



Southwestern white pine (*Pinus strobiformis*) species distribution models project a large range shift and contraction due to regional climatic changes

Andrew J. Shirk^{a,*}, Samuel A. Cushman^b, Kristen M. Waring^c, Christian A. Wehenkel^d,
Alejandro Leal-Sáenz^d, Chris Toney^e, Carlos A. Lopez-Sanchez^d

^a Climate Impacts Group, College of the Environment, University of Washington, Box 355674, Seattle, WA 98195-5762, USA

^b USDA Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll Drive, Flagstaff, AZ 86001, USA

^c School of Forestry, Northern Arizona University, PO Box 15018, Flagstaff, AZ 86011, USA

^d Instituto de Silvicultura e Industria de la Madera, Universidad Juarez del Estado de Durango, Durango, Durango, Mexico

^e USDA Forest Service, Rocky Mountain Research Station, 507 25TH St., Ogden, UT 84401 USA



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ABSTRACT

Southwestern white pine (*Pinus strobiformis*; SWWP) is a conifer species that occurs at mid to high elevations in the mountains of Arizona, New Mexico, and northern Mexico. A key component of mixed conifer forests in the region, SWWP is an important species for wildlife and biodiversity. The dual threats of the non-native fungal pathogen that causes white pine blister rust (WPBR) and a warmer, drier projected future climate have created an uncertain future for SWWP. In this study, we used a novel multi-scale optimization approach including an ensemble of four species distribution modeling methods to explore the relationship between SWWP occurrence and environmental variables based on climate, soil, and topography. Spatial projections of these models reflecting the present climate provide an improved range map for this species that can be used to guide field data collection and monitoring of WPBR outbreaks. Future projections based on two emissions scenarios and an ensemble of 15 general circulation models project a large range shift and range contraction by 2080. Changes in the future distribution were particularly extreme under the higher emissions scenario, with a more than 1000 km northerly shift in the mean latitude and 500 m increase in the mean elevation of the species' suitable habitat. This coincided with a range contraction of over 60% and a significant increase in habitat fragmentation. The ability of SWWP to realize its projected future range will depend on colonization at the leading edge of the range shift, including dispersal dynamics, resistance to WPBR, competition with other species, and genetic adaptations to local climate. Our results provide information that can be used to guide monitoring efforts and inform conservation planning for this keystone species.

1. Introduction

The southwestern white pine (*Pinus strobiformis*; SWWP), the southernmost white pine (*Pinus* subgenus *strobus*) species in the United States, occurs primarily at mid to high elevations in the Rocky Mountains of Arizona and New Mexico as well as the Sierra Madre ranges of Mexico (Fig. 1). At least one species of white pine occurs in every high mountain region of western North America, where they play important ecological roles (Tomback and Achuff, 2010). Their large, nutritious seeds are important dietary components for many birds and mammals (Tomback and Achuff, 2010).

The southwestern white pine is currently considered a 'species of least concern' with a stable population trend (Kyne et al., 2013). However, it is highly susceptible to white pine blister rust (WPBR;

Kinloch and Dupper, 2001; Schoettle and Snieszko, 2007), caused by the fungus *Cronartium ribicola*. This pathogen was first introduced to North America from Asia in the late 1800s (Kinloch, 2003). Since then, it has spread throughout the range of most white pine species and caused more than 90% mortality in some affected areas (Campbell and Antos, 2000). WPBR has recently spread into parts of Arizona and New Mexico (Hawksworth, 1990; Wilson et al., 2014), posing an increasing threat as it enters the core of the SWWP range. The threat is particularly acute given that genetic resistance to WPBR has been found in only a small percentage of SWWP trees to date, leaving most of the population vulnerable to mortality (Snieszko and Kegley, 2008).

In addition to the increasing threat from WPBR, climatic changes in the region also pose risks to the future viability of SWWP populations. Climate across the range of SWWP is expected to become warmer and

* Corresponding author.

E-mail address: ashirk@uw.edu (A.J. Shirk).

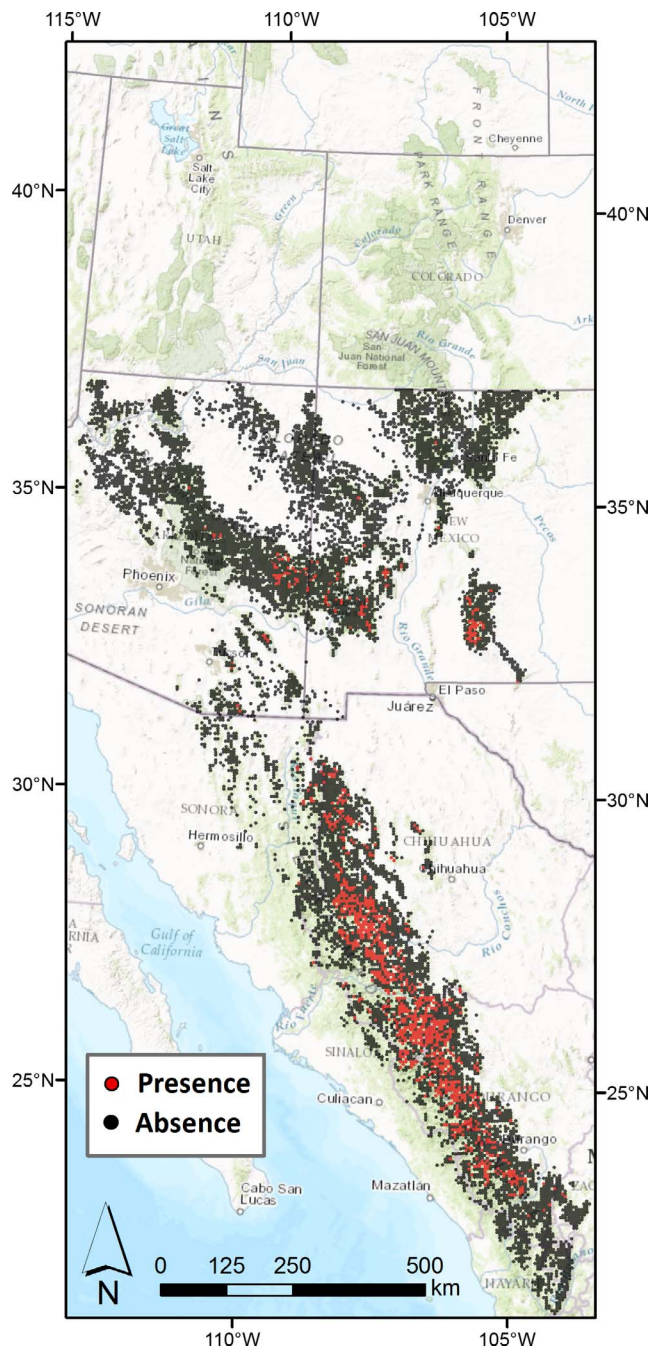


Fig. 1. Study area and sampling sites for southwestern white pine (*Pinus strobiformis*). The study area encompassed 193.4 Mha in the southwestern United States and Mexico. Field surveys to detect the presence (red dots, $n = 1077$) or absence (black dots, $n = 9071$) of southwestern white pine were limited to Arizona, New Mexico, and northwestern Mexico. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

drier with increasing drought frequency (Seager and Vecchi, 2010). This may put SWWP at a competitive disadvantage because it is more drought sensitive than potential competitors like Douglas-fir (*Pseudotsuga mensiesii*) and Ponderosa Pine (*Pinus ponderosa*; Barton and Teeri, 1993). Phenological events are also highly sensitive to changes in temperature regimes (Richardson et al., 2013). For example, budburst in many temperate and boreal tree species, including SWWP, is regulated by a winter chilling and spring forcing (i.e. thermal time). In a warmer future climate, the chilling requirement may take longer to achieve, leading to a delay in budburst and thereby reducing growth and ultimately survival (Harrington and Gould, 2015).

Currently, the distribution of SWWP has only been delimited by expert opinion (Little, 1971), and the environmental variables controlling its distribution are poorly understood. Efforts are underway to genetically sample the population to identify loci associated with WPBR resistance (Sniezko and Kegley, 2008) as well as adaptations to climate variability (Goodrich et al., 2016). In addition, monitoring efforts are tracking the spread and severity of WPBR outbreaks. To support these efforts, more accurate range maps of the SWWP distribution are required. In addition, greater understanding of the relationship between SWWP distribution and environmental controls will improve our ecological knowledge of this poorly understood species. Projecting those relationships into the future given climate change projections for the region will help inform conservation planning to mitigate the impacts of SWWP range shifts and range contractions. For example, assisted migration and assisted gene flow (Aitken et al., 2008) are strategies being explored to maximize WPBR resistance and adaptation to a rapidly changing regional climate.

To meet these needs, the goals of this study were to (1) model the relationship between observed patterns of SWWP occurrence and environmental variables related to climate, topography, and soil, (2) apply the model to the current landscape and recent climate to produce a continuous probability of occurrence map for SWWP, (3) project the model into the future based on future climate projections, and (4) assess the potential future distribution of SWWP habitat.

2. Material and methods

2.1. Study area

Our study area (Fig. 1) comprised 193.4 Mha encompassing nearly the entire historical distribution of SWWP, plus potentially suitable future habitat areas in Colorado and Utah. The elevation of the study area varied from sea level to over 4400 m. At the lowest elevations, the climate is warm and dry, with mean annual temperature (MAT) reaching as high as 26.3°C and mean annual precipitation (MAP) as low as 6.5 cm. At the highest elevations, the climate is cool and wet, with MAT as low as 1.2°C and MAP as high as 204.1 cm. The lower elevations are generally covered in sparse desert scrub vegetation, including a variety of shrubs, grasses, forbs, and cacti. At progressively higher elevations, pinyon-juniper woodlands, ponderosa pine forests, dry and wet mixed conifer forests and spruce fir forests predominate. Areas above treeline are covered in sparse alpine tundra vegetation.

2.2. Occurrence data collection

We evaluated SWWP occurrence at 6308 sites in the US and 7590 sites in Mexico (surveyed once between 2001 and 2015). The US sites consisted of all Forest Inventory and Analysis (Smith, 2002) program plots maintained by the US Forest Service in Arizona and New Mexico. The Mexican sites consisted of National Forest and Soil Inventory plots in temperate forests of the Sierra Madre Occidental range. Both sets of plots were based on the same design consisting of four circular 400 m² subplots. The center subplot was surrounded by three outer subplots spaced 45.14 m apart. Plots were distributed in forested areas in a regular grid approximately 5 km × 5 km (Fig. 1). We defined presence as the occurrence of one or more live SWWP seedlings, saplings, or mature trees in any subplot.

Species distribution models are sensitive to the geographic distribution of absences relative to presences (Barve et al., 2011). We constrained the geographic scope of our analysis by removing absences from level III ecoregions (Environmental Protection Agency, 2010) where no presence locations were recorded. This resulted in the removal of 3750 absence locations occurring primarily in low elevation areas unsuitable for SWWP.

Table 1

Environmental variables used to project southwestern white pine (*Pinus strobiformis*) distribution in Utah, Colorado, Arizona, New Mexico, and Mexico during the 1981–2010 reference period and in 2080 under two future emissions scenarios (RCP 4.5 and RCP 8.5). Variables are grouped by type, including climate, soil, and topography.

Variable type	Variable	Abbreviation
Climate	Annual Heat Moisture Index	AHM
	Beginning Frost Free Period (Julian day)	bFFP
	End Frost Free Period (Julian day)	eFFP
	Hargreave's Climatic Moisture Index	CMI
	Freezing Degree Days (< 0C)	FDD
	Growing Degree Days (> 5C)	GDD
	30-year Extreme Minimum Temperature (C)	EMT
	30-year Extreme Maximum Temperature (C)	EXT
	Hargreaves Reference Evaporation	HRE
	Mean Annual Precipitation	MAP
	Mean Annual Temperature	MAT
	Mean Coldest Month Temperature	MCMT
	Mean Warmest Month Temperature	MWMT
	Number of Frost Free Days	NFFD
	Precipitation as Snow (mm)	PAS
	Summer (Jun to Aug) Precipitation (mm)	MSP
	Winter (Dec to Feb) Precipitation (mm)	MWP
	Summer Heat Moisture Index	SHM
	Mean Summer (Jun to Aug) Temperature (C)	MST
	Mean Winter (Dec to Feb) Temperature (C)	MWT
	Temperature Differential (MCMT – MWMT)	TD
	Mean Annual Relative Humidity	RH
Soil	Silt Percentage (%)	SLT
	Sand Percentage (%)	SND
	pH	SpH
	Organic Carbon Content (g/kg)	OCC
Topography	Diurnal Anisotropic Heating index	DAH
	Morphometric Protection Index	MPI
	Slope (degrees)	SLP
	Topographic Position Index	TPI
	Topographic Wetness Index	TWI

2.3. Spatial predictor variables

A priori, we identified 22 climate, 4 soil, and 5 topographic variables we hypothesized may influence the distribution of SWWP based on our knowledge of the species and the study area (Table 1). We obtained gridded data for all climate variables at 1 km resolution from AdaptWest (Wang et al., 2016). AdaptWest climate data is based on an extension of the ClimateWNA statistical downscaling algorithm (Wang et al., 2016, 2012). We obtained gridded data at 250 m resolution for all soil variables from SoilGrids250m (Hengl et al., 2017). SoilGrids250m is derived from an ensemble of machine learning algorithms used to relate empirical soil profile data to remote sensing data. Topographic variables were based on a 30 m resolution digital elevation model (DEM) we obtained from the Shuttle Radar Topography Mission (Rabus et al., 2003). We used the System for Automated Geoscientific Analyses (SAGA; Conrad et al., 2015) Geographical Information System (GIS) software (version 3.0.0) to calculate each of the topographic variables from the DEM.

We resampled all climate, soil, and topography variable raster grids to 250 m resolution. The spatial scale at which environmental variables are important predictors of occurrence may vary, depending on the species and variable (McGarigal et al., 2016). To address this issue, we evaluated a range of additional spatial scales (> 250 m) using the mean of a circular moving window with a radius of 500 m, 1000 m, 2000 m, and 4000 m. All manipulation of the spatial data layers was performed in the R statistical environment (R Core team, 2015) using the 'raster' package (Hijmans et al., 2014).

We extracted the values of all variables at each of the five spatial scales at all sampled locations. For each variable at each spatial scale, we used a student's *t*-test to evaluate the difference in the means between SWWP presence and absence locations. We excluded from

further analysis all variables with no significant difference ($\alpha = 0.05$) between the means after correcting *p* values for multiple tests using the method of Benjamini & Yekutieli (2001). We then calculated a correlation matrix from the remaining significant variables based on their values at all sampled locations. If any significant variables had a correlation > 0.70 to another variable, only the variable with the largest absolute value of the *t*-score was retained.

2.4. Species distribution modeling

We fit species distribution models for SWWP using four methods, including boosted regression trees (BRT), random forests (RF), generalized additive models (GAM), and generalized linear models with a logit link (GLM; i.e., logistic regression). The first three methods allow for non-linear relationships between the response and predictors, but GLM does not unless they are explicitly defined in the model. Because we expected non-linear relationships between SWWP occurrence and environmental variables, we fit GLMs in three ways including (1) only linear terms, (2) linear and quadratic terms, and (3) linear, quadratic, and cubic terms. We then chose one of the three approaches using AIC model selection (Burnham and Anderson, 2004). All models used the same response variable (SWWP occurrence as described above) and predictor variables (i.e., the subset of spatial variables that were not highly correlated to other variables and had significant differences between presence and absence, as described above). Each model was fit 25 times in five repetitions of a 5-fold cross-validation (i.e., models were fit using 80% of the data for training and the remaining 20% for model evaluation). During model fitting for all methods, observations were weighted based on their prevalence, which has been shown to improve accuracy in model performance and projections (Meynard et al., 2013).

We fit BRT models using the 'dismo' package (Hijmans et al., 2011) in R. We fixed the number of trees at 1500 and evaluated a range of values for the interaction depth (1–9) and learning rate parameters (0.001–0.1), choosing the combination that maximized area under the receiver operator curve (AUC) when the model was used to predict occurrence from the withheld test data. We fit RF models using the 'randomForest' package (Breiman et al., 2015) in R. We fixed the number of trees at 1500 and evaluated a range of values for the number of variables randomly sampled as candidates at each split (1–9), choosing the value that maximized AUC of the model applied to the withheld test data. We fit GAM and GLM models with the 'mgcv' (Wood and Wood, 2013) and 'stats' packages respectively, in R.

2.5. Model assessment, projection, and analysis

We evaluated model performance for each method and replicate in several ways, including AUC, True Skill Statistic (TSS; Allouche et al., 2006), Cohen's Kappa (Cohen, 1968), proportion correctly classified (PCC), specificity, and sensitivity. To calculate Cohen's Kappa and PCC required a binary model, which we created based on a threshold probability where sensitivity equaled specificity (i.e., we equally weighted errors of omission and commission).

We projected the fitted models onto spatial projections of the climate, soil, and topographic variables reflecting three scenarios at 250 m resolution. The first was based on the same spatial data from which the model predictor variables were extracted (i.e., they represent the 30-year normal climate from 1981 to 2010). The other two scenarios represent future climate projections for 2080 under different emissions pathways. The first, Representative Concentration Pathway (RCP) 4.5, assumes climate policies limit greenhouse-related emissions and total radiative forcing is stabilized at 4.5 W m^{-2} in the year 2100 without ever exceeding that value in prior years (Thomson et al., 2011). The second, RCP 8.5, assumes continued increases in greenhouse gases following recent trends, reaching a total radiative forcing of 8.5 W m^{-2} in the year 2100 (Riahi et al., 2011). We obtained 2080 projections for

all climate variables included in the model for both emissions scenarios from AdaptWest (Wang et al., 2016). These climate projections were based on an ensemble of 15 General Circulation Models (GCMs) from the Coupled Model Intercomparison Project phase 5 (CMIP5; Taylor et al., 2012), chosen to represent all major clusters of similar GCMs with high validation statistics. We applied the binary threshold above to each future scenario to create binary SDM projections for all models. For each scenario, we also created an ensemble model based on an average of the projected models across all modeling methods, folds, and replicates.

For the current and future scenarios, we used FRAGSTATS 4.2 (McGarigal et al., 2002) to quantify the area of habitat and degree of habitat fragmentation based on the binary ensemble models. We quantified suitable habitat area in three ways, including total area (TA) in the study area, mean patch area (MPA), and largest patch index (LPI; the percentage of the landscape encompassed by the largest patch). We quantified fragmentation using the aggregation index (AI), which equals 0 when suitable habitat is maximally disaggregated into single grid cell patches disconnected from all other patches and increases to 1 as suitable habitat is increasingly aggregated into a single, compact patch. We also quantified the degree of change for each future scenario relative to the 1981–2010 30-year normal, classifying habitat as either stable, expanding, or contracting. Finally, we used density plots to quantify the distribution of each variable at all locations where SWWP was present in each of the three scenarios.

3. Results

Of the 10,148 sites surveyed, SWWP was present at 1077 sites and absent at 9071 (Fig. 1), resulting in a prevalence of 0.106. SWWP was present at elevations ranging from 684 m to 3711 m (mean elevation = 2104 m). The latitudinal distribution of SWWP among sampled sites ranged from 21.22 degrees north to 36.99 degrees north (mean latitude = 31.04 degrees north).

We observed a significant difference in the means between presence and absence locations for 28 of the 31 candidate variables for at least one of the five spatial scales we evaluated. Among the 22 climate variables, MCMT, RH, and MST were not significant at any scale. All other climate variables were significant at all scales. Among the four soil variables, all were significant at all scales. Among the five topographic variables, TWI, MPI, and SLP were significant at all scales, DAH was significant at ≤ 1000 m, and TPI was significant at ≥ 2000 m. The t -score and corrected p -values for all candidate variables is provided in Table S1 (Supporting Information).

After removing highly correlated variables (keeping the ones with the highest absolute value of the t -score) among the significant candidate variables noted above, six variables remained. They included the climate variables FDD (at the 4000 m scale), MWP (at the 250 m scale), and MWMT (at the 250 m scale), the soil variable SpH (at the 1000 m scale), and the topographic variables TWI (at the 4000 m scale) and SLP (at the 250 m scale). A matrix of the correlation among variables is provided in Table S2 (Supporting Information). In addition, we provide density plots showing the distribution of each of the six variables for presence and absence locations in Fig. S1 (Supplemental Information). Based on variable importance scores (averaged across the 4 modeling approaches), FDD and SpH together contributed 61% of the importance score (Table 2). The other 4 variables contributed the remaining 39%.

The functional form of the marginal response plots varied among the six variables (Fig. 2). MWMT and SpH exhibited a sigmoidal relationship, with higher occurrence probability at cooler temperatures and lower SpH. FDD, MWP, TWI, and SLP exhibited a unimodal relationship with the maximum probability of presence at intermediate levels of the variable.

Model performance was excellent for all methods on both the training data and the test data (Table 3). AUC varied from 0.930 to 0.971, PCC varied from 0.857 to 0.919, TSS varied from 0.710 to 0.838,

Table 2

Variables included in southwestern white pine (*Pinus strobiformis*) species distribution models, including their class (soil, climate, or topography), scale, (i.e. the moving window radius over which the variable was calculated that was most related to occurrence), and variable importance (mean and standard deviation is shown for the four different modeling methods). Variable importance scores were normalized such that they sum to unity.

Variable	Class	Scale (m)	Importance (SD)
FDD	Climate	4000	0.342 (0.142)
SpH	Soil	1000	0.268 (0.147)
MWP	Climate	250	0.177 (0.088)
MWMT	Climate	250	0.104 (0.073)
TWI	Topography	4000	0.071 (0.036)
SLP	Topography	4000	0.038 (0.020)

sensitivity varied from 0.852 to 0.919, and specificity varied from 0.857 to 0.919. The AUC of the ensemble of all four modeling methods was 0.978, which was higher than any method individually.

The binary ensemble model projection for the 1981–2010 30-year normal period estimated 6.733 Mha of suitable habitat. By comparison, the only published range map for SWWP (Fig. 3; Little, 1971) estimated 17.31 Mha of suitable habitat within the study area extent. The binary ensemble projection was not simply a subset of the Little (1971) distribution map. For example, only the ensemble model projected suitable habitat where we detected SWWP in the Sangre de Cristo and Nacimiento mountain ranges of north central New Mexico.

Binary ensemble projections of the fitted models to 2080 reveal projected range shifts in the distribution of suitable habitat for SWWP, with the magnitude of the shift varying between emissions scenarios (Fig. 4). Substantial range contractions were evident in both scenarios in Mexico, southern Arizona, and southern New Mexico. In northern New Mexico, Colorado, and Utah, substantial expansions of suitable environmental conditions were evident in both future scenarios. There was strong model agreement among the four different SDM approaches in areas which were suitable for SWWP during the 1981–2010 period as well as in both future projections for 2080 (Fig. S2, Supporting Information).

Under RCP 4.5 (the lower emissions scenario), the mean latitude of suitable habitat shifts almost 2 degrees north (220 km) and nearly 180 m higher in elevation. Under this scenario, the total area of suitable habitat decreases by 43% (a loss of nearly 3 Mha), average patch area becomes 54% smaller, the largest patch (i.e., the large patch in the Sierra Occidental range of Mexico) becomes 68% smaller, and the aggregation index of suitable habitat decreases 7% (Fig. 5). Under RCP 8.5 (the higher emissions scenario), the mean latitude of suitable habitat shifts nearly 10 degrees north (1000 km) and 540 m higher in elevation, the total area of suitable habitat decreases by 61% (a loss of over 4 Mha), average patch area becomes 78% smaller, the largest patch becomes 90% smaller, and the aggregation index of suitable habitat decreases 18%.

At sites where SWWP was present, the distribution of the three climate variables shifts under the two future climate scenarios for 2080 (Fig. 6). The future projections reveal a large shift towards fewer chilling degree days and warmer summer temperatures, such that under the most extreme future scenario (RCP 8.5), there is little overlap between the historical 30-year normal and future distribution. The future projections also reveal a shift towards less winter precipitation, but the magnitude is small compared to that of the temperature-related variables.

4. Discussion

This study was motivated by concerns about the future of the SWWP ecosystem given the recent spread of WPBR within the study area and a rapidly changing regional climate. Broadly, our results contribute to the growing body of literature projecting potentially dramatic range shifts

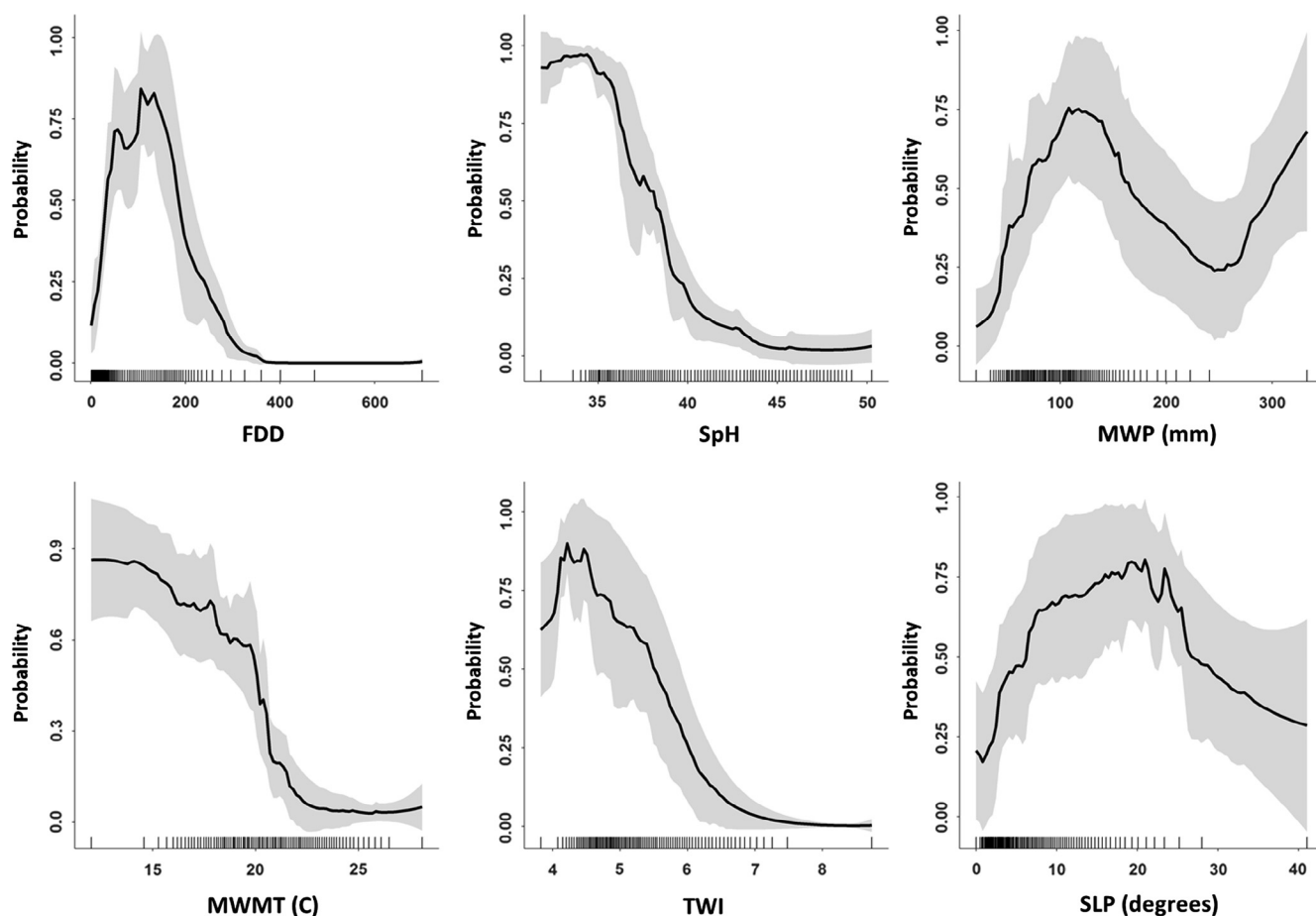


Fig. 2. Marginal response curves for the six variables included in southwestern white pine (*Pinus strobiformis*) species distribution models, including freezing degree days (FDD), soil pH (SpH), mean winter precipitation (MWP), mean warmest month temperature (MWMT), topographic wetness index (TWI), and slope (SLP). The normalized probability of occurrence is shown as a function of each variable while holding all other variables at their median values at presence locations. The mean (black line) and standard deviation (grey area) of the occurrence probability is based on 25 replicate model runs of each of the four species distribution modeling methods. The rug at the bottom of each plot represents the distribution of the variable at all surveyed locations.

Table 3

Model fit metrics for each of the four species distribution modeling methods applied to southwestern white pine (*Pinus strobiformis*) occurrence data within the study area in the southwestern United States and Mexico. Methods included boosted regression tree (BRT), random forest (RF), generalized linear model (GLM), and generalized additive model (GAM). Model fit metrics included area under the receiver operator curve (AUC), proportion correctly classified (PCC), true skill statistic (TSS), Cohen's kappa, sensitivity, and specificity. Model fit was assessed on the training data used to fit the model as well as the withheld test data used for model evaluation. Model fit metrics for the ensemble of all methods are also provided. All values represent the mean of 25 model runs (i.e. 5 replicates, each with 5-fold cross-validation).

Method	Dataset	AUC	PCC	TSS	Kappa	Sensitivity	Specificity
BRT	Test	0.943	0.899	0.719	0.575	0.809	0.909
	Train	0.971	0.919	0.838	0.663	0.919	0.919
RF	Test	0.941	0.875	0.752	0.534	0.877	0.875
	Train	0.940	0.873	0.747	0.529	0.873	0.873
GLM	Test	0.928	0.857	0.710	0.486	0.852	0.857
	Train	0.930	0.859	0.718	0.492	0.859	0.859
GAM	Test	0.932	0.864	0.720	0.502	0.855	0.865
	Train	0.935	0.866	0.733	0.510	0.866	0.866
Ensemble		0.978	0.910	0.819	0.633	0.909	0.910

for conifers in the region by the end of the century. More specifically, our results provide three key pieces of information that will help guide conservation and management of this species. First, the historical projection more accurately reflects the observed distribution of SWWP

compared to the only existing range map (Little, 1971), allowing for more efficient genetic sample collection (for the purposes of identifying WPBR resistance and genetic adaptations to climate variability) as well as improved monitoring of WPBR outbreaks. Second, the variables identified and their functional relationship to SWWP occurrence suggests mechanisms by which climate, soil, and topography may influence the distribution of this poorly studied species. Identifying the key constraints on species' distributions and their functional relationship to occurrence is critical to devising effective conservation strategies. Third, our results provide a preview of the potential future distribution of environmental conditions suitable for SWWP, providing lead-time to enact forward-looking strategies (e.g. assisted migration and assisted gene flow; Aitken et al., 2008; Aitken and Bemmels, 2016) designed to conserve high elevation white pine ecosystems within the study area. The magnitude of these changes projected by our models underscores the need for conservation planning.

An important aspect of our approach to SDM is the optimization of the scale at which each variable is related to occurrence. The presence of a species at a particular location is potentially influenced by multiple factors operating at different spatial scales, from several meters to many kilometers (reviewed in McGarigal et al. (2016)). Despite this, the scale at which variables are optimally related to species occurrence is rarely hypothesized or evaluated in SDMs. Rather, variables are most commonly assessed at the base resolution of the input data. We have previously shown that multi-scale analysis of habitat selection increases model accuracy, sensitivity, and specificity as well as providing ecological insights about the scales at which variables affect occurrence

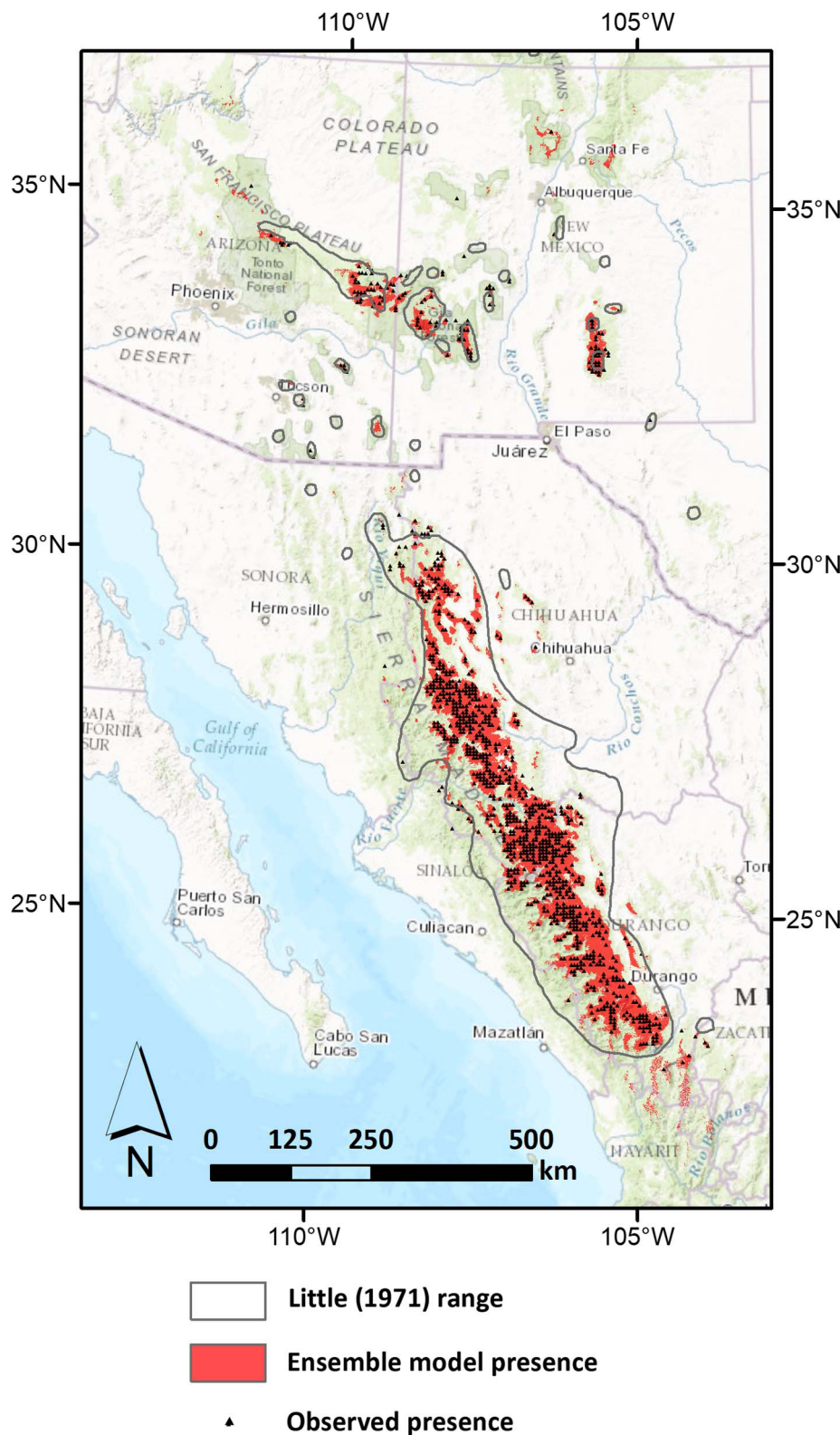


Fig. 3. Spatial distribution of southwestern white pine (*Pinus strobusiformis*) in the southwestern United States and northern Mexico. Grid cells where the majority of species distribution model runs across the 4 methods and 25 replicates project presence are shown in red. The polygons outlined in black represent the published range map for this species, from Little (1971). The small black triangles represent sites where southwestern white pine was present. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Shirk et al., 2014). Here, we extend this concept to the analysis of species' ranges. In the case of SWWP, we found the relationship of climate and soil variables to occurrence did not differ strongly over the spatial scales we considered. However, the topographic variables (slope and topographic wetness) were much more correlated with occurrence over broad scales (4000 m). Thus, the topographic controls on SWWP distribution within the study area appear to be tied to broad regional

patterns of slope and soil moisture rather than finer-scale site-level characteristics.

Because soil and topography were assumed to be constant over time, range shifts projected by our models were due solely to changes in the three climate variables. Based on variable importance scores, warming winter low temperatures (modeled as degree days below freezing) was the main driver of the shift. Winter warming has potentially profound

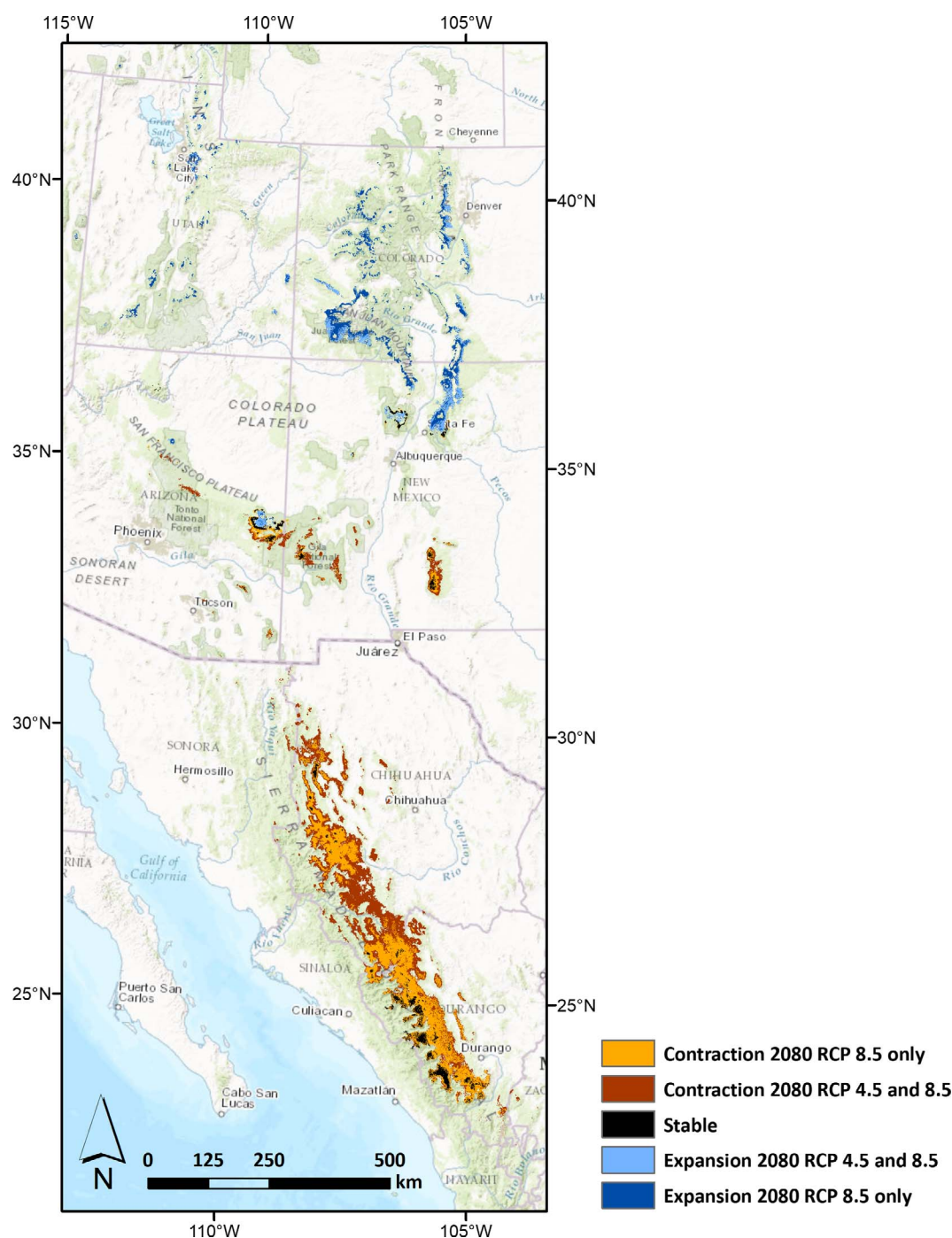


Fig. 4. Projected changes in the future range of southwestern white pine (*Pinus strobiformis*) in the southwestern United States and northern Mexico. Black grid cells represent areas where southwestern white pine is projected by the ensemble species distribution model to be present now and also present in 2080 under both future emissions scenarios (RCP 4.5 and RCP 8.5). Orange and red grid cells represent areas where the distribution of suitable environmental conditions is projected by the ensemble model to contract by 2080 under both RCP 4.5 and RCP 8.5, or RCP 8.5 only, respectively. Light blue and dark blue grid cells represent areas where the distribution of suitable environmental conditions is projected to expand by 2080 under both RCP 4.5 and RCP 8.5, or RCP 8.5 only, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

consequences for the many temperate and boreal tree species that require prolonged exposure to cold winter temperatures before bud growth can initiate in spring (Heide, 2003). Indeed, our results indicate the projected distribution of freezing degree days by 2080 under RCP 8.5 is almost entirely outside the historical range of variability at sites where SWWP was present. Importantly, the marginal response curve projects SWWP to have a low probability of occurrence within the future distribution of freezing degree days. Thus, failure to meet the chilling requirement appears to pose a considerable threat to SWWP within its current range and is therefore a potential driver of future

range shifts. Chilling requirements have been identified as an important determinant of southern distributional limits for other temperate and boreal North American tree species (Morin et al., 2007), and winter warming impeding the chilling requirement has been proposed as a mechanism driving range shifts and extirpation under future climate scenarios (Aitken et al., 2008).

Future projections of lower mean winter precipitation also contributed to the range contraction and range shift apparent in the 2080 scenarios. Within the occupied range of SWWP, historically wet winters at high elevations result in saturated soils near the surface in early

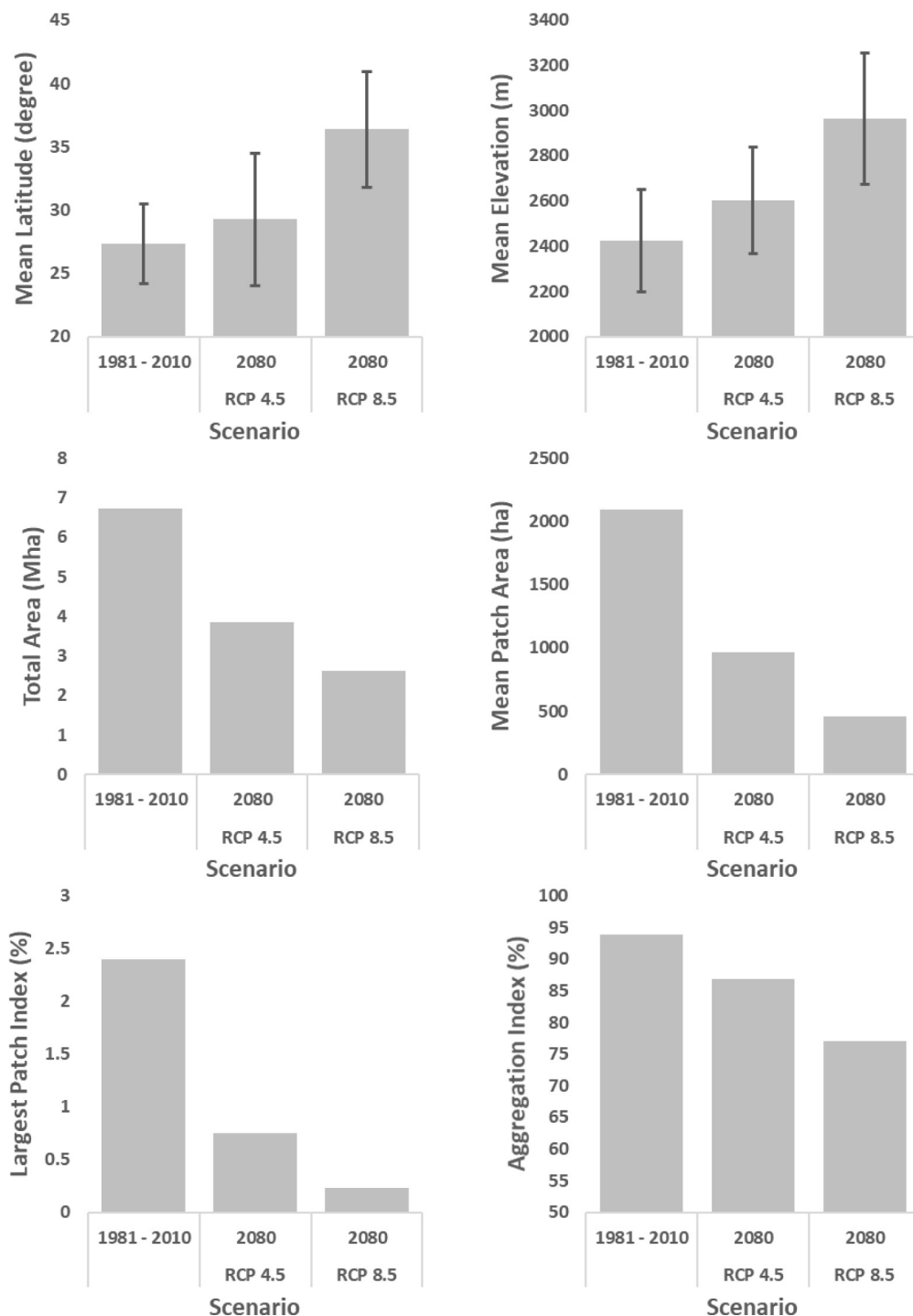


Fig. 5. Changes in the distribution, area, and fragmentation of southwestern white pine (*Pinus strobiformis*) habitat in the southwestern United States and northern Mexico under three scenarios, including the 1981–2010 reference period, 2080 under the RCP 4.5 emissions scenario, and 2080 under the RCP 8.5 emissions scenario. The top two panels show the mean latitude and elevation for all grid cells where the majority of model runs across 25 replicates and four species distribution modeling methods project presence. The bottom four panels show metrics quantifying the area and fragmentation of grid cells in the ensemble model where southwestern white pine was projected to be present, including total area, mean patch area, largest patch index (i.e. the percent of the study area occupied by the single largest patch), and aggregation index (a measure of fragmentation that varies from 0 to 100, with zero reflecting conditions where all suitable grid cells are maximally dispersed from each other across the landscape).

spring and recharge of soil moisture at greater depths (Notaro et al., 2010). In most of the SWWP range, melting winter snowpack also contributes to spring soil saturation and recharge. Like other high-elevation white pine species, SWWP requires saturated surface soils for seed germination and deep soil moisture recharge for early survival (Gans, 1978). Climate projections for the southwestern United States show strong agreement in projecting less winter and spring precipitation (Baker and Huang, 2014). In conjunction with warming in both summer and winter, this is driving a decline in winter snowpack, reduced soil moisture recharge, and increased drought severity throughout the region (Mote et al., 2005). These trends have been implicated in widespread die-offs among conifers in the study area and elsewhere in the western United States in recent years (Van Mantgem

et al., 2009), and are projected to accelerate in the future, with concomitant reductions in spring–summer soil moisture and summer drought in mountainous regions (Gergel et al., 2017; Klos et al., 2014).

The role of mean warmest month temperature in shaping the projected distribution of SWWP is likely also related to drought stress because warmer temperatures increase the vapor pressure deficit, which drives rates of transpiration in plants (Williams et al., 2012). The response curve for mean warmest month temperature shows a steep decline in SWWP occurrence probability above 20 °C, and much of the future range of this variable is expected to shift well beyond this threshold, particularly under RCP 8.5. Drought stress is an increasingly common cause of tree mortality in North America (Hember et al., 2017), particularly in water-limited ecosystems like our study area.

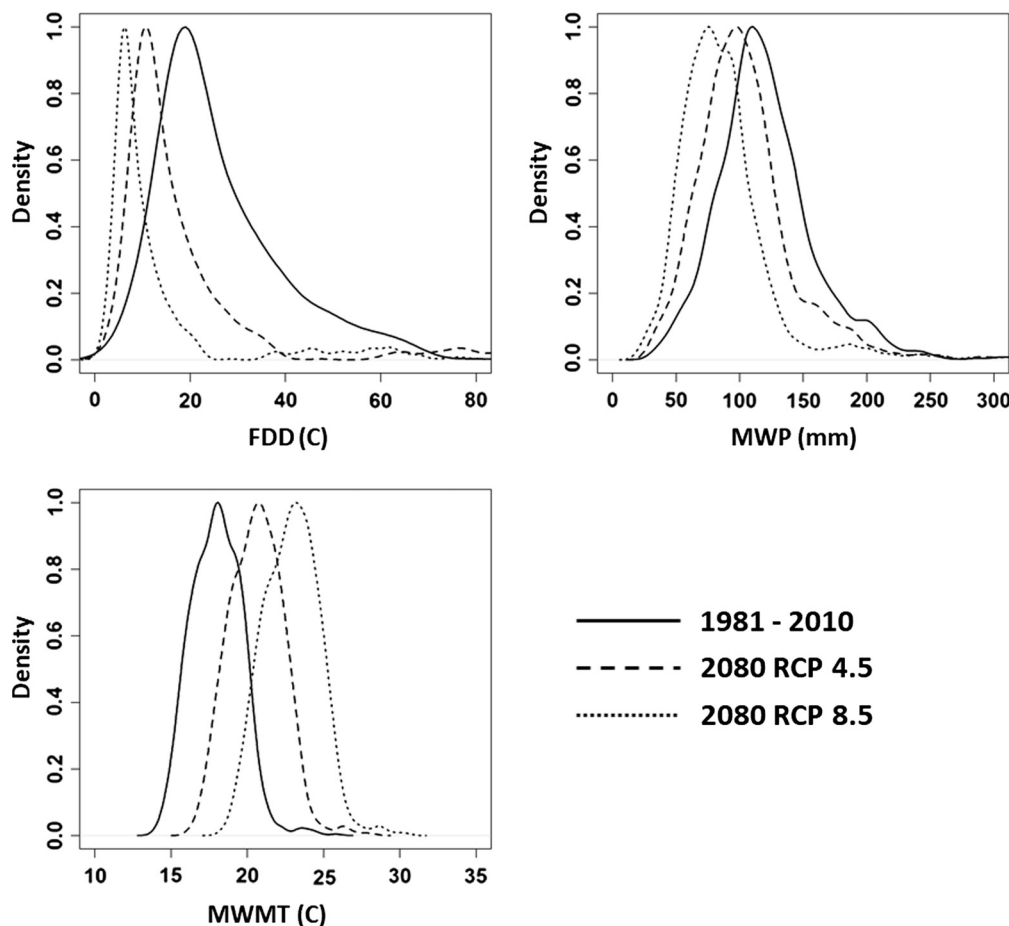


Fig. 6. Distribution of climate variables at sites where southwestern white pine (*Pinus strobi-formis*) is present in Arizona, New Mexico, and northwestern Mexico under three scenarios, including the 1981–2010 reference period (solid black line), 2080 under the RCP 4.5 emissions scenario (dashed black line), and 2080 under the RCP 8.5 emissions scenario (dotted black line). The variables shown are the three climate variables used in the species distribution models, including freezing degree days (FDD), mean winter precipitation (MWP), and mean warmest month temperature (MWMT).

Future projections of vapor pressure deficit in the southwestern US indicate that by the 2050s, mean forest drought stress will exceed that of the most severe droughts in the past 1000 years (Williams et al., 2012), leading researchers to predict massive die-offs of conifer forests in the region (McDowell et al., 2015).

Two other studies have assessed the future distribution of SWWP under climate change scenarios. Laughlin et al. (2011) projected a 500 m shift upwards in elevation assuming a 2.5 °C increase in temperature by 2060. This shift was driven by changes in functional relationships between climate and traits related to tree growth and phenology. Though the methods and predictors were very different from this study, the 500 m elevational shift agrees with our model expectations under RCP 8.5 by 2080. In contrast, our study differs markedly from the Gómez-Mendoza and Arriaga (2007) analysis, which projected the SWWP range in Mexico would expand slightly under a climate change scenario of a 1.6 °C temperature increase by 2050 and decrease slightly under a more severe 2.5 °C temperature increase over the same period. Their analysis used a much more limited set of environmental variables, at a much coarser spatial resolution, with a single GCM that was not included in our ensemble. Their analysis was also based on only 33 sites sampled, compared to 10,148 in this study. Furthermore, they did not provide validation statistics, so model accuracy is unknown. For these reasons, comparison with our study is difficult.

The SWWP range shift projected by our models can be thought of as two simultaneous processes. On the trailing edge of the population, projections of rising temperature (in both summer and winter) and decreasing precipitation would be expected to result in failure to achieve the chilling requirement during winter, drier soils in the spring, and greater drought-stress during summer. Reduced growth initiation and drought stress would be expected to eventually kill mature trees. If lack of soil moisture limits germination and survival of seedlings,

regeneration would fail to replace adult trees and extirpations would occur along the trailing edge of the population. Under the RCP 8.5 scenario, our models project nearly the entire population of SWWP in Mexico, southern Arizona, and southern New Mexico become extirpated, except for a few high-elevation refugia. This fits with other regional assessments of conifer extirpation under future climatic conditions (McDowell et al., 2015).

As the trailing edge of the population contracts, the leading edge of the environmental space suitable for SWWP is projected to expand dramatically northward in latitude and upward in elevation, far into Colorado and Utah. However, several constraints may limit the ability of SWWP to colonize this potential future niche. First, colonization requires seed dispersal, which is poorly understood for SWWP. In the northern portion of its range, avian dispersal has been observed by Clark's Nutcracker (Samano and Tomback, 2003), a common agent of dispersal for other white pine species, including the closely related limber pine (*Pinus flexilis*; Lanner and Vander Wall, 1980; Hutchins and Lanner, 1982). The colonization rate for tree species with avian dispersers is generally greater compared to other species, but is still limited to 0.1–1 km/year during rapid shifts in climate (Clark et al., 2014). The projected range shift of 15 km/year under RCP 8.5 suggests SWWP will not be able to keep pace with the northerly shift of its climatic niche. The disparity between colonization rates and the rate at which SWWP habitat is shifting would be expected to create a substantial lag between when expansion is environmentally possible and when expansion actually occurs.

In addition to seed dispersal, germination, survival, and reproduction are also required for successful colonization. The degree to which these requirements are met is influenced by many factors, including competition with other species, genetic resistance to disease, genetic adaptations to the local climate of the colonized area, timing of

phenology, and rates of disturbances (Caplat et al., 2008; Chuine and Beaubien, 2001; Petit et al., 2004). The high rate of change projected in the near-future climate, coupled with range expansion of WPBR, suggest it may be difficult for SWP to fill its potential future environmental niche as rapidly as it shifts. If so, the degree of range contraction and fragmentation of the future population may far exceed our estimates. Indeed, if contraction at the population's trailing edge occurs faster than colonization of new habitat at the leading edge, the population could ultimately be at risk of extinction.

The ecological impacts of the projected range shift and contraction for SWWP may be modified by corresponding shifts in other white pine species that play similar functional roles in high elevation habitats. The limber pine and Mexican white pine (*Pinus ayacahuite*) are closely related to SWWP, and the two species overlap with the distribution of SWWP in the north and south parts of its range, respectively. Together, these species form a complex that spans a broad environmental gradient. It is possible the ecological role of SWWP will be maintained by other members of the complex in areas where it becomes extirpated.

We note two important limitations of our study. First, the uncertainty in our model projections for the year 2080 is entirely a function of the variance among the four SDM methods we used. Because we used an ensemble of 15 GCMs, rather than assess GCMs individually, our model projections for 2080 do not account for the uncertainty in the future projections of the climate variables. Though there is strong agreement among CMIP5 models for warming and decreased precipitation in the study area (Gao et al., 2014), the magnitude of those changes varies among the GCMs, and it would be valuable to understand the degree to which that variability affects future projections of SWWP occurrence.

A second limitation of our study is the potential for the assumptions inherent in correlative SDM (Wiens et al., 2009) to be violated in our study area, and thereby reduce the accuracy of the projected future distribution of SWWP. Of particular concern are the assumptions that species distributions are determined only by environmental factors controlling their niche (e.g. climate, soils, and topography) and that all suitable habitat is fully occupied. In practice, species distributions may also be strongly influenced by biotic interactions among species such as competition, predation, amensalism, and mutualism (Godsoe et al., 2017). Biotic and abiotic disturbances (primarily WPBR and fire, respectively), modulated by forest management practices (Sakulich and Taylor, 2007), also limit the range of SWWP. Adding to this complexity, forest management practices and changes in the regional climate may interact with and modify these species interactions and disturbance regimes (Keane et al., 2013; Tylisanakis et al., 2008). To incorporate these ecological processes into future projections of the SWWP distribution would require mechanistic models that explicitly define them (Kearney and Porter, 2009). However, in our view, there is not currently sufficient understanding of the dynamics of competition with close competitors like Douglas-fir (*Pseudotsuga menziesii*; Looney and Waring, 2012), disturbance (primarily WPBR and fire), and climate changes to reliably parameterize such models, hence our reliance on correlative approaches. Despite the potential for the assumptions of correlative SDMs to be violated, they have been shown to be, in some cases, equally or even more accurate than mechanistic models (Hijmans and Graham, 2006; Shabani et al., 2016). Indeed, both approaches have strengths and weaknesses, and the most robust inferences of future species distributions may come through integrating the projections of both mechanistic and correlative approaches (Kearney et al., 2010).

Our model projections offer insight into how potential climatic changes in the southwestern United States and Mexico may shape the future distribution of SWWP. Phenotypic plasticity and local adaptation may modify rates of contraction and expansion at the trailing and leading edges of a population, respectively (Valladares et al., 2014). However, given the magnitude of the projected range shift, relying on these natural mechanisms of resiliency alone may not be sufficient. To help conserve SWWP, efforts are underway to identify genotypes that

are resistant to WPBR and adapted to the climatic conditions that are expected to predominate across the region in the future. The improved range map provided by this study will help those efforts. Assisted gene flow may then be used to introduce individuals with adaptive genotypes into populations that lack those traits (Aitken and Bemmels, 2016). Given that natural colonization rates are unlikely to keep pace with the projected range shift, assisted migration into areas our study identified as suitable in the future may also be warranted (Vitt et al., 2010).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.01.025>.

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