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Effect of increasing temperatures on the distribution of spruce beetle in Engelmann spruce forests of the Interior West, USA



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ABSTRACT

The spruce beetle (*Dendroctonus rufipennis*) is a pervasive bark beetle indigenous to spruce (*Picea* spp.) forests of North America. In the last two decades outbreaks of spruce beetle have increased in severity and extent. Increasing temperatures have been implicated as they directly control beetle populations, potentially inciting endemic populations to build to epidemic (outbreak) proportions. However, stand structure and composition conditions will also influence beetle populations. We tested the effect of temperature variables (minimum cool season temperature and maximum warm season temperature), and habitat controls (structure and composition) on the prediction of spruce beetle presence/absence for 4198 Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) plots in the Interior West, USA. Predictions were applied to three global climate models (GCMs) for three time periods. While both temperature variables were important, results suggested habitat variables (spruce basal area and spruce composition) were more influential for the prediction of current beetle presence. Future beetle prevalence varied from 6.1% to 24.2% across GCMs and time periods. While both temperature variables increased over time, in some cases the increases were not proportional, which led to differential predictions of beetle population prevalence in space and time among GCMs. Habitat variables that characterized current spruce beetle susceptibility changed as future temperatures increased. Application of results to forest management will include adjusting monitoring programs to reflect the potential increased overall prevalence of the beetle, and modifying the characterization of high hazard spruce stands to reflect increasing beetle presence in stands with lower basal area and spruce composition than currently observed.

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1. Introduction

Spruce beetle (*Dendroctonus rufipennis* Kirby) is a native species endemic to spruce (*Picea* spp.) forests across North America. In western North America, spruce beetle outbreaks have been increasing in extent and severity over the last two decades (Dymerski et al., 2001; Berg et al., 2006; Garbutt et al., 2006; Raffa et al., 2008; DeRose et al., 2011; DeRose and Long, 2012), resulting in substantial spruce mortality and fundamental shifts in forest structure, composition and function (Veblen et al., 1991; Zhang et al., 1999; DeRose and Long, 2007). The recent increase in spruce mortality caused by the spruce beetle suggests conditions conducive for beetle populations to attain outbreak levels are becoming increasingly common (Bentz et al., 2010). The causes of growing spruce beetle activity in western US Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) forests have received relatively little attention

and are not entirely understood, however, both climatic variability and increasing habitat suitability have been implicated (Berg et al., 2006; Hansen et al., 2006; Bentz et al., 2010; DeRose and Long, 2012).

Spruce beetle populations most often exist at very low densities over large areas and periodically build to outbreak population levels that can cause high levels of tree mortality. Because spruce beetle needs a suitable host for reproduction its fundamental niche is necessarily constrained by the presence of spruce. However, the realized niche for spruce beetle can be defined as environmental conditions where they have been observed, regardless of population phase (e.g., endemic, incipient, or epidemic). The realized niche can be described by a combination of the temperature and habitat controls that drive developmental success and reproduction. For example, spruce beetle developmental rate is highest at relatively warm temperatures (Hansen et al., 2001) and a facultative prepupal diapause can be evaded when summer and fall temperatures are above a critical threshold (Hansen et al., 2011). Individuals that avoid prepupal diapause are able to complete their lifecycle in a single year (univoltine), an outcome that increases the

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probability for exponential population growth (Hansen and Bentz, 2003), ultimately increasing the risk of an outbreak (Bentz et al., 2010). The amelioration of minimum annual temperature can also potentially influence population growth through increased brood survival (Miller and Werner, 1987; Rousseau et al., 2012). Increases in minimum temperatures have been greater than increases in maximum temperatures over the past several decades (Easterling et al., 1997), and effects have been greater at high elevations (Diaz et al., 1997). These temperature trends result in high elevation habitats that are highly susceptible to temperature-driven population changes of several insect species, including spruce beetle (Bentz et al., 2010).

In addition to temperature, successful brood production is dependent on habitat conditions such as host trees and stands that exhibit particular structural and compositional characteristics conducive to spruce beetle population growth. Susceptible hosts and stands typically have the following attributes: (1) large individual trees (i.e., large surface area of phloem); (2) high density (i.e., strong competition); (3) a high proportion of spruce; and (4) vast expanses of spruce forest (Schmid and Frye, 1976; Hansen et al., 2010). The interactions between large contiguous areas of susceptible habitat and temperature increases are likely responsible for recent large-scale spruce beetle outbreaks (Berg et al., 2006; DeRose and Long, 2012) and increasing beetle presence in general, i.e., high pre-outbreak population levels (DeRose et al., 2009; DeRose and Long, 2012).

With rising temperature predicted as a consequence of global climate change (IPCC, 2007), increased future spruce beetle activity is likely (Bentz et al., 2010), and it is therefore imperative that we gain an enhanced understanding of areas within the Interior West with potential for increased population success. Indeed, although the effects of increasing spruce beetle activity on mortality in spruce forests for some regions has been severe, e.g., central and southern Utah, (Dymerski et al., 2001; DeRose and Long, 2007), the influence of climate change on potential spruce beetle distribution at a regional scale has not been thoroughly investigated.

Given the spruce beetle realized niche is defined by the combination of both climatic (i.e., temperature) and habitat variables, a niche-based modeling approach can be used to determine potential distributional shifts under future climate change scenarios. This approach has received widespread application in assessing the influence of global climate change on insect (e.g., Evangelista et al., 2011), plant (e.g., Keenan et al., 2011), and animal (Araújo et al., 2005), distributions. Generally, niche models assume the current realized climatic niche characterizes the future climatic niche, (i.e., niche conservation *sensu* Pearman et al., 2008). Based on this assumption, niche models that include both climatic and habitat variables could be manipulated to evaluate the effects of varying one variable while holding another constant. By pairing forecasted temperature change with current habitat conditions we have the opportunity to more effectively make spatially explicit predictions of future spruce beetle realized niche.

In this study, USDA Forest Service, Forest Inventory and Analysis (FIA) data are coupled with downscaled global climate data to predict current and future distributions of spruce beetle in spruce forests of the Interior West, USA. A niche-modeling approach is applied via an ensemble model to forecast future spruce beetle realized niche. Modeled outcomes are used to suggest habitat conditions where proactive spruce beetle monitoring and management can effectively be focused in the future. The goals are: (i) use an ensemble model to predict current and future spruce beetle habitat in the Interior West with habitat and climate data; and (ii) based on simulated climate data and current habitat conditions, test whether the spruce beetle realized niche will expand or contract under global climate change. We use the forecasted spruce beetle niche, in combination with current habitat data, to quantify

potential shifts in conditions that characterize future spruce forest susceptibility to spruce beetle.

2. Methods

2.1. Study area

The Interior West was defined as our study area and includes the following western US states: Arizona, Colorado, Idaho, Nevada, New Mexico, Montana, Utah, and Wyoming. We further refined our study area to include all spatially unique FIA periodic and annual inventory plots that included at least one Engelmann spruce >12.7 cm diameter at breast height over the period 1981–2008. Engelmann spruce forests in the Interior West extend from 32.71 N to the US–Canada border (49.00 N) and from 104.9 W to 117.14 W. Spruce range in elevation from 670 m at the northernmost locations to over 3600 m on the Colorado Plateau. Over such a large geographic area, climate varies widely, but generally the northernmost part of this range receives a majority of its precipitation during the winter from storm tracks originating in the Pacific Ocean (Mock, 1996) while the southernmost part can receive up to half its annual precipitation during the summer monsoon. However, the entire western US region exhibits strong locally coherent cycles of aridity that occur at multi-decadal time scales (Cook et al., 1999; Shinker et al., 2006).

The predictor data set included a unique combination of forest stand data from FIA plots (spruce beetle habitat data) (<http://fia.fs.fed.us/tools-data/>) and climate data (bioclimatic data) determined to be most influential for discerning spruce beetle presence in spruce forests. Latitude and longitude of FIA plots were used to derive potential bioclimatic variables from the WorldClim gridded climate data sets v 1.4 (Hijmans et al., 2005) (<http://www.worldclim.org>). In no case did more than one FIA plot fall within the same WorldClim grid cell. The FIA sampling design is characterized as a geographically unbiased, equal probability sample of field plots established on a hexagonal grid with each hexagon encompassing $\sim 2403 \text{ ha}^{-1}$ (Bechtold and Patterson, 2005). In the Interior West, the hexagon panel is divided into 10 equal interpenetrating, non-overlapping panels, where 10% per year are selected for sampling (McRoberts et al., 2005). Each plot consists of four non-overlapping subplots covering a total area of 0.4 hectare that were designed to characterize the forest condition (McRoberts et al., 2005). On each plot substantial forest mensuration data were collected including individual tree species, diameter and species, and was assigned a disturbance agent code that indicated the presence of bark beetles (i.e., whether there are spruce beetle in the tree, or a spruce that had been killed by spruce beetle recently, i.e., last five years). Therefore, the dependent variable in this study, the presence/absence of spruce beetle, was determined by assessing whether any tree on each plot was: (1) spruce; and (2) had a disturbance agent code indicating bark beetle activity on the tree (not necessarily mortality) within the last 5 years for the period 1981–2008, which we interpreted as the presence of spruce beetle. Two distinct advantages were conferred by this approach: (1) presence/absence data were determined in the field so that absence data did not need to be synthetically generated during modeling; and (2) the presence/absence data occurred entirely within the known range of spruce forests, which necessarily limited the analysis to the spruce beetle fundamental niche *sensu* Sauer et al. (2012).

2.2. Spruce beetle habitat data

Variables that described spruce beetle habitat were calculated from FIA data for unique plots with at least one spruce present in the overstory (diameter at breast height >12.7 cm). This resulted

Table 1

Independent variables for Engelmann spruce plots from the Interior West Forest Inventory and Analysis data ($n = 4198$), and current WorldClim bioclimatic variables used for the prediction of spruce beetle presence/absence.

Variable	Mean (SD)	Min	Max
Stand basal area ($\text{m}^2 \text{ha}^{-1}$)	11.93 (5.58)	0.32	40.16
Percent Engelmann spruce composition	0.40 (0.29)	0.01	1.0
Quadratic mean diameter > 10 cm	16.04 (4.45)	10.09	48.99
Stand density index ratio	0.84 (0.17)	0.16	1.0
Minimum temperature of coldest month (C)	-15.17 (2.7)	-21.8	-6.2
Maximum temperature of warmest month (C)	21.85 (2.37)	15.2	29.6

in 4198 plots measured over the period 1981–2008 to conduct the analysis. Independent variables were calculated for each plot from forest stand attributes that have been shown to characterize suitable habitat for non-outbreak (i.e., endemic) populations of spruce beetle to persist, and potentially build (Schmid and Frye, 1976; Hansen et al., 2010). These variables included: plot basal area ($\text{BA m}^2 \text{ha}^{-1}$); percent spruce (%ES, percent by BA); and quadratic mean diameter greater than 10 cm (QMD). The spruce beetle hazard rating (Schmid and Frye, 1976) indicates susceptible stands have some combination of high densities ($>14 \text{ m}^2 \text{ha}^{-1}$ BA), a large percentage of spruce ($>65\%$), and large average spruce diameters ($>40 \text{ cm}$ mean dbh). In addition, we calculated the stand density index ratio (SDIr), which characterizes individual stands based on their structure across a gradient of complex (uneven-aged) to simple (even-aged) structures (Ducey, 2009, Table 1).

2.3. Bioclimatic data

The current bioclimatic data represented interpolated monthly weather station measurements averaged for the period 1950–2000, which did not overlap entirely with our habitat data observations (1981–2008). Rather than reducing our empirical data, we included observations from 2001 to 2008 when modeling the current bioclimatic conditions, because averaged measurements are likely to fundamentally change over this short period. We used future predicted bioclimatic data based on the 4th IPCC A2a scenario (IPCC, 2007), which reflects increases of CO_2 emissions due to high population growth and increased energy use. The spatial resolution of all gridded bioclimatic data was $\sim 1 \text{ km}^2$. The Delta Method-downscaled climate predictions from three different atmosphere–ocean global climate models were used: (1) Hadley Center for Climate Prediction, Hadley Centre Coupled Model 3 (HADCM3, <http://www.metoffice.gov.uk/research/modelling-systems/unified-model/climate-models/hadcm3>), (2) Canadian Center for Climate Modeling and Analysis, Coupled Global Climate Model 2 (CGCM2, <http://www.ec.gc.ca/ccmac-cccma/default.asp?lang=En&n=40D6024E-1>), and (3) the Commonwealth Scientific and Industrial Research Organization, Atmospheric Research Mark 2 (MK2) (Hirst et al., 1996, 2000) at three different time steps (2020, 2050, and 2080).

2.4. Species distribution modeling

Extensive, preliminary Biodiversity Modeling (BIOMOD, see below) was performed before we chose our final predictor variables, and indicated that, of the 19 available bioclimatic variables, two were ultimately successful in the prediction of spruce beetle presence/absence, minimum temperature of coldest month (minT), and maximum temperature of the warmest month (maxT). Not surprisingly, these two bioclimatic variables presumably described the known controls on spruce beetle development and survival, i.e., warm summer temperatures (e.g., Hansen et al., 2011) and high

winter minimum temperatures (e.g., Miller and Werner, 1987). Bioclimatic variables from each GCM, time step, and their associated FIA plot were extracted from the WorldClim data set. The combined habitat and bioclimatic predictor variable data were subjected to correlation analysis to ensure no redundancy in highly correlated (defined as $r > 0.6$) variables existed. While elevation is commonly used in species distribution modeling (Hof et al., 2012), as it effectively proxies for environmental conditions, e.g., radiation, that might effect species distributions, it varied widely within the FIA data set. Furthermore, both maxT ($r = 0.83$) and minT ($r = 0.65$) were highly correlated with elevation in the data set, so it was not included in the predictor data set.

Because multiple modeling methods can yield widely varying results, ensemble models have been suggested as an approach to simultaneously take into account results from multiple modeling scenarios (Thuiller, 2003; Araújo and New, 2007). We used the niche-based BIOMOD ensemble model in the R computing environment (R development core team, Thuiller, 2003) to make ensemble predictions and forecasts of the spruce beetle realized niche based on current presence/absence data. This approach assumes niche conservatism (Pearman et al., 2008), i.e., the factors controlling the species niche will remain similar for future realizations of spruce beetle niche. The seven individual niche-based modeling approaches we used were: artificial neural networks; generalized additive model; generalized boosting model; generalized linear model; multivariate adaptive regression splines; flexible discriminant analysis; and random forests. To evaluate model predictions we performed a threefold cross-validation after splitting the data into training (70%) and testing sets (30%) using a random partition (Araújo et al., 2005) before running a final model incorporating all the data. Model results were evaluated using area under the curve (AUC) from a receiver operating characteristic and the true skill statistic (TSS) because of their known independence from prevalence in the data set (Allouche et al., 2006). The AUC score can range from 0.5 to 1.0 and were evaluated as follows: AUC: $1 > \text{good} > 0.8 > \text{fair} > 0.7 > \text{poor}$. The TSS statistic can range from -1 to 1 where 0 indicates no skill and was evaluated as follows: TSS: $1 > \text{good} > 0.6 > \text{fair} > 0.4 > \text{poor}$. We also report the sensitivity and specificity of the model (Fielding and Bell, 1997). At each plot, future predictions for each GCM (3) and each time step (3) were generated from probabilities of occurrence for each of the seven modeling approaches, transformed to presence/absence using the AUC, and averaged to get the ensemble consensus mean.

2.5. Determining future spruce beetle niche

Unlike other niche-based modeling applications, our approach necessarily constrained the spatial range of observations to the current range of spruce forests (spruce beetle host). Although it is possible that climate change could influence the spruce realized niche over the analysis time frame (current–2080) via regeneration at novel sites or mortality on at-risk sites (Rehfeldt et al., 2006), no empirical analysis has documented actual Engelmann spruce range

Table 2

Mean independent variable importance and SD among the seven models in the ensemble (see methods).

Variable	Mean Importance	(SD)
Percent Engelmann spruce composition	0.4975	(0.2002)
Stand basal area ($\text{m}^2 \text{ha}^{-1}$)	0.4957	(0.2458)
Stand density index ratio	0.1274	(0.0693)
Maximum temperature of warmest month (C)	0.1197	(0.1662)
Quadratic mean diameter > 10 cm	0.1100	(0.2253)
Minimum temperature of coldest month (C)	0.1094	(0.1464)

expansion or contraction. Therefore, we made a reasonable and key assumption that the realized niche will remain similar to current conditions. This approach allowed us to hold habitat variables constant while the global climate change-driven bioclimatic predictors were varied by GCM and time step. In other words, we could directly assess the influence of temperature change on spruce beetle distribution within the current geographic range of spruce in the Interior West and among the distribution of current spruce habitat characteristics, which nearly approximate population-level estimates for Interior US as a result of the sampling design (McRoberts et al., 2005).

3. Results

Ensemble model performance was reasonable based on both the ensemble mean AUC (0.77) and TSS (0.458). The model correctly predicted 198 of the 250 plots observed to have spruce beetle (i.e., sensitivity = 0.79), and correctly predicted 3871 of the 3948 observation plots without spruce beetle (i.e. specificity = 0.98). Factors important in the prediction of the presence/absence of spruce beetle included both habitat and climate variables (Table 2). While the bioclimatic variables, minimum cold season temperature (minT) and maximum warm season temperature (maxT) were important predictors, the habitat variables %ES and BA were the most influential in the model. Excellent spatial coherence was found between observed spruce beetle presence and ensemble model-predicted locations in the Interior West (Fig. 1). In particular, there was good agreement between the higher occurrence of spruce beetle on FIA plots south of $\sim 42^\circ$ latitude and the modeled observations (Fig. 1). Observational data indicated spruce beetle occurred on 5.9% of the total FIA plots whereas the ensemble

model predicted presence on 6.1% of plots. The vast majority of Engelmann spruce plots with spruce beetle, both observed and predicted, occurred in Colorado and Utah (Fig. 1).

All future projections of spruce beetle presences in FIA plots showed an increase from the current prediction of 6.1% that ranged from 6.2% to 6.6% for 2020, 5.6–10.8% for 2050, and 8.1–24.2% by the end of the analysis period 2080 (Fig. 2). The HADCM3 was the most conservative model, followed by the MK2; the largest increase in predicted spruce beetle occurred under the CGCM2 (24.2% by 2080). In all cases, the increase in future spruce beetle presence was associated with increasing minT and maxT (Fig. 3). While future increases of spruce beetle presence were manifest under all GCMs, they varied by GCM, which was a direct result of the non-proportionality of temperature increases among GCMs (Fig. 4). For example, the HADCM3 predicted higher presence over time in Colorado and Utah, which reflected a substantial increase in maxT compared to minT by 2080 (Fig. 4). In comparison, the CGCM2 GCM also predicted large increases in spruce beetle at intermediate latitudes and longitudes, i.e., Wyoming and Idaho (Fig. 2), which was the result of a strong increase in minT relative to maxT, particularly in 2080 (Fig. 4). While the MK2 GCM predicted increased spruce beetle further north near the US-Canadian border (Fig. 2), this appeared to reflect a proportional increase in minT/maxT by 2080 (Fig. 4).

Because habitat variables were held constant in the analysis, the changes in BA and %ES habitat conditions associated with increasing spruce beetle presence over time were the result of increasing susceptibility due to warming conditions. In other words, spruce habitats with low susceptibility to spruce beetle during the period 1981–2008 are now more susceptible because of warming. The median and range of BA for spruce plots forecasted as suitable for spruce beetle showed a general decreasing pattern over time with median values decreasing from $\sim 19 \text{ m}^2 \text{ ha}^{-1}$ in 2020 to $\sim 15 \text{ m}^2 \text{ ha}^{-1}$ in 2080 averaged across GCMs (Fig. 5). Similarly, the median and range of %ES for suitable spruce beetle plots also exhibited a decrease over time (Fig. 6), and median %ES varied between GCMs in 2080 from $\sim 60\%$ for MK2 to 75% in HADCM3. The results for the independent variables of lower importance (i.e., SDIr, and QMD, Table 1) did not change perceptibly over time or GCM (data not shown).

4. Discussion

We found the current spruce beetle realized niche could be reasonably modeled using a combination of habitat and climate variables determined *a priori* (Saupe et al., 2012). This result is consistent with contemporary understanding of bark beetle dynamics, which suggest both habitat and climate exhibit control on population dynamics, but the effect, timing, and interactions depend on the current population level of the insect (i.e., endemic, incipient, or epidemic, Raffa et al., 2008; Bentz et al., 2010). It is important to note that our results are not intended to explicitly portend future spruce beetle outbreaks, and that our future predictions were statistically dependent on stand and climate conditions that affected spruce beetle presence/absence between 1981 and 2008. The results, however, are relevant in the context of whether or not spruce forest will become increasingly suitable habitat. Additionally, population level was not taken into account in the analysis as has been done in other studies (Hansen et al., 2006; DeRose and Long, 2012).

The geographically unbiased sample design under which the majority of the FIA data were collected adds perspective to the true (i.e., measured) impact of spruce beetle in the Interior West. Given the dire warnings of increasing spruce beetle activity in the western US it is telling to note that between 1981 and 2008 only

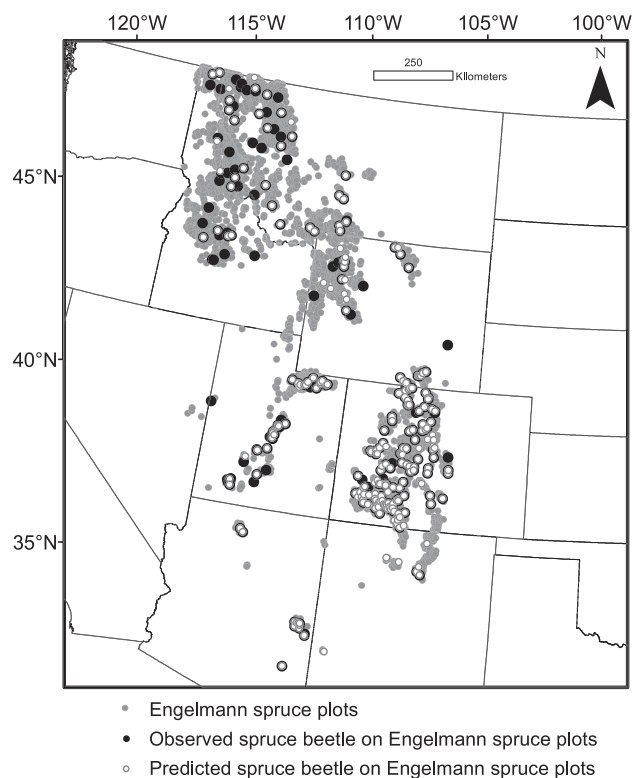


Fig. 1. Engelmann spruce plots without spruce beetle (gray circles) and Engelmann spruce plots with observed spruce beetle (black circles) on Forest Inventory and Analysis plots in the Interior West for the period 1981–2008. White circles outlined in black indicate Engelmann spruce plots with observed spruce beetle presence and also positively modeled as spruce beetle presence.

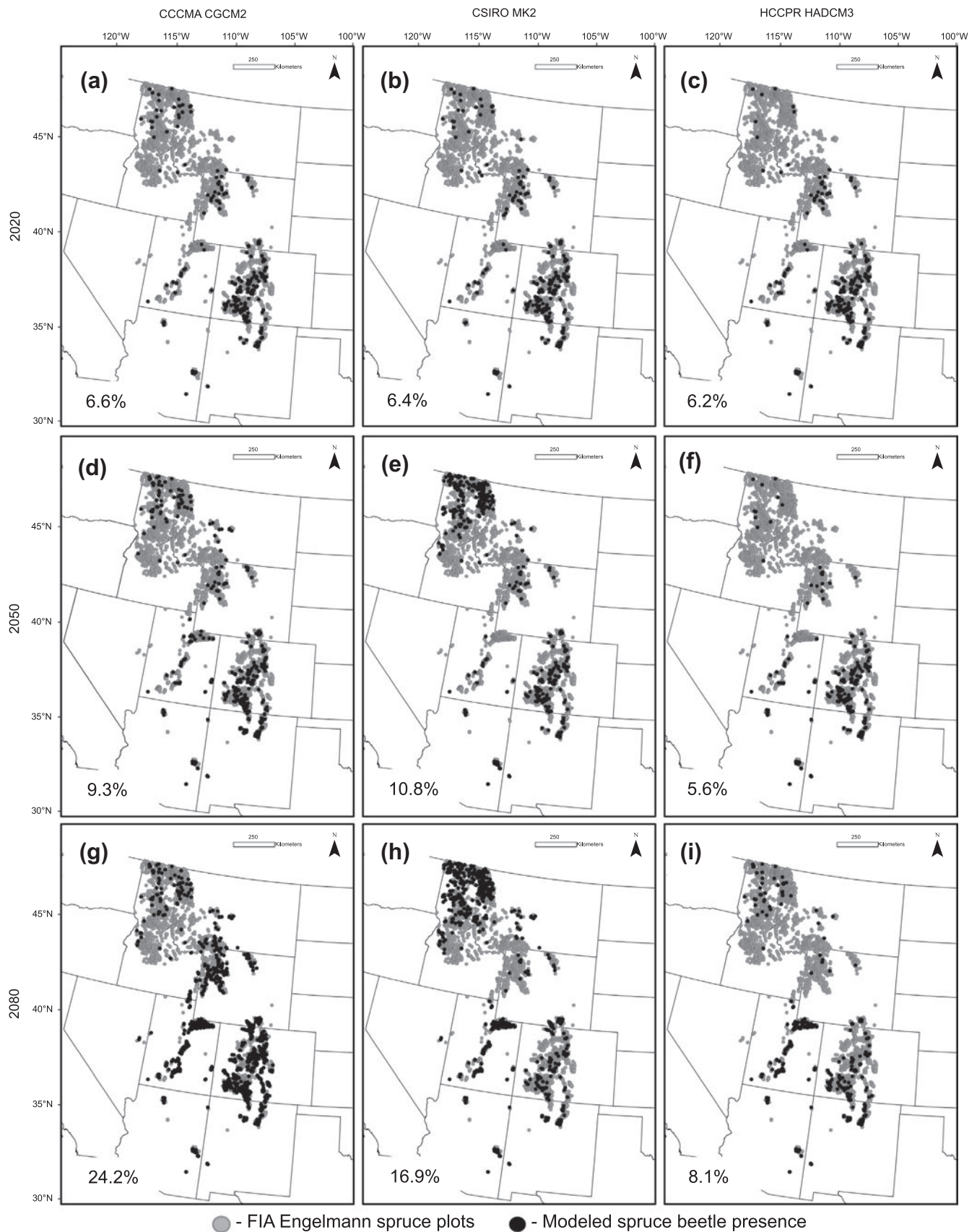


Fig. 2. Interior West Forest Inventory and Analysis Engelmann spruce plots predicted as unsuitable for spruce beetle (gray circles), and plots predicted to be suitable for spruce beetle (black circles) under three climate change scenarios (HADCM3, CGCM2, MK2) at three time periods (2020, 2050, and 2080). Numbers in lower left corner indicate percentage of plots suitable for spruce.

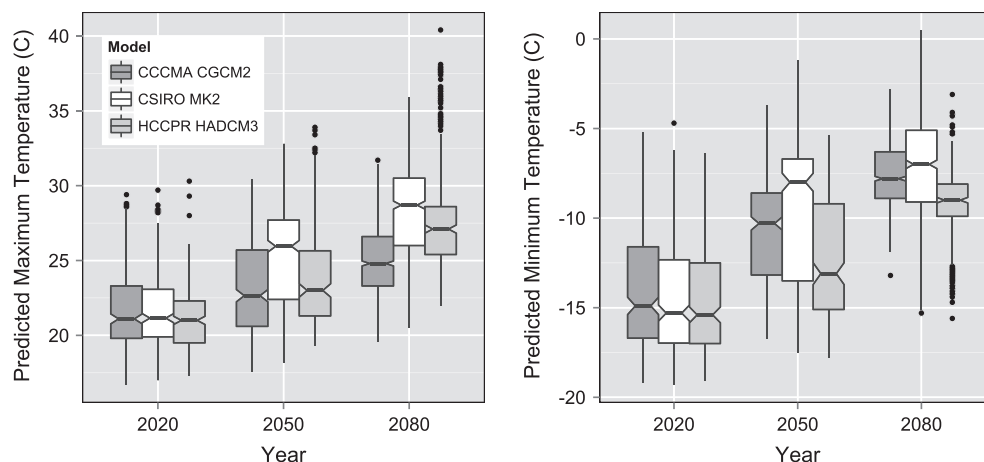


Fig. 3. Boxplots showing the median, interquartile range, and outliers of (a) minimum temperature (minT) and (b) maximum temperature (maxT) on Engelmann spruce plots predicted to be susceptible to spruce beetle under three climate change scenarios (HADC3, CGCM2, MK2) and at three time periods (2020, 2050, and 2080). The upper and lower hinges correspond to the 1st and 3rd quartile, whiskers extend from the hinges (above and below) to 1.5 times the inter-quartile range and points beyond the whisker are outliers. Non-overlapping notches suggest differences between medians.

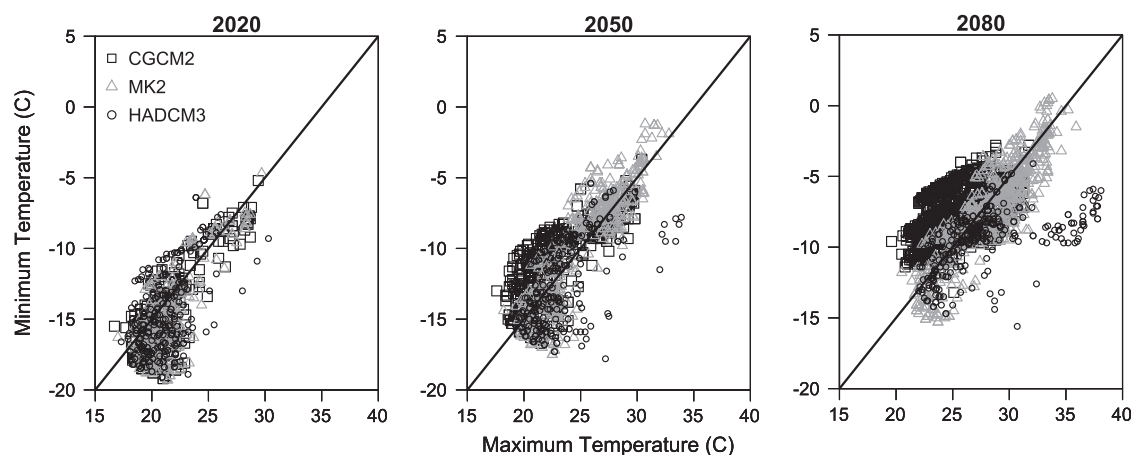


Fig. 4. Scatterplots showing the non-proportional shifts in increasing temperatures on Engelmann spruce plots predicted to be susceptible to spruce beetle under three climate change scenarios (HADC3, CGCM2, MK2) and at three time periods (2020, 2050, and 2080).

5.9% of the inventoried spruce plots were infested, and by 2020 on average just over 6% of spruce forests were predicted to be suitable hosts. In other words, very little difference occurred between inventoried spruce beetle activity and that modeled for 2020, which bolsters support for our use of the 2001–2008 data although it did not overlap temporally with current bioclimatic data (1950–2000). By 2080 the most extensive predictions of spruce beetle change, which incorporated large temperature increases, resulted in, at most, 24.2% of spruce forests suitable for spruce beetle. Because a much larger proportion of the total spruce landscape is predicted to become suitable habitat, there could be an increased likelihood of outbreak initiation due to increased windthrow and avalanche events, which could subsequently spread to areas predicted as unsuitable (DeRose and Long, 2012). Another possibility is that by holding habitat constant, we have revealed the extent to which spruce beetle migration might occur based strictly on temperature change. Future work that allows beetle habitat to change at current or elevated temperatures might indicate increased migration potential and possibly larger areas of susceptible Engelmann spruce forests.

The climate variables were important, and necessary to predict future spruce beetle presence, but habitat variables exerted more

influence in the model. Therefore, while temperatures may directly control beetle population dynamics, the presence of suitable habitat, and more importantly, the structure and composition of that habitat, were more influential in determining whether or not spruce beetle will occur on a particular plot. In other words, regardless of temperature conditions, suitable hosts must be available for spruce beetle to infest. These results highlight the importance of including host tree habitat in predictive models of forest insects in a changing climate (see Bentz et al., 2010). The results also corroborate many decades of work that has indicated that mature, dense, high composition spruce stands are most susceptible to spruce beetle (Schmid and Frye, 1976; Reynolds and Holsten, 1994; Berg et al., 2006; DeRose and Long, 2012). To rear a successful brood sufficient substrate (i.e., spruce phloem) is necessary and spruce beetle is more likely to find this on bigger trees (larger QMD). When occurring in a sufficiently dense (high BA) or relatively pure stand (high %ES), spruce beetle has a higher likelihood of finding a host. Furthermore, patches of dense stand conditions provide spruce with reduced host vigor and subsequent reduced defense mechanisms that facilitate outbreak initiations. The predicted increases in growing season maxTs (Fig. 3), and therefore increased vapor pressure deficit, might also result in increased

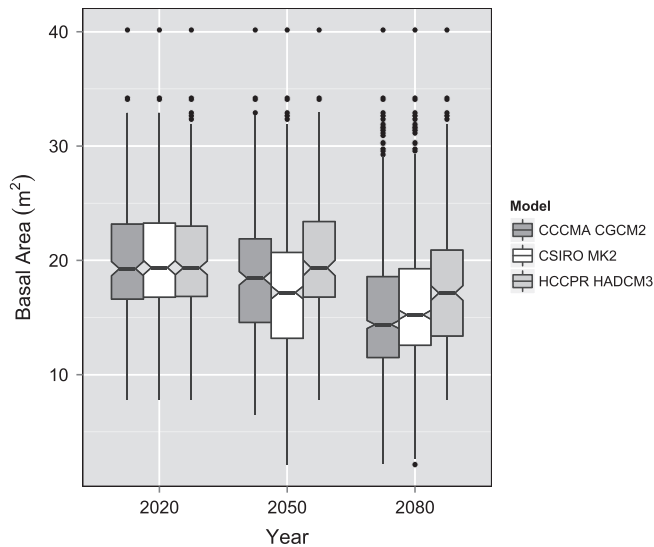


Fig. 5. Boxplots showing the median, interquartile range, and outliers for basal area of Engelmann spruce plots predicted to be susceptible to spruce beetle under three climate change scenarios (HADCM3, CGCM2, MK2) and at three time periods (2020, 2050, and 2080). The upper and lower hinges correspond to the 1st and 3rd quartile, whiskers extend from the hinges (above and below) to 1.5 times the inter-quartile range and points beyond the whisker are outliers. Non-overlapping notches suggest differences between medians.

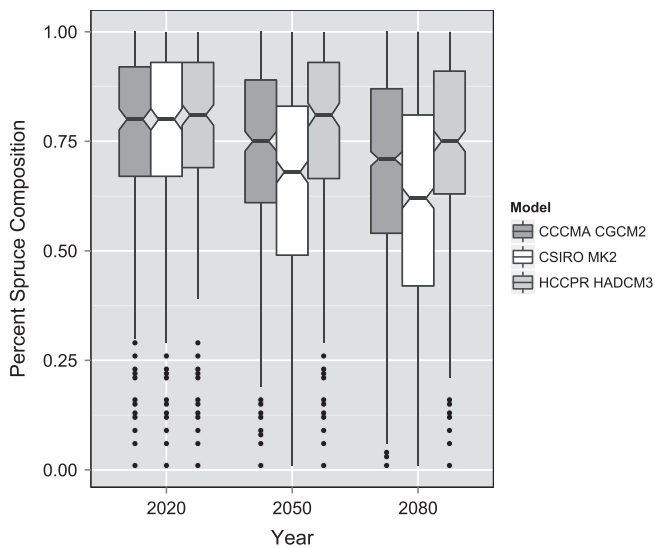


Fig. 6. Boxplots showing the median, interquartile range, and outliers for percent spruce composition of plots predicted to be susceptible to spruce beetle under three climate change scenarios (HADCM3, CGCM2, MK2) and at three time periods (2020, 2050, and 2080). The upper and lower hinges correspond to the 1st and 3rd quartile, whiskers extend from the hinges (above and below) to 1.5 times the inter-quartile range and points beyond the whisker are outliers. Non-overlapping notches suggest differences between medians.

drought-stress in spruce forests, potentially exacerbating low vigor conditions. Future predictions, however, suggest that increased temperatures will allow spruce beetle to be successful in stands of lower BA and %ES, stand conditions that may not promote landscape wide outbreaks despite the climatic release on spruce beetle population dynamics.

Spatial inconsistencies of predicted spruce beetle presence between GCMs was likely primarily due to the non-proportional changes of minT and maxT over time (Fig. 4). Specifically, predicted increases in minT are likely to result in much higher brood survival

during the winter, especially as historic winter cold spikes become rare or obsolete (Rousseau et al., 2012). The effects of increasing minT was particularly pronounced in the CGCM2 scenario where future spruce beetle presence increased virtually throughout the Interior West, but was particularly acute at higher latitudes (Fig. 2). Similarly, the observed increases in maxT will result in larger percentages of beetles potential shifting from semivoltinism to univoltinism, which would increase the number available to infest spruce, assuming the presence of host. Bentz et al. (2010) observed similar spatial and temporal patterns of increased spruce beetle univoltinism across the western US using the CGCM2 scenario. Increased spruce beetle presence predicted by the HADCM3 GCM in the high-elevation forests of Utah and Colorado (Fig. 2) likely indicated the influence of maxT on voltinism because of the non-proportional increase in maxT by 2080 (Fig. 4). The combined, relatively proportional, increase in both minT and maxT was the ultimate driver of the predicted increase in spruce beetle susceptibility for the MK2 GCM.

While the overall increase in potential spruce beetle habitat was not striking, the spatial distribution was much more concerning (Fig. 2). Lower latitude and, to a lesser degree, high-elevation spruce (i.e., the four corners states, Arizona, Colorado, New Mexico, and Utah) exhibited the highest percent increase in predicted spruce beetle habitat across all GCMs in 2020. However, by 2050 the variation in minT and maxT (Figs. 3 and 4), and therefore GCM predictions, started to differ (Fig. 2). The modest increase in temperatures under the HADCM3 model resulted in modest increases in spruce beetle habitat, which occurred almost entirely at lower latitudes, higher elevations and higher relative maxT. In contrast, larger temperature increases predicted by the MK2 model resulted in a substantial increase in potential spruce beetle habitat at northern latitudes in addition to the spruce forests of the four corners. The CGCM2 model predicted the largest increase in both minT and maxT (Fig. 3) and therefore the largest percentage of potential spruce beetle habitat. While the percentage of susceptible plots under the CGCM2 scenario was highest at low latitudes, this GCM predicted more plots suitable for spruce beetle overall, and predicted a larger number at mid-latitudes than either of the other two GCMs.

This study marks a substantial advancement in the modeling of spruce beetle activity at a regional scale. The predictive ability is particularly good when considering the model was constrained to nearly two decades of *in situ* empirical observations of presence/absence data that described the spruce beetle realized niche. It is unlikely a comparable observational data set exists to evaluate the influence of warming on spruce beetle populations. Furthermore, no spatial averaging of dependent or independent data was done, and no proxies for presence/absence were used, so results reflect actual variability in measured attributes. For example, most species distribution studies rely solely on remotely sensed presence data (e.g., Aerial Detection Survey, modeled presence, etc.), proxies for species presence such as a temperature regime for insects, or other presence data collected at coarse resolutions that: (1) have limited or no quality control to determine the actual presence of beetles, and; (2) require the generation of random pseudo-absences. In comparison, part of the rigorous FIA quality control protocol involves revisiting 10% of the sample plots annually (Bechtold and Patterson, 2005), which ought to assuage concerns regarding positive identification of bark beetle affected trees or repeatability in the data set. Additionally, false negatives associated with generating pseudo-absences were avoided.

Our approach also differed from other species distribution models in that locations outside the current geographic distribution of Engelmann spruce were not modeled. Because predicted spruce beetle habitat was contingent upon both bioclimatic

variables and habitat conditions necessary to support beetle populations, we were necessarily limited to the current geographic extent of spruce in the FIA database and their contemporary conditions (i.e., spruce beetle habitat data). While seemingly a shortcoming, the strength of this approach was that the direct influence of temperature on potential spruce beetle habitat could be isolated from habitat, and areas of potentially increasing susceptibility identified. Future warming will likely also eventually affect the distribution of spruce, but it is unlikely to alter the outcomes of this analysis. First, species distribution changes in response to climate change are likely to be lagged, especially for very long-lived species such as spruce. Although new spruce stands may establish in novel places in the next ~80 years, they would not become suitable spruce beetle habitat in that time period (Veblen et al., 1994). Second, in comparison to some of our GCM predictions for spruce beetle, recent envelope modeling of the geographic distribution of its host, Engelmann spruce, indicated upward (elevation) and poleward (northern) shifts (Rehfeldt et al., 2006); however, to date no empirical analyses have documented any expansion or contraction of Engelmann spruce forests. Similarly, no modeling of potential demographic changes to Engelmann spruce forests (e.g., spruce beetle habitat data) as a result of warming have been conducted. Because the spruce beetle niche is necessarily restricted to spruce forests, a complete understanding of the differential response to warming for both the host and insect species warrants future research.

We showed a niche-based species distribution model could be used with empirical data to predict the current and future potential habitat for spruce beetle in the Interior West. While this represents an important first step, fine-scale resolution data sets, such as FIA, could be combined with larger scale data, e.g., the Aerial Detection Survey data, to better characterize current spruce beetle distribution regionally. Given the nature of spruce beetle outbreaks to build locally before spreading (DeRose and Long, 2012), the combination of these two scales might provide increased accuracy and resolution for predicting spruce beetle presence in the Interior West. We modeled known structural and compositional constraints of host tree habitat and direct constraints of temperature on beetle population success using average maximum and minimum temperatures. Further refinement in predictive capability is likely possible by adding temperature-dependent process-based models of spruce beetle population success (Hansen et al., 2001; Hansen et al., 2011), that incorporate species-specific phenological constraints (Morin and Thuiller, 2009; Buckley et al., 2011). We acknowledge that other factors including host tree defenses, community associates and the spatial nature of host trees may also play a role in outbreak dynamics, although information sufficient for inclusion in a predictive model is not available.

5. Management implications

Factors identified here that are linked to potential future increases in spruce beetle presence can directly inform forest management that seeks to maintain or promote spruce forests in the Interior West. In particular, the results indicate characteristics of Engelmann spruce forests at risk for spruce beetle infestation under warming conditions. Once identified, proactive management employing monitoring or mitigation of spruce beetle activity can be implemented. Specifically, as temperature increases (both minT and maxT), more area of Engelmann spruce forest will become suitable spruce beetle habitat, and the structural constraints to spruce beetle infestation, i.e., BA, and compositional constraints, i.e., %ES, will be lowered. These insights can be incorporated into sustainable forest management by modifying monitoring protocols and the timely initiation of mitigation strategies.

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