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Using spatiotemporal correlative niche models for evaluating the effects of climate change on mountain pine beetle

AARON M. SIDDER,[1,2,3,5,†] SUNIL KUMAR,[1,2,3] MELINDA LAITURI,[1,2,3] AND JASON S. SIBOLD[3,4]

[1] *Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523 USA*
[2] *Department of Ecosystem Science and Sustainability, Colorado State University, Natural and Environmental Sciences Building, 1231 East Drive, Fort Collins, Colorado 80523 USA*
[3] *Graduate Degree Program in Ecology, Colorado State University, 1401 Campus Delivery, Fort Collins, Colorado 80523 USA*
[4] *Department of Anthropology, Colorado State University, B-219 Andrew G. Clark Building, Fort Collins, Colorado 80523 USA*

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Abstract. Over the last decade, western North America has experienced the largest mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in recorded history, and Rocky Mountain forests have been severely impacted. Although bark beetles are indigenous to North American forests, climate change has facilitated the beetle's expansion into previously unsuitable habitats. We used three correlative niche models (maximum entropy [MaxEnt], boosted regression trees, and generalized linear models) to estimate (1) the current potential distribution of the beetle in the U.S. Rocky Mountain region, (2) how this distribution has changed since historical outbreaks in the 1960s and 1970s, and (3) how the distribution may be expected to change under future climate scenarios. Additionally, we evaluated the temporal transferability of the niche models by forecasting historical models and testing the model predictions using temporally independent outbreak data from the current outbreak. Our results indicated that there has been a significant expansion of climatically suitable habitat over the past 50 yr and that much of this expansion corresponds with an upward shift in elevation across the study area. Furthermore, our models indicated that drought was a more prominent driver of current outbreak than temperature, which suggests a change in the climatic signature between historical and current outbreaks. Projections under future conditions suggest that there will be a large reduction in climatically suitable habitat for the beetle and that high-elevation forests will continue to become more susceptible to outbreak. While all three models generated reasonable predictions, the generalized linear model correctly predicted a higher percentage of current outbreak localities when trained on historical data. Our findings suggest that researchers aiming to reduce omission error in estimates of future species responses may have greater predictive success with simpler, generalized models.

Key words: climate change; *Dendroctonus ponderosae* Hopkins; disturbance ecology; forest ecology; insect pests; model transferability; species distribution models.

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[5] Present address: U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, Colorado 80526 USA.

† **E-mail:** aaron.sidder@gmail.com

INTRODUCTION

Global surface temperatures have warmed over the last three decades, with each successive decade warmer than the preceding decade (IPCC 2014). Substantial warming is projected in the U.S. Rocky Mountain region (Colorado, Utah, Wyoming, Montana, and Idaho) by mid-century with temperature increases exceeding the global mean. These increases are expected to have a particularly pronounced effect at higher elevations (Bentz et al. 2010, Lukas and Gordon 2015).

Combined with a shift in the timing and frequency of precipitation events, the Rocky Mountain region is forecasted to be hotter and more susceptible to drought in the coming decades (Seager et al. 2007, Lukas and Gordon 2015). These climatic changes portend significant ecological changes, including species range shifts and an increase in landscape-shaping disturbances such as outbreaks of the mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins; Coleoptera: Curculionidae, Scolytinae), one of the principal drivers of landscape-level change in western North America (Dale et al. 2001, Parmesan 2006, Lenoir et al. 2008, Negrón and Fettig 2014).

The recent MPB epidemic is a historically large outbreak that has impacted over 6.5 million hectares of forest in the western United States (Bentz et al. 2010, USDA Forest Service 2011). The MPB is a major disturbance agent that causes widespread tree mortality and substantially alters the structure, composition, and function of North American coniferous forests (Logan and Powell 2001, Carroll et al. 2006, Raffa et al. 2008). Given the severity of the recent beetle epidemic, there has been a considerable focus on the ecology and long-term ramifications of the infestation on North American forests (Bentz et al. 2010, Negrón and Fettig 2014). The Rocky Mountain region has previously experienced large MPB outbreaks, but fire suppression, reduced habitat heterogeneity, and the climatic release of previously unsuitable habitats have driven an outbreak unique in its scope and intensity (Taylor and Carroll 2003, Carroll et al. 2006, Raffa et al. 2008, Assal et al. 2014).

The two most important host species for MPB are lodgepole pine (*Pinus contorta* var. *latifolia*) and ponderosa pine (*P. ponderosa*), which are found in montane forests throughout the American West. The pine beetle prefers large-diameter trees, and although it will infest any native pine in its range, some species like piñon pine (*P. edulis*) are poor hosts (Amman 1978, Logan and Powell 2001). The recent outbreak, which initiated in the mid-1990s, has also expanded into high-elevation subalpine forests (3000–3500 m) that were previously deemed too climatically harsh for eruptive MPB outbreaks (Logan and Powell 2001, Carroll et al. 2006). Potential hosts in subalpine forests include five-needle pines such as whitebark pine (*P. albicaulis*), limber pine (*P. flexilis*), and both Rocky Mountain and Intermountain bristlecone pines (*P. aristata* and *P. longaeva*, respectively) (Logan and Powell 2001). During an outbreak, MPB will overwhelm its host via a pheromone-driven "mass attack" that results in the establishment of egg galleries in the phloem (Negrón and Fettig 2014). Host trees are killed through a combination of high beetle pressure and the blue-stain fungus introduced by the beetle; adults and larvae girdle the tree by feeding on the phloem, and the fungus penetrates the xylem and blocks water transport from the soil to the canopy (Fairweather et al. 2006, Hubbard et al. 2013).

Climate influences MPB in three ways: through adaptive seasonality, cold-induced mortality, and drought stress on host trees (Creeden et al. 2014). Many stages of the beetle's life cycle are regulated by temperature, and adaptive seasonality occurs when the MPB experiences a one-year life cycle as a result of climatically synchronized adult emergence from host trees at the appropriate time of year (Amman 1978, Safranyik 1978, Hicke et al. 2006, Safranyik and Carroll 2006, Sambaraju et al. 2012). Adaptive seasonality is conducive for large outbreaks, while maladaptive seasonality (two- or three-year life cycles) can restrict outbreak potential (Creeden et al. 2014). In contrast to adaptive seasonality, which facilitates large outbreaks, extremely cold temperatures may restrict the MPB population by reducing overwinter survival and causing widespread beetle mortality (Safranyik 1978, Campbell 2007, Sambaraju et al. 2012). Cold-induced mortality of overwintering larvae is an important factor in MPB population dynamics, but MPB cold tolerance varies geographically and among seasons (Régnière and Bentz 2007). Drought indirectly drives MPB outbreaks by restricting the host tree's ability to defend itself against beetle attacks and increases the probability of eruptive outbreaks (Safranyik 1978, Creeden et al. 2014). Drought is an important component of beetle outbreaks, although many past studies have emphasized warming temperatures as the primary climatic driver behind the recent epidemic (Logan and Powell 2001, Hicke et al. 2006, Bentz et al. 2010, Jewett et al. 2011).

The relationship between climate and MPB has been modeled using a variety of statistical approaches, both mechanistic and correlative.

Mechanistic, or process-based, models have been used to incorporate the explicit relationships between climate and MPB performance to predict adaptive seasonality (Logan and Powell 2001, Hicke et al. 2006), cold-induced mortality (Régnière and Bentz 2007), and climatic suitability (Safranyik et al. 1975, 2010, Carroll et al. 2006, Bentz et al. 2010). Correlative models, which statistically correlate MPB outbreaks and climate, have been used to determine the climatic associations of MPB outbreaks and to better understand the climatic conditions that support eruptive beetle outbreaks (Aukema et al. 2008, Evangelista et al. 2011, Jewett et al. 2011, Sambaraju et al. 2012, Creeden et al. 2014). Many of these models have been applied to future climate change scenarios to predict the climatic suitability for MPB outbreaks in a warming environment (Carroll et al. 2006, Hicke et al. 2006, Bentz et al. 2010, Safranyik et al. 2010, Evangelista et al. 2011, Sambaraju et al. 2012). While many of these studies evaluated MPB ecology through time, none explicitly compared the climatic drivers of historical outbreaks with the drivers of the recent epidemic in the Rocky Mountain region.

We used three correlative niche models to spatiotemporally evaluate the climatic correlates of MPB outbreaks since 1960. Correlative niche models—also known as bioclimatic envelopes, species distribution models, or ecological niche models—are probabilistic models that statistically correlate species' occurrences with its present environment, and are often used to estimate a species' distribution and predict the changes in their distribution under changing climatic conditions (Guisan and Zimmermann 2000). The technical foundations and the relative performance of niche models have been widely reviewed (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith et al. 2006, Elith and Leathwick 2009), and these models have been implemented to explore the potential impacts of climate change on a variety of species (Thuiller et al. 2008, Anderson 2013, Khanum et al. 2013, Monahan et al. 2013).

We investigated how the climatic niche, potential distribution, and climatic drivers of MPB have changed across three time periods: 1960–1980 (historical), 1997–2010 (current), and 2040–2069 (future). Additionally, we tested the niche models' transferability through time, or how well they project into different time periods with conditions not currently found in the study area. We define the climatic niche as the range of climatic conditions that could support an MPB outbreak, for example, the upper and lower temperature bounds found in occupied habitat. The potential distribution refers to the spatial extent of climatically suitable habitat, or the abiotic conditions (topographic and climatic) that could support an outbreak. Climatic drivers refer to the variables that most prominently influence MPB outbreaks.

Four primary questions guided the research: (1) How has the potential distribution of MPB shifted under changing climatic conditions between historical and current outbreaks, and how will this be expected to change under future climate change scenarios? (2) What were the primary climatic drivers of the historical and current outbreaks, and how do they differ? (3) How will the utilized climatic space of the beetle be expected to shift under projected future climatic conditions, and how might this modify the distribution of the species? and (4) Which correlative niche model is most appropriate for predicting suitable habitat under future climate conditions (i.e., temporal transferability)?

Data and Methods

The study was conducted across five U.S. states (Colorado, Idaho, Montana, Utah, and Wyoming) that have experienced, and continue to experience, extensive MPB outbreaks (Fig. 1, Appendix S1). To evaluate the changes in the potential distribution and climatic drivers of MPB outbreaks, we used past and current U.S. Forest Service (USFS) aerial detection survey (ADS) data and a spatiotemporal modeling scheme that covered three time periods: 1960–1980 (historical), 1997–2010 (current), and 2040–2069 (future) (Fig. 2). Additionally, we used a principal components analysis (PCA) to show changes in the occupied climatic niche between historical and current outbreaks. Model transferability was assessed by training each niche model on historical data and projecting into current climate conditions, using current occurrence data as the test (or evaluation) data set (Fig. 2).

Occurrence data

The species occurrence data used in the analysis were generated from USFS ADS polygons

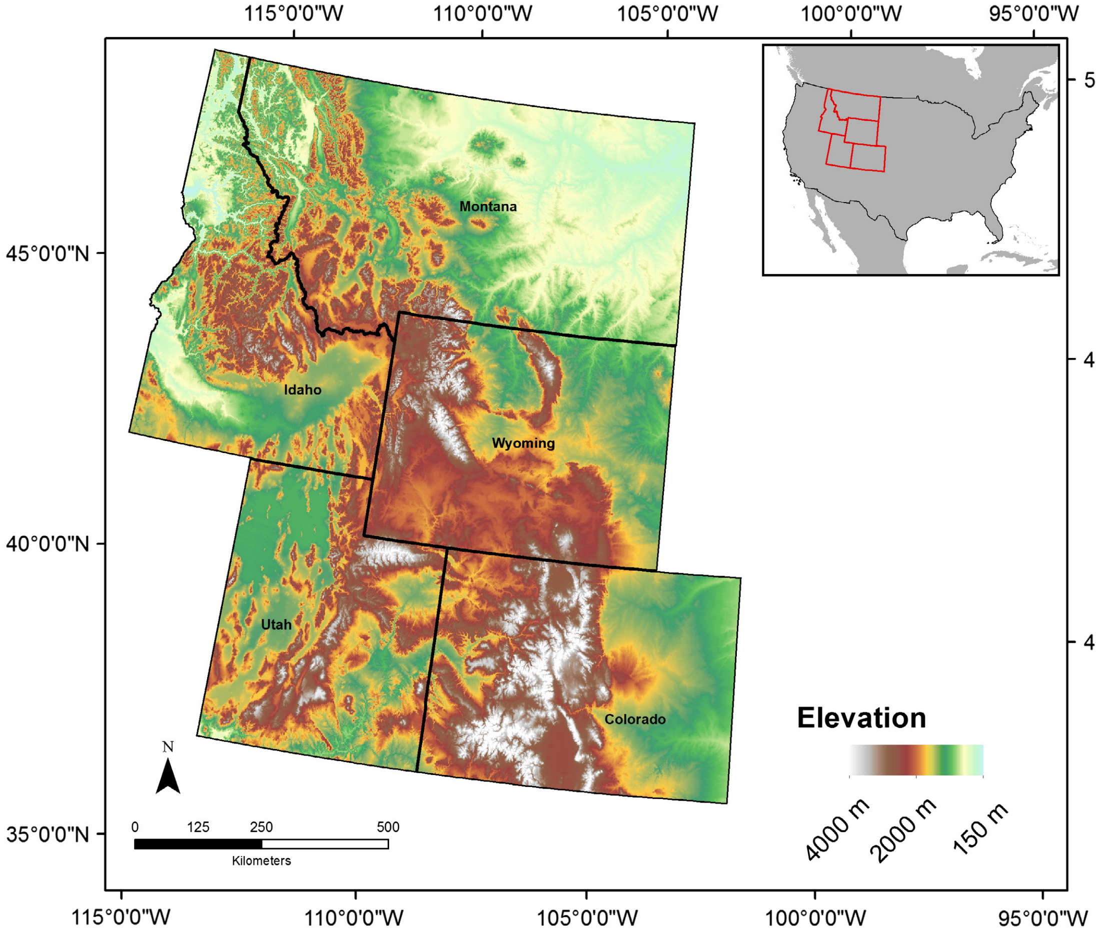

Fig. 1. The five-state Rocky Mountain region comprising Colorado, Utah, Wyoming, Montana, and Idaho. The map shows topographic relief (1-km cells) across the region.

that delineate the annual extents of MPB infestation and other forest disturbance across the five-state Rocky Mountain region (McConnell et al. 2000). Survey data were collected for historical (1960–1980) and current (1997–2010) time periods. All data were reprojected into the North American Datum 1983 (NAD83) Albers Equal Area Projection to reduce latitudinal background selection of pseudo-absence (background) points in the niche models (Brown 2014). All MPB polygons from each study period were dissolved into a single layer, and a sample of 5000 stratified random points (where strata are polygons) was generated from within this layer using the *Geospatial Modelling Environment* software (Beyer 2012). This sample of occurrence localities was spatially filtered with the *SDMToolbox* so that no occurrence localities were within 10 km of another occurrence (Brown 2014). Spatial filtering can reduce model overfitting and spatial autocorrelation, and ensures independence of the test and training data when using a cross-validation evaluation technique (Veloz 2009, Boria et al. 2014, de Oliveira et al. 2014, Radosavljevic and Anderson 2014). We filtered at 10 km because MPB generally occurs in mountainous terrain with high spatial heterogeneity, similar to previous modeling studies that used the 10-km filter in mountainous regions (Pearson et al. 2007, Anderson and Raza 2010, Boria et al. 2014). Spatial filtering reduced the historical data set from 5000 original points to 882 points. The current data exhibited a wider geographic spread and contained more data points than the historical data, so to maintain consistency

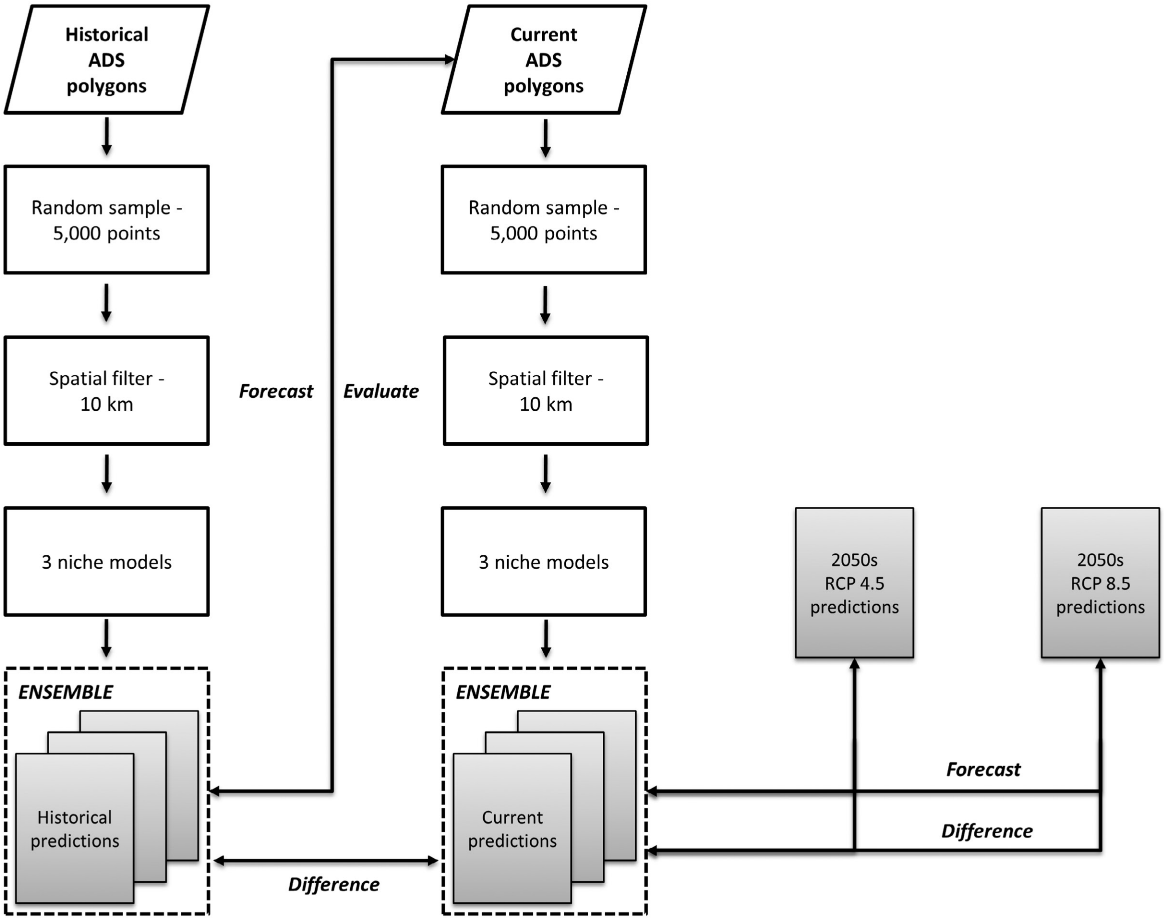

Fig. 2. A schematic representation of the modeling workflow. Models were trained on both historical and current outbreak data, and the difference in predicted climatic suitability between the two time periods represents the expansion of climatically suitable habitat over the past half-century. Historical models were evaluated by forecasting the model to current climate conditions and comparing the predictions to current outbreak data. To assess the future climatic suitability, the current models were forecast to future climate conditions under RCP 4.5 and RCP 8.5 scenarios. See Data and Methods for more details; ADS, aerial detection survey; RCP, representative concentration pathways.

between time periods, the current data were also reduced to 882 points via random point selection.

Historical data were acquired from individual USFS Regional Offices. The historical data were originally collected on marked topographic quadrangles and georeferenced and digitized in a geographic information system (ArcGIS v10.2, ESRI, Redlands, California, USA). Because there are historical surveys that remain undigitized, and therefore unavailable for use in this study, it should be noted that the historical data set is partially incomplete and may not reflect the full range of MPB presence during the years 1960–1980. Current data were downloaded from the Insect and Disease Detection Survey (IDS) Data Explorer (USDA Forest Service 2014).

Climate data

Climate data were acquired from ClimateWNA (version 5.10) at 1-km grid cell resolution (Wang et al. 2012). Historical climate data were selected for the 30-yr period spanning 1951–1980, and current climate data for 1981–2010. The 30-yr period for future climate projections covers the years 2040–2069, which we collectively refer to as "2050." We used the global mean of 15 global climate models for two representative concentration pathways (RCP), RCP 4.5 and RCP 8.5. These scenarios were selected from phase five of the Coupled Model Intercomparison Project (CMIP5) multi-model data set that corresponds with the Fifth Assessment Report from the Intergovernmental Panel on Climate Change (IPCC) (Moss et al. 2010, Taylor et al. 2012, Wang et al. 2012). RCP 4.5 is considered a medium stabilization scenario (~650 ppm CO_2 equivalent by 2100) that encompasses the vast majority of the scenarios assessed in the Fourth Assessment Report (van Vuuren et al. 2011). RCP 8.5 is considered a very high emissions scenario (~1370 ppm CO_2 equivalent by 2100) that assumes no current or future climate policy (van Vuuren et al. 2011).

Forty-five initial variables were chosen from the full ClimateWNA data set (Appendix S2: Table S1) based on the known climatic and environmental influences on MPB biology and ecology. These variables were tested for correlation based on the Pearson, Spearman, and Kendall coefficients, and highly correlated variables ($|r| \geq 0.7$) were filtered using expert knowledge of MPB ecology, and were chosen to represent seasonal climatic influences on MPB. However, four pairs of highly correlated variables were retained in the final analysis to examine the seasonal influences on the beetle. The final predictors included 14 climatic and topographic variables (Table 1).

Spatiotemporal modeling

We used three correlative niche models and a PCA to evaluate historical and current MPB outbreaks. The niche models were used to estimate the potential distribution of MPB, and the PCA was used to evaluate the potential climatic niche shift in multidimensional space. Three distinct models were run for this analysis: maximum entropy (MaxEnt) (Phillips et al. 2006), boosted regression trees (BRT) (Elith et al.

Table 1. Predictor variables used in the three niche models. For a detailed description of climate variables, see Wang et al. (2012).

Variables	Description	Rationale
CMD	Hargreaves climatic moisture deficit (CMD). Sum of the monthly difference between reference atmospheric evaporative demand (E_{ref}) and precipitation. A higher CMD reflects a greater moisture deficit.	Drought affects the host tree's ability to defend itself against bark beetle attack (Safranyik 1978, Creeden et al. 2014). Below-average precipitation across the growing season correlates with an increased MPB (Amman 1978, Carroll et al. 2006).
PAS	Precipitation as snow (PAS, mm) between August of previous year and July of current year.	
PPT_sp	Spring precipitation between March–May.	
PPT_sm	Summer precipitation between June–August.	
PPT_at	Autumn precipitation between September–November.	Reduction in autumn moisture immediately following an attack benefits larval overwinter survival (Amman 1978).
bFFP	Julian date on which the frost-free period (FFP) begins.	Spring temperature affects the larval development (Amman 1978, Aukema et al. 2008).
eFFP	Julian date on which the frost-free period ends.	Early onset of frost period in the late summer and autumn may affect the egg and larval development (Safranyik 1978).
Tmin_wt	Winter mean minimum temperature (°C).	Severe winter temperatures can reduce overwinter survival and cause widespread beetle mortality (Safranyik 1978, Campbell 2007, Sambaraju et al. 2012).
DD_0_wt	Winter degree-days below 0°C.	
DD_0_sp	Spring degree-days below 0°C.	Spring temperature affects the larval development (Amman 1978, Aukema et al. 2008).
DD18_sm	Summer degree-days above 18°C.	Summer heat accumulation affects many aspects of the MPB life cycle, including emergence, flight, and egg hatch (Sambaraju et al. 2012).
elevation	Digital elevation model (DEM) at 1-km resolution.	Topographic variables roughly define a suitable topography for host species (Safranyik 1978, Sambaraju et al. 2012).
slope	Maximum change in elevation between each cell and its eight neighbors.	
aspect	Downslope direction of a grid cell.	

2008), and generalized linear models (GLM) (McCullagh and Nelder 1989, Austin 2002). For details on model parameterization and function, see Appendix S3. These three models have consistently demonstrated high performance across species functional groups, and compare favorably with other correlative models (Elith et al. 2006, Austin 2007, Guisan et al. 2007, Stohlgren et al. 2010). All models were trained using the same 14 variables across all time periods (Table 1). Each model was tested internally using a 10-fold cross-validation (Fielding and Bell 1997). The potential geographic overlap between the models was calculated with Schoener's *D* statistic via the "ENMeval" package in R v.3.1.2 (Warren et al. 2008, Muscarella et al. 2014, R Core Team 2015). All final maps were clipped to the combined forest classifications denoted by the National Land Cover Dataset (NLCD) for the years 2001, 2006, and 2011 (Homer et al. 2007, Fry et al. 2011, Jin et al. 2013). Forested areas include the sum of forest land cover classification codes 41 (deciduous forest), 42 (evergreen forest), and 43 (mixed forest).

MaxEnt is a general-purpose machine-learning method that was run in its stand-alone software package (Phillips et al. 2006). A number of recent studies have underscored the importance of carefully calibrating the MaxEnt model (Merow et al. 2013, Shcheglovitova and Anderson 2013, Radosavljevic and Anderson 2014). To parameterize MaxEnt models for MPB, we experimentally tuned the parameters using the "ENMeval" package in R v.3.1.2 (Appendix S3: Figs. S1, S2; Muscarella et al. 2014, R Core Team 2015). We ran all MaxEnt models (historical, current, and projected) using the "all features" setting, with a regularization multiplier of 3.0 and 20,000 background samples. Based on the ENMeval metrics, these settings produced the best performing models with biologically reasonable response curves (Appendix S4: Figs. S1, S2).

Boosted regression trees (BRT) are an ensemble method for fitting statistical models that use regression trees and boosting to combine many simple models and improve performance (De'ath 2007, Elith et al. 2008). Boosted regression trees tend to overfit models, so regularization methods are used to constrain the fitting procedure by optimizing three parameters: the number of trees, the learning rate, and tree complexity (Elith et al. 2008). The BRT models were fitted using the Software for Assisted Habitat Modeling (SAHM), and we experimentally parameterized the learning rate and tree complexity to derive models with at least 1000 trees and biologically sensible response curves (Morisette et al. 2013). For the historical model, the best settings that resulted in at least 1000 trees for the historical model had a learning rate of 0.005 and tree complexity of 5; the current model was parameterized at 0.005 and 3.

Generalized linear models are a regression approach that fits parametric terms using some combination of linear, quadratic, and/or cubic terms (Elith et al. 2006). Within SAHM, we fit the GLM to a binomial distribution with a logit link function, and the SAHM algorithm chose the optimal model based on a bidirectional stepwise procedure that selected covariates based on Akaike's information criterion (AIC; Morisette et al. 2013).

We evaluated elevational range shifts, range expansion, and range contraction to assess the geographic trends across time periods (Fig. 2). In addition to calculating these values for each individual model, we created an ensemble prediction for each time period to assess the average progression through time. Ensemble models are a solution to intermodel variation and capture the areas of agreement across models (Araújo and New 2007). To create the ensemble, binary suitability maps were produced using a fixed 95% sensitivity threshold; that is, the threshold equaled the lowest predicted probability that encompassed 95% of the occurrence localities (Peterson et al. 2011). The binary maps for each model were combined so that the resulting ensemble map contained only pixels that were deemed environmentally suitable by all three models (Stohlgren et al. 2010).

The correlative niche models encompass two strategies for modeling presence-only data. MaxEnt draws pseudo-absences from a random sample of background pixels to account for the presence-only structure of the occurrence data, whereas the BRT model and GLM are derived from regression techniques generally associated with presence–absence data (Phillips et al. 2006). Because absence data were not available for the historical period, we used background data as pseudo-absences for the BRT model and GLM (Phillips et al. 2009). Background samples were constrained by a kernel density estimator (KDE) to account for potential sampling bias that may exist when aerial surveys are primarily flown over federal lands (Kumar et al. 2014*a*, *b*). The KDE restricted background sampling to general "use areas" for MPB so that all background samples were drawn from environmental conditions the species is most likely to reach (Merow et al. 2013). The constrained background sampling corrects for sampling bias in the species occurrences by applying the same bias to the background points, thereby canceling out the bias in the modeling process (Phillips et al. 2009). The KDE was generated in SAHM using a 95% isopleth on MPB occurrence data; that is, the resulting mask represented the smallest area providing a 95% probability of finding MPB (Fieberg 2007, Morisette et al. 2013). We created separate surfaces for both historical and current occurrence data that were used to restrict the background "absences" in BRT and GLM. These surfaces were used as a bias file in MaxEnt.

Models were evaluated using AUC (the area under the receiver-operating characteristic curve), a threshold independent metric, and sensitivity (the true-positive rate), a threshold-dependent metric. The AUC metric is a commonly used statistic that represents an overall measure of a model's predictive accuracy and summarizes the model's ability to distinguish between a species' presence and absence (Peterson et al. 2011). Although AUC can be a misleading measure of model performance, it was useful for this study because all models were trained on the same geographic extent, and background samples were extracted from the general use area defined by the KDE (Lobo et al. 2008). To assess the model performance through time when climatic conditions may differ, we also evaluated sensitivity. Sensitivity is the rate of known presences correctly predicted by the model prediction (1—the omission error rate) and represents the absence of omission error (Peterson et al. 2011).

To assess the temporal transferability of the various modeling techniques, we trained each model on the historical data (historical occurrences and climate data) and projected them onto current climate conditions (Fig. 2). To assess the quality of the predictions of the forecast model, we tested the predictions, trained with historical occurrence data, against current occurrence localities, and generated AUC and sensitivity statistics for each model. Sensitivity was calculated by thresholding the projection at the same 95% sensitivity threshold of the historical model. For example, if the 95% threshold for the historical model was 0.26, then this value was used as the threshold for the projected model as well. We calculated AUC values for the projected models using the ROC/AUC calculator (Schroeder 2006) and created multivariate environmental similarity surface (MESS) maps to quantify the extent of extrapolation in model projections (Elith et al. 2010). The MESS maps were generated within SAHM (Morisette et al. 2013). All current models were then projected to two climate scenarios for 2050, RCP 4.5 and RCP 8.5. The models were trained using the current occurrence localities and climate data, and forecast climate conditions were substituted to provide a projection of future climatic suitability.

Lastly, we used a PCA model in R (v.3.1.2; R Core Team 2015), adapted from Broennimann et al. (2012), to assess the potential shifts of the climatic niche in multivariate environmental space. We ran three separate PCAs with all 14 environmental variables to contrast the fundamental niche shift of MPB across time periods: historical to current, current to RCP 4.5, and current to RCP 8.5. To prepare the data for the PCA, 20,000 random background points were selected from across the study extent and variable values were extracted at each point. Additionally, data were extracted at each of the 882 occurrence localities for each time period. Contrasting principal components were overlaid to determine the extent of MPB in ordinal space and to assess the niche overlap between time periods (West et al. 2015). Additionally, we calculated niche overlap in climatic space using Schoener's D metric, which varies from 0 (no overlap) to 1 (complete overlap) (Warren et al. 2008, Broennimann et al. 2012).

RESULTS

Historical models

MaxEnt and BRT were the top-performing historical models (Table 2). All models displayed a good fit, meaning that they captured a large fraction of the total variability in the data, with

Table 2. Model summary and results; higher AUC values indicate better model performance.

	Model description		Model evaluation		
Model	No. of variables†	Top variables	Training AUC	Test AUC	ΔAUC
Historical					
MaxEnt	12	Summer precipitation, summer degree-days (18°C), precipitation as snow	0.86	0.85	0.01
BRT	10	Summer degree-days (18°C), precipitation as snow, climatic moisture deficit	0.88	0.85	0.03
GLM	6	Summer degree-days (18°C), winter degree-days below 0°C, elevation	0.81	0.81	0
Current					
MaxEnt	12	Climatic moisture deficit, summer precipitation, summer degree-days (18°C)	0.82	0.82	0
BRT	6	Climatic moisture deficit, summer degree-days (18°C), slope	0.84	0.82	0.02
GLM	7	Climatic moisture deficit, summer degree-days (18°C), end of frost-free period	0.8	0.8	0

Notes: The training AUC shows the fit of the model to the data, while the test AUC was calculated based on withheld data applied to the model using a 10-fold cross-validation. ΔAUC, the difference between the training and test AUC, is a measure of model overfit (overparameterization), and lower values indicate better fit.

† All variables were included in the initial run, but were reduced through a jackknife test of variable importance. In MaxEnt, variables of low importance were manually removed. The BRT and GLM algorithms in SAHM automatically removed the variables of low importance.

minimal difference between training and test AUC values for the MaxEnt model and GLM. A pairwise comparison of niche overlap predicted by the models revealed a strong agreement among the models. MaxEnt and BRT overlapped by 85% (as calculated by Schoener's *D* statistic), MaxEnt and GLM had 80% overlap, and GLM and BRT also had 80% overlap. Summer degree-days above 18°C was the only top predictor common to all three models.

Current models

Similar to the historical models, MaxEnt and BRT were the top-performing current models (Table 2). Again, all models produced strong predictions, although with a slight decrease in performance across the board, and all models also showed good fit with low ΔAUC values. A comparison of the niche overlap between current model predictions again showed high agreement among the models. MaxEnt and BRT overlapped by 86%, MaxEnt and GLM had 82% overlap, and GLM and BRT had 84% overlap. The top predictors for the current outbreak showed more consistency among the models than for the historical models: Summer degree-days above 18°C and climatic moisture deficit were the top predictors in all three models.

All models estimated a substantial range expansion for the pine beetle between the historical and the current time periods with the BRT predicting the highest net expansion (Table 3). In addition to an overall range expansion, the model results suggest that this range expansion correlates with an upward shift in elevation (Fig. 3, Table 3). All of the individual models show a statistically significant upward shift in the mean elevation. Again, the ensemble models demonstrated the greatest elevational shift ($P < 0.0001$), and the BRT showed the greatest shift among the individual models ($P < 0.0001$).

Future projections

Under the RCP 4.5 scenario, all models predicted a net contraction of climatically suitable habitat for MPB, with the GLM showing the greatest contraction (Fig. 4, Table 3). There was greater disagreement among model projections under RCP 4.5 than for the historical and current models. The MaxEnt and BRT models had a predicted niche overlap of 78%; MaxEnt and GLM overlapped by 87%; and the BRT model and GLM overlapped by 75%.

The second forecast projected the models onto the data from the RCP 8.5 scenario. The patterns of contraction seen in the RCP 4.5 projections held true for the RCP 8.5 forecasts as well: GLM

Table 3. The predicted area (km^2) of climatically suitable habitat for the mountain pine beetle across historical, current, and future time periods.

Models	Total area	Range expansion (km^2)	Range contraction (km^2)	Net (km^2)	Elevation shift (m)
Historical					
MaxEnt	275,565	…	…	…	…
BRT	267,840	…	…	…	…
GLM	311,565	…	…	…	…
Ensemble	249,002	…	…	…	…
Current					
MaxEnt	311,142	41,254	5677	35,577	+79
BRT	306,284	45,510	7066	38,444	+99
GLM	322,123	17,224	6666	10,558	+22
Ensemble	295,207	52,350	6145	46,205	+115
Future					
RCP 4.5					
MaxEnt	267,970	2987	46,069	−43,082	+41
BRT	273,949	3830	36,165	−32,335	+19
GLM	240,570	46	81,599	−81,553	+110
Ensemble	228,111	1570	68,666	−67,096	+87
RCP 8.5					
MaxEnt	243,738	1440	68,844	−67,404	+74
BRT	260,798	2381	47,867	−45,486	+24
GLM	205,133	0	116,990	−116,990	+171
Ensemble	194,420	731	101,518	−100,787	+139

Notes: Predicted changes in area for current and 2050 estimates show the calculated areas of suitable habitat and the extent of expansion and contraction from the preceding time period (i.e., range expansion for the current estimates reflects the change compared to the historical predictions). The elevation shift reflects the mean elevation of climatically suitable habitats. All values reflect the suitable habitat clipped to the National Land Cover Dataset forest layers.

predicted the greatest contraction, followed by MaxEnt and BRT (Table 3). The RCP 8.5 projections had the least agreement of all the temporal segments. MaxEnt and BRT models showed a predicted niche overlap of 74%; MaxEnt and GLM overlapped by 86%; and the BRT and GLM overlapped by 70%.

Model transferability

All three historical models demonstrated good fit and high AUC values when projected into the current climate conditions. Based on the test AUC values, each model performed better than the current models trained on the current occurrences (Table 4). Based on AUC, the MaxEnt and BRT models were the top-performing models. MaxEnt had a slightly higher sensitivity compared to BRT, but both were lower than GLM (Table 4). Overall, all three models provided reasonable predictions across time periods.

While evaluating the model transferability, we used MESS maps to track the extent of extrapolation in model projections (Fig. 5, Elith et al. 2010). The MESS maps show minimal extrapolation in all projections, from historical to current and current to 2050 (RCP 4.5 and RCP 8.5). Areas of high extrapolation were generally outside the estimated climatic niche of MPB, in alpine environments or the southern reaches of the study extent dominated by non-forested grassland, shrubland, and desert.

Potential niche shift

We evaluated the shifts in the climatic niche space utilized by the mountain pine beetle across time periods using PCA, which shows the relative niche occupancy along each axis. The first PCA compared the historical climatic niche to the current niche and was run with all 14 climatic and topographic variables. The comparison revealed a significant shift in the climatic niche between outbreaks (Fig. 6). Three variables displayed similar loadings for the first principal component (PC1): winter degree-days below 0°C, beginning of the frost-free period, and

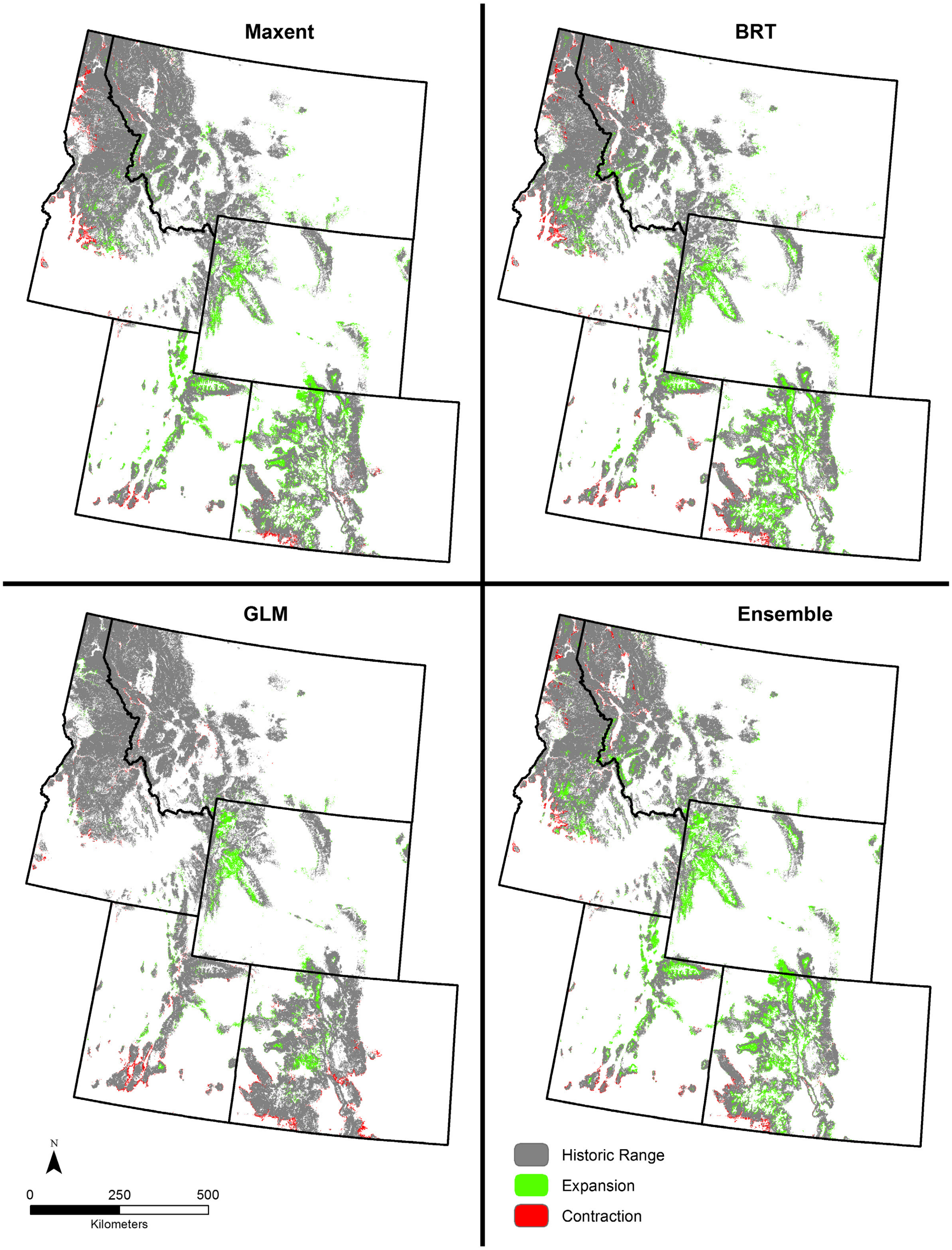

Fig. 3. Estimated shift in climatically suitable areas between historical and current outbreaks as predicted by the models. The map shows the suitable conditions in both historical and current outbreaks (gray), the range expansion between outbreaks (green), and the range contraction between outbreaks (red).

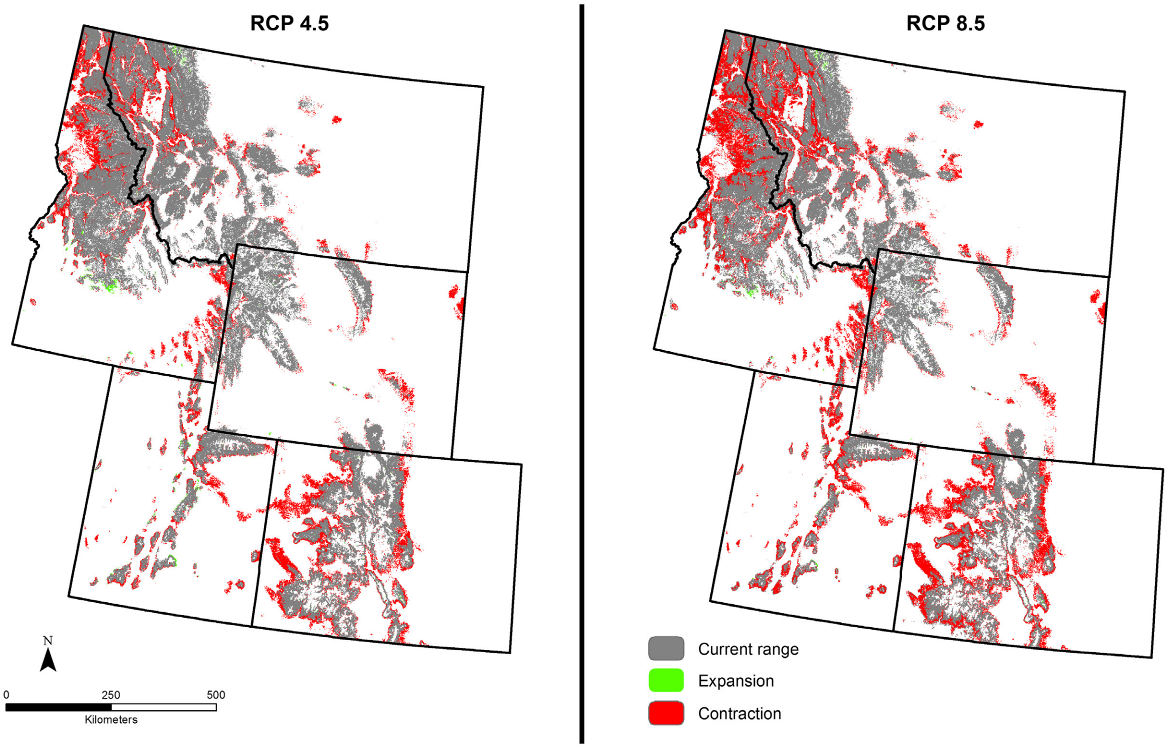

Fig. 4. The ensemble models showing the shift in climatically suitable conditions under both the RCP 4.5 and RCP 8.5 future climate scenarios. The map shows the suitable conditions in current outbreaks (gray), predicted range expansion under future conditions (green), and predicted range contraction under future conditions (red).

Table 4. Evaluation of model transferability from historical to current climate conditions.

Model	Test AUC	Sensitivity
MaxEnt (historical projected to current)	0.87	82% (728/882)
BRT (historical projected to current)	0.87	81% (717/882)
GLM (historical projected to current)	0.85	90% (798/882)

Notes: Sensitivity is based on the 95% sensitivity threshold used for the historical model and applied to projections with the current climate data. The current occurrence localities were used as test data, temporally independent from the training data. Sensitivity is the number of correctly predicted current occurrences out of 882 occurrence localities.

spring degree-days below 0°C. The highest loading of the second component (PC2) was autumn precipitation. The niche overlap (Schoener's *D*) between the two time periods was 0.30. This suggests that only 30% of the ordinal historical niche was utilized by the species during the current outbreak. This shift showed that the historical niche and current climatic niche were not significantly similar ($P = 0.207$).

We ran the PCA comparing the current climatic niche with the potential niche under two future climate change scenarios, RCP 4.5 and RCP 8.5, under the assumption that the current occurrence localities would remain suitable habitat under future conditions (Fig. 6). The results were similar under both future scenarios. The top loadings of the PC1 were winter degree-days below 0°C, beginning of the frost-free period, and spring degree-days below 0°C. The PC2 was loaded primarily by autumn and spring precipitation. The niche shift was slightly more pronounced under RCP 8.5, which shared 54% of the ordinal climate space with the current niche. The overlap between the current niche and RCP 4.5 was 61%.

Discussion

The models used in this study represent approximations of climatic suitability for MPB

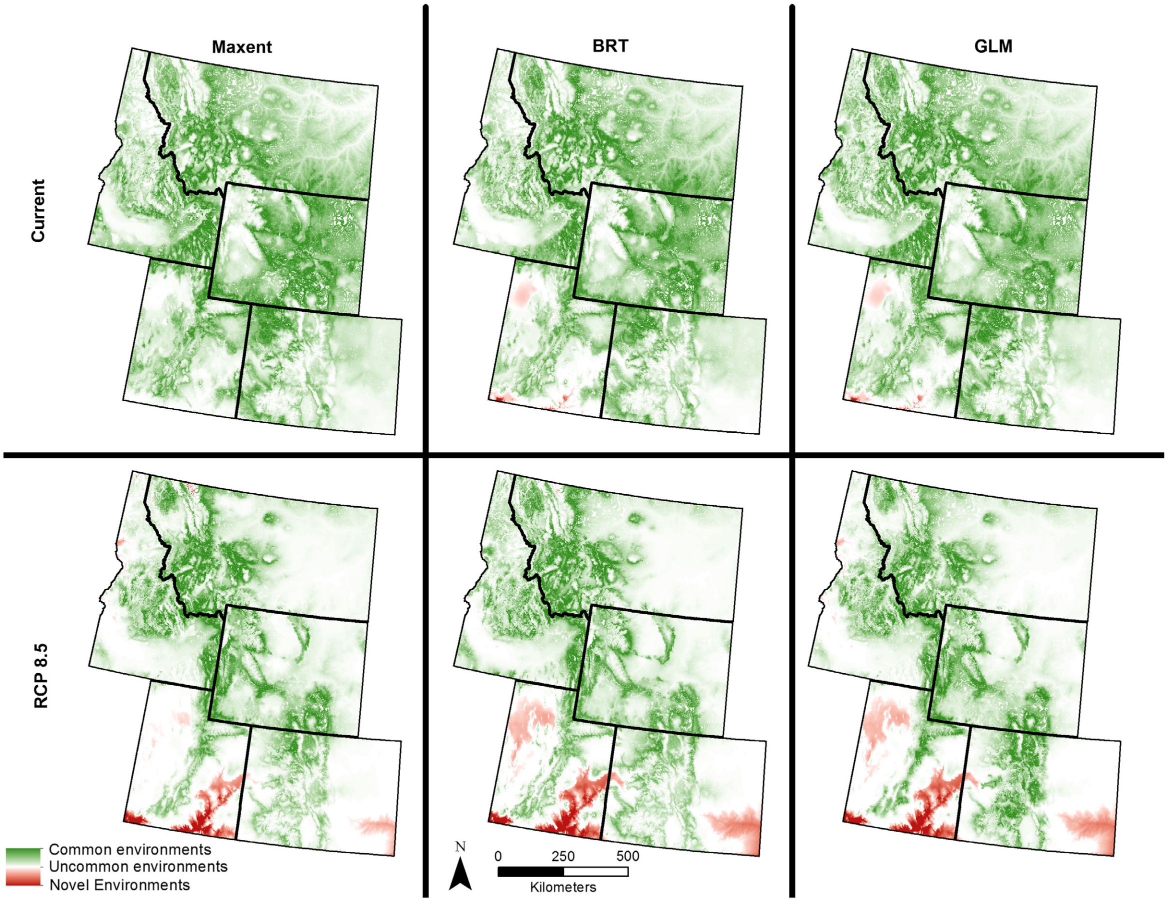

Fig. 5. A comparison of predictor variables using multivariate environmental similarity surface (MESS) maps. The MESS calculation represents how similar a point is to a reference set of points. Negative values (red) indicate novel environments where at least one variable has a value outside the range of environments found in the reference data. Sites with positive values indicate that the full range of environmental variables was found in the reference data; high positive values (green) are fairly common and lower values (white) represent a relatively unusual environment (Elith et al. 2010). Darker colors indicate more extreme values.

outbreaks. Shifts in suitable area were estimated based on the correlative relationships between the predictors and the occurrence localities. The model results should be treated as distributional hypotheses that are limited to the predictors, extent of the study region, and location of MPB occurrences (Lobo et al. 2008). Our results imply that climatic changes in the latter half of the 20th century significantly increased the amount of climatically suitable habitat for MPB in the U.S. Rocky Mountain region and that the recent MPB outbreak displayed a different climatic signature than historical outbreaks. The expansion of climatically suitable habitat reflects an upward elevational shift into previously unsuitable habitats and a change in MPB's climatic niche. Yet, despite the recent expansion of suitable habitat for MPB, future projections suggest that climate warming will reduce the amount of climatically suitable areas by mid-century.

Climatic drivers of mountain pine beetle outbreak and range expansion

Our results revealed both direct and indirect climatic drivers of MPB outbreaks. The primary climatic drivers for both the historical and current outbreaks were summer heat accumulation and drought (Table 2), which align with past findings on the climatic influence on MPB

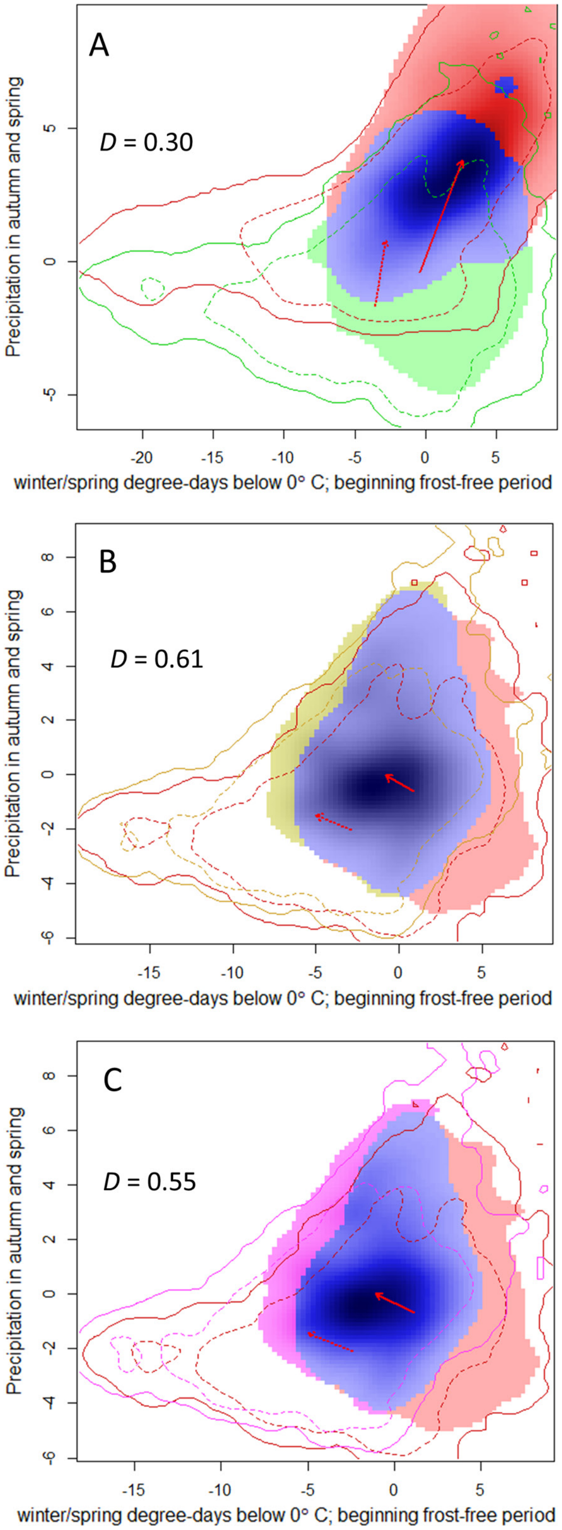

Fig. 6. Principal component analysis of niche shift in environmental space for *Dendroctonus ponderosae*. Blue shading represents the overlap between periods. The solid and dashed contour lines illustrate, respectively, 100% and 50% of the available (background) environment. The solid arrows represent the shift of the niche for occupied sites, and the dashed lines represent the shift across the full study area extent. Axes show the primary loadings of each principal component: (A) historical (green) and current (red); (B) current (red) and future under RCP 4.5 (gold); (C) current (red) and future under RCP 8.5 (purple).

outbreaks (Bentz et al. 2010, Evangelista et al. 2011, Chapman et al. 2012, Creeden et al. 2014). However, our model results showed different climatic signatures between historical outbreaks and the recent epidemic. All three correlative niche models agree that the climatic moisture deficit was the most important predictor variable for the current outbreak, suggesting that drought has played a larger role in the current outbreak than in historical outbreaks. Over the past 50–60 yr, the Rocky Mountain region has experienced drier summers with reduced moisture availability, and an earlier onset of spring that diminishes snowpack sooner than the historical norm (Westerling et al. 2006, Bentz et al. 2010). This has led to long-term drought that has contributed to increased tree mortality in the region and has made host trees far more susceptible to eruptive MPB outbreaks (Hicke et al. 2006, van Mantgem et al. 2009). Increased summer heat accumulation, particularly at higher elevations, was also important in making conditions more conducive to MPB outbreak. Increased summer heat facilitates adaptive seasonality and reduces the risk of overwinter mortality, in turn boosting the intensity of the recent outbreak. Our results indicate that these climatic trends are critical elements in intensified MPB outbreaks and shifts in the species' distribution.

These climatic drivers resulted in a substantial expansion of the climatically suitable habitat of MPB between 1960 and 2010. Although there was some variability among the models, all three models, as well as the ensemble model, showed a net expansion of suitable habitat during the current outbreak (Table 3). As conditions grew warmer over the past 50 yr, MPB expanded into previously unfavorable high-elevation forests (Carroll et al. 2006), which is reflected in the primary habitat gains along the range margins and an increase in the average elevational range of the species (Table 3). A considerable portion of this expansion occurred in northwest Wyoming in the Greater Yellowstone Ecosystem. This ecosystem has recently experienced high rates of whitebark pine mortality driven by warmer, drier conditions (Jewett et al. 2011). These climatic conditions correspond with the primary climate variables that drove the expansion of suitable environment for MPB throughout the region. Although the study area has previously experienced MPB epidemics in whitebark pine ecosystems (Perkins and Swetnam 1996), our results support the arguments that climate change is increasing the susceptibility of these ecosystems by reducing the climatic deterrents to widespread outbreaks (Logan and Powell 2001, Carroll et al. 2006). Our estimates of the current expanse of suitable environment are also similar to those of Evangelista et al. (2011); however, by using climate data through 2010, we were able to capture suitable habitat in northwest Wyoming that was not predicted by their models, which only used climate data through the year 2000.

The transition of MPB into high-elevation forests is also shown in the utilized climatic niche of the species. Three predictors contained a majority of the variability in the first principal component: the beginning of the frost-free period (bFFP) and degree-days below 0°C in both the winter and spring seasons. The shift in the second principal component was driven by increases in precipitation in the spring and autumn. The climatic niche of the current outbreak shifted positively along both axes of the PCA, which indicates higher correlation with the principal loadings of the axes. Higher elevations would be expected to have a later last frost, more cold days in the winter and spring, and more precipitation in the spring and fall. The positive correlations of these variables with MPB occupancy in the current outbreak suggest that the current outbreak occupied suitable habitats at higher elevations than in the historical outbreak.

With regard to future predictions of climatic suitability, our models projected a net contraction under both future scenarios, RCP 4.5 and RCP 8.5. The net contraction was more pronounced under RCP 8.5, the high emissions scenario, but both projections indicate a decrease in climatically suitable habitat for MPB. There are a number of possible explanations for this trend, although none were tested explicitly in the modeling. The life cycle of MPB is under direct temperature control, and population success is closely tied to phenology; adult beetles must emerge late enough in the summer to avoid lethal freezing, but not so late as to reduce ovipositional potential through fall and winter cooling (Logan and Bentz 1999). Projected decreases in suitable habitat are likely related to a reduction in areas of adaptive seasonality. Conditions that promote earlier emergence would result in early oviposition, which may expose cold-intolerant life stages (e.g., pupa) to extremely cold winter temperatures (Hicke et al. 2006). Further warming could also disrupt current suitable habitat by promoting maladaptive seasonality or disrupting the beetle's physiology (e.g., flight), which could reduce the effectiveness of the species' "mass attack" strategy and other key life stages (McCambridge 1971, Safranyik 1978, Logan and Bentz 1999). Although climate change is expected to intensify all aspects of insect outbreaks, warming at lower elevations and latitudes could result in the reduction in suitable environments for MPB, as shown in the model predictions (Fig. 4, Logan et al. 2003). There is less confidence in forecasts of precipitation in climate models, so anticipating the effects of drought on climatically suitable habitat in the future may be more difficult than linking the potential changes to warming temperatures.

The PCA revealed a potential niche shift under both RCP 4.5 and RCP 8.5 (Fig. 6). Without knowing future occurrences, we were only able to estimate the background environment and extract forecast conditions at the current outbreak localities. Our approach assumes that the current suitable habitat will also be suitable, biologically and climatically, in the future. Moreover, this approach does not take into account any future range expansion, biotic interactions, and currently unaccounted localities. The two principal components were loaded similarly to the historical/current PCA. The first component reflected the beginning of the frost-free period (bFFP) and degree-days below 0°C in both the spring and winter, and the second principal component was loaded by precipitation in the spring and autumn.

The future niche space was similar under both climate scenarios, but expansion of the niche under RCP 8.5 was slightly more pronounced than that under RCP 4.5, as expected because RCP 8.5 is a more severe forecast. Overall, the future climatic space shifted negatively along the x-axis and positively along the y-axis, suggesting a reduction in degree-days below 0°C in the winter and a warmer, earlier spring. The shift along the y-axis indicates an increase in precipitation in the spring and fall, although this was fairly minimal compared to the horizontal shift. The PCA suggests that currently occupied habitats will continue to grow warmer and that the high-elevation habitats will become more conducive to beetle outbreaks.

Spatiotemporal model transferability

Predicting a species' response to climate change assumes that models are transferable through time and that models adequately extrapolate to novel conditions (conditions not currently found in the study area). Predicting species' responses to novel conditions often involves extrapolation beyond the range of the data used to train the model, which can be more complicated than interpolative forecasting because temporally or spatially independent data are often unavailable to test model predictions (Williams et al. 2007). This transferability (also called "generality") refers to a model's ability to make useful predictions in a different context from which it was trained, and models with better transferability would be expected to make more useful predictions (Dobrowski et al. 2011). In general, broadly applicable models provide more useful predictions than those that only accurately predict occurrence based on a narrow set of conditions (Wenger and Olden 2012).

Multiple studies have addressed the issue of temporal transferability for a range of models (Araújo et al. 2005, Pearman et al. 2008, Kharouba et al. 2009, Dobrowski et al. 2011, Heikkinen et al. 2012), but such investigations are still fairly uncommon given the relative lack of temporally independent data sets (Araújo et al. 2005). Because a species' observed distribution alone cannot provide information on how a species may respond to novel conditions, assessments of temporal transferability are important for determining the usefulness of predicted responses to climate change (Fitzpatrick and Hargrove 2009). In our study, all three model projections provided reasonably good predictions (test AUC values >0.85) when projected through time, and there was little difference in model performance (Table 4). Given past research on transferability, the relative similarity between model projections was expected; in general, the functional traits of species influence transferability more than differences in the modeling algorithms (Kharouba et al. 2009, Dobrowski et al. 2011, Heikkinen et al. 2012). The results from this study may be useful for predicting the climate change responses of other native bark beetles (Coleoptera: Curculionidae, Scolytinae) such as the spruce beetle (*D. rufipennis* Kirby) and western pine beetle (*D. brevicomis*).

The choice of modeling algorithm for forecasting will largely be determined by the goals of the project, but our analysis suggests that a simpler model, such as the GLM, may be more appropriate for future predictions that seek to limit omission error. GLM performed 8–9% better than the BRT and MaxEnt models, but did not adequately discriminate between unsuitable high-elevation environments and the mid-elevation environments that are the primary habitats of the beetle. Because of this generality, the GLM predicted a much narrower elevational shift and less expansion of suitable habitat between the time periods; however, the generalized prediction yielded more accurate predictions of current outbreaks. The GLM had the lowest omission error, and this is especially important in the analyses of relocation, translocation, or species reintroduction, as well in the assessments of risk from invasive species or disease (Araújo and Peterson 2012).

The MESS maps reveal that despite projection across temporal domains, extrapolation in the model projections was fairly limited (Fig. 5). None of the forecasts either from the historical to current time period or from the current to future scenarios exhibit significant novelty in regard to the variables used in the models, and regions that did exhibit novel conditions are not generally susceptible to MPB outbreaks (non-forested, high-elevation alpine and southern shrub and desert ecosystems). There are a couple of possible explanations for this. The first explanation is that the chosen time periods may not be separated by enough time to show significant climatic changes. Yet, the past three decades have shown unprecedented warming, a trend that is anticipated to continue over the next three decades (IPCC 2014). Both current and future climate data should reflect this warming, and novel conditions would be expected. Instead, it is more likely that the projections lacked novel conditions because the models were trained on data drawn from a heterogeneous landscape. Rocky Mountain landscapes are highly varied and have a significant topographic relief throughout the region in addition to a large latitudinal gradient. As a result, although certain locations might see drastic climatic changes, the new conditions are likely found elsewhere in the study area and were used to train the model. For MPB, estimates of climatically suitable areas in the future can be viewed with a higher degree of confidence than a species with a more restrictive elevation or latitudinal range because model projections are not extrapolating to novel conditions.

Modeling future suitability requires a number of assumptions that may not be true under novel climatic and environmental conditions. For example, over the past 20–30 yr, the study region has undergone a significant population growth in exurban areas that overlap with MPB habitat, and the current outbreak largely coincides with an increase in large forest fires (>400 ha) across the same habitats (Westerling et al. 2006, Maestas et al. 2011). These changes have introduced a substantial environmental change to habitats that support MPB, and as a result, current MPB occurrences may not reflect a species at equilibrium with its environment. This is one of the key assumptions of correlative niche models that can be problematic when applying modeling algorithms to novel temporal domains under future climate scenarios (Wiens et al. 2009, Araújo and Peterson 2012). Correlative niche models are also unable to account for evolutionary adaptations that may occur over time (Pearson and Dawson 2003). When projecting future responses of MPB to climate change, we can estimate future suitable habitat, but cannot forecast the effects of warming on host trees or how the beetle may respond to other rapidly changing environmental conditions (Bentz et al. 2010). We have high confidence in the modeled response of the beetle to 20th-century warming because the predictions are rooted in actual occurrences, but future projections should be interpreted cautiously.

Furthermore, there is an inherent uncertainty in the data used in this analysis. Improvements in global positioning systems (GPS), geographic information systems (GIS), and aerial detection techniques have reduced the uncertainty of recent outbreak polygons, but there are still geographic errors in the data. For example, rates of omission—when a category other than “no damage” is found on the ground but no observation was recorded on the aerial survey map—can be as high as 35% in lodgepole pine forests (Johnson and Ross 2008). The historical MPB data set may have even higher error rates resulting from the process of georeferencing and digitizing old topographic quadrangles (Johnson and Ross 2008). For this analysis, we can reasonably expect that a 1-km pixel would encompass most of the uncertainty from the aerial survey; however, this geographic error may result in an MPB occurrence correlating with different conditions than the species experienced in the environment.

The climate data products and analytical programs used in this study also contain varying levels of uncertainty. For example, the interpolative and downscaling techniques used by ClimateWNA introduce uncertainty into the data, and future climate forecasts retain internal model variability (Beaumont et al. 2007, Wang et al. 2012). Additionally, there may be unknown errors associated with the software used in the analysis. These errors are likely not additive, but augment one another in synergistic fashion. Through careful calibration and a deliberate consideration of this uncertainty, we were able to reduce some of the uncertainty in our modeling, but model predictions—particularly forecasts into future domains—should be interpreted as estimates and geographic approximations, not certainties.

CONCLUSIONS

We have demonstrated that three common correlative niche models provide fairly reliable estimates of species response to climate change. While studies utilizing correlative models should always be aware of the assumptions and limitations of the models, correlative niche models can be an effective and reliable tool in predicting change across temporal domains (Pearson and Dawson 2003, Araújo and Peterson 2012). Simpler algorithms, like the GLM, may provide more general predictions that project better across temporal domains and reduce omission error.

Our research reveals a significant expansion of climatically suitable area for MPB over the past half-century in both geographic and climatic space; however, projected warming may reduce climatic suitability under future climate scenarios. Furthermore, our results suggest that the recent MPB epidemic showed a different climatic signature than historical outbreaks as drought drove model predictions more so than temperature increases. The shift of climatically suitable habitats into higher elevations is expected to continue in the future, and this shift threatens sensitive high-elevation ecosystems such as those dominated by whitebark pine. This shift may also reflect the destabilization of currently suitable habitats at lower elevations (Jewett et al. 2011). Our results confirm that climate change has driven a range expansion of MPB and corroborates past research on the effects of climate on the spatial distribution of MPB outbreaks.

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