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

R. Justin DeRose [a,*], Barbara J. Bentz [b], James N. Long [c], John D. Shaw [a]

[a] Forest Inventory and Analysis, Rocky Mountain Research Station, 507 25th Street, Ogden, UT 84401, United States
[b] Rocky Mountain Research Station, 1200 E. 800 N., Logan, UT 84321, United States
[c] Department of Wildland Resources and Ecology Center, Utah State University, 5230 Old Main Hill, Logan, UT 84322-5230, United States

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ABSTRACT

The spruce beetle (*Dendoctronus 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

* Corresponding author. Tel.: +1 801 625 5795; fax: +1 801 625 5723.
E-mail addresses: rjderose@fs.fed.us (R.J. DeRose), bbentz@fs.fed.us (B.J. Bentz), james.long@usu.edu (J.N. Long), jdshaw@fs.fed.us (J.D. Shaw).

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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 ~2403 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* Saupe 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