

Integration of Population Genetic Structure and Plant Response to Climate Change: Sustaining Genetic Resources Through Evaluation of Projected Threats

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Abstract

To assess threats or predict responses to disturbances, or both, it is essential to recognize and characterize the population structures of forest species in relation to changing environments. Appropriate management of these genetic resources in the future will require (1) understanding the existing genetic diversity/variation and population structure of forest trees, (2) understanding climatic change and its potential impacts on forest species and populations, and (3) development and use of new tools to identify populations at risk and geographic areas that will provide suitable habitat in the future. Forest trees exist within distinct geographic populations created by climatic shifts, evolutionary processes, the availability of suitable habitats, and other environmental factors. These processes have occurred over millennia and continue to shape the biogeography and genetic structure of these species. Forest trees in Western North America are being defined on the basis of molecular markers and quantitative traits. For example, studies of whitebark pine (*Pinus albicaulis*) and western white pine (*P. monticola*) demonstrate the existence of several distinct populations that likely developed via the long-term processes described above. These studies and others have shown that distinct populations exist within western conifer species and further indicate that the biogeographies of forest species are quite dynamic over time and space. Here, we present a case study using genetic data from whitebark pine and western white pine coupled with landscape-based, plant-climate modeling. Suitable contemporary habitat is

accurately predicted for both species based on presence/absence of field observations. General circulation models were used to predict areas of suitable habitat for both species under the current climate and the projected climate around the year 2030. These models predict that these species will respond differently to projected climate change. Suitable habitat (i.e., climate space) for whitebark pine is predicted to decline dramatically by ca. 2030. Populations in the lower latitudes (below 45° N) and those persisting at the low elevation limits show the greatest threat to extinction from climate change. Predictions also indicate that suitable habitat for western white pine will be reduced in some southern latitudes, whereas the suitable habitat will be increased in the northern latitudes of its distribution. For whitebark and western white pine, both molecular markers and quantitative traits frequently reveal congruent genetic structure for species conservation. The combination of genetic studies with climate modeling can provide base-line tools that will enable managers to focus genetic conservation efforts on populations at highest risk while restoring areas that have the lowest risk for predicted climatic extirpation. The ability to define forest populations and predict landscape-level effects of climate change is critical for sustaining future forest health.

Keywords: Bioclimatic models, biogeography, genetic conservation, western white pine, whitebark pine.

Introduction

Climate change and associated glacial/interglacial cycles have had a profound impact on the biogeography of plant communities. Paleocological data from pollen sediment cores and packrat middens have been used to uncover many of the past plant-climate associations (e.g., Thompson and Anderson 2000, Thompson and others 1993, Whitlock 1993). These climatic oscillations have also affected intra-species genetic relationships that are recorded in changes in gene frequencies or adaptive traits, or both (Davis and Shaw 2001). In western North America, most forest trees have

broad, disjunct distributions that are associated with variable environmental conditions. The combination of disjunct intra-species distributions and environmental variables can contribute to barriers in gene flow and changes in adaptive or neutral gene frequencies, or both, caused by selection or genetic drift (Richardson and others 2005). Population genetics typically assess neutral genetic variation and provide estimates of genetic diversity and partitioning among a spatial hierarchy. Population genetic studies can estimate both contemporary and historical gene flow, and thereby aid in elucidating past intraspecies relationships and distributions. Such genetic data, coupled with paleoecological data, provide inferences to historical changes in plant biogeography and postglacial expansion/contraction (e.g., Godbout and others 2005, Jackson 2006, Magri and others 2006, Petit and others 2004, Richardson and others 2002, Thompson and Anderson 2000). Knowledge of the population genetic structure and adaptation is critical for successful forest health management and conservation/restoration efforts.

Five-needled pines are keystone species in numerous ecosystems in western North America. This paper focuses on two case studies: whitebark pine (*Pinus albicaulis* Engelm.) and western white pine (*P. monticola* Dougl. ex D. Don). Whitebark pine occupies subalpine habitats across the northern Rocky, Cascade, and Sierra Nevada Mountains and mountains of northern Nevada. Seed dispersal is dependent on a coevolved mutualism with Clark's nutcracker (*Nucifraga columbiana*) that deposits seeds in caches for later consumption (Tomback 2001). Flight distances with seeds vary but have been reported as far as 22 km (Richardson and others 2002, Vander Wall and Balda 1981). Whitebark pine has been recognized as critical for wildlife (Mattson and others 2001) and watershed stability (Arno and Hoff 1989).

Western white pine occupies a wider ecological niche than whitebark pine, occurring from sea level in Washington and British Columbia to a predominately subalpine distribution from Sierra Nevada northward to the Cascades. In the northern Rocky Mountains, this species occupies wet montane to subalpine habitats (Wellner 1962). It is valued as a timber species because of its rapid growth, straight

bole, and ability to regenerate as a seral species from wind-dispersed seeds. Since the early 1900s, the abundance of both five-needled pines has dropped precipitously, mainly from white pine blister rust caused by the fungus *Cronartium ribicola* (McDonald and Hoff 2001). Major efforts and resources have been directed toward restoration of five-needled pine ecosystems. Unfortunately, most restoration efforts have been operating on the assumption that the climate will remain stable. For successful management and restoration of five-needled pine ecosystems, future climate change must be considered and integrated into current efforts and plans for species management/conservation.

Research corroborated by diverse sciences provides strong evidence that the Earth is experiencing a warming process driven by increased greenhouse gas concentrations. Records indicate that mean global temperature increased 0.6 °C during the 20th century, and global temperature is expected to further increase 1.4 to 5.8 °C over the next 100 years (IPCC 2001). This predicted rate of climate change is unprecedented within the available historical records. Because of the extremely fast rate of predicted climate change, determining the responses of forest tree species and populations is one of the major challenges for future threat assessment (Jump and Peñuelas 2005). Recent studies have developed plant-climate models that are highly accurate in predicting a suitable contemporary climate envelope for several western North American species (Rehfeldt and others 2006). These models serve as means to project future climate scenarios using general circulation models (GCMs).

It is well known that historical climatic oscillations have dramatically shifted species distributions. However, these historical climate changes typically occurred at a relatively slow rate over the course of millennia. The predicted rate of climate change, due to the anthropogenic release of greenhouse gases, will greatly exceed historical rates (IPCC 2001). Studies based on several climate models have shown the predicted rate of climate warming could jeopardize plant taxa with limited seed dispersal distances or disjunct habitats (Malcolm and others 2002). In this analysis, we develop an approach to evaluate potential impacts of future climate change on genetic diversity and biogeography of whitebark pine and western white pine. Our objectives include:

1. Assess the existing genetic diversity and population structure of whitebark pine and western white pine.
2. Model each species climate space (i.e., suitable habitat) for contemporary and year 2030 climate.
3. Use the predicted biogeographical changes to prioritize genetic conservation efforts by identifying populations at risk and determining areas suitable for restoration.

Material and Methods

Population Genetic Analyses

Sampling of needle and bud tissue was conducted across the range of both whitebark pine and western white pine. For whitebark pine, 28 sites were sampled and were combined into 6 regions (n = 21 to 72, Richardson and others 2002). Western white pine was sampled from 15 sites (n = ~30) across the range (Kim and others unpublished). Plant tissue was used to extract genomic DNA using previously published protocols (Kim and others 2003, Richardson and others 2002).

For whitebark pine, two types of DNA markers were used: mitochondrial DNA (mtDNA) and chloroplast microsatellites (cpSSR) haplotypes. These markers are uniparentally inherited enabling separate estimates of gene flow via pollen by cpSSR and via seed dispersal by mtDNA. Protocols for DNA typing and analyses are described by Richardson and others (2002). For western white pine, an amplified fragment length polymorphism (AFLP) approach was used to provide high-resolution markers that are typically biparentally inherited (i.e., nuclear markers). Western white pine AFLP protocols and analyses are described in Kim and others (2003).

Plant-Climatic Modeling

Whitebark pine and western white pine bioclimatic models used species presence/absence data for more than 118,000 point locations described geographically by latitude, longitude, and elevation (see “Acknowledgments”). Climate was estimated for each of these locations using a spline climate model (Rehfeldt 2006). This procedure yielded a

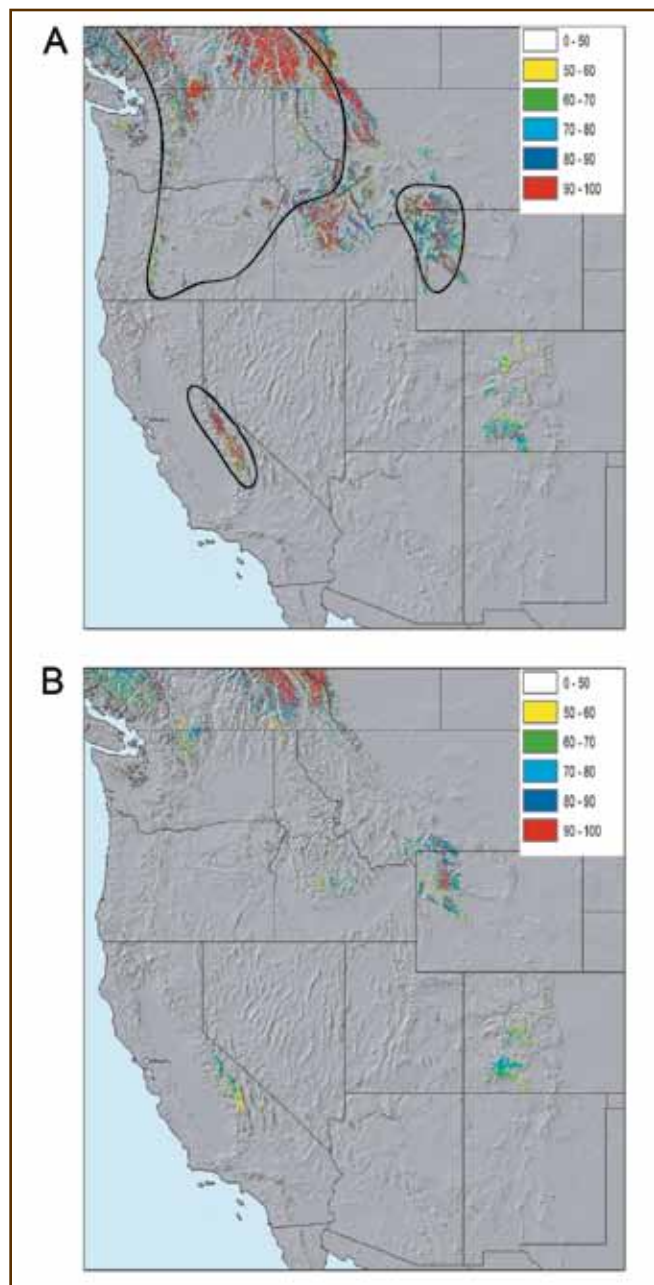


Figure 1—(A) The predicted contemporary distribution of whitebark pine (*Pinus albicaulis*) in the Western United States and southwestern Canada using a plant-climate model (Rehfeldt and others 2006). Pixel colors represent votes for whitebark pine occurrence; votes between 0 and 50 are not shown. The black drawn lines represent predicted metapopulations of whitebark pine based on chloroplast microsatellite molecular markers (Richardson and others 2002). (B) The predicted 2030 distribution of whitebark pine using the average of two general circulation models.

data set that described species presence or absence based on 33 climate variables representing simple interactions of

temperature or precipitation, or both, in relation to time, all of which have some relationship to plant responses. Random forests multiple classification tree analysis (Breiman 2001) was then used to identify climate variables important for predicting species presence and to build decision-tree-based bioclimatic models.

Arc map software (ESRI Inc.) was used to project the models predictions on a map. For this approach, the spline climate model was used to estimate climate in each 1-sq-km grid across the Western United States (more than 5.9 million pixels). Each pixel was then assessed using 100 independent decision trees. For each decision tree, a vote for or against species presence was cast. Pixels receiving vote tallies of 50 percent or greater were defined as having suitable climate space. These pixels are represented by the colored areas in Figures 1 and 2. These procedures are described in depth elsewhere (Rehfeldt and others 2006).

The response of a species contemporary suitable climate space under climate change was then assessed. The spline climate model was updated to the predicted climate of beginning in ca. 2030 using an average from the HadCM3GGA1 of the Hadley Centre (Gordon and others 2000) and CGCM2 of the Canadian Centre for Modeling and Analysis (Flato and Boer 2001) general circulation models. The procedure described in the previous paragraph was then repeated using the updated climate model to predict future climate for each pixel space.

Results

Whitebark Pine

Population Genetics—

Analysis of mtDNA reveals three haplotypes that are discretely partitioned among regions with two introgression zones. One introgression zone apparently occurs across a broad area in central Idaho, and another introgression zone occurs across a narrow area in the northern Cascades near Mount Rainier, Washington. The introgression of mtDNA haplotypes in the northern Cascades has been proposed to have resulted from the colonization of previously glaciated habitat during Holocene warming (Richardson and others 2002).

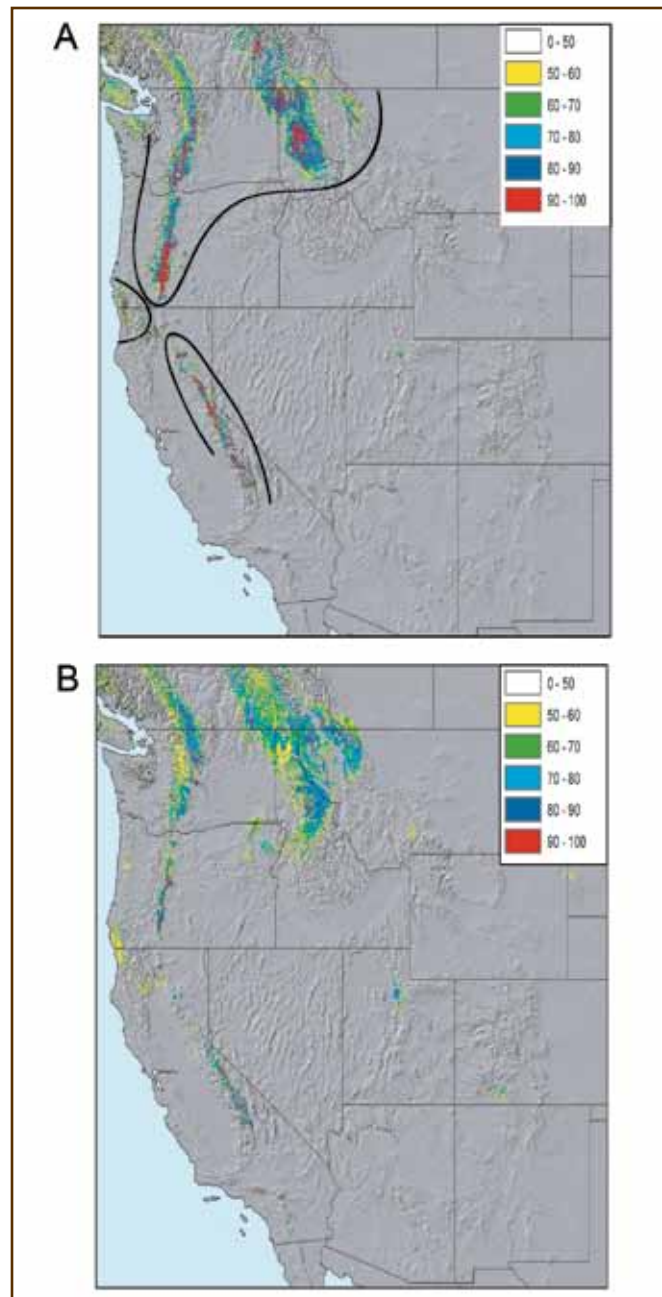


Figure 2—(A) The predicted contemporary distribution of western white pine (*Pinus moniticola*) in the Western United States and southwestern Canada using a plant-climate model (Rehfeldt and others 2006). Pixel colors represent votes for western white pine occurrence. The black drawn lines represent the predicted metapopulations of western white pine based on AFLP analyses. (B) The predicted 2030 distribution of western white pine using the average of two general circulation models.

Analysis of pollen gene flow using cpSSRs reveals broader population boundaries that include mtDNA

introgression zones. These data circumscribe three metapopulations: the Sierra Nevada Mountains, the Yellowstone region, and a large Pacific Northwest region that includes the northern Rocky Mountains and the Cascade (Figure 1A). Private alleles were typically found at low frequency within each region; however, one notable exception was the Sierra Nevada metapopulation that had a private allele at high frequency. Genetic diversity has been described as moderately high for cpSSR markers (Richardson and others 2002) to moderately low using allozyme analysis (reviewed in Bruederle and others 2001). Furthermore, genetic characterization of isolated populations in southern Oregon, northern California, and Nevada are still needed to assess genetic conservation efforts in these areas.

Plant-Climate Modeling—

The contemporary plant-climate model for whitebark pine fits its present distribution with remarkable precision. Comparisons between ground-truthed whitebark pine locations and predicted areas of suitable habitat showed an overall error rate of only 2.47 percent (Figure 1A). The mapped predictions for the occurrence of whitebark pine were more accurate than Little's (1971) published range maps (Warwell and others 2006). Based on two GCMs (Hadley and Canadian Centre for Climate Change), the projected climatic space for whitebark pine in ca. 2030 shows a dramatic change in comparison with the contemporary prediction. An estimated 70 percent of the current climate space for whitebark pine will be lost by 2030. Most of predicted loss occurs in the southern latitudes of the whitebark pine range, including the Oregon Cascades, Siskiyou, and northern Nevada mountain ranges, where current suitable habitats are limited to mountaintops in many locations (Figure 1B). The elevation of suitable climate space is also expected to rise 330 m, thereby leaving only the Sierra Nevada Mountains as a potential refuge with suitable climate space below 40° N latitude. In contrast, the model does predict suitable climate space will occur in central Colorado, which may represent a fundamental climate niche for whitebark pine. In the northern Rockies and Cascades, whitebark pine climate space is predicted to persist only among the highest elevations found in Yellowstone, south-central Idaho, Glacier National Park, and the northern Cascades. Areas north

of 50° N will also likely fit climatic space for whitebark pine, but these areas fell outside of the geographic window and are not included in the analyses.

Western White Pine

Population Genetics—

Analyses of AFLP loci discern three metapopulations in western white pine. These include a Pacific Northwest metapopulation that extends from the northern Rockies west to the Pacific and south along the Cascade Mountains to central Oregon. A distinct metapopulation exists in the Siskiyou Mountains of southern Oregon and northern California, and another metapopulation extends into the Sierra Nevada Mountains (Figure 2A). Like most other pines, western white pine contained moderate to high levels of heterozygosity in all three metapopulations (Kim and others unpublished).

Plant-Climate Modeling—

For western white pine, the contemporary climate space also fits with the current distribution with a small overall error of 3.85 percent. The projected current distribution of western white pine is shown in Figure 1A. The predicted 2030 climate space for western white pine provides a strong contrast with that of whitebark pine. Western white pine climate space is expected to increase 29 percent by 2030 (Figure 2B). Overall, suitable climate space for western white pine is expected to increase 157 m in elevation by 2030. This predicted expansion occurs in the northern latitudes, with notable expansion into northwestern Montana and northward into the Canadian Rocky Mountains. In the more southern latitudes of California and southern Oregon, populations are projected to persist at higher elevations. Predicted climate space is reduced in southern Oregon, thereby rendering the projected Sierra Nevada population more disjunct from the southern Cascades.

Discussion

Whitebark Pine

Past climate change has shaped the biogeography of whitebark pine and, hence, genetic relationships and potential adaptive traits. Since the last glacial maximum, whitebark

pine has apparently responded to the warming climate after the last glacial maximum by colonizing new habitat opened up by receding glaciers of the Canadian Rocky Mountains and the northern Cascades. Holocene expansion into the northern Cascade Mountains likely originated from source populations to the south and east of the north Cascades, based on the mtDNA at the contact zone (Richardson and others 2002). In contrast, a wider distribution of whitebark pine in more southern latitudes during the last glacial maximum was probably constricted to higher elevations by subsequent Holocene warming. This constriction in suitable habitat appears particularly dramatic in northern Nevada, where whitebark pine currently persists only on the highest mountaintops.

Population genetics of whitebark pine have identified distinct regional metapopulations occupying the Pacific Northwest (i.e., northern Rockies and Cascade Mountains), the greater Yellowstone region, and the Sierra Nevada. Other populations in the Great Basin and central Oregon have not been analyzed with mtDNA or cpSSR markers. However, allozyme analyses have shown distinct genetic structure among the Great Basin whitebark pine populations (Yandell 1992). Further studies to characterize genetic diversity and structure of whitebark pine in Washington and Oregon are in progress (Personal communication. C. Aubry. 2006. Area Geneticist, Olympia National Forest, 1835 Black Lake Blvd. Suite A, Olympia, WA 98512), and studies are assessing rangewide and regionwide adaptive traits in whitebark pine (Bower and Aitken 2006, Warwell and others unpublished). These studies and population genetic analyses are essential to determine appropriate genetic conservation efforts and proactive management that consider predicted climate change.

The contemporary climate space predicted using the plant-climate model is extremely precise for the distribution of whitebark pine. This precision has also been demonstrated with other western plant species (Rehfeldt and others 2006). The predicted suitable climate space for whitebark pine shows a dramatic reduction in the year 2030. At the highest risks are populations that currently only exist on mountaintops, where projected suitable climate space will be entirely lost from the region. Loss of local whitebark pine

populations is predicted to occur throughout the Oregon Cascades and mountaintops of northern Nevada, and further result in disjunct populations in the Sierra Nevada that will persist only at the highest elevations. These populations that face the highest risk of extirpation from predicted climate change and the white pine blister rust fungus should take priority for seed bank collections. Besides the Sierra Nevada, the plant-climate model predicts four major regions where climate space remains in the Western United States. These regions include the highest mountain ranges: the northern Cascades, Glacier National Park, south-central mountain ranges in Idaho, and the greater Yellowstone region. These regions that contain suitable climate space in 2030 predictions should be considered as priority regions for restoration efforts.

Western White Pine

Like whitebark pine, western white pine populations were also shaped by past climate change. This process created genetic structure with similarities to whitebark pine: a large Pacific Northwest metapopulation with partitions in southern Oregon and northern California (Kim and others unpublished). This population structure is also supported by an earlier study of isozyme markers (Steinhoff and others 1983). In addition, similar findings were reported in a study of adaptive traits for western white pine, showing a relationship between latitude and shoot elongation with a transition zone in southern Oregon (Rehfeldt and others 1984).

Again, the bioclimatic model predicted an excellent fit to the known distribution of western white pine. However, predicted 2030 climate space for western white pine shows a stark contrast to whitebark pine. The predicted increase in climate space is evident as an expansion in the northern Rocky Mountains that apparently relates to a slight increase in moisture. In the Sierra Nevada and Siskiyou Mountains, predicted climate space in 2030 does not show expansion. In these areas, moisture levels are predicted to increase more dramatically relative to the Pacific Northwest, and predicted climate becomes less suitable for western white pine, possibly owing to increased competition. Whereas losses of genetic diversity seem relatively small compared to whitebark pine, some areas of western white pine may

be at risk. Reductions in the abundance or extirpation of small isolated populations are conceivable for the Siskiyou Mountains and other areas of northern California where the western white pine populations exhibit a unique and diverse genetic background. Such populations should be considered as a priority for genetic conservation efforts.

Model Refinements and Uncertainties

Further refinements in the plant-climate model can be achieved by integrating knowledge from molecular and quantitative genetics. An important point is that this model currently utilizes ground-truthed locations for the entire distribution of each species for current and future predictions, ignoring genetic adaptation to local/regional climate. This model assumes that each climate-adapted population will be able to occupy its climate space in the future regardless of the geographic distance. For example, it is clear that the Sierra Nevada metapopulation of western white pine is genetically different and occupies a climate that is different from western white pine in the more northern latitudes. However, it is unclear where the populations occupying current climate space in Sierra Nevada may move in the future. Future plant-climate model improvements should be able to correlate climate variables and genetic data. Ongoing studies are focused on the delimiting population-based adaptive traits and refining molecular genetic data from western white pine populations to project suitable climates for these populations under current and future climate scenarios. Similar studies can be conducted with whitebark pine and other tree species, but this will require investing in efforts to conduct thorough, rangewide genetic studies.

Most uncertainty in the plant-climate model is associated with future climate scenarios and the GCMs. Precipitation is a major factor for predicting suitable climate space of plant species. For the Western United States and Canada, models display consistency for increased winter precipitation; however, summer precipitation predictions remain inconsistent (IPCC 2001). In addition, the time scale between loss of suitable climatic space and extirpation of local populations remains uncertain. Much of this uncertainty comes from site-specific biotic interactions. For example, two potential scenarios can be envisioned: (1) slow

attrition from succession where whitebark pine persists for decades or (2) stress from maladaptation leading to insect (e.g., bark beetle) outbreaks or disease (e.g., root rots) epidemics resulting in local extirpation within years. Projected scenarios are further complicated by mortality and loss of cone crops to white pine blister rust and insect attack. Continued studies are needed to address these uncertainties and improve predictions of climate-change impacts on distribution and population genetic structure of whitebark pine and western white pine.

Summary

Case studies were presented for whitebark pine and western white pine using plant-climate modeling of current and future climate predictions and genetic studies. These studies indicate dramatic differences in these two species' responses to climate change from the past and the future. These responses are largely dependent on the breadth of the ecological niches and life-history characteristics of each species. For whitebark pine, specialization for subalpine habitat is predicted to severely limit its distribution under future climate scenarios. Alternatively, coevolved relationships with Clark's nutcracker have enabled this species to colonize new habitat following Holocene warming. This characteristic may also aid its migration northward in the future, but successful migration to newly established suitable climate space is contingent upon the rate of climate change and the severity of impact from white pine blister rust and insect attack. Because western white pine has broader ecological range, it may be better suited to buffer effects of climate change. This ecological range is reflected in its predicted resilience under the future climate scenario. The creation of the plant-climate models and determining the impact from future climate scenarios for a particular species are dependent upon basic genetic research, both ecological and population genetics. Current research is focused on integration of genetic and climate data for these species. This approach represents a synthesis of multidisciplinary research to provide useful guidelines for forest management plans for genetic conservation and restoration that consider future climate change projections.

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- Forest Inventory and Analysis (FIA)
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- CalFlora Database (Yosemite National Park Natural Resource Inventory)
- Donna Dekker (Lynn Wells and Ray Wiseman 1991 Report)
- John King and Mike Carlson, British Columbia Ministry of Forests
- Jodie Krakowski, Master's Thesis, University of British Columbia
- RMRS Field Data
- RMRS Northern Idaho Habitat Type Data
- Ulla Geralyn Yandell, Master's Thesis, University of Nevada, Reno
- USFS Whitebark Limber Pine Information System

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