

The past, present and future: climate change and the foxtail pines (*Pinus balfouriana*) and whitebark pines (*Pinus albicaulis*) in the Klamath Mountains

Abstract

Over time a changing climate has perpetually resulted in shifts of the biogeographic distribution of flora and fauna across landscapes. It is therefore important to consider how future environmental change will affect species—both globally and regionally. The Klamath Mountains are renowned for botanical diversity that has persisted since the Tertiary—this region has been a meeting ground for plants as climatic conditions have shifted for at least 60 million years. Will this botanical diversity persist close to its current level of diversity? Will numerous microclimates that have fostered the survival of relict plants and the evolution of new species endure as our climate warms to levels never seen before? This paper will explore potential effects of these changes on the rare, spatially restricted, high elevation microsites in the Klamath Mountains where two rare conifers persist.

Past

The Klamath Mountains are a museum of sorts, hiding relicts of epochs gone by and fostering the growth of new species through complex abiotic interactions. The ecoregion is an ancient meeting ground because of a historically moderate climate and a central location along, and continuity within, the western cordillera. Species from the Sierra Nevada, Cascades, Great Basin and Coast Range interact where they reach the northern, southern, eastern or western extent of their range. Here, a plant's fecundity is not just measured in success across a vast segment of the landscape but also in terms of its persistence in spatially restricted microsites.

In ecology, a microsite is defined as a pocket within an environment with unique conditions, features, or characteristics. In the Klamath Mountains, microsites protect rare or unusual botanical diversity because of the absence of competition. This has historically enabled outliers to secure habitat or remain in a habitat where otherwise, under less demanding

conditions, the species would be outcompeted. The Klamath Mountains are a safe haven, and because of this, organisms continue to flourish here as ecological outliers—surviving either on the edge of a broader range or speciating into an endemic (Sawyer 2006).

Botanically unique microsites occur throughout the Klamath Mountains and are advanced by complex interactions of climate, geology, and geomorphology. A north to south trending spine in the east-central Klamath creates a relatively predictable and repeated microsite at high elevation. This is a region of transition, where unique growing conditions are nurtured by a combination of complex soils and an orographic effect. Mesic west-side forests meet xeric east-side forests, and complex floristic associations are created. These climax vegetation types are crowned by charismatic mega-flora—conifers. Specifically, two rare conifers survive along this spine—foxtail pine (*Pinus balfouriana* ssp. *balfouriana*), which is an endemic (Oline et al 200, Eckart 2006, 2007), and whitebark pine (*Pinus albicaulis*), which is an outlier from a much broader range (Arno et al 1989, Murray 2005). These two species have survived for millennia on these isolated sky islands from 2000-2750m.

In the Klamath Mountains the number of plant species, as well as plant associations created by this diversity, has long been noted for its botanical importance (Whittaker 1960, Sawyer 2004). The conservation of this diversity relates to the maintenance of small spatial scale habitat. The continued persistence of relict plants in the regions must be considered as humans continue to influence climatic conditions. Plant assemblages have been stable across this ancient meeting ground since the mid-Pleistocene (Whittaker 1960, Millar et al. 1999) when major shifts in biota began to occur as the climate warmed. With respect to conifers for example, 15,000 years ago in western North America the number of species of Cupressaceae began to decline as the number of species of Pineaceae increased (Millar 2004).

One means to an end to understand this regional biodiversity, where it has been, and where it might be going, is to study the localized conifers. As dynamic climatic conditions relate to the Klamath Mountains, the high elevation sky islands are of particular importance because this ecosystem is rare and long-lived conifer species are nurtured. High-elevation ecosystems are likely to be the first to register the impacts of global climate change (Bunn et al. 2005) and can thus serve as a catalog for trends in vegetation and climatic shifts. What effects will accelerated climate changes have on these ecologically restricted high elevation conifers of the Klamath Mountains?

Conifers at tree line in western North America survive at these sites because conditions are optimal in the absence of competition. This is particularly true of whitebark pine (WBP) and foxtail pine (FP), which are both shade-intolerant. In the Sierra Nevada, FP have shown visible signs of stress like branch and needle dieback when sampled growing with hemlocks and firs (Eckart 2006). These two species also endure harsh climatic extremes. For instance, many plants would suffer cavitation in either extreme cold or extreme heat coupled with drought, because of the loss of turgor pressure. Turgor pressure maintains the pressure within the cells of the plant. If the pressure in the xylem, which transports water from the roots to the leaves, is broken by an undesirable formation of air bubbles through freezing or drought, the cells above the rupture will die. Conifers in general and especially those at high elevation are specially adapted to avoid cavitation events during extreme cold and drought. Because of this adaptation, WBP have exhibited predictable dominance on xeric sites with warm summer temperatures in Oregon (Ettl 2007).

Soil type can also play an important role in the success of these species. This is particularly true in the Klamath Mountains, where inhospitable serpentine soils are more common than any other geographic region in North America (Sawyer 2006). In the situation

where serpentine is the soil above 2000m, FP thrive because of their ability to handle nutrient deficiencies where other conifers cannot (Eckert 2006). At high elevation where soil is more nutrient rich, WBP and FP only persist amongst boulder fields. On a small spatial scale, these large rocks inhibit shade tolerant species' expansion where the shade intolerant are already established (Eckert 2006). In other words, these are conditions that keep the firs and hemlocks from growing too close and causing die-back in the shade intolerant pines. There are only a handful of WBP-FP groves in the Klamath Mountains where hemlock and fir cannot grow because the high elevations restrict their success. Above 2600m, only in the High Trinity Alps and approaching the summit of Mount Eddy, WBP and FP survive in the absence of competition regardless of soil type.

The populations of FP and WBP that exist at high elevations in the Klamath are generally small (300-600 individuals but often smaller). Over time, this has created genetic bottle necks where populations vary greatly from one ridgetop population to another (Oline et al 2000). It is clear that these two species are living on the edge—as outliers of the overall North American range (*figure 1*) and fragmented within that range. The importance of these relicts (foxtail pines) and outliers (whitebark pines) lies in their ability to recolonize a shifting climatic landscape over time with varied genetics coded over centuries of sky island isolation. They are important for the maintenance of biodiversity and ecosystem services that diversity offers. These services are varied but include shading snow to maintain headwaters later in the summer season as well as simple aesthetic beauty. As the climate changes the long-term implications, both potentially positive and negative, must be understood.

Historically, there have been repeated documented cycles of downslope and upslope expansion of treeline throughout the West as a function of regional climate change (Millar 2004). Whitebark pine and foxtail pine colonized their current locations in the Klamath Mountains in

the mid-Pleistocene. Foxtail pine separated from the Sierra Nevada population and became restricted here 15,000 years ago (Bailey 1970). After progressing across the Great Basin from the Rocky Mountains in the Pleistocene, whitebark pines established populations in the high elevations of the Oregon Cascades 10,000 years ago—climbing upslope to colonize xeric mountain tops as climate warmed (Murray 2005). This is also the time frame in which they must have reached the Klamath Mountains—most likely distributed to the sky islands by birds. In both cases, these forests have been relatively static since their establishment in the Holocene.

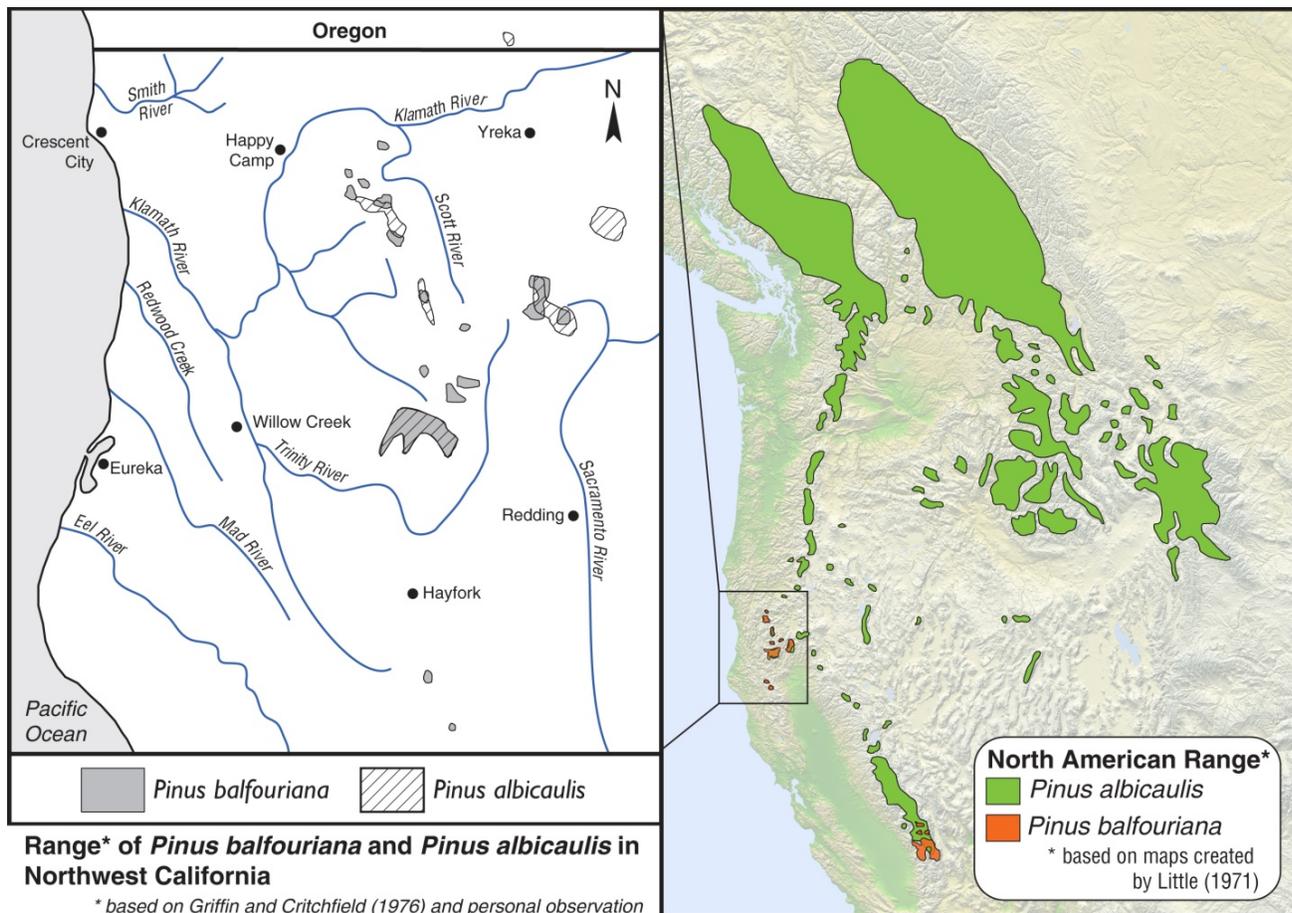


figure 1

Once populations are established, these species can live for many years—both can attain significant ages. WBP have been recorded to over 1000 years (Arno et al 1989) while FP attain ages of more than 2000 years (Lanner 2007) in the Sierra Nevada. Being long-lived, trees may delay reproductive events to correspond with availability of resource. When optimal resources

are available, cone mastings events might only occur every 50 years in WBP (Arno et al 1989). At these times, trees are able to allocate significant resources so as to produce massive amounts of cones—enough to ensure that there will be too many seeds for predators to consume and thus increase the chance of seedling establishment. Over a 1000 year lifetime, even if reproductive events are limited to every 25 years on average, a WBP will ensure at least 40 individual years of seed production.

At high elevation, sunlight for photosynthesis is rarely as limiting as other abiotic factors are. Instead, restrictions for growth include moisture variability throughout the year, low levels of winter snowpack that causes drought stress, and extreme temperature in both summer and winter. All of these variables can restrict growth and ultimately survivorship. Fluctuations in tree ring growth patterns for FP and WBP have been observed over the last several thousand years in association with the variability of these conditions. It appears that the genetics are in place to endure a warming climate; but how much warming can be tolerated? Can it be tolerated if the climate also becomes increasingly xeric?

Sticky and viscous resin, made in resin ducts, forms the first line of defense against creatures like mountain pine beetles or other decomposers that hope to make a home in a tree. But, winter cold coupled with summer dryness can limit the action of decomposers because these are not good condition to foster their success (Logan 2001) particularly at high elevations. This ensures a long life potential for these and other high elevation pines. In fact, a close relative of the FP, bristlecone pines, are the longest-lived species in nature—attaining ages approaching 5,000 years (Lanner 2007). With age in trees it was thought that senescence—or degeneration with age—would occur. It appears that this does not play a role in the decline of high elevation pine species either. Tracheids—elongated cells in the xylem of conifers that transport water and nutrients—in the cells of ancient bristlecone pines were no different than those in young

bristlecones (Lanner et al. 2001). There has been no degradation witnessed in even the most ancient species on Earth. The success and survival in the Klamath Mountains over the past 15,000 years is most likely due to the cold, xeric conditions in which they grow—ultimately culling a strong genetic code through natural selection.

Both tree-ring growth and moderate fluctuations in upslope and downslope colonization suggest that, even with long life cycles, these two species are ecologically pliable. In the Little Ice Age there was a noticeable decline in Foxtail pine, and its close relative the bristlecone pine. However, as the climate warmed in the mid-1800's, these two species responded by doubling their growth rates (Graumlich 1991). This variability of ring size was significantly correlated with higher levels of winter precipitation (Hughes 2003).

If, in addition to a warmer climate, the climate does become wetter, it is expected that trees at elevation will continue the trend of increased tree ring width which is directly correlated with increases in temperature and moisture levels (LaMarche 1974, Hughes et al. 2003, Salazar et al. 2009). Increased tree ring growth is also found in long-lived high elevation pines of the Great Basin (Hughes et al. 2003) and in the white mountains of California (Salazar et al. 2009) which is correlated to recent warming trends and possibly increased carbon in the atmosphere (Cole et al. 2009).

Present

We are in a period where average annual temperatures are increasing which is therefore lengthening the growing season—conservative estimates are an increase of 3-5 days per year since 1951 (Bunn et al 2005). This average is potentially higher at elevation, particularly at altitudes where mountain tops of moderate topography have little shade cast upon them. In the Klamath Mountains, almost all mountain tops are rounded and open—unlike the granitic spires in the Sierra Nevada or European Alps which cast more shade throughout the year. Because the subalpine trees are exposed to more solar radiation on rounded mountain tops, with global

warming, growing season should come earlier and stay longer across all high elevations of the Klamath Mountains. This is not the case in a canyon bottom or on north-facing mountain slope. At lower elevation, where shading due to the angle of the sun will persist for the same duration year to year.

Worldwide, average yearly temperatures are on the rise because atmospheric concentrations of carbon dioxide are increasing due to the burning of fossil fuels. With this trend comes the potential for a positive response from plants through carbon fertilization. During the daily cycles, plants open their stomata to maintain transpiration of water through the xylem. Water moves out and draws more water up from the soil, maintaining flow in the xylem which keeps the possibility of cavitation at bay and also maintains turgor pressure in leaves. When stomata are open carbon dioxide enters the leaves for consumption during photosynthesis—the carbon is used to make the sugars. In xeric condition, plants must balance the opening of the stomata and the potential for cavitation if water were to be unavailable from the soil. Ultimately, plants must keep the stomata closed more often when it is dry which limits the amount of carbon that can enter the leaves.

However, if more carbon enters because of increased levels in the atmosphere, there is the potential for increasing net photosynthesis (Cole et al. 2009, Frank et al. 2009). This will enhance net primary production in plants—particularly when combined with longer growing seasons (Cole et al. 2009). The combination of increased growing seasons, precipitation levels that continue close to current averages, and increased carbon dioxide have the potential to be beneficial to high elevation conifers, at least in the short-term.

Coupled with a warming climate, carbon dioxide fertilization could lead to upslope migration into uncolonized habitat. In the Klamath Mountains, however, there are no higher elevations into which a conifer could migrate. Populations of FP on serpentine and in boulder

fields are expanding, measured as an increase in seedling recruitment on to south and west slopes (Eckart 2007) but this trend is only seen on restrictive soil mediums. In the nearby Cascades of California mountain hemlock (*Tsuga mertensiana*) seedling establishment in Mount Lassen was greatest during periods with above normal annual and summer temperatures, and normal or above normal precipitation (Taylor 1995). This expansion began at the end of the Little Ice Age and if global warming continues at projected rates, the dynamics of and structure within forests near timberline in the Pacific Northwest will change as shade tolerant firs and hemlocks move upslope (Taylor 1995). If the diverse conifer forests of the Klamath Mountains exhibit similar patterns, in addition to invasion from mountain hemlock, other montane conifers like Shasta fir (*Abies magnifica* var. *shastensis*), white fir (*Abies concolor*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), Jeffrey pine (*Pinus jeffreyi*), Douglas-fir (*Pseudotsuga menziesii*), and incense-cedar (*Calocedrus decurrens*) could accelerate upslope expansion and compete to a greater degree with FP and WBP. With new competition comes exclusion initially through reduced seedling recruitment potential and then by branch dieback because of shade-intolerance.

Mountain pine beetles (*Dendroctonus ponderosae*) are also of concern with respect to high elevation conifers and a warming climate. Most western pines are suitable hosts for the beetle but currently the most important hosts are ponderosa pine (*Pinus ponderosa*) and lodgepole pine (Logan et al. 2001). The beetle is a native insect, having co-evolved with western pine forests in fluctuations of periodic disturbance often followed by cleansing fire regime events. More recently, mass beetle infestations have been correlated with increased climatic warming (Mock 2007). At previous times in the Holocene there were events where mountain pine beetles (MPB) established populations in sub-alpine ecosystems, these were short lived.

Conversely, since the early 1990's, MPB have exhibited a continued high elevation invasion and persistence in the Rocky Mountains (Mock et al 2007).

Mountain pine beetles require sufficient thermal input to complete the life cycle in one season. Historically, high elevation ecosystems did not meet these conditions. However, due to recent warming trends, there is significant thermal input at high elevations for the lifecycle and infestations of whitebark pine are now increasingly common (Logan et al. 2001). Interestingly, they are even infesting downed WBP wood at high elevation, a phenomenon that has not been witnessed in other pines at lower elevations (Mock et al 2007). This MPB adaptation is probably due to the scarcity and density of wood in high elevation ecosystems. The preponderance of mass infestations at elevation have been witnessed in the Rocky Mountains. While observations of high elevation infestations in the Klamath Mountains are lacking, potential is there.

In addition to native insects, a non-native fungal pathogen is affecting high elevation forests. For WBP this may be the greatest risk for long-term survival. In 1910 white pine blister rust (*Cronartium ribicola*) arrived in a British Columbia port and by 1930 had spread to southern Oregon, infecting western white pine (*Pinus monticola*) and sugar pine (*Pinus lambertiana*) (Murray 2005) along the way. The Klamath Mountains foster one of the most diverse temperate coniferous forests on Earth and hold within its boundaries four 5-needle pines—all of which are potential hosts for the pathogen. In addition, the climate of the Klamath Mountains is often cloudy, foggy, and rainy—which are prime condition for the lifecycle of white pine blister rust (WPBR). Finally, the lifecycle completion requires WPBR to utilize a *Ribes* ssp. as an alternate host. The Klamath Mountains are highly diverse with respect to that genus—where 2/3 of the *Ribes* species in the state can be found (Sawyer 2006). The region is clearly a prime breeding ground for this western conifer-killing pathogen.

In late summer spores from *Cronartium ribicola* are blown from the *Ribes* host and then enter 5-needle pines through stomata. Upon successful entry, hyphae grow, spread through the phloem, then ultimately swell and kill tissue above the site of infection. Infected trees can survive for over 10 years but the infection inhibits reproduction (Murray 2005). Instead of sugars from the phloem being directed to cone production the infections become sugar sinks in an attempt to compartmentalize decay (Malloy 2001). For species like WBP, which live in fringe habitat and therefore delay reproductive events until conditions are optimal, having an infection that further inhibits cone production is a dangerous proposition. The fungus is found on foxtail pine and whitebark pine in northwest California (Maloy 2001) where variability in microsite infestation occur (Ettl 2007). On Mount Ashland in the Siskiyou Mountains blister rust has infected 4 of the 9 WBP trees in the population (Murray 2005). All 5-needle native western pines have shown some heritable resistance in the past 100 years (Schoettle et al. 2007), but enduring an infection works against a long-lived pine's survival strategy because this fungus—and other decomposers—are not typically at high elevations.

Seedling establishment for organisms that are on the ecological edge is also jeopardized because of the effects of climate change. Foundations of unsuccessful seedling recruitment are many but at high elevation include the effects of fire suppression over the past 100 years. While fire has never been a common phenomenon in high-elevation forests, a shift in fire regime occurred in WBP populations during the Holocene, around 4500 years ago. Before that time fire was not a significant factor in WBP ecology but since has become significant (Murray 2004). Across the mountains of the Pacific Northwest, fire was observed either on the tree or on the ground in 88% of WBP forests (Murray 2007) which signifies the prevalence of fire in the high elevations of the Cascades. The introduction of fire regime suppression in the 1930s has ultimately led to an impending synergistic disaster when coupled with the effects of climate

change. Where shade tolerant species are moving back into WBP habitat in Montana, WBP are showing decline (Keane and Arno 1993). Whitebark pines need open space for seedling establishment and historically some of this open space has been created by fire events.

Fire suppression has also lead to increased fire intensity which could be compounded by pathogens. If blister rust and mountain pine beetles move into high elevations of the Klamath Mountains, they will potentially generate more dead and downed wood. This would exacerbate the potential for the risk of stand replacing fire. This is would not mimic historical fire regimes—which has been of low intensity and often focused on individual trees by lightning strikes (Murray 2007). As discussed, downed wood at high elevation has never decomposed at high rates in xeric conditions and this too would lead to a higher intensity fire with continued suppression.

Whitebark pines and Clark's nutcrackers (*Nucifraga columbiana*) are keystone mutualists. It is virtually impossible to be in a WBP forest and not hear the robotic squawk of the Clark's nutcracker. The wingless seeds of the WBP are dependent on the Clark's nutcracker for dispersal—and disperse them they do. Individual birds often cache over 25,000 seeds a year in pockets of 5-10 seeds (Lanner 1996). The nutcracker inevitably loses track of some caches and those forgotten pockets will sprout and establish seedlings in new territory. However, if a cone masting event is perpetually delayed because of insect or fungus infestation, drought-like conditions, or a lack of proper habitat due to fire suppression the Clark's nutcracker would be left with little choice but to find another source of food. While this is highly speculative, nutcracker's provide the only avenue for a wingless WBP seed to move upslope (Logan 2001). High elevation pines, particularly WBP, could potentially be left without a seed disperser or a way to progress to cooler habitats.

Foxtail pines and WBP overlap ranges in the Klamath Mountains and Clark's nutcrackers have taken FP seeds as a food source. The birds must ultimately disperse these seeds between the sky islands as they do with WBP seeds. Because of this range overlap and the fact that seed crops for these two species vary from year to year—with FP producing cones more regularly (at least in the past 10 years) than WBP—it appears Clark's nutcrackers will not leave in search of another food source if WBP cone masting become infrequent. However, the close relationship between WBP and nutcrackers is still a fragile one, as is a tree's relationship to a high elevation environment.

Future

It is an epic struggle of nature against the element—in an environment shaped by wind, water, sun, soil, and time. The temporal visitor can revel as witness to dramatic existences where windswept branches on contorted trees are the norm and where this distortion ensures survival. In the grand scheme of land management, many high elevations environments are protected because there is little perceived value beyond the overwhelming aesthetics—the trees here have no commercial value. However, there is eminent danger of losing species diversity if humans do not create favorable conditions for survival of these isolated species—particularly the whitebark pine.

There are positive signs that high elevation conifers are responding favorably to certain aspects of global change. First, when substantial moisture falls in the winter and followed by a warm summer, FP and WBP have shown increases in growth of annual rings (Hughes et al. 2003, Salazar et al. 2009). Additionally, as carbon dioxide levels in the atmosphere increase, it appears that carbon dioxide fertilization could be a boon for plants (Cole et al. 2009, Frank et al. 2009).

If whitebark pines and foxtail pines are to survive potential drought, subsequent bark beetle attacks, the threat of white pine blister rust, increased fire frequency due to climate change

and then establish seedlings—the trees that endure will have to be selected, naturally or artificially (Schoettle et al. 2007, Richardson et al. 2002). The question becomes will there be time for natural selection to occur? For instance, ponderosa pines of the San Francisco Peaks in Arizona that trees that have survived bark beetle attacks had resin ducts that were >10% larger, >25% denser (# of resin ducts mm^{-2}), and composed of >50% more area per unit growth ring (Kane et al. 2010). These traits have been naturally selected by climate and bark beetles in a shorter-lived species. For characteristics like these to evolve rapidly enough in a long-live species, humans may need to step in and proactively manage threatened forests to facilitate long-term survival. The risk for potential destruction of high elevation ecosystems lies in the fact that MPB have co-evolved in ponderosa pine and lodgepole pine forests and these forests are the antithesis of the long-lived WBP and FP survival strategies.

All five needle pines have shown heritable resistance to blister rust but within these restricted populations, the number of resistant individuals will not increase rapidly (Schoettle 2007). To ensure even-aged forests, a selective breeding programs for blister rust resistance needs to be implemented, fire should also be prescribed to promote open space for potential seedling recruitment via Clark's nutcrackers, and silviculturists must create canopy openings if shade tolerant species begin to encroach where they have historically been absent (Richardson et al. 2002). Other possible proactive actions include spraying insect pheromones on WBP to ward off beetle attacks (Murray2005) and to attempt suppression of MPB at lower elevation so upslope expansion is moderated. The truth is that the climate is changing more rapidly than it has since at least the Cenozoic and humans must play a proactive role to prevent catastrophic mortality, fire, and ecological conversions. Can we accept this role as managers without over managing?

The Klamath Mountains have been an ancient meeting ground for millions of years of climatic fluctuations. Will climate be more moderated across northwest California as it has over the past 60 million years? Will this wild landscape be able to absorb some of the impacts of global change? Will species continue to be able to hold out, survive, and evolve to fit these changing conditions? Clearly, there are more questions than answers but at least the questions are being asked.

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