Climate Change and Whitebark Pine: Compelling reasons for restoration

There is confusion in the research and management communities about the fate of whitebark pine (*Pinus albicaulis*) as climates slowly warm. Many feel that projected warmer conditions will severely reduce whitebark pine habitat and push whitebark pine off the tops of mountains or restrict the species to north of the Canadian border (Koteen 1999; Schrag et al. 2008; Warwell et al. 2007). These speculations have been used by some land managers and agency leaders to discontinue whitebark pine restoration activities and funding. Others feel that climate-mediated changes in the disturbance regimes will serve to keep whitebark pine within its current range, albeit at lower levels (Loehman et al. 2011). The reality, of course, is more complex because of high uncertainty in regional climate change predictions, the high genetic diversity and resilience of the species, and the localized changes in disturbance regimes and interactions. Therefore, we suggest that the question of whether to restore whitebark pine is not dependent on future climates since we really can't predict them, and, more importantly, we cannot predict how landscapes will respond to them, but restoration is instead dependent on whether society can afford the loss of this widely distributed foundation and keystone species and the ecosystems that it creates (Tomback et al. 2001a). Climate variation and change, like insects, disease, fire, and land management, is a factor that must be mitigated in restoration attempts and not a reason for curtailing restoration actions. Here, we present background on whitebark pine and climate change, discuss reasons to restore whitebark pine forests under changing climates, and then explore how to ensure restoration effectiveness considering climate-mitigated changes in disturbance regimes. We wrote this paper to dispel beliefs that whitebark pine is doomed no matter what we do because of warming climates and to present a logical strategy for restoring the species.

Whitebark pine decline and climate change

Whitebark pine, an important component of high-elevation forests in the western United States and Canada, has been declining since the early Twentieth Century from the combined effects of native mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, contemporary fire exclusion policies, and the spread of the exotic disease white pine blister rust (caused by the pathogen *Cronartium ribicola*) (Schwandt et al. 2010, Tomback and Achuff 2010). The pine was initially listed as endangered in the province of Alberta, Canada; it is now a candidate species for listing under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2011) and listed as Endangered in Canada under the federal Species at Risk Act. Within the last decade, major outbreaks of pine beetle and increasing damage and mortality from blister rust have resulted in cumulative whitebark pine losses that have altered high-elevation community composition and ecosystem processes in many regions of the U.S. and Canada. Whitebark pine is a keystone species because it supports community diversity and it is a foundation species because of its roles in promoting community development and stability (Tomback et al. 2001a, Tomback and Achuff 2010). Since more than 90 percent of whitebark pine forests occur on public lands in the

U.S. and Canada, maintaining whitebark pine communities requires a coordinated effort across federal, state, and provincial land management agencies (Keane et al. 2012).

Climate-induced changes in disturbance regimes will overwhelm most vegetation responses to climate change (Dale et al. 2001). Many climate change studies consistently project drier conditions in the range of whitebark pine and that will result in large increases in the annual number, area burned, and severity of wildfires (Flannigan et al. 2009, Krawchuk et al. 2009, Marlon et al. 2009). With increased fire, whitebark pine will have an unique opportunity to maintain its range or even increase in distribution in the future because it has bird-mediated (Clark's nutcracker) seed dispersal mechanisms that can disseminate seed great distances into the large, severe burns predicted in the future, well before wind can disperse the seeds of its competitors (Tomback 1978, 1982, Tomback et al. 1990, Lorenz et al. 2008, Lorenz and Sullivan 2009). Whitebark pine is a fire-adapted species that readily regenerates in large burned areas (Arno and Hoff 1989; Tomback et al. 1990, Tomback et al. 1995, Tomback et al. 2001b) and has morphology that enables it to survive low to moderate severity fires (Ryan and Reinhardt 1988). Therefore, whitebark pine is uniquely positioned as a species that can increase under the more frequent fire regimes that result from warming climates. And since nutcrackers may be harvesting seeds from trees that have survived blister rust, there is some chance that seeds from unclaimed nutcracker caches may become blister rust-resistant trees.

Unfortunately, climate-mediated mountain pine beetle outbreaks are occurring in many areas within whitebark pine's range (Carroll et al. 2003), and this has, and will, kill many cone-bearing whitebark pines (Hicke and Logan 2009). Most of these trees would have eventually died from the exotic blister rust, but the blister rust-resistant survivors are also targeted by the beetles. To mitigate this loss, it is important that beetle-killed stands be planted with rust-resistant whitebark pine seedlings following one of the main principles of the range-wide restoration strategy (Keane et al. 2012). This reforestation will create more resilient young to old forests of whitebark pine that are more likely to withstand increased fire, beetles, and blister rust. Another way to ensure resilient whitebark pine forests in the future is to create heterogeneous landscapes composed of many age classes and successional stages of whitebark pine to reduce the scale and intensity of fire and mountain pine beetle outbreaks (Schoettle and Sniezko 2007). Another critical goal is to protect valuable rust-resistant, cone-bearing whitebark pine trees on the landscape so that they can provide seeds for future reforestation after wildfire as well as provide food for many wildlife species (Hutchins 1994).

Historical analogs of warmer climates in the paleoecological record indicate whitebark pine was maintained and even increased in some places under past warmer and drier climates in some parts of its range (Tausch et al. 1993). Whitebark pine can grow within a broad upper elevation zone in the west; the pines happen to grow best at high elevations where there is little competition from other species. In fact, Arno et al. (1995) found that whitebark pine's elevational range extended over 500 feet below the current lower elevation limits of whitebark pine in the Bitterroot Mountains of Montana. Whitebark pine occupies the largest range of any five-needled white pine in the U.S. and Canada, including about 18˚of latitude and 21˚ longitude, indicating some tolerance to different climates (Tomback and Acuff 2010).

Anecdotal evidence shows that some whitebark pine forests are experiencing abnormally high growth and more frequent cone crops due to warmer summers and longer growing seasons. The notion that whitebark pine will stop growing and reproducing at high elevations under future climates is unsubstantiated, and it is entirely possible that as long as wildland fire creates areas where birds will cache seeds and seedlings can grow without competition, whitebark pine will continue to thrive throughout its range. This is supported for some region-based scenarios using computer modeling (Loehman et al. 2010).

Most of the studies that predict the demise of whitebark pine in much of its range from climate warming use Species Distributional Models (SDMs) to project future geographical ranges (Koteen 1999, Warwell et al. 2007). SDMs, also called Bioclimatic Envelope models, niche models, and species envelope models, are developed by linking current climate with current distribution of a species of interest by means of advanced statistical modeling. Then, using the statistical model, a future species distribution is computed using projected climate data as inputs. However, SDMs are inherently flawed for predicting future species distributions in that they relate only climate to species occurrence resulting in predictions of potential species habitat, not species distribution. The critical processes of cone production and pollination, seed dispersal, seed germination, seedling establishment, tree growth, species interactions with mycorrhizae, competitive interactions, herbivores and mutualists, and mortality, as well as the phenology of many processes, are not represented in SDMs. Moreover, the climates used to develop SDMs represent a very small slice of time (50-100 years) relative to the long time periods that trees, such as the long-lived whitebark pine (>1000 years of age) may survive, so they do not capture the climate for all stages of the tree's life cycle. The mature trees used to evaluate species occurrence in the statistical model may have lived for 100s to 1000s of years and continued to survive despite major changes in climate. Moreover, SDMs assume that the current distribution of the species is a consequence of climate alone, yet we know that fire exclusion, exotic disease, and management actions have also reduced whitebark pine occurrence (Tomback et al. 2001a). Therefore, it is difficult to have any confidence in SDM projections; they are informative, but not prognostic, especially on short time scales of decades and half-centuries required by land management.

All the climate models that predict rapidly warming climates have a high degree of uncertainty that often precludes planning for mitigation (IPCC 2007). While there is little debate that atmospheric CO_2 is increasing and this increase will cause major changes in climate (IPCC 2007), there is a great deal of uncertainty about the magnitude and rate of change (Stainforth et al. 2005, Roe and Baker 2007). This uncertainty will undoubtedly increase as climate predictions are made (1) at finer resolutions, (2) for different geographical areas, and (3) for longer time periods. The range of possible predictions of future climate from General Circulation Models (GCMs) (anywhere from a 1.6 to 8°C increase in global average annual temperature) is much greater than the variability of climate over the past two or three centuries (Stainforth *et al.*, 2005), and the variability across GCMs is greater than the variability in each model's weather projections. Since it is impossible to know whether society will respond to climate change by employing technological innovations to minimize CO_2 emissions or to mitigate its effects, most GCMs also simulate a suite of scenarios that capture a range of possible strategies to deal with

climate change, introducing yet another source of uncertainty. Moreover, it is the high variability of climate extremes, not the gradual change of average climate, that will drive most ecosystem responses to the climate-mitigated disturbance and plant dynamics, and these rare, extreme events are the most difficult to predict (Easterling et al. 2000).

Yet another source of uncertainty will be introduced when we try to predict how the earth's ecosystems will respond to the already highly uncertain effects of climate change (Araujo et al. 2005). Mechanistic ecological simulation of climate, vegetation, and disturbance dynamics across landscapes is still in its infancy (Sklar and Costanza 1991, Walker 1994, Keane and Finney 2003). Many ecosystem simulation models are missing the important interactions of disturbance, hydrology, and land use that will dictate climate effects on plant distributions (Notaro et al. 2007). As an example, major mountain pine beetle outbreaks currently occurring in western North America have been attributed to climate change (Logan and Powell 2001, Carroll et al. 2003), yet these outbreaks were not predicted by any of the major Dynamic Global Vegetation Models, because insect and disease processes are not explicitly simulated due to a lack of knowledge of epidemic mechanisms and inappropriate scale (Neilson et al. 2005). If this one critical disturbance is not represented in ecological models, then there must be a host of other unanticipated disturbances and ecological relationships that are also missing, which could result in still higher levels of uncertainty in describing future conditions. Little is known about the interactions among climate, vegetation, and disturbance or critical plant and animal life cycle processes of reproduction, growth, and mortality (Keane et al. 2001, Gworek et al. 2007, Ibanez et al. 2007, Lambrecht et al. 2007) as they interact with climate in different ways. 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 the interactions among different disturbance regimes (fire and beetles, for example) could also create novel landscape behaviors.

Therefore, given the high uncertainties in predicting climate, vegetation, and disturbance responses to increasing CO_2, we feel that 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. Long-lived whitebark pine forests have already experienced great variation in past climate and clearly have broad amplitudes of resilience with respect to climate. Considering the high uncertainty of future climate and vegetation projections, and knowing the resilience of whitebark pine, we suggest that any conclusions about the feasibility of whitebark pine restoration against changing climate are imprudent. On one hand, 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 data. But improving ecosystem models may take decades before simulations can be used to predict species and landscape response to climate change with reasonable accuracy, and while we wait, we lose valuable populations and rust-resistant trees, and our options for restoration diminish greatly. Even with climate change, restoration activities in whitebark pine will probably be appropriate, considering the considerable genetic variation across the range of this species, which provides

the foundation for adaptation (Rehfeldt et al. 1999; Bower and Aitken 2006, 2008, Mahalovich and Hipkins 2011).

Restoring whitebark pine forests in changing climates

There are many compelling reasons to restore whitebark pine, including the ecosystem services, biodiversity, and ecosystem functions that it provides (Tomback et al. 2001a). Ultimately, healthy whitebark pine forests are critical to enabling future response to climate, particularly at the "climate change fronts" of upper subalpine and treeline elevations and the northern-most latitudes. Climate has changed significantly and repeatedly, from the Pleistocene through the Holocene, albeit at a slower pace than we now see in the Anthropocene, and future changes--whether from anthropogenic causes or not—are inevitable. The goal of today's restoration efforts should be to create whitebark pine forests that are resistant and resilient in tomorrow's climate and disturbance regimes. This may be accomplished by spreading genetic resistance to the blister rust pathogen by (1) saving putative and screened blister rust-resistant trees to provide seeds for dispersal by Clark's nutcrackers, enabling the natural spread of rust-resistance, (2) collecting seeds from rust-resistant trees, growing seedlings from these seeds, and planting the seedlings or direct seeding in recently burned or treated areas that are free of competition, and (3) allowing natural disturbances, especially wildfires, to create competition-free growing spaces or creating similar open seedbeds with prescribed burning and/or mechanical cuttings.

We also must manage future whitebark pine landscapes to reduce the scale of future mountain pine beetle outbreaks by fostering a diversity of forest ages, compositions, and structures, not only in whitebark pine forests, but in all mountain pine beetle-susceptible forests. We can mitigate potential climate warming effects on the species by being strategic in our restoration efforts. For example, we can prioritize higher elevation whitebark pine stands for restoration, but also plant seeds and seedlings on colder aspects and in colder areas of a region. We also should ensure that planted seedlings or sown seeds represent high genetic diversity (Keane et al. 2012). If we follow these simple guidelines, we will enable whitebark pine forest to prosper under future climates--even with naturalized blister rust, eventually restoring the species to dominance on our high mountain landscapes.

While it is true that whitebark pine forest are likely to become more vulnerable under warming climates, the same is true for all ecosystems from prairie grasslands to arctic tundra. This may be the single most important reason to institute restoration measures now rather than wait for most of the trees to die, including those rust-resistant individuals that are the foundation of the restoration strategy. The blister rust pathogen has spread across most of the range of whitebark pine, and the demise of the tree has been accelerated in many areas by the recent mountain pine beetle outbreaks. Regions such as the Northern Continental Divide Ecosystem now illustrate that a threshold can be crossed in whitebark pine decline, leading to non-functional ecosystems, even without major recent losses from mountain pine beetles (McKinney et al. 2009, Barringer et al. 2012). If we want to conserve whitebark pine, we must act now to create resilient and resistant forests that include rust-resistant whitebark pine on

landscapes that are able to withstand future changes in fire regimes, pine beetle outbreaks, and species competition. There is a small chance that the benefits of the proposed restoration efforts might be negated by climate change effects. However, the proposed actions are infinitely better than the alternative of doing nothing. The "no action" alternative will almost certainly result in major, if not complete, losses in whitebark pine populations, even without climate change. Since projections of climate change and ecosystem response have such great uncertainty, we should attempt to "save all the parts of today's ecosystems," to paraphrase Aldo Leopold. It seems irrational to base a decision on whether to save a major, widespread ecosystem and the considerable biodiversity that it supports based on the results of highly uncertain climate change models.

Finally, the process of restoring whitebark pine will require commitment and tenacity from agencies and managers. This program is going to take several human generations to complete. The sooner it is begun, the more likely we will have a successful outcome. Restoration must be viewed as a long-term program because we should not restore all whitebark pine forests at once (Keane et al. 2012). All types of restoration efforts, from removing competition through prescribed fire and mechanical thinning to planting rust-resistant whitebark pine seedlings must be continually assessed to refine and modify techniques to ensure future success. Local land managers must work closely with scientists and the public to implement the restoration activities that have the highest chance of success, given the current state of ecological knowledge. This adaptive approach is the best hedge against future adverse climate effects on whitebark pine restoration. We don't know if today's restoration actions will be ineffective in the future, and we will probably never know until we try.

Risks to restoration

The major risk to achieving successful whitebark pine restoration is that we are too late to protect these valuable forests before mountain pine beetle, fire, and competition remove rust-resistant whitebark pine trees from the landscape. Land managers in the most highly impacted regions of whitebark pine's range are currently protecting mature cone-producing trees from wildfire, protecting potentially blister rust-resistant trees from mountain pine beetles, planting seedlings in accessible competition-free areas, and in some cases removing competing tree species from all age classes of whitebark pine to ensure their future, but there is much more to be done. We need to implement these actions in less-impacted areas as well, where we still have "all the parts" to the ecosystem, and restoration is highly feasible (e.g., Schoettle and Sniezko 2007, Keane et al. 2012).

Another risk to implementation of whitebark pine restoration is "agency/manager fatigue," resulting in loss of interest and of funding. Agencies must commit to the "long-haul" to see this work completed and the ecosystem restored. Essentially, we "broke" the ecosystem through various activities, including importing blister rust on plantation stock, suppressing fires, and adding greenhouse gases to the atmosphere (Tomback and Achuff 2010, U.S. Fish and Wildlife 2011), and we are ethically and ecologically obligated to "fix it." Additional research and development will help identify treatments, activities, and protocols that will speed restoration

and make restoration more efficient, stretching precious federal dollars. Funding at the local levels is desperately needed to implement those indispensable restoration activities that research has identified as beneficial. Managers and researchers must continue to work together to monitor those activities to determine efficacy and success. And most importantly, continued education of the public and government officials, and the establishment of public and private partnerships, will be important to maintain interest and funding.

Administrative and regulatory barriers are also a risk in that they might limit collaboration among land management agencies in effective restoration efforts. These barriers must be identified and overcome for the most efficient restoration implementation and outcome. The range-wide restoration strategy (Keane et al. 2012) provides detailed information on the planning and implementation of whitebark pine restoration activities across the U.S. and Canadian borders, with collaboration among governments and their agencies, universities, and other organizations. Many local land management units are developing whitebark pine management strategies to prioritize areas for restoration and protection. A variety of implementation projects are funded each year with the top priority including cone collection and screening trees with potential blister rust resistance.

The feasibility of restoration in the face of climate change

The goals of the whitebark pine range-wide strategy (Keane et al. 2012) are certainly achievable and actions to realize these goals are being implemented in small-scale projects across the range of whitebark pine by innovative land managers. To date managers have been quite successful on local scales in protecting rust-resistant cone-producing whitebark pine from mountain pine beetle with the application of Verbenone packets or by spraying trees with Carbaryl. Both managers and scientists have monitored successes and failures to ensure we continue to effectively protect valuable trees. They continue to improve application techniques and share their results widely so others can learn. Planting techniques that maximize seedling survival have been developed over the last 30 years from whitebark pine planting experience and were recently summarized in a document for managers (McCaughey et al. 2009). Operational planting efforts are continually improving, acres of planting are increasing, and seedling survival rates continue to increase. Each year managers request assistance from researchers to develop new techniques to improve the efficiency of Verbenone applications, to develop new approaches for planting, such as direct seeding and seedling mycorrhizal inoculation, and to develop planting strategies to mitigate for climate change. Long-term monitoring of projects and sharing information have led to increased knowledge and experience in application of restoration techniques, and also increasing interest across the range of whitebark pine.

Conclusions

In summary, we believe that restoration is the only course of action for managing whitebark pine ecosystems. The anthropogenic-caused loss of a major ecosystem is irreversible: with it go tremendous biodiversity, ecosystem services, and ecosystem function, seriously impoverishing

our biological heritage. Restoration will include the implementation of strategies that hedge the effects of climate warming on whitebark pine ecosystems. However, we point out that the high uncertainty inherent in most current climate and ecosystem models may limit predicted distributional shifts that are extremely coarse-scaled and should not be used as justification for a "no restoration" response, especially considering the resiliency exhibited by whitebark pine over time and across its range. We must use the best information available and the most efficient restoration approaches in our toolkit of restoration techniques. We also need to educate and recruit new generations of managers and researchers, as well as new generations of agency administrators and other government officials, so that they understand the value of restoring these ecosystems and the rich biological heritage we hope to leave for future generations.

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