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Effective actions for managing resilient high elevation five-needle white pine forests in western North America at multiple scales under changing climates

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ABSTRACT

Many ecologically important high elevation five-needle white pine (HEFNP) forests that historically dominated upper subalpine landscapes of western North America are now being impacted by mountain pine beetle (*Dendroctonus* spp.) outbreaks, the exotic disease white pine blister rust (*Cronartium ribicola*), and altered fire regimes. And more recently, predicted changes in climate may reduce HEFNP habitat and exacerbate adverse impacts of fire, beetles and rust. Management intervention using specially designed tactics implemented at multiple scales (range-wide, landscape, stand, and tree levels) are needed to conserve these keystone tree species. A goal of this intervention is to promote self-sustaining HEFNP ecosystems that have both resilience to disturbances and genetic resistance to white pine blister rust in the face of climate change. Many tools and methods are available for land managers, and in this paper, we summarize possible multi-scaled actions that might be taken as steps toward restoration of these valuable HEFNP forests. Long-term programs, such as inventory, mapping, planning, seed collection, seedling production, education, and research provide the materials for effective restoration at finer scales. Stand- and landscape-level passive and active treatments, such as silvicultural cuttings and prescribed fires in both healthy and declining forests, are described in detail and grouped by objectives, methods, and tactics. And last, there are critical pro-active tree-level actions of planting and protection that may be used alone or together to enhance success of other restoration actions. Administrative, policy, legislative, and societal barriers to implementation of an effective restoration effort are also discussed.

1. Introduction

It is now evident that many high elevation five-needle pine (HEFNP) forests in western North America are declining because of complex interactions across multiple disturbance factors (Keane et al., 2011) (Fig. 1). Forests consisting of two of the most widespread HEFNPs, whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*), are rapidly declining primarily due to the exotic disease white pine blister rust (WPBR)(*Cronartium ribicola),* but also recent frequent outbreaks of the native mountain pine beetle (MPB) (*Dendroctonus ponderosae*) (Tomback and Achuff, 2010; USFWS, 2018). Furthermore, the exclusion of wildland fire in these ecosystems over the last 100 years through fire suppression has resulted in greater surface and canopy fuel loadings and successional replacement of some HEFNPs with more shade tolerant conifers (Keane, 2001). Climate change, however, has the potential to exacerbate WPBR and MPB outbreaks, increase wildfires above historical levels, and reduce suitable HEFNP habitat (Koteen, 1999; Kendall and Keane, 2001b; Keane et al., 2012; Smith-McKenna et al., 2014; Dudney et al., 2020). Forests of the other HEFNPs – foxtail pine (*P. balfouriana*), Great Basin bristlecone pine (*P. longaeva*), southwestern white pine (*P. strobiformis*), and Rocky Mountain (RM) bristlecone pine (*P. aristata*) – have yet to experience the major declines observed in limber and whitebark pine forests, but all are also in imminent danger from WPBR, and some from MPB mortality under climate change (Keane and Schoettle, 2011). Upper subalpine and treeline HEFNP forests cover a great portion of the western North American landscape (Arno and

Abbreviations: HEFNP, High Elevation Five Needle Pines; MPB, Mountain Pine Beetle; WPBR, White Pine Blister Rust; HRV, Historical Range of Variability; RAD, Resist, Accept, Direct climate mitigation strategy; RM, Rocky Mountain.

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Hoff, 1990; Keane, 2000; Keane et al., 2011) and contain high biodiversity and unique landscape structures that provide extensive ecosystem services, including watershed protection, reduction of soil erosion, wildlife food and habitat, protection against soil erosion and avalanche, as well as recreational and aesthetic values (Tomback and Kendall, 2001; Tomback and Achuff, 2010). Therefore, restoring these valuable ecosystems is imperative to sustain regional ecological biodiversity and ecosystem services (Naughton et al., 2018).

The case for management intervention in these threatened, iconic HEFNP ecosystems was first made by Tomback et al. (2001a) who emphasized the inherent value of these forests as many HEFNPs are both keystone and foundational species in many high mountain ecosystems (Tomback and Kendall, 2001; Tomback and Achuff, 2010). WPBR infections in tree populations poorly adapted to resist the fungus, coupled with major MPB outbreaks that kill mature trees that could have resistance to WPBR, pose the real possibility of local extirpations of HEFNP forests (Kendall and Keane, 2001a; Wong and Daniels, 2016; Holtz and Schoettle, 2018). Paradoxically, fire exclusion policies reduced burned areas on the high mountain landscapes that were the ideal environments for shade-intolerant HEFNP trees to regenerate and grow to maturity (Tomback, 1989; Morgan et al., 1994b; Larson et al., 2010). Now, frequent and intense wildfires, fostered by climate change-mediated drought and suppression-era fuel buildups, occur on many high elevation landscapes and kill HEFNPs that are potentially resistant to both MPB and WPBR (Loehman et al., 2011; Keane et al., 2017b; Shepherd et al., 2018). Few healthy cone-bearing trees remain in stands decimated by MPB and/or WPBR, especially in the US northern Rocky Mountains (Keane et al., 2012). In hard-hit stands, seeds from the relatively few surviving HEFNP trees may be quickly harvested before seed ripening by pine squirrels (*Tamiasciurus* spp.) or Clark's nutcrackers (*Nucifraga columbiana*), the bird species that is the major seed disperser for several HEFNP species (e.g., (Tomback, 1998; McKinney and Tomback, 2007). These interacting factors create a possible extirpation pathway for keystone HEFNP forests in many parts of their ranges. Therefore, proactive restoration measures are critically needed to ensure the HEFNP species remain on high elevation North American landscapes (Schwandt, 2006; Schoettle and Sniezko, 2007; Keane et al., 2012).

As stated in Keane et al. (2012), the overarching goals of most restoration and conservation actions are (1) facilitating increases in WPBR-resistance on the landscape, whether it is through natural selection or planting of WPBR-resistant pine seedlings after disturbance; (2) maintaining or increasing genetic diversity of natural and planted seedlings to ensure HEFNPs forests are able to adapt as changes in climate alter historical landscape processes, and (3) enhancing vigor and reproductive capacity of HEFNP forests and trees (Keane et al., 2012; Mahalovich, 2013; Keane et al., 2017a; Schoettle et al., 2019a). The free flow of genetic material across the landscape through wide-spread pollen dissemination, bird-assisted seed caching, and management-assisted planting, may be our best strategy for sustaining pines on high elevation western North American landscapes.

Here, we present an interrelated set of multi-scaled management actions that we feel will meet those goals and maintain or restore HEFNP forests under climate change (Fig. 2) (Keane and Schoettle, 2011). This paper complements compilations of current conservation and management practices presented in Tomback et al. (2021, this issue). First, we synthesize projected climate change impacts in HEFNP forests to set a context for the remaining sections in the paper. Second, we detail a set of on-going, long term programs that need to be implemented to support restoration efforts at all scales (Fig. 2). Then we present potential restoration activities, treatments, and considerations at four spatial scales (range-wide, landscape, stand, and tree; Fig. 2) that are intended to mitigate potential adverse impacts of climate change on HEFNP populations (Simonson et al., 2021). Climate change considerations are addressed at each scale to ensure each action is designed to enhance all other actions at both finer and coarser scales into a more effective, integrative, and comprehensive restoration strategy. All summarized actions are described in detail in Keane and Schoettle (2011), Keane et al. (2012, 2017a) to present a catalog of potential restoration actions rather than a set of best management practices for restoring these valuable ecosystems.

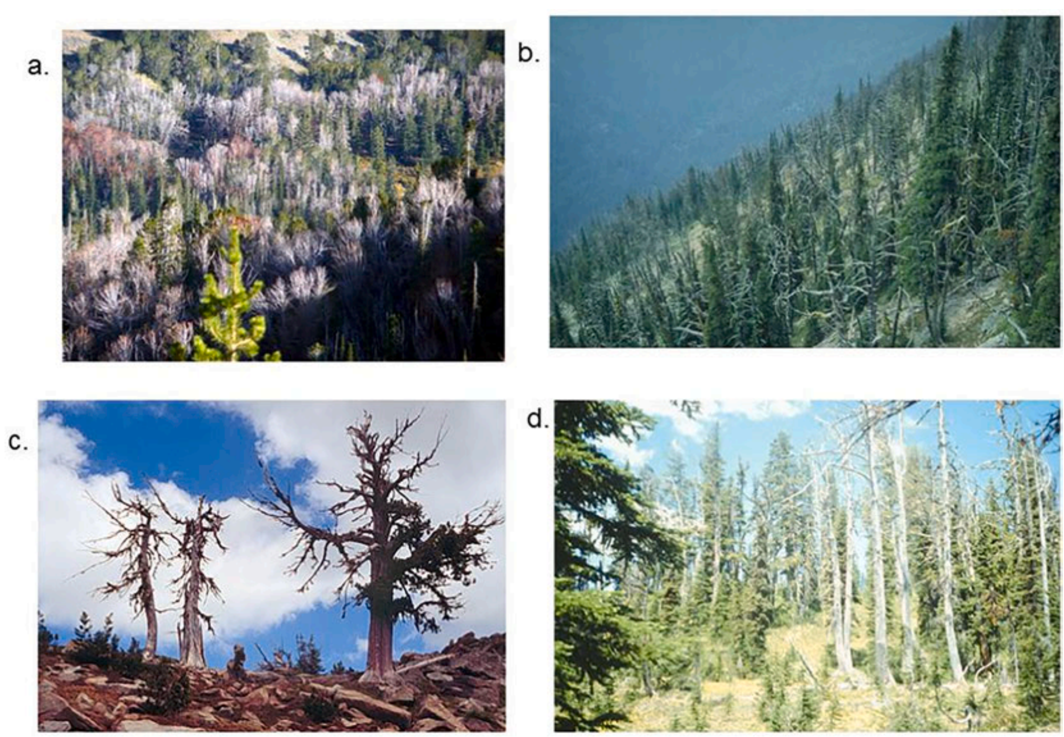

Fig. 1. Declining whitebark pine forests across the species range. (a) Mountain pine beetle (MPB) mortality in central Idaho, (b) white pine blister rust (WPBR) mortality in west-central Montana, (c) WPBR mortality in the Great Burn of Idaho, and (d) extensive WPBR mortality in the Bob Marshall Wilderness Area of Montana. Whitebark pine is one of the six high elevation five needle pine species (Photos a, b, d, Bob Keane, USDA Forest Service; photo d, Steve Arno).

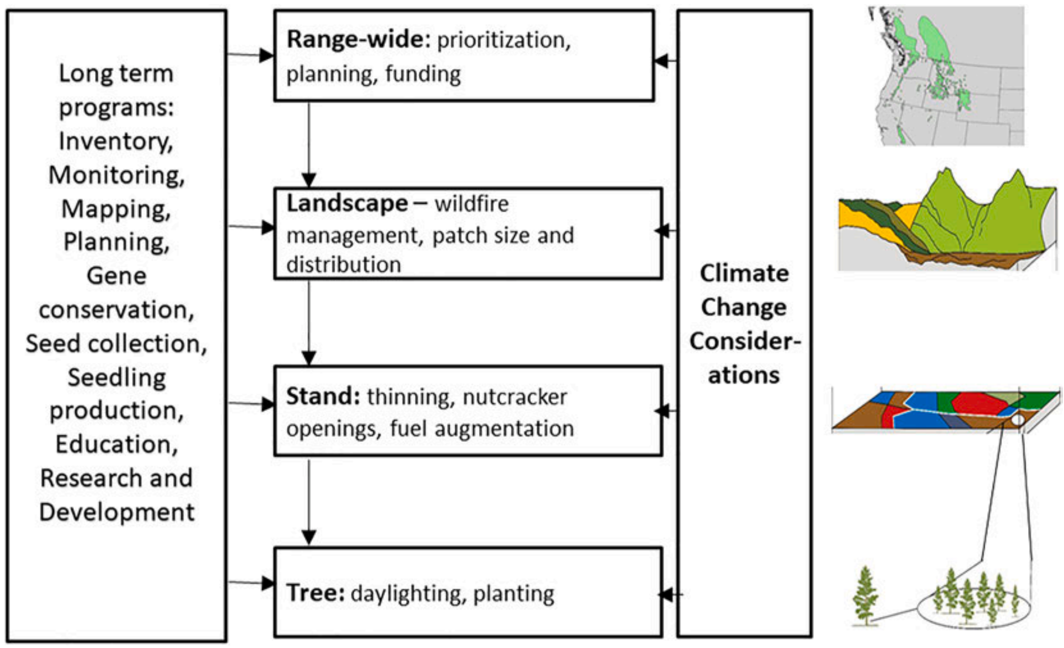

Fig. 2. The primary structure of the principles and actions needed for effective restoration and management of High Elevation Five Needle Pines (HEFNPs). A large group of long-term programs are listed to aid in the implementation of restoration actions at multiple scales from the entire range, to landscape then stand then tree scales. A list of some example actions is provided at each scale. Climate change considerations are addressed at every scale and within all long-term programs.

2. Climate change impacts

2.1. Climate projections for high elevation forests

Over the last 100 years in western North America, including most HEFNP forests, temperatures have increased while precipitation patterns have not changed consistently (Mote and Salathé, 2010). In HEFNP forests of the Greater Yellowstone Area, however, recent evidence shows that there has been a decrease in precipitation with a larger percent falling as rainfall instead of snowfall (Mahalovich, 2013). From 1895 to 2011, temperatures warmed 1.3°F in the Pacific Northwest (Cayan et al., 2001; Mote and Salathé, 2010). For 1901 to 2009, heat waves expressed as high nighttime minimum temperatures have increased since 1980. No significant trend in precipitation has been found, although variability appears to be 16% higher since 1970 than in the preceding 75 years. Increases in extreme precipitation events have been modest (Mote and Salathé, 2010).

Increases in temperature and decreases in precipitation may cause other impacts. High elevation areas may experience an increase of 50+ frost-free days a year, a significant change over historical averages (Littell et al., 2011). Higher temperatures also cause lower snowpacks throughout the western US, which are expected to decrease by 20 to 70% with the greatest reductions in the Cascade Range of Washington and Oregon. The earlier snowmelt, coupled with higher temperatures, could result in lower soil water during the growing season, but the already high precipitation amounts in the upper subalpine forests of the Pacific Northwest will ensure plenty of water throughout the year; many Global Circulation Models (GCMs) predict increases in soil water for some high mountain areas.

2.2. Climate change effects

There is much uncertainty about the fate of HEFNP forests as climates slowly warm. Conventional wisdom has projected warmer and drier conditions severely reducing high-elevation pine habitat and pushing HEFNPs “off the tops of mountains” or “farther north" (Koteen, 1999; Schrag et al., 2007; Warwell et al., 2007). This assumes that less hardy, shade-tolerant conifer species would establish in those higher-elevation stands and HEFNPs would “migrate” upslope to the limited areas above its current elevational range (Romme and Turner, 1991). Three main responses to climatic change may occur for all HEFNP ranges: decline, maintain, and expand. Species Distributional Modeling (SDM) studies have shown dramatic decreases in whitebark pine habitat over the next 50 years (Warwell et al., 2007; McDermid and Smith, 2008). Hamann and Wang (2006) predict a 100% decline in whitebark pine in British Columbia with climate warming. These same models also predict that whitebark pine may transition to timberline environments (above current species elevational range), but these transitional areas are smaller in size than whitebark pine’s traditional range, thereby resulting in a net loss of the species. Bell et al. (2014) computed 10–20% range losses in high elevation forests by 2090. Others feel that climate-mediated changes in the disturbance regimes will serve to keep HEFNP within its current range, albeit at lower levels (Loehman et al., 2011; Ireland et al., 2018). Realistic predictions are more complex because of (1) high uncertainty in regional climate change predictions, (2) high genetic diversity and resilience of HEFNP species, and (3) localized changes in disturbance regimes and their interactions (Keane et al., 2017a). Climate can adversely impact growth and mortality of whitebark pine in several ways (Bugmann and Cramer, 1998; Keane et al., 2018), but primarily, projected decreases in water availability may result in less water being available for some droughty sites.

Some HEFNP forests may have positive responses to warming climates. Loehman et al. (2011) simulated high growth and more frequent cone crops in the U.S. northern Rocky Mountains due to warmer summers and longer growing seasons. Recent modeling efforts have shown that whitebark pine might be maintained on the landscape providing that predicted increases in stand-replacement fires create large, competition-free burned areas (Clark et al., 2017; Keane et al., 2017a). Whitebark pine also shows some promise for climate change resistance because of high levels of genetic diversity (Richardson et al., 2002; Mahalovich and Hipkins, 2010); moderate to high heritabilities in key adaptive traits (Landguth et al., 2017); demonstrated blister rust resistance (Mahalovich et al., 2006); minimal inbreeding (Bower and Aitken, 2007; Mahalovich and Hipkins, 2010); increased diameter growth (Kichas et al., 2020); and generalist adaptive strategies (Mahalovich, 2013). Xeric conditions predicted by many climate change studies may also foster large increases in the annual number, area burned, and intensity of wildfires (Whitlock et al., 2003; Gergel et al., 2017; Hessburg et al., 2019b; Pansing et al., 2020). With increased fire, some HEFNPs will have an unique opportunity to maintain their range or even increase in distribution in the future because they have bird-mediated (Clark's nutcracker) seed dispersal; the bird 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, 1982, 2005). Whitebark pine is a quasi-fire-adapted species that readily regenerates in large burned areas (Arno and Hoff, 1990; Tomback, 2001) and has morphology that enables it to survive low to moderate severity fires (Ryan and Reinhardt, 1988).

In general, HEFNP forests are not expected to do well under future climates, not because they are poorly adapted to shifts in climate regimes, but rather because they are currently experiencing major declines caused by other disturbances that preclude successful regeneration into future burned areas. Current MPB outbreaks appear to be more frequent than historical records indicate, probably a result of warmer winter temperatures that facilitate establishment and expansion of MPB populations in the higher-elevation zone (Logan and Powell, 2001). Warmer climates may also accelerate spread of WPBR (Smith-McKenna et al., 2014; Shepherd et al., 2018). HEFNPs are at great exposure to any climate changes because of their (1) confined distribution to the upper subalpine environments, (2) currently depressed populations, and (3) lack of an ability to regenerate when populations are low because of nutcracker and squirrel seed predation (Keane et al., 2017a).

3. Long-term programs

There are a number of important restoration programs that are most efficiently implemented across all geographic scales by public and private land management agencies to provide the data, knowledge, expertise, materials, and methods needed to properly implement rangewide, landscape, stand and tree level restoration activities that mitigate climate change (Fig. 2) (Simonson et al., 2021). These ongoing programs may last years to decades, perhaps until HEFNP ecosystems are deemed restored, or they may be short-lived, such as research studies and educational programs. Significant coordination and collaboration across all land management agencies will be needed to ensure success of these programs over the large geographical ranges of all HEFNP species. Admittedly, many of the programs described below are missing for most of the HEFNPs; whitebark pine and limber pine have the most active long-term programs to date.

New and existing long-term programs must integrate climate change mitigation tactics and strategies into the design of restoration actions to succeed into the unknown future (Millar et al., 2007; Keane et al., 2017b). For example, historical ranges of variability (HRV) may be an impossible target condition for land management in the future as climate may render some HEFNP habitat unsuitable (Millar et al., 2007; Schuurman et al., 2020). However, HRV can be used as a reference to define resilience and resistance indices for determining new landscape conditions (Keane et al., 2020c). The RAD (Resist-Accept-Direct) decision framework (Schuurman et al., 2020) is a simple tool that defines a decision space for responding to ecosystems facing the potential for rapid, irreversible ecological change to assists managers in making informed, purposeful choices about how to respond to the trajectory of change and provides an approach for collaborating at larger scales across jurisdictions. Millar et al. (2007) mentions that no single solution fits all future challenges, especially considering the wide range of GCM climate projections, and that the best strategy is to mix different approaches for different situations. They suggest three main adaptive strategies: (1) forestall impacts and protect highly valued resources (resistance), (2) improve the capacity of ecosystems to return to desired conditions after disturbance (resilience), and (3) facilitate transition of ecosystems from current to new conditions (response). Both Millar et al. (2007) and von Holle et al. (2020) found that there are few examples of successful landscape restoration strategies under climate change in the literature. Therefore, each individual long-term program should be designed and revised with these and other climate change principles in mind.

3.1. Inventory and monitoring

Most HEFNP restoration activities require forest health and stand attribute data to guide planning, design, and implementation. Projected impacts of a changing climate on threats to HEFNP, such as WPBR and drought mortality, may be important reasons for accelerating inventory and monitoring activities (Keane et al., 2017a). HEFNP forest condition databases provide context for restoration actions so that the best available information can be used to evaluate health and decline which then leads to prioritizing areas for restoration, identifying appropriate treatments, designing effective treatments, and implementing additional actions for mitigating future adverse impacts (Wilson, 2002; Schoettle and Sniezko, 2007). Inventory or monitoring efforts should include an assessment of those factors that are contributing to HEFNP decline or putting the populations at risk, such as WPBR infection incidence, WPBR-caused canopy kill, MPB-caused mortality, regeneration, shade tolerant tree species density, and ground cover (see Keane et al. (2012) for more guidance). And most importantly, climate-related variables should be included to provide context for unexpected responses (e.g., georeferenced coordinates for plot can be used to reference modeled weather and climate data for past, present, and future).

Many existing inventory and monitoring systems can be used to field-sample stand attributes, including FIREMON (Lutes et al., 2006), FSVEG (Nelson et al., 2015), and FFI (Lutes et al., 2009). Tomback (2005) developed standardized methods for repeated surveys of whitebark and limber pine stand health that are focused on assessment of tree-level and plot-level WPBR and MPB mortality and incidence that have been adopted for use in other HEFNP forest communities (e.g. Schoettle and Coop (2017)). These standardized methods allow comparison among geographic areas and improved trend analyses of disease severity and pine population; and their application to plot network monitoring (Tomback et al., 2021, this issue). For whitebark pine and limber pine, a US Forest Service database of cross-agency forest health assessments was developed as a repository to organize and facilitate access to existing data for assessing changes in condition over time. The database was initially called the WLIS (Whitebark and Limber pine Information System) (Lockman et al. (2007)) but is now expanded to include other HEFNPs.

Allocating resources for monitoring restoration treatments using statistically credible sampling designs are critical for providing the essential information needed to fine-tune restoration strategies to local areas and adjust treatment designs to improve efficacy (Churchill et al., 2013; McKelvey et al., 2021). Successes of future HEFNP restoration efforts will be greatly dependent on the lessons learned in current and past attempts, especially under climate change (Keane et al., 2017a) (Tomback et al., 2021, this issue). Results from monitoring efforts also need to be published so they are readily available to the public, managers, and researchers. Monitoring efforts for any given treatment need to be extended well into the future because of the long response times in HEFNP ecosystems and impeding climate change (Agee and Smith, 1984). The co-production of restoration monitoring plans by both management and research will improve evaluation of treatment efficacy and contribute to adaptive management (McKelvey et al., 2021). Tracking moisture availability or summer maximum temperatures after treatment using local climate data (e.g., Snotel weather stations, remote weather stations, or algorithm-based sources such as, PRISM), for example, may provide insight into success or failure of some projects under climate change, and provide context for interpreting levels of seedling survival, growth, or seed germination in restoration projects. Other effects could include tree mortality from drought stress or a failure of natural regeneration after restoration treatments (van Mantgem and

Schwik, 2009; Leirfallom et al., 2015; Stevens-Rumann et al., 2018).

3.2. Mapping

Mapping distributions of HEFNP species, threats to these species, spatial management context (e.g., land ownership, wilderness, and roads), forest structure, and stand condition (i.e., mortality and its causes) at multiple scales is an important first step towards planning effective restoration (Aubry et al., 2008b; Burns et al., 2008; Keane et al., 2012). Standard GIS spatial analysis techniques (Brown et al., 1994) can be used with available digital maps representing HEFNP ecology and management issues to provide the critical spatial information needed for many restoration efforts (see Keane et al. (2012) and Jenkins et al., in preparation, this issue). For example, gene conservation and seed collection guidelines can be geographically stratified by species distribution, biophysical settings, and ecological conditions following specified guidelines (e.g., see (Aubry et al., 2008b; Schoettle and Coop, 2017; Schoettle et al., 2019a)). Risk maps of WPBR infection levels may be useful to identify areas to monitor, collect seeds, and assess for intervention prioritization (Schoettle et al., 2019a) (Jenkins et al., in preparation, this issue). Effective mapping of HEFNP ranges and resources is best done at coarse spatial scales. Future HEFNP habitat layers have been modeled by several projects using empirical species distribution modeling approaches (Iverson and Prasad, 1998; Rehfeldt et al., 2006; McKenney et al., 2007), but this statistical approach has many limitations (Keane et al., 2020b).

3.3. Planning

The success of HEFNP restoration attempts will be greatly enhanced if a coordinated strategy can be developed that integrates the latest scientific findings into a comprehensive plan for species conservation across multiple scales of time, space, and organization. Because over 88% of whitebark pine forests (USFWS, 2020), and most other HEFNP forests, exist on public lands managed by state, provincial and federal agencies in the U.S. and Canada (Keane, 2000; Tomback and Achuff, 2010), government land management agencies play key roles in ensuring the survival of these ecologically valuable tree species. It is important that these government agencies employ a coordinated plan for species restoration to ensure that there are few conflicting actions that could result in further declines of HEFNP.

An inter-agency, trans-boundary restoration strategy for whitebark pine was crafted by Keane et al. (2012) to emphasize infrastructure, expertise, and agency strengths for implementation, and to make efficient use of scarce resources. This integrated strategy was then augmented with another report that accounted for climate change impacts on restoration strategies (Keane et al., 2017a). Together these provide guidance for planning successful, cost-effective actions for restoring declining whitebark pine forests. This effort is complemented by the National Whitebark Pine Restoration Plan, currently in development, which emphasizes priority areas for restoration work within units managed by different federal agencies (Tomback and Sprague, in preparation, this issue). Numerous regional or agency-based management guides and strategies have also been written to facilitate restoration of declining HEFNP ecosystems, especially whitebark pine forests. Regional developed strategies include the BLM whitebark pine strategy (Perkins et al., 2016), the Greater Yellowstone Ecosystem (Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee, 2011), limber pine forests of the US Southern Rockies (Schoettle et al., 2019a), and whitebark pine forests of the Pacific Northwest (Aubry et al., 2008a). At local scales are the Crater Lake National Park (Beck and Holm, 2013), Greater Rocky Mountain National Park Area (limber pine) (Schoettle et al., 2019a), and Glacier National Park (Peterson, 1999). The Crown of the Continent (CCE) Pilot restoration strategy for whitebark pine is an ambitious multi-jurisdictional, transboundary plan that includes both whitebark and limber pine on US and Canadian lands (Jenkins et al., in preparation, this issue). The CCE strategy and Keane et al. (2017a) efforts directly incorporate climate change impacts into the planning process, which is critically needed to be addressed in future planning documents.

An important step towards effective active restoration planning is to identify those areas that, with the proper management, have the greatest likelihood of success to support sustainable HEFNP populations and provide ecosystem services at the stand, landscapes, and regional levels under future climate change (Keane et al., 2012, 2017a). Even in regions where HEFNP mortality rates are comparatively low, such as the southern Rocky Mountains, the Sierra Nevada and interior Great Basin ranges, proactive prioritization strategies (see Schoettle and Sniezko (2007), Schoettle et al. (2019a)) may help prevent the severe declines experienced elsewhere. Prioritizing landscapes for restoration require assessments of those factors that have caused the decline of high elevation pines and those factors that could restrict or facilitate restoration activities, most importantly climate change. Assessments performed at this scale may be for several purposes: (1) to determine overall health and condition of the landscape or stand, (2) to inform design of restoration treatments, (3) to provide a context for assessing restoration goals (land ownership, accessibility for example), (4) to identify issues that could restrict or facilitate restoration efforts (e.g., grizzly bears, remote locations, wilderness), (5) to explain disturbance regimes that can be used to guide restoration design, (6) to locate areas that provide critical ecosystems services (watershed protection, recreation) and (7) to determine those areas that might support HEFNP forests under climate change. Collectively, these factors and others can be used to rank areas for restoration priority.

3.4. Conserving genetic diversity

Tree mortality from WPBR and MPB reduce both genetic diversity and population size of the HEFNP hosts. WPBR kills all age classes of HEFNP, including mature trees, but MPB especially targets larger-diameter individuals, which are cone-bearing (e.g., McDonald (1992). Both threats reduce effective population size in HEFNPs and potentially create isolated groups and individuals, leading to inbreeding (Tomback and Kendall, 2001; Bower and Aitken, 2007). Before these threats significantly impact a HEFNP population, there is opportunity to capture native species' genetic diversity for gene conservation (Schoettle and Sniezko, 2007; Keane and Schoettle, 2011). Millar et al. (2007) mentioned retaining of genetic diversity as an important action to enhance resilience to allow forests to respond to new disturbance regimes; prioritizing seed collections from only fast-growing trees may be counter-indicated in tomorrow's forests. Collections of seeds are the primary means to assess and conserve genetic diversity; gene conservation has been supported by the U.S. Forest Service (see Tomback et al., 2021, this issue). Seed collections, for example, began in 2001 for RM bristlecone pine and in 2003 for limber pine in the Southern Rocky Mountains (Schoettle, 2004). Extensive seed collections are being made before the occurrence of high mortality caused by MPB, WPBR, or wildland fire, enabling research on adaptive traits, genetic structure, and rust resistance screening to proceed. Range-wide Rocky Mountain bristlecone pine collections, accompanied by stand condition plot information for each sampling location, have been completed (Schoettle and Coop, 2017). Comparison of whitebark pine growth characteristics over geographic areas or large-scale common garden studies for whitebark pine indicate geographic variation in adaptive traits, particularly those related to climate (Bower and Aitken, 2006; Mahalovich et al., 2006).

Healthy ecosystems provide opportunities to gain information on the genetic structure of the pine host and population vulnerabilities to WPBR and other novel stresses, such as climate change (Schoettle et al., 2011; Schoettle et al., 2012). Seed zones in the U.S. were established for whitebark pine and limber pine (Mahalovich, 2006), and zones are being defined for RM bristlecone pine to aid in defining seed transfer guidelines. To further refine seed zones and guide gene conservation collections, the genetic structure of RM bristlecone pine in the core portion of its range was studied (Schoettle et al., 2012). Rust resistance testing of RM bristlecone began in 2004 and 2005 (Schoettle et al., 2011). The first extensive family-based rust resistance testing for limber pine confirmed rust resistance and found that frequencies of those resistances vary geographically (Schoettle et al., 2014; Schoettle et al., 2019a).

3.5. Collecting seed

Seeds from HEFNP trees are collected for three general reasons: (1) to grow seedlings for operational planting, (2) to directly sow seeds, and (3) to use in studies, such as WPBR resistance and cold hardiness determinations (Keane et al., 2012). Costs of collecting whitebark pine seed for operational planting and sowing is high because cones must be caged to prevent squirrels and nutcrackers from harvesting the seed, which requires climbing trees in early summer to install cages, and then climbing trees again in late summer to harvest caged cones. See Tomback et al. (2021, this issue) for detailed discussions on seed collection methods.

Seed collection and storage for operational seedling production, and cataloging seed origins, are essential for HEFNP restoration, primarily because the planting of areas burned in wildfires has become one of the most effective restoration techniques (Keane et al., 2017a). A promising alternative to reducing regeneration costs is to sow seeds instead of planting seedlings (Smith et al., 2011; Pansing and Tomback, 2019). Even though the technology for sowing seed has yet to become cost-effective, the effective sowing of seeds may allow managers to regeneration remote burned areas where transporting seedlings may be problematic and in designated Wilderness where mechanical applications are restricted.

3.6. Growing seedlings

A concerted effort should be given to creating or maintaining a network of tree nurseries that are highly successful at both growing HEFNP seedlings and storing HEFNP seeds (Eggers, 1990; Burr et al., 2001). Recent improvements in nursery techniques have reduced some of the cost of growing HEFNP seedlings and have increased seedling survival. However, the cost of growing whitebark pine seedling is still high (~$1-$3 USD per seedling), making effective large-scale restoration plantings difficult with limited funding (Burr et al., 2001). Nursery techniques for growing seedlings of whitebark, limber, southwestern white, and RM bristlecone pines have been developed, but there needs to be more work for the other HEFNPs. Inoculation of seedlings with ectomycorrhiza appears to increase seedling survival in both the nursery and in the planted areas, especially in environments that are somewhat arid (Mohatt et al., 2008; Lonergan et al., 2014).

3.7. Educating and engaging

Implementing conservation measures and treatments in the historically unmanaged HEFNP ecosystems requires the acceptance, commitment, and engagement of both land managers and the public (Keane and Schoettle, 2011). The recent proposed listing of whitebark pine as Threatened under the Endangered Species Act has, through media outlets, alerted the public to the decline of this widely-ranging forest species and can serve as a major impetus for public education concerning HEFNPs in general (US Fish & Wildlife Service, 2020). Education and outreach programs for the public are necessary to help citizens understand why management actions are essential to the survival of these pines, and, at the same time, informational and training programs must be conducted for government agency personnel responsible for restoration so they can plan and implement successful HEFNP restoration programs. Current scientific knowledge and research findings must be organized and presented in media formats that are easily understood by both agency staff and the public at large. Overview documents, such as Samman et al. (2003) and Schwandt (2006), are useful to put threats to the HEFNP into perspective, as are regional management plans (Aubry et al., 2008a). The more public and agency people know about HEFNP ecology, the easier it will be to engage them in restoration activities to fund multi-scale restoration plans across HEFNP ranges (Meldrum et al., 2020; McKelvey et al., 2021).

Providing forums for information exchange and dialogue among diverse interest groups, from recreationists to conservation advocates to wilderness advocates to government skeptics, is also essential for restoration success. Educational websites that serve as primers on HEFNPs and the factors that threaten them provides easily accessible information for managers, teachers, and the public (www.whitebarkfound.org) (Schoettle and Laskowski, 2006). Extensive seminars and training sessions for environmental, native plant and botanic garden interest groups also increase awareness. Coordination with local chapters of the Society of American Foresters has led to field tours in Colorado and Wyoming and their volunteer assistance with cone collections on the Medicine Bow National Forest. News media also helps increase awareness through targeted outlets such as newspapers, newsletters, and public radio.

3.8. Conducting research

New research is desperately needed in all phases of HEFNP ecology and management to ensure that all actions mentioned in this paper and Tomback et al. (2021, this issue), and those implemented by land management agencies, utilize the best scientific information to effectively return HEFNPs to high mountain settings. Detailed basic research is needed in all fields of ecology, but especially in ecophysiology (e.g., used in modeling and understanding climate change responses), genetics (e.g., promoting rust resistance), disturbance regimes (e.g., describing fire regimes and tree-fire resistance), bird interactions (e.g., dispersal densities and distances), and community dynamics (e.g., successional trajectories). Applied research topics include improved technology and information for harvesting and sowing seed; effective prescriptions for fire and silviculture activities under climate change; planting seedlings, especially after wildfires; and protection of high values trees from disturbance.

The most pressing research need may be to address important effects and consequences of current and future pro-active restoration treatments, such as assessing regeneration success; evaluating silvicultural treatments to promote regeneration; and characterizing WPBR resistance frequencies, mechanisms, and distributions across the landscapes (Keane and Schoettle, 2011; Maher et al., 2018). For example, many high elevation restoration projects are proposing or implementing treatments designed to release individual whitebark pine trees using "daylighting" techniques. However, there have been few research efforts that show suppressed seedlings and saplings of whitebark pine, a moderate shade tolerant species, will actually release to increase in growth and become cone-bearing mature trees (Maher et al., 2018; Retzlaff et al., 2018); Keane et al. (2007a), for example, found that only a third of the whitebark pine trees released immediately, while another third released decades later and the remaining did not release. In another example, there is a great need for research to assess prescribed fire impacts in HEFNP ecosystems as some studies have shown high mortality in HEFNPs after some prescribed burns and wildfires (Keane and Parsons, 2010b; Keane et al., 2020a). It is vital that research provide the information needed by managers to conduct successful treatments for the sustainable management of whitebark pine ecosystems.

4. Range-wide actions

There are several range-wide activities that support fine scale restoration treatments. Range-wide digital maps and databases provide context for fine scale planning; the whitebark pine range map developed by Keane (2000) and the WLIS database (Lockman et al., 2007), for example, provided spatial context and site information for the range-wide strategy (Keane et al., 2012). Legislation, regulation, and policy are also implemented at this scale; the USFWS's possible inclusion of whitebark pine on the threatened species list is a good example. Along similar lines, the collaboration, lobbying, support, and advocacy of HEFNP by various Non-Governmental Organizations is best served at this scale; an example is the collaborative effort between the Whitebark Pine Ecosystem Foundation with American Forests and various governmental agencies has resulted in a National Whitebark Pine Restoration Plan (NWPRP) (Tomback and Sprague, in preparation, this issue). Planning, prioritization, and preparation are also vital activities that inform finer scale efforts; the NWPRP will eventually provide a means to prioritize whitebark pine restoration projects at landscape, stand, and tree scales. All mentioned activities must specifically address climate change in their implementation (e.g., both future and current range maps should be developed; prioritization should address climate change impacts). To do this, there must be a clear and consistent message on climate change and their impacts on HEFNPs.

5. Landscape activities

5.1. Integrating historical disturbance ecology

It is vitally important to understand disturbance ecology of HEFNP species at landscape scales to plan restorative actions at finer spatial scales (Schoettle and Sniezko, 2007). In short, different forest communities at elevations below the HEFNP communities, with respect to their stand structure, composition, fire regime, and pattern, may influence HEFNP forest management (Hobbs et al., 2014; Hessburg et al., 2019a). Wildland fire is the keystone disturbance that shaped many HEFNP landscapes in the past, especially throughout the Rocky Mountains (Morgan and Bunting, 1989; Murray et al., 1995a; Arno et al., 2001); therefore, many restoration treatments should be designed at both the landscape- and stand-level to somewhat emulate fires' effects (Murray et al., 1995b; Keane and Arno, 2001; Perkins, 2015; Keane, 2018). Stand-level prescribed fire and silvicultural thinning projects, for example, should be designed to mimic effects of stand-replacing, mixed severity, or non-lethal surface fires in high elevation landscapes (Keane and Arno, 2001; Keane et al., 2017a). Patchworks of treatment unit sizes and shapes should be similar to patterns left by historical fires (Hessburg et al., 1999; Swetnam et al., 1999; Hessburg et al., 2007) and treatment designs should account for available pine seed source in surrounding stands and the modes of seed dispersal for the target HEFNP (Coop and Schoettle, 2009; Leirfallom et al., 2015). As an example, burn patches of 5 to 50 acres were found to be attractive to Clark's nutcrackers for caching whitebark pine seeds (Norment, 1991), so Keane and Arno (1996) designed similar sized treatment unit sizes to enhance nutcracker caching to promote natural regeneration (Keane and Parsons, 2010b). Treatments that create large areas for whitebark pine regeneration in landscapes where few seeds are available because of WPBR and MPB mortality should only be attempted if planting rust-resistant seedlings is planned (McKinney, 2004; Leirfallom et al., 2015; Keane et al., 2017a).

Historically, HEFNP landscapes also were shaped by other disturbance regimes, such as MPB outbreaks, interacting with fire, vegetation dynamics, and climate to create shifting mosaics of diverse HEFNP communities (Turner, 1987; Millar and Delany, 2019). This created landscape heterogeneity (pattern diversity) that is critically important in maintaining resilient HEFNP forests in the face of climate change (Churchill et al., 2013; Keane et al., 2017a). HEFNP forests often have great variation in patch size, shape, and distribution because they were created by the highly variable interactions between vegetation, multiple disturbances, and climate (Murray, 1996; Millar and Delany, 2019). This great heterogeneity in both time and space facilitated optimal biological assemblages, species diversity, adaptive capacity, and most importantly, ecological resilience (Gunderson, 2000; Schoettle and Sniezko, 2007; Desjardins et al., 2015). Many positive landscape characteristics are associated with high landscape heterogeneity (Turner, 1987). Landscapes with diverse structure (mosaic of successional communities) and composition (species diversity) are often considered more resilient and resistant to disturbances (Haire and McGarigal, 2010). In heterogeneous landscapes, MPB outbreaks, for example, are less severe and their effects are more short-term on landscapes with diverse age structures of host tree species (Schoettle and Sniezko, 2007). Heterogeneous landscapes also promote population stability (Oliver et al., 2010); fluctuations in plant and animal population are dampened when landscape structure is diverse (Turner et al., 1993). Heterogeneous landscapes may also have more connecting corridors, buffers, and refugia for wildlife and plant migration (Camp et al., 1997; Wilkin et al., 2016). And last, biodiversity is greatest in heterogeneous landscapes; the most species can be found when there are diverse communities across space (Bannerman, 1997; Cohn et al., 2015). Management activities that promote homogenization of landscape conditions may probably render future landscapes more susceptible to disturbance; lead to losses in biodiversity; and cause declines in critical plant and animal species populations through loss of successional diversity (Morgan and Bunting, 1989). Fire exclusion, for example, has homogenized landscapes by creating large contiguous patches of older, denser stands with high surface and canopy fuel accumulations making them more susceptible to insects and disease because of low tree vigor from intense competition (Keane and Arno, 2001; Kendall and Keane, 2001b). The abundances of surface and canopy biomass could also fuel future wildfires that may be unprecedented in their size, frequency, and pattern (Keane et al., 2002).

A major question facing HEFNP land managers is "what is the appropriate level of heterogeneity for their landscapes?" A benchmark or set of reference conditions that can be used to evaluate, plan, and implement activities designed to facilitate landscape heterogeneity and mitigate climate change effects is needed. Using HRV is one method for estimating optimal heterogeneity (historical range and variation of landscape characteristics) (Morgan et al., 1994a; Nonaka and Spies, 2005; Keane et al., 2009). While HRVs of landscape metrics may poorly represent future landscapes under changing climates (Millar, 1997; Millar and Woolfenden, 1999), it may provide the best estimate of landscape conditions under which HEFNP ecosystems have evolved over the last several thousand years, and it is probably a good assumption that these historical conditions produced healthy ecosystems and landscapes (Landres et al., 1999; Wiens et al., 2012). Departures of contemporary landscapes from historical landscape compositions and structures can be used to plan, design, and sometimes, to implement effective restoration actions (Keane et al., 2009; Dickinson, 2014; Keane et al., 2019). We feel HRV reference conditions should be used in tandem with climate adaptation strategies (Millar et al., 2007; Ireland et al., 2018) to ensure successful restoration actions.

5.2. Wildfire management

Wildfires (uncontrolled wildland fires) burning in declining HEFNP landscapes can be both a benefit and a threat (Keane et al., 2017b). Wildfires can be an effective means of killing encroaching shade-tolerant, fire-sensitive conifer competition in late seral HEFNP stands, especially if the pines are declining due to MPB and WPBR (Keane and Parsons, 2010a). However, wildfire can also kill healthy HEFNP trees, trees that survived MPB and WPBR damage and may be putatively beetle- and rust-resistant. Their loss from wildfires severely limits chances for successful future HEFNP regeneration with increased rust-resistance (Hoff et al., 2001; Sniezko, 2008).

Wildfire management is often described using a circular continuum (Fig. 3). There are wildfire planning and proactive activities that can be implemented before the wildfire occurs (pre-fire environment) to both (1) control wildfire behavior allowing firefighters to fight wildfires more safely and (2) to improve the resilience of the forest (Moritz et al., 2005;

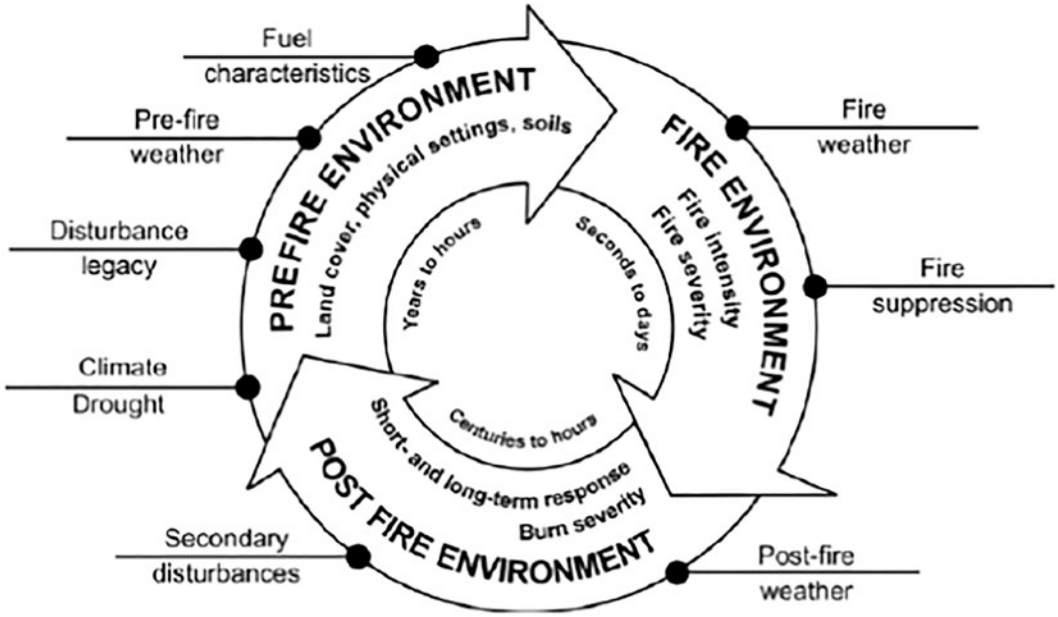

Fig. 3. The continuum of fire management. In this paper, wildfire management is stratified by actions that occur before the wildfire burns (pre-fire environment), during the fire (fire environment), and after the fire has occurred (post-fire environment) (from Graham et al. (2004)).

Keane et al., 2019). These management actions attempt to reduce wildland fuels to lessen wildfire severities (i.e., fuel treatment), but should also be designed to enhance resilience by (1) protecting fire-adapted species from unwanted damage or mortality; (2) improving tree vigor to facilitate survival after wildfires and other disturbances, and (3) enhancing regeneration by opening the stand to those tree species that can survive wildfire. There are generally three options for wildfire management while the wildfire is burning on HEFNP landscapes (fire environment. Fig. 3): (1) full suppression (FS), (2) partial suppression (PS), and (3) allowing wildfires to burn under an acceptable set of conditions (WFU; wildland fire use). Suppression tactics are best used to protect valuable elements of HEFNP ecosystems (detailed in Keane (2018)), but the consequences of suppression are usually greater fuel buildups, thereby increasing future wildfire severities. Perhaps the most effective restoration tool at the landscape level is managed wildfires or WFU (Black, 2004). WFUs are lightning-started fires that are allowed to burn under acceptable weather and site conditions specified in a local fire plan (Tanner, 1992). Aggressive use of WFU has the potential to be an efficient, economical, and ecologically viable method of restoring HEFNP forests in many areas, especially in wilderness areas (Keane et al., 2012). Landscapes where WFU might be contra-indicated are those with few HEFNP seed sources (e.g., high MPB and WPBR mortality) and where planting might be difficult.

6. Stand restoration treatments

The Keane et al. (2012, 2017a) range-wide whitebark pine strategies emphasized the need to create stand conditions that encourage natural regeneration (if WPBR resistance is high), conserve seed sources, promote rust resistance, and create resilient forests under changing climates. Objectives for most treatments, especially under changing climates (Keane et al., 2017a), include facilitating natural regeneration and planting rust-resistant seedlings, increasing HEFNP tree vigor, and reducing disturbance impacts. This can be accomplished by creating nutcracker caching habitat, reducing competing vegetation, decreasing surface and canopy fuels, manipulating forest structure and composition, and diversifying age class structure (Prichard et al., Millar et al., 2007). These actions can be implemented using a host of passive and active management actions to create areas where vigorous HEFNP trees can prosper in the face of climate change and impending disturbance regimes (Swanston and Janowiak, 2012). In general, this usually involves some combination of locally designed silvicultural cuttings, prescribed burning, and planting rust-resistant seedlings. Any restoration action should also improve landscape heterogeneity while also facilitating HEFNP resilience, rust resistance, and sustainable cone crops (Keane et al., 2017a; Ireland et al., 2018). Stand-level treatment should be designed to address multiple objectives at landscape scales. Fuel reduction treatments, for example, should reduce competition and allow for natural and artificial pine regeneration, while also reducing fire hazard and risk (Prichard et al., 2021).

Mechanical cuttings include treatments that manipulate whitebark pine stand structure and composition, often by using chainsaws, to remove competing shade-tolerant, fire-sensitive tree species, such as subalpine fir, spruce, and mountain hemlock (example in Fig. 4). Traditional silvicultural approaches may have limited effectiveness in these high mountain stands because of the severity of the sites, unique ecology of HEFNPs, diverse disturbance regimes, and bird-mediated seed dispersal of some of the HEFNPs (Keane et al., 2017a). Silvicultural strategies must be specifically tailored to individual stands to address restoration concerns in high elevation pine forests (Waring and O'Hara, 2005). Six types of mechanical cuttings are currently being used in restoration treatments for whitebark pine. Keane and Parsons (2010b) created ***nutcracker openings,*** areas within which all trees except whitebark pine were cut, in successionally advanced subalpine fir stands containing both healthy and dying WPBR-infected whitebark pine (Fig. 5). Nutcracker openings can also mimic patchy, mixed severity wildfires. Other cutting treatments include ***group selection cuts*** where all trees except whitebark pine are felled, and ***thinnings*** where all non-whitebark pine trees below a threshold diameter are cut (Chew, 1990; Eggers, 1990). ***Girdling*** subalpine fir trees has also been used to reduce whitebark pine competition because it is a fast, cost-effective means of killing competing subalpine fir (Jenkins, 2005), but the lowest live branches must be cut and the girdled trees are fuel that could foster future high severity wildfires that could kill those pine trees being restored. ***Daylighting*** (cutting of shade-tolerant competing species in a circle around whitebark pine trees) has been gaining favor among managers because it is cheap and easy, but there is little research on its effectiveness (see Fig. 4). One last cutting is ***fuel enhancement*** where subalpine fir trees are directionally felled to increase fuel loadings to better spread the fire (Keane and Arno, 2001). Keane and Parsons

Fig. 4. Mechanical cutting in whitebark pine treatment area. This person is performing a mechanical removal of trees around a whitebark pine, also called a “daylighting” treatment.

(2010b) found this treatment highly effective for widening of prescribed burning windows (lengthen flammability of fuelbed). In any mechanical treatment, it is important that slash be removed from treated sites to (1) allow nutcrackers full access to the ground for caching (Keane and Parsons, 2010b), (2) reduce potential pine mortality from *Ips* spp. beetles (Baker and Six, 2001), and (3) reduce severity of future unplanned future wildfires (Keane, 2018).

Prescribed burning may be the most ecologically desirable treatment because it best emulates wildland fire (Fig. 6), but it is also the most difficult and riskiest to implement (Keane et al., 2020a). Prescribed burns can be implemented at three intensities to mimic the three types of fire regimes common in HEFNPs forests: non-lethal surface fires, mixed severity burns, and stand-replacement fires (Murray et al., 1995a; Brown and Schoettle, 2008; Coop and Schoettle, 2010). The primary objectives of low intensity prescribed fires are to kill competing overstory and understory, to preserve the HEFNP component, and prepare the site for natural regeneration or planting (Keane, 2018). Moderate intensity prescribed burns mimic mixed severity fires where patches of variable size are burned depending on wind, canopy contagion, and fuel moisture conditions. A high intensity prescribed burn creates burned patches that are so large that seeds from competitors are unable to disperse into the center of the burn, allowing HEFNP regeneration decades of competition-free growth after germinated seeds are cached by nutcrackers. Mechanical cuttings and prescribed burns can be used together or separately to accomplish treatment objectives. Many populations of HEFNPs may be highly susceptible to fire mortality and prescribed burning may not be an option (Keane et al., 2020a). Research is needed to evaluate effective prescribed burning ignition patterns (Hiers et al., 2020), desirable ranges of wind, moisture and weather conditions (Keane and Parsons, 2010b), effective fuel loads to facilitate desired fire effects (Keane et al., 2020a).

6.1. Tree competition removal

Eliminating vegetation that competes with HEFNP trees is needed to improve tree vigor, which is increasingly important as the climate warms because it promotes resilience (Keane et al., 2017a; Retzlaff et al., 2018). Improved vigor often results in greater forest resilience because the trees have more resources to allocate to defenses against increasing

Fig. 5. A view of a “nutcracker opening” in the Keane and Parsons (2010b) restoration study that was implemented at the stand level and planned at the landscape level. In a nutcracker opening, all non-whitebark pine trees are cut and left on site. Slash is piled and burned. The openings were planted with rust-resistant seedlings three years later.

Fig. 6. Prescribed burning in the same landscape shown in Fig. 5. The objective of the prescribed fire was to kill all subalpine fir and Engelmann spruce, but leave whitebark pine mature trees alive. Auxiliary objectives were fuel reduction and seedling site preparation.

disturbance events (Churchill et al., 2013). Improved vigor may also increase the abundance of cone crops because trees may allocate more resources to reproduction (Morgan and Bunting, 1991). Increased vigor will also contribute to longevity and allow trees to remain on the landscape longer.

Mechanical thinning is the primary tool used for competition removal treatments (Keane and Arno, 2001). It is important that all competing shade-tolerant conifers be cut, including unwanted regeneration. However, this is rarely done because of the cost. Any residual trees of competing species, even small fir seedlings, will compromise efficacy of mechanical treatments, especially when future climate-mediated increases in productivity may accelerate successional advancement (Joyce, 1995; Fei et al., 2017; Gustafson et al., 2017). Therefore mechanical treatments may be enhanced by prescribed burning because, hopefully, 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, 2010a).

6.2. Wildland fuel reduction

Fuel treatments will undoubtedly play an important role in reducing future wildfire impacts on living rust-resistant HEFNP trees, and should therefore, be considered a viable restoration action (Rehfeldt and Jaquish, 2010; Spittlehouse and Stewart, 2004). 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, cutting, or piling. Reducing fuels in or near stands that contain valuable rust-resistant trees may be an important hedge against losing them to future wildfires. Fuel treatments can also be designed in the context of HEFNP restoration treatments, and vice versa, with any reduction of canopy and surface fuels considered a secondary objective. Many contemporary fuel treatments, such as mastication, canopy thinning, and chipping, are rarely designed with ecological relationships in mind. There is also some risk that live HEFNP 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.

7. Tree level actions

7.1. Planting

As HEFNP forests continue to decline, there will be fewer seeds produced and thus fewer available for pine regeneration (Keane and Parsons, 2010b). For example, in whitebark pine stands with high WPBR and MPB mortality, the low number of cones produced by surviving trees are highly sought after by pre-dispersal seed predators–especially pine squirrels, which may take unripe cones, but also nutcrackers—leaving few seeds to ripen and be available for nutcracker caching (McKinney and Tomback, 2007; McKinney et al., 2009). There also may be insufficient whitebark pine seed to naturally regenerate burned areas because of high nutcracker retrieval of caches (Keane and Parsons, 2010b; Tomback and Achuff, 2010). This same reasoning can also be applied to other HEFNP, and especially those pines that depend on Clark's nutcrackers for long distance seed dispersal (Tomback and Kendall, 2001; Tomback et al., 2011). Therefore, planting rust-resistant seedlings may be the only option to regenerate the species in large-scale high elevation burned areas (Howard, 1999; Hoff et al., 2001; Scott and McCaughey, 2006; Schoettle et al., 2019b). In addition, if local seed sources contain little or no heritable resistance to WPBR, artificial regeneration with rust-resistant seedlings may both increase population size and augment resistance into the future (Schoettle et al., 2019a). If high elevation landscapes have higher than 60% HEFNP mortality, it may be necessary to plant with putatively rust-resistant pine seedlings (Keane et al., 2012; Leirfallom et al., 2015).

Effective planting guidelines have been developed for whitebark pine (Scott and McCaughey, 2006; Izlar, 2007; McCaughey et al., 2009) and limber pine (Casper, 2015). The new guidelines have resulted in improvements in whitebark pine seeding survival (Izlar, 2007), but planting guidelines for the other HEFNPs are still needed. Appropriate microsites and shelter (i.e., nurse objects such as boulders, cobble, logs, and tree trunks) are important for successful establishment of both wind and bird-dispersed HEFNPs species (Coop and Schoettle, 2009). When practical, planting crews could remove non-HEFNP conifers to make planting effective in the long-term. Climate change adaptation actions of assisted migration (anticipating climate change by planting in new areas) (McLane and Aitken, 2011) and modified planting guidelines (expanding elevational and geographical seed zones to accommodate future climates) are often proposed to improve future planting successes. However, we feel that the models that predict where new planting sites may exist in the future are highly uncertain and not ready for operational use (Keane et al., 2017b). However, higher variabilities of drought, seed crop abundance, and microsite potential are expected and efforts should be made to account for these variabilities (Stewart et al., 2021).

Direct sowing of HEFNP seed instead of planting seedlings may significantly reduce costs of regenerating sites if sowing guidelines and technologies improve (Schwandt et al., 2011; Pansing and Tomback, 2019). Broadcast seeding results in nearly 100 percent consumption of whitebark pine seed by rodents (McCaughey and Weaver, 1990); therefore, HEFNP seeds must be sown correctly to reduce predation. A potential tactic may be to plant two to four seeds about 2–3 cm deep in one planting site with a specially designed dibble. Direct seeding may be the only cost-effective method for regenerating large high elevation burns in wilderness areas and remote settings (Keane, 2000; Tomback, 2008; Tomback et al., 2021, this issue). Considerable research must be done on sowing before it becomes operational.

7.2. Protection

Protection is a set of actions or treatments that safeguard high-value, mature, cone-producing, rust-resistant HEFNP trees to ensure they remain on the landscape so that their seeds provide natural regeneration and are also available for collection by managers for WPBR resistance screening and restoration plantings. A common tree-level protection activity is to safeguard trees from disturbance agents, primarily fire, MPB, and WPBR. These protection activities can be done prior to and after silvicultural treatments to ensure continued pine seed production. The most important trees to protect from these agents are those that have been identified as important sources for genetic and phenotypic rust-resistant seeds (aka “plus” or “elite” trees) (Mahalovich et al., 2006).

Protection of trees from damage from wildland fire (prescribed, wildland fire use, or wildfire) using tree-level fuel treatments is difficult and costly, yet it can be successful (Murray, 2007; Keane and Parsons, 2010b). Mechanical manipulations of fuel surrounding the trees have been done with mixed success by (1) raking or blowing (via leaf blower) litter and duff away from tree bases, (2) cutting competing fir and spruce, and (3) manually removing downed woody, shrub, and herbaceous fuels (Knapp et al., 2011; Ottmar and Prichard, 2012). Fire crews have wrapped large whitebark pine with fire shelters to protect against fire mortality, also with mixed results (Keane and Parsons, 2010b). There are also anecdotal stories of marginal successes by foaming trees to lessen fire damage (Adams and Simmons, 1999). For prescribed burning and wildfire control, modification of ignition patterns to control burn severity using thin strip head fires and avoiding igniting large pine trees may be the most successful way to minimize fire-caused pine mortality (Hood and Lutes, 2017).

Most HEFNP species historically avoided damage by MPB by inhabiting cold, inhospitable mountain environments where MPBs rarely completed their life cycle (Tomback et al., 2001b). However, the recent winter-time warming trend has facilitated successful MPB outbreaks in HEFNP forests across western North America (Williams and Liebhold, 2002; Carroll et al., 2003; Bentz et al., 2010). Improving individual tree vigor by removing competing trees may not always increase HEFNP’s ability to survive MPB attacks, especially in extreme outbreaks (Carroll et al., 2003), and it sometimes may make trees more susceptible to MPB attack (Baker and Six, 2001). Managers can protect valuable WPBR-resistant trees from MPB using either pesticides or pheromone treatments (Kegley and Gibson, 2004; Bentz et al., 2005) at limited spatial scales. Carbaryl is probably the most effective pesticide treatment, especially when beetles are below outbreak levels; it sometimes provides over 90 percent protection for two years. The anti-aggregation pheromone Verbenone is currently being used to protect whitebark and limber pine trees during beetle epidemics (Kegley and Gibson, 2004; Bentz et al., 2005; Randall, 2008; Schoettle et al., 2019a).

Pruning rust-infected branches from HEFNP pines may delay the spread of WPBR in the early stages of infection (Schoettle et al., 2019a), but this also delays the selection against susceptible pines and therefore delays the selection for rust resistance (Schoettle and Sniezko, 2007). Sanitation pruning of infected limbs may be effective for extending survival of high value trees but is not suitable for application on a landscape scale (Dooling, 1974; Hungerford et al., 1982; Hunt, 1998; Jacobi et al., 2016). Use of fungicides to battle WPBR is costly, ineffective, and impractical because of the sheer number of trees that need protection and the collateral damage to other native organisms. The best approach for reducing WPBR hazard over time is to promote natural regeneration to enhance genetic diversity while increasing rust-resistance, especially where rust resistance is known to occur, plant blister rust-resistant seedlings in appropriate sites to build population resilience, and to diversify age class structures order to maintain seed production and ecosystem function over time, and provide large populations for selection for rust resistance (Schoettle and Sniezko, 2007).

8. Discussion

There are two important factors that will govern successes of restoring HEFNP forests: (1) resources to conduct restoration efforts, and (2) commitment of natural resource agencies to restore declining HFNPF communities for many human generations to come. Resources can be in the form of funding, personnel, collaborative planning efforts, or public support. The efficacy of treatments to restore HEFNPs will always depend on the abilities of managers to account for highly localized topographic and biotic factors in the treatment design to anticipate future changes in climate (Keane et al., 2017a). Even the most carefully crafted treatments are rarely appropriate across all whitebark pine regions because of the uncertain future climate, let alone all HEFNP forests, and therefore each action will need to be carefully modified to account for local conditions and future climate. Because HEFNP ecosystems have little value as timber, it is doubtful that any restoration treatment or activity will generate appreciable incomes, so success of any restoration strategy depends on effective and strategic allocation of limited government and non-profit-generated funding and resources across multiple spatial scales. Government agencies should consider a long-term commitment to HEFNP restoration because it takes a long time for high elevation ecosystems to respond to the effects of most restoration treatments so it may take decades to evaluate treatment success or failure (Agee and Smith, 1984). Moreover, climate change may exacerbate adverse fire, WPBR, and mountain pine beetle impacts for many years so it is important that agencies commit to long-term restoration strategies to prevent local extirpation later.

Restoring high elevation pine ecosystems is further complicated by political and administrative barriers (Salwasser and Huff, 2001). Because most HEFNP forests are on public lands that have little commercial potential, agency funding and support may wax and wane over time as governmental priorities shift. Social acceptance of management in these high elevation ecosystems may be less of an obstacle. Initial surveys document that people value HEFNP forests and may support management to sustain their existence for future generations (Meldrum et al., 2011; Naughton et al., 2018). Integration of public preferences with economic and ecological trade-offs will provide further insights into potential optimal management strategies (Bond et al., 2011). For example, the US Forest Service policy of disallowing planting rust-resistant pine seedlings in Wilderness Areas may stifle restoration efficacy across many high elevation ecosystems within designated Wilderness Areas (Keane, 2000; Keane et al., 2012).

Most barriers can be overcome if comprehensive strategies can (1) demonstrate the value of these iconic ecosystems, (2) provide a viable process for restoring and sustaining these forests, and (3) describe the dire consequences if these species are lost from the high elevation landscape through inaction. The crisis for whitebark pine has brought increased awareness to the severity of the combined threats of WPBR, MBP, and climate change to the other HEFNPs that have yet to be severely impacted. A shift is beginning toward managing these still healthy ecosystems for resilience against these novel stressors to position them on a different trajectory from that followed by whitebark pine (Schoettle et al., 2019a). HEFNP restoration will take centuries and we must commit to a strategy for the "long haul". While it may seem that restoring high elevation pine forests is a monumental task with questionable outcomes, we believe that sustaining and restoring these forests is both achievable and essential for the long-term sustainability of high mountain landscapes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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