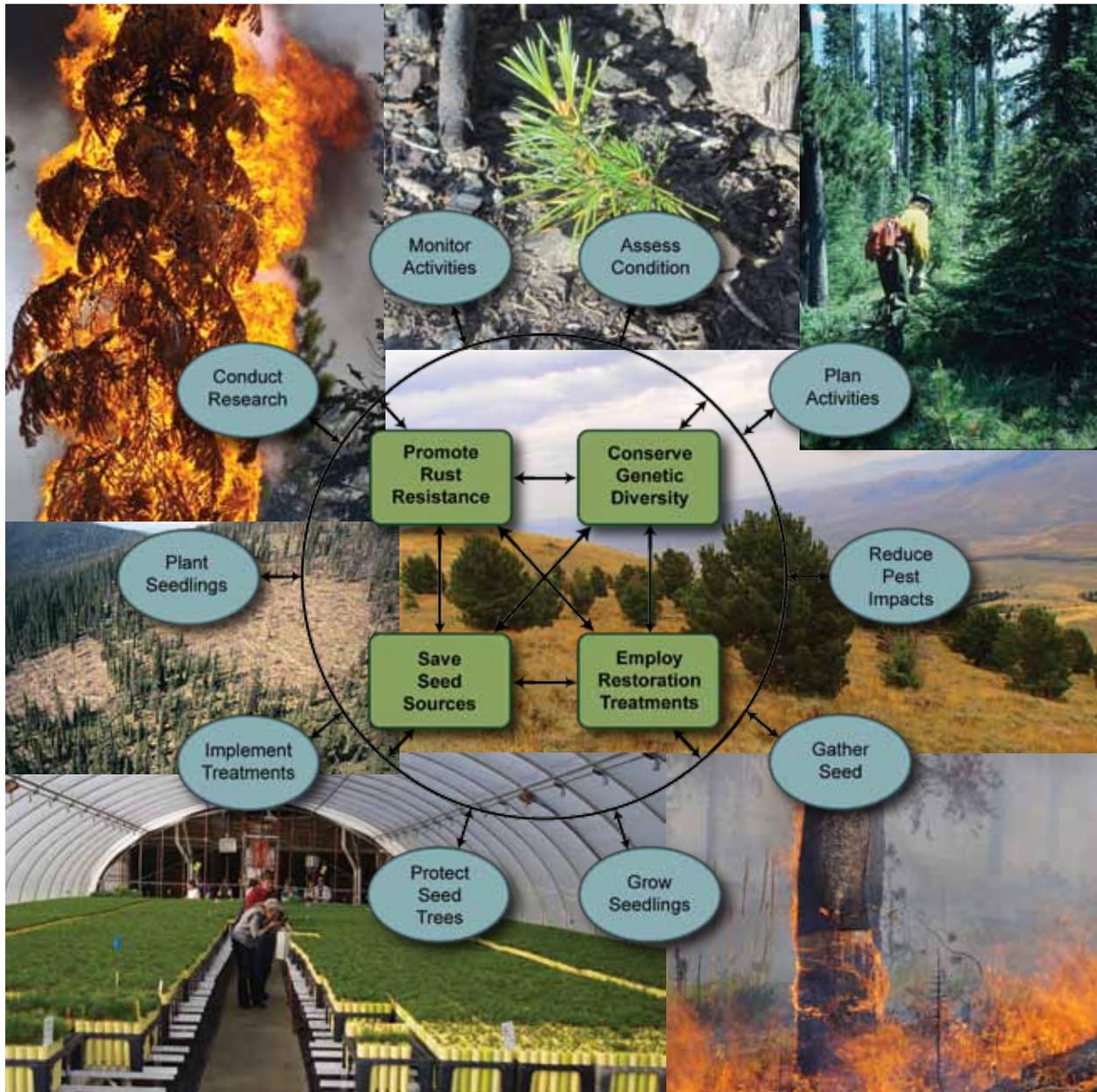


Restoring Whitebark Pine Ecosystems in the Face of Climate Change

Robert E. Keane, Lisa M. Holsinger, Mary F. Mahalovich, and Diana F. Tomback



Abstract

Whitebark pine (*Pinus albicaulis*) forests have been declining throughout their range in western North America from the combined effects of mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, fire exclusion policies, and the exotic disease white pine blister rust (*Cronartium ribicola*). Projected warming and drying trends in climate may exacerbate this decline; however, whitebark pine has a wide climatic tolerance because of its broad distribution coupled with high genetic diversity. A rangewide whitebark pine restoration strategy (Keane et al. 2012b) was developed recently to inform restoration efforts for whitebark pine across Federal, State, and Provincial land management agencies. This strategy, however, did not address the effects of climate change on existing whitebark pine populations and restoration efforts. In this report, we present guidelines for restoring whitebark pine under future climates using the rangewide restoration strategy structure. The information to create the guidelines came from two sources: (1) a comprehensive review of the literature and (2) a modeling experiment that simulated various climate change, management, and fire exclusion scenarios. The general guidelines presented here are to be used with the rangewide strategy to address climate change impacts for planning, designing, implementing, and evaluating fine-scale restoration activities for whitebark pine by public land management agencies.

Keywords: whitebark pine, climate change, fire regime, blister rust, mountain pine beetle, Clark's nutcracker, seed dispersal, regeneration, upper subalpine, restoration

Photo credits: All photos were taken by Forest Service employees except as noted.

Cover photos: This cover is similar to the cover for the rangewide strategy (Keane et al. 2012b); which is the companion document to this publication, but the photos are different. In the center are the actions and guiding principles of the restoration strategy and clockwise from top: wildfire in a subalpine fir; a natural seedling after a wildfire; a sawyer removing subalpine fir in a restoration cutting; encroaching whitebark pine into sagebrush grasslands; a prescribed burn in whitebark pine; thousands of rust-resistant whitebark pine seedlings; treatments called nutcracker openings in whitebark pine forests. All photos taken by Bob Keane.

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Executive Summary

Whitebark pine (*Pinus albicaulis*) forests are declining across most of their range in North America because of the combined effects of mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, fire exclusion policies, and the exotic pathogen *Cronartium ribicola*, which infects five-needle white pines and causes the disease white pine blister rust. Predicted changes in climate may exacerbate whitebark pine decline by (1) accelerating succession to more shade tolerant conifers, (2) creating environments that are unsuitable for the species, (3) increasing the frequency and severity of mountain pine beetle outbreaks and wildland fire events, and (4) facilitating the spread of blister rust. Yet, whitebark pine tolerates a variety of stressful conditions and the broad genetic diversity to adapt to changes in climate and disturbance.

The ongoing decline in this high-elevation tree species poses serious consequences for upper subalpine and treeline ecosystems and, as a result, whitebark pine is a candidate species for listing under the Endangered Species Act. The large, nutritious seeds produced by this pine are an important food for many bird and mammal species, such as the endangered grizzly bear (*Ursus actos horribilis*), and whitebark pine communities provide nesting sites and habitat for many other wildlife species. Whitebark pine seeds are dispersed long distances by Clark's nutcrackers (*Nucifraga columbiana*), which cache seeds in a variety of terrain and plant community types, including recent burns and other disturbed areas. Unclaimed seeds often germinate and produce hardy seedlings. These seedlings can survive on harsh, arid sites, and act as nurse trees to less hardy conifers and vegetation.

Because more than 90 percent of whitebark pine forests exist on public land in the United States and Canada, a rangewide whitebark pine restoration strategy (Keane et al. 2012b) was developed to coordinate and inform restoration efforts across Federal, State, and Provincial land management agencies. This restoration strategy, however, failed to fully address the projected effects of climate change on whitebark pine restoration efforts and existing populations.

In this report, we present guidelines for restoring whitebark pine under future climates using the rangewide restoration strategy structure. General restoration guidelines considering effects of climate change are given for each of the strategy's guiding principles: (1) promote resistance to blister rust, (2) conserve genetic diversity, (3) save seed sources, and (4) employ restoration treatments. We then provide specific guidelines for each of the strategy's actions: (1) assess condition, (2) plan activities, (3) reduce disturbance impacts, (4) gather seed, (5) grow seedlings, (6) protect seed sources, (7) implement restoration treatments, (8) plant burned areas, (9) monitor activities, and (10) support research.

We used information from two sources to account for climate change impacts on whitebark pine restoration activities. First, we conducted an extensive and comprehensive review of the literature to assess climate change impacts on whitebark pine ecology and management. Second, we augmented this review with results from a comprehensive simulation experiment using the spatially explicit, ecological process model FireBGCv2. This modeling experiment simulated various climate change, management and fire exclusion scenarios. We also ran FireBGCv2 to evaluate the effects of specific rangewide restoration actions with and without climate change. We analyzed two simulated response variables (whitebark pine basal area, proportion of the landscape dominated by whitebark pine) to explore which restoration scenarios are likely to succeed.

Our findings indicate that management intervention actions such as planting rust-resistant seedlings and employing proactive restoration treatments, can return whitebark pine to the high mountain settings of western North America to create resilient upper subalpine forests for the future. The report is written as companion guide to the rangewide restoration strategy for planning, designing, implementing, and evaluating fine-scale restoration activities for whitebark pine by addressing climate change impacts.

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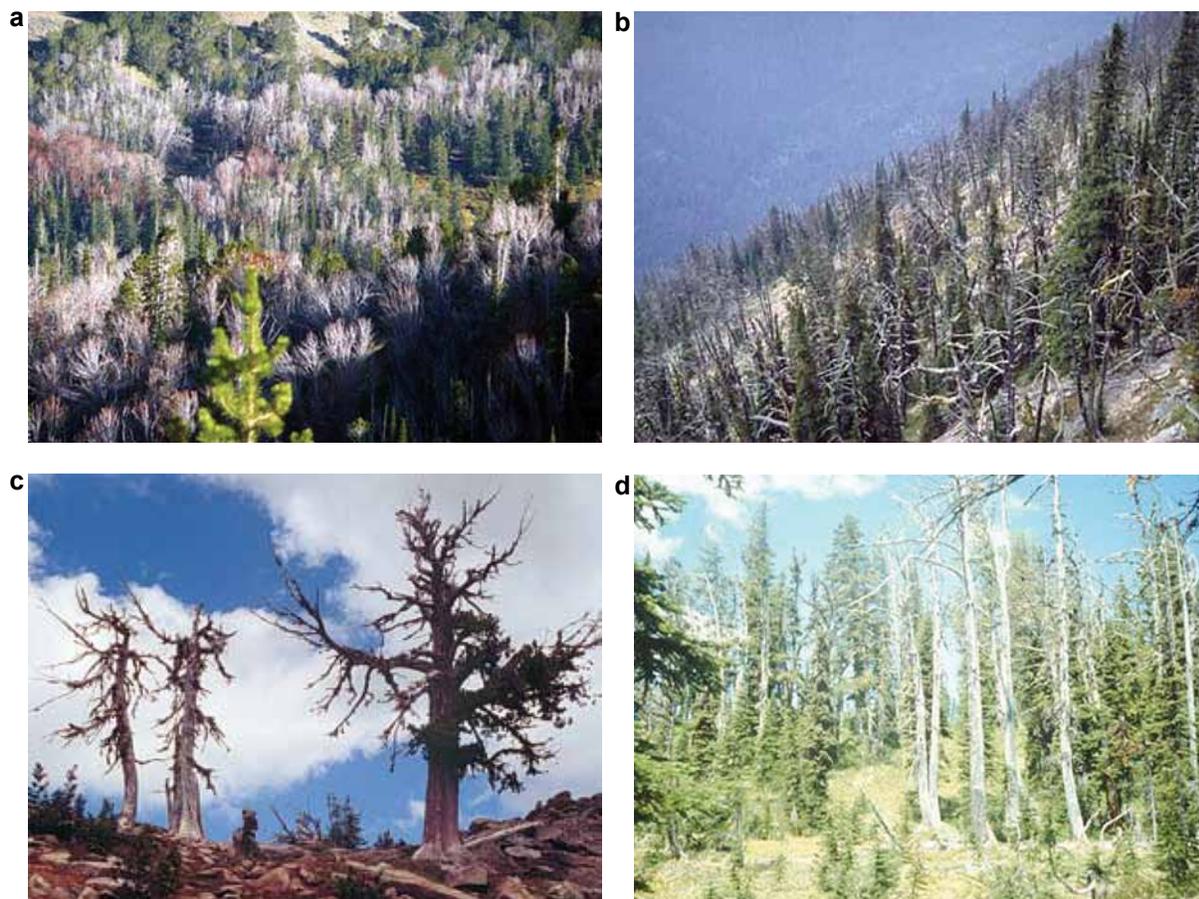


Figure 1—Declining whitebark pine forests across the species range. (a) mountain pine beetle (MPB) mortality in central Idaho, (b) white pine blister rust (WPBR) mortality in west-central Montana, (c) WPBR mortality in the Great Burn of Idaho, and (d) extensive WPBR mortality in the Bob Marshall Wilderness Area of Montana (photos a,b,c, Bob Keane, USDA Forest Service; photo d, Steve Arno, USDA Forest Service, retired).

1. Introduction

Upper subalpine whitebark pine (*Pinus albicaulis* Engelm.) forests are rapidly declining throughout western North America because of the interaction among and cumulative effects of historical and current mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins *Coleoptera*: *Curculionidae*, *Scotlytinae*) outbreaks, more than 90 years of fire exclusion policies, and white pine blister rust, caused by the introduced pathogen *Cronartium ribicola* (Keane and Arno 1993; Kendall and Keane 2001; Murray and Rasumussen 2003; Schwandt 2006; Tomback and Achuff 2010) (fig. 1). To make matters worse, many scientists believe that projected warmer future climates will severely reduce high elevation whitebark pine habitat, thereby restricting populations to mountaintops or to the northern parts of its range (Funk and Saunders 2014; Koteen 1999; McKenney et al. 2007; Schrag et al. 2007; Warwell et al. 2007). While it is widely held that whitebark pine will decline under future climates, the magnitudes and directions of whitebark pine ecosystem responses to projected climate changes are still unknown. This may confound attempts at restoring this valuable ecosystem.

The loss of this iconic high-elevation tree species has serious consequences for high mountain ecosystems, both in terms of the impacts on biodiversity and in losses of valuable ecosystem processes and services (Funk and Sanders 2014; Lee 2003; Tomback and Achuff 2010; Tomback et al. 2001a). The large, nutritious seeds produced by whitebark pine are an important food for birds and mammals, and whitebark pine communities provide important habitat for many wildlife species (Lorenz et al. 2008; Tomback and Kendall 2001). Whitebark pine seedlings survive on harsh, high elevation sites and, when fully grown, often act as nurse trees to less hardy conifers and undergrowth vegetation (Callaway 1998; Callaway et al. 1998; Tomback et al. 2001b). At upper subalpine elevations, mature whitebark pine trees help to regulate snowmelt and reduce soil erosion (Farnes 1990). For these collective functions, whitebark pine is considered both a keystone species for promoting

community diversity and a foundation species for promoting community stability (Ellison et al. 2005; Mills et al. 1993; Paine 1995; Tomback and Achuff 2010; Tomback et al. 2001a). The loss of whitebark pine also potentially impacts fire regimes, recreational experiences, and aesthetic perceptions (Keane et al. 2002a; McCool and Freimund 2001; Tomback and Achuff 2010; Tomback et al. 2001a). As a result, whitebark pine is a candidate species for listing under the Endangered Species Act (FWS 2011).

There are many compelling reasons to restore whitebark pine forests (Tomback et al. 2001a). As mentioned, losing a foundation and keystone species due to exotic diseases and adverse management actions might result in the decline of the many species of flora and fauna that depend on whitebark pine, such as grizzly bears, Clark's nutcrackers, and blue grouse (*Dendragapus obscurus*). Changes in ecosystem services, such as reduced late summer streamflows may also result (Tomback et al. 2001b). In addition, healthy whitebark pine forests maintain resilient upper subalpine ecosystems in the face of climate change, particularly at the "climate change fronts" of high elevations and northern-most latitudes (Tomback and Achuff 2010). Whitebark pine forests may be more resilient to climate change than those forests that might replace them. For example, the late successional spruce-fir forests have more shade-tolerant conifers that pose greater risks to society, such as higher fire hazard, lower biodiversity, and greater water demand, than whitebark pine forests (Keane et al. 2012b). These spruce-fir forests may also provide fewer ecosystem services, such as late summer irrigation water, snowpack stability, and wildlife habitat.

A detailed restoration strategy was recently developed to coordinate restoration activities across the entire range of whitebark pine at several spatial scales (Keane et al. 2012b). This "rangewide strategy" is an important reference for researchers and managers involved in coordinating efforts to restore declining whitebark pine forests. In short, the strategy outlines several broad actions for whitebark pine restoration

including protecting putative rust-resistant trees to provide seeds for natural rust-resistant regeneration, collecting seed from proven rust-resistant (elite or plus) trees to grow genetically diverse rust-resistant seedlings for planting, and allowing wildfire and management treatments to create competition-free growing spaces for planting rust-resistant seedlings.

The strategy, however, is critically lacking validation of these actions under future climates because it doesn't consider the impacts of climate change or the interactions between climate change, the recommended management actions, and other environmental stressors. Recommendations in the strategy do not address how to select the best areas to plant, burn, and treat given a changing climate, or how to determine how much of the landscape needs to be treated to ensure sustainability of whitebark pine forests.

1.1 This Report

This report provides managers with the latest information to integrate climate change impacts into plans to restore whitebark pine forests. It is intended to be a companion to the Keane et al. (2012b) range-wide strategy by addressing climate change impacts for each of the strategy's guiding principles and restoration actions. The report begins with some basic ecological principles and knowledge that are important in addressing climate change effects on whitebark pine forests (Section 2). We then present a general summary of possible climate change projections for whitebark pine habitats and address the impacts of those projections on whitebark pine populations by summarizing information from the literature (Section 3). Next, we present simulation modeling effort that was used to help develop climate change considerations in the rangewide restoration strategy (Section 4). The FireBGCv2 model was used in a carefully designed experiment to simulate climate change impacts on landscape dynamics. Section 5 presents climate change considerations and recommendations for each of the rangewide restoration strategy's guiding principles and restoration actions based on the literature review and FireBGCv2 simulation experiment. We also used independent runs of FireBGCv2 to illustrate potential ecosystem responses to restoration actions

under changing climates. Finally, we discuss the limitations and caveats of this report (Section 6).

Predicting the response of whitebark pine to projected climate change is an immensely complicated task involving myriad complex ecological interactions for whitebark pine at multiple spatial and temporal scales. Climate warming, for example, may foster more high elevation fires that will burn more whitebark pine forests and kill trees that may be genetically resistant to blister rust, thereby reducing regeneration potential. Thus, it is nearly impossible to comprehensively assess the magnitude and direction of all impacts of climate change on all whitebark pine forests. We have attempted to address some of these interactions using the FireBGCv2 model, but only two landscapes could be simulated due to computational and logistical considerations. The model also lacks a simulation of other stressors in new climates. Therefore, we used an approach that integrates qualitative assessments from the climate change literature with the FireBGCv2 simulation results to develop recommendations for implementing effective restoration measures. Since most interactions occur at fine scales, such as the tree- and stand-level, we recommend that information in this report be modified to incorporate local conditions in restoration actions.

1.2 Rangewide Restoration Strategy Summary

The rangewide whitebark pine restoration strategy consists of a set of principles with associated actions to guide the design, planning, and implementation of restoration activities throughout the range of whitebark pine (Keane et al. 2012b) (fig. 2). The guiding principles (in bold type) represent broad areas of emphasis that should be addressed when restoring whitebark pine.

The most important guiding principle is to ensure that future populations of the species have some resistance to blister rust by increasing the total number of trees with genetic resistance to the blister rust pathogen (**Promote rust resistance**). The full genetic diversity across the range of whitebark pine must be preserved for the future by collecting and archiving seeds and growing and planting genetically diverse

Whitebark Pine Strategy

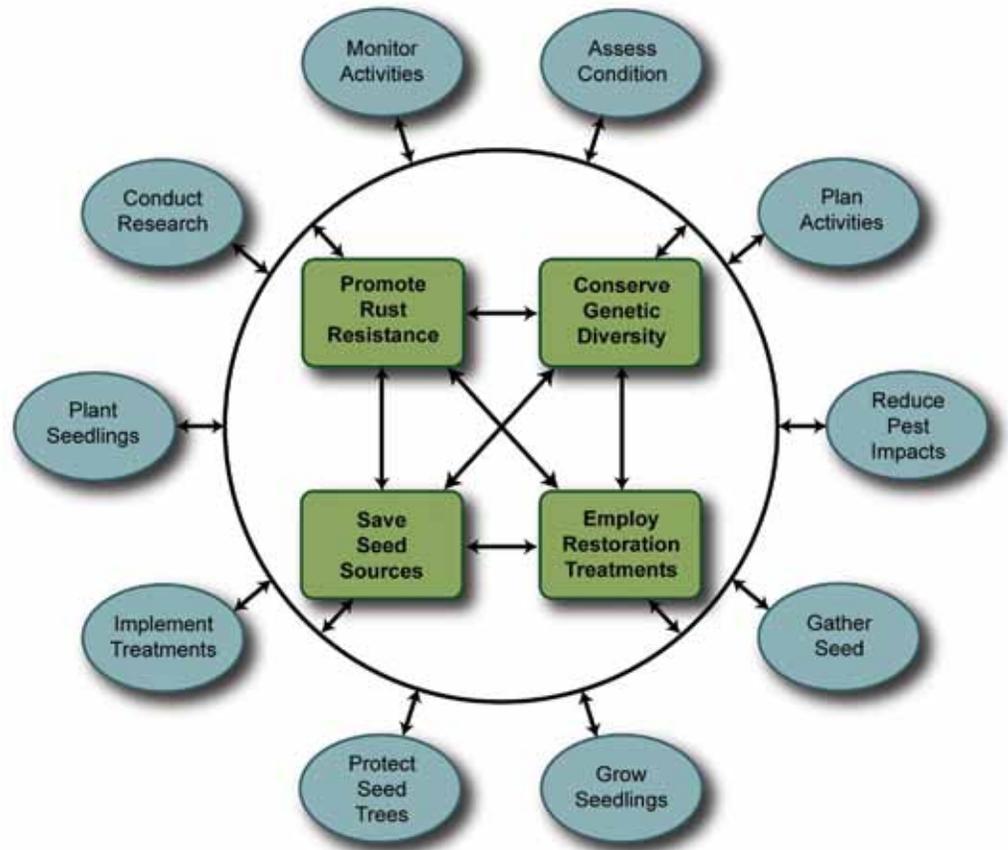


Figure 2—The rangewide whitebark pine restoration strategy with the Guiding Principles (in green) implemented by the set of management actions (in blue) (Keane and others 2012b).

seedlings (**Conserve genetic diversity**). Mature, seed-producing, putatively rust-resistant whitebark pine trees in regions that are experiencing rapid decline must be protected from other native or exotic disturbances so that the apparent rust-resistant seed can be harvested in the future (**Save seed sources**). In areas where whitebark pine forests are declining due to insects, disease, or advanced succession, it might be appropriate for proactive or passive restoration treatments to create sustainable whitebark pine populations (**Employ restoration treatments**).

These principles are used to guide whitebark pine restoration plans at various spatial scales and are implemented using a set of ten possible management actions. One or more of these actions constitute meaningful steps toward restoring whitebark pine ecosystems.

1. *Assess condition.* Conduct assessments that document the status and trend of whitebark pine forests within regions.

2. *Plan activities.* Develop plans and design possible treatments for restoring whitebark pine ecosystems.
3. *Reduce disturbance impacts.* Implement proactive measures to reduce blister rust, mountain pine beetle, and other disturbance impacts on whitebark pine forests.
4. *Gather seed.* Collect seeds from trees that are proven rust-resistant or phenotypically rust-resistant in areas exposed to blister rust, and from trees not tested in areas yet to be exposed to blister rust for archiving genetic diversity and variation.
5. *Grow seedlings.* Grow whitebark pine seedlings from seeds of proven (genetically tested in a rust screening process) rust-resistant trees.
6. *Protect seed sources.* Protect valuable rust-resistant, seed-producing whitebark pine from future mortality caused by disturbance, climate change, and advanced competition.

7. *Implement treatments.* Create conditions that encourage whitebark pine regeneration, conserve seed sources, and promote rust resistance.
8. *Plant seedlings.* Plant rust-resistant seedlings or sow seeds directly in treated or burned areas, especially in areas experiencing heavy whitebark pine mortality.
9. *Monitor activities.* Pre- and post-activity field sampling is critical to document the success or failure of restoration treatments.
10. *Conduct research.* Researchers must continuously develop new and more efficient methods and techniques for effective ecosystem restoration.

The rangewide strategy provides direction at six spatial scales of analysis (fig. 3): (1) coarse scale, the whitebark pine’s entire range in the United States; (2) regional scale using the U.S. Forest Service Pacific Northwest and Northern Regions as examples; (3) forest scale that is equivalent in size to National Forests and National Parks; (4) landscape scale, which could be watersheds, management units, or landforms; (5) stand scale where most proactive restoration activities take place; and (6) tree level, where intensive treatments are needed to protect individual whitebark pines.

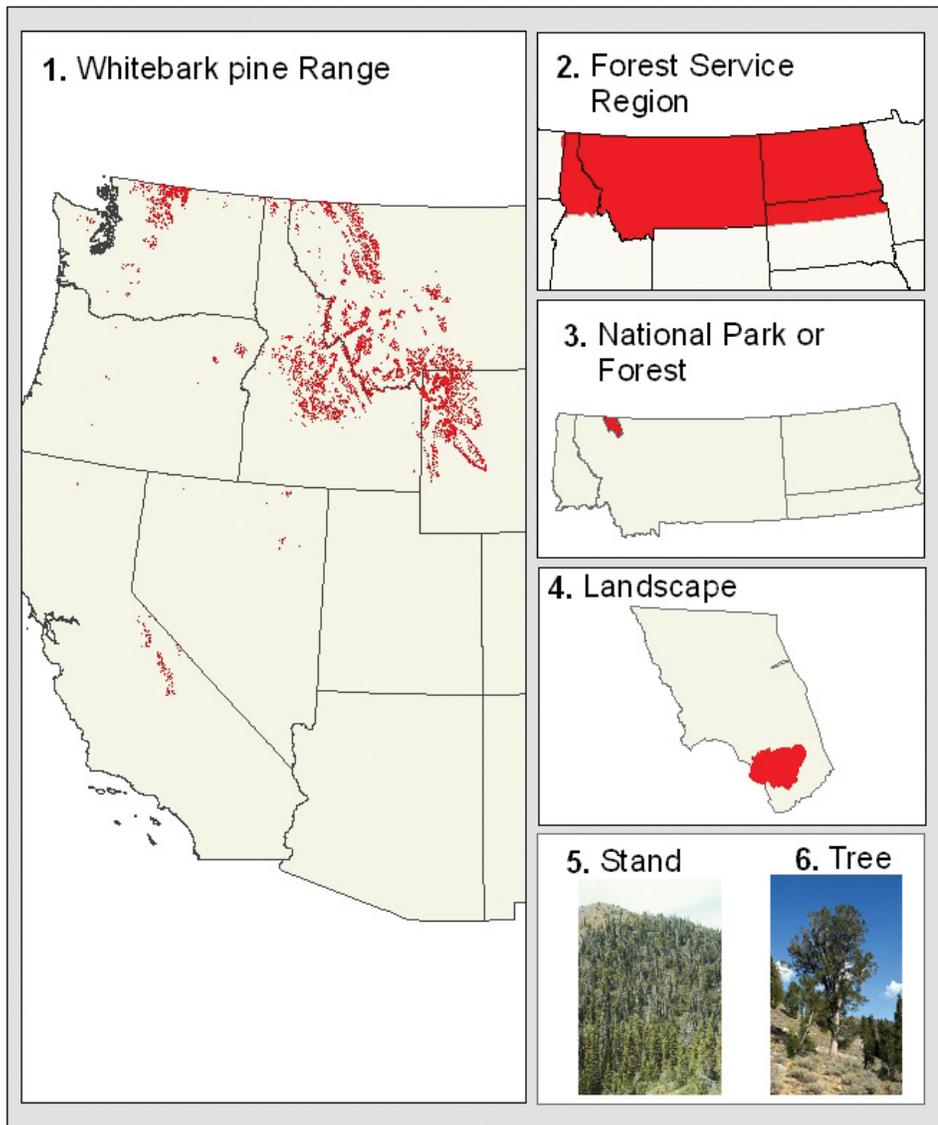


Figure 3—The five scales of the rangewide whitebark pine restoration strategy from tree (~10 m²) through stand (10³ m²) to landscape (10⁵ m²) to Park or Forest (10⁷ m²) to Region (10¹⁰ m²) and its entire range in the United States (Keane and others 2012b).

2. Whitebark Pine Ecology

Restoration efforts, especially those that consider climate change, demand some basic knowledge of the ecology of species to be restored. While the Keane et al. (2012b) rangewide strategy includes extensive background material, we included this section to provide a brief synopsis of whitebark pine ecology to understand the potential response of the species to climate change. The material was taken from Arno and Hoff (1990), Keane et al. (2012b), and Tomback et al. (2001a).

2.1 Autecology

Whitebark pine forms extensive forests in the upper subalpine areas of the northern Rocky Mountains of

the U.S. and the southern Rocky Mountains in Canada (fig. 4). It is abundant, with a patchy distribution on the eastern slopes of the Cascades and Coast Ranges and at the northern end of its distribution in the Canadian Rockies and Coast Ranges of British Columbia. It is also present but confined to specialized environments in the Sierra Nevada and in northern Nevada (Arno and Hoff 1990; Day 1967). Whitebark pine typically is less abundant on limestone soils, except in wetter areas near and north of the Canadian border (reviewed in Weaver 2001). In the northernmost Canadian Rocky Mountains, whitebark pine grows exclusively on siliceous soils as opposed to limestone soils.

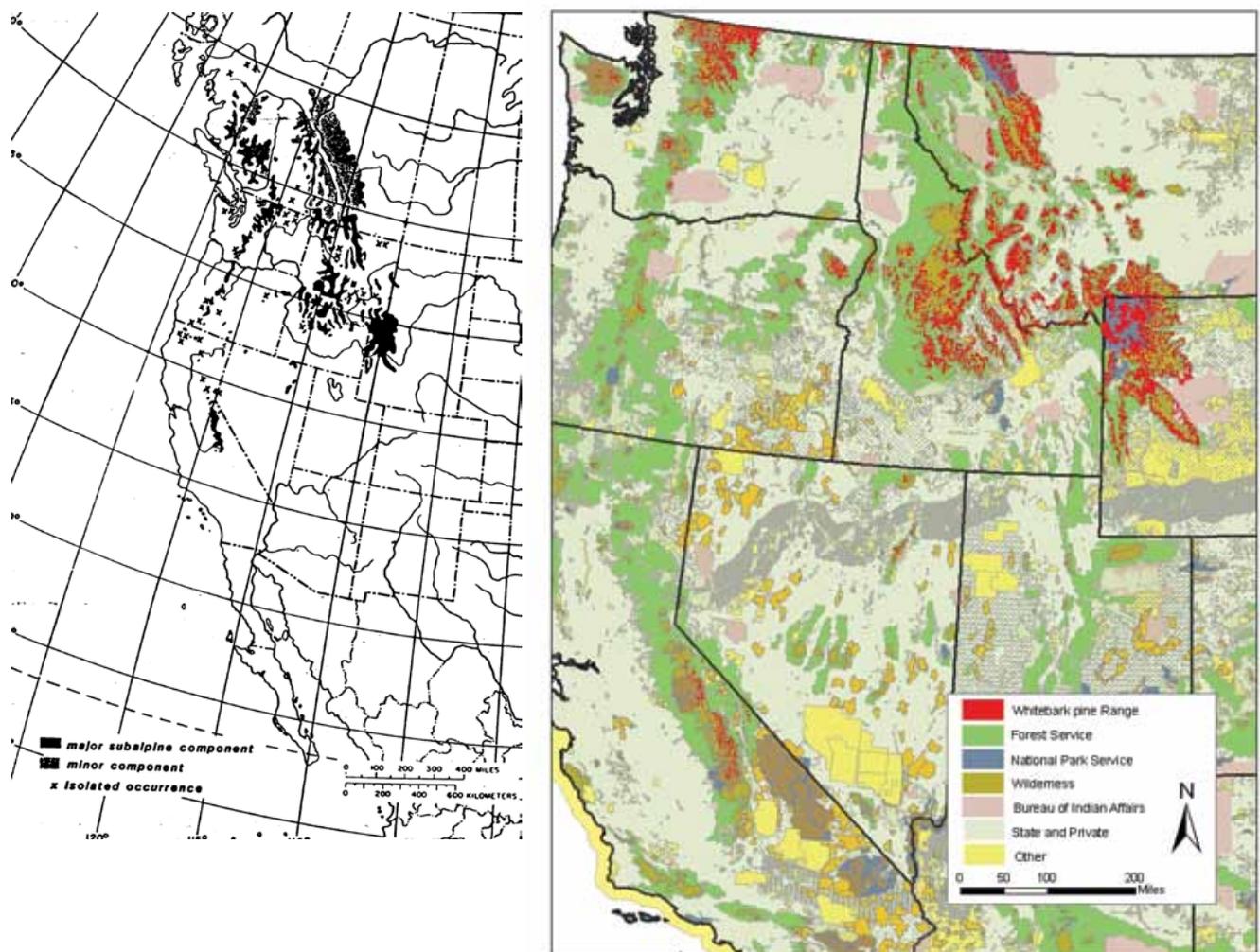


Figure 4—The range of whitebark pine from left, Arno and Hoff (1990) and right, Keane et al. (2011). Whitebark pine is a major seral species in the upper subalpine zone in these areas (seral sites) and, in some areas, whitebark pine is the only species able to maintain dominance because of cold, windy, droughty conditions (climax sites).



Figure 5—Typical appearance of a mature whitebark pine on a climax site. This tree is over 400 years old and displays the lyrate growth form that is commonly observed in the species.

Whitebark pine is a long-lived tree of moderate shade tolerance (Minore 1979). It is common to find mature whitebark pine trees well over 400 years of age, especially on harsh growing sites (fig. 5). The oldest known individual is more than 1,275 years (Luckman et al. 1984; Perkins and Swetnam 1996). Whitebark pine is slow-growing in both height and diameter, and it rarely grows faster than most of its competitors except on the most severe sites (Arno and Hoff 1990). In fact, it rarely exhibits rapid height growth even on the most productive sites. Whitebark pine is one of the most drought tolerant species in

the upper subalpine of North America (Arno and Hoff 1990). It reaches reproductive maturity by 40 to 60 years and doesn't reach optimal cone production capability until it is well over 200 years old (Arno and Hoff 1989).

2.2 Clark's Nutcracker Interactions

Whitebark pine seeds are primarily dispersed by Clark's nutcracker (*Nucifraga columbiana* Wilson), a bird related to crows, ravens, and jays (avian Family Corvidae) (fig. 6). The Clark's nutcracker and whitebark pine coevolved mutualistic interaction where both species gain from the relationship (Lanner 1982; Tomback 1978, 1982, 1983; Tomback and Linhart 1990). Whitebark pine has evolved dependence on nutcrackers to disperse its large wingless seeds, and in turn, nutcrackers utilize fresh and stored whitebark pine seeds as an important food source. Nutcrackers bury thousands of whitebark pine seeds each year as food stores in small clusters or "seed caches" across diverse forest terrain (Hutchins and Lanner 1982; Tomback 1982). Seeds in some of the caches are retrieved by nutcrackers primarily in spring and summer



Figure 6—A Clark's nutcracker harvesting seed from whitebark pine cones (photo courtesy of Diana Tomback from Keane et al. 2011).

months as an important food source for themselves and their young. However, not all seed caches are recovered, particularly after a large cone crop. Moist conditions from snowmelt and summer rains stimulate germination in the seeds; this leads to regeneration newly established whitebark pine forests (Tomback 1982; Tomback et al. 2001c). Although whitebark pine depends nearly exclusively on nutcrackers, nutcrackers are not dependent on whitebark pine and harvest, cache, and eat seeds of other large-seeded pines (Tomback 1978, 1998).

In years with cone production, nutcrackers begin to harvest seeds as early as mid-July, removing pieces of unripe seeds from unripe, resinous cones, to feed themselves or their dependent juveniles (Tomback 1978). Throughout the summer, nutcrackers also retrieve whitebark pine seed caches made the previous year (Tomback 1978; Vander Wall and Hutchins 1983). Nutcrackers compete with pine squirrels for whitebark pine seeds—the Douglas squirrel or chickaree (*Tamiasciurus douglasii*) of the Pacific ranges and the widely distributed American red squirrel (*T. hudsonicus*)—which cut and store cones as a winter food supply. When cone crops are small, most of the seed crop will be depleted between the pine squirrels and early nutcracker foraging (e.g., McKinney and Tomback 2007, 2011).

Nutcrackers select diverse microsites for caching, burying caches 1 to 3 cm under various substrates, such as forest litter, mineral soil, gravel, or pumice. Nutcrackers place a large proportion of their caches at the base of trees; these microsites tend to experience early snowmelt. Nutcrackers also cache next to fallen trees and rocks, in fallen trees, in open terrain, among plants, on rocky ledges, and in rock fissures (Tomback 1978). They place some of their caches in trees, tucking seeds in cracks, holes, and under the bark, which may allow easier access to seeds, especially in regions with heavy winter snowpack (Lorenz et al. 2008; Tomback 1978). They will also cache whitebark pine seeds in the ground at and above treeline among patches of krummholz conifers. Whitebark pine seeds may be cached near source trees or transported 32 km or farther, often to higher or to lower elevations, where whitebark pine cannot grow as well (Lorenz et al. 2011; Tomback 1978). Nutcrackers appear to cache

across a variety of terrain within their home range, but also within communal storage areas that are within 3 to 4 km of source trees (Tomback 1978; Hutchins and Lanner 1982).

2.3 Mycorrhizae

Whitebark pine, like other western conifers, requires ectomycorrhizal fungi (ECM) for survival in the cold, infertile upper subalpine environs (Mohatt et al. 200; Read 1998). Mycorrhizae considerations should be taken into account in management strategies to help ensure establishment, maintenance, and conservation of this pine species under changing climates (see Keane et al. 2012b for details). Ectomycorrhizal fungi are important because they (as species or strains) vary in host specificity; soil preference; host age requirements; dispersal strategies; ability to enhance nitrogen (N) or phosphorus (P) uptake; types of N and P accessed; and protective abilities against pathogens, drought, heavy metals, and soil grazers (Tedersoo et al. 2009). There are 7,000 to 10,000 species of ectomycorrhizal fungi associated with trees and woody shrubs (Taylor and Alexander 2005) (fig. 7). Whitebark pine hosts only a small subset of ectomycorrhizae, currently assessed at fewer than 50 species (Cripps and Grime 2009; Mohatt et al. 2008; Molina and Trappe 1994). Fourteen of those species are shared with limber pine (Cripps and Antibus 2010). Practices and impacts potentially threatening to the maintenance of ectomycorrhizal diversity in the soil include tree-cutting, soil removal, mechanical disturbance, soil compaction, erosion, mining activities, liming, N-deposition, fertilization, high severity fire, reduction of tree age diversity, and promotion of certain grasses (Cripps and Antibus 2010). Additional



Figure 7—Ectomycorrhizae on whitebark pine (photo courtesy of Cathy Cripps, Montana State University).

detrimental effects may result from the removal of certain understory or reservoir plants, woody debris, nurse trees, and other microsite components (reviewed by Wiensczyk et al. 2002). In general, these practices should be minimized to maintain high ECM fungal diversity in the soil.

Fire can affect ectomycorrhizal communities in soil in different ways, depending on the severity of the fire, forest type, and other factors (Cairney and Bastias 2007). High intensity fires may eliminate ectomycorrhizal communities because of the deep depth of heating in the soil, the loss of original tree hosts, and changes in abiotic conditions, including an increase in soil surface temperature (Neary et al. 1999). Although some fungal species survive and rapidly recolonize after fire, others do not, and consumption of the duff layer can inhibit establishment of some ectomycorrhizal fungi (Smith et al. 2005). Five years after a high severity fire, seedlings were partially colonized by suilloids, likely due to availability of a nearby inoculum (an adjacent unburned forest), the presence of dispersal vectors (deer and small mammals), and a management plan that included planting 1 year after the burn (Trusty and Cripps 2010). Under other circumstances, recolonization of suilloids might take decades.

2.4 Community Characteristics

Whitebark pine forests occur in two high mountain biophysical settings (fig. 8). On productive, upper

subalpine sites, whitebark pine is the major seral species that is eventually replaced, in the absence of disturbance, by the more shade-tolerant subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm), or mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière), depending on geographic region (Arno and Weaver 1990). These sites, referred to as “seral whitebark pine sites” here, support upright, closed-canopy forests in the upper subalpine zone, just above or overlapping with the elevational limit of the shade-intolerant lodgepole pine (*Pinus contorta* Douglas ex Loudon) (Arno and Weaver 1990; Pfister et al. 1977). These two species can often share dominance of a site. Other minor to rare species found with whitebark pine on these sites in the northern Rocky Mountains are Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western larch (*Larix occidentalis*), western white pine (*Pinus monticola* Dougl.), and limber pine (*Pinus flexilis* James).

Biophysical settings where whitebark pine is the major, and sometimes only, tree species able to successfully dominate in high-elevation settings are called “climax whitebark pine sites.” Climax sites are often harsh and severe, and occur above the seral sites and just below tree line on relatively dry, windswept, cold slopes (Arno 1986; Arno and Weaver 1990; Steele et al. 1983) (fig. 9a). The stands tend to be open and well-spaced, sometimes mixed with other species, such as subalpine fir, spruce, and lodgepole pine in

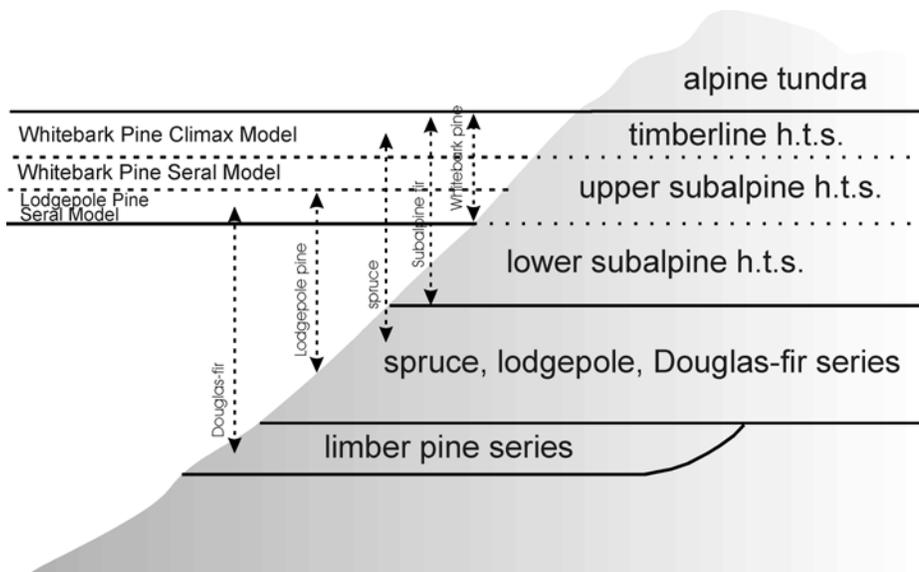


Figure 8—Elevational range of whitebark pine showing the two site types often associated with this species (Arno 2001). The climax type is dominated by whitebark pine because it is the only species able to inhabit these inhospitable environments. The seral type is where the shade-intolerant whitebark pine is eventually replaced by the more shade tolerant subalpine fir, spruce, and mountain hemlock.



Figure 9—Typical whitebark pine stands on the two site types: (a,b) climax sites where whitebark is often the only tree species able to gain dominance (photos courtesy of Steve Arno) and (c,d) seral sites where whitebark pine is often found with lodgepole, subalpine fir, and spruce, and is often outcompeted by fir and spruce in the absence of fire (photos by Bob Keane, USDA Forest Service).

the Rocky Mountains (fig. 9b). Co-occurring species in seral communities vary geographically and include western white pine (*Pinus monticola*), foxtail pine (*Pinus balfouriana*), red fir (*Abies magnifica*), and mountain hemlock (*Tsuga mertensiana*) (Tomback and Achuff 2010). On climax sites, these species may co-occur with whitebark pine, but only as scattered individuals with truncated growth forms and they rarely dominate (Arno and Hoff 1990; Arno and Weaver 1990; Cooper et al. 1991; Pfister et al. 1977). Alpine larch (*Larix lyallii*) is often found on north-facing climax whitebark pine sites, often in association with sub-surface water (Arno and Habeck 1972). Whitebark pine also occurs as krummholz, elfin forests, clusters, groves, tree islands, and timber atolls in the alpine

treeline ecotone (Arno and Hoff 1990; Resler and Tomback 2008; Tomback 1989; Tomback et al. 2014) and as a minor seral species in lower subalpine sites (Cooper et al. 1991; Pfister et al. 1977).

In the absence of fire, whitebark pine is eventually replaced by shade-tolerant competitors, namely subalpine fir, spruce, and mountain hemlock on the more productive seral whitebark pine sites (Arno and Hoff 1990; Campbell and Antos 2003; Keane 2001b) (fig. 9c,d). It can take 50 to 250 years for subalpine fir to replace whitebark pine in the overstory depending on the local environment and previous fire history (Arno and Hoff 1990; Keane 2001b; Kipfmüller and Kupfer 2005). Successional processes and rates vary considerably among and within the species range

(Campbell and Antos 2003; Keane 2001b). On seral sites, whitebark pine may occur as a minor to major seral component depending on biophysical settings, available seed sources, and disturbance type and severity.

2.5 Genetics

A key component of any whitebark pine restoration program is the planting of rust-resistant seed or seedlings for reforestation (Keane and Parsons 2010b; Mahalovich and Dickerson 2004; Mahalovich and Foushee, submitted; Mahalovich et al. 2006). However, the planting of seed away from its source of collection increases the risk of maladaptation, which could lead to reduced growth and survival (Campbell 1979; Rehfeldt 1994). Seed transfer should be guided by natural levels of genetic variation and local adaptation in adaptive traits specific to the species in question (Hufford and Mazer 2003; McKay et al. 2005; Morgenstern 1996). Understanding genetic structure and levels of inbreeding are also necessary for predicting the possible effects of climate change (St. Clair et al. 2005).

Current predictions of future climates may complicate seed transfer. A diverse mixture of seed sources can balance suitability of resultant seedlings to current and future environments (Bower and Aitken 2008). The degree of diversity, however, must be balanced to offset possible adverse impacts of outbreeding depression. An individual tree's genetic makeup and its interaction with the environment determine the amount of variation in measurable characteristics such as growth, survival, and tolerance to biotic and other stressors, such as disease resistance, insect tolerance, drought tolerance, and cold hardiness.

Genetic variation is critical because it provides the raw material for adaptation to new environments and it is the foundational component of biodiversity. The amount and structure of genetic variation within a population are influenced by many factors including gene flow, mutation, genetic drift, and selection (Frankham et al. 2002). Knowledge of a species' genetic structure is essential to ensure that management activities do not adversely affect the amount and patterns of genetic diversity. Moreover, because

whitebark pine is an outcrossed species (unrelated genetic material is introduced to the breeding line) (Bower and Aitken 2007; Jørgensen and Hamrick 1997; Mahalovich and Hipkins 2011), it is imperative that management activities do not adversely contribute to an increase in inbreeding.

A few studies have assessed the genetic variation of whitebark pine in adaptive traits such as cold hardiness, growth, phenology, stem form, and disease resistance. Mahalovich et al. (2006) found significant differences between seed sources for late winter cold injury (cold hardiness), survival, height growth, and blister rust resistance. Most of the differentiation is attributed to broadscale differences among geographic regions, with sources from the Greater Yellowstone Area distinct from other sources in Montana, Idaho, and eastern Washington. Cold hardiness and rust resistance show weak and opposite geographic patterns, with sources in the Pacific Northwest having higher rust resistance and lower cold hardiness, and southeastern sources having lower rust resistance and higher cold hardiness. Bower and Aitken (2006) found that the level of cold hardiness varies throughout the year from below -70°C in the winter to -9°C in the summer. Acclimation and de-acclimation to cold often occur rapidly over a period of 2 to 3 weeks in the fall and spring, respectively; however, even during the period of active shoot elongation, whitebark pine shows greater hardiness to cold than most conifers. Most trait correlations are favorable; unfavorable correlations with cold hardiness can be managed through zoning, a restricted selection index (Mahalovich et al. 2006, Mahalovich and Foushee, submitted), or site-specific planting prescriptions to avoid frost pockets and swales (McCaughy et al. 2009). Family heritabilities for survival, height, cold hardiness, and blister rust resistance are moderate to high ($h^2_F = 0.68\text{--}0.99$) (Mahalovich et al. 2006). Gentle clines in elevation for height and rust resistance and moderate clines in cold hardiness characterize whitebark pine as having a generalist adaptive strategy in the Northern Rockies. Moreover, adaptation to heterogeneous environments does not appear to be as strongly related to phenotypic plasticity as western white pine (Potter et al., in prep.).

2.6 Disturbance

2.6.1 Wildland Fire

Whitebark pine fire regimes often contain elements of all three types of fire severities: non-lethal, mixed severity, and stand-replacing (Arno and Hoff 1990; Barrett 2008; Campbell et al. 2011; Larson et al. 2010; Morgan et al. 1994b; Murray 2008; Siderius and Murray 2005) (fig. 10). Some whitebark pine stands may experience low-intensity, non-lethal surface fires because of sparse surface and canopy fuel loadings and unique topographical settings. These sites are mostly found in the southern parts of the species' range in the Rocky Mountains or on high, dry ridges and represent less than 10 percent of existing whitebark pine forests (Keane et al. 1994; Morgan et al. 1994b). Whitebark

pine can survive low-intensity surface fires better than most of its competitors, especially subalpine fir, because it has somewhat thicker bark, higher and thinner crowns, and deeper roots (Arno and Hoff 1990; Morgan and Bunting 1990; Ryan and Reinhardt 1988). Non-lethal surface fires have historically maintained whitebark pine dominance in the overstory and prolonged whitebark pine cone production by delaying succession (Keane 2001b).

The more common mixed-severity fire regime is characterized by fire severities that are highly variable in space and time, creating complex patterns of tree survival and mortality on the landscape (Murray et al. 1998; Romme and Knight 1981; Siderius and Murray 2005) (fig. 10). Mixed-severity fires can occur at 60 to 300+ year intervals and sometimes

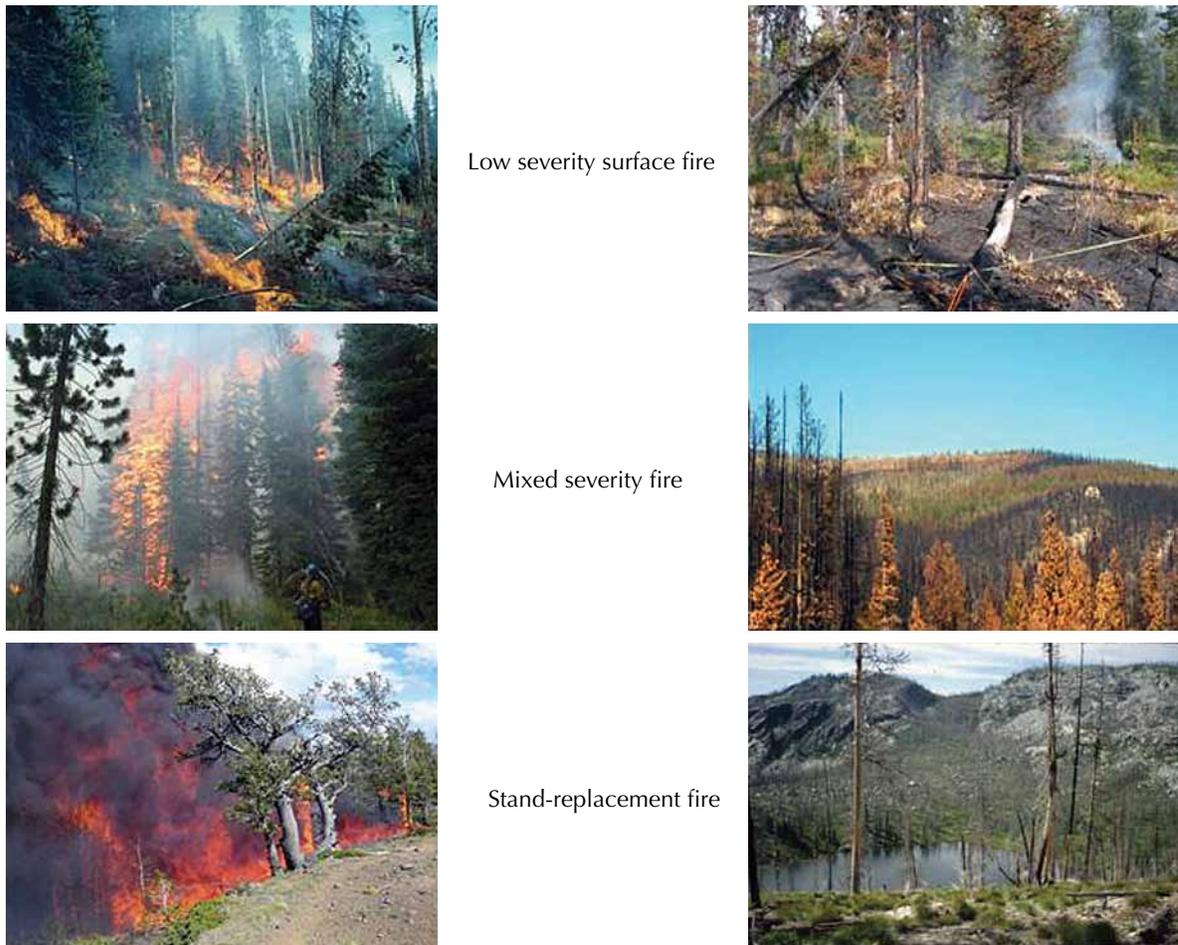


Figure 10—The three severities of fire that occur in whitebark pine ecosystems. The low severity surface fire is a low intensity fire that creeps along on the ground killing small seedlings, saplings, and fire-sensitive trees. The mixed severity fire burns in a patchy pattern with some patches having high tree mortality and other patches have low tree mortality. The stand-replacement fire kills most (>90 percent) trees in large patches (Keane and others 2012b; photos taken by R. Keane, USDA Forest Service and anonymous photographers).

over 500 years, depending on drought cycles, fuel conditions, landscape burn history, and frequencies of high wind events (Arno and Hoff 1990; Morgan et al. 1994b; Walsh 2005). Individual mixed-severity fires can include patches of non-lethal surface fires with differential mortality mixed with patches of variable mortality stand-replacement fires (Morgan et al. 1994b). Sometimes fires burn in sparse ground fuels at low severities, killing the smallest trees and the most fire-susceptible overstory species, often subalpine fir (Walsh 2005). Severity increases if the fire enters areas with high fuel loads or under high wind or drought conditions because these situations facilitate ignition of tree crowns, thereby creating patches of fire-killed trees (Lasko 1990). Burned patches vary widely in size depending on topography and fuels; these openings provide important seed caching habitat for the Clark's nutcracker (Norment 1991; Tomback et al. 1990).

Many whitebark pine forests in the northern Rocky Mountains, Cascades, and Greater Yellowstone Area historically experienced periodic large, stand-replacement fires that occurred at intervals of over 250 years) (fig. 10). Stand-replacement fires also occurred within mixed-severity fire regimes, but as infrequent events (Morgan and Bunting 1989; Romme 1980). Stand-replacement fires are usually wind-driven and often originate in lower, forested stands (Murray et al. 1998), and they create large burned patches that may be distant from tree seed sources (Beighley and Bishop 1990). Whitebark pine has an advantage over its competitors in that it readily colonizes large, stand-replacement burns because its seeds are transported great distances by Clark's nutcracker (Lorenz et al. 2008; Tomback 1982, 2005). Nutcrackers can disperse whitebark pine seeds up to 100 times farther (over 10 km) than wind can disperse seeds of subalpine fir and spruce (McCaughey et al. 1985; Tomback et al. 1990, 1993). Since nutcrackers often cache in open sites with many visual cues, stands burned by mixed- or stand-replacement fire provide favorable sites for seed caching and competition free seedling growth (McCaughey and Weaver 1990; Sund et al. 1991; Tomback 1998). Murray et al. (1995) found that larger burns were associated with a greater volume per hectare of whitebark pine as compared to smaller burns in the Bitterroot Mountains.

Whitebark pine benefits from wildland fire because it is better adapted to surviving fire and also to regenerating in burned areas than associated shade-tolerant trees (Arno and Hoff 1990). Without fire, most seral whitebark pine forests would be successional replaced by subalpine fir or some other shade-tolerant high-elevation species. Fire, whitebark pine, and the Clark's nutcracker form an important high-mountain ecological triangle (Tomback 1989). Fire burns areas thereby enhancing fine-scale patterns thereby increasing visual cues that then facilitate nutcracker caching. Unretrieved whitebark pine seed cached in burned areas can germinate and become seedlings that can grow into mature trees unfettered by competition.

2.6.2 Mountain Pine Beetle

The primary insect that kills whitebark pine trees is the mountain pine beetle (MPB) (Arno and Hoff 1990). Mountain pine beetles range from the Pacific Coast east to the Black Hills of South Dakota and from northern British Columbia and western Alberta south into northwestern Mexico. It is a native, cambial-feeding bark beetle of all the western pines, including western white, limber, ponderosa, and lodgepole pines. Its entire life cycle is spent beneath the bark of host trees, except when adults emerge from brood trees in the early summer and fly in search of new host trees. Trees defend themselves with various secondary chemicals and by exuding pitch, but these matchhead-size beetles can overwhelm these defenses with a mass attack strategy through sheer numbers of beetles (Logan and Powell 2001).

Beetles develop through four stages: egg, larva, pupa, and adult (Amman and Cole 1983). Adults mate and then lay eggs that hatch into larvae that develop in the phloem of the tree through the pupa stage, thus completing the life cycle—a 1-year or univoltine life cycle. Larval growth is aided by one of two symbiotic fungi—*Grosmannia clavigera* or *Ophiostoma montium* (Adams and Six 2007; Six 2003; Six and Paine 1998). Adult beetles deposit the fungi in the tree as they excavate galleries where the females lay eggs. The fungi colonize the phloem and sapwood of the infected tree with the fungal hyphae providing nutrition to beetle larvae (Six 2003). Adult beetles also feed on fungal spores in the pupal chambers before emergence and

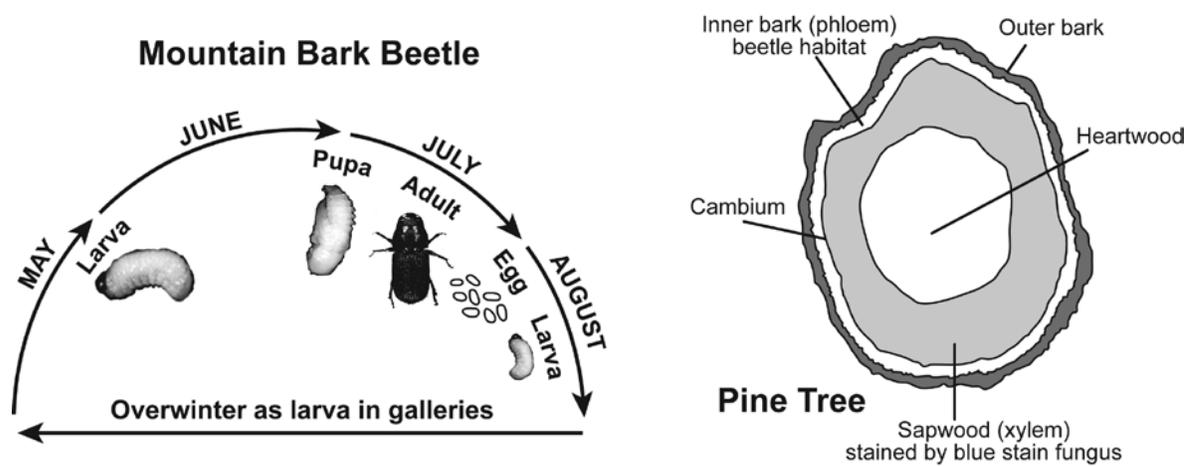


Figure 11—The complex life cycle of the mountain pine beetle (taken from Logan and McFarlane 2010). The eggs are laid inside the bark in mid-summer and then hatch and overwinter as larva in galleries.

dispersal from the host tree. One to several months after the tree is infested by MPB, the sapwood discolors to a bluish tint caused by the fungi.

Beetle life cycles take 1 to 2 years, and many empirical, laboratory, and modeling research studies have been undertaken to understand the causes of life cycle variability (Bentz et al. 1991; Logan and Powell 2001; Powell et al. 1996) (fig. 11). Over most of its range, the beetle has one generation per year, but two generations have been observed in high-elevation areas, including whitebark pine forests, when warm temperatures prevail (Logan and Bentz 1999). The traditionally cold environment of the whitebark pine forest creates an unfavorable heat balance for beetle development in most years (Amman 1973; Logan and Bentz 1999). Mountain pine beetles have mechanisms to survive in sub-zero temperatures; however, sustained, sub-freezing temperatures may result in mortality in all life stages (Amman and Cole 1983; Regniere and Bentz 2007). Beetle development is under direct temperature control (Logan and Bentz 1999), and warm temperatures favor successful brood development, beetle survivorship, and successful attacks (Amman 1972, 1973; Bentz et al. 1991; Logan and Bentz 1999; Reid and Gates 1970). Generally, epidemics collapse due to one of two factors: an extreme cold snap (less than -18°C) in early fall or late spring and winter temperatures below -37°C (Cole et al. 1989); or a lack of susceptible host trees.

Once inside the bark, the MPB disrupts the connectivity of the water transport system of the tree,

damaging the tree by mechanically girdling the stem as adults and larvae create galleries in the phloem. More importantly, the MPB introduces a blue stain fungus that inhibits water transport and may eventually kill the tree (Six 2003; Six and Paine 1998). Some trees have the ability to exude pitch at the attack sites as a defense mechanism, but these are infrequent in whitebark pine. Whitebark pine, like other pines, may sustain “strip attacks” where a vertical portion of inner bark is killed while the rest of the stem is unaffected and continues to transport water and nutrients. Foliage of successfully attacked trees generally fades uniformly through the crown from yellowish green to shades of orange, rust and red. Whitebark pine crowns generally fade to a rust color the year after attack, but may take 2 to 3 years in some hearty individuals.

The severity of the current MPB outbreak in high elevation pines is attributed to warmer winters that have increased survival and warmer summers that have allowed some proportion of broods to shift from a 2-year life cycle to a 1-year life cycle (Bentz et al. 2011, 2014; Dooley 2012; Logan and Powell 2001; Logan et al. 2010). Within the past decade, 47 million ha across all pine types in the Rocky Mountains have been affected by the mountain pine beetle (Raffa et al. 2008). Recent climate projections indicate this trend will continue in the future, with a possible increase in the frequency of back-to-back MPB outbreaks subjecting surviving host trees for further attacks (reviewed in Mahalovich 2013).

2.6.3 White Pine Blister Rust

White pine blister rust (WPBR) is an exotic fungal disease caused by the fungus *Cronartium ribicola* and infects all five-needle pines including sugar, western white, limber, southwestern white, bristlecone, and foxtail pines (Burns et al. 2007; Geils et al. 2010; McDonald and Hoff 2001). It was introduced to eastern North America in the 1890s and into western North America in the first decade of the 20th century on infected eastern white pine nursery stock grown in France and shipped to Vancouver British Columbia. Since then, the pathogen has spread across all or part of the ranges of all five-needle pines in the United States and Canada, except for Great Basin bristlecone pine. It was once thought that the dry environments of western North America were inhospitable to WPBR, but the rust has since infected pines in even the most severe and hostile climates (Burns et al. 2008; Resler and Tomback 2008; Tomback and Achuff 2010).

WPBR has a complex life cycle involving five different spore types on three groups of alternate hosts. Blister rust cankers on the white pine hosts produce aeciospores, which transmit the disease to the alternate hosts. Shrubs of genus *Ribes* are the most common hosts, but herbaceous plants of the genera *Pedicularis* and *Castilleja* also serve as hosts (Geils et al. 2010; McDonald et al. 2006). Basidiospores produced by the alternate hosts are fragile, short-lived spores that infect pines by entering needle stomata. This stage of the life cycle is most climatically limited, requiring moderate temperatures and high humidity for spore production and transmission to pines (Van Arsdel 1967; Van Arsdel et al. 1956). As reviewed in Mahalovich (2013), regional geography and local physiographic features dictate whether pine infections originate predominately from sources within the pine stand (local spread) or from distant sources (long-distance dispersal) (Zambino 2010).

There are two modes of WPBR dispersal:

1. Diffusion. Basidiospores may be dispersed by diffusion at the local scale, where the density of spores for deposition and infection from a single source declines in magnitude with the square root of distance. In this mode, basidiospores usually travel only a short distance, averaging 300 m since

the delicate spores are vulnerable to desiccation and sunlight (Kinloch 2003). Local spread (diffusion) and intensification of blister rust in five-needle pines progresses concentrically and relatively slowly (Kinloch 2003).

2. Turbulent mixing. Long distance flow can occur at multiple scales as a result of distinct air masses with a combination of laminar flow and disruption by turbulent mixing (Van Arsdel et al. 2006).

The range of basidiospore dispersal also varies by position of blister rust cankers within an infested crown. Hunt (1983) found that within western white pine stands in British Columbia, cankers near the ground resulted from *Ribes* spp. inoculum produced in the stand, whereas cankers high in the crown resulted when inoculum from a distant source was carried into the stand by down-slope air flow. Thus, average distance estimates of basidiospore transport range from 15 m (diffusion) to 27 km (turbulent mixing), where patterns of pine infection and distances of effective dissemination also vary from year-to-year with annual variation in the weather (Zambino 2010). Lastly, moist air masses in late summer form the backdrop of wave years, where basidiospores can survive traveling farther over wider geographic areas (Van Arsdel 1967).

Spores that germinate within the needle tissue produce hyphae, which then grow into the vascular system and the needle stem (see McDonald and Hoff 2001; Geils et al. 2010 and references therein). The hyphae grow down the branch and eventually into the tree bole. There, 2 to 3 years later, it eventually forms a canker in which spore structures called pycnia produce pycniaspores, which are not infectious but are needed for fertilization by insects. Aeciospores are produced from fertilized pycnia found in bright orange blisters in the early summer of the following year. These aeciospores are hardy with thick walls and can travel long distances to infect *Ribes* spp. Aeciospore transmission to *Ribes* spp. has been estimated to be as far as 300 km (Fujioka 1992) to 500 km during wave years (Mielke 1943). Wave-year events can either be a significant local intensification of rust infection or a long-distance jump of blister rust (Mahalovich 2013). Wave years need not be particularly wet; however, “dry” events are typically preceded by 1 or 2 wet years

(Fujioka 1992). Fragile orange urediniospores are produced on the underside of the alternate host leaves and infect other alternate hosts throughout the summer. In the fall, teliospores form on infected *Ribes* spp. leaves, and these germinate to form the basidiospores that infect the pine.

WPBR damages and then kills whitebark pine trees from the top down by girdling branches and stems (Hoff 1992), which reduces cone production before death. Kinloch (2003) argued that the most insidious impact of rust is its destruction of host natural regeneration, which consequently alters natural succession. This reduction in regeneration potential is further exacerbated by a suite of interactions among vertebrate predation and pine cone production that are altered both directly and diffusely by disproportionate whitebark pine mortality and reduced seed cone availability.

Current estimates of whitebark pine resistance to WPBR in high rust-mortality areas ranged from 33 percent in a small sample ($n = 3$) (Hoff et al. 1980) to 47 percent ($n = 108$) (Mahalovich et al. 2006) in the Inland Northwest and 26.3 percent ($n = 43$) on the Pacific Coast (Snieszko et al. 2007). Seeds from the healthy trees in stands heavily infected and damaged by blister rust would have the highest probability of having some resistance to blister rust. Resistance to rust can be manifest in many mechanisms or adaptations including no spotting (failure of the germinating basidiospore to penetrate the stomatal cavity), premature shedding of infected needles, fungicidal short-shoot reaction, bark reactions walling off canker development with callous tissue, and canker tolerance (Hoff 1992; Hoff et al. 1980; Mahalovich 2013; Zambino and McDonald 2004). If whitebark pine continues to decline, the surviving (rust-resistant) trees that have these resistance mechanisms will be at such low numbers that virtually all of their seeds will be eaten and little of the resistance will be passed to the future generations (McKinney and Tomback 2007). Some landscapes in the northern Rocky Mountains contain so few undamaged trees and apparent rust-resistant whitebark pine seed sources that there is major concern that whitebark pine seed dispersal is not occurring at any magnitude. Between the pine squirrels cutting down cones and nutcrackers consuming

unripe seeds, there may be few ripe seeds available for seed caching.

2.7 Current Status

The rapid decline of whitebark pine across most of its range in North America is mostly a result of multiple concurrent human-caused and natural events (Arno 1986; Kendall 1995; Kendall and Keane 2001; Raffa et al. 2008; Tomback et al. 2001b; Zeglen 2007; for recent reviews, see Tomback and Achuff 2010 and Tomback et al. 2011a). First, several major natural MPB outbreaks over the last 70 years have killed many cone-bearing whitebark pine trees across its range (Arno 1986; Baker et al. 1971; Waring and Six 2005). The most recent MPB outbreak, which began in the late 1990s, apparently has achieved unprecedented intensity and geographic extent, driven by higher temperatures that many associate with anthropogenic climate-warming (Logan and Powell 2001).

Next, an extensive and successful fire exclusion program in western North America for most of the 20th century has reduced the area that can be potentially inhabited by the shade-intolerant whitebark pine. Because there were fewer fires, late successional whitebark pine communities became increasingly common and early successional communities increasingly rare. This resulted in a cumulative decline of whitebark pine at a landscape scale over time (Keane and Arno 1993; Kipfmueller and Kupfer 2005; Morgan and Bunting 1990).

And finally, the potentially most threatening events were multiple introductions of the exotic fungal pathogen *Cronartium ribicola* to the western United States and Canada in the early 1900s (Hunt 1983), which causes WPBR (Geils et al. 2010; McDonald and Hoff 2001). Whitebark pine was historically considered the most susceptible of the five-needle white pines to blister rust (Hoff et al. 1980; Kendall and Keane 2001; Schwandt 2006). More recent rust screening trials from 2006 to 2014 involving larger and geographically widespread samples have shown that whitebark pine exceeded western white pine seedlings in percent rust resistance in two of the three tests (Mahalovich and Foushee, submitted).

3. Climate Change Impacts: A Literature Review

The cumulative interactions of these three agents have resulted in a rapid decrease in mature whitebark pine, particularly in the more mesic parts of its range (>80 percent mortality in northern Idaho, northwestern Montana, northern Cascades) (Campbell and Antos 2000; Elder et al. 2008; Fiedler and McKinney 2014; Keane and Arno 1993; Six and Adams 2007). Moreover, predicted changes in the Pacific Northwest climate brought about by global climate change could further accelerate the decline of this important tree species by directly influencing the regeneration, growth, and mortality of whitebark pine and indirectly by increasing the frequency, intensity, and duration of MPB, WPBR, and fire (Blaustein and Dobson 2006; Logan and Powell 2001; Romme and Turner 1991; Running 2006).

When incorporating climate change into restoration strategies, it is important to evaluate effects of climate change across all of the ecological interactions and processes that influence whitebark pine abundance. All life stages, including reproduction, seed dispersal, regeneration, phenology, and mortality, should be considered, not just growth response (Koteen 1999). All ecosystem processes, specifically disturbance regimes, hydrology, and successional dynamics, should also be appraised. Climate change impacts on spatial processes, such as seed dispersal and disturbance spread, must also be assessed (Chuine 2010; Loehle and LeBlanc 1996; Price et al. 2001).

Moreover, climate change effects should be assessed at multiple spatial and temporal scales to ensure all interactions are appropriately evaluated (Gardner et al. 1996; Keane et al. 2015). Regeneration and mortality responses, for example, are best evaluated at the tree level, while disturbance dynamics are more appropriately assessed at landscape scales. While climate change may adversely affect whitebark pine populations across its entire range (Chang et al. 2014; Hansen and Phillips 2015; Koteen 1999), climate response must be evaluated locally to determine any exceptional regions of continued dominance and the most efficient set of restoration goals (Keane et

al. 2008b). Maintaining whitebark pine on the high mountain landscape using controlled wildfires and prescribed fires, for example, may only be possible in a narrow set of situations dictated by local constraints (e.g., smoke regulations, nearby developments, whitebark pine abundance). Restoration actions are probably more effective if implemented at landscape scales (see Section 4). Matching restoration objectives and climate change impacts with local landscape conditions will more effectively create resilient and resistant landscapes that are crucial for future conservation of whitebark pine (Craig 2009; Diggins et al. 2010).

Predicted warming, drought, and highly variable precipitation patterns have the potential to significantly impact whitebark pine ecosystems (Bartlein et al. 1997; Romme and Turner 1991), but the directions and magnitudes of these changes on high elevation landscapes in the range of whitebark pine are still largely unknown (Loehman et al. 2011b). Some aspects of whitebark pine ecology, such as drought tolerance, may enable the species to adjust to rapid climate change. Because of its long life span and phenotypic plasticity, whitebark pine is a hardy species that may have the adaptations to live through major climatic cycles such as those experienced in the past (Arno and Hoff 1990).

This Section 3 describes some important aspects of whitebark pine ecosystems that may make them more or less susceptible to climate change impacts over the next century. First, a climate projection was taken from the Northern Region Assessment Program vulnerability assessment for the northern Rocky Mountains (Keane et al., in press). Then, various ecological aspects of whitebark pine that are important to assessing climate change responses are discussed: species life cycles, genetics, and succession dynamics. Next, changes in the biophysical environment as a consequence of climate change are evaluated. Following that are some assessments of how climate change may alter those disturbance processes important in whitebark pine dynamics, specifically

Table 1—A summary of important climate change impacts on those biophysical processes that affect vegetation response for the CMIP5 RCP8.5 climate scenario outputs.

Evaluation category	Climate change impact
Precipitation	No trends in precipitation over the last century; higher variability range wide (16% higher). No significant trends for the western portions of whitebark pine's range and lower variation for east of the Continental Divide (CD) with a slight increase in precipitation.
Seasonal precipitation	West of the CD there is a decrease of 30% summer precipitation, and slightly higher in other seasons. East of the CD, it appears there might be a slight increase. Precipitation in all areas are highly uncertain and variable.
Average temperature	Temperatures have increased by 0.8 °C this past century. Considerable warming of 1.2–4.8 °C for areas west of the CD and 1.6–4.6 °C for areas east of the CD. Most warming occurs in the daily minimum than in the daily maximum; higher nighttime temperatures;
Maximum summer temps	Considerable warming of 1.9–5.3 °C west of CD and even higher east of the CD. Heat extremes will increase.
Minimum winter temps	Increased by 1.1–4.6 °C; greater in the shoulder seasons. Cold extremes will decrease
Freeze days	Decrease by 35 days in west of CD and 24 days east of the CD
Frost free days	Increase by 35 days west of the CD and 23 days east of the CD.
Drought duration	Droughts will be longer, but no indication of how much longer
Fire	Increased fire frequencies (1–3 times more fire). Possible increase in fire size (mostly as a result of fire exclusion). Possible increases in fire severity although highly variable and ecosystem dependent.
Insect outbreaks	Increased frequencies but depends on host and disease species.
Disease outbreaks	Increased frequencies but depends on host and disease species.
Extreme weather	Increased high precipitation events (>2.5 cm) by 13%.

fire, MPB, and WPBR responses to climate change. Finally, possible climate change influences on the Clark's nutcracker are discussed. The climate projections for the whitebark pine's range are summarized in table 1. Responses of whitebark pine ecosystems to these climate projections are presented in table 2 for reference when evaluating the mitigating actions recommended in Section 5.

3.1 Climate Projections

3.1.1 Understanding Climate Change Predictions

Predicting spatially explicit daily weather for the next century is an incredibly difficult task considering the complexity of the earth's interacting physical and biological systems. These predictions are usually made using global circulation models (GCMs), which are three-dimensional physical models that simulate weather and climate using conservation of mass and momentum approaches (Edenhofer et al. 2011). Many

GCMs are currently used to simulate future climate at coarse scales. Although it is clear that all models are predicting warming climates because of increasing atmospheric greenhouse gases (GHGs), specifically CO₂ (Stocker et al. 2013), there is a great deal of difference in the magnitude and rate of change across model projections (Roe and Baker 2007; Stainforth et al. 2005) (fig. 12). Not only do these GCMs simulate complex biophysical processes and feedback systems, they must also simulate society's response to climate change through the use of technological innovations to minimize or mitigate the effects of increasing GHG emissions.

Societal responses to GHG emissions are usually accounted for in various GCM simulation scenarios (fig. 12). As a result, there are vast differences in climate forecasts among GCMs and GHG scenarios contributing to a high degree of uncertainty in climate forecasts. This diversity of projections ultimately makes it difficult to design restoration strategies and actions under future climates (Stocker et al. 2013)

Table 2—Summary of the effects of climate change on whitebark pine ecosystems at multiple scales (Tree, Community, Landscape) and multiple interactions (Disturbance, Nutcracker). Columns in the table include Factor (the ecosystem characteristic or process being impacted by climate change), the Climate Effect (the effect of climate change on that factor), Impact (the severity of that effect on the factor), Direction (the trend in whitebark pine population stability), Importance (the importance of the change in the factor to the decline of whitebark pine and the effectiveness of restoration on a scale of 1-low to 10-high), and Notes (any other material deemed important).

Factor	Process affected	Climate effect	Impact	Direction	Importance	Notes
Tree						
Reproduction	Cone crop frequency and abundance	Increase	Moderate	Increase	4	Fine scale and coarse scale climate dynamics can influence cone crop dynamics
Regeneration	Germination	Decrease	Low	No change	2	
	Establishment	Uncertain	Moderate	Unknown	7	Difficult to evaluate if upper subalpine areas will be so hot and dry that seedlings will die
	Dispersal	Uncertain	Low	No change	5	Little is known of nutcracker-climate relationships
Growth	Tree diameter and height growth	Increase	High	Increase	5	It is unknown if understory whitebark pine seedlings and saplings will release
	Tree death	Uncertain	High	Increase	7	It is unknown if gains in vigor reduce mortality rates
Community						
Successional replacement	Competitor growth	Accelerate towards shade tolerant species	High	Decrease	8	Rate of successional replacement of whitebark pine to subalpine fir, spruce, and hemlock will increase
	Competitor growth and regeneration	Low soil moisture causes high competitor mortality	Low	Increase	3	Droughty sites
Disturbance						
Wildland fire	Increased fire frequency and intensity	May kill more whitebark pine, especially rust-resistant individuals	High	Decrease	7	Frequency might be so quick that fires burn regeneration before they reach reproductive maturity
	Larger and more severe fires	Increased burn areas create more caching sites free from competition	High	Increase	7	May kill those mature, cone-bearing trees that are somewhat rust-resistant thereby causing a loss of genetic diversity
MPB-caused Mortality	Increased frequency and severity of outbreaks	May kill more whitebark pine, especially rust-resistant individuals	High	Decrease	8	High mortality in cone-bearing trees resulting in a loss of rust-resistance and genetic diversity
WPBR-caused mortality	Increased spread	Increased spore production and spread	Moderate	Decrease	5	Highly variable climate may facilitate mutations in WPBR

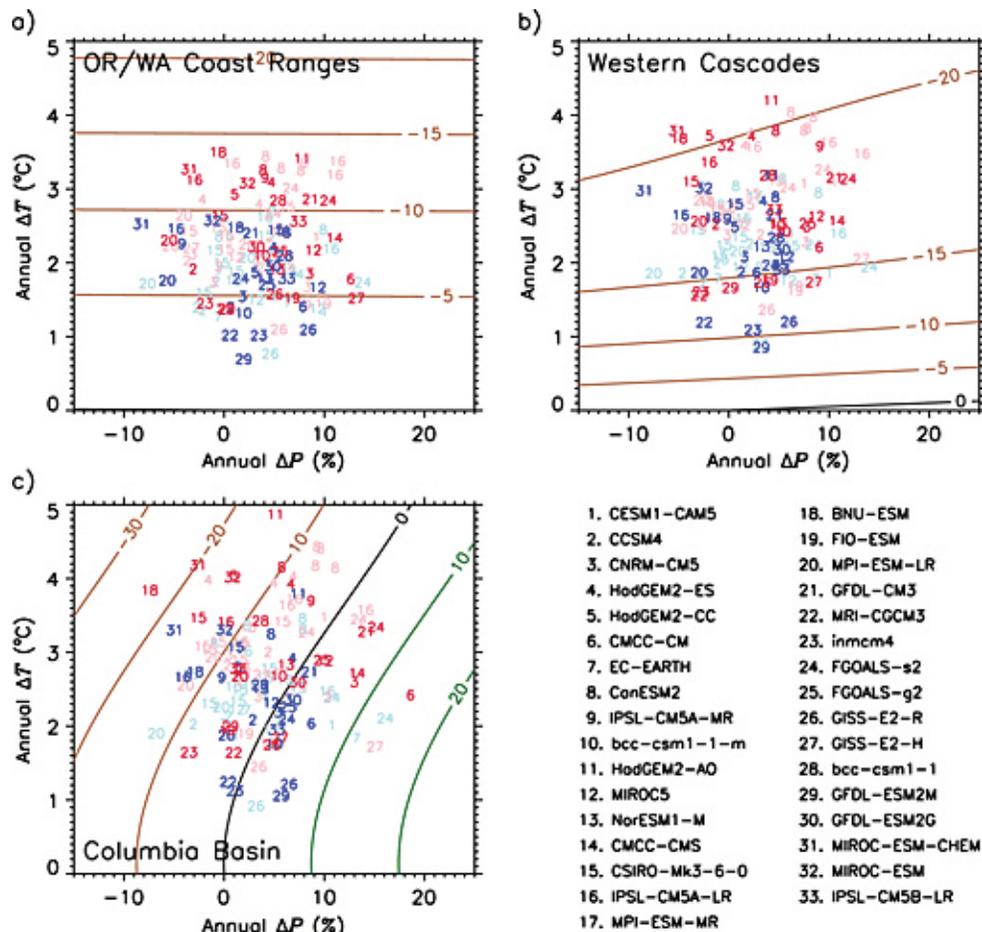


Figure 12—Figure from Vano et al. (2015) showing the differences in climate projections among Global Circulation Models (GCMs) and two emissions scenarios (RCP4.5, RCP8.5) from the CMIP study. This graph shows isolines that represent constant change in vegetation carbon for the three regions: (a) OR/WA Coast Ranges, (b) Western Cascades, and (c) Columbia Basin. All three of these regions are within the range of whitebark pine. GCM positions in ΔP - ΔT space are identified with performance ranking numbers. Blue numbers are RCP4.5 and red numbers are RCP8.5, where lighter numbers indicate multiple runs for the same GCM. Note the high uncertainty across all models and scenarios.

(figs. 12, 13). Moreover, the spatial resolutions of GCM predictions are usually quite coarse (1 to 5 degrees longitude and latitude), so another suite of models are often used to extrapolate GCM gridded daily data to finer scales (4 to 50 km pixel sizes) (Wilby and Wigley 1997).

Unfortunately, even these fine scale weather extrapolations are still too coarse to accurately describe local, landscape-level climate changes for most whitebark pine forests because the species occurs in unique landscape settings (tops of mountains) that are highly patterned at resolutions finer than the resolution of most downscaled GCM extrapolations

(e.g., 4 km). Mountain ridges, for example, are long, thin linear features that are only detected at scales below 4 km. Another confounding factor is that these model extrapolations have shallow temporal depth; most GCMs only simulate climate for 50 to 100 years, which is often too short to detect changes in whitebark pine populations.

In 1995, the Coupled Model Intercomparison Project (CMIP; see Meehl et al. 2000) was created to provide climate change scientists with a spatial database of coupled GCM simulations to use in other climate change studies. CMIP also was created to determine why different models gave different

The global climate of the 21st century

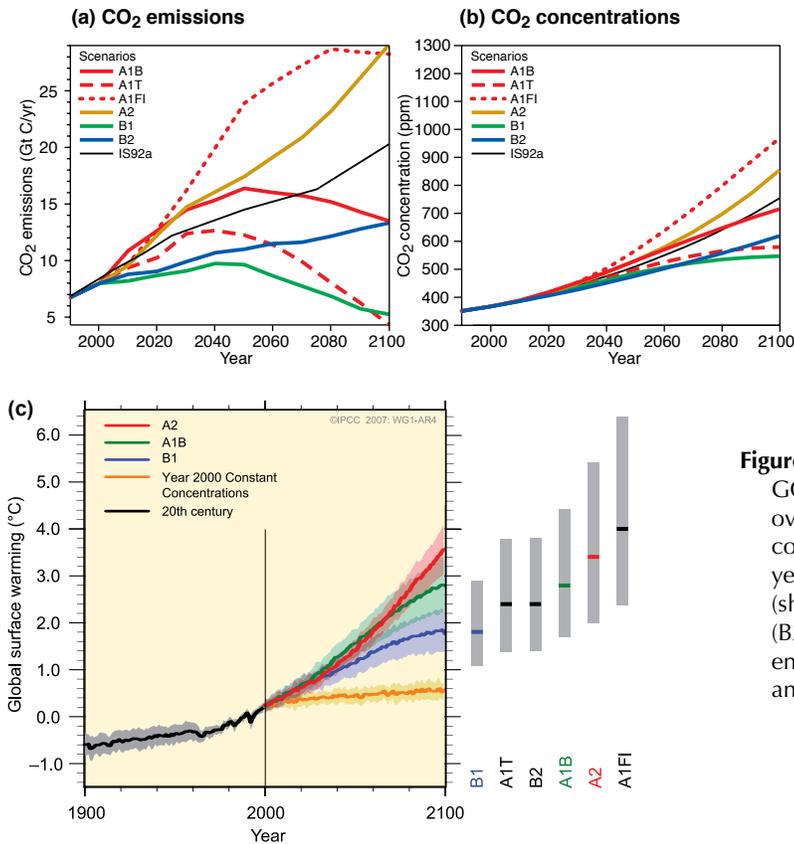


Figure 13—A set of emission scenarios for one GCM showing the (a) projected CO₂ emissions over the next century, and (b) atmospheric CO₂ concentrations that those emissions will create till year 2100. Also shown (c) is the great uncertainty (shaded bars) within and across emission scenarios (B2, A1T, B2, A2, A1F1) especially towards the latter end of the century (taken from Solomon et al. 2007 and Houghton et al. 2001. Used with permission).

outputs in response to the same input and to simply identify “consensus” in model predictions. In CMIP, the complete physical climate system, including the oceans and sea ice, adjust to prescribed atmospheric concentrations of carbon dioxide (CO₂). The first phase of CMIP, called CMIP1, collected output from coupled GCM control runs in which CO₂, solar brightness and other external climatic forcings are kept constant. A subsequent phase, CMIP2, collected output from both model control runs and matching runs in which CO₂ increases at the rate of 1 percent per year. Climate projections from CMIP3 and CMIP5 are used in this report. The CMIP3/5 data were downscaled to an 8 km resolution and are stratified by the time frames 2000 to 2050 and 2050 to 2090.

Two sets of climate change emission scenarios are used for illustration in this paper because of shifts in Edenhofer et al. (2011) scenario development. The B2 and A2 scenarios are part of the IPCC Special Report Emission Scenarios (SRES) created prior to

2011 to describe potential effects of society’s reaction to climate change (fig. 13). The A2 scenario is considered the hot, dry scenario. It represents a world with less international cooperation and more self-reliance on natural resources and government structures (Stocker et al. 2013). In the B2 world, there is increased concern for environmental and social sustainability. Environmentally aware citizens across the globe develop government, business, and social strategies for decreasing emissions and mitigating climate change.

In the Edenhofer et al. (2011) report, the SRES scenarios were replaced by a set of four scenarios that represented the total radiative forcing of the cumulative effects of human emissions of GHGs, expressed in W m⁻² of additional energy. These representative concentration pathways (RCPs) are indirectly tied to society’s response to climate change (fig. 14). The two RCP scenarios used in this report are RCP4.5 and RCP8.5 representing 4.5 W m⁻² and 8.5 W m⁻² of additional energy due to GHG emissions. Although it is

difficult to compare the SRES scenarios with the RCP scenarios, it may be convenient to think of B2 and RCP4.5 as the more moderate warm, dry scenarios and A2 and RCP8.5 as the severe hot, dry scenarios. Both scenarios are depicted here so that climate change studies using the earlier SRES A2/B2 scenarios can be linked to the more recent research that used RCP 4.5/8.5 scenarios in the literature synthesis of this section of the report.

3.1.2 Climate Projections for the Range of Whitebark Pine

Over the last 100 years in the Pacific Northwest, which encompasses most of whitebark pine's range, temperatures have increased while precipitation amounts have changed little (Mote and Salathé 2010). In the Greater Yellowstone Area (GYA), however, recent evidence shows that there has been a decrease in precipitation with a larger percentage falling as rainfall instead of snowfall (Mahalovich 2013). From 1895 to 2011, temperatures warmed 1.8 °C. During the period 1901 to 2009, observed temperatures,

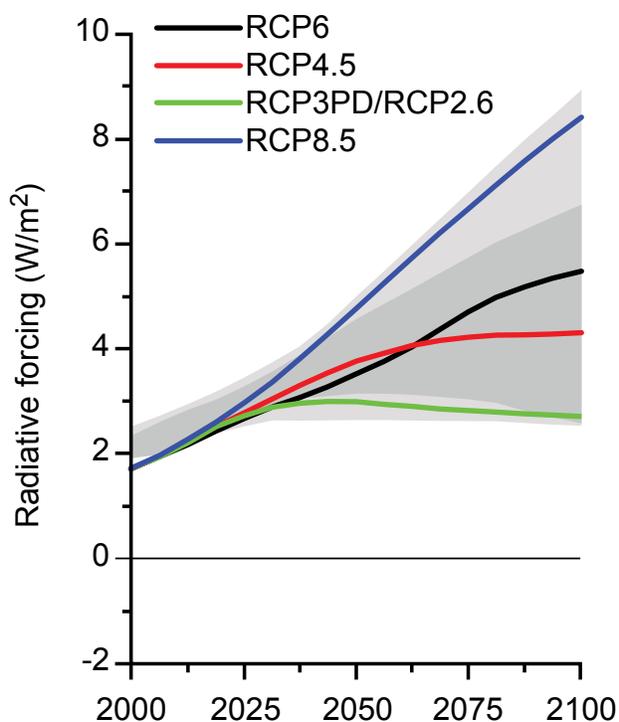


Figure 14—The new set of Representative Concentration Pathway scenarios used by the GCMs to predict future climate change. This report uses RCP4.5 and RCP8.5, which reflect the amount of additional radiative forcing caused by increased greenhouse gases (taken from Stocker et al. 2013).

especially high nighttime minimum temperatures, have increased since 1980 (fig. 15). No significant trend in precipitation has been found, although variability appears to be 16 percent higher since 1970 than in the preceding 75 years. Increases in extreme precipitation events have been modest (Mote and Salathé 2010).

Future projections suggest there will be greater warming in the northern Rocky Mountains than in the previous century (fig. 16). Compared to a baseline of 1970 to 1999, CMIP5 models project warming of 2–5 °C for the Pacific Northwest from 2041 to 2070, with the lower end of warming occurring for a scenario with moderate greenhouse gas emissions (RCP4.5) (Mote and Salathé 2010). CMIP3 and CMIP5 efforts project increases of at least 4 °C across all seasons with the greatest warming projected for the summer; the CMIP5 RCP8.5, the high emissions scenario, projects 3–8 °C warming for the summer. Heat extremes are projected to increase, whereas measures of cold extremes are projected to decrease. The biggest changes will be in minimum temperatures. NARCCAP simulations for 2041 to 2070 under the emissions scenario SRES to A2 project the duration of freeze to frost-free days to increase by 35 days (6 day standard deviation), and the number of days under 0 °C to decrease by 35 days (6 day standard deviation) (Mote and Salathé 2010).

Projections for precipitation are less certain (fig. 17). There are no significant trends in precipitation projections for the 2010 to 2100 timeframe for the Pacific Northwest (Mote et al. 2010). Despite lack of consensus among models for total annual precipitation, nearly all models project lower summer precipitation (some as much as 30 percent lower), and higher winter, spring, and fall precipitation. Increased precipitation is projected for high elevations (above 1,800 m mean sea level approximately), whereas decreased precipitation is projected for low elevations. CMIP3 projections for precipitation extremes are more uncertain; moderate events (days >1 inch of precipitation) are projected to increase by 13 percent (7 percent standard deviation), but scenarios of other extremes are less certain (Mote et al. 2010).

Observed U.S. Temperature Change

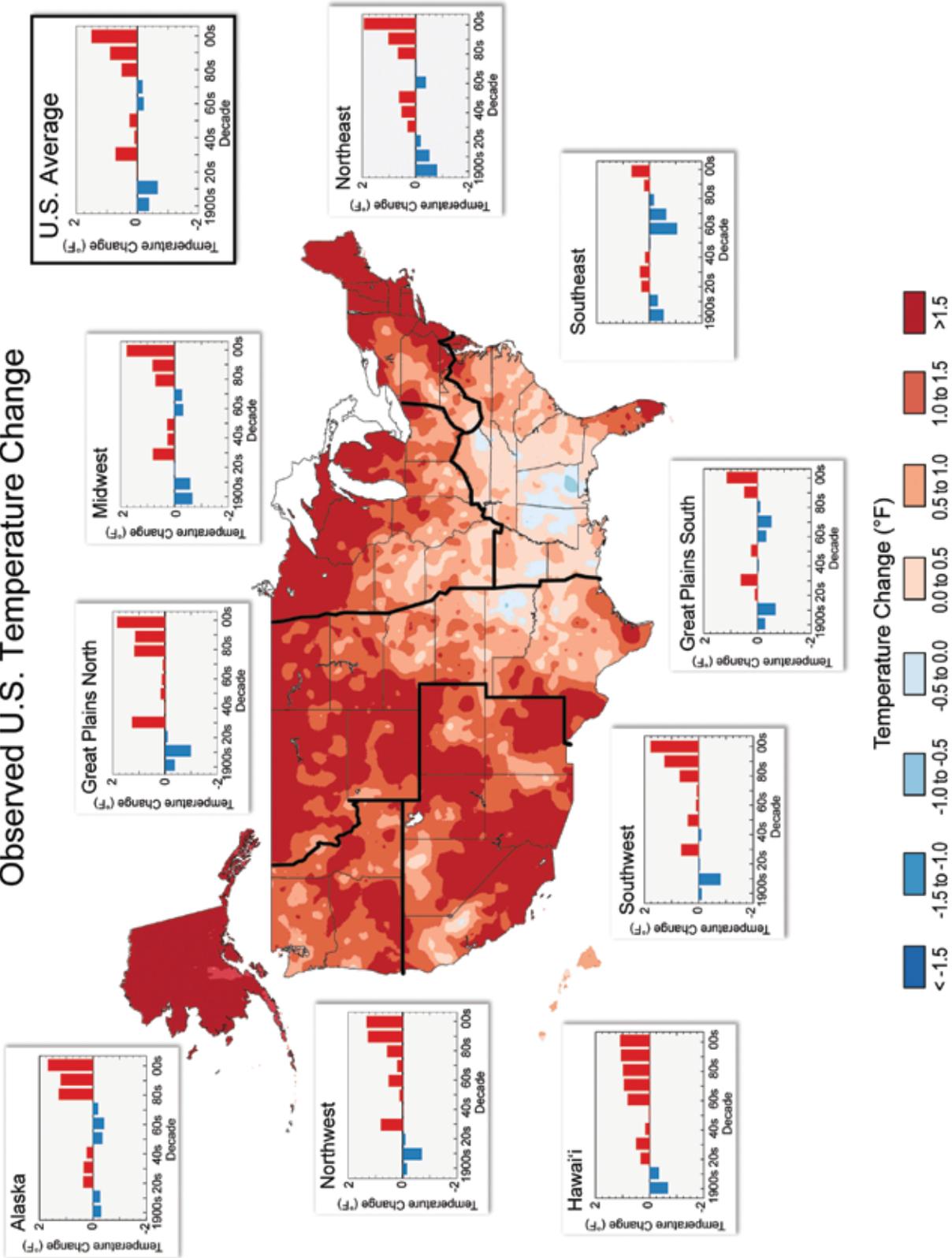


Figure 15—Changes in observed temperature over the last century across the contiguous United States. Colors in the map reflect temperature changes from 1991–2012 compared to the 1901–1960 average and graphs show average temperature changes by decade (source: NOAA National Climate Data Center).

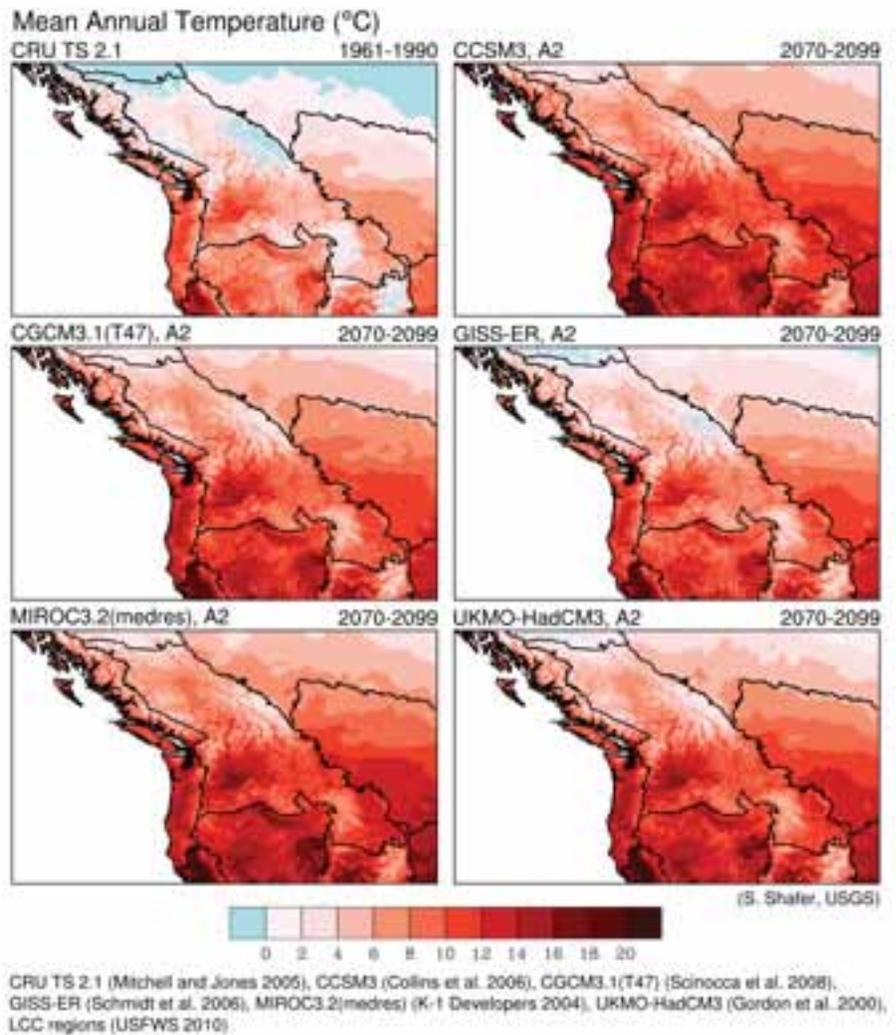


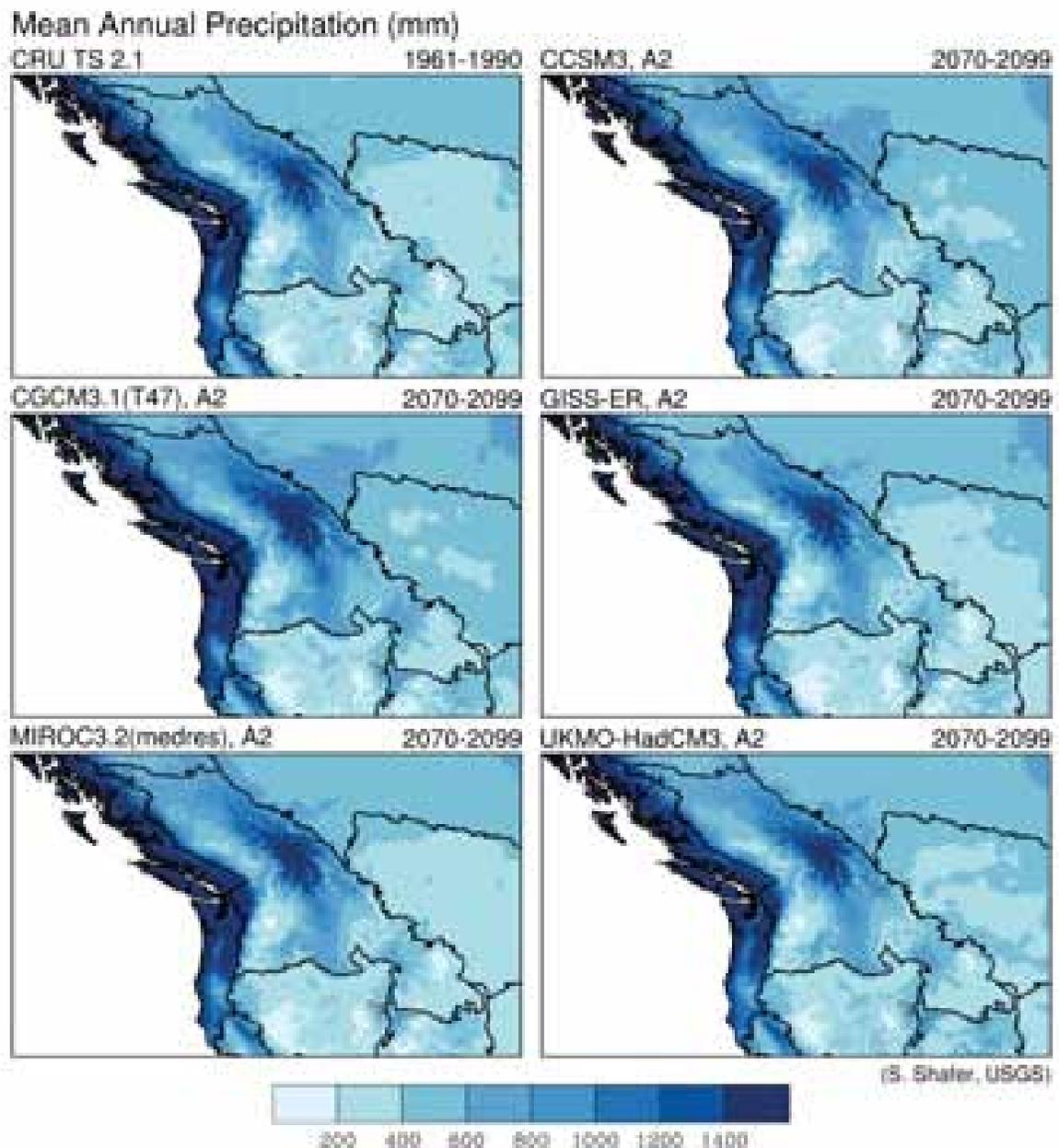
Figure 16—Projected temperatures for two GCMs and one SRES scenario (A2, which is similar to RCP8.5) for the Pacific Northwest to year 2100. Note the extensive warming in the high elevation whitebark pine ecosystems of the Northern Rocky Mountains and Cascades.

Many other changes in climatic factors are related to the increases in temperature and decreases in precipitation. First, the number of frost-free days is predicted to increase substantially, especially in the range of whitebark pine (fig. 18). High elevation areas throughout whitebark pine’s range may experience an increase of over 50 frost-free days a year, a significant increase over historical averages (Littel et al. 2011). The higher temperatures would also result in lower snowpacks throughout the western United States (fig. 19). Mountain snowpacks within the range of whitebark pine are predicted to decrease by 20 to 70 percent with the greatest reductions in the Cascade Range of Washington and Oregon. The earlier snowmelt, coupled with higher temperatures, could result in less soil water during the growing season in some parts of whitebark pine’s range, but the already high precipitation amounts in the

upper subalpine forests of the Pacific Northwest will ensure plenty of water throughout the year (fig. 20). Many GCMs actually predict increases in soil water for some high mountain areas. Climate trends are summarized in table 1.

3.1.3 Understanding Species Response to Climate Change

In general, there are four techniques used to assess effects of climate change on vegetation and any other resource concern. The first is *expert opinion*; this involves having experts in the fields of climate change, ecology, and vegetation dynamics qualitatively judge what will happen to vegetation under various climate change scenarios. The majority of papers about climate change impacts on vegetation were written by experts who have evaluated future climate projections and used their valuable



CRU TS 2.1 (Mitchell and Jones 2005), CCSM3 (Collins et al. 2006), CGCM3.1(T47) (Scirocco et al. 2006), GISS-ER (Schmidt et al. 2006), MIROC3.2(medres) (K-1 Developers 2004), UKMO-HadCM3 (Gordon et al. 2000), LCC regions (USFWS 2010)

Figure 17—Projected precipitation (mm) for two GCMs and one SRES scenario (A2, which is similar to RCP8.5) for the Pacific Northwest to year 2100. Note the relative little change in precipitation across the range of whitebark pine.

experience to deduce how vegetation would respond to different climates.

The second technique is *field assessment*, where extensive field sampling or remote sensing projects monitor vegetation change as the climate warms. This empirical technique involves establishing plots in networks across the landscape and detecting change

between plot measurements and correlating those changes to climate data. Demography studies track individual plants over time, rather than use periodic plot-level inventories, to fully understand the role of climate relative to other risk factors such as competition, variation in physiology and function, and vulnerability to insects and pathogens.

Projected Changes in Frost-Free Season Length

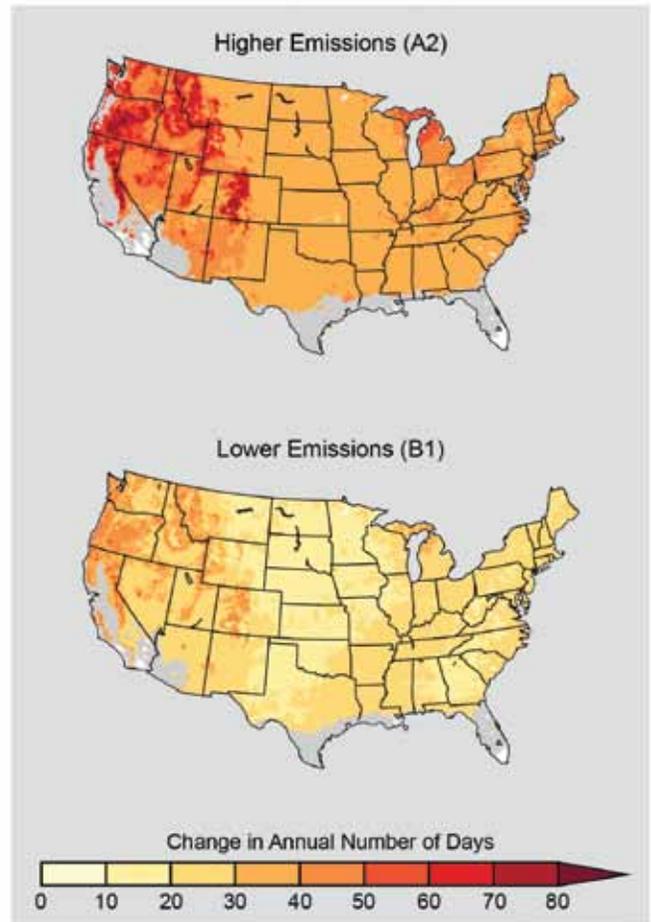


Figure 18—Projected changes in the number of frost-free days for the contiguous United States for the A2 and B1 scenario at year 2100. Percent increase (red) indicates that growing seasons in many high elevation areas in the western United States will increase by at least 40 days (source NOAA National Climate Data Center). The A2 scenario is most similar to the RCP8.5 scenario.

Percent Change in Average Annual Snowfall (Future vs. Present)

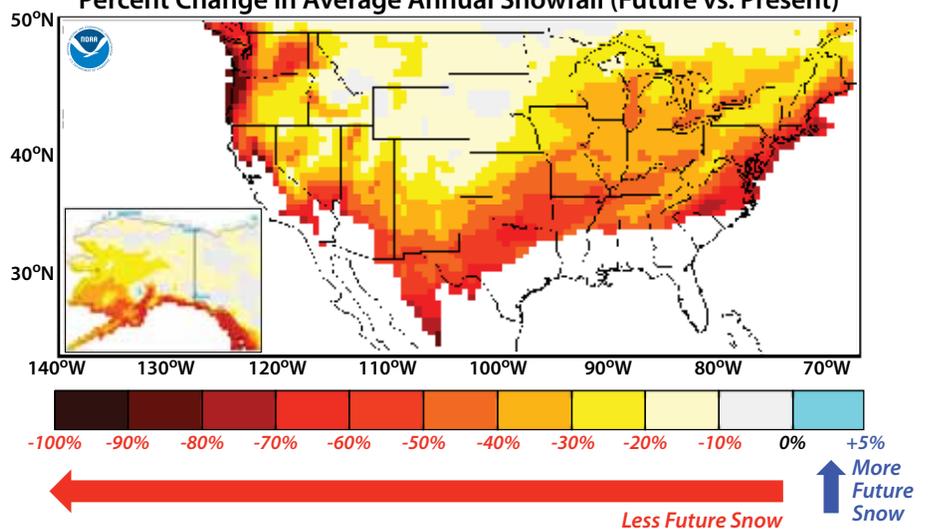


Figure 19—Projected changes in annual snowfall for the contiguous United States for the A2 (close to RCP8.5) scenario at year 2100. Percent increase (blue) and decrease (red) indicate that snowpacks are predicted to decrease in whitebark pine's range although there is a great deal of variability from 10 percent in central Montana to over 70 percent in the Cascades (Source: NOAA National Climate Data Center).

Projected Changes in Soil Moisture for the Western U.S.

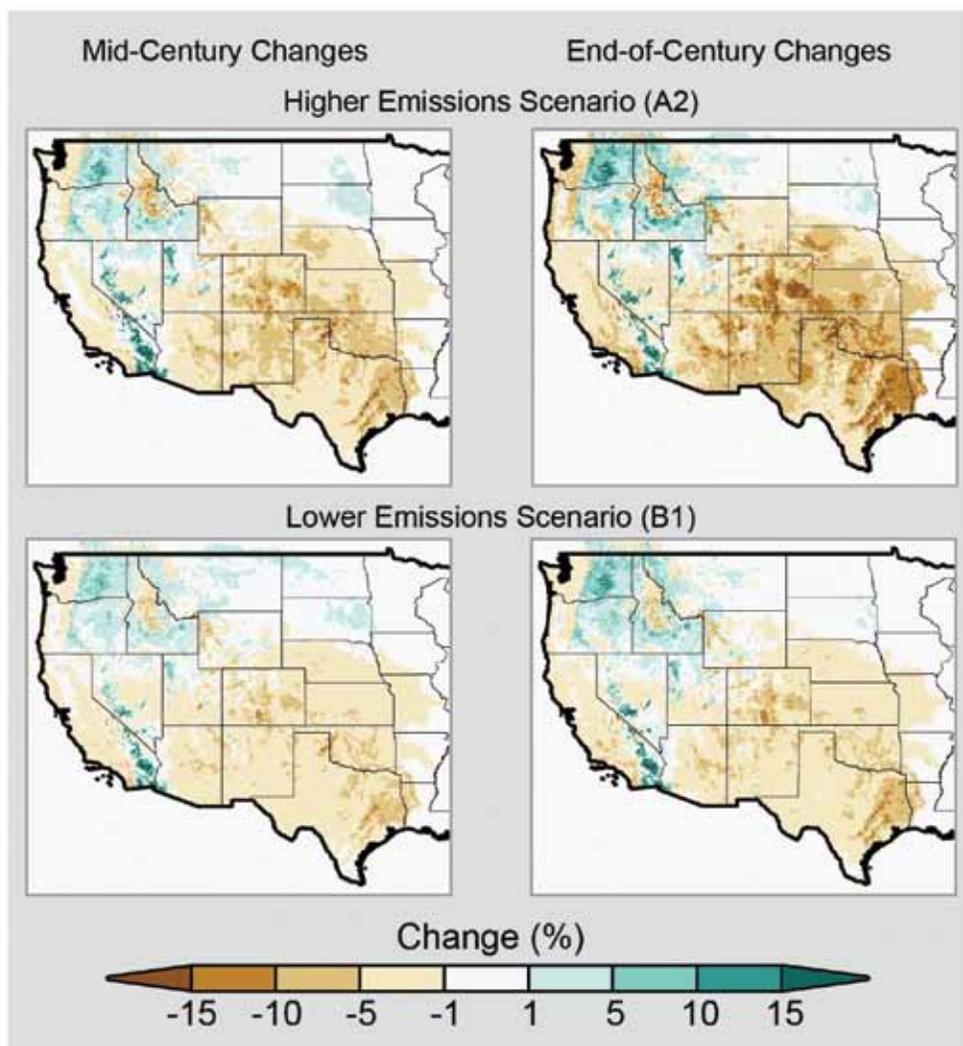


Figure 20—Projected changes in soil moisture for the A2 and B1 scenarios at 2050 and 2100. Percent increase (blue) and decrease (red) are shown for the western United States. Note that most high elevation areas in the range of whitebark pine will experience greater soil moisture (Solomon et al. 2007).

One demographic study in the southeastern United States tracked more than 27,000 individuals of 40 species for about a decade to address climate-vegetation interactions (Clark et al. 2011). Although this field technique is the most reliable and most useful, it is often intractable because of the large areas and long time periods needed to sample vegetation at the appropriate scales to detect or anticipate changes as a result of climate.

The third method involves the use of advanced *statistical analysis* to create empirical models that predict climate change response. Most of the studies that predict the demise of whitebark pine from climate warming use Bioclimatic Envelope Models (BEMs) to project future geographical ranges (Chang et al. 2014; Crookston et al. 2010; Hansen and Phillips 2015;

McDermid and Smith 2008; Rehfeldt et al. 2012; Warwell et al. 2007) (fig. 21). BEMs, also called species distributional models, niche models, or species envelope models, are developed by associating current climate conditions to the current distribution of a species of interest by means of advanced statistical modeling. Climate variables are correlated to species presence as determined from field data using statistical models to predict probabilities of species occurrence. Future species distributions are then computed using the projected future climate data, such as CMIP or downscaled GCM data, as inputs to the statistical model. A major BEM assumption is that current distribution of a species adequately defines the entire bioclimatic niche of that species. The presence data used to create BEMs, however, often represent

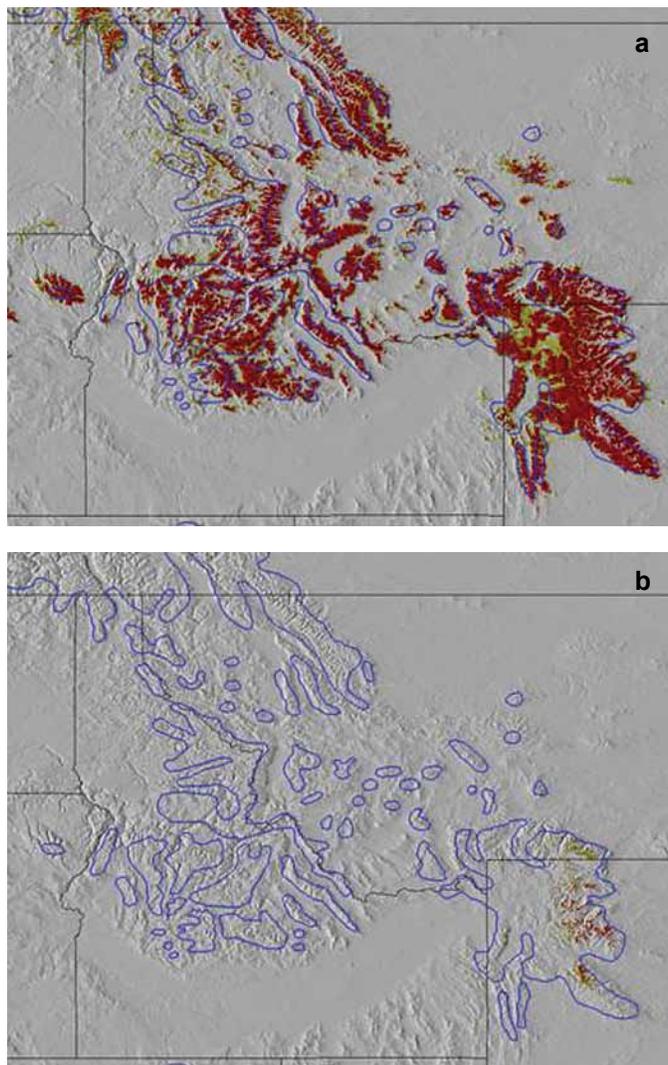


Figure 21—The decline in the range of whitebark pine over the next 80 years as predicted from a bioclimatic species envelope (BEM) modeling approach for the A2 (hot, dry) climate scenario (Warwell et al. 2007). Part (a) shows whitebark pine distribution modeled from NOAA weather station data and (b) shows whitebark pine distribution at year 2090 under the A2 (similar to the RCP8.5) climate scenario. Red indicates areas where the statistical model predicts occurrence with greater certainty, these are the areas that the model predicts the species will most likely occur.

current species habitat and not the actual spatial distribution of a species. Most field data do not recognize all places where the species is missing but could still exist. This is the major limitation in BEM modeling. Whitebark pine can be missing from many areas for any number of reasons, including disturbance effects, dispersal limitations, and land-use activities; therefore, BEM projections may underestimate future whitebark pine distributions.

There are other problems with the BEM approach that warrant discussion so results from literature search presented in this report can be put in the right context. First and most importantly, many critical life cycle processes, such as cone production and pollination, nutcracker-mediated seed dispersal, seed germination, seedling establishment, tree growth, mycorrhizae associations, competitive interactions, phenology, and mortality are not represented or included in BEMs; only climate and species occurrence are considered. Dullinger et al. (2012), for example, found that range shifts predicted by BEMs retracted by over 40 percent when seed dispersal was included in the prediction process. Another limitation is that many studies have now found that most species distributions are *not* in equilibrium with climate, thereby causing BEMs to miss those areas that are conducive for the species, but where the species is currently absent because it hasn't migrated there yet. Moritz and Agudo (2013), for example, found that many species in the fossil record existed over a wider range of climates than is recorded today. BEMs assume that the current distribution of the species is a consequence of climate alone, yet we know that many other factors, such as fire exclusion, exotic diseases, and management actions have reduced whitebark pine occurrence so much so that the current distribution of whitebark pine is greatly contracted over historical conditions (Tomback et al. 2001a).

There are also scale problems in BEM analyses. The data used to represent climates in BEM model development represent a small slice of time (50 to 100 years) relative to the long time periods that living trees, especially the long-lived whitebark pine (>1000 years of age), have survived. Thus, these limited climate data sets rarely capture the full range of climate experienced by existing trees sampled in the field data. Along these same lines, BEM-projected changes in species habitat are uncorrelated to actual rates of change in future species distributions; the long-lived whitebark pine can certainly live longer than the 100-year projections of habitat declines. Climate data are often summarized as monthly or annual averages to simplify their correlation to species occurrence, yet we know that many climate impacts on species distributions result from short-term (daily)

weather phenomena, such as early frosts. Current and projected climate data are too coarse spatially to adequately represent those local conditions that may impact species distribution, such as frost pockets, cold air drainages, microsites, and topographic shading (Pypker et al. 2007).

Some BEM efforts recognize species occurrence in the field data by setting a threshold level below which the species is considered absent. For example, whitebark pine is present on a field plot when it exceeds a minimum basal area or canopy cover requirement. These thresholds may be high (e.g., >10 percent cover), thereby excluding areas where the species currently exists at low levels but could potentially support greater abundances of the species. Moreover, the sampling and analysis methods used to estimate species characteristics to compare against thresholds are sometimes too coarse to detect the presence of a species, especially if the species occurs as scattered regeneration. Whitebark pine is often found as seedlings and saplings at low levels throughout the landscape due to widely dispersed nutcracker seed caching (Arno and Hoff 1990), yet these small and rare individuals are often missed by common sampling protocols. These limitations make it difficult to have any confidence in BEM projections; they are informative, but not prognostic, especially on short time scales of decades and half-centuries required by land management and at spatial scales of project implementation.

The last and most rigorous approach uses *simulation modeling* to assess climate-mediated vegetation responses (Keane et al. 2015; McKenzie et al. 2014). Future projections of climate from GCMs are input into simple to complex ecological models to simulate climate change effects on whitebark pine. Spatially explicit models that simulate the major biophysical processes that control ecosystem dynamics are important tools for exploring climate change effects on vegetation under possible future climates. A variety of existing models simulate ecological change at broad (global, regional) and fine (point, ecosystem, stand) scales (Keane et al. 2015). However, landscape scale models simulating areas of 100 to 250 km² are perhaps the most critical for predicting climate change effects because a landscape scale is where many ecosystem processes and linkages are manifest and

the scale at which most management decisions are made (Cushman et al. 2007; Littell et al. 2011). Finer-scale stand models (0 to 1 km²) cannot incorporate important exogenous disturbance regimes because of their limited spatial extent. Coarse-scale models (1,000 km² to global) are unable to simulate important plant-, species- and canopy-level competition and disturbance effects, such as successional shifts, community dynamics, and differential disturbance effects among species (McKenzie et al. 2014).

To be effective at realistically predicting climate change effects, models must simulate disturbances, vegetation, and climate as well as their interactions across fine multiple scales. For whitebark pine, we believe the processes identified in figure 22 should be included at a minimum. Yet few models simulate ecosystem processes with the mechanistic detail needed to realistically represent important interactions among landscape processes, vegetation dynamics, disturbance regimes, and climate. Direct interactions between climate and vegetation, for example, may be more realistically represented by simulating daily carbon (photosynthesis, respiration), water (evapotranspiration), and nutrient (nitrogen, phosphorous) dynamics at the plant level rather than by simulating annual vegetation development using state-and-transition modeling approaches (Keane et al. 2015). Moreover, few GCMs project climate at scales useful for landscape models.

3.2 Species Responses

There are three modes of response of a tree species to climate change. A species can (1) change in productivity and health in situ or within its current range; (2) become extirpated from its current range due to adverse environmental conditions; or (3) migrate into new areas that were not part of its historical range (Aitken et al. 2008). Tree species range limits, both in the past and into the future, are highly dynamic because of high climate variability. Any assessment of climate change impacts on species range expansion and contraction demands a long temporal evaluation (Aitken et al. 2008), which makes evaluating BEM results difficult. But overall, these three modes may provide the foundation for evaluating whitebark pine

response to climate change. Predicting the future of whitebark pine in western North America is a great deal more difficult than some have theorized because of the complex interactions of whitebark pine with all the other ecological processes that form the ecosystem (see fig. 22).

Predicted increases in productivity for upper subalpine areas throughout the range of whitebark pine may allow whitebark pine to remain in some of its current geographical range (Aston 2010; Chhin 2008). Whitebark pine may experience gains in diameter growth, cone production, bumper cone crop frequencies, and leaf area under the predicted climate. Recent ecological simulation modeling efforts have shown that whitebark pine growth will increase in the future (Loehman et al. 2011b). Lenihan et al. (2003) predicted increases in productivity in upper subalpine whitebark pine forests and expansion of this forest into the alpine areas of California. Whitebark pine also shows promise for being maintained in situ in the Northern Rockies because of high levels of genetic diversity (Mahalovich and Hipkins 2011; Mahalovich et al. 2006; Richardson et al. 2002a); moderate to high heritabilities of key adaptive traits; demonstrated blister rust resistance (Hoff et al. 1980; Mahalovich et al. 2006; Sneizko et al. 2007); minimal inbreeding (Bower and Aitken 2007; Mahalovich and Hipkins 2011); and generalist adaptive strategies (Mahalovich, in prep.).

A preponderance of the studies contends that whitebark pine’s range will decrease in the future because of increasing temperatures, but most of these studies were conducted using BEMs (McKenney et al. 2007; Hamann and Wang 2006). Most qualitative, expert opinion synthesis papers speculate that climate change could “push” whitebark pine off the top of the mountain by moving its lower elevational limits above the height of the tallest peaks (Bartlein et al. 1997; Schrag et al. 2007). Other statistical modeling studies, similar to Warwell et al. (2007) presented in figure 21, support this hypothesis by showing dramatic decreases in whitebark pine suitable habitat over the next 80 years (Chang et al. 2014; Crookston et al. 2010; Funk and Saunders 2014; McDermid and Smith 2008; Rehfeldt et al. 2012). McKenzie et al. (2003) predict major range retractions of whitebark pine in the Pacific Northwest, as do Nitschke and Innes (2008). Forecasts of severe droughts at the lower elevational limits of whitebark pine’s range (see Section 3.1.2) may create inhospitable conditions for regeneration. The projected increase in productivity of all species in the upper subalpine forests may also foster more intense competition and accelerate succession of shade tolerant tree species associated with whitebark pine. Also, lower elevational species, such as lodgepole pine and Douglas-fir, might invade the lower portions of the upper subalpine forest zone and outcompete whitebark pine.

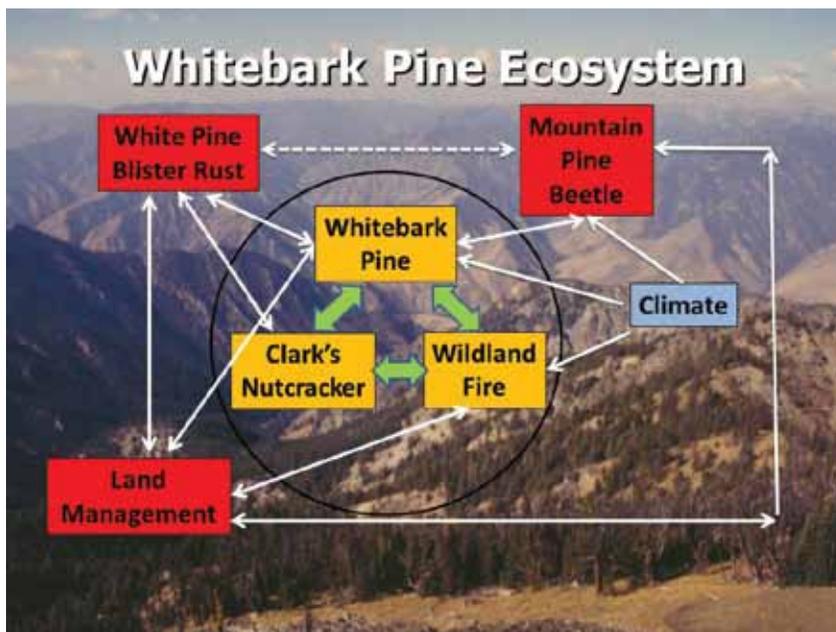


Figure 22—The important interactions and feedbacks in the whitebark pine ecosystem to consider when evaluating climate change effects on whitebark pine ecosystems. The yellow boxes in the black circle indicate the three critical elements of the whitebark pine ecosystem: the species, wildland fire, and the bird. The red boxes indicate the important disturbance processes that impact whitebark pine dynamics: the mountain pine beetle, white pine blister rust, and humans. Climate is in the blue. The dotted line indicates a minor impact. Less significant interactions are not shown.

Evidence of warmer climates in paleoecological records indicates that whitebark pine was maintained and sometimes increased in some places under past warmer and drier climates in some parts of its range (Iglesias et al. 2015; Krause et al. 2015; Whitlock and Bartlein 1993). Whitebark pine can grow within a broad upper elevation zone in western North America but it is a poor competitor; it grows best on those sites that are inhospitable to other tree species. In fact, Arno et al. (1993) found that whitebark pine's elevational range extended more than 500 feet below the current lower elevational limits of whitebark pine in the Bitterroot Mountains of Montana, USA, prior to the modern fire exclusion era (circa 1910). Whitebark pine occupies the largest latitudinal range of any five-needled white pine in the western United States and Canada, indicating some tolerance to a wide range of climates (Tomback and Achuff 2010).

There is other evidence that whitebark pine may continue to inhabit high mountain landscapes in warming climates. Anecdotal evidence shows that some whitebark pine forests are experiencing abnormally high growth rates and more frequent cone crops due to warmer summers and longer growing seasons. Loehman et al. (2011a,b) used a mechanistic landscape model to simulate higher productivities in whitebark pine in the future, but the species continued to decline, not from warming climates, but from WPBR, especially when wildland fire was not allowed to burn. Moreover, WPBR screening trials and other common garden (genecology) studies indicate whitebark pine has both the adaptive capacity and phenotypic plasticity to favorably respond to climate change (Mahalovich, in prep.). The notion that whitebark pine will stop growing and reproducing at high elevations under future climates is mostly unsubstantiated. It is entirely possible that as long as wildland fire creates areas where birds can cache seeds and seedlings can grow without competition, whitebark pine will continue to thrive throughout its range. This is supported for some of the region-based scenarios using computer modeling (Loehman et al. 2011b).

Climate change can impact each phase of the life cycle processes of a species including reproduction, regeneration, growth, and mortality. The following subsections are summaries from the literature about

possible climate change effects on whitebark pine by life cycle processes.

3.2.2 Regeneration

Regeneration is probably the life cycle phase most susceptible to shifts in climate (Solomon and West 1993). Microsite conditions needed for successful regeneration may be so demanding that seed germination is rarely successful. Bunn et al. (2003) emphasized the importance of accounting for microsite variability in assessing climate change response; high elevation microsite climate amelioration, coupled with increased fire activity, could increase whitebark pine regeneration and growth as climates change. High snow depth and long duration snow cover often govern high elevation tree regeneration. Most years are moist enough for regeneration but snow may remain on the site for a long time thereby limiting the number of days that a seedling can actually photosynthesize and grow. Warm years in the upper subalpine often result in waves of regeneration and can be dated from seedling and sapling ages (Little et al. 1994). With projected temperature increases, earlier snow melt might give more time for seedlings to grow. Recent observations of invasions of subalpine meadows and open, sparsely vegetated areas (balds) by subalpine fir, alpine larch, and spruce are a result of a string of warm years with low snowpack over the last decade that have facilitated high mountain regeneration (Dullinger et al. 2004). Moreover, there is often abundant precipitation in upper subalpine settings and future projections indicate roughly the same; therefore, future seedling mortality from drought might be minimal.

Future climates and their high variability may affect the ability of the cached and forgotten whitebark pine seeds to germinate. Seed chilling requirements may not be met during mild winters (Arno and Hoff 1990) thereby reducing germination. Germination may also be delayed to the driest parts of the growing season resulting in higher seedling mortality (McCaughey 1993; Tomback et al. 2001c). Because of longer growing seasons and increased warming, soil temperatures may be too high, especially for the critical initial post-germination growth stages, causing greater mortality to both germinants and

also to established seedlings (Rocheffort et al. 1994). Conversely, longer growing seasons may result in more effective establishment of whitebark pine seedlings through additional root growth which can stabilize seedlings against high snow loads or allow the seedlings access to more water (Keane and Parsons 2010a), thereby mitigating the negative consequences of drought. And most importantly, the projected longer, drier, and warmer growing seasons may have such high variability that infrequent hot, dry years may kill young seedlings, especially on southern slopes in lower elevation settings.

Climate change can also affect dispersal of seeds, especially those of competing tree species. Stronger winds (Gedalof et al. 2005) coupled with longer growing seasons may result in longer and more successful seed dispersal over a longer period of time for whitebark pine's competitors. However, since whitebark pine's seed are dispersed great distances by the Clark's nutcracker (see Section 3.5) and wildland fire size is predicted to increase in the future (see Section 3.4.1), whitebark pine might have a competitive advantage over other tree species in that it will be able to populate new habitats before the wind-blown seeds of its competitors arrive in these areas (Tomback et al. 1990). Longer summers and autumns might also mean that seed dispersal takes place when the ground and litter are the warmest and driest, which may adversely affect seed germination and establishment of competing tree species (Neilson et al. 2005). Changes in spatial heterogeneity due to shifts in disturbance regimes may also influence bird-mediated dispersal by shifting potential seed sources and changing patch size that might affect nutcracker behavior.

3.2.1 Reproduction

Whitebark pine cone and seed crops could be both adversely and beneficially affected by climate change. In high elevation, historically cold environments, increasing temperatures may lengthen growing seasons and thereby increase the potential for more frequent and more abundant cone crops with greater numbers of seed. Thus, decreases in species abundance and associated cone production may be offset by climate-driven increases in cone crops. Alternatively, lodgepole pine, subalpine fir, and spruce might also

experience increased seed production and thereby heighten competition with whitebark pine.

Climate change and its variation may also affect the phenology of cone crops, but impacts may be minimal. Some predict higher frost mortality of emerging cones due to earlier onset of the growing season coupled with high daily temperature variability (Chmura et al. 2011). Others suggest that cone crops will be reduced in both magnitude and frequency in the future because of the high drought stress (Mutke et al. 2005). Because whitebark pine is both drought tolerant and cold tolerant (Bower and Aitken 2007; Mahalovich et al. 2006), changes in climate variability and timing may have a minimal impact on species cone production and reproduction. Reduced tree density due to mortality from MPB, WPBR, wildland fire, and stand isolation is more likely to reduce seed cone abundance and have an impact on future cone crops than climate (Rapp et al. 2013). Pease and Mattson (1999) characterized high mast years as those with more than 20 cones per tree. McKinney et al. (2009) report that a threshold of 900 cones ha⁻¹ is needed to ensure seed dispersal by Clark's nutcrackers. This threshold equates to 25 to 50 cone-bearing trees per ha (or 20 to 50 cone-bearing trees ha⁻¹). For an effective pollination cloud to provide adequate pollination of receptive ovules, a minimum of 25 reproductively mature *Pinus* spp. per ha are required (Mahalovich 2013). Furthermore, for wind-pollinated conifers, 50 to 125 reproductively mature trees per ha ensure a genetically diverse cone crop with minimal consequences of inbreeding depression.

3.2.3 Growth and Mortality

Climate can adversely impact growth and mortality of whitebark pine in a number of ways (Bugmann and Cramer 1998; Keane et al. 2001d). Projected decreases in water availability may result in more droughty sites. Longer periods of drought might cause whitebark pine to close their stomata more often and for longer times resulting in slow growth. The projected increased temperatures will increase both maintenance and growth respiration, especially during periods when stomata are closed, thereby requiring additional photosynthetic gains to counterbalance respirational losses that will require even more water

in the future. If photosynthesis doesn't exceed respirational demands, then the plant becomes stressed thereby increasing direct mortality and its susceptibility to insect and disease attacks. Moreover, Aitken et al. (2008) note that the genetically controlled timing of the growth flush may be out of synchrony with the new environment, because it is occurring in drier parts of the season.

Projected warmer upper subalpine climates may have a positive impact by increasing whitebark pine diameter growth in established trees and decreasing mortality, especially in those mesic seral whitebark pine forests. Wu et al. (2011) found increases in plant growth for many forest and rangeland ecosystems worldwide. Earlier growing seasons with sufficient moisture, such as that predicted for the upper subalpine forests, would result in increased productivity and greater growth. This is especially true for the widespread higher mountain areas where cold, not moisture, limits tree growth. Longer, warmer growing seasons may result in higher vegetative productivities and greater biomass, especially considering the high amounts of precipitation that currently fall in upper subalpine forests. The abundant moisture may enable longer periods of tree growth at high elevations. Higher biomass could result in increased canopy bulk density and therefore, higher crown fire potential and more intense, severe fires and, possibly, more intense insect and disease outbreaks. More importantly, the higher amounts of biomass may increase cone crop abundance and frequency (Ibanez et al. 2007; LaDeau and Clark 2001). This increased production, however, may also heighten competitive interactions between whitebark pine and its associated species thereby favoring the more shade-tolerant individuals in the absence of disturbance.

Increased atmospheric carbon dioxide and greenhouse gas levels may also modify basic eco-physiological growth processes. Oxygen and carbon dioxide compete for active RuBisCo (the primary enzyme used in photosynthesis) binding sites, particularly under high temperatures. Higher atmospheric CO₂ concentrations increases internal leaf CO₂ concentrations via diffusion, thereby favoring CO₂ attachment to RuBisCo sites. This results in photosynthetic increases of 2 to 250 percent, depending on

the site and species. Increased water use efficiency for conifers in water-limited environments might compensate for decreases in water availability and might increase growth rates in water-rich environments. Water use efficiency is the ratio of water used for plant metabolism (photosynthesis and respiration) to the water lost to transpiration. With higher CO₂ concentrations in the atmosphere, the plant would obtain more CO₂ during the time the stomata are open resulting in lower transpiration losses. Whitebark pine may have the plasticity to adapt to low water conditions by decreasing transpiration through other avenues. However, this is totally dependent on many other ecological conditions such as nitrogen, soil nutrients, water, and light availability.

Whitebark pine diameter and height growth may be directly enhanced by the elevated CO₂ levels in the atmosphere (Chmura et al. 2011). Physiological adaptations allow the plant to utilize more CO₂ in photosynthesis because of higher atmospheric concentrations, and this increased photosynthesis might increase plant biomass. Leaf biomass is usually the first to increase as plants attempt to optimize photosynthesis by growing more photosynthetically active foliage (i.e., more leaf area). Increases in leaf biomass often lead to increases in leaf area, usually measured as leaf area index (ratio of leaf area to projected ground area), but these increases are often transient and greatly dependent on available nitrogen. Increases in leaf area index would likely result in greater rainfall interception, higher snow collection, greater canopy evaporation, and shadier forest floors, which might increase forest soil aridity. Elevated CO₂ levels may also change root:shoot ratios, with more aboveground biomass and fewer roots due to higher levels of photosynthesis and water use efficiency. Increased CO₂ levels and increasing temperatures may also interact to increase growth. The temperature optima for photosynthesis differs by tree species, and those temperature optima may change under new atmospheric CO₂ levels. Warmer temperatures might be closer to the new temperature optima, especially during the cooler early growing season, resulting in higher growth. In summary, because most whitebark pine occurs in cool to cold environs that rarely experience moisture deficits, growth rates of whitebark

pine in most areas may increase as a result of higher carbon dioxide levels and longer growing seasons.

3.3 Community Response

As climates warm, less hardy but more shade-tolerant conifer species may be able to establish in those higher-elevation stands where whitebark pine currently is dominant (Hansen and Phillips 2015; Koteen 1999; Romme and Turner 1991; Schrag et al. 2007). Succession toward fir, spruce, and mountain hemlock may accelerate on seral whitebark pine sites and initiate on climax whitebark pine sites. Many of whitebark pine's shade tolerant associates can grow faster in height than whitebark pine with increasing productivity (Arno and Hoff 1990). Conifers invading from lower elevation forests, in addition to the shade-tolerant conifers already present, could out-compete whitebark pine and shift the upper subalpine areas to a more spruce and fir-dominated community composition. Moreover, as growth rates increase, the rate of succession may also increase, accelerating the shift from whitebark pine to more shade-tolerant species (Aston 2010). Because of intense competition, whitebark pine is often relegated to those high elevation sites where it is the only tree adapted to the harsh conditions at and below timberline (Koteen 1999). This scenario of heightened competition assumes that wildland fire is minimal across the range of whitebark pine.

It is also possible that some seral whitebark pine sites, such as south-facing aspects in the upper subalpine zones, may experience longer and more frequent soil water deficits throughout the summer, especially in drought years. Whitebark pine appears to have a greater ability to survive and prosper through periods of low available soil moisture than nearly all of its competitors, especially during the critical establishment phases (Arno and Hoff 1990; Callaway et al. 1998). Therefore, it may be that whitebark pine is able to maintain dominance on these sites providing low WPBR and MPB activity. In fact, Coops and Waring (2011) predict whitebark pine will expand in range under future climates in some areas, especially into the lower treeline.

3.4 Disturbance Changes

Climate-induced changes in disturbance regimes may overwhelm most direct vegetation responses to climate change (Dale et al. 2001). Most landscape and ecosystem shifts caused by global climate change will probably be facilitated by major modifications in disturbance regimes (Gardner et al. 1996; Swetnam and Betancourt 1998). Some of these shifts may have already been observed in some whitebark pine ecosystems (Larson et al. 2010; Millar et al. 2012). Recent MPB outbreaks are killing whitebark pine trees at rates greater than previously documented in the historical records (Raffa et al. 2008). These unprecedented outbreaks are probably a result of warmer winter temperatures that facilitate expansion and establishment of beetle populations in the higher-elevation whitebark pine zone (Logan and Powell, 2001; Logan et al. 2003). A warmer climate may accelerate the spread of blister rust (Koteen 1999; Resler and Tomback 2008) or it could disrupt the complex life cycle and reduce spore production (see Section 2.6.3).

If disturbances are predicted to increase (Flannigan et al. 2008; Logan and Powell 2001), then disturbance adaptations, not species competitive interactions, might determine the future composition and structure of landscapes. Whitebark pine has many adaptations to disturbance that might allow it to remain on the high-elevation landscape, especially in comparison to all of its competitors. Although climate change impacts could be severe for whitebark pine, they are also complex and difficult to predict because of disturbance interactions (Hobbs and Cramer 2008). Therefore, it is important that potential shifts in fire, beetles, and blister rust dynamics caused by changing climates be anticipated and built into the design, approach, and kinds of restoration activities across the range of whitebark pine. Moreover, a unique set of activities might be emphasized in each bioclimatic region, site, or at more local levels such as the stand level. The following sections detail projected changes in the regimes of the three major disturbance agents in whitebark pine forests—wildland fire, MPB, and WPBR.

3.4.1 Wildland Fire

Many climate change studies consistently project that the warmer conditions in the range of whitebark pine will result in large increases in the length of the fire season, annual number of fires, area burned, size, and intensity of wildfires (Flannigan et al. 2009; Krawchuk et al. 2009; Marlon et al. 2009). Some predict as much as 2 to 6 times more fire in the future as a result of climate change (Brown et al. 2004; Running 2006; Westerling et al. 2006) (fig. 23). Loehman et al. (2011b) simulated increases in burned area under the A2 climate that were 2.5 times more than historical averages in a whitebark pine landscape in Glacier National Park. Wildfire frequency in western forests has increased fourfold during the period 1987 to 2003 as compared to 1970 to 1986, while the total area burned increased six-fold (Westerling et al. 2006). Earlier snowmelt dates have been shown to correspond to increased wildfire frequency (Running 2006). Trouet et al. (2006) confirm that increases in area burned are tied to climate conditions. Prolonged dry and hot periods are generally required for large fires (Gedalof et al. 2005) and projected climates will likely make these droughts and resultant wildfires more likely (Keeton et al. 2007).

In most years, whitebark pine forests remain moist for the majority of the fire season, resulting in long fire return intervals (Morgan and Bunting 1990), but the projected warmer climates will probably result in greater drying that may cause earlier and longer fire seasons. Historically moist high elevation areas, which normally act as fire breaks, could become dry enough to carry fire in some years. This means that future fires might be larger because fuels are dry enough to facilitate fire growth across larger areas (i.e., entire landscapes) (Loehman et al. 2011b). Moreover, fire seasons are also predicted to be hotter and drier with deep, prolonged droughts that may carry over to consecutive years. Climate models also predict increased lightning and wind because the increased temperatures add more energy to the atmosphere (Price and Rind 1994; Reeve and Toumi 1999; Romps et al. 2014). The increased temperatures, drought, lightning, and wind, coupled with more fuel due to higher biomass productivity (Section 3.2.3), may also result in more fire starts that

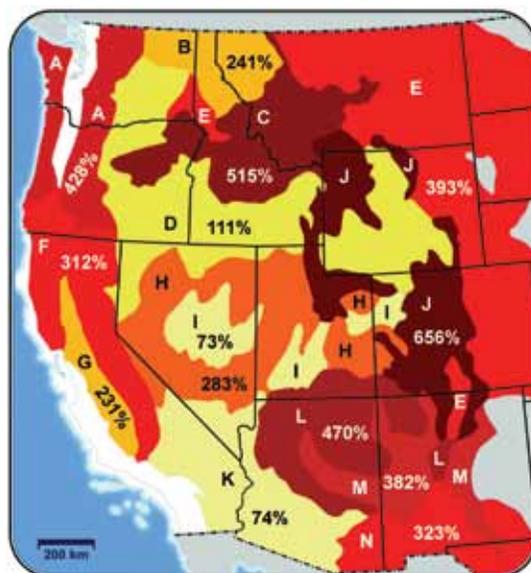


Figure 23—Projected percent increase in burned areas in the West for a 1 °C increase in global average temperatures relative to the median area burned during 1950–2003 (National Research Council 2011). The darker colors indicate the greatest increases in fire with over five-fold more burned areas.

foster more intense fires (Flannigan et al. 2008, 2009). Fires may also be more severe, especially considering that the existing heavy accumulations of canopy and surface fuels, which resulted from successful fire exclusion over the last century, that when burned, may cause atypical postfire mortality in many plants and animals. However, Keane et al. (2008a) mention that fire severities may remain the same because of inherent fire adaptations in the biota, and only fire intensities may increase.

With increased fire frequency and intensity, whitebark pine may have a unique opportunity to maintain, or even increase, its range in the future because of bird-mediated (Clark’s nutcracker) seed dispersal. Nutcrackers can disseminate seeds great distances into large, severe burns well before wind can disperse the seeds of its competitors (Lorenz et al. 2008; Lorenz and Sullivan 2009; Tomback 1978, 1982; Tomback et al. 1990). Whitebark pine seedlings are hardy, tolerant of poor seedbeds, and readily regenerate in large burned areas (Arno and Hoff 1990; McCaughey and Tomback 2001; Tomback et al. 1990, 1995, 2001c). Whitebark pine morphology (deep roots, high crowns, somewhat thick bark) enables it to survive low to moderate severity fires (Ryan and Reinhardt 1988). Therefore,

whitebark pine could be uniquely positioned as a species that may increase under future fire regimes.

A major drawback of more frequent and intense fire on the high elevation landscape is that these fires are also more likely to kill those whitebark pine trees that are resistant to WPBR. These rust-resistant trees are the foundation of the restoration strategy in two ways. They provide rust-resistant seeds for nutcracker caching into burned areas, and the cones are collected to grow rust-resistant whitebark pine seedlings in the nursery for planting in areas lacking seed sources. If these trees are killed by fire, the potential for seed dispersal by nutcrackers is reduced and with this, opportunities to spread genes for rust resistance to succeeding pine generations of whitebark pine.

Increased fire frequency and intensity due to climate change could also reduce wildland fuels by burning more of the landscape and creating firebreaks that may potentially protect rust-resistant whitebark pines from future fire damage. Allowing wildfires to burn, especially in moderate fire weather years, may increase the area subject to lower intensity fire in declining whitebark pine stands. This would reduce fuels and protect those valuable surviving rust-resistant trees against future fires that might occur in severe weather years. Fire in moderate years can reduce fuel in two ways. First, these fires have low intensities that might allow whitebark pine to survive, but may kill the more fire-susceptible subalpine fir and other potential conifer invaders, thereby reducing canopy fuels. This in turn would lower the potential for damaging crown fires (Keane and Parsons 2010a). Low-intensity fires can also creep through high elevation stands and consume surface fuel and reduce severities of future fires (Lasko 1990). Fires that consume surface and canopy fuels may create burned areas that could stop the spread of future fires (Larson et al. 2010).

Future fires might also become so frequent that whitebark pine trees may not be able to grow to a size where the foliage is above lethal scorch heights. As a result, newly established trees may be killed by fire before reaching reproductive maturity. In model simulations, Holsinger et al. (2014) found that future fires were so frequent in a western Montana watershed that lodgepole pine seedlings were killed by fire before they could grow the 15 years needed for cone production.

Whitebark pine trees need especially long intervals between fires in order to remain on the landscape because the species has an older age to reproductive maturity (>60 years) (Arno and Hoff 1990; Holsinger et al. 2014).

Predicted increases in fire size and intensity could also be detrimental to whitebark pine ecosystems in other ways. First, fires may be so frequent and intense that they reduce mycorrhizal populations (see Section 2.3), which may have negative impacts on whitebark pine growth and regeneration (Keane et al. 2012b; Mohatt et al. 2008). Many high elevation species of mycorrhizae respond poorly to fire, especially stand-replacing fires. The absence of whitebark pine trees on the burned site may cause a corresponding decline in mycorrhizae populations that may ultimately result in poor survival of whitebark pine regeneration (Mohatt et al. 2008, Lonergan et al. 2013). Native shrubs, which often share mycorrhizae with whitebark pine, may be reduced so much by frequent fire that their populations will be insufficient for maintaining healthy mycorrhizae communities.

3.4.2 Mountain Pine Beetle (MPB)

Unfortunately, climate-mediated MPB outbreaks have occurred in many areas within whitebark pine's range (Carroll et al. 2003, 2006; Gibson et al. 2008) killing many cone-bearing whitebark pines (Hicke and Logan 2009). Most of these trees might have eventually died from the exotic WPBR, but those trees that would have survived WPBR because they were somewhat rust-resistant may now be targeted by the beetles. Logan et al. (2010) suggest that MPB might be the main driver of future losses in whitebark pine trees, especially in the Greater Yellowstone Area.

Temperature is a major driver of bark beetle population survival and growth (Bentz et al. 1991, 2014; Logan and Powell 2004). Recent warming temperatures, especially daily minima, have resulted in increased overwintering survival of MPB, particularly in forests with historically severe winters (Bentz et al. 2009). Warm temperatures in other parts of the year also play a significant role because they influence timing of adult emergence and generation cycles (Bentz et al. 2014). Slight differences in temperature, even within a single tree or stand, can result in dramatic

differences in MPB generation time. Mountain pine beetles will complete their lifecycles in one year rather than two in warmer climates, and this often leads to increased population growth and associated beetle-caused tree mortality (Safranyik et al. 2010). If adult emergence occurs in early summer, a generation can be completed by the next fall. Completion of a generation over the winter is constrained, however, due to evolved thresholds for development (Bentz et al. 2014). Short-term drought often associated with warm temperatures can create both a pool of weakened host trees and the appropriate thermal conditions for population outbreaks of multiple bark beetle species (Chapman et al. 2012; Hart et al. 2013). The greatest density of pine occurs at 2,000–3,000 m in elevation, and these stands are predicted to have greater univoltine population growth rates than historic, through 2030–2050 (Loehman et al., in press).

One major adverse effect of MPB outbreaks on whitebark pine stand dynamics is that the heavy beetle-caused mortality in overstory whitebark pine may release the shade-tolerant but suppressed understory of subalpine fir and other associated conifer competitors (Amberson 2014). Once released, these trees can rapidly occupy the overstory canopy space vacated by the dying whitebark pine resulting in a swift conversion of whitebark pine forests to fir-spruce forests (Campbell 1998; Keane 2001a). As mentioned, these fir-spruce forests tend to have lower canopy bases and high canopy densities resulting in a dramatic increase in crown fire potential. Moreover, whitebark pine will be unable to regenerate in MPB-killed stands because of intense competition with the fir-spruce component.

3.4.3 White Pine Blister Rust (WPBR)

Direct responses of WPBR to climate change greatly depends on the conditions for dispersal and germination in late summer and early autumn. At this time, basidiospores are released from the telia on the undersides of *Ribes* spp. leaves and travel before landing on five-needle pine needles to germinate. This is a delicate time, because for WPBR to germinate on pine needles and for the hyphae to grow into the stomata, the spores need warm (>10 °C) and moist (>95 percent relative humidity) conditions. Since future climates are predicted to be warmer, there may be

an increased temperature window for spore infection of pines (Mahalovich 2013). However, there is great uncertainty as to whether the high relative humidity needed for spore germination and hyphae growth during the potentially warmer part of late summer and early autumn will occur. Increases in infection due to favorable fall temperatures might be negated by forecast decreases in humidity. This, of course, is all dependent on the ability of all species involved (WPBR, pine, and all alternate hosts) to adjust their phenology to the predicted newer climates.

Fall mesoscale weather events may also accelerate the spread of WPBR by influencing the frequency and length of infection periods or “wave years.” Koteen (1999) suggested that selective weather conditions required for basidiospore germination and infection of pine needles may be longer and more frequent in future climates for upper subalpine forests. Wave years occur when cooler temperatures and higher relative humidity or monsoon-like climatic conditions occur in late summer and early fall. These conditions favor long distance basidiospore transport, while facilitating regional and local rust infection amplification. Kinloch (2003) and Sturrock et al. (2011) speculate that wave years will actually decrease for most pine forests because of projected hotter, drier climates. Helfer (2014) believes that warmer temperatures would negatively impact rusts, where the higher concentrations of atmospheric carbon dioxide could also cause declines in rust populations. He also mentions that the highly variable and extreme weather projected in the future will aid in WPBR spore dispersal resulting in increases in WPBR range and higher spore loads on existing pines.

Indirect WPBR climate change response will be mediated by the host species’ ability to respond to climate change under changing disturbance regimes. Changes in the abundance of whitebark pine and its alternate host species from climate warming in the upper subalpine areas will surely change WPBR dynamics (Koteen 1999). White pine blister rust infection will certainly continue to increase in the new disturbance regimes that favor the alternate hosts and other five-needle pines, such as *Pinus monticola* and *P. flexilis*, to complete its life cycle. It may be that future climates will increase vigor of whitebark pine’s

shade-tolerant competitors, in which case, increases in competition might stress the hosts and increase WPBR infection. Rust infection and mortality appear to occur regardless of tree condition and vigor. Thus it is doubtful that any direct responses of the tree or alternate hosts to future climates, such as increased growth due to a longer growing season, will enhance or reduce the ability of whitebark pine to ward off infections (Hoff et al. 2001; Smith and Hoffman 2001).

Climate-mediated changes in host regeneration dynamics, however, could restrict or expand host ranges, which could also affect the range of WPBR (Helfer 2014). Higher leaf biomass for the pine and host species under warmer, enriched CO₂ environments (see Section 3.2.3) means greater spore germination surfaces and a higher chance for rust infection on both pine and hosts. High elevation areas may experience warming temperatures along with continued high precipitation that may facilitate the expansion of the alternate hosts into areas that were historically too cold and snowy. Conversely, low elevation areas where *Ribes* spp. are currently abundant might experience more drought. This might cause a decline in their abundance and a decline in premature leaf fall in July, thereby disrupting completion of the rust cycle (Mahalovich 2013; Zambino 2010). Moreover, increased drought may cause extended and extensive stomatal closure in the pines, which would prevent hyphae entry. The shifting mosaics of the alternate hosts into new, higher elevation mesic areas are driven by drought in lower elevations and may result in the spread of WPBR into areas where it currently has not been detected.

3.4.4 Interactive Effects

While climate is a key driver of wildland fire, MPB, and WPBR dynamics, the impact of climate change on whitebark pine forests will most likely result from the interactions of these disturbances on high mountain landscapes (Hicke et al. 2012; Jenkins et al. 2012; Loehman et al. 2016; Mahalovich 2013) (fig. 22). Most of the research exploring these interactions has primarily focused on the potential for increased fire hazard following MPB and WPBR outbreaks (see Hicke et al. 2012 for a summary). Acting independently or interacting synchronously in space

and time, wildland fires, MPB outbreaks, and WPBR epidemics can substantially influence forest structure, composition, and function, abruptly reorganize landscapes, and alter biogeochemical processes such as carbon cycling, water supply, and nutrient cycles (Edburg et al. 2012; Falk 2013; Fettig et al. 2007; Hansen 2014; Kurz et al. 2008).

3.4.4.1 Fire and Beetles

MPB can often be found in pine trees damaged by fire (Davis et al. 2012; Geiszler et al. 1984; McHugh et al. 2003; Schwilk et al. 2006; Six and Skov 2009). However, MPB may make only minor contributions to postfire tree mortality (Geiszler et al. 1984; Jenkins et al. 2014; Powell et al. 2012). This mortality is usually limited to the immediate vicinity of the fire (Ryan and Amman 1996). Although fires rarely initiate MPB outbreaks (Mitchell and Sartwell 1974; Powell et al. 2012), they may maintain local MPB populations (Davis et al. 2012; Elkin and Reid 2004; Powell et al. 2012). Fire effects on MPB populations are time-dependent; fire-weakened trees, for example, are colonized by MPB only when the fires occurred when beetles were searching for new host trees (Parker et al. 2006). Although MPB often reproduce in fire-damaged trees, this lasts only a few months or years after a fire (Davis et al. 2012; Powell et al. 2012). Wildland fires can affect MPB activity indirectly over longer time periods by altering species composition and forest structure (e.g., removing fire intolerant species) and providing increased water, light, and nutrients to surviving trees, thus improving vigor of suitable host trees (Fettig et al. 2007; Hessburg et al. 2005; Keeling and Sala 2012). Stand-replacing fires reduce the likelihood of MBP attack until regenerating forests have attained a sufficient size to attract beetles, especially when beetle populations are relatively low (Kulakowski et al. 2012).

Mountain pine beetle activity influences wildland fire by altering the quantity, type, vertical and horizontal arrangement, and chemical and moisture properties of dead and live biomass (fuel) (Hicke et al. 2012). In the endemic phase, MPBs are restricted to stressed or damaged trees, so there is little influence on fuels and subsequent fire behavior as few trees are affected (Page and Jenkins 2007). In the epidemic and post-epidemic phases, in which large beetle populations attack and

kill as many as 80–95 percent of susceptible host trees within stands, fine surface and canopy fuels change in a variety of ways (Hicke et al. 2012). One to 3 years after the initial attack, needles of attacked trees are yellowing or red, but still attached to branches. These needles have lower foliar moisture contents, contributing to higher flammability and torching potential than green trees. Because aerial fuel continuity is maintained, active crown fire potential is high (Jenkins et al. 2014; Page et al. 2012). Four to 10 years after an attack, standing dead trees have lost their needles and small branches, active crown fire potential is lower than in non-attacked stands, but increased fine surface fuel loads result in higher surface fire rates of spread, flame lengths, and torching potential (Hicke et al. 2012; Schoennagel et al. 2012). The highest fire hazard is assumed to occur in the post-epidemic phase, decades after attack, as a result of high snag fall contributing to the accumulation of heavy, large-diameter fuels. These stands also have increased shrub, herb, and tree regeneration biomass, and the loss of forest canopy contributes to increased wind speeds and radiation, thereby drying fuels more rapidly (Jenkins et al. 2008).

3.4.4.2 Fire and WPBR

Severe fires that kill rust-resistant pine trees may ensure continued high WPBR mortality in the future because there will be fewer resistant whitebark pine for natural selection to increase the frequency of rust-resistant genes in the subsequent progeny (Keane et al. 2012b). However, where rust-resistant five-needle pines survive fire, they can provide the seeds for populating future landscapes consisting of whitebark pine trees that are resilient to both WPBR infection and fire mortality (Keane et al. 2012b). Conversely, other studies have shown that fire exclusion has increased competition stress, weakening pine trees and perhaps facilitating rust infection and mortality (Heward et al. 2013; Parker et al. 2006).

Rust-infected whitebark pine stands may have a greater potential for postfire tree mortality. Trees infected with WPBR are weakened with dead branches and tops, and therefore may be more susceptible to fire-caused damage and mortality (Stephens and Finney 2002). As WPBR kills mature pine trees, dead foliage and wood added to the fuelbed may increase fire

intensity, which in turn may increase tree mortality. White pine blister rust infection results in elimination of the shade-intolerant pine overstory, allowing shade-tolerant competitors, such as subalpine fir, to quickly occupy the openings. This creates substantially different canopy fuel conditions, such as lower canopy base heights, higher canopy bulk densities, and greater canopy cover, which facilitate more frequent and intense crown fires (Keane et al. 2002c; Reinhardt et al. 2010). Shade-tolerant competitors are also more susceptible to fire damage, resulting in higher postfire tree mortality of these species in rust-infected landscapes.

3.4.4.3 MPB and WPBR

Interactions between MPB populations and WPBR are rarely studied. In their endemic phase, MPB populations may weaken five-needle pines and facilitate infection by WPBR, but these interactions are strongly governed by climate and biophysical environment (Bockino 2008; Tomback and Achuff 2010). Mahalovich (2013) outlines some concerns regarding correlated response in whitebark pine, particularly an unfavorable interaction between WPBR infection and MPB incidence levels that have been put forth by Six and Adams (2007), Bockino and Tinker (2012), and Dooley (2012). Host selection ratios developed by Macfarlane et al. (2013) assume that trees with more blister rust infection are prone to MPB attacks. Schwandt and Kegley (2008) found that mountain pine beetle preferred trees infected with blister rust in north Idaho when beetle populations were low; however, during outbreaks, beetles preferentially attacked trees with little or no WPBR. Dooley (2012) hypothesized that MPB tree selection is nonlinear and increased with WPBR infection levels to a point, after which it decreased. More importantly, MPB indirectly influences WPBR and vice versa through regulation of the tree species that are host to both disturbance agents, especially by killing those five-needled host trees that are resistant to blister rust (Campbell and Antos 2000).

Effects of WPBR on MPB infestations are also highly variable and subtle. Campbell and Antos (2000) found less MPB activity in trees that had high WPBR damage, whereas Bockino and Tinker (2012) found that whitebark pine selected as hosts for MPB

had significantly higher WPBR infection, but this varied by tree size (diameter), stand type, and disturbance pattern (Larson 2011). Kulhavy et al. (1984) found that over 90 percent of western white pine trees infected by bark beetles had either WPBR or some type of root disease, whereas Six and Adams (2007) found little evidence of interaction effects between MPB and WPBR. Simulations of MPB disturbance under current climate result in increased mortality of both lodgepole and whitebark pine, with a corresponding increase in subalpine fir and Douglas-fir, and there is little change with the addition of WPBR (Clark et al. 2017). These projected trends were enhanced under a warmer climate, where lodgepole pine declines are greater and stands are mainly replaced by Douglas-fir, but WPBR interaction has minor effects on species composition.

Between two traits, correlated response from a genetics perspective has a basis in linked genetic loci, overlapping genetic loci, or both (Mahalovich 2013). Plus trees in the genetics program provide a biological basis for testing the hypothesis that there are one or more unfavorable, correlated responses among traits. Pearson mean correlations among the plus trees do not indicate an unfavorable correlation between WPBR infection and high MPB outbreaks, whether those data are pooled across years or analyzed by year. Blister rust infection is weakly correlated with MPB incidence ($r = 0.01$, $P < 0.88$), as is average canker count ($r = 0.03$, $P < 0.67$) (Mahalovich 2015). Blister rust was first identified in the Greater Yellowstone Ecosystem in 1937; so within the recent evolutionary history (1.3 generations), this timeframe is not long enough for whitebark pine to have established a correlated response between an introduced pathogen and an endemic insect. Moreover, blister rust infection, number of cankers, and MPB incidence are weakly related geographically, increasing with latitude and longitude and decreasing with elevation.

3.4.4.4 Fire, MPB, and WPBR

Real-world studies of the complex interactions among all three disturbances—fire, beetles, and rust—are rare, but, in our opinion, the net result is that MPB and WPBR serve to reduce five-needle populations and create high fuel loads. When ignited,

these fuelbeds may foster fires that are more intense than historical fires, and this may result in greater fire-caused mortality for all plants within the burned area. However, fire, while reducing pines in the short term, appears to ensure their long-term persistence by eliminating competitors, as noted by Keane and Morgan (1994a). Fire also creates conditions suitable for the germination of seed cached by Clark's nutcrackers. In previous modeling efforts, decades or centuries were required to reestablish populations of rust-resistant pines after die-off (such as would occur with MPB) (Loehman et al. 2011b). Simulated wildland fires killed some trees, but prevented encroachment by shade-tolerant, non-pine species and maintained five-needle pines on the landscape (Loehman et al. 2011b). Observationally, the greatest decline in whitebark pine has been found in those areas affected by both WPBR and MPB, but not fire (Campbell and Antos 2000).

3.5 Nutcracker Responses

Given the obligate dependency of whitebark pine on Clark's nutcrackers for seed dispersal and regeneration (Tomback and Linhart 1990), the response by the bird to predicted climate warming and changing forest landscapes should generate as much concern as the likely changes in disturbance regimes and threats for whitebark pine. Nutcracker distribution and numbers will determine the distribution and continuity of whitebark pine (Tomback 2001, 2005). Any modeling of future distribution of whitebark pine should be constrained by the predicted future distribution of Clark's nutcracker (Keane et al. 1990). Direct connections between the two species have not been properly recognized with respect to the implications for whitebark pine.

Nutcrackers determine the distribution of whitebark pine geographically, regionally, and locally, as well as population structure, growth forms, and other aspects of whitebark pine ecology. Sites selected by nutcrackers for seed caching, along with the environmental suitability of these sites for seed germination and seedling survival, determine where whitebark pine occurs on the landscape (Tomback 1983, 2001, 2005). The tendency of nutcrackers to cache seeds below and above the current elevational distribution of whitebark

pine enables whitebark pine to respond rapidly to climate cooling or warming with changes in elevational and even latitudinal distribution. This influence is particularly important now, as climate warming is predicted to cause an upward and northward shift in whitebark pine distribution (e.g., McKenney et al. 2007; Schrag et al. 2007; Tomback 2005; Tomback and Achuff 2010).

Secondly, seed dispersal by nutcrackers is responsible for the genetic population structure of whitebark pine at several spatial scales (Tomback 2005). At the local level, the seed caching mode of seed dispersal results in a unique fine-scale genetic population structure. Because two or more whitebark pine seeds are often cached together, several seedlings from a cache may survive and produce a “tree cluster” growth form. This growth form appears as a single tree with multiple stems, which are tightly clustered or fused at the base or part way up the stem. Also, because nutcrackers harvest several seeds to an entire pouch-load of seeds from a single tree, there is a high probability that the seeds within a cache are genetically related (Tomback and Linhart 1990). Within a given area, nutcrackers cache at random with respect to caches already present, and with seeds from different source trees. Therefore, seedlings among neighboring caches are usually unrelated, resulting in a random genetic pattern among clusters. Finally, nutcrackers transport seeds for caching typically over distances of several kilometers to more than 30 km. Consequently, gene flow from nutcracker seed dispersal occurs across greater distances than seed dispersal by wind, resulting in genetically diverse populations (Rogers et al. 1999; Tomback et al. 1990). This high genetic diversity may facilitate local adaptation and whitebark pine resilience in the climates of the future.

Loss of cone production capacity within declining whitebark pine forests coupled with the tendency of nutcrackers to emigrate when cone crops are small could result in fewer seed dispersal events in many whitebark pine forests. Whitebark pine stands with extensive damage or high mortality from MPB and WPBR have lower cone abundance and relatively higher pre-dispersal squirrel and nutcracker predation (McKinney and Tomback 2007). Yet these stands could harbor a higher frequency of rust-resistant

alleles than similar stands with low mortality if trees with some resistance were most likely to have survived over time (Hoff et al. 1994). In general, as cone production declines from tree mortality and damage, the likelihood of stand visitation by nutcrackers and seed dispersal declines (Barringer et al. 2012; McKinney et al. 2009).

Bioclimatic envelope models (BEMs) predict that whitebark pine will move to higher elevations and more northern latitudes (e.g., McKenney et al. 2007; Schrag et al. 2008) (Section 3.1.3). However, these assessments are made without considering interaction with nutcrackers, or even other mutualists such as mycorrhizae, and how nutcrackers will respond to climate change. Since nutcrackers determine the distribution of whitebark pine on several spatial scales, the influence of climate on nutcracker distribution will also affect whitebark pine distribution. One major limitation of the use of assisted migration in the management of whitebark pine (e.g., McLane and Aitken 2012), for example, is that the range extension may not represent suitable habitat, or include the BEM, for nutcrackers.

What is the likely influence of a warming climate on nutcracker distribution? The National Audubon Society has simulated the effects of climate change for the North American bird species they consider to be the most climatically vulnerable. The distributional requirements for each species were defined in terms of temperature range, precipitation, and seasonal changes. Determination of “climate suitability” was based on three decades of data collected through citizen science projects including the Audubon Christmas Counts (December) and the North American Breeding Bird Surveys (usually June). Clark’s nutcrackers were classified as climatically vulnerable because of their dependence on high elevation forest communities, which are projected to shift in distribution and contract in areal extent (National Audubon Society 2014). The simulations started with the species distribution in the year 2000 and examined projected changes in winter and summer distributions in 2020, 2050, and 2080, based on “a range of... greenhouse gas emission scenarios.” By 2080, the projections indicated that only 16 percent of the summer range of nutcrackers present in 2000 was usable, with an overall

decrease in suitable summer range of 72 percent. Only 25 percent of winter range was usable in 2080, with an overall decrease of 68 percent. Some of the new climatically suitable areas identified for nutcrackers are geographically disjunct and distant from the dependable nutcracker range and thus are unlikely to be occupied, or are in areas with unsuitable habitat.

For most North American birds, Christmas counts and breeding bird surveys provide a reasonable picture of distribution. For Clark's nutcrackers, however, neither survey may capture their primary, high elevation range or the extent of their range, and thus provide an incomplete BEM. Nutcrackers are mobile, traveling widely in search of food resources, especially in years of poor seed production (Lorenz and Sullivan 2009; Tomback 1978; Vander Wall et al. 1981). In fact, this mobility appears to result in the absence of a rangewide population genetic structure for nutcrackers (Dohms and Burg 2013). In December, when Christmas bird counts are conducted, many nutcrackers may have left their summer range (Tomback 1998; Lorenz and Sullivan 2009). Most nutcrackers complete nesting by April and May (Tomback 1998), whereas breeding bird surveys tend to be in June. Also, bird watchers conducting these surveys are often not in the forest types that are favored by nutcrackers, which limits information on bioclimatic tolerances.

Although we tend to associate nutcrackers with cold, high mountain environments, the reliable distribution of Clark's nutcrackers may be quite broad, including a disjunct population on the high peak Cerro Potosí, in Nuevo León, Mexico (latitude 25°N), and a former population in Sierra San Pedro Mártir, northern Baja, California. Populations are also found in the desert ranges of southern California and the sky island forests of southern New Mexico and Arizona (Tomback 1998). At the northern limits, the numbers of nutcrackers are reported to decline above 53°N in the coastal ranges of British Columbia and

in the Rocky Mountain distribution (Tomback 1998). Within some regions, nutcrackers also have a wide elevational distribution, even within local areas (e.g., Lorenz et al. 2011; Tomback 1978).

Thus, the nutcracker distribution, which encompasses 28 degrees of latitude, several hundred meters of local elevational range, a multitude of forest types and various weather and disturbance regimes, represents a large bioclimatic envelope that should encompass future climates as well as future distributions of whitebark pine. However, Clark's nutcracker distribution may be limited by ecological requirements as opposed to climatic. Nutcracker populations require multiple seed sources, as backup for years of poor cone production by whitebark pine. Other important seed sources include ponderosa pine and Douglas-fir in the northern range, as well as pinyon pines and other high elevation five-needle white pines in more central and southern portions of its range (Lorenz et al. 2011; Tomback 1978, 1998; Vander Wall and Balda 1977). In the northernmost range of whitebark pine, only Douglas-fir—which produces small, less preferred seeds—serves as an alternative seed source, and its range ends at lower latitudes than whitebark pine on the eastern slope of the Rocky Mountains. The lack of additional seed sources at the northern end of the nutcracker distribution may preclude a dependable disperser population, which will limit the extent of northward shifts in whitebark pine.

Regardless of the nutcracker bioclimatic niche and predicted distributional shifts, loss of cone-producing whitebark pine as a result of WPBR and MPB infestations diminishes the energetic reward for nutcrackers locally, and reduces the likelihood of whitebark pine seed dispersal and regeneration. Maintaining or restoring healthy stands of whitebark pine is the best means of insuring continued stand visitation by nutcrackers and seed dispersal leading to regeneration, even with changing climate (Barringer et al. 2012; McKinney et al. 2009).

4. The Simulation Effort

The complexity of most ecosystem processes and interactions preclude traditional approaches of predicting climate impacts such as expert opinion, statistical modeling, and field experiments because of the long time spans and large areas needed to properly evaluate vegetation, disturbance, and ecosystem responses to changing climates. Mechanistic ecological simulation of the climate, vegetation, and disturbance dynamics in a spatial domain is probably the best approach, but this field of landscape modeling is still in its infancy (Keane and Finney 2003; Sklar and Costanza 1991; Walker 1994). Some ecosystem simulation models are missing the important interactions of disturbance, hydrology, and land use that might dictate climate effects on plant distributions (Notaro et al. 2007). Many landscape models also fail to include disturbances and spatial relationships that may be minor now, but are likely to be important in the future (e.g., exotics). This could result in still higher levels of uncertainty in describing future conditions.

Little is known about the interactions among climate, vegetation, and disturbance, along with interactions of critical plant and animal life cycle processes of reproduction, growth, and mortality with climate (Gworek et al. 2007; Ibanez et al. 2007; Keane et al. 2001d; Lambrecht et al. 2007). Therefore, it is difficult to determine which interaction might be the most important in determining species response to climate change, especially in upper subalpine whitebark pine ecosystems (Price et al. 2001; Walther et al. 2002). Climate influences on interactions among different disturbance regimes and vegetation could create novel landscape behaviors (Williams and Jackson 2007; Williams et al. 2007). Therefore, even though landscape ecosystem modeling is not yet mature, we think that a simulation approach is still the best way to objectively address complex interactions among climate, disturbance, and vegetation. Hence, we have included a simulation modeling experiment in this report to support various climate change recommendations. We have also included independent model runs to illustrate various responses of restoration actions in the future.

4.1 The Model

FireBGCv2 is best described as a mechanistic, individual-tree, gap model that is implemented in a spatial domain (see Keane et al. 2011 for complete model documentation, also <http://www.firelab.org/project/firebgcv2-simulation-platform-and-projects> [accessed October 2015]). The model was developed by integrating empirically derived deterministic functions with stochastically driven algorithms to approximate landscape and ecosystem behavior across time and space (Keane et al. 2011). Empirical and deterministic functions are used to represent those ecological processes, such as autotrophic respiration and photosynthesis, which are often heavily studied so the processes are somewhat understood and predictable. Stochastic functions are used to represent ecological processes that are highly variable, somewhat unstudied, and difficult to quantify, such as fire ignition, tree mortality, and snag fall. FireBGCv2 is a cumulative effects model that is best used to study long-term changes to landscape and ecosystem dynamics regimes rather than as a prognostic model to predict what will happen in the near future. The FireBGCv2 model is best used to simulate the long-term interactions of disturbance, climate, and vegetation across several model runs to determine patterns and trends in landscape behavior and response.

FireBGCv2 simulates ecological processes across and within multiple spatiotemporal scales including cross-scale interactions that can drive landscape behaviors (fig. 24). Wildland fire ignition and spread, along with cone crop production and seed dispersal, are simulated at the landscape level at the end of each simulation year. Most of the action in a FireBGCv2 simulation occurs at the stand level (fig. 24) where the flows of carbon, nitrogen, and water are distributed across various terrestrial and atmospheric components within the model (fig. 25). Ecological processes modeled at the stand level include decomposition of leaf and litter fall, which dictates forest floor dynamics; the interaction of precipitation and temperature,

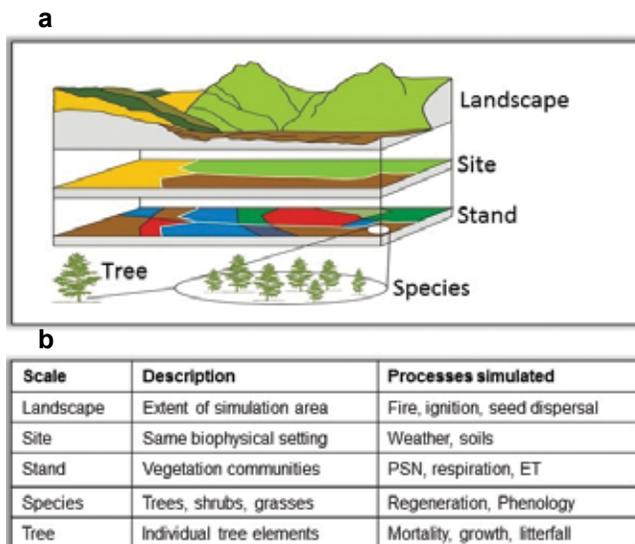


Figure 24—The FireBGCv2 model was designed to simulate multiple spatial and temporal scales. (a) A description of the five spatial and organizational scales implemented in the design. The landscape is the entire simulation area. Sites are the unique biophysical settings of the landscape based on soils, topography, aspect, and slope. Stands are patches of vegetation within a site of different successional status, and these stands are made of species of trees and undergrowth. (b) There are unique ecological processes simulated at each of the inherent scales of FireBGCv2.

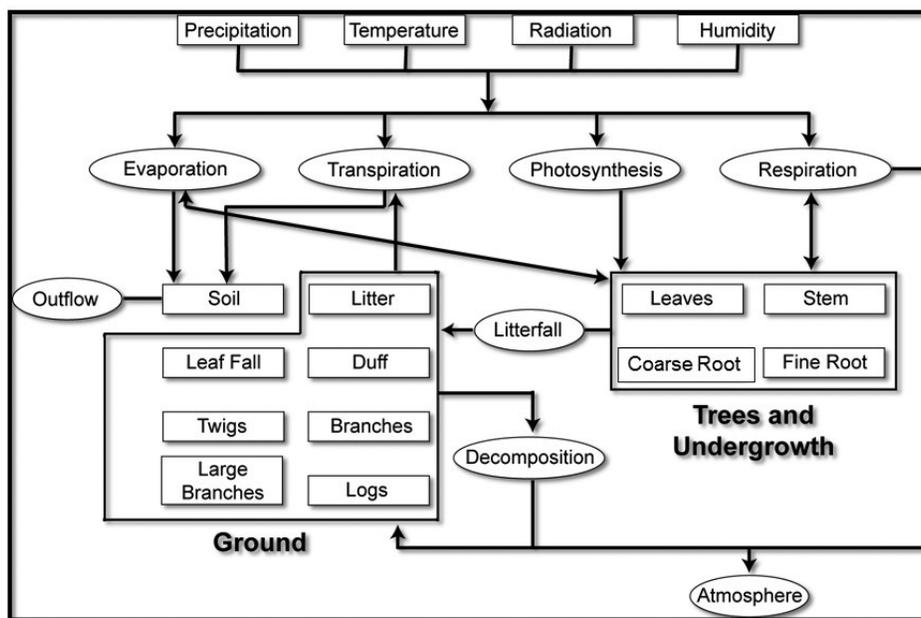
which influences leaf area production and governs water dynamics; and photosynthesis and respiration, which dictate carbon dynamics. Weather and species phenology are simulated at the site level at a daily time step. Tree growth, establishment, and mortality are simulated at the individual tree level. Disturbance

effects, such as fuel consumption, tree mortality, and soil heating, are computed at each of the scales.

All simulated processes have cross scale implications. For example, carbon is fixed by tree leaves (needles) via photosynthesis, which is simulated using solar radiation and precipitation weather inputs, and the carbon is then distributed to leaves, stems, and roots. A portion of this plant material is lost each year and accumulates on the forest floor in the litter, duff, and soil, eventually providing fuel for a fire. These forest floor compartments also lose carbon through decomposition. Nitrogen is cycled through the system from the available nitrogen pool.

Because FireBGCv2 has many stochastic elements, the model should be run for long time periods that are at least two to five times the longest fire return interval and each run should be replicated at least five times (Keane et al. 2012). Simulation results should be summarized to emphasize relative trends in ecological change rather than absolute change. And, as with most mechanistic models, the simulation results are best used when compared across simulation scenarios to evaluate differential patterns. Using a complex landscape simulation model to develop climate change guidelines demands thoughtful design of a comprehensive simulation experiment because the strength of modeling is in the comparison of alternative scenarios, rather than interpretation of singular predictions.

Figure 25—A diagram showing the flow of carbon, water, and nitrogen to some of the many compartments in the FireBGCv2 model which represent the basic ecophysiological processes needed to simulate climate change responses.



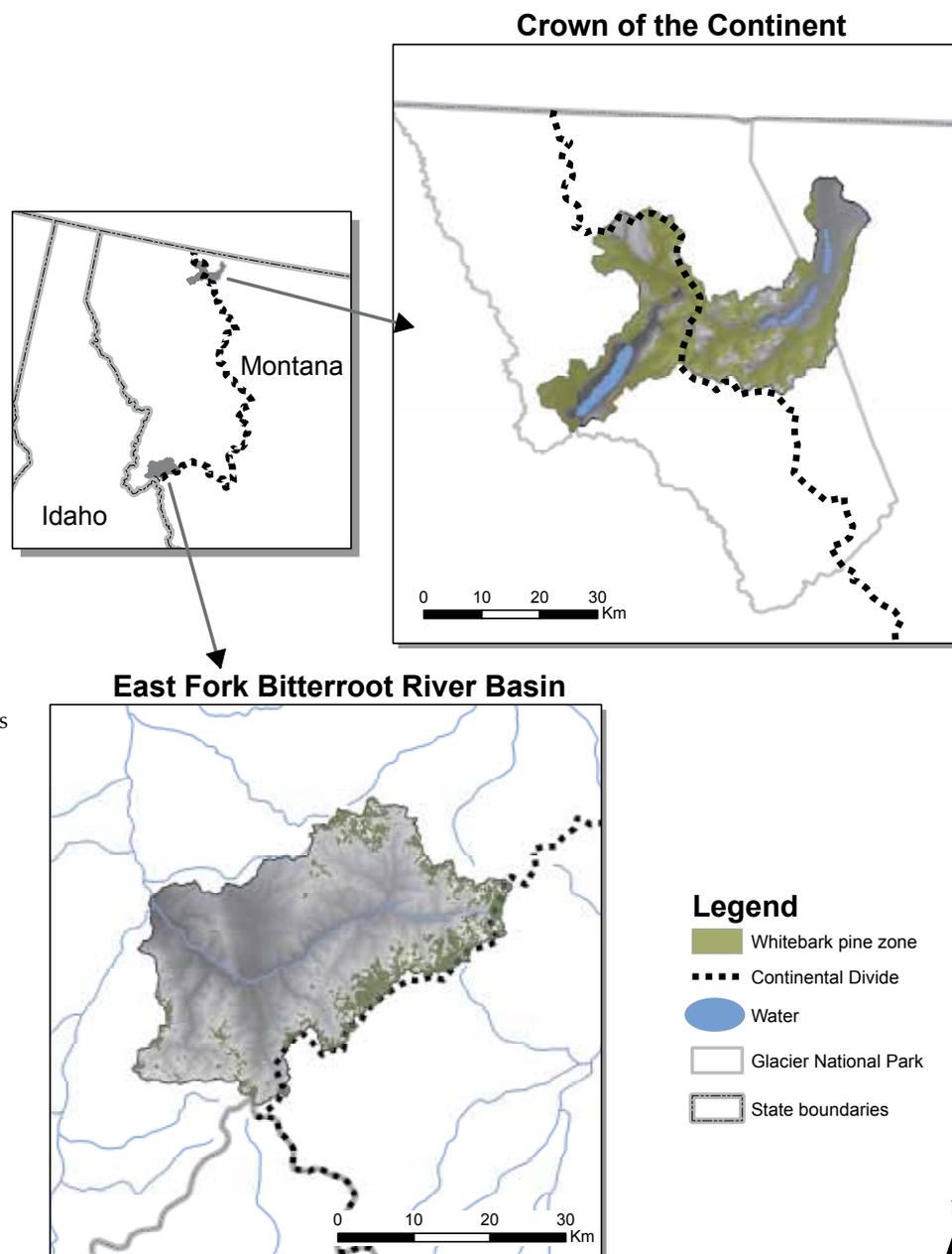
4.2 The Simulation Experiment

Our simulation experiment used FireBGCv2 to explore climate change impacts on whitebark pine and fire dynamics and their effects on ecosystem components, including interactions with insects (MPB), diseases (WPBR), fire management (suppression), and restoration activities. It would be impossible to simulate the complex interactions of climate, fire, and landscape dynamics over the entire range of whitebark pine. Therefore, we assessed resilience and persistence of whitebark pine under future climates on two landscapes that are broadly representative of a wide range of climate, vegetation, and fire regime types

for whitebark pine in the northern Rocky Mountains. These landscapes were previously calibrated for FireBGCv2 execution and represent a considerable investment. It typically requires about 3 to 6 months of intensive field sampling to collect data to initialize and parameterize FireBGCv2 for a target landscape and another 6 to 8 months to prepare the initial input maps and files. We selected the following landscapes for inclusion in this project (fig. 26):

- East Fork Bitterroot River (**EFBR**), Bitterroot National Forest. A 128,000-ha dry mixed-conifer ecosystem with a mixed frequency and severity fire

Figure 26—The two landscapes that were included in the FireBGCv2 simulation experiment and that were used in the illustrative independent simulations. The landscapes are described in the text.



regime. Whitebark pine forests currently make up 8 to 12 percent of the landscape.

- Crown of the Continent (**CROWN**), including portions of Glacier National Park and the Flathead National Forest. A 100,000-ha high-elevation mesic mixed-conifer ecosystem with fire regimes of variable frequency and severity. Whitebark pine forests compose 8 to 14 percent of the landscape.

All lands with the potential to support whitebark pine were explicitly identified on each landscape using biophysical parameters and field data (fig. 26). In FireBGCv2 simulations, each landscape was delineated into two zones. The first zone consists of areas that readily support whitebark pine communities. These are typically higher elevation subalpine areas, which in the EFBR basin elevation ranged from 1,305 to 2,876 m and elevations 956 to 3,010 m in the CROWN landscape. The second zone is all other areas with lands that are generally unsuitable for whitebark pine.

In prior studies, we found that a fully factorial approach works well with a suite of factors that represent the important objectives of the simulation effort (Loehman et al. 2011b). In this project, our simulation objective was to evaluate the impact of climate change on whitebark pine abundance under fire management and restoration treatments. Therefore, we designed a simulation experiment using a set of factors that represent climate, restoration approaches, and fire management. We varied each factor to explore a range of treatment intensities or frequencies. We then replicated each simulation across all factors to account for model stochasticity (table 3).

The four factors included in the simulation experiment were (1) fire suppression level (S), (2) restoration activity (R), (3) whitebark pine planting (P), and (4) climate (C). Within each factor, we simulated a number of factors that span a reasonable array of potential outcomes (table 3). For S, we simulated three levels of fire suppression: (1) 0 percent suppression (mimics historical fire regime), (2) 50 percent suppression (mimics wildland fire use management option), and (3) 92 percent suppression (operational fire suppression) (Loehman et al. 2011b). For R, we simulated three restoration treatment strategies:

(1) no restoration treatments, (2) moderate restoration where mechanical cuttings of subalpine fir (thinning, removal) in concert with prescribed burning were used to remove whitebark pine competitors across a small proportion (3 percent per year) of the landscape, and (3) extensive restoration where mechanical cuttings and prescribed burning treatments were imposed across a substantial portion (30 percent per year) of the landscape. The P factor had three treatments: (1) no planting, (2) planting rust-resistant whitebark pine seedlings at 10 ha yr⁻¹ at a density of 275 seedlings ha⁻¹; and (3) planting seedlings at 100 ha yr⁻¹ at a density of 550 seedlings ha⁻¹. Each year, seedlings were simulated to be planted on any areas that burned within the last 30 years either from wildfire or prescribed burning in an attempt to mimic a full restoration program. If there were insufficient newly burned areas for planting (i.e., no prescribed fire or new wildfires occurred during a particular year in the simulation), then seedlings were planted in old burns up to 50 years old. If no burned areas were available, then no seedlings were planted that year. The proportions of seedlings with rust resistance in these simulations were set at 30 percent. This is at the upper range of whitebark pine seedling resistance as determined from the Inland West Whitebark Pine Genetic Restoration Program at the USDA Forest Service Coeur d'Alene (ID) (Mahalovich and Foushee, submitted). However, natural levels of rust resistance at high spore loads similar to a wave-year event were estimated below 1.0 percent (Mahalovich 2015); we included simulations and analysis at this lower level as well.

The climate (C) factor had two scenarios: (1) historical climate and (2) a future climate predicted by the Coupled Model Intercomparison Project Phase 5 (CMIP5) with an 8.5 Representative Concentration Pathway (RCP). In the future climate scenario, average temperatures are projected at about 5 °C above pre-industrial levels. This is an emissions scenario that predicts the highest temperature increases among various possible emission scenarios and the one scenario that appears increasingly most likely to occur (Peters et al. 2013). A summary of the RCP8.5 CMIP5 data is provided in table 1.

Table 3—The multifactorial simulation experiment used to assess impacts of climate change on whitebark pine restoration attempts. The factors and treatments were used to explore climate change effects on whitebark pine distribution and abundance. We performed 10 replicates of each factor. Also presented are acronyms of the tree species included in all simulations as referenced in other figures and tables in this section.

Factor	Number of levels	Values for each level
Fire suppression (S) —Levels of fire suppression expressed as percent of fires that are suppressed	3	No suppression (SN)- historical fire regime; Low suppression (SL)- 50% suppression (wildland fire use); High suppression (SH) 92% suppression (current management)
Restoration activities (R) —Three levels of area treated with mechanical cuttings coupled with prescribed burns	3	No treatments (RN); low restoration levels (RL) 3% of landscape treated per year; high restoration (RH) 30% landscape treated per year
Whitebark planting (P) —Three levels of area treated with planting whitebark pine seedlings	3	No planting (PN); low planting (PL) 10 ha per year at 275 seedlings per ha; high planting (PH) 100 ha per year at 550 seedlings per ha
Climate (C) —Current and projected daily climate streams for 95 years	2	Historical and warm-dry (RCP8.5) scenarios
Tree species and plant guilds included in the simulations		
Scientific Name	Abbreviation	Common name
<i>Abies lasiocarpa</i>	ABLA	Subalpine fir
<i>Pinus albicaulis</i>	PIAL	Whitebark pine
<i>Pinus contorta</i>	PICO	Lodgepole pine
<i>Pinus engelmannii</i>	PIEN	Engelmann spruce
<i>Populus tremuloides</i>	POTR	Quaking aspen
<i>Pseudotsuga menziesii</i>	PSME	Douglas-fir
<i>Pinus ponderosa</i>	PIPO	Ponderosa pine
<i>Pinus flexilis</i>	PIFL	Limber pine
<i>Larix occidentalis</i>	LAOC	Western larch
<i>Pinus monticola</i>	PIMO	Western white pine
<i>Larix lyallii</i>	LALY	Alpine larch
<i>Thuja plicata</i>	THPL	Western red cedar
<i>Tsuga heterophylla</i>	TSHE	Western hemlock
Riparian Herb	RHRB	Wetland herbaceous communities
Grass	GRSS	Grassland dominated communities

Typically, it is recommended that at least ten global circulation models (GCMs) be used to describe future climate or impacts models to sufficiently capture the range of uncertainty in climate projections (Mote et al. 2011). Due to limited time and capacity for FireBGCv2 simulation, we chose one GCM from the numerous models available. Based on an evaluation of a suite of GCMs by Rupp et al. (2013) for the Pacific Northwest and surrounding region, we chose the CNRM-CM5 (National Centre of Meteorological

Research, France), which was the highest ranked model overall for the northern Rocky Mountains region. Landscape climate input data were taken from a statistical downscaling of the GCM data from CMIP5 using the Multivariate Adaptive Constructed Analogs (Abatzoglou and Brown 2012) method with the METDATA (Abatzoglou 2011) observational dataset as training data. We also derived weather data for our historic scenario simulations from downscaled grids of historical climate modeled from the CNRM-CM5

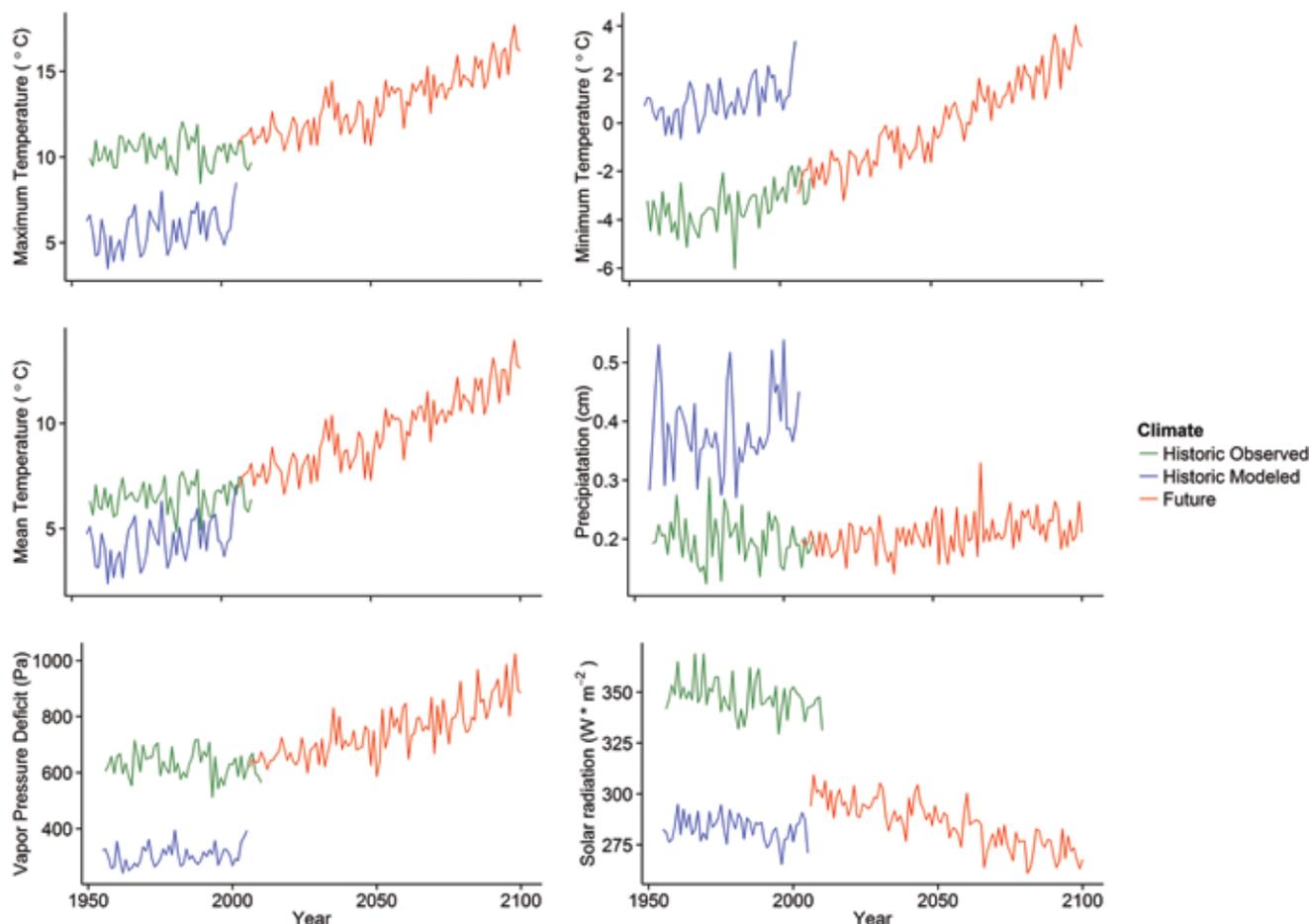


Figure 27—Simulated and observed weather data for EFBR simulation landscape, including average annual maximum, minimum and mean temperature (°C), precipitation (cm), vapor pressure deficit (Pa), and solar radiation (W m⁻²). Historic observed data were taken from a weather station at Sula, Montana, and historic and future modeled data were derived from the CNRM-CM5 GCM. Note the following: (1) lack of transition from simulated historical (blue line) to simulated future (red); (2) difference between simulated historical (blue) and observed historical climate (green); and (3) the same precipitation predicted for the future (red: no decrease).

GCM for the baseline period of 1950–2005 (56 years). The GCM modelers recommend that the simulated historical climate be used instead of the actual observed climate in order to match the resolution and detail of the simulated future projections (Peters et al. 2013). However, the average annual conditions simulated for the six weather variables input to FireBGCv2 for the EFBR (fig. 27) and CROWN (fig. 28) were different from the observed historical patterns from weather station data and often did not match the start of future projections.

Each level for each factor was simulated in a multifactorial design with ten replicates for each of these simulations resulting in a total of 540 simulations (3 S x 3 R x 3 P x 2 CC x 10 reps = 540 runs) for each landscape. We used the same species list for

each simulation run (shown in table 3); this species list dictated which species could inhabit the landscape during the simulation. Data for the future climate scenarios were available for years 2006–2100 (95 years). For comparable results, we simulated both historical and future scenarios for this same length of time. We output simulation results every 10 years to create a simulated time series of nine observations for each simulation run. For the historical simulations, we repeated the 56-year weather record for both study areas to achieve 95-year long simulations. Results from these simulations provided the basis for the set of recommendations that we crafted future whitebark pine management.

A suite of response variables that comprehensively describe ecological dynamics across the combinations

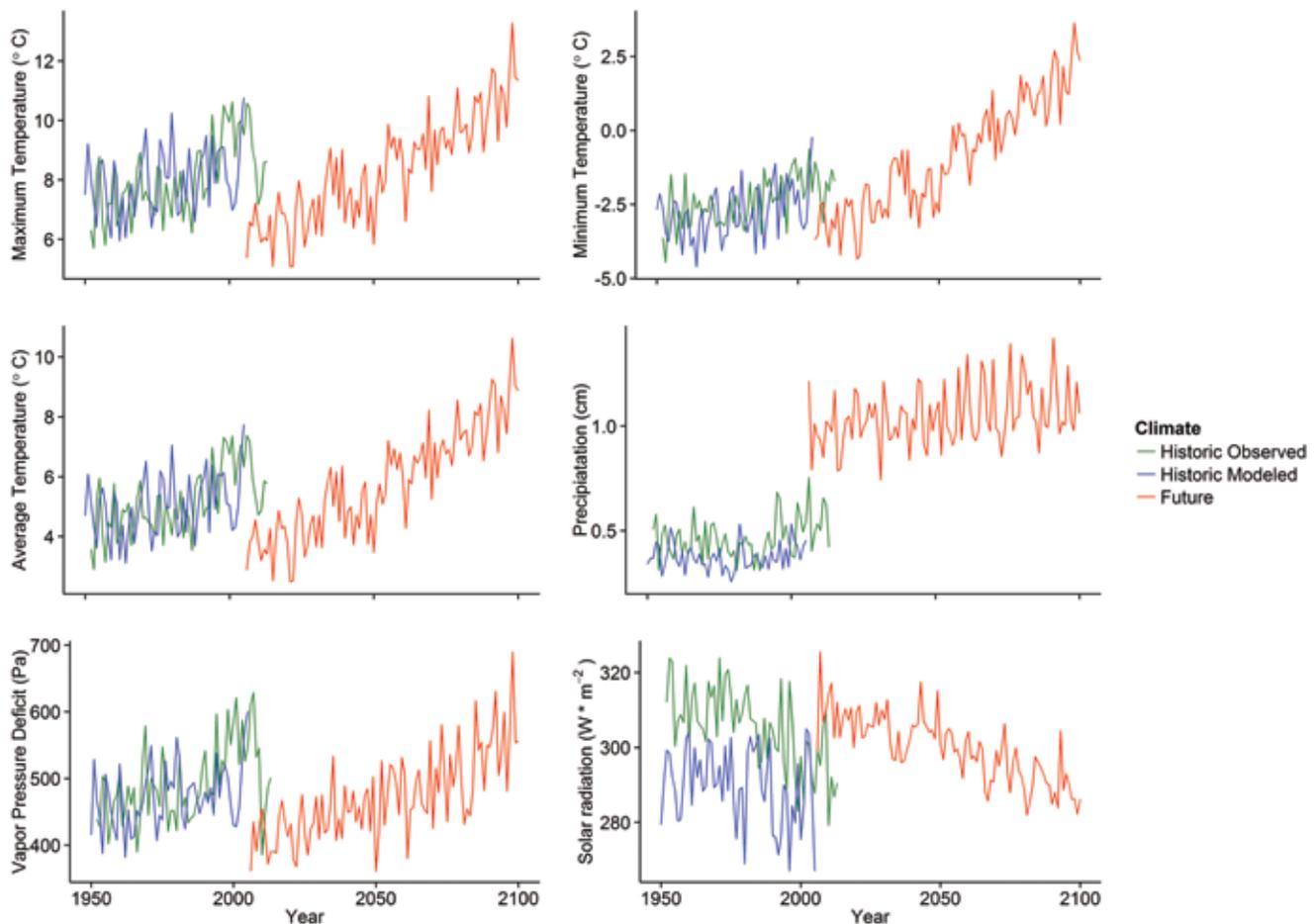


Figure 28—Simulated and observed weather data for CROWN simulation landscape, including average annual maximum, minimum and mean temperature (°C), precipitation (cm), vapor pressure deficit (Pa), and solar radiation ($W \cdot m^{-2}$). Historic observed data were taken from a weather station at Sula, Montana, and historic and future modeled data were derived from the CNRM-CM5 GCM. Note the following: (1) lack of transition from simulated historical (blue line) to simulated future (red); (2) difference between simulated historical (blue) and observed historical climate (green); and (3) the same precipitation predicted for the future (red: no decrease).

of factors detailed above was used to assess climate change impacts. Most importantly, we analyzed the response of whitebark populations to restoration and planting treatments at the **stand scale** using “basal area ($m^2 \text{ ha}^{-1}$) in whitebark pine,” and at the **landscape scale** using “proportion of the simulation area in whitebark pine dominated stands (proportion landscape cover).” We summarized the basal area and proportion landscape cover in the whitebark pine zone only (upper elevation areas that readily support whitebark pine) (fig. 26).

We used generalized linear mixed models (GLMM) for repeated measures to test for significant differences in restoration, planting, fire suppression, and climate, and we also built GLMMs to evaluate historical and future climate conditions separately.

To evaluate the amount of basal area, we used R (R Development Core Team 2014) with the “lme” package (Bates et al. 2014) and an AR(1) random residual structure to account for temporal autocorrelation. We also included multiple comparisons of the main treatment effects. We used GLIMMIX in SAS to evaluate proportion cover, with an AR(1) structure and a beta probability distribution (appropriate for proportion data), and conducted multiple comparisons of main effects. In addition, we developed GLMMs to include comparisons of plantings with rust resistance at two levels: 5 percent (approximate maximum native resistance under intense spore loads indicative of wave year events) and 30 percent (average WPBR-resistance level in breeding program). We performed multiple comparisons of main treatment effects, as

well as their two-way interactions to better explore relationships between rust resistance and restoration, planting, and fire suppression.

We also qualitatively described forest community responses to climate change and wildfire management by summarizing percent of the upper subalpine landscape (whitebark pine zone) comprised by each tree species cover type and by six structural stages (seedling d.b.h. < 1 cm, sapling d.b.h. 1–10 cm, pole d.b.h. 10–30, mature d.b.h. 30–70 cm, large d.b.h. 70–120 cm, and very large d.b.h. > 120 cm). We also evaluated a host of other ecosystem related explanatory variables including fuels (canopy bulk density), fire (average annual area burned, landscape fire rotation, fire size), fire effects (tree mortality, fuel consumption), and wildlife habitat (lynx and grizzly bear) summarized to the landscape scale. Because whitebark pine is a keystone and foundation species and its distribution overlaps with other forest types that provide important habitat for other key conservation targets, we also included the simulation of grizzly bear and lynx habitat suitability in our model runs. The Loehman et al. (2011b) matrix that rates habitat suitability to combinations of cover type and structural stage was used in this step.

4.3 Independent Model Runs

The FireBGCv2 model was also used as an illustrative tool to show effects of a particular action or strategy on whitebark pine dynamics over the long term. It would have been impossible to include all possible factors in our multifactorial simulation experiment because of logistical concerns (i.e., it took about 4 months to conduct the full simulation experiment). Further, including all other possible restoration actions, such as tree protection and patterns of genetic variation, would have made the simulation experiment unwieldy. As a result, we employed the FireBGCv2 model to illustrate important impacts and recommendations for specific cases. To support our climate change considerations discussed in Section 5, we ran the model independently of the simulation experiment to evaluate effects of restoration guiding principles and actions. We did this because responses of whitebark pine to climate change are relatively unknown

for many geographic regions so the only reference available is a FireBGCv2 model run.

Independent runs used different weather data than our simulation experiment. The GCM CMIP5 data represented only 95 years into the future, which is often insufficient for the impacts of climate change to manifest. Fire regimes, for example, need several centuries of simulation to be described appropriately. Therefore, we used the methods presented in Holsinger et al. (2014) to simulate five centuries of climate change by offsetting the daily historical recorded weather data presented in figures 27 and 28 using parameters calculated from the CMIP5 data for the RCP8.5 scenario (approximately 4.5 °C in temperature and 1.05 percent increase in precipitation) (see Holsinger et al. 2014 for details). Results from these independent runs are presented throughout this report.

4.4 Simulation Results

4.4.1 Whitebark Pine Abundance

In the EFBR, restoration treatments had the greatest success under a future climate for increasing both whitebark pine basal area and the proportion landscape cover of whitebark pine in the upper elevations of this landscape (figs. 29, 30; table 4). Basal area doubled when restoration treatments were implemented at either low or high levels as compared to no treatment. The proportion of upper subalpine landscape in whitebark pine was almost four times as high in low or high levels compared to no restoration (table 5). In addition, fire suppression had a significant but minimal effect on the proportion in whitebark pine in the upper subalpine with significantly higher canopy cover (3 to 5 percent higher) in the full suppression scenario as compared to the no suppression simulations (tables 4, 5).

For the historical climate, we obtained similar results, but also with a significant two-way interaction between suppression and restoration for basal area amount. Both climate and restoration had the greatest effects on the amount of basal area and proportion of landscape in whitebark pine. High suppression was also important for the landscape proportion in whitebark pine, where more whitebark pine was

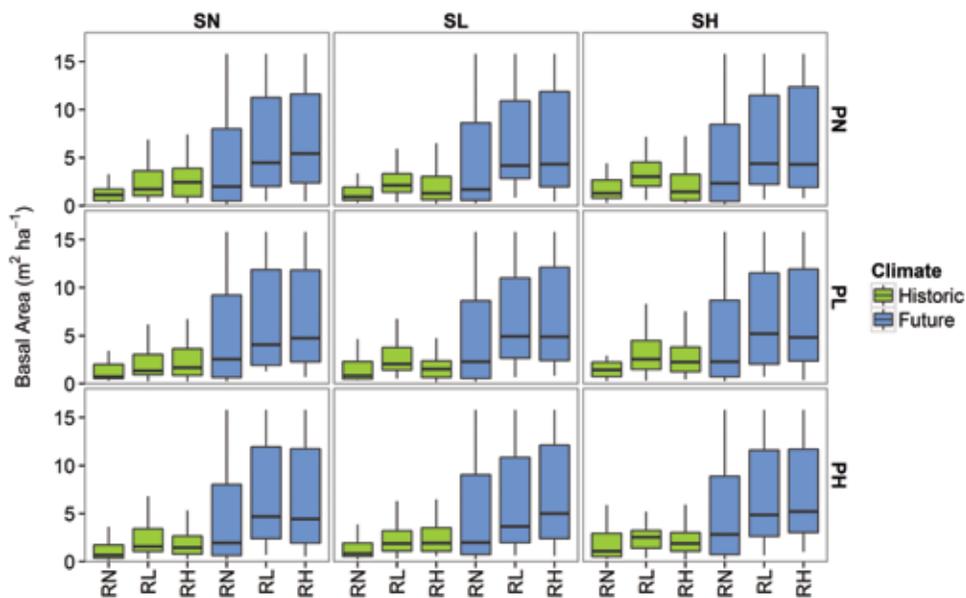


Figure 29— Basal area ($\text{m}^2 \text{ha}^{-1}$) of whitebark pine in upper elevations (whitebark pine zone) of the EFBR landscape across all scenarios including: historic (green) and future (blue) climate; fire suppression at none (SN), low (SL) and high (SH) levels; planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). FireBGCv2 predicts greater whitebark pine basal areas in the future, especially when restoration measures are taken.

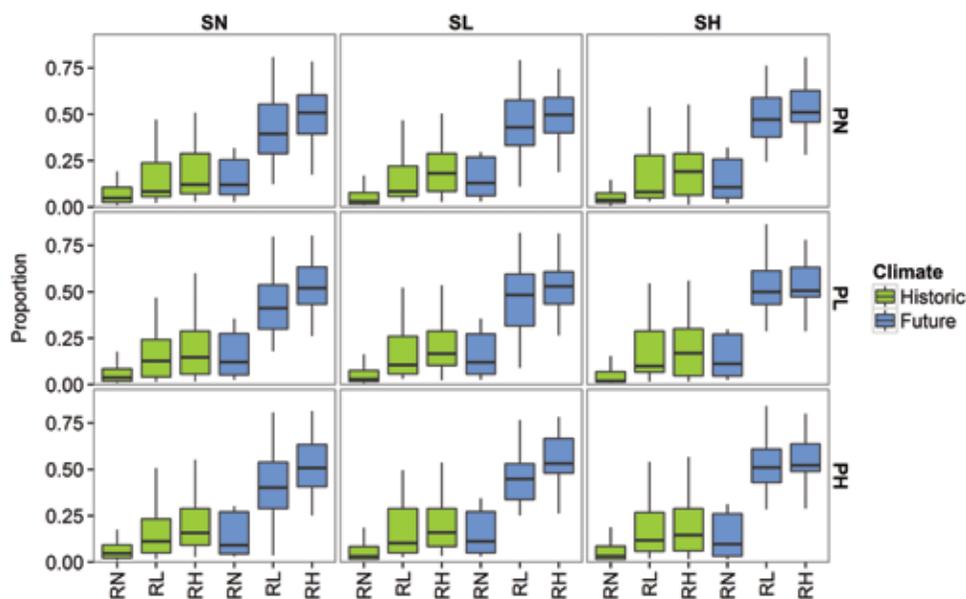


Figure 30—Proportion of landscape in whitebark pine in upper elevations (whitebark pine zone) of EFBR across all scenarios including: historic (green) and future (blue) climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). There is over twice the area occupied by whitebark pine in the future when restoration measures are taken

evident compared to no suppression. We found that the amount and proportion of whitebark pine was significantly higher in the EFBR under the future climate as compared to the historical (P value < 0.0001). Over twice as much whitebark pine was predicted for the future (3.72 vs. $1.69 \text{ m}^2 \text{ha}^{-1}$) and for proportion landscape cover (33 vs 12 percent for future and historical climate, respectively) (figs. 29, 30). Planting whitebark pine seedlings did not significantly affect the amount or proportion of whitebark pine in any of the EFBR simulations. The greatest whitebark pine basal areas are found under future climates with high restoration and fire suppression.

In contrast, simulation results for the CROWN landscape showed that there were significantly fewer whitebark pines, overall, in the future as compared to the historical simulations (3.33 vs $10.05 \text{ m}^2 \text{ha}^{-1}$ basal area and 0.24 vs 0.32 proportion cover for future and historic respectively) (figs. 31 and 32; tables 4, 5). Wildfire suppression had the greatest effect on basal area and proportion landscape cover in whitebark pine under both future and historical climates. In each climate scenario, the amount of basal area in whitebark pine was significantly higher with low or high suppression compared to without suppression. Similarly, the proportion of landscape in whitebark

Table 4—Results of generalized linear mixed models for the effects of planting, restoration, suppression climate and year for the amount of whitebark pine basal area and the proportion landscape area in whitebark pine dominated communities in the whitebark pine zone of the East Fork of the Bitterroot River (EFBR) and Crown of the Continent (CROWN) landscapes for Future only, Historic only, and Future and Historic combined. Asterisk indicates significant interaction between effects. Asterisk indicates significant interaction between effects.

Type III tests of fixed effects						
Effect	EFBR			CROWN		
	F statistic	Degrees of freedom Numerator; denominator	P-value	F statistic	Degrees of freedom Numerator; denominator	P-value
Whitebark pine basal area ($m^2 ha^{-1}$)						
<i>Future</i>						
Restoration	145.80	2; 263	<0.0001	0.79	2; 263	0.45
Planting	0.98	2; 263	0.38	1.46	2; 263	0.23
Suppression	2.05	2; 263	0.13	8.06	2; 263	0.0004
Year	760.92	9; 2421	<0.0001	11871.20	9; 2421	<0.0001
<i>Historic</i>						
Restoration	31.89	2; 259	<0.0001	0.21	2; 263	0.81
Planting	0.70	2; 259	0.50	0.08	2; 263	0.92
Suppression	1.55	2; 259	0.21	77.21	2; 263	<0.0001
S * R	3.69	4; 259	0.006	3254.78	9; 2421	<0.0001
Year	894.39	9; 2421	<0.0001			
<i>Future and Historic</i>						
Restoration	130.97	2; 532	<0.0001	0.54	2; 532	0.58
Planting	0.03	2; 532	0.97	1.04	2; 532	0.35
Suppression	2.29	2; 532	0.10	57.57	2; 532	<0.0001
Climate	234.11	2; 532	<0.0001	14512.15	2; 532	<0.0001
C * Year	356.83	9; 4842	<0.0001	3017.36	9; 4842	<0.0001
Year	1274.36	9; 4842	<0.0001	14110.61	9; 4842	<0.0001
Proportion of whitebark pine in landscape (%)						
<i>Future</i>						
Restoration	511.94	2; 156	<0.0001	1.19	2; 276	0.30
Planting	1.35	2; 154	0.26	1.04	2; 276	0.36
Suppression	3.58	2; 154	0.03	27.55	2; 276	<0.0001
Year	256.02	9; 1961	<0.0001	1721.78	9; 2233	<0.0001
<i>Historic</i>						
Restoration	218.12	2; 256	<0.0001	0.63	2; 317	0.53
Planting	0.11	2; 252	0.90	0.72	2; 317	0.49
Suppression	0.76	2; 252	0.47	63.96	2; 317	<0.0001
Year	316.23	9; 2166	<0.0001	328.32	9; 2356	<0.0001
<i>Future and Historic</i>						
Restoration	459.27	2; 542	<0.0001	0.62	2; 518	0.54
Planting	0.71	2; 536	0.49	0.44	2; 518	0.65
Suppression	3.23	2; 536	0.04	46.72	2; 518	<0.0001
Climate	950.84	2; 533	<0.0001	789.15	2; 518	<0.0001
Year	261.53	9; 4452	<0.0001	934.17	9; 4578	<0.0001

Table 5—Multiple comparisons of the main treatment effect's least square means (\pm standard error) on whitebark pine (PIAL) basal area and proportion landscape area of the EFBR and CROWN landscapes in the whitebark pine zone for planting, restoration, suppression and climate factors. Tukey's honestly significant difference (HSD) test was used to evaluate whether means were significantly different from each other with corrections for unbalanced replication using the Tukey-Kramer. Future and historical climates evaluated separately and combined.

Variables	EFBR landscape			
	Restoration			P-value ^a
	None	Low	High	
Basal area (Future)	2.32 \pm 1.03	4.77 \pm 1.03	4.77 \pm 1.03	a, <0.0001
Basal area (Historic)	1.34 \pm 1.04	2.08 \pm 1.04	1.72 \pm 1.04	b, <0.0001
Basal area (Future/Historic)	1.77 \pm 1.03	3.13 \pm 1.03	2.83 \pm 1.03	c, <0.0001
Prop. PIAL (Future)	0.1217 \pm 0.006	0.4558 \pm 0.009	0.5025 \pm 0.009	b, <0.0001
Prop. PIAL (Historic)	0.0642 \pm 0.003	0.1271 \pm 0.004	0.1605 \pm 0.004	d, <0.0001
Prop. PIAL (Future/Historic)	0.0901 \pm 0.004	0.2772 \pm 0.006	0.3210 \pm 0.007	d, <0.0001
Planting				
Variables	None	Low	High	P-value ^a
	None	Low	High	
Basal area (Future)	3.71 \pm 1.03	3.86 \pm 1.03	3.60 \pm 1.03	n.s.
Basal area (Historic)	1.72 \pm 1.04	1.62 \pm 1.04	1.72 \pm 1.04	n.s.
Basal area (Future/Historic)	2.51 \pm 1.03	2.51 \pm 1.03	2.48 \pm 1.03	n.s.
Prop. PIAL (Future)	0.3177 \pm 0.009	0.3380 \pm 0.009	0.3302 \pm 0.009	n.s.
Prop. PIAL (Historic)	0.1097 \pm 0.003	0.1098 \pm 0.003	0.1116 \pm 0.004	n.s.
Prop. PIAL (Future/Historic)	0.2023 \pm 0.006	0.2112 \pm 0.006	0.2090 \pm 0.006	n.s.
Suppression				
Variables	None	Low	High	P-value ^a
	None	Low	High	
Basal area (Future)	3.53 \pm 1.03	3.90 \pm 1.03	3.74 \pm 1.03	n.s.
Basal area (Historic)	1.82 \pm 1.04	1.77 \pm 1.04	1.60 \pm 1.04	n.s.
Basal area (Future/Historic)	2.44 \pm 1.03	2.61 \pm 1.03	2.46 \pm 1.03	n.s.
Prop. PIAL (Future)	0.3133 \pm 0.009	0.3265 \pm 0.009	0.3463 \pm 0.009	e,<0.05
Prop. PIAL (Historic)	0.1071 \pm 0.003	0.1120 \pm 0.004	0.1120 \pm 0.004	n.s.
Prop. PIAL (Future/Historic)	0.1976 \pm 0.006	0.2080 \pm 0.006	0.2173 \pm 0.006	e, <0.05
CROWN landscape				
Variables	Restoration			P-value ^a
	None	Low	High	
	None	Low	High	
Basal area (Future)	3.53 \pm 1.01	3.53 \pm 1.01	3.29 \pm 1.01	n.s.
Basal area (Historic)	9.97 \pm 1.01	10.07 \pm 1.01	9.97 \pm 1.01	n.s.
Basal area (Future/Historic)	5.81 \pm 1.01	5.81 \pm 1.01	5.75 \pm 1.01	n.s.
Prop. PIAL (Future)	0.2193 \pm 0.002	0.2187 \pm 0.002	0.2223 \pm 0.002	n.s.
Prop. PIAL (Historic)	0.3326 \pm 0.003	0.3326 \pm 0.003	0.3366 \pm 0.003	n.s.
Prop. PIAL (Future/Historic)	0.2761 \pm 0.002	0.2760 \pm 0.002	0.2794 \pm 0.002	n.s.
Planting				
Variables	None	Low	High	P-value ^a
	None	Low	High	
Basal area (Future)	3.32 \pm 1.01	3.29 \pm 1.01	3.39 \pm 1.01	n.s.
Basal area (Historic)	10.07 \pm 1.01	9.97 \pm 1.01	10.07 \pm 1.01	n.s.
Basal area (Future/Historic)	5.81 \pm 1.01	5.75 \pm 1.01	5.81 \pm 1.01	n.s.
Prop. PIAL (Future)	0.2189 \pm 0.002	0.2222 \pm 0.002	0.2192 \pm 0.002	n.s.
Prop. PIAL (Historic)	0.3314 \pm 0.003	0.3341 \pm 0.003	0.3363 \pm 0.003	n.s.
Prop. PIAL (Future/Historic)	0.2753 \pm 0.002	0.2783 \pm 0.002	0.2779 \pm 0.002	n.s.
Suppression				
Variables	None	Low	High	P-value ^a
	None	Low	High	
Basal area (Future)	3.22 \pm 1.01	3.40 \pm 1.01	3.38 \pm 1.01	a, <0.05.
Basal area (Historic)	9.12 \pm 1.01	10.07 \pm 1.01	11.02 \pm 1.01	a, <0.0001
Basal area (Future/Historic)	5.41 \pm 1.01	5.82 \pm 1.01	6.11 \pm 1.01	b, <0.0001
Prop. PIAL (Future)	0.2107 \pm 0.002	0.2205 \pm 0.002	0.2294 \pm 0.002	c, <0.0001
Prop. PIAL (Historic)	0.3119 \pm 0.003	0.3324 \pm 0.003	0.3584 \pm 0.003	b, <0.0001
Prop. PIAL (Future/Historic)	0.2552 \pm 0.002	0.2765 \pm 0.002	0.2945 \pm 0.003	b, <0.0001

^a Significant differences among factors indicated by a, RN v RL and RH are significantly different from each other; b, RN v RL and RH at <0.0001, RH v RL at 0.001; c, RN v RL and RH at <0.0001, RH v RL at <0.05; d, all treatments are significantly different from each other; e, SH v SN.

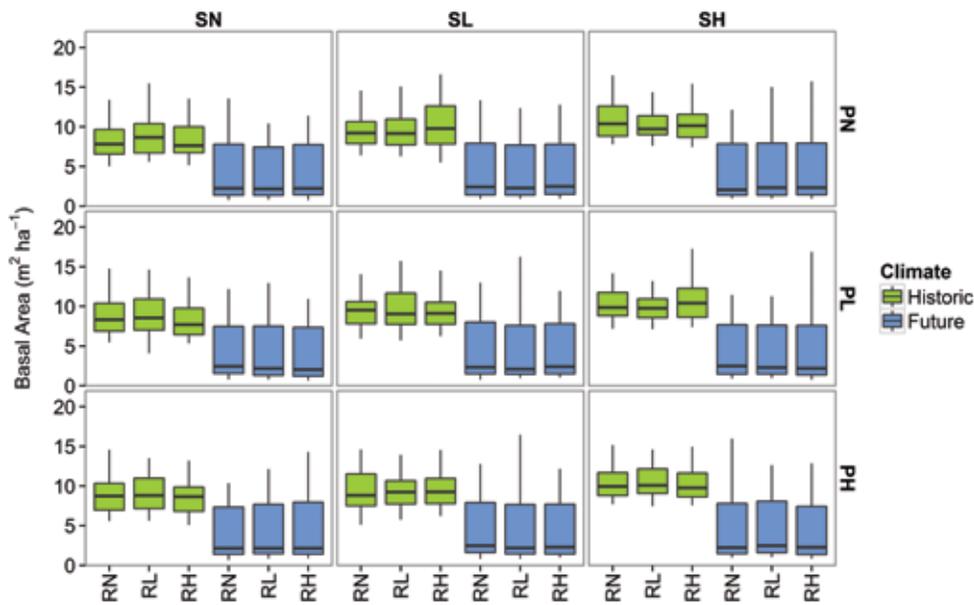


Figure 31—Basal area (m²ha⁻¹) of whitebark pine in upper elevations (whitebark pine zone) of CROWN landscape across all scenarios including: historic (green) and future (blue) climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). These results are dramatically different than those for the EFBR in that future whitebark pine stands will have lower basal areas regardless of restoration treatment.

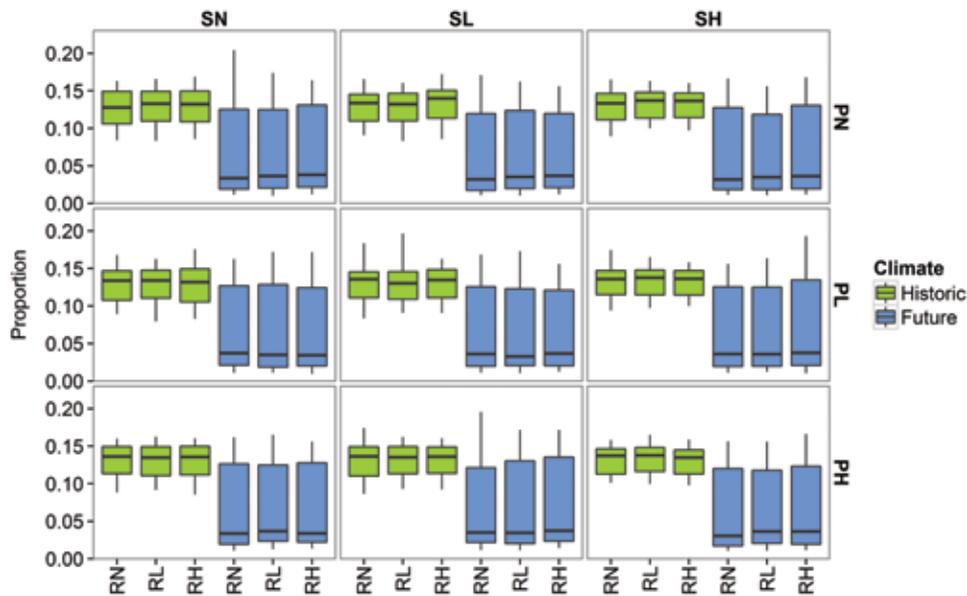


Figure 32—Proportion of landscape in whitebark pine in upper elevations (whitebark pine zone) of the CROWN landscape across all scenarios including: historic (green) and future (blue) climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). These results are dramatically different than those for the EFBR in that whitebark pine will have lower occurrence in the future regardless of restoration treatment.

pine increased with increasing levels of suppression (each level significantly different from each other to varying degrees; table 4). When climate was included as a factor, suppression and climate were the most important influences. Finally neither restoration nor planting treatments had any notable influence on whitebark pine basal area in the CROWN landscape.

When WPBR resistance (two levels, 5 percent and 30 percent resistance) was considered with the other factors, both rust resistance and restoration had the greatest effects on basal area in the EFBR under both future and historical climates (table 6). Rust resistance

interacting with restoration and suppression were also highly significant, and to a lesser degree, planting. In general, basal area was higher when restoration measures were implemented at both low and high levels of rust resistance (table 7). Perhaps most striking is that under future climates at the 5 percent resistance level, both low and high restoration treatments had 7 to 8 times more whitebark pine basal area than without restoration. Basal area was also significantly higher with low and high suppression compared to historical fire regimes—at the low rust resistance level—in every climate scenario. Similar results occurred at the

Table 6—Results of generalized linear mixed models for the effects of planting, restoration, suppression, climate and rust resistance for the amount of basal area ($m^2 ha^{-1}$) and the proportion of the landscape covered in whitebark pine (PIAL) in the upper elevation areas of EFBR landscape. Asterisk indicates significant interaction between effects.

Type III tests of fixed effects			
Effect	F statistic	Degrees of freedom numerator; denominator	P-value
Whitebark pine basal area			
<i>Future</i>			
Rust resistance	10634.30	1; 5114	<0.0001
Restoration	139.72	2; 263	<0.0001
Planting	0.84	2; 263	0.43
Suppression	1.35	2; 263	0.26
Year	1681.82	9; 5114	<0.0001
Rust * Rx	307.90	2; 5114	<0.0001
Rust * Planting	4.01	2; 5114	0.02
Rust * Suppression	11.92	2; 5114	<0.0001
<i>Historical</i>			
Rust resistance	8631.48	1; 5116	<0.0001
Restoration	54.36	2; 259	<0.0001
Planting	0.30	2; 259	0.74
Suppression	0.62	2; 259	0.54
Year	2054.37	9; 5116	<0.0001
Suppression * Restoration	3.73	4; 259	0.006
Rust * Restoration	58.01	2; 5116	<0.0001
Rust * Suppression	34.53	2; 5116	<0.0001
<i>Future and Historical</i>			
Rust resistance	18300.44	1; 10246	<0.0001
Restoration	184.11	2; 532	<0.0001
Planting	0.09	2; 532	0.91
Suppression	1.90	2; 532	0.15
Climate	422.71	1; 532	<0.0001
Climate * Year	636.84	9; 10235	<0.0001
Year	3134.90	9; 10235	<0.0001
Rust * Rx	269.73	2; 10235	<0.0001
Rust * Planting	3.00	2; 10235	0.05
Rust * Suppression	39.89	2; 10235	<0.0001
Landscape proportion area (%)			
<i>Future</i>			
Rust resistance	0.01	1; 266	0.92
Restoration	1064.68	2; 270	<0.0001
Planting	1.27	2; 266	0.28
Suppression	2.91	2; 285	0.06
Year	539.37	9; 3750	<0.0001
Restoration * Suppression	2.75	2; 279	0.03
<i>Historical</i>			
Rust resistance	2.06	1; 460	0.15
Restoration	404.64	2; 467	<0.0001
Planting	0.07	2; 460	0.93
Suppression	5.02	2; 460	0.007
Year	592.71	9; 4337	<0.0001
<i>Future and Historical</i>			
Rust resistance	0.24	1; 1056	0.62
Restoration	952.60	2; 1067	<0.0001
Planting	0.68	2; 1056	0.51
Suppression	4.33	2; 1088	0.01
Climate	1927.29	1; 1048	<0.0001
Year	547.39	9; 8875	<0.0001
Restoration * Suppression	2.49	4; 1077	0.04

Table 7—Multiple comparisons of the main treatment effect’s least square means (\pm standard error) and interactions for planting, restoration, suppression, rust resistance and climate using Tukey’s honestly significant difference (HSD) test to evaluate whether means were significantly different from each other with corrections for unbalanced replication using the Tukey-Kramer adjustment for Basal Area in whitebark pine (PIAL) and the proportion of area dominated by whitebark pine in upper elevations of EFBR. Future and historic climates evaluated separately and combined. Only significant results are shown. Asterisk indicates significant interaction under noted variable.

Variables	None	Low	High	P-value ^a
Basal area				
<i>Future</i>				
Restoration	2.34 \pm 1.04	4.75 \pm 1.04	4.73 \pm 1.04	a, <0.0001
Rust = 5% * Restoration	0.72 \pm 1.04	5.78 \pm 1.04	5.33 \pm 1.04	a, <0.0001
Rust = 30% * Restoration	3.18 \pm 1.04	3.90 \pm 1.04	4.19 \pm 1.04	b, <0.0001
Rust = 5% * Suppression	3.38 \pm 1.04	3.94 \pm 1.04	3.98 \pm 1.04	c, <0.05
<i>Historic</i>				
Restoration	1.33 \pm 1.03	2.18 \pm 1.03	1.77 \pm 1.03	d, <0.0001
Rust = 5% * Restoration	1.20 \pm 1.04	2.53 \pm 1.04	1.77 \pm 1.04	e, <0.0001
Rust = 30% * Restoration	1.48 \pm 1.04	1.88 \pm 1.04	1.78 \pm 1.03	f, <0.0001
Rust = 5% * Suppression	1.57 \pm 1.04	1.73 \pm 1.04	1.98 \pm 1.04	g, <0.0001
Rust = 30% * Suppression	1.54 \pm 1.04	1.79 \pm 1.04	1.79 \pm 1.04	c, <0.05
<i>Future and Historic</i>				
Restoration	1.76 \pm 1.03	3.22 \pm 1.03	2.89 \pm 1.03	h, <0.0001
Rust = 5% * Restoration	1.43 \pm 1.04	3.86 \pm 1.04	3.07 \pm 1.04	e, <0.0001
Rust = 30% * Restoration	2.18 \pm 1.04	3.69 \pm 1.04	2.73 \pm 1.04	a, <0.0001
Rust = 5% * Suppression	2.29 \pm 1.04	2.62 \pm 1.04	2.81 \pm 1.04	c, <0.05
Proportion landscape area				
<i>Future</i>				
Restoration	0.12 \pm 0.004	0.46 \pm 0.006	0.50 \pm 0.006	e, <0.0001
Restoration = Low * Suppression	0.43 \pm 0.011	0.45 \pm 0.011	0.50 \pm 0.011	i, <0.0001
<i>Historic</i>				
Restoration	0.07 \pm 0.002	0.13 \pm 0.003	0.16 \pm 0.003	e, <0.0001
Suppression	0.10 \pm 0.003	0.11 \pm 0.003	0.12 \pm 0.003	i, <0.05
<i>Future and Historic</i>				
Restoration	0.09 \pm 0.002	0.28 \pm 0.005	0.32 \pm 0.005	e, <0.0001
Suppression	0.20 \pm 0.004	0.21 \pm 0.004	0.22 \pm 0.004	i, < 0.05
Restoration = Low * Suppression	0.26 \pm 0.007	0.28 \pm 0.008	0.31 \pm 0.008	j, <0.0001

^a Significant differences (repeated measures ANOVA with Tukey’s HSD) among factors indicated by a, RN v RL and RH significantly different, b, RN v RH at <0.0001, RN v RL at <0.05; c, SN v SL and SH; d, RN v RL and RH at <0.0001, RL v RH at <0.05; e, all treatments significantly different; f, RN v RL at <0.0001, RN v RH at <0.05; g, SN v SH at <0.0001, SL v SH at <0.05; h, RN v RL and RH at <0.0001, RL v RH at 0.05; i, SN v SH; j, SN v SH at <0.0001, SL v SH at <0.05.

high rust resistance level in the historical climate only. In contrast, the proportion of canopy in whitebark pine was not evidently influenced by rust resistance under any of the climate scenarios (tables 6, 7).

In the CROWN landscape, rust resistance also had a significant effect on the amount of basal area, as did suppression and their interactions under both climate scenarios (tables 8, 9). Whitebark pine basal area was significantly higher with increasing levels of suppression at both low and high rust resistance levels, except under the future climate scenario, where this was only the case at low rust resistance (table 8). Similar relationships were observed for the proportion of landscape area in whitebark pine, where rust

resistance and suppression had the greatest effects in each of the climate scenarios (table 9). Also, as with basal area, the proportion of landscape cover in whitebark was greater with each increasing suppression level (table 9).

4.4.2 Forest Species Community Response

Whitebark pine (PIAL in table 3) was the dominant species (46 to 53 percent on average) under a future climate in the upper elevations (whitebark pine zone) of the EFBR when either low or high levels of restoration treatments were implemented (fig. 33). Without any restoration, subalpine fir (ABLA) was dominant (76 percent), with whitebark pine as the second most dominant specie (9 percent). Under the historical

Table 8—Results of generalized linear mixed models for the effects of planting, restoration, suppression, climate and rust resistance for the amount of basal area (m² ha⁻¹) and proportion of landscape cover in whitebark pine (PIAL) in the upper elevation areas of CROWN. Asterisk indicates significant interaction between effects

Type III tests of fixed effects			
Effect	CROWN		
Effect	F statistic	Degrees of freedom numerator; denominator	P-value
Whitebark pine basal area			
<i>Future</i>			
Rust	58213.34	1; 58213	<0.0001
Restoration	0.54	2; 263	0.59
Planting	1.21	2; 263	0.30
Suppression	13.43	2; 263	<0.0001
Year	13.36	9; 518	<0.0001
Rust * Suppression		2; 5118	<0.0001
<i>Historic</i>			
Rust	12053.97	1; 5118	<0.0001
Restoration	0.22	2; 263	0.80
Planting	0.13	2; 263	0.87
Suppression	117.03	2; 263	<0.0001
Year	5905.59	9; 5118	<0.0001
Rust * Suppression	38.45	4; 5118	<0.0001
<i>Future and Historic</i>			
Rust	63599.78	1; 10239	<0.0001
Restoration	0.50	2; 532	0.61
Planting	0.87	2; 532	0.42
Suppression	88.95	2; 532	<0.0001
Climate	24586.45	1; 532	<0.0001
Climate * Year	6485.98	9; 10239	<0.0001
Year	34326.02	9; 10239	<0.0001
Rust * Suppression	33.04	3; 10239	<0.0001
Proportion of landscape cover of whitebark pine			
<i>Future</i>			
Rust	8178.95	1; 5381	<0.0001
Restoration	0.60	2; 5381	0.55
Planting	0.38	2; 5381	0.68
Suppression	3.36	2; 5381	0.04
Year	1440.62	9; 5381	<0.0001
Rust * Suppression	4.61	2; 5381	0.01
<i>Historic</i>			
Rust	15316.4	1; 576	<0.0001
Restoration	1.51	2; 573	0.22
Planting	1.11	2; 573	0.33
Suppression	45.95	2; 577	<0.0001
Year	646.48	9; 4692	<0.0001
Rust * Suppression	27.51	2; 577	<0.0001
<i>Future and Historic</i>			
Rust	870.44	1; 10780	<0.0001
Restoration	0.53	2; 10780	0.59
Planting	0.23	2; 10780	0.79
Suppression	12.76	2; 10780	<0.0001
Climate	870.44	1; 10780	<0.0001
Year	1170.36	9; 9862	<0.0001
Rust * Suppression	9.4	2; 10780	<0.0001

Table 9—Multiple comparisons of the main treatment effect's least square means (\pm standard error) and interactions for planting, restoration, suppression, rust resistance and climate using Tukey's honestly significant difference (HSD) test to evaluate whether means were significantly different from each other with corrections for unbalanced replication using the Tukey-Kramer adjustment for basal area in whitebark pine (PIAL) and percent of whitebark pine in upper elevations of CROWN. Future and historic climates evaluated separately and combined. Only significant results shown. Asterisk indicates significant difference under the noted variable.

Variables	None	Low	High	P-value ^a
Basal area				
<i>Future</i>				
Rust	–	3.42 \pm 1.01	3.22 \pm 1.01	<0.0001
Suppression	3.26 \pm 1.01	3.42 \pm 1.01	3.42 \pm 1.01	a, <0.0001
Rust = 5% * Suppression	3.25 \pm 1.01	3.49 \pm 1.01	3.54 \pm 1.01	a, <0.0001
<i>Historic</i>				
Suppression	9.19 \pm 1.01	9.95 \pm 1.01	10.88 \pm 1.01	b, <0.0001
Rust = 5% * Suppression	8.89 \pm 1.01	9.88 \pm 1.01	11.13 \pm 1.01	b, <0.0001
Rust = 30% * Suppression	9.50 \pm 1.01	10.03 \pm 1.01	10.62 \pm 1.01	c, <0.0001
<i>Future and Historic</i>				
Rust	–	5.83 \pm 1.00	5.78 \pm 1.00	<0.05
Suppression	5.47 \pm 1.01	5.84 \pm 1.01	6.10 \pm 1.01	b, <0.0001
Rust = 5% * Suppression	5.37 \pm 1.01	5.87 \pm 1.01	6.28 \pm 1.01	b, <0.0001
Rust = 30% * Suppression	5.58 \pm 1.01	5.82 \pm 1.01	5.94 \pm 1.01	a, <0.0001
Proportion PIAL				
<i>Future</i>				
Rust	–	0.06 \pm 0.001	0.22 \pm 0.002	<0.0001
Suppression	0.11 \pm 0.002	0.12 \pm 0.002	0.12 \pm 0.002	e, <0.05
Rust = 30% * Suppression	0.21 \pm 0.003	0.22 \pm 0.003	0.23 \pm 0.003	f, <0.0001
<i>Historic</i>				
Suppression	0.20 \pm 0.001	0.21 \pm 0.002	0.22 \pm 0.001	b, <0.0001
Rust = 30% * Suppression	0.31 \pm 0.002	0.33 \pm 0.002	0.36 \pm 0.002	b, <0.0001
<i>Future and Historic</i>				
Suppression	0.15 \pm 0.002	0.16 \pm 0.002	0.17 \pm 0.002	f, <0.0001
Rust = 30% * Suppression	0.26 \pm 0.003	0.28 \pm 0.003	0.30 \pm 0.003	c, <0.0001

^a Significant differences (repeated measures ANOVA with Tukey's HSD) among factors indicated by a, SN v SL and SH significantly different, b, all treatments significantly different from each other; c, SH v SN and SL at <0.0001, SL v SN at <0.05; e, SN v SH; f, SN v SH at <0.0001, SL v SN and SH at <0.05.

climate, applying high restoration resulted in aspen (POTR) as the dominant species (59 percent), and comparable amounts of subalpine fir (21 percent) and whitebark pine (17 percent) (fig. 34). Both low and high levels of restoration kept whitebark pine on the landscape (>12 percent), but subalpine fir was still the dominant cover type (40 percent) followed by aspen (35 percent). Without restoration, subalpine fir dominated the high elevation landscape (76 percent) using historical weather data.

In contrast, there was little variation in community composition among treatments and climate in the CROWN landscape (figs. 35, 36). Subalpine fir dominated the upper elevation areas across all treatments in both the future (about 45 percent in fig. 35) and historical (about 35 percent in fig. 36) climates. Whitebark pine continues to remain on the high elevation landscape in both historical and future climates,

but at low levels (10 percent) probably because restoration isn't nearly as effective on this landscape compared to EFBR. The other species occurring under both future and historical climates were mainly a mixture of aspen, Douglas-fir (PSME), lodgepole pine (PICO) and Engelmann spruce (PIEN) at about 10 percent each.

In terms of structural stage distributions, forest structure in the upper elevations of the EFBR were balanced in the low and high levels restoration treatments with a mixture of sapling (25 percent for low levels and 38 percent for high), pole (37 percent for low, 25 percent for high) and mature (23 percent for low, 18 percent for high) stages with low and high levels of restoration under the future climate (fig. 37). Without restoration measures, trees were mainly in the mature stage (48 percent), followed by the pole stage (40 percent). Under the historical climate scenario,

there were similar distributions where low and high restoration treatments had stands with mixtures of sapling (17 percent for low, 40 percent for high), pole (51 percent for low, 30 percent for high), and mature (22 percent for low, 15 percent for high) trees (fig. 38). Without restoration, trees were mainly in

the mature (47 percent) and pole (39 percent) stages under the historical climate. In the CROWN landscape, trees were primarily mature (50 percent) across all treatments and climates, followed by the pole (20 percent), sapling (15 percent) and large (10 percent) structural stages (figs. 39, 40).

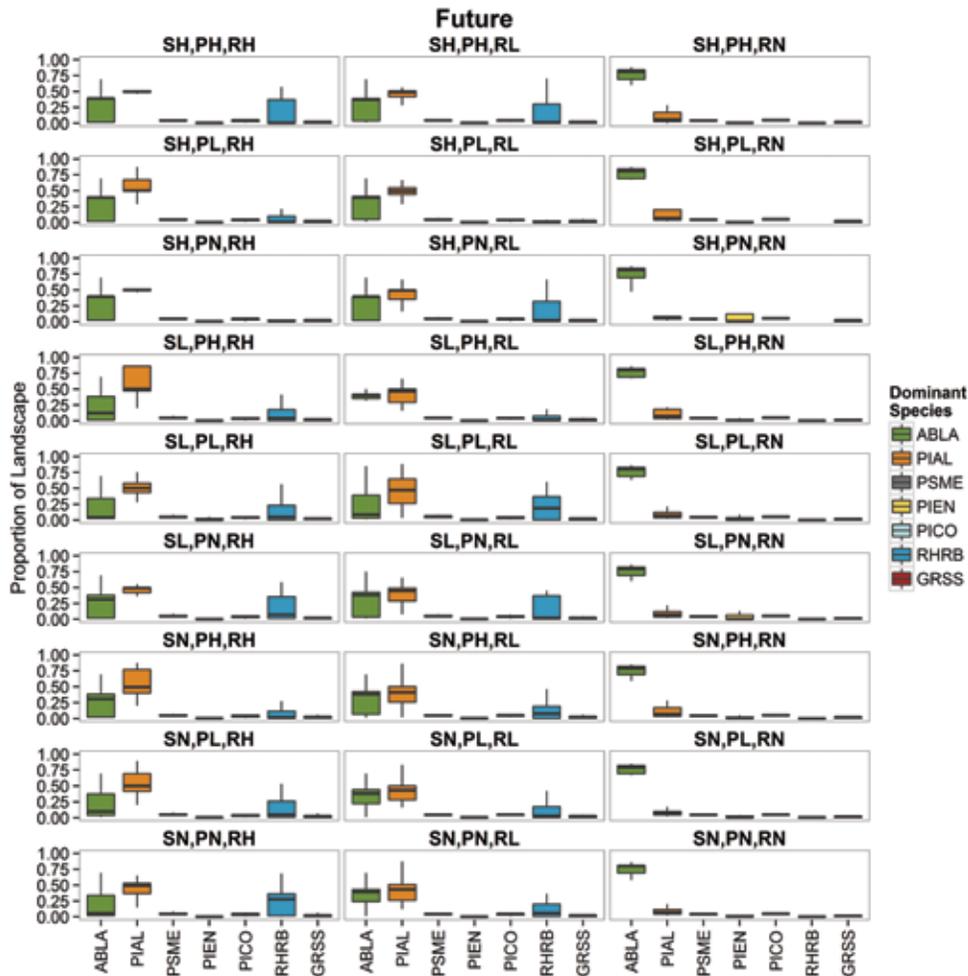


Figure 33—Forest species composition for the upper elevations of the EFBR landscape under a future climate for fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). See table 3 for species abbreviations. Whitebark pine will comprise more of the EFBR landscape in the future, especially with decreasing fire suppression and increasing restoration measures.

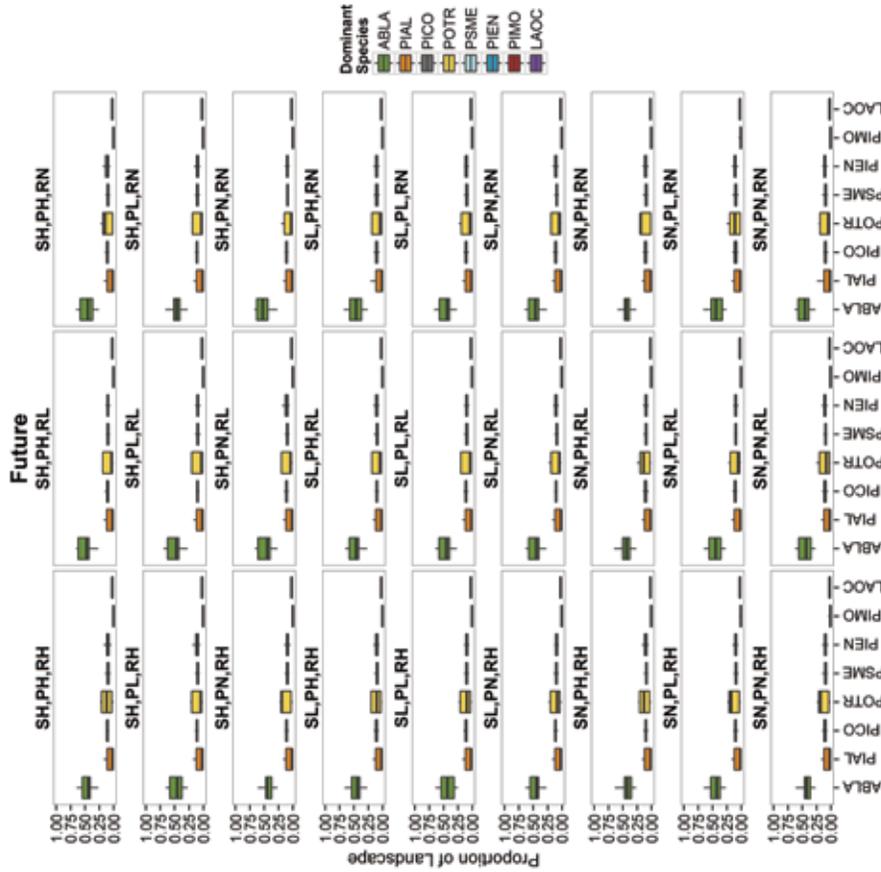


Figure 34—Forest species composition for the upper elevations of the EFBR landscape under a historical climate for fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). See table 3 for species abbreviations. Historically, whitebark pine dominated only 20 percent of the EFBR landscape with WPBR and that proportion is dramatically reduced with fire suppression and it is enhanced by restoration measures.

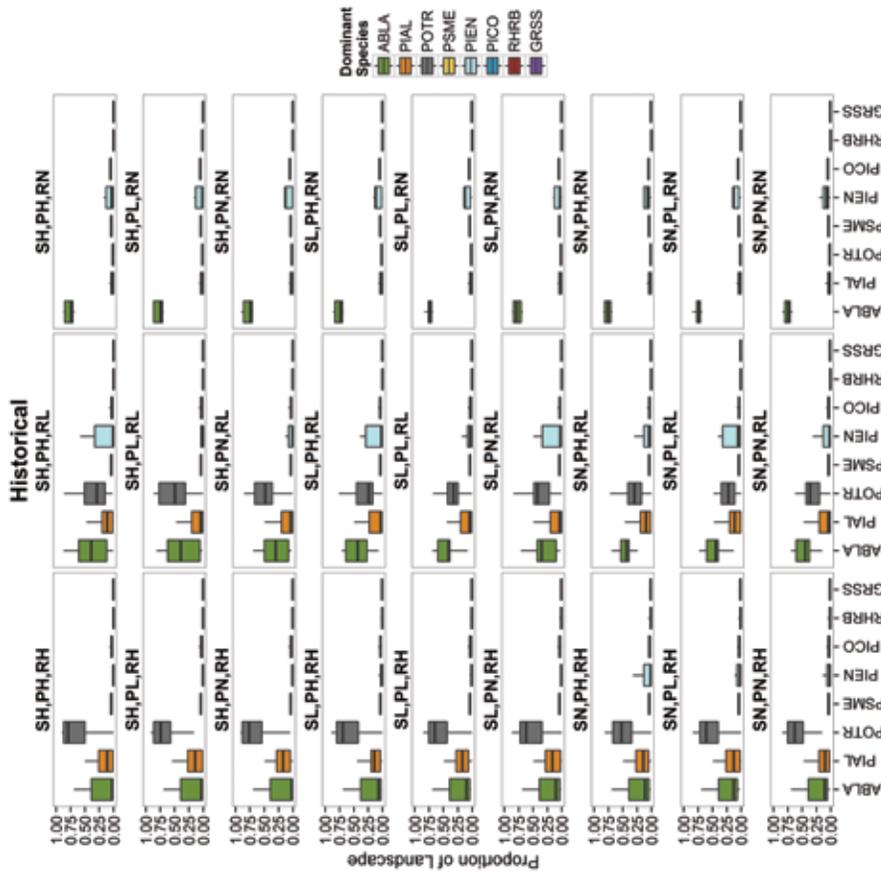


Figure 35—Forest species composition for the upper elevations of the CROWN landscape under a future climate for fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). See table 3 for species abbreviations. Whitebark pine dominates less than 10 percent of the landscape regardless of restoration activities or suppression efforts.

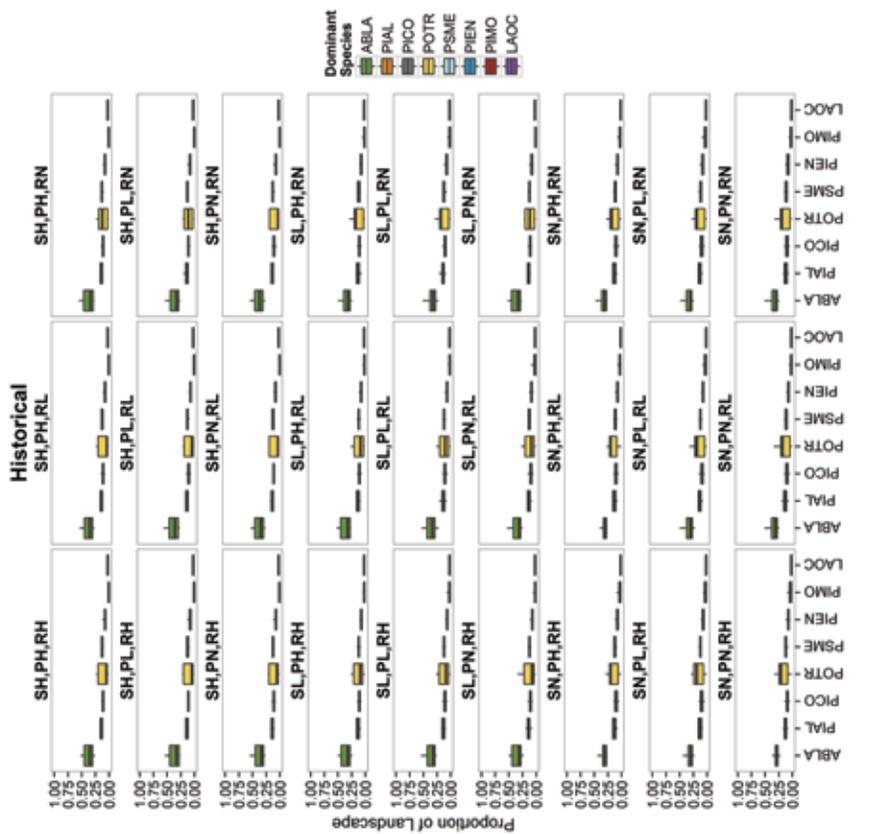


Figure 36—Forest species composition for the upper elevations of the CROWN landscape under a historical climate for fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). See table 3 for species abbreviations. Similar to future predictions, whitebark pine dominates less than 10 percent of the landscape regardless of restoration activities or suppression efforts.

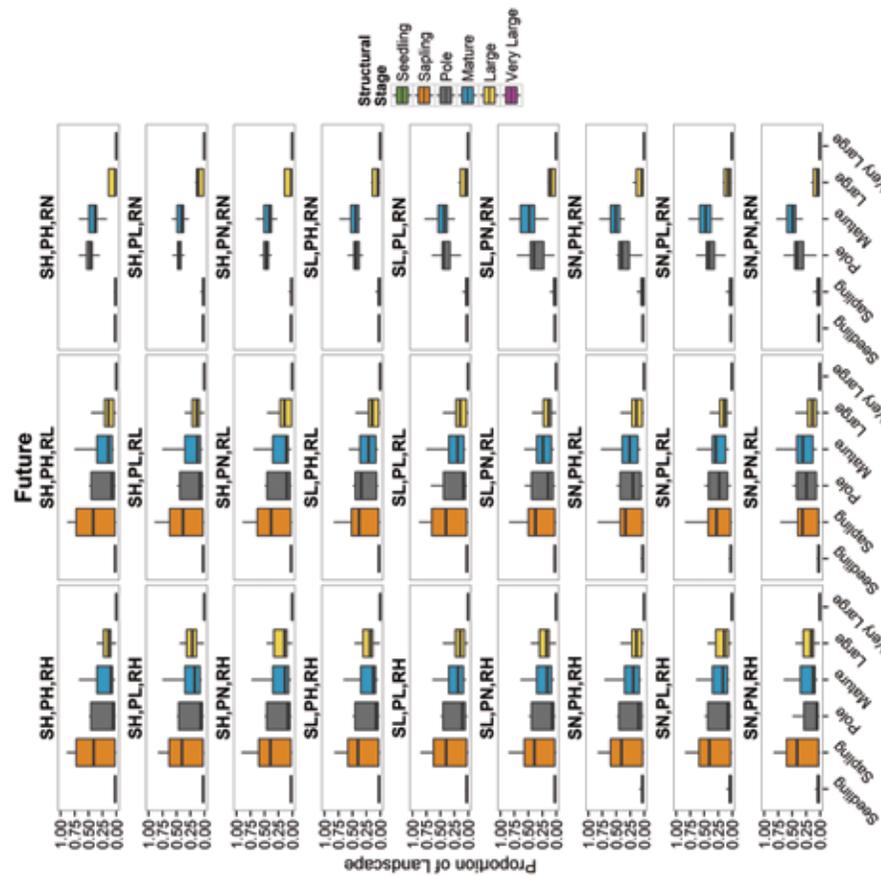


Figure 37—Structural stage distributions across the upper elevation areas of the EFBR landscape under a future climate for fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). In the future, the EFBR landscape was dominated by early seral whitebark pine stands when fires are allowed to burn regardless of restoration measures.

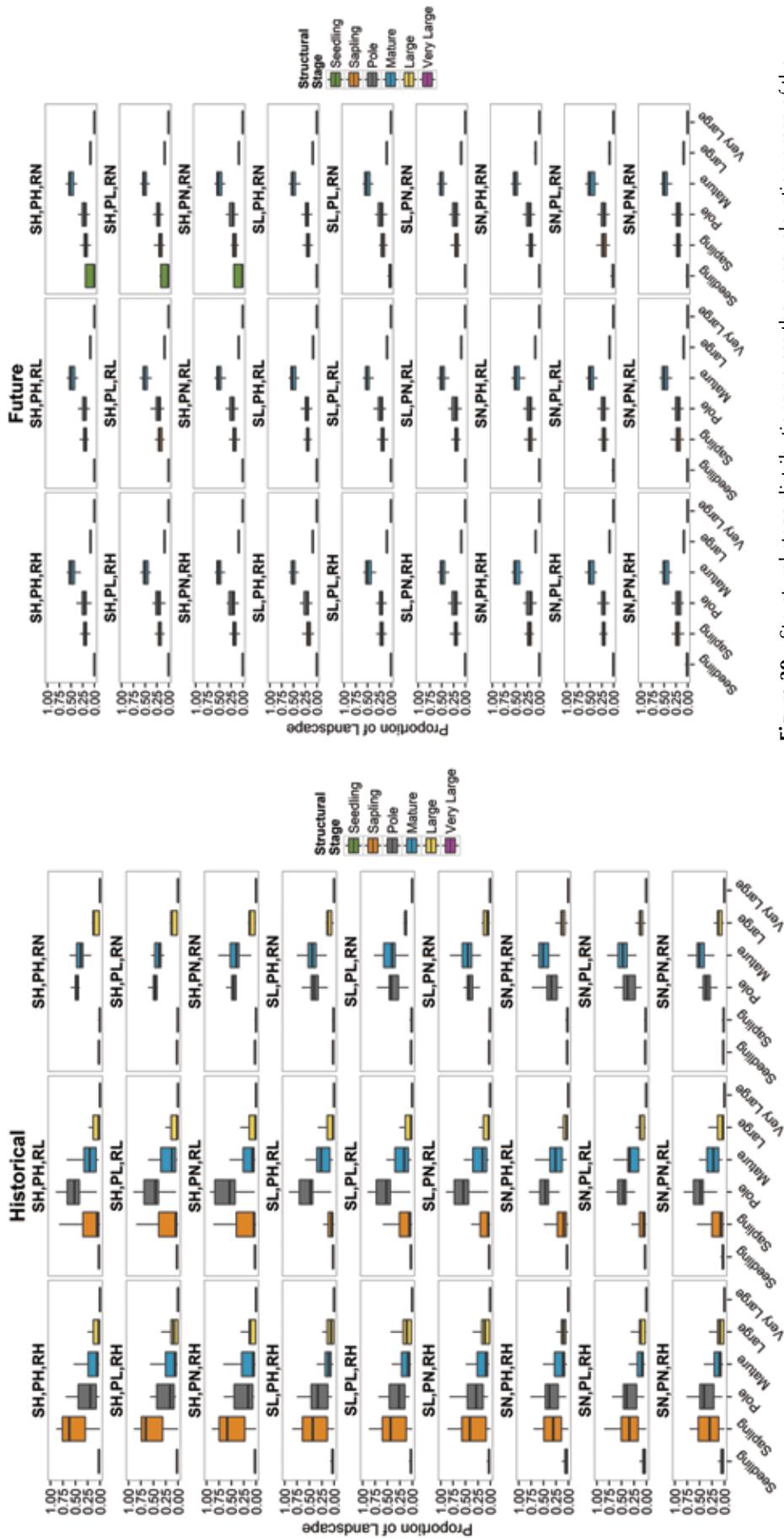


Figure 38—Structural stage distributions across the upper elevation areas of the EFBR landscape under a historic climate for fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). There was much less area in mature stands in the past than in the future (fig. 37) and late seral stands dominate when fires are suppressed.

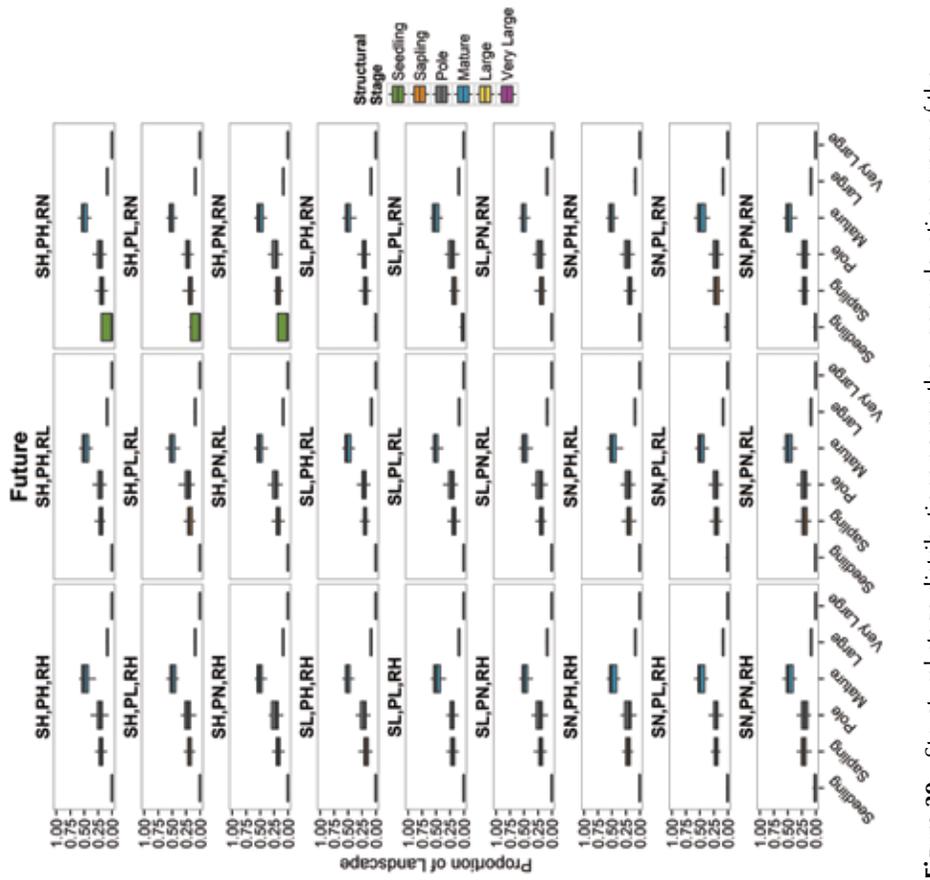


Figure 39—Structural stage distributions across the upper elevation areas of the CROWN landscape under a future climate for fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). In the future, the CROWN landscape was dominated by mature whitebark pine stands regardless of suppression or restoration measures.

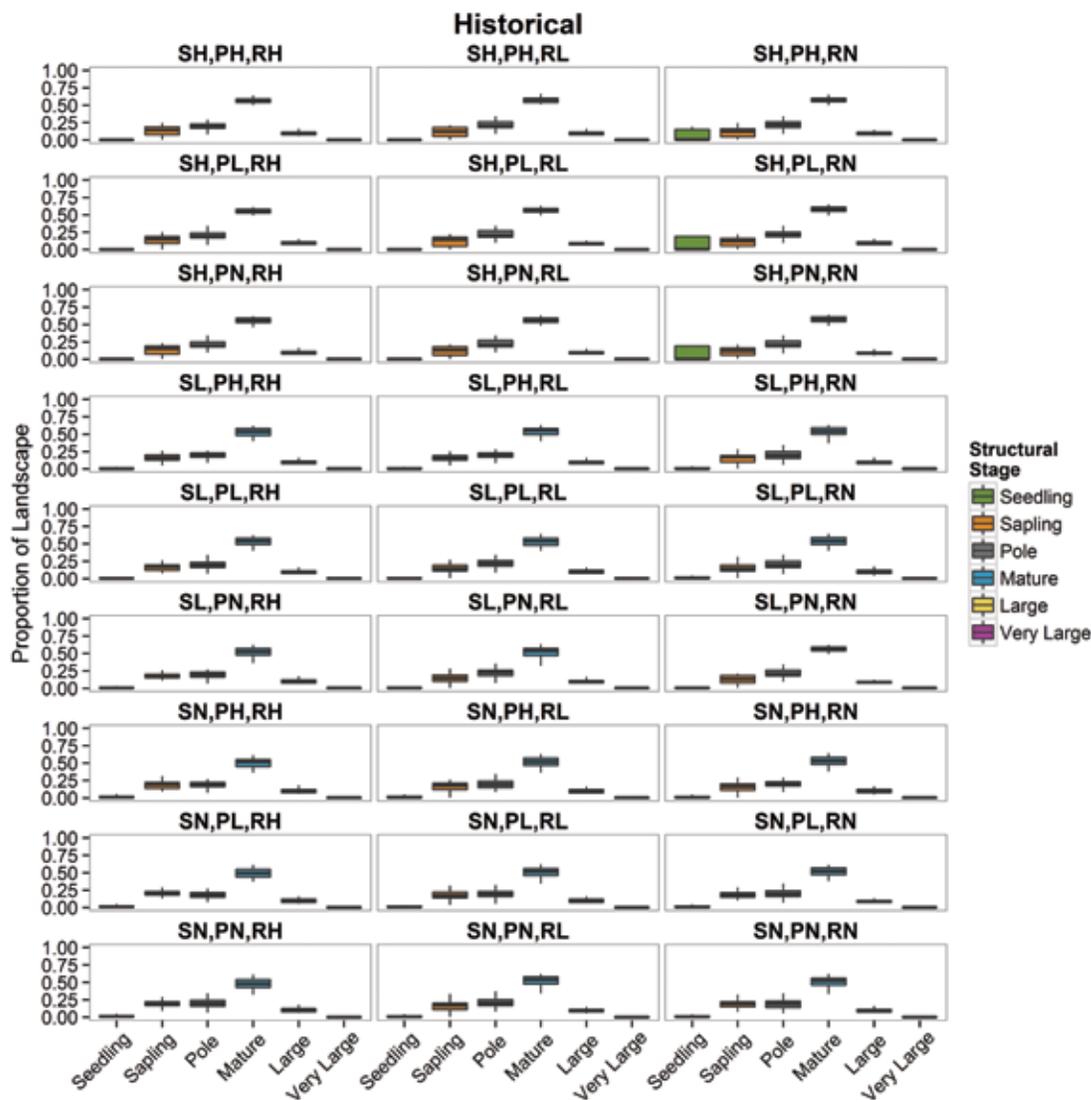


Figure 40—Structural stage distributions across the upper elevation areas of the CROWN landscape under a historic climate for fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). The distribution of structural stages on the CROWN landscape in the past was similar to that predicted for the future regardless of suppression or restoration.

4.4.3 Fuel Characteristics

Canopy bulk densities in the EFBR landscape were slightly higher under the historical climate (13 percent on average) compared to the future (10 percent) (fig. 41). Among treatments, canopy bulk densities were slightly higher without restoration treatment (up to 0.03 kg m⁻³) compared to low or high restoration in the historical and future climates. In the CROWN landscape, canopy bulk densities were quite similar between climates (20 percent for historical, 21 percent for future; fig. 42). Across treatments, canopy bulk densities were also similar (about 20 percent), with

the greatest differences in simulations without suppression (up to 0.02 kg m⁻³ lower) compared to low or no suppression.

4.4.4 Fire Regimes

On average, more area burned under a future climate than the historical climate in the EFBR (157 percent increase). Without suppression, a median of 550 ha burned annually under the future climate compared to 350 ha under the historical climate. With low suppression, 186 ha vs 155 ha burned annually, and 52 ha vs 58 ha with high suppression in the future vs historical climates, respectively. The historical climate

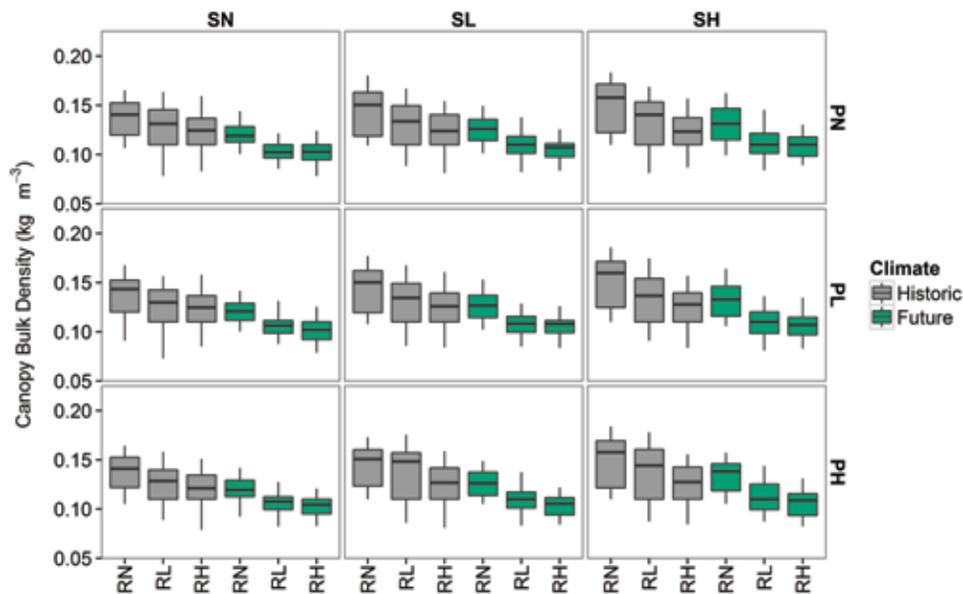


Figure 41—Canopy bulk density in the EFBR across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). Canopies were less dense in the future, especially with high restoration, which results in less chance of crown fires.

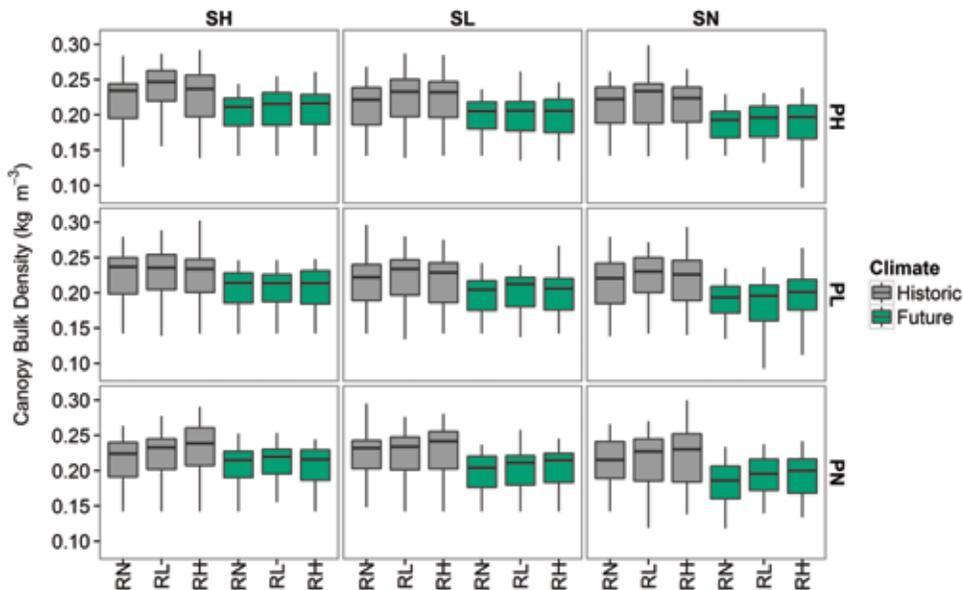


Figure 42—Canopy bulk density in the CROWN across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). Canopies were roughly the same density across all scenarios for the crown, but maybe a bit less dense in the future.

scenario generated few large fire years (years 11, 54 and 67) that were not observed in the future climate (fig. 43), but these high burn years had little overall effect on the central tendency across simulations. We estimated about 1 to 2 fewer ha burned annually under the historical climate when those fire years were removed. The percent of the landscape burned each year was only slightly less (10 percent) in the historical climate scenario than in the future scenario with corresponding levels of fire suppression (fig. 44). The median percentage burned annually under the historical versus the future scenario was: 0.48 percent versus 0.56 percent without suppression; 0.21 percent vs

0.25 percent with low suppression; and 0.059 percent vs 0.062 percent with high suppression. Average fire sizes across all scenarios were relatively invariant with a median of about 50 ha (fig. 45).

In the CROWN landscape, about half as much area was burned (median of 70 ha annually across all scenarios) compared to the EFBR (143 ha). Moreover, more area burned annually under the historical climate than the future without suppression (135 ha vs 79 ha respectively) and with low suppression (68 ha vs 62 ha, respectively). With high suppression, less area burned under the historical climate (53 ha annually) than the future (58 ha). Similar to the EFBR, there were

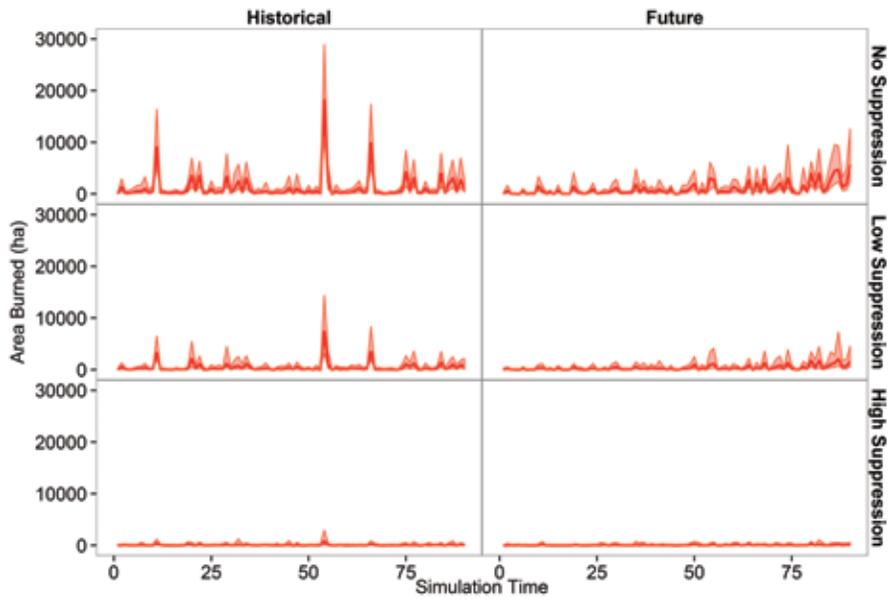


Figure 43—Average annual area burned (ha) by simulation time in the EFBR under historic and future climate and with fire suppression at none, low and high levels. More land burns in the future especially at the end of the simulation, but there was more variability in the past.

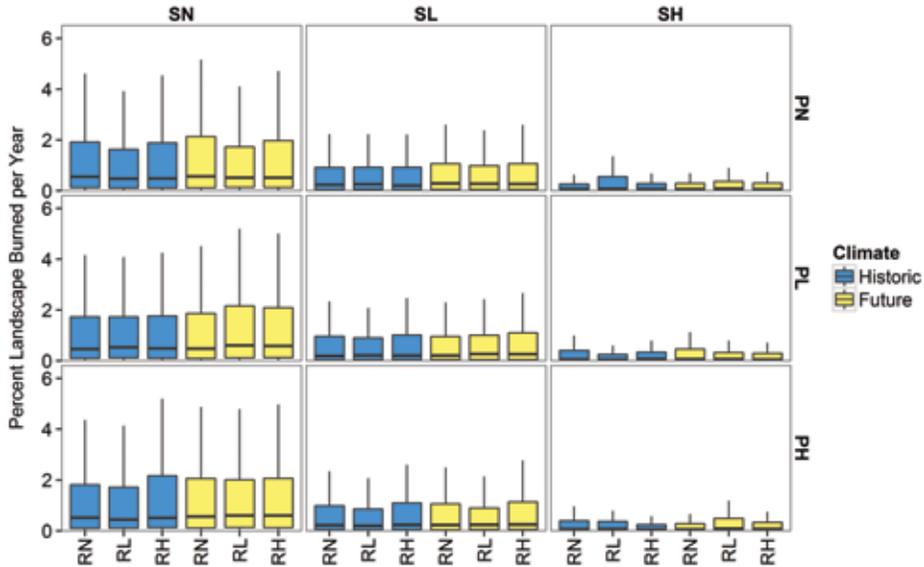


Figure 44—Percent of landscape burned per year in the EFBR across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). There was slightly more area burned in the future for the EFBR landscape. Suppression is the main factor that reduces landscape fire rotation.

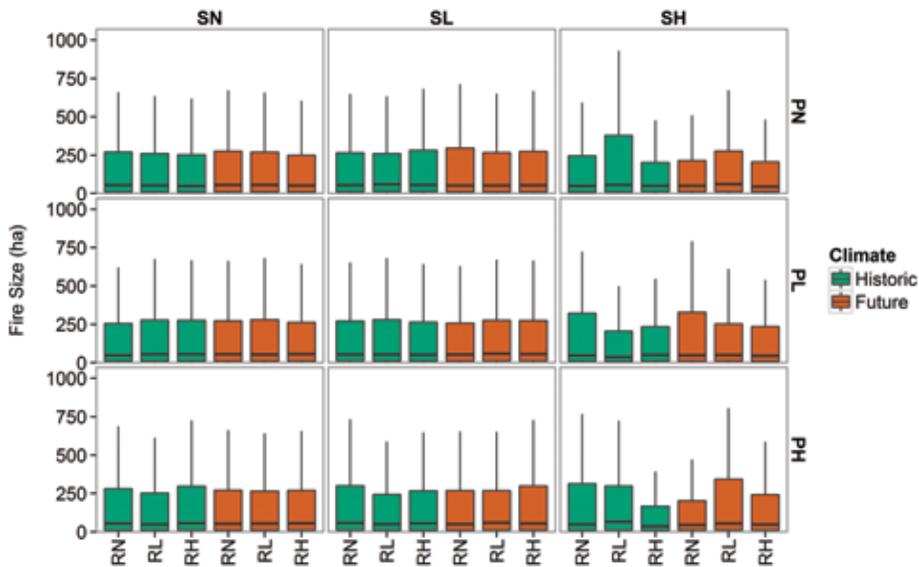


Figure 45—Fire size (ha) in the EFBR across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). Fires were about the same size regardless of scenario on the EFBR landscape.

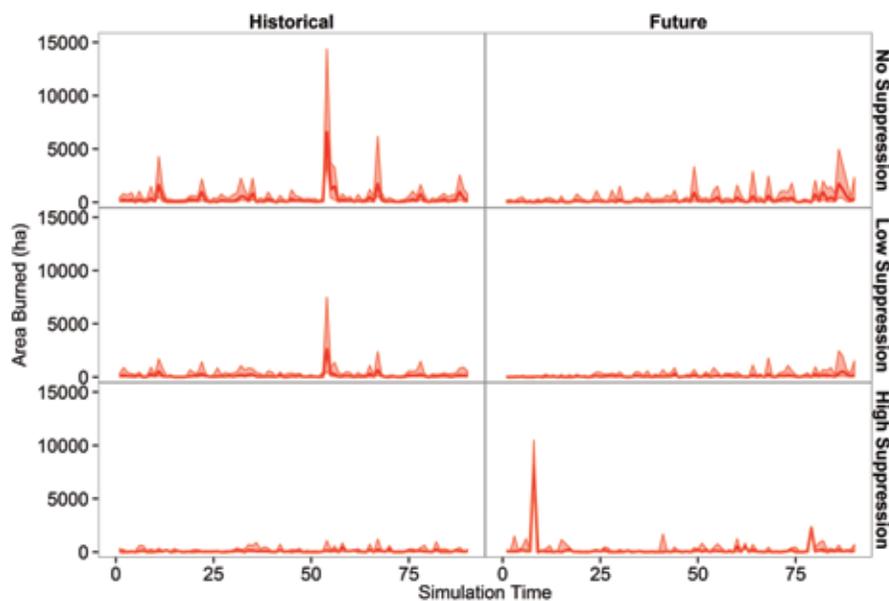


Figure 46—Average annual area burned (ha) by simulation time in the CROWN landscape under historic and future climate and with fire suppression at none, low and high levels. Fires become more frequent in the future towards the end of the simulation. Note that fires increase in the future towards the end of the simulation time span and also there is less variability in the future. Even high suppression strategies can sometimes result in a large fire year (bottom right).

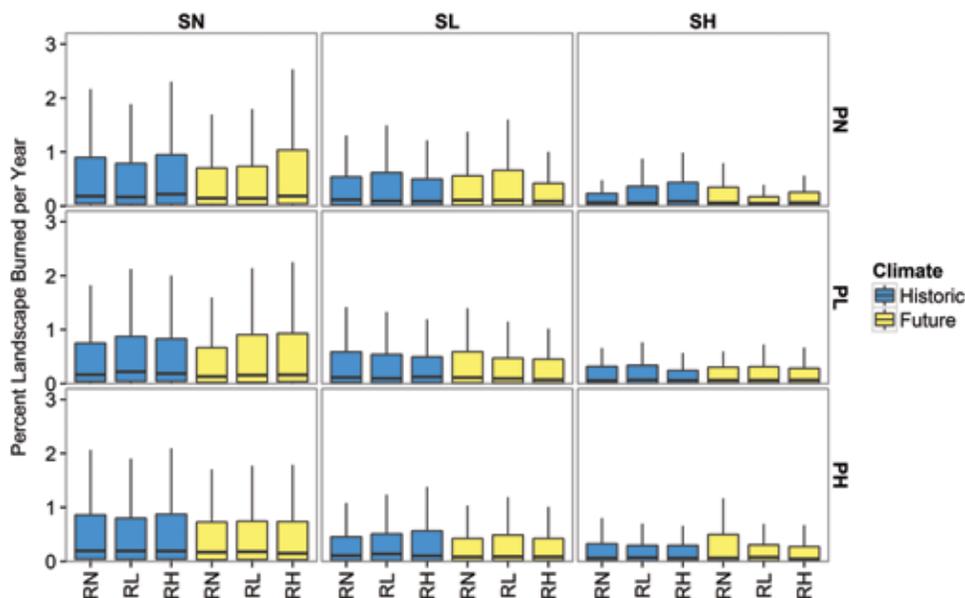


Figure 47—Percent of landscape burned per year in the CROWN landscape across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). Burned area rate was about the same in the future as it was in the past for the CROWN. Suppression is the only factor that reduces landscape fire rotation.

three very large fire years (11, 54, and 67) under the historical climate scenario to extents not observed in the future (fig. 46). When these fire years are removed from the historical dataset, the amount of area burned annually was relatively unaffected in the low and high suppression scenarios (67 ha and 52 ha respectively), but substantially lower when fires were allowed to burn (125 ha). The percent of the landscape burned each year was essentially the same between climates with low suppression (0.1 percent) and high (0.06 percent) and marginally higher without suppression under the historical climate (0.19 percent) as compared to the future scenario (0.16 percent) (fig. 47).

As in the EFBR, fire sizes in the CROWN landscape were very similar across all scenarios having a median size of 49 ha (fig. 48).

4.4.5 Fire Effects

The fire-caused tree mortality in the EFBR landscape was somewhat higher under the historical climate as compared to the future (fig. 49). We simulated average tree mortality to be 20 percent for the historical simulations versus 16 percent of trees killed annually in the future without suppression; 21 percent versus 17 percent with low suppression; and 22 percent versus 17 percent with high. Similar relationships

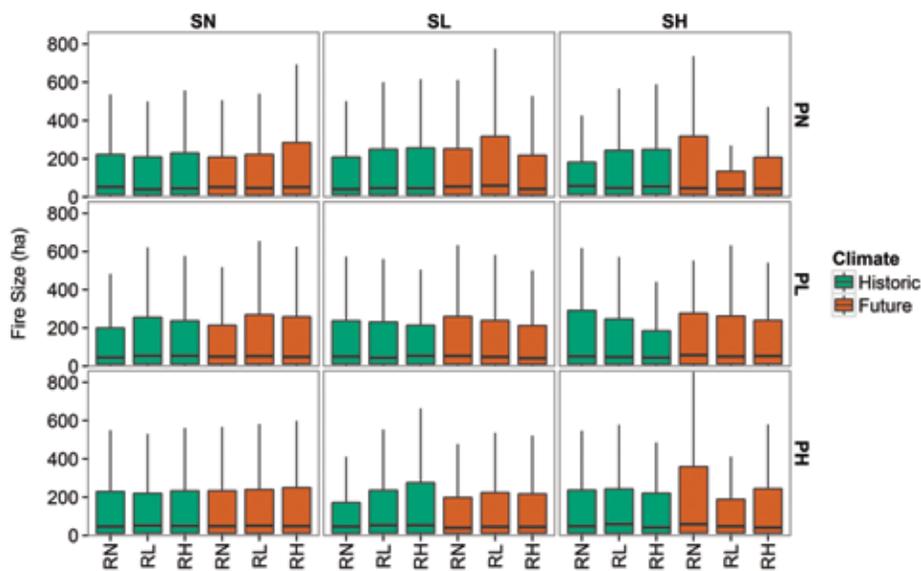


Figure 48—Fire size (ha) in the CROWN landscape across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). There was little difference in fire size across suppression, restoration, and planting scenarios.

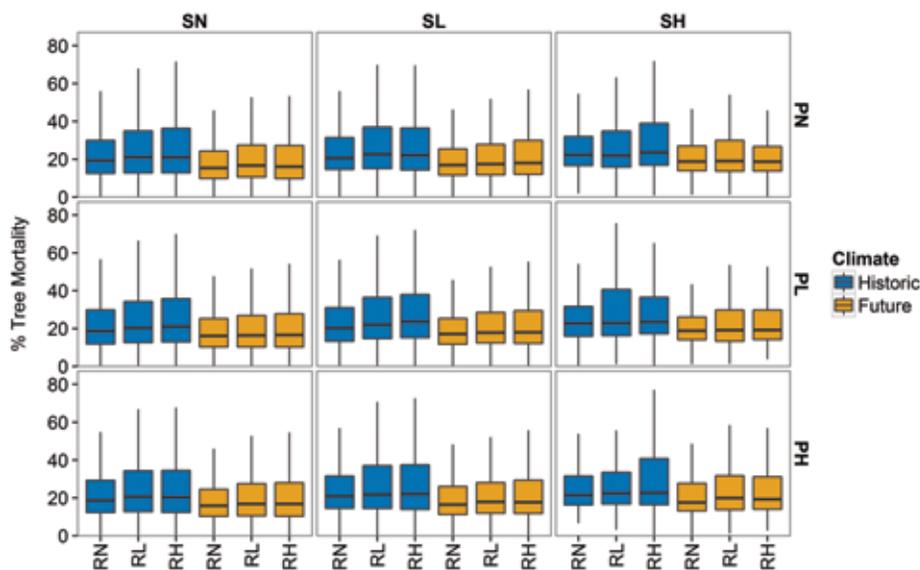


Figure 49—Percent tree mortality in the EFBR landscape across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). There was less tree mortality in the future regardless of suppression or restoration action.

for fire effects occurred in the CROWN landscape although with substantially greater magnitudes. Fire caused tree mortality was slightly higher under the historical versus future climate: 63 percent vs 61 percent without suppression; 62.5 percent vs 61.6 percent with low suppression; and 62 percent and 60 percent with high suppression (fig. 50).

Conversely, the amount of biomass consumed by fire annually in the EFBR landscape was slightly lower under the historical versus the future climate: 0.0018 kg m⁻² versus 0.0023 kg m⁻² without suppression; 0.0018 kg m⁻² versus 0.0025 kg m⁻² with low suppression; 0.0019 kg m⁻² versus 0.0026 kg m⁻² with high suppression (fig. 51). Marginally less biomass

was consumed by fire on an annual basis under the historical versus future climate: without suppression (0.0052 kg m⁻² versus 0.0053 kg m⁻²) and with low suppression (0.0055 kg m⁻² versus 0.0067 kg m⁻²). With suppression, slightly more biomass was consumed in the historical versus future climate (0.0063 kg m⁻² versus 0.0059 kg m⁻²) (fig. 52).

4.4.6 Lynx and Grizzly Bear Habitat Suitability

Habitat suitability for lynx in the EFBR declined only slightly in the future scenario (46 percent of the landscape on average) as compared to the historical climate scenario (44 percent) (fig. 53). Most notably, more lynx habitat was available when no restoration

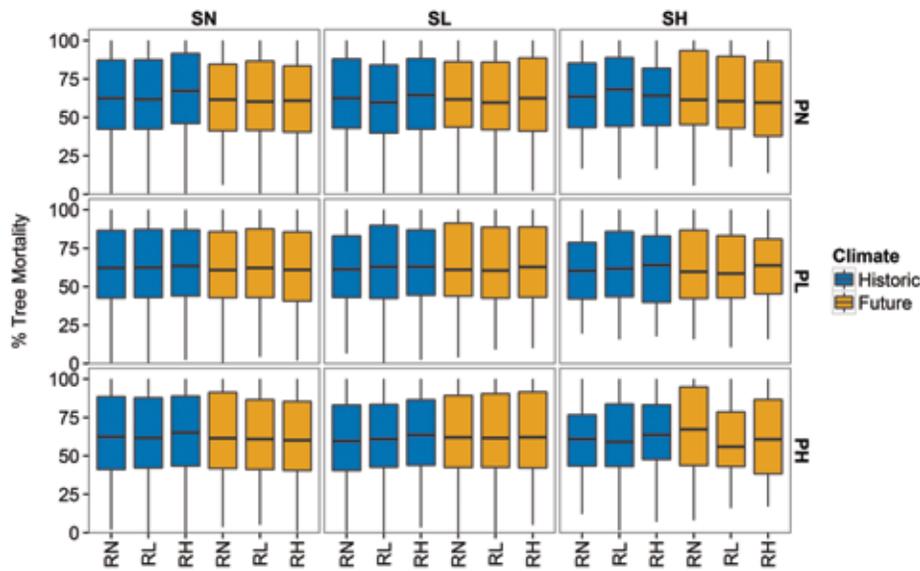


Figure 50—Percent fire-caused tree mortality in the CROWN landscape across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). There was little difference in fire mortality across suppression, restoration, and planting scenarios.

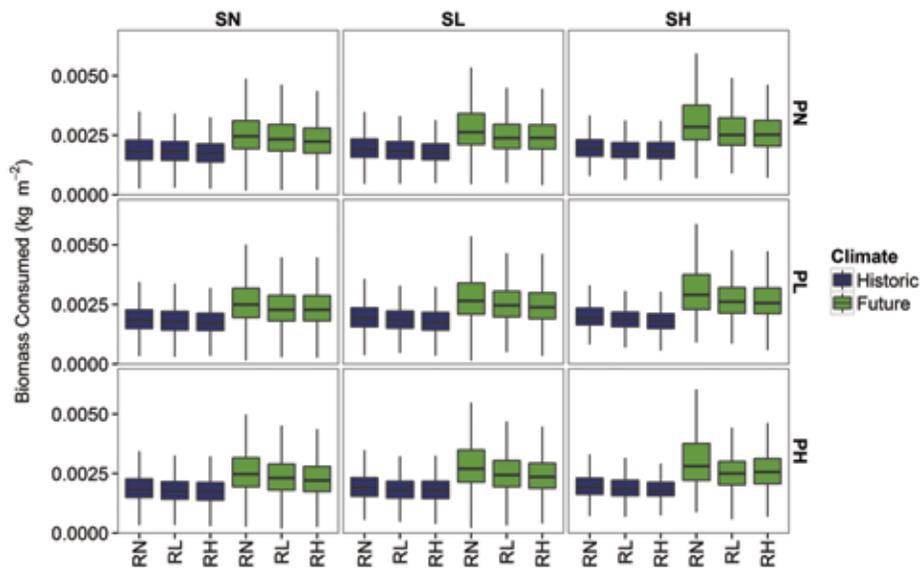


Figure 51—Biomass consumed by fire (kg m^{-2}) in the EFBR landscape across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). It appears more biomass will be consumed in the future but restoration actions may also reduce biomass consumed.

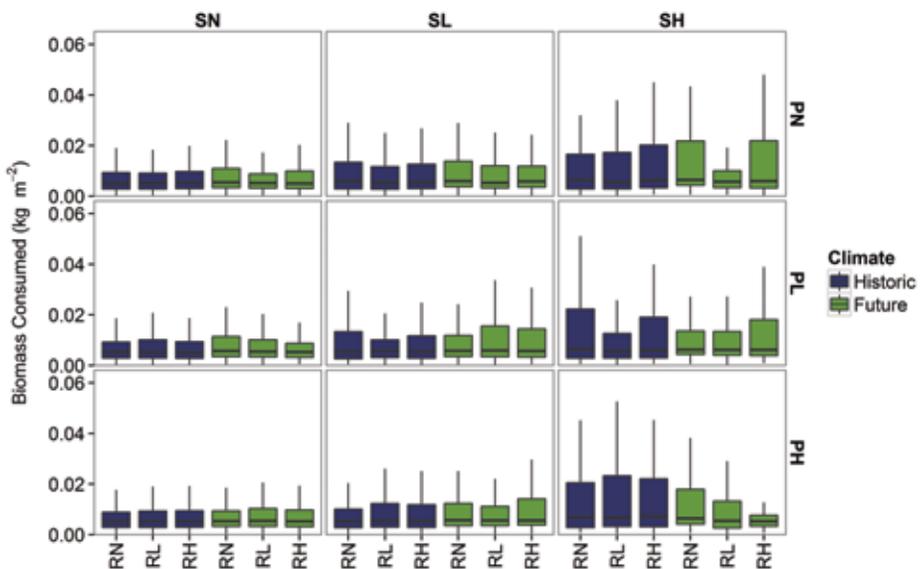


Figure 52—Biomass consumed by fire (kg m^{-2}) in the CROWN landscape across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). Amount of biomass consumed varied little over restoration actions, but it appears more biomass was consumed when fires are suppressed.

treatments were implemented in either the future or historic climates; restoration treatments reduced subalpine fir on the landscape. For grizzly bears, the amount of habitat available was essentially the same under both the historical and future climates (44 percent) (fig. 54). But restoration had the reverse effect with bear habitat increasing at low and high treatments. Planting and suppression had little effect on either lynx or bear habitat.

The response of lynx and grizzly habitat was quite different in the CROWN landscape with the dominant

influence being climate. For lynx, more habitat was available in the future climate scenario (59 percent) compared to the historical climate (53 percent) (fig. 55). Grizzly bear habitat suitability declined slightly in the future climate scenario (52 percent) as compared to the historical climate scenario (55 percent; fig. 56). None of the other treatments (restoration, suppression, planting) had any discernable influence on either lynx or grizzly bear habitat.

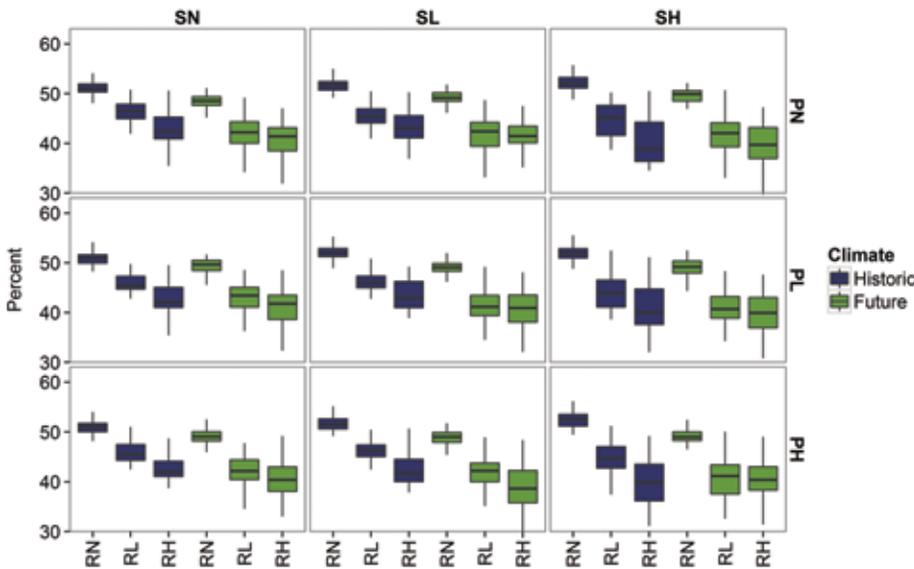


Figure 53—Percent of the EFBR landscape with habitat suitable for lynx across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). It appears lynx habitat will decrease because of restoration actions in both the future and past.

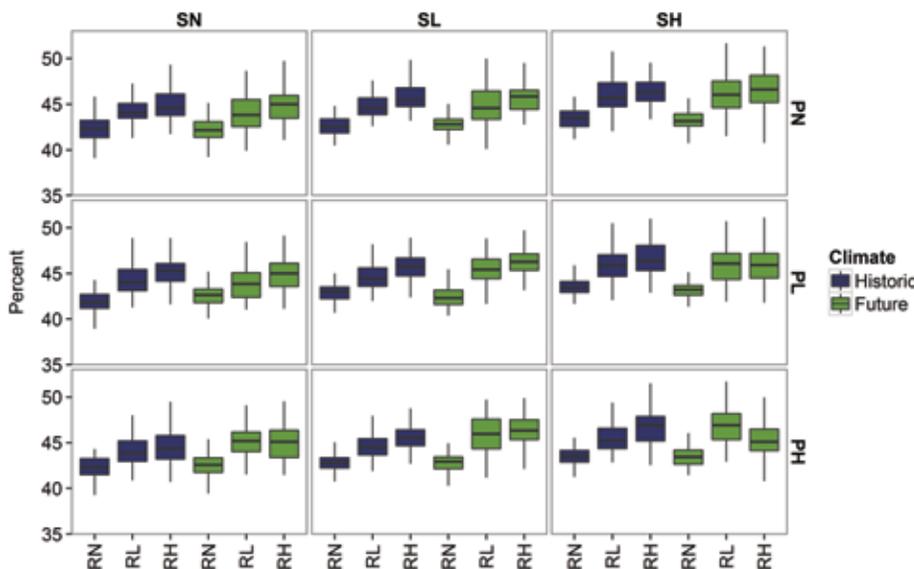


Figure 54—Percent of the EFBR landscape with habitat suitable for grizzly bear across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). It appears grizzly bear habitat may increase with restoration actions in both the future and past.

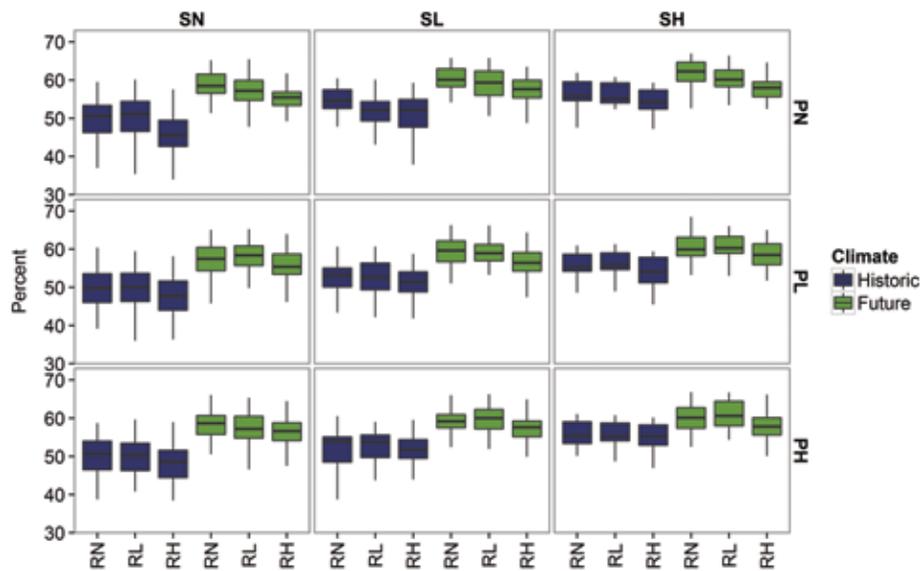


Figure 55—Percent of the CROWN landscape with habitat suitable for lynx across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). It appears lynx habitat will increase by 3–4 percent in the future regardless of restoration or suppression actions.

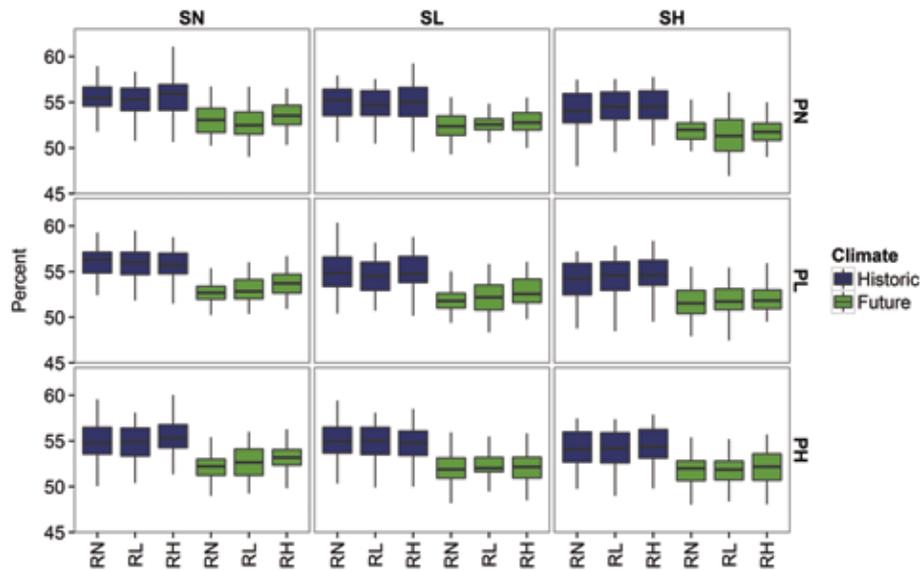


Figure 56—Percent of the CROWN landscape with habitat suitable for grizzly bear across all scenarios including: historic and future climate; fire suppression at none, low and high levels (SN, SL, SH respectively); planting at none, low and high levels (PN, PL, PH); and restoration at none, low and high levels (RN, RL and RH). It appears grizzly bear habitat will decrease by about 4 percent in the future regardless of restoration activities and suppression actions.

4.5 Simulation Summary

4.5.1 Findings

It appears from our simulations that there may be landscapes in whitebark pine’s range where the species will actually do well in abundance and extent under a future of warming climates (for example, the EFBR; figs. 29, 30). However, these future gains are only realized if there is some sort of restoration activity; even low levels of restoration will ensure potentially resilient whitebark pine forests in the future. Conversely, there are other landscapes, such as CROWN, where whitebark pine will not do well in the future (figs. 31, 32), even with restoration

and increased planting of rust-resistant seedlings. Knowing which landscapes will support future whitebark pine forests will be difficult without the aid of models such as FireBGCv2 because the interactions of fire, climate, and vegetation will dictate future landscape dynamics.

While FireBGCv2 simulation results show that whitebark pine appears to be more productive in the next of 95 years of climate warming (figs. 29, 30) for the EFBR landscape, the long-term future for whitebark pine for both simulation landscapes is (fig. 57). Our independent simulations show a downward trend in whitebark pine basal area over the next 100 years regardless of restoration level (fig. 57)

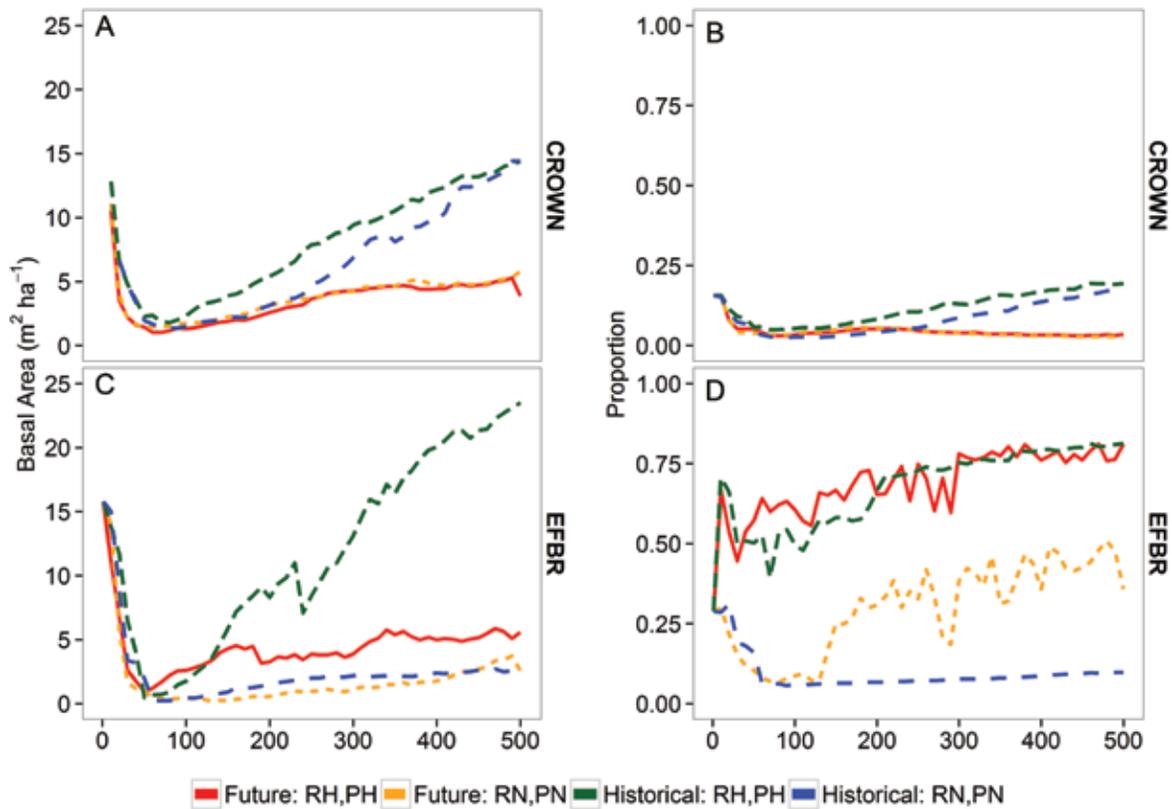


Figure 57—Independent simulations (Section 4.3) of the long-term dynamics (500 year simulations) of whitebark pine basal area ($m^2 ha^{-1}$) and landscape extent (proportion) for the two landscapes for historical (blue, green) and future climates (red, yellow) for no (RN-PN; yellow, blue) and high (RH-PH; green, red) restoration efforts (table 5): (A) CROWN landscape showing changes in whitebark pine (PIAL) basal area, (B) CROWN landscape showing changes in whitebark pine (PIAL) landscape extent as a proportion, (C) EFBR landscape showing changes in whitebark pine (PIAL) basal area, (D) EFBR landscape showing changes in whitebark pine (PIAL) landscape extent as a proportion. It appears whitebark pine will be reduced from both landscapes over the long-term but restoration treatments will ensure it will endure on the high mountain landscape.

that is primarily a result of the damaging impacts of WPBR; climate plays a minor role. However, there is an increase in whitebark pine basal area and landscape proportion after 120 years of simulation as rust resistance increases on the landscape from both natural selection and planting. Without any restoration measures, whitebark pine abundance remains low because of poor seed dispersal by nutcrackers. It appears that whitebark pine can eventually overcome the damaging effects of WPBR in about 150 years under the historical climate. Increased fire and higher temperatures in the future, however, may keep whitebark pine populations low but trending upwards. Whitebark pine levels stay low without restoration measures, but trend upwards as whitebark pine populations become more rust-resistant and as restoration activities are implemented (fig. 57).

Planting rust-resistant seedlings doesn't seem to enhance whitebark pine abundance in our simulations (figs. 29, 31; tables 5–8), but this is primarily an artifact of the short simulation period (95 years). Previous simulations by Loehman et al. (2011b) showed that it took at least 90 years for populations of whitebark pine to become sufficiently resistant to WPBR. Independent model runs of 500 years for the EFBR landscape shows that it takes about a century for the pine to rebound against WPBR and develop enough resistance to combat the disease (fig. 57). We attempted to rectify the short time period by simulating both 5 and 30 percent levels of resistance in the whitebark pine population and found that the higher resistance improved both whitebark pine basal area and proportion cover (tables 8, 9). The real payoff from planting rust-resistant seedlings probably won't

be realized for a century and its main effect is to shorten the time it takes to create rust-resistant populations of seed-producing whitebark pine.

Interestingly, simulated future wildland fire activity increased by only 57 percent in area burned over historical EFBR simulations (fig. 44), and actually went down 10 percent for CROWN simulations (fig. 47). Increases in wildland fire are one reason why whitebark pine has responded both well and poorly in future climates. Increased wildfires created ample competition-free places for nutcracker seed caching and rust-resistant seedling planting, but these same fires also killed many whitebark pine. Minor increases in burned area can result in major gains in fire-tolerant species over long time spans, but if fire is too frequent, it may kill the planted and natural whitebark pine regenerated stands. Decreases in fire activity in the CROWN are primarily due to the warmer but wetter climate projections; precipitation is projected to increase while temperatures actually start out lower and end up marginally higher in future projections (fig. 28). It is also interesting that the characteristics of the fire, primarily biomass consumed and tree mortality, remained the same under future climates for the CROWN landscape, but changed on the EFBR landscape—more biomass was consumed and fewer trees were killed. This could also explain why whitebark pine increased under future climates on the more xeric EFBR landscape. Future projections also have fire-caused tree mortality decreasing on the EFBR landscape, and this is primarily because the increases in whitebark pine basal area are creating more resilient forests in the future (fig. 49).

The large contrast in simulation results between EFBR and CROWN landscapes is probably a consequence of four interacting factors: (1) delineated whitebark pine zone, (2) climate, (3) whitebark pine abundance, and (4) landscape characteristics. The area of suitable whitebark pine was much larger on the CROWN landscape (>30,000 ha) than on the EFBR landscape (<10,000 ha) (fig. 26). The majority of the CROWN area could not support viable whitebark pine forests because of rock, glaciers, snowfields, and lodgepole pine dominance (>20 percent of the mapped whitebark pine zone). This meant that all the basal area and proportion of the landscape for

whitebark pine was heavily biased towards areas that could never support the species and explains why it was difficult to see differences across the scenarios. When we restricted the zone to its current range in the CROWN landscape, we got results somewhat similar to those from the EFBR landscape (fig. 58). Moreover, past and future climates for the CROWN landscape were colder and wetter (figs. 26, 62) than those simulated for EFBR, resulting in significantly less wildland fire (fig. 47) and more subalpine fir (figs. 33 to 36). Previous simulations by Loehman et al. (2011b) showed significantly more fire and more whitebark pine on the CROWN landscape using the offset observed historical weather rather than the simulated dataset used in this study. In addition, the CROWN landscape consists of high elevation alpine tundra, rock, and barren areas with fuel loadings so low that wildland fire could not spread to many parts of the high elevation settings. As a result, fire return intervals are also low (>400 years; fig. 47) and shade-tolerant species (subalpine fir) dominate and easily outcompete the shade-intolerant whitebark pine, even under future climates (fig. 35). If we had used a warmer, drier climate scenario for the CROWN, such as the A2 scenario used by Loehman et al. (2011b) or Holsinger et al. (2014), we would have simulated significantly more fires. And, as a result, would have seen more whitebark pine coverage but less basal area. This provides insight into the consequences regarding the high uncertainty of future climate projections. Small, subtle changes in high elevation climate can lead to a substantially different set of landscape dynamics, and it is nearly impossible to predict restoration success in the future without accurate climate projections.

The distributions of structural stages on the simulation landscape were used to evaluate two important issues: (1) the continued presence of mature, cone-producing whitebark pine (d.b.h. >20 cm) that provides food for wildlife and (2) high heterogeneity in the upper subalpine landscape. We found that all restoration treatments created landscapes that were heterogeneous with respect to stand development stages and these landscapes also contained an abundance of cone-producing whitebark pine trees (figs. 37 to 40). High levels of fire suppression nearly

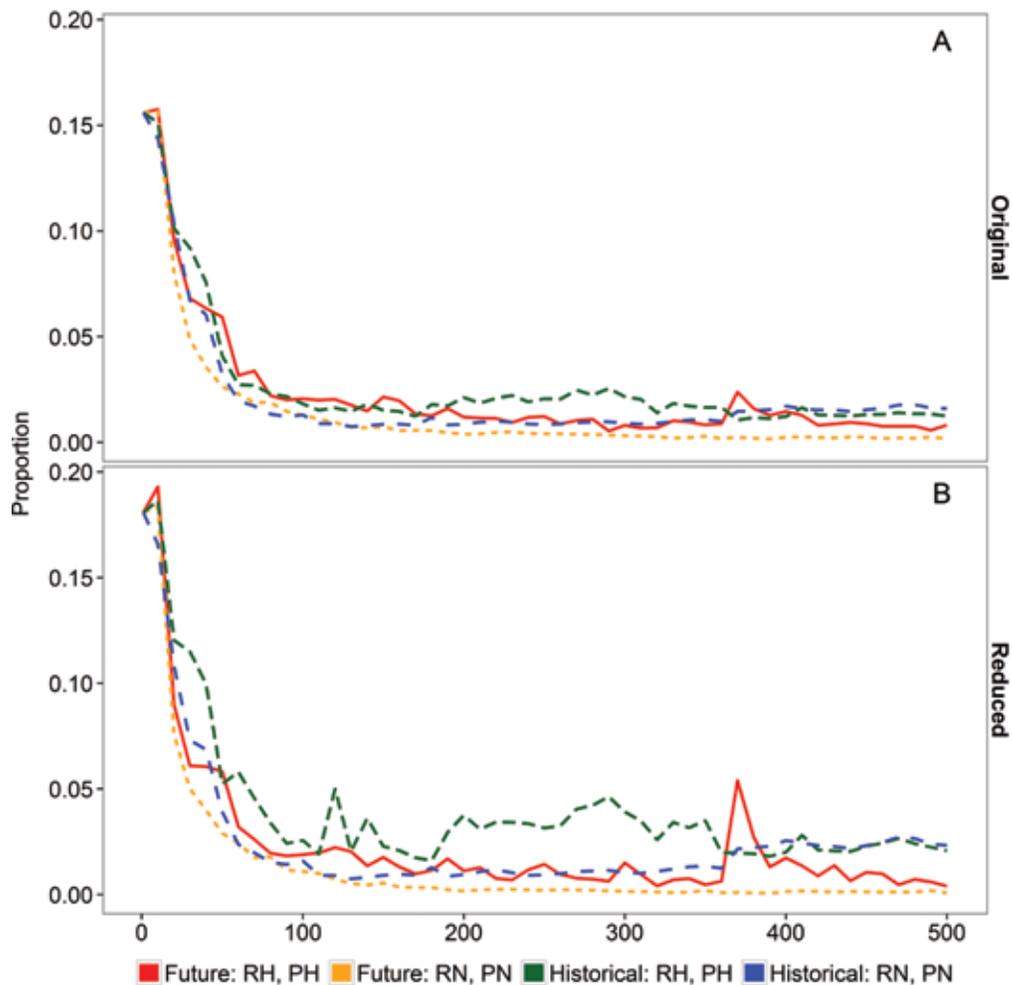


Figure 58—The large area of whitebark pine habitat in the CROWN whitebark pine zone influenced results. Shown are independent simulations (Section 4.3) of the long-term dynamics (500-year simulations) of whitebark pine landscape extent (proportion) for the CROWN landscape for historical (blue, green) and future climates (red, yellow) for no (RN-PN; yellow, blue) and high (RH-PH; green, red) restoration efforts (table 5): (A) CROWN landscape showing changes in whitebark pine (PIAL) landscape extent as a proportion using the whitebark pine zone shown in figure 27, (B) CROWN landscape showing changes in whitebark pine (PIAL) landscape extent as a proportion using a whitebark pine zone that was reduced by over 30 percent. As climates warmed, whitebark pine was quickly lost from the lower habitats and there were few upper habitats that it could populate in the short time span.

always created landscapes with lower heterogeneity where one or two structural stages comprised over 70 percent of the landscape. We also found that both wildfires and restoration created landscapes that had significant portions of the landscape in seedling and pole stages thereby ensuring long-term cone-production and resilient forests.

Another interesting finding is that the simulation results show that variations of whitebark pine basal area and proportion landscape are significantly greater under future climates for both landscapes (figs. 27 to 37). It appears that whitebark pine can remain on the

landscape over a wide range of fire, MPB, and WPBR conditions. This is in contrast to the lower variability of future weather predictions compared to observed weather (figs. 26, 27). This high variability provides for more resilient whitebark pine forests in the future because simulations show it can remain on the landscape under a wide range of conditions.

Last, we found it interesting that simulated habitat suitability for wildlife species are significantly different under future climates, but the trend in suitability depends on the wildlife species in question (Loehman et al. 2011b). Lynx habitat appears

to decline in the future while grizzly bear habitat increases. This demonstrates why management for a single species may be ineffective in the future. Complex ecological interactions could multiply over time to make a short-term plan for habitat restoration become ineffective under long-term climate change. An ecosystem approach that balances all ecological processes and characteristics is the only way to have a successful restoration program, especially for white-bark pine (Keane et al. 2012b).

4.5.2 Simulation Limitations

There are several limitations of this simulation experiment that must be addressed when interpreting the modeling results. First, there is a major drawback with the climate scenarios that demands future attention—the simulated historical weather record does not match the historical observed weather for both landscapes (figs. 27, 28). We used the simulated historical weather because it was recommended by GCM modelers, but our simulation results did not match results simulated from the real historical weather as found by Holsinger et al. (2014). This adds another level of uncertainty to interpretation and clouds the findings because the simulated historical climate does not produce the vegetation dynamics actually observed in the landscapes. Second, there appears to be the same or less variability in future projections, especially for precipitation and especially on the EFBR landscape (fig. 27, 28). This may be a result of the downscaling of the GCM climate data or it could be inadequate

GCM simulations. This lack of variability probably resulted in unrealistic fire dynamics, especially for the EFBR landscape (fig. 43), where large fire years were rare in the future simulations. And last, there appears to be a problem with the transition of the historical simulation to the future. Many of the temperature, precipitation, and radiation projections at the end of the historical simulation do not match the start of the future projections (figs. 27, 28). This compromises the validity of the short 95 year future projection if it is starting at a different point than the end of the historical data.

The list of tree species used in the simulations of both landscapes (table 3) represents those species that exist on the landscape today and the species that could possibly inhabit the landscape in the future. It is impossible for species not on the list to immigrate into the simulation landscape in the 95-year simulation period. It may be that the new climates could support tree species that were not in our list, but we assumed that the slow rate of tree species migration would preclude any new species becoming established. Our tree species list might need to include other tree species if simulation runs are longer than 500 years so that other species have the opportunity to become established in the new climates. We also used the same species parameter set for both landscapes (see Keane et al. 2012b) when in reality, there may be subtle differences in some species parameters between landscapes, such as cone crop frequency, adaptive strategies, and site index.

5. Climate Change Adaption Strategies and Tactics for Restoring Whitebark Pine Ecosystems

This section presents important strategies and tactics for incorporating the climate change information from the previous two sections into each of four guiding principles and, more appropriately, into each of the management actions of the whitebark pine rangewide restoration strategy (Keane et al. 2012b) (fig. 1; Section 2). Generalized approaches for addressing climate change impacts in restoration designs are presented in the “Guiding Principles” subsections below to set the context for understanding and implementing the climate change tactics and strategies detailed for each management action. There may be redundancy across the guiding principles and management actions because we structured each subsection to stand on its own.

The information presented in this section was compiled from material collected from the comprehensive literature search summarized in Section 3 and the FireBGCv2 simulation experiment presented in Section 4. Background material on whitebark pine ecology that may be needed to understand some climate change impacts can be found in Section 2 and the rangewide strategy (Keane et al. (2012b). Limitations, caveats, and concerns regarding the use of these recommendations are presented in the “Discussion” below (Section 6.2).

Some may find that this section lacks sufficient detail for managers to implement the proposed considerations in restoration actions, and that may be true for some of the recommendations. However, this lack of detail is because of the difficulty in implementing any of these actions without knowledge of local conditions. An appropriate action on one landscape or stand might be ineffective on other landscapes and stands as evidenced from our simulation results (see “Simulation Effort,” Section 4). The strategies, approaches, and tactics presented here must be further adjusted to account for local surroundings.

Several important findings from this study’s literature review (Section 3) and simulation experiment

(Section 4) provide the framework of this section. The first is that whitebark pine forests may be the tree species most resilient and resistant to climate change as compared to forests comprised of any of its upper subalpine associates if it weren’t for WPBR. The second is that without proactive restoration, whitebark pine, on those sites where it is seral to subalpine fir, will continue to decline and become a minor, if not absent, component on high elevation landscapes in western North America. Even a low level of restoration activity may help keep these whitebark pine forests from vanishing on the high mountain landscape. It appears that if we do nothing, whitebark pine will cease to function as a keystone species, regardless of climate conditions. Third, we found that whitebark pine can continue to exist under future climates on many landscapes, especially with more frequent fire, but probably at lower than historical levels. Next, we found that the impacts of climate change on whitebark pine populations are highly governed by local conditions. As the simulated outputs presented in Section 4.4 show, whitebark pine actually increases in abundance and stature on one landscape with future warming while it decreases on another. This is a direct consequence of the complex interactions of climate with vegetation and disturbance. Thus, there is no “magic bullet” or “one-size-fits-all” solution for restoring this iconic and valuable ecosystem; managers must tailor broad strategies to local conditions for the most effective restoration treatments (Diggins et al. 2010). And last, we found that the best approach to restoring whitebark pine forests and for creating resilient landscapes in the face of climate change is to implement the recommendations proposed in the rangewide strategy (Keane et al. 2012b) (see Section 1.2 for details). However, modifications to the rangewide strategy are needed to account for future changes in climate. These changes are the subject of this section.

5.1 Climate Change Adaptation Primer

The real question now facing land managers is how to mitigate the adverse impacts of changing climates so that restoration actions will be effective in the long term. The climate change community often uses the word “adaptation” to describe any actions toward mitigating climate change effects (Aitken et al. 2008; Chmura et al. 2011). Adaptation actions range from the simple, such as planting rust-resistant seedlings, to the complex, such as implementing thinning treatments to increase whitebark pine vigor (Janowiak et al. 2014) and to reduce the risk of high severity fire to protect whitebark pine seed trees (Spittlehouse and Stewart 2004).

Most land managers already have the tools, knowledge, and resources to begin to address climate change impacts. But as Swanston and Janowiak (2012) argue, managers will need a new perspective to expand their thinking to include consideration of new climates, spatial scales, treatment timing, and prioritization of efforts (Diggins et al. 2010). Often, all that is needed is to integrate climate change concerns into land management plans is to account for the high variability and trend of climate in the design of alternative land management actions (Janowiak et al. 2014).

There are some fundamental principles that can serve as starting points for climate change adaptation design and approaches (Joyce et al. 2008; Millar et al. 2007; West et al. 2009):

1. *Prioritization*. It will be increasingly important to prioritize management actions for adaptation based on both the vulnerability of species to climate change and the likelihood that adaptation actions to reduce vulnerability will be effective.
2. *Adaptive Management*. Adaptive management principles must provide a decisionmaking framework that maintains flexibility and incorporates new knowledge and experience over time
3. *Low hanging fruit*. Management actions that result in a wide variety of benefits under multiple scenarios, but have little or no risk, may be initial places to look for near-term implementation.

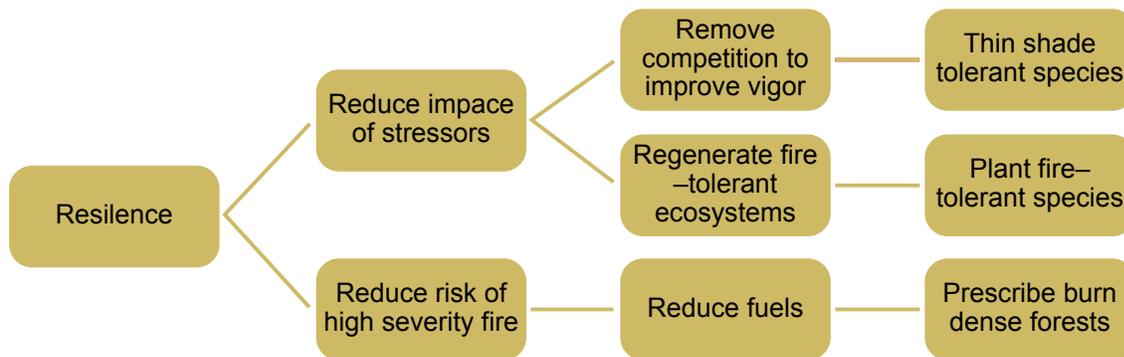
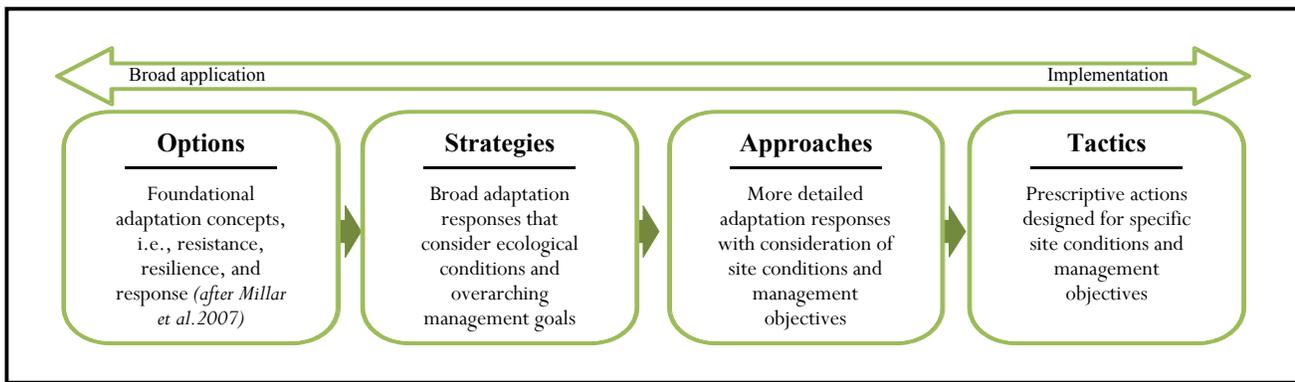
4. *Triage*. Where vulnerability to whitebark pine communities is high, precautionary actions to reduce risk in the near term, even with existing uncertainty, may be extremely important.
5. *Variability*. It is important to remember that climate change is much more than increasing temperatures. Increasing climate variability across all components of climate, such as precipitation, humidity, and radiation, may lead to equal or greater impacts that will need to be addressed.
6. *Multiple Objectives*. Many adaptation actions are often complementary with other land management and adaptation actions (e.g., thinning may increase vigor, resilience, and carbon sequestration rates); multiple actions to adapt forests to future conditions may also help restore these forests.

The concepts of resistance, resilience, and response serve as the fundamental framework for managers to consider when responding to climate change using adaptation actions (Millar et al. 2007; Swanston and Janowiak 2012) (fig. 59). Resistance options improve ecosystems’ defenses against anticipated climate change responses or directly defend ecosystems against disturbance to maintain current conditions. Resistance actions are often effective in the short term, but they may require greater effort over the long term as the climate shifts further from historical norms. Moreover, there is a risk that the ecosystem will undergo irreversible change because of large climatic shifts thereby rendering all resistance activities ineffective.

Resilience options allow some change, but emphasize a return to prior conditions after a disturbance. Resilience actions are also short term and should be used for high-value resources or areas that are buffered from climate change impacts.

Response options intentionally accommodate change and allow ecosystems to adaptively respond to changing and new conditions. A wide range of actions exists under this option, all working to influence ways in which ecosystems adapt to future conditions.

Resistance, resilience, and response options serve as the broadest and the most widely applicable level of a continuum or gradient of adaptation responses to climate change. They are most often called the



Modified from “Forest adaptation resources: Climate change tools and approaches for land managers.”
 Source: <https://www.treeseearch.fs.fed.us/pubs/40543>

Figure 59—Climate change adaptation action hierarchy taken from Swanston and Janowiak (2012) and illustrated by a set of specific actions at each scale of the hierarchy.

adaptation options (fig. 59). Along this continuum, adaptation actions become increasingly specific from options (resilience, resistance, and response), to strategies (broad adaptation responses that consider ecological conditions and overarching management goals), to approaches (detailed adaptation responses with consideration of local site conditions and management objectives), and to tactics (prescriptive actions designed for specific site conditions and management objectives) (fig. 59).

Adaptation strategies describe how adaptation options could be employed, but they are still broad and general in their application across ecosystems. In this report, an adaptation strategy would be comparable to the guiding principles in the rangewide strategy (Keane et al. 2012b). Approaches provide greater detail in how managers may respond to climate change effects and major differences in application among

ecosystems are now more evident. Ultimately, tactics are the most specific adaptation response and they provide prescriptive directions on how actions can be applied on the ground. Adaptation tactics are detailed actions using these strategies and approaches, but tactics are designed for regional to local situations and for specific objectives, species, cover types, or resource concerns.

This section is dedicated to the adaption strategies, approaches, and tactics that managers may use to design effective tactics to mitigate climate change effects in restoring whitebark pine forests. Adaptation strategies and approaches are linked to the rangewide strategy’s guiding principles and adaptation tactics are linked to the rangewide strategy’s management actions. A summary of all climate change adaptation options, approaches strategies and tactics is presented in table 10.

Table 10—Summary of climate change tactics in developing and implementing effective whitebark pine restoration actions in the future of climate change. Abbreviations include MPB-mountain pine beetle, WPBR-white pine blister rust. See Section 5 for descriptions of Adaptation option definitions.

Adaptation option	Strategy	Climate change impact	Adaptation tactic and restoration recommendation in the face of climate change
Guiding principles—Adaptation strategies			
Resistance	Promote rust resistance	Rust mutation	Collect seed and pollen from a wide variety of individuals. Replace plus-trees frequently. Rotate seed orchard stock.
Resistance	Conserve genetic diversity	Loss of genetic variation	Gather and archive seed and pollen from a wide variety of trees. Conduct extensive genetic surveys. Create spatial products depicting genetic diversity.
Resilience	Save seed sources	Increasing wildland fire frequency, intensity, size	Proactive fuel treatments around living individuals; allowing wildfires to burn in moderate years (wildland fire use); suppression tactics that include protecting living whitebark pine trees during a wildfire event
Resistance		Increasing frequency of MPB outbreaks	Create heterogeneous landscapes within historical range of variation; prescribe fire and silvicultural treatments to improve tree vigor; individual tree protection using anti-aggregating pheromones or insecticides
Resistance		Unwanted human activities	Modify suppression tactics in whitebark pine forests to save living trees; allow fires to burn, especially those in moderate years; avoid cutting rust-resistant trees in timber sales; do not plant competitors of whitebark pine in suitable habitat;
Resistance	Employ restoration treatments	Unanticipated loss of mature whitebark pine	Implement treatments to save rust-resistant seed-producing trees and plant rust-resistant seedlings in the best sites for survival and growth; design treatments to increase the likelihood trees will survive in future climates (details presented in each management action)
Resilience		Create resilient landscapes	Use a landscape approach; create heterogeneous landscapes; use historical range and variation of composition and structure as a reference for landscape heterogeneity until better spatial models are available.
Management actions			
Resistance, Resilience	Assess condition	Warmer temperatures; longer growing season	Add biophysical descriptors to inventory and monitoring protocols; use potential vegetation site classifications to describe climate in context of vegetation; Include spatial data layers of climate change predictions; use climate change projections to identify those areas that will experience the greatest warming and drying.
Resistance, Resilience	Plan activities	All predicted climate change conditions	Prioritize areas for restoration that are in the upper elevational range of local seral whitebark pine types; prioritize areas on the cooler aspects from northwest to northeast; select landscapes that have abundant seral and climax whitebark pine stands; consider wilderness restoration

continue Table 10 on next page

Table 10—Continued.

Adaptation option	Strategy	Climate change impact	Adaptation tactic and restoration recommendation in the face of climate change
Management actions			
Resilience	Reduce disturbance impacts	All disturbances	Create heterogeneous landscapes; take a landscape approach to planning and prioritizing; emphasize whitebark pine ecology and avoid treatments designed only to reduce disturbance agents, such fuel treatments
Resilience		Increasing fire	Embrace a more holistic wildland fire policy that balances wildfires, prescribed fires, and fire suppression; manage fire to balance losses in rust-resistant trees with gains in competition-free burned areas;
Resilience		Increasing MPB	Remove competition using fire, silvicultural cuttings; create landscape diversity of age classes
Resistance, Resilience		Increasing WPBR	Promote rust resistance through planting or direct sowing; promote natural rust resistance by providing regeneration opportunities where seed sources are intact;
Resistance, Resilience	Gather seeds	All predicted climate change conditions	Collect from many different seed sources; store as many seeds as possible; create seed libraries and central storage areas.
Resistance, Resilience	Grow seedlings	All predicted climate change conditions	Grow as many seedlings as possible and outplant to burned areas; inoculate seedlings with mycorrhizae to facilitate establishment on harsh sites;
Resilience	Protect seed sources	Increasing fire under warming climates	Proactive fuel treatments around living individuals; widening the treated area around protected trees in anticipation of future disturbances; allowing wildfires to burn in moderate years (wildland fire use); modifying suppression tactics that include protecting living whitebark pine trees during a wildfire event
Resistance, Resilience		Increasing MPB	Spray with insecticides (Carbaryl); use anti-aggregation pheromones; trap the beetles
		Against increasing WPBR	Spray with fungicides; remove <i>Ribes</i> spp. from surrounding area
Resistance, Resilience	Implement treatments	Against increasing disturbances; warming climates	Be more liberal with cutting and burning prescriptions; burn under hotter conditions; lower diameter limits on thinnings; cut or burn more seedling and sapling shade-tolerant species; reduce fuels in treated stands to ensure seed source survival after wildfire; Augment fuelbed to widen prescribed burn window; create ground conditions that facilitate the planting of rust-resistant seedlings (e.g., do not leave slash)
Resistance, Resilience	Plant seedlings	All predicted climate change conditions	Plant at the highest elevations of the treated areas first; plant in favorable microsites and create these microsites if missing from a planting site; make sure mycorrhizae are available; focus on areas within the current range of whitebark pine (i.e., do not attempt assisted migration as “restoration”)
Resistance, Resilience, Response	Monitor activities	All predicted climate change conditions	Conduct monitoring over long time spans; always include a control unit; measure additional variables at the sample site to understand and mitigate climate warming effects in future treatments; increase sampling intensity; improve sampling design to accommodate increasing variabilities caused by climate change; create centralized databases and standardized protocols.
Resistance, Resilience, Response	Conduct research	All predicted climate changes	Support research on the efficacy of these different treatment approaches.

5.2 Guiding Principles for Adaptation Strategies and Approaches

5.2.1 Promote Rust Resistance

The central principle in the rangewide strategy (Keane et al. 2012) is to enhance the level of rust resistance in whitebark pine populations at local to rangewide scales for restoration treatments to be effective. It is critical that future populations of the species have high frequencies of resistance to WPBR, otherwise all restoration treatments will be ineffective (Schultz 1989). This happens because WPBR occurs range-wide, and infection levels continue to increase when site and climatic conditions favor completion of the rust life cycle (Mahalovich 2013).

To increase rust resistance, the rangewide strategy emphasizes the importance of a three-pronged approach: (1) supporting existing and developing new selective breeding programs to produce blister rust-resistant whitebark pine, (2) facilitating and accelerating natural selection for blister rust-resistant genotypes in stands by reducing competition to increase survival of healthy trees in high blister rust areas, and by providing openings for natural seed dispersal and seedling survival, and (3) planting seedlings from seed sources known to have some level of blister rust resistance based on blister rust screening trials.

There are several major caveats connected with the enhancement of blister rust resistance independent of climate change. The most important caveat is that all programs for collecting seed from plus-trees, breeding for rust-resistant pines, and planting rust-resistant seedlings diversify the genetic mechanisms of resistance and the underlying genetic variation of resistance mechanisms. *Cronartium ribicola* has mutated and could mutate further and overcome a limited set of resistance mechanisms (Garrett et al. 2006).

The most important step towards assuring enduring rust resistance is to collect seed from a wide variety of individuals that survived in a wide range of high rust-mortality areas. To improve blister rust resistance, a sufficient number of plus trees designated for selective breeding programs must include population sizes large enough to sustain gains in rust resistance while minimizing the negative consequences of inbreeding

(Mahalovich and Dickerson 2004; Mahalovich and Foushee, submitted). In the absence of reproductively mature seed orchards, trees selected for operational cone collections in areas with high rust mortality should be rotated to safeguard against using the same rust-resistance genetics in future whitebark pine populations. All operational cone collections should be evaluated for rust resistance levels to further guide site-specific restoration prescriptions, as rust resistance levels vary by ecosystem (Mahalovich and Foushee 2015; Mahalovich et al. 2006; Sniezko et al. 2007). We are hopeful that advances in genomics will result in genetic evaluations of rust-resistance traits of new trees more quickly and less expensively than the current common garden techniques, which take 5–7 years.

A similar approach can be used in designing the whitebark pine seed orchards of the future. Scions should be taken from diverse collections of proven rust-resistant donors from more than one area. Recurrent selection programs for general combining ability—that portion of genetic variation that can be passed on to the next generation—can be augmented with new selections after they have been robustly tested to ensure that gains in rust resistance are not lost (reduction in selection intensity). Further, thorough analysis of pedigrees can ensure that related individuals are not added to the testing, breeding, or seed orchard populations.

5.2.2 Conserve Genetic Diversity

Genetic diversity across the entire range of whitebark pine must be conserved for the future. Climate change may facilitate more frequent and perhaps more severe disturbance processes that may compromise the genetic legacy of the species (Bower and Aubry 2009). Preserving genetic diversity is accomplished by collecting and archiving seeds from known rust-resistant parent trees throughout the range of whitebark pine, and then growing and planting genetically diverse, rust-resistant seedlings. We must be careful not to lose the broad genetic diversity inherent in the species while disturbances increase during the process of selecting rust-resistant lineages for growing seedlings for planting (Mahalovich and Hipkins 2011).

We should also consider other critical activities including archiving pollen and developing seed orchards to produce blister rust-resistant seed, and establishing clone banks. Clone banks would be used to archive the selections possessing desirable characteristics of blister rust resistance, drought tolerance, cold hardiness, and perhaps tolerance to mountain pine beetle (Bower et al. 2011). We should also strive to identify representative samples of live, putative rust-resistant whitebark pine trees to replenish those plus-tree selections that are lost to mortality. Similarly, even under optimum storage conditions (6–8 percent moisture content), seed and pollen do not stay viable indefinitely. Active genetic conservation efforts should include the periodic replenishing of seed and pollen stores. A bet-hedging restoration

strategy that preserves genetic variation and enhances rust resistance is to plant rust-resistant seedlings in restoration treatments from the current seed transfer zone (fig. 60). It is hoped that this would diversify the genetic variation present for cold hardiness, growth, phenology, and resistance traits.

The climate change considerations detailed here mirror some of those presented in the discussion about promoting rust resistance (see above). We should collect seed and pollen from many individuals within each of the seed zones of whitebark pine to ensure broad genetic diversity. For example, Mahalovich et al. (2006) found that in parts of the Northern Rockies there was a decrease in cold hardiness in seedlings grown from seed with high rust resistance ($r = -0.18$, $P < 0.01$). We need to collect, store, and catalog the

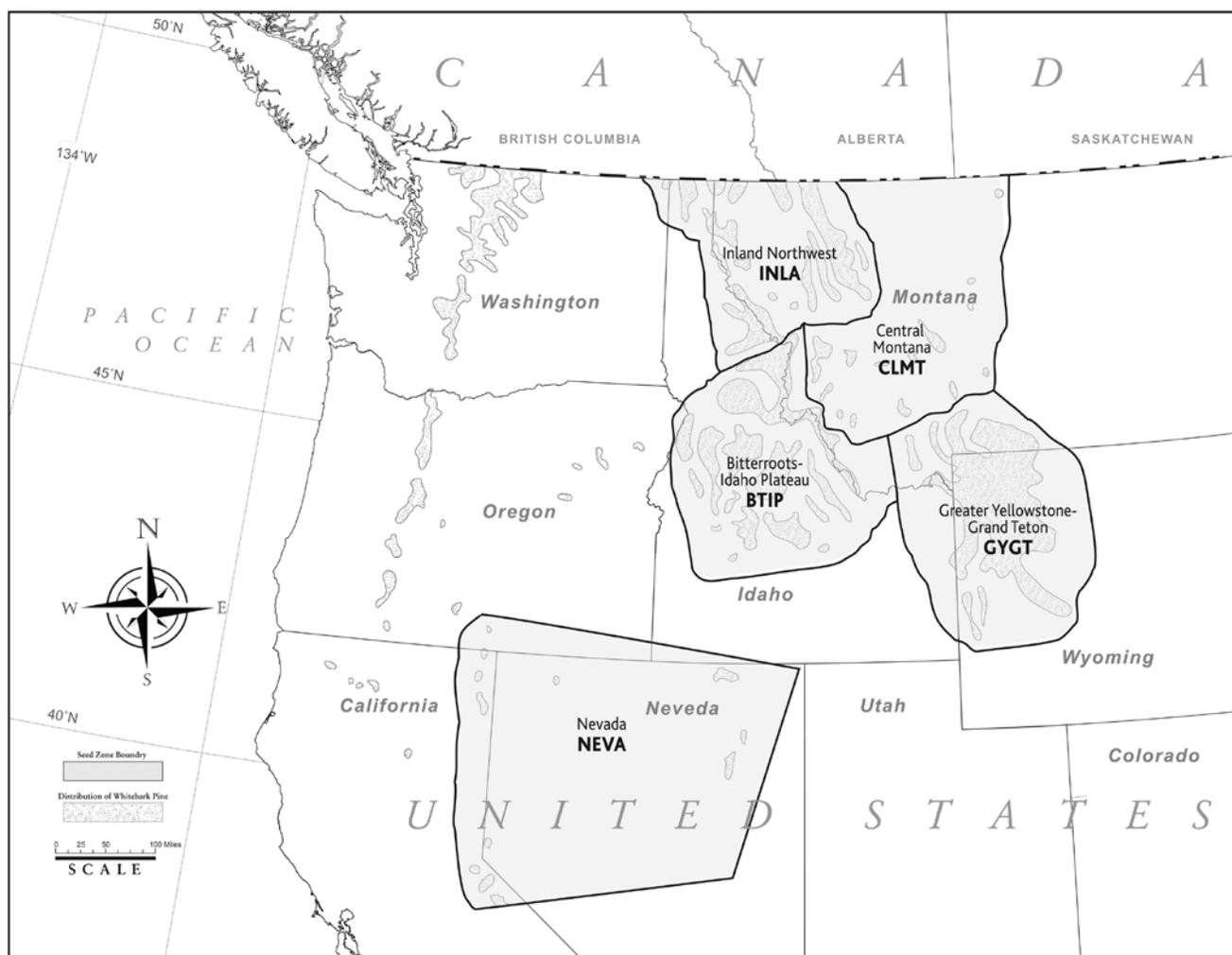


Figure 60—Genetic zone maps used as seed zones for whitebark pine from Mahalovich et al. (2011). When used in restoration treatments, rust-resistant seedlings from these seed transfer zones would preserve genetic variation and enhance rust resistance. At this time it is probably best to not transfer seed across seed zones under climate change.

baseline levels of genetic diversity, genetic variation in adaptive traits, and levels of inbreeding throughout the range of whitebark pine. These samples would serve as a reference for future management and research projects (e.g., to reconstruct entire populations that may be lost to disturbance) (Bower et al. 2011). Seed collections from a wide variety of individual trees will be incredibly important if local whitebark pine populations go below thresholds where they are no longer viable (see McKinney et al. 2009). These seed collections should be stored using methods that will ensure their long-term viability (Bower 2011). The pedigrees of these collections should be documented and periodically reviewed so that new and innovative genetic approaches can be used to restore the species. Detailed genetic analysis of these collections using next generation sequencing can reveal both individual variation and geographic differences. New technologies may uncover population differences in the frequency of genes that contribute to rust resistance (Snieszko et al. 2011).

5.2.3 Save Seed Sources

Mature, seed-producing, putatively rust-resistant whitebark pine trees, especially in regions that are experiencing the most severe decline, must be protected from severe disturbances so that genetically diverse seed can be harvested well into the future. Major perturbations to protect against include unwanted wildland fire, MPB, and silvicultural cuttings. Localized disturbances include clearing forests for ski area runs, mining, road-building, and avalanches (Tomback et al. 2001b).

There is no effective protection of trees from WPBR, as most proactive treatments (such as pruning, fungicide application, or removing alternate hosts) are ineffective. Further, these practices do not promote rust resistance. Identification and prioritization of areas that contain rust-resistant and genetically diverse trees can be accomplished with comprehensive genetics profiles using data generated from regional genetics programs and collaborative research partnerships. Nevertheless, all whitebark pine trees still living after prolonged rust infection have great value to the restoration program because they have a high probability of carrying genes related to resistance.

Wildland fire may endanger many individual whitebark pine seed sources and are the biggest threat to rust-resistant individuals, but mitigation actions are possible. Since fires are predicted to be more frequent, more intense, and larger in the upper subalpine areas where whitebark pine is commonly found (Section 3.4.1), precautions to protect known rust-resistant whitebark pine trees from fire damage are recommended. Policies designed to exclude fires from these high elevation forests are mostly ineffective, unrealistic, and costly; wildfires will eventually burn many whitebark pine stands regardless of the level of fire suppression (Loehman et al. 2011b).

We advocate a more holistic fire management policy for whitebark pine forests that balances wildfires, prescribed fires, and fire suppression (Black 2004). This approach entails proactive fuel reduction treatments, perhaps using prescribed fire, around potential and known rust-resistant trees as the first line of defense against wildfires. Wildland fire use (WFU: letting fires burn under prescribed weather conditions) in moderate years may also be effective, but some highly valuable trees would likely be lost without prior fuel reduction treatments in WFU fires.

Suppression is warranted in seed orchards or stands containing known rust-resistant trees where whitebark pine populations are in severe decline, and where seed sources are rare. Suppression tactics that implement fuel treatments during a wildfire event may help preserve key whitebark pine stands such as backfires. This approach is only realistic if saving whitebark pine trees is considered as a resource priority in suppression decisionmaking.

On a related issue, the anthropogenic policy of fire exclusion often results in a disrupted fire regime, high accumulations of fuels, and more intense future fires (Keane et al. 2002c). Policies supporting full suppression actions under projected warmer and drier climates might be counter-productive and potentially damaging in the long run, especially for whitebark pine restoration. Suppression efforts may cause declines of whitebark pine on seral sites by advancing succession towards subalpine fir domination in many parts of the species range. But this was not always the case in our 95-year simulation results (Section 4.4.2). Moreover, fire suppression activities may be harder

to successfully employ as canopy and surface fuels increase in the absence of fire.

Fire exclusion policies have resulted in excessive fuel accumulations that when burned generate fire intensities that tend to kill most of those trees that we want to remain on the landscape (Keane 2001b). Advocating for allowing fires to burn on high elevation landscapes, especially during moderate fire years, may appear contradictory as these fires may kill rust-resistant whitebark pine trees. But this is probably a more desirable alternative than protecting trees from the predominantly high severity fires resulting from prolonged fire exclusion. Genetic diversity can be ensured by archiving seed and tissue sources in secure, off-site locations. Allowing more fires to burn in moderate years will result in lower severity fires and create burn mosaics that satisfy many restoration objectives from creating fire breaks to reducing competition from subalpine fir.

Another disturbance to negatively impact whitebark pine is MPB (see Section 3.4.2). Beetle outbreaks are also predicted to increase in intensity and frequency in the future, so it is important to minimize losses of rust-resistant pine trees. This can be done using a multiple-scale design where coarse scale approaches create heterogeneous landscapes with patch structures within the historical range of variability (HRV) (Keane et al. 2002b, 2010a). This will limit excessive buildups of MPB populations by minimizing the number of host species that are of adequate size to sustain major MPB outbreaks (Schoettle and Sniezko 2007). Finer scale approaches include treatments implemented at both the stand and tree levels, such as thinning, verbenone, and daylighting (Keane et al. 2012b).

Silvicultural treatments to improve tree vigor and increase tree defenses, such as release thinnings and group selection cuts, might be effective in stands that are dominated by subalpine fir. Protecting individual trees from MPB attack using various proactive techniques, such as release cuttings (Keane and Parsons 2010a), anti-aggregation pheromones (Bentz et al. 2005), and insecticides (Gibson and Bennett 1985), may also be effective (Keane et al. 2012b).

Land management practices that may impact whitebark pine populations in the future are those that

involve removing potential and known rust-resistant, cone-producing whitebark pines. This includes fire suppression activities as detailed above, but also commercial harvesting and tree cutting for ski area runs and power line construction. Valuable seed sources can be saved by training crews to identify whitebark pine, to avoid cutting potentially rust-resistant trees. Managing forests for carbon sequestration to mitigate climate change should never supersede whitebark pine restoration efforts. Cutting mature cone-producing whitebark pine trees to create more productive stands that sequester more carbon are counter-productive to the restoration of whitebark pine ecosystems.

5.2.4 Employ Restoration Treatments

Areas where whitebark pine seed sources are still in reasonable health but may be threatened by MPB, WPBR, or advanced succession should be considered for restoration treatments. Treating these seed sources will create sustainable whitebark pine populations. Restoration treatments include any combination of prescribed fire, silvicultural treatments, and regeneration plantings as described below.

Prescribed fire can be used to manage the spread of WPBR when used in successional advanced communities. Treatments would encourage whitebark pine regeneration and increase the presence of rust-resistant genotypes. Silvicultural treatments (cutting trees) at the local scale can be used to remove competing vegetation. This would increase the vigor of surviving trees and reduce the likelihood of mountain pine beetle attacks. Finally, planting rust-resistant seedlings would accelerate stocking of whitebark pine and rust resistance in the populations.

A landscape approach should be taken when implementing treatments at stand scales to ensure heterogeneity of stand compositions and structures across a landscape so that there are large populations for natural selection for rust resistance. A landscape approach would also ensure a diversity of age class structures to maintain ecosystem function and reduce MPB hazard. The landscape scale includes areas across elevation zones where whitebark pine occurs, including the uppermost subalpine zones and transition zones to treeline.

The first step towards employing restoration treatments under changing climates is to design restoration treatments with an understanding of the landscape context. Several restoration objectives can be met when treatments are designed within a landscape context. First, the severity of future MPB, WPBR, and wildfire events can be reduced. The overall efficacy of the restoration treatments is increased because stand-level treatments would not be overwhelmed by adverse stand conditions at the landscape-level. Finally, landscape-scale treatments would create corridors and improve the connectivity and transfer of genes and individuals between disjunct populations. Landscapes evaluated for treatments must include not only the upper subalpine forests, but all forests susceptible to fire, blister rust, and mountain pine beetle. Fuel reduction treatments, for example, may be best implemented in whitebark pine stands that are adjacent to more fire-prone, lower elevation areas. The foundation of a landscape approach is to ensure resilient whitebark pine forests in the future by creating heterogeneous landscapes composed of many age classes and successional stages of whitebark pine. This, in turn, will reduce the scale and intensity of fire, WPBR, and MPB events (Schoettle and Sniezko 2007) (see Section 4.4.2). We can mitigate the potential climate warming effects on whitebark pine by being strategic in our restoration efforts to increase community heterogeneity in targeted upper subalpine areas.

The dilemma facing most land managers is estimating the right mix of whitebark pine communities for these high elevation settings to ensure optimal landscape heterogeneity. This is best accomplished by using spatially explicit ecological modeling to simulate the range of landscape conditions that will occur under both past (HRV) and future climates (Keane 2013; Keane et al. 2008b) (see Section 4.1). Unfortunately, most managers do not have access to these types of models so other means must be used.

Therefore, we think most recommendations in the rangewide strategy (Keane et al. 2012b) still apply under climate change and we advocate that the concept of HRV (Landres et al. 1999) be used to estimate and design for landscape heterogeneity under future conditions. While past conditions might not be the best analog for future conditions, we think that HRV

represents our best knowledge of the landscape conditions and disturbance regimes under which species have evolved. HRV is the reference conditions that provide least uncertainty that are the most ecologically appropriate (Keane et al. 2009; Loehman et al. 2011b; Millar et al. 2007). However, there may be times when future climate will make it impossible to restore whitebark pine landscapes back into HRV. This is why a quantification of the future range and variation (FRV) of landscape conditions is also important. By comparing HRV with FRV we are able to use the range of overlap as a possible target. Judging from the results of our simulation efforts (see Section 4.4), it appears that landscape conditions of historical and future climates often have large overlaps and these may be our target zone for restoration treatment designs (figs. 29 to 55). Moreover, our modeling shows landscape conditions for the high elevation settings are quite different if WPBR is included, so we suggest that any FRV include WPBR.

Most of the other climate change considerations for this guiding principle often concern the locations and designs of restoration treatments. The most important treatment with respect to long-term benefits in the rangewide strategy is planting rust-resistant seedlings in burned areas. But other restoration actions may be necessary in support of planting, such as cutting or using prescribed fire or WFU to reduce whitebark pine competition and create optimal planting sites. For the last decade, sowing seeds (direct sowing) from potential or known rust-resistant trees, as opposed to planting seedlings, has been explored as a more cost-efficient option that would enable restoration in remote terrain (e.g., Schwandt et al. 2011). In some landscapes, germination rates and seedling survival may be high enough for direct sowing to be a viable and more economical alternative. The biggest climate change consideration when implementing planting or sowing treatments is deciding where exactly to apply these treatments so they will be most effective and last the longest. Modifying the design criteria, such as increasing prescribed fire intensity, decreasing minimum cutting diameters, and increasing planting densities to anticipate climate-mediated change could improve the chances of success (Diggins et al. 2010). All of these climate considerations are described in

detail in several of the management actions presented in the following section.

5.3 Management Actions

5.3.1 Assess Condition

The first step in designing whitebark pine restoration projects is assessing the conditions of upper subalpine stands to determine if they are suitable for restoration. Assessments consist of inventory and monitoring projects, GIS mapping, spatial modeling, and remote sensing. These tools document the status and trend of whitebark pine across multiple spatial scales from the stand to landscape to regional levels. Assessments are used in nearly all other management actions as a reference for design and implementation of treatments so they most effectively restore whitebark pine landscapes (see Section 5.3.8 below).

An assessment should include a comprehensive description of the biophysical setting to appropriately evaluate and mitigate effects of climate change at all scales. Biophysical classifications such as seral vs. climax sites, habitat types, landforms, and elevation zones can also be used to stratify landscapes into areas that represent environmental gradients that provide the context in which to plan and evaluate climate change strategies. These classifications can also be used to fine-tune coarse scale climate change projections using various extrapolation techniques. Slope, aspect, and elevation, for example, can be used in weather extrapolator software to downscale coarse scale (e.g., 50 km pixel size) climate change predictions to the site level to account for local conditions into the future (Hungerford et al. 1989; Keane and Holsinger 2006; Thornton et al. 1997).

Inventory and monitoring protocols and methods should include comprehensive descriptions of site conditions so that climate change predictions and mitigation activities can be modified to account for local variation and scale. Regeneration success from stakerow surveys, for example, could be more useful in the future if microsite (e.g., planting site condition) and macrosite site conditions (e.g., habitat type) are recorded. This could provide a basis for deciding which site characteristics can be used to evaluate where to put restoration treatments. Possible site

assessments include topography (e.g., slope, aspect, elevation), landscape position (e.g., valley bottom, frost pocket, bench), topographic shading, and georeferenced location (e.g., longitude-latitude, UTM) (Bush and Kies 2012; Lutes et al. 2006, 2009).

Collectively, biophysical stratifications can then be used to guide inventory, monitoring, prioritization, and implementation efforts in large scale adaptive management projects. For example, colder whitebark pine sites may warrant a higher restoration priority.

Maps of site classifications such as habitat types (Pfister et al. 1977) and plant associations (Henderson et al. 1989), are also important. They can be created for both current and future conditions based on climate inputs (Holsinger et al. 2006; Rollins et al. 2004). Potential vegetation classifications are more suitable for bioclimatic envelop modeling (see Section 3.1.3) than species distributions to predict where whitebark pine habitat will be in the future. Potential vegetation classes represent those unique biophysical conditions that may support late-seral or climax vegetation and therefore are more easily and accurately correlated to climate than individual species distributions (Keane et al. 2008b). These classifications also provide a more comprehensive description of a plant community and its possible movement across a landscape than the independent projections of species distribution models.

One drawback of predicting future potential vegetation communities using climate projections is the disparate rates of seed dispersal and migration among the species that comprise a potential type (Keane 2000). Tree species move across landscapes at different rates so the movement of potential vegetation types and their community associations might not consist of the same species assemblages in the future as occurred in the past. The time spans used in most climate change evaluations (e.g., 50–100 years) may be too short to allow for the terminal migration of most vegetation species that comprise the subalpine landscape.

The acquisition of spatial data products that describe both historical and future weather and climate are also important in addressing climate change in spatial analyses of restoration assessments. Daily weather data captured at 1 to 10 km resolutions,

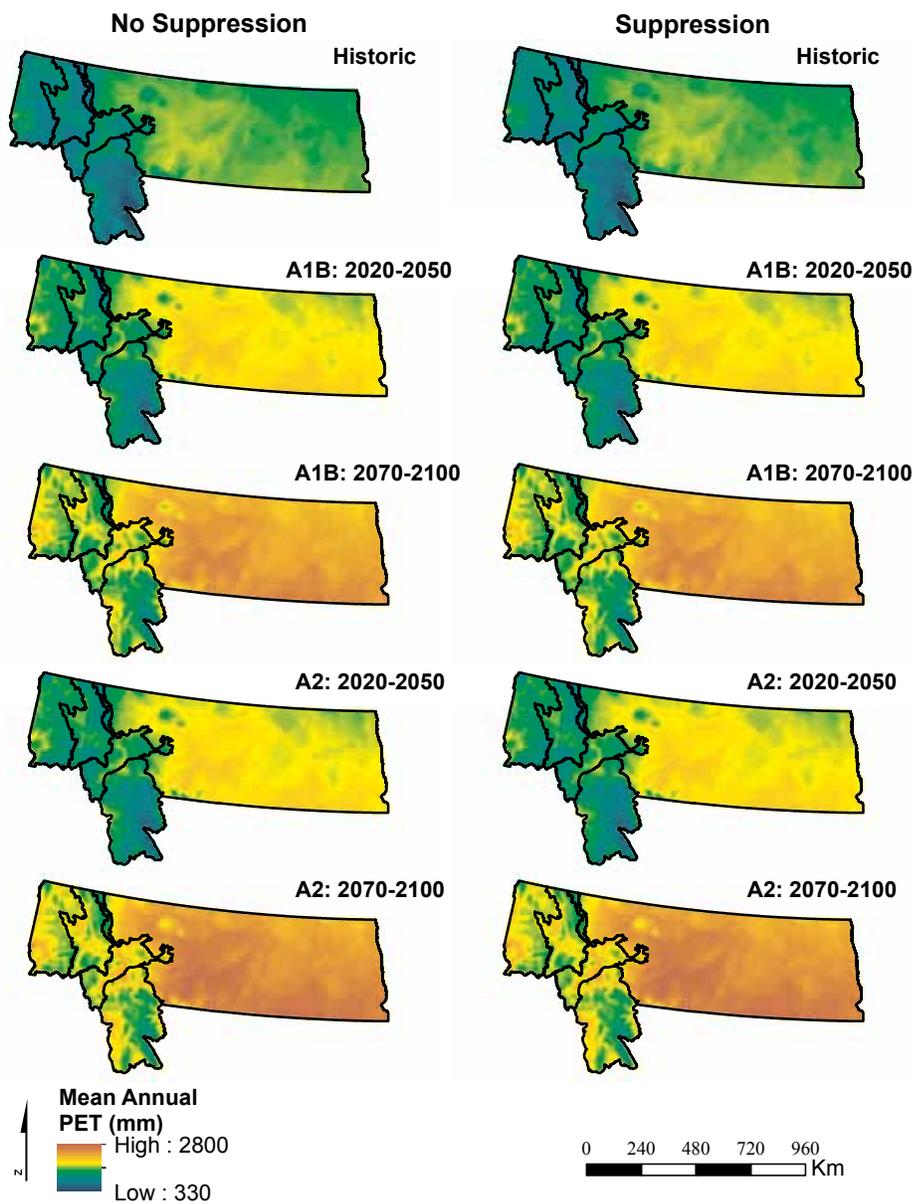


Figure 61—Maps of potential evapotranspiration averaged across each of three time spans (historic, 2020–2050, 2070–2100) and without and with fire suppression for two climate change scenarios (A1B and A2) used in the NRAP project (Keane et al., in press). Note, the highest increases in potential evapotranspiration in the future are in the low elevation forest types, not in the high elevations where whitebark pine is found.

can be used to directly represent climate changes in restoration assessments. This weather data is available through DAYMET (Thornton et al. 1997), PRISM (Di Luzio et al. 2008), and future gridded climate projections (Meehl et al. 2007; Taylor et al. 2012). The Northern Region Adaptation Partnership project, for example, used 4 km pixel resolution to describe potential evapotranspiration across the Northern Region of the National Forest System (fig. 61) (Keane et al., in press). Downscaled climate projections are available in many spatial data formats across whitebark pine’s range.

When conducting spatial assessments, it is important to emphasize trends in temperature and

precipitation from historical to future conditions rather than absolute values because most global circulation model predictions have a high degree of uncertainty (Section 3.1.1). Using data from the weather stations nearest to the restoration site, landscape, or region may also be important. Extrapolating recorded weather to local conditions can more realistically describe local climate (Hungerford et al. 1989). Climate descriptions can then be used to assess where restoration activities are possible or most successful, such as conducting restoration treatments on the cooler, moister parts of the project area.

Lastly, it is important that assessments be done at multiple scales using landscape approaches. Given

projected increases in the frequency of disturbance events, it makes little sense to analyze potential restoration areas at only the stand level when most of the future disturbances originate from outside stand boundaries. Conducting all assessments at the landscape scale ensures that spatial relationships are included in the evaluations, especially processes such as nutcracker-mediated seed dispersal (Barringer et al. 2012). For example, it would be futile to reduce fuels in a 10-acre stand when it is surrounded by vast expanses of dense subalpine fir stands with high fuel loadings. Restoration treatments on ridgetops with isolated whitebark pine populations, as another example, would require significantly different designs than treatments implemented in large, continuous landscapes of whitebark pine habitats. Assessment areas must be big enough to encompass those future disturbance regimes that might impact treatments, but also be small enough so that treatments can be properly designed and their effects monitored. This means that assessments should include lower elevation settings to evaluate if fires or other disturbances can spread into treatment areas from below.

5.3.2 Plan Activities

Every restoration project needs a plan. Planning includes prioritizing landscapes for restoration and identifying which stands to restore, designing possible treatment alternatives, evaluating alternatives for efficacy, and scheduling areas to treat. Accounting for climate change in restoration planning will increase the likelihood that the outcome of restoration will be effective over the long term and create those forests that will be resilient in the future.

The primary recommendation for planning is to prioritize stands for restoration based on site-specific considerations. Seral whitebark pine communities, which occur on more productive sites than climax sites, are often the most in need of restoration (Keane et al. 2012b). Elevation is one of the easiest biophysical characteristic to use to prioritize stands and landscapes. However, climate data layers, habitat types, and other land classifications can also be used to augment prioritization. Both the literature synthesis (Section 3) and our FireBGCv2 modeling effort (Section 4) indicate that restoring stands that are at

the local upper elevations of whitebark pine seral sites might be more effective than restoration in lower elevations in the future for several reasons (Koteen 1999; Warwell et al. 2007) (fig. 62). First, it could be that lower portions of whitebark pine seral sites may be too harsh (i.e., high radiation loads, drier, warmer) for survival of whitebark pine seedlings in the majority of years, thereby limiting effective natural regeneration (Larson and Kipfmüller 2010; Lonergan et al. 2013; McCaughey and Weaver 1990). Second, the lower portions of seral sites, especially those on southern slopes, may have warmer climates that facilitate rapid successional replacement of whitebark pine by subalpine fir, spruce, and perhaps a suite of lower elevation species, such as Douglas-fir, especially in areas that already experience abundant precipitation (Arno and Hoff 1990). Lodgepole pine might also increase in productivity on seral sites in the future and out-compete whitebark pine (Keane 2001a). Seral whitebark pine sites with little snow cover because of strong winter winds might also favor establishment of subalpine fir and spruce because of the longer growing seasons and longer snow-free periods. Conversely, warming climates in the lower elevations and south-facing aspects of seral sites, especially in southernmost latitudes of whitebark pine's range in the Rocky Mountains and Sierra Nevada where summer moisture deficits are more common, may receive lower priority for restoration. This requires evaluating the lowest and highest elevations that encompass whitebark pine seral communities at local scales, and assigning a higher priority for restoration to the top half of this elevational range.

We believe that whitebark pine climax communities across the range are probably more resilient in the long run than seral communities—even those with lower mortality from WPBR or MPB and less climatic influences (Keane et al. 2012b). As a result, proactive restoration treatments may often be confined to those sites where whitebark pine will be lost through competitive interactions.

Disturbance responses to climate change might also favor upper elevational whitebark pine seral sites for restoration projects. Wildland fire, MPB, and WPBR are all projected to increase in the future and this increase will be especially prominent on the warmer,

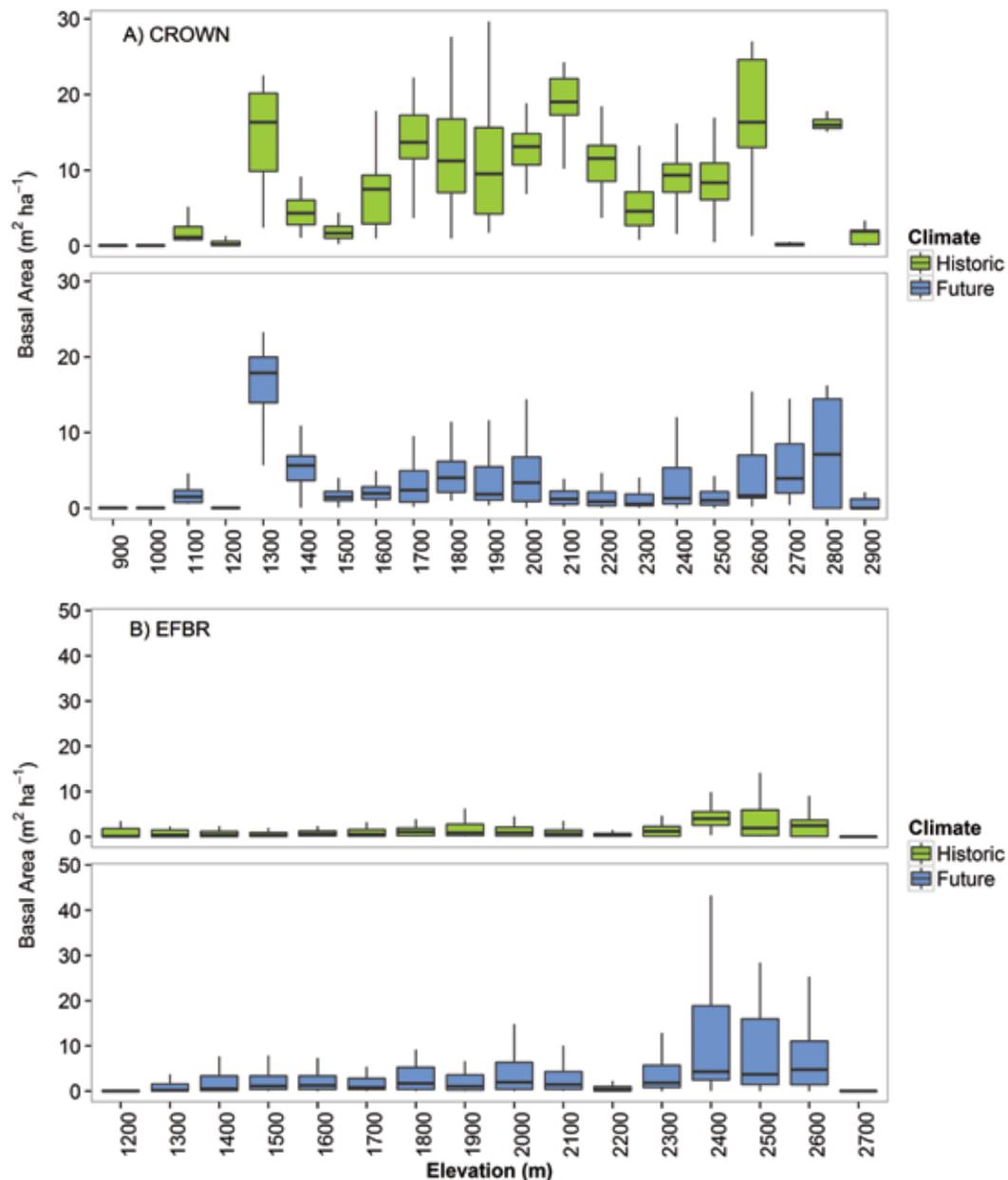


Figure 62—Results from the FireBGCv2 independent simulation runs. Increases in whitebark pine basal area in the future would occur on the higher elevation sites of the whitebark pine zone in the (A) CROWN and (B) EFBR landscapes. And whitebark pine on the CROWN landscape decline rapidly because there is more whitebark pine habitat at the lower elevations.

drier seral whitebark pine sites, which tend to be at lower elevations (see Section 3). Both MPB and rust will kill mature whitebark pine trees and thereby accelerate succession towards shade-tolerant fir and spruce. Fire, on the other hand, may kill whitebark pine trees, but it will also create competition-free growing space that may be suitable for planting rust-resistant seedlings. Fire may also reduce fuels and lower the potential for future crown fires that could kill even more whitebark pine trees, especially those

that are rust-resistant. However, if exposed burned sites become drier and experience higher insolation, whitebark pine regeneration may not survive and the fuels may become dry enough to foster more frequent fire regimes.

Restoration treatments implemented on isolated ridges that are distant from other whitebark pine seed sources are important because these are the settings in which whitebark pine may likely go locally extinct (Keane et al. 2012b). However, this may not

be the most efficient use of restoration funding under rapidly warming climates because seed production of these isolated seral whitebark pine communities will continue to decline into the future, despite treatment. Locations with a diversity of seral and climax whitebark pine communities covering large areas might rate a higher priority for restoration because these are more likely to persist into the future. It is essential that the evaluation process include an assessment of the magnitude and condition of proximate whitebark pine seed sources to heighten the effectiveness of any treatment or disturbance.

Finally, we should start to think about restoring whitebark pine in designated wilderness areas as a hedge against adverse climate change impacts outside of wilderness. Over 48 percent of whitebark pine's range occurs in designated wilderness (Keane 2000) and most of these wilderness locations have unique whitebark pine populations living in settings that are important to the long-term conservation of the species, especially as the climate warms. It is important that the entire range of whitebark pine be considered to account for the great variability in climate change, species response, and plant genetics. To exclude half the species range from restoration may compromise the effectiveness of local, non-wilderness efforts and fail to preserve the genetic diversity needed to maintain the species on the changing landscape. Wilderness restoration, however, is often considered an unacceptable action by some wilderness advocates (Landres 2010).

5.3.3 Reduce Disturbance Impacts

Various local treatments are implemented to mitigate and control WPBR, MPB, and fire effects, such as removal of *Ribes* spp., spraying fungicide or pesticide, use of anti-aggregation pheromones, thinning, and reducing fuels in stands with cone-bearing trees (Keane et al. 2012b). Most disturbances in whitebark pine forests are predicted to increase in frequency and perhaps severity under future climates (see Section 3.4), so management actions are needed to reduce their impacts on whitebark pine populations. Except for wildland fire, there are few viable proactive treatments that can mitigate expected climate-mediated changes in WPBR and MPB

disturbances over the long term. We believe that the long-term solution is to manage non-fire disturbances indirectly through a holistic ecosystems management approach. The money saved from protective actions designed to directly reduce MPB or WPBR populations could be more effectively used for other restoration treatments that will in turn mitigate impacts of these disturbances.

Fire is the one disturbance we can manage at a multitude of scales. At the coarsest scale, fire exclusion policies, through the suppression of all high elevation fires, may seem like a viable approach for saving cone-bearing, rust-resistant whitebark pine trees. But we think that fire exclusion in a future of climate change may expedite the decline rather than conserve this foundation species over the long term. This is evidenced by our simulation results in Section 4 and illustrated in figure 63. Long-term fire exclusion often results in two unwanted effects: (1) a buildup of surface and canopy fuels that, when burned, often kills all remaining rust-resistant pine trees, and (2) increased competition from fir and spruce that will reduce whitebark pine vigor, thus causing more infrequent and smaller cone crops and reductions in resistance to other potential disturbances.

A more effective way to reduce impacts from fire is to create landscapes where the impacts from future fire are mitigated using a mix of fire management approaches. Tree-level treatments (see Section 5.3.6) and stand-level actions (see Section 5.3.7) are integrated with a landscape-level wildland fire use approach in which most fires are allowed to burn, especially those mixed severity fires that burn in moderate fire danger years (Keane et al. 2012b). Moderate or mixed severity fires promote several beneficial restoration objectives: (1) reduce competition and thereby increase whitebark pine vigor that will enhance resilience to other future disturbances, (2) produce burned patches that facilitate nutcracker seed caching, and (3) create burn perimeters that reduce fuel loads and act as fuelbreaks to protect surviving rust-resistant trees from future fires (Keane and Parsons 2010b). If known rust-resistant trees and stands are protected from wildfire using fuel treatments or if their genetic legacy is archived in clone banks, then perhaps fires can be allowed to burn,

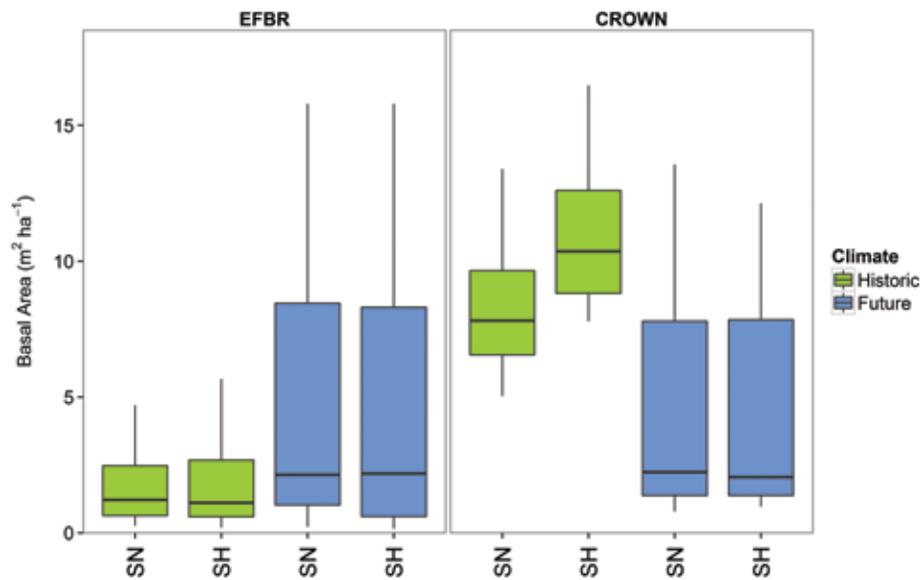


Figure 63—The difference in whitebark pine basal area under a fire exclusion management approach (SH-high suppression) vs a more historically appropriate management policy of letting fires burn (SN-No suppression) in both a historical climate and a RCP8.5 scenario climate. Note that this is only 95 years of simulation in areas with a 250-year fire return interval for the whitebark pine zone. Thus, major differences are clearly only manifest in the CROWN landscape, not the EFBR (East Fork Bitterroot River) landscape.

even in severe weather years. If high elevation forest fires must be suppressed, then special care must be taken to ensure that critical rust-resistant individuals are protected from future fire suppression activities, especially the damaging impacts of back burns, which often have the highest fire severities (Amiro et al. 2001).

Many interacting factors could increase the future rate of spread of the WPBR pathogen, both geographically and within landscapes, making the reduction of WPBR impacts difficult, especially in the uncertain climate future (see Section 3.1, *Climate Change*). *Ribes* spp., the most important alternate hosts for *Cronartium ribicola*, regenerate well after disturbances, especially fire. And the prevalence of *Ribes* spp. may well increase in the high country with more frequent fire events and less competition from other species (Zambino 2010). Therefore, any treatment to reduce *Ribes* spp. by mechanical removal, spraying herbicide, or burning might require prohibitive amounts of resources and time (Carlson 1978), and these treatments have been proven to be ineffective (Geils et al. 2010). Pruning rust-infected branches will also be ineffectual as the incidence of rust intensifies, especially if the tree has little resistance. This also applies to the repetitive use of fungicide for containing or eliminating the rust, which must be limited to a small number of trees. Not only is the application of fungicide labor-intensive and expensive, it forestalls the effects of natural selection: The key to the

future survival of whitebark pine populations is the enhancement of resistance to *Cronartium ribicola*. Protecting highly susceptible trees is counter to this process and will often fail over time. Therefore, we believe that the best way to reduce WPBR impacts on future whitebark pine populations is by following the first guiding principle of promoting rust resistance (Section 1.2; Keane et al. 2012b).

Treatments at the stand or tree level for MPB are similarly problematic, with some exceptions. Use of pesticides or pheromones to protect high value trees against attack by MPB may be appropriate in small areas or at the individual tree level for short-term preservation and mitigation (see Section 5.3.6; Keane et al. 2012b). These applications, however, must be repeated and are highly impractical at the operational scales of multiple stands and landscapes, especially when future climates are predicted to heighten MPB population dynamics (Bentz et al. 2011). There is some indication that thinning stands to increase tree vigor may increase the amount of radiation and wind to the stand and create conditions that withstand MPB attacks. But these thinning treatments may be financially prohibitive in the long run because most whitebark pine stands do not contain commercial timber and most whitebark pine have few defenses against MPB, especially during outbreak years. It is better if thinning is part of a suite of proactive, multi-purpose restoration actions meant to improve whitebark pine vigor by reducing competition from

shade-tolerant conifers while also reducing canopy fuels to minimize fire-caused tree mortality (Section 5.3.7).

As mentioned in the Guiding Principles, creation of heterogeneous upper subalpine landscapes that contain a wide variety of whitebark pine communities is potentially the best defense against large-scale MPB outbreaks, as well as protection against wildfire. Landscapes with multiple age classes of whitebark pine along with plantings of rust-resistant seedlings are the best hedge against all disturbance agents. Upper subalpine landscapes should contain a diversity of successional stages in proportions that anticipate the disturbance regimes of tomorrow's climates (Schoettle and Snieszko 2007). Possibly the most economical and effective means to accomplish this is to allow wildfires that occur in moderate fire danger years to burn, as mentioned above (Keane and Arno 2001). Wildfires that burn under moderate drought conditions often stay small and burn in a mixed severity pattern (Lasko 1990). Granted, no mature whitebark pine tree is safe when MPB is in outbreak mode or when wildfires are severe (Millar et al. 2012), but as upper subalpine landscapes become heterogeneous, the severity, intensity, and frequency of MPB outbreaks and severe fire should also diminish. Declines in the size and abundance of host trees across the landscape may restrict MPB populations to an endemic level, and the greater extent of burned area and heterogeneous forest types may reduce future severe fires.

Other strategies to create heterogeneous landscapes include use of the restoration treatments incorporating prescribed burning and silvicultural cuttings detailed in Keane and Parsons (2010b), summarized in the rangewide strategy (Keane et al. 2012b), and discussed in the context of climate change in Section 5.3.7 (*Implement Treatments*) here. Given the great uncertainty in the climate future, it is especially important that any tree and stand level treatment be designed in a landscape context. It makes little sense to treat a single tree or stand when it lies within a matrix of stands that are highly susceptible to increased disturbances predicted for the future. Thinning to remove competition from one stand without considering the entire landscape might be ineffective in the

long run because fires or MPB outbreaks that occur on that landscape might be so severe that they may overwhelm the minor treatment area.

Treatments implemented for the landscape approach should reduce competition and open up the upper subalpine stands. Open-grown whitebark pine forests have lower canopy fuels and the tree crowns are more heterogeneously distributed across the stand than successional advanced pine forests with fir in both the understory and overstory. This openness reduces the potential for crown fires, and, if there is a crown fire, it may be patchy and passive (Keane and Parsons 2010b). Mature, healthy and vigorous whitebark pine trees are better able to defend against endemic (low level) MPB outbreaks and, if some of these trees have WPBR-resistance, they have a better chance of surviving. The challenge facing land managers and research scientists is estimating how much of the landscape to treat so that it will be most resilient in the future. This depends on local conditions and the current state of the landscape (Keane et al. 2012b). Again, we suggest using the concept of HRV to determine the ranges of landscape compositions for the near term and then compare against some approximation of the FRV compiled from an ecological model that simulates future climate and ecosystem processes and the landscape compositions they create (Keane et al. 2009).

5.3.4 Gather Seed

Collecting seeds from trees that are proven or phenotypically rust-resistant (level of resistance is unknown) is important for many reasons. First, a collection of seeds throughout the range of whitebark pine is important for archiving genetic diversity and variation so that viable populations suited for future warmer climates are available for planting (Sections 5.2.1, 5.2.2). Stored seed from source trees known to have rust resistance can be used for operational planting and direct seeding. Seeds can also be used by research to pioneer new methods for improving nursery techniques, planting guidelines, and direct seeding protocols.

Now more than ever, seed collections should be made throughout the geographical distribution of whitebark pine to capture the greatest range of genetic

diversity, including locally and regionally rare alleles, before the species declines to very low levels as a result of disturbance and climate threats (Hoban and Schlarbaum 2014). Seed inventories should be managed and periodically assessed for seed viability and to ensure that effective population sizes are being maintained both in space and time. This will enable agencies to be proactive in current conservation efforts and to provide a buffer for large-scale disturbance and climate change. Agencies need to identify and test rust resistance in a sufficient number of plus trees to maintain genetic variation throughout the range of whitebark pine, since no region will be free of WPBR. Although costly, we suggest that more plus trees be selected and tested to provide a hedge against the anticipated mortality expected from increases in future abiotic and biotic disturbances caused by warming climates. Future plus trees should be identified as we lose current plus trees to disturbance.

We also suggest that cone collections from known rust-resistant trees in areas where genetic testing has occurred, vary spatially and temporally to further enhance genetic diversity and capture the spatial heterogeneity of different rust-resistant traits. This will minimize the chance that WPBR may overcome rust resistance gains from selective breeding programs (Mahalovich and Foushee, submitted). Collecting cones from the same collection areas and the same trees does not effectively capture the full range of genetic variation in key adaptive traits. Moreover, it increases the levels of related offspring and the subsequent consequences of inbreeding depression.

In anticipation of climate change, we also suggest that the proven rust-resistant trees from which most seeds are harvested within an area be replaced with other proven rust-resistant trees over time to increase genetic diversity and diversify tree resistance mechanisms. This will minimize the chance that rust will evolve and overcome these resistance mechanisms. Continued harvests of seed for operational planting from only one set of trees over time may not ensure that the full range of rust resistance be captured in the seedlings that will be planted on the landscape. With current technology, it is expensive to constantly test new plus trees for their level of rust resistance, but confining seed collection from a small plus tree

population may reduce the genetic variability that is so important in responding to climate change fluctuations. We hope that the application of genomics will provide faster, cheaper tests to determine whether individual trees carry key genes contributing to polygenic resistance.

We also advocate that managers harvest additional seed in anticipation of future increases in planting treatments. Although it is difficult to store the seed for more than 14 years, we think that a large seed collection will provide the critical materials for implementing future restoration treatments. The seed may have a wide variety of uses such as (1) growing seedlings for operational planting and research studies, (2) cataloging genetic diversity, (3) supplying a source of seed for other land management agencies that have few seed resources, (4) use in research and management studies, and (4) sustaining gene conservation cone collections in seed stores where typical grow-out procedures for other annual and biannual species to replenish inviable seed is impractical for a long-lived conifer. It is acknowledged that rust resistance by these means is based solely on the performance of the maternal (cone-bearing) parent, as these cone collections are a result of open-pollination from random (both resistant and susceptible) pollen donors.

There are several other important activities that fall within this management action (Mahalovich 2000; Mahalovich and Dickerson 2004; Mahalovich and Foushee, submitted; Nelson 2014). We need to build up a comprehensive pollen bank to use in special breeding programs and genetic efforts. We also need to create a clone bank. The primary advantage of a clone bank is to archive valuable genetic material scattered across several areas into a well-protected location (White et al. 2007). Plus trees of interest (i.e., proven, rust resistance, cold hardiness, drought tolerance, etc.) are commonly propagated through grafting as a means of *ex situ* conservation. Protecting valuable genetic material in a centralized location serves as an added buffer if the original plus tree dies and also reduces the costs of protecting scattered plus trees in the field. Moreover, this form of gene conservation would afford more flexibility in designing treatments (mechanical cuttings and prescribed fire) in the field to promote whitebark pine regeneration if

backup copies of plus trees are established in a clone bank (Mahalovich and Foushee 2015).

5.3.5 Grow Seedlings

Now, and increasingly over time, we need to grow thousands of whitebark pine seedlings from seeds gathered from trees that demonstrate rust resistance (Burr et al. 2001). Restoration activities are increasing, and as fire size and frequency increase, we will need to supply the seedlings to plant in the extensive areas that have been treated or burned, especially where seed sources are dead or damaged. Rust-resistant seedlings are especially important for the future if wildland fire increases in areas with high damage and mortality from WPBR and MPB. This is because red squirrels, especially, will cut cones and nutcrackers will act as predators and eat most of the cached seed in highly damaged areas (Keane and Parsons 2010a; McKinney and Tomback 2007). Planting is the most important restoration activity in those areas with high whitebark pine mortality (>50 percent) to ensure continued whitebark pine regeneration and increase the frequency of rust resistance on the landscape.

Mycorrhizae are critical for whitebark pine establishment so it may be beneficial, especially in this time of warming climates in the upper subalpine areas, to inoculate seedlings with mycorrhizae. This would improve their survival because of increased water, phosphorus, and nitrogen uptake (Cripps and Antibus 2010). At the time sowing requests are submitted, nurseries should be told that seedling stock is going to be planted in settings that might be devoid of mycorrhizae (e.g., after a severe fire, a re-burn, or a hot prescribed burn), to determine if mycorrhizal inoculation is appropriate in a nursery setting. Perhaps the best approach may be to inoculate all seedlings regardless of where they are planted, depending on the expense (Cripps and Grimme 2010). Continued research to determine the efficacy of nursery inoculations of mycorrhizae is critically needed.

When planting programs within a recognized ecosystem or seed zone exceed 40,000 seedlings annually, managers should consider the benefits of establishing grafted seed orchards. Seed orchards can be carefully designed to optimize genetic diversity,

minimize the negative consequences of inbreeding depression, double the levels of blister rust resistance with both rust-resistant maternal (cone) and paternal (pollen) parents, manage correlated response with other adaptive traits (e.g., cold hardiness and drought tolerance), provide early and abundant flowering to overcome infrequent and variable cone crops, and provide a cost effective means of harvesting seed for planting programs. Establishing seed orchards should have been included among the management actions in the Keane et al. (2012b) rangewide strategy. And, because branch tips (scions) remember their age and position in the tree crown, 80 to 300-year old scions from the better performing plus trees grafted onto 3–6 year old rootstock initiate cone production shortly thereafter. Abundant conelets and pollen catkins are routinely observed on greenhouse whitebark pine grafts. Cones in orchard crowns can be easily protected with wire cages so that tree climbing or traveling long distances to backcountry, high elevation sites is unnecessary. Developing cone crops in seed orchards can be readily monitored for maturity to ensure that only the well-developed cones and mature seed are harvested. Smaller sized orchards (one to five acres) are easier to finance, can be customized for site specific management objectives, and can reflect a broader genetic base by varying the genetic constitution of each seed orchard.

5.3.6 Protect Seed Sources

Protecting rust-resistant, seed-producing whitebark pine trees against mortality from future disturbance and climate regimes will be important for maintaining genetically diverse populations on the landscape. These mature trees are key to effective restoration in times of rapid climate change because they enhance resistance to WPBR and contain unique genetic legacies. The more rust-resistant screened plus trees that can be retained in the future, the more likely we can maintain genetically diverse populations on the landscape. Thus, it is important that these trees don't die in wildfires, avalanches, and MPB outbreaks that are likely to be more frequent and severe in the future. These seed-source trees fall in two classes: (1) the high priority plus trees that have been selected for seed collection and tested for rust resistance,

and (2) the lower priority future plus trees that are identified as potentially rust resistant, but have yet to be screened for resistance. The latter class of trees are all those currently growing in high rust-mortality areas (Hoff et al. 2001). All trees of both classes warrant protection. One last and important point is that any protection treatment should attempt to satisfy multiple objectives when implemented; for example, fuel treatments should also be thinnings that increase whitebark pine tree vigor and cone production and planting rust-resistant whitebark pine seedlings should be part of the treatment design.

The most common tree-level restoration activity is the protection of trees from disturbance agents, primarily fire, MPB, and WPBR. Protecting trees against wildland fire (prescribed, wildland fire use, or wildfire) is difficult and costly, but it can often be effective, especially in moderate fire danger years (Keane and Parsons 2010a; Murray 2007). Fire protection has been implemented, with mixed success, using any combination of the following actions: (1) mechanical or manual manipulation of surface fuel surrounding the plus trees by raking or blowing (via leaf blower) downed wood, litter, and duff away from tree bases; (2) cutting competing fir and spruce; (3) mechanical reduction of shrub, and herbaceous fuels using mowers or clippers; and (4) prescribed burning to kill competing vegetation and reduce surface fuels (Keane and Parsons 2010b).

The most important design criterion is deciding the amount of area to treat around each tree. A general rule of thumb is a circular area around the tree that has a radius equal to the average stand height (Keane and Parsons 2010b; Keane et al. 2012b). That area, however, can be increased or decreased depending on canopy and surface fuel conditions in adjacent stands, especially in the prevailing downwind stands. We believe that it may be more effective to increase the fuel treatment radii around selected trees and to treat more trees to anticipate future impacts. Tree-level protection treatments against fire are most effective when little woody surface fuel is present in the treated area and that there are few competing tree and shrub fuels surround the tree being protected. Fire crews have wrapped large whitebark pine with fire shelters to protect against fire mortality, but with limited

success (Keane and Parsons 2010b). These tree-level fuel treatments are commonly done by people with chainsaws cutting trees around the target tree and then removing, piling, and burning the slash. The slash should be piled away from the target tree to minimize *Ips* spp. beetle damage and prolonged soil heating when piles are burned (Keane and Parsons 2010b).

Methods of protecting known or potential rust-resistant trees from MPB and WPBR fall into two categories: indirect and direct protection. Indirect protection comes from increasing tree vigor by cutting competing vegetation and by eliminating the factors that favor the spread of MPB or WPBR. Treatments that remove competing vegetation around individual trees, often called “daylighting” (tree level) or thinning (stand level), provide the target tree competition-free growing space for a long time span (Keane et al. 2012b). Daylighting treatments can also function as fuel-removal treatments that reduce surface and canopy fuels surrounding the target tree (see previous paragraph). Daylighting has other benefits, many of which have yet to be extensively studied. Some think that the post-daylighting environment increases radiation to the stems of the target trees, thereby increasing temperature and perhaps limiting MPB attack. This open environment also increases wind speeds that may better disperse the aggregating pheromones produced by MPB in the surrounding attacked trees. Increased wind and radiation could also decrease humidity that may decrease the incidence of new WPBR infections on the target trees in moderate fire years. Again, the size of treatment area is critical in the design of daylighting treatments (see above). Many treatments have used a circle around the target tree with the radius that is equal to the height of the surrounding canopy or 1–3 times the height of the target tree. Daylighting treatments should also include fuel reduction to protect against multiple disturbances. Thinnings have the same benefits of daylighting if done correctly, but most thinnings will be more effective into the future if paired with a prescribed burn (see Section 5.3.7).

Direct protection treatments for MPB and WPBR are any action designed to reduce populations or prevent attack. These include tree-level treatments that kill the damaging pathogens or pests, such as

fungicides for WPBR (Brown 1969) and insecticides for MPB, and treatments that change the behavior of the organism, such as the anti-aggregating pheromone Verbenone (Bentz et al. 2005; Kegley and Gibson 2004). Pruning has also been suggested by some as a means to retard or eliminate WPBR infections (Hungerford et al. 1982; Hunt 1998). However, direct approaches are costly and may take funding away from projects that make more effective and longer-term contributions to restoration. Direct approaches could be valuable for protecting small numbers of whitebark pine in local situations that may have disproportionate impacts, such as within ski areas, for isolated stands of whitebark pine, and around a municipal watershed (Keane et al. 2012b).

All of these tree-level treatments demand a long-term commitment, especially as we progress into the uncertain future when we know restoration efforts might be compromised. It is hoped that protection methods for these important rust-resistant trees will be improved as other restoration actions create landscape heterogeneity, increase rust resistance, and allow natural landscape processes to occur. Ultimately, we need to ensure that there are other trees to take the place of plus trees lost from disturbance.

5.3.7 Implement Treatments

The rangewide strategy emphasizes the need to create conditions that encourage whitebark pine regeneration, conserve seed sources, and promote rust resistance (Shoal et al. 2008). Objectives for treatments include creating nutcracker caching habitat, reducing competing vegetation, decreasing surface and canopy fuels, manipulating forest structure and composition, and diversifying age class structure. These actions can be implemented using a host of passive and active treatments to create areas where whitebark pine can prosper. As mentioned in the guiding principles (Section 5.2.4), before stand- and tree-level treatments are implemented, managers need to take a landscape approach and manage for heterogeneous landscapes and plan treatments as part of a landscape level evaluation.

Many types of treatments can accomplish the primary restoration objectives of facilitating whitebark pine regeneration, increasing whitebark pine cone

crops by increasing vigor, and reducing disturbance impacts. This usually involves some combination of silvicultural cuttings, prescribed burning, and planting rust-resistant seedlings. These treatments should attempt to improve landscape heterogeneity while also facilitating whitebark pine resilience, rust resistance, and sustainable cone crops. We discuss prescribed burning, cuttings, and plantings as the primary tools for implementing treatments in the context of the primary reason or objectives for the treatment—competition removal, fuel reduction, fuel augmentation, and regeneration facilitation. Any treatment should be designed to address multiple objectives. Fuel reduction treatments, for example, should also reduce competition and allow for natural and artificial regeneration.

5.3.7.1 Competition Removal

Eliminating vegetation that competes with whitebark pine trees is meant to improve tree vigor, which is increasingly important as the climate warms. Improved vigor often results in greater forest resilience because the trees are now about to allocate resources to defenses against increasing incidences of disturbance events. Improved vigor may also increase the frequency and quantity of cone crops because trees may allocate more resources to reproduction. And last, increased vigor will contribute to longevity and allow trees to remain on the landscape for longer times.

Mechanical thinning where chainsaws are used to cut competing subalpine fir, spruce, and mountain hemlock is the primary tool used for competition removal treatments. It is important that all competing shade-tolerant conifers be cut, including the regeneration; this is rarely done because of the cost. Any residual trees of competing species, even small fir seedlings, will compromise the efficiency of the mechanical treatment, especially when productivity increases projected for the future will accelerate successional advancement. Therefore, many cutting treatments can be improved by including prescribed burning after the cut because, hopefully, the fire will tend to kill most of the small and large shade-tolerant tree competitors and leave the more fire-tolerant whitebark pine individuals (Keane and Parsons

2010b). Prescribed burning alone, however, is not as exacting as mechanical cuttings. Prescribed fires are highly variable across space and may miss parts of the stand thereby leaving many fir and spruce trees alive. These fires can also severely burn parts of the stand resulting in high mortality in mature whitebark pine trees (Keane and Parsons 2010b). If done correctly, prescribed fires can kill most of the shade-tolerant understory layer that otherwise would take significant effort to remove if mechanical cuttings were used. This is especially true when fuels are augmented prior to the fire treatment (see following sections).

Since climate change may result in significant increases in vegetative productivity in upper subalpine areas, it is important to remove as many shade-tolerant competitors as possible to make any restoration treatment last longer. Therefore, several modifications of these competition removal treatments are needed to account for potential climate change. First, mechanical cuttings and prescribed burning treatments should take a more liberal approach and remove more of the competitors than normal. Cutting non-merchantable trees or removing advanced regeneration is probably best. In prescribed burning, it is better to burn on the hotter side of the prescription while protecting those valuable plus trees. This may be difficult in most operational settings because the fuelbed may be quite dry; this might increase the risk of escape and spotting, and result in high whitebark pine mortality. Therefore, we suggest using a pre-fire mechanical treatment, here called fuel augmentation, to add more fuels (needles and small branches) to the normally sparse fuelbed. With fuel augmentation (discussed below), a greater fire intensity can be obtained while the weather conditions are still moist, thus protecting whitebark pines (Keane and Parsons 2010b). It is vitally important that any mechanical thinning or cutting to improve whitebark pine growing conditions should also treat the fuels surrounding the apparent rust-resistant trees to minimize the chance that they are lost from fire.

5.3.7.2 Fuel Reduction

Fuel treatments will undoubtedly play an important role in reducing wildfire impacts on living rust-resistant trees and are therefore considered a viable

restoration action. Treating fuel through the use of controlled and uncontrolled wildfires will be important in the future as a protection in the role of creating heterogeneous landscapes. Wildfires, however, can't be planned and can be difficult to manage, especially once they get above 50 ha in size. There is always a chance that they will adversely impact whitebark pine restoration efforts by killing rust-resistant trees or planted seedlings rather than providing benefits by creating competition-free growing space for future populations. Therefore, mechanical and prescribed fire fuel treatments may be more desirable and manageable than wildfires in the future.

Fuel treatments involve reducing canopy fuels by cutting, masticating, or burning living subalpine fir, spruce, and other shade-tolerant conifer trees and reducing surface fuels by burning or cutting. Reducing fuels in or near stands that contain valuable rust-resistant trees can be an important hedge against losing them to future wildfires. It is critically important that any fuel treatment be also designed in the context of a whitebark pine restoration treatment, and vice versa. This means that the reduction of canopy and surface fuels should be considered a secondary objective. Many contemporary fuel treatments, such as mastication, canopy thinning, and chipping, are not designed with ecological relationships in mind. It is entirely possible that live whitebark pine trees could be cut during fuel reduction treatments. And conversely, restoration treatments that do not also reduce fuels may result in unnecessary losses of seed sources from future wildfires.

5.3.7.3 Fuel Augmentation

Fuel augmentation is the process of changing the fuelbed to facilitate a wider prescribed burning window and a more comprehensive and consistent burn once the fire is ignited. Usually fuel augmentation involves felling the shade-tolerant, fire susceptible competing trees in areas where surface fuels are insufficient to achieve the prescribed burning objective. The red needles and small twigs of the felled trees create additional fine surface fuels that allow ignition of hotter fires under cooler and moister conditions. This creates a wider temporal burn window thereby allowing fire specialists the ability to ignite

a prescribed burn when fuel moistures are higher, such as towards the end of the autumn burning season (Keane and Parsons 2010b). Many seral whitebark pine stands have discontinuous fuelbeds with highly variable fuel loadings that, when burned under typical prescriptions, do not generate enough heat to kill the shade tolerant competitors, so fuel augmentation is often a necessity (Keane and Parsons 2010b).

The successful melding of fuel augmentation and prescribed burning will be an important treatment in the near-term but it may become even more important as climate changes become manifest in high elevation landscapes. The treatment that accomplishes the most restoration objectives is often prescribed burning. To get the best results from prescribed fires, it is important to augment surface fuels when needed to provide additional control to fire managers. In anticipation of future increases in wildland fire, fuel augmentation and prescribed burning can be used together as fuel reduction treatments to protect rust-resistant pine trees and also as competition removal treatments to improve whitebark pine vigor. Keane and Parsons (2010a) found that those stands that were treated with prescribed fire after fuel augmentation acted as effective fuelbreaks against wildfires that occurred after the prescribed burn. Therefore, the importance of fuel augmentation coupled with prescribed burning will be to condition current stands against future increases in disturbances, primarily fire (through fuel reduction), but also insects and disease (through improved vigor).

5.3.7.4 Regeneration Facilitation

Some proactive, stand-level restoration treatments are designed to remove competition in order to improve natural regeneration of whitebark pine (Keane and Parsons 2010b). This involves creating stand conditions that facilitate seed caching by the Clark's nutcracker on the treated site. If nutcrackers cache enough seeds, then they may not recover some caches, or snowmelt and spring and summer rains may trigger germination before nutcrackers retrieve the seeds (Tomback 2001). Seedlings from these caches become the whitebark pine forests of the future. Regeneration restoration treatments usually involve removing vegetation from the overstory and understory to create open ground conditions that are used by nutcracker

for seed caching (Keane and Arno 2001; Tomback 2001). A variety of mechanical cutting and prescribed burning treatments can be used to create conditions that facilitate regeneration. The most common approaches are group selection harvests and moderately severe prescribed burns (Keane and Parsons 2010a).

Facilitating natural regeneration using management treatments may not be dependable in the near-future, especially with changing climates and continued losses from MPB and WPBR. Relying on natural regeneration is a risky business considering that many areas may have insufficient populations of mature, cone-bearing whitebark pine to sustain viable regeneration because the Clark's nutcracker eats most of the seed it caches. Keane and Parsons (2010a) found little natural whitebark pine regeneration in their treated areas probably because the nutcracker reclaimed most of the cached seed in areas of low seed-producing trees. Even if natural regeneration does occur, the majority of the nutcracker cached seeds may be from whitebark pine trees that are susceptible to rust. Therefore, most regeneration facilitation treatments should attempt to create suitable ground conditions to allow the successful planting of rust-resistant seedlings. This may be the best option under changing climates, especially in those stands decimated by MPB and WPBR.

5.3.8 Plant Seedlings

To mitigate the loss of whitebark pine due to climate-mediated changes in disturbance regimes, we must plant those disturbed or treated areas where whitebark pine seed sources have lost cone-producing capacity through MPB mortality or WPBR infection with rust-resistant whitebark pine seedlings (Fiedler and McKinney 2014). This is one of the main principles of the rangewide restoration strategy (Keane et al. 2012b). Reforestation with rust-resistant seedlings will increase the representation of blister rust-resistant genotypes in the next generation and eventually create resilient whitebark pine forests of diverse age structures that are more likely to withstand frequent fire, MPB outbreaks, and the spread of WPBR. Planting rust-resistant seedlings is recognized as the key management action in the rangewide strategy (Keane et al. 2012b). Sowing seeds from rust-resistant

sources directly in treated or burned areas, if shown to be efficacious, may be a cost-efficient alternative to growing seedlings and planting them. Areas with declining whitebark pine seed sources are unlikely to produce enough seeds to attract and support nutcrackers, so natural seed dispersal is unlikely (Barringer et al. 2012; McKinney et al. 2009). Because blister rust is at the northern limit of whitebark pine's range, as well as its upper elevational limits, both important climate change fronts, seedlings from rust-resistant parent trees should be planted at both limits. Most other restoration actions will be ineffective without the planting of rust-resistant seedlings.

We have several suggestions for planting seedlings to mitigate the effects of climate change and ensure high seedling survival. First, planting probably should be prioritized first on the higher portions of whitebark pine seral sites based on results of our simulation experiment (Section 4). Given the high costs of growing rust-resistant seedlings and of planting them in remote settings, planting should start at the highest regions in burned areas below climax whitebark pine sites where they are most likely to survive in the future, and then progress downwards in elevation.

Second, seedlings should be planted in microsites that best mitigate harsh conditions and provide shade or wind protection (McCaughey et al. 2009). For example, they should be planted on the side of a rock, stump, or other object that provides some protection. Microsites may moderate seasonally arid conditions when the planted seedling is most susceptible to drought effects, or protect against hard frosts, deep snow packs, prolonged insolation, drought, and soil erosion during the critical time of seedling establishment (Scott and McCaughey 2006). Since snags eventually fall, planting next to snags should be avoided, but planting next to stumps often provides good protection. If no favorable microsites for planting exist, then we suggest that planting crews be instructed to create the microsite using a log, rock, or wood stake, or other protection device.

Next, selection of planting sites should be based on whether they might contain important mycorrhizae needed to ensure seedling survival (Loneragan et al. 2013). Seedlings planted in proximity to sapling or mature whitebark pine regeneration have a chance

to be colonized by the appropriate mycorrhizae (Mohatt et al. 2008; Perkins 2015). Moreover, it may be advantageous to wait for undergrowth vegetation, particularly shrubs, to develop before planting whitebark pine seedlings on burned sites, although this could require a number of years for extreme sites. There may be excessive erosion and soil movement during the years directly after a burn that may dislodge planted seedlings, and undergrowth shrubs may provide partial shade that is favorable to seedling survival (Tomback et al. 2011b). Waiting until shrub and herbaceous plants have reestablished before extensive planting is implemented may be more effective, except when beargrass (*Xerophyllum tenax*) is present (Izlar 2007; McCaughey et al. 2009).

In the future, special attention should be given to the planting guidelines of McCaughey et al. (2009) and Scott and McCaughey (2006). Large, hardy seedlings with well-developed root systems will survive best in the highly variable climates of the future. Seedlings should be planted in competition-free environments so that shading effects are minimized and the seedling can grow its best to be more resilient. However, some partial shade and physical protection may enhance survival by using shade cards and planning site mitigation, such as placing logs or rocks around the seedling. Moist soils will be critical for high survival after planting seedlings; managers are now waiting until the fall to plant whitebark pine seedlings to avoid summer droughts. So it might also be more effective to wait until autumn rains have wet the soils before planting, especially with future warmer and drier climates.

Our simulation efforts show that the gains in planting rust-resistant trees are not manifest in the short simulation time (90 years) (see Section 5). However, the real gains in planting may take centuries not decades to become manifest (fig. 57). By planting rust-resistant seedlings, we may reduce by half the amount of time it would take natural selection to create viable, rust-resistant populations. We also avoid the possibility that the species might decline to such low levels that it is unable to create rust-resistant populations naturally without management intervention (Keane et al. 2012b). While some areas will regenerate naturally from surrounding seed sources, the surviving seedlings

might have a low frequency of resistance to WPBR and most may eventually die after WPBR wave years, which could be more frequent in the future. One general way to restore whitebark pine and mitigate for climate change is to plant all burned or treated areas with rust-resistant seedlings, including those burned areas in somewhat healthy whitebark pine landscapes with abundant live, mature trees. However, in the interest of effectiveness and cost containment, the higher elevations in a treatment landscape or stand should be targeted for planting first.

Assisted migration is broadly defined as the translocation of a species into more habitable locations outside of their current range (McLachlan et al. 2007). This treatment option has been promoted as a means of saving species or vulnerable populations from extinction due to climate change (McLane and Aitken 2012). While this may seem like a viable approach, we think it is fraught with uncertainty and pitfalls that may render most plantings ineffective. First of all, rust-resistant seedlings at this time are not available in sufficient quantities, and they are quite expensive. Planting expensive seedlings in a foreign environment is probably not a good use of funding.

Secondly, it will be nearly impossible to decide the best places to plant these expensive rust-resistant seedlings based on the highly uncertain simulated climate change predictions (see Section 3). The high uncertainty in climate predictions among global circulation models and scenarios, coupled with the high uncertainty in extrapolating predicted coarse scale weather to finer scales, make it challenging to identify which areas will be climatically suitable for whitebark pine planting beyond its current range, especially at the microsite scale. Bioclimatic envelope models (BEMs) are often used to locate potential assisted migration areas (see Section 3), but BEMs often are based on the distribution of mature trees and do not account for regeneration processes in their design.

Third, sown seeds and planted seedlings may not survive the near term climates in these new areas; cold, snow, frost, lack of mycorrhizae, and novel soil conditions in the new areas may kill the seedlings long before the climate changes sufficiently. However, a recent study of sown seeds at treeline has shown good seedling germination and survival in the Greater

Yellowstone Area (Pansing 2014). McLane and Aitken (2012) found that whitebark pine in British Columbia could establish in model-predicted climate zones north of the current species range in a small assisted migration trial. Their BEM, however, could be enhanced by adding snow-duration variables to facilitate capturing the influence of snow on seedling germination and survival. We think it is best to use the limited resources available to restore whitebark pine within its historical range, with the goal of maintaining healthy, cone-producing populations that can naturally expand distribution (Breed et al. 2013). Nutcrackers cache seeds within and above treeline in alpine tundra—essentially providing “assisted migration” at the upper elevation climate change front (Tomback 1986, 2001). Little is known about nutcracker seed dispersal at the northern limits of whitebark pine, but nutcrackers may well occasionally cache seeds beyond the current distributional limits.

5.3.9 Monitor Activities

The success of future whitebark pine restoration efforts will be greatly dependent on the lessons learned in previous attempts (Keane and Parsons 2010b). Future implementation of restoration protocols and tools will benefit by the detailed documentation of the successes and failures of all previous restoration attempts, especially in this time of climate change (Logan et al. 2008; White et al. 1990). Therefore, the monitoring of restoration treatments with pre- and post-treatment sampling is vital for providing the critical information needed to fine-tune future treatment planning, designs, and implementation to adjust both for local conditions and for changing climates. Historically there has been little financial support for the comprehensive monitoring needed to evaluate the effectiveness of land management actions, and these monitoring efforts will be even more important with climate change.

Monitoring requires a system of uniform protocols, databases, and sampling methods; it also requires the free exchange of data across agencies and the public (see Lockman et al. 2007). Several field monitoring systems are available (Tomback et al. 2005), including FIREMON (Lutes et al. 2006), the FIREMON-FEAT Integration (FFI; Lutes et al. 2009), the U.S. Forest

Service's FSVEG (USFS 2016), and the National Park Service's Fire Monitoring Handbook (NPS 2001).

All monitoring data should be entered into one interactive database for analysis by both research and management and analyzed at various spatial and temporal scales, from local to regional and from yearly to decadal, to comprehensively document ecosystem responses to restoration treatments. The results are best for feedback on restoration treatment efficacy. The time frame for monitoring is also a consideration: Should treated areas be assessed within a year after restoration is implemented, or should 3, 5, or 10 years elapse first? In the case of planted seedlings, information on first-year survival seems essential; similarly, soon after application of prescribed fire, effectiveness of treatment should be evaluated.

Modifying current monitoring project designs is an important way to accommodate the potential impacts of climate change. First and foremost, all monitoring should be done over long time periods to ensure that any ecological response from changing climates is manifest in quantifying treatment effects. This means that we need to monitor over decades to centuries. This will entail monitoring of legacy projects from previous generations of restoration initiatives, along with revised agency work priorities. It is also important that monitoring networks be continually revisited to detect if restoration activities are still effective under these new climates. Moreover, whitebark pine ecosystem response to disturbance, especially wildland fire, often takes a long time, up to 50 years in some areas (Agee and Smith 1984; Keane and Parsons 2010b). Most importantly, all monitoring should always include a control unit to document those changes that results from climate alone so that the responses resulting from restoration actions can be interpreted in the appropriate context.

Monitoring sample designs might also include variables that might be important to describe climate impacts on restoration treatments. Most monitoring efforts are designed to evaluate some restoration objective. For example, if a restoration objective is to regenerate recent burned areas, then the monitoring design might only include methods to quantify seedling density using fixed-area plots. In times of changing climates, the count of seedlings by species

and size in the plot could be augmented with a variable that indicates if seedlings are next to protected microsites or specific shrub or herb plant species. Variables that describe biophysical attributes of the fixed area plot could be assessed, such as aspect, soil type, percent cover by lifeform, and ground cover. The primary monitoring data can then be stratified by or analyzed by the secondary variables as covariates to detect differences and adjust restoration designs accordingly.

Because ecological processes are dynamic, they tend to be highly variable, and the predicted climates of the future will surely increase that variability. Therefore, another recommendation is that sampling intensities (number of plots) be increased to accommodate changing variabilities over time. Of course, it will be difficult to determine just exactly how many plots or sampling units will be needed to quantify future variabilities because of the high uncertainty in climate prediction and ecosystem response. There are, however, minor things that can be done to mitigate declining sampling power. First, tighter tolerances can be used to compute sample sizes from an estimate of contemporary variability. Instead of using a 20 percent threshold for estimating how close the sample should approximate the mean, for example, 15 percent could be used. Next, a more conservative approach can be used to approximate the sample size and design. The parameters detailed in the methods presented in FIREMON (Lutes et al. 2006) or Keane (2015) for estimating sample size can be computed for a best case and worst case scenario; under climate change, the worst case scenario might be appropriate. Next, those variables being estimated in a sample plot must be measured using the most accurate techniques to minimize high uncertainty in final estimates. Tree height, for example, is more accurately estimated using laser rangefinders rather than clinometers, and plant cover could be more accurately estimated with digital photos rather than visual estimates. Last, sampling could be confined to those variables that best assess restoration objectives and have lower natural variabilities. Total fine woody surface fuel load, for example, has a lower variability than the variability of any of the three surface fuel components that comprise fine woody fuels (0 to 0.25 in diameter, 0.25 to

1 inch diameter, and 1 to 3 inches in diameter) (Keane et al. 2012a, 2013).

5.3.10 Conduct Research

New research in all phases of whitebark pine restoration is needed to ensure that all management actions utilize the most scientifically credible methods to effectively return the species to high mountain settings. Unfortunately, there continues to be little interest in funding basic and applied whitebark pine ecological research, especially in the context of climate change, and this could impact the future success of restoration treatments. For example, many whitebark pine restoration projects are proposing or implementing treatments designed to release understory whitebark pine. However, there is little research to show that the suppressed seedlings and saplings of this moderate shade tolerant species will actually release to increase in growth and become cone-bearing mature trees. In a limited sample, Keane et al. (2007a) found that about a third of the trees released, but many released years later or didn't release at all. The key then is to conduct the research that develops methods to identify which species will release and which will remain at the same size. This lack of comprehensive research is perhaps the most important barrier for efficient and successful restoration treatments. In general, few research dollars are being spent on this endangered foundation species and the forests it creates, and there are few scientists that have an extensive knowledge of this complex ecosystem. It is vital that research provide the information needed by managers to conduct successful treatments for the sustainable management of whitebark pine ecosystems.

Several high priority topics for guiding future research in whitebark pine restoration are presented in Keane et al. (2012b), but there are many others that should be included to account for climate change. We present these topics by major categories and also by the four guiding principles (Sections 5.2.1 to 5.2.4), but our examples are by no means exhaustive.

Basic Ecological Research

- Study basic ecophysiological relationships of whitebark pine to climate and environmental conditions.
- Study the recent and long-term past climates of whitebark pine sites.

- Carefully study the regeneration processes of whitebark pine as it is probably the most sensitive to climate change impacts.
- Improve current information on the survival of whitebark pine after fires, MPB, and WPBR and develop predictive models from this information (Perkins and Roberts 2003).

Silvicultural Investigations

- Evaluate those characteristics of whitebark pine seedlings and saplings that indicate if individuals will release from competition or remain suppressed (Keane et al. 2007a).
- Create a classification system that easily identifies those whitebark pine trees that will increase in growth after removal of competition.
- Improve planting guidelines to optimize planting success.
- Develop better ways to harvest cones, clean seeds, and grow seedlings (Ward et al. 2006).
- Develop better cutting prescriptions for ecosystem restoration in whitebark pine with rust (Waring and O'Hara 2005);
- Determine optimal thinning designs for whitebark pine forests.

Nutcracker Interactions

- Continue to study the interacting dynamics of seed predation by birds, mammals, and insects.
- Estimate the density of cone production needed to sustain natural whitebark pine regeneration in most cone years and at what cone production density nutcrackers become seed predators rather than dispersal vectors.
- Determine whether regional populations of nutcrackers fluctuate over time and how population size may influence seed dispersal.
- Determine if whitebark pine is extirpated regionally and then restored, whether nutcrackers may return in future decades.

Modeling

- Design and develop spatially explicit, ecophysiological models that simulate whitebark pine landscape

dynamics over the entire range of the species (Nelson 2014).

- Develop methods to simulate both the past and future ranges of variation of whitebark pine community dynamics to use as reference in management analyses (Keane et al. 2009).
- Obtain more accurate, realistic and comprehensive daily climate data for both the past and future.
- Improve methods to downscale climate predictions to local settings.
- Develop simulation protocols and modules to simulate alternative management treatments on whitebark pine stands in landscapes (Mladenoff and Baker 1999).
- Simulate how much of the landscape needs to be treated to ensure the optimal efficacy of whitebark pine restoration treatments (Loehman et al. 2011b).

Promote Rust Resistance

- Develop genomics-based cost-efficient methods to evaluate the presence of rust resistance in individual whitebark pine trees and at the population level.
- Determine what frequency of rust resistance in a whitebark pine population is needed to sustain that population in the future with different climate change and blister rust response scenarios.
- Add the impact of MPB and fire to these models.
- Invent new ways to accelerate natural selection for rust resistance in whitebark pine.
- Explore tree breeding and other ways to improve rust resistance in seedlings;
- Monitor genetic variation in *Cronartium ribicola* both geographically and over time to determine rates of evolution.

Conserve Genetic Diversity

- Create methods to assess the durability of rust resistance under operational conditions and natural inoculum.
- Determine the genetic diversity of outplanted rust-resistant seedlings in relation to natural populations.
- Periodically reassess seed transfer guidelines and seed source performance under changing climatic conditions to ensure the highest seedlings survival.
- Plant beyond seed transfer guidelines, using genotypes from more southerly locations that have climatic conditions more similar to future climates.

Save Seed Sources

- Develop new techniques to protect rust-resistant trees from fire, MPB, and future climates.
- Develop protocols for protecting cone-bearing whitebark pine trees from future severe fire during wildfire suppression efforts.
- Develop new techniques to accelerate cone production in seed orchards.

Employ Restoration Treatments.

- Evaluate efficacy of current and future restoration treatments; develop new techniques to harvest seeds from trees and grow seedlings in the nursery to reduce the high cost.
- Explore new techniques for planting the seeds of whitebark pine in burned and treated areas.
- Explore how to increase seed germination and seedling survival, and reduce rodent seed theft in direct sowing projects.
- Determine when is the best time to plant whitebark pine seedlings after a severe wildfire.

6. Discussion

6.1 Restoring Whitebark Pine in the Face of Climate Change

Several important findings from this study's literature review (Section 3) and simulation experiment (Section 4) may dictate how we approach whitebark pine restoration in the future. The first finding is that whitebark pine will continue to decline over the next several decades, mostly from WPBR and MPB mortality and only indirectly by direct climate change impacts (Section 4). This agrees with another modeling effort by Smith-McKenna et al. (2014). The second finding is that this decline can be reversed with proactive restoration actions; if no restoration activities are attempted, whitebark pine forests will continue to decline and become a minor, if not missing, component on the high elevation landscapes in western North America. Even a low level of restoration activity will help keep whitebark pine forests from vanishing on the high mountain landscape (Section 4). We also found that the effects of planting rust-resistant seedlings on whitebark pine ecosystem restoration take a long time to become manifest, probably more than a century. Third, we found that the recommendations proposed in the rangewide strategy (Keane et al. 2012b) (see Section 2 for details) are still valid. Only a few modifications to the rangewide strategy are needed to account for future changes in climate (Section 5). We also found that whitebark pine can do quite well under future climates on many landscapes, especially with more frequent fire, but there are some landscapes where whitebark pine will continue to decline (Sections 3, 4). In fact, whitebark pine appears to be able to create the most resilient and resistant upper subalpine forest under climate change compared to any other of its associates, primarily subalpine fir (Sections 3, 4). We also found that creating heterogeneous landscape structures will also mitigate the severity of disturbances. And last and most important, we found that the impacts of climate change on whitebark pine populations vary across its range based on local conditions. As the simulated output presented in Section 4 shows, whitebark pine actually increases

in abundance and stature on one landscape with future warming while it decreases on another. This implies that there is no magic bullet or one-size-fits-all solution for restoring this enigmatic ecosystem; managers must tailor broad strategies to local conditions for the most effective restoration treatments.

There is great concern among managers that treating declining whitebark pine ecosystems during a time of widespread climate change, WPBR infections, and MPB outbreaks might destroy the important remaining whitebark pine seed sources. It is possible that allowing lightning fires to burn as controlled wildfires and proactively lighting prescribed fires might kill valuable rust-resistant, cone bearing whitebark pine trees. However, we should consider the alternative. Wildfires will happen regardless of our best suppression efforts, especially in this high-elevation ecosystem where uncontrolled wildfires would have a greater chance of killing valuable rust-resistant individuals than managed fires because they burn under drier, hotter, and windier conditions. Even if uncontrolled wildfires don't occur, vegetation succession will occur, and the result will put an even greater competitive stress on the remaining shade-intolerant whitebark pine trees. Seeds from these surviving trees would have less chance of being planted in favorable sites free of competition because there are fewer burned areas on the landscape due to fewer fires. Mountain pine beetle impacts on whitebark pine are devastating, but these impacts provide little reason to suspend restoration activities. In fact, the most important time to initiate restoration actions on the landscape might be right now while we still have remaining whitebark pine populations on the high mountain landscapes.

The key to successful restoration in the future is the planting of rust-resistant whitebark pine seedlings after wildland fires, whether these fires are controlled wildfires, uncontrolled wildfires, or prescribed fires (Keane et al. 2012b). It is also important that the genetic diversity of these seedlings is optimized to ensure whitebark pine remains on the landscape as

the climate changes. Maintaining a diversity of age classes that contain rust-resistant whitebark pine is critical to sustaining the species over long time periods because it provides the resilience to survive unwanted wildfires and the resistance to outbreaks, disease, and climate shifts.

Undoubtedly, land managers and researchers will need to assess the future of whitebark pine with and without restoration for various projects and we think that the primary vehicle that will be used to conduct these prognostications is simulation modeling. The problem, then, is deciding which modeling technique, model, or model output to use to develop the projections. We suggest that perhaps the best guide to use for evaluation is to determine if the model in question simulates the major interacting factors presented in figure 22. If a model doesn't explicitly include these interactions, then certain assumptions and caveats must be made and used in the interpretations of the model projections. Bioclimatic enveloping models, for example, fail to account for several factors in figure 22. Therefore, if people want to use BEMs to decide the future of whitebark pine, then they must interpret the results in that context that the major disturbance effects are missing. Unfortunately, models that include explicit simulations of all the factors in figure 22 are rare and difficult to use at present. Thus, managers and researchers may often have to forgo modeling, and use the material in this report as context, or partner with modelers to simulate whitebark pine dynamics for their targeted landscapes. Models that integrate climate and management actions with ecosystem and landscape processes are rare, especially for whitebark pine, and there are no management oriented models as yet. This report represents perhaps the most comprehensive modeling effort for the species at landscape levels.

Given the high uncertainties in predicting climate, vegetation, and disturbance responses to increasing carbon dioxide levels, restoring whitebark pine ecosystems is much more likely to lead to a successful outcome than deciding not to restore based on the uncertain predictions for the future. It may be more prudent to wait until simulation technology has improved to include credible pattern and process interactions with regional climate dynamics coupled

with significant model validation before we base decisions on the restoration of whitebark pine on uncertain future climate projections. Ecosystem models may take decades of further development before their simulations can be used to predict species and landscape response to climate change with reasonable accuracy. While we wait, we may lose valuable populations and rust-resistant trees, and our options for restoration diminish greatly. There is a small chance that the benefits of the proposed restoration efforts might be negated or compromised by climate change effects, but any restoration action implemented today might be better than the alternative of doing nothing. The no action alternative will almost certainly result in major, if not complete, losses of whitebark pine populations, even without climate change.

6.2 Caveats

The Keane et al. (2012b) rangewide strategy and this report provide critical information for planning and implementing whitebark pine restoration efforts at multiple scales in the face of climate change. Successful restoration, however, depends on the ability of managers to tailor restoration designs to fit local conditions. It is impossible to design a restoration approach that will work everywhere with the same level of effectiveness in the projected climates of the future because of the high variability in site conditions across the range of whitebark pine. The manager must craft restoration plans that will be successful for a specific area and effective under changing climates by addressing critical local conditions such as rust infection levels, MPB mortality, fuel loadings, successional status, public issues, and whitebark pine mortality. We hope that this report coupled, with the rangewide strategy, provides helpful direction on how to design restoration projects while detailing those efforts that need to be accomplished at the appropriate scale.

The climate change considerations for the rangewide restoration strategy presented here have their limitations for implementation. First, findings in this report are based on information, technology, models, and data that were available at the time of writing. The field of climate change science is moving quickly so there may be more current information now that

can be included in any restoration evaluation (see Keane et al. 2011). The recommendations in Section 5 may be improved as (1) new restoration technologies are developed, (2) additional research is completed, and (3) more data become available. The guidelines presented in this document are provided for reference and are not designed to be implemented in the same way across the range of whitebark pine. This report is

meant to guide land managers as to which attributes to consider when evaluating the condition of their whitebark pine communities and to demonstrate the need for active restoration. Managers should use this information along with specific management direction established for lands to determine when, where, and if restoration and planting should occur.

7. Summary

Active restoration appears to be the only course of action for conserving whitebark pine ecosystems. Restoration must include the implementation of strategies that hedge the effects of climate warming on whitebark pine ecosystems, as well as mitigate the anthropogenic threats. However, the high uncertainty inherent in most current climate and ecosystem models and assessments may limit our ability to design restoration actions that are effective in the face of climate change. Uncertain climate change warming predictions are not justifications for inaction and allowing this important high mountain resource to continue to decline, especially considering the resiliency exhibited by whitebark pine forests over time and in response to wildland fire.

The best available information must be used to design effective restoration approaches and the toolkit of potential restoration techniques. Managers have the knowledge, skills, and experience to successfully

restore whitebark pine forests across the entire species' range, even though WPBR and climate change will make this task more difficult and complex. These factors only further underscore the need for immediate action to prevent the loss of this species and provide a solid rationale for strategic research and management planning for the conservation of this ecosystem. Sustaining these valued upper subalpine landscapes so that they will be resistant and resilient to climate change requires that we conserve as many parts of this ecosystem as we can. Losing whitebark pine ecosystems before the full range of climate change impacts are manifest could lead to a less resilient forest and dramatic shifts in high-elevation ecosystems of western North America. The set of management actions and adaptation strategies, approaches, and tactics presented in Section 5 will hopefully provide guidance in developing effective restoration actions using the rangewide strategy.

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