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Regeneration for resilience framework to support regeneration decisions for species with populations at risk of extirpation by white pine blister rust

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Abstract

Natural forests are increasingly invaded by nonnative pests and pathogens that threaten host species with population extirpation and cascading ecological impacts. The regeneration for resilience (R4R) framework provides a decision structure to prioritize limited resources and utilize artificial and natural regeneration management to offer the best likelihood of success in positioning stands and landscapes to support multi-generational self-sustaining host populations in the presence of the nonnative invader by (1) increasing host population size to offset invader-caused mortality, (2) increasing the frequency of genetic resistance traits in host populations in habitats that enable their expression and durability to retard future mortality and facilitate population sustainability and recovery, and (3) maintain host genetic diversity, adaptive capacity, and population connectivity. This application is designed for conditions where the nonnative invader is expected to be a persistent threat, the host species naturally has some genetic resistance to the invasive species, and the forest host populations are integral to support valued ecosystem processes and services. The R4R framework has been developed for application in high elevation five-needle pine ecosystems of North America impacted and threatened by the nonnative pathogen *Cronartium ribicola* that causes the lethal disease white pine blister rust (WPBR). Several examples using the R4R framework to integrate information on current forest condition, WPBR risk or hazard, genetic resistance to WPBR, and host population dynamics and silvics to prioritize areas and design interventions are discussed. Effective management of forest regeneration dynamics can increase forest resilience and adaptive capacity to mitigate impacts of invasive species.

Keywords *Pinus albicaulis* · *Pinus flexilis* · *Pinus aristata* · *Pinus strobiformis* · Five-needle pine · White pine blister rust · Genetic resistance · Natural regeneration · Artificial regeneration · Invasive species

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Introduction

Insects and diseases shape forest composition, structure, and function. Native pests (insects) and pathogens in forests that have coevolved with host species are often in relative balance and a natural part of the disturbance regimes that contribute to forest dynamics. However many factors can create imbalance in these co-evolved systems including forestry practices and climate events resulting in epidemics of unusual scale or impact (Dale et al. 2001; Bentz et al. 2010; Millar and Stephenson 2015). Introduction of nonnative pests and pathogens can cause unprecedented disturbance and lead to extirpation of local host populations or near extinction of a species with cascading ecological impacts (e.g. Boyd et al. 2013). The speed that these threats can impact forest ecosystems requires rapid adaptive approaches to reduce vulnerabilities and mitigate impacts at relevant temporal and spatial scales (Jacobs et al. 2015; Stanturf 2015). The common management responses to an invasive species are prevention of introduction, detection of the invasive species, control and management of the invasive species, and restoration and rehabilitation of the impacted host species, forests, and ecosystems (see Lovett et al. 2016). The first elements often focus on invasive species eradiation or limiting population size with biocontrol agents or chemical applications. Finally, if eradiation and control fail and the invasive species is expected to be a permanent resident and persistent threat, restoration activities begin for valued resources. While these activities and foci are often considered a linear sequence, they don’t have to be. Research to provide the science foundation for restoration and management to increase the resilience of the host forests to invasive species can begin at any time upon detection of the invasive species threat.

Host defense can be lacking or at low levels to nonnative pests and pathogens due to the lack of evolutionary history shared by the organisms giving the advantage to the invasive species. Host genetic resistance is “…the ability of an individual host tree to use genetically encoded mechanisms to defend against or withstand attack by an invading organism, with an associated and measurable increase in fitness compared with hosts who do not employ these mechanisms…” (Telford et al. 2015). In the case of American chestnut (*Castanea dentata*) challenged by the accidental introduction of the chestnut blight fungus (*Cryphonectria parasitica*) in the late 1800s, 3.5 million American chestnut trees were killed over the course of 50 years (Jacobs et al. 2013). Genetic resistance to the blight is not present at detectable frequencies within American chestnut. Hybridization of American with Chinese chestnut (*Castanea mollissima*) trees, which carry genes conferring resistance to the fungus, has produced hybrid backcross material with improved blight resistance (Hebard 2005), yet deployment still has biological and social challenges (Jacobs et al. 2013; Dumroese et al. 2015; Holtz et al. 2017). Hosts that lack genetic resistance to the invasive species cannot utilize natural regeneration approaches to fostering genetic resistance in natural populations and will require artificial regeneration to introduce genetic resistance on the landscape (Jacobs et al. 2013; Steiner et al. 2017). Fortunately, genetic resistance to some nonnative pests and pathogens is present naturally within some forest species. Although the frequency of resistance can be very low, it provides the genetic variation on the landscape on which natural selection can operate (Schoettle and Sniezko 2007; Woodcock et al. 2017) and for use in tree improvement programs to develop improved seed (Sniezko and Koch 2017). Tree improvement programs have historically been established for tree species of commercial interest using plantation forestry practices. These breeding programs take considerable time and investment, especially for long-lived tree species, making timely development and deployment of genetically improved trees in natural forests for conservation challenging (Woodcock et al. 2017). These programs offer technologies for identifying genetic resistance which can be very useful even if the investment in a breeding program is unlikely for a non-commercial host. Decision and deployment strategies for increasing the frequency of genetic resistance in natural forests using regeneration management are not well developed.

Land management is increasingly focusing on sustaining ecosystem processes and services and building resistance and resilience in natural forests (Alexander 2010; DeRose and Long 2014; Seidl 2014; Dumroese et al. 2015; Seidl et al. 2016). We define forest resistance (not to be confused with "genetic resistance" to an invasive species which can contribute to both forest resistance and resilience) as forests that can withstand rapid change and maintain relatively unchanged conditions; forest resilience is defined as those forests that may change following disturbance but ultimately return to the original condition [Millar et al. 2007, as applied to interventions in Nagel et al. (2017)]. Forest resilience is characterized as the influence of disturbance on structure and composition (DeRose and Long 2014) and is therefore a function of the specific invasive species disturbance. Resilience can therefore be assessed using factors that influence adaptive capacity and demographic thresholds for host populations challenged by specific invasive species (Baho et al. 2017). Transition strategies (Nagel et al. 2017), that would shift the forest to non-host species, provide an additional management option to sustain forested landscapes threatened by both invasive species and climate change.

Tree–invasive species interactions in natural forests necessitate consideration of large landscape scales and the often patchy distribution of both host and invasive species populations. This meta-population perspective also highlights the potential for independent disease processes to occur in individual populations (Thrall et al. 2001). The complexity of natural ecosystems makes mitigating disease impacts more difficult than in managed forests (Oliva et al. 2013). Sustaining natural forest resilience in the presence of an invasive species requires maintenance of the host population's recovery and adaptive capacity on a landscape spatial and multi-generational temporal scale.

Regeneration management, whether it be planting genetically resistant seedling stock, maintaining and augmenting the size of host species populations, or generating a diverse mosaic of stand ages across a landscape, is a key component of forest resilience that can foster forest adaptation and mitigate impacts caused by invasive species that have failed to be eradicated. This component of an overall management approach for invasive pests and pathogens in natural, traditionally unmanaged, forests can incorporate a long-term demographic and evolutionary perspective (Schoettle et al. 2012b; Carlson et al. 2014; Whiteley et al. 2015; Ennos 2015) to complement other activities such as invasive species eradication or sanitation efforts (e.g. Schwandt et al. 2010; Jacobs et al. 2013), and host genetic conservation programs (e.g. Potter et al. 2017; Schoettle and Coop 2017). Deploying seedlings with genetic resistance traits is only one of several interventions that will affect the overall outcome of a host-invasive species interaction in natural forests (Waring and O'Hara 2005; Schoettle and Sniezko 2007; Field et al. 2012; Jacobs et al. 2013; Woodcock et al. 2017). Interventions to support natural regeneration and connectivity to promote natural selection and gene flow of genetic resistance can be combined with targeted plantings of genetically resistant trees (Schoettle and Sniezko 2007; Landguth et al. 2017; Cavers and Cottrell 2014). Positioning forests for accelerated adaptation to new conditions while sustaining viable population sizes will promote resilience (Keane and Schoettle 2011). Therefore it is the adaptive capacity and trajectory of the host population (and any species that depend on it) that need to be the focus of regeneration interventions in natural forests.

These interventions entail integrating genetic resistance information into an ecological context to prioritize and inform regeneration interventions to sustain healthy landscapes.

In this paper we present the regeneration for resilience (R4R) decision framework to guide when, where, and how to utilize regeneration to increase forest resistance and resilience to invasive nonnative pests and pathogens in natural forests. The R4R decision framework has been developed for the North American high elevation five-needle pine populations to mitigate impacts by *Cronartium ribicola*, the nonnative pathogen that causes the lethal disease white pine blister rust (WPBR). This application is designed for conditions where (1) eradication of the nonnative invader has failed, (2) the forest host populations are integral to support valued ecosystems processes and services, and (3) the host species naturally has some genetic resistance to the invasive species. The goal of the R4R framework is to guide regeneration decisions to offer the best likelihood of success in positioning stands and landscapes to support self-sustaining host populations over multiple generations in the presence of the nonnative invader by (1) increasing host population size to offset invader-caused mortality, (2) increasing the frequency of genetic resistance traits in the host population in habitats that enable their expression and durability to retard future mortality and facilitate population sustainability and recovery, and (3) maintain host genetic diversity, adaptive capacity, and population connectivity.

We present (1) a brief review of the WPBR-pine pathosystem to help define the features that will confer resilience in host populations to WPBR, (2) the science-based inputs needed to guide decisions, (3) demonstrations of how those criteria can be integrated using R4R decision trees to prioritize when, where, and how to utilize regeneration management for the greatest likelihood of sustaining five-needle pine populations, and (4) specific examples of its application to Rocky Mountain bristlecone pine (*P. aristata*) and limber pine (*P. flexilis*) in the Southern Rocky Mountains, whitebark pine (*P. albicaulis*) in western North America, and southwestern white pine (*P. strobiformis*) in the U.S. Southwest. The R4R framework provides guidance for prioritizing intervention actions based on biological, genetic, and ecological considerations. The recommended actions from this framework need to be integrated and reconciled with social, administrative, and institutional constraints on a case-by-case basis by the land manager.

High-elevation five-needle pine—white pine blister rust situation

Cronartium ribicola, the fungal pathogen that causes the lethal disease WPBR on five-needle pines, was accidently introduced into North America over a century ago and eradication efforts failed (see Geils et al. 2010). Upon introduction to western North America, the pathogen spread rapidly and resulted in the collapse of the western white pine (*Pinus monticola*) forest industry (Neuenschwander et al. 1999), the endangerment of whitebark pine and limber pine in northern portions of their distributions, as well as impacts to other five-needle pines (Tomback and Achuff 2010). The U.S. Fish and Wildlife Service (2011, 2015) determined that whitebark pine warranted Endangered Species status protection under the Endangered Species Act, and Canada designated whitebark pine as endangered in 2012 under the Species at Risk Act (Government of Canada 2012). Assessment of limber pine by the Committee on the Status of Endangered Wildlife in Canada determined it to be endangered in Canada, and the species was recommended for legal listing in November 2014 (Government of Canada 2014); the formal proposal for the national listing as endangered is pending. Both pines have been listed as endangered in Alberta for several years (Government of Alberta 2014). Limber pine in Wyoming, where it is more common than in any other state, is on the Bureau of Land Management's Special Status Species list (Bureau of Land Management Wyoming 2013) and several of the five-needle pines are designated as species of management concern in National Parks (Schoettle et al. 2013). The pathogen is now a permanent resident and continues to spread putting populations of all of the North American five-needle pines at risk. As *C. ribicola* continues to spread, interest in implementing interventions in the threatened but not yet heavily impacted five-needle pine populations has increased in attempt to shift these populations from following the same trajectory as those that have been impacted (Schoettle and Sniezko 2007). Opportunities for conservation of healthy stands in the impacted areas still exist as disease pressure is not uniform resulting in some populations escaping heavy infection (Smith et al. 2013a, b; Cleaver et al. 2015).

Cronartium ribicola has a complex life cycle that requires two hosts, five-needle pines and *Ribes* spp. or other alternate hosts (see Geils et al. 2010). Consequently, there is no tree-to-tree spread of *C. ribicola*. Five-needle pines can only be infected by basidiospores produced on the alternate host species. Infections on the pines are perennial, and the fungus continues to colonize tissues spreading from the point of infection in the needles to the main stem of the tree. The disease causes cankers to form on branches and the main bole; as a canker enlarges over time it can girdle and kill branches, and once in the main stem can cause top-kill and ultimately tree death. Infections on the alternate hosts must be initiated each spring from aeciospores produced on the pine host and fungal colonization is restricted to the leaves which are naturally shed in autumn from these deciduous plants. The specific infective spore types are dispersed between the hosts through the air and require specific humidity and temperatures conditions to survive and germinate on their respective hosts; long distance transport of aeciospores is also possible (see Geils et al. 2010). In areas conducive to spore production, dispersal, and host infection, pines accumulate infections over time sometimes having 10–100 s of cankers. These areas are considered high hazard and disease-caused mortality can be rapid and high. Low hazard areas are those that have the conditions less conducive to infection, and the opportunity for infection may occur infrequently.

WPBR kills five-needle pines of all ages. The fungus can kill small trees within a few years of infection due to the short distance from the infection site in the needles to the main stem while it may take 10 or more years to kill a large tree. Branch girdling and death can severely reduce cone production and vigor well before the disease kills the tree. As a result, WPBR directly reduces the regeneration capacity of five-needle pines (McKinney et al. 2009; Tomback and Achuff 2010) and forest recovery following other stand-replacing disturbances such as fire or bark beetle epidemics. Genetic resistance to *C. ribicola* exists in all of the nine North American five-needle species (King et al. 2010). Its expression and efficacy in retarding fungal colonization and prolonging host survival are functions of resistance mechanism, *C. ribicola* race, and disease pressure. Even resistance that is conferred by multiple genes can be overwhelmed by high spore doses (e.g. Jacobi et al. 2018); hence under high hazard conditions, genetic resistance to *C. ribicola* can be less effective.

Tree improvement programs to harness genetic resistance to WPBR in the commercial timber species (*Pinus monticola*, western white pine; *P. lambertiana*, sugar pine; and *P. strobus*, eastern white pine) have been underway since the mid-1900s (King et al. 2010). Technologies to effectively artificially inoculate seedling families have been developed to screen progeny for resistance and infer heritable resistance in the parent trees (Sniezko 2006). These methods have been adapted for application to the high elevation five needle-pine species (see Sniezko et al. 2011). Progeny testing can only assess the resistance status of reproductive trees. However, molecular markers for genetic resistance to WPBR are also under development which will enable resistance to be detected with needle tissue collected from trees of any age (e.g. Richardson et al. 2010; Liu et al. 2016).

The high elevation five-needle pines are slow growing, long-lived trees (Tomback and Achuff 2010). With the possible exception of southwestern white pine, most of the species in this group are slow to reach reproductive maturity and to recolonize disturbed sites (Coop and Schoettle 2009). The species tend to be tolerant of environment stresses and can occupy harsh sites unsuitable for other subalpine species (Schoettle 2004). Because their long generation time reduces their natural capacity for rapid adaptation to novel stresses such as *C. ribicola*, management to increase the frequency of heritable genetic resistance is an accepted restoration approach (e.g. Schoettle and Sniezko 2007; Aubry et al. 2008; Keane et al. 2012). Strategies to deploy resistant stock and foster selection for genetic resistance in natural forests however are not well defined—hence we propose the R4R framework to help guide regeneration management.

Criteria inputs for the regeneration for resilience (R4R) framework

Key information needs emerge from understanding that the sustainability of five-needle pine populations in natural forests is a function of numerous interacting factors determining and affecting the biology of *C. ribicola*, the five-needle pines, and the disease interaction. The R4R framework for WPBR integrates science-based information on (1) current forest health condition, (2) genetic resistance to WPBR, (3) WPBR risk and hazard, and (4) host population dynamics to prioritize when and where interventions will have the greatest likelihood of success in sustaining high elevation forests in the presence of WPBR. A description of each criterion and how the information can be gathered is presented below.

Current forest health condition

First and foremost the condition of the natural forest will affect its response to both invasion and intervention. Before or at the initial stages of invasion by *C. ribicola*, when the incidence and intensity of infestation is nil or low, the forest processes are still functioning and ecosystem services are still provided. Monitoring forest health condition can effectively characterize the extent and intensity of the disease outbreak and other disturbance factors. Disease detection can be difficult in the early phases; timing monitoring efforts during the time of year when the pathogen is fruiting increases reliable detection. Genetic tools to identify species from non-fruiting fungal tissue will further accelerate infestation confirmation from otherwise limited signs of disease; this will be especially useful for species such as *C. ribicola* that cannot be cultured in the lab. Inclusion of metrics in monitoring protocols that also characterize key ecological processes and host population dynamics (e.g. competing vegetation, seed production, age class distribution, seedling density, species silvics) adds further information on the condition of the forest and its potential to respond to management. This can be particularly important for forest types that have been historically understudied such as the high elevation five-needle pines and other non-timber species where basic ecological relationships may be poorly understood.

Repeated monitoring of the same plots or areas over time provides information on the dynamics of the nonnative pathogen spread and disease intensification as well as baseline ecological information on changes in forest structure and function; these data are just becoming available for the high elevation five-needle pine species impacted by WPBR and other disturbances (e.g. Looney and Waring 2012; Smith et al. 2013a, b; Cleaver et al. 2015). These data resources are essential to calculate accurate parameter estimates for population and epidemiology modeling (Field et al. 2012; Jacobi et al. in press). Estimates of annual infection probability and time since invasion can also help distinguish if impacts are due to the duration of *C. ribicola* exposure (e.g. accumulated impacts over time), ecological interactions (e.g. changes in disease pressure), or virulence of the pathogen race (e.g. its lethality). Monitoring WPBR incidence and *C. ribicola* virulence over time is also important as pathogen evolution may affect the durability and therefore expression of genetic resistance to the pathogen in the host (Kinloch et al. 2004; Xhaard et al. 2011; Cleaver et al. 2017a).

Current forest condition will distinguish areas suitable for restoration intervention options and those that offer proactive opportunities to prepare the landscape for pathogen invasion or disease intensification before impacts develop (Fig. 1). The most impacted areas may have limited response to treatment and therefore have low restoration potential (e.g. Keane and Parsons 2010). To utilize natural processes to assist the effectiveness of interventions to augment forest resilience, the extent of ecosystem impairment can be an important decision point when prioritizing when, where, and how to intervene.

Genetic resistance to the nonnative pathogen

The presence of heritable genetic resistance to nonnative pathogens in the host and its frequency in the natural forest is critical information for projecting population trajectories and making regeneration intervention decisions. Genetic resistance to WPBR in the pines influences the effect of infection on tree growth, seed production, and survival, and the frequency of resistance traits in the stand influences the trajectory of the population in the presence of the pathogen (Field et al. 2012; Maloney et al. 2011; Landguth et al. 2017). Genetic resistance traits can be qualitative or quantitative and both are present, in different degrees, in the five-needle pines (Sniezko 2006). Qualitative genetic resistance, also known as Major Gene Resistance (MGR) or R gene resistance, is inherited by a single dominant allele and confers immunity to the infected host. Due to its simple inheritance, a mutation in the associated allele of the pathogen can overcome qualitative genetic resistance in the host and permits the disease to develop. Quantitative genetic resistance is thought

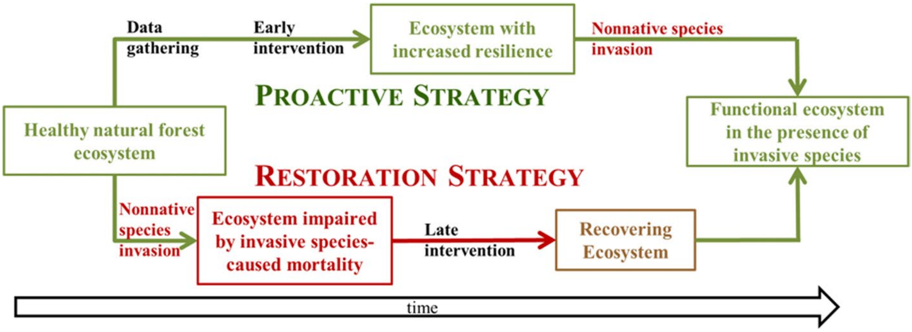

Fig. 1 A schematic of pathways for facilitating sustainable natural forest ecosystems in the presence of a nonnative invasive species. Adapted from Schoettle et al. (2012b)

to be a result of small contributions of multiple genes and consequently is less likely to become overcome by the pathogen and is therefore considered more durable than qualitative genetic resistance. However expression of quantitative resistance traits can be reduced at high inoculum doses (Jacobi et al. 2018). Quantitative genetic resistance slows, but generally does not preclude, pathogen colonization prolonging host survival with the disease. Expression of some mechanisms of resistance can also depend on the maturity of the host (ontogenetic), morphological barriers to infection (escape), or endophyte community interactions (e.g. Woo et al. 2001; Ganley et al. 2008). Because these mechanisms are often not expressed in all tree age classes and may therefore may not contribute to the multigenerational trajectory of the host, we will focus our consideration of genetic resistance mechanisms to those that are qualitative and quantitative as discussed above.

Surveys, trials with and without experimental controlled exposure to the invasive species, and molecular tools, if available, can be used to identify trees with genetic resistance to WPBR and other nonnative pests and pathogens (Woodcock et al. 2017; Sniezko and Koch 2017; Liu et al. 2016). Sampling surviving trees in stands where infestation is high and selection has already culled susceptible trees is an efficient means to identify putatively resistant individuals in the field. Testing these trees through progeny screening under artificial inoculation protocols can assess if the differential disease expression in the field is a result of heritable genetic resistance, ontogenetic resistance, or escape. Upon identifying genetically resistant sources, the trees can serve as seed sources for artificial regeneration or be used in breeding programs. Experimental screening approaches can be refined and further used to characterize genetic resistance types, heritability, and durability (Sniezko 2006). This knowledge and technology facilitates testing for the genetic resistance traits in other parts of the host distribution, estimating frequencies of genetic resistance, and identifying field seed trees with genetic resistance in naïve, not yet invaded, populations (e.g. Schoettle et al. 2014, 2018a).

The R4R framework uses the current frequency of genetic resistance in populations and the availability of planting stock enriched with resistant genotypes in making intervention decisions. Genetic resistance to WPBR and other nonnative pathogens is generally not distributed uniformly across the species (Laine et al. 2011; Kinloch 1992; Schoettle et al. 2014). Information on genetic resistance mechanisms and their frequencies helps identify the populations where selection for genetic resistance can occur in the presence of the pathogen. Early identification of the frequency of genetic resistance and genetic resistance types offers insight into potential genetic resistance durability which should be considered in management planning. For example, healthy populations with higher baseline frequencies will be high priority for managers to maintain in the landscape, providing leverage to fund treatments and protection (e.g. decreasing tree and stand susceptibility to disturbances such as fire, insects and drought through density reduction, or designation as a resource to protect from wildfire).

Disease risk or hazard

Geographic variation in forest health condition, site factors, and site climate can also be used to identify and predict conditions conducive to invasion and disease intensification and therefore management treatment efficacy. Each organism has its own mode of dispersal and preferred environmental conditions set by its life history and tolerances; how the favorable conditions for the pathogen overlap with the distribution of the host determines the areas at risk for disease, and the likelihood and severity of infestation determines disease hazard (Zeglen et al. 2010). The modeling efforts that generate hazard maps for areas already invaded and risk maps for areas threatened but not yet invaded provide managers with practical tools to reduce uncertainty about the expected distribution of the disease (e.g. Meentemeyer et al. 2004; Kearns et al. 2014). Research suggests that the conditional probabilities of *C. ribicola* infection play an important role in disease impacts in the decision of which threatened stand should be treated if a choice is available to the manager (Field et al. 2012; Bond et al. 2011). Risk and hazard maps also offer guidance to prioritize and align types of intervention based on projected disease pressure. In areas of very high risk or hazard, the probability of successfully sustaining the host can be greatly diminished due to disease pressure overwhelming genetic resistance mechanisms (e.g. King et al. 2010; Schwandt et al. 2010). Risk and hazard analyses will need to be updated periodically with current forest health conditions and climate data as climate changes.

While areas of high disease impact may attract attention and therefore appear to be a restoration priority, they may not offer the most efficient use of resources for sustaining the larger host population and ecosystem type. Restoration of these areas can require planting to completely rebuild the host population in the decimated forest. However, high mortality of those seedlings can still be expected under such high disease pressure. The R4R framework proposes a triaged approach that prioritizes lower risk or hazard areas for intervention as they provide a greater likelihood that genetic resistance will be durable and contribute to slowing mortality and sustaining the host species. Keeping those forests that are still functioning from severe decline via pre-emptive interventions to facilitate adaptation in the presence of the disease and climate change will help sustain host populations and ecosystem services in at least part of the pine's range. Prioritizing areas of lower hazard for interventions may lead to extirpation of the pine host in some high hazard areas; their loss may be unavoidable, even with intervention, and may be the cost of preventing species-wide extinction with limited time and resources.

Host population dynamics and ecological context

Life history traits (i.e. species silvics), such as time to reproductive maturity, regeneration capacity, fire and shade tolerance, and lifespan affect survival during and recovery from disturbance and, in combination with genetic diversity and gene flow, the rate of adaptation to new conditions across the landscape (Aitken et al. 2008; Field et al. 2012). Minimum demographic factors that support the regeneration cycle (seed dispersal, seedling establishment, overstory recruitment, and reproduction) will set the threshold for population sustainability and when not met, population decline. Regeneration capacity varies among habitats and environmental conditions (e.g. Coop and Schoettle 2009; Gärtner et al. 2014). For the high elevation five-needle pines, overstory stand density and regeneration capacity, as well as the current frequency of genetic disease resistance, are critical forest attributes that contribute to seedling recruitment and genetic combinations on which natural selection can act (Field et al. 2012; Schoettle et al. 2012b).

Understanding patterns of local adaptation for other traits for the development of seed zones is essential if local seed sources lack the desired genetic resistance traits and appropriate distant seed sources must be identified and used. If targeted supplemental planting of trees resistant to WPBR is warranted to introduce genetic resistance into a population, it is best, though not always possible, to identify genetically resistant sources within the same seed or climate zone to reduce the risk of failure due to maladaptation (Mahalovich and Dickerson 2004). This is especially important when seed sources for outplanting will be collected from field grown trees which is most often the case for species that lack breeding programs and seed orchards. Trait variation within a species is typical and common garden studies, where individuals from different environments are grown together in a single or multiple common environments, are a powerful tool to provide an experimental means to quantify the genetic contribution to observed population differences (Kawecki and Ebert 2004). Seed transfer guidelines can be based on geographic variation in traits yet use of climate-based seed source selection is becoming more common for climate adaptation management (McKinney et al. 2009; Bower et al. 2014; Dumroese et al. 2015). Common garden studies can also be used to refine seed zones defined prior to rapid climate change and pathogen invasion. For example, provisional seed zones first published in 1973 for southwestern white pine (Schubert and Pitcher 1973) may be broadened to accommodate low frequencies of genetic resistance to WPBR (Goodrich et al. 2016). Alternatively, common garden studies suggest that movement of limber pine seedlings with genetic resistance to WPBR within the broad Southern Rocky Mountain seed zone (Mahalovich 2006) may need to be narrowed to reduce the risk of maladaptation (Borgman et al. 2015). Every effort should be made to use the best available science to identify seed sources that have genetic resistance to WPBR and are adapted to current and future conditions at the planting site to hedge against failure in future climates.

Demonstrations of the R4R framework—prioritizing when, where, and how to intervene

The R4R framework provides decision trees to prioritize when, where, and how to intervene with regeneration management for maximum ecological benefit. Prerequisites for the application of the framework are that (1) the nonnative pathogen, such as *C. ribicola*, cannot be eradicated and is expected to be a persistent threat and (2) genetic resistance to the invasive species is present in the host species. The R4R framework is not intended to replace or preclude other control measures which can be implemented concurrently with regeneration management. In the case of WPBR, there is some evidence that highly selected seed sources may also have lower genetic diversity (e.g. Kim et al. 2003) making them less desirable for extensive use for conservation purposes in natural forests (Woodcock et al. 2017). Silvicultural interventions to stimulate natural regeneration are the most natural treatments and, when appropriate and feasible, are a desirable intervention type (Waring and O'Hara 2005; Schoettle and Sniezko 2007).

Timing the interventions before or early in the *C. ribicola* invasion process will minimize the length of time the recovery capacity (i.e. resilience) of the population is compromised by high mortality of reproductive trees. To warrant the expense of an intervention planting to increase genetic resistance in the population it is imperative to test and know the frequency of the genetic resistance traits in the seedling source material to ensure objectives are being met; this information will also allow planting densities to be adjusted in anticipation of seedling mortality by WPBR in addition to natural planting losses (Schoettle et al. 2018a; Goodrich et al. 2018). Demonstrations of high rates of host planting success in both experimental and management plantings is also needed to maintain optimism among managers and increase efficiency of funds invested (Waring and Goodrich 2012).

Intervention options

Interventions are specific to the pathogen-host interaction. Here we present those interventions for the WPBR-high elevation five-needle pine pathosystem, including those where the pathogen can infect and kill trees of all ages and for which genetic resistance naturally exists within the host. Intervention actions can include:

1. Stimulate natural regeneration to increase the population size (1) to offset pathogen-caused mortality, and (2) if the population already contained genetic resistance, to increase the genetic combinations on the landscape to accelerate selection for genetic resistance to increase the frequency of genetic resistance in the surviving population (Fig. 2, lower green arrows). Silvicultural approaches to stimulate regeneration will depend on the host species ecology and can include:
    a. Treatments to remove competing tree species to increase seed production and open the stand for natural seedling establishment and eventual overstory recruitment;

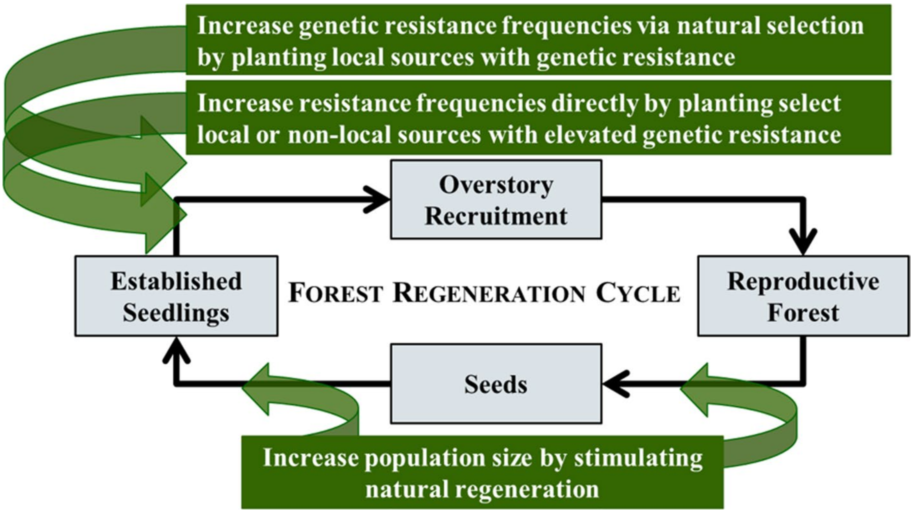

Fig. 2 Flow diagram of the forest regeneration cycle (narrow black arrows) showing intervention options (broad arrows) to increase the population size, genetic resistance to the invasive species, and contribute to host population sustainability. Maintaining all compartments and their connections is essential for multigenerational population persistence and to provide individuals with genetic combinations on which natural selection can act for species adaptation. In a functioning forest, overstory densities in the reproductive forest need to be sufficient to support seed production and natural regeneration yet structured to maintain vigor of the established seedlings to enable recruitment into the overstory in a reasonable time period. On a landscape basis however, natural regeneration or planting can be accomplished outside the forest in nearby canopy openings to develop a mosaic of areas of different age classes. The lower arrows depict an intervention to stimulate natural regeneration in a healthy host population that contained genetic resistance to increase the number of individuals and the genetic combinations to accelerate natural selection for genetic resistance and increase the frequency of genetic resistance in the population in the presence of the invader. The upper arrows depict interventions that can be implemented in forests where the regeneration cycle is intact or impaired to increase or restore population size and introduce seedling with genetic resistance into the population. Adapted from Schoettle et al. (2009)

   b. Seed bed preparation near healthy seed sources, such as prescribed fire or mechanical treatment, to favor natural seedling establishment of the host.

2. Planting seedlings or seed (Fig. 2, upper green arrows) by under planting within a stand or in canopy openings using seed from:
   a. The local population that contains durable genetic resistance to the nonnative pathogen of known frequency to retain genetic diversity of the target population and accelerate selection for genetic resistance to increase the frequency of genetic resistance in the young cohort and population;
   b. Select seed trees in the local population that are significantly healthier than the neighbor trees with respect to pathogen-caused impact (i.e. putatively resistant seed trees) and preferably have been tested and therefore the seed lot has a known frequency of genetic resistance. If the putatively resistant trees haven't been tested, testing the bulked seed lot to estimate the frequency of genetic resistance in the lot is recommended so appropriate planting densities can be calculated. If genetic resistance testing is not possible, estimates of overstory recruitment rates based on understory infection levels can be used to calculate regeneration densities needed for sustainability (Goodrich et al. 2018).

3. Direct supplementation of genetic resistance to the population by planting seedlings or direct seeding with seed sources from select field trees from other populations (Fig. 2, upper green arrows). Seeds can be collected from trees:
   a. Within the same seed zone that have a known frequency of genetic resistance (via testing) to augment the existing natural forest;
   b. Outside of traditional seed zone boundaries but within recommended planting guidelines for the area, based on climate matching strategies between seed source and planting locations (e.g. McKenney et al. 2009).

Application scenarios

The following scenarios will demonstrate how this framework can be applied to natural forests of five-needle pines challenged and threatened by WPBR. The framework steps through the decision-making factors outlined above to prioritize areas for management and proposes intervention(s) to increase host population resilience in that setting (Figs. 3, 4). The stage of invasion and impacts to the reproductive capacity of the host are the first considerations. If the area is heavily impacted and extensive WPBR-caused mortality has reduced its regeneration capacity, only restoration options are available (Figs. 1, 3). If the area is also high hazard, the area will have the lowest priority for intervention due to the low probability of restoration success resulting from high mortality of both susceptible and resistant genotypes. In areas of moderate hazard, forest regeneration surveys can ascertain if seedling establishment is low or absent in otherwise suitable habitats, and therefore the population has likely fallen below the demographic threshold to support natural regeneration. If the threshold has been passed due to WPBR impacts alone or in combination with other disturbances, interventions to stimulate natural regeneration from the compromised seed source will not be effective (e.g. Keane and Parsons 2010; Maher et al. 2018) even if those few remaining overstory trees have genetic resistance to WPBR. Therefore the only

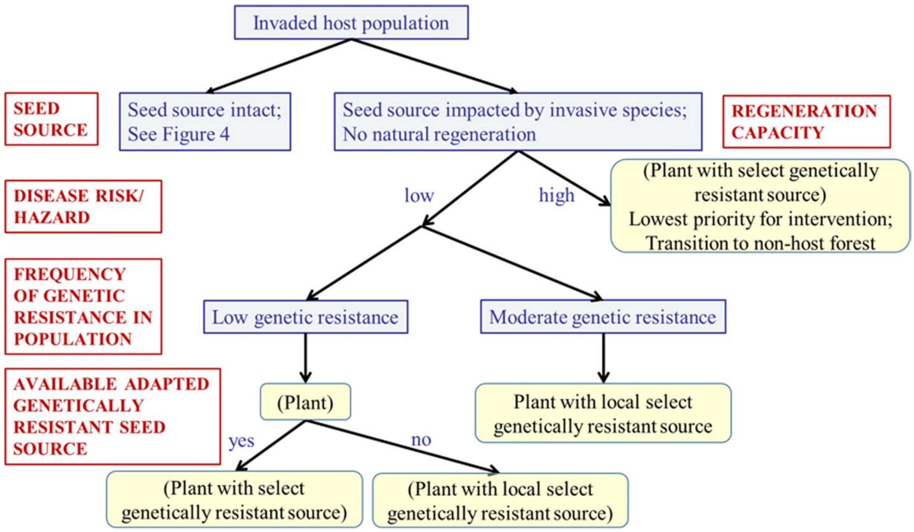

Fig. 3 A demonstration of the regeneration for resilience (R4R) decision framework for a natural forest that is currently invaded by *C. ribicola*. The diagram steps through the decision-making factors (unconnected boxes with capitalized text) to prioritize conditions suitable for intervention and proposes interventions (rounded rectangular boxes) to increase host population resilience in that setting. Those interventions with text in parentheses have a lower probability of contributing to the multi-generational sustainability of the host population and are therefore a lower priority for implementation

feasible intervention is to supplement the small surviving population with seed or seedlings of known genetic resistance frequency to increase the population size (Fig. 3). If durable genetic resistance is present in the surviving population, increase the population size by planting the opened stand with seed from the greater area. If the standing genetic resistance in the surviving population of seed trees is low, the site can be planted with a resistant seed source from another area but would be lower priority for intervention (Fig. 3).

Prioritizing areas for intervention that are threatened but not yet heavily impacted by WPBR offer opportunities to supplement existing populations before WPBR impacts the regeneration cycle (Fig. 4). Interventions in areas of low WPBR risk and hazard should be prioritized over areas of higher risk and hazard (Schoettle and Sniezko 2007). If genetic resistance already exists in the population, the population size can be increased by stimulating natural regeneration with silvicultural treatments and letting future selection by WPBR increase the proportion of trees with genetic resistance in the surviving population (via mortality of susceptible trees). However if there are other factors that impact the seed source (e.g. large stand replacing fire, native or invasive insect pests or diseases) supplemental planting may be required. If the frequency of genetic resistance is low it can be increased, along with population size, by planting seedlings that carry genetic resistance traits to WPBR. It is critical that the frequency of genetic resistance of the planting stock is known or estimated with site-based data so planting densities can be calculated; note that seed lots that are considered resistant lots can still contain a high proportion of susceptible individuals. Planting seedlings that do not contain heritable genetic resistance is of limited benefit as it will take valuable labor resources and will not contribute to the multi-generational sustainability of the population in the presence of WPBR. Because mortality of susceptible individuals cannot be prevented (nor is that desirable for the future

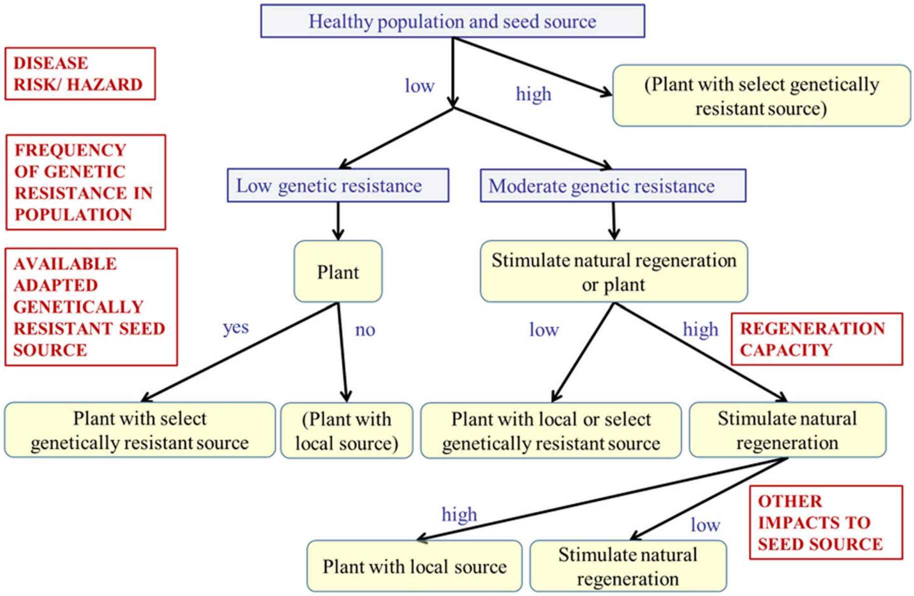

Fig. 4 A demonstration of the regeneration for resilience (R4R) decision framework for a natural forest that is currently healthy or in the early stages of invasion by *C. ribicola*. The diagram steps through the decision-making factors (unconnected boxes with capitalized text) to prioritize conditions suitable for intervention and proposes interventions (rounded rectangular boxes) to increase host population resilience in that setting. Those interventions with text in parentheses have a lower probability of contributing to the multi-generational sustainability of the host population and are therefore a lower priority for implementation

sustainability of the population), increasing the population size for selection to act on may increase the number of survivors enough to sustain the regeneration cycle and support population dynamics. Application of the decision tree to multiple management units within a landscape will ultimately generate a matrix from which gene flow can extend the reach of the treatment over time. It is critical to keep all life stages on the landscape available for selection to manage the distribution of mortality, buffer against other disturbances, and sustain ecosystem services. In addition, WPBR selection against susceptible individuals is rapid in young trees and slower in older, larger trees, therefore managing for a diverse size-class structure across the landscape can diffuse the speed and effect of selection (i.e. mortality) in any one size-class to help maintain overall ecosystem function (Schoettle and Sniezko 2007).

Application to Rocky Mountain bristlecone and limber pine in the Southern Rocky Mountains

The R4R framework can be applied for evidence-based conservation practices for Rocky Mountain bristlecone pine (bristlecone pine hereafter) and limber pine in the Southern Rocky Mountains. Risk analyses suggest that approximately half of the limber pine and bristlecone pine coverage in Colorado regularly has temperature and relative humidity conditions that will support *C. ribicola* infection (Kearns et al. 2014; Howell et al. 2006).

Some of these populations have already been invaded (Burns et al. 2011) while others are at risk of invasion. The highest risk areas are those near streams where suitable alternate host species (*Ribes*) and climatic conditions provide inoculum and the environment to support infection of the nearby pines. The R4R framework designates these areas as low priority for intervention (Fig. 4). Where WPBR-caused mortality is low to moderate, most areas still support natural regeneration (Cleaver et al. 2017b). Guided by neutral and adaptive variation studies, seed and tissue collections have been archived for ex situ conservation, and in situ protection of the populations' seed sources from mountain pine beetle (*Dendroctonus ponderosae*) are ongoing (Schoettle et al. 2011a, 2018a; Schoettle and Coop 2017). Individual tree seed collections are being used for genetic disease resistance testing (see Sniezko et al. 2011; Schoettle et al. 2011b, 2014). Quantitative resistance to WPBR has been found in both species, and early results suggest it is more common in bristlecone than limber pine populations in the southern Rockies (Jacobi et al. 2018; Schoettle et al. 2011b). Qualitative resistance is present in limber pine at unexpectedly high frequencies in the southern Rockies (5% average) and ranges in frequency among populations (0–13.9%) (Schoettle et al. 2014); no qualitative resistance has been found in bristlecone pine (Vogler et al. 2006). Studies indicate that the regeneration capacity of bristlecone and limber pine is variable across environments and disturbances (Coop and Schoettle 2009 and references therein). Artificial regeneration (seedling planting) can be successful for both species (Schoettle et al. 2018b) with particularly good survival for under planted limber pine (Casper et al. 2016).

Integration of this site- and species-specific information within the R4R framework generates priorities and intervention recommendations for each species. Most of the bristlecone pine distribution has not yet been invaded by *C. ribicola*, therefore the recommendations are based on healthy seed sources, moderate frequency of genetic resistance to WPBR, low regeneration capacity, and moderate risk (Fig. 4). Because the natural regeneration response is so slow in this species and moderate genetic resistance is present, we recommend planting local bulked seed lots in low risk habitats to increase the population size to offset future mortality and therefore increase forest resilience. The use of bulked seed lots will maintain genetic diversity and increase the opportunity for rare genotypes to persist on the landscape, which is important since the genetic diversity in this species is naturally low (Schoettle et al. 2012a). To accelerate selection for genetic resistance we recommend considering planting bristlecone pine in moderate hazard zone sites, and we recommend no treatments in high risk areas (i.e. riparian areas). Because forest health surveys suggest that competing species (*Picea* and *Abies* species predominantly) limit cone production in bristlecone pine (Schoettle and Coop 2017), a secondary intervention to remove competing trees may also help increase regeneration and the size of the population over time. This intervention may be particularly effective at augmenting natural regeneration in forests near disturbances that cause canopy openings such as stand-replacing fire, wildlife habitat treatment areas, or insect epidemics. In addition, prioritizing planting and promoting natural regeneration in areas projected to continue to have suitable climatic condition in the future for bristlecone pine is also advised (Malone et al. 2018). Diversifying the age class structure across the landscape will be particularly important for this species as selection by WPBR against susceptible host genotypes can be rapid in young trees and much slower for older trees (Schoettle et al. 2011b). Continued research on genetic resistance to determine mechanisms and diversity is needed to further refine this recommendation and develop select seed sources.

Limber pine in the southern Rockies is in a slightly different situation. In Colorado, most seed sources are still healthy and populations have a relatively high frequency of qualitative genetic resistance, a low frequency of quantitative genetic resistance, and a high regeneration capacity after disturbance. To increase the population size, stimulating natural regeneration and planting can be employed in low WPBR risk areas. Removing competing trees and understory vegetation to open existing stands may increase reproductive output and seedling establishment. Use of prescribed fire and wildland fire management to create forest openings will help diversify the age class structure within the landscape mosaic and as well as reduce vulnerability of the populations to loss by mountain pine beetle. Management can also reduce the probability of accelerating the proliferation of the virulent strain of *C. ribicola*, should it evolve from mutation, which can overcome qualitative resistance in limber pine. We recommend planting bulked seed lots in low WPBR risk areas only to increase population size and retain susceptible pine genotypes on the landscape to reduce the selective pressure for a virulent strain of *C. ribicola* (Schoettle et al. 2018a). Monitoring WPBR for virulence is also recommended (see Cleaver et al. 2017a). Planting seed sources with qualitative genetic resistance in populations lacking it, in low risk or low hazard areas only, may reduce mortality upon invasion in the short run but the genetic resistance may not be durable for long and therefore is not a high priority. When seed sources with quantitative genetic resistance are identified through controlled inoculation progeny testing, we recommend immediately supplementing the natural forests with plantings from seed collected from these select seed trees or populations to increase the frequency of durable genetic resistance in case of a breakdown of the qualitative genetic resistance. The sooner trees with quantitative genetic resistance can be established, the sooner they will mature and become reproductive and sustain the population and support ecosystem function. Rocky Mountain National Park has adopted this strategy to conserve limber pine (Schoettle et al. 2018a).

Application to whitebark pine in western North America

Whitebark pine is a keystone species in high elevation regions of western North America, and its distribution is often included within national parks and wilderness areas. Many whitebark pine populations have declined precipitously in the central and northern Rocky Mountains due to WPBR, bark beetles, and fire suppression (Tomback and Achuff 2010; Keane et al. 2012) while other portions of the distribution are faring better yet are still threatened. As mentioned earlier, whitebark pine is designated as endangered in Canada and considered for such in the USA. Mortality in some areas has reached levels that constrain natural regeneration and the density of cone-producing trees has fallen too low to reliably attract visitation by the species' obligate seed disperser Clark's nutcrackers (*Nucifraga columbiana*) (McKinney et al. 2009). Consequently canopy openings by silvicultural treatment or wildfire in these decimated populations are not consistently recolonized naturally by whitebark pine (Keane and Parsons 2010; Maher et al. 2018). Like the other high elevation five-needle pines, even in areas with sufficient seed production, natural regeneration can be slow (Tomback and Achuff 2010). Methods for direct seeding and seedling planting have been developed (Keane et al. 2012). Quantitative resistance to WPBR is present in whitebark pine and varies geographically; qualitative resistance traits have not been found in this species (Sniezko et al. 2011; Mahalovich and Dickerson 2004).

Existing restoration strategies largely emphasize treatments in heavily impacted populations and have been met with mixed success (Aubry et al. 2008; Keane and Parsons 2010; Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee 2011;

Keane et al. 2012; Alberta Whitebark and Limber Pine Recovery Team 2014b). The R4R framework recommends more treatments in areas of moderate and low WPBR risk and hazard (Fig. 3). In the areas with a compromised seed source, planting with seed lots with a known and confirmed frequency of genetic resistance to WPBR is the best option to rebuild the populations in low to moderate hazard sites. Because of the large geographic area that is impacted, planning for connectivity between remaining and restored populations is important to support future adaptive capacity. Unfortunately, the young planted stands will not contribute to the regeneration capacity or gene flow of genetically resistant genotypes until the seedlings mature and become reproductive, which may take several or more decades. Opportunities in populations that are relatively healthy in the southern and southwestern portions of the species distribution or lower hazard areas of the north, still exist for both artificial and natural regeneration methods to be implemented (e.g. Fig. 4). Greater landscape resilience for whitebark pine, and the wildlife species that depend on it, will be achieve in areas less impacted where a mosaic of newly planted (with known genetic resistance) and naturally regenerated (if the local seed sources have genetic resistance) stands are interspersed within and around existing mature whitebark pine forests. The seedlings will be that much closer to maturity by the time WPBR impacts the remaining forests. Spreading treatments over a diversity of current stand conditions and WPBR hazards will increase the likelihood that some whitebark pine forests will avoid extirpation to sustain the species.

Application to southwestern white pine in the U.S. Southwest

In the case of southwestern white pine (SWWP), most of the range has yet to be invaded by *C. ribicola*, and its range lies primarily south of the US border in Mexico. In the US Southwest, over 30 distinct, disjunct populations are found separated by other forest types, grasslands, deserts and non-forested areas (Conklin et al. 2009). Many of the populations are found in dense mixed conifer forests that are susceptible to stand-replacing wildfire events, leaving populations vulnerable to rapid extirpation. Over 10% of forest monitoring plots established in 2010–2011 were burned at high severity (100% tree loss) by 2016 (Waring, unpublished data). Proactive and ongoing collections of genetic material as an intervention strategy is critical. Lack of surface fire over the past 120 years has led to an increase in understory SWWP in some areas, including at lower elevations under a ponderosa pine (*P. ponderosa*) overstory. Reconstructions of forest composition indicate that SWWP was a minor stand component under frequent fire regimes and overstory density has also increased in recent years. Interventions to increase resilience to WPBR will need to balance SWWP sustainability with increasing pressure to meet restoration objectives that include lowering densities of SWWP. For areas where WPBR has not been established long, it may be difficult to develop risk rating systems, while areas with a longer disease history may exhibit more patterns related to environmental risk for infection (Looney et al. 2015; Geils et al. 1999). However, not all of the disjunct populations have the alternate host for WPBR, *Ribes* spp. present, which may decrease population-level hazard due to escape and offer opportunities for interventions to sustain healthy forests as *C. ribicola* continues to spread (Fig. 4). Qualitative genetic resistance to WPBR is present, with putative genetic resistance found in only one stand to date. Quantitative genetic resistance appears to be more common but still infrequent. Reducing overstory density in the mixed conifer forest, while favoring a higher proportional density of overstory SWWP in areas with genetic resistance will yield desired understory seedlings that are vigorous and likely to recruit into the overstory. Managing for multiple canopy layers can increase ladder fuels and fire hazard, so we recommend stand-level densities be relatively low (e.g. 40–120 ft^2 basal area ac^{-1} [9.1–27.4 m^2 basal area ha^{-1}] for dry mixed conifer, Reynolds et al. 2013). Low stand densities are also recommended to increase forest resistance to other disturbances, including drought and bark beetles.

Pairing the R4R framework for five-needle pines with other management objectives

In the above examples, the primary objective of interventions is to artificially and naturally regenerate five-needle pine populations to mitigate WPBR impacts. However, progress toward increasing the resilience of the landscape to WPBR impacts can also be made in conjunction with management of other disturbances. Including five-needle pines in the species planting plans after extensive areas of overstory mortality by insect outbreaks (e.g. spruce beetle, *Dendroctonus rufipennis*, or mountain pine beetle) or wildfires can help with reforestation. Five-needle pines can establish in harsh habitats and tend to be poor competitors, so they can contribute to forest cover while posing little risk of displacing other desirable tree species within a planting area (Schoettle 2004). Targeted plantings of five-needle pines in dry habitats can improve reforestation and reduce erosion in the overall treatment area, as well as increase the number of five-needle pines on the landscape. Likewise, the five-needle pines are tolerant of some root diseases and planting them in these areas can retain forest cover. Sparing five-needle pines during fuels treatments to reduce fire hazard will also assist with facilitating gene flow connectivity among populations and treatment areas. It is clear that interventions that benefit five-needle pines can also fit into schemes for meeting more general restoration, fire hazard reduction, or other management objectives.

Other considerations

The R4R framework does not include site value (e.g. tourist, historical, or cultural areas) in the prioritization of areas and interventions. It can, however, be applied to areas with different management authorities such as US wilderness areas. Knowing the forest health condition and the frequency of genetic resistance may help provide context for treatment proposals in wilderness (see Hahn and Landres 2017). Stimulating natural regeneration with wildland fire use for early seral host species such as the five-needle pines is a viable treatment option in wilderness if durable genetic resistance is present in the population and regeneration processes are still functional. If populations require direct supplementation with genetic resistance, and planting or direct seeding is permitted, utilizing seed sources that have been tested from within the wilderness would be preferred to retain the natural genetic background. Intervention options and priority areas can be further refined using the most current host and pathogen species distribution models under predicted climate change scenarios (sensu Lenoir et al. 2017; Malone et al. 2018; Millar et al. 2018).

The condition of the overall landscape, including disturbances by fire and native and non-native pests and pathogens, should also be taken into consideration when deciding priorities and intervention options. Recent fires can increase the abundance of alternate host species for *C. ribicola* and therefore increase disease hazard in the area. Fire or other stand replacing disturbances may also provide natural regeneration or planting opportunities. Native pests and pathogens may require control to limit their impacts before managing the target host population is possible. There are, of course, many scenarios that may be encountered and additional criteria could be added; the R4R framework provides a decision structure from which to compare and prioritize different areas for regeneration management to determine when, where and how to treat to achieve the best probability of success for sustaining the host species. Regeneration management will not restore or sustain all host populations under all levels of pathogen impact; but if natural resistance is present in the host species it will help prioritize and position areas for treatment that can accelerate adaptation to the new conditions while sustaining viable population sizes to promote resilience and prevent host species extirpation.

Summary

The proposed R4R framework provides a decision structure to guide artificial and natural regeneration decisions in five-needle pine ecosystems impacted and threatened by WPBR to optimize limited resources to shift the trajectory of a pine population way from extirpation and toward resilience and sustainability. There are non-market benefits to managing WPBR in high-elevation five needle pine forests (Meldrum et al. 2013). Regeneration management is one component of an overall response strategy and the R4R framework provides guidance for its use. Areas heavily impacted by WPBR that can no longer support natural regeneration are not highly prioritized for intervention due to the low probability of timely success in rebuilding the population. In areas with lower disease pressure and fewer impacts, natural processes are still functional and can be utilized to help increase forest resilience and prepare the landscape for invasion and disease intensification. Interventions, when conducted in priority conditions, can increase population size and generate and retain age class diversity to maintain demographic and evolutionary processes. Selection against susceptible genotypes (i.e. disease-caused mortality) will occur more rapidly in young stands than older stands. Therefore, management that generates a mosaic of patches of different stand ages across a landscape can effectively generate patches with different rates of selection upon *C. ribicola* invasion, thereby mitigating the effect of mortality in any one cohort or stand on overall ecosystem function and resilience of the greater landscape (Schoettle et al. 2012b). Timely informed management can help position the ecosystems for increased forest resilience. The R4R framework can be applied to any of the North American five-needle pines. The concept of the R4R framework can be adapted for application to other situations in which genetic resistance in the host to the nonnative invasive species is present at detectable levels within natural populations. Appropriate decision criteria will need to be defined for the specific host and invader. If genetic resistance is not present in the host species, than the restoration aspects of this framework (e.g. Fig. 3) can be applied to guide efficient deployment of planting material with genetic resistance when it is developed, though the R4R framework does not consider any social or regulatory trade-offs associated with deploying genetically engineered trees.

Conclusions

Science-based conservation practices prioritized for application where the probability of success is the greatest will help avert host population extirpation and sustain resilient natural forests. A sustainable multi-generational outcome for natural forests threatened by

WPBR will be a function of the interaction of current forest health condition, invasive species risk or hazard, genetic resistance to the invasive species, and host population dynamics and silvics. The R4R framework presented here highlights factors to target through interventions to sustain and restore threatened or declining populations, respectively. Utilizing natural processes to aid sustainability in the face of impacts is desirable to retain genetic diversity and adaptive capacity. Natural regeneration offsets mortality and is therefore a stabilizing force in forests. Regeneration also provides the individuals and genetic combinations to support the dynamic natural selection for genetic resistance and other traits important for long-term adaptation in a changing climate. Artificial regeneration via seed or seedling planting may also be needed to further increase population size and introduce or supplement the population with genetic resistance traits. More natural forest types are challenged by nonnative invasive pests and pathogens than can be reasonably expected to be the focus of tree breeding programs. However, the R4R framework adapts and builds on knowledge gained from these programs and provides guidelines for regeneration decisions in natural forests with conservation rather than production goals.

This framework is being applied to the high elevation five-needle pines in the southern Rocky Mountains. It can be applied to the WPBR pathosystem throughout North America including areas that have been invaded for decades as well as the threatened natural forests of the southern Rockies, Great Basin, Southwest, and Mexico. The conceptual R4R framework approach can be adapted for application to other invasive species-host interactions with species specific modifications. The key factors that determine the outcome of the invasive species-host interaction may vary due to differences in invasive species' dispersal, risk factors and preferences, and host traits, but the decision process can still apply: (1) take the long view with an evolutionary approach to build and sustain resilience, (2) prioritize areas for intervention that have the highest probability of success to promote self-sustaining host populations in the presence of the invader, and (3) time interventions early in the invasion process to better utilize natural ecosystem processes to attain conservation goals.

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