

Climate influences on whitebark pine mortality from mountain pine beetle in the Greater Yellowstone Ecosystem

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Abstract. Extensive mortality of whitebark pine, beginning in the early to mid-2000s, occurred in the Greater Yellowstone Ecosystem (GYE) of the western USA, primarily from mountain pine beetle but also from other threats such as white pine blister rust. The climatic drivers of this recent mortality and the potential for future whitebark pine mortality from mountain pine beetle are not well understood, yet are important considerations in whether to list whitebark pine as a threatened or endangered species. We sought to increase the understanding of climate influences on mountain pine beetle outbreaks in whitebark pine forests, which are less well understood than in lodgepole pine, by quantifying climate–beetle relationships, analyzing climate influences during the recent outbreak, and estimating the suitability of future climate for beetle outbreaks. We developed a statistical model of the probability of whitebark pine mortality in the GYE that included temperature effects on beetle development and survival, precipitation effects on host tree condition, beetle population size, and stand characteristics. Estimated probability of whitebark pine mortality increased with higher winter minimum temperature, indicating greater beetle winter survival; higher fall temperature, indicating synchronous beetle emergence; lower two-year summer precipitation, indicating increased potential for host tree stress; increasing beetle populations; stand age; and increasing percent composition of whitebark pine within a stand. The recent outbreak occurred during a period of higher-than-normal regional winter temperatures, suitable fall temperatures, and low summer precipitation. In contrast to lodgepole pine systems, area with mortality was linked to precipitation variability even at high beetle populations. Projections from climate models indicate future climate conditions will likely provide favorable conditions for beetle outbreaks within nearly all current whitebark pine habitat in the GYE by the middle of this century. Therefore, when surviving and regenerating trees reach ages suitable for beetle attack, there is strong potential for continued whitebark pine mortality due to mountain pine beetle.

Key words: climate change; *Dendroctonus ponderosae* Hopkins; forest disturbance; Greater Yellowstone Ecosystem; logistic regression; *Pinus albicaulis*; *Pinus contorta* var. *latifolia*.

INTRODUCTION

Globally, there is evidence that climate change during the last several decades has affected natural systems (Rosenzweig et al. 2008, IPCC 2014). Extensive and severe tree mortality, linked to climate change, has occurred on all continents (Allen et al. 2010), and biotic disturbance agents are often key components of this mortality. Recent outbreaks by bark beetles have resulted in >11 million hectares of tree mortality in western North America (Meddens et al. 2012) and have been associated with warm and dry conditions (Bentz et al. 2010, Weed et al. 2013). Given projections of future warming, there is strong potential for increases in insect-induced tree mortality in the future (Bentz et al. 2010).

Large-scale mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks have historically been relatively uncommon and short-term in whitebark pine (*Pinus albicaulis*) forests (Logan et al. 2010) because these high-elevation forests were typically outside the beetle's thermal limits of development and cold tolerance (Amman 1973). However, during the 2000s, widespread outbreaks occurred in whitebark pine stands across the western USA (Gibson 2006) with particularly severe tree mortality in the Greater Yellowstone Ecosystem (GYE), where 82% of catchments containing whitebark pine experienced significant tree mortality (Macfarlane et al. 2013). The recent outbreak in the GYE caused whitebark pine mortality of greater spatial extent and severity than any previously recorded event for this host species (Logan et al. 2010).

Whitebark pine is a keystone and foundation species of high-elevation forests (Tomback et al. 2001). Whitebark pines promote community diversity through production

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of highly nutritious seeds, which are a food source for grizzly bears (*Ursus arctos horribilis*) and other animals (Tomback et al. 2001). Whitebark pine seedlings are able to establish in conditions too harsh for other tree species (Tomback and Linhart 1990, Tomback et al. 1993), and mature whitebark pine trees then provide shelter from wind and ice abrasion, allowing less hardy species to establish (Callaway 1998). Whitebark pines also regulate snowmelt, stabilize rocky soils, and reduce soil erosion (Arno and Hammerly 1984, Farnes 1990, Hann 1990, Tomback et al. 2001).

Because of the recent extensive tree mortality and continuing threats that include climate change, white pine blister rust caused by the nonnative invasive fungus *Cronartium ribicola*, and the legacy of fire exclusion, whitebark pine was recommended for listing as a threatened or endangered species (USFWS 2011). Climate influences on mountain pine beetles (e.g., Logan et al. 2010) was a major reason for the finding (USFWS 2011). However, the climatic drivers of the recent outbreak and the potential for future events of this magnitude are not well established (USFWS 2011).

Mountain pine beetle is a native insect that reproduces within the main stems of pines. Adult females select potential hosts, enter the phloem, attract mates, and oviposit. The brood feed on phloem and adult-vectored fungi as larvae, pupate, develop into teneral adults, emerge, and seek new hosts. Effective dispersal distance is typically approximately 5 km, but beetles can sometimes fly longer distances on convection currents (Safranyik et al. 1992, Jackson et al. 2008). Pines are equipped with multifaceted constitutive and induced defenses that can repel or kill beetles (Raffa et al. 2008). However, mass attacks by sufficiently large numbers of beetles can overcome these defenses. The aggregation pheromones that mediate mass attacks exploit specific host compounds as precursors and or synergists (Blomquist et al. 2010). Moreover, a variety of biotic and abiotic environmental stresses on trees can compromise their defense mechanisms (Raffa et al. 2005, Lindgren and Raffa 2013).

There is substantial understanding of climate influences on mountain pine beetle outbreaks in lodgepole pine (*Pinus contorta* var. *latifolia*) forests (e.g., Raffa et al. 2008, Bentz et al. 2010). Temperature affects beetles by regulating development rates. Ideal temperatures allow for a one-year lifecycle and synchronized emergence of adults in late summer, which permits mass attack of trees and enables the brood to enter winter as late instar larvae, the most cold-hardy life stage; this effect has been termed “adaptive seasonality” (Logan and Powell 2001). Beetles may require more than one year to complete their lifecycle in regions with colder temperatures common at higher elevations (Bentz et al. 2014). Temperature also influences winter beetle mortality (Régnière and Bentz 2007). Some beetle mortality occurs when temperatures are lower than -30°C , and 100% mortality occurs when conditions are below -40°C

(Wygant 1940). Unseasonably cold weather (but above -30°C) during fall and spring can kill beetles that are not fully cold-hardened (Wygant 1940). Drought stress limits a tree's ability to defend itself against beetle attack (Kane and Kolb 2010). However, severe drought stress can result in thin phloem that limits food resources for larvae (Amman and Baker 1972) and desiccates quickly (Safranyik and Carroll 2006), thereby reducing brood production.

Critical knowledge gaps remain concerning effects of climate on mountain pine beetle outbreaks in whitebark pine forests and the potential for future outbreaks given a changing climate. Few field, experimental, or empirical studies of mountain pine beetles in whitebark pine exist relative to lodgepole pine, but the available data indicate important differences (Raffa et al. 2013). For example, whitebark pines can have a lower defensive capacity, especially in induced reactions, and a chemical composition more amenable to beetle pheromone communication (i.e., higher proportions of precursors and synergists, and lower induced quantities of inhibitors) than lodgepole pines (Raffa et al. 2013). Hence, beetles that entered whitebark pines were 38% more likely to succeed in generating mass attacks than those that entered lodgepole pines, even though beetles retain a behavioral preference for lodgepole pine, in mixed stands (Bentz et al. 2015). Thermal requirements for completing a beetle generation vary across latitudinal and elevational gradients (Bentz et al. 2014), and therefore models that have been developed to predict effects of temperature on beetle survival and development in lower-elevation lodgepole pines (e.g., Bentz et al. 1991) may be less applicable in higher-elevation whitebark pines. These complex interactions could yield different relationships between climate and outbreak initiation or progression in different forest types.

Although past observational studies have analyzed the recent widespread whitebark pine mortality in the GYE (Logan et al. 2010, Jewett et al. 2011, Simard et al. 2012), these studies do not consider the full range of important factors that include the effects of temperature, moisture, the number of attacking beetles, and stand structure. Thus, more detailed quantitative analyses that link whitebark pine mortality from mountain pine beetle to beetle populations, stand structure, and multiple climate variables will increase understanding of the causes of the recent outbreak and allow for estimates of outbreak potential under future climate conditions. This understanding can foster more informed recommendations for future listing and management of whitebark pine (Keane et al. 2012). Given its important role in high-elevation ecosystems of the western USA (Tomback et al. 2001), increased understanding about future trajectories for whitebark pine is also critical to understanding potential cascading effects on wildlife, hydrology, and forest structure and function.

We investigated climate–beetle relationships in whitebark pine in the GYE and projected climate suitability

for whitebark pine mortality from mountain pine beetle colonization under future climate scenarios. Our objectives were to (1) quantify climate–beetle relationships that influence whitebark pine mortality from mountain pine beetle, (2) assess relative climate influences on the initiation and progression of the recent outbreak, and (3) project future climate suitability for whitebark pine mortality from mountain pine beetle. We developed and evaluated a logistic regression model of the probability of whitebark pine mortality from mountain pine beetle. This model included variables that represent temperature effects on beetle survival and development, precipitation effects on host tree stress and subsequent influences on attack success, stand characteristics, and beetle population size. We used the model to describe climate–beetle relationships and diagnose climate influences on the recent outbreak. Finally, we applied the model to future climate projections to estimate climate suitability for whitebark pine mortality from mountain pine beetle and foster development of subsequent mortality probability models.

METHODS

Our spatial domain for developing the model of whitebark pine mortality was the GYE in the western USA (see Fig. 2b). The GYE encompasses Yellowstone and Grand Teton National Parks and surrounding lands, of which the national parks comprise approximately 25% (Clark and Zaunbrecher 1987). Lower elevations are predominately grass-shrub communities, with willows (*Salix* spp.) and cottonwoods (*Populus* spp.) along streams and rivers. At higher elevations, coniferous forest types include Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine, subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine, which are intermixed with montane meadows (Knight 1994). We defined the range of whitebark pine as those 1-km grid cells within the GYE with at least 108 (10%) 30-m grid cells that have whitebark pine (Landenburger et al. 2008). The 30-m map was developed from satellite imagery and overall classification accuracies exceeded 90% (Landenburger et al. 2008). Given that whitebark pine is a slow-growing species (Arno and Hoff 1989), its distribution likely has not changed substantially since this map was developed in 1999. Using this range definition, 1-km grid cells containing whitebark pine occurred from 2,000 to 3,800 m, with an average elevation of 2,732 m.

Data sets used in model development

Response variable.—We used the USDA Forest Service Aerial Detection Survey (ADS) database to define the response variable as the presence of whitebark pine mortality in each voxel (1-km pixel by year) within the range of whitebark pine. ADS observers in aircraft recorded tree mortality from mountain pine beetle indicating forest type (whitebark pine) and damage severity

(number of killed trees). In the GYE, we assumed that recent whitebark pine mortality has been primarily due to mountain pine beetle attack and infection by blister rust (Shanahan et al. 2014), with mortality from mountain pine beetle much higher than mortality from blister rust (Shanahan et al. 2014). Blister rust does not cause all needles on a tree to turn red in a single year as mountain pine beetle colonization does; therefore misidentification of sources of mortality by observers was unlikely.

Meddens et al. (2012) converted these ADS data to 1-km grids of the number of trees killed for each beetle and tree species combination for the western USA. We subtracted one year from the year of detection to convert to year of beetle colonization because whitebark pines attacked and killed in one summer turn red (allowing for detection) the following summer. From this data set, we identified the voxels with whitebark pine trees killed by mountain pine beetle from 1996 to 2009. Voxels having at least one tree killed were coded as having mortality (0 = absence of mortality, 1 = presence). The aerial surveys also report locations flown each year. Voxels that were not flown during ADS surveys in a given year were excluded from the model development data set.

Whitebark pine mortality from mountain beetles was noted in Yellowstone Park in 1971–1979 and in 1983–1984 (R. Renkin, *unpublished data*). ADS reports for the GYE (*available online*) and observations (R. Renkin, *personal communication*) indicated no mountain pine beetle activity in whitebark pine stands from 1985 through 1995.⁷ We therefore set all voxels from 1985 through 1995 to zero trees killed.

Explanatory variables.—Explanatory variables were chosen to represent known factors that influence mountain pine beetle outbreaks in lodgepole pine, including (1) winter beetle mortality, (2) adaptive seasonality, (3) host tree defensive capabilities, (4) stand characteristics, and (5) the number of attacking beetles the previous year (Aukema et al. 2008, Boone et al. 2011, Preisler et al. 2012, Sambaraju et al. 2012). We created a suite of candidate variables to represent each of these factors (Table 1) and calculated an annual value for the time of colonization (late summer) for each factor that represented the conditions leading up to attack. For example, for colonization in 2001, the corresponding winter minimum temperature (a potential variable representing beetle mortality) was the minimum of monthly minimum temperatures during December 2000 through February 2001 (i.e., the winter before colonization). Temperature variables were calculated over one year, representing a one-year life cycle, and over two years, representing a two-year life cycle. For each factor affecting beetle outbreaks, one explanatory variable (or in the case of adaptive seasonality, two) was selected from the suite of

⁷http://www.fs.usda.gov/detailfull/r1/forest-grasslandhealth/?cid=fsbdev3_016103

TABLE 1. Description of candidate explanatory variables in generalized additive models of the probability of whitebark pine mortality from mountain pine beetle in the Greater Yellowstone Ecosystem during 1985–2009.

Process	Rationale	Variable	Description	Original data source	Temporal resolution of source data
Climate conditions					
Beetle winter mortality	Unseasonably and/or extremely low temperatures can cause direct mortality of overwintering insects.	T _{min}	minimum monthly minimum temp in December–February†	PRISM	monthly
		Coldt	probability of winter survival from the cold tolerance model developed by Régnière and Bentz (2007)†	BioSIM	daily
		ECS	presence/absence of an early cold snap, defined as four consecutive days with temp ≤−20°C between 15 October and September–30 November†	BioSIM	daily
		Drop20	number of days with >20°C drop in mean temperature†	BioSIM	daily
		Min40	number of days with min temp ≤−40°C†	BioSIM	daily
Adaptive seasonality	Temperature conditions can promote outbreaks by allowing for a one-year life cycle and near-synchronous adult emergence.	Logan	0/1 of whether conditions were suitable for univoltinism according to the adaptive seasonality process model developed by Logan and Powell (2001)†	BioSIM	daily
		Tmean	average temp 1 August–31 July†	PRISM	monthly
		FallT	average temp September–November†	PRISM	monthly
		TMAA	average temp April–August†	PRISM	monthly
		CDD	cumulative degree-days above 5.5°C from 1 August to 31 July; DD = max(0,T-Tthresh)†	BioSIM	daily
Tree drought stress	Drought stressed trees have lower defensive capabilities than healthy trees.‡	BDD	binary of whether 833°C degree-days accumulated between 1 August and 31 July†	BioSIM	daily
		VPD01 through 05	average monthly vapor pressure deficit in current and previous five growing seasons§¶	PRISM	monthly
		CWD01 through 05	cumulative climatic water deficit in current and previous five growing seasons¶	PRISM	monthly
		PPT01 through 05	cumulative monthly October–August precipitation in current and previous five years¶	PRISM	monthly
		JJAPPT01 through 05	cumulative monthly June–August precipitation in current and previous years¶	PRISM	monthly
Stand characteristics					
Available host	Outbreaks will collapse when available host is depleted.	RMWBP	remaining whitebark pine = cumulative mortality area since 1998; *percentage of pixel with whitebark pine	Meddens et al. (2012)	annual
Stand composition	More homogenous stands will provide more host trees for beetles.	PCTWBP	percentage of pixel with whitebark pine	Landenburger et al. (2008)	NA
Stand age	Beetles prefer older, larger trees.	Age	age in years	Pan et al. (2011)	NA
Beetle populations					
Local beetle pressure (number attacking beetles originating from within pixel)	Beetles can kill healthy trees at high populations.	lY1	Log(number of mountain pine beetle-killed trees in the focal cell last year)	Meddens et al. (2012)	annual
Adjacent beetle pressure (number attacking beetles originating from outside pixel)		ldsp	Log(weighted linear function of number of mountain pine beetle-killed trees in surrounding cells up to 6 km distant)	Meddens et al. (2012)	annual

Notes: †Two variables: year of attack and previous year. ‡The effect of drought stress was allowed to vary with prior year beetle pressure to account for large beetle populations being capable of killing healthy trees. §Growing season is May–October. ¶Six variables: 0, 0–1, 0–2, ..., 0–5.

candidate variables as described in the statistical model development section below.

Beetle winter mortality was represented by candidate temperature-based variables that were derived from either daily or monthly climate data. The BioSIM program (Régnière 1996) was used to spatially interpolate daily station data from the National Weather Service Cooperative Observer Program stations to each 1-km grid cell using inverse distance weighting and derived vertical lapse rates. These daily temperature values were used to calculate several climate metrics to estimate cold snaps (Table 1). BioSIM was also used to calculate cold tolerance, the probability of beetle survival over the winter, with the process model of Régnière and Bentz (2007). This model tracks cold-hardiness fluctuations as a function of daily temperature. Finally, we also considered the lowest monthly minimum temperature from December through February, using monthly 800-m Parameter-elevation Regressions on Independent Slopes Model (PRISM) data (version LT71m; Daly et al. 2008).

To represent adaptive seasonality, we considered both daily and monthly temperature metrics (Table 1). The adaptive seasonality process model within BioSIM calculates the probability of beetles achieving a one-year life cycle and mass emergence in August using daily temperatures and laboratory measurements of beetle development rates for each life stage (Logan and Powell 2001). Other metrics computed from BioSIM-derived daily temperatures assessed development based on degree-days. We also considered monthly PRISM metrics: fall (September–November) mean temperature (FallT) representing development rate, appropriate timing for entering winter in the most cold-hardy stage, and population synchrony; and spring-summer (April–August) means (TMAA) representing development rate and emergence.

We represented tree drought stress and consequently reduced defensive capabilities with a set of candidate variables that included May–October vapor pressure deficit (VPD), water-year and summer precipitation (PPT; JJAPPT), and growing season climatic water deficit (CWD) calculated for the current through previous five years, resulting in six candidate variables for each drought stress metric (Table 1). We used monthly 800-m PRISM data for these variables. Climatic water deficit was computed using the AET Calculator program (Gavin and Hu 2006), which estimates water balance using a modified Thornthwaite method (Willmott et al. 1985); we assumed a field capacity of 100 mm. We also assessed the occurrence of drought by inspecting drought conditions from the US Drought Monitor (*available online*), which integrates multiple drought indices.⁸

To isolate the effects of climate variables, we also needed to account for the effects of non-climate variables in our model. Local beetle pressure (the number of beetles in the focal cell, IY1) was represented by the number of

trees, of any species, killed by mountain pine beetles in each grid cell the previous year (Preisler et al. 2012) using 1-km gridded ADS data (Meddens et al. 2012). Beetle pressure from outside the cell of interest, or adjacent beetle pressure (ldsp), was calculated from the number of trees, of any species, killed by mountain pine beetle in the neighborhood using an inverse-distance-weighted linear function that declined to 0 at a 6-km radius (Turchin and Thoeny 1993, Raffa et al. 2008), then subtracting the number of trees killed in the focal grid cell. These beetle population variables are important because of the positive density feedback exerted by pheromone-mediated cooperative behavior (Raffa et al. 2008) and because higher beetle populations increase the likelihood of successful colonization and subsequent tree mortality (Boone et al. 2011).

We calculated several variables representing stand characteristics. The percent of each grid cell containing whitebark pine (PCTWBP) was determined by summing the area of 30-m grid cells defined by Landenburger et al. (2008) in each 1-km grid cell. We estimated the area of available host trees, here termed remaining whitebark pine (RMWBP), by calculating 100 ha (the total area of each 1-km grid cell) minus the cumulative hectares with mortality since 1985 from Meddens et al. (2012). Stand age (Age) was estimated from a 1-km resolution map of average stand age for North America based on forest inventory data, fire histories, and remote sensing data (Pan et al. 2011). Data sets of biomass (Blackard et al. 2008), basal area (Krist et al. 2007), and quadratic mean diameter (Krist et al. 2007) were available for this study area, yet many grid cells with recorded beetle-caused mortality from ADS data had zeros for biomass or basal area. We were therefore not confident these data adequately represented stand structure in the study area and so did not use them in our models. We also evaluated a map of whitebark pine distribution developed by the Whitebark Pine Subcommittee of the Greater Yellowstone Coordinating Committee (GYCCWPSC 2010) that has a categorical size class attribute but found noticeable political boundaries (perhaps due to differences in measurement protocols) and did not want to introduce those delineations into the modeled climate suitability estimates, so did not use these data.

Statistical model development

We modeled the probability of whitebark pine mortality from mountain pine beetle with logistic regression, defined by the equation

$$\text{logit}(P) = \beta_0 + \sum_i^I s_i(C_i) + \sum_j^J s_j(X_j) \quad (1)$$

where P is the probability of tree mortality (at least one tree killed) by mountain pine beetle and $s_i(C_i)$ through $s_j(X_j)$ are tensor product smooth functions of the explanatory variables. C_i through C_J represent climate variables

⁸ <http://droughtmonitor.unl.edu>

affecting beetle winter mortality, beetle adaptive seasonality, and host tree stress; X_j through X_J represent variables describing remaining live host trees, stand structure, and previous year beetle population (Table 1). The estimated smooth functions of the explanatory variables are the change in the log-odds of whitebark pine mortality over the range of the variable, with log-odds set to zero at the average value of all variables. Confidence intervals around smooth functions were calculated through jackknifing by year: A population of smooth functions was estimated from models developed from a set of data with one year withheld at a time and confidence intervals calculated from this population (Preisler et al. 2012). Because beetles can kill healthy trees when beetle populations are high (Boone et al. 2011), we allowed the drought stress variable to vary with beetle pressure by including an interaction term, $s(C_{mi}, X_{mj})$, between drought variables and beetle pressure. This interaction is not shown in Eq. 1 because it was not significant and hence not included in the final model used in our analyses (see *Results*).

We used a model selection process ranking models according to Aikake's information criterion (AIC), following Burnham and Anderson (2002), to select the best-fitting variable from our set of candidate variables for each of the factors in Table 1. To assess correlation among variables, we calculated concavity (akin to multiple collinearity in a linear model) among variables in the model (Hastie and Tibshirani 1990). Concavity was >0.5 only between the variables percent whitebark pine and remaining whitebark pine. PCTWBP was retained in the final model because it was the stronger variable (lower AIC). All models included (by prescription) percent whitebark pine (PCTWBP), stand age (Age), local beetle pressure (IY1), and adjacent beetle pressure (ldsp). We refer to the model containing the prescribed and selected best-fitting variables as the "top" model (Fig. 1).

Spatial autocorrelation has the potential to incorrectly increase confidence in a model, produce erroneous relationships between variables, and generate incorrect predictions. We therefore evaluated the potential for spatial autocorrelation by calculating autocorrelation in the residuals from our top model as well as from our top model with the addition of a spatial term (x, y in UTM coordinates). We also compared the log-odds plots of these two models because differences between them may indicate a spatial pattern not accounted for by the other explanatory variables.

We assessed model goodness-of-fit model by comparing observed and predicted values both temporally and spatially. The skill of the model in predicting total area with mortality for each year in the study was assessed by summing the modeled probabilities for each grid cell over all whitebark pine locations in the study. The latter sum was then used as our model estimate of expected area with mortality in a given year. Predictions were calculated through a cross-validation procedure, whereby data from the year being predicted were withheld and model

parameters were calculated using the remaining years of data. The result is the time series shown in Fig. 2a. In an analogous way, we evaluated model predictions spatially using cross-validation. We withheld data from each of ten regions in the study area, estimated model parameters, then compared the predicted number of years with whitebark pine mortality in that region with the observed number of years of mortality. The results are the maps in Fig. 2c. Following Pineiro et al. (2008), We plotted observed vs. predicted area and number of years with mortality and report the linear regression equations, R^2 values, and P values from significance tests that the slopes and intercepts differ from 1 and 0, respectively.

Application of statistical model

We applied the final statistical model, defined as the model with the lowest AIC with one variable substitution because of input data limitations (see *Results*), to assess climate suitability for whitebark pine mortality from mountain pine beetle for the past few decades and future decades (see Fig. 1). We developed a climate suitability index (CSI) based on the estimated log-odds in Eq. 1. The CSI for a given voxel, m , was defined as the change in log-odds due only to the climate variables. Specifically, from Eq. 1 we have

$$CSI_m = \sum_i^I s_i(C_{im})$$

This index is used to project the effects of climate change on the odds of whitebark pine mortality. By focusing only on the effect of the climate variables, we were able to forecast climate change effects regardless of the levels of other variables (e.g., beetle pressure, stand structure) that were not available for future projections. Forecasting the probability of whitebark pine mortality is beyond the scope of this study.

In terms of the odds, our model is

$$\text{Odds} = e^{\beta_0} \times e^{\sum s(X)} \times e^{\sum s(C)} \quad (2)$$

Consequently, a log-odds value, $CSI = \sum s(C)$, of zero implies no increase in the odds due to climate, since $e^{\sum s(C)} = e^0 = 1$, while a suitability estimate >0 implies an increase and <0 a decrease in the odds of mortality over the average odds. The average of an explanatory variable in our model is the mean over all voxels used to develop the model. Finally, we developed an overall average climate suitability index per year by summing the CSI_m over all pixels (locations) for each year.

To estimate historical climate suitability and diagnose influences of climate variables during recent decades, we applied the final model to monthly 800-m PRISM data. We initially sought to apply our statistical model back to 1900 to provide more context for recent patterns and to evaluate our predicted climate suitability against known

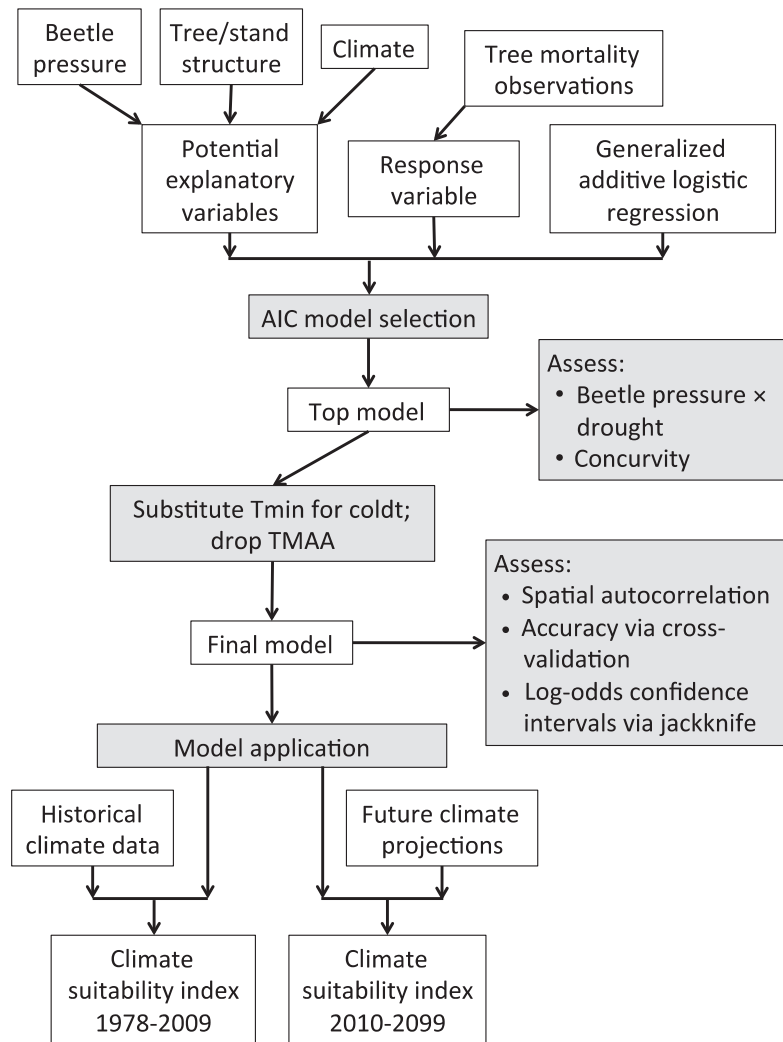


FIG. 1. Flow diagram showing data inputs and models (open boxes) and processing steps (shaded boxes) used in the analyses of climate influences on whitebark pine mortality from mountain pine beetle colonization, resulting in the final model, and application of this model to estimate historical and future climate suitability for whitebark pine mortality.

past outbreaks in the GYE in the 1930s and 1970s (Furniss and Renkin 2003, Lynch et al. 2006). Inspection of low- and high-elevation weather stations revealed frequent temperature inversions in the GYE. However, the list of weather stations used in PRISM interpolations indicated there were very few high-elevation stations contributing observations before 1978, leading to more uncertainty in PRISM temperatures at whitebark pine locations in these times. PRISM interpolations after 1978 include weather stations at elevations ranging from 1,102 to 3,078 m. Thus, we chose to focus on the period 1978–2009. A comparison of temperature and precipitation variables from PRISM, Daymet (Thornton et al. 1997), TopoWx (Oyler et al. 2015), and weather station data during 1978–2009 showed similar temporal patterns in all weather variables, indicating our results and conclusions are robust with respect to the choice of gridded historical climate data set.

To estimate future climate suitability, we applied the final model to future climate projections. We included projections from ten global climate models (GCM; Appendix S1: Table S1) from the fifth Coupled Model Inter-comparison Project results (Taylor et al. 2012), selected based on their historical (1950–2010) fidelity to observed climate in the western USA as determined by Rupp et al. (2013), that were forced with low (RCP 2.6), moderate (RCP 4.5), and high (RCP 8.5) emissions scenarios. We used downscaled GCM output from monthly NASA Earth Exchange Downscaled Climate Projections at 30 arc-second resolution (Thrasher et al. 2013). We checked for consistency between historical GCM and PRISM data to ensure we could (1) apply our statistical model developed using PRISM data to future GCM climate projections and (2) calculate future climate suitability estimates that would be comparable with historical climate suitability

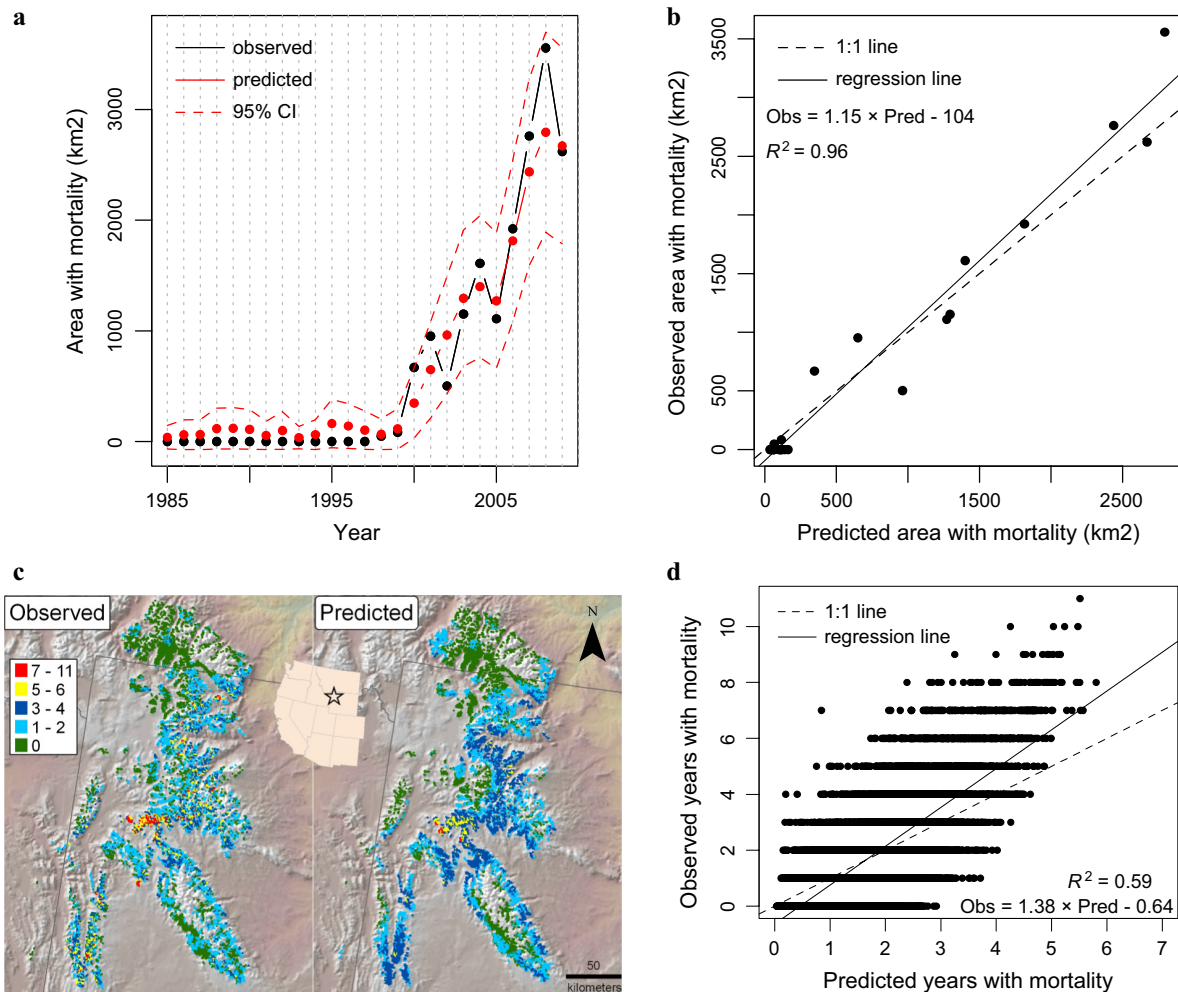


FIG. 2. Model evaluation in (a) time, showing observed (black line) and predicted (red line) area with whitebark pine mortality from mountain pine beetle (dashed red lines are 95% confidence intervals calculated from cross-validation by year, RMSE = 243 km²), with (b) showing linear regression of observed area with mortality as a function of predicted area with mortality (significance test slope = 1: $P = 0.08$, significance test intercept = 0: $P = 0.37$); and (c) space, showing observed (left map) and predicted (right map) number of years with whitebark pine mortality between 1985 and 2009 (RMSE = 1.2 yr), with (d) showing linear regression of observed years with mortality as a function of predicted years with mortality (significance test slope = 1: $P < 0.05$, significance test intercept = 0: $P < 0.05$). Colors in (c) indicate the number of years with observed and predicted mortality for each pixel. Star on inset map shows location of study area within western USA.

based on PRISM data. Historical climate data for the period 1978–2006 from each downscaled GCM projection were similar to historical PRISM weather data; averaged over the study area and time period, GCM winter temperatures were within 1°C of PRISM winter temperatures and summer precipitation was within 6% (Appendix S1: Fig. S1).

RESULTS

Whitebark pine mortality from mountain pine beetle in the GYE increased from below-observable levels in the late 1980s to a peak of just over 3,500 km² in 2008, followed by a decline in 2009 (Fig. 2a). The area with mortality each year represents new mortality in each

year, as opposed to the cumulative area with mortality since 1985. Our cross-validated model predicted the observed annual (Fig. 2a, b) and spatial (Fig. 2c, d) patterns of tree mortality well. The slopes and intercepts of observed vs. predicted values (Fig. 2b, d) indicate the model tended to overestimate when mortality was low and underestimate when mortality was high. However, these trends were only significant for the spatial regression (Fig. 2d), due in part to the large number of spatial subsamples compared to temporal subsamples. Autocorrelation in the residuals at a distance of 1 km was low (0.11) in the model without a spatial term, and including a spatial term only reduced this correlation to 0.09. Including a spatial term did not noticeably change the log-odds plots of the explanatory variables, and

therefore we did not include a spatial term in subsequent analyses.

According to the AIC model selection process (Appendix S1: Table S2), beetle winter mortality was best represented by cold tolerance (Coldt), adaptive seasonality was best represented by the average fall temperature the year prior to colonization (FallT) and the average April–August temperature in the year of colonization (TMAA), and tree drought stress was best represented by the cumulative precipitation during the summer of colonization and previous summer (JJAPPT01; Appendix S1: Table S2). Cold tolerance is a computationally expensive variable, and our objectives included applying the model to large future climate data sets. Substituting the minimum temperature of the coldest winter month in the winter prior to attack (T_{\min}), which was the second best winter mortality variable (Appendix S1: Table S2), for Coldt did not substantially change the annual patterns of mortality nor alter our interpretation of the influence of beetle winter mortality or the other explanatory variables. We therefore used T_{\min} in our final model (Appendix S1: Table S2), and all subsequent results shown are from this model.

Higher probability of tree mortality was associated with stands with greater percentages of whitebark pine, older stands, and increasing local (within the grid cell) and adjacent (from outside the grid cell) beetle pressure (Appendix S1: Fig. S2). According to the stand age map (Pan et al. 2011), average stand age was $137 (\pm 7)$ years, and 75% of stands were at least 87 years old.

Climate–beetle relationships that influence whitebark pine mortality from mountain pine beetles

Whitebark pine mortality from mountain pine beetle was more likely as winter temperature increased up to about -12°C (Fig. 3a) and as fall temperature increased up to about -2°C (Fig. 3b). The effect of April–August temperature was similar but was not well estimated by the model as indicated by the wide standard errors (Fig. 3c) and was therefore not included in the final model. Decreasing summer precipitation generally led to an increasing probability of whitebark pine mortality. However, at the lowest levels of precipitation whitebark pine mortality appeared to decline, though not significantly (Fig. 3d).

Relative climate influences on the initiation and progression of the recent outbreak

Observed whitebark pine mortality began in 1998, and the combined climate suitability index indicates greater than average odds of suitable climate conditions for tree mortality from beetle colonization after 1995, with exceptions in 1998, 1999, and 2005 (Fig. 4). Winter and fall temperatures were more suitable beginning around 1995. From 1978 to the early 1990s, winter minimum temperature frequently had low or very low suitability values, whereas after 1992, winter temperature suitability was consistently higher. With a few exceptions, fall temperatures were typically suitable during 1978–2009. Suitability due to precipitation was higher in 1995–1996 and after 1999 (except 2005). Declines in the observed area with

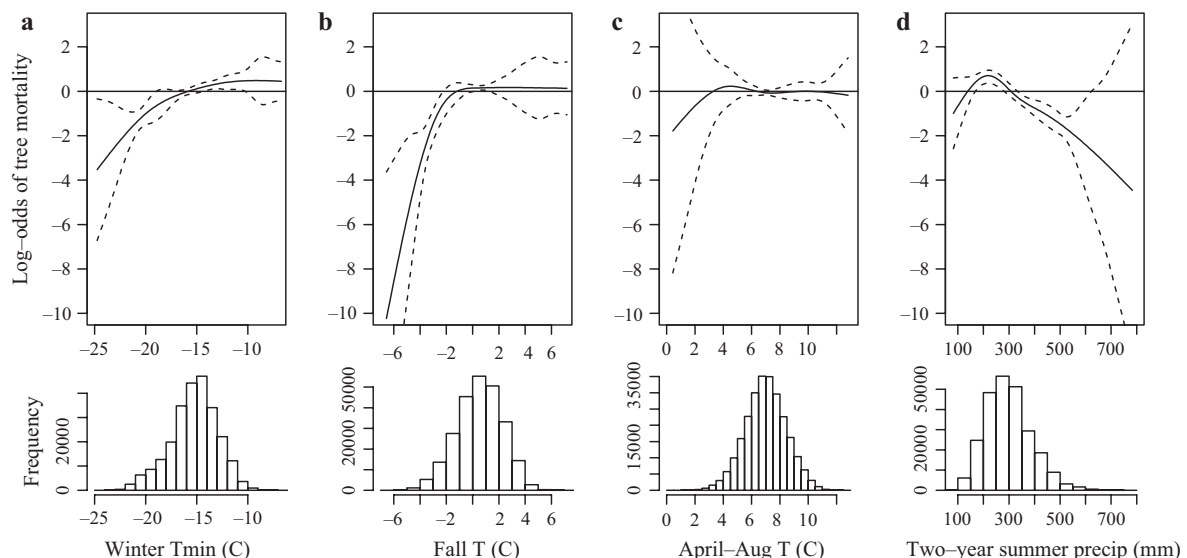


FIG. 3. Effects of climate variables on the log-odds of whitebark pine mortality from mountain pine beetle. (a) Minimum temperature of coldest winter month (representing beetle winter mortality), (b) average September–November temperature (representing temperature control of life stage development rate and population synchrony), (c) average April–August temperature (representing temperature control of life stage development rate), and (d) cumulative two-year summer precipitation (representing drought effects on whitebark pine hosts). Dashed lines are pointwise 95% confidence intervals calculated from jackknifing by year. Histograms show distributions of data used in model development.

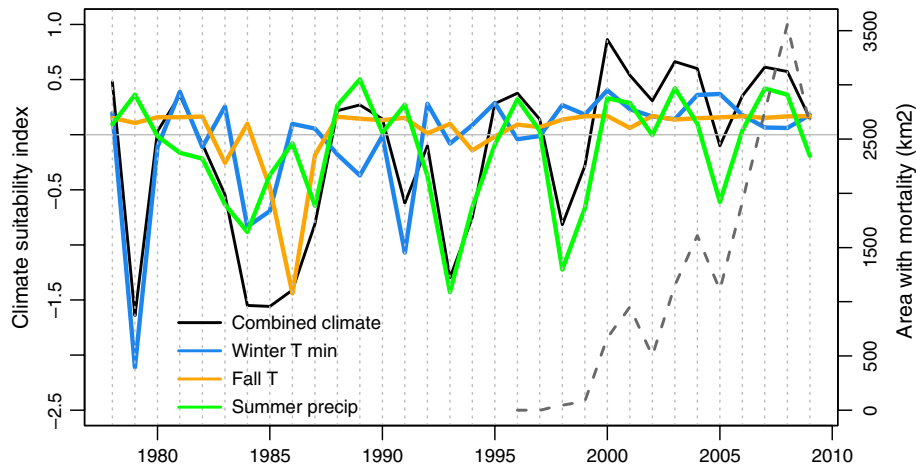


FIG. 4. Average modeled climate suitability for whitebark pine mortality from mountain pine beetle, spatially averaged over the Greater Yellowstone Ecosystem. Dashed gray line and right y-axis show observed area with mortality (km^2) in the study area from aerial detection surveys. Higher index (log-odds) values indicate greater probability of mortality.

mortality occurred in years with lower precipitation suitability (2002 and 2005).

US Drought Monitor maps of late August indicate abnormally dry to severe drought conditions during 2000–2008, with multiple years of extreme to exceptional drought. Additionally, plots of summer (Appendix S1: Fig. S3) and water-year precipitation from PRISM data show that multiple consecutive years of low precipitation occurred in the 2000s more often than in previous decades. In our study, this is reflected in the multiple years of higher than average suitability levels for summer precipitation observed between 2000 and 2008 (Fig. 4).

Whitebark pine mortality from mountain pine beetle was recorded in Yellowstone National Park from 1971 to 1978 and 1981 to 1983, (R. Renkin, *unpublished data*), although the spatial extents of these outbreaks were far less than the most recent outbreak. The lack of mortality in 1979 and for multiple years beginning in 1984 (not shown) coincides with predicted low suitability of winter minimum temperature (Fig. 4).

Future climate suitability for whitebark pine mortality from mountain pine beetles

Future climate projections show increasing winter and fall temperatures, with greater increases under higher emissions scenarios and later in the century (Appendix S1: Fig. S4). Projections of cumulative two-year summer precipitation are more variable (Appendix S1: Fig. S4). Given these projections, modeled future climate suitability for whitebark pine mortality from mountain pine beetle increases in the future and is higher under higher emissions scenarios and later in the century (Fig. 5; Appendix S1: Fig. S5). Under the highest emissions scenario (RCP 8.5), most projections indicate climate suitability from 2010 forward that is similar to suitability that occurred during the recent outbreak (Fig. 5a). Modeled T_{\min} suitability is

relatively more consistent among climate projections than other climate variables, with the near disappearance of years with the extremely low winter temperature suitability that occurred prior to the recent outbreak (Fig. 5a). Future FallT suitability shows less intermodel variability and, on average, has continuously high values after 2010 (not shown). JJAP01 suitability varies widely among climate projections and does not show any long-term change relative to the historical period (Fig. 5b). Combined future climate suitability varies substantially because of future precipitation estimates, with more precipitation leading to lower climate suitability and less precipitation leading to higher climate suitability for beetles (Fig. 5b, c). Regardless of future precipitation projections, GCM projections agree on warming, which increases suitability for beetle survival and development, and consequently fewer years when climate is unsuitable for beetle-induced mortality to whitebark pine (Fig. 5c).

We mapped T_{\min} suitability (Fig. 6) because the temporal patterns of this climate variable (Fig. 4) show a clear difference before and after the recent outbreak. Because spatial patterns of future climate suitability were similar among GCM projections, we show results from the multi-model average. Across the current range of whitebark pine in the GYE, the proportion of winters with high T_{\min} suitability (defined as the T_{\min} suitability index >0) for whitebark pine mortality increases in the future (Fig. 6). Prior to the recent outbreak, in 1978–1997 (not mapped), the spatially averaged proportion of a highly suitable winter was 0.47, and during the recent outbreak, in 1998–2009, the proportion increased to 0.56. Future projections indicate that the proportions will increase to 0.75, 0.87, and 0.94 in 2010–2039, 2040–2069, and 2070–2099, respectively. In the near term, spatial variability exists, with the lowest suitability occurring in portions of the Wind River Range (southeast GYE) and the northeast GYE (Fig. 6).

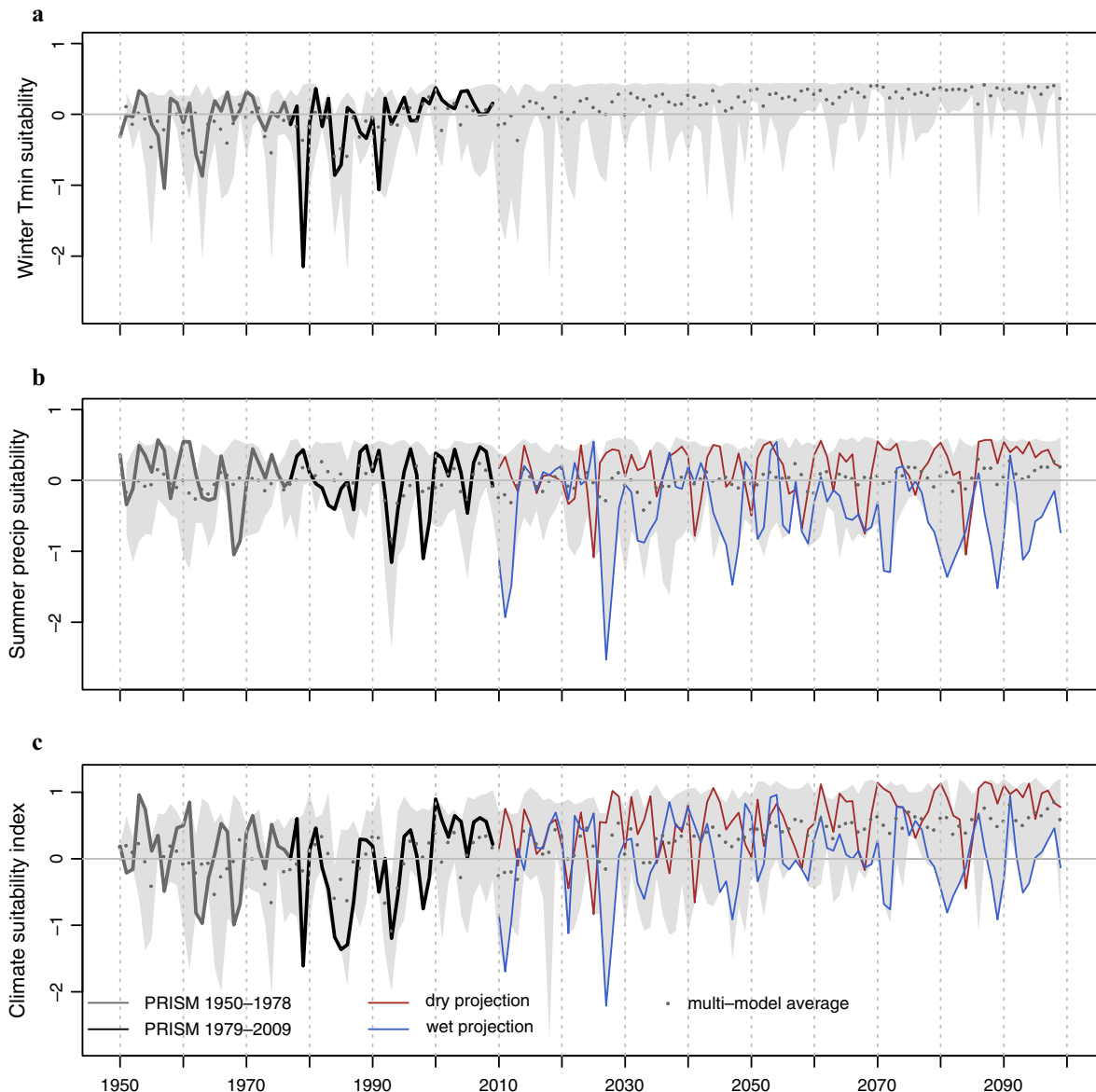


FIG. 5. Climate suitability for whitebark pine mortality from mountain pine beetle for (a) winter minimum temperature, (b) two-year summer precipitation, and (c) combined weather suitability averaged across the Greater Yellowstone Ecosystem for each year. Gray line is 1950–1978 and black line is 1970–2009 suitability using PRISM weather data; gray dots are the average suitability using ten general circulation model (GCM) projections downscaled to 1-km resolution (Table S3); gray shading bounds the range of results from all GCMs; blue line is from one GCM with wetter projections (CanESM2); red line is from one GCM with drier projections (IPSL-CM5A-MR). GCMs were forced with RCP 8.5, a high emissions scenario.

DISCUSSION

Climate–beetle relationships that influence whitebark pine mortality from mountain pine beetle

Whitebark pine mortality from mountain pine beetle was predicted to increase with increasing temperatures in fall, winter, and spring/summer seasons. Our modeling structure allowed us to investigate the different effects of temperature on beetle development and synchrony of host-seeking adults. In our model, fall temperatures were

more important than spring/summer temperatures, suggesting beetle population synchrony was an important factor in the recent outbreak. Fall temperatures act to synchronize beetle populations through differential development rates among life stages (Logan and Powell 2001): when low temperatures arrive in late fall/early winter, development stops for later life stages but continues for earlier stages, allowing individuals in the earlier stages to catch up to individuals in later stages. Our modeling suggested a positive, though inconclusive, influence of spring/summer (April–August) temperature

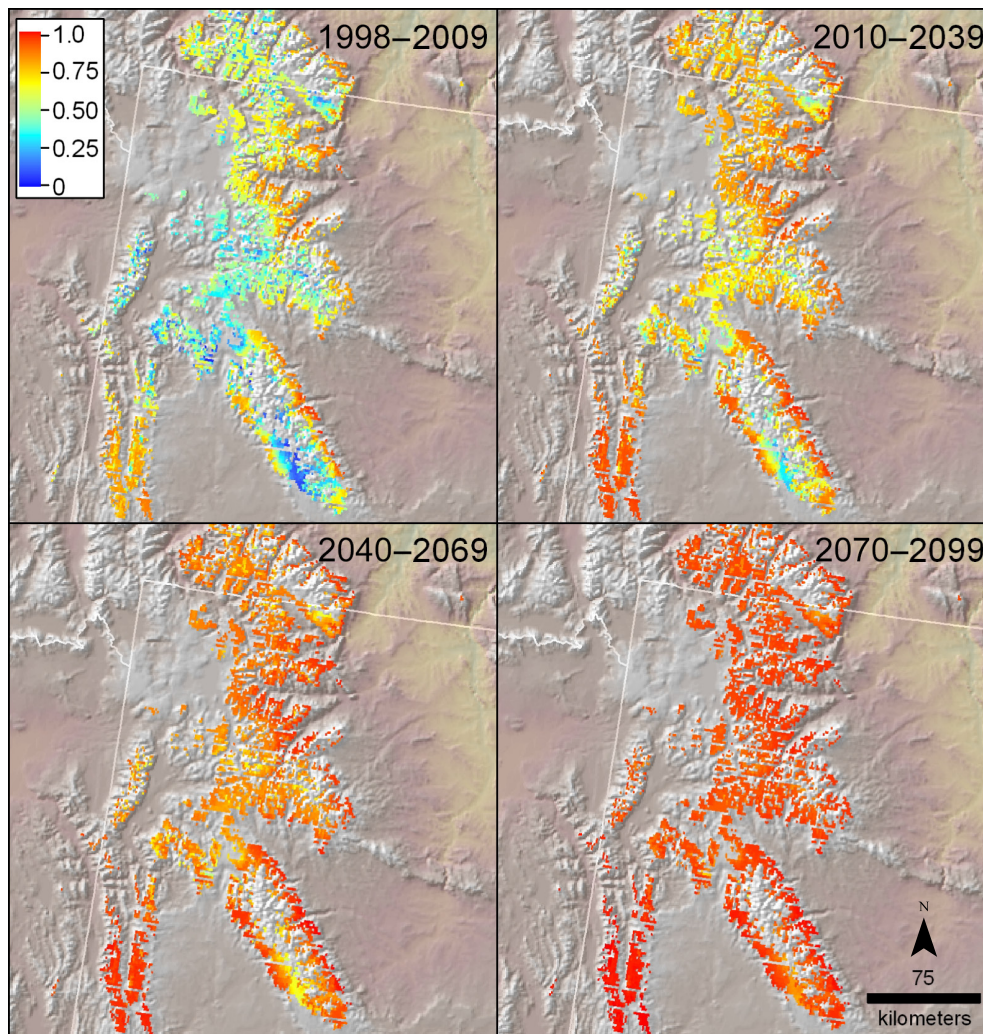


FIG. 6. Proportion of years in range of years listed in each panel with winter minimum temperature suitability for whitebark pine mortality from mountain pine beetle >0 (indicating more suitable winter conditions for beetle survival) during historical and future time periods. Historical proportions were calculated from PRISM data. Future proportions are multi-model means of ten downscaled climate projections forced with a high emissions scenario (RCP 8.5). Winter temperature suitability increases through time, but in some regions of the study area the suitability increases more slowly than other regions.

on whitebark pine mortality. The range of spring/summer temperatures over the period of model development may have been insufficient to detect a conclusive influence.

Temperature effects on whitebark pine mortality from mountain pine beetle were similar to those previously found in the beetles' primary host, lodgepole pine (Logan and Powell 2001, Régnière and Bentz 2007, Aukema et al. 2008, Raffa et al. 2008, Bentz et al. 2010, Preisler et al. 2012, Creeden et al. 2014, Weed et al. 2015). Increases in minimum winter temperatures have been related to beetle outbreaks in lodgepole pine (Creeden et al. 2014) and mountain pine beetle population growth in colder regions of the western USA (Weed et al. 2015). Increasing temperatures also affect mountain pine beetle phenology in lodgepole pine systems (Powell and Bentz 2009). These similarities suggest that although the thermal requirements

necessary to complete a beetle generation vary across latitudinal and elevational (and hence temperature) gradients (Bentz et al. 2001, 2014), temperature is an important influence on beetle survival, development, and population synchrony across different forest types (and therefore different thermal regimes). Average fall and spring/summer temperatures were a better predictor of whitebark pine mortality than was the adaptive seasonality process model, indicating that continued research on beetle development rates will increase our understanding of and ability to predict temperature effects on beetle life cycles.

We found that whitebark pine mortality increased as precipitation declined, which is consistent with previous mechanistic and correlative studies suggesting a reduction in tree defense. However, at the very lowest levels of precipitation there appeared to be a decline in tree mortality

(albeit not significant), suggesting reduced brood production due to thinner phloem (Preisler et al. 2012). Multiple studies have documented the co-occurrence of tree-killing bark beetle outbreaks with decreased precipitation (Rouault et al. 2006, Negron et al. 2009, Chapman et al. 2012, Preisler et al. 2012, Gaylord et al. 2013, Hart et al. 2014) and drier site topographic conditions (Kaiser et al. 2013). Tree susceptibility to beetle attack increases with increasing levels of drought stress (Raffa and Berryman 1983, Kane and Kolb 2010) because severe stress can decrease the ability of trees to produce and translocate defensive compounds (Ayres 1993, Breshears et al. 2009, Bentz et al. 2010). For example, drought stress reduced the production of resin canals in ponderosa pine (*Pinus ponderosa*; Kane and Kolb 2010), which are an integral part of tree defense against beetle attack (Kane and Kolb 2010). Whitebark pine growth has been positively correlated with precipitation (Perkins and Swetnam 1996, Millar et al. 2012), and Perkins and Roberts (2003) found whitebark pine mortality from beetles was higher when precipitation was lower and tree growth was less. We therefore interpret summer precipitation as an index of tree drought stress and hence tree defensive capability. Combined with the inherently lower defensive capacity of whitebark than lodgepole pine (Raffa et al. 2013), additional drought stress may be particularly problematic for whitebark pine. The declines (or leveling off) in mortality probability we found at the lowest levels of precipitation could arise from highly stressed trees having phloem too thin to support substantial brood development (Amman 1969, Amman and Baker 1972, Cole 1975, Safranyik and Carroll 2006).

Other factors affecting whitebark pine mortality from mountain pine beetle

Stand structure influences mountain pine beetle attack in lodgepole pine (Amman and Baker 1972) and whitebark pine (Perkins and Roberts 2003) stands; older trees and denser stands are more susceptible (Shore and Safranyik 1992, Shore et al. 2000). There was insufficient data to quantify potential stand density effects in our modeling. We found that tree mortality increased with stand age, but as can be seen from the magnitude of the change in the log-odds (Appendix S1: Fig. S1), this effect was much less than other variables. We found similar relationships between susceptibility and stand age in whitebark pine, though shifted to slightly older stands, as reported for lodgepole pine (Shore et al. 2000). Based on this relationship and the average stand age in the GYE (137 ± 7 yr; Appendix S1: Fig. S2d), most stands have probably been susceptible to beetle colonization for at least 50 yr, and had climate conditions been suitable, extensive outbreaks could have occurred. Hence the lack of extensive continuous whitebark pine mortality during previous decades, in contrast to the duration and scale of recent outbreak (Logan et al. 2010), provides additional evidence of the important role of recent climate change.

Relative climate influences on initiation and progression of the recent outbreak

By applying our statistical model using climate data since 1978, we were able to analyze climate influences before the recent outbreak as well as during its initiation. Winter temperatures were more suitable, and consistently so, during the recent outbreak than in prior years, suggesting higher winter temperatures allowed greater beetle survival and beetle population growth, leading to the recent outbreak. Preliminary analyses of temperatures from long-term weather stations in the region and PRISM over the 20th century suggest that low winter minimum temperatures occurred more frequently in the GYE during the early and mid-1900s than in recent decades (see Appendix S1: Fig. S2).

Drought appears to have facilitated beetle population increases, potentially by stressing host whitebark pines and making them more susceptible to colonization. Low precipitation prior to the outbreak, in 1995–1997, may have lowered tree defenses and favored growth of low (endemic) beetle populations. Tree mortality increased during 1998–1999 when beetle populations were high and precipitation was likewise high (and drought stress would have been alleviated). Later in the outbreak, precipitation (and hence drought stress) appeared to continue to exert an influence on whitebark pine mortality as can be seen from the high correlation between precipitation and area with mortality during 2004 through 2009. This continued correlation during high mountain pine beetle populations in whitebark pines differs from the outbreak patterns in lodgepole pines (Creeden et al. 2014), in which beetles switch their preferences to unstressed trees during epidemics (Boone et al. 2011). The mechanisms behind interspecific differences in relationships between precipitation and tree mortality during mountain pine beetle outbreaks are not well understood. They could potentially arise from a number of factors, including the beetle's higher behavioral preference for lodgepole pine (Raffa et al. 2013, Bentz et al. 2015), the higher drought tolerance of whitebark pine (Weaver 2001), or differences in how constitutive vs. induced defense mechanisms respond to moisture deficit (Lewinsohn et al. 1993, Kane and Kolb 2010). Further research is needed to better understand the mechanisms, roles, and context-dependency of drought during beetle outbreaks in whitebark pine.

Future climate suitability for whitebark pine mortality from mountain pine beetle

A combination of suitable tree, stand, landscape, and climatic conditions is required for bark beetle outbreaks (Raffa et al. 2008, 2015). We focused on estimating the suitability of future climate conditions. Given projections of future warming, we estimate that by mid-century, climate conditions across most of the current whitebark pine range in the GYE will commonly be as suitable for

beetle colonization as conditions that occurred during the recent outbreak. Under all climate projections, combined climate suitability is higher at the end of this century than at the beginning. Increased temperatures are primarily responsible; precipitation projections and their influence on suitability are variable among models and years. The upper limits of temperature suitability are less variable than lower limits (see Fig. 4), because at higher temperatures the probability of whitebark pine mortality plateaus and additional increases in temperature do not increase beetle survival.

Caveats

Our measures of whitebark pine mortality and beetle pressure relied on ADS data, which have spatial and host tree identification error. Johnson and Ross (2008) evaluated the presence of bark beetle-caused tree mortality in various tree species recorded by aerial surveys and found errors of commission and omission decreased with stand homogeneity and decreasing spatial resolution. Whitebark pine tends to be homogeneous in the GYE (Weaver 2001), and therefore spatial accuracy of ADS observers was likely high. The inconsistent coverage of areas flown in the GYE (Macfarlane et al. 2013) introduces some uncertainty into our results, although we partially accounted for this in our use of only flown areas for defining the presence and absence locations used to develop the statistical model of whitebark pine mortality. Because whitebark pines have a distinctive crown shape compared to lodgepole pine, misidentification of host species, while possible, was likely minimal. Increasing the accuracy, spatial, and temporal coverage of beetle outbreak data, such as by using satellite imagery (e.g., Meddens et al. 2013) will improve studies of climate influences.

Implications

The recent outbreak has substantially altered whitebark pine forest structure (Gibson et al. 2008). Because whitebark pines grow slowly, requiring up to 250 yr to achieve diameters of 50 mm (Arno and Hoff 1989), stands that experienced high mortality of large trees may not have enough suitable trees to support large mountain pine beetle populations for decades into the future. However, beetles may continue to persist in nearby lodgepole pine, which did not recently experience severe mortality in the GYE (Meddens et al. 2012). Given the suitability of future climate projections, whitebark pines in the GYE will face a strong potential for beetle colonization as they achieve sizes preferred by beetles.

The future structural composition of whitebark pine stands will likely be quite different from before the recent outbreak: large whitebark pines may not be prevalent in the GYE. Instead, whitebark pines may primarily exist as young and/or small trees, which will still be vulnerable to other threats such as white pine blister rust (Greater

Yellowstone Whitebark Pine Monitoring Working Group 2013).

Our results provide additional evidence for the potential for major shifts in vegetation types in the GYE. Climate change can affect the distribution and abundance of whitebark pines and other forest types through direct effects on the species themselves (Chang et al. 2014) as well as indirect effects through abiotic (e.g., fire; Westerling et al. 2011) and biotic (e.g., mountain pine beetles) disturbance agents.

Whitebark pine restoration may be most successful in locations where beetle survival is limited by low winter minimum temperatures. Our results indicate that several regions in the GYE offer potential refugia from beetle colonization in the early to middle decades of this century. However, finer-resolution features not captured in our results, especially locations with cold air drainage or significant temperature inversions, will be important when identifying potential refugia for whitebark pine. Reducing greenhouse gas concentrations will limit future temperature increases, decreasing suitability for beetle survival and increasing the likelihood of whitebark pine persistence into the future.

Warming and drought have been identified as important drivers of forest insect outbreaks across the globe, including those of bark beetles in Europe (e.g., Marini et al. 2012) and North America (e.g., Bentz et al. 2010). However, variability exists among which systems are most affected and how climate effects are manifested. Some major beetle outbreaks are initiated by windthrow (e.g., Okland and Berryman 2004) and others are coupled to drought (Raffa et al. 2008). In contrast to less aggressive species such as piñon ips (*Ips confusus*), more aggressive beetle species such as mountain pine beetle are able to kill healthy trees during epidemics (Boone et al. 2011) and therefore become less coupled to drought after they surpass an eruptive threshold (Raffa et al. 2008). Our findings of a continued influence of drought well into a mountain pine beetle outbreak in whitebark pine indicates that further research is required to better understand the role of drought stress on host-beetle interactions.

Our study quantifies the role of past and future climate in an important biotic disturbance that caused a widespread forest die-off in a temperate forest. This adds to an emerging body of evidence (Breshears et al. 2005, Berg et al. 2006, Pureswaran et al. 2015) on the importance of climate change impacts via trophic interactions and provides a foundation for illustrating climate change impacts on ecological systems in a visible and meaningful way.

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LITERATURE CITED

- Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660–684.
- Amman, G. D. 1969. Mountain beetle emergence in relation to depth of lodgepole pine bark. Research Note INT-96. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Amman, G. D. 1973. Population changes of the mountain pine beetle in relation to elevation. *Environmental Entomology* 2:541–547.
- Amman, G. D., and B. H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. *Journal of Forestry* 70:204–209.
- Arno, S. F., and R. P. Hammerly. 1984. *Timberline: mountain and arctic forest frontiers*. Mountaineers, Seattle, Washington, USA.
- Arno, S. F., and R. J. Hoff. 1989. *Silvics of whitebark pine (Pinus albicaulis)*. General Technical Report INT-253. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Aukema, B. H., A. L. Carroll, Y. Zheng, J. Zhu, K. F. Raffa, R. D. Moore, K. Stahl, and S. W. Taylor. 2008. Movement of outbreak populations of mountain pine beetle: influence of spatiotemporal patterns and climate. *Ecography* 31:348–358.
- Ayres, M. P. 1993. Global change, plant defense, and herbivory. Pages 75–94 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Bentz, B., C. K. Boone, and K. F. Raffa. 2015. Tree response and mountain pine beetle attack preference, reproduction and emergence timing in mixed whitebark and lodgepole pine stands. *Agricultural and Forest Entomology* 17:421–432.
- Bentz, B., J. Vandygriff, C. Jensen, T. Coleman, P. Maloney, S. Smith, A. Grady, and G. Schen-Langenheim. 2014. Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients in the western United States. *Forest Science* 60:434–449.
- Bentz, B. J., J. A. Logan, and G. D. Amman. 1991. Temperature-dependent development of mountain pine beetle and simulation of its phenology. *Canadian Entomologist* 123:1083–1094.
- Bentz, B. J., J. A. Logan, and J. C. Vandygriff. 2001. Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. *Canadian Entomologist* 133:375–387.
- Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience* 60:602–613.
- Berg, E. E., J. D. Henry, C. L. Fastie, A. D. De Volder, and S. M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227:219–232.
- Blackard, J. A., et al. 2008. Mapping U.S. forest biomass using nationwide forest inventory data and moderate resolution information. *Remote Sensing of Environment* 112:1658–1677.
- Blomquist, G. J., R. Figueroa-Teran, M. Aw, M. M. Song, A. Gorzalski, N. L. Abbott, E. Chang, and C. Tittiger. 2010. Pheromone production in bark beetles. *Insect Biochemistry and Molecular Biology* 40:699–712.
- Boone, C. K., B. H. Aukema, J. Bohlmann, A. L. Carroll, and K. F. Raffa. 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. *Canadian Journal of Forest Research* 41:1174–1188.
- Breshears, D. D., et al. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences USA* 102:15144–15148.
- Breshears, D. D., O. B. Myers, C. W. Meyer, F. J. Barnes, C. B. Zou, C. D. Allen, N. G. McDowell, and W. T. Pockman. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* 7:185–189.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer, New York, NY.
- Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos* 82:561–573.
- Chang, T., A. J. Hansen, and N. Piekielek. 2014. Patterns and variability of projected bioclimatic habitat for *Pinus albicaulis* in the Greater Yellowstone Area. *PLoS ONE* 9:e11169.
- Chapman, T. B., T. T. Veblen, and T. Schoennagel. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* 93:2175–2185.
- Clark, T. W., and D. Zaunbrecher. 1987. *The Greater Yellowstone Ecosystem: the ecosystem concept in natural resource policy and management*. Renewable Resources Journal 5:8–15.
- Cole, W. E. 1975. Interpreting some mortality factor interactions within mountain pine beetle broods. *Environmental Entomology* 4:97–102.
- Creeden, E. P., J. A. Hicke, and P. C. Buotte. 2014. Climate, weather, and recent mountain pine beetle outbreaks in the western United States. *Forest Ecology and Management* 312:239–251.
- Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology* 28:2031–2064.
- Farnes, P. E. 1990. SNOWTEL and snow course data: describing the hydrology of whitebark pine ecosystems. Pages 302–305 in W. Schmidt and K. McDonald, editor. *Proceedings-symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource*; 1989 March 29–31. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Furniss, M. J., and R. A. Renkin. 2003. Forest entomology in Yellowstone National Park, 1923–1957: a time of discovery and learning to let live. *American Entomologist* 43:198–209.
- Gavin, D. G., and F. S. Hu. 2006. Spatial variation of climatic and non-climatic controls on species distribution: the range limit of *Tsuga heterophylla*. *Journal of Biogeography* 33:1384–1396.

- Gaylord, M. L., T. E. Kolb, W. T. Pockman, J. A. Plaut, E. A. Yepez, A. K. Macalady, R. E. Pangle, and N. G. McDowell. 2013. Drought predisposes pinon-juniper woodlands to insect attacks and mortality. *New Phytologist* 198:567–578.
- Gibson, K., K. Skov, S. Kegley, J. Jorgensen, S. Smith, and J. Witcosky. 2008. Mountain pine beetle impacts in high elevation five-needle pines: current trends and challenges. R1-08-020. Forest Service, Forest Health Protection, Missoula, Montana, USA.
- Gibson, K. E. 2006. Mountain pine beetle conditions in whitebark pine stands in the Greater Yellowstone Ecosystem. R1Pub06-03. Forest Health Protection Report. USDA Forest Service, Northern Region, Missoula, Montana, USA.
- Greater Yellowstone Whitebark Pine Monitoring Working Group. 2013. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2012 annual report. Natural Resource Data Series NPS/GRYN/NRDS-2013/498, National Park Service, Fort Collins, CO.
- Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee. 2010. 2010 whitebark pine distribution and condition assessment for the Greater Yellowstone by N. Bockino and W. Macfarlane. Cooperation with USDA Forest Service–Forest Health and Protection and Grand Teton National Park, National Park Service, Kelly, WY.
- Hann, W. J. 1990. Landscape and ecosystem level management in whitebark pine ecosystems. Pages 335–339 in *Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Elevation Mountain Resource*. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Hart, S. J., T. T. Veblen, K. S. Eisenhart, D. Jarvis, and D. Kulakowski. 2014. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* 95:930–939.
- Hastie, T. J., and R. J. Tibshirani. 1990. Generalized additive models. Chapman and Hall, London, UK.
- IPCC. 2014. Climate Change 2014: impacts, adaptation, and vulnerability. Part a: global and sectoral aspects. In C. B. Field et al., editors. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, New York, USA.
- Jackson, P. L., D. Straussfogel, B. S. Lindgren, S. Mitchell, and B. Murphy. 2008. Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 38:2313–2327.
- Jewett, J. T., R. L. Lawrence, L. A. Marshall, P. E. Gessler, S. L. Powell, and S. L. Savage. 2011. Spatiotemporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. *Forest Science* 57:320–335.
- Johnson, E. W., and J. Ross. 2008. Quantifying error in aerial survey data. *Australian Forestry* 71:216–222.
- Kaiser, K. E., B. L. McGlynn, and R. E. Emanuel. 2013. Ecohydrology of an outbreak: mountain pine beetle impacts trees in drier landscape positions first. *Ecohydrology* 6: 444–454.
- Kane, J. M., and T. E. Kolb. 2010. Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. *Oecologia* 164:601–609.
- Keane, R. E., et al. 2012. A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). General Technical Report RMSR-GTR-279. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Knight, D. H. 1994. Mountain and plains: the ecology of Wyoming landscapes. Yale University Press, New Haven, Connecticut, USA.
- Krist, F. J., F. J. Sapio, and B. M. Tkacz. 2007. Mapping risk from forest insects and diseases. FHTET 2007-06. USDA Forest Service, Washington, D.C.
- Landenburger, L., R. L. Lawrence, S. Podrutzny, and C. C. Schwartz. 2008. Mapping regional distribution of a single tree species: whitebark pine in the Greater Yellowstone Ecosystem. *Sensors* 8:4983–4994.
- Lewinsohn, E., M. Gijzen, R. M. Muzika, K. Barton, and R. Croteau. 1993. Oleoresinosis in grand fir (*Abies grandis*) saplings and mature trees: modulation of this wound response by light and water stresses. *Plant Physiology* 101: 1021–1028.
- Lindgren, B. S., and K. F. Raffa. 2013. Evolution of tree killing in bark beetles (Coleoptera: Curculionidae): trade-offs between the maddening crowds and a sticky situation. *Canadian Entomologist* 145:471–495.
- Logan, J. A., W. W. MacFarlane, and L. Wilcox. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecological Applications* 20:895–902.
- Logan, J. A., and J. A. Powell. 2001. Ghost forests, global warming and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47:160–173.
- Lynch, H. J., R. A. Renkin, R. L. Crabtree, and P. R. Moorcroft. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. *Ecosystems* 9:1318–1327.
- Macfarlane, W. W., J. A. Logan, and W. R. Kern. 2013. An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. *Ecological Applications* 23:421–437.
- Marini, L., M. P. Ayres, A. Battisti, and M. Faccoli. 2012. Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. *Climatic Change* 115:327–341.
- Meddens, A. J. H., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications* 22:1876–1891.
- Meddens, A. J. H., J. A. Hicke, L. A. Vierling, and A. T. Hudak. 2013. Evaluating methods to detect bark beetle-caused tree mortality using single-date and multi-date Landsat imagery. *Remote Sensing of Environment* 132:49–58.
- Millar, C. I., R. D. Westfall, D. L. Delany, M. J. Bokach, A. L. Flint, and L. E. Flint. 2012. Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 42:749–765.
- Negron, J. F., J. D. McMillin, J. A. Anhold, and D. Coulson. 2009. Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona, USA. *Forest Ecology and Management* 257:1353–1362.
- Okland, B., and A. Berryman. 2004. Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*. *Agricultural and Forest Entomology* 6:141–146.
- Oyler, J. W., A. Ballantyne, K. Jensco, M. Sweet, and S. W. Running. 2015. Creating a topoclimatic daily air temperature dataset for the conterminous United States using homogenized station data and remotely sensed land skin temperature. *International Journal of Climatology* 35: 2258–2279.
- Pan, Y., J. M. Chen, R. Birdsey, K. McCullough, L. He, and F. Deng. 2011. Age structure and disturbance legacy of North American forests. *Biogeosciences* 8:715–732.

- Perkins, D. L., and D. W. Roberts. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. *Forest Ecology and Management* 174:495–510.
- Perkins, D. L., and T. W. Swetnam. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. *Canadian Journal of Forest Research* 26:2123–2133.
- Pineiro, G., S. Perelman, J. P. Guerschman, and J. M. Paruelo. 2008. How to evaluate models: Observed vs. predicted or predicted vs. observed? *Ecological Modelling* 216:316–322.
- Powell, J. A., and B. J. Bentz. 2009. Connecting phenological predictions with population growth rates for mountain pine beetle, an outbreak insect. *Landscape Ecology* 24: 657–672.
- Preisler, H. K., J. A. Hicke, A. A. Ager, and J. L. Hayes. 2012. Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. *Ecology* 93:2421–2434.
- Pureswaran, D. S., L. De Grandpre, D. Pare, A. Taylor, M. Barrette, H. Morin, J. Regniere, and D. D. Kneeshaw. 2015. Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. *Ecology* 96:1480–1491.
- Raffa, K. E., B. H. Aukema, N. Erbilgin, K. D. Klepzig, and K. F. Wallin. 2005. Interactions among conifer terpenoids and bark beetles across multiple levels of scale: an attempt to understand links between population patterns and physiological processes. *Recent Advances in Phytochemistry* 39: 80–118.
- Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, and T. E. Kolb. 2015. Responses of tree-killing bark beetles to a changing climate. Pages 173–201 in C. Bjorkman and P. Niemela, editors. *Climate change and insect pests*. CABI, Wallingford, UK.
- Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58:501–517.
- Raffa, K. F., and A. A. Berryman. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* 53:27–49.
- Raffa, K. F., E. N. Powell, and P. A. Townsend. 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proceedings of the National Academy of Sciences USA* 110:2193–2198.
- Régnière, J. 1996. A generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. *Environmental Entomology* 25:869–881.
- Régnière, J., and B. Bentz. 2007. Modeling cold tolerance in the mountain pine beetle, *Dendroctonus ponderosae*. *Journal of Insect Physiology* 53:559–572.
- Rosenzweig, C., et al. 2008. Attributing physical and biological impacts to anthropogenic climate change. *Nature* 453:353–358.
- Rouault, G., J. N. Candau, F. Lieutier, L. M. Nageleisen, J. C. Martin, and N. Warzee. 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Annals of Forest Science* 63:613–624.
- Rupp, D. E., J. T. Abatzoglou, K. C. Hegewisch, and P. W. Mote. 2013. Evaluation of CMIP5 20th century climate simulations for the Pacific Northwest USA. *Journal of Geophysical Research, Atmospheres* 118:10884–10906.
- Safranyik, L., and A. Carroll. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. Pages 3–66 in L. Safranyik and W. R. Wilson, editors. *The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada.
- Safranyik, L., D. A. Linton, R. Silversides, and L. H. McMullen. 1992. Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie* 113:441–450.
- Sambaraju, K. R., A. L. Carroll, J. Zhu, K. Stahl, R. D. Moore, and B. H. Aukema. 2012. Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. *Ecography* 35:211–223.
- Shanahan, E., K. M. Irvine, D. A. Roberts, A. Litt, K. Legg, and R. Daley. 2014. Status of whitebark pine in the Greater Yellowstone Ecosystem: a step-trend analysis comparing 2004–2007 to 2008–2011. *Natural Resource Technical Report NPS/GRYN/NRTR—2014/917*, Fort Collins, Colorado, USA.
- Shore, T. L., and L. Safranyik. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. BC-X-336, Forestry Canada, Victoria, B.C.
- Shore, T. L., L. Safranyik, and J. P. Lemieux. 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. *Canadian Journal of Forest Research* 30:44–49.
- Simard, M., E. N. Powell, K. F. Raffa, and M. G. Turner. 2012. What explains landscape patterns of tree mortality caused by bark beetle outbreaks in Greater Yellowstone? *Global Ecology and Biogeography* 21:556–567.
- Taylor, K. E., R. J. Stouffer, and G. A. Meehl. 2012. An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society* 93:485–498.
- Thornton, P. E., S. W. Running, and M. A. White. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology* 190: 214–251.
- Thrasher, B., J. Xiong, W. Wang, F. Melton, A. Michaelis, and R. Nemani. 2013. Downscaled climate projections suitable for resource management. *Eos, Transactions American Geophysical Union* 94:321–323.
- Tomback, D. F., S. F. Arno, and R. E. Keane. 2001. *Whitebark pine communities: ecology and restoration*. Island Press, Washington, D.C., USA.
- Tomback, D. F., and Y. B. Linhart. 1990. The evolution of bird-dispersing pines. *Evolutionary Ecology* 4:185–219.
- Tomback, D. F., S. K. Sund, and L. A. Hoffmann. 1993. Postfire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 23:113–119.
- Turchin, P., and W. T. Thoeny. 1993. Quantifying dispersal of southern pine beetles with mark recapture experiments and a diffusion model. *Ecological Applications* 3:187–198.
- United States Fish and Wildlife Service. 2011. Endangered and threatened wildlife and plants; 12-month finding on a petition to list *Pinus albicaulis* as endangered or threatened with critical habitat. *Federal Register* 76:42631–42654.
- Weaver, T. 2001. Whitebark pine and its environment. Page 440 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. *Whitebark pine communities: ecology and restoration*. Island Press, Washington, D.C., USA.
- Weed, A. S., M. P. Ayres, and J. A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs* 83:441–470.
- Weed, A. S., B. J. Bentz, M. P. Ayres, and T. P. Holmes. 2015. Geographically variable response of *Dendroctonus*

- ponderosae* to winter warming in the western United States. *Landscape Ecology* 30:1075–1093.
- Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences USA* 108:13165–13170.
- Willmott, C. J., C. M. Rowe, and Y. Mintz. 1985. Climatology of the terrestrial seasonal water cycle. *Journal of Climatology* 5:589–606.
- Wygant, N. D. 1940. Effects of low temperature on the Black Hills beetle (*Dendroctonus ponderosae* Hopkins). Dissertation. State College of New York, Syracuse, New York, USA.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1396/supinfo>

DATA ACCESSIBILITY

Data associated with this manuscript have been deposited in the Northwest Climate Science Center: <https://nccwsc.usgs.gov/display-project/4f8c64d2e4b0546c0c397b46/5006c438e4b0abf7ce733f44>