



Climate Change and Tree-line Ecosystems in the Sierra Nevada

Habitat Suitability Modeling to Inform High-elevation Forest Dynamics Monitoring

Natural Resource Report NPS/SIEN/NRR—2017/1476





ON THIS PAGE

Whitebark pine (*Pinus albicaulis*) near treeline, North Goddard Creek, Kings Canyon National Park, California.
Photograph by: Peggy E. Moore

ON THE COVER

Foxtail pine (*Pinus balfouriana* ssp. *austrina*), Bighorn Plateau, Sequoia National Park, California.
Photograph by: Peggy E. Moore

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Executive Summary

Whitebark pine and foxtail pine serve foundational roles in the subalpine zone of the Sierra Nevada. They provide the dominant structure in tree-line forests and regulate key ecosystem processes and community dynamics. Climate change models suggest that there will be changes in temperature regimes and in the timing and magnitude of precipitation within the current distribution of these species, and these changes may alter the species' distributional limits. Other stressors include the non-native pathogen white pine blister rust and mountain pine beetle, which have played a role in the decline of whitebark pine throughout much of its range. The National Park Service is monitoring status and trends of these species. This report provides complementary information in the form of habitat suitability models to predict climate change impacts on the future distribution of these species within Sierra Nevada national parks.

We used maximum entropy modeling to build habitat suitability models by relating species occurrence to environmental variables. Species occurrence was available from 328 locations for whitebark pine and 244 for foxtail pine across the species' distributions within the parks. We constructed current climate surfaces for modeling by interpolating data from weather stations. Climate surfaces included mean, minimum, and maximum temperature and total precipitation for January, April, July, and October. We downscaled five general circulation models for the 2050s and the 2090s from $\sim 125 \text{ km}^2$ to 1 km^2 under both an optimistic and an extreme climate scenario to bracket potential climatic change and its influence on projected suitable habitat.

To describe anticipated changes in the distribution of suitable habitat, we compared, for each species, climate scenario, and time period, the current models with future models in terms of proportional change in habitat size, elevation distribution, model center points, and where habitat is predicted to expand or contract.

The current whitebark pine model compared favorably with the distribution of species occurrence samples across park landscapes. The total amount of suitable habitat for whitebark pine in the parks was projected to be nearly equivalent in the 2050s under scenario B1 as under the more extreme scenario, A2, but with increases over the current model of 20% to 22% across the study area. In Yosemite National Park (YOSE), the amount of suitable habitat decreased 16% to 28% for the 2050s and increased in Sequoia & Kings Canyon National Parks (SEKI) by 44% to 49%.

For the 2090s, the amount of whitebark pine habitat was predicted to remain unchanged, on average, in YOSE and increase in SEKI by an average of 14%, again with little difference between scenarios. However, the distribution of habitat by elevation was similar for whitebark pine among models in both YOSE and SEKI and under both climate scenarios, while model center points indicated slight geographic shifts to the south under both scenarios in both YOSE and SEKI. Models indicated bioclimatically suitable habitat in the current model will decrease for whitebark pine at a rate of 17% to 20% for the 2050s and 20% to 23% for the 2090s across the study area. These results contrast with changes in habitat abundance from modeling results in the Greater Yellowstone Area but echo the increase in suitable habitat predicted for the full range of whitebark pine.

The distribution of suitable foxtail pine habitat in the current climate-topography model also compared favorably with the current distribution reflected in occurrence samples. The future distribution of suitable habitat for foxtail pine was projected to be similar in SEKI under the two climate scenarios, and it was not projected to extend north into YOSE. Compared with the current model, the amount of habitat was projected to decrease, with a greater decrease for the 2090s than for the 2050s and more under the extreme scenario than under the optimistic scenario. Model center points reflected geographic shifts in suitable habitat, largely to the north. Currently suitable habitat for foxtail pine is predicted to be lost at rates of 25% to 35% compared with the current model. Loss is similar between scenarios for the 2050s but greater under A2 than under B1 for the 2090s.

Overall, models indicated that suitable habitats for whitebark and foxtail pine are more likely to shift geographically within the parks by 2100 rather than decline precipitously. This implies park managers might focus conservation efforts on stressors other than climate change, working toward species resilience in the face of threats from introduced disease and elevated native insect damage. More specifically, further understanding of the incidence and severity of white pine blister rust and other stressors in high elevation white pines would help assess vulnerability from threats other than climate change.

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Introduction

Many western North American coniferous forests are currently facing unprecedented challenges, including upsurges of native pests and pathogens, invasive exotic species, and altered disturbance regimes (Raffa et al. 2008; Tomback and Achuff 2010; Taylor 2000). Increased atmospheric warming, carbon dioxide concentration, and nitrogen deposition, as well as changes in precipitation patterns (i.e., timing, magnitude, and type) pose additional short- and long-term threats. Each factor alone can alter forest ecosystem structure, function, and species composition, while additive or synergistic effects are possible if multiple agents act jointly (Paine et al. 1998). Coincident with these changes, increased tree mortality rates over the last several decades have been documented recently across a broad range of latitude and forest types in western North America (Allen et al. 2015; van Mantgem et al. 2009).

Declines of foundation tree species pose an especially compelling problem because these species provide fundamental structure to a system and are thereby irreplaceable (Ellison et al. 2005). Foundation species generally occupy low trophic levels, create locally stable conditions required by many other species, and stabilize fundamental ecosystem processes (Ellison et al. 2005). In temperate zone forests (e.g., western North America) there often are only one or two foundation species, and therefore little functional redundancy is present in the system. If a foundation tree species is lost from these systems, it will likely lead to a cascade of secondary losses, shifts in biological diversity, and ultimately affect the functioning and stability of the community (Ebenman and Jonsson 2005).

High elevation white pines serve foundational roles in the subalpine zone (Tomback et al. 2014; Schoettle 2004). These include whitebark pine (*Pinus albicaulis*) and foxtail pine (*P. balfouriana* ssp. *austrina*) in the Sierra Nevada. These species provide the dominant structure in tree-line forests and regulate key ecosystem processes and community dynamics such as moderating snow melt, providing habitat and food resources for wildlife, and influencing soil and geomorphic processes (Farnes 1990; Tomback et al. 2001, 2014).

High elevation white pines are threatened by climatic change, native pine beetles, and the non-native pathogen white pine blister rust (WPBR, *Cronartium ribicola*) (Tomback and Achuff 2010). Since introduction of WPBR to British Columbia in 1910, this Eurasian fungus has spread throughout western North America to most of the five-needle white pines, causing significant mortality in some areas. The higher incidence of this fatal pathogen in the northern portion of these species' ranges and at lower elevations within the Sierra Nevada implies a climatic influence on its current distribution. Climate change models suggest that there will be changes in temperature regimes and in the timing and magnitude of precipitation within the current range of these species, and these changes may alter the distributional limits of white pines. The interaction of climate change and WPBR could have profound impacts on the structure and function of tree-line ecosystems in the Sierra Nevada.

Abundance of whitebark pine has been decreasing throughout much of its range due to a combination of WPBR, a reduction in suitable (burned) sites for seedling establishment (Tomback et al. 1995; Kendall and Keane 2001; Keane and Parsons 2010), and outbreaks of mountain pine beetle (*Dendroctonus ponderosae*; Waring and Six 2005). Specific effects of WPBR are reduced pre-

dispersal seed survival and seed dispersal (McKinney and Tomback 2007; McKinney et al. 2009), death of cone-bearing limbs, increased vulnerability to pine-beetle attack (Arno 1986; Keane and Arno 1993), and tree mortality within three years of canker development (Hoff and Hagle 1990). Tree mortality in whitebark pine from the combined impacts of WPBR and mountain pine beetle exceeds 50% in northwestern Montana, north-central Idaho, and northern Washington (Kendall and Keane, 2001). Elevated threats from mountain pine beetle are associated with climate change in parts of the West (Carroll et al. 2003; Logan and Powell 2001). Climate change and WPBR are the primary factors in the Sierra Nevada where some of the first extensive outbreaks of mountain pine beetle were only recently reported from the eastern slope (Millar et al. 2012). WPBR continues to spread throughout the range of white pines in western North America and continues to intensify where it occurs, resulting in increasing levels of damage and increasing tree mortality (Campbell and Antos 2000; Smith and Hoffman 2000). In December 2008, a proposal to list whitebark pine under the U.S. Endangered Species Act was submitted to the U.S. Fish and Wildlife Service (USFWS) (Tomback 2009). On July 19, 2010, the USFWS determined that there was sufficient evidence to warrant a 12-month status review, and in 2011 placed whitebark pine on the candidate species list of Endangered or Threatened species (U.S. Fish and Wildlife Service 2011).

Although blister-rust-induced declines in foxtail pine have not yet been documented, foxtail pine is susceptible to blister rust, and rust infection of foxtail pine has been found in both its northern (Dunlap 2006) and southern (Duriscoe and Duriscoe 2002) populations.

The Sierra Nevada (SIEN), Klamath (KLMN), and Upper Columbia Basin (UCBN) networks of the U.S. National Park Service Inventory & Monitoring Program are implementing long-term monitoring of white pines with data collection on whitebark pine, foxtail pine, and, within UCBN, limber pine (*Pinus flexilis*) (McKinney et al. 2012). Response variables in the monitoring design include species composition; stand structure; individual recruitment, growth, mortality; cone production; and the incidence and severity of WPBR and mountain pine beetle. Monitoring results will provide managers with the relative frequency and effects of WPBR within and among parks across the three NPS networks, but they will not produce information needed to predict the likely impact of climate change on the distribution of the white pines in the long term.

The primary objective of this project was to model the future distribution of high elevation white pines within SIEN parks. It was beyond the scope of this project to evaluate potential impacts of WPBR on the two species or the interacting effects of changes in temperature, precipitation, and rust intensity and distribution. However, by modeling the distribution of suitable habitat based on the fundamental aspects of temperature and precipitation, this project provides a scenario within which the other major stressors could act to further alter potential distribution.

Distribution and ecology of whitebark pine and foxtail pine in SIEN

Whitebark Pine

Whitebark pine has the broadest distribution of all eight western five-needle white pine species, occurring from 37° to 55° N latitude and from 107° to 128° W longitude (McCaughy and Schmidt 2001). It occurs in two main subregions: the northern Rocky Mountains from central Alberta and

British Columbia south through Montana and Idaho and into western Wyoming; and the Cascade and Coastal Ranges of central British Columbia south through the Cascades and Sierra Nevada (Figure 1). It reaches its southern limit in the Mt. Whitney vicinity of the southern Sierra Nevada. Whitebark pine occurs on both the west and the more arid east side of the Sierra Nevada in scattered treeline stands, and its areal extent in Yosemite National Park (YOSE) and Sequoia & Kings Canyon National Parks (SEKI) is nearly equivalent at over 18,000 ha each (Table 1).

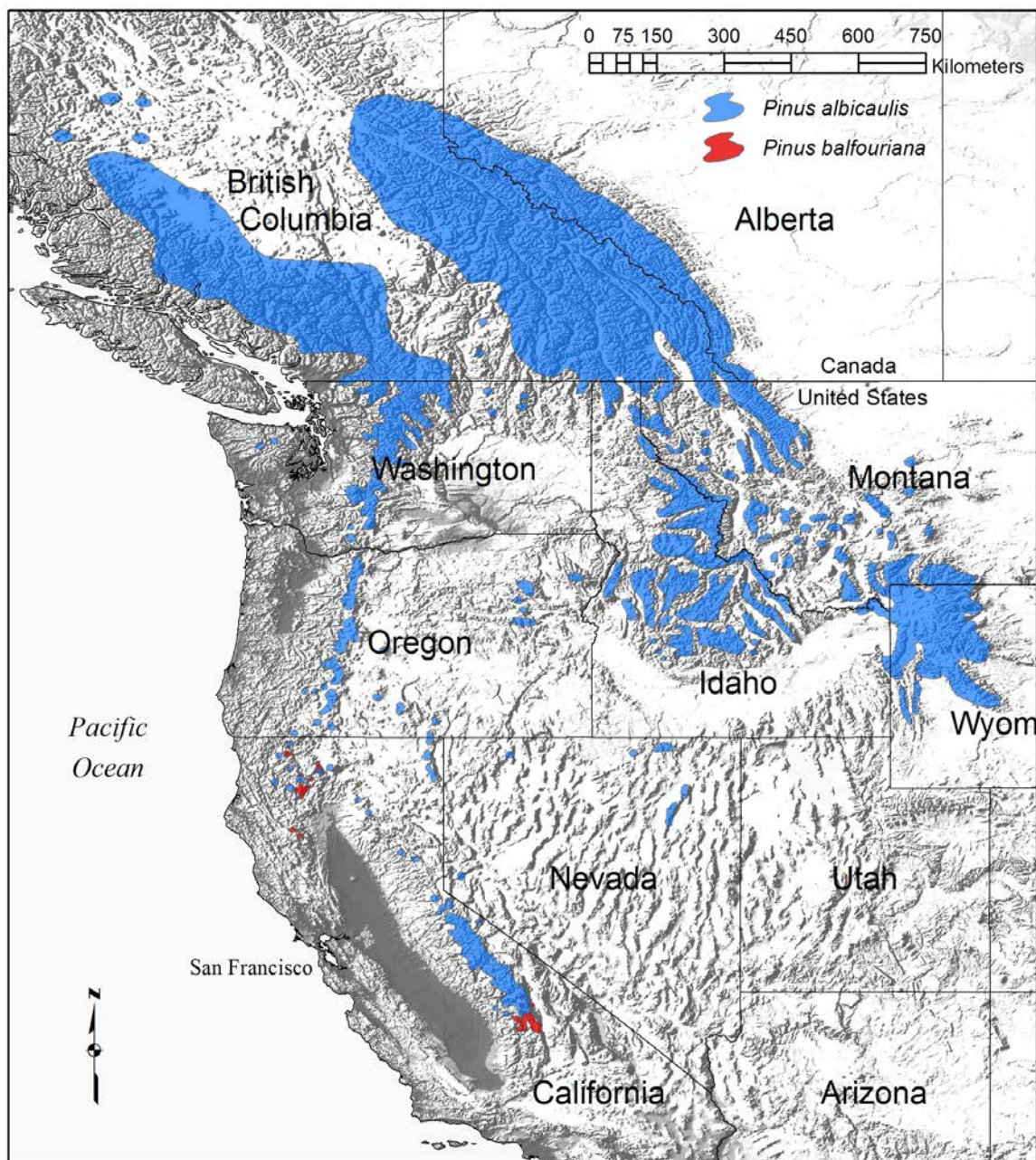


Figure 1. Whitebark pine (*Pinus albicaulis*) is at the southern extent of its range in Sierra Nevada Network as is foxtail pine (*P. balfouriana* var. *austrina*). Distribution maps based on Little (1971). Digital versions courtesy of USGS Geosciences and Environmental Change Center (<http://esp.cr.usgs.gov>). (Geographic Coordinate System projection, North American Datum of 1983)

Table 1. Areal extent (in hectares) of the distribution of white pine species by U.S. National Park Service unit according to mapping by photointerpretation of 1997 (YOSE) and 2000 & 2001 (SEKI) aerial photography. SEKI = Sequoia & Kings Canyon National Parks. YOSE = Yosemite National Park.

Park Unit	Whitebark Pine	Foxtail Pine	Limber Pine	Total
SEKI	18,312	24,056	221	42,589
YOSE	18,089	0	0	18,089

Whitebark pine is the dominant tree-line species in the northern portion of the Sierra Nevada Network. It forms upright stands in protected settings and has horizontal, stunted forms known as krummholz (crooked wood) where it is sculpted by high winds, low temperatures, and blowing snow and ice.

Throughout its range, whitebark pine occupies a narrow elevational band from the upper subalpine zone to tree line (Arno and Hoff 1990; 1370-3660 m range wide). It occurs as the only tree species on the coldest and driest sites near treeline and, in the north, as a seral species on protected, slightly lower sites more favorable for its shade-tolerant competitors (Arno and Weaver 1990).

In the Sierra Nevada, associates are mainly mountain hemlock (*Tsuga mertensiana*) and lodgepole pine (*Pinus contorta* ssp. *murrayana*). The latter is a shade intolerant species that is the most prominent host of the current mountain pine beetle outbreak in the northern portion of the species' range.

Blister rust infections on whitebark pine decrease from north to south in the Pacific West region, mirroring the Rocky Mountain trend. Blister rust is relatively rare in whitebark pine at LAVO, YOSE, and SEKI (Dunlop 2006; Jackson et al. 2015; Nesmith 2015). Mountain pine beetle is currently abundant in the northern Cascades, but also decreases with decreasing latitude (Gibson et al. 2008) in the Pacific West.

Whitebark pine acts as a foundational species in high-elevation forest communities by regulating ecosystem processes, community composition, and dynamics and by influencing regional biodiversity (Ellison et al. 2005; Tomback and Kendall 2001). Whitebark pine plays a role in initiating community development after fire, regulating snowmelt and stream flow, and preventing soil erosion at high elevations (Tomback et al. 2001; Farnes 1990). The large, wingless seeds of whitebark pine are high in fat, carbohydrates, and lipids and provide an important food source for many granivorous birds and mammals (Tomback and Kendall 2001). Whitebark pine is dependent upon Clark's nutcracker (*Nucifraga columbiana*) for seed dispersal (Tomback 1982). Nutcrackers extract seeds from indehiscent cones in late summer and early fall and often cache seeds in recently disturbed sites accounting for the pine's early successional status. Whitebark pine also provides important habitat structure for high-elevation vertebrates. For example, white-tailed jackrabbits (*Lepus townsendii*) have been documented using dense, low-growing whitebark pine mats for shelter in the Sierra Nevada. The hare is a species of concern in California and has become uncommon in the Sierra Nevada where its southern range limit coincides with whitebark pine (Storer et al. 2004). The

second largest hare in the western hemisphere, white-tailed jackrabbits can be an important prey source for large raptors, mountain lions, and other high-elevation predators.

Foxtail Pine

In the southern portion of SIEN, foxtail pine is the dominant tree-line species. It is limited to high-elevation slopes, ridges, and peaks (1,525 – 3,650 m range wide) often in pure to nearly-pure, open stands with little other vegetation. Its distribution is much smaller than that of whitebark pine (Figure 1). It is a California endemic confined to two discrete regions separated by 500 km: the Klamath Mountains of northwestern California and the southern Sierra Nevada, where it is scattered over a large area of SEKI at tree line.

Research on community and population dynamics is lacking for foxtail pine. However, given its position as the major stand component of high-elevation environments (e.g., > 3,000 m) in the southern Sierra Nevada, it likely provides important habitat and food resources for birds and mammals and ecosystem services such as influencing snow melt and soil erosion. Foxtail pine seeds are wind dispersed.

Objectives

The objectives of this project were to produce habitat suitability models for two high elevation white pine species under climate change scenarios, evaluate their reliability with appropriate techniques, and compare them with suitable habitat under current climate. A primary goal was to use basic inventory products to inform this effort, including vegetation plot data collected for classification and mapping, digital elevation models, and other spatially explicit data on factors influencing the distribution of high elevation pine species (e.g., climate, potential solar radiation).

Study Area

We limited our area of study to SEKI and YOSE (Figure 2). SEKI represents two contiguous units of the U.S. National Park Service and a single administrative unit, and we hereafter refer to them as a single unit.

YOSE (302,693 ha) and SEKI (349,527 ha) are located on the western slope of the central and southern Sierra Nevada, respectively. SEKI extends from 36.299 degrees to 37.237 degrees N latitude and YOSE from 37.492 degrees to 38.186 degrees N latitude. The parks span environmental gradients from the foothills to the alpine at the crest of the range. YOSE elevations vary from 640 m to 4000 m at Mt. Lyell and those of SEKI from 415 m to 4421 m atop Mt. Whitney.

Granitics dominate bedrock geology of the parks. In YOSE, metamorphic features occur along the western boundary in the foothills and the southeastern and eastern boundaries along Sierra Nevada crest. Metamorphics along the western boundary are largely sedimentary in origin, while the eastern belt along the crest is composed of both metasedimentary and metavolcanic rock. Bedrock geology in SEKI is predominantly Mesozoic, granitic rock, particularly at middle and high elevations. Erosional processes that formed the deeply incised landscape removed 95% of metamorphics that once overlaid the intruding plutonic rock (Huber 1987). The result is a sparsely scattered distribution of pre-Cretaceous metamorphics. Volcanics are even less common with only the most minor exceptions.

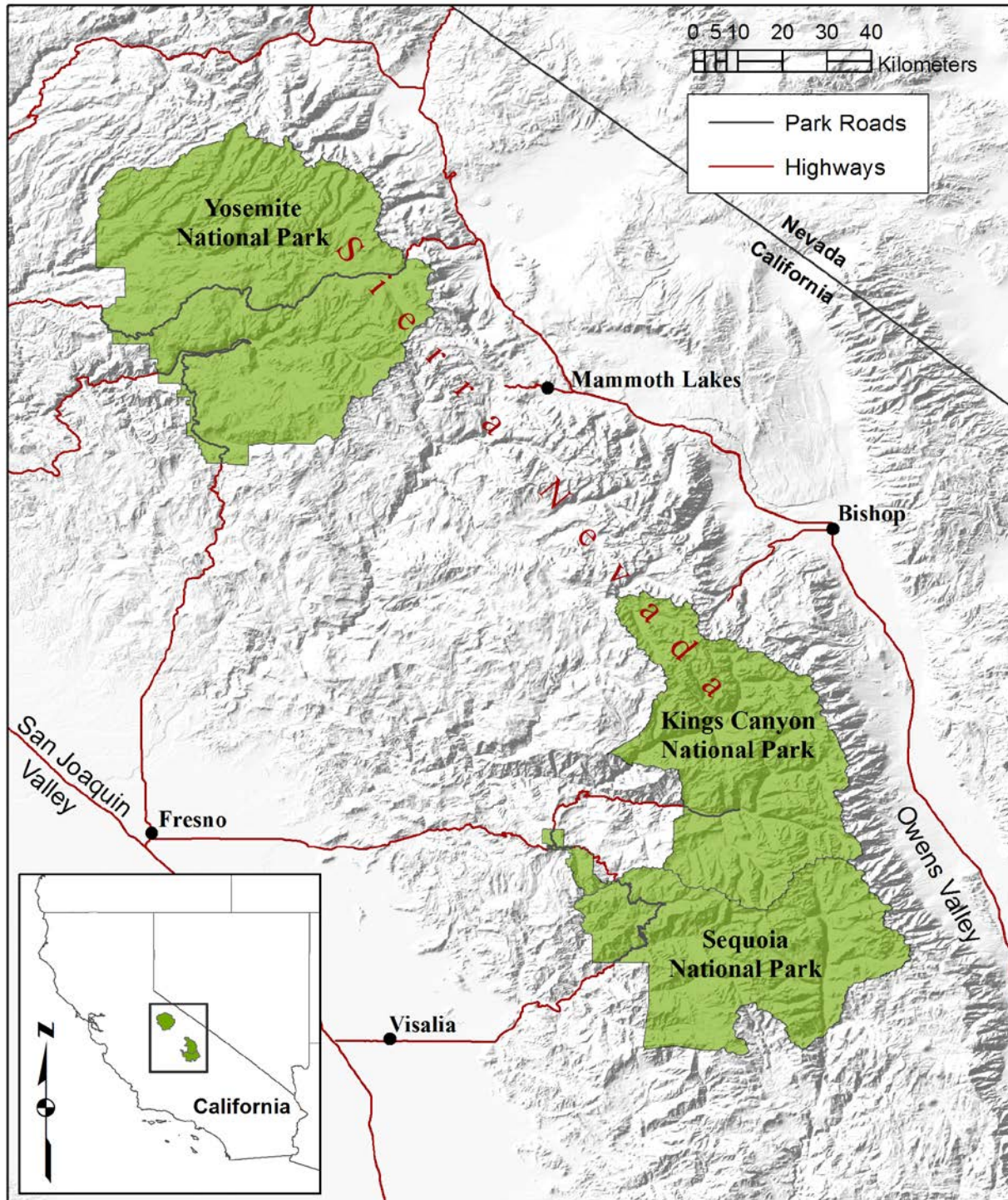


Figure 2. Yosemite and Sequoia & Kings Canyon national parks are located on the west slope of the Sierra Nevada. Environmental gradients tend to be extreme due to topography, geology, and glacial history.

The climate at the lower elevations is Mediterranean with warm, dry summers and cool, moist winters. At the crest of the range, an alpine climate predominates with cold, snowy winters and

warm, dry summers with periodic afternoon thunderstorms. Temperatures are comparable between the parks for the same elevations. Precipitation is slightly less in many portions of SEKI, but this is influenced by significant topographic variation (California Department of Water Resources 2014). Precipitation is concentrated in the winter months between October and March and is mostly in the form of snow above 1800 m.

Methods

We used maximum entropy modeling (Maxent) to build habitat suitability models by relating species presence to environmental variables (Phillips et al. 2006). Maxent is a machine learning system that requires only presence data for training and does not require data on confirmed absences (Li et al. 2011). It estimates the probability of species occurrence by cell (Phillips et al. 2006), is considered robust across different location accuracies and sample sizes, and has been found to perform well according to a number of evaluation measures (Elith et al. 2006). Maxent provides good estimates of range shifts with climate change compared with mechanistic models that isolate the effect of climate, and it estimates range size more accurately than Bioclim or Domain (two other leading modeling tools), which have been shown to underestimate range size (Hijmans and Graham 2006). Regarding how Maxent works, Phillips et al. (2006, Page 234) put it succinctly:

“The idea of Maxent is to estimate a target probability distribution by finding the probability distribution of maximum entropy (i.e., that is most spread out, or closest to uniform), subject to a set of constraints that represent our incomplete information about the target distribution. The information available about the target distribution often presents itself as a set of real-valued variables, called “features”, and the constraints are that the expected value of each feature should match its empirical average (average value for a set of sample points taken from the target distribution).”

We combined climate and topographic variables in constructing models because the combination was more likely to capture landscape-defined refugia (Austin and Van Niel 2010). We projected all environmental variables to North America Albers Equal Area Conic projection to meet the assumption in maximum entropy modeling of equal area among grid cells. Models were fitted using default feature types and default regularization parameters in Maxent.

Maxent output is expressed as continuous values of probability of species occurrence. Prior to modeling, we split sample data into three random sets: 60% for training the model, 20% for validation, and 20% for testing. This was done only for the current models to determine model accuracy. To assist with interpretation and presentation of results, we used the validation data to identify threshold values for converting output to binary models of species occurrence (Pearson et al. 2004). To do this, we sorted model output extracted for each validation point (occurrence probabilities) from lowest to highest and set a 5% omission rate as the threshold above which the model shows a species to be present.

We compared results for current models with projected future models based on the same combinations of topographic and climatic factors to describe anticipated changes in the distribution of suitable habitat.

Species occurrence information

For species occurrence, we obtained vegetation plot data from YOSE and SEKI documenting presence of whitebark pine and foxtail pine. These data were collected during vegetation classification and mapping efforts between 1985 and 2004. Plot size was 0.1 ha.

Plot locations were determined using random stratified (YOSE NRI), systematic (SEKI NRI), or stratified (SEKI vegetation mapping full plots [SEKI VM] and SEKI & YOSE mapping accuracy assessment [AA]) sampling designs and thus avoided the pitfalls of modeling based on subjective samples (Yackulic et al. 2013). Plots with whitebark pine present totaled 580, and those with foxtail pine present totaled 404. Spatial autocorrelation can affect the magnitude of forecasted change in species' distributions under climatic change (Crane et al. 2014). To reduce this bias and avoid having 1 km sq cells (our model resolution) represented by more than one plot, we randomly selected one plot per species per kilometer cell. This resulted in 328 whitebark pine points and 244 foxtail pine points on which to base habitat suitability models (Table 2). We assumed a detection probability = 1.0 because our study species were sessile and conspicuous, and plot size allowed for complete censuses.

Table 2. Ecological plots providing species occurrence data for distribution models of whitebark pine (*Pinus albicaulis*, 328 locations) and foxtail pine (*Pinus balfouriana* ssp. *austrina*, 244 locations) in Kings Canyon, Sequoia, and Yosemite national parks. YOSE=Yosemite National Park; SEKI=Sequoia & Kings Canyon National Parks.

Park	Data Set	Sample Years	Whitebark Pine Plots	Foxtail Pine Plots
YOSE	Natural Resource Inventory	1991-1993	27	0
YOSE	Vegetation Mapping Accuracy Assessment	2002-2003	73	0
SEKI	Natural Resource Inventory	1985-1996	39	46
SEKI	Vegetation Mapping Full Plots	2000-2003	13	3
SEKI	Vegetation Mapping Accuracy Assessment	2002-2004	176	195

Plot locations documenting species occurrence were widely distributed across the landscape and environmental gradients (Figure 3). They spanned the known latitudinal range of each pine species within the parks and ranged in elevation from 2,342 m to 3,865 m for whitebark pine and from 2,536 m to 3,630 m for foxtail pine. Temperature and precipitation gradients across these ranges generally parallel the elevational gradient but are also influenced by latitude.

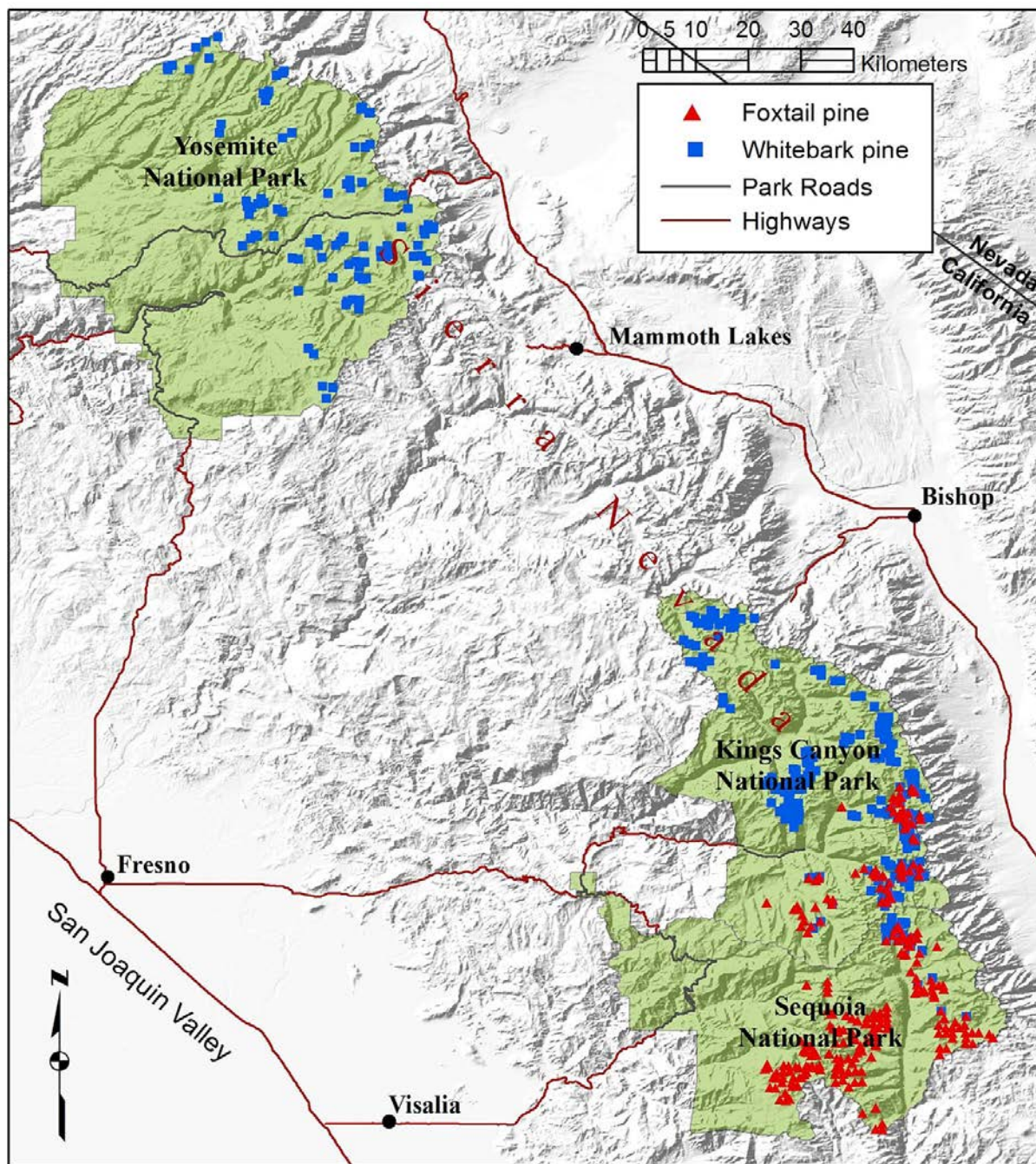


Figure 3. Locations of samples documenting species presence for foxtail pine (*Pinus balfouriana* ssp. *austrina*) and whitebark pine (*P. albicaulis*) in Sequoia- & Kings Canyon and Yosemite national parks.

Current Habitat Suitability Models

Current climate surfaces

Historic and localized weather data are used by climatologists to determine climate patterns in the past, to represent current patterns, and to make predictions for the future. This is done by using points in geographic space (i.e., weather stations) to make assumptions about areas where we do not have historic weather data using spatial analysis. The result of this interpolation is known as a climate

surface. The application of climate surfaces is widespread in ecological studies (Bonan et al. 2003; Guo et al. 2005; Chen et al. 2007; Loarie et al. 2009; Mbogga et al. 2009).

We generated climate surface models from weather station data. We created a new current climate surface from weather station data rather than using available surfaces (e.g., PRISM, Daly et al. 2008) to take advantage of a more accurate covariate for estimating precipitation (RADAR rather than elevation) and to reduce error by creating new surfaces at 860 m resolution rather than downscaling from 4 km sq (e.g., PRISM).

We obtained weather station data from the Food and Agriculture Organization (2001; FAOCLIM 2.0) and the Global Historical Climatology Network Dataset (NOAA 2011; Peterson and Vose 1997). We focused on the period 1950 to 1999 to permit comparisons with other widely used climate surfaces (e.g., WorldClim). After applying multiple temporal and spatial outlier detection algorithms, removing any records that were not from the time period of interest, and verifying location accuracy, we obtained 552 stations for precipitation, 357 stations for maximum temperature, 381 stations for minimum temperature, and 415 stations for mean temperature. These stations are arrayed over multiple states in the Western U. S. and formed the basis for current climate surfaces over that extent (Figure 4). The extent of our analysis for this project was within the SIEN parks between 38.2° N and 36.3° N latitude and 119.9° W and 118.2° W longitude.

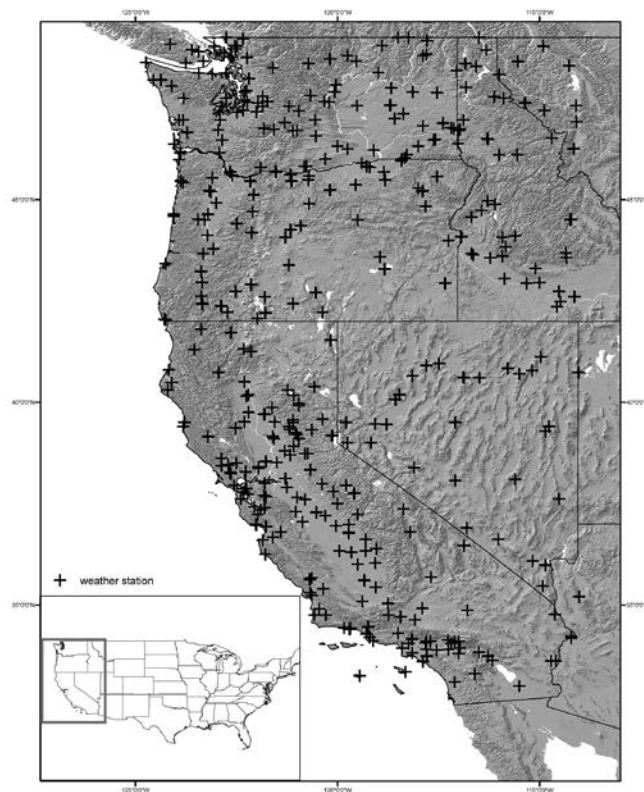


Figure 4. Spatial distribution of the weather stations, indicated by plus symbols, across the western U.S. used to construct current climate surfaces.

To generate the current climate surfaces, we used Thin Plate Spline (TPS) in the package ‘fields’ version 6.3 in R version 2.7.1 (Furrer et al. 2011). TPS was selected because it allows one to use multiple covariates and change the polynomial function degree (m) and also for its computational efficiency (Wood 2003). TPS was used when trying to derive coherent signals and remove noise from the interpolation (Wahba and Wendelberger 1980; Wahba 1990) and was first applied to climatology by Hutchinson (Hutchinson 1995; Hutchinson and Gessler 1994).

We used a tenfold cross-validation approach (Kohavi 1995) on each climatic variable to evaluate which covariates and polynomial degrees were associated with the lowest uncertainty. Each climatic variable was first divided randomly into 10 sub-samples and we then ran TPS with only 9 out of 10 sub-samples, retaining one sub-sample to validate the model. We repeated the process ten times, guaranteeing that all of the points were used for both training and validation. We determined model accuracy using Root Mean Square Error (RMSE). After selecting the best covariates and m parameter, we used all the points to create the monthly average from 1950 to 1999 for each climate surface at a spatial resolution of 1 km². Using the same parameters, we generated a monthly climate surface for each year, producing 50 years x 12 months = 600 climate surfaces per climatic variable. Leading covariate candidates were: precipitation polynomial function degree of 2 with radar being the covariate, maximum temperature polynomial function degree of 2.4, and mean and minimum temperature polynomial function degree of 1.8. For all three temperatures, elevation was the covariate with the lowest error.

Current models

To establish a basis for assessing expected change in the future models, we produced current habitat models using the same set of topographic variables (elevation, slope, and aspect) and the same climatic factors as future models (temperature and precipitation) but under the current climate regime.

To capture the effect of seasonality on species distributions (Weltzin and McPherson 2000), we included measures of temperature and precipitation from January, April, July, and October among our candidate models. Although July precipitation represents a small fraction of annual moisture, we included it because it can affect seedling establishment. Maxent is less influenced by multicollinearity than stepwise regression (Elith et al. 2011), supporting our inclusion of temperature for more than one month to capture this seasonality.

Future habitat suitability models

Future climate surfaces

We obtained the future model data from the WCRP CMIP3 Multi-Model Data (<https://esg.llnl.gov:8443/index.jsp>), which is the data portal for the Intergovernmental Panel on Climate Change (IPCC). The general circulation models (GCMs) we downscaled were: Bergen Climate Model Version 2 (BCCR BCM 2.0; Bjerknes Centre for Climate Research, University of Bergen, Norway, 2005); Community Climate System Model, Version 3.0 (NCAR CCSM 3.0, National Center for Atmospheric Research, Boulder, CO, 2006); CSIRO Mark 3.0 (Commonwealth Scientific and Industrial Research Organisation Mk 3.0; CSIRO, Australia, 2001); CSIRO Mark 3.5 (CSIRO Mk 3.5, CSIRO, Australia, 2006); and Model for Interdisciplinary Research on Climate

Version 3.2 medium resolution (MIROC 3.2 med res, CCSR/NIES/FRCGC, Japan, 2004). We downscaled only these five GCMs because they had to meet three criteria. First, the 20th century experiment (scenario 20c3m for the fourth IPCC assessment) had to be provided for each GCM. Second, all four climatic variables (precipitation, mean temperature, minimum temperature, and maximum temperature) had to be available for each GCM. Finally, all of the GCMs had to be available for each of the two extreme scenarios from the Special Report on Emissions Scenarios, SRES B1 and SRES A2, of the Fourth Assessment Report (IPCC 2007).

These two scenarios differ in their assumptions regarding demographic change, economic development, and technological change (IPCC 2007). Scenario B1 assumes economies change rapidly toward service and information, reductions in material intensity, and the introduction of cleaner, more efficient technologies. The associated atmospheric CO₂ concentration under scenario B1 is projected to be near the minimum expected, staying below 550 ppm by the year 2100 (Nakicenovic et al. 2000), and the global average temperature to increase by 1.1° C to 2.9° C.

Scenario A2 assumes continuously increasing global population, globally fragmented economic development and growth, and slower, more fragmented technological change. Associated atmospheric CO₂ concentration under scenario family A2 is projected to surpass 850 ppm by 2100 and the global average temperature to increase by 2° C to 5.4° C.

We obtained climate models from the IPCC Fourth Assessment Report (IPCC 2007) in 2011. IPCC 5 became available in 2012; however, it had only 3 of the 5 GCMs we were using, would not have improved results, and would have involved information loss. So we continued to work with IPCC 4 and ran models using those GCMs.

We applied the Statistical Downscale and Bias Correction algorithm (Wood et al. 2002; Wood et al. 2004; Maurer 2007) to downscale the GCMs from ~125 km² to 1 km². This algorithm determines the bias between the past model (20c3m) and the current climate surfaces. This assumes that the past bias will be the same as the future bias, keeping it constant, no matter the time period analyzed. We compared our future downscaled surfaces with the “Bias Corrected and Downscaled” (BCD) data set (Maurer et al. 2007), which was at ~12 km² and had mean temperature and precipitation from 2000 to 2100. Our future downscaled climate surfaces showed similar patterns to the BCD product but with differences at the higher elevations. This disagreement is likely due to different weather station data, different interpolation methods, and different covariates that were used in the interpolation.

We downscaled climate data and aggregated environmental data to 1 km² spatial resolution for the following reasons: 1) 1 km² resolution is well established in published literature, 2) future projections will be made at 1 km² resolution because that is the resolution of downscaled climate models, and 3) older plot location data have lower positional accuracy. For these reasons, we believe that 1 km² resolution provided the most meaningful information.

Future models

We constructed models based on the two extreme emissions scenarios described above, B1 and A2, to bracket potential response. Only 5 of 20 GCMs have meaningful variables (temperature, etc.) and

each has 2 scenarios. For the future models, we produced five models each for whitebark pine and foxtail pine x two scenarios x two future time periods (2050s and 2090s) for a total of 40 habitat suitability models.

We constructed climate variables for each climate scenario and each GCM as follows: mean, minimum, and maximum monthly temperatures for January, April, July, and October over the 50 year period 1950-1999 (IPCC 2007); mean, minimum, and maximum monthly precipitation for January, April, July, and October; and topographic variables of elevation, aspect, and slope (Shuttle Radar Topography Mission, NASA 2007; Farr et al. 2007). We used a linear conversion of aspect in degrees to convert southwest aspects to the lowest values and northeast aspects to the highest values with resulting values varying from 0 to 2:

$$\text{Linear Aspect} = 1 + (\text{COS}(\text{Pi} * (\text{aspect} - 45)/180))$$

Using Maxent model output, we then determined agreement among the models for the five different GCMs within each climate scenario within each species, with greater agreement among GCMs (e.g., 4-5 GCMs) reflecting greater confidence in the modeled result and lesser agreement among GCMs (e.g., 1-2 GCMs) reflecting lower confidence.

Model Evaluation

To assess model ability to discriminate between suitable and unsuitable areas for each species, we used area under the receiver operating characteristic curve (AUC). We interpreted AUC values as relative to other models using the same data and not as absolute measures of performance (Yackulic et al. 2013). To assess variable contribution, we also examined training gain for how well a model performed using only a particular environmental factor and how well it performed when excluding that factor.

In a separate exercise, we produced a set of hypothesis-driven current models for each species to assess the relative performance of the climate-topography models. We constructed hypotheses based on species ecology and produced models using additional environmental data that could not be projected into the future (and therefore would not serve as a basis for comparing future models). We used the Contrast Validation Index (CVI; Hirzel and Arlettaz 2003; Hirzel et al. 2006) to rank the models and AUC as another measure of model performance (Appendix B).

The final set of future models included 20 models each for whitebark pine and foxtail pine based on the five GCMs x two climate scenarios x two future time periods (2050s and 2090s) for a total of 40 future habitat suitability models. They took the form of binary models representing suitable/unsuitable habitat. To illustrate and evaluate model output, we took a conservative approach and considered habitat to be suitable only where all five GCMs agreed. As a result, we presented final models as agreement among five GCMs, resulting in four sets of model concurrence per species: two climate scenarios each for the 2050s and the 2090s.

Current versus Future Model Comparisons

We assessed changes in the distribution of suitable habitat for the two high elevation white pine species by evaluating differences between current and future models. We used ArcGIS 10.2.2 (ESRI

2014) for analysis of model output, comparing models with the projection set to the geographic coordinate system and the datum to WGS 1984.

McNemar's test

To compare current climate-topography models with projected future models, we used McNemar's chi-square test for paired nominal data with continuity correction (Yates 1934; McNemar 1947). Data were arranged in a 2 x 2 contingency table prior to calculating the McNemar statistic:

	Future Habitat Suitable	Future Habitat Not Suitable
Currently Suitable	a	b
Currently Not Suitable	c	d

where cell frequencies are numbers of 1 km² cell pairs.

McNemar's chi-square statistic is calculated as:

$$\chi^2 = \frac{(|b - c| - 0.5)^2}{b + c}$$

where b and c are the values for discordant cells, which represent cells that differ between models with respect to habitat suitability. The concordant cells do not contribute any information about a difference between pairs so they are not used to calculate the test statistic. The null hypothesis was that the proportions of suitable habitat are equal between the models. With multiple McNemar tests planned for comparing models, we did a Bonferroni correction to adjust the p-value needed for significance as $\alpha = 0.05/\text{number tests} = \text{adjusted } \alpha$.

We also examined projected geographic shifts in suitable habitat by comparing, for areas of GCM agreement, proportional change in habitat size, elevation distribution, and model centroids. Because of the geographic gap in both samples and environmental variables between the parks, we made comparisons separately for YOSE and SEKI.

Suitable Habitat Size

We compared the area of suitable habitat as the percent change (+/-) between models using the number of 1 km² cells where presence was predicted among all five GCMs.

Elevation

We derived elevation (m) for each model using DEM at 1 km resolution (same as model input) and compared elevation patterns among models, seeking insights into ways in which suitable habitat might shift topographically. To avoid the bias inherent in arbitrary bin sizes of histograms, we plotted elevation data in violin plots using the functions `geom_violin` and `geom_boxplot` in the package

ggplot2 1.0.1 2015-03-16 (Wickham 2009) in R version 3.1.3 (R Core Team 2015). Violin plots are box plots with kernel density plots on each side illustrating the probability density of the data at different values.

Model Centroids

To calculate shifts in centroids of suitable habitat, we converted models from raster to vector using the Raster to Polygon tool. We then converted them to multipart features using the *Dissolve* tool (i.e., one polygon per species range), converted those features to feature classes (i.e., centroids) using the Feature to Point tool, and compared point coordinates. We derived distances between centroids of current climate-topography models and future model centroids using the *Generate Near Table* tool.

Habitat Shifts

To locate where models differed in the availability of suitable habitat, we identified areas of overlap between current and future models, areas of contraction (in current but not in future models), and areas of extension (in future but not in current models) using the Con tool in ArcGIS 10.2.

Results

Current and Future Climate Surfaces

In comparisons of current and projected future climate surfaces using data extracted with species presence points, there were substantial differences among surfaces that affected model outcomes. Our goal is to characterize the climate surfaces for the reader. However, we are focusing summary statistics on the variables that made the greatest contributions in the models (mostly over 5%).

Whitebark pine

Under scenario B1, all 5 GCMs indicated somewhat wetter January conditions by the 2050s and 3 of 5 GCMs indicated nearly double January precipitation by the 2090s (Appendix A). Miroc v. 3.2 and the North American GCM, NCAR CCSM v. 3.0, indicated the least change in January precipitation at 6% to 12% increase for the 2090s under B1. Not surprisingly, July precipitation remains very low to near zero in all GCMs for both the 2050s and the 2090s. GCMs indicate less than a 1° C increase in January minimum temperatures by the 2050s under B1, and less than a 2° C increase by the 2090s (except for BCCR BCM v. 2.0). All 5 GCMs indicate little change in July maximum temperatures under B1 between the 2050s and the 2090s. The direction of change in July minimum temperatures is inconsistent for the 2050s under B1.

Under scenario A2, 4 of 5 GCMs indicate greater January precipitation for both the 2050s and the 2090s while July precipitation is unchanged under 4 GCMs but dramatically higher under CSIRO Mk v. 3.5 (Appendix A). The degree of winter warming increases over time with a 3° C to 10° C increase in January minimum temperatures by the 2050s and a 3° C to 21° C increase by the 2090s. July minimum temperature varies little from the current range with the median staying within about 3° C among the various GCMs and the range shifting slightly downward for climate models Mk 3.0 and Mk3.5 for both the 2050s and the 2090s. The July maximum behaves similarly with the median projected to stay within 3° C to 5° C by the 2090s and the ranges remaining within the current minimum and maximum modeled temperatures.

Foxtail pine

Within the range of foxtail pine based on species occurrence samples, all five GCMs indicate wetter winter conditions with January precipitation increasing 12% to 135% by the 2050s and increasing 8% to 98% by the 2090s under scenario B1 (Appendix A). The pattern is similar under A2, with four of five GCMs showing increasing January precipitation for the 2050s and the 2090s. There is strong agreement among GCMs for continued dry summer conditions under B1 with July precipitation of less than 5 mm. With the exception of Mk v 3.5, there is agreement for continued dry summer conditions under A2 as well.

Consistent with conditions over the broader range of whitebark pine, January temperatures within the range of foxtail pine are predicted to increase under B1 mostly by less than 4° C by the 2050s (with the exception of BCM v. 2.0; Appendix A). The magnitude of change is greater for the 2090s. Under scenario A2, January minimum temperatures will increase 5° C by the 2050s and 11° C by the 2090s. Again July minimum temperatures vary little from the current model (within 1° C to 4° C) for either

scenario or time period, and the July maximum temperature remains within 2° C to 5° C of the current maximum by the 2090s.

Current Habitat Suitability Models

Whitebark pine

Areas of suitable habitat in the current climate-topography model compared favorably with species occurrence samples as expected (Figure 5a).

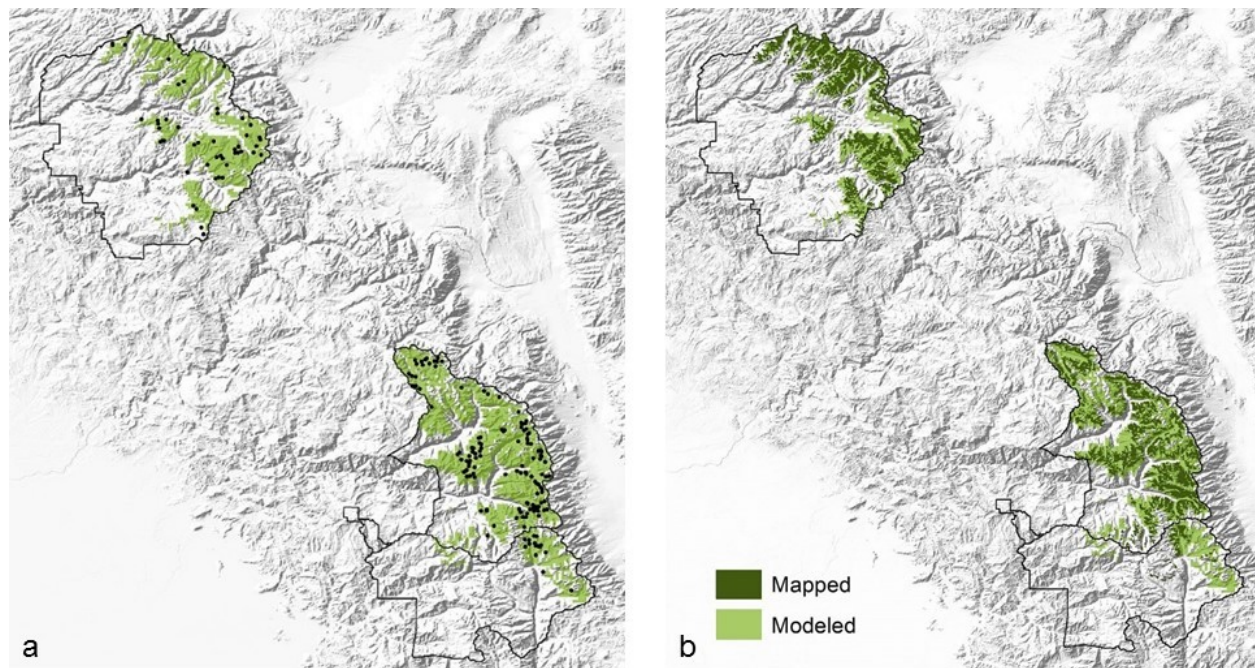


Figure 5. a) The current climate-topography model for whitebark pine within Yosemite and Sequoia & Kings Canyon national parks. Closed circles: training samples. b) Current climate-topography model for whitebark pine in relation to the distribution of whitebark pine vegetation types photointerpreted from 1997 (YOSE) or 2001 (SEKI) aerial photography.

Elevation had the greatest influence on the whitebark pine climate-topography model (50% contribution) followed by July precipitation (18%) and July maximum temperature (8%). January minimum temperature contributed 6%, but all other topographic and climate variables contributed 5% or less. Probability of whitebark pine presence was above 50% for a narrow range of elevation and a narrow range of July maximum temperature, and there appeared to be a threshold effect for July precipitation.

Elevation and January minimum temperature, equally, provided a fairly good fit to the training data in the climate-topography model, and no covariate, when removed, reduced the gain substantially. July precipitation reduced gain only slightly.

The climate-topography model for whitebark pine, which formed the basis for comparisons with future projections, ranked 17th among 20 current models according to the CVI (Appendix B). Although the CVI value did not approach that of the top four CVI-ranked models, the AUC value

(0.927) tied for highest. The model with an equally high AUC value included a broad array of habitat factors, including elevation, summer precipitation, winter conditions (January minimum temperature and snow-covered conditions), normalized difference vegetation index (NDVI), topographic wetness, and solar potential. Without these additional covariates, the climate-topography model discriminated equally well between suitable and unsuitable areas.

A visual comparison of the current climate-topography model with the mapped distribution of whitebark pine based on photointerpretation of 1997 (YOSE) and 2001 (SEKI) aerial photography (1:15,850 scale) indicated distributions aligned well geographically, but the model identified suitable habitat over a greater area (Figure 5b). The model predicted more extensive presence in southern SEKI with occurrence north and south of some isolated mapped stands in southeastern SEKI. It also filled interstices of mapped distributions throughout the whitebark pine distribution within the parks.

Foxtail pine

The distribution of suitable habitat in the climate-topography model compared favorably with species occurrence samples (Figure 6a).

Spring and summer precipitation and temperature made the greatest contributions to the current climate-topography model for foxtail pine with contributions of 29% for April precipitation, 23% for July precipitation, and 8% to 10% for April and July temperatures. Response curves indicated that, as spring and summer precipitation increase, the probability of foxtail pine presence declines. Elevation contributed just 8% to the model.

April precipitation was the most important covariate to the climate-topography model according to jackknife results, but the gain varied little among temperature and precipitation covariates when they were used in isolation. Only slope and aspect had very low importance. No covariate reduced gain substantially when removed from the model, indicating redundancy in information among the covariates.

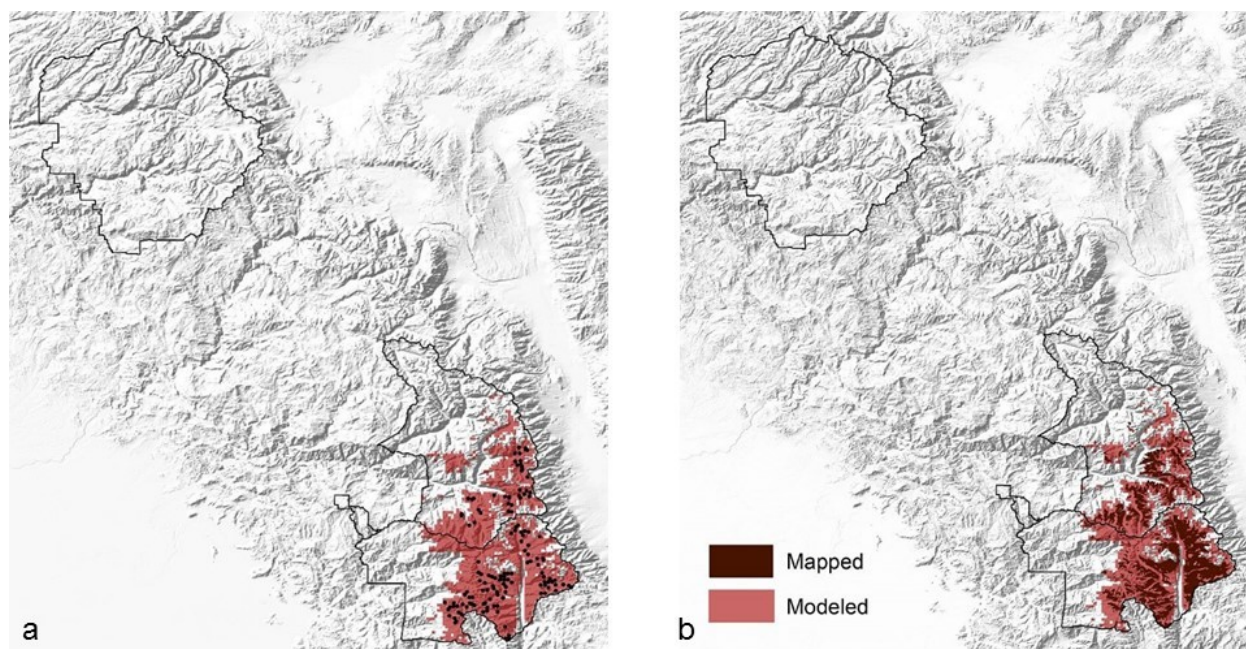


Figure 6. a) The current climate-topography model for foxtail pine within Sequoia & Kings Canyon national parks. Closed circles: training samples. b) Current climate-topography model for foxtail pine in relation to the distribution of foxtail pine vegetation types photointerpreted from 2001 aerial photography.

An AUC value of 0.958 indicated the climate-topography model performed as well as the highest ranked hypothesis-driven models (AUC values between 0.949 and 0.964) (Appendix B). The CVI value for that model of 0.774, higher than the top four CVI-ranked models (CVI values between 0.730 and 0.743), provided further support.

A visual comparison of the current climate-topography model with the mapped distribution of foxtail pine based on photointerpretation of 2000 and 2001 aerial photography (1:15,840 scale) indicated distributions aligned well geographically, but the model covered more area (Figure 6b). The model predicted more extensive suitable habitat in southern SEKI, particularly in the western portion of the parks. It also filled interstices throughout the mapped distribution of foxtail pine within the parks.

Future Habitat Suitability Models

Whitebark pine

Similar to the current climate-topography model, elevation made the greatest contribution to whitebark pine future models (62%) followed by July precipitation (17.5%) and April and October precipitation (approximately 5% each). Unlike the current climate-topography model, no temperature covariates had greater than 2% contribution.

Results of jackknife tests paralleled the contribution levels outlined above to an uncommon degree. Elevation was the covariate with the highest gain when used in isolation (0.75 regularized training gain), and it reduced gain the most when it was removed from the model. July precipitation had the second highest gain (0.39) when used in isolation, but it reduced the gain to only a minor degree when it was removed.

The total amount of suitable habitat for whitebark pine in the parks was projected to be nearly equivalent in the 2050s under scenario B1 (3254 km²) as under the more extreme scenario A2 (3,302 km², Figure 7). For the 2090s, model comparison showed more suitable habitat under scenario A2 (3,034 km²) than under scenario B1 (2864 km²) but 8% to 12% less than for the 2050s. Suitable habitat was not projected to extend as far south in SEKI in the 2090s under scenario B1 compared with scenario A2 and compared to the 2050s. It was also projected to be less abundant for the 2090s in northern SEKI and more abundant in southern SEKI under A2. Please see ‘Current versus Future Models’ section and Table 4 below.

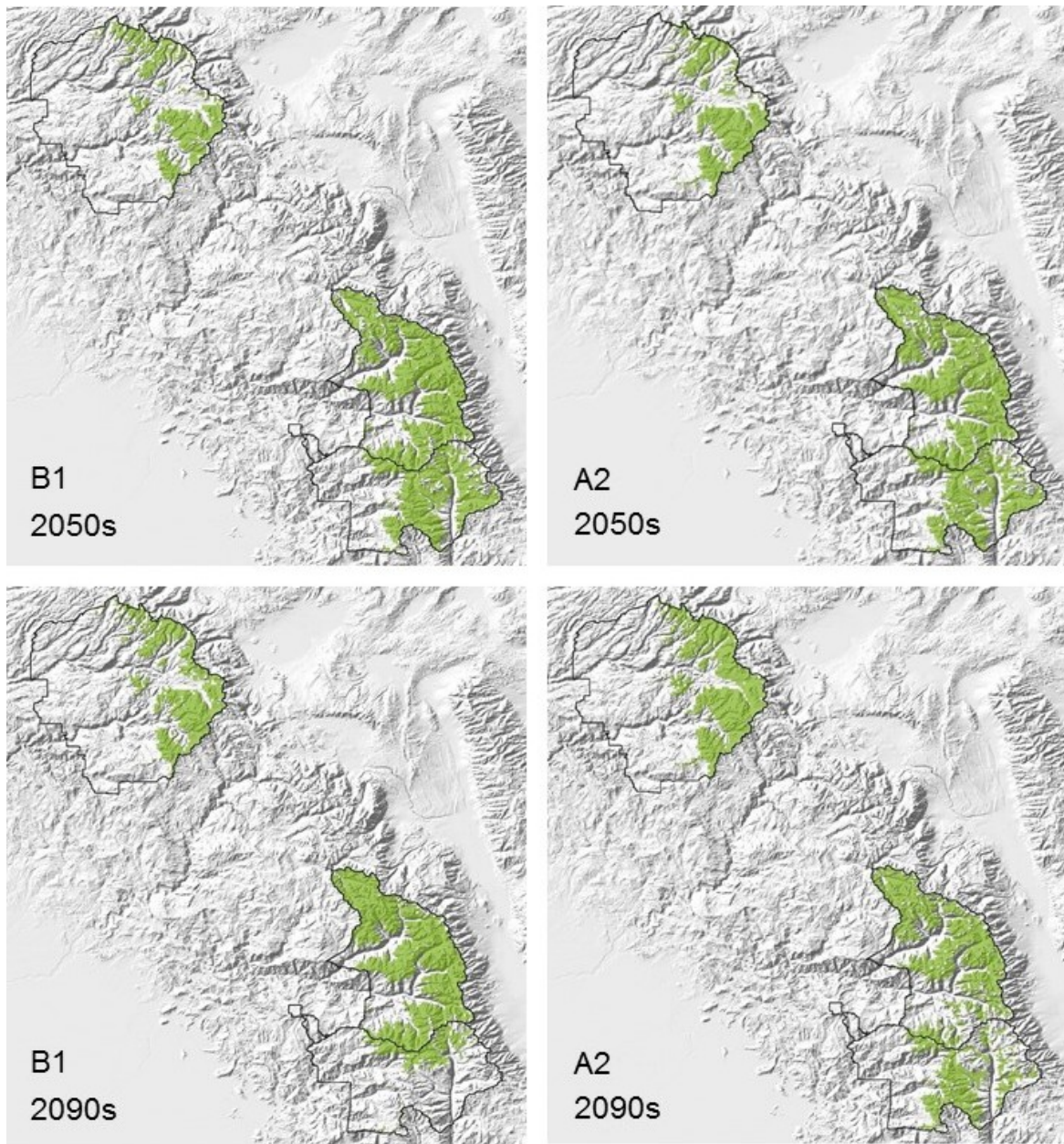


Figure 7. Suitable habitat for whitebark pine in the 2050s is projected to be less abundant under scenario B1 than under scenario A2. For the 2090s, suitable habitat is not projected to extend as far south under scenario B1 compared with scenario A2.

Foxtail pine

Similar to the current climate-topography model, April and July precipitation and elevation were important contributors to foxtail pine models for the 2050s and 2090s. Although April and July precipitation contributed at levels similar to those in the climate-topography model (21% to 27%), elevation had a stronger influence on foxtail pine future models (30%). January precipitation contributed 9.3% and October precipitation 5.1%. All other covariates contributed less than 5%.

Jackknife results paralleled contribution levels for foxtail pine as well. April, January, and July precipitation were the covariates with the highest gain. Only elevation decreased the gain when it was omitted and only to a minor degree, but it had at least some information that the precipitation covariates did not.

The general distribution of suitable habitat for foxtail pine was projected to be similar in SEKI under scenarios B1 and A2 (Figure 8), and it was not projected to extend north into YOSE. For the 2050s, suitable habitat appeared comparable under scenarios B1 and A2. For the 2090s, the distribution of suitable habitat was projected to be comparable under both scenarios in southern SEKI but to be somewhat less extensive to the N and NW under scenario A2 in northern SEKI. In terms of area, models indicated a decline of 10% to 17% in the amount of habitat between the 2050s and the 2090s from 1686 km² to 1516 km² under B1 and from 1587 km² to 1321 km² under A2.

Current versus Future Models

Whitebark pine

In paired comparisons of habitat suitability models, McNemar's tests indicated future whitebark pine models differed from the current climate-topography model under both scenarios and within both YOSE and SEKI (Table 3). Differences appeared to be greater in models for the 2050s than in models for the 2090s.

Table 3. Comparisons of current climate-topography models for whitebark pine, by park, with future projected models, based on GCM agreement, indicated by year and scenario, using McNemar's chi-square test with continuity correction of 0.5 (Yates 1934). Critical value for the test is 3.84 at $\alpha = 0.05$, $df = 1$.

Park	Scenario	Model	Chi-square	p-value
YOSE	B1	2050	193.4	<<0.05
	B1	2090	37.00	<0.05
	A2	2050	58.0	<<0.05
	A2	2090	48.5	<0.05
SEKI	B1	2050	565.0	<<0.05
	B1	2090	106.6	<<0.05
	A2	2050	528.4	<<0.05
	A2	2090	31.7	<0.05

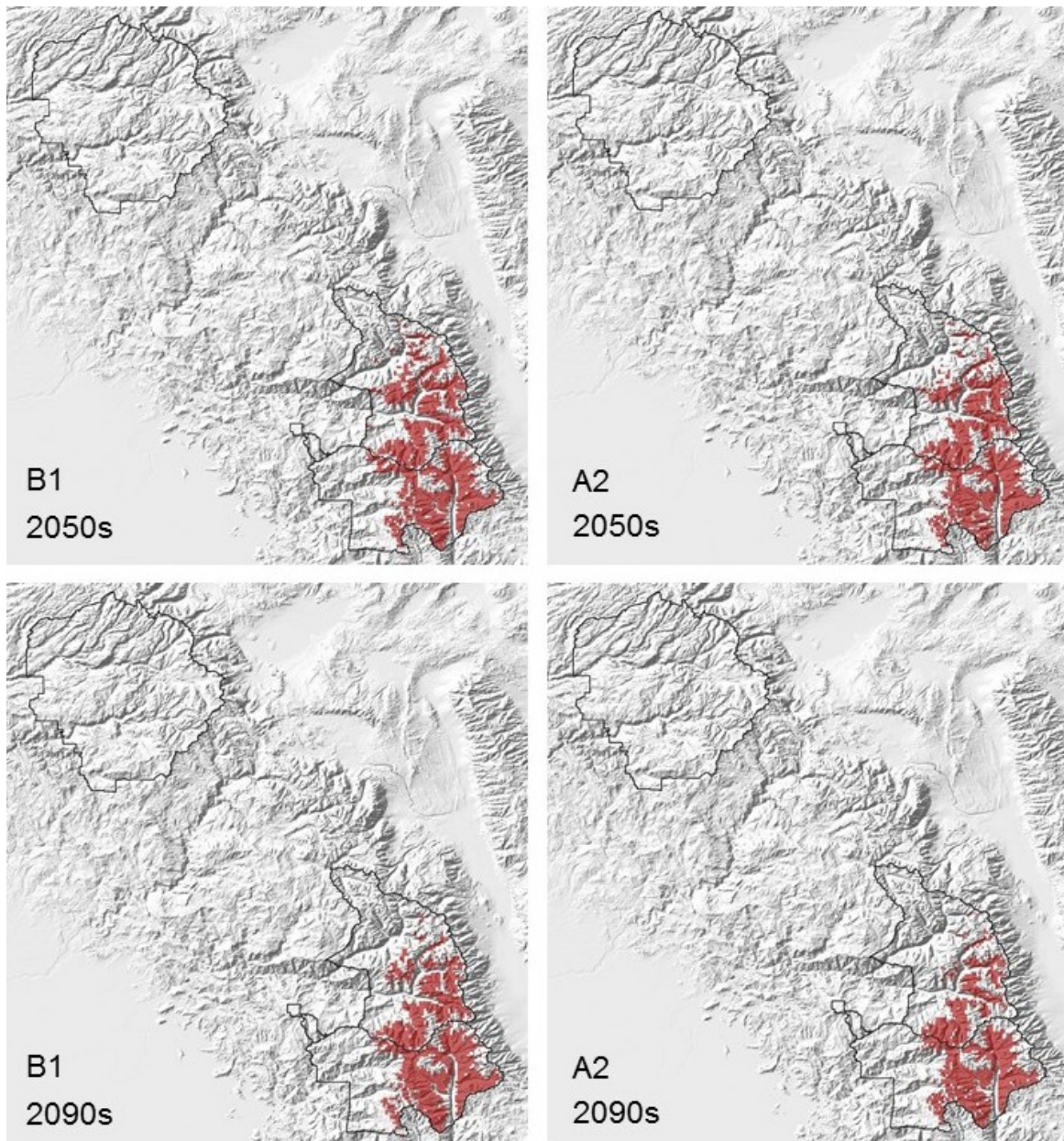


Figure 8. Suitable habitat for foxtail pine in the 2050s appeared comparable under scenario B1 and under scenario A2. In the 2090s, suitable habitat is similar under scenario B1 to that under scenario A2 in southern SEKI but extends somewhat farther north and northwest under B1 in northern SEKI.

Consistent with the McNemar tests, differences in the amount of suitable habitat for whitebark pine differed consistently from the current climate-topography model according to projections (Table 4). These differences varied in magnitude and direction from a decrease of 13% to 28% in YOSE to an

increase of 11% to 49% in SEKI. Just within YOSE, magnitude differed for the 2050s between B1 and A2, and the sign differed for the 2090s with a decrease under B1 and an increase under A2. Under A2, reduction in habitat area for the 2050s in YOSE was comparable to that under B1 for 2090. The amount of suitable habitat was projected to increase in SEKI under both scenarios but increases were greater for the 2050s than for the 2090s.

Table 4. Area (km²) of suitable habitat projected under climate scenarios B1 and A2, by park, compared with the current climate-topography model for whitebark pine. The current climate-topography model had 1012 km² of suitable habitat in YOSE and 1695 km² in SEKI.

Park	Scenario	Model	Area (km ²)	(%)
YOSE	B1	2050	727	-28.2
	B1	2090	879	-13.1
	A2	2050	853	-15.7
	A2	2090	1155	14.1
SEKI	B1	2050	2527	49.1
	B1	2090	1985	17.1
	A2	2050	2449	44.5
	A2	2090	1879	10.9

The distribution of elevation was similar for whitebark pine among models in both YOSE and SEKI and under both scenario B1 and A2, but there were subtle differences (Figure 9). In YOSE, the amount of suitable habitat by elevation remained proportionally similar in the current model versus future projections, peaking around 3000 m to 3100 m and gradually declining in probability of occurrence to approximately 3600 m. However, under B1, there was less suitable habitat below 3000 m, somewhat more suitable habitat between 3000 m and 3100 m, and an increase in the median elevation. Under A2, there was negligible increase in median values, and the probability of occurrence had a similar distribution among elevations as the current model. In SEKI, whitebark pine habitat under both scenarios was projected to shift away from a peak around 3500 m to a peak closer to 3200 m to 3300 m by the 2090s particularly under A2. This is consistent with a slight decrease in the median elevation for whitebark pine in SEKI. Suitable habitat is projected to be more normally distributed between 2500 m and 3800 m than either the current model or models in YOSE.

Model centroids reflected geographic shifts between the current climate-topography models and future habitat models (Table 5). Centroids shifted to the south and east under both scenarios in YOSE, averaging 3.2 km under B1 and 5.2 km under A2. Centroids of whitebark pine models shifted south from the centroid of the current climate-topography model in SEKI as well under both B1 and A2 (Table 5). Shifts averaged 8.3 km under B1 and 11.8 km under A2. Shifts appeared more modest for the 2090s than for the 2050s.

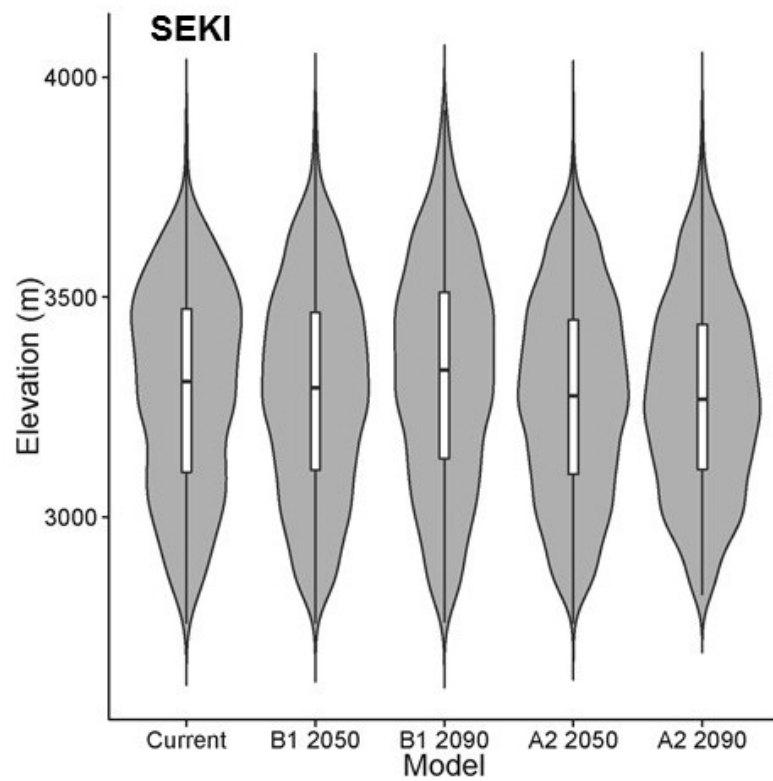
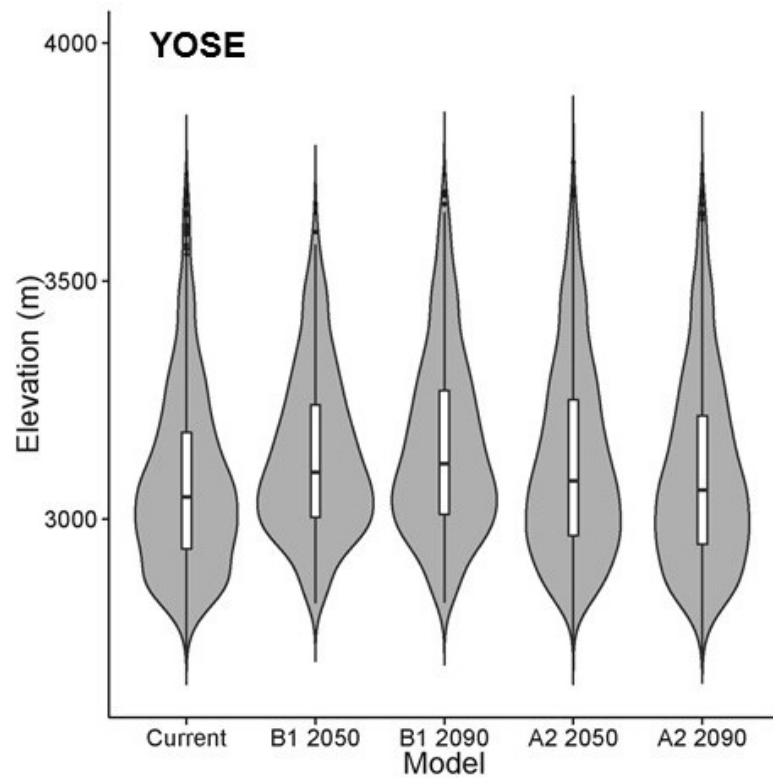


Figure 9. Violin plots (box plots embedded within 95% kernel density estimates) of projected elevation distributions for current climate and for the 2050s and 2090s under climate change scenarios B1 and A2 for whitebark pine in Yosemite and in Sequoia & Kings Canyon national parks.

Table 5. Distance and direction from centroid of current climate-topography model for whitebark pine to centroids of future projected models along with centroid elevations.

Park	Scenario	Model	Elev (m)	Dist (km)	Direction
YOSE	B1	2050	2658	2.51	SSE
	B1	2090	2672	3.88	SE
	A2	2050	3291	6.53	SSE
	A2	2090	2699	3.82	SE
SEKI	B1	2050	2689	14.05	S
	B1	2090	3289	2.57	SW
	A2	2050	2435	13.51	S
	A2	2090	2186	9.99	SSW

In the assessment of where suitable habitat contracted and expanded under future scenarios, habitat for whitebark pine contracted at a rate across the parks of 17% to 20% for the 2050s and 20% to 23% for the 2090s (Table 6). There was greater contraction of suitable habitat in SEKI for the 2090s than for the 2050s particularly under scenario A2. However, in YOSE there was less contraction for the 2090s than for the 2050s particularly under A2. Most models indicated the primary areas of contraction in whitebark pine habitat were in the farthest northern reaches of YOSE and in southeastern SEKI (Figure 10).

Table 6. Contraction and extension of suitable habitat in models for the 2050s and 2090s under scenarios B1 and A2 compared with the current climate-topography model for whitebark pine.

Park	Scenario	Model	Contraction (%)	Extension (%)
Study Area	B1	2050	20	40
	B1	2090	20	26
	A2	2050	17	39
	A2	2090	23	35
YOSE	B1	2050	34	6
	B1	2090	29	16
	A2	2050	29	14
	A2	2090	13	27
SEKI	B1	2050	12	60
	B1	2090	15	32
	A2	2050	10	54
	A2	2090	29	40

Suitable habitat extended into new areas beyond the current climate-topography model at a rate of approximately 39% to 40% across the study area for the 2050s and more modestly at 26% to 35% for the 2090s (Table 6). There was greater habitat extension for the 2090s than the 2050s in YOSE. In SEKI, there was the opposite trend with percent extension reduced in the 2090s compared to the 2050s under both scenarios. The primary areas of additional habitat in YOSE for the 2090s were in the eastern portion of the park (Figure 10). However, the most notable change was the extensive

additional habitat in southern SEKI for all but the 2090s under scenario B1, which showed additional habitat in southern SEKI was limited to the northern Great Western Divide, the head of Kern Canyon, and west along the Kings-Kaweah Divide. For the remaining models, suitable habitat extended well south in SEKI in the vicinity of the Great Western Divide and east of the Kern Canyon as well as the head of Kern Canyon and west along the Kings-Kaweah Divide.

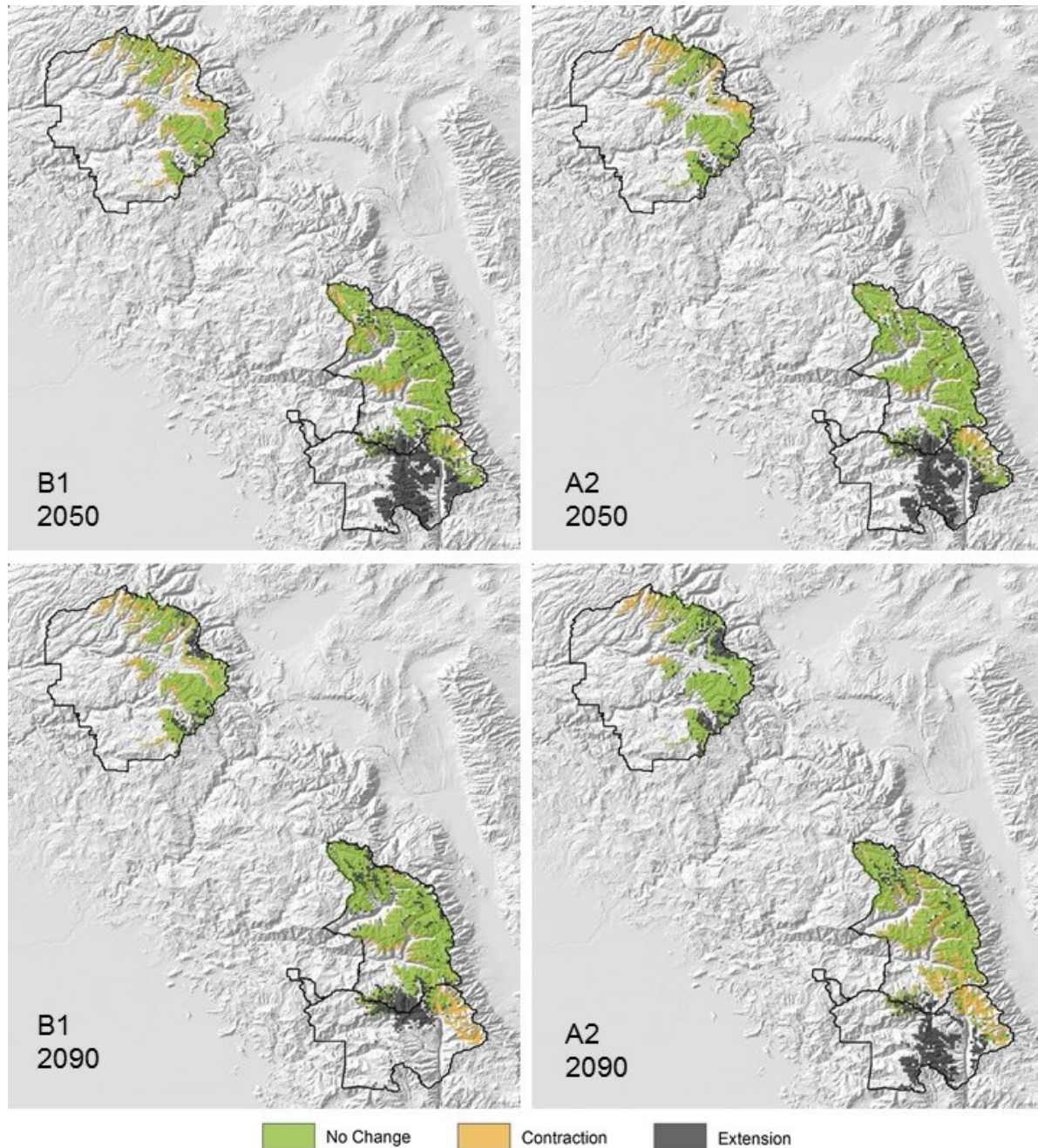


Figure 10. Suitable habitat model comparisons for whitebark pine showing where habitat is to remain unchanged (green), where it is to contract (orange), and where models indicated extension into new areas (gray). Comparisons are between the current climate climate-topography model and models under scenario B1 for 2050 and 2090 and models under scenario A2 for 2050 and 2090.

Foxtail pine

In paired comparisons of suitable habitat, McNemar tests indicated foxtail pine models differed from the current climate-topography model under both scenarios in whether the proportions of suitable habitat were equal (Table 7). Although all results were highly significant, models for the 2090s were more highly significant than those for the 2050s, and the difference was more highly significant for the model under A2 than for the model under B1.

Table 7. Comparisons of current climate-topography models for foxtail pine with future projected models, based on GCM agreement, indicated by year and scenario, using McNemar's chi-square test with continuity correction of 0.5. Critical value for the test is 3.84 at $\alpha = 0.05$, $df = 1$.

Park	Scenario	Model	Chi-square	p-value
SEKI	B1	2050	108.6	<<0.05
	B1	2090	322.5	<<0.05
	A2	2050	225.2	<<0.05
	A2	2090	561.9	<<0.05

Again, consistent with McNemar results, the area of suitable habitat for foxtail pine was projected to decrease under both scenarios compared with the current climate-topography model (Table 8). Decreases were greater for the 2090s than for the 2050s under both scenarios, and the decrease was greater under scenario A2 than under scenario B1.

Table 8. Area (km²) of suitable habitat in SEKI projected under climate scenarios B1 and A2 compared with the current climate-topography model for foxtail pine. The area of suitable habitat in the current climate-topography model is 1962 km².

Park	Scenario	Model	Area (km ²)	Difference (%)
SEKI	B1	2050	1686	-14.1
	B1	2090	1516	-22.7
	A2	2050	1587	-19.1
	A2	2090	1321	-32.7

The distribution of elevation among foxtail pine models was similar with probability of suitable habitat peaking at approximately 3,250 m in all models, including the current model and under both B1 and A2 scenarios (Figure 11). However, it appeared to increase between 3,250 m and 3,500 m and to diminish abruptly below 2,750 m compared with the current model. Probability of occurrence dropped off steeply above 3,500 m elevation in all models. Median elevation was not predicted to shift under either scenario compared with the current model.

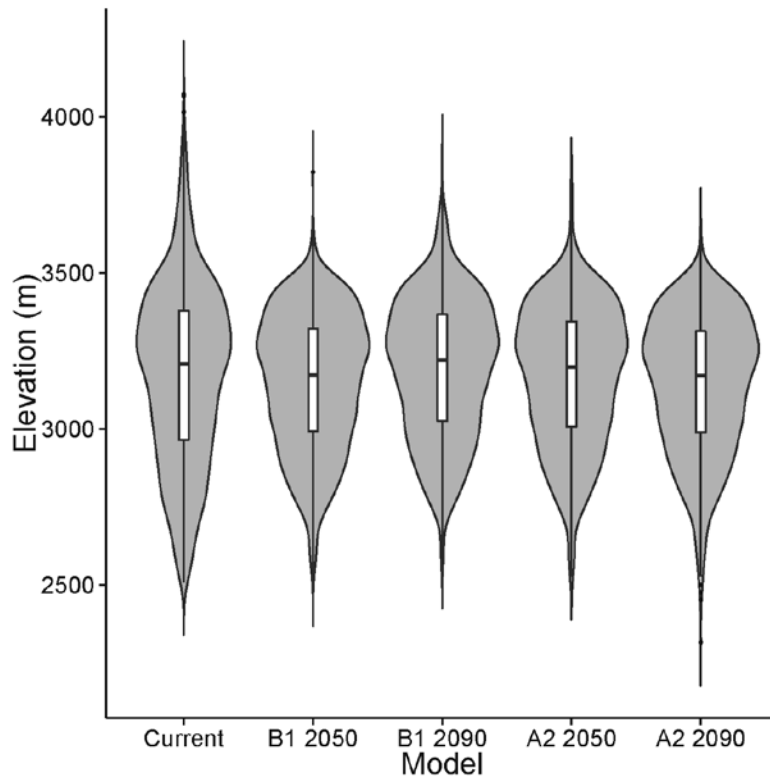


Figure 11. Violin plots (box plots embedded within 95% kernel density estimates) of projected elevation distributions for current climate and for the 2050s and 2090s under climate change scenarios B1 and A2 for foxtail pine in Sequoia & Kings Canyon national parks.

Model centroids reflected geographic shifts between the current climate-topography model and future habitat models (Table 9). Centroids under both scenarios shifted largely to the north, averaging 4.0 km under B1 but only 2.4 km under A2. As with whitebark pine, centroid shifts were greater for the 2050s than for the 2090s.

Table 9. Distance and direction from centroid of current climate-topography model for foxtail pine to centroids of future projected models along with centroid elevations.

Park	Scenario	Model	Elev (m)	Dist (km)	Direction
SEKI	B1	2050	3374	5.92	NNW
	B1	2050	3602	2.12	NNE
	A2	2090	3729	4.04	N
	A2	2090	3108	0.84	SSE

Contraction of suitable habitat for foxtail pine was at rates of 25% to 35% compared with the current climate-topography model (Table 10) and was well distributed throughout the range of the species in SEKI (Figure 12). The amount of contraction did not appear to differ between scenarios for the 2050s but was greater under A2 than under B1 for the 2090s. Extension of suitable habitat was much more

modest, was limited largely to northern SEKI, and was greater for the 2050s than for the 2090s. The relatively small amount of additional habitat that was predicted under B1 for the 2090s was in the vicinity of the east end of Monarch Divide at elevations from 2490 m to 3475 m.

Table 10. Contraction and extension of suitable habitat in models for the 2050s and 2090s under scenarios B1 and A2 compared with the current climate-topography model for foxtail pine.

Park	Scenario	Model	Contraction (%)	Extension (%)
SEKI	B1	2050	25	11
	B1	2090	27	4
	A2	2050	25	6
	A2	2090	35	2

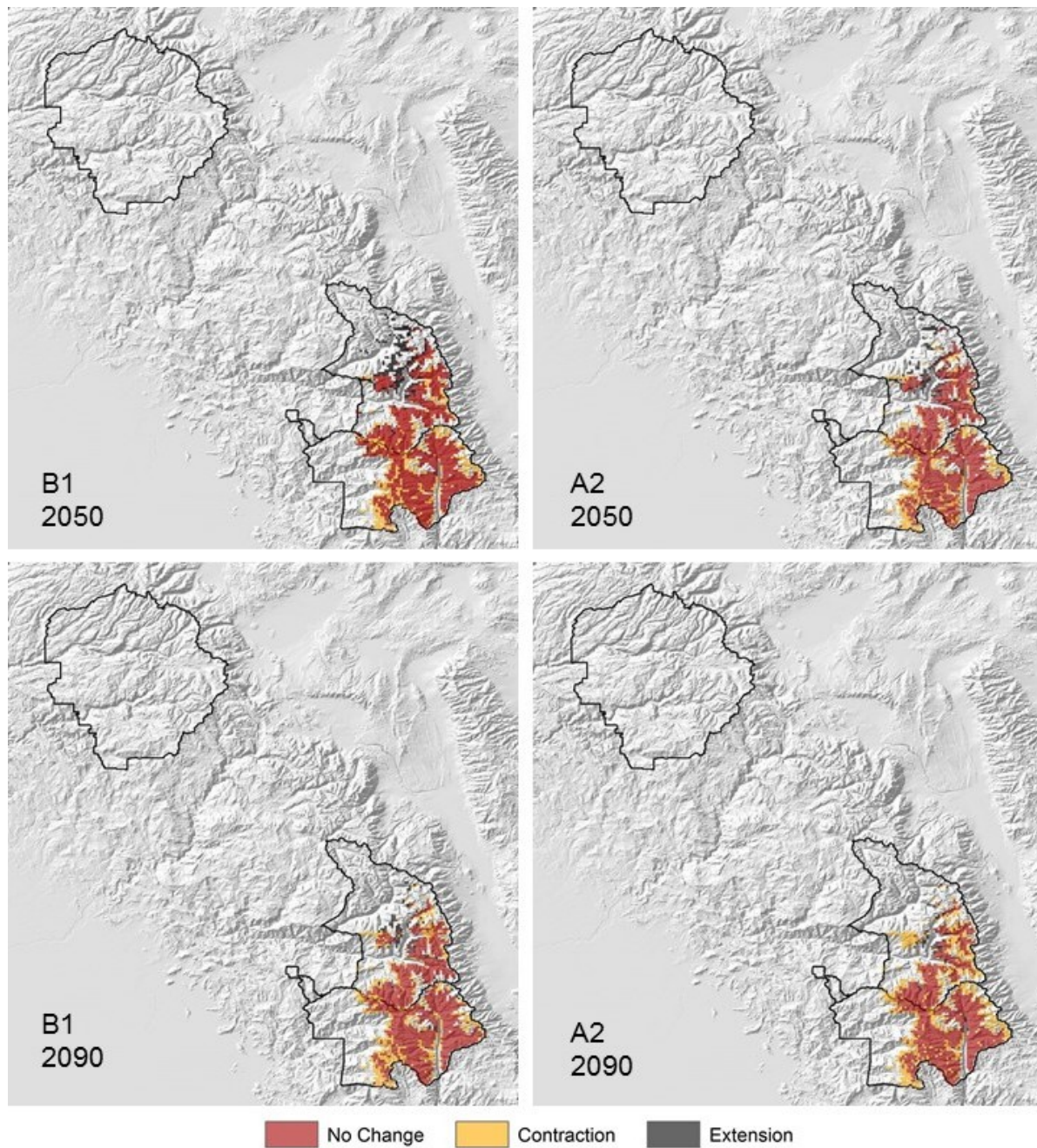


Figure 12. Suitable habitat model comparisons for foxtail pine showing where habitat is to remain unchanged (green), where it is to contract (orange), and where models indicated extension into new areas (gray). Comparisons are between current climate-topography model and models under scenarios B1 and A2 for the 2050s and the 2090s.

Discussion

Climate Surfaces

Although climate surfaces indicated higher winter precipitation by the 2090s, GCMs are least reliable for forecasting precipitation levels. The North American climate model was the least consistent with 124% and 6% increases predicted for precipitation within the range of whitebark pine for the 2050s and 2090s, respectively, under B1 (slightly greater for foxtail pine). The relatively subtle changes in temperature in the climate surfaces under B1 but more consistent increases in winter temperature under A2 are consistent with projections presented in the IPCC fourth assessment report (IPCC 2007), which reported greater increase in global average surface air temperature under A2 than under B1 by mid-century.

Current habitat suitability models

Whitebark pine

The upper elevation of whitebark pine is limited by growing season length (Weaver 2001). At lower elevations, it is a poor competitor in more shaded conditions (Arno 2001). Its mutualistic disperser, the Clark's Nutcracker, moves seeds to lower elevations, but establishment is low to non-existent below its typical elevation range. Therefore, a close relationship with elevation, which contributed 50% to the current model, is not surprising. Mixed-species stands are the exception in the Sierra Nevada region, reflecting the narrow environmental setting in which the species occurs.

The cold hardiness of whitebark pine varies geographically, increasing across the species' range from south to north, but overall it has a high level of hardiness compared to other conifer species (Bower and Aitken 2006). The contribution of January minimum temperature to the current model, at 6%, supports the hypothesis of cold hardiness in whitebark pine or at least the competitive advantage it may have in colder climatic regimes (Weaver 2001). Alternatively, January minimum temperature may be a surrogate for the range of conditions under which whitebark pine has superior hardiness, including cold, a short growing season, and desiccating high winds.

The basis for the strong contribution of July precipitation, at 18%, is more subtle. The range of values for July precipitation is just 1 mm to 11 mm across the study area, much lower magnitude than the 73 mm to 220 mm range of January precipitation, and, unlike January precipitation, it shows little fidelity to general topography. The highest values occur in the southeastern quadrant and northwest edge of YOSE, the lowest values in southern SEKI. Middle values occur in northern SEKI (3 mm to 4 mm) and the remainder of YOSE (mostly 4 mm to 5 mm). Whitebark pine samples occur across this range with the greatest concentrations between 2 mm and 4 mm in SEKI and between 4 mm and 6 mm in YOSE.

In the comparison of the current climate-topography model with the mapped distribution of whitebark pine, more extensive suitable habitat in the model may have resulted in part from the model's relatively coarse 1 km² resolution compared with 0.005 km² minimum mapping unit of the vegetation map. The latter had the advantage of distinguishing patterns of occurrence that varied with microtopography, soil depth and other fine scale habitat characteristics that were not available at the

1 km² resolution. Also, accuracy of photointerpreted whitebark pine mapping classes was estimated with 235 field samples at 78% to 85% in YOSE and at 67% to 100% in SEKI, indicating a basis for additional differences between the two products. Errors of omission could account for some of the discrepancies between modeled and photointerpreted whitebark pine extent. Lack of mapped stands does not preclude species presence but only indicates the species was not detected. Also, lack of species presence can result from site history or lack of propagule dispersal and not necessarily that the habitat is unsuitable. Finally, the purpose of the modeling was not to distinguish individual stands but to assess potential shifts in the distribution of suitable habitat in response to anticipated climatic shifts.

Foxtail pine

The importance of April and July precipitation, with contributions of 31% and 22%, respectively, to the foxtail pine current model is unlikely to be due exclusively to its close relationship with elevation. That is because they do not parallel topography nearly as much as January precipitation. More likely, it is the fidelity with which the species occurs at the lowest levels of July precipitation within the study area. Increased summer precipitation can enhance tree establishment (Agee and Smith 1984), and the model may have reflected this relationship.

Elevation made a more modest contribution to the current foxtail pine model, at 8%, than to that of whitebark pine. The relationship between elevation and precipitation in general is somewhat complex. January precipitation is correlated with elevation at $r = 0.68$, but the correlation declines for the remainder of the months evaluated from $r = 0.54$ for April to $r = 0.23$ for October precipitation. Winter and spring precipitation increase from the xeric foothill zone to the montane zone where they peak at middle elevations around 2600 m to 2,800 m. They then decline at higher elevations so that above 2,800 m to 3,000 m there may be 25% less precipitation than at middle elevations. Due to the summer dry Mediterranean-type climate, July precipitation is an order of magnitude lower than in winter, but it increases from mid to high elevation by approximately the same proportion as winter precipitation decreases across that gradient.

Similar to whitebark pine, the more extensive suitable habitat for foxtail pine in the current climate-topography model in southern SEKI compared with mapped occurrence may have resulted in part from the relatively coarse 1 km² resolution of the model compared with 0.5 ha minimum mapping unit of the vegetation map. Map accuracy was estimated with 153 field samples at 67% to 90% for foxtail pine mapping classes. Again, errors of omission could account for some of the discrepancies between modeled and photointerpreted foxtail pine extent, and detectability varies among species in a photointerpretation context.

Future habitat suitability models

Whitebark pine

After elevation and July precipitation, Maxent reported that April and October precipitation had the greatest influence on future whitebark pine models. However, because April precipitation is highly correlated currently with January precipitation, comparisons of contribution levels are not reliable, and January precipitation may have as strong an influence on future habitat suitability as that of April

precipitation. In addition, we cannot predict how correlations among covariates may change in the future, making conclusions among the relative contribution of covariates difficult.

Future models for the 2050s may display greater differences from current models than those for the 2090s for several reasons. The conservative approach of requiring agreement among all 5 GCMs might have had an effect. If that requirement were relaxed (e.g., requiring agreement among only 4 or more GCMs), it is possible there would be less difference between the 2050s and the 2090s. Another possible but untested explanation is, when elevation or centroid location changes, the amount of suitable area might change. That is, elevation affects many of the driving variables, yet the counter-intuitive results are that suitable area might increase over time or be inconsistent in the amount and direction of change. This could be simply because the elevation that becomes more suitable comprises a greater (or lesser) area within the parks. However, without estimates of uncertainty (variance, 95% CI, etc.), it is difficult to determine whether these differences are truly meaningful, i.e., whether confidence intervals overlap.

The predicted reduction in suitable habitat in YOSE of 13% to 28% is consistent with an increase in elevation and a geographic shift to the southeast under both scenarios. The highest elevation portions of the YOSE landscape are in the southeast in the vicinity of Mts. Dana and Gibbs, the Kuna Crest, Mts. Lyell and Maclure, and the Clark Range (Gesch 2007; Gesch et al. 2002), making a geographic shift to the southeast consistent with an increase in elevation.

Whitebark pine is likely to be more vulnerable to warmer January minimum temperatures predicted under scenario A2 than to rises in summer temperature (Iglesias et al. 2015); however, predicted increases in January precipitation could mediate that effect.

SEKI has a higher proportion of high-elevation habitat than YOSE. As a result, there is more high elevation habitat for whitebark pine expansion consistent with predicted increases in the amount of suitable habitat in SEKI under both scenarios. Although models indicated a narrowing in elevation range, suitable habitat was predicted to be slightly more evenly distributed within that range. High-elevation habitat is more evenly distributed north to south in SEKI than in YOSE, but there is a greater proportion of high-elevation habitat in southeastern SEKI in the vicinity of the Kaweah Peaks Ridge, Great Western Divide, Kings-Kern Divide, and the Sierra Nevada crest in the Mt. Whitney region. Therefore, a geographic shift to the southeast is consistent with an increase in elevation in SEKI as well. Although projected range shifts have been typically to the north under more extreme climate scenarios (Kueppers et al. 2005), other species of high elevations in the Sierra Nevada have been predicted to shift south as well (Loarie et al. 2008).

The extension of whitebark pine suitable habitat to the south corresponds to the pattern of centroid shift, which was to the south for both the 2050s and 2090s under both scenarios. This extension falls outside not only the current modeled range and current mapped range of whitebark pine in SEKI but south of the known range limit for whitebark pine. The prominent extension for the 2090s in northeastern YOSE, however, falls within an area mapped as whitebark pine and may reflect a gap in the model more than a likely shift in habitat. The extension south in SEKI would extend the species' southern range limit should whitebark pine shift south into the newly suitable habitat. Dispersal

limitation should not be a factor because the range of Clark's Nutcracker includes that portion of SEKI. Nevertheless, we recommend caution in interpreting predicted species expansion since factors beyond climate can influence species distributions (Chardon et al. 2015).

Although models and mapped current vegetation are not directly comparable (due to differences in resolution, species versus species assemblage models, etc.), it is interesting to note what is currently mapped within areas predicted to be suitable whitebark pine habitat in the future. Approximately half of newly suitable habitat is mapped as barren, consisting of mostly non-alpine talus and rock outcrops (85%) and alpine talus and scree (15%) (Appendix C). Only the areas of extension for scenario A2 for 2090 in YOSE are much below 50% barren, at 35%, and only scenario B1 for 2090 in SEKI is much above 50% barren at 71%. Most of the remaining portions of the extensions are mapped as Sierra lodgepole pine, mountain hemlock, and whitebark pine in YOSE and as foxtail pine, Sierra lodgepole pine, and California red fir (*Abies magnifica*) in SEKI (in declining order). The areas currently mapped as whitebark pine types may represent gaps in the model, errors in mapping, or both. Areas mapped as whitebark pine represent less than 15% of newly suitable habitat in YOSE and less than 3% in SEKI, reflecting well on model accuracy in one respect. There are few differences in proportions of mapped habitats within YOSE or SEKI when comparing models for different scenarios or decades.

Reductions of suitable habitat in YOSE under B1 and under A2 for 2050 are consistent with bioclimatic habitat modeling that predicted 82% to 100% reduction in whitebark pine habitat in the southern Sierra Nevada (M. D. Schwartz, Univ. Calif. Davis, unpublished data). In addition, Gonzalez (2012) found 20% of the southern Sierra Nevada is highly vulnerable to biome change based on Dynamic Global Vegetation Models, and subalpine forest overall has among the highest projected losses. The 11% to 49% increase in suitable habitat in YOSE under A2 and in SEKI for both time scenarios and both time periods contrasts with these results. Whitebark pine habitat models for the Greater Yellowstone Area also project substantial reductions by 2100 (Chang et al. 2014; Miller et al. 2015). Interestingly, Maxent models using 3 GCMs and 2 emissions scenarios for the full North American range of whitebark pine, projected a 29% increase in the size of the bioclimatic envelope but also a shift north of 6.5 degrees latitude (McKenney et al. 2007).

Differences in the direction and magnitude of modeling results may be attributable to differences in methods, techniques, data, variables, spatial resolutions, climate scenarios, GCMs, or ecosystems. These factors make it difficult to interpret either similarities or differences among results. Gonzalez (2012) used biome as the unit of analysis and a spatial resolution of 50 km². Miller et al. (2015) used state transition models constructed for the GYA with its substantially different climate and included interactions with blister rust and mountain pine beetles. Very little comparable work has been done for the Sierra Nevada and none that considers these biotic interactions.

Foxtail pine

Although April and July precipitation had the greatest proportional influences on foxtail pine future models (27% and 21%, respectively), response curves indicated the greatest probability of foxtail pine occurrence when April and July precipitation values were low, between 2 mm and 4 mm. In

contrast, although January precipitation contributed less than half that of April and July precipitation (9.3%), the response curve indicated probability of occurrence increased with increasing January precipitation, peaking above 0.8 probability at the highest levels of over 200 mm precipitation. It is tempting to interpret this as being due to the orographically-influenced increase in winter precipitation with elevation, but this may be an over-simplification for two reasons. First, response curves are difficult to interpret if covariates are strongly correlated, and they reflect how each environmental variable individually affects Maxent output; whereas Maxent models can be as influenced by the behavior of variable groups as that of individual variables (Phillips 2005). Second, the range of values for precipitation in July (1 mm to 12 mm) differs by an order of magnitude from those in January (60 mm to 230 mm), complicating interpretation.

When only January precipitation is included in the model, the marginal response curve indicates the probability of foxtail pine occurrence is high at lower values of 60 mm to 100 mm and drops to zero above 140 mm. This may reflect the occurrence of foxtail pine predominantly in the eastern portion of SEKI in the arid Kern River watershed east of the Great Western Divide and other areas east of the maximum winter precipitation zone, which is at middle elevations (Haultain 1994).

Finally, as with the whitebark pine models, because January precipitation is highly correlated currently with April precipitation, while October precipitation is not, contribution levels between these are not reliable, and January precipitation may have as strong an influence on future habitat suitability as that of April precipitation. Again, we cannot predict how correlations among covariates may change in the future, making conclusions among the relative contribution of covariates difficult.

The extension of foxtail pine suitable habitat to the north is consistent with the pattern of centroid shift: most pronounced for the 2050s and least pronounced for the 2090s particularly under scenario A2. Rather than extending farther north, change in suitable habitat for the 2090s is characterized primarily by contraction of 27% to 35%, compared with the current model, under scenarios B1 and A2, respectively.

Within the areas of foxtail pine extension indicated by the models, approximately 40% to 55% is currently mapped as barren with the remaining consisting of Sierra lodgepole pine, western white pine (*Pinus monticola*), and California red fir (Appendix C). While areas mapped as foxtail pine cover well under 10% of newly suitable habitat, they climb to 15% for 2090 under A2. For the 2090s, however, the amount of barren area in newly suitable habitat is less under scenario A2 than under B1, and there are greater proportions of foxtail pine, Sierra juniper (*Juniperus grandis*), and western white pine under A2.

Paleological record

Despite differences in seed dispersal mechanisms between the two species, there are important similarities to how their distributions have responded to past climates. These similarities provide context to the interpretation of these modeling results and insight into management.

The genetic diversity of both whitebark pine and foxtail pine in the Sierra Nevada was likely influenced by Pleistocene glaciation. Timing of the Sherwin glacial maximum (the largest

Pleistocene glacial episode in the Sierra Nevada) corresponds with estimates of divergence from northern populations (e.g., Klamath Mountains) (Eckert et al. 2008; Richardson et al. 2002). Low levels of gene flow since divergence are documented only from cpDNA (i.e., pollen), and Sierra Nevada populations of both species are significantly different from northern populations in cpDNA haplotype frequencies (Eckert et al. 2008; Richardson et al. 2002). Thus the biogeography of both species has been profoundly shaped by geographical isolation and by large shifts in the subalpine ecosystem associated with climate change and glaciation between the Pleistocene and early Holocene.

The picture is clearer for the more intensively studied whitebark pine. The following is derived from Richardson et al. (2002) who performed mtDNA analysis from samples throughout the range of whitebark pine. Their results identified three distinct haplotypes, and one of them occurs in the Sierra Nevada and the Cascade Range. The geographic structure of the three mtDNA haplotypes is suggestive of the existence of large (> 100 km) areas of unsuitable habitat that create hard barriers to seed dispersal. At lower latitudes (e.g., Sierra Nevada), full glacial climates apparently led to a sizeable expansion of subalpine and montane habitats, which were displaced as much as 1000 m below present limits. This climate probably favored expansion into the northern Great Basin and central Oregon. As warming occurred, whitebark pine from these lower latitude regions were reduced to remnant populations on the highest peaks. In the north, the retreating Cordilleran ice sheet provided new expanses of subalpine habitat that were colonized by whitebark pine, as indicated by macrofossils found in early Holocene strata. The Sierra Nevada apparently exhibited limited gene flow with other regions. Geographic isolation and a possible founder effect may have created comparatively low genetic diversity and high genetic divergence that distinguishes the Sierra Nevada populations. Whitebark pine in the Sierra Nevada and in smaller areas in northern Nevada could be considered to inhabit contemporary refugia, making climatic warming and other novel stressors even greater threats to overall genetic conservation.

The paleological record indicates that the distributions of both species have responded to climate fluctuation, and while speciation has not occurred, genetic differentiation from northern populations is in evidence. What does this history tell us about the potential for these species to adapt to anticipated climatic change in the Sierra Nevada? In general, there are three responses that can reduce the threat of extinction from changing climatic conditions: phenotypic plasticity, tracking suitable climate through range shifting, and adapting to changing conditions by rapid evolution (Parmesan 2008; Bell 2012). The most widely accepted view is that most species will more likely shift distribution or respond by phenotypic plasticity rather than adapt in situ to new conditions. This is largely because range shifting and plasticity are likely faster responses to matching environmental conditions than evolutionary processes. Dispersal is a key determinant of population dynamics and the main response mechanism is the spread of newly arising, beneficial alleles. Spatially structured populations have a greater chance of surviving periods of deteriorating growth conditions and adapting to the new environment when dispersal allows for gene flow across subpopulations (Schiffers et al. 2012). However, despite the beneficial effect of dispersal for rapid evolution, dispersal is known to have an overall negative influence on population fitness under most scenarios of local adaptation (Schiffers et al. 2012). Mismatches between immigrants' genotypes and

environmental conditions at the new site result in a reduction in overall fitness, known as migration load. Migration load increases with the degree of habitat heterogeneity under gene flow through both pollen and seed movement (Schiffers et al. 2012).

Results from genetic analyses and investigations into the species' past and current distributions provide some optimism for their potential to respond to climate warming. Both species have persisted through large changes in climatic conditions, and presently both occur in patchy but spatially structured populations with low to intermediate levels of gene flow. Schiffers et al. (2012) conclude that optimized fitness occurs in patchy populations distributed across an environmental gradient with intermediate rates of dispersal. Our modeling results predict small changes in species distribution over the remainder of this century. However, our project addressed a very short time period when considering the relative likelihood of adaptation versus extinction. The time to first reproduction for a young seedling that exists today would likely occur after our first modeled time period (2050s), making interpretation of predicted climate on adaption extremely difficult. However, Lloyd (1997) speculated that long-lived tree species (> 500 yrs) with long reproductive lifespans (> 100 yrs) could exhibit population-level inertia during periods of inhospitable climates. Recruitment could be low to non-existent, and stand structural density could decline, but adults could persist until favorable conditions return. This would make populations somewhat buffered against variation in environmental conditions. Moreover, paleo-reconstruction of treeline forests indicate that lags of 150 years or more are likely between the initiation of a warming period and the establishment of a forest community (Lloyd 2005). Thus, while a high degree of uncertainty exists beyond the modeled time period of our project, the paleological and genetic record and key characteristics of the two species (e.g., long lived) suggest the potential for persisting through a changing climate. The rate and magnitude of climatic change will be paramount in influencing this potential.

Conclusions

Models indicate that suitable habitats for whitebark pine and foxtail pine are more likely to shift geographically within the parks by 2100 rather than decline precipitously. This implies park managers might focus conservation efforts on stressors other than climate change, working toward species resilience in the face of threats from introduced disease and elevated native insect damage (e.g., mountain pine beetle).

Tracking the incidence of biotic interactions such as pathogens (e.g., WPBR), parasites, (e.g., dwarf mistletoe), and insect damage (e.g., mountain pine beetle) are among the primary objectives of the NPS high elevation white pine monitoring protocol (McKinney et al. 2012). Other objectives include tracking tree species composition and structure; tree birth, death, and growth rates; and reproductive effort (i.e., cone production). Habitat suitability models do not directly consider biotic interactions or demographic trends but can inform the interpretation of monitoring results. Because warming temperatures play a role in the duration and magnitude of mountain pine beetle outbreaks (Logan and Bentz 1999), models may be helpful with interpreting changes in the incidence of bark beetles. Although the paleoecological record indicates increasing temperatures are unlikely to cause an expansion of subalpine forests if water supply is elevated as predicted, changes in forest structure (e.g., increased density) can be a precursor to landscape-scale shifts in distribution, which show a lagged response in long-lived species (Lloyd and Graumlich 1997).

Estimates of species physiological capacity to respond to climate change are more informed when niche models are for the full range of species' distribution. Such models would complement those presented here for the parks, which were designed to inform managers about likely species response within their areas of responsibility. The spatial extent of model training has a substantial effect on model outcomes and neither local nor range-wide location guarantees consistent results in the magnitude and direction of change in suitable habitat extent and characteristics (Monahan et al. 2013). The species occurrence samples we used were well distributed across the range of the species in the parks and provided for the best opportunity for modeling species' local responses to climate projections.

Although the average elevation of snowline is predicted to increase and a greater proportion of winter precipitation in the parks is likely to be received as rain, whitebark pine habitat will continue to be above snowline in the foreseeable future, and snow cover can be expected to continue to shelter seedlings over winter and late-lying snow to provide moisture into the growing season.

To better understand how these species are responding to observed warming and drying trends in the near term, we offer the following suggestions. SIEN monitoring plot locations were originally drawn from previously mapped locations that did not include the areas identified as extensions in our modeling effort. Surveying for species occurrence or installing monitoring plots in areas where future suitable habitat is predicted to occur (particularly above current treeline) could assist the SIEN monitoring program in understanding the status and trend of these species across the parks. Furthermore, it would be informative to identify plots that are in areas predicted to contract and determine if mortality rates are higher, and regeneration rates lower, than areas where contraction is

not expected based on modeling results. Both of these approaches would assist in validating results from this modeling effort and, more importantly, would provide a more well-informed understanding of the influence of temperature and precipitation on the distribution and viability of the two species.

High elevation white pine management needs to be informed by both habitat suitability models and a greater understanding of introduced white pine blister rust and native pine beetles for a comprehensive approach to managing these foundational species (Millar et al. 2012). Further understanding of the incidence and severity of white pine blister rust and other stressors in high elevation white pines would help assess vulnerability from threats other than climate change.

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Appendix A. Climate Surface Summaries

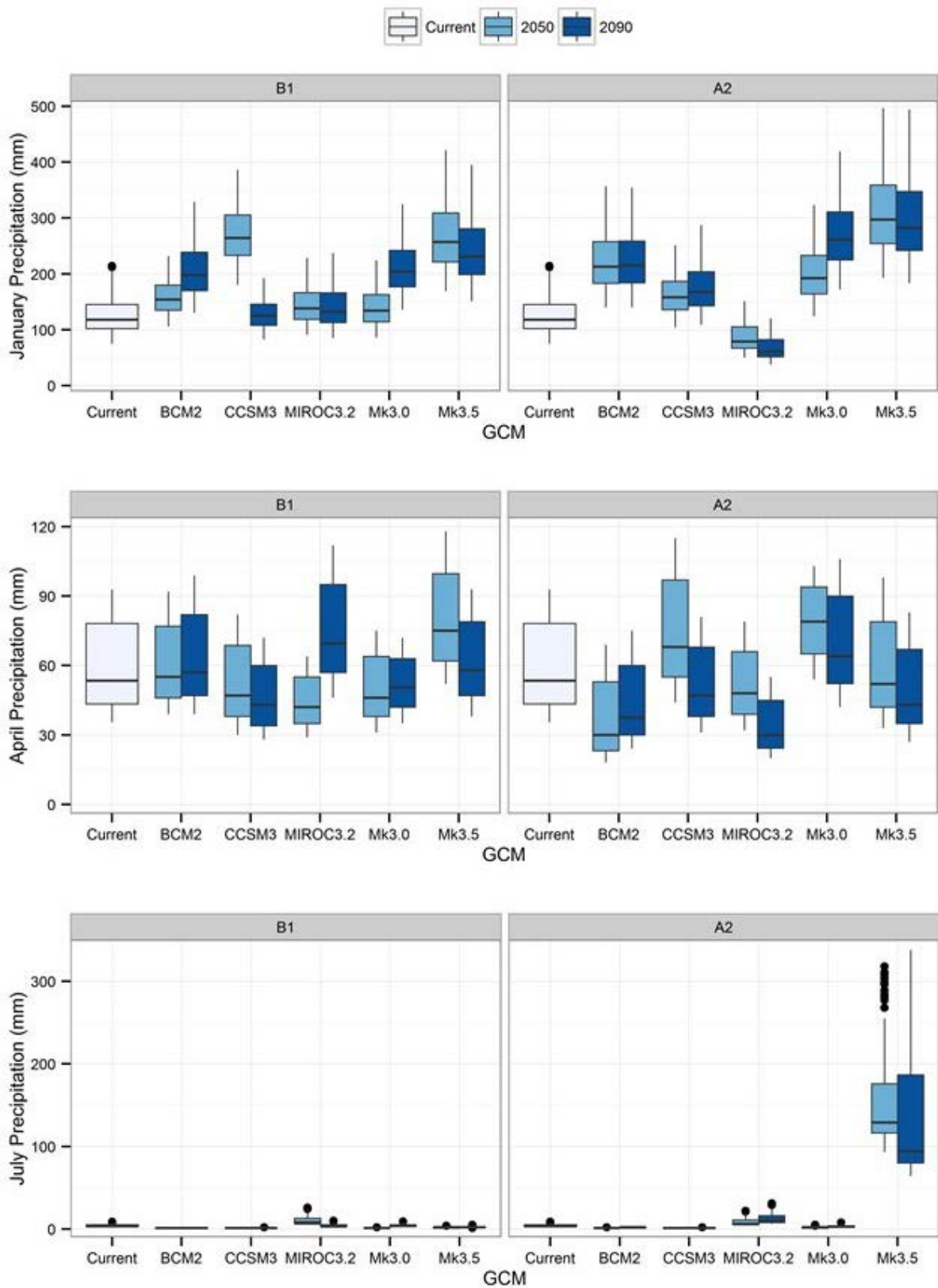
The following pages present box and whisker plots displaying the distribution of data from climate surfaces for select climate covariates that were useful in predictions of suitable habitat for whitebark pine (*Pinus albicaulis*) and foxtail pine (*P. balfouriana* ssp. *austrina*).

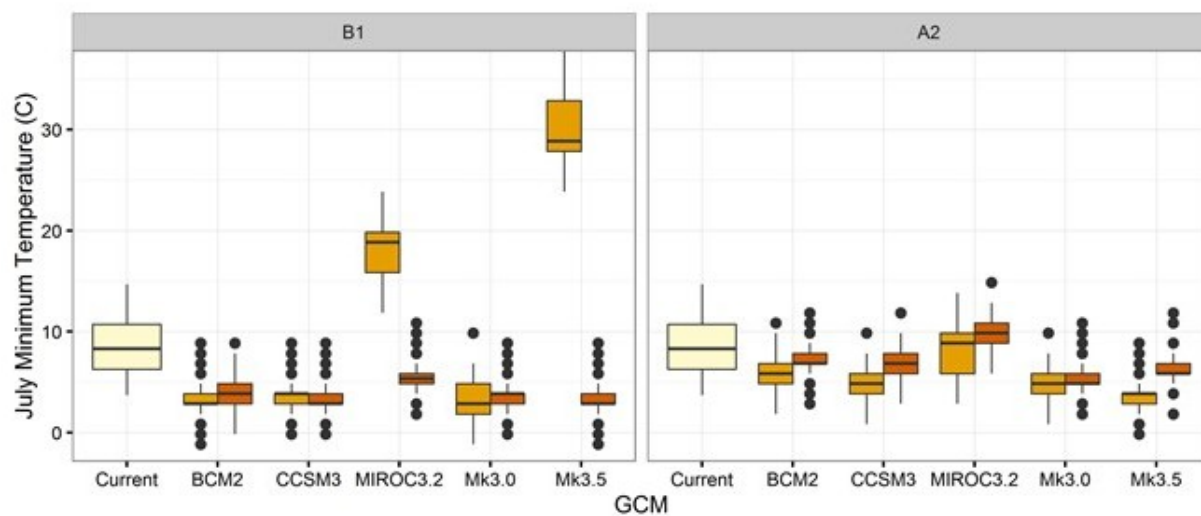
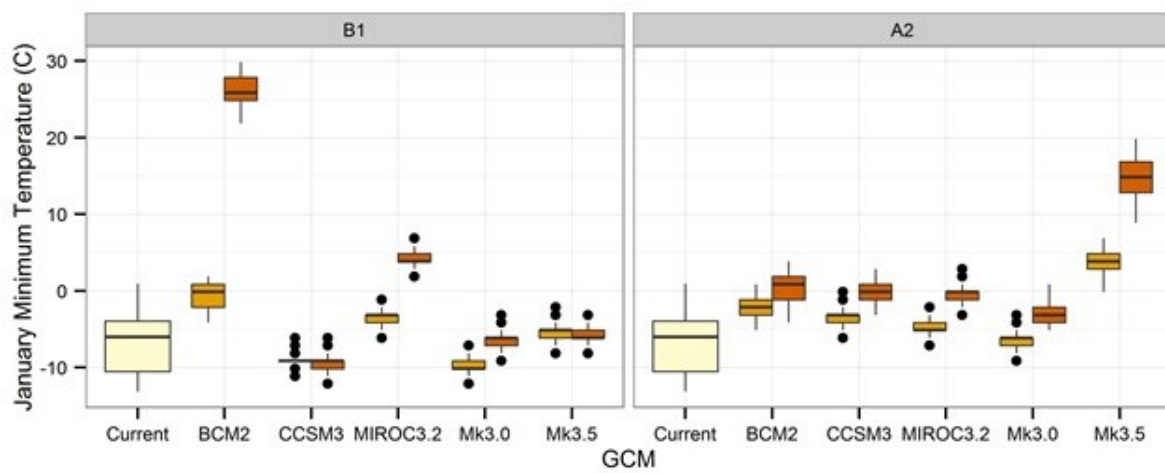
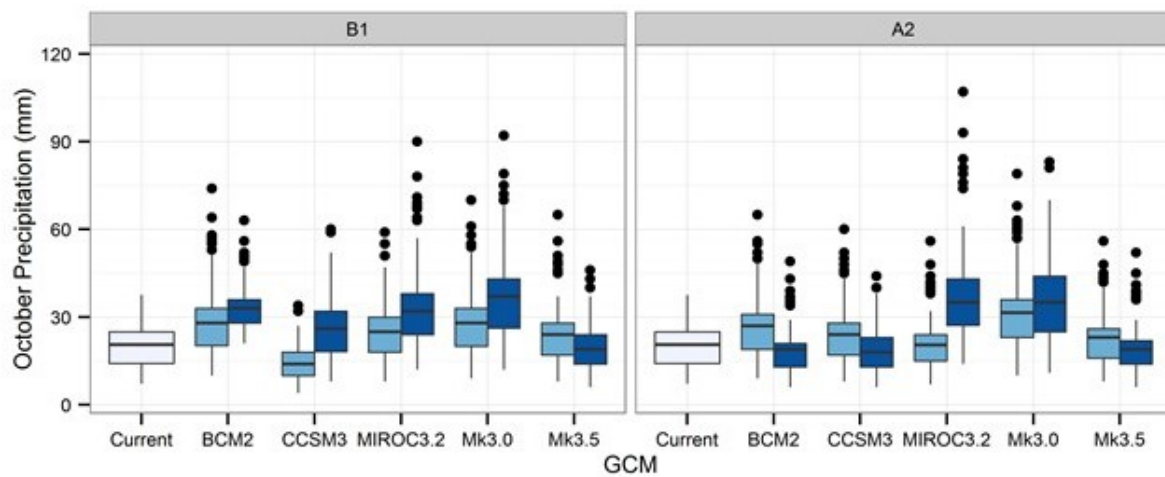
The plots compare data from current climate surfaces with those for the 2050s and the 2090s to reflect changes expected under the respective climate scenarios and General Circulation Models (GCMs) downscaled to the local landscape. They are based on values from each climate surface for locations where each species occurred using the same samples as those used for model input with 328 points for whitebark pine and 244 points for foxtail.

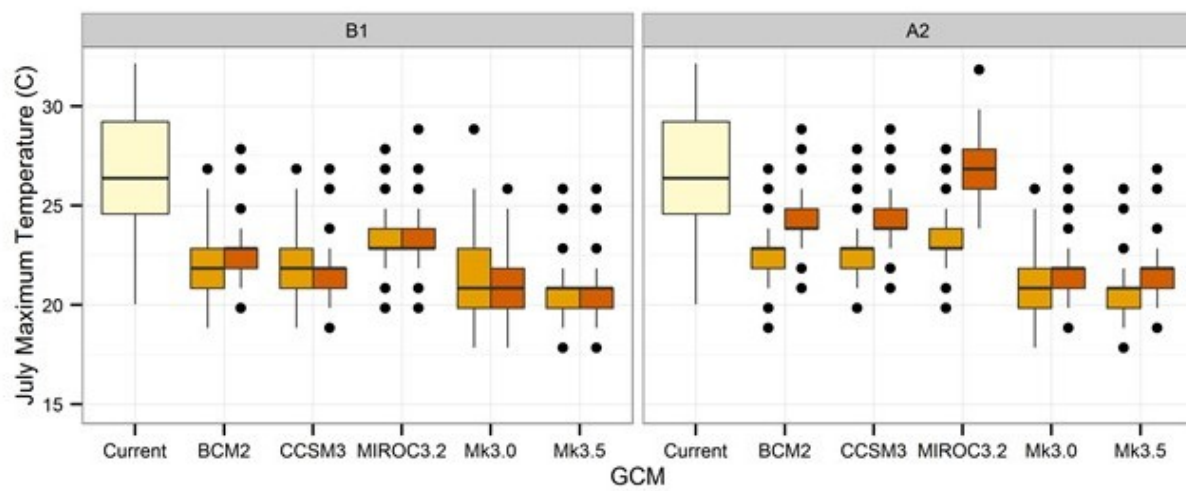
Precipitation is shown for January, April, July, and October for both species. January minimum and July minimum and maximum temperature are shown for both species with the addition of April maximum and October minimum temperature for foxtail pine. Boxes show first quartile (bottom of box), median (horizontal line within box), and third quartile (top of box), and whiskers (vertical lines) display minimum and maximum values (line terminus). Closed circles represent outliers. Y axes were allowed to vary because the primary focus was on differences between climate scenarios B1 and A2 rather than among months, and standardized axes precluded comparisons among GCMs within these scenarios for some covariates.

GCMs used in modeling were BCM2.0 = Bjerknes Centre for Climate Research, Bergen Climate Model v. 2.0, CCSM3 = National Center for Atmospheric Research Community Climate System Model v. 3.0, MIROC3.2 = Model for Interdisciplinary Research on Climate medium resolution v. 3.2 (2004), Mk3.0 = Commonwealth Scientific and Industrial Research Organisation, Mk v. 3.0, and Mk3.5 = Commonwealth Scientific and Industrial Research Organisation, Mk v. 3.5 (see main text for more information).

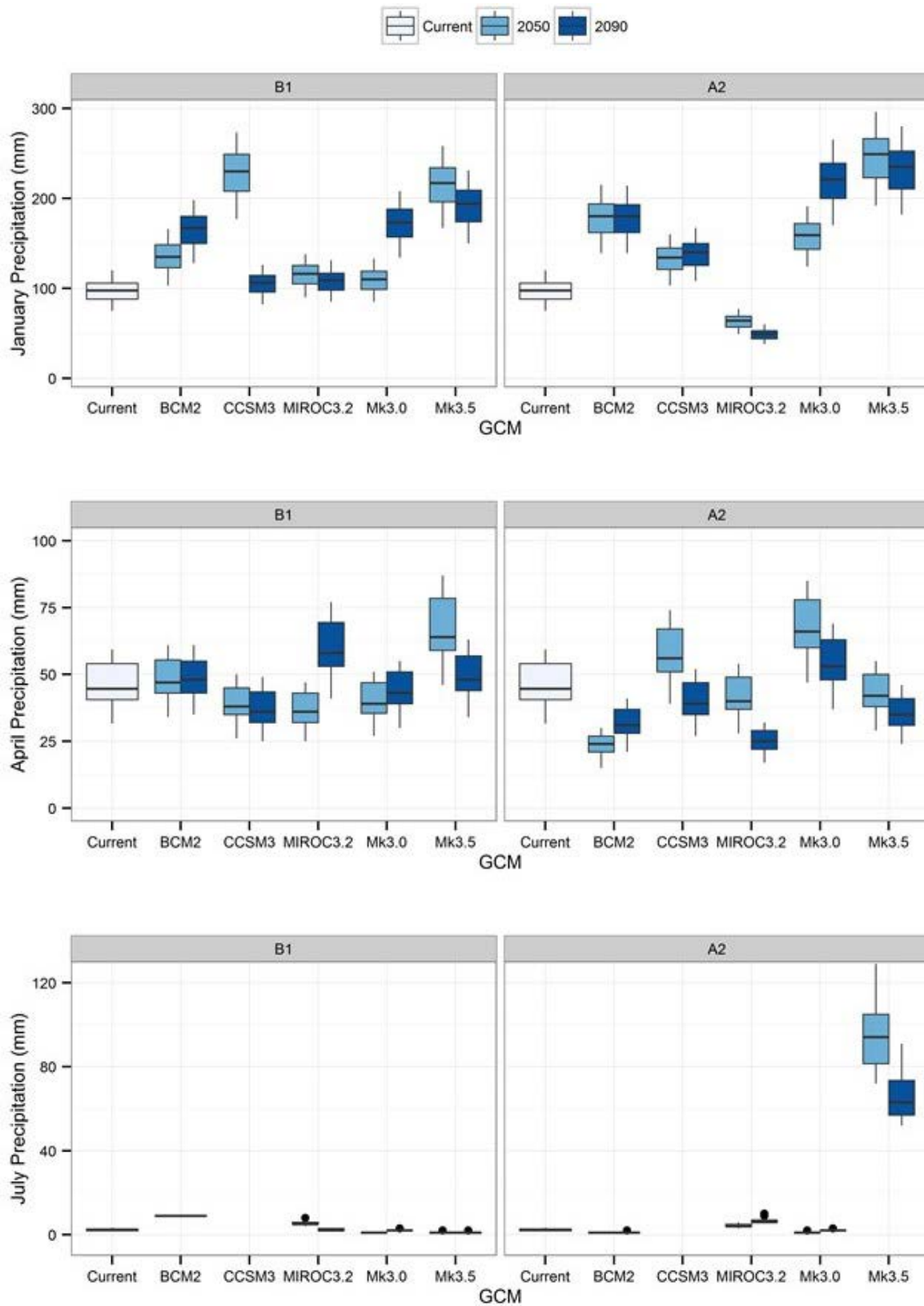
Whitebark Pine

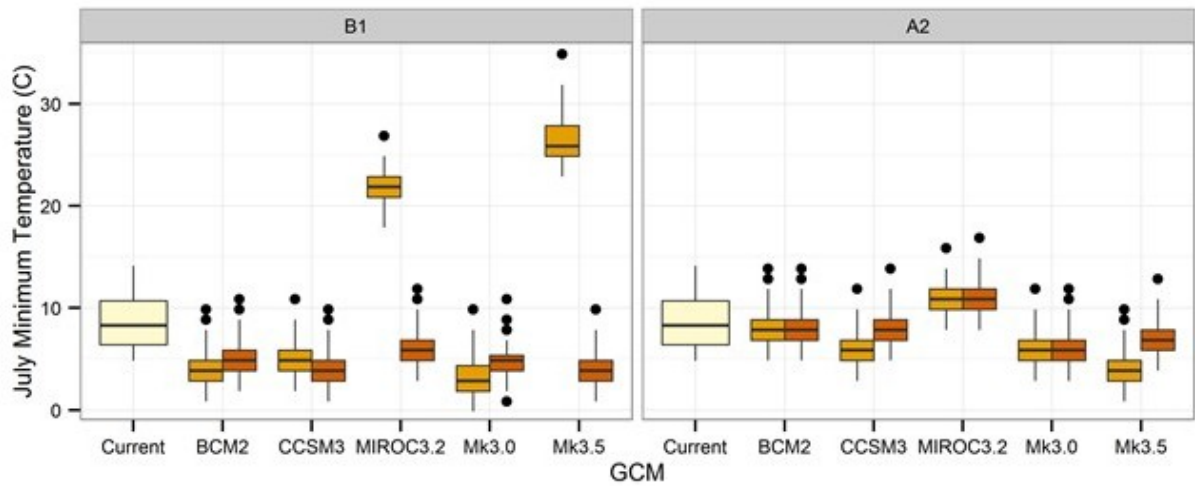
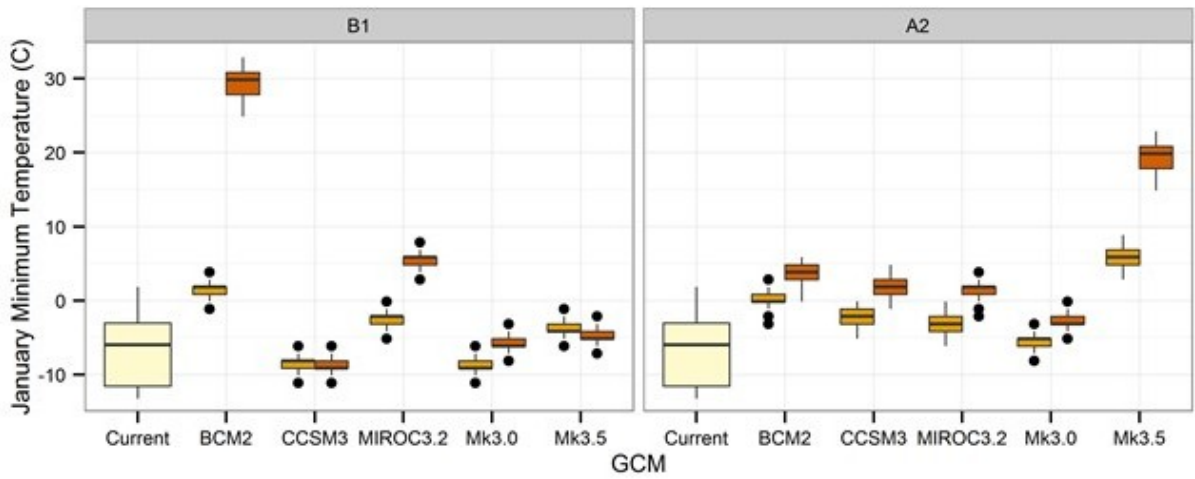
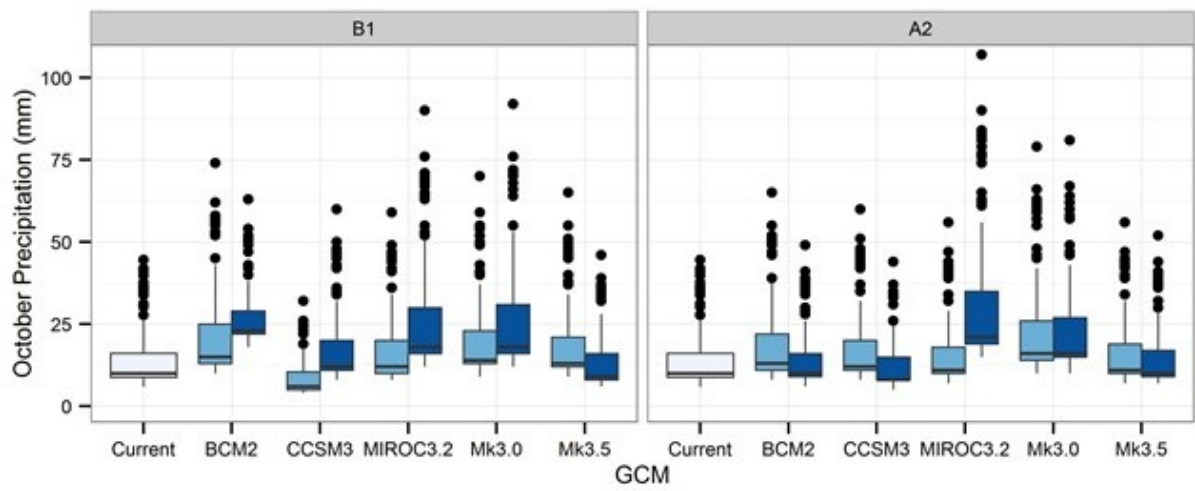


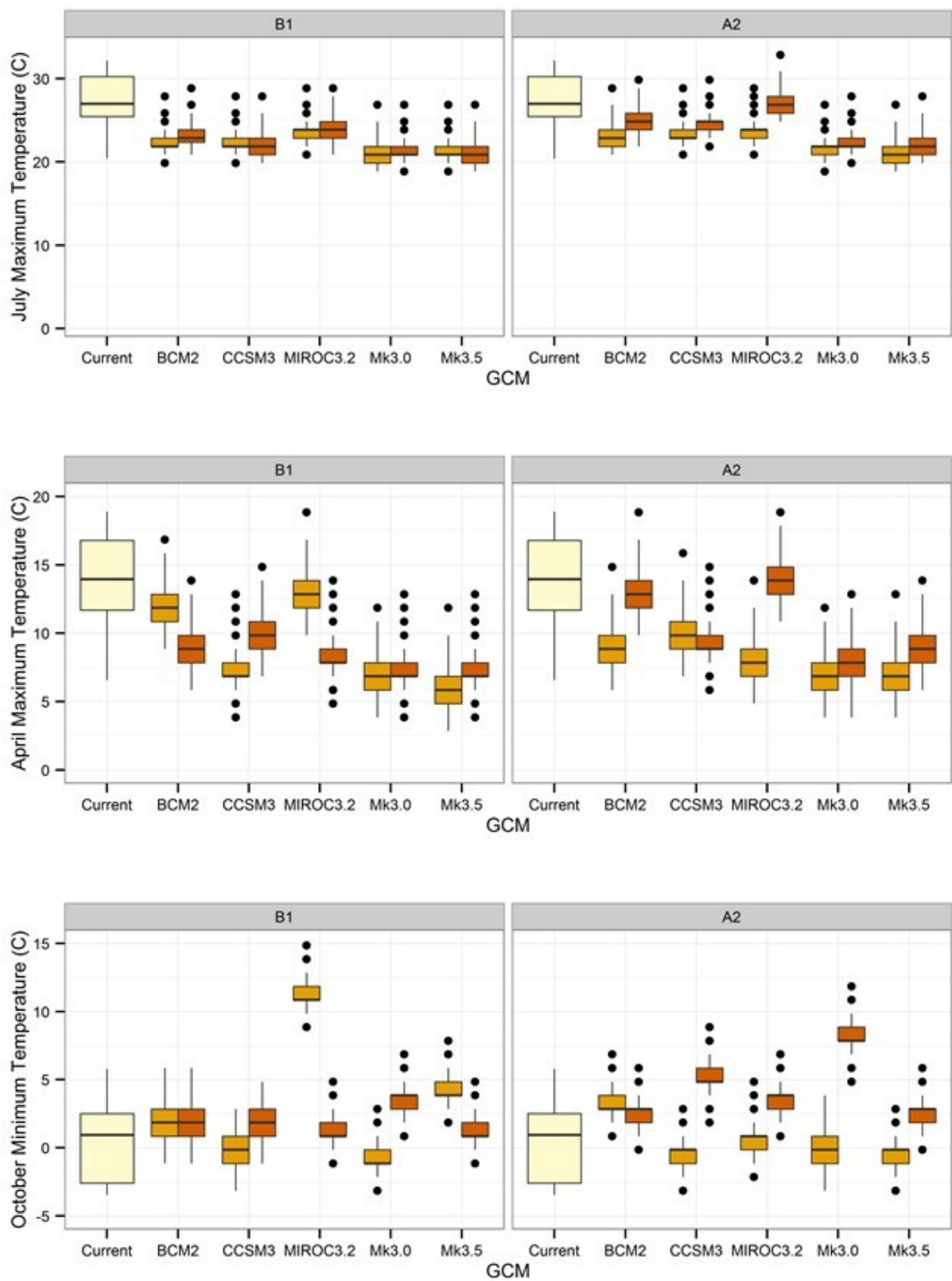




Foxtail pine







Appendix B. A Comparison of Current Climate-topography Models with Hypothesis-driven Current Models

To assess our confidence in how well the climate-topography models defined the species' environmental niche, we compared current climate-topography models for each species with models fit to a larger set of ecologically relevant environmental variables.

Methods

Hypothesis driven current models

For the purpose of the comparisons, we constructed models of current habitat suitability using additional environmental variables not projectable to the future. We identified variables based on three factors: 1) hypotheses regarding factors driving species distributions, 2) the degree of correlation among variables, and 3) the relative contribution of each variable to species distributions according to preliminary jackknife results. Although Maxent is not highly sensitive to multicollinearity, we used $r = 0.7$ as the threshold for variable inclusion to minimize its effect. Hypotheses took the form of variable combinations representing factors likely to influence habitat suitability (Table B1a and B1b). In hypothesis development, we focused on temperature and moisture inputs to capture direct and indirect influences on species distributions related to their physiological requirements (Woodward and Williams 1987). These included air temperature, precipitation, a topographic moisture index, potential soil irradiance as a surrogate for potential energy input, and snow cover for its influence on reproduction and recruitment. We also included an index of vegetation greenness as a surrogate for biomass and associated competition.

The vegetation greenness index was based on MODIS (Moderate Resolution Imaging Spectroradiometer, <http://modis.gsfc.nasa.gov/>) Normalized Difference Vegetation Index (NDVI, resolution=250 m² rescaled to 1 km²) data for July to October from 2000 to 2006. Using a data frequency of every 16 days, we took the maximum of each growing-season month per year (if multiple images were available per month) and used values from all months and all years to calculate NDVI mean.

Soils data were not available across the distribution of whitebark pine within the parks, and they do not contribute to projecting distributions into the future, so we relied on topography to represent moisture availability. We calculated, for each 1 km² cell, a topographic wetness index (Wetness) for park landscapes as a function of slope and contributing area using DEM and an algorithm available from Environmental Systems Research Institute (Pathak 2010). More specifically, it is a function of the natural logarithm of the ratio of local upslope contributing area and slope steepness. The wetness index represents potential, not actual, moisture as defined by topography.

Table B1a. Model covariates based on hypotheses developed as candidate habitat suitability models for whitebark pine (*Pinus albicaulis*) in Sequoia & Kings Canyon and Yosemite national parks. Elev is elevation (m) from digital elevation model data. Pr1, -4, -7 and -10 are precipitation in January, April, July, and October (see text). Tmin1, -4, -7, -10 are mean minimum temperatures in the same months. The same pattern is used for tmean and tmax. Solar_p is solar potential based on digital elevation models and latitude. Ndvi = mean NDVI values over 7 years based on MODIS data. Snow_dur, tsfd, and ssd are snow duration in days, total number of snow-free day, and first day of snow covered conditions based on MODSCAG between 2000 and 2010. Wetness is a topographic moisture index as a function of slope and contributing area. Covariates are presented in order of topography, precipitation, temperature, and all others alphabetically. Covariates for the climate-topography model are presented for comparison. (See text for more detail)

Model	Environmental Covariates
Climate- Topo	Elev, slope, aspect, pr1, pr4, pr7, pr10, tmin1, tmin4, tmin7, tmin10, tmean, tmean4, tmean7, tmean10, tmax1, tmax4, tmax7, tmax10
1	Elev, pr1, tmin1
2	Elev, pr1, tmin1, ndvi
3	Elev, pr1, pr7, tmin, ndvi, solar_p, wetness
4	Elev, pr1, pr7, tmin1, ndvi, snow_dur, solar_p, tsfd, wetness
5	pr1, pr10
6	tmin1, tmax7
7	Elev, slope, aspect, pr7, pr10, tmin1, ndvi, snow_dur, solar_p, ssd, tsfd, wetness
8	pr7, tmin1, ndvi, snow_dur, solar_p, ssd, tsfd,
9	pr10, pr7, tmin1, ndvi, snow_dur, tsfd
10	pr1, pr10, tmin, ndvi, snow_dur, tsfd
11	pr7, tmean7, ndvi, solar_p, snow_dur, tsfd
12	Elev, pr7, tmin1, ndvi, snow_dur, tsfd
13	pr1, tmin1, ndvi, solar_p, snow_dur, tsfd
14	Elev, pr7, pr10, tmin1, ndvi, solar_p, wetness
15	pr7, tmin1, ndvi, solar_p
16	pr7, pr10, tmin1, ndvi
17	pr1, pr10, tmin1, ndvi
18	pr7, tmean7, ndvi, solar_p
19	pr7, tmin1, ndvi, solar_p

Table B1b. Model covariates based on hypotheses developed as candidate habitat suitability models for foxtail pine (*Pinus balfouriana* ssp. *austrina*) in Sequoia & Kings Canyon National Parks. Elev is elevation (m) from digital elevation model data. Pr_1, -4, -7 and -10 are precipitation in January, April, July, and October (see text). Tmin_1, -4, -7, -10 are mean minimum temperatures in the same months. The same pattern is used for tmean and tmax. Solar_p is solar potential based on digital elevation models and latitude. ndvi = mean NDVI values over 7 years based on MODIS data. Snow_dur, tsfd, and ssd are snow duration in days, total number of snow-free days, and first day of snow covered conditions based on MODSCAG between 2000 and 2010. Wetness is a topographic moisture index as a function of slope and contributing area. Covariates are presented in order of topography, precipitation, temperature, and all others alphabetically. Covariates for the climate-topography model are presented for comparison. (See text for more detail)

Model	Environmental Covariates
Climate- Topo	Elev, slope, aspect, pr1, pr4, pr7, pr10, tmin1, tmin4, tmin7, tmin10, tmean1, tmean4, tmean7, tmean10, tmax1, tmax4, tmax7, tmax10
1	Elev, pr4, pr7, pr10, ndvi, tmin1
2	Elev, pr7, pr10, tmin1, ndvi
3	Elev, pr1, pr7, pr10, ndvi, solar_p
4	Elev, pr4, pr7, pr10, tmin1, ndvi, solar_p
5	Elev, pr1, pr7, pr10, tmin1, ndvi, snow_dur, solar_p
6	pr1, pr7, pr10, tmax7
7	tmax7
8	Elev, pr4, pr7, pr10, tmin1, ndvi, slop, snow_dur, solar_p, tsfd_min, wetness
9	Elev, pr7, pr10, tmin1, ndvi, snow_dur, solar_p, tsfd_min, wetness
10	Elev, pr4, pr7, pr10, tmin1, ndvi, snow_dur, solar_p, tsfd, wetness
11	Elev, pr4, pr7, pr10, tmax10, ndvi, snow_dur, solar_p, tsfd, wetness
12	Elev, pr1, pr7, pr10, ndvi, snow_dur, solar_p, tsfd_min, wetness
13	Elev, pr4, pr7, pr10, tmin1, ndvi, solar_p, wetness
14	Elev, pr7, pr10, tmin1, ndvi, solar_p, wetness
15	Elev, pr1, pr7, pr10, tmin1, ndvi, solar_p, wetness
16	Elev, pr1, pr7, pr10, ndvi, solar_p, wetness

We developed potential soil irradiance (Solar_p) using digital elevation models (DEMs) and latitude using a simple calculation and a resolution matching that of the models. Solar potential is a function of aspect, slope, latitude of each location, and time (Alvarez et al. 2014). We used the amount of potential solar energy (solar constant) that can reach a specific location on the earth at a certain time of the year, and integrated it over time and date. It was generated using the hemispherical viewshed algorithm:

$$\text{PointRadiation} = \text{Direct}_{\text{Total}} + \text{Diffuse}_{\text{Total}}$$

where Direct_{Total} and Diffuse_{Total} are the sum of radiation of all sectors (Rich et al. 1994). We used the ArcGIS solar radiation toolbox (ESRI 2009) and slope and aspect generated from SRTM (Shuttle Radar Topography Mission, NASA 2007; Farr et al. 2007) to generate the hourly solar radiation for 2010. The output was then averaged per month and then for the growing season, leading to a mean solar radiation layer at 1 km² spatial resolution. We did not apply atmospheric correction for cloud cover and atmospheric conditions. These data therefore represent potential but not actual solar insolation.

Snow cover in these mountainous areas represents prolonged moisture availability into the growing season, and the timing and duration of snow cover affects ecological processes in these settings (Brooks and Williams 1999). We included snow cover duration, snow cover start date, and total number of snow-free days among our hypothesis-driven current models. To capture the effect of variable snow cover and its influence on seedling survival and moisture availability, we used snow cover variables from MODSCAG (MODIS Snow Covered-Area and Grain size retrieval; Painter et al. 2009) data. Imagery covered the period 2000 to 2010 at a spatial resolution of 500 m² and at a daily temporal resolution. Raw data were stored as percent snow cover (Rittger et al. 2013). We defined snow covered condition as > 15%. The outputs were binary, with 1 representing snow covered conditions and 0 as not snow covered. From the binary results, we generated the three primary products of snow duration (Snow_{dur}, expressed as mean and minimum number of days), snow-free conditions (TSFD, expressed as minimum and maximum number of days), and first day of snow covered conditions (SSD, expressed as maximum). Snow cover measures were not correlated above the threshold we set of $r=0.7$ with either of the other snow cover measures or with any other environmental covariates (e.g., elevation, temperature), and we included more than one measure of snow cover in some hypothesis-driven current models (e.g., Model 4 for whitebark pine).

Modelling Process

For each hypothesis regarding habitat suitability, we produced a current model. We projected all environmental variables to North America Albers Equal Area Conic projection to meet the assumption in maximum entropy modeling of equal area among grid cells.

We fitted models using default feature types and default regularization parameters. Maxent output is expressed as continuous values of probability of species occurrence. Prior to modeling, we split sample data into three random sets: 60% for training the model, 20% for validation, and 20% for testing. This was done only for the current models to determine model accuracy. To assist with interpretation and presentation of results, we used the validation data to identify threshold values for

converting output to binary models of species occurrence (Pearson et al. 2004). To do this, we sorted model output extracted for each validation point (occurrence probabilities) from lowest to highest and set a 5% omission rate as the threshold above which the model shows a species to be present.

Model Evaluation

To assess the relative performance among current models, we ranked the current distribution models using the statistic Contrast Validation Index (CVI; Hirzel and Arlettaz 2003; Hirzel et al. 2006). The CVI reflects whether model accuracy outperforms a random model, and it varies from 0 to 1. Ranking the resulting CVI scores provided a basis for identifying the best models from among hypothesis-driven models. To assess model ability to discriminate between suitable and unsuitable areas for each species, we used area under the receiver operating characteristic curve (AUC). We interpreted AUC values as relative to other models using the same data and not as absolute measures of performance (Yackulic et al. 2013). We also considered unregularized training gain to assess how much better the Maxent distribution fit the presence data compared to a uniform distribution.

Current climate-topography vs current hypothesis-driven models

To test for differences between the current climate-topography model and the top performing hypothesis-driven current models, we employed McNemar's chi-square test for paired nominal data with continuity correction (Yates 1934, McNemar 1947). The null hypothesis was that the proportions of suitable habitat are equal between the models. With multiple McNemar tests planned for comparing current models, we did a Bonferroni correction to adjust the p-value needed for significance as $\alpha = 0.05/4 \text{ tests} = 0.0125$ adjusted α .

Less formally we compared the area of current climate-topography models with those of top ranked hypothesis-driven models as well as centroid locations as ways of assessing their comparability.

Results

Environmental Settings

Based on whitebark pine occurrence points, elevation ranged from 2,287 m to 3,788 m ($\bar{x} = 3,202$, SE = 12.5; Table B2) while for foxtail pine the range was 2,224 m to 3,716 m ($\bar{x} = 3,157$, SE = 15.0; Table B3). Both species occur over the full range of aspect: from 0 to 2 in the linear conversion from aspect in degrees. NDVI spanned most of the NDVI range for the study area (36 – 229), but the mean for both species is below that of the study area. Snow cover variables were comparable for the two species. Snow duration averaged approximately two months and the average first day of snow cover fell in late December. The number of snow-free days was somewhat greater for foxtail than for whitebark, which may be due to the lower latitudes of its range. Elevation, aspect, and slope were used in current and future models. All remaining environmental covariates were used in current, hypothesis-driven models only.

Table B2. Environmental covariates used in current habitat suitability models for whitebark pine. Statistics are based on species occurrence samples (n=328).

Covariate	Min	Max	Mean	SE
Elevation (m)	2287	3788	3202	12.5
Slope (%) ¹	89	89	89	0.01
Aspect (linear conversion)	0.0	2.0	0.8	0.04
Solar potential (W/m ²)	1,356	1,037,280	597,860	15,019
NDVI (index)	57.0	181.0	101.7	1.3
Wetness (index)	-2.0	14.9	2.2	0.2
Snow Duration (days)	6.9	88.2	59.3	0.9
Snow Start Day	358.0	366.0	361.6	0.2
Total Snow-free Days (days)	105.0	211.0	138.1	0.9

¹Slope values were limited to the 89-90% range due to averaging slope changes within 1 km sq resolution.

Table B3. Environmental covariates used in current habitat suitability models for foxtail pine. Statistics are based on species occurrence samples (n=244).

Covariate	Min	Max	Mean	SE
Elevation (m)	2224	3716	3157	15.0
Slope (%)	89	89	89	0.0100
Aspect (linear conversion)	0	2	0.8	0.05
Solar potential (W/m ²)	8,210	1,030,820	640,494	16,774
NDVI (index)	69	177	110	1.4
Wetness (index)	-1.8	15.4	2.3	0.3
Snow Duration (days)	6	91	55	1.0
Snow Start Day	358	366	363	0.2
Total Snow-free Days (days)	112	219	160	1.5

¹Slope values were limited to the 89-90% range due to averaging slope changes within 1 km sq resolution.

Hypothesis-driven current models

Whitebark pine

The top-ranked current models for whitebark pine according to the CVI statistic were models 3, 4, 12, and 1 (Table B4). Fourth-ranked model 1 showed whitebark habitat farther south than the other models and had more suitable habitat predicted at high elevations in the northern portion of SEKI, but the distribution of suitable habitat was otherwise similar among the top four models (Figure B1).

Elevation made the greatest contribution to the top-ranked models followed by summer precipitation or winter temperature (January minimum) (Table B4). NDVI made approximately 10% contribution to the three models ranked highest by CVI. Two of the top models also had among the highest AUC values, models 3 and 4 (AUC = 0.911 and 0.915, respectively). The two models with the highest AUC and training gain, models 7 and 14, had the same four variables as models 3 and 4 making the greatest contributions: elevation, July precipitation, NDVI, and January minimum temperature. The addition of a wetness index and solar potential in models 7 and 14 did not elevate their CVI rankings to within the top four models, although CVI values were only 0.050 and 0.055 below the top ranked

model, respectively. At the same time, models 7 and 14 had the best discrimination between background and species presence among the hypothesis-driven models according to AUC values (AUC = 0.927 and 0.922, respectively). Similarly, the addition of other topographic variables, slope and aspect, did not elevate their CVI rankings to near the top. When elevation was included in a model, it frequently made the greatest relative contribution (46% - 51%). The contribution of NDVI to three of the four top-ranked models was significantly lower than that of elevation (10% to 11%) but not negligible.

Table B4. Hypothesis-driven current models for whitebark pine ranked by Contrast Validation Index (CVI) statistic. Model 0 is the climate-topography current model for comparison with hypothesis-driven models. Elev is elevation (m) from digital elevation model data. Pr1, -4, -7 and -10 are precipitation in January, April, July, and October (see text). Tmin1, -4, -7, -10 are mean minimum temperatures in the same months. The same codes are used for tmean and tmax. Solar_p is solar potential based on digital elevation models and latitude. Ndvi = mean NDVI values over 7 years based on MODIS (250 m2) data. Snow_dur, tsfd, and ssd are snow duration in days, total number of snow-free days, and first day of snow covered conditions based on MODSCAG between 2000 and 2010. Wetness is a topographic moisture index as a function of slope and contributing area. (See text for more detail)

CVI Rank	CVI	Model	Training Gain	AUC	Variables in Decreasing Order of Percent Contribution
1	0.577	3	1.432	0.911	elev + pr7 + ndvi + tmin1 + pr1 + wetness + solar_p
2	0.576	4	1.480	0.915	elev + pr7 + tmin1 + ndvi + pr1 + wetness + tsfd + snow_dur + solar_p
3	0.575	12	1.331	0.902	elev + pr7 + ndvi + tmin1 + tsfd + snow_dur
4	0.566	1	1.049	0.868	elev + tmin1 + pr1
5	0.560	2	1.154	0.883	elev + tmin1 + ndvi + pr1
6	0.559	11	1.364	0.906	tmean7 + pr7 + tsfd + ndvi + solar_p + snow_dur
7	0.557	13	1.229	0.890	tmin1 + ndvi + tsfd + solar_p + pr1 + snow_dur
8	0.545	8	1.384	0.907	tmin1 + pr7 + ndvi + tsfd + solar_p + snow_dur + ssd_max
9	0.545	15	1.319	0.902	tmin1 + pr7 + ndvi + solar_p
10	0.545	19	1.319	0.902	tmin1 + pr7 + ndvi + solar_p
11	0.538	18	1.288	0.898	tmean7 + pr7 + ndvi + solar_p
12	0.527	7	1.611	0.927	elev + pr7 + tmin1 + ndvi + pr10 + wetness + solar_p + snow_dur + tsfd + aspect + ssd_sd
13	0.522	14	1.546	0.922	elev + pr7 + ndvi + tmin1 + pr10 + wetness + solar_p + aspect + slope
14	0.512	9	1.415	0.910	tmin1 + pr7 + ndvi + pr10 + tsfd + snow_dur
15	0.510	6	0.910	0.850	tmin1 + tmax7
16	0.464	10	1.269	0.895	tmin1 + ndvi + tsfd + pr10 + snow_dur + pr1
17	0.456	0	1.558	0.927	elev + pr7 + tmax7 + tmin1 + pr10 + pr4 + tmean7 + aspect + slope + pr1 + tmax1 + tmin10 + tmean4 + tmax10 + tmax4 + tmin4 + tmin7 + tmean1 + tmean10
18	0.435	16	1.360	0.905	tmin1 + pr7 + ndvi + pr10
19	0.415	17	1.194	0.886	tmin1 + ndvi + pr10 + pr1
20	-0.006	5	0.397	0.740	pr10 + pr1

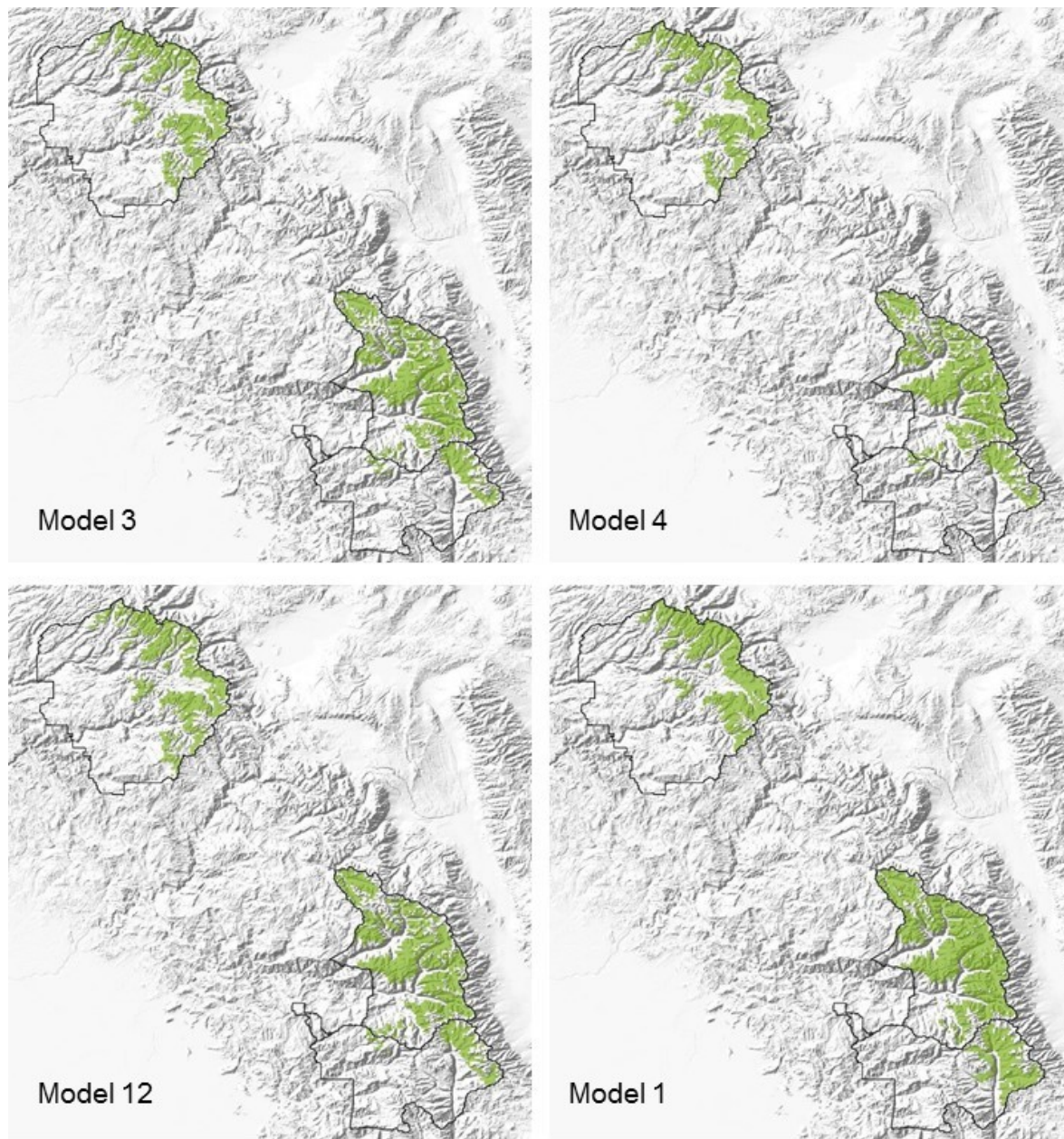


Figure B1. Current habitat suitability models for whitebark pine based on *a priori* hypotheses. Models are in order of rankings by the Contrast Validation Index. See Table B4 for model covariates.

Elevation and January minimum temperature were equivalently the most important covariates to all the top-ranked models according to jackknife results from using each variable in isolation. NDVI and July precipitation (Model 3) or the total number of snow-free days (Models 4 and 12) followed in importance, depending on which were included. No variable reduced gain substantially when removed, but July precipitation reduced gain the most, indicating it may contain some information lacking in other covariates. July precipitation contributed 19% to models 7 and 14 versus 3% contributed by January precipitation in three of the four top-ranked models.

In comparison with the hypothesis-driven current models, the climate-topography model performed well (AUC = 0.927), exceeding the AUC value of 0.911 for top-ranked model 3 (Table B4). However, its CVI value (0.456) was better than only three hypothesis-driven models, 5, 16 and 17 (CVI = 0.0, 0.435, 0.415, respectively).

Areas of suitable habitat in the current climate-topography model appeared similar to those of models 3, 4, and 12 (Figure 5a in body of report).

Foxtail pine

The top-ranked current models for foxtail pine according to the CVI statistic were models 12, 2, 8, and 1 (Table B5). These four models produced fairly comparable habitat suitability maps (Figure B8). Models 12 and 8 appear similar while model 2 shows additional suitable habitat in the western portions of SEKI and Model 1 displays slightly less habitat in northern SEKI.

Table B5. Hypothesis-driven models for foxtail pine ranked by Contrast Validation Index (CVI) statistic. Elev is elevation (m) from digital elevation model data. Pr1, -4, -7 and -10 are precipitation in January, April, July, and October (see text). Tmin1, -4, -7, -10 are mean minimum temperatures in the same months. The same codes are used for tmean and tmax. Solar_p is solar potential based on digital elevation models and latitude. Ndvi = mean NDVI values over 7 years based on MODIS (250 m²) data. Ssd_sd and ssd are first day of snow cover (standard deviation and maximum). Snow_dur and tsfd are snow duration in days and total number of snow-free days based on MODSCAG between 2000 and 2010. Wetness is a topographic moisture index as a function of slope and contributing area. (See text for more detail)

CVI Rank	CVI	Model	Training Gain	AUC	Variables in Decreasing Order of Percent Contribution
1	0.774	0	2.191	0.958	pr4 + pr7 + tmax4 + tmin7 + elev + tmin10 + pr10 + tmin4 + pr1 + tmean4 + tmean7 + tmax7 + tmax1 + tmean10 + tmin1 + tmean1 + tmax10
2	0.743	12	2.173	0.960	elev + pr1 + pr7 + tsfd + pr10 + ndvi + solar_p + wetness + snow_dur
3	0.742	2	1.962	0.949	pr7 + tmin1 + ndvi + elev + pr10
4	0.733	8	2.255	0.964	pr4 + pr7 + tmin1 + tsfd + elev + pr10 + ndvi + solar_p + slope + wetness + snow_dur
5	0.730	1	2.058	0.954	pr4 + pr7 + tmin1 + elev + ndvi + pr10
6	0.730	9	2.146	0.959	pr7 + tmin1 + tsfd + elev + pr10 + ndvi + solar_p + wetness + snow_dur
7	0.729	11	2.261	0.964	pr4 + tmax10 + pr7 + tsfd + ndvi + elev + pr10 + solar_p + wetness + snow_dur
8	0.726	10	2.245	0.963	pr4 + pr7 + elev + tmin1 + tsfd + ndvi + pr10 + solar_p + wetness + snow_dur
9	0.721	4	2.097	0.956	pr4 + pr7 + tmin1 + elev + ndvi + pr10 + solar_p
10	0.719	15	2.097	0.956	pr1 + pr7 + tmin1 + elev + ndvi + pr10 + solar_p + wetness
11	0.717	5	2.100	0.956	pr1 + pr7 + tmin1 + elev + ndvi + pr10 + snow_dur + solar_p
12	0.709	14	2.047	0.954	pr7 + tmin1 + ndvi + elev + pr10 + solar_p + wetness
13	0.704	16	2.087	0.956	elev + pr1 + pr7 + ndvi + pr10 + solar_p + wetness
14	0.702	6	1.916	0.947	tmax7 + pr1 + pr7 + pr10
15	0.694	13	2.122	0.957	pr4 + pr7 + tmin1 + elev + ndvi + pr10 + solar_p + wetness
16	0.688	3	2.053	0.954	elev + pr1 + pr7 + ndvi + pr10 + solar_p
17	0.494	7	1.033	0.864	tmax7

Among the four top-ranked models for foxtail pine, spring and summer precipitation figured more prominently than in those for whitebark (Table B4). Although January minimum temperature was still an important contributor, it did not predominate with 14% to 27% contribution in 3 of the top 4 models. Surprisingly, elevation made the greatest contribution only to model 12 (28%) and made less than 13% contribution to the other three out of the four top-ranked models. Mean NDVI contributed 4% to 12% among the top-ranked models, but most other environmental covariates contributed below 5% to 10%. CVI values did not drop off precipitously below the top four models but remained fairly comparable for the first 8 rankings (CVI = 0.721 to 0.743).

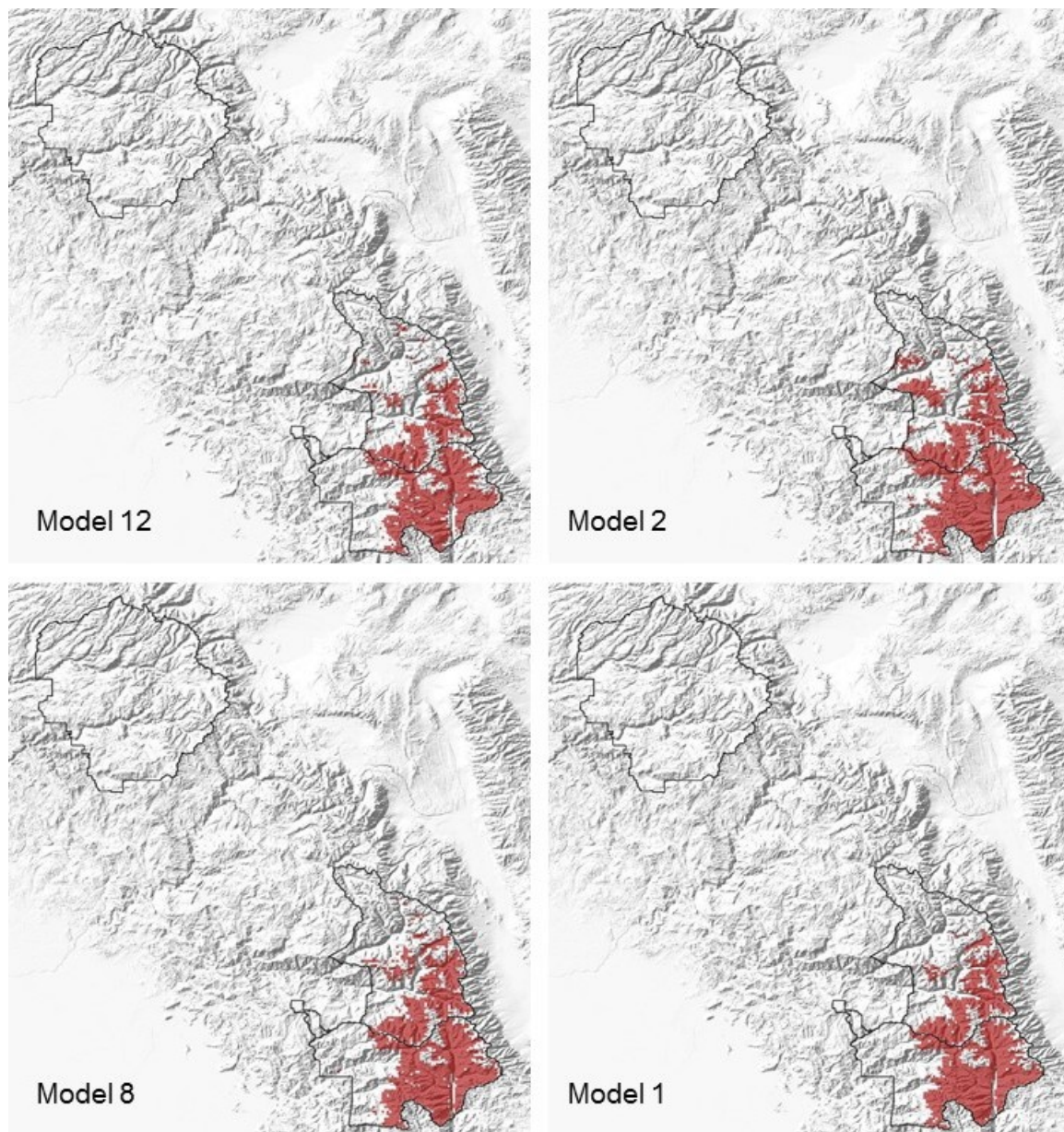


Figure B2. Current habitat suitability models for foxtail pine based on a priori hypotheses. Models are the four highest rankings according to the Contrast Validation Index. See Table B5 for model covariates.

Precipitation covariates provided the highest gain among top-ranked models when used in isolation. July precipitation alone (Model 2) or equally with April precipitation (Models 8 and 1) or January precipitation (Model 12) provided the highest gain followed by elevation and January minimum temperature (Models 1, 2, and 8). Maxent achieved almost no gain when it used topographic wetness in isolation (Models 2 and 8) and very little when it used NDVI alone (Model 1).

Most foxtail pine current models performed well in discriminating between background and species presence. AUC values were high for all models (0.947 to 0.964) with the exception of model 7, which was based only on July maximum temperature. The climate-topography model had the highest CVI value, the sixth highest AUC value, and was within the range of AUC values for the top four CVI-ranked models (0.958 versus 0.954 to 0.960).

The distribution of suitable habitat in the climate-topography model appeared similar to hypothesis-driven current models 12, 2, and 8 (Figure 6a in main text).

Current Model Comparisons

Whitebark pine

McNemar chi-square tests indicated that all four of the top-ranked hypothesis-driven models differed in paired comparisons with the current climate-topography model for whitebark pine in both YOSE and SEKI ($p < 0.05$). In terms of area, hypothesis-driven models predicted an average of 11.6% less habitat in YOSE than the climate-topography model and an average of 8.5% less in SEKI (Table B6). Overall, top-ranked models predicted an average of 10.6% less suitable habitat in the study area than the climate-topography model.

Table B6. Area (km²) of the climate-topography model compared with each of the four top-ranked hypothesis-driven current models for whitebark pine.

Park	Model	Area (km ²)	Difference from Climate-Topography Model (%)
YOSE	Climate-topography	1012	
	3	865	-14.5
	4	883	-12.7
	12	874	-13.6
	1	957	-5.4
SEKI	Climate-topography	1695	
	3	1438	-15.2
	4	1434	-15.4
	12	1448	-14.6
	1	1885	11.2

Centroids of whitebark pine hypothesis-driven current models are farther north in YOSE by 2 km to 5 km compared with the climate-topography model and farther south in SEKI by 1 km to 3 km (Table B7). Although centroid elevations are noted, differences among centroids are likely not significant because elevations change dramatically over short distances in the parks.

Table B7. Distance and direction from centroid of current climate-topography model for whitebark pine to centroids of current, top-ranked, hypothesis-driven models along with centroid elevation. Centroid elevations for current models are 2,568 m in YOSE and 2,908 m in SEKI.

Park	Model	Elev (m)	Dist (km)	Direction
YOSE	3	2648	1.8	NNE
	4	2624	2.0	NNE
	12	2635	2.0	NNE
	1	2680	5.6	NNE
SEKI	3	2712	1.3	S
	4	2643	1.4	SE
	12	2967	1.7	S
	1	2126	3.1	SE

Foxtail pine

McNemar chi-square tests indicated that three of four hypothesis-driven models (models 12, 2, and 1) differed in paired comparisons with the current climate-topography model for foxtail pine ($p < 0.05$), whereas model 8 was similar ($p > 0.05$). The hypothesis-driven models for foxtail pine predicted an average of 4% less habitat in SEKI than the climate-topography model, but the models varied from 6% more (model 2) to 14% less (model 12) suitable habitat (Table B8). Model 8 was similar in area to the climate-topography model, but the habitat appeared less contiguous. Model 12 had less area and was less contiguous while Model 1 had less suitable habitat but was similar in its geographic distribution.

Table B8. Area (km²) of the climate-topography model compared with each of the four top-ranked hypothesis-driven current models for foxtail pine.

Park	Model	Area (km ²)	Difference from Climate-Topography Model (%)
SEKI	Climate-topography	1962	
	12	1680	-14.4
	2	2075	5.8
	8	1969	0.4
	1	1801	-8.2

Centroids of current hypothesis-driven models did not reflect much geographic shift when compared with the climate-topography model centroid (Table B9). Model 2 shows the greatest shift at 2.3 km NW, but the remaining centroids are all within 1 km. Although centroid elevations are noted, differences likely are not significant because elevations change dramatically over short distances in the parks.

Table B9. Distance and direction from centroid of current climate-topography model for foxtail pine to centroids of current, top-ranked, hypothesis-driven models along with centroid elevation. Centroid elevation for current climate-topography model is 3,308 m.

Park	Model	Elev (m)	Dist (km)	Direction
SEKI	12	3140	0.6	S
	2	3620	2.3	NW
	8	3460	0.9	N
	1	3079	0.8	SE

Discussion

Hypothesis-driven current models

Whitebark pine

Whereas elevation made the greatest contribution to the four top-ranked hypothesis-driven models with contribution levels greater than 45%, July precipitation, NDVI, and January minimum temperature made consistent rather than highly influential contributions at 10% to 22% each. See the Discussion section in the body of this report for comments on the contribution of elevation and July precipitation to the current climate-topography model

The high contribution of January minimum temperature to top-ranked models supports, as it did for the current climate-topography model, the hypothesis of cold hardiness in whitebark pine or at least represents the range of conditions under which whitebark pine has superior hardiness.

The contribution of NDVI at 10% to 11% in three of four top-ranked current models may reflect that NDVI is not a driver of habitat suitability, but a response to habitat characteristics and stand structure. NDVI is lowest at the high elevations where whitebark pine occurs and highest from foothill to montane zones where canopy is more continuous. Whitebark pine typically occurs in a patchwork of open woodlands with low vegetative cover between patches, resulting in some of the lowest NDVI values for forested areas. NDVI may be a good tool for modeling current conditions but may represent a surrogate for competition rather than a predictor of species occurrence.

Although we contrasted covariate contribution levels among Maxent models, we endeavored to interpret these percentages with caution where environmental variables were highly correlated. This is because they can result from how the Maxent code derived the model and not about which of two or more correlated variables is more important to the species (Phillips 2005). Importantly, high covariate contribution reflects its value in prediction and not necessarily its importance to species ecology.

Foxtail pine

As with the current climate-topography model, the importance of July precipitation to the foxtail pine hypothesis-driven models is unlikely to be due exclusively to its close relationship with elevation. See the Discussion section in the body of the report for comments on July precipitation and foxtail pine.

The proportionally higher contributions of spring and summer temperatures in the top-ranked climate-topography model (3rd and 4th highest contributions at 10% and 8%, respectively) indicate they may have been useful covariates to include in more hypothesis-driven models. July temperature was included only in model 6 and April temperature was not a covariate among the models. At the same time, temperature covariates are highly correlated ($r > 0.999$ for all temperature covariate pairs), and a temperature variable was included in all but three of the 16 candidate models (models 3, 12, and 16), so temperature was well represented.

NDVI was included in 14 out of 16 foxtail pine candidate models, so it was not surprising it occurred consistently among top-ranked models; however, it made only modest contributions at 4% to 11%. According to Maxent response curves, the logistic prediction of foxtail pine presence is greatest at moderate values of NDVI. NDVI values varied from approximately 20 to 245 with the greatest response by foxtail pine between index values of approximately 50 and 100. Greater values of NDVI occurred within lower elevation mixed conifer and California red fir forest and the lowest values of NDVI occurred at the highest elevations in such habitats as alpine scree and talus and alpine rock outcrops. Again, the modest contribution by NDVI may reflect that NDVI is not a driver, but a response to typical stand structure of foxtail pine.

In the two models in which we included the total number of snow-free days, it had greater contribution levels than either wetness or snow duration, which were both less than 1%. Tsfd was not highly correlated with elevation ($r > -0.25$) and instead may reflect the availability of growing-season moisture within relatively dry foxtail pine habitat. Response curves indicate species presence is predicted in the middle range of tsfd values between about 100 and 140 days for both model 12 and model 8.

Current Model Comparisons

Whitebark pine

McNemar chi-square tests detected proportional differences for whitebark pine between the climate-topography model and each of the four top ranked hypothesis-driven models. The climate-topography model identified suitable habitat over a greater area compared to all top ranked hypothesis-driven models except Model 1 in SEKI. Although Model 1 had the second poorest discrimination between presence and background according to its AUC value, the AUC value of 0.868 is high, and the model was ranked among the top four models by CVI. The limited information in Model 1, with covariates limited to elevation, January minimum temperature, and January precipitation, may have reduced its discrimination somewhat. Suitable habitat appeared to be more contiguous at high elevation in the climate-topography model compared with the three top-ranked models, and fourth-ranked Model 1 predicted suitable habitat farther south than the climate-topography model, accounting for its greater area. Suitable habitat under Model 1 may have been both more continuous at high elevations and more extensive across high elevations in SEKI because it was more exclusively driven by elevation (87% contribution to the model) and January minimum temperature (17% contribution). We included elevation and January minimum temperature together in several models in spite of a correlation coefficient of $r = 0.78$ because multicollinearity does not have a strong influence on Maxent results (Elith et al. 2011) and because removing elevation from

models with January minimum temperature resulted in extremely exaggerated predictions of suitable habitat across park landscapes.

Hypothesis-driven models may have identified less area of suitable habitat because they were more complex models. This was due to the inclusion of multiple covariates such as NDVI and snow cover that were not projectable to the future and therefore not available for comparison with models under future climate scenarios. However, differences in area were not great, averaging 10.6% less suitable habitat in hypothesis-driven models than in the current climate-topography model and lending support to the utility of the current climate-topography model.

While more rugged topography in SEKI likely accounts for the elevational differences among model centroids, there appeared to be little significant geographic shift in suitable habitat among current whitebark pine models as reflected in their centroids.

Although the current climate-topography model for whitebark pine ranked 17th according to CVI, it equaled the highest AUC and training gain values among the hypothesis-driven models. By this measure of performance, it ranked among the top-performing models. This supported the use of the climate-topography model as a basis for comparison with models under future climate scenarios, and the covariates used in the climate-topography model were useful for modeling suitable habitat under climate scenarios.

Foxtail pine

Although there were significant differences in the extent of suitable habitat between the current climate-topography model and top-ranked hypothesis-driven models, the proportional difference averaged only 4% among the four paired comparisons. The four hypothesis-driven models differentiated well between presence and background as evidenced by consistently high AUC values of 0.949 to 0.960. The addition of covariates such as NDVI and snow cover did little to refine current models beyond what was possible with climatic and topographic covariates for which the AUC value was comparable at 0.958.

There appeared to be more contiguous habitat in the climate-topography model than in the top-ranked hypothesis-driven model (model 12); however, there was more variability among the current foxtail pine models for area and contiguity than among the whitebark pine models.

Nevertheless, in addition to the minor differences in area, the minor differences among current model centroids reflect the comparable nature of the hypothesis-driven models compared with the climate-topography model. All five models show similar geographic distribution and compare favorably with the known species distribution.

Although all AUC values, with the exception of model 7, were high, the top ranking of the climate-topography model, according to both AUC and CVI, supports its use as a basis for comparison with models under future climate scenarios.

Appendix C. Current Habitats in Areas Predicted to be Newly Suitable Habitat under Climate Envelope Models.

Vegetation types within areas predicted to represent newly suitable habitat in species distribution models differ in composition more between scenarios for the 2090s than for the 2050s. Mapped vegetation types not shown represent less than 2% of newly suitable habitat identified by models.

Whitebark Pine

Park	Scenario	Model	Alliance	Percent of New Habitat
YOSE	B1	2050	Barren	43
	B1	2050	Mountain hemlock	9
	B1	2050	Sierra lodgepole pine	21
	B1	2050	Western white pine	4
	B1	2050	Whitebark pine	14
	B1	2050	Meadow	4
	B1	2090	Barren	51
	B1	2090	Mountain hemlock	6
	B1	2090	Sierra lodgepole pine	15
	B1	2090	Western white pine	4
	B1	2090	Whitebark pine	13
	B1	2090	Meadow	5
	A2	2050	Barren	50
	A2	2050	Mountain hemlock	8
	A2	2050	Sierra lodgepole pine	13
	A2	2050	Western white pine	8
	A2	2050	Whitebark pine	10
	A2	2050	Meadow	<2
	A2	2090	Barren	35
	A2	2090	Mountain hemlock	13
	A2	2090	Sierra lodgepole pine	21
	A2	2090	Western white pine	9
	A2	2090	Whitebark pine	11
	A2	2090	Meadow	4
SEKI	B1	2050	Barren	52
	B1	2050	Foxtail pine	16
	B1	2050	Sierra lodgepole pine	6
	B1	2050	California red fir	6
	B1	2050	Western white pine	3
	B1	2050	Whitebark pine	1
	B1	2090	Barren	71
	B1	2090	Foxtail pine	4
	B1	2090	Sierra lodgepole pine	2
	B1	2090	California red fir	4
	B1	2090	Western white pine	2
	B1	2090	Whitebark pine	2

A2	2050	Barren	52
A2	2050	Foxtail pine	17
A2	2050	Sierra lodgepole pine	6
A2	2050	California red fir	4
A2	2050	Western white pine	3
A2	2050	Whitebark pine	1
A2	2090	Barren	52
A2	2090	Foxtail pine	16
A2	2090	Sierra lodgepole pine	7
A2	2090	California red fir	5
A2	2090	Western white pine	3
A2	2090	Whitebark pine	1

Foxtail Pine

Park	Scenario	Model	Alliance	Percent of New Habitat
SEKI	B1	2050	Barren	39
	B1	2050	California red fir	5
	B1	2050	Foxtail pine	2
	B1	2050	Sierra juniper	6
	B1	2050	Sierra lodgepole pine	11
	B1	2050	Western white pine	8
	B1	2050	Whitebark pine	10
	B1	2090	Barren	56
	B1	2090	California red fir	1
	B1	2090	Foxtail pine	6
	B1	2090	Sierra juniper	2
	B1	2090	Sierra lodgepole pine	12
	B1	2090	Western white pine	6
	B1	2090	Whitebark pine	8
	A2	2050	Barren	41
	A2	2050	California red fir	4
	A2	2050	Foxtail pine	5
	A2	2050	Sierra juniper	5
	A2	2050	Sierra lodgepole pine	9
	A2	2050	Western white pine	7
	A2	2050	Whitebark pine	11
	A2	2090	Barren	26
	A2	2090	California red fir	5
	A2	2090	Foxtail pine	15
	A2	2090	Sierra juniper	10
	A2	2090	Sierra lodgepole pine	6
	A2	2090	Western white pine	12
	A2	2090	Whitebark pine	4

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