Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Evaluating future success of whitebark pine ecosystem restoration under climate change using simulation modeling

Robert E. Keane[1,2], Lisa M. Holsinger[1], Mary F. Mahalovich[3], Diana F. Tomback[4]

Major declines of whitebark pine forests throughout western North America from the combined effects of mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, fire exclusion policies, and the exotic disease white pine blister rust (WPBR) have spurred many restoration actions. However, projected future warming and drying may further exacerbate the species' decline and possibly compromise long-term success of today's restoration activities. We evaluated successes of restoration treatments under future climate using a comprehensive landscape simulation experiment. The spatially explicit, ecological process model FireBGCv2 was used to simulate whitebark pine populations on two U.S. Northern Rocky Mountain landscapes over 95 years under two climate, three restoration, and two fire management scenarios. Major findings were that (1) whitebark pine can remain on some high mountain landscapes in a future climate albeit at lower basal areas (50% decrease), (2) restoration efforts, such as thinning and prescribed burning, are vital to ensure future whitebark pine forests, and (3) climate change impacts on whitebark pine vary by local setting. Whitebark pine restoration efforts will mostly be successful in the future but only if future populations are somewhat resistant to WPBR. Results were used to develop general guidelines that address climate change impacts for planning, designing, implementing, and evaluating fine-scale restoration activities.

Key words: fire regime, mountain pine beetle, range-wide restoration strategy, regeneration, seed dispersal, upper subalpine, white pine blister rust

Implications for Practice

- Restoration treatments will still be effective in the future under warmer climates, and they might be the only actions that keep whitebark pine forests on high elevation landscapes.
- Thinning of shade-tolerant competitors, coupled with prescribed burning, will allow whitebark pine to continue to produce cones and provide microsites for bird-mediated dispersal and regeneration.
- Planting rust-resistant whitebark pine seedlings is an important restoration action, but the effects will not be manifest for more than a century.
- Restoration prescriptions will need to be tailored to local conditions to be effective as climate change impacts will not be the same across all high mountain ecosystems.

Introduction

High elevation whitebark pine (*Pinus albicaulis* Engelm.) forests are rapidly disappearing throughout western North America because of the cumulative effects of historical and current mountain pine beetle (MPB, *Dendroctonus ponderosae*) outbreaks, over 90 years of fire exclusion policies, and the introduced pathogen *Cronartium ribicola*, which causes the exotic disease white pine blister rust (WPBR) in five-needle white pines (Keane & Arno 1993; Kendall & Keane 2001; Murray & Rasumussen 2003; Schwandt 2006; Tomback & Achuff 2010). Exacerbating an already stressed ecosystem, projected future climates may accelerate whitebark pine declines and further reduce whitebark pine habitat thereby possibly restricting populations to the tops of mountains or to the northern portions of its range (Koteen 1999; McKenney et al. 2007; Schrag et al. 2007; Warwell et al. 2007; Funk & Saunders 2014). However, magnitudes and directions of whitebark pine ecosystem responses to projected climate changes are largely unknown because of the species' unique ability to survive fire, colonize disturbed environments, and tolerate drought (Loehman et al. 2011*b*). The high uncertainty of future climate predictions coupled with limited information on disturbance and climate interactions

Author contributions: RK created and parameterized the model and designed the study; LH initialized the model and conducted simulations and statistical analyses; MM, DT assisted in initialization, parameterization, and calibration of the model and helped in the analysis; RK, LH, MM, DT wrote parts of the article.

[1]Missoula Fire Sciences Laboratory, U.S. Forest Service, Rocky Mountain Research Station, 5775 Hwy 10 West, Missoula, MT 59808, U.S.A.
[2]Address correspondence to R. E. Keane, email rkeane@fs.fed.us
[3]U.S. Forest Service, Northern, Rocky Mountain, Southwestern, and Intermountain Regions, Forestry Sciences Laboratory, Moscow, ID 83844, U.S.A.
[4]Department of Integrative Biology, University of Colorado Denver, Denver, CO 80202, U.S.A.

doi: 10.1111/rec.12419
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.12419/suppinfo

may confound planning restoration activities for this valuable ecosystem (Keane et al. 2015). The primary goal of restoration is to promote rust resistance in this five-needle pine ecosystem with actions such as planting rust-resistant seedlings while also ensuring continued bird-mediated seed dispersal (Keane et al. 2012).

The loss of this iconic high-elevation tree species will result in serious consequences for high mountain ecosystems, both in terms of the impacts on biodiversity and in losses of valuable ecosystem processes and services (Tomback et al. 2001*a*; Lee 2003; Tomback & Achuff 2010; Funk & Saunders 2014). The large, nutritious seeds produced by whitebark pine are an important food for many bird and mammal species, and whitebark pine communities provide important habitat for many wildlife species (Tomback & Kendall 2001; Lorenz et al. 2008). In fact, the Clark's nutcracker (*Nucifraga columbiana*), a large bird of the Corvidae family, is the primary seed disperser for whitebark pine, and both species are coevolved mutualists (Tomback 1982, Tomback & Linhart 1990). Whitebark pine seeds buried by nutcrackers in caches throughout montane terrain as future food may germinate and grow into trees that often act as nurse trees to less hardy conifers and other vegetation, promoting regeneration (Callaway 1998; Callaway et al. 1998; Tomback et al. 2001*b*). At upper subalpine elevations, mature whitebark pine trees help to regulate snow melt and reduce soil erosion (Farnes 1990). For these reasons, whitebark pine is considered both a keystone species for promoting community diversity and a foundation species for promoting community stability (Paine 1995; Tomback et al. 2001*a*; Ellison et al. 2005; Tomback & Achuff 2010). If not for WPBR, whitebark pine forests may be more resilient to climate change than any other forest that might replace it, such as forests of the shade-tolerant conifers subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), or mountain hemlock (*Tsuga mertensiana*), because of the pine's superior ability to survive fire (Ryan & Reinhardt 1988).

Predicting responses of whitebark pine to projected climate change and restoration actions is a complicated task involving consideration of complex ecological interactions at multiple spatial and temporal scales. Climate warming, for example, may foster more high elevation fires that may burn more whitebark pine forests that may provide additional sites for nutcracker caching that may promote future regeneration, but fires may also kill trees that may be genetically resistant to WPBR thereby reducing regeneration potential (Loehman et al. 2011*a*, 2011*b*; Keane et al. 2012). This complexity precludes traditional approaches for evaluating climate impacts, such as expert opinion, statistical modeling, and field experiments, because of the long time spans and large areas needed to properly assess vegetation, disturbance, and ecosystem responses to changing climates (Keane et al. 2015). Mechanistic ecological simulation of climate, vegetation, and disturbance dynamics in a spatial domain may be the best approach at this time even though the field of landscape modeling is still in its infancy (Gustafson 2013). Biophysical landscape models that integrate mechanistic algorithms allow the spatial simulation of complex interactions among climate, vegetation, and disturbance, along with interactions of critical plant and animal life cycle processes of reproduction, growth, and mortality with climate (Gworek et al. 2007; Lambrecht et al. 2007; Keane et al. 2015).

We used the mechanistic landscape model FireBGCv2 (Keane et al. 2011) to determine if restoration actions proposed in the whitebark pine range-wide strategy (Keane et al. 2012) will be successful in the future with projected climates. The Keane et al. (2012) strategy suggests 10 restoration actions, but only two were applicable for this article: (1) implement treatments (silvicultural thinnings, prescribed burning, and wildland fire use) and (2) plant rust-resistant seedlings; the other eight cannot be simulated at this time. A fully factorial design experiment was used to simulate various climate, restoration, and fire management scenarios on whitebark pine abundance to determine if current and proposed restoration strategies will be effective in the future. Results from this simulation experiment were integrated with a comprehensive literature review to create a companion document to the range-wide restoration strategy of Keane et al. (2012) that presents various recommendations of modifying restoration actions under climate change (Keane et al. 2016).

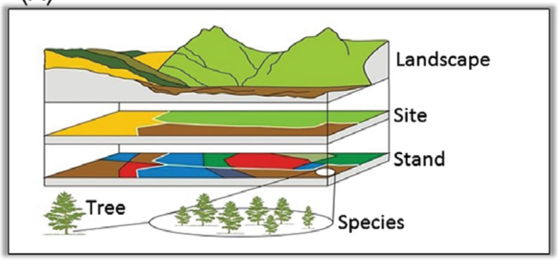
Methods

FireBGCv2 Model

FireBGCv2 is a mechanistic, individual-tree, gap model that is implemented in a spatial domain (see Keane et al. 2011 for complete model documentation, assumptions, and parameters). The model was developed by integrating empirically derived deterministic functions with stochastically driven algorithms to approximate landscape and ecosystem behavior across time and space (Keane et al. 2011). Physical and empirical functions are used to represent some well-studied ecological processes, such as autotrophic respiration and photosynthesis. Stochastic functions are used to represent ecological processes that are highly variable, under-studied, and difficult to quantify, such as fire ignition, tree mortality, and snag fall. FireBGCv2 is a cumulative effects model that is best used to study long-term landscape dynamics rather than as a prognostic model to project short-term future conditions.

FireBGCv2 simulates ecological processes across multiple spatiotemporal scales including cross-scale interactions that can drive landscape behaviors (Fig. 1). Wildland fire ignition and spread, along with cone crop production and seed dispersal, are spatially simulated at the landscape level at the end of each simulation year. Most of the FireBGCv2 fine-scale simulation occurs at the stand level where the flow of carbon, nitrogen, and water are distributed across various terrestrial and atmospheric components within the model. Important ecological processes modeled at the stand level include litterfall, decomposition, snow dynamics, soil water, transpiration, and evaporation. Many processes are simulated at a daily time step including species phenology, litterfall, and soil water. Tree growth, establishment, and mortality are simulated at the individual tree level, while

(A)



(B)

Scale	Description	Processes simulated
Landscape	Extent of simulation area	Fire, ignition, seed dispersal
Site	Same biophysical setting	Weather, soils
Stand	Vegetation communities	PSN, respiration, ET
Species	Trees, shrubs, grasses	Regeneration, Phenology
Tree	Individual tree elements	Mortality, growth, litterfall

(C)

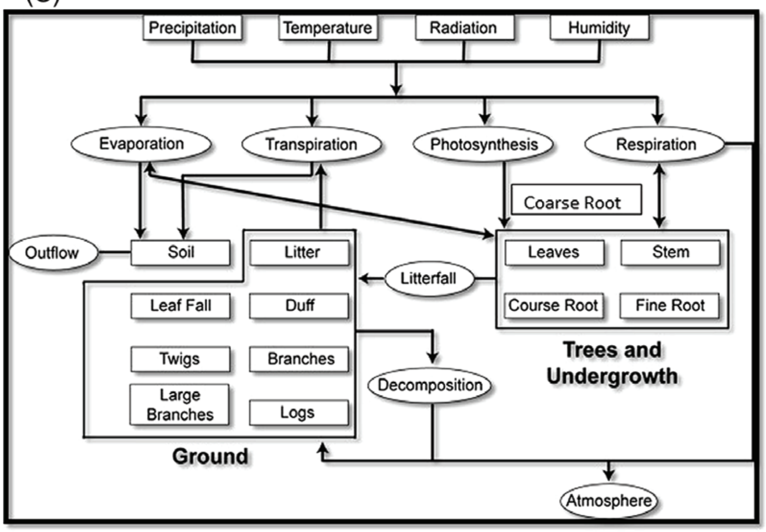


Figure 1. A diagram showing the important aspects of the FireBGCv2 model. (A) The five scales incorporated into the model and (B) some of the important processes simulated at each scale. (C) The flow of energy, carbon, water, and nitrogen is simulated at the stand scale across each of the carbon pools using mechanistic algorithms detailed in the work of Keane et al. (2012); biophysical processes of evaporation, transpiration, photosynthesis, and respiration (ovals) are calculated from five daily weather variables (precipitation, maximum and minimum temperature, radiation, and humidity—top rectangles) to simulate the flux of energy, water, carbon, and nitrogen across the important ecosystem components (other rectangles).

disturbance effects, such as fuel consumption, tree mortality, and soil heating, are computed across all scales.

Several FireBGCv2 components are important in this study and warrant mention here. First, the model includes simulation of WPBR dynamics using weather, stand conditions, and tree phenology as intermediate variables (Keane et al. 2011). The blister rust module was adapted from McDonald et al. (1981) and parametrized using Hoff et al. (2001). We set rust resistance at 0.01 for all input living whitebark pine trees and set rust resistance at 0.30 for all planted seedlings based on results from the Inland West Whitebark Pine Genetic Restoration Program (Mahalovich & Foushee, submitted). And even though FireBGCv2 has a MPB module, we decided not to simulate MPB dynamics to simplify interpretation of results. There is a complex simulation of Clark's nutcracker-caching dynamics and its influence on whitebark pine regeneration along with empirical seed dispersal algorithms for this bird-dispersed species (Keane et al. 1990). There is also an extensive module that simulates a wide variety of management actions, including partial harvest, planting, wildland fire use, and prescribed burning at the stand scale (Keane et al. 2011); this module was used to simulate restoration actions. There are also detailed fire algorithms that simulate (1) ignition based on weather, fuels, and topography, (2) spread based on vectors of wind and slope, (3) effects based on fire intensity, and (4) management based on proportion of fires suppressed, an input parameter (Keane et al. 2011).

Study Areas

Simulation of the complex interactions of climate, fire, and vegetation dynamics over the entire range of whitebark pine is computationally intractable at this time. Instead, we simulated whitebark pine dynamics on two large landscapes that we felt represented the wide range of climate, vegetation, and fire regime types for whitebark pine in the U.S. Northern Rocky Mountains (Fig. 2):

(1) East Fork of the Bitterroot River (EFBR) on the Bitterroot National Forest, Montana, U.S.A.: a 128,000 ha dry mixed-conifer ecosystem with a mixed frequency and severity fire regime currently comprised of 8–12% whitebark pine based on plot data and statistical modeling (Holsinger et al. 2014).

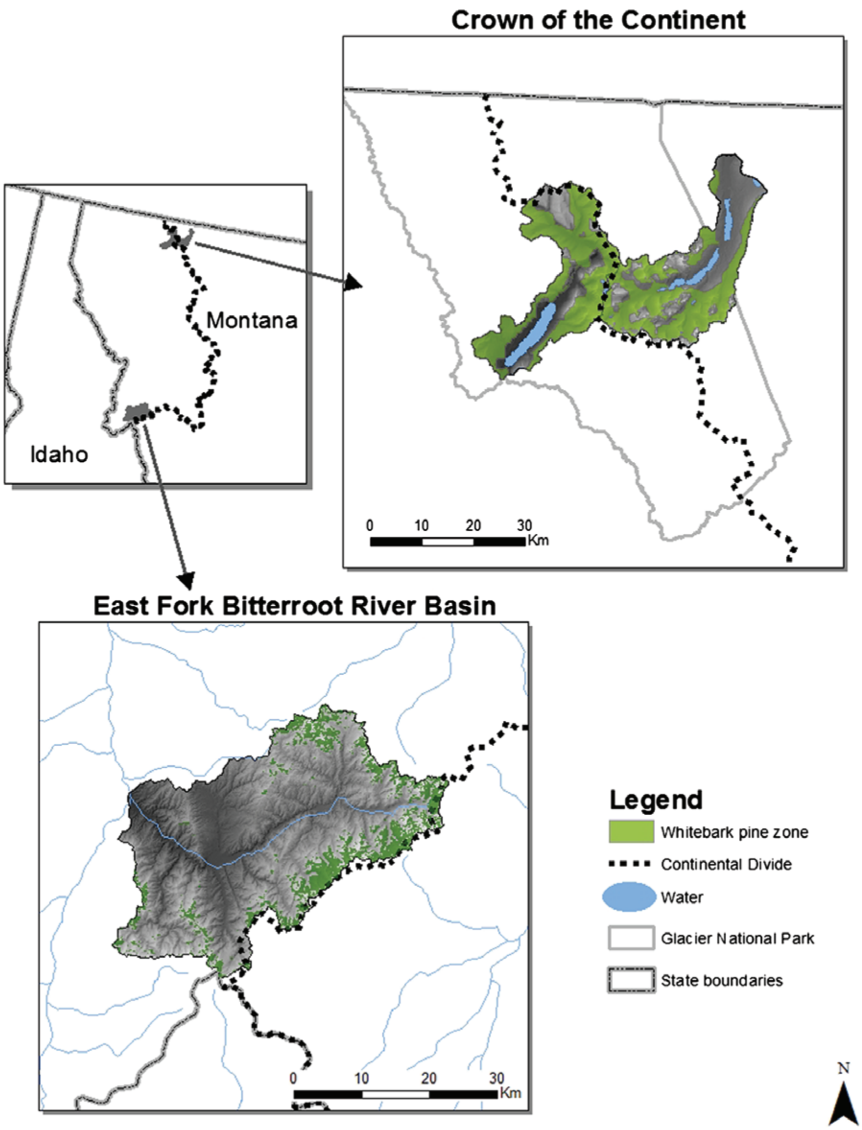


Figure 2. The two landscapes that were included in the FireBGCv2 simulation experiment and that were used in the illustrative independent simulations.

(2) Crown of the Continent (CROWN) comprised of the McDonald and St. Mary's drainages of U.S. Glacier National Park: a 100,000 ha mesic mixed-conifer landscape with fire regimes of variable frequencies and severities, and comprised of about 8–14% potential whitebark pine habitat based on plot data and empirical modeling (Loehman et al. 2011*a*).

All lands with the potential to support whitebark pine were explicitly identified as the "whitebark pine zone" on each landscape using biophysical parameters and field data (green in Fig. 2, Loehman et al. 2011*a*; Holsinger et al. 2014). These two landscapes were selected because they had been used in previous FireBGCv2 studies (Loehman et al. 2011*b*; Holsinger et al. 2014) (it takes over 10 months to parameterize a FireBGCv2 landscape) and they contained a significant amount of whitebark pine habitat in the high elevation settings.

Simulation Experiment

The overarching objective of this simulation project was to evaluate the success of two whitebark pine restoration activities under future climate and fire management scenarios. We used a fully factorial design to answer this objective where a set of four factors were used to represent climate, restoration cutting, planting rust-resistant whitebark pine, and fire management and within each factor we nested two or three treatments to explore a range of restoration options (Table 1). The four factors included in the simulation experiment were (1) fire suppression (S), (2) restoration cuttings (R), (3) planting (P), and (4) climate (C). For S, we simulated three levels of fire suppression: (1) 0% suppression (mimics historical fire regime), (2) 50% suppression (mimics wildland fire use management option), and (3) 92% suppression (operational fire suppression) (Loehman et al. 2011*b*).

Table 1. The multifactorial simulation experiment used to assess impacts of climate change on whitebark pine restoration attempts. The factors and treatments were used to explore climate change effects on whitebark pine distribution and abundance. We performed 10 replicates of each factor. Also presented are acronyms of the tree species included in all simulations as referenced in other figures and tables.

Factor	*Num Levels*	*Values for Each Level*
Fire suppression (S)—levels of fire suppression expressed as percent of fires that are suppressed	3	No suppression (SN); historical fire regime; 50% suppression to emulate wildland fire use (SL); 92% suppression to represent current management (SH)
Restoration (R)—three levels of area treated with mechanical cuttings coupled with prescribed burns	3	No treatments (RN); low restoration levels (RL) 3% of landscape treated per year; high restoration (RH) 30% landscape treated per year
Planting (P)—three levels of area planted with rust-resistant (25% resistance) whitebark pine seedlings	3	No planting (PN); low planting (PL) 10 ha per year at 275 seedlings per ha; high planting (PH) 100 ha per year at 550 seedlings per ha
Climate (C)—current and projected daily climate data for 95 years	2	Historical and warm-dry (RCP8.5) scenarios

Tree Species and Plant Guilds Included in the Simulations

Scientific Name	*Abbreviation*	*Common Name*
Abies lasiocarpa	ABLA	Subalpine fir
Laryx occidentalis	LAOC	Western larch
Larix lyallii	LALY	Alpine larch
Pinus albicaulis	PIAL	Whitebark pine
Pinus contorta	PICO	Lodgepole pine
Pinus engelmannii	PIEN	Engelmann spruce
Pinus flexilis	PIFL	Limber pine
Pinus ponderosa	PIPO	Ponderosa pine
Populus tremuloides	POTR	Quaking aspen
Pinus monticola	PIMO	Western white pine
Pseudotsuga menziesii	PSME	Douglas-fir
Thuja plicata	THPL	Western red cedar
Tsuga heterophylla	TSHE	Western hemlock
Shrubs	SHRB	Upland shrublands
Riparian Herb	RHRB	Wetland herbaceous communities
Grass	GRSS	Grassland dominated communities

For the restoration cutting (R), we simulated three restoration treatment strategies: (1) no restoration cuttings (RN), (2) low restoration where mechanical cuttings removing subalpine fir and Engelmann spruce (thinning) were used in concert with prescribed burning to eliminate whitebark pine competitors at a rate of approximately 3% of the landscape per year (RL), and (3) extensive restoration where mechanical cuttings and prescribed burning treatments were implemented at a rate of 30% per year (RH in Table 1). Stand-level restoration treatment design was based on recommendations from Keane et al. (2012) where all subalpine fir and spruce above 4 cm DBH (Diameter Breast Height) were cut and taken off-site followed by a low intensity prescribed burn (~400 kW/m fireline intensity).

The planting (P) factor had three treatments: (1) no planting (PN), (2) low planting where rust-resistant whitebark pine seedlings are planted at 10 ha/year at a density of 275 seedlings/ha (PL), and (3) high planting (PH) where whitebark pine seedlings at 100 ha/year at a density of 550 seedlings/ha (densities taken from Keane et al. 2012). Seedlings were planted on areas that burned within the last 30 years either from wildfire or prescribed burning. If there were insufficient burned areas for planting, seedlings were planted in old, unplanted burns (<50 years since fire). The proportion of seedlings with rust resistance in these simulations was set at 30%, which is at the upper range in whitebark pine seedlings resistance determined from the Inland West Whitebark Pine Genetic Restoration Program at the USDA Forest Service Coeur d'Alene Nursery (Mahalovich & Foushee, submitted).

The climate (C) factor had two scenarios: historical climate and a future climate (Fig. 3). The historical and future climate data were taken from the Coupled Model Intercomparison Project Phase 5 (CMIP5) with an 8.5 Representative Concentration Pathway (RCP8.5) where average temperatures are projected at about 5°C above pre-industrial levels—an emissions scenario that predicts the highest temperature increases among various possible emission scenarios but the one that appears increasingly most likely to occur (Peters et al. 2013). Based on an evaluation of a suite of GCMs by Rupp et al. (2013) for the Pacific Northwest and surrounding region, we chose the CNRM-CM5 (National Centre of Meteorological Research, France) GCM, which was the highest ranked model overall for the Northern Rocky Mountains region. Landscape daily weather input data were taken from a statistical downscaling of CNRM-CM5 GCM data from CMIP5 using the Multivariate

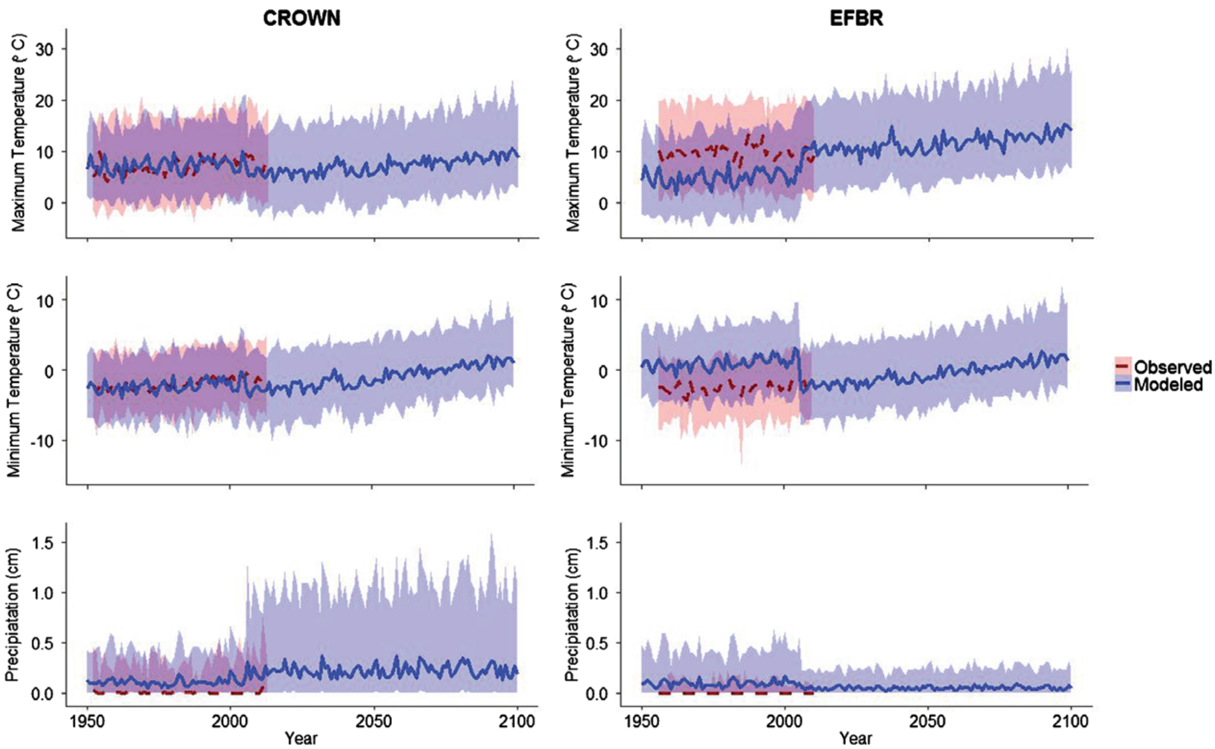


Figure 3. Modeled and observed weather data for CROWN and EFBR simulation landscape, including average annual maximum and minimum temperature (°C), and precipitation (cm). Historic observed data were taken from Saint Mary, MT and West Glacier, MT for the CROWN; Sula, MT weather station for the EFBR; and historic and future modeled data derived from the CNRM-CM5 GCM. Dark blue and red lines are median values; light blue and red indicate 25th to 75th percentile ranges.

Adaptive Constructed Analogs (Abatzoglou & Brown 2011) method with the METDATA (Abatzoglou 2011) observational dataset as training data. We derived weather data for our historic scenario simulations from downscaled 800 m grids of historical climate modeled from the CNRM-CM5 GCM for the baseline period of 1950–2005 (56 years) (Fig. 3). The historical simulations were only 56 years long and the future projections were comprised of only 95 years of daily weather.

Each level for each factor was simulated in a multifactorial design with 10 replicates for a total of 540 simulations for each landscape (3S × 3R × 3P × 2CC × 10 reps = 540 runs). We used the same species list for each simulation run (Table 1), which dictated which species could inhabit or migrate into the landscape during simulations. We simulated both historical and future scenarios for this same length of time (95 years). We output values for response and exploratory variables every 10 years to create a simulation time series of nine observations for each simulation run. For the historical simulations, we cycled the 56-year weather record for both study areas to create 95 year-long simulations.

We evaluated restoration success from simulated response variables that represent whitebark pine population response to restoration and planting treatments: *Whitebark pine basal area* (m^2/ha) averaged across all stands on each landscape and the proportion of the simulation area in whitebark pine dominated stands (*proportion landscape*). We summarized basal area for the whitebark pine zone only (Fig. 2). We used generalized linear mixed models (GLMM) for repeated measures to test for significant differences in restoration, planting, suppression, and climate. We also used GLMMs to evaluate differences in historical and future climate conditions separately. To evaluate the amount of basal area, we used the software R (R Development Core Team 2014) with the *lme* package (Bates et al. 2014) including an AR(1) random residual structure to account for temporal autocorrelation and multiple comparisons of the main treatment effects. We used GLIMMIX in SAS to evaluate proportion cover with an AR(1) structure and a beta probability distribution and conducted multiple comparisons of main effects. There were few significant main effects interactions.

We qualitatively described forest community responses to climate change and wildfire management by summarizing the percent of the upper subalpine landscape (whitebark pine zone) comprised by each tree species cover type evaluated by the plurality of basal area. In addition, we evaluated a number of other ecosystem related explanatory variables (see Keane et al. 2016), but only present two fire variables (area burned, fire rotation) here.

Because we anticipated that 95 years was too short to evaluate whitebark pine landscape dynamics, we also conducted ancillary simulations for longer time periods (500 years) to explore potential long-term dynamics of whitebark pine for illustrative purposes. These simulations included only a small

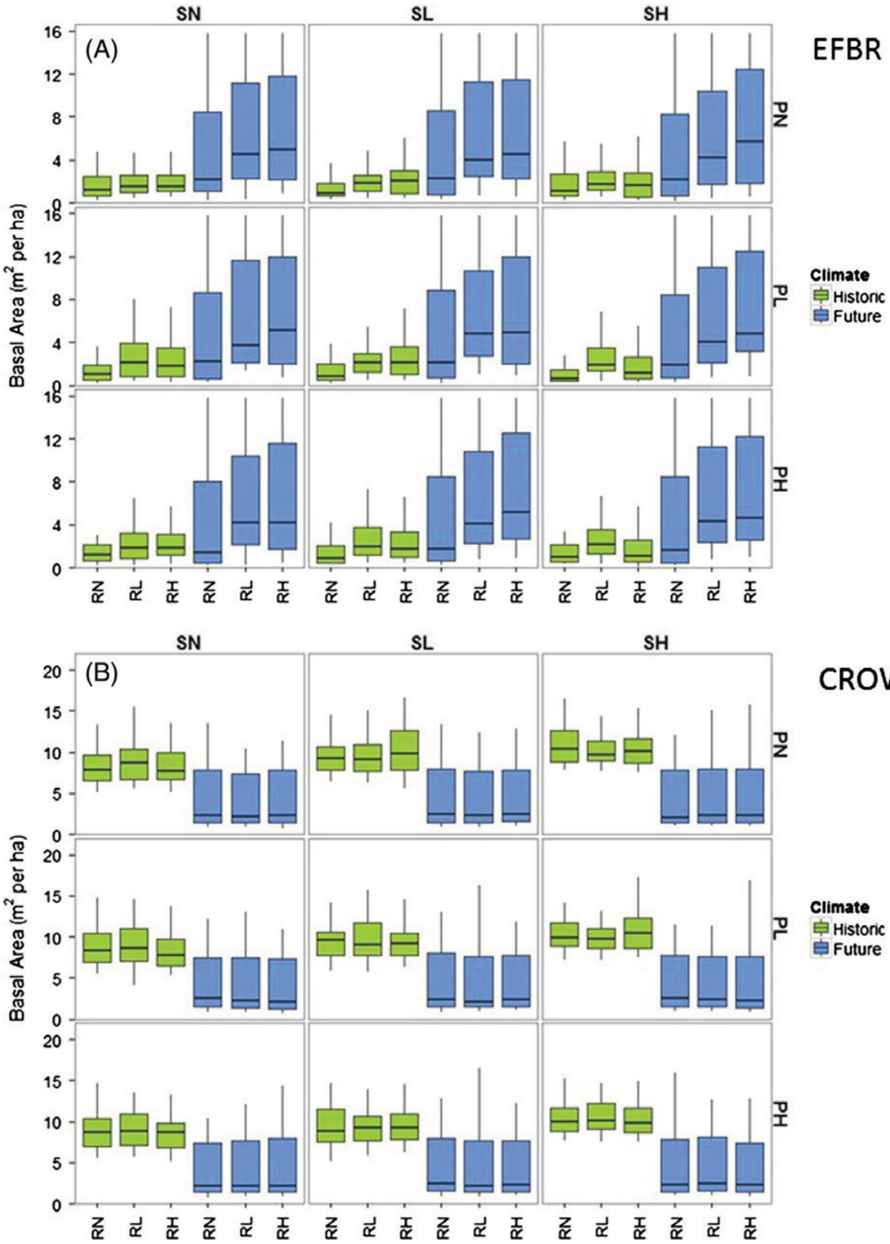


Figure 4. Simulated basal area (m^2/ha) of whitebark pine over 95 years in whitebark pine zone for the (A) East Fork of the Bitterroot River (EFBR) and (B) Crown of the Continent (CROWN) landscapes across all scenarios including: historic (green) and future (blue) climate; fire suppression at none (SN), low (SL) and high (SH) levels; planting at none, low, and high levels (PN, PL, and PH); and restoration at none, low, and high levels (RN, RL and RH). In the box and whisker diagrams, the box represents 25th and 75th percentiles, the whiskers represent the range of the data, and the horizontal line is the median.

combination of the scenarios in Table 1; the highest levels of restoration and planting treatments with 50% fire suppression. To simulate weather across the lengthy 500-year period, we relied on previous methods as described in detail by Loehman et al. (2011*b*) where observed historical weather station data from the two landscapes (West Glacier, MT and Saint Mary, MT for CROWN; Sula, MT for EFBR; Fig. 3) was cycled in sequence over the 500-year simulation period. For the climate change scenario, we adjusted historical weather data using offsets derived from the Hadley Centre (UK) HadCM3 GCM for the A2 emissions scenario (Nakicenovic et al. 2000), which corresponded to the RCP 8.5 emissions scenario used in our formal simulation experiment.

Results

East Fork Bitterroot River Landscape

We found that basal area (Fig. 4A) and proportion cover (Fig. 5A) of whitebark pine were significantly higher in the

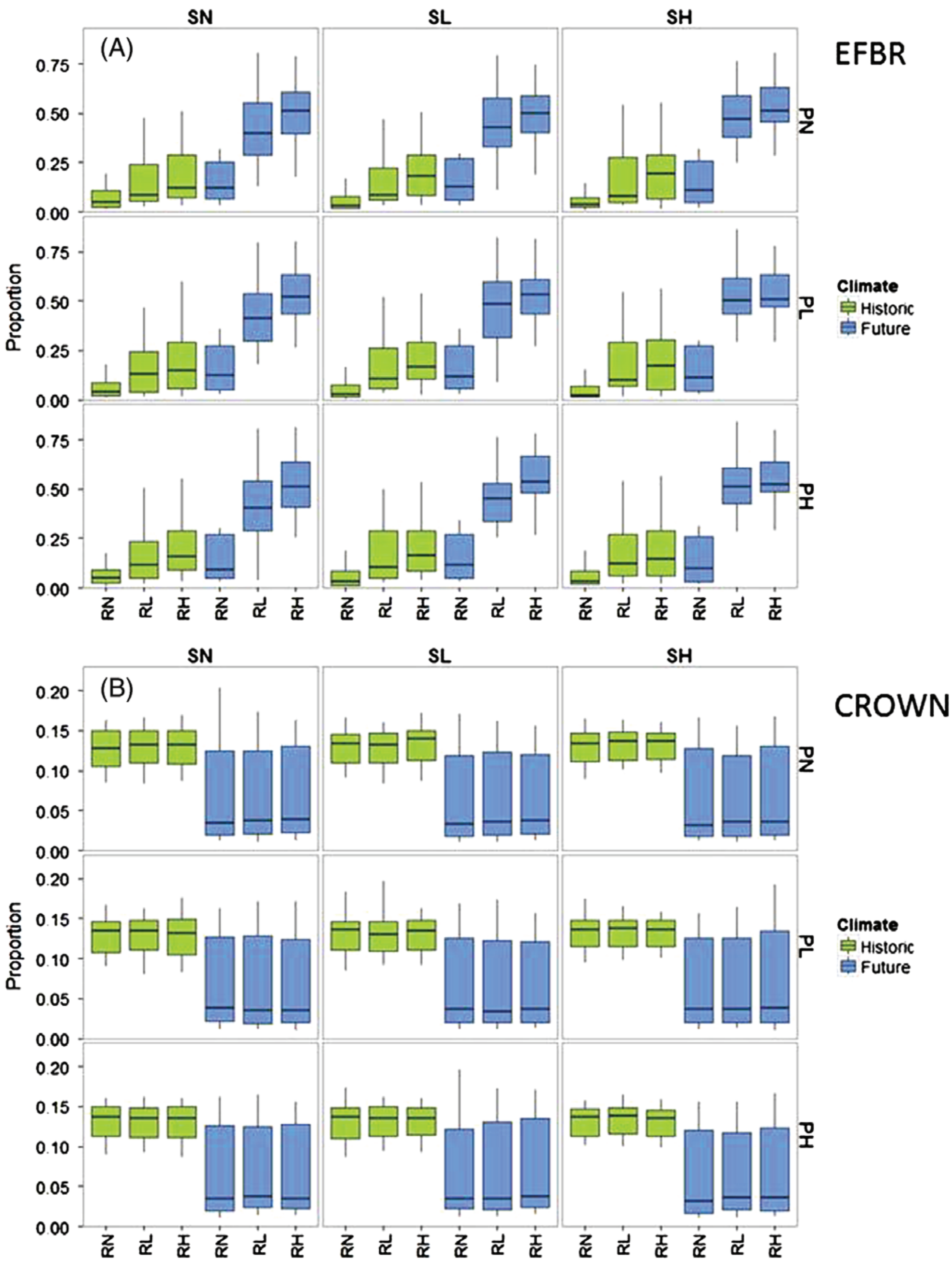


Figure 5. Simulated proportion of landscape in whitebark pine over 95 years in whitebark pine zone for the (A) East Fork of the Bitterroot River (EFBR) and (B) Crown of the Continent (CROWN) landscapes across all scenarios: historic (green) and future (blue) climate; fire suppression at none, low, and high levels (SN, SL, and SH respectively); planting at none, low, and high levels (PN, PL, and PH); and restoration at none, low, and high levels (RN, RL, and RH). In the box and whisker diagrams, the box represents 25th and 75th percentiles, the whiskers represent the range of the data, and the horizontal line is the median.

EFBR under future climate compared to the historical scenario (p-value < 0.0001) with over twice as much whitebark pine predicted for the future (3.72 vs. 1.69 m^2/ha) and for proportion landscape (33 vs. 12%), respectively (Table S1, Supporting Information). Basal area doubled when restoration treatments were implemented at either low or high levels compared to no treatment, while the proportion of upper subalpine landscape in whitebark pine was almost four times higher in low (47%) or high (54%) restoration levels compared to no restoration (13%). Planting whitebark pine seedlings did not significantly affect the basal area or proportion landscape of whitebark pine in any of the EFBR simulations (Table S1; Figs. 4A & 5A).

Of the three factors simulated, climate and restoration had the greatest effects on whitebark pine basal area and proportion landscape compared to planting or fire suppression (Table S1; Figs. 4A & 5A). However, fire suppression had a significant

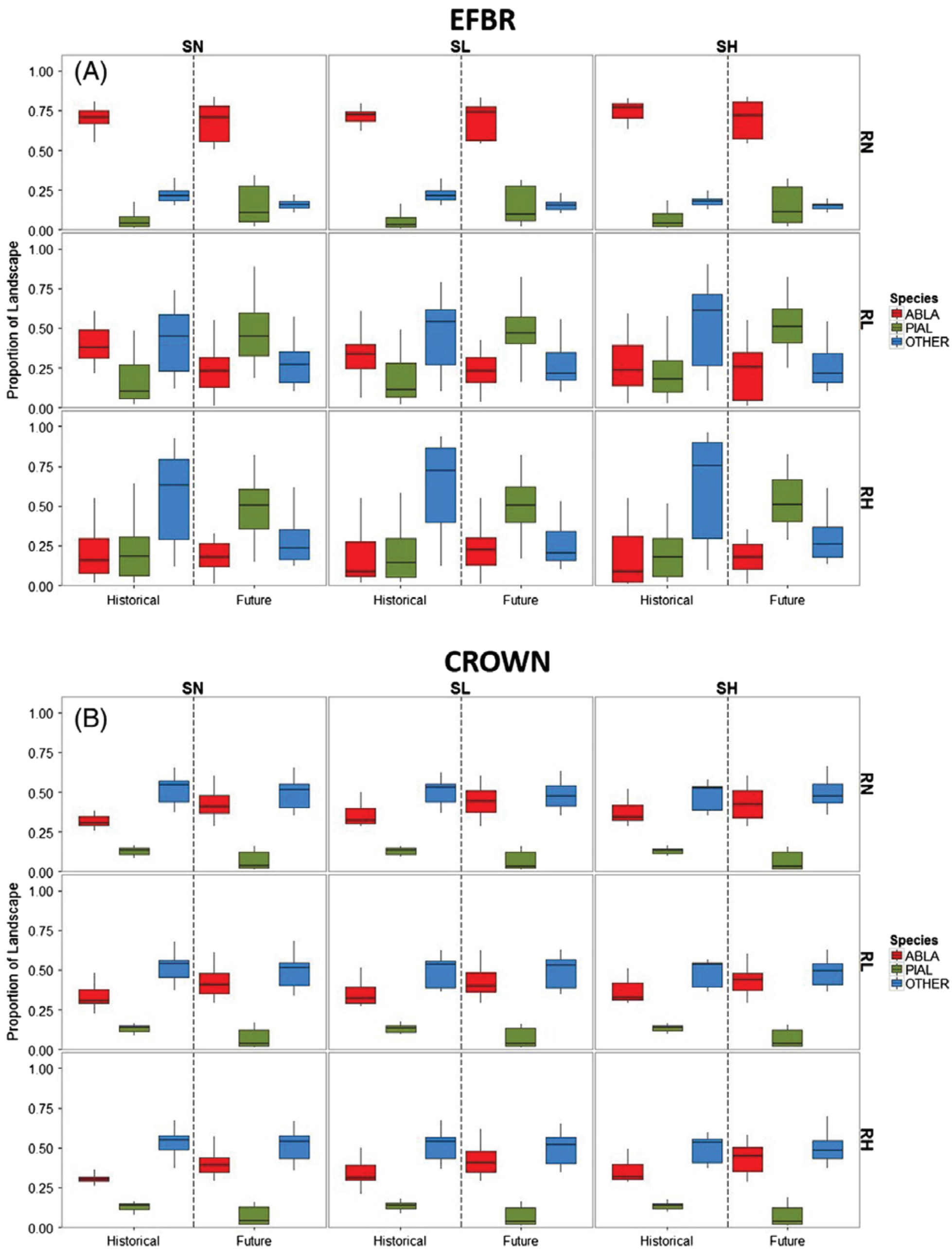


Figure 6. Simulated forest species composition over 95 years for the upper elevations of the (A) East Fork of the Bitterroot River (EFBR) and (B) Crown of the Continent (CROWN) landscapes under historical and future climates for fire suppression at none, low, and high levels (SN, SL, and SH, respectively) and restoration at none, low, and high levels (RN, RL, and RH). Planting was not included because of its minimal effects within the 95-year period. See Table 1 for species abbreviations: ABLA (red)-subalpine fir, PIAL (green)-whitebark pine, OTHER (blue)-includes mostly Engelmann spruce, quaking aspen, and lodgepole pine. In the box and whisker diagrams, the box represents 25th and 75th percentiles, the whiskers represent the range of the data, and the horizontal line is the median.

but minimal effect on the proportion in whitebark pine in the upper subalpine under future climates with higher landscape cover (3–5% higher) in the full suppression scenario compared to the no suppression simulations (Figs. 4A & 5A).

Whitebark pine was the dominant species (46–53% on average) under a future climate in the upper elevations (whitebark pine zone) of the EFBR when either low or high levels of restoration treatments were implemented (Fig. 6A). Without restoration, subalpine fir (ABLA) was dominant (76%), with whitebark pine as the second most dominant species (9%). Under the historical climate, applying high restoration resulted in aspen (POTR; *Populus tremuloides*) as the dominant species (59%), and comparable amounts of subalpine fir (21%) and whitebark pine (17%). Low and high levels of restoration kept whitebark pine on the landscape (>12%), but subalpine fir was still the dominant cover type (40%) followed by aspen (35%). Without restoration, subalpine fir dominated the high elevation landscape (76%) under historical weather.

On average, more area burned under a future climate than a historical climate in the EFBR (157% increase). Without suppression, a median of 550 ha burned annually in the future climate compared to 350 ha in the historical. With low suppression, 186 versus 155 ha burned annually, and 52 versus 58 ha with high suppression in the future versus historical climates, respectively. The historical climate generated some large fire years (years 11, 54, and 67) that were not observed in the future climate, but these high burn years had little overall effect on the central tendency across simulations (Keane et al. 2016).

Results from the 500-year simulations show that declines in whitebark pine basal area on the EFBR are rapid for all four scenarios (historical RHPH, historical RNPN, future RHPH, and future RNPN) over the first 100 years, but basal area starts to increase after year 100 for the high restoration scenarios for both historical and future climates (Fig. S1A). Whitebark pine basal area increases to 24 m^2/ha after 500 years in the historical RHPH scenario (25% higher than current levels), but grows to only 5 m^2/ha in the future RHPH scenario (75% less than current). Whitebark pine comprises a large portion of the whitebark pine zone for both climate scenarios (>50%) but only if restoration is implemented (Fig. S1C). Interestingly, with restoration, the proportion of the landscape dominated by whitebark pine increases from current levels (~30%) to over 70% of the landscape.

Crown of the Continent Landscape

In contrast to EFBR, simulation results for the CROWN landscape showed that there were significantly fewer whitebark pine, overall, in the future compared to the historical simulations (3.33 vs. 10.05 m^2/ha basal area and 0.03 vs. 0.13 proportion landscape for future and historic, respectively, Table S1; Figs. 4B & 5B). Wildfire suppression had the greatest effect on basal area and proportion landscape in whitebark pine under both future and historical climates unlike results from EFBR. In each climate scenario, the amount of basal area in whitebark pine was marginally higher but significant with low or high suppression compared to no suppression. Similarly, proportion of landscape in whitebark pine increased with increasing levels of suppression (each level significantly different from each other to varying degrees). When climate was included as a factor, suppression and climate were the most important influences (Table S1). Neither planting nor restoration treatments had any notable influence on simulated whitebark pine basal area or landscape proportion in the CROWN landscape.

There was little variation in community composition among treatments and climate in the CROWN landscape (Fig. 6B). Subalpine fir dominated the upper elevation areas across all treatments in both the future (about 45%) and historical (about 35%) climates. Whitebark pine continues to remain on the high elevation landscape in both historical and future climates, but at low levels (10%). The other species occurring under both future and historical climates were mainly a mixture of aspen, Douglas-fir (PSME; *Psuedotsuga menziesii*), lodgepole pine (PICO), and Engelmann spruce (PIEN) at about 10% each.

In the CROWN landscape, about half as much area burned (median of 70 ha annually across all scenarios) compared to the EFBR (143 ha). Moreover, more area burned annually in the historical climate than the future without suppression (135 vs. 79 ha, respectively) and with low suppression (68 vs. 62 ha, respectively). With high suppression, somewhat less area burned in the historical climate (53 ha annually) than the future (58 ha). Similar to the EFBR, there were three large fire years (11, 54, and 67) in the historical climate yet no large fires were observed in the future.

The 500-year simulation results support the 95-year runs where basal area decreased to low levels (67% decline to <5 m^2/ha) and areal extent shrank (60% decline to <5% of whitebark pine zone) in future climates regardless of restoration attempts (Fig. S1B & S1D). Restoration in the historical scenarios resulted in 20–30% higher basal areas period and 30–50% more area over time compared to no restoration, but both were roughly the same after 500 years.

Discussion

Several important findings from this simulation experiment may influence how we manage whitebark pine forests in the future. The first is that whitebark pine will likely continue to decline over the next several decades, but mostly from WPBR and, to a lesser extent, from climate change. This finding agrees with other simulation modeling efforts by Loehman et al. (2011*b*) and Smith-McKenna et al. (2014). However, while the FireBGCv2 EFBR simulation results show more productive whitebark pine populations in the next of 95 years of climate warming, the long-term future for whitebark pine for both simulation landscapes is less encouraging. Our 500-year independent simulations show a downward trend in whitebark pine basal area over the next 100 years regardless of treatment and planting intensities as a result of the damaging impacts of WPBR. Whitebark pine basal area and landscape proportion in the future RCP8.5 scenario started to increase after 100 years of simulation as rust resistance increases on the landscape from natural selection, treatments, and planting, and whitebark pine populations peak after 500 years at less than half of historical basal areas but high coverage in the EFBR landscape. Restoration success must be evaluated over centuries.

The second finding is that this decline can be mitigated on some landscapes with proactive restoration actions; even a low level of restoration activity may keep whitebark pine forests from vanishing on the high mountain landscape. Without restoration measures, whitebark pine basal areas remain low. The long-term simulations show that whitebark pine can eventually overcome the damaging effects of WPBR in about 100 years, but only with restoration activities to keep whitebark forests on the landscape.

We also found that effects of planting rust-resistant seedlings were negligible over the 95-year simulations, but only because planting impacts take a long time to become manifest in this high elevation ecosystem. Whitebark pine is a slow-growing tree with cone production occurring at about 30–80 years old and the optimal cone period occurring when trees are 100–200 years old (McCaughey & Tomback 2001). Thus, a 95-year simulation is too short for planted rust-resistant whitebark pine seedlings to grow into cone-producing trees to supply seeds for the next generation of seedlings. Previous simulations by Loehman et al. (2011*b*) and our 500-year simulations showed that it took at least 100 to 120 years for populations of whitebark pine to become sufficiently resistant to WPBR. The real payoff from planting rust-resistant seedlings will likely take at least a century and its main effect will probably be to shorten the time for rust resistance to become important in seed-producing whitebark pine.

And last, we found that the impacts of climate change on whitebark pine populations vary across its range based on local conditions; simulation output for EFBR and CROWN show completely different results. This implies that there is no "one-size-fits-all" solution for restoring this important and widely distributed high elevation ecosystem; managers must tailor broad strategies to local conditions for the most effective restoration treatments. The large contrast in simulation results between the EFBR and CROWN landscapes is likely a consequence of both the input climate and landscape setting. In the EFBR, whitebark pine populations increased in response to prescribed burning and thinning treatments (and to a lesser extent from removing suppression) under future hotter and drier conditions. In contrast, past and future climates for the CROWN landscape were colder and wetter than those simulated for EFBR, resulting in significantly less wildland fire, greater subalpine fir abundance, and higher mortality in whitebark pine from WPBR (Keane et al. 2016). In fact, precipitation in the CROWN landscape increased by over 10% on average into the future and mortality from WPBR reached as high as six times that of fire-related mortality, presumably due to higher humidity levels that enhance WPBR infections. Previous simulations by Loehman et al. (2011*b*) for a smaller portion of our CROWN landscape in Glacier National Park used observed historical weather and modeled future climate with offsets derived from A2 emissions scenarios (Nakicenovic et al. 2000) that corresponds to our RCP8.5 CNRM-CM5 modeled weather dataset and, interestingly, they simulated significantly more fire than this study using different climate inputs and climate warming parameters with future area burned over twice as much as historical (we observed less fire activity into the future), but they similarly predicted that whitebark pine populations will drop precipitously in the future. Correspondingly, Loehman et al. (2011*b*) attributed the decline largely to increased wildfire, where as we noted above, WPBR was the major source of mortality in these simulations of the CROWN landscape. This incongruity provides insight into the consequences of high uncertainty of future climate projections; small, subtle changes in high elevation climate can lead to a substantially different set of landscape futures and to a different set of conclusions regarding whitebark pine population dynamics. Such uncertainty highlights the difficulty of predicting the success of restoration strategies in the future, and emphasizes the need to improve climate projections and the importance of adaptive management approaches for whitebark pine. And last, the whitebark pine zone in the CROWN is composed of rock, glaciers, and snowfields (>20%) that are mostly unsuitable to whitebark pine (i.e. the 95-year simulation time too short for melted ice/snowfields to develop adequate soil profiles). As such, whitebark pine populations in the CROWN had inherently less potential to respond to the interactions of fire and climate dynamics than in the EFBR landscape where fire could more readily increase suitable habitat.

Our simulation results disagree with many contemporary studies that predict the demise of whitebark pine with climate change (e.g. Koteen 1999; McKenney et al. 2007; Schrag et al. 2007; Warwell et al. 2007). Most of these studies used Bioclimatic Envelope Model (BEMs) techniques to project future geographical ranges (McDermid & Smith 2008; Crookston et al. 2010; Rehfeldt et al. 2012; Chang et al. 2014; Hansen & Phillips 2015). BEMs, also called climate envelope models, niche models, or species envelope models, are developed by associating current climate conditions to the current distribution of a species by means of advanced statistical modeling. Future species distributions are then computed using the projected future climate data as inputs to the statistical model. There are many other limitations with the BEM approach. First, many critical life cycle processes, such as cone production, nutcracker-mediated seed dispersal, seedling establishment, and competitive interactions, are not represented in BEMs—only climate and species occurrence were included. Dullinger et al. (2004), for example, found that range shifts predicted by BEMs were reduced by over 40% when seed dispersal was included in the prediction model. BEMs also miss those areas that are now suitable for the species but where species is currently absent because it has not migrated there yet or has been removed by disturbance. Moritz and Agudo (2013), for example, found that many species in the fossil record existed over a wider range of climates than is recorded today. BEMs also assume that current species distribution is a consequence of climate alone, yet we know that many other factors, such as fire exclusion, exotic diseases, and management actions, have reduced whitebark pine occurrence over historical conditions (Tomback et al. 2001*a*). Data used to represent climates in BEM model development represent a small slice of time (50–100 years) relative to the long time that long-lived trees, especially whitebark pine, which can live longer than 1000 years, have survived, so these limited climate datasets rarely capture the full range of climate experienced by trees sampled in the field. Along these same lines, whitebark pine can certainly live longer than the 100-year projections of future climate. And perhaps most important, future climate inputs are well outside of the weather data used to develop the statistical model. These limitations make it difficult to use BEM projections to restore whitebark pine; they are informative, but not prognostic, especially on short time scales of decades and half-centuries required by land management and at spatial scales of project implementation.

There are several limitations of this simulation experiment that are important when interpreting our modeling results. First, there are several problems with the GCM simulated future climate data that demands attention, such as the limited temporal range, mismatch of historical and simulated historical weather, and improper transition from historical simulation to future simulation. For this study, we used the 95-year CMIP5 simulated historical and future weather as recommended by several GCM modelers and climate change experts, whereas our earlier methods, and in the 500-year ancillary runs in this study, we relied on observed historical weather and offsets for future conditions (see Loehman et al. 2011*b*; Holsinger et al. 2014). The documented inaccuracy of the historical CMIP5 weather data adds another level of uncertainty to interpretation of our simulation results and clouds our findings because FireBGCv2 simulations using CMIP5 simulated historical weather often did not result in realistic vegetation dynamics; however, we simulated realistic conditions when actual observed historical weather was used (Keane et al. 2011; Loehman et al. 2011*b*; Holsinger et al. 2014). Second, there appears to be the same or less variability in future projections, especially for precipitation and especially on the EFBR landscape. This may be a result of the downscaling of the GCM climate data or it could be inadequate GCM simulations. This lack of variability probably resulted in unrealistic fire dynamics, especially for the CROWN landscape where large fire years were rare in the future simulations. And last, there appears to be a problem with the transition of the historical simulation to the future; temperature projections at the end of the EFBR historical simulation do not match the start of the future projections. This compromises the validity of the short 95-year future projection if it is starting at a different value than the historical end.

Management Implications

Active restoration involving thinning, burning, and planting appears to be critical for conserving some Northern Rocky Mountain U.S.A. whitebark pine ecosystems. The loss of a major high elevation ecosystem from WPBR, MPB, fire exclusion, and climate change might be irreversible and with it goes tremendous biodiversity, ecosystem services, and ecosystem function, thereby impoverishing our biological heritage (Tomback et al. 2001*a*; Tomback & Achuff 2010). Restoration provides a hedge against the adverse effects of climate warming on whitebark pine and mitigates anthropogenic threats. However, the high uncertainty inherent in most current climate and ecosystem models and assessments may limit our capacity to assess whether restoration actions will be effective in the face of climate change on certain landscapes. Silvicultural cuttings, prescribed burning, wildland fire use, and planting are all effective treatments to restore this valuable ecosystem now and in the future, and without these treatments, our model predicts that whitebark pine forests will continue to decline. Managers are recommended to prioritize higher elevations of whitebark pine's current range for treatment, avoid planting in predicted future ranges because of uncertainty in climate projections, and utilize microsites for planting to mitigate possible climate change effects. More detailed management recommendations from this simulation study that supplement the Keane et al. (2012) whitebark pine range-wide strategy are available in the study of Keane et al. (2016).

Acknowledgments

This effort was mostly funded by the Great Northern Landscape Conservation Cooperative (GNLCC). We also thank M. Retzlaff, U.S. Forest Service, Rocky Mountain Research Station, for extensive editing and quality control; R. Nelson, Crown of the Continent Conservation Initiative; A. Bower, U.S. Forest Service; S. McKinney, USGS; and K. Ireland, Montana State University, for extensive reviews of various versions of the document.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Results of generalized linear mixed models for the effects of planting, restoration, suppression climate, and year.

Figure S1. Independent simulations of the long-term dynamics (500-year simulations) of whitebark pine basal area (m^2/ha) and proportion of landscape area in whitebark pine zone.

Coordinating Editor: Beth Newingham

Received: 13 January, 2016; First decision: 9 March, 2016; Revised: 1 July, 2016; Accepted: 1 July, 2016; First published online: 16 August, 2016