Modeling Climate Changes and Wildfire Interactions: Effects on Whitebark Pine (*Pinus albicaulis*) and Implications for Restoration, Glacier National Park, Montana, USA

Paper

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Abstract—Climate changes are projected to profoundly influence vegetation patterns and community compositions, either directly through increased species mortality and shifts in species distributions, or indirectly through disturbance dynamics such as increased wildfire activity and extent, shifting fire regimes, and pathogenesis. High-elevation landscapes have been shown to be particularly sensitive to climatic change and are likely to experience significant impacts under predicted future climate change conditions. Whitebark pine (*Pinus albicaulis*), a keystone and foundation five-needle pine species, is vulnerable to multiple and interacting disturbances that have already caused major changes in species distribution and abundance. We used the mechanistic simulation model FireBGCv2 to assess potential interacting effects of future climate changes and wildfire patterns on the presence and persistence of whitebark pine in a high-elevation watershed in Glacier National Park, Montana, USA. We did not include white pine blister rust and mountain pine beetles as disturbance factors in our simulation so that we could isolate climate-fire impacts, and because these disturbance factors have already so severely reduced whitebark pine populations in the area that few live trees remain. Hence, our results presume the establishment of initial populations of live, rust-resistant trees on the MD-GNP landscape through successful restoration efforts. Our results indicate that climate changes may significantly impact whitebark pines in this region through indirect mechanisms including altered distributions of competing tree species and increased fire frequency and fire size. The sensitivity of the species to a complex suite of interacting disturbance agents suggests that conservation efforts must address and mitigate these multiple threats through a suite of restoration treatments including planting of rust-resistant stock, fuels treatments, and prescribed burning to restore whitebark pine to its current range. In addition, additional simulation modeling experiments should be developed to identify areas suitable for restoration under potential future climate regimes and test efficacy of restoration strategies under these new climate conditions.

Introduction

Climate changes are projected to profoundly influence landscape patterns and biotic community compositions either directly through increased species mortality and shifts in species distributions, or indirectly from factors such as increased wildfire activity and extent, shifting fire regimes, and pathogenesis (Bentz and others 2010; Dale and others 2001; Flannigan and others 2000; Lenihan and others 2003; McKenzie and others 2004). High-elevation landscapes have been shown to be particularly sensitive to climatic change and are likely to experience significant impacts under predicted future climate change conditions (Fagre and Peterson 2000). Whitebark pine (*Pinus albicaulis*), an important high-elevation five-needle pine that is both a keystone and foundation species (Logan and others 2010), is particularly sensitive to a complex set of interacting disturbances—climatic change, anthropogenic fire exclusion, white pine blister rust (*Cronartium ribicola*), and mountain pine beetles (*Dendroctonus ponderosae*)—that have already caused major changes in species distribution and density (Keane and Parsons 2010). Further changes in abiotic and biotic conditions will likely pose additional threats to the success of this treeline species, with likely negative consequences for snowpack accumulation and retention, timing and amount of surface water runoff, wildlife habitat and food availability, and forest succession and structure in subalpine environments in the northern Rocky Mountains (Keane and Parsons 2010; Klasner and Fagre 2002; Tomback and others 2001).

We developed a simulation modeling experiment using the mechanistic ecosystem process model FireBGCv2 (Keane and others 2011) to assess the effects of predicted future climate changes and wildfire patterns on whitebark pines in the Northern Rocky Mountains. Our objective was to test whether different trajectories of climate change would result in markedly different wildfire patterns and abundance and persistence of whitebark pine-dominated stands within the study landscape. We incorporated two climate change scenarios designed to span a range of potential regional climate futures from warmer and wetter to hotter, drier conditions. Differences in these climate projections result from alternate trajectories of global anthropogenic drivers and associated greenhouse gas emissions (IPCC 2007). We hypothesized that warming temperatures would negatively affect whitebark pine stands at lower elevations within their current range as the result of species thermal limits and competitive replacement by lower-elevation conifers; but

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

that habitat areas for whitebark pine would increase at the upper margins of subalpine niches as temperature isotherms shifted upslope. Such upward and latitudinal migration of high-elevation forests has been previously noted in response to long-term climate trends (IPCC 2007; Millar and others 2004). Ecological niche shifts may be further complicated by altered fire regimes, which have been associated with observed and predicted changes in temperature and moisture regimes at multiple temporal and spatial scales (Heyerdahl and others 2008; Littell and others 2009; Schoennagel and others 2004; Westerling and others 2006). For example, climate changes may increase fire frequencies in high-elevation forests that historically experienced stand-replacement wildfires at long fire return intervals, as warmer temperatures and altered moisture patterns contribute to changes in fuel availability and fuel moisture. Although the important role of climate as a driver of wildfires (Heyerdahl and others 2008; Kitzberger and others 2007; Morgan and others 2008) together with the dominant role of wildfires in shaping vegetation composition and structure (Flannigan and others 2000) suggests that predictive modeling approaches for species distributions must incorporate wildfire-climate dynamics, few models are capable of integrating these complex dynamics. For example, correlative species distribution or bioclimatic envelope models are commonly used to assess climate change effects on species ranges, but are widely criticized for failing to take complex ecological interactions and species life histories into account (Hampe 2004; Heikkinen and others 2006; Sinclair and others 2010). In contrast, FireBGCv2 provides a method for mechanistically modeling the interactive effects of climate changes and wildfires on vegetation dynamics.

The FireBGCv2 modeling platform combines a mechanistic, individual tree succession model with a spatially explicit fire model incorporating ignition, spread, and effects on ecosystem components, all with stochastic properties implemented in a spatial domain (Keane and others 2011; Keane and others 1999; Keane and others 1998; Keane and others 1996). The model is designed around five hierarchical levels of spatial organization from coarse, fixed-boundary sites defined on the basis of similar topography, weather, soils, and potential vegetation; to dynamically-created stands that differ by existing vegetation composition and structure; to simulation plots on which ecosystem processes are modeled for computational efficiency; to species with well-defined physiological parameters; to individual trees, each of which is explicitly represented with attributes such as age, height, diameter at breast height, and height to live crown (Figure 1).

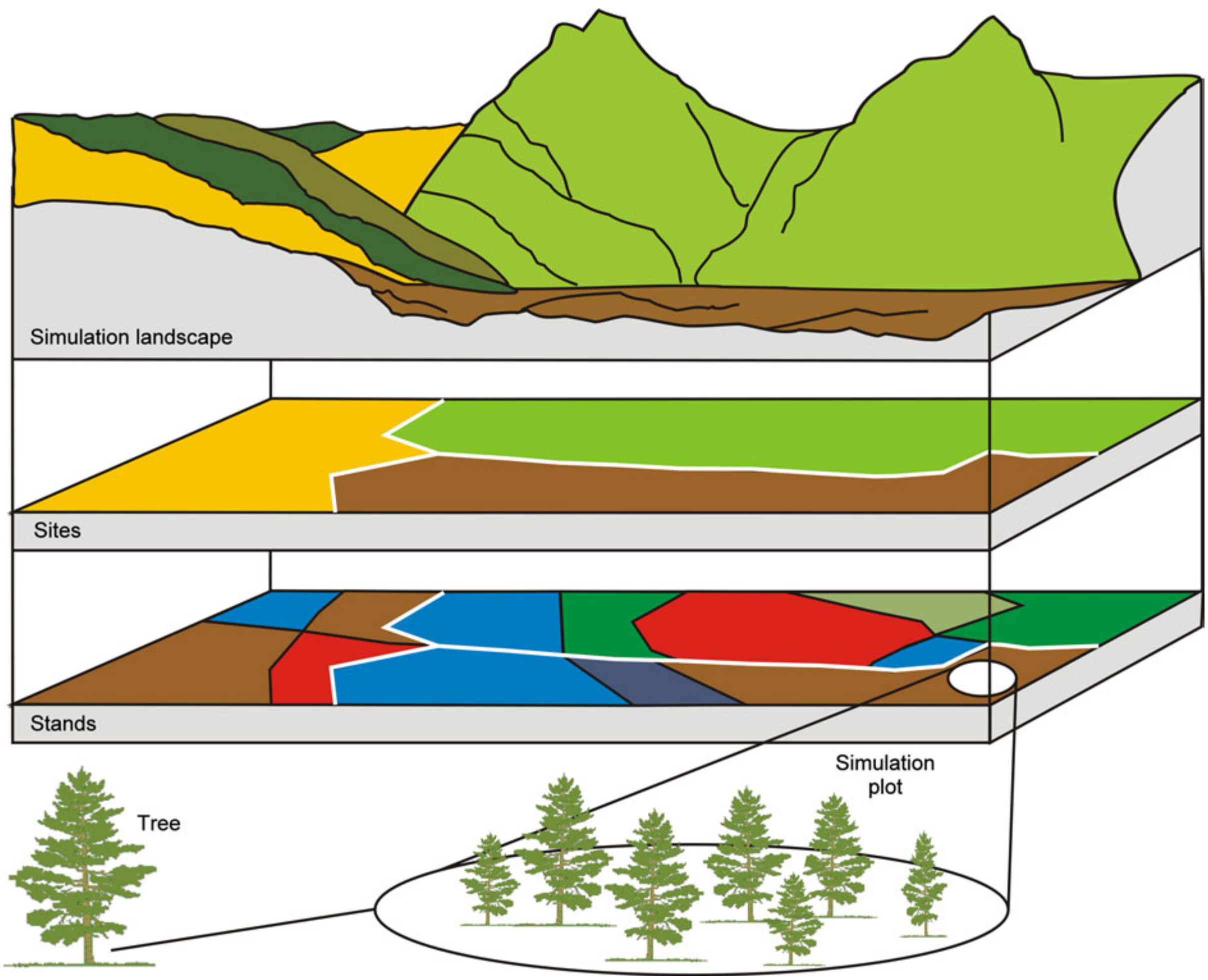


Figure 1. Hierarchical levels of spatial organization in the FireBGCv2 simulation modeling platform.

Weather and climate are important inputs to FireBGCv2 because they drive the primary canopy processes of transpiration, photosynthesis and respiration. Potential climate change effects on ecosystems are incorporated into the simulation through a series of parameters that alter daily observed (instrumental) weather streams along user-defined climate pathways including projected offsets of seasonal precipitation and temperature and annual offsets of atmospheric CO_2. Weather and climate also dynamically affect the simulation of wildfires through stand-level effects on fuel availability and fuel moisture.

Tree growth, regeneration, organic matter decomposition, litterfall and other ecological processes are simulated using detailed physical biogeochemical relationships for individual tree species. Tree establishment and mortality are modeled using probability functions with ecologically-derived parameters. Annual carbon and nitrogen gains computed daily for each stand are allocated to each tree in the stand at the end of each year and then apportioned to the stem, roots and leaves. Carbon allocation to the stem of a tree is used to calculate a corresponding diameter and height growth. Material from trees (fallen needles, leaves, and branches) is added to the fuelbed and eventually decomposes based on available water, nitrogen, and light. Whitebark pine regeneration is accomplished through a species-specific module that simulates the effects of seed crop, seed dispersal by the Clark's nutcracker, and light on whitebark tree sapling establishment (Keane and others 1990). Although FireBGCv2 can also be used to simulate effects of additional mortality factors such as white pine blister rust and mountain pine beetles, these factors were not included in the current simulation experiment.

Methods

Study Area

We simulated climate-disturbance interactions on the McDonald drainage of Glacier National Park, Montana, USA (MD-GNP, Figure 2). The MD-GNP watershed is a long, narrow, glaciated valley approximately 45,000 ha in area that contains a large lake at its base and is surrounded by rugged mountains. Elevations range from approximately 830 to 2,900 meters above sea level (masl), and the watershed is characterized by diverse and complex topography, climate, vegetation, and fire regimes. Climate within the MD-GNP watershed is mainly inland-maritime with cool, wet winters and short, warm-dry summers (Finklin 1986). Average annual precipitation ranges from 760 millimeters at West Glacier to over 1,980 millimeters at Flattop Mountain, and the majority of annual precipitation occurs as snow (Finklin 1986). Maximum July daily temperatures range from 26 °C in the lower valleys to 18 °C at 2,000 masl.

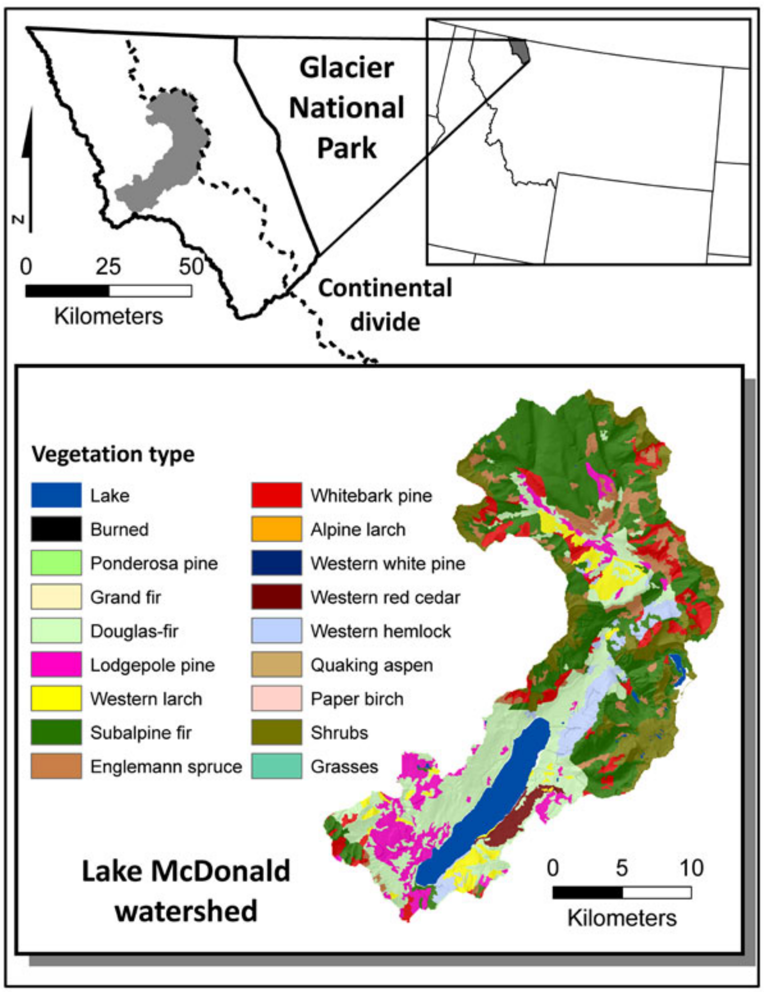


Figure 2. McDonald drainage of Glacier National Park, Montana, USA (MD-GNP).

Vegetation in the MD-GNP watershed consists of low-elevation forests of western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) in relatively, warm, moist lakeside environments, and western larch (*Larix occidentalis*), western white pine (*Pinus monticola*), interior Douglas-fir (*Pseudotsuga menziesii* var *glauca*), and lodgepole pine (*Pinus contorta* var. *contorta*) in drier low-elevation areas (Habeck 1970a; Kessell 1979). Upper subalpine forests consist primarily of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) (Habeck 1970a). Alpine environments (2,200 masl and above) support Krummholz conifer and forb meadow communities (Habeck and Choate 1963). Although historically whitebark pine communities were a significant component on up to 20 percent of forested lands in Glacier National Park, currently an estimated 44 to 90 percent of these trees are dead and more than 75 percent of remaining trees are lethally infected with white pine blister rust and likely to die within the next 20 years (Graumlich 2006; Kendall and Keane 2001). Additional threats to whitebark pine persistence in Glacier National Park and elsewhere include mountain pine beetle outbreaks that have killed larger, cone-bearing trees and fire exclusion practices that have allowed for the incursion of shade tolerant tree species (notably subalpine fir) into whitebark pine forests (Keane and Parsons 2010). Although our field data indicated that whitebark pines were present as a stand-level dominant tree species on approximately seven percent of the MD-GNP watershed, the presence of stumps and snags within study plots suggests that combined biotic and abiotic disturbances had already significantly reduced the abundance of the tree species at the time of data collection (Keane and others 1999).

Two distinct fire regimes are historically evident on the MD-GNP landscape: large, stand-replacement fires at return intervals of 120 to 350 years on moist sites and mixed-severity surface fires with approximately the same return intervals on drier areas of the watershed (Barrett 1986; Barrett and others 1991; Habeck 1970b) (Table 1). This mixed fire regime features a combination of fires that kill all trees in some areas and nonlethal underburns that kill only small trees and fire-intolerant species in other areas (Habeck 1970a). The complex topography of MD-GNP has considerable influence on fire behavior and effects via the spatial arrangement of fuels on the landscape. Rocky areas with low accumulation of woody fuels impede fire spread across and within the watershed, and moist conditions on north-facing slopes often prevent spread of fire from the drier south-facing slopes (Habeck 1970a).

Table 1. Biophysical characteristics and historical fire frequency for the McDonald drainage of Glacier National Park, Montana, USA.

Site ID	Site Potential Vegetation	Average elevation (m)	Historical Fire Frequency (yrs)
1	Subalpine fir (low/wet)	1334	300
2	Subalpine fir (upper/dry)	1954	250
3	Subalpine fir (middle/dry)	1682	250
4	Subalpine fir (upper/wet)	1850	350
5	Subalpine fir (low/dry)	1288	250
6	Subalpine fir (middle/wet)	1513	300
7	Western hemlock (wet)	1086	350
8	Western hemlock (dry)	1006	300
9	Barren/Low vegetation	2180	450

Simulation Methods

We implemented three climate scenarios on the MD-GNP landscape over a 350-year simulation period. Detailed simulation methods are given in Keane and others (1996); briefly, site, stand and tree input spatial data layers and data files needed to parameterize and initialize the MD-GNP simulation landscape were quantified from field data, the literature, existing spatial data layers, and satellite imagery. Parameters that describe various site-level ecological processes and conditions across the simulation landscape were quantified from summaries of the field data, as were stand-level input parameters for fuels and tree and understory species. We modeled multiple climate regimes because although, as mentioned above, anthropogenic climate changes are projected to significantly alter ecosystem processes and patterns, few modeling studies examine potential future terrestrial landscape changes in the context of restoration (but see Covington and others 2001; Diggins and others 2010; Ravenscroft and others 2010). We suggest that simulation models provide one of the best vehicles to investigate the dynamic interactions among climate, fire, vegetation, and management, and can provide useful assessment tools for land managers designing restoration efforts under conditions of rapid ecological change, particularly where multiple trajectories of future climate regimes may exist.

Climate

We tested the effects of three climate regimes (historical conditions and two climate change scenarios) on landscape and fire dynamics. Historical conditions were derived from a 44-year (1950-1994) daily instrumental weather stream from the West Glacier weather station located within the McDonald watershed (NCDC 2011). We further used the Mountain Climate Simulator (MT-CLIM) (Hungerford and others 1989; Running and others 1987) to extrapolate the historical weather stream to sites on the simulation landscape with different elevations, slopes, and aspects. To simulate an historical climate regime the model cycled through this 44-year weather record in sequence for the duration of the simulation period. Warmer-wetter and hotter-drier climate regimes represent potential future climate trajectories for the northern Rocky Mountain region in the coming centuries, and provide insight into the conditions under which whitebark pine restoration may be implemented in the future. Both climate change scenarios used the West Glacier historical weather data set as a baseline, adjusted by modifying seasonal temperature and precipitation and starting and ending atmospheric CO_2

Table 2. Temperature (ΔT, °C) and precipitation (ΔP, cm) offsets and starting and ending atmospheric CO_2 concentrations (ppmv) for historical, A2, and B2 climate scenarios. Offsets are implemented seasonally, where Winter = January/February, Spring = March/April/May, Summer = June/July/August, and Fall = September/October/November/December.

	Element	HIST	B2	A2
Winter	ΔT	0.00	1.80	2.50
	ΔP	0.00	0.99	1.11
Spring	ΔT	0.00	1.00	3.00
	ΔP	0.00	1.17	1.02
Summer	ΔT	0.00	2.10	6.70
	ΔP	0.00	1.24	0.66
Fall	ΔT	0.00	1.60	4.60
	ΔP	0.00	1.05	0.93
	start CO_2	287	369	369
	end CO_2	287	621	856

levels (Table 2). Values for these offsets were derived relative to a 1950-1999 base period from the Hadley Centre (UK) HadCM3 general circulation model (GCM), using an average of grid points corresponding to the Pacific northwest region (Mote 2003) for Intergovernmental Panel on Climate Change (IPCC) Special Report on Emission Scenarios (SRES) A2 and B2 emissions scenarios (Nakicenovic and others 2000). The A2 scenario describes a heterogeneous world with high population growth, slow economic development and slow technological changes and is associated with significant changes in regional climatology; specifically hotter-drier summers (+6.7 ˚C, -34 percent precipitation) and warmer-wetter winters (+2.5 ˚C, -11 percent precipitation) as compared with current conditions. The B2 scenario describes a world with intermediate population and economic growth, emphasizing local solutions to economic, social, and environmental sustainability, and is projected to result in warmer- wetter summer conditions (+2.1 ˚C, +24 percent precipitation) and warmer but slightly drier winters (+1.8 ˚C, -1.0 percent precipitation) across the study region. Temperature and precipitation offsets and CO_2 levels were ramped up in even annual increments for the first 100 years of the simulation and then held at those levels for the following 250 simulation years.

Whitebark pine

Although none of the whitebark pines present in the input tree list for MD-GNP were live at the time of field data recording due to high mortality from white pine blister rust as described above, we recoded them as live trees to produce a viable parent population. Even so, this tree list describes a relatively low initial proportion of whitebark pine-dominated stands on the simulation landscape (approximately seven percent), likely because of long-term competitive exclusion from subalpine fir. We further did not include white pine blister rust as a disturbance factor in the simulations because it is likely that few whitebark pines would have persisted long enough for seed dispersal to occur, as when white pine blister rust is specified as a factor a 99 percent rust mortality probability is imposed on all five-needle pines. Mountain pine beetle mortality can be selected as an additional simulated disturbance type, but this mortality factor was not included in this experiment so that we could isolate climate-fire impacts. Thus our experimental results assume an initial population of live, rust-resistant, reproductively mature whitebark pines on the MD-GNP landscape such as would result from the implementation of a successful integrated restoration program.

Wildfire

All simulations were performed under natural fire regime conditions in which all fires simulated on the study area were allowed to burn without enacting fire suppression factors. We defined historical fire return intervals using fire chronologies, fire history data, and fire atlases for Glacier National Park and elsewhere (Keane and others 1999). The frequency of ignition and points of origin of simulated fires were stochastically predicted at a yearly time step across the simulation landscape and climate, fuels and fire management were mechanistically linked such that the stand-level probability of fire occurrence was scaled to the size of the stand, level of fire management, and climate. The potential for a stand to experience ignition (burnability) was determined by the amount and type of fuel in the stand (Keane and others 2011).

Analysis

Our simulation experiment produced both non-spatial and spatial output files. Non-spatial, stand-level output contained an array of variables aggregated by simulation year; we summarized stand area and dominant tree species per stand based on basal area using data management and analysis tools in the R and MATLAB software packages (MATLAB 1984-2009; R Development Core Team 2010). Non-spatial, landscape-level output included cumulative number of wildfires, average and maximum fire size, and cumulative area burned during each simulation year. We produced spatial output in the form of thematic map layers for specific annual stand-level variables including dominant species by basal area and cumulative number of fires. ESRI ArcMap software was used to display and analyze spatial data layers (ESRI 1999-2009).

Results

We observed significant changes in abundance and persistence of whitebark pine on the MD-GNP simulation landscape across the 350-year simulation period (Figure 3). The proportion of the landscape dominated by whitebark pine decreased sharply during the first 100 years of the simulation for all modeled climate scenarios, consistent with an increase in wildfires under our modeled natural fire regime. Subsequently, under historical climate conditions the proportion of whitebark pine increased as newly germinated trees reached minimum reproductive age (60 years) and produced seed. Thus, by simulation year 190 whitebark

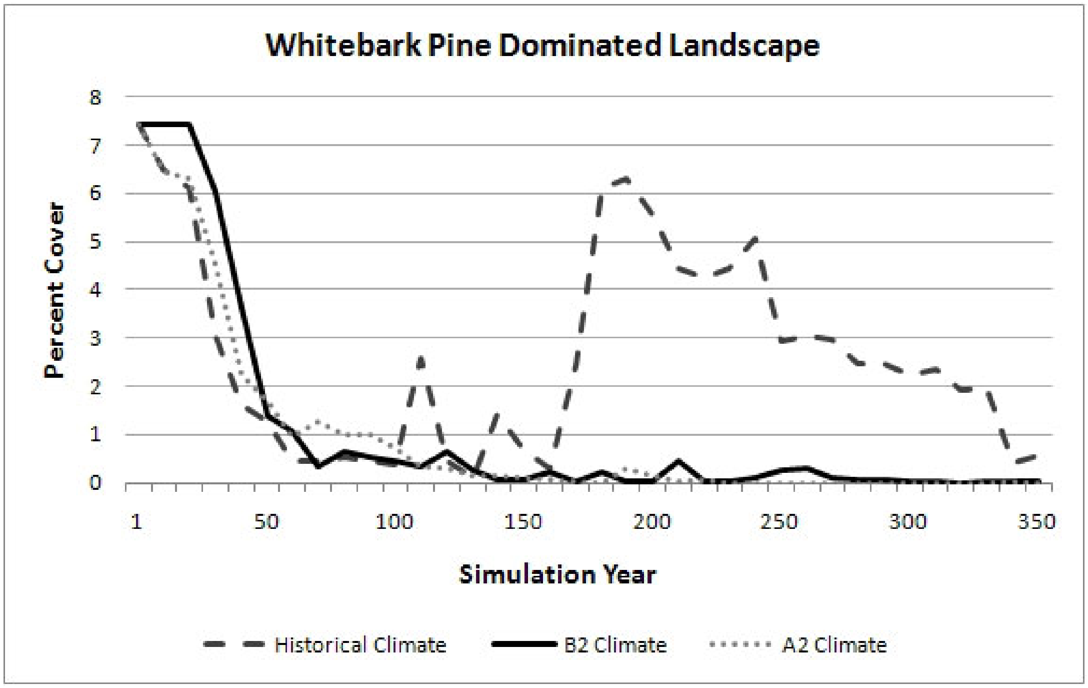


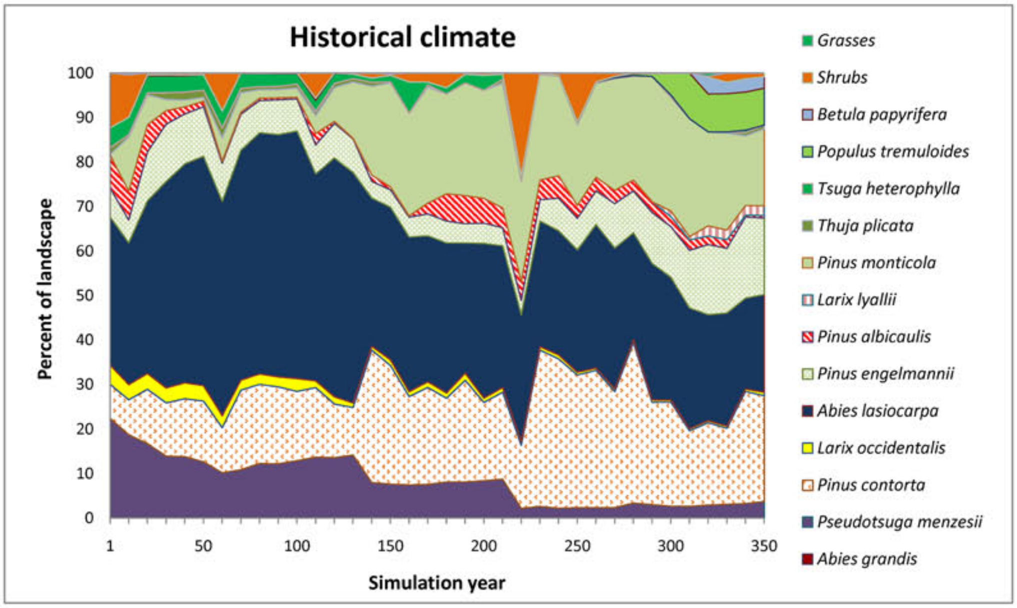
Figure 3. Changes in abundance and persistence of whitebark pine on the MD-GNP simulation landscape across the 350-year simulation period for historical (solid line), B2 (dash) and A2 (dot) climate scenarios.

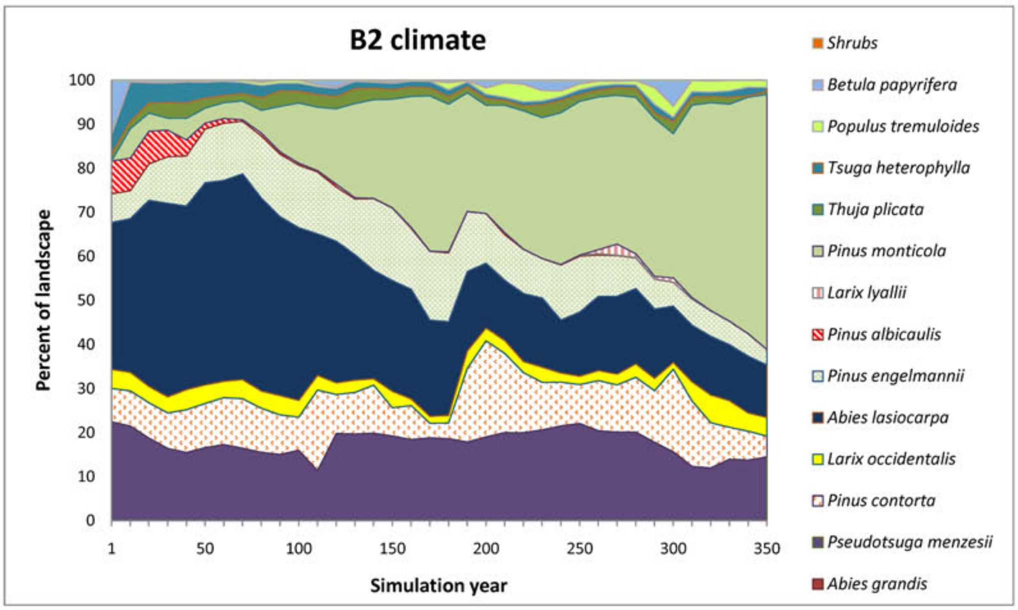
pines were dominant in over six percent of the MD-GNP landscape, nearly to the level described by our input data. For the A2 and B2 climate scenarios less than one percent of the landscape retained whitebark pines as a dominant overstory component from simulation years 60 onward, and no whitebark-pine dominated stands existed under A2 climate conditions beyond simulation year 230.

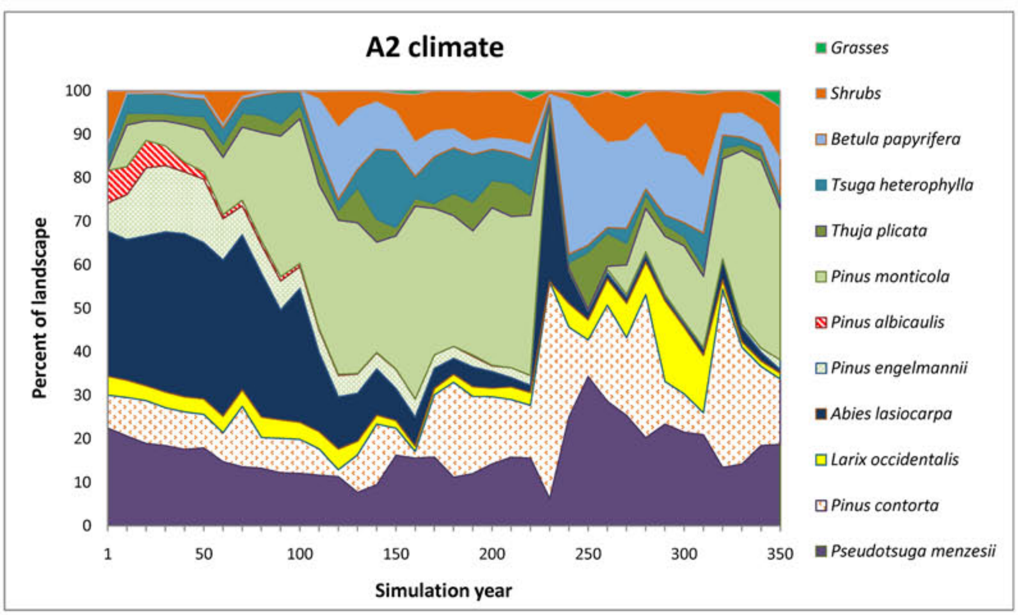
Simulated historical climate conditions resulted in temporal variation in the proportion of the MD-GNP watershed occupied by subalpine fir, Douglas-fir, lodgepole pine, and western white pine (Figure 4). The abundance of western white pines was facilitated by the exclusion of blister rust and mountain pine beetles as disturbance factors in the simulation experiment; although these trees were historically a major constituent of landscapes in the inland northwest before the 20th century, they have declined greatly in both distribution and extent (Tomback and Achuff 2010).

The percent of the MD-GNP landscape dominated by shade tolerant tree species decreased across the simulation period for all climate scenarios (Figure 5), likely as the result of our imposed natural fire management scenario and its effect on reducing overstory biomass developed during the 20th century period of fire exclusion in the northern Rocky Mountains. Increases in shade tolerant species within scenarios occurred during periods of decreased wildfire activity, as expected in forested landscapes where shade-tolerant species usually dominate later stages of succession (Keane and others 1998). In addition, the spatial arrangement of vegetation types differed among scenarios and as simulations progressed as the result of climate-fire interactions. Under historical climate conditions some upper elevation areas of the watershed initially dominated by subalpine fir were replaced by Englemann spruce and, to a lesser extent, subalpine larch and aspen-dominated stands, while lodgepole pine and western white pine increased in lower elevation areas (Figure 6). For the B2 and A2 scenarios upper elevation subalpine fir stands were almost completely replaced by western white pine and Douglas-fir dominated stands, with an additional component of lodgepole pine and paper birch *(Betula papyrifera)*. The dominant role of wildfires in shaping landscape vegetation is evident in thematic maps of overstory structural stage showing the decrease in mature trees with increasing fire activity on the landscape (Figure 7).

Wildfire patterns differed across historical and climate change scenarios. The model simulated 251 wildfires in 170 fire years for the historical climate scenario, as compared with 304 wildfires in 180 fire years for the B2 scenario and 536 fires in 253 fire years for the A2 scenario (Table 3). Maximum and average wildfire size were larger for the A2 climate than simulated historical or B2 climates, and over the 350 years of the simulation two and a half times more area burned under the A2 scenario than under simulated historical conditions (Figure 8, Table 3). Fires burned a majority of the landscape area under all simulated climate conditions, and only a very small proportion of the landscape was left unburned under A2 climate conditions (0.03 percent). Warmer-wetter conditions associated with the B2 climate scenario decreased average and maximum wildfire size and cumulative area burned and increased the proportion of unburned landscape as compared with the historical climate scenario. Repeat fires (reburns) occurred across much of the simulation landscape for all modeled climate regimes. Approximately 78 percent of the simulation landscape reburned under the modeled historical climate regime as compared with 85 percent for the B2 scenario and 95 percent for the A2 scenario (Figure 9). Shifts in temperature and precipitation associated with the A2 and B2 scenarios did not markedly alter the distribution







Figures 4a-4c. Percent of the MD-GNP simulation landscape occupied by tree species, shrubs, and grasses for the 350-year simulation period, where colored bands represent individual cover types and the width of the area fill at each timestep represents the percentage of the landscape occupied by that cover type.

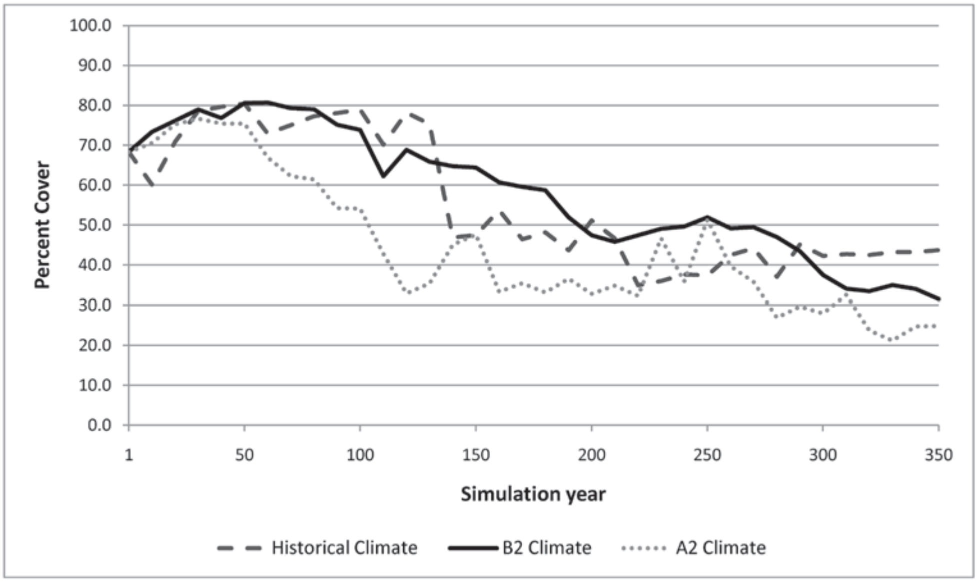


Figure 5. Temporal changes in the percent of the MD-GNP landscape dominated by shade tolerant tree species for historical, A2, and B2 climate scenarios. Shade tolerant tree species are grand fir, Douglas-fir, subalpine fir, Englemann spruce, western red cedar, and western hemlock.

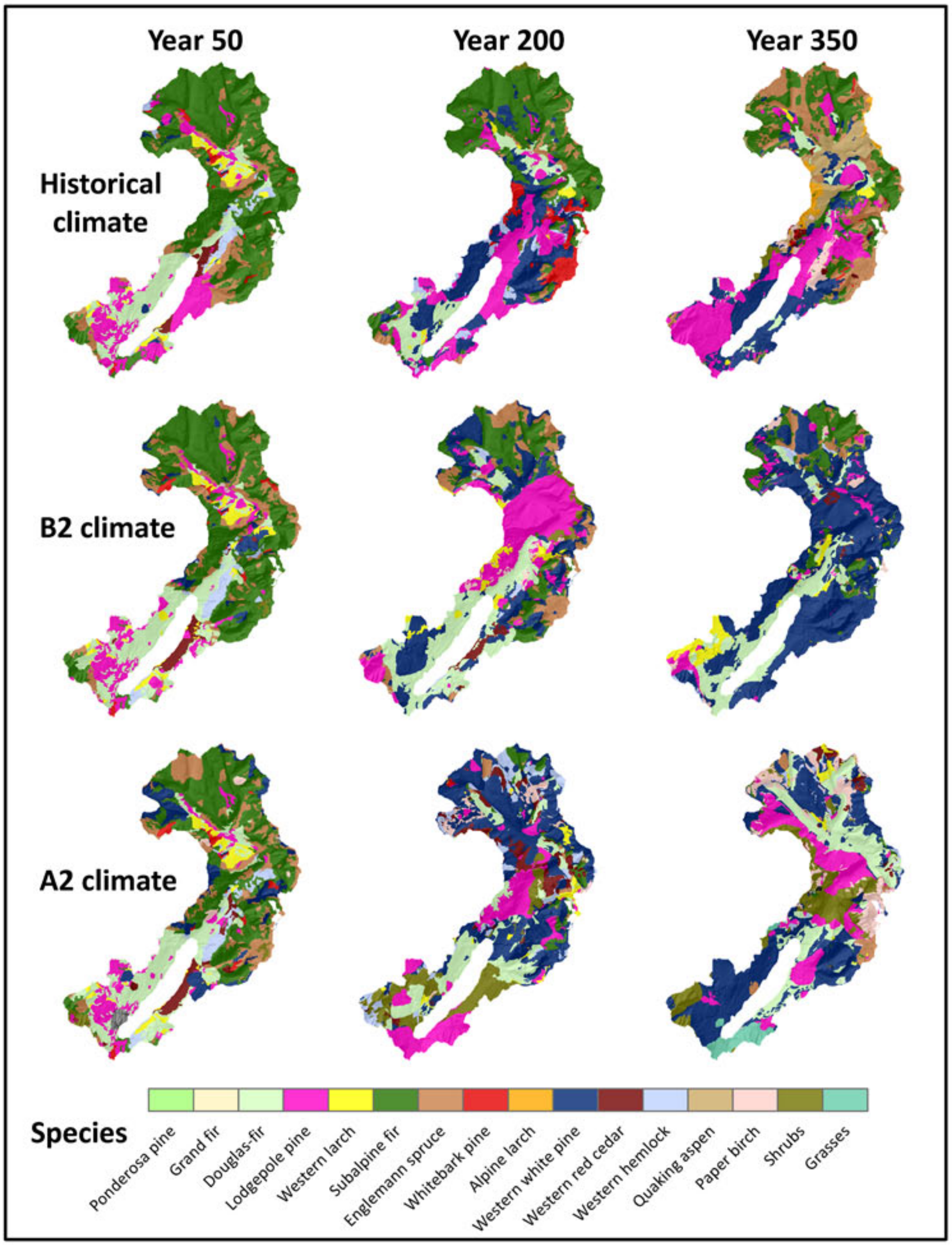


Figure 6. Dominant species by basal area on the MD-GNP simulation landscape for historical, B2, and A2 climate scenarios, simulation years 50, 200, and 350.

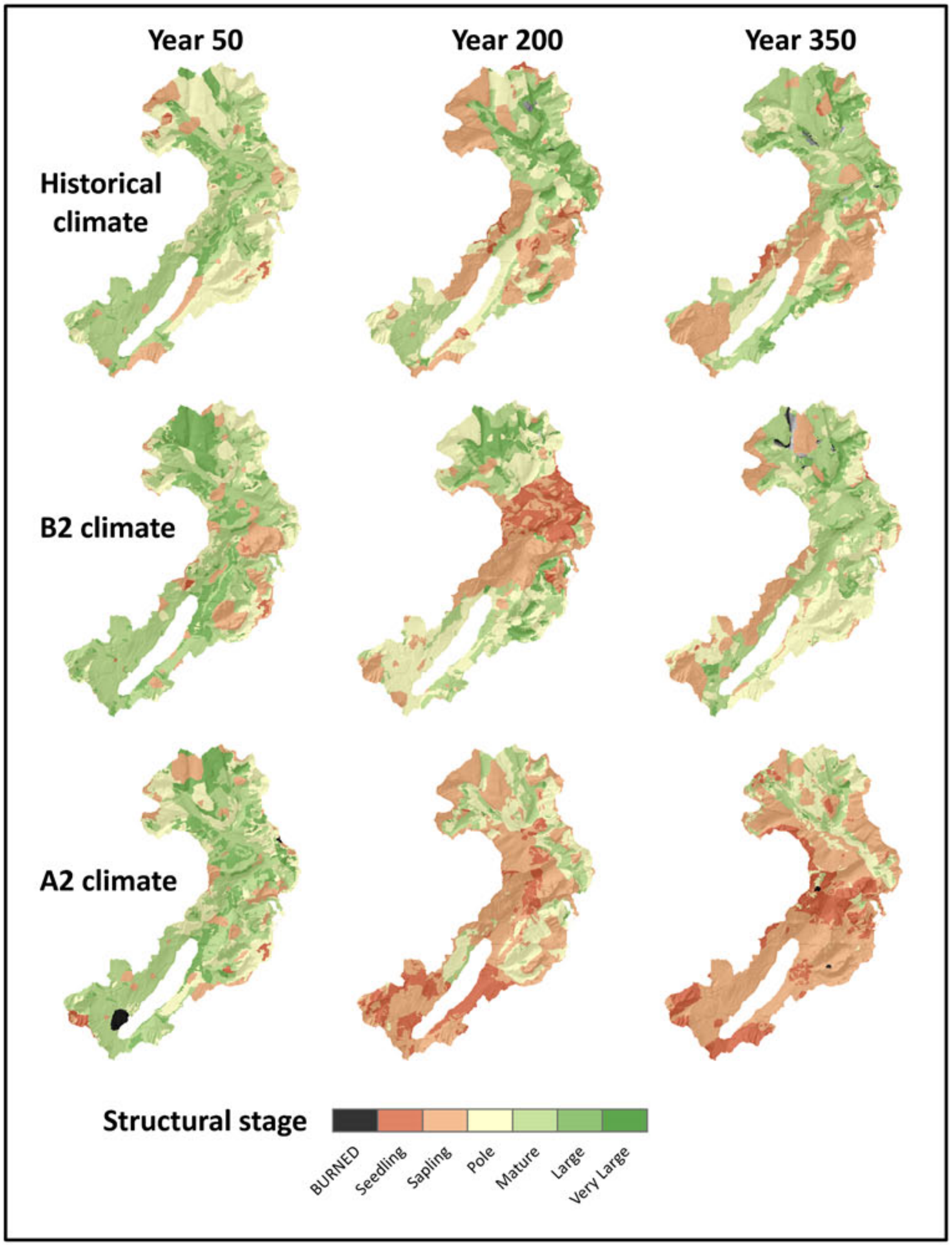


Figure 7. Overstory structural stage on the MD-GNP simulation landscape for historical, B2, and A2 climate scenarios, simulation years 50, 200, and 350.

Table 3. Simulated wildfire dynamics for the McDonald drainage of Glacier National Park, Montana, USA under historical, B2, and A2 climate scenarios for a 350-year simulation period.

Parameter	Historical climate	B2 climate scenario	A2 climate scenario
Cumulative number of wildfires	251	304	536
Cumulative number of wildfire years (yrs)	170	180	253
Cumulative area burned (ha)	126774.72	112406.94	314900.37
Landscape burned area multiplier	2.94	2.61	7.31
Percent of landscape unburned (%)	8.77	10.29	0.03
Average fire size (ha)	505.10	369.76	587.50
Maximum fire size (ha)	14233.33	7281.63	27383.4

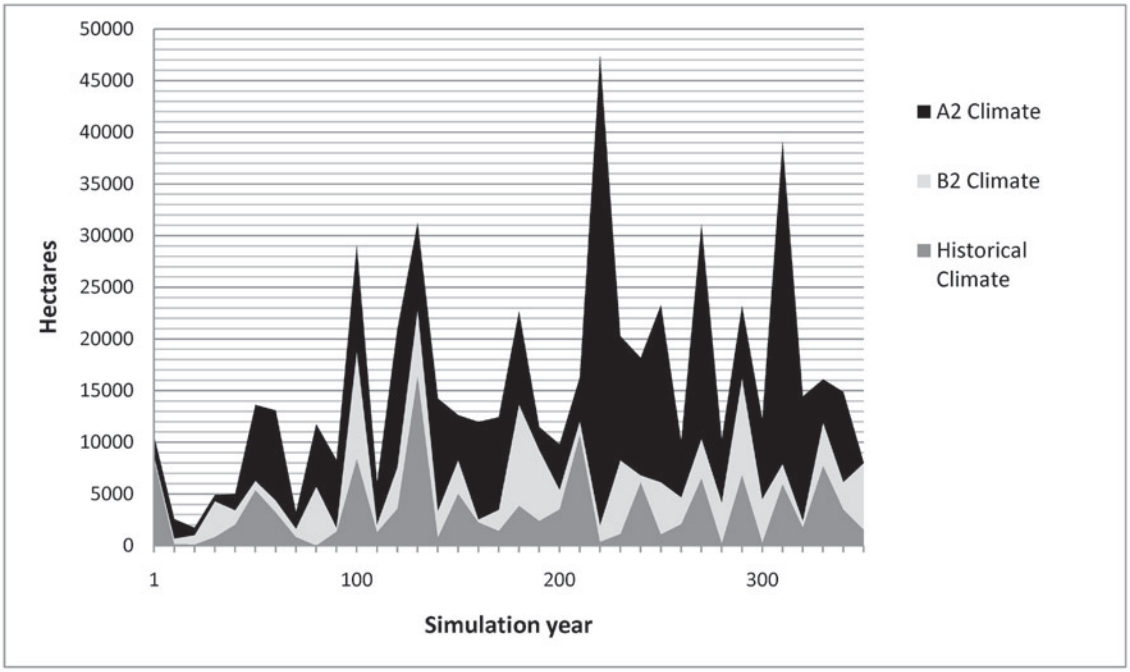


Figure 8. Annual burned area on the MD-GNP simulation landscape for historical, B2, and A2 climate scenarios for a 350-year simulation period.

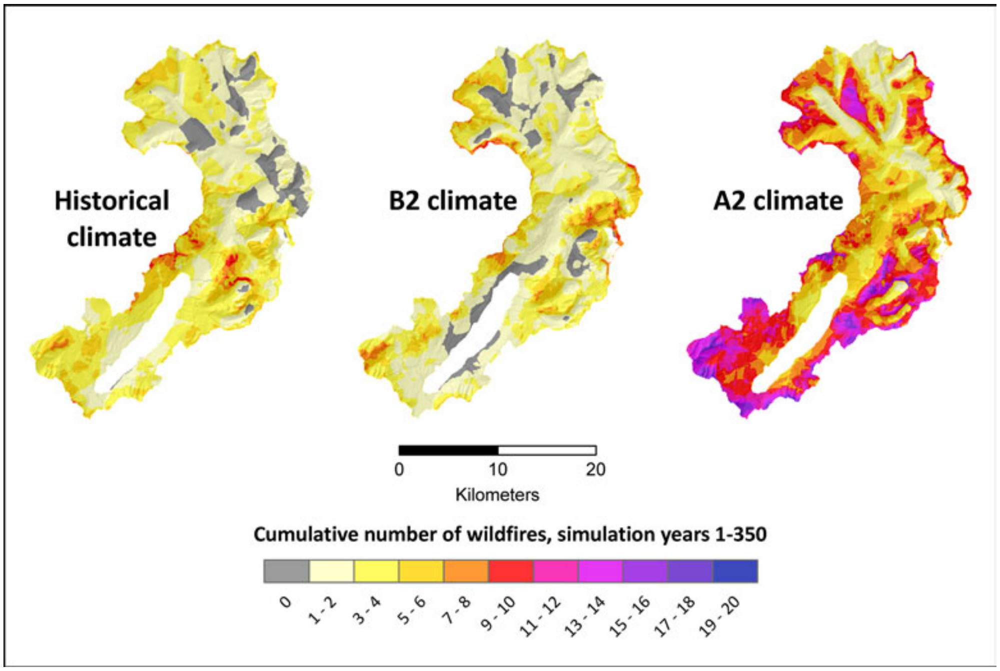
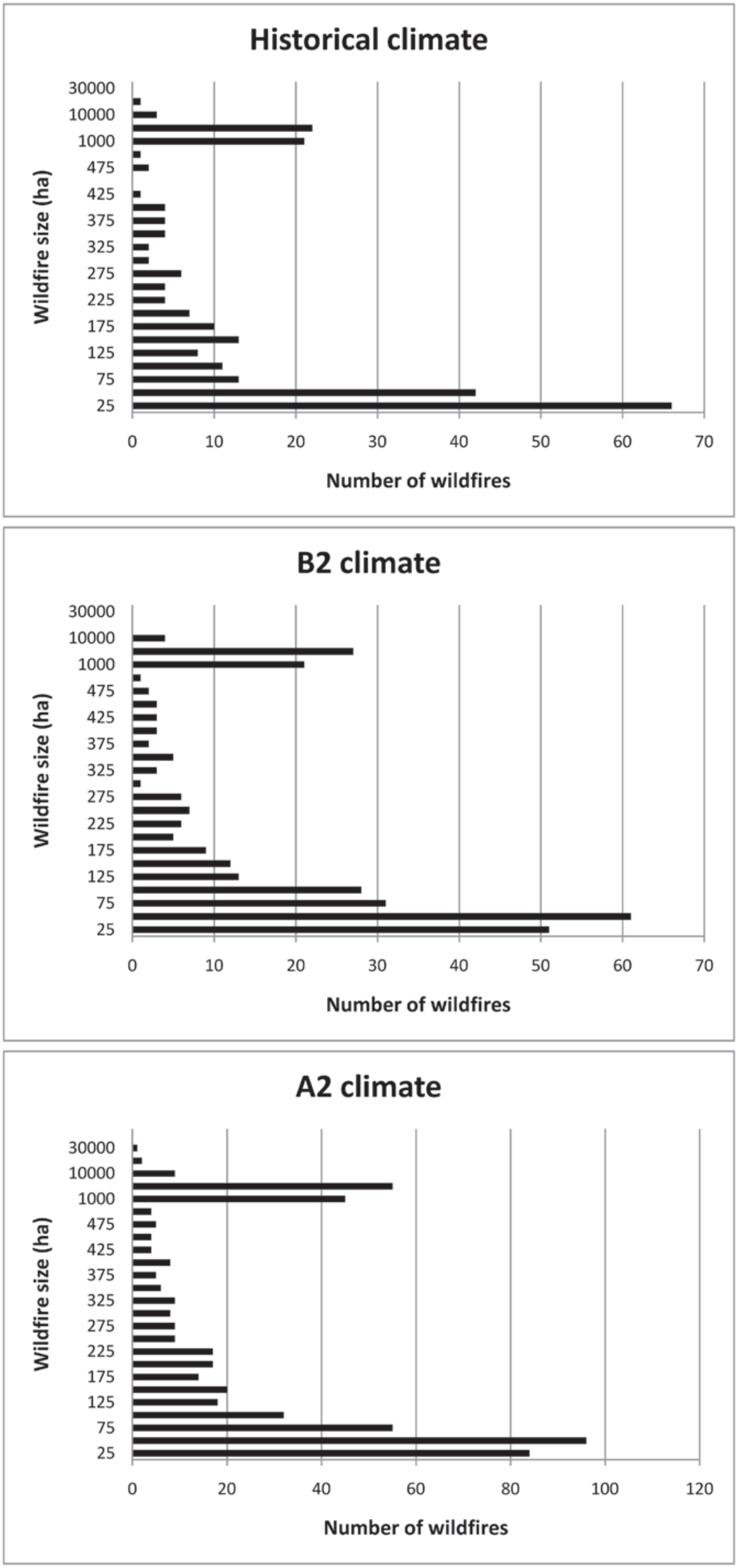


Figure 9. Cumulative number of wildfires on the MD-GNP simulation landscape for historical, B2, and A2 climate scenarios for a 350-year simulation period.

of fire sizes across the simulation period as compared with the historical simulation, but instead influenced the overall number of fires burning within coarse fire size classes (Figure 10).

Discussion

Our objective was to test whether climate and disturbance interactions influenced abundance and persistence of whitebark pine-dominated stands within the MD-GNP watershed. The study location provided an ideal context within which to perform this simulation experiment because it is a landscape where whitebark pine was an historically significant component but has declined severely in recent decades as the result of the combined effects of white pine blister rust, mountain pine beetles, and fire exclusion. Recent attention has been focused on restoring whitebark pines to this region (Keane and Parsons 2010), but current recommendations do not incorporate potential effects of climatic change as a factor in long-range management plans although shifts in climate are predicted to further reduce



Figures 10a-10c. Distribution of fire sizes simulated under historical, B2, and A2 climate scenarios.

whitebark pine populations either directly through increased climate-related mortality or indirectly through increased activity of pests and pathogens and competition from lower-elevation conifer species (Koteen 2002; Logan and others 2010; Logan and Powell 2001; McKenney and others 2007).

We hypothesized that climate changes, and in particular warming temperatures, would shift the whitebark pine distribution in GNP-MD upward in elevation via expansion of suitable habitat in upper subalpine zones and competitive replacement from lower elevation tree species in response to warming temperatures in the subalpine zone. We further posited potential synergistic interactions of climate changes and wildfires in which increased fuel loading in upper, previously lightly vegetated zones might result in an increase in wildfire frequencies and extents within those zones. Although our results suggest that hotter-drier conditions associated with the A2 climate scenario increased wildfire frequency and the number of large fires in GNP-MD, we did not observe shifts in whitebark pine distribution or increased abundance for either of the climate change scenarios. In fact, whitebark pine decreased in abundance by the end of the 350-year simulation period for the three climate scenarios. For the historical climate scenario we attribute this decline to competitive exclusion by shade-tolerant Englemann spruce and subalpine fir that dominated in the absence of few repeat fires. Given the historical (pre-fire exclusion) fire rotation of 250 years or more in areas of the simulation landscape suitable for whitebark pine establishment, it is likely that the abundance of whitebark pine would peak again were the simulation period extended for additional centuries. Keane and Parsons (2010) note that it may take 50 to 250 years for shade-tolerant trees to replace whitebark pine in the overstory, a period that matches the temporal dynamics of our simulation. Specifically, whitebark pine abundance peaked at about year 200 in the simulation, but decreased over the following 150 years as shade-tolerant species readily colonized recently-burned stands.

We attribute the rapid decline of whitebark pine in the B2 scenario to increasing abundance of western white pines within subalpine habitats (Figure 4). Western white pine has the least restricted distribution of all white pine types, and exists within elevations of 0-3,350 masl and a geographic range that spans 17 degrees of latitude and 13 degrees of longitude (Tomback and Achuff 2010). Characteristics of western white pine that enable its success under warmer-wetter climate conditions as compared with whitebark pine include its increased heat tolerance and faster reproductive maturity. The extirpation of whitebark pine from GNP-MD under the A2 climate regime was caused by the combined effects of climate-mediated vegetation shifts in stands that were initially dominated by whitebark pines, especially in higher elevation areas of the simulation landscape; and by the marked increase in wildfire activity. The two and a half times increase in area burned under A2 climate conditions coupled with the increase in number of repeat fires over the simulation period resulted in the entrainment of much of the landscape in early seral stage, immature forests. Because the cone-bearing age for whitebark pine is 60 to 100 years on most sites (Arno and Hoff 1989), trees that germinated post-fire likely did not reach either cone-producing age or grow taller than a lethal scorch height before the next wildfire occurred.

Changes in vegetation observed under climate change scenarios result from the interaction of temperature and precipitation-driven changes in species habitats and wildfire dynamics. Wildland fire was historically an important component of many forests in the western U.S., as evidenced by many resident species that exhibit morphological and physiological adaptations that provide survival advantages during fire events (Agee 1996; Habeck and Mutch 1973). It is believed that past uncontrolled fires did not, at any one point in time, completely burn over a given landscape, because many stages of successional development are usually present (Habeck and Mutch 1973). Although historical and B2 climate conditions do not seem to violate this description of fire-adapted landscapes, the wildfire and vegetation patterns resulting from our A2 climate simulations do. This drastic change in vegetation composition and structure, and its attendant shift in wildfire regimes, suggests that future forests within the northern Rocky Mountain region may appear and function very differently than the forests of the past.

Management Implications

Our results demonstrate that potential future regional climatic changes described by the SRES B2 and A2 emissions scenarios will likely have significant impacts on the abundance and persistence of whitebark pines in the MD-GNP watershed, and perhaps within other high-elevation areas with similar biotic and abiotic characteristics. Our modeling results indicate that the mechanisms influencing whitebark pine success are different for each of our simulated climate regimes, suggesting that each of these climate trajectories may require different management strategies to maintain the tree species on the landscape. Keane and Parsons (2010) recommended restoration treatments for whitebark pine forests that include emulation of historical fire regimes through prescribed burning and wildland fire management and manual planting of whitebark pine seedlings. Although these treatments may be effective under current climate conditions, the results of our experiment indicate that these strategies may not be appropriate given potential future climate changes.

Our recommendations for restoring whitebark pines to treeline environments in the northern Rocky Mountains include the following: first and foremost, augment existing populations through intensive outplanting of proven rust resistant stock. This activity should be initiated immediately so that trees reach cone-bearing age under climate conditions as close to the historical range as possible. Second, identify areas where whitebark pine establishment and growth are viable under both current and future conditions, and proactively restore these areas. Restoration treatments should include rust-resistant planting, fuels treatments to reduce shade-tolerant competitors, insect protection strategies such as verbenone, and prescribed burning to emulate historical fire regimes. Third, anticipate effects of hotter, drier future climate conditions on increasing wildfire frequency and size and design a program of fuels treatments and prescribed burning to reduce fuel loading in areas of historically mixed-severity fire regimes. Finally, implement additional research projects that (1) include the synergistic effects of white pine blister rust, mountain pine beetles, and climate changes on whitebark pine populations; (2) identify levels of rust resistance necessary for successful establishment and persistence of whitebark pine forests; and (3) use simulation modeling experiments to test the efficacy of alternative suites of management activities in the context of multiple disturbances.

Acknowledgements

This research was funded in part by the Joint Fire Sciences Program under Project JFSP 09-3-01-17. The authors gratefully acknowledge the contributions of the large number of skilled researchers, ecologists, and biological technicians who have participated in many phases of this research. In particular, we thank Alisa Keyser (UC Merced), Dan Fagre (USGS), Matt Rollins (USGS), and Signe Leirfallom and Greg Cohn (USDA Forest Service Rocky Mountain Research Station Fire Sciences Lab). We also thank Ilana Abrahamson and Eva Karau (USDA Forest Service Rocky Mountain Research Station Fire Sciences Lab) and Michael Murray (BC Forest Service) for their editorial comments during preparation of this manuscript.

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