



Recent and future climate suitability for whitebark pine mortality from mountain pine beetles varies across the western US



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ABSTRACT

Recent mountain pine beetle outbreaks in whitebark pine forests have been extensive and severe. Understanding the climate influences on these outbreaks is essential for developing management plans that account for potential future mountain pine beetle outbreaks, among other threats, and informing listing decisions under the Endangered Species Act. Prior research has focused on one geographic region, but geographic variability in beetle and tree physiological responses to climate conditions have been documented. Here we evaluate geographic variability in climate influences on recent beetle outbreaks in whitebark pine and estimate future climate suitability for outbreaks across much of the range of whitebark pine in the western US. To accomplish these objectives, we developed and analyzed statistical models for three different geographic regions as well as a Westwide model, then applied the Westwide model to a suite of climate projections. The general patterns of climate-tree mortality relationships were similar across the three regions of our study. However, the relative importance of individual climate metrics preceding and during the recent outbreaks varied geographically because of the different climates in the regions. Winter minimum temperatures appeared to be limiting prior to outbreaks in the colder regions. All regions experienced low summer precipitation prior to or during outbreak initiation. Future climate suitability for beetle outbreaks is estimated to increase or remain stable in the coldest regions and decline slightly in the warmest region by the end of this century. Across the study area, projections of higher winter temperatures and decreased summer precipitation (with lower confidence than for temperatures) contribute to increased climate suitability for outbreaks, while projected higher fall/spring/summer temperatures contribute to decreased suitability. Some regional variability exists; in particular, the effect of winter warming is muted in the warmest region (Cascades) where winter temperatures appear to be less limiting. However, all regions are projected to experience fewer years with very low suitability, which commonly occurred prior to the recent outbreaks and may have limited beetle populations. Given the inherent uncertainty in climate projections and ecological responses to novel climates, management plans that incorporate sites that are expected to experience a range of expected future climate conditions might increase the chances of whitebark pine persistence in a warmer future.

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1. Introduction

Understanding changing disturbance regimes is important for developing a portfolio of management tactics to reduce the impacts of disturbances (Turner, 2010). Expansions in the geographic range of mountain pine beetle (*Dendroctonus ponderosae*)

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outbreaks (Carroll et al., 2004; Logan et al., 2010) indicate that disturbance regimes due to tree mortality from mountain pine beetle attack are changing. Climate change is likely to have an important influence on mountain pine beetle outbreaks (Bentz et al., 2010; Logan et al., 2010; Buotte et al., 2016), as it has in other instances of tree mortality documented globally (Allen et al., 2010), such as piñon pine dieoff in the southwestern US in the early 2000s (Breshears et al., 2005). Therefore, understanding climate influences on future mountain pine beetle outbreaks is one prerequisite

for developing comprehensive forest management plans in areas with the potential for beetle outbreaks.

Historically, mountain pine beetle outbreaks affected limited areas of whitebark pine (*Pinus albicaulis*) forest, and for limited periods (Perkins and Swetnam, 1996; Logan et al., 2010), because temperatures were typically too low to allow successful mountain pine beetle development and survival (Amman, 1973). Accordingly, whitebark pine management plans have been primarily focused on mitigating the effects of fire exclusion and infection from white pine blister rust (*Cronartium ribicola*) (Keane et al., 2012). Recent beetle outbreaks, however, have been severe and extensive (Logan and Powell, 2001; Meddens et al., 2012; Macfarlane et al., 2013), and are a contributing reason whitebark pine has been listed as warranting Endangered Species protection by the US Fish and Wildlife Service (USFWS, 2011). Understanding climate influences on beetle outbreaks in whitebark pine is therefore crucial for developing rangewide management plans and informing future Endangered Species Act listing decisions for whitebark pine.

Previous research has provided a strong understanding of climate influences on mountain pine beetle outbreaks in their primary host, lodgepole pine (*Pinus contorta*) (for reviews, see Raffa et al., 2008; Bentz et al., 2009, 2010). The limited research on climate drivers of outbreaks in whitebark pine forests indicates that the risk of mountain pine beetle attack is linked to higher temperatures (Logan et al., 2010; Buotte et al., 2016) and lower summer precipitation (Buotte et al., 2016). Past studies of mountain pine beetle outbreaks in whitebark pine have primarily focused on one geographic region, the Greater Yellowstone Ecosystem (Perkins and Roberts, 2003; Logan et al., 2010; Jewett et al., 2011; Buotte et al., 2016). However, substantial outbreaks have occurred outside this region: during 1997–2009, over 6000 km² of mortality occurred across the range of whitebark pine in the western US (Meddens et al., 2012).

Previous research in lodgepole pine systems indicates beetles' physiological responses to climate influences can vary geographically (Bentz et al., 2001, 2011, 2014; Weed et al., 2015). Beetle development rates are adapted to the local temperature regimes they experience (Bentz et al., 2001), and the importance of temperature to beetle-caused tree mortality can vary across geographic regions (Weed et al., 2015). Field measurements (Bentz et al., 2014) have shown that although the number of days required to complete a life cycle are similar, the thermal units required varies across latitudinal and elevational gradients.

Temperate forest tree species (Breda et al., 2006; Littell et al., 2008), including conifers (Graulich and Brubaker, 1995; Littell et al., 2008), are also adapted to their local climate conditions. Whitebark pines exhibit genetic variation in their growth response to temperature (Millar et al., 2012) and cold-hardiness (Keane et al., 2012). Taken together, this previous research suggests the potential for geographic variability in climate influences on whitebark pine mortality from mountain pine beetle colonization.

Our objectives were to assess geographic variability in climate influences on whitebark pine mortality from mountain pine beetles across much of the western US by (1) evaluating the potential for geographic variability in climate-whitebark pine mortality relationships; (2) comparing climate influences on the recent beetle outbreaks; and (3) estimating future climate suitability for whitebark pine mortality from mountain pine beetles. To understand climate influences on whitebark pine mortality, we developed statistical models of whitebark pine mortality from mountain pine beetles with and without geographically variable effects of climate. We then applied our model without geographically variable effects of climate (Westwide model, see results) to 1979–2009 climate data to assess climate influences on the recent beetle outbreaks,

and to climate projections to estimate future climate suitability for whitebark pine mortality from mountain pine beetles.

2. Methods

Our study area covered the range of whitebark pine in the US outside of California and Nevada (Fig. 1). Given variability in seasonal temperatures and precipitation across this range (Fig. S1), we divided the study area into three geographic regions: the Greater Yellowstone Ecosystem (GYE), Northern Rockies (NR), and Cascades (Fig. 1), generally following Level III ecoregion classifications of the Environmental Protection Agency (Omernick, 2004) which are defined based on similar areas of climate and vegetation type. Due to a lack of whitebark pine mortality data, we did not include locations in California and Nevada.

2.1. Input data

We assigned the presence of whitebark pine mortality from mountain pine beetles based on US Forest Service Aerial Detection Survey (ADS) data (USDA Forest Service, 2000) covering our study area. During surveys, observers in aircraft record tree mortality by host and mortality agent. These data were gridded to a 1-km resolution (Meddens et al., 2012). From this data set, we identified the voxels (grid cells by year) with whitebark pine killed by mountain pine beetle from 1996 to 2009. Because trees that are successfully attacked and killed turn red the following summer, the year of attack is the year prior to the year recorded in the ADS data. In the GYE region, ADS reports indicate no observed whitebark pine mortality from mountain pine beetles from 1986 to 1995 so we defined all voxels as having no mortality from 1986 to 1995. Reports from other regions indicate low levels of mortality prior to 1996; however, mortality absence could not be assumed and we did not extend the study period backward for these regions.

We defined the spatial distribution of whitebark pine in the NR and Cascades by combining the 1-km pixels where ADS data recorded whitebark pine and locations with a map of the potential for blister rust infection in whitebark pine (R. Keane, pers. com.). In the GYE, we selected those 1-km pixels that had at least 10% whitebark pine according to a 30-m map of whitebark pine distribution developed from Landsat data (Landenburger et al., 2008). In all

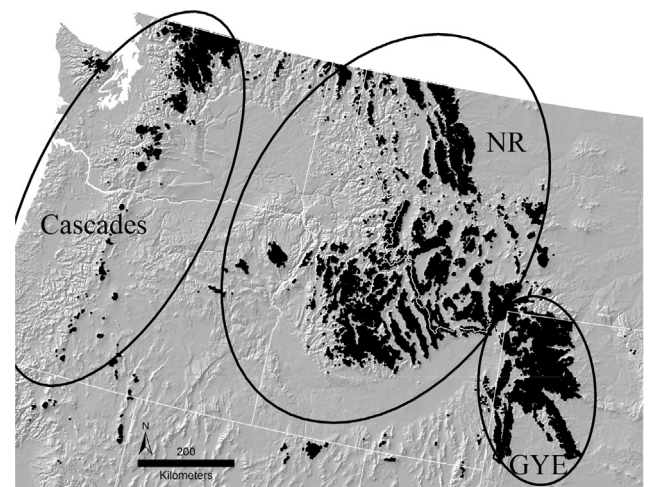


Fig. 1. Whitebark pine range in the western US and approximate boundaries of geographic regions for developing and applying models of the presence of whitebark pine mortality from mountain pine beetle (GYE = Greater Yellowstone Ecosystem, NR = Northern Rockies). Locations in California and Nevada were excluded due to a lack of tree mortality data.

regions we defined the absence of whitebark pine mortality as those voxels within the distribution of whitebark pine defined above that were flown during annual Aerial Detection Surveys that did not have recorded mortality. Voxels that were not flown in the aerial surveys were excluded from model development data sets.

We selected explanatory variables (Table 1) that represented five processes known to influence mountain pine beetle outbreaks in the beetles' primary host, lodgepole pine (Aukema et al., 2008; Preisler et al., 2012; Sambaraju et al., 2012) and in whitebark pine (Buotte et al., 2016): the number of attacking beetles, or beetle pressure; stand structure; and climate conditions affecting beetle winter mortality; beetle development and population synchrony, also known as "adaptive seasonality" (Logan and Bentz, 1999); and host tree defensive capabilities. We did not have a direct measure of the number of attacking beetles in the previous year; therefore we used the number of trees killed by beetles last year as a surrogate. We acknowledge that other factors, such as tree vigor and tree size are also important in determining the number of attacking beetles that could be produced. We derived two beetle pressure variables for each cell using 1-km gridded aerial detection survey data (Meddens et al., 2012): the number of trees killed in the focal cell last year and the number of trees killed in the surrounding 6-km neighborhood last year. Because the number of trees killed depends on factors other than the size of the beetle population, we reiterate that this variable represents an index of beetle populations. Stand structure variables included the area of remaining living trees, from gridded aerial detection survey data (Meddens et al., 2012) and stand age (Pan et al., 2011). Climate variables representing beetle winter mortality, beetle adaptive seasonality, and host tree defenses were derived from either 800-m PRISM climate data (Daly et al., 1997), or daily weather station data interpolated within the BioSIM software environment (Régnière et al., 1996). All candidate climate variables were gridded to a 1-km resolution and associated with the year of beetle colonization. We did not measure tree defensive ability directly; instead we used climate variables that have been shown to be correlated with tree defenses (Rigling et al., 2003; Kane and Kolb, 2010). Additional processing details for each variable are provided in Table 1 and further descriptions of explanatory variables are provided in Buotte et al. (2016).

2.2. Statistical model

We modeled the probability of tree mortality with logistic regression, defined by the equation

$$\text{Logit}(p) = \beta_0 + \text{Reg} + s_{m1}(X_{m1}) + \cdots s_{mi}(X_{mi}) \quad (1)$$

where p is the probability of whitebark pine mortality (at least one tree killed in a given 1-km pixel per year) from mountain pine beetle, Reg is a factor for geographic region, and $s_{m1}(X_{m1})$ through $s_{mi}(X_{mi})$ are tensor product smooth functions of the explanatory variables representing beetle winter survival, beetle development and synchrony, host tree defenses, previous year beetle population, and stand structure (see Table 1).

We created a set of candidate models in which every model contained a representation of each of the five important processes described above and in Table 1. Given differences in the relative area of mortality in each geographic region (Fig. 2), we included region as a factor. This variable adjusts the intercept such that each region may have a different overall mean probability of mortality. We used a model selection process following Burnham and Anderson (2002), ranking models according to AIC, to determine the variable or combination of variables that best represented each of the five processes. The combination of variables from the model selection exercise defined our final model. To investigate the potential for geographic variation in the relationships between tree mortality and climate we developed a statistical model in which

the climate smooth functions in Eq. (1) were allowed to vary by geographic region. We also developed a Westwide model that pooled observations from all regions and performed model selection to identify the variables that defined the best model.

The relationship between each explanatory variable and the presence of tree mortality was assessed through log-odds plots. We calculated standard errors around the mean response through jackknifing by year (Preisler et al., 2012). To do this we estimated the parameters of the model with one year of data withheld, repeating for each year. Jackknife standard errors were then calculated from that population of parameter estimates. Ecological significance of an explanatory variable was determined from visual inspection of the log-odds plots. When the 95% confidence interval of the log-odds bounded zero, we determined that the variable was not contributing to either an increase or a decrease in the probability of tree mortality. Those variables with 95% confidence bounds that did not include zero were assumed to have a significant effect on the model prediction, and the greater the range of the log-odds (y-axis on these plots), the greater the magnitude of that variable's effect.

We evaluated the potential for spatial autocorrelation in the residuals by adding a spatial term (x, y in UTM coordinates) in the final model. We plotted the autocorrelation in the residuals of the final model with and without a spatial term at increasing lag distances. We also compared the log-odds plots from the models with and without the spatial term.

We evaluated the final model goodness-of-fit by plotting observed and predicted total area with mortality by year and calculating a linear regression of the observed area as a function of predicted area. Predicted area was calculated through cross-validation, in which the year being predicted was withheld from the data used to estimate the model parameters. The yearly predicted area was calculated as the sum of the predicted probabilities over all grid cells in that year.

2.3. Model application

To better understand the effects of climate on outbreaks, we defined climate suitability indices (CSI) that isolate the influence of climate on whitebark pine mortality (Buotte et al., 2016). A CSI for each individual explanatory variable was calculated as the average of that variable's log-odds over all grid cells for a given year. We also calculated a combined CSI by summing the log-odds of all climate variables in each grid cell and taking the average for a given year. Indices were calculated for the entire study area and separately for each of the three geographic regions. A mean CSI greater than zero implies an increase in the odds of whitebark mortality (hence an increase in climate suitability for tree mortality) over the average odds of mortality.

We used the climate suitability indices to assess climate effects on the recent outbreaks and future climate suitability for whitebark pine mortality from mountain pine beetle attack. To calculate climate suitability indices for years prior to and during the recent outbreaks, we applied the final model to PRISM climate data (Daly et al., 2008) for the period 1979–2009; 1979 and after is when multiple high-elevation climate station records were available for inclusion in PRISM (Buotte et al., 2016). We applied the model to all grid cells within the distribution of whitebark pine in the study area.

To estimate future climate suitability we applied the final model to future climate projections from ten general circulation models (Table S1) (Taylor et al., 2012). Because the current trend indicates that anthropogenic carbon emissions are on or exceed the trajectory of the high emissions (RCP 8.5) scenario (IPCC, 2007; Sanford et al., 2014), we show results for climate projections generated with the RCP 8.5 emissions scenario. The future climate

Table 1

Description of candidate explanatory variables in generalized additive models of the probability of whitebark pine mortality from mountain pine beetle.

Process	Rationale	Variable	Description	Data source	Temporal resolution
<i>Beetle pressure</i>					
Local beetle pressure (#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 (#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
<i>Stand structure</i>					
Available host	Outbreaks will collapse when available host is depleted	RMWBP	Remaining whitebark pine = cumulative mortality area since 1998 * % of pixel with whitebark pine	Meddens et al. (2012)	Annual
Stand age	Beetles prefer older, larger trees	Age	Age in years	Pan et al. (2011)	NA
<i>Climate conditions</i>					
Beetle winter mortality	Unseasonably and/or extremely low temperatures can cause direct mortality of over-wintering insects	Tmin	Minimum monthly minimum temp in December–February ^a	PRISM	Monthly
		Coldt	Probability of winter survival from the cold tolerance model developed by Régnière and Bentz (2007) ^a	BioSIM	Daily
		ECS	Presence/absence of an early cold snap, defined as 4 consecutive days with temp ≤ −20 °C between Oct 15–September–November 30 ^a	BioSIM	Daily
		Drop20	Number of days with > 20 °C drop in mean temperature ^a	BioSIM	Daily
		Min40	Number of days with min temp ≤ −40 °C ^a	BioSIM	Daily
		Logan	0/1 of whether conditions were suitable for univoltinism according to the adaptive seasonality process model developed by Logan and Powell (2001) ^a	BioSIM	Daily
		Tmean	Average temp August 1–July 31 ^a	PRISM	Monthly
		FallT	Average temp September–November ^a	PRISM	Monthly
		TMAA	Average temp April–August ^a	PRISM	Monthly
		CDD	Cumulative degree-days above 5.5 °C from August 1–July 31. DD = max(0, T-Tthresh) ^a	BioSIM	Daily
Adaptive seasonality	Temperature conditions can promote outbreaks by allowing for a one-year life cycle and near-synchronous adult emergence	BDD	Binary of whether 833 °C degree-days accumulated between Aug 1–July 31 ^a	BioSIM	Daily
		VPD01 through 05	Average monthly vapor pressure deficit in current and previous 5 growing seasons ^{c,d}	PRISM	Monthly
		CWD01 through 05	Cumulative climatic water deficit in current and previous 5 growing seasons ^d	PRISM	Monthly
		PPT01 through 05	Cumulative monthly October–August precipitation in current and previous 5 years ^d	PRISM	Monthly
Tree defensive capabilities	Drought stressed trees have lower defensive capabilities than healthy trees ^b				

^a Variables: year of attack and previous year.^b 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.^c Growing season = May–October.^d Six variables: 0, 0–1, 0–2, ..., 0.

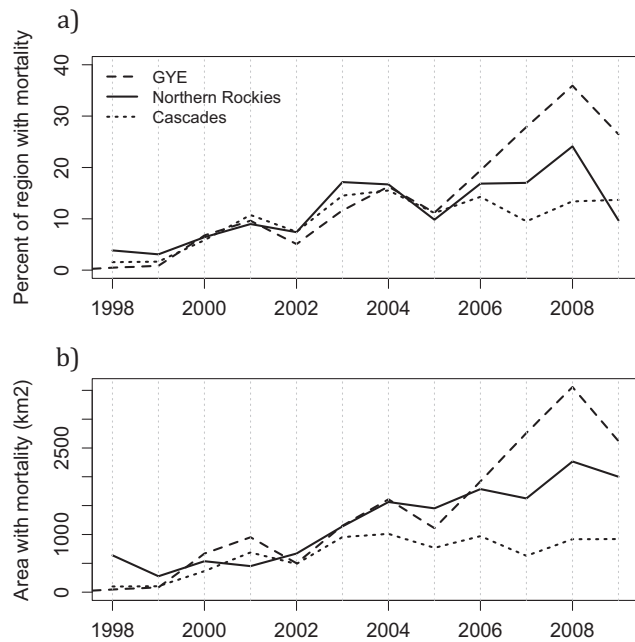


Fig. 2. Annual area with whitebark pine mortality from mountain pine beetle in three geographic regions of the western US in terms of (a) percent of total area flown and (b) absolute area (GYE = Greater Yellowstone Ecosystem).

projections were downscaled to 30-arc-second resolution using PRISM data and a bias correction spatial downscaling algorithm (Thrasher et al., 2013). Future projections of climate variables were limited to the range of observed climate during the period of tree mortality model development.

The set of GCM experiments used in the historical forcing or RCP scenarios are not designed to match or be compared to observed climate for an individual year. However, bias correction procedures (Thrasher et al., 2013) are designed to allow climatological statistics taken over a longer time period (30 years) from GCMs run over historical forcing experiments to match the corresponding statistics from PRISM. We therefore confirmed the consistency between historical GCM climate and PRISM climate data distributions to ensure we could apply our statistical model to future GCM climate projections and calculate future climate suitability estimates that would be comparable with historical climate suitability estimates based on PRISM climate data (Fig. S2).

3. Results

3.1. Model goodness of fit

In all regions, annual area of whitebark pine mortality from mountain pine beetles began increasing in the late 1990s (Fig. 2). Regional trends diverged during the mid-2000s as the outbreak in the GYE continued until the late 2000s whereas outbreaks in the NR and Cascades declined or plateaued (respectively) in the mid-2000s (Fig. 2). The GYE experienced the highest annual area with mortality relative to the area of whitebark pine range flown during aerial detection surveys (Fig. 2).

Baseline climate conditions during 1997–2009 were different across the three regions. The GYE was the coldest region across all seasons, and the Cascades region was the warmest in winter and the driest in summer (Fig. S1). Annual patterns of seasonal temperature and precipitation also varied across regions, with patterns in the Cascades the least similar to the other regions (Fig. S3).

The final Westwide model captured the annual trends in area with whitebark pine mortality with relatively little bias (Fig. 3).

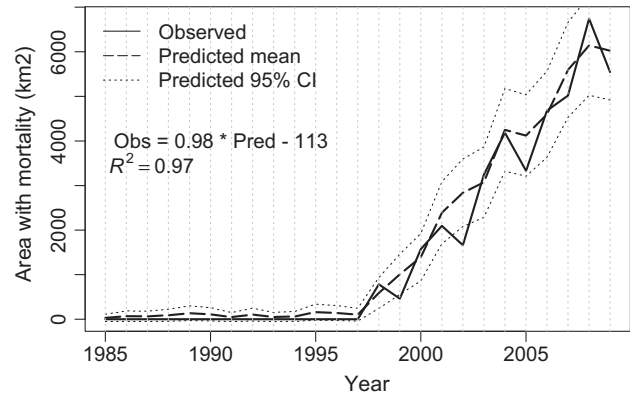


Fig. 3. Model evaluation showing observed (solid line) and predicted (long-dashed line) area with whitebark pine mortality from mountain pine beetle (short-dashed lines are 95% confidence intervals calculated from cross-validation by year, RMSE = 774 km²). Equation and R^2 are from a linear regression of observed area with mortality as a function of predicted area with mortality.

Autocorrelation in the residuals at a distance of 1 km was low (<0.2) in the final model, and including a spatial term only slightly reduced this correlation. Including a spatial term did not change the log-odds plots of the explanatory variables and therefore a spatial term was not included in the final model. The region effect indicated tree mortality was equally likely in the Cascades and Northern Rockies, and 1.6 times as likely in the GYE ($p < 0.001$) compared to the other regions.

3.2. Climate influences on whitebark pine mortality from beetles

Geographic differences in the effect of climate on whitebark pine mortality across regions were due to differences in the observed range of climate conditions each region experienced, not to geographic variability in the relationship between climate variables and tree mortality (Fig. 4). When climate relationships were allowed to vary by region, the resulting relationships were similar among regions: the 95% confidence intervals of regional log-odds overlapped along the majority (5–95% of the distribution) of the range of observed values. Slight differences occurred at the edges of the ranges, where there were little data available to estimate the effects with confidence. In addition, the mean log-odds among the different regions exhibited broadly similar patterns. Therefore, in the final, Westwide, model, the effects of climate on whitebark pine mortality were held constant across geographic regions (i.e., smooth functions were not allowed to vary by region).

Whitebark pine mortality was more likely with increasing winter minimum temperature up to 13 °C, suggesting higher beetle winter survival at higher temperatures (Fig. 4a); with increasing fall temperature up to 0 °C, suggesting increasing adaptive seasonality (Fig. 4b); and decreasing summer precipitation, suggesting lowered tree defenses (Fig. 4d). Plots of estimated effects of all other, non-climatic, variables in the model are provided in Supplemental Figures (Fig. S4).

3.3. Climate influences on recent beetle outbreaks

Climate suitability for whitebark pine mortality, averaged across the study area, was typically low prior to the recent outbreaks; increased as the area with whitebark pine mortality increased; and declined coincident with declines in the area with mortality (Fig. 5a). There were, however, differences in both the timing and magnitude of climate suitability across geographic regions (Fig. 5b–d). Prior to the recent outbreaks, winter temperature suitability for tree mortality was at times low (i.e., winter

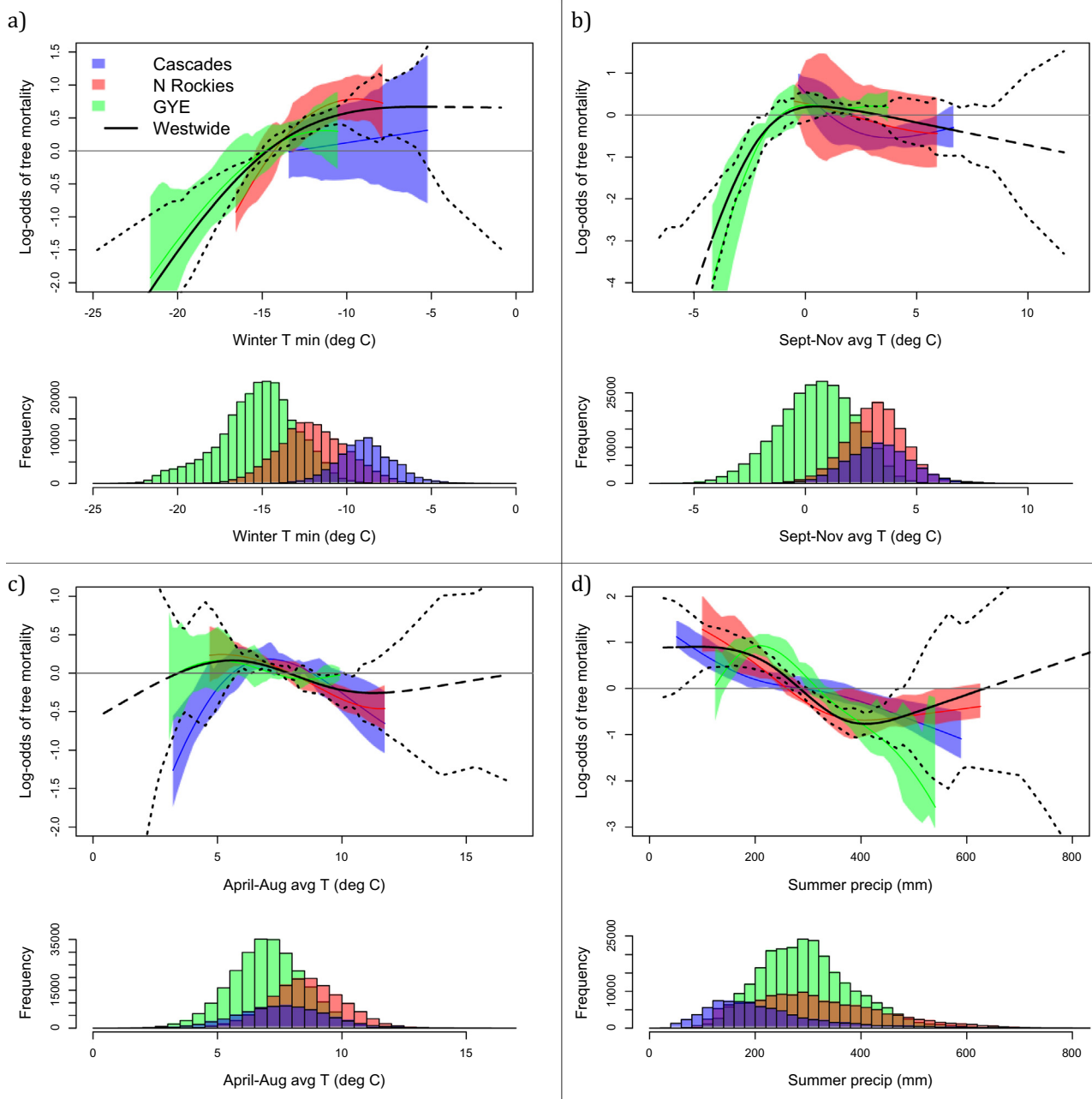


Fig. 4. Log-odds of whitebark pine mortality from mountain pine beetle given climate metrics selected to represent (a) beetle winter mortality from very low temperatures, (b) beetle adaptive seasonality effects from fall temperatures, (c) beetle adaptive seasonality effects from spring-summer temperatures, and (d) host tree defensive ability represented by summer precipitation. Colored lines and shading indicate means and 95% confidence intervals from regional models. Regional log-odds are only shown where distributions are within 5th and 95th percentiles. Solid black and dotted lines shows mean and 95% confidence intervals from a model using all data (Westwide model). Black dashed lines indicate Westwide mean outside of the 5th through 95th percentiles. Confidence intervals were calculated by jackknifing by year. Histograms indicate distributions of observations used to build models.

minimum temperatures were low) in the GYE and Northern Rockies, but was rarely low in the Cascades. In all regions, increases in area with mortality coincided with increases in precipitation suitability (i.e., less precipitation). Except for a few years of very low September–November temperature suitability in the GYE and Northern Rockies, seasonal average temperature suitability showed little variability.

3.4. Future climate suitability for beetle outbreaks

Under RCP 8.5, future temperatures are projected to substantially increase and summer precipitation is projected to slightly decrease relative to historical conditions, although precipitation

is more uncertain from model to model (Fig. S5). These projections tend to lead to increasing climate suitability for whitebark pine mortality from mountain pine beetles during this century across the western US (Fig. 6a).

There are, however, regional differences. Projected winter minimum temperature suitability increases the most in the GYE (the coldest region) and declines in the Cascades (the warmest region) by the end of this century (Fig. 7). Increases in fall and spring-summer temperatures lead to declines in future climate suitability compared to historical suitability, and decreases in summer precipitation lead to increases in climate suitability for whitebark pine mortality (Fig. 7). These differences in individual climate suitability metrics lead to increased combined climate suitability projections

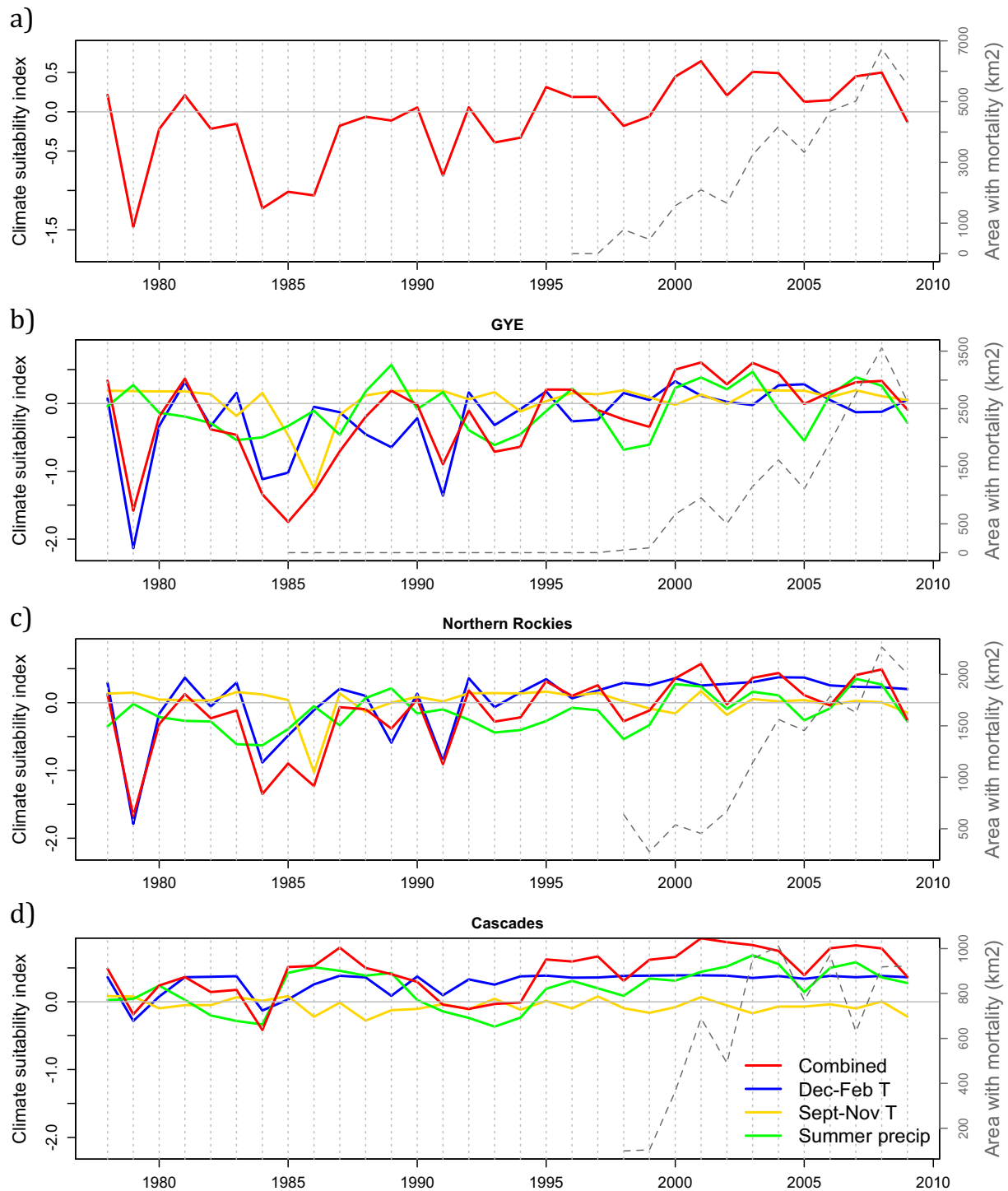


Fig. 5. Combined climate suitability index averaged over (a) entire study area (Westwide) and (b–d) three geographic regions, calculated as the sum of the climate terms in the logistic regression model of whitebark pine mortality from mountain pine beetle. Dashed lines and right y-axis show area with whitebark pine mortality each year. April–August temperature suitability is not shown due to lack of variability.

increase in the GYE (Fig. 6b), relatively constant climate suitability in the Northern Rockies (Fig. 6c), and declines in the Cascades (Fig. 6d).

4. Discussion

Whitebark pine mortality was more likely in the GYE than in other regions after accounting for the effect of all other climate, beetle pressure, and stand structure effects. Higher levels of white-

bark pine mortality in the NR prior to 1997 (Keane and Arno, 1993), and the greater homogeneity of whitebark pine stands in the GYE (Weaver, 2001) likely meant there were more whitebark pine available as host trees in the GYE at the beginning of the outbreak than in the NR and Cascades and thus relatively greater mortality in the GYE than the other regions.

The relationships between individual climate effects and whitebark pine mortality from mountain pine beetles were generally consistent across the study area. Differences in climate suit-

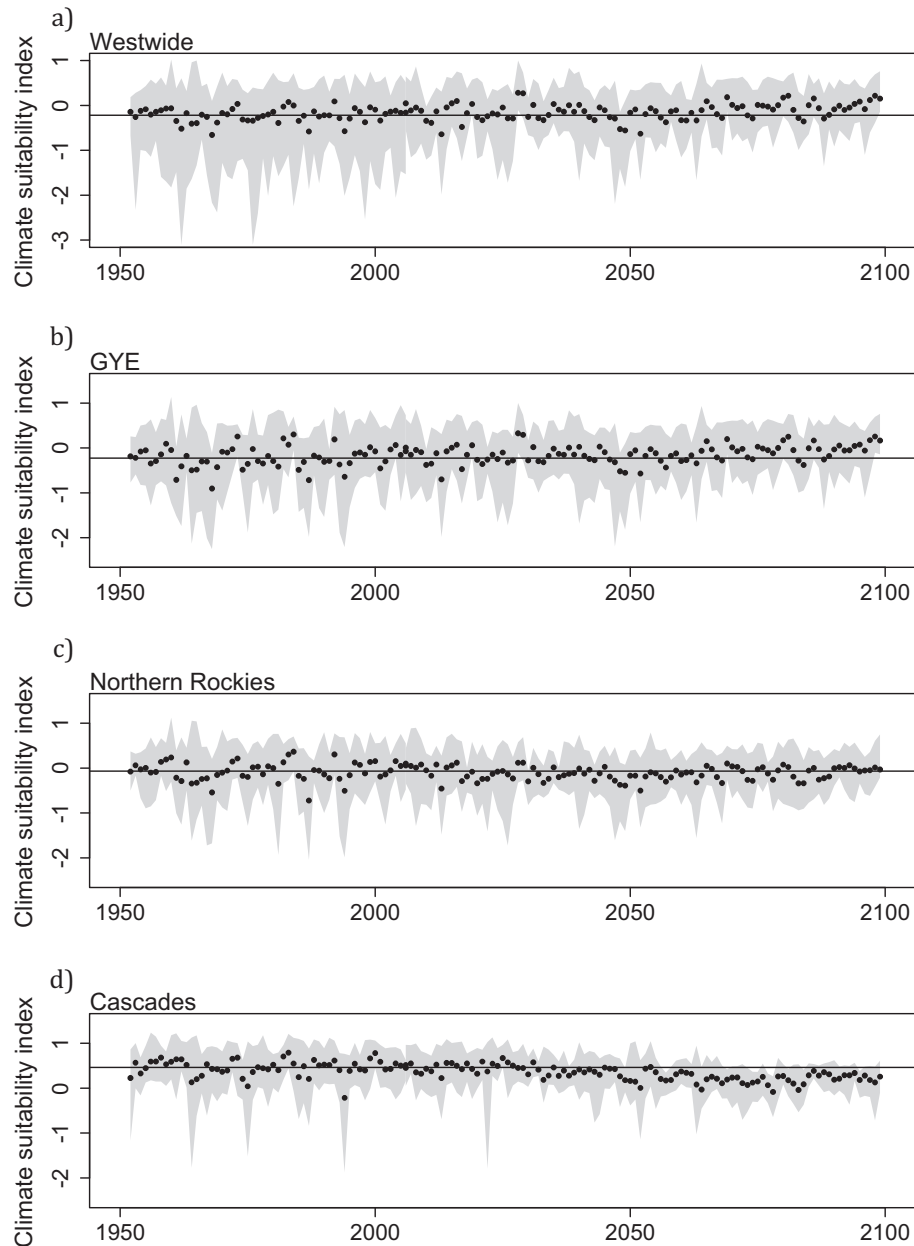


Fig. 6. Future combined climate suitability for whitebark pine mortality from mountain pine beetle averaged across (a) the study area, (b) the Greater Yellowstone Ecosystem, (c) the Northern Rockies, and (d) the Cascades. Gray shading indicates the range of suitability and dots the average suitability from applying the logistic regression model to ten global climate models forced with a high emissions scenario (RCP 8.5).

ability among regions seem to be mostly accounted for by differences in the range of observed climatic values among regions rather than geographic differences in the relationships between climate variables and whitebark pine mortality. In laboratory studies, (Bentz et al., 2011, 2014) found that beetle development rates and emergence dates varied by population source and latitude. Our methods used tree mortality as the dependent variable. Therefore, we could not assess the potential for a range of beetle emergence dates for those voxels with dead trees. There may be differences in development rate or emergence date across geographic regions, but we were not able to detect an influence on the probability of tree mortality. Possibly, there is a range of emergence dates that allows for successful attack. Alternatively, the monthly PRISM climate data we used may not capture variability in daily temperatures that were important variables in previous laboratory studies.

Our modeled relationships between climate and whitebark pine mortality agree well with other studies in both lodgepole and whitebark pine forests. Lethal minimum temperatures have been established experimentally (Wygant, 1940), and increases in winter temperatures have been related to beetle outbreaks in lodgepole (Preisler et al., 2012; Creeden et al., 2014) and whitebark pine (Buotte et al., 2016). Our findings were consistent with these studies in that we found higher odds of tree mortality as winter minimum temperatures increased from the minimum observed temperature to about -13°C , after which no further increase in the odds was observed. We found that the likelihood of tree mortality increased as fall temperatures increased. Seasonal temperatures strongly influence mountain pine beetle phenology (Powell and Bentz, 2009), with fall temperatures serving to synchronize individual development stages (Logan and Powell, 2001). Declines in tree mortality at the highest fall temperatures may be a manifes-

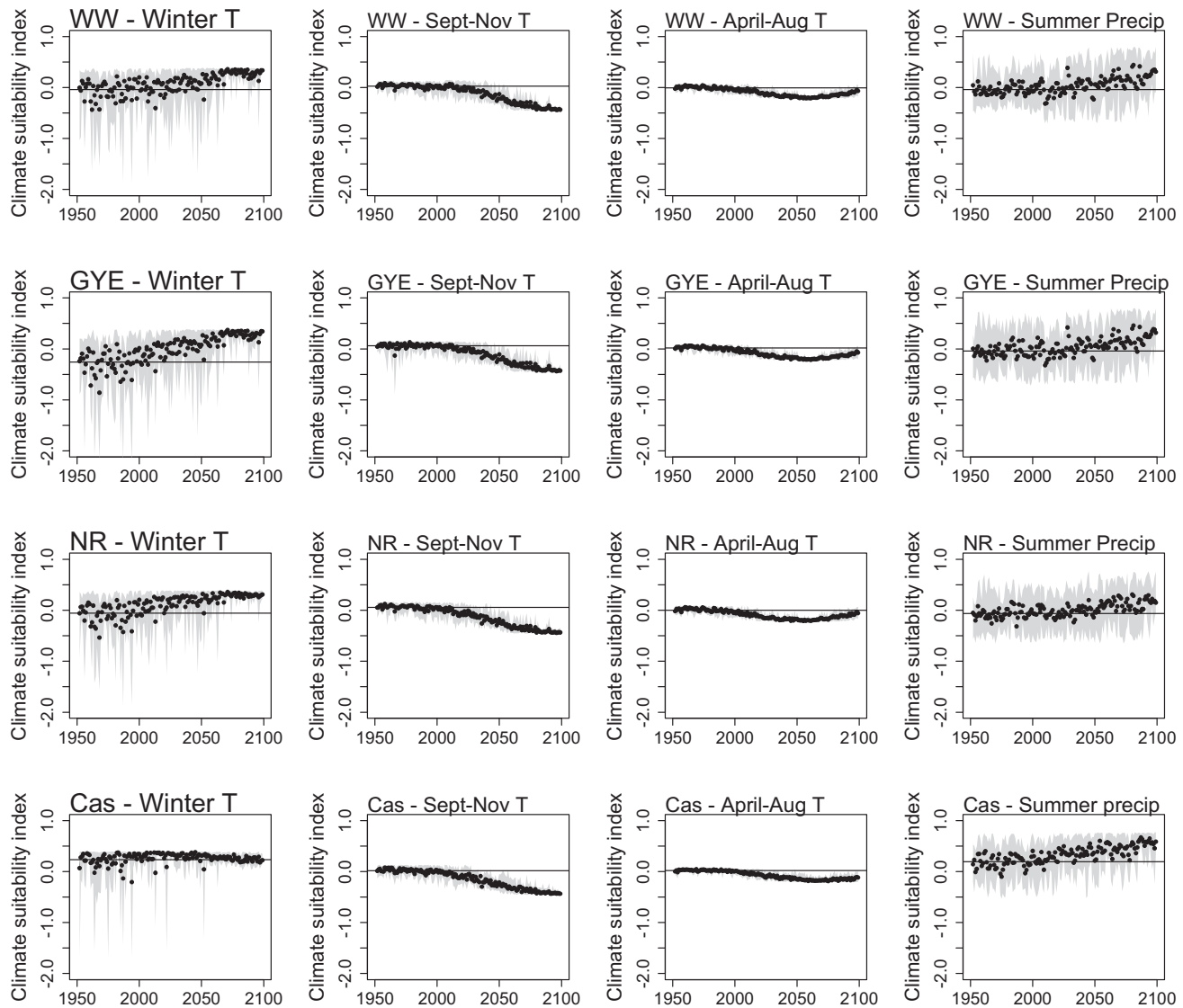


Fig. 7. Historical and future winter temperature, fall temperature, spring–summer temperature, and two-year summer precipitation suitability for whitebark pine mortality from mountain pine beetle averaged across the western US (WW) and three geographic regions (GYE = Greater Yellowstone Ecosystem, NR = Northern Rockies, Cas = Cascades). Gray shading indicates the range of suitability, and dots the average suitability, predicted by applying the logistic regression model to ten global climate models forced with a high emissions scenario (RCP 8.5).

tation of maladaptive seasonality in which temperature-driven beetle development rates do not allow for a one-year life cycle with mass emergence in late summer (Logan and Powell, 2001; Hicke et al., 2006). Based on previous work linking tree defensive abilities to drought stress (Rigling et al., 2003; Kane and Kolb, 2010) the success of beetle attacks relative to tree defenses (Raffa and Berryman, 1983; Boone et al., 2011) and documented whitebark pine growth response to precipitation (Perkins and Swetnam, 1996), we interpret precipitation as a potential index of tree defensive ability due to severe drought stress. The likelihood of tree mortality increased with decreasing precipitation, potentially due to resulting declines in tree defenses.

Although the functional form of the climate relationships were similar across geographic regions, the relative influence of individual climate metrics prior to and during the recent outbreaks varied geographically due to differences in observed climate among regions. Prior to the recent outbreaks, winter minimum temperature was most unsuitable for beetle outbreaks in the coldest regions (GYE and NR), and became more suitable at the beginning

of the outbreaks, when winter minimum temperatures were increasing. This pattern of outbreaks occurring during years of higher temperatures is indicative of beetles taking advantage of typically unsuitable habitat (Logan and Powell, 2001). Though not unprecedented, beetle outbreaks in whitebark pine forests in the GYE have been rare in the past (Perkins and Swetnam, 1996; Logan et al., 2010). In the warmer Cascades region, winter temperatures rarely appeared to be limiting prior to or during the recent outbreak. Similarly, previous studies in lodgepole pine forests have demonstrated that winter temperatures are limiting to beetle outbreaks only in colder regions (Weed et al., 2015).

In all regions, the recent outbreaks coincided with years of less precipitation, indicating the potential for reduced tree defensive abilities due to drought stress. In lodgepole pine systems (Boone et al., 2011), tree defenses strongly reduced attack success when mountain pine beetle populations were low but not once populations had risen. In the current study, precipitation appeared to influence whitebark pine mortality throughout the course of the outbreaks, as greater precipitation was followed by declines in area

with mortality during some years in all regions. This indicates that further work is needed to increase our understanding of the role of precipitation and tree drought stress in whitebark pine resistance to beetle attack.

Climate conditions, stand age, and prior year beetle population size (the explanatory variables in our model), are likely not the only factors that determine whitebark pine mortality from mountain pine beetles. Stand composition may play a role in determining which trees beetles select for attack (Bentz et al., 2015), and tree size, age, and density are also important (Perkins and Roberts, 2003). Due to a lack of sufficient data, we were not able to investigate the effect of stand structure characteristics other than stand age in this study.

Spatial, forest type, severity, and mortality agent errors exist in the ADS data. Johnson and Ross (2008) found that such errors decreased with decreasing spatial resolution and ADS data achieved a 78% accuracy at 500-m resolution. Because we used a 1-km spatial resolution, the effects of errors in the ADS data were minimized.

Future climate projections produce patterns of climate suitability similar to patterns during the recent outbreaks. Across the West, future climate suitability for whitebark pine mortality from mountain pine beetle tends to increase. Historically, periodic years with low winter temperatures resulted in low climate suitability for whitebark pine mortality, likely due to high beetle winter mortality. However, in all regions, there is agreement among GCMs of higher winter temperatures, resulting in fewer years with low winter temperature suitability in the future. Regionally, future climate suitability patterns are similar to recent patterns as well. Winter temperatures continue to become more suitable for whitebark mortality (greater beetle survival) in the colder regions, but remain constant (and suitable) in the warmer Cascades region. Toward the middle to end of this century, fall and spring-summer temperature suitability declines. Our model was developed with little data in this warmer temperature range and so conclusions of declines in suitability are less certain. However, similar declines in beetle population growth have been predicted using a process model of adaptive seasonality as yearly temperatures increase (Hicke et al., 2006), providing a measure of confidence. We interpret this decrease in suitability with increasing fall temperatures as leading to maladaptive conditions that adversely affect beetle emergence timing (during winter) and/or asynchrony in emergence and therefore the lack of mass attack (Logan and Powell, 2001).

5. Conclusions

We did not detect differences in the relationships between whitebark pine mortality from mountain pine beetle and individual climate metrics across geographic regions of the western US. However, we did find that different climate conditions among regions led to regional differences in the importance of climate variables before and during the recent beetle outbreaks. Our results suggest that projected warming will lead to more favorable climate conditions for outbreaks of mountain pine beetle and whitebark pine mortality in the coming decades, although the magnitude of this effect depends on emission scenario and climate model.

Understanding the geographic variability of this changing disturbance regime provides opportunities for creating site-specific management plans to promote whitebark pine persistence in a future climate that may be more favorable to beetle outbreaks. Recent winter warming appears to have increased whitebark pine mortality from mountain pine beetles in the colder regions of its range in the western US (GYE and Northern Rockies), and future climate conditions are increasingly suitable for beetle outbreaks.

Therefore, management plans could include restoration sites where winter temperatures can be expected to remain low, due to cold air drainage for example, causing high levels of beetle winter mortality. In the warmer Cascades region, or warmer microclimates of the GYE and NR regions, management plans could include low-elevation sites where future fall warming may cause disruptions in beetle development and population synchrony and thereby limit future beetle outbreaks. Further research on the effectiveness of whitebark pine defensive abilities against beetle attack success, especially as related to tree stress induced by drought, high stem density, or other environmental conditions, would be informative to management plans in all regions. Here we examined the potential effects of future climate, but future stand structure conditions and the defensive capacities of trees will be important for determining whitebark mortality as well.

Future climate projections, and how ecological systems will respond to novel conditions, contain some degree of uncertainty. Therefore, a regional whitebark pine management portfolio that spreads the risk of mortality from mountain pine beetles across sites with a range of future climate conditions could increase the chances of whitebark pine persistence.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.05.032>.

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