Ecology, 93(11), 2012, pp. 2421–2434

Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon

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Abstract. Widespread outbreaks of mountain pine beetle in North America have drawn the attention of scientists, forest managers, and the public. There is strong evidence that climate change has contributed to the extent and severity of recent outbreaks. Scientists are interested in quantifying relationships between bark beetle population dynamics and trends in climate. Process models that simulate climate suitability for mountain pine beetle outbreaks have advanced our understanding of beetle population dynamics; however, there are few studies that have assessed their accuracy across multiple outbreaks or at larger spatial scales. This study used the observed number of trees killed by mountain pine beetles per square kilometer in Oregon and Washington, USA, over the past three decades to quantify and assess the influence of climate and weather variables on beetle activity over longer time periods and larger scales than previously studied. Influences of temperature and precipitation in addition to process model output variables were assessed at annual and climatological time scales. The statistical analysis showed that new attacks are more likely to occur at locations with climatological mean August temperatures >15°C. After controlling for beetle pressure, the variables with the largest effect on the odds of an outbreak exceeding a certain size were minimum winter temperature (positive relationship) and drought conditions in current and previous years. Precipitation levels in the year prior to the outbreak had a positive effect, possibly an indication of the influence of this driver on brood size. Two-year cumulative precipitation had a negative effect, a possible indication of the influence of drought on tree stress. Among the process model variables, cold tolerance was the strongest indicator of an outbreak increasing to epidemic size. A weather suitability index developed from the regression analysis indicated a 2.5× increase in the odds of outbreak at locations with highly suitable weather vs. locations with low suitability. The models were useful for estimating expected amounts of damage (total area with outbreaks) and for quantifying the contribution of climate to total damage. Overall, the results confirm the importance of climate and weather on the spatial expansion of bark beetle outbreaks over time.

Key words: adaptive seasonality; aerial detection survey data; climate suitability; Dendroctonus ponderosae; *logistic regression; mountain pine beetle; multinomial probabilities; spatial regression; spline functions.*

Introduction

Recent mesoscale epidemics of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae) in conifer forests of North America have concerned scientists, forest managers, and the public, especially where outbreaks have resulted in expansive areas of dead forests in areas of high social and ecological values. There is strong evidence that climate is a driver of these epidemics (Carroll et al. 2004, Raffa et al. 2008). Given future projections of warming in the coming decades and associated predictions of changes in outbreaks (Logan and Powell 2001, Hicke et al. 2006, Bentz et al. 2010), it is important to understand the effect climate has on these widespread forest disturbances.

Climate plays a major role in influencing large outbreaks of mountain pine beetle through several mechanisms. First, temperatures directly affect beetles. Seasonal temperatures control life stage development rates. Daily temperature regimes exist that synchronize populations (Logan and Powell 2001), thereby maximizing the potential to mass attack and overcome defenses of host trees. Temperatures also control voltinism: a one-year life cycle allows populations to build more quickly than multi-year life cycles as well as possibly avoid unfavorable weather conditions. In addition, temperatures influence developmental timing that ensures that the appropriate life stage enters the cold season. Year-round temperatures that cause synchronous emergence of a beetle population at an

Manuscript received 3 August 2011; revised 9 April 2012; accepted 30 April 2012. Corresponding Editor: J. D. Reeve.

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appropriate time of year with a one-year life cycle result in "adaptive seasonality" (Logan and Powell 2001). Temperature also controls beetle cold tolerance in winter. Beetle larvae progressively develop cold tolerance with decreasing fall temperatures, but abnormally cold weather results in mortality (Régnière and Bentz 2007). Temperatures below −15°C to −40°C can result in significant larval mortality (Wygant 1940). Finally, thermal effects (August temperatures) have also been noted for flight characteristics and mass attack success of mountain pine beetles (McCambridge 1971), and thus have been included in a climate suitability model (Carroll et al. 2004).

Second, climate impacts on beetle dynamics are manifested in the host trees because tree defense mechanisms can be compromised under high temperatures and drought (Raffa et al. 2008, Bentz et al. 2010; A. L. Carroll, J. Régnière, S. W. Taylor, and L. Safranyik, *unpublished manuscript*). For instance, unstressed lodgepole pine (*Pinus contorta*) has a significant capacity to mount defenses against mountain pine beetle attack, including exuding toxin resin to pitch out attacking beetles (Raffa et al. 2008). However, drought stress may make host trees more susceptible to attack, because such trees cannot produce resin in sufficient quantities (Safranyik et al. 1975, Raffa et al. 2008, Grulke et al. 2009). Drought stress also reduces tree phloem thickness, and phloem thickness has been shown to be positively related to beetle brood production (Amman and Cole 1983). Thus, beetle epidemics may also be facilitated by healthy, unstressed trees.

Studies of climate drivers of bark beetle outbreaks have used process models representing one or more of these influences. Models of adaptive seasonality have been generated from laboratory measurements of life stage development rates (Bentz et al. 1991, Logan and Powell 2001) as well as from empirical methods based on degree-days (Safranyik et al. 1975, Carroll et al. 2004). Logan and Powell (2009) demonstrated that when model results indicated adaptive seasonality in the Sawtooth Valley region of central Idaho, USA, observed attacks by mountain pine beetle increased as well. Simple (Carroll et al. 2004) and more complex (Régnière and Bentz 2007) models have been developed to simulate cold tolerance. Régnière and Bentz (2007) showed good agreement between their mechanistic model of cold tolerance and observations of beetle supercooling points. A model incorporating drought stress has been developed from observations of mountain pine beetle outbreaks and precipitation (Safranyik et al. 1975, Thomson and Shrimpton 1984, Carroll et al. 2004).

Statistical analyses have also informed our understanding of climate drivers. Williams and Liebhold (2002) found that temperature and precipitation in several months were important variables for explaining mountain pine beetle outbreaks in the northwestern United States in their study of the effects of climate change on future bark beetle outbreaks. Aukema et al. (2008) statistically analyzed presence/absence of mountain pine beetle attacks within the area of one outbreak in British Columbia, Canada, considering neighborhood beetle populations, temperature metrics, and topography as drivers. The authors identified several temperature variables in addition to beetle presence in surrounding cells that significantly affect probability of beetle presence. Duehl et al. (2011) performed a similar analysis for southern pine beetle outbreaks in the southeastern United States, also reporting the importance of nearby beetle populations and climate.

Despite these and other studies, our understanding of the relative importance of the three primary climate drivers discussed above (adaptive seasonality, winter mortality, drought stress on hosts) on mountain pine beetle outbreaks is limited. Climatological variables have been used in past studies as indicators of climate suitability, for example, as part of forecasting climate change effects (Hicke et al. 2006, Bentz et al. 2010). Empirical validation of the laboratory-derived suitability models under a range of conditions and for multiple mountain pine beetle outbreaks over large areas has not been conducted. Yet such understanding is critical for developing and evaluating predictions of these epidemics at large spatial scales, particularly in view of future climate change projections that could significantly alter key climate drivers of beetle outbreaks.

Here we examined the extent to which individual climate and weather variables and climate suitability indices produced by process models can explain the spatial and temporal patterns of three decades of mountain pine beetle epidemics over 50 672 km^2 of lodgepole pine forests in Oregon and Washington, USA. Spatial data on historical mountain pine beetle outbreaks were obtained from annual survey data collected by the USDA Forest Service. We examined the explanatory ability of simple climate variables (e.g., mean annual temperatures) as well as complex climate suitability indices developed from simulation models. We assessed explanatory variables in terms of both short-term (annual) and long-term climatological (means over three decades) time scales. The long-term time scale is the one that has been presented in previous studies (Carroll et al. 2004, Bentz et al. 2010, Safranyik et al. 2010). Our focus was to study influences of weather drivers on mountain pine beetle outbreaks within 1-km^2 grid cells. The findings of the study contribute to the broader understanding of the potential effects of climate change on mountain pine beetle epidemics.

METHODS

Study area and data

The study area consisted of lodgepole pine forests in Oregon and Washington, USA (Fig. 1). We determined the location of stands composed primarily of lodgepole pine using three data sources: (1) a 1-km map of forest types from satellite observations (Zhu and Evans 1994); (2) a 30-m map of forest types from a classification of

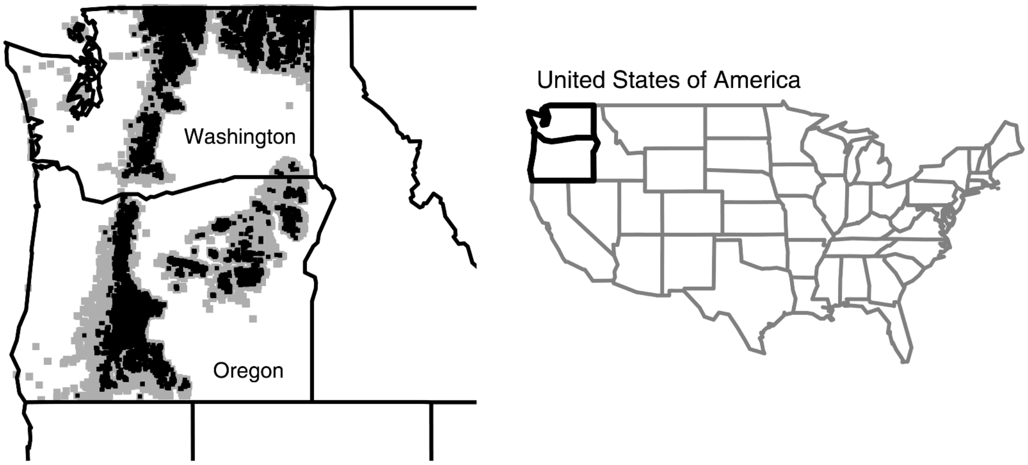

FIG. 1. Lodgepole pine forests in Oregon and Washington, USA (gray) and 1-km^2 cells with >100 trees killed by mountain pine beetle (small black squares, which merge together) in at least one year during the study period 1980–2006.

Landsat imagery produced by the USGS Gap Analysis (*available online*);[5] and (3) a similar map of existing vegetation types from 30-m Landsat imagery published by the LANDFIRE program (Rollins and Frame 2006; *available online*).[6] We combined the data sources by assuming the presence of lodgepole pine if any of the three data sources listed its presence. The resulting host map covered 5 067 200 ha, located primarily on the central and eastern portions of the states, corresponding to 50 672 1-km^2 grid cells.

Response variables

Our response variables were derived from the number of trees killed by mountain pine beetle, which we used as an indicator of beetle populations. We used the Aerial Detection Survey (ADS) database maintained by Forest Health Protection in Region 6 (Washington and Oregon) of the USDA Forest Service (*available online*).[7] ADS data have been widely analyzed for monitoring and other assessments by forest health staff in the Forest Service (Johnson and Wittwer 2006, 2008). The data were collected with aerial sketchmapping procedures in which the locations of infestations were mapped annually. Flights typically occurred in late summer, and the observer estimated several attributes, including the infested area boundaries; the density (trees per unit area) of newly attacked trees based on the presence of red needles; and host tree species and damage causal agent (in our case, mountain pine beetle attacking lodgepole pine).

Because a one-year lag exists between beetle attack and the appearance of red needles, the ADS data actually identify trees attacked in the prior year. Mountain pine beetles disperse to new trees in late summer, and successfully attacked trees are girdled during egg gallery construction and inoculated with fungi that penetrate the xylem. However, needles on attacked trees do not turn red (and thus are not observable by ADS sketchmappers) until the following summer. Thus we defined the attack year as the year prior to when ADS reported red trees.

Tree mortality due to beetle outbreaks was aggregated from the ADS database for each 1 × 1 km grid cell in the study area, and for each year between 1980 and 2006. Thus all data were kilometer × kilometer × year voxels (grid cells/pixels [locations] by time [year]). Our initial analysis used the number of trees killed as the response variable. However, it was difficult to detect influences of the explanatory variables on the exact numbers of trees killed due to the amount of noise in such data. As an alternative, we decided to group the number of trees killed into four classes, as explained below, and study the influence of the climate drivers on each of these classes.

Outbreak classes.—We classified outbreaks by number of killed trees per voxel. Class 0: 0–2.5 trees killed per voxel. Class I: 2.5–100 trees killed per voxel. Class II: 100–1000 trees killed per voxel. Class III: $\geq$1000 trees killed per voxel. A 2.5 trees killed cutoff point was used following Amman (1984), who identified 2.5 trees killed/km^2 as a threshold between endemic (background) and epidemic population levels.

Outbreak initiation (new attacks).—Cells in Class I and higher categories ($\geq$2.5 trees killed) were defined as being in the outbreak initiation stage when they were surrounded by cells that were in endemic stage in the previous year (<2.5 trees killed).

Explanatory variables

We divided explanatory variables into three major groups as follows (Table 1 and Appendix C).

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[5] http://gap.uidaho.edu/index.php/gap-home/Northwest-GAP/landcover

[6] http://landfire.cr.usgs.gov/NationalProductDescriptions21.php

[7] http://www.fs.fed.us/r6/nr/fid/as/index.shtml

TABLE 1. Description of the explanatory variables used in the study.

Variable	Description
A) Variables included in all models	
btp	beetle pressure within neighborhood in previous year
ctree5	cumulative number of trees killed over previous five years
spatial	longitude and latitude of center of cell
B) Weather and process-modeled output variables; annual time scale	
Drought variables	
prec01	cumulative precipitation (Jun–Aug) in current and previous year
prec1	precipitation (Jun–Aug) in previous year
water01	cumulative precipitation (Oct –Sep) in current and previous year
water1	precipitation (Oct–Sep) in previous year
moist01	cumulative 1 Sep soil moisture (0–40 cm depth) (mm) current and previous year
moist1	1 Sep soil moisture (0–40 cm depth) (mm) in previous year
Mean temperature	
tmean	mean temperature between Oct and Sep
tmaa	mean temperature between Apr and Aug
tma	mean temperature for Aug
Loganp and Loganb	logan probability; adaptive seasonality (see Appendix A)
Minimum winter temperature	
tmin	minimum monthly temperature between Dec and Feb
coldt	probability of winter survival based on cold tolerance (see Appendix A)
Climate suitability	
SafP3P4 and SafP4	Safranyik model (see Appendix A)
C) Climatological variables	
All variables in B above (except for the lagged variables) evaluated over the 27-year study period.	

Variables included in all models.—

1) *Beetle pressure in the previous year* (btp). Beetle pressure represented the size and proximity of nearby beetle populations that can disperse and attack other stands (Shore and Safranyik 1992). Greater beetle pressure (from either closer and/or larger beetle populations) is expected to result in higher probability of tree mortality in a stand (Shore and Safranyik 1992). Few studies have documented the dispersal distances of mountain pine beetles and bark beetles generally, with reports including dispersal events within 30–500 m (Safranyik et al. 1992, Robertson et al. 2007, Kautz et al. 2011) or within 5 km (Turchin and Thoeny 1993, Wallin and Raffa 2004, Raffa et al. 2008), and low-probability, long-distance events (Safranyik and Carroll 2006, Chen and Walton 2011). In this study, the spatial resolution of our grid (1 km^2) is comparable to the size of a stand and $>$500 m, suggesting that many dispersal events are within a grid cell. We also included nearby cells that may be a source of dispersing beetles. We calculated the beetle population in the surrounding neighborhood using inverse-distance weighting of the number of trees killed in the cell of interest and in surrounding cells (out to 10 km). We applied an inverse sigmoidal curve with weights of 1 in the cell of interest and 0.5 and 0.1 at cells 3 and 6 km distant, respectively. Beetle pressure was defined as the beetle population size in this neighborhood in the previous year. The population was considered endemic if btp $<$ 2.5. An examination of effect of beetle pressure at lag times longer than one year indicated no discernible effect on beetle populations when included in models with previous year btp.
2) *Cumulative number of trees killed in a 1×1 km cell in the previous five years* (ctree5). The variable ctree5 was used as a surrogate for the number of uninfested host trees (which we did not have); mountain pine beetle populations are dependent on the presence and density of host trees within a stand (Shore and Safranyik 1992).
3) *A spatial location variable (longitude, latitude)* (spatial). The spatial location variable was used as a surrogate for effects such as soil fertility or other site conditions that were not available but may have affected mountain pine beetle population levels in the study area. The spatial term accounts for correlations in the data due to persistent trends in the landscape that are not changing over time.

Annual weather variables and process model outputs.— Daily weather data from local weather station observations within the study area and for the period 1980–2006 were interpolated for each voxel via inverse distance weighting and vertical lapse rates. We used the BioSIM program for this purpose (Régnière et al. 1996) and generated both temperature and precipitation variables (Table 1). BioSIM was also used to generate annual outputs of modeled climate suitability indices for mountain pine beetle (Loganp, Loganb, Coldt, SafP3P4, and SafP4) (Safranyik et al. 2010) (Table 1 and

Appendix A). We also included soil moisture (0–40 cm, top two model layers) for 1 September from the Variable Infiltration Capacity (VIC) model (Elsner et al. 2010), which represented a measure of tree stress in the early fall. A plot of a select group of annual weather variables averaged over the study area (Appendix D: Fig. D1) demonstrates some of the overall trends in these variables over the study period.

Climatological variables.—The weather variables described previously were averaged over the 27 years in our study (1980–2006) to generate variables that described the long-term climate in the study area. Long-term climate suitability indices were also generated with BioSIM.

Weather and climate explanatory variables were categorized into three groups that represented the different climate drivers of mountain pine beetle outbreaks according to past literature: adaptive seasonality (based on year-round temperatures), winter mortality (based on minimum cold-season temperatures), drought-related host tree stress (based on two-year cumulative precipitation), and brood size (based on amount of precipitation in the previous year, which influences production of brood that emerges in the current year). The relative importance of explanatory variables within each group was then assessed to identify the most influential variables in that group.

Statistical methods

We used logistic regression to identify the explanatory variables most influential on the probabilities of outbreak initiation (new attacks) and intensification, and to quantify the skill of these variables in predicting large outbreaks at specific locations. The logistic regression equation was

$$\text{logit}(p) = \log - \text{odds} = \beta_0 + s(\text{lon}, \text{lat}) + \sum_m s_m(X_m) \qquad (1)$$

where p was either the probability of outbreak initiation or intensification (further details are given in Appendix B); lon, lat, were the longitude and latitude of the 1-km^2 grid cell; X_m, for $m = 1, \ldots, M$ is the vector of values of the mth explanatory variable; s(lon, lat) is a time-invariant, two-dimensional cubic spline for the location variables, and $s_m(X_m)$ are tensor product smooth functions of the explanatory variables (Wood 2006). Plots of the estimated smooth functions describe the potentially nonlinear relationships between each of the explanatory variables and the log-odds of the probabilities, after controlling for the rest of the variables in the model.

Variable selection was done using the following stepwise regression (Appendix C: Tables C1–C4). All models included beetle pressure in the surrounding cells in the previous year (btp), and cumulative number of trees killed in the previous five years (ctree5). All models except those with the climatological variables also included spatial location (lon, lat). Having the above variables in each model allowed us to select and study the effects of each of the weather drivers after controlling for differences in beetle pressure and host conditions in each voxel. We considered three groups of variables that represented the three climate/weather processes (Table 1). At each selection step, only one type of variable from each group was included in the model. For example, no model included both precipitation and soil moisture. However, lagged values of the same variable (e.g., precipitation for the present and previous year) were tested by including multiple lags at each selection step. The variable from each group that produced the largest drop in the Akaike Information Criteria (AIC) was selected.

We assessed the level of spatial correlation in the data by producing correlogram plots measuring the correlation between data points at various distances from each other. Spatial correlation in the residuals was minimal (<0.13) at distances >4 km (Appendix D: Fig. D2). Significance of each of the selected drivers in the "best" model was assessed using jackknife standard errors, rather than the standard errors produced directly by the statistical package, in order to account for between-year variability (i.e., a random year effect). Jackknife standard errors were evaluated from 27 different estimates for each of the parameters of concern. Each estimate uses data from all years but one (see Appendix B for details).

For the analyses involving the long-term climatological variables, all models included btp and ctree5. We did not include the spatial location variable because many of the climatological variables exhibited a spatial trend. For example, there was a strong decreasing west–east trend in the values of the climatological cold tolerance variable. Because these variables did not change over the span of the study (unlike the annual variables), they were confounded with a spatial term that also mainly estimates trends over space. This confounding effect makes it difficult to interpret the results for the climatological variables.

Goodness-of-fit of the logistic regression was assessed by first grouping the data over space to produce observed and expected trends of large outbreaks over time. Specifically, by summing the estimated probabilities of a Class II or larger outbreak over all grid cells in a given year, we estimated the expected area (in square kilometers) with >100 trees killed in Oregon and Washington separately. We compared this number to the observed total area in Washington or Oregon (lodgepole pine lands) that had at least 100 trees killed by mountain pine beetle. For our 1-km^2 grid cells, total area is the same as total number of grid cells. Because the number of beetles in the previous year is likely to be a strong predictor of outbreak size in the next year, we anticipated that most of the models ability to predict observed outbreak sizes would be due to beetle pressure and thus would mask the contribution of weather. To

Table 2. List of the selected annual variables with significant influence on mountain pine beetle outbreaks in a 1 km × 1 km × 1 year voxel.

	Outbreak class								
	New attacks†			≥Class II‡			≥Class III§		
Variable	Sign¶	df#	ΔAIC‖	Sign	df	ΔAIC	Sign	df	ΔAIC
spatial	var	22	2233	var	22	1873	var	19	980
btp	na††	na	na	+	4	9938	+	4	1277
ctree5	0	–	–	var	4	973	var	4	628
coldt	0	–	–	na	na	na	+	4	205
tmin	na	na	na	+	4	1897	na	na	na
tmean	na	na	na	var	4	1276	na	na	na
tmaa	0	–	–	na	na	na	+	4	224
prec01	var	4	799	–	4	465	–	0	–
prec1	var	4	962	+	4	1547	–	4	434

Notes: Only variables found to have significant influence on at least one of the probability classes are included in the table. The variables are defined in Table 1.

† New attacks represent at least 2.5 trees killed by mountain pine beetles at locations with negligible previous year attacks (<2.5 trees killed in neighborhood in previous year).

‡ ≥Class II are at least 100 trees killed by mountain pine beetles in cells with beetle presence (≥2.5 trees killed).

§ ≥Class III are at least 1000 trees killed by mountain pine beetles in cells with ≥Class II outbreaks (≥100 trees killed).

¶ The + symbol indicates an overall increasing influence; – indicates a decreasing influence; 0 no significant influence, and var indicates both increasing and decreasing influence. The exact shapes of these relationships are seen in Fig. 2 and Appendix D: Figs. D3 and D4.

Degrees of freedom of the smooth term; df = 1 indicates a linear relationship.

‖ Amount of increase in AIC when the variable is removed from the model. Larger increases indicate greater relative influence.

†† Not applicable. Throughout the table "na" indicates that the variable was not selected (via AIC analysis) to be included in the model (see Appendix C: Table C1), or for new attacks, it was not included because beetle pressure in the surrounding area in the previous year is negligible by definition of new attacks (btp < 2.5).

ascertain the total contribution of the weather variables on the estimated total area attacked in a given year while keeping beetle pressure constant, we calculated a measure of the contribution of each type of driver (beetle pressure vs. weather) using a weighted average of the corresponding additive terms in the logistic model (Eq. 1). Additional details of these analyses are included in Appendix B. The contribution of the individual weather variables on the probability of outbreaks was studied via the plot of the estimated odds from the logistic regression fit as described previously.

We also studied the goodness-of-fit of our model in predicting the spatial distribution of large outbreaks in the last three years (2004–2006) by first estimating the parameters of the selected model using only prior years' data (before 2004). Next we produced maps showing locations with predicted low, medium, high, or extreme probabilities for 2004–2006, and compared those with the observed locations of large outbreaks for the corresponding years. The four categories based on the predicted probabilities are: low = 0.0–0.25; medium = 0.25–0.5; high = 0.5–0.75; extreme = 0.75–1.00. We expect that the fraction of observed large outbreaks among all voxels with a low prediction to be 0–0.25, and so on for the other categories.

Finally, we produced a table showing the observed increase in the odds of Class II outbreaks or greater given beetle presence in the cell, for voxels with low and high weather suitability. We evaluated an overall weather suitability index by summing the estimates of the weather terms in the logit line (Eq. 1). Weather conditions in a given voxel were defined as highly suitable if the sum of the weather terms was greater than the 75th percentile of the index, and low if it is less than the 25th percentile. Because the logit-line is the log-odds of an outbreak, higher values of the suitability index imply higher odds when all other terms in the model are kept fixed. To control for the variable beetle pressure, odds in each of the high and low suitability groups were calculated after grouping the voxels in five categories according to the observed surrounding beetle pressure in the previous year (btp).

Results

Influence of annual variables

Beetle pressure in the previous year was one of the most important variables for all stages of mountain pine beetle outbreaks. The estimated odds of Class I or greater outbreaks (i.e., presence of killed trees) in a cell surrounded by attacks in previous years (btp ≥ 2.5) was on average 30 times larger than for new attacks. The probability of new attacks, i.e., attacks being introduced to a new location where beetle pressure in the surrounding area in the previous year was negligible (<2.5), was marginally influenced by the precipitation levels in current and previous years (Table 2; Appendix C: Table C1 and Appendix D: Fig. D3). New attacks appeared to be more likely at locations with low two-year cumulative precipitation and low previous-year precipitation (Fig. D3e, f). The cold tolerance (coldt) and April to August mean temperature (tmaa) variables, although selected as the best variables in their group

(Appendix C: Table C1), were not found to have significant effects on the probability of new attacks (Appendix D: Fig. D3b, c). In summary, none of the tested variables had a large influence on the probability of new attacks in areas lacking prior mountain pine beetle activity.

The most influential variable for intensification of outbreaks (i.e., Class II or greater) was previous year beetle pressure (Table 2). The estimated log-odds increased sharply with increasing pressure up to ~50 000 trees, after which the effect seemed to level off (Fig. 2b). The cumulative number of dead trees was also significant. The log-odds increased with increasing ctree5 up to ~2000 trees/km^2, after which the odds decreased, possibly as an indication of a decrease in the number of available host trees (Fig. 2c). The influence of the spatial term, which may be considered as a surrogate for stand conditions and topography, although significant, was smaller than that of the combined weather variables (Table 2). The weather variables selected from each of the groups were tmin, tmean, prec01, and prec1 (Appendix C: Table C2). The influence of the weather variables tmin and tmean was significant with the log-odds increasing with increasing tmin values above −10°C and decreasing with tmean values above 1°C (Fig. 2d, e). For the selected drought variables (precipitation), the pattern was as follows: the odds of at least a Class II outbreak increased with increasing precipitation in the previous year but decreased with increasing two-year cumulative precipitation (Fig. 2f, g).

For the largest outbreak class in our study, the weather drivers that appeared to be most influential on outbreak transition from Class II to Class III were coldt followed by tmaa (Table 2; Appendix D: Fig. D4). The odds of a Class III outbreak in voxels with at least Class II increased 4.5-fold as coldt increased from 0 to 0.5. However, no additional increase in the odds was seen for cold tolerance values greater than 0.4 (Fig. D4).

Influence of climatological variables

The three long-term average (climatological) variables selected by the AIC analysis to be included in the model for probability of new attacks were coldt, tma, and prec (Appendix C: Table C3). A spatial component was not included in the study of the climatological variables for the reasons given in *Statistical methods*. Of the three climatological variables, only the mean August temperature (tma) had a statistically significant influence on probability of new attacks (Table 3; Appendix D: Fig. D5a). The log-odds for new attacks increased linearly with tma values >15°C. This result needs to be interpreted with caution, given the confounding effect of the climatological variables with location-related effects (e.g., elevation, aspect, soil conditions). However, the significant influence of tma was consistent with mountain pine beetle ecology (Bentz et al. 2010), and it is likely that the landscape-scale relationship seen here between temperature and outbreak initiation is not simply spurious. Further studies are required (possibly on a larger landscape) to arrive at more conclusive results regarding beetle outbreak initiation.

The three climatological variables selected for Class II outbreaks or greater were coldt, tmean, and precipitation (Appendix C: Table C4). Of these variables, the influence of coldt and tmean were statistically significant, with coldt having the largest influence (Table 3; Appendix D: Fig. D5b). We found an estimated 1.3 ± 2 times increase (mean ± SE), interval = 1.2–1.5) in the odds of an outbreak of at least Class II for each 0.1 increase in coldt. There was a 3.5 (3–4) times increase in the odds over the range of coldt (range = 0.6) observed in the region. For the conditional probability of Class III outbreak, variables coldt and tmean were found to have significant effects (Table 3; Appendix C: Table C3 and Appendix D: Fig. D5c). None of the climatological drought variables had a significant effect on outbreak initiation or intensification. This may not be surprising given that the climatological variable is on average >27 years and our results on the annual variables indicated a lagged effect of drought, with the different lags having opposite effects.

Model assessment and regional level results

Total area affected by mountain pine beetle attacks per year was predicted for each state (Oregon and Washington) and plotted against time (Fig. 3). The outputs reproduced the fluctuations in the observed numbers, and in particular the increasing trend of attacks starting in the year 2000 (Fig. 3). However, the model did not predict as large a drop in the beetle activity observed in the ADS data for Oregon between 1987 and 1988. Scarcity of suitable hosts during these years may be a reason for this sharp drop in area attacked. A better measure of host availability than the one used (ctree5) in our study may improve results.

We studied the partial contributions of the two main groups of explanatory variables, the combined weather variables and the beetle pressure variable, on the total area attacked in a given year to understand the combined influence of weather after controlling for beetle presence in the region (Fig. 4). Consistent with our results above, beetle pressure had the largest influence on the probability of intensification of an outbreak. Also consistent with our logistic regression results, these figures demonstrate the role weather plays in increasing and decreasing outbreaks at the landscape level. Increasing beetle populations in Oregon in the early 1980s and 2000s and in Washington in the early 2000s appear to be facilitated by favorable weather conditions in those years. In contrast, outbreak levels in Oregon in 1985–1987 decreased because weather was unsuitable despite high pressure.

As a further check of the influence of weather on beetle outbreaks, we calculated the observed odds of an outbreak for voxels with low and high overall weather suitability (Table 4). Regardless of the beetle pressure,

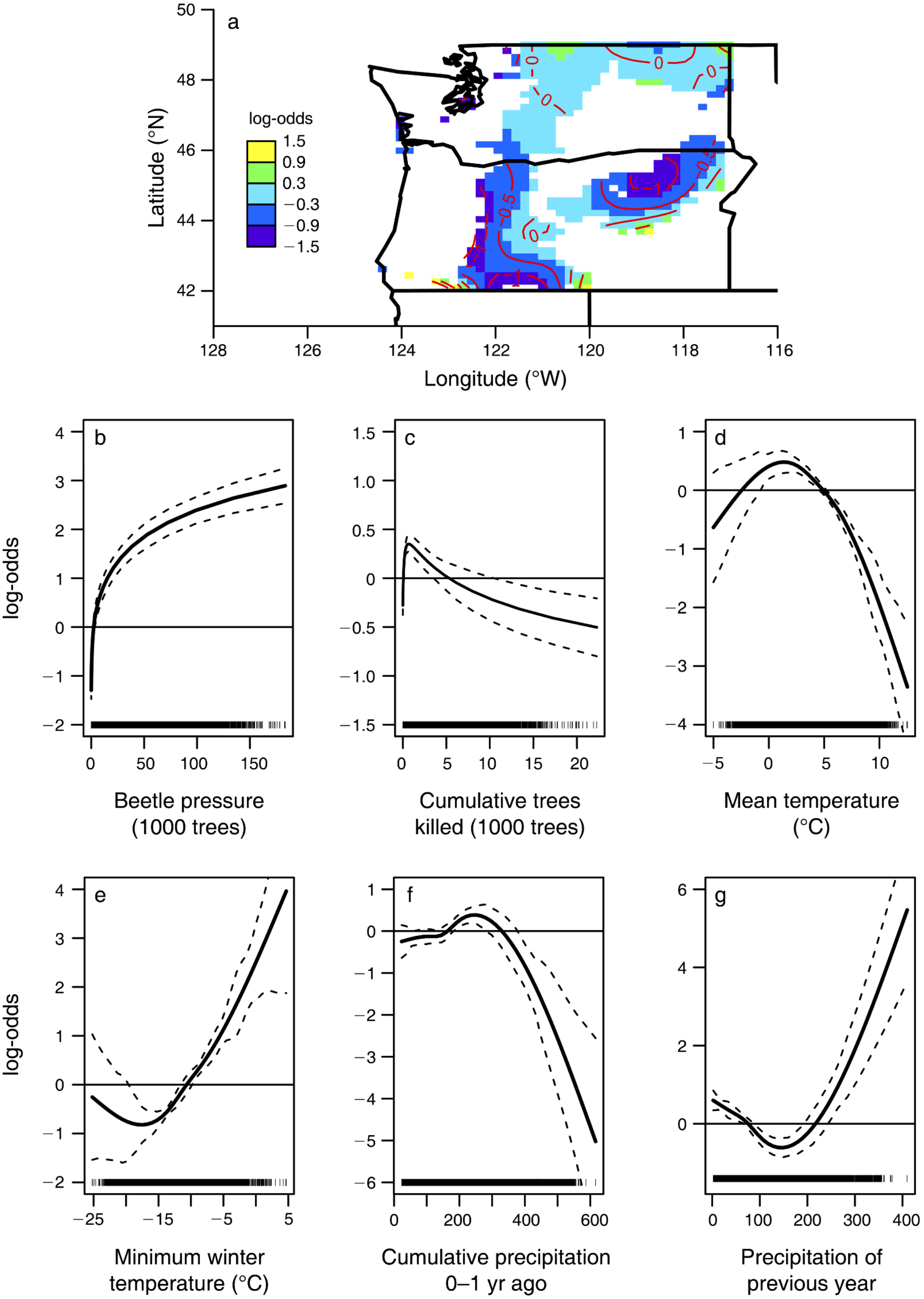


FIG. 2. Estimated change in log-odds for the conditional probability of at least 100 trees killed in a 1 km × 1 km × 1 year voxel (at least Class II) due to the influence of (a) the spatial variables, (b) beetle pressure, (c) cumulative trees killed, and (d, e, f, g) the climate/weather variables selected from each of the groups listed in Table 1. A variable is assumed significant if the ±2 SE bands (dashed lines) do not include the horizontal line at zero. Hatched marks at the bottom are the locations of the observed values for the corresponding variable. (Gaps indicate that there were no observations.)

TABLE 3. A list of the selected climatological variables with significant influence on mountain pine beetle outbreaks in a 1 km × 1 km × 1 year voxel.

	New attacks			≥ Class II			≥ Class III		
Variable†	Sign	df	ΔAIC	Sign	df	ΔAIC	Sign	df	ΔAIC
btp	na	na	na	+	4	11 516	+	4	1309
ctree5	na	na	na	var‡	3	381	var	4	496
coldt	0	–	–	+	4	888	+	3	581
tmean	na	na	na	var	3	381	var	4	545
tma	+	4	248	na	na	na	na	na	na

Note: Only variables found to have significant influence on at least one of the probability classes are included in the table.

† No spatial term was included in models when studying the climatological variables. See *Methods* for further details.

‡ The shape of the relationships between the various variables and the odds of attack for each of the classes is seen in Appendix D: Fig. D5.

the odds of a Class II or larger outbreak in voxels with highly suitable weather conditions (in the upper 75th percentile) was ~2.5 times larger than the odds in corresponding voxels with low weather suitability (in the lower 25th percentile).

Maps of predicted low, medium, high, or extreme probabilities for the likelihood of Class II outbreaks for 2004–2006 demonstrate the models' ability to predict locations of outbreaks (Fig. 5). Good spatial agreement was observed between predicted and observed outbreak areas. Agreement between observed and predicted values is also seen for 2004–2006 when the observed frequency of outbreaks is compared to the predicted range of probabilities in each category (Table 5). For example, for voxels in the high category, the observed frequency of voxels with large outbreaks for the years 2004–2006 were all in the predicted range of 0.5–0.75. The same comparisons for 1988 were not as good. Here the model overestimated the frequency of attacks in each category. This result is another indication that the variables in our model (and in particular the ctree 5 variable) were not adequate for predicting the sharp drop in attacks between 1987 and 1988, and that a better measure of host availability may improve model predictions.

Discussion and Conclusions

Among all the variables tested in this study, the most influential on the probability of outbreak intensification was beetle pressure in the neighborhood in the previous year. The number of beetles that disperse within a stand (grid cell) as well as from neighboring stands (as represented in our analysis) to attack new hosts is critical for determining the success of beetles in killing host trees (Shore and Safranyik 1992, Safranyik and Carroll 2006). Cumulative number of killed trees was an

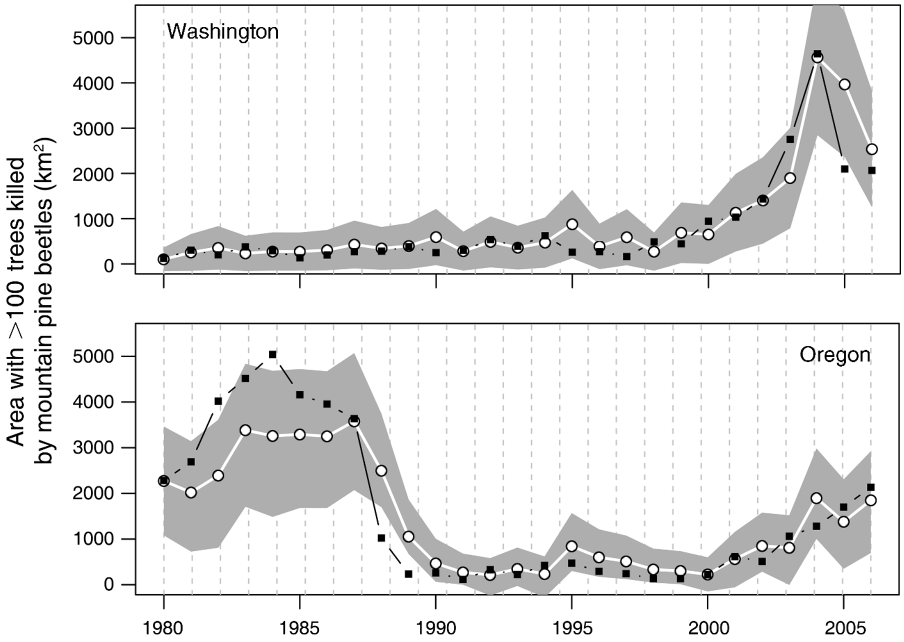


FIG. 3. Observed (solid squares) and estimated (open circles) area (measured in km^2) with at least 100 trees killed by mountain pine beetle (at least Class II) in a given year, grouped by state. The shaded gray area is the ~95% confidence bounds of the estimated curve.

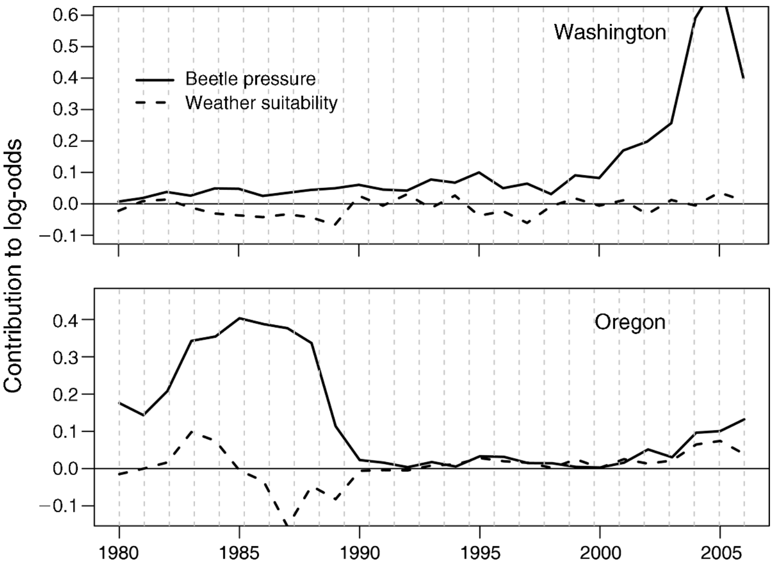


FIG. 4. Estimated incremental contribution of beetle pressure (solid curve) and weather suitability (dashed curve) to the probability of ≥Class II outbreaks within the entire study area in Washington (top panel) and Oregon (bottom panel). Contributions were weighted by the estimated probability of beetle presence in a cell to focus on cells with beetle attack only.

important explanatory variable as well, showing a positive effect at low mortality values, probably related to correlation with beetle pressure, and then a negative relationship as mortality increased, representing stands in which the lack of an available host limited subsequent beetle attacks.

Weather variables, including mean annual temperature, summer precipitation, and winter low temperature, had significant effects on outbreak intensification (Table 6). Higher winter temperatures were associated with increased odds of large outbreaks, likely because of increased winter survival of beetles. In contrast, intermediate mean annual temperatures, which represent the effect of year-round temperatures on adaptive seasonality, were optimal for large outbreaks. Higher temperatures decreased the odds of large outbreaks, perhaps related to conditions too warm to support adaptive seasonality, as suggested by previous modeling studies (Hicke et al. 2006, Bentz et al. 2010, Littell et al. 2010). There was some evidence that precipitation in the previous year had increased the probability of outbreak intensification; we hypothesize that this effect may be related to increased beetle brood production with thicker phloem (Amman and Cole 1983). The relationship with total precipitation 0–1 years prior indicated the role of drought stress on hosts and a negative relationship between precipitation and outbreaks (Safranyik et al. 1975, Raffa et al. 2008).

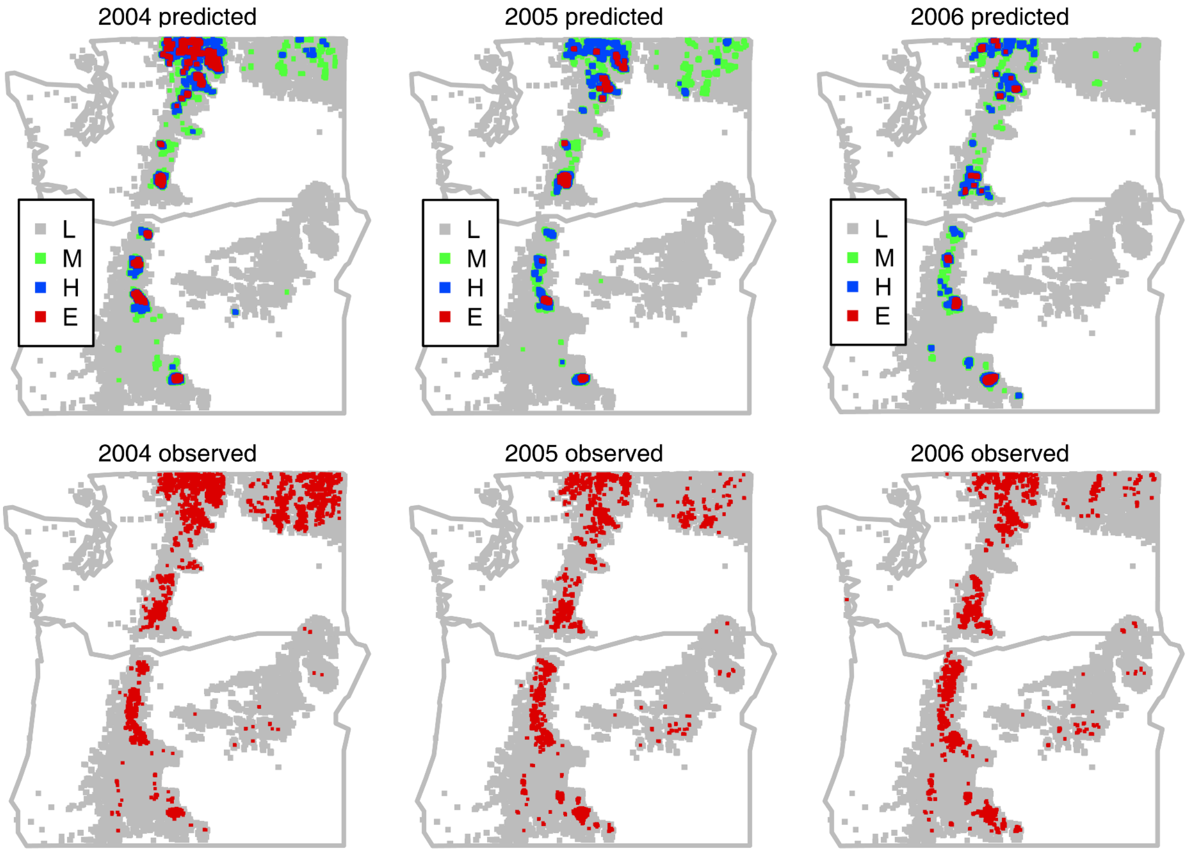
Except for cold tolerance, climate suitability indices from process models (e.g., Logan probability of adaptive seasonality) were not selected in any of our models as alternatives to the weather variables used in developing these indices. In the models of outbreak initiation, the cold tolerance variable decreased AIC slightly more than minimum winter temperature. In the models of larger outbreaks, cold tolerance decreased

TABLE 4. The observed percentage of voxels with >100 trees killed per beetle pressure category grouped for voxels with high or low weather suitability.

Beetle pressure (btp)	Voxels observed				High to low odds ratio
	Low suitability†		High suitability		
	Voxels (%)	Sample size	Voxels (%)	Sample size	
0, 10	10	2 444	22	2 911	2.5
10, 100	10	2 814	22	3 670	2.5
100, 1500	22	8 534	39	9 878	2.3
(1.5–15) × 10^4	44	13 129	63	14 066	2.2
(15–150) × 10^4	67	7 902	85	5 078	2.7

Note: Regardless of the beetle pressure, the odds of a Class II or larger outbreak are ~2.5 times larger in voxels with highly suitable weather when compared to voxels with low weather suitability.

† Weather suitability is defined as low when the sum of the estimated weather terms in the logistic regression is in the lower 25th percentile and high when it is in the upper 75th percentile.


2004 predicted

2005 predicted

2006 predicted

2004 observed

2005 observed

2006 observed

FIG. 5. (Top panels) Predicted probabilities of at least 100 trees killed per km^2 (at least Class II) grouped into four categories (L, <0.25; M, 0.25–0.5; H, 0.5–0.75; E, >0.75). (Bottom panels) Study area (gray) and outbreak cells with at least 100 trees killed per km^2 (red).

AIC substantially compared with winter temperature, suggesting that the model for cold tolerance (Régnière and Bentz 2007) is useful for predicting transition of outbreaks to epidemics at regional scales, although the relationship is not linear. There are several possible reasons for the lack of additional explanatory power provided by process model results. First, population-scale genetic variation exists in the climate response of mountain pine beetles (Bentz et al. 2001, Mock et al. 2007); the Logan model of adaptive seasonality was not developed with populations from our study region (Bentz et al. 1991). In addition, the Logan adaptive seasonality model included in BioSIM results in a binary outcome (0, 1) only under optimal thermal conditions. However, near-optimal thermal conditions could still produce large populations of beetles that are effective at mass dispersal and attack, suggesting that the model may be too restrictive in its outcomes (Bentz et al. 2010). Another explanation is that the BioSIM mountain pine beetle model does not consider temporal lags in drought or the potential positive effects of precipitation (Safranyik et al. 2010). Our study indicates that the intensification of an outbreak was more likely when there were drought conditions 0–1 years prior, and wetter conditions during the year before an outbreak.

Although weather variables were not as important as beetle pressure (Fig. 4) when estimating probabilities of large outbreaks, they were ecologically significant at critical times. First, larger positive contributions of

TABLE 5. Observed fraction of voxels with >100 trees killed per probability category developed for four selected years. Voxels are assigned to one of four categories (low, medium, high, extreme) based on their predicted probabilities.

	Predicted probability category			
Year	Low 0.0–0.25	Medium 0.25–0.50	High 0.50–0.75	Extreme 0.75–1.00
2004	0.020	0.39	0.59	0.81
2005	0.010	0.46	0.74	0.86
2006	0.120	0.32	0.62	0.82
1988	0.002	0.20	0.21	0.49

Notes: In each category, the observed number of voxels with more than 100 trees killed was divided by the total number of voxels in that category to obtain the values in the table. For a good fit, the observed fractions should be within the predicted probability range in the corresponding category. Lower than expected values are observed in all categories for 1988 (see possible explanation in *Results: Model assessment and regional level results*).

TABLE 6. A summary of the influential drivers for optimal conditions for a large outbreak.

Driver variable	Potential explanation	Optimal conditions for large outbreaks
Beetle pressure	beetle pressure	high levels
Number of trees killed in past five years	available host for beetles	lower levels
Minimum winter temperature	beetle mortality from very cold conditions	highest levels (> −5°C)
Year-round temperature	adaptive seasonality: one-year life cycle synchrony of mass attack emergence at appropriate time of year	intermediate levels (0–2°C)
Precipitation in previous year	thickness of phloem/quantity of food resource	highest levels (>200 mm)
Cumulative precipitation in current and previous year	drought stress of host trees	lowest levels (<200 mm)

weather occurred at the beginning of major epidemics, aiding population increases (Fig. 4). Second, weather variables contributed to population decreases in Oregon in the late 1980s and in Washington after 2004. High beetle pressure resulted in an estimated high probability of large outbreaks, whereas climate variables may reduce these probabilities (Fig. 2). Model estimated population decreases, which generally matched observed decreases, were caused by variables other than beetle pressure (like climate).

Several limitations of the study are important to consider in relation to the main findings. The lack of data on stand structure (tree density and size), which is known to affect susceptibility to mountain pine beetle attack (Shore and Safranyik 1992), precluded its use in the statistical models. Many of the lodgepole pine stands in the study area are highly susceptible, but there is substantial variation in conditions (Hicke and Jenkins 2008). Some of the variation in stand structure was included in our model by the spatial terms. Uncertainty in the aerial survey data may have further contributed to modeling errors. Aerial survey information was recorded by observers, suggesting some subjectivity and reduced confidence in these data. We reduced this effect by considering classes of beetle-killed trees that allow for some variability in the accuracy of number of trees killed. Aerial survey information also included live and killed trees within affected area polygons, and thus was not designed to be analyzed at fine spatial scales. Our relatively coarse-resolution analysis (1-km grid cells) and study of climate variables that vary slowly in space minimized negative impacts of this effect. Adaptation of beetle or host tree populations to local climate may hide responses of beetle populations to weather. For example, life stage development rates of different mountain pine beetle populations respond differently to temperature (Bentz et al. 2001). The more limited spatial extent of our study and similar climate across the study area suggest that this may not be an issue here, although more research is needed to address this question.

Our analysis did not explicitly include some drivers of beetle population dynamics such as natural enemies, competition, or symbionts, which are clearly important (Safranyik and Carroll 2006, Raffa et al. 2008), particularly at low population levels. These processes operate at spatial scales below our 1-km spatial resolution, and may be most important before aerial surveys detect killed trees, making inclusion of these drivers in our study difficult. Dispersal also acts to influence outbreaks, although little is known about the importance and spatial patterns of dispersal. We included a representation of dispersal in our analysis, and many dispersal events likely occur within one of our grid cells (Robertson et al. 2007). However, future statistical analyses may benefit from a more informed representation of dispersal as new information is obtained.

Our results are similar to evaluations of bark beetle/climate relationships reported previously. For instance, Aukema et al. (2008) studied a mountain pine beetle outbreak in British Columbia, also finding that beetle pressure was the most important driver of beetle outbreaks. The authors also determined that winter and summer temperatures were the most important climatic variables, with higher probability of beetle presence in warmer winters and summers. However, Aukema et al. (2008) did not consider drought or adaptive seasonality variables. Duehl et al. (2011) used a statistical analysis of southern pine beetle outbreaks to assess potential drivers, including climate variables. Similar to our study, these authors found that nearby beetle populations in the previous year were most important, and that temperature (minimum winter temperatures) and precipitation were also significant. Precipitation in the last two years compared with average had a negative relationship with beetle populations (attributed to host stress and lack of defensive capability), whereas fall precipitation had a positive relationship that the authors attributed to increased nutritional quality of food resource, a finding similar to ours.

Our study confirms the important role of climate variables driving bark beetle outbreaks that has been noted at smaller scales and in different geographic locations. The relative importance of different variables depended on the lag times, with some effects such as drought stress switching the sign of their influence, depending on the lag value. We also found that process model outputs, with the exception of cold tolerance, did not lead to additional explanatory power at the landscape level beyond the simple climate or weather variables. Empirical validation of process model results over large areas and long time spans will be difficult without new sources of data on host distribution, weather, and beetle mortality maps. The findings here increase our understanding of bark beetle ecology and contribute to the development of future models of climate suitability. These latter models will be critical for understanding effects of future climate change on bark beetle epidemics and resulting forest successional dynamics (Bentz et al. 2010).

Acknowledgments

We thank Eva Strand and Terri Stamper (University of Idaho), Julie Johnson (USFS), and Marketa McGuire Elsner (University of Washington) for assistance with data acquisition and processing. Rémi St-Amant and Jacques Régnière helped with the BioSIM model. We thank the USFS Pacific Southwest Research Station and Western Wildland Environmental Threat Assessment Center for support. J. A. Hicke also acknowledges support from the USGS Western Mountain Initiative and DOE National Center for Climate Change Research.

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SUPPLEMENTAL MATERIAL

Appendix A

Descriptions of the process model explanatory variables used in the analyses (*Ecological Archives* E093-228-A1).

Appendix B

Detail about the multinomial model and calculation of jackknife standard errors, and goodness-of-fit analysis (*Ecological Archives* E093-228-A2).

Appendix C

Supplemental tables with AIC values evaluated for selection of variables in the various models (*Ecological Archives* E093-228-A3).

Appendix D

Figures showing observed yearly total areas attacked and mean values for the weather drivers with significant influence on the probability of outbreaks, spatial correlation of data, and for model residuals, estimated log-odds for the probability of new attacks, estimated log-odds for the conditional probability of at least 1000 trees killed, and estimated influence of the selected climatological temperature and drought variables (*Ecological Archives* E093-228-A4).