Understanding and Capturing Geographic Variability in Vulnerability of Natural Resources to Climate Change Through Modeling and Workshops

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Abstract

Climate patterns exert a strong influence on many ecological systems. Understanding how a changing climate will affect our natural systems is a necessary prerequisite for developing appropriate management strategies that will enable these systems to persist into the future. The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is a native species that is strongly influenced by climate and recently, unprecedented outbreaks have occurred in Canada and at high elevations in the U.S. I investigated weather influences on the recent beetle outbreak in whitebark pine forests in four geographic regions of the western U. S. I used a generalized additive logistic regression model of the presence of whitebark pine mortality from mountain pine beetles to: 1) understand weather effects on the recent outbreaks, 2) diagnose the relative importance of weather conditions prior to and during the recent outbreaks, and 3) estimate future weather suitability for whitebark pine mortality from mountain pine beetles. Whitebark pine mortality increased with increasing winter minimum temperature in all regions, but the magnitude of the effect at a given temperature was different. The effects of seasonal (September-November and April-August) temperatures and summer precipitation were different across regions at the outer ranges of observed temperature and precipitation. In all regions the recent outbreaks appeared to be initiated by warm winters. In some regions outbreaks coincided with low precipitation as well. These differences in weather influences led to differences in estimates of future weather suitability, even though there is a common pattern of increasing temperatures across regions, with future weather suitability increasing in two regions and declining in two regions. Statistical modeling is one way to assess geographic variability in vulnerability to climate change. Conducting workshops to elicit expert opinion is another. I developed and tested a framework for capturing geographic variability in climate change vulnerability during a regional-scale vulnerability assessment. My revised framework is structured around pathways of climate influence on species or resources. This structure provides a means of capturing potential hypotheses of climate influence that can then be used to develop an adaptive monitoring program that is tailored to geographic regions but coordinated across administrative and ecological boundaries.

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Introduction

Our Changing Planet

We're lucky. We live on a planet with just the right atmosphere that's just the right distance from the sun. The sun emits shortwave radiation, some of which is absorbed by the atmosphere and the planet's surface. At night, heat from the atmosphere and surface is emitted as longwave radiation. Greenhouse gases (primarily water vapor, carbon dioxide, methane, ozone, and nitrous oxide) in the lower atmosphere reflect some of this longwave radiation back to the surface. Without this natural greenhouse effect, Earth's surface would be about 60° F cooler (Walsh et al. 2014).

But it's possible to have too much of a good thing. One of the primary greenhouse gases is carbon dioxide. Atmospheric carbon dioxide concentration has varied substantially over Earth's history. Over the last 800,000 years, carbon dioxide concentrations have fluctuated between around 170 to 300 parts per million (Fischer et al. 1999). Concentrations have been increasing since the mid-1700s due to human activities, and current concentrations have exceeded 400 parts per million (Walsh et al. 2014). As a result, there has been a 1.5° F increase in average global temperature since 1880 (Walsh et al. 2014). Additional indicators of a changing global climate include increases in sea surface temperatures, higher sea level, and decreased Arctic sea ice (IPCC 2013). We are changing our atmosphere and thereby changing our climate (IPCC 2013).

If anthropogenic sources of greenhouse gases continue to increase, future global average temperatures will continue to rise (IPCC 2013). Future precipitation projections across the planet are variable, though contrasts between wet and dry regions are likely to increase (IPCC 2013). Precipitation is generally expected to decline in the subtropics and increase at higher latitudes (Walsh et al. 2014). Extreme precipitation events are projected to occur two to five times as often over all regions of the United States, even those that are projected to receive less annual precipitation (Walsh et al. 2014).

Globally, there is evidence that climate change during the last several decades has impacted natural systems (Walther et al. 2002, Rosenzweig et al. 2008, IPCC 2014). Impacts include changes in phenology (Walther et al. 2002, Parmesan and Yohe 2003), species' ranges and distributions (Walther et al. 2002, Parmesan and Yohe 2003), community composition and interactions (Walther et al. 2002, Walther et al. 2009), ecosystem structure (Walther et al. 2002), and disturbance regimes (Westerling et al. 2006, Turner 2010).

Observed and projected changes in climate vary across global (IPCC 2013) and regional (Luce and Holden 2009, Deser et al. 2012, Abatzoglou and Barbero 2014) scales. Therefore, associated impacts also vary across scales (O'Brien et al. 2004). Understanding this variability is an import prerequisite for managing our natural systems.

Coping with Change

Developing natural resource management plans requires understanding how climate conditions influence natural resources and our management of those resources (Joyce et al. 2008, Peterson et al. 2011). This understanding can be achieved in multiple ways. Classical natural history, or direct observation of the natural world, provides the most basic starting point. To understand, we have to be aware of our world and learn about how it functions and our place in it. This awareness, combined with curiosity, often leads to questions and hypotheses about how the system functions. These questions and hypotheses form the basis of ecological research. They can also form the basis for adaptive management programs

(Nichols and Williams 2006, Lindenmayer and Likens 2009) that evaluate the effects of our interventions.

Ecology and natural resources are broad fields. In my dissertation work, I focused on mountain pine beetle outbreaks in whitebark pine forests and climate influences on wildlife populations. My questions were:

1. How has weather influenced the recent mountain pine beetle outbreak in whitebark pine forests of the Greater Yellowstone Ecosystem and what is the potential for future outbreaks?
2. How do weather influences on mountain pine beetle outbreaks in whitebark pine forests, and hence future outbreak potential, vary across the western U.S.?
3. How can geographic variability in the vulnerability of natural resources to climate change, specifically wildlife populations, be captured during regional-scale climate change vulnerability assessments?

I used two different methods for answering these questions of how climate change affects natural resources. One method was statistical modeling, based on hypotheses of controls on ecological processes. The second method was using a questionnaire in a workshop setting to capture the knowledge and insights of people spending their careers investigating ecological questions and managing natural resources.

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Chapter 1: Historical and Future Climate Influences on Mountain Pine Beetle Outbreaks in Whitebark Pine in the Greater Yellowstone Ecosystem[1]

1.1 Abstract

Extensive mortality of whitebark pine is occurring in the Greater Yellowstone Ecosystem of the western US primarily from mountain pine beetle colonization, though disease is another factor. The climatic drivers and the potential for future tree mortality from mountain pine beetles are not well established, yet are important considerations in whether to list whitebark pine as a threatened or endangered species. We sought to add to the understanding of climate influences on mountain pine beetle outbreaks in whitebark pine forests, which are less well understood than outbreaks in lodgepole pine, by quantifying climate-beetle relationships in whitebark pine, understanding climate influences on the recent outbreak, and estimating the suitability of future climate for beetle colonization. We developed a statistical model of the probability of whitebark pine mortality that included the effects of beetle population size, beetle development and survival, and stand characteristics. Estimated probability of whitebark pine mortality increased with higher winter minimum temperature, allowing for greater beetle winter survival; higher fall temperature, allowing for synchronous beetle emergence; and lower two-year summer precipitation, leading to enhanced host tree stress. Mortality probability also increased with increasing beetle pressure, stand age, and increasing

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[1] Buotte, P. C., J.A. Hicke, H.K. Preisler, J.T. Abatzoglou, K.F. Raffa, J.A. Logan. 2015. Historical and Future Climate Influences on Mountain Pine Beetle Outbreaks in Whitebark Pines in the Greater Yellowstone Ecosystem. Global Change Biology. In Revision.

dominance of whitebark pine within a stand. The recent outbreak appeared to have resulted from a combination of higher than normal winter temperatures, suitable fall temperatures, and low summer precipitation. Projected temperature increases will provide favorable conditions for MPB survival and development within almost all current whitebark pine habitat in GYE by the end of this century. When these temperatures coincide with low precipitation, whitebark pine's relatively low defenses against mountain pine beetle colonization will be further compromised. Therefore, when surviving and regenerating trees reach ages suitable for beetle colonization, there is strong potential for continued whitebark pine mortality.

1.2 Introduction

Globally, there is evidence that climate change during the last several decades has impacted natural systems (IPCC, 2014, Rosenzweig *et al.*, 2008). Extensive and severe tree mortality, linked to climate change, has occurred on all continents (Allen *et al.*, 2010), and biotic disturbance agents are often key components of this mortality. Recent outbreaks by bark beetles have resulted in >11 million hectares of tree mortality in western North America (Meddens *et al.*, 2012) and have been linked to warm and dry conditions (Bentz *et al.*, 2010, Berg *et al.*, 2006, Carroll *et al.*, 2004, Creeden *et al.*, 2014, Preisler *et al.*, 2012, Weed *et al.*, 2013). Given projections of future warming, there is strong potential for increases in insect-induced tree mortality in the future (Adams *et al.*, 2009, Bentz *et al.*, 2010).

Large-scale mountain pine beetle (*Dendroctonus ponderosae Hopkins)* outbreaks have been relatively uncommon and short-termed in whitebark pine (*Pinus albicaulis*) forests (Logan *et al.*, 2010), because these high-elevation forests were typically outside the beetle's thermal limits of development and cold tolerance (Amman, 1973). However, during the

2000s, a widespread outbreak occurred in whitebark pines across the western US with particularly severe mortality in the Greater Yellowstone Ecosystem (GYE), where 82% of catchments containing whitebark pine experienced significant tree mortality (Macfarlane *et al.*, 2013). This outbreak caused whitebark pine mortality that was greater in spatial extent and severity than any previously recorded outbreak for this host species (Logan *et al.*, 2010).

Whitebark pine is both a keystone and foundation species of high-elevation forests of the GYE, which is centered on Yellowstone National Park, a United Nations-designated World Heritage Site. Whitebark pines promote community diversity through production of highly nutritious seeds, which are a food source for grizzly bears (*Ursus arctos horribilis*), and other animals (Tomback *et al.*, 2001). Whitebark pine promotes community stability in several ways. Clark's nutcrackers (*Nucifraga columbiana*) cache the seeds in open or recently disturbed areas, but do not recover all of these seeds, and regeneration occurs rapidly (Hutchins & Lanner, 1982, Tomback, 1982, Tomback *et al.*, 2001). The seedlings are able to establish in conditions too harsh for other tree species (Tomback & Linhart, 1990, Tomback *et al.*, 1993). Mature whitebark pine trees then provide shelter from wind and ice abrasion, allowing less hardy species to establish (Callaway, 1998). Whitebark pines also regulate snowmelt, stabilize rocky soils, and reduce soil erosion (Arno & Hammerly, 1984, Farnes, 1990, Hann, 1990, Tomback *et al.*, 2001).

Because of extensive tree mortality and future threats, whitebark pine was recommended for listing as a threatened or endangered species (USFWS, 2011). Climate influences on mountain pine beetles (e.g., Logan *et al.*, 2010) was a major reason for the finding (USFWS, 2011). However, the climatic drivers of the recent outbreak and the potential for future events of this magnitude are not well established (USFWS, 2011).

There is substantial understanding of mountain pine beetle outbreaks in lodgepole pine (*Pinus contorta* var. *latifolia*) forests (e.g., Bentz *et al.*, 2010, Raffa *et al.*, 2008). Temperature affects beetles by regulating development rates. Ideal conditions for beetles allow for a one-year life cycle and synchronized emergence of adults in late summer, which permits mass attack of host trees and enables populations to enter winter as late instar larvae, the most cold-hardy life stage (Logan & Powell, 2001). Beetles may require more than a single year to complete their lifecycle in regions with colder temperatures common at higher elevations (Bentz *et al.*, 2014). Cold tolerance describes the probability that beetles will survive the winter (Régnière & Nealis, 2007). Temperatures below -40° C cause nearly 100% beetle mortality (Safranyik, 1978), and unseasonably cold weather during fall and spring can kill beetles that are not fully cold-hardened (Wygant, 1940). Drought stress limits a host tree's ability to defend itself against beetle attack (Kane & Kolb, 2010, Raffa & Berryman, 1983). However, severe drought stress can result in thin phloem that limits food resources for beetles (Amman & Baker, 1972) and that desiccates quickly (Safranyik & Carroll, 2006), thereby reducing mountain pine beetle brood production.

Critical knowledge gaps, however, remain about the effects of climate on mountain pine beetle outbreaks in whitebark pine forests and the potential for future outbreaks given a changing climate. Few field, experimental, or empirical studies of mountain pine beetles in whitebark pine exist relative to lodgepole pine, yet climate influences may differ from lodgepole pine (Raffa *et al.*, 2013). For example, in lodgepole pine drought stress is an important factor in determining attack success (Raffa & Berryman, 1983), however whitebark pine trees can have a lower defensive capacity then lodgepole pine trees (Raffa *et al.*, 2013) which could yield different relationships between drought and outbreak initiation or progression in different habitats. Beetle development rates vary across latitudinal and elevational gradients (Bentz *et al.*, 2014), therefore models that have been developed to predict the effects of temperature on beetle survival and development in lodgepole pine may not be applicable in whitebark pine. Although there have been observational studies of the recent widespread whitebark pine mortality in the GYE (Jewett *et al.*, 2011, Logan *et al.*, 2010, Simard *et al.*, 2012), these studies do not partition the effects of temperature, moisture, the number of attacking beetles, and stand structure. Thus, more detailed quantitative analyses that link mountain pine beetle outbreaks in whitebark pine to beetle populations, stand structure, and multiple climate variables will increase understanding of the causes of the recent outbreak and allow for estimates of outbreak potential under future climate conditions, thereby leading to a more informed recommendation for future listing and potential management. Given its important role in high-elevation ecosystems of the western US, increased understanding about the future for whitebark pine is also critical to understanding potential cascading effects on wildlife, hydrology, and forest structure and function.

Here we investigated observed climate-beetle relationships in whitebark pine in the GYE (see Fig. 1.1) and projected weather suitability for whitebark pine mortality from mountain pine beetle colonization under future climate scenarios. Our objectives were to 1) understand weather influences on whitebark pine mortality from mountain pine beetles, 2) assess relative weather influences on the initiation and progression of the recent outbreak, and 3) project future climate suitability for whitebark pine mortality from mountain pine beetles. We developed and evaluated a logistic regression model of the probability of whitebark pine mortality from mountain pine beetle colonization. The model accounted for the effects of beetle population size, stand structure, and weather effects on beetle development and survival and tree stress. This model was used to describe climate-beetle relationships and diagnose weather influences on the recent outbreak. We then applied the model to future climate projections to estimate future climate suitability for whitebark pine mortality from mountain pine beetle colonization.

1.3 Methods

1.3.1 Study Area

The spatial domain for developing the model of tree mortality is the GYE of the western US (Fig. 1.1b). The GYE encompasses Yellowstone and Grand Teton National Parks and the surrounding lands (Clark & Zaunbrecher, 1987). Lower elevations are predominately grass-shrub communities, with willows (*Salix* spp.) and cottonwoods (*Populus* spp.) along streams and rivers. At higher elevations, coniferous forest types include Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine, subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine, which are intermixed with montane meadows (Knight, 1994). We limited our model development to those 1-km grid cells within the GYE with at least 10% whitebark pine based on a 30-meter resolution map of whitebark pine presence in the GYE developed from Landsat imagery (Landenburger *et al.*, 2008). Overall classification accuracies for this map exceeded 90% (Landenburger *et al.*, 2008). Using this range definition, grid cells containing whitebark pine ranged from 2000-3800 meters, with an average elevation of 2732 meters.

1.3.2 Response Variable

We used the USDA Forest Service Aerial Detection Survey (ADS) database to define the response variable as the presence of whitebark pine mortality each year in each 1-km pixel within the range of whitebark pine. ADS data were collected by observers in aircraft who recorded tree mortality from mountain pine beetles, forest type (here, whitebark pine), and damage severity (here, number of killed trees). Meddens et al. (2012) converted these data to 1-km grids of the number of trees killed for each beetle and tree species combination for the western United States. We subtracted one year from the year of detection to convert to year of beetle colonization because whitebark pines attacked and killed in one summer turn red (allowing for detection) the following summer. From this data set, we identified the voxels (grid cells by year) with whitebark pine trees killed by mountain pine beetles from 1996-2009. Voxels having at least one tree killed from mountain pine beetles were coded as having mortality (0=absence of mortality, 1=presence). The aerial surveys also report locations flown (not every location is flown every year). Voxels that were not flown during ADS surveys in a given year were excluded from the data used to develop the model. Whitebark pine mortality from mountain beetles was noted in Yellowstone Park in 1971-1979 and in 1983-1984 (R. Renkin, unpublished data). However, ADS reports for the GYE (available at http://www.fs.usda.gov/detailfull/r1/forest-grasslandhealth/?cid=fsbdev3_016103) and observations (pers. comm. Roy Renkin, Vegetation Ecologist, Yellowstone National Park) indicated no mountain pine beetle activity in whitebark pine stands from 1985 through 1995. We therefore set all voxels from 1985 through 1995 to zero trees killed. To reduce the potential for the inclusion of beetle-killed trees other than whitebark pine, we limited our model development dataset to those 1-km pixels that contained at least 10% whitebark pine, as described above. Given whitebark pine is a slow-growing species (Weaver, 2001), its distribution would not have changed substantially since this map was developed in 1999. Confusion with other sources of mortality is unlikely. In the GYE, mortality from mountain pine beetles is higher than mortality from blister rust (Shanahan *et al.*, 2014), blister rust does not cause trees to turn red all at once as mountain pine beetle colonization does.

1.3.3 Explanatory Variables

Explanatory variables were chosen to represent known factors that influence mountain pine beetle outbreaks in lodgepole pine, including the number of attacking beetles, or beetle pressure, from the previous year, beetle mortality due to low winter temperatures, successful beetle development for survival to reproductive age the summer of colonization, population synchrony, stand structure, and host tree defensive capabilities (Aukema *et al.*, 2008, Boone *et al.*, 2011, Preisler *et al.*, 2012, Sambaraju *et al.*, 2012). Temperature affects beetles by regulating development rates. Ideal conditions allow for a one-year life cycle and synchronized emergence of adults in late summer, which permits mass attack of host trees and enables populations to enter winter as late instar larvae, the most cold-hardy life stage (Logan & Powell, 2001). Temperatures below -40° C can cause near 100% mortality in beetles in any life stage (Safranyik, 1978), and unseasonably cold weather during fall and spring can kill beetles that are not fully cold-hardened (Wygant, 1940). Drought stress limits a host tree's ability to defend itself against beetle attack (Kane & Kolb, 2010, Raffa & Berryman, 1983). However, severe drought stress can result in thin phloem that limits food resources for beetles (Amman & Baker, 1972) and that desiccates quickly (Safranyik & Carroll, 2006) thereby reducing mountain pine beetle productivity.

Temperature variables representing beetle winter mortality and beetle development rates (Table 1.1) were calculated over the year of attack, representing a one-year lifecycle, and over the year of attack and previous year, representing a two-year lifecycle. We represented tree drought stress with a set of candidate variables including vapor pressure deficit, precipitation, and water balance metrics calculated over the current through previous five years, resulting in six candidate variables for each drought stress metric (Table 1.1).

We created a set of candidate variables to represent each of the factors described above (Table 1.1) and calculated these variables for each 1-km pixel for each year (i.e. voxel). Several candidate temperature variables were derived from daily temperature data using National Weather Service Cooperative Observer Program stations interpolated to a 1-km resolution through inverse distance weighting and vertical lapse rates within the BioSIM program (Régnière, 1996). BioSIM and interpolated daily data were also used to derive variables from process models of cold tolerance (Régnière & Bentz, 2007) and adaptive seasonality (Logan & Powell, 2001) at 1-km resolution. The cold tolerance model calculates the probability of beetle survival over the winter (Régnière & Bentz, 2007). The adaptive seasonality model calculates the probability of beetles achieving a one-year life cycle and mass emergence in August (Logan & Powell, 2001). Several candidate climate variables were derived from monthly 800-m Parameter-elevation Regressions on Independent Slopes Model (PRISM) data version LT71m (Daly *et al.*, 2008). Climatic water deficit was computed using the AET calculator program (Gavin & Hu, 2006) with monthly 800-m PRISM data. This program calculates water balance using a modified Thornthwaite method (Willmott *et al.*, 1985) and we assumed a field capacity of 100 mm. We additionally assessed the occurrence of drought by inspecting drought conditions from the US Drought

Monitor (http://droughtmonitor.unl.edu, accessed 09 December 2014), which integrates multiple drought indices. Regardless of the original data source, all candidate variables were interpolated to a 1-km resolution and assigned to each pixel according to the year of colonization. For example, winter minimum temperature was the minimum of monthly minimum temperatures during December-February the winter prior to colonization in each 1-km pixel.

To isolate the effects of climate variables, we need to also account for the effects of non-climate variables in our model. Local beetle pressure (the number of beetles in the focal cell) was represented by the number of trees killed by mountain pine beetles in each grid cell the previous year (Preisler *et al.*, 2012) using 1-km gridded ADS data (Meddens *et al.*, 2012). Beetle pressure from outside the cell of interest, or dispersal beetle pressure, was represented by calculating an inverse-distance-weighted linear function of the number of trees killed by mountain pine beetles that declined to 0 at a 6-km radius (Raffa *et al.*, 2008, Turchin & Thoeny, 1993), minus the number of trees killed in the cell of interest. These beetle pressure variables are important because of the positive density feedback exerted by pheromone-mediated corporative behavior (Raffa *et al.*, 2008) and because higher beetle populations increase the likelihood of successful colonization and subsequent tree mortality (Boone *et al.*, 2011). Percent whitebark pine was determined by summing the area of 30-m grid cells defined as whitebark pine from the Landenberger et al. (2008) map of whitebark pine in each 1-km grid cell in the study area. As noted previously, because whitebark pine is a slow growing species (Weaver, 2001), a distribution map based on satellite imagery from 1999 (Landenburger *et al.*, 2008) is valid well beyond the time span of our study. To estimate the food supply available to beetles, we calculated remaining whitebark pine as 100 hectares minus the cumulative area (ha) with mortality since 1985 from the Meddens et al. (2012) data set. Stand age was defined from a 1-km resolution map of average stand age for North America based on forest inventory data, fire histories, and remote sensing data (Pan *et al.*, 2011). In the databases of biomass and basal area available for this study area (Blackard *et al.*, 2008, Krist *et al.*, 2007) many grid cells with recorded mortality had zeros for biomass or basal area. We therefore did not feel these data were adequate representations of stand structure in the study area and did not use them in the models. We investigated using quadratic mean diameter data from the National Risk Assessment mapping program as a variable describing stand structure, but there were spatial inconsistencies across the study area, most notably around Yellowstone Lake, which indicated there was a problem with georeferencing. We also evaluated a map of whitebark pine distribution developed by the Whitebark Pine Subcommittee of the Greater Yellowstone Coordinating Committee (GYCCWBPSC, 2010) that has a categorical size class attribute, but found noticeable political boundaries and did not want to introduce those delineations into the modeled weather suitability estimates, so did not use these data.

1.3.4 Historical Weather Data

To estimate historical weather suitability (described below), we applied our statistical model to yearly variables generated from 800-m PRISM data from 1978-2009. We sought to apply our statistical model back to 1900, using PRISM climate data, to provide more context for recent patterns and to evaluate our predicted weather suitability against known past outbreaks in the GYE in the 1930s, 1970s, and early 1980s (Furniss & Renkin, 2003, Lynch *et al.*, 2006). However, by comparing temperature records at low- and high-elevation weather stations, we noted that frequent temperature inversions occur in the GYE. After examining period of record for Natural Resources Conservation Service Snow Telemetry stations in the study area, we found there were very few high-elevation stations that contributed observations to PRISM algorithms before 1978. Therefore, there is more uncertainty in PRISM temperatures at whitebark pine locations earlier in the 1900s and we decided not to use past outbreaks for model evaluation. We suggest trends in weather suitability for mountain pine beetle output in whitebark pine forests earlier than 1978 but emphasize the uncertainty in these trends. A comparison of temperature and precipitation variables from PRISM, Daymet (Thornton *et al.*, 1997), TopoWx (Oyler *et al.*, 2014), and weather station data during 1978-2009 showed similar temporal patterns in all weather variables, indicating our results and conclusions are robust with respect to the choice of climate dataset.

1.3.5 Future Climate Projections

To estimate future climate suitability (described below) we applied our model to yearly variables generated from future projections from ten general circulation models forced with low (RCP 2.6), moderate (RCP 4.5), and high (RCP 8.5) emissions scenarios, at the same temporal resolution as variables used in model development. We used NASA Earth Exchange Downscaled Climate Projections at 30 arc-second resolution (Thrasher *et al.*, 2013), which were downscaled from the Fifth Coupled Model Inter-comparison Project results (Taylor *et al.*, 2012). Due to natural variability in atmospheric conditions, GCM climate projections cannot be expected to represent a particular year and match weather station data from that year. We can, however, expect GCM climate projections and weather station data distributions of temperature or precipitation to match over a longer time period. We therefore checked for consistency between historical GCM climate and PRISM weather 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 weather suitability based on PRISM weather data. Historical climate data for the period 1978–2006 from each downscaled GCM projection were similar to historical (1978-2006) PRISM weather data (Fig. 1.5); averaged over the study area and time period, GCM winter temperatures were within 1 ºC of PRISM winter temperatures and summer precipitation was within 6%.

1.3.6 Statistical Model

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

$$logit(p) = \beta_o + s_{m1}(X_{m1}) + \cdots s_{mi}(X_{mi}) \qquad \text{Eq. 1}$$

where *p* is the probability of tree mortality (at least one tree killed) from mountain pine beetle colonization and $s_{m1}(X_{m1})$ through $s_{mi}(X_{mi})$ are tensor product smooth functions of the explanatory variables representing the factors of beetle winter mortality, beetle adaptive seasonality, host tree stress, previous year beetle population, remaining food supply, and stand structure (see Table 1.1). The estimated smooth functions of the explanatory variables are the change in the log-odds of whitebark pine mortality over the range of the variable, with change set to zero at the average. Because beetles can kill healthy trees when beetle populations are high (Boone *et al.*, 2011), we allowed the drought stress variables to vary with beetle pressure by including an interaction term, $s(X_{mi}, X_{mj})$, between drought variables and beetle pressure. This interaction is not shown in Eq. 1 because it was not included in our final model (see results below). We used a model selection process following Burnham and Anderson (2002), ranking models according to AIC, to select the best-fitting variable from our set of candidate variables for representing each of the factors in Table 1.1.

Because weather variables in particular tend to be correlated, we calculated concurvity (akin to multiple colinearity in a linear model) among variables in the top model (Hastie & Tibshirani, 1990). When concurvity was greater than 0.5, we assessed the effects of removing one of the concurved variables on the smoothing functions of the other variables. In cases where removing variables altered the response curves of the remaining variables, we computed AIC scores from models with only uncorrelated variables to determine which of the concurved variables would remain in the final model.

We evaluated model goodness-of-fit in several ways. First, to determine if the model captured the temporal pattern of area with mortality, we plotted observed and predicted area of mortality by year (Fig. 1.1a). Because our response variable was the presence of whitebark pine mortality in each 1km voxel, we summed the modeled probabilities of mortality to calculate the predicted area with mortality in Figure 1.1a. 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 computed as the sum of the predicted probabilities over all grid cells in that year. We calculated the R^2 and root mean square error (RMSE) between the observed and predicted yearly total mortality areas. Second, we plotted maps of observed and predicted mortality to determine if the model captured the spatial pattern of mortality within the GYE (Fig. 1.1b). These predictions were calculated through spatial cross-validation, in which the area being predicted was withheld from the data used to estimate the model parameters. Using these maps, we compared the sum of the number of years with observed mortality with the sum of the predicted yearly mortality probabilities.

We evaluated the potential for spatial autocorrelation by calculating autocorrelation in the residuals from both our top model as well as from our top model with the addition of a spatial term (x, y in UTM coordinates). We plotted the autocorrelation in the residuals of both models at increasing lag distances. We also compared the log-odds plots from the two models because changes in these plots would indicate there is a spatial pattern that was not accounted for by the other explanatory variables. Autocorrelation in the residuals at a distance of 1 km was low (0.11) in the model without a spatial term, and including a spatial term only reduced this correlation to 0.09. Including a spatial term did not change the log-odds plots of the explanatory variables.

1.3.7 Weather Suitability for Whitebark Pine Mortality from Mountain Pine Beetle Colonization

We define weather suitability indices for tree mortality from mountain pine beetle colonization in reference to the log-odds of tree mortality. We do not project historical or future probabilities of whitebark pine mortality. Therefore, we set non-weather variables to a constant and applied our model to historical weather data and future climate projections. We calculated weather suitability indices for a given year for each of the explanatory weather variables by computing the mean log-odds over all pixels in a given year. We calculated a combined weather suitability index by summing the log-odds of all the weather variables for each pixel and then computing the mean of these summed log-odds over all pixels in a given year. Because a log-odds value of zero implies no increase in the odds of mortality relative to the odds evaluated at the average level, a mean suitability estimate greater than zero implies an increase in the odds of mortality (hence an increase in suitability) over the average odds of mortality. The average of an explanatory variable in our model is the mean over all voxels used to develop the model. As we discussed previously, GCM projections are not representative of a given year, but rather are representative of temperatures and precipitation over a longer time period. We therefore refer to future suitability as climate suitability instead of weather suitability.

1.4 Results

Whitebark pine mortality from mountain pine beetle colonization in the GYE increased from below-observable levels in the late 1980s to a peak of just over 3,500 km^2 in 2008, followed by a decline in 2009 (Fig. 1.1a). Yearly mortality areas represent new mortality in each year, as opposed to the cumulative area of mortality since 1985. Our cross-validated model predicted the observed annual (Fig. 1.1a) and spatial (Fig. 1.1b) patterns of tree mortality well.

1.4.1 Weather Influences on Whitebark Pine Mortality from Mountain Pine Beetles

In the top model, beetle mortality due to low winter temperature was best represented by cold tolerance, calculated using a previously-developed process model in the BioSIM software; beetle development was best represented by the average fall temperature the year prior to colonization and the average April-August temperature in the year of colonization; tree drought stress was best represented by the cumulative precipitation in the summer or colonization and previous summer; and stand structure was best represented by stand age (Table 1.2). Cold tolerance is a computationally expensive variable, and our objectives included applying the model to large future climate data sets. Substituting the minimum temperature of the coldest winter month in the year of attack, which was the second best winter mortality variable (Table 1.2), for cold tolerance did not substantially change the annual patterns of mortality nor alter our interpretation of the influence of beetle winter mortality or the other explanatory variables. We therefore used minimum temperature of the coldest winter month in our final model, and all results shown are from this model.

Plots of the interaction between the number of trees killed last year and drought stress indicated no difference in the effect of drought at higher beetle. Therefore, the final model did not contain this interaction. Concurvity between the percent of whitebark pine and the area of remaining whitebark pine in the previous year was high (0.91), and dropping one of these variables altered the response function of the other. Percent whitebark pine was the more skillful variable according to AIC scores, and so we retained percent whitebark pine in the final model.

Estimated probability of tree mortality increased significantly with higher winter minimum temperature then plateaued above -12°C (Fig. 1.2a). A similar pattern occurred for fall temperature (Fig. 1.2b). The effect of April-August temperature was similar but was not well estimated by the model as indicated by the wide standard errors (Fig. 1.2c), and was therefore not included in the final model. Probability of tree mortality increased significantly with decreasing summer precipitation across most of the range of precipitation. However, at the lowest levels of precipitation, the relationship switched to a declining probability of tree mortality (Fig. 1.2d).

Higher probability of tree mortality was associated with increasing local and dispersal beetle pressure, in older stands, and in stands with greater amounts of whitebark pine (Fig. 1.3). Average stand age was 137 years, and 75% of stands were at least 87 years old.

1.4.2 Weather Influences on the Recent Outbreak

Observed whitebark pine mortality began in 1998, and the combined weather suitability index indicates more suitable weather conditions for tree mortality from beetle colonization in 1995 forward, with exceptions in 1998 and 1999 (Fig. 1.4). Winter and fall temperatures were more suitable beginning around 1995. From 1978 to the early 1990s, winter minimum temperature frequently had low or very low suitability values, whereas after 1992, winter temperature suitability was higher. With a few exceptions, fall temperatures were typically suitable during 1978-2009. Suitability due to precipitation was higher in 1995-1996 and after 1999 (except 2005). Declines in the observed area with mortality occurred in years (2002 and 2005) with lower precipitation suitability. US Drought Monitor maps of late August indicate abnormally dry to severe drought conditions during 2000-2008, with multiple years of extreme to exceptional drought. Additionally, plots of summer (Fig. 1.4) and water-year (not shown) precipitation from PRISM data show that multiple consecutive years of low precipitation occurred in the 2000s more often than in previous decades.

Whitebark pine mortality from mountain pine beetles was recorded in Yellowstone National Park from 1971 through 1978, and 1981 through 1983 (R. Renkin, unpublished data), although the spatial extents of these outbreaks were far less than the most recent outbreak. The lack of mortality in 1979 and for multiple years beginning in 1984 coincides with low suitability of winter minimum temperature (Fig. 1.4).

1.4.3 Future Weather Suitability for Whitebark Pine Mortality from Mountain Pine Beetles

Applying our statistical model to future climate projections allowed us to estimate future climate suitability for mountain pine beetle colonization. Future climate projections show increasing winter and fall temperatures, with greater increases under higher emissions scenarios and later in the century, and intermodel and interannual variability in cumulative two-year summer precipitation (Fig. 1.5). As a result, modeled future climate suitability for whitebark pine mortality from mountain pine beetle colonization increases in the future and is higher under higher emissions scenarios and later in the century (Fig. 1.6 & 1.7). Under the highest emissions scenario (RCP 8.5), most projections indicate climate suitability similar to values that occurred during the recent outbreak from 2010 forward (Fig. 1.7c). Modeled winter minimum temperature suitability is relatively more consistent among climate projections than other climate variables, with the near disappearance of years with the extremely low winter temperature suitability that occurred prior to the recent outbreak (Fig. 1.7a). Future fall temperature suitability shows less intermodel variability and, on average, has continuously high values after 2010 (not shown). Precipitation suitability varies widely among climate projections and does not show any long-term change relative to the historical period (Fig. 1.7b). Combined future climate suitability varies most with future precipitation estimates, with more precipitation leading to lower climate suitability and less precipitation leading to higher climate suitability (Fig. 1.7b,c). Regardless of future precipitation projections, strong climate model agreement of warming increases suitability for beetle colonization, and consequently the number of years with low combined climate suitability declines in the future (Fig. 1.7c).

We mapped winter minimum temperature suitability (Fig. 1.8) because the temporal patterns of this climate variable (Fig. 1.2) show a clear difference before and after the recent outbreak and because future projections were consistent across climate models. Because spatial patterns of future climate suitability were similar across all projections and time periods, we show results from the multi-model average. Across the current range of whitebark pine in the GYE, the proportion of winters with high suitability (defined as the weather suitability model term > 0) for whitebark pine mortality increases in the future (Fig. 1.8). Prior to the recent outbreak, in 1978-1997 (not mapped), the spatially averaged proportion of a highly suitable winter was 0.47, and during the recent outbreak, in 1998-2009, the proportion increased to 0.56. Future projections indicate that the proportions will increase to 0.75, 0.87, and 0.94 in 2010-2039, 2040-2069, and 2070-2099, respectively. In the near term, spatial variability exists, with the lowest suitability occurring in portions of the Wind River Range (southeast GYE) and the northeast GYE (Fig. 1.8).

1.5 Discussion

Our study indicates that climate is an important driver of mountain pine beetle colonization of whitebark pines of the Greater Yellowstone Ecosystem, similar to results in lodgepole pines. Higher temperatures and drought appear to facilitate colonization through enhanced beetle survival, synchronous attacks, and increased host tree susceptibility. Future climate suitability for whitebark pine mortality due to mountain pine beetle colonization is expected to increase due the effects of increasing fall and winter temperatures, and increases are expected to be greater when accompanied by summer drought, for which the projections are more variable.

1.5.1 Climate Influences on Whitebark Pine Mortality from Mountain Pine Beetle Colonization

An increase in tree mortality with increasing winter minimum temperatures has been found in lodgepole pine (Aukema *et al.*, 2008, Chapman *et al.*, 2012, Creeden *et al.*, 2014, Preisler *et al.*, 2012) and whitebark pine (Jewett *et al.*, 2011, Logan *et al.*, 2010, Perkins &

Roberts, 2003). These, and our results of increasing whitebark pine mortality from beetle colonization with increasing winter minimum temperatures, are likely due to increased beetle survival (Amman, 1973, Bentz *et al.*, 1991) leading to a larger beetle population attacking trees the following summer.

Our modeling structure allowed us to separate the different effects of temperature on beetle development and population synchrony; we found that fall temperatures were more significant than spring/summer temperatures. Fall temperatures serve to synchronize life stage development of beetle populations because when fall temperatures are warmer, eggs that were laid late in the fall can continue to develop and enter winter as late-instar larvae (Logan & Powell, 2001). Our modeling suggested a positive, though insignificant, influence of April-August temperature on tree mortality probability. The range of April-August temperatures over the period of model development may have been insufficient to detect a conclusive influence. Jewett et al. (2011) found whitebark pine mortality in the GYE was related to higher spring temperatures, though mortality was not directly attributable to mountain pine beetle colonization. In British Columbia, the probability of outbreaks in lodgepole pine increased with warmer summers (Aukema *et al.*, 2008).

We found similar temperature effects on whitebark pine mortality from mountain pine beetle colonization as has been found in the beetles' primary host, lodgepole pine (Bentz *et al.*, 2010, Logan & Powell, 2001, Raffa *et al.*, 2008, Régnière & Bentz, 2007). These similarities suggest that although beetle development rates vary across latitudinal and elevational (and hence temperature) gradients (Bentz *et al.*, 2014, Bentz *et al.*, 2001), temperature is an important influence on beetle survival and development and population synchrony across different forest types.

Although we found similar temperature drivers of mortality from beetle colonization in whitebark pine forests as in lodgepole pine forests, a process model that predicts the probability of adaptive seasonality that was parameterized with data from beetle development rates in a lodgepole pine system (Logan & Bentz, 1999) did not have a better predictive value for estimating the effects of beetle development and synchrony on whitebark pine mortality than average seasonal temperatures. This suggests continued research on beetle development rates across temperature gradients (e.g. , Bentz *et al.*, 2014), and further process model regional parameterization, would increase our understanding of and ability to predict temperature effects on beetle lifecycles in high elevation forests.

Multiple studies have documented the co-occurrence of beetle outbreaks with drought stress (Gaylord *et al.*, 2013, Hart *et al.*, 2014, Kaiser *et al.*, 2013, Negron *et al.*, 2009, Rouault *et al.*, 2006). Tree susceptibility to beetle colonization increases with increasing levels of tree drought stress (Bentz *et al.*, 2010, Kane & Kolb, 2010, Raffa & Berryman, 1983) because severe drought stress can decrease the ability of trees to produce and translocate defensive compounds (Ayres, 1993, Bentz *et al.*, 2010, Breshears *et al.*, 2009). Drought stress also reduces tree growth (Ayres, 1993, McDowell *et al.*, 2008). Whitebark pine growth has been positively correlated with precipitation (Millar *et al.*, 2012, Perkins & Swetnam, 1996), and Perkins and Roberts (2003) found whitebark pine mortality from beetles was higher when precipitation was lower and tree growth was less. We therefore interpret summer precipitation as an index of tree drought stress and hence tree defensive capability.

We found increasing odds of whitebark pine mortality as precipitation declined, until the very lowest levels of precipitation where the likelihood of tree mortality declined. This pattern is suggestive of drought's opposing effects on beetles through tree defense and phloem thickness. The increasing likelihood of tree mortality with increasing drought agrees with the relationship found in lodgepole pine(Chapman *et al.*, 2012, Kaiser *et al.*, 2013, Preisler *et al.*, 2012, Raffa & Berryman, 1983), spruce (Hart *et al.*, 2014), piñon-juniper woodlands (Gaylord *et al.*, 2013), ponderosa pine (Negron *et al.*, 2009), and whitebark pine (Millar *et al.*, 2012, Perkins & Roberts, 2003). Millar et al. (2012) found that drought in the previous one to two years was associated with whitebark pine mortality in the Sierra Nevada, CA. Combined with the inherently lower defensive capacity of whitebark compared with lodgepole pine (Raffa *et al.*, 2013) additional drought stress may be particularly problematic for whitebark pine. The declines in mortality probability we found at the highest levels of drought stress (lowest precipitation) could be a result of those trees having thinner phloem that cannot support substantial brood development (Amman, 1969, Amman & Baker, 1972, Cole, 1975, Safranyik & Carroll, 2006).

Stand structure is known to influence mountain pine beetle attack in lodgepole pine (Amman & Baker, 1972) and whitebark pine (Perkins & Roberts, 2003) such that older and larger trees and denser stands are more susceptible to mountain pine beetle attack (Shore *et al.*, 2000). We found that tree mortality increased with stand age, but, as can be seen from the relative magnitude of the change in the log-odds over the range of each variable, the effect of stand age on the odds of whitebark pine mortality was much less than the effect of any other variable in the model. Shore et al. (2000) showed that lodgepole pine susceptibility to beetle colonization was low in stands less than 60 years old, increased sharply in stands 61-80 years old, and stands greater than 80 years old were highly susceptible and did not pose a limit to beetle colonization. Effects of stand age were similar in our model, though shifted to slightly older stands. Based on this relationship between age and susceptibility to colonization and the typical stand age in the GYE, most stands have been susceptible to colonization throughout the last century, and had weather conditions been suitable, extensive outbreaks could have occurred. However, there is no evidence of prior tree mortality that was as extensive as recent mortality (Logan *et al.*, 2010). Stand density is an important factor in beetle colonization in lodgepole pine (Shore & Safranyik, 1992). Due to a lack of sufficient data, we were not able to quantify the effects of stand density in our modeling.

1.5.2 Climate Influences on Initiation and Progression of the Recent Outbreak

Winter minimum temperature suitability for whitebark pine mortality was consistently higher during the recent outbreak than in the years prior, suggesting warmer winter temperatures allowed beetle survival to increase and beetle populations to grow large enough to colonize whitebark pines. The historical warming that resulted in the recent absence of low winter minimum temperatures is likely a result of anthropogenic climate change (Abatzoglou *et al.*, 2014, Barnett *et al.*, 2008, IPCC, 2013, Walsh *et al.*, 2014). Preliminary analyses of temperatures from long-term weather stations in the region and PRISM over the 20th century suggest that low winter minimum temperatures occurred more frequently in the GYE during the early and mid-1900s than in recent decades. However, due to a lack of high elevation weather stations, PRISM temperatures at whitebark pine locations may be less reliable before 1978.

Drought appears to have facilitated beetle population increases by stressing host trees and making them more susceptible to colonization (Raffa & Berryman, 1983). Low summer precipitation for most years after 2000 indicated favorable conditions for the beetle outbreak by increasing the number of stressed host trees. US Drought Monitor data indicates more severe drought and PRISM data shows less precipitation in the 2000s than in years prior, confirming that precipitation was relatively low during the recent outbreak. Thus, drought stress appears to have facilitated outbreak initiation and continuation.

The role of precipitation is host-mediated, and hence more complex than that of temperature. The mechanisms behind the effects of precipitation on tree mortality from beetle colonization are less well understood, particularly in whitebark pines, and may vary with different modalities of defense (Kane & Kolb, 2010, Lewinsohn *et al.*, 1993). Declines in area with mortality in 2005 and 2009 coincided with higher precipitation and therefore relief from drought stress. However, during 1998-1999 mortality area was increasing when precipitation was high and drought stress low. Further research, as has been done in lodgepole pine (Raffa & Berryman, 1983), is necessary to better understand the mechanisms, roles, and context-dependency of drought in whitebark pines.

1.5.3 Caveats

Our measures of whitebark pine mortality and beetle pressure relied on ADS data. Although these data necessarily have spatial error, Johnson and Ross (2008) evaluated recorded presence of bark beetle-caused tree mortality in various species and found errors of commission and omission decreased at coarser spatial scales. Johnson and Ross (2008) also suggest stand homogeneity influences error rates because errors in lodgepole stands, which tended to be homogeneous in the region sampled, declined from 33% within a spatial buffer of 50 meters to 13% within a spatial buffer of 500 meters. In their study, errors for whitebark or limber pine were high (50-75%) within a spatial buffer of 500 meters. However, they sampled primarily at the southeastern edge of the range of whitebark pine (Johnson & Ross, 2008). Because whitebark pine stand conditions tend to be homogeneous in the GYE

(Weaver, 2001), identifying whitebark pine stands is likely easier and spatial accuracy therefore likely greater in our study area.

We were unable to include the effects of stand density in our statistical model. However, removing stand age from our model did not alter the shape of any of the weather variable response curves. We therefore expect that including stand age would also not alter our interpretations of the effects of weather variables.

1.5.4 Future Climate Suitability for Whitebark Pine Mortality from Mountain Pine Beetle Colonization

Given projections of future warming, we estimate that by approximately 2040 climate conditions across most of the current whitebark pine range in the GYE will likely be as suitable for beetle colonization as conditions that occurred during the recent outbreak. Thus, newly establishing whitebark pines will face a strong potential for beetle colonization as they achieve sufficient size, and the future structural composition of whitebark pine stands will likely be quite different from before the recent outbreak: large whitebark pines may not be prevalent in the GYE. Instead, whitebark pines may primarily exist as young and/or small trees, which will still be vulnerable to other threats, such as white pine blister rust (Greater Yellowstone Whitebark Pine Monitoring Working Group, 2013).

Estimates of future climate suitability depend on future climate projections. Because future temperature and precipitation projections vary across GCMs (Rupp *et al.*, 2013), we applied our statistical model to a range of GCM projections to capture multiple possible futures. As noted previously, further research is required to more fully understand the influence of drought on whitebark pine susceptibility to beetle colonization. Additionally, projected changes in summer precipitation are less certain than projected changes in temperature. We therefore have the highest confidence in our estimates of future climate suitability due to temperature effects. Regardless of future precipitation projections, however, combined climate suitability is higher at the end of this century than at the beginning under all climate projections. Upper limits of temperature suitability are less variable among GCM projections than lower limits because the effect of temperature on the probability of whitebark pine mortality plateaus at higher temperatures.

1.6 Conclusions

The recent outbreak has substantially altered whitebark pine forest structure, reducing the number of suitable host trees (Gibson *et al.*, 2008), which will influence the future potential for mortality from mountain pine beetles. Because whitebark pine are slow-growing trees (Weaver, 2001), stands that experienced high mortality of large trees may not have enough suitable trees to support large mountain pine beetle populations for decades into the future. However, beetle populations may continue to exist in nearby lodgepole pine, which did not experienced severe mortality recently, providing a potential beetle population source for attacking whitebark pines as they attain suitable size.

Locations with lower minimum temperatures and therefore reduced suitability for mountain pine beetle outbreaks will allow whitebark pine to persist longer, and management actions to restore and conserve whitebark pines may be most successful in these areas. Spatial patterns of our results indicate that several regions in the GYE are potential locations for refugia from beetle colonization in the early to mid parts of this century. In addition, finer-resolution features not captured in our results, especially locations with cold air drainage, or significant temperature inversions, will be important for defining areas that are likely to experience low winter temperatures that will limit beetle survival. The smallest increase in temperature is projected to occur under the lowest emissions scenario. Thus reducing greenhouse gas concentrations will decrease suitability for beetle survival and likely increase the chances of whitebark pine persistence into the future.

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Table 1.1. Description of explanatory variables included in generalized additive models of 1) the probability of mountain pine beetle (MPB) outbreaks and 2) the number of MPB-killed trees, in whitebark pine forests of the Greater Yellowstone Ecosystem during 1985-2009.

Process	Rationale	Variable	Description
Climate Conditions			
Winter mortality	Unseasonably low temperatures and/or extreme low temperatures can cause direct mortality of over-wintering insects	Tmin	Minimum monthly minimum temp in Dec-Feb
		Coldt	Probability of winter survival from the cold tolerance model developed by Regniere & Bentz (2007)
		Ecs	Presence/absence of an early cold snap, defined as 4 consecutive days with temp <=-20°C between Oct 15 –Nov 30.
		Drop20	Number of days with >20°C drop in avg temperature
		Min40	Number of days with min temp <=-40°C
Adaptive seasonality	Temperature conditions can promote outbreaks by allowing for a one-year life cycle and synchronous adult emergence	Logan	0/1 of whether conditions were suitable for univoltinism according to the adaptive seasonality process model developed by Logan and Powell (2001)
		Tmean	Average temp Aug 1 – July31
		Tmaa	Average temp April-Aug
		FallT	Average temp Sept-Nov
		CDD	Cumulative degree days above 5.5°C from Aug 1 – July31. DD = max(0,T-Tthresh)
		BDD	Binary of whether 833°C degree days accumulated between Aug 1 – July 31
Drought stress	Drought stressed trees have lower defensive capabilities than healthy trees[1]	VPD0-5	Average monthly vapor pressure deficit in current and previous 5 growing seasons[2] (six variables: 0, 0-1, 0-2, …, 0-5)
		CWD0-5	Cumulative climatic water deficit in current and previous 5 growing seasons (six variables: 0, 0-1, 0-2, …, 0-5)

		PPT0-5	Cumulative monthly Oct-Aug precipitation in current and previous 5 years (six variables: 0, 0-1, 0-2, …, 0-5)
		JJAPPT 0-5	Cumulative monthly June-Aug precipitation in current and previous years (six variables: 0, 0-1, 0-2, …, 0-5)
Stand characteristics			
Available host	Outbreaks will collapse when available host is depleted	RMWBP	Remaining whitebark pine = cumulative mortality area since 1998 * % WBP in the pixel
Stand composition	More homogenous stands will provide more host trees for beetles	PCTWBP	Percent whitebark pine in the 1km^2 pixel
Stand age	Beetles prefer older, larger trees	Age	Age in years from Pan et al 2011
Beetle pressure			
Local beetle pressure	Beetles can kill healthy trees at high populations	lY1	Log(Number of MPB-killed trees in the focal cell last year)
dispersal beetle pressure		ldsp	Log(Weighted linear function of number of MPB-killed trees of any host species in surrounding 1km cells up to 6 km distant, outside the focal cell)

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[1] 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

[2] growing season = May-October

Table 1.2. AIC values from the model selection process to determine the top model of mortality probability from mountain beetles in whitebark pine forests of the Greater Yellowstone Ecosystem during 1985-2009. Base model contained the variables lY1, ldsp and PCTWBP. See Table 1.1 for variable definitions.

Logistic Model	AIC	ΔAIC
Base Model	52642	
Beetle Winter Mortality		
Tmin	52178	-463
Coldt	52082	-560
ecs+ctmin40+cdif20	52592	-50
ecs	52603	-39
ctmin40	52607	-35
cdif20	52577	-65
ecs+ctmin40	52581	-61
ecs+cdif20	52605	-37
ctmin40+cdif20	52579	-63
Beetle Adaptive Seasonality		
loganP	52643	2
tmean	51787	-854
tmaa	52555	-87
cdd	52299	-343
bdd	52522	-120
fallt	52221	-421
fallt+tmaa	51751	-891
fallt+cdd	52226	-416
fallt+ bdd	52445	-197
Tree Drought Stress		
VPD0	52158	-484
VPD01	52121	-520
VPD02	52411	-231
VPD03	52515	-127
VPD04	52562	-80
VPD05	52593	-49
cwd0	52247	-395
cwd01	52208	-434
cwd02	52176	-466
cwd03	52397	-245
cwd04	52511	-131
cwd05	52546	-96
water0	52481	-161
water01	52520	-121
water02	52511	-130

water03	52501	-141
water04	52500	-142
water05	52494	-147
JJA0	52165	-477
JJA01	52093	-548
JJA02	52328	-314
JJA03	52440	-202
JJA04	52429	-213
JJA05	52539	-103
Stand Structure		
Age	52338	-304

Table 1.3. General circulation models from the CMIP5 experiment used to estimate future weather suitability for whitebark pine mortality from mountain pine beetles in the Greater Yellowstone Ecosystem.

Modeling Center or Group	**Model Name**
Beijing Climate Center, China Meteorological Administration	BCC-CSM1.1
Canadian Centre for Climate Modelling and Analysis	CanESM2
University of Miami – RSMAS	CCSM4
Community Earth System Model Contributors	CESM1(BGC)
Community Earth System Model Contributors	CESM1(CAM5)
Centro Euro-Mediterraneo per I Cambiamenti Climatici	CMCC-CESM
Centre National de Recherches Météorologiques / Centre Européen de Recherche et Formation Avancée en Calcul Scientifique	CNRM-CM5
Met Office Hadley Centre	HadGEM2-CC
Met Office Hadley Centre	HadGEM2-ES
Institut Pierre-Simon Laplace	IPSL-CM5A-MR

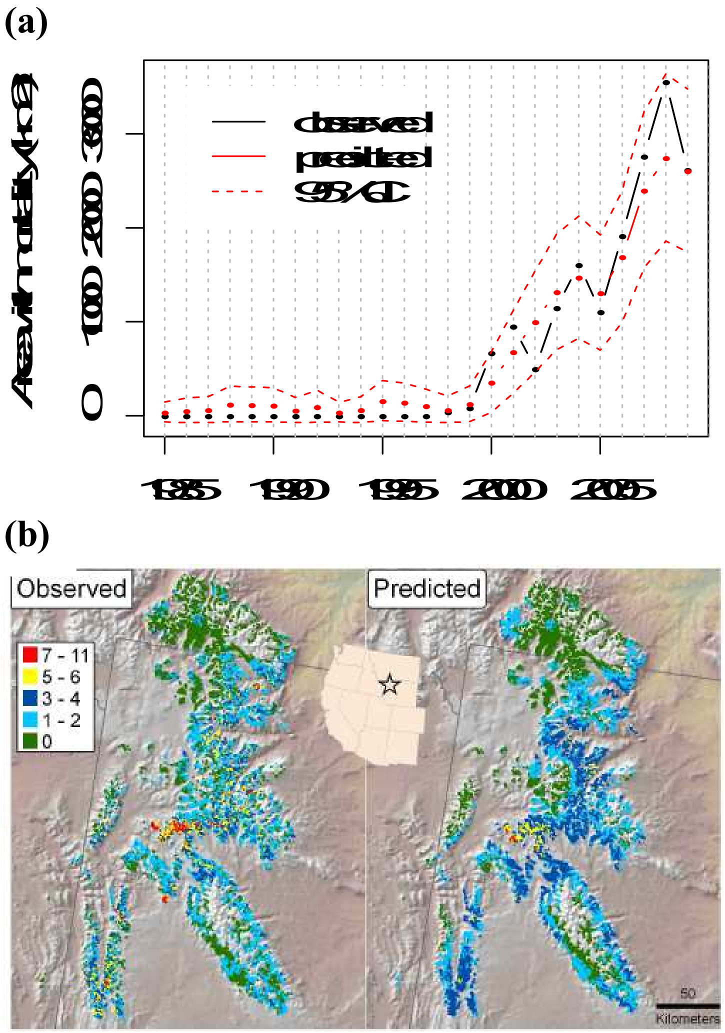

Figure 1.1. Model evaluation in (a) time, showing observed (black line) and predicted (red line) area with mortality by year (dashed red lines are 95% confidence intervals calculated from cross-validation by year) (RMSE=339 km^2, R^2=0.87); and (b) space, showing observed (left map) and predicted (right map) number of years with mortality between 1985 and 2009. Predicted mortality was determined by summing the modeled probabilities for each grid cell over (a) whitebark pine locations or (b) the study period. (b) also delineates whitebark pine locations in the study area. Star on inset map shows location of study area within western US.

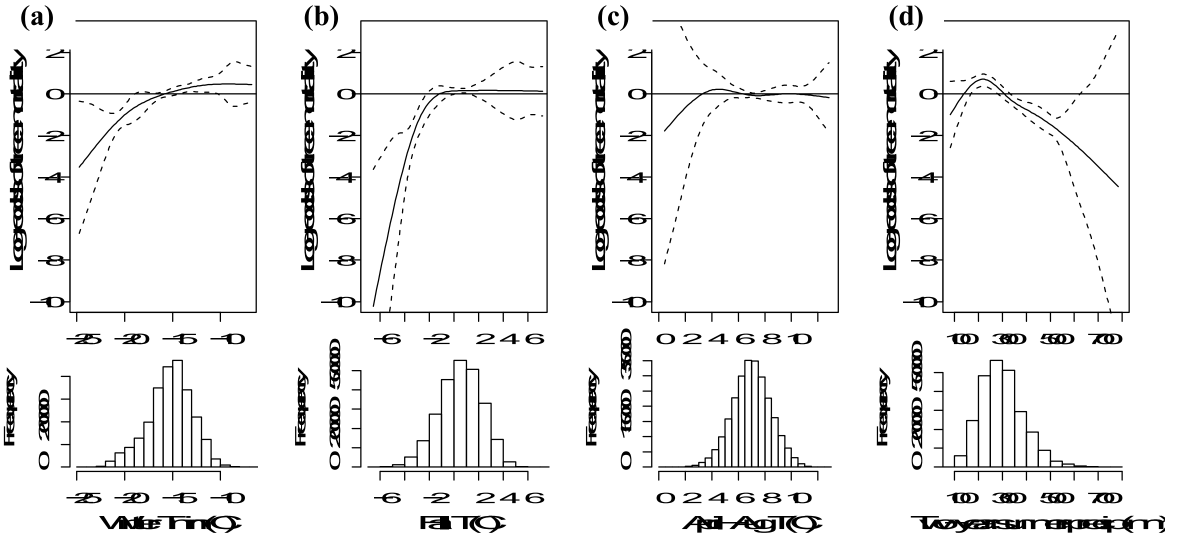

Figure 1.2. Effects of explanatory variables on the probability of whitebark pine mortality from mountain pine beetles. (a) Winter minimum temperature (representing beetle winter mortality), (b) average September-November temperature (representing temperature control of life stage development rate and population synchrony), (c) average April-August temperature (representing temperature control of life stage development rate), and (d) cumulative 2-year summer precipitation (representing drought effects on whitebark pine hosts). Dashed lines are 95% confidence intervals calculated from jackknifing by year (see SI text). Histograms show distributions of data used in model development.

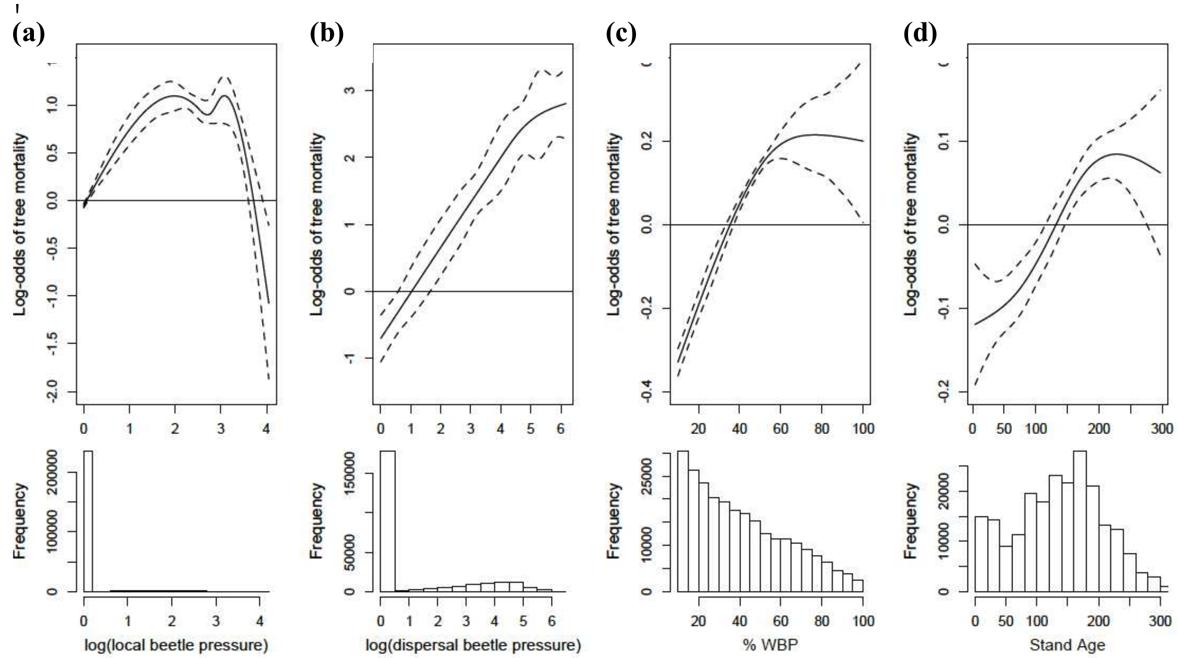

Figure 1.3. Effects on the probability of whitebark pine mortality from mountain pine beetles of (a) the logarithm of local beetle pressure (represented by the number of trees killed within each grid cell), (b) the logarithm of dispersal beetle pressure (represented by the number of trees killed in a 6-km radius outside of the center grid cell), (c) percent whitebark pine, and (d) stand age. Dashed lines are 95% confidence intervals calculated from jackknifing by year. Histograms show distributions of the data used in model development.

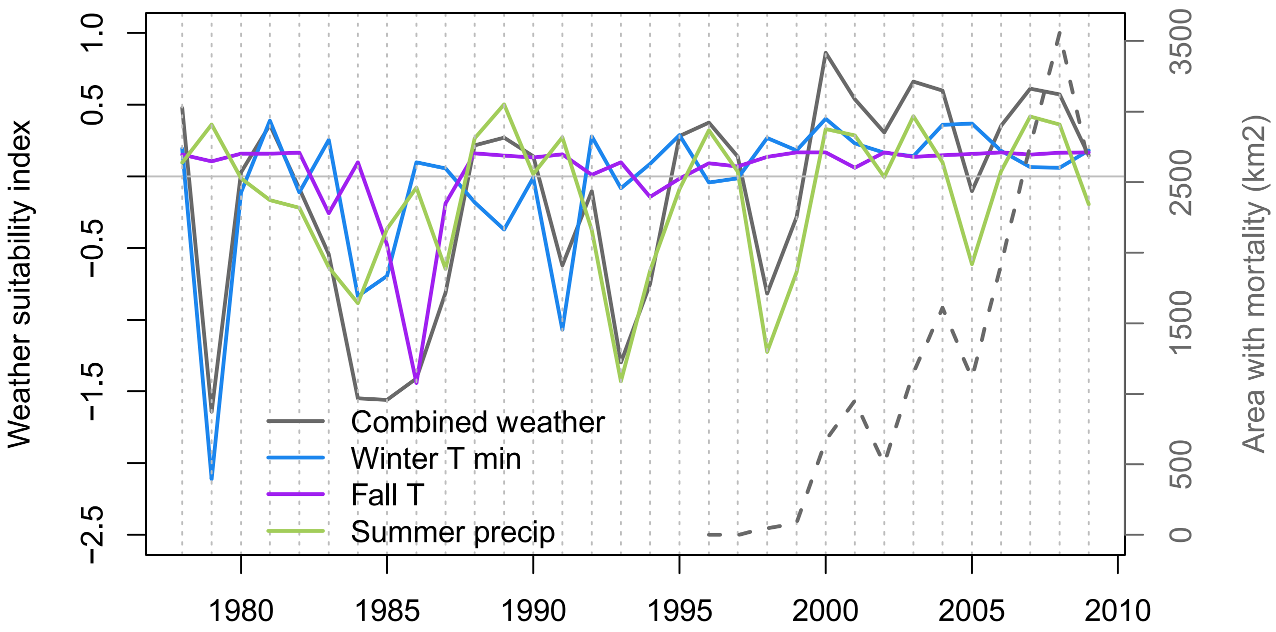

Figure 1.4. Average modeled weather suitability for whitebark pine mortality due to mountain pine beetles calculated from 800-m PRISM climate data spatially averaged over the Greater Yellowstone Ecosystem. Dashed gray line and right y-axis show observed area with mortality (km^2) in the study area from aerial detection surveys.

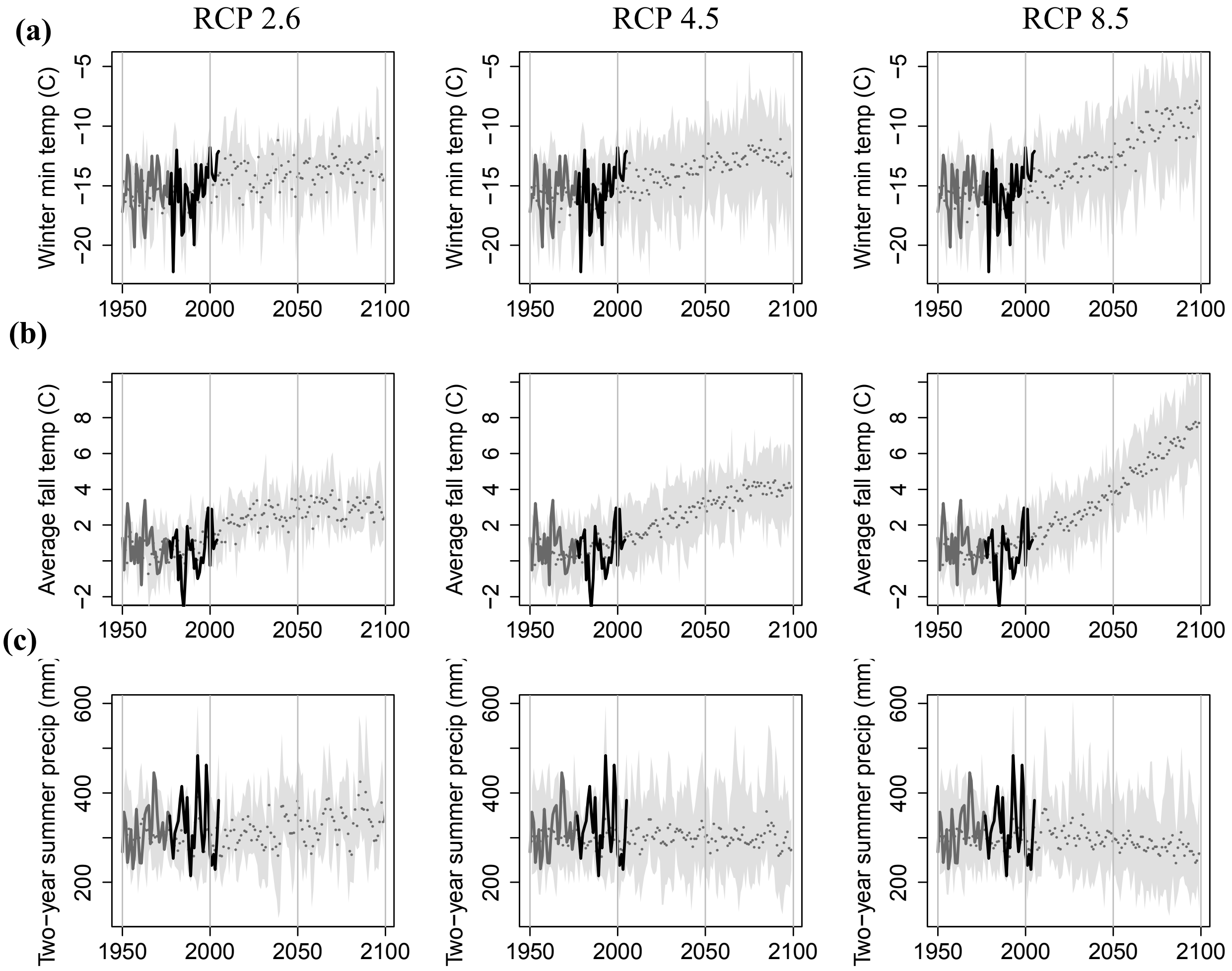

Figure 1.5. Range (gray shading) and average (gray dots) of key climate variables from ten general circulation models (Table 1.3) downscaled to 1-km resolution and from 800-m PRISM data (gray line 1950-1978, black line, 1979-2006) averaged over whitebark pine locations in the Greater Yellowstone Ecosystem for each year. (a) Winter minimum temperature, (b) average September-November temperature, and (c) cumulative two-year summer precipitation. Projections are from general circulation models forced with low (RCP 2.6, left column), moderate (RCP 4.5, middle column), and high (RCP 8.5, right column) emissions scenarios. Due to a lack of high-elevation weather stations before 1978, results from PRISM data then are less certain than after 1978 and are shown with a gray line.

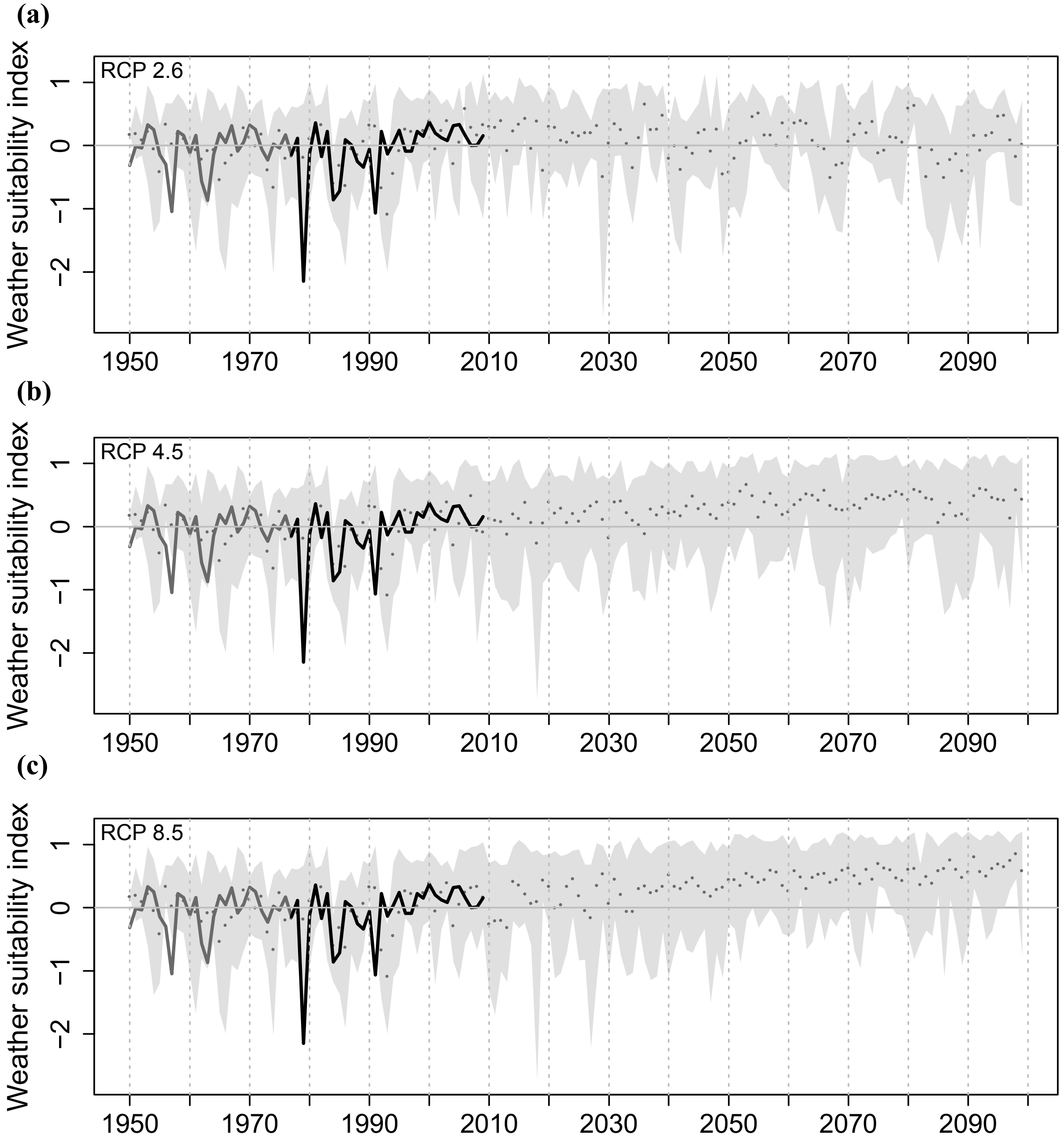

Figure 1.6. Weather suitability for whitebark pine mortality from mountain pine beetles calculated from ten general circulation models (Table 1.3) forced with (A) low (RCP 2.6), (B) medium (RCP 4.5), and (C) high (RCP 8.5) emissions scenarios and downscaled to 1-km resolution. Weather suitability averaged over whitebark pine locations in the Greater Yellowstone Ecosystem. Dark gray line indicates the spatial average derived from 800-m PRISM data during 1950-1978, black line indicates derived from 800-m PRISM data from 1979-2009, gray points indicates the multi-model average suitability, and light gray shading indicates the range of suitability spanned by the ten GCMs. Due to a lack of high-elevation weather stations before 1978, results from PRISM data then are less certain than after 1978 and are shown with a gray line.

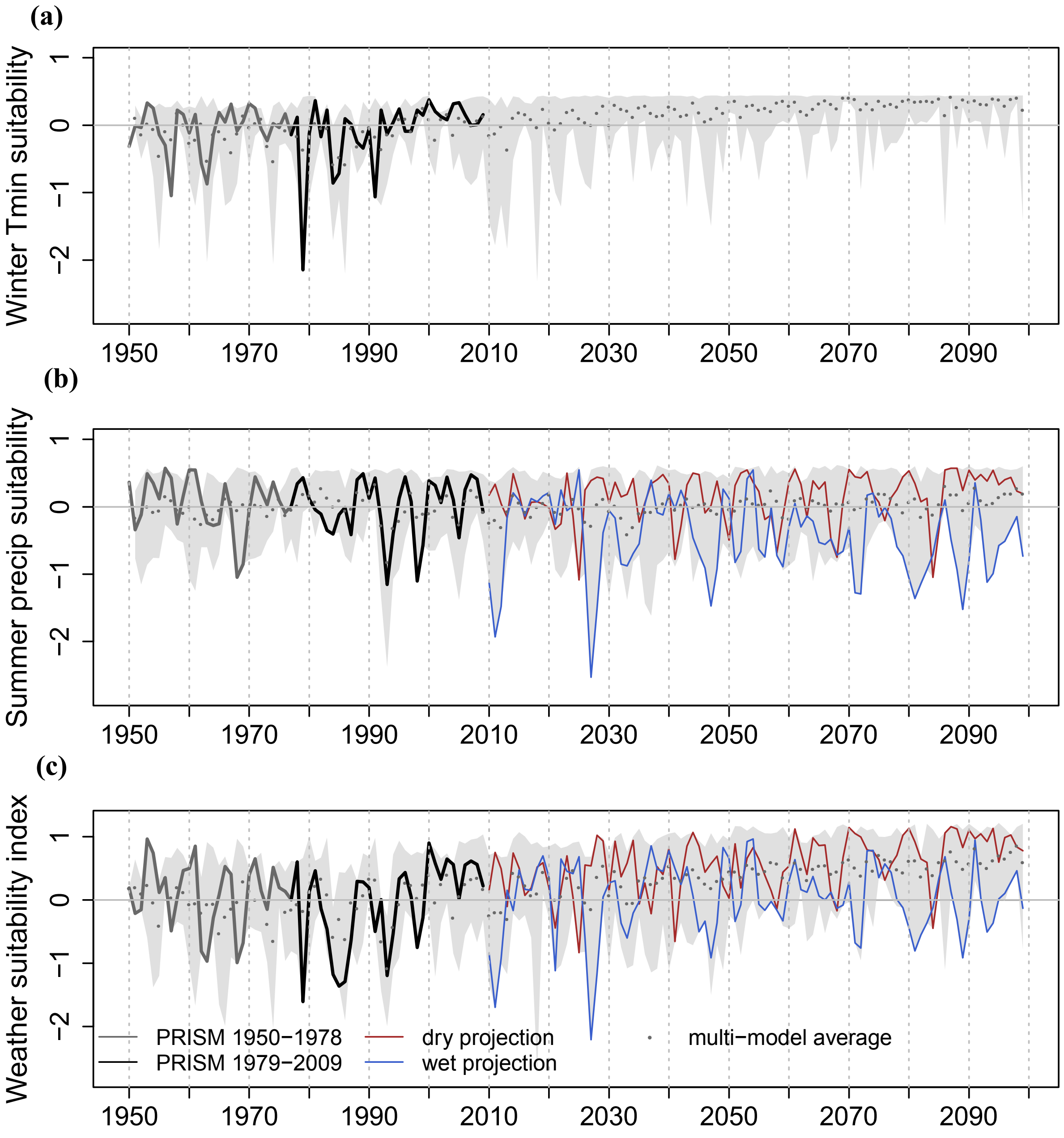

Figure 1.7. Weather suitability for whitebark pine mortality from mountain pine beetles for (a) winter minimum temperature, (b) two-year summer precipitation, and (c) combined weather suitability averaged across the Greater Yellowstone Ecosystem for each year. Gray line is 1950-1978 and black line is 1970-2009 suitability using 800-m PRISM data; gray dots are the average suitability using ten general circulation model (GCM) projections downscaled to 1-km resolution (Table 1.3); blue line is from one GCM with wetter projections (CanESM2); red line is from one GCM with drier projections (IPSL-CM5A-MR); gray shading bounds the range of results from all GCMs. GCMs were forced with RCP 8.5, a high emissions scenario.

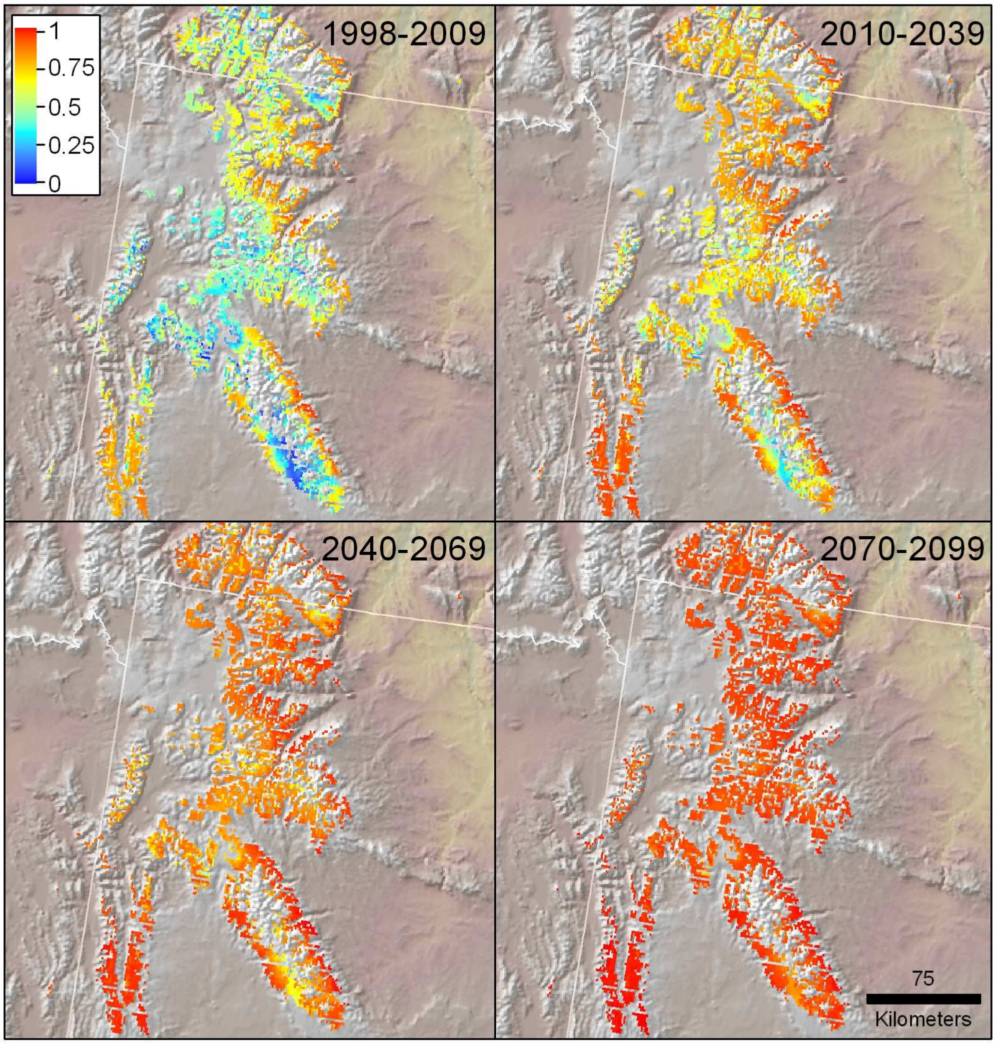

Figure 1.8. Proportion of years with winter minimum temperature model term greater than 0 (indicating more suitable winter conditions for beetle survival) during historical and future time periods. Historical proportions were calculated from 800-m PRISM data. Future proportions are multi-model means of ten downscaled climate projections (Table 1.3) forced with a high emissions scenario (RCP 8.5).

Chapter 2: Geographic Variability in Past and Future Weather Influences on Whitebark Pine Mortality from Mountain Pine Beetles[2]

2.1 Abstract

Whitebark pine is in decline across its range, prompting consideration as a threatened or endangered species in the United States. Colonization by mountain pine beetles is a primary source of recent mortality. There is potential for geographic variability in weather influences on beetle outbreaks in whitebark pine. Here we developed regional predictive models of the probability of whitebark pine mortality from mountain pine beetle colonization, compared weather influences and conditions during the recent beetle outbreaks across regions, and estimated future weather suitability for tree mortality across whitebark pine distribution in the western US. Factors affecting beetle winter mortality, beetle development rates and mass emergence, and host tree stress were important in all regional models. Beetle winter mortality was best represented by the minimum winter temperature, and climate influences on beetle development and mass emergence by the average September through November temperature and the average April through August temperature. Depending on the region, host tree stress was represented by summer precipitation during the summer of attack or the summer of attack plus the previous summer. In all regions, the probability of tree mortality generally increased with increasing winter minimum temperature and declining summer precipitation. The magnitude of the effects of winter minimum

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[2] Buotte, P.C., J.A. Hicke, H.K. Preisler, J.T Abatzoglou, K. F. Raffa, J. A. Logan. 2015. Influences of Weather on Whitebark Pine Mortality from Mountain Pine Beetles Vary Geographically. Ecological Applications. In Preparation.

temperature and summer precipitation, however, differed across regions. The effects of seasonal temperatures were similar across regions. Future weather suitability for whitebark pine mortality from beetle colonization is projected to increase in the Greater Yellowstone Ecosystem and the Northern Rockies, remain steady in the Cascades, and decline in the Central Rockies. In all regions, future suitability increases due to increases in winter minimum temperature. Future declines in the Central Rockies and Cascades are primarily due to declines in suitability at higher seasonal temperatures, which is where for multiple reasons we have the least confidence in the models. These results confirm the importance of winter temperatures in regions cold enough to induce beetle winter mortality, reveal the importance of assessing multiple aspects of future weather suitability, and suggest areas for further research.

2.2 Introduction

Understanding changing disturbance regimes is important for developing a portfolio of management tactics (Turner 2010). Expansions in the geographic range of mountain pine beetle (*Dendroctonous ponderosae*) outbreaks (Carroll et al. 2004a, Logan et al. 2010) indicate tree mortality from mountain pine beetle attack is a changing disturbance regime. Climate change is likely to have an important influence on mountain pine beetle outbreaks (Bentz et al. 2010, Logan et al. 2010), as it has in other instances of tree mortality (Allen et al. 2010). Recent beetle expansion into whitebark pine (*Pinus albicaulis*) forests across the western United States has caused extensive tree mortality, prompting consideration of whitebark pine as a U. S. threatened or endangered species (USFWS 2011).

There has been considerable research on mountain pine beetle outbreaks in their primary host, lodgepole pine (*Pinus contorta*) (for reviews, see Raffa et al. 2008, Bentz et al.

2009). However, due to the infrequency of outbreaks at higher elevations (Logan et al. 2010) and lack of economic importance of whitebark pine, there has been relatively little research on mountain pine beetle outbreaks in whitebark pine forests. The limited research on climate drivers indicates risk of mountain pine beetle outbreaks in whitebark pine forests is linked to higher temperatures (Logan et al. 2010) and lower summer precipitation (Buotte et al. in review). Lodgepole pine host trees have evolved defenses against beetle attack, producing resin to physically eject the attacking beetle, and producing toxins in areas of attack (Raffa and Berryman 1983). However, whitebark pine have relatively lower defensive capabilities compared with lodgepole pine (Raffa et al. 2013).

Previous research in lodgepole pine systems suggests physiological responses to climate influences on mountain pine beetle outbreaks may vary geographically (Bentz et al. 2001, Bentz et al. 2011, Bentz et al. 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). Recent field measurements (Bentz et al. 2014) have shown that although the thermal units required to complete a life cycle are similar, the amount of time required varies across latitudinal and elevational gradients. Temperate forest tree species (Breda et al. 2006, Littell et al. 2008), including conifers (Graumlich and Brubaker 1995, Littell et al. 2008), are also adapted to their local climate conditions. Whitebark pines exhibit genetic differences in their growth response to temperature (Millar et al. 2012) and cold-hardiness (Keane et al. 2012), indicating the potential for genetic variability across the range of whitebark pine. Taken together, this research suggests a strong potential for geographic variability in climate influences on whitebark pine mortality from mountain pine beetle colonization.

Past studies of mountain pine beetle outbreaks in whitebark pine have primarily focused on one geographic region, the Greater Yellowstone Ecosystem forests (Perkins and Roberts 2003, Logan et al. 2010, Jewett et al. 2011, Buotte et al. in review). However, substantial outbreaks have occurred outside this region: during 1997-2009, over 4,000 km^2 of mortality occurred across the range of whitebark pine in the western US (Meddens et al. 2012). Understanding how weather conditions influence outbreaks in whitebark pine forests will enable identification of regions most likely to experience mortality in the future and aid in prioritizing management and restoration efforts.

Our objective was to quantify geographic variability in weather influences on whitebark pine mortality from mountain pine beetles across the western US by assessing 1) differences in weather influences among geographic regions; 2) weather effects on recent beetle outbreak initiation and progression; and 3) climate suitability for whitebark pine mortality from mountain pine beetles during the rest of this century. To understand weather influences on whitebark pine mortality from mountain pine beetles, we developed generalized additive logistic regression models of the probability of whitebark pine mortality from mountain pine beetle attack in four geographic regions of the western US. We applied our models to 1979-2009 weather data assess weather effects on the recent beetle outbreaks and to future climate projections to estimate future weather suitability for whitebark pine mortality from mountain pine beetles.

2.3 Methods

The study area covered the range of whitebark pine in the United States, outside of California and Nevada (Figure 2.1). Given variability in seasonal temperatures and precipitation across this range (Fig. 2.2), and previous indications of geographic variability in beetle populations' (Bentz et al. 2001) and whitebark pine's (Perkins and Swetnam 1996, Millar et al. 2012) response to climate, we divided the range into four geographic regions: the Greater Yellowstone Ecosystem (GYE), Northern Rockies (NR), Central Rockies (CR), and Cascades (Fig. 2.2), generally following Level III ecoregion classifications of the Environmental Protection Agency (Omernick 2004). Due to a lack of whitebark pine mortality data, we did not include California and Nevada.

2.3.1 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). During surveys, observers in aircraft record tree mortality by host (here whitebark pine) and mortality agent (here mountain pine beetle). 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 trees killed by mountain pine beetles from 1996-2009. 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, because ADS reports indicate below-observable levels of whitebark pine mortality from mountain pine beetles from 1986-1995, we set all voxels as having no mortality during this time period. Reports form other regions indicate low levels of mortality prior to 1996; therefore, although beetle activity was likely to be low, mortality absence could not be assumed, and therefore we did not extend the study period back for these regions.

In the NR, CR, and Cascades we defined the spatial distribution of whitebark pine using the combination of 1-km pixels where either ADS data recorded whitebark pine or locations were included in 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 modeled using Landsat data (Landenburger et al. 2008). We defined the absence of whitebark pine mortality as those voxels within the distribution of whitebark pine that were flown during annual Aerial Detection Surveys and did not have mortality recorded. Voxels that were not flown were excluded from model development data sets.

Our explanatory variables (Table 1.1) represented processes that are known to influence mountain pine beetle outbreaks in the beetles' primary host, lodgepole pine: the number of attacking beetles, or beetle pressure; beetle winter mortality; beetle development and population synchrony; stand structure; and host tree defensive capabilities (Aukema et al. 2008, Preisler et al. 2012, Sambaraju et al. 2012). All candidate variables were gridded to a 1-km resolution and associated with each year of beetle colonization. Detailed descriptions of explanatory variables are provided in Chapter 1.

2.3.2 Statistical Model

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

$$logit(p) = \beta_o + s_{m1}(X_{m1}) + \cdots s_{mi}(X_{mi}) \qquad \text{Eq. 1}$$

where p is the probability of tree mortality (at least one tree killed in each 1-km pixel per year) from mountain pine beetles and $s_{m1}(X_{m1})$ through $s_{mi}(X_{mi})$ are tensor product smooth functions of the explanatory variables representing the processes of beetle winter survival, beetle development, host tree stress, previous year beetle population, and stand structure (see Table 1.1). The smooth functions of the explanatory variables are estimates of the expected change in the log-odds over the range of the variable.

We developed separate statistical models for each geographic region (Fig. 2.1), as well as one Westwide model using all the data. Every model contained a representation of each of the important processes described above and in Table 1.1. 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 those processes.

The relationship between each explanatory variable and the presence of tree mortality was assessed through the log-odds plots. We calculated standard errors in these plots by 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 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 log-odds for a variable was zero, and the other variables were in the model and held constant, that variable was not contributing to either an increase or a decrease in the probability of 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.

Wherever the confidence bounds included 0, we concluded that the variable did not have a significant effect in that range. When confidence bounds included zero along the entire range of an input variable, that variable was not included in the final model.

We plotted observed and predicted total area with mortality by year for each region to evaluate the final model goodness-of-fit. 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 computed as the sum of the predicted probabilities over all grid cells in that year. We calculated the R^2 and root mean square error (RMSE) between the observed and predicted yearly total mortality areas.

We evaluated the potential for spatial autocorrelation 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 two models. Autocorrelation in the residuals at a distance of 1 km was low (<0.2) in the top models, and including a spatial term only slightly reduced this correlation. For all regional models, including a spatial term did not change the log-odds plots of the explanatory variables.

To isolate the effects of weather on outbreaks, we defined weather suitability indices (WSI) in reference to the log-odds of tree mortality. The WSIs of each individual variable were evaluated by calculating the average of the corresponding log-odds over all grid cells in the region for a given year. Combined WSI was evaluated by summing the log-odds of all weather variables in each grid cell, and then evaluating the average over each region for a given year. A log-odds value of zero implies no increase in the odds of mortality relative to the odds evaluated at the average level. Thus, a mean suitability estimate greater than zero implies an increase in the odds of mortality (hence an increase in suitability) over the average odds of mortality when all variables are held at their means.

2.3.3 Model Application

We used the weather suitability indices to assess weather effects on the recent outbreaks and estimate future weather suitability for whitebark pine mortality from mountain pine beetle attack. To calculate weather suitability indices for years prior to and during the recent outbreaks, we applied each final regional model to PRISM weather data (Daly et al. 2008) for the period 1979-2009; 1979 is when multiple high-elevation weather station records were available for inclusion in PRISM (Buotte et al. In Review). We applied models to all grid cells within the distribution of whitebark pine in each region. To estimate future weather suitability we applied the models to future climate projections from ten general circulation models (Table 1.3) forced with low (RCP 2.6; IPCC 2013), medium (RCP 4.5), and high (RCP 8.5) emissions scenarios (Thrasher et al. 2013). The future climate projections were downscaled to 30-arc-second resolution using PRISM data as the reference in a bias correction algorithm (Thrasher et al. 2013).

We clamped future projections to the range of temperature and precipitation that occurred in the model development data. That is, when future seasonal temperature exceeded the observed seasonal temperature in that region, we set future temperature to the maximum observed. Projected future temperatures were never lower than observed (Fig 2.8 & 2.9) and projected precipitation was usually within the range of observed precipitation (Fig. 2.10). We summarized future weather suitability estimates for three 30-year periods between 2010 and 2099 by calculating the yearly spatial average of WSI estimates from our regional models applied to each GCM projection individually. As described in Chapter 1, a

GCM climate "hindcast" projection for a given past year cannot be expected to represent the weather station observations for that particular year. Because of the bias correction procedure applied during downscaling (Thrasher et al. 2013) we can, however, expect statistical distributions of GCM hindcast projections and temperature or precipitation observations from weather stations to match over a longer time. We therefore checked for consistency between historical GCM climate and PRISM weather data distributions to ensure we could apply our statistical model to future GCM climate projections without further modification and calculate future climate suitability estimates that would be comparable with historical weather suitability based on PRISM weather data.

2.4 Results

Weather conditions and outbreak patterns during recent decades were different across the four regions. The GYE was the coldest region across seasons and the Cascades the warmest in winter and the driest in summer (Fig. 2.3 B-E). In all regions, annual area of whitebark pine mortality from mountain pine beetles began increasing in the late 1990s. Regional trends diverged during the mid-2000s as outbreaks in the GYE and CR continued until the late 2000s whereas outbreaks in the NR and Cascades declined and plateaued in the mid-2000s (respectively) (Fig. 2.3A). The GYE had the greatest area with mortality relative to the area of whitebark pine range (Fig. 2.3A). Time series of seasonal temperature and precipitation also varied across regions, with the Cascades showing the greatest differences compared to the other regions (Fig. 2.3B-D).

Our models captured the annual trends in area with whitebark pine mortality quite well in the GYE, Northern Rockies (NR), and Central Rockies (CR), but less well in the

Cascades (Fig. 2.4). All regional models performed better than the Westwide model, with lower root-mean-square error and higher R^2 (Fig. 2.4).

2.4.1 Weather Influences on Mountain Pine Beetle Outbreaks in Whitebark Pine

In all regions the variables selected to represent weather influences were the same, with the exception of tree drought stress. Beetle winter mortality was best represented by winter (coldest month) minimum temperature; beetle development and population synchrony by average fall (September-November) and April-August temperatures; and tree drought stress by cumulative two-year (year of attack plus previous year) summer (June-August) precipitation in the GYE, and current (year of attack) summer precipitation in the other three regions. The best variable representing each process was always at least 10 AIC units better than the next best variable.

The general shapes of the response curves, which describe the effects of each variable on the probability of whitebark pine mortality, were similar across regions (Fig. 2.5). The log-odds of tree mortality increased with increasing beetle winter survival, represented by increasing winter minimum temperature, but the magnitude of the negative effect of low temperatures was different (relative to the magnitude at the average for that region) among the GYE, CR, and NR (Fig. 2.5A). The effects of beetle development and population synchrony, represented by the average fall and average April-August temperatures, were less certain (as indicated by wide confidence bounds) (Fig. 2.5B). Mortality declined with decreasing temperature at very low fall temperatures in the GYE, but we were not able to make similar conclusions for the CR, Cascades, or NR regions because fall temperatures were never that low (Fig. 2.5B). The standard errors around the mean estimate of the effect of fall temperature in the NR bounded zero along the entire range of temperature, and therefore this variable was not included in the final NR model. The log-odds of whitebark pine mortality declined at very low April-August temperatures in all regions (Fig. 2.5C), although this effect was not statistically significant (as indicated by the 95% confidence bounds that included zero). Confidence bounds included zero along the entire range of April-August temperature in the GYE and NR regions and so this variable was not included in those final regional models. In all regions, tree mortality increased with increasing tree drought stress, represented by decreasing precipitation, except at the very highest levels of drought stress in the GYE and the very lowest levels of drought stress in the NR (Fig. 2.5D). Except for stand age, the effects of non-weather variables were also similar but differed in magnitude across regions (Fig. 2.6).

2.4.2 Weather Effects on Recent Outbreak Initiation and Progression

Temporal patterns of weather suitability for whitebark pine mortality before and during the recent outbreaks showed both similarities and differences across regions (Fig 2.7). In all regions, combined weather suitability was higher during the recent outbreaks than in years prior. In the GYE and NR, and the CR in 2009, declines in the area with mortality corresponded with low combined weather suitability. In all regions, winter minimum temperature was more suitable during the recent outbreaks than in years prior (Fig. 2.7), but the magnitude of the winter minimum temperature suitability index varied across regions. In the GYE, winter minimum temperatures were consistently suitable during the outbreak period and changes in mortality area fluctuated with changes in summer precipitation (Fig. 2.7A). In the NR, changes in annual area with mortality tended to fluctuate with changes in winter temperature suitability and summer precipitation had little influence (Fig. 2.7B).

Annual patterns of mortality corresponded less well with annual weather suitability in the CR and Cascades, though both regions show that outbreak onset coincided with more suitable (warmer) winter temperatures and increased suitability for whitebark mortality due to decreased summer precipitation (Fig. 2.7C-D).

2.4.3 Future Weather Suitability for Whitebark Pine Mortality from Mountain Pine Beetles

Future temperatures are projected to rise in all regions, with the greatest increases later in the century and under higher emissions scenarios (Fig. 2.8-2.9). Nearly all precipitation projections are within the historical range of variability (Fig. 2.10), but vary substantially by GCM. Applying our statistical models of whitebark pine mortality to these projections over the range of whitebark pine results in variability in estimates of future weather suitability for whitebark pine mortality across regions (Fig 2.11). Relative to suitability calculated using both historical PRISM and hindcast GCM weather data for the 30-year period centered on 1985, future weather suitability increases in the GYE and NR, declines slightly in the CR, and remains stable in the Cascades.

Some similarities in trends in future weather suitability across regions are apparent when looking at individual weather suitability. In all regions, under RCP 8.5, suitability for whitebark pine mortality increases due to less beetle winter mortality with increasing winter minimum temperature (Fig. 2.12). In the future, all regions have higher median winter minimum temperature suitability than during the historical period (1970-1999), and by mid-century, winter minimum temperature suitability is higher than what occurred during the recent outbreak. Additionally, the number of years with very low suitability declines in the future (Fig. 2.12). Variability in future suitability due to summer precipitation is similar to variability in historical precipitation suitability in all regions (Fig. 2.13).

The differences among regions in future combined weather suitability are a result of slight differences in responses (Fig. 2.5) to increasing seasonal temperatures (Fig. 2.9). In the CR and Cascades declines in suitability at higher fall (Fig 2.14) and April-August (Fig. 2.15) temperatures lead to declines in future combined weather suitability for whitebark pine mortality (Fig. 2.11).

2.5 Discussion

Weather influenced the probability of whitebark pine mortality from mountain pine beetle attack in the western US. Whitebark pine mortality primarily increased with increasing beetle winter survival, as measured by winter minimum temperature, and with increasing drought stress, as measured by summer precipitation. In all geographic regions, winter minimum temperature suitability was higher during the recent outbreaks than in years prior to the outbreaks. The magnitude of the effect of winter temperature, however, varied across regions. The influence of September-November and April-August temperatures was similar, though less certain, across regions. However, the odds of whitebark pine mortality declined at the highest seasonal temperatures in the CR and Cascades, but not in the GYE. These differences led to differences in estimates of future weather suitability for whitebark pine mortality from mountain pine beetle colonization across regions. Future weather suitability increased in the GYE and NR, but declined in the CR and Cascades.

Reliable future estimates of weather suitability depend on a reliable statistical model of the probability of whitebark pine mortality. There were less data available for estimating the climate relationships at the edges of the observed range of explanatory variables, as evident in the wide standard errors in the log-odds plots at these locations (Fig. 2.5). Predictions of future weather suitability given these temperatures are more uncertain, particularly when the mean values of the log-odds plots were increasing or decreasing at the highest temperatures. Under RCP 8.5, projected average fall temperatures in the CR and Cascades are in the upper range of observed temperatures, where the log-odds began to decline, and the standard errors were wide, in the first 30 years of this century. Projected April-August temperatures are in the range of high uncertainty in the CR and Cascades late in this century. We therefore have less confidence in the estimated seasonal temperature and combined future weather suitability in these two regions. In all regions we have the highest confidence in our estimates of increasing future weather suitability due to the effects of increasing winter minimum temperature.

2.5.1 Influence of Winter Minimum Temperature

Our results are broadly consistent with previous winter temperature effects found for beetle outbreaks in lodgepole pine (Aukema et al. 2008, Chapman et al. 2012, Preisler et al. 2012, Sambaraju et al. 2012, Creeden et al. 2014) and whitebark pine (Perkins and Roberts 2003, Logan et al. 2010, Jewett et al. 2011, Buotte et al. in review). Increasing winter temperature leads to a higher beetle survival rate (Amman 1973, Bentz et al. 1991) and more beetles attacking trees the following summer.

A lack of cold winters has been suggested as a primary reason for recent mountain pine beetle outbreaks at high elevations (Logan and Powell 2001, Logan et al. 2010) and in northern forests (Carroll et al. 2004b, Safranyik et al. 2010, Sambaraju et al. 2012). Our results add to the evidence of the importance of winter temperature for beetle outbreaks in high elevation forests. The occurrence of unsuitable winter temperatures (i.e. very low temperatures) from 1979 through the mid-1990s suggests outbreaks in all of these regions were previously limited by winter mortality and a lack of cold winters after the mid-1990s enabled the recent outbreaks to occur. Similar results have been found when examining the influence of winter temperature on tree mortality from mountain pine beetles across all pine species (Weed et al. 2015).

We found a stronger influence of very low winter minimum temperatures in the NR and CR compared to the GYE. We suggest this may be due to variability in beetle development rates given the typical climate they inhabit. Bentz et al. (2001) showed that, under identical laboratory temperatures, beetles from colder regions developed faster than beetles from warmer regions. Field measurements have shown that although the time required to complete a generation was similar, fewer thermal units were required at colder sites than at warmer sites (Bentz et al. 2014). Therefore, beetle mortality due to cold temperature may occur at a higher temperature in regions that are typically warmer (e.g. NR, CR, Cascades) as compared to regions that are typically colder (e.g. GYE). Future research on beetle development rates at high elevations across a rage of winter temperature, as well as including weather variables defined in terms of departures from normal conditions, could help to clarify this hypothesis.

2.5.2 Influence of Average Seasonal Temperatures

Our results of increasing tree mortality with increasing fall temperature in the GYE fit well with previous work showing the effect of beetle development rates on population synchrony and mass emergence (Bentz et al. 1991, Powell et al. 2000, Logan and Powell 2001, Powell and Logan 2005). Tree mortality generally declined at the lowest April-August temperatures, though the confidence bounds included zero and this variable was not included in two regional models. The potential for such a decline being a reflection of unfavorable beetle development at low temperatures is supported by past research. For example, in the Sawtooth Valley of Idaho, a beetle outbreak in lodgepole pine was temporarily halted by very low summer temperature (Logan and Powell 2009).

Because beetle development at each life stage has an optimal temperature profile (Bentz et al. 1991, Logan and Powell 2001), differences in the effects of seasonal temperatures may be a reflection of different beetle development rates across regions. Beetle population synchrony depends on development rates (Bentz et al. 1991, Logan and Powell 2001, Powell and Logan 2005) and previous modeling has shown that increases in temperature may lead to maladapted population synchrony in lodgepole pine systems (Hicke et al. 2006). The slight decline in the log-odds of tree mortality at the highest fall temperatures may be a result of cumulative thermal accumulation causing maladapted population synchrony. The lack of an observed negative influence at the lowest fall temperatures in the NR, CR, and Cascades may be due the lack of very low fall temperatures in those regions.

We found large uncertainty in the effects of seasonal temperatures. However, estimates of adaptive seasonality using previously developed process models (Logan and Powell 2001) were not better predictors. Taken together, these results suggest further research on mountain pine beetle development rates across climatic gradients at high elevations is necessary to fully understand the effects of temperature on beetle outbreaks in whitebark pine forests.

2.5.3 Influence of Drought

We found tree mortality generally increased with increasing drought stress, as measured by summer precipitation, in all regions. Greater tree susceptibility to beetle attack due to drought stress has been shown in previous research in lodgepole pine (Raffa and Berryman 1983). In Idaho, whitebark pine growth patterns were positively correlated with precipitation (Perkins and Swetnam 1996) and mortality coincided with periods of low growth (Perkins and Roberts 2003). In California, Millar et al. (2012) also found that whitebark pine mortality was associated with drought.

The declines in mortality probability in the GYE at the highest levels of drought stress (lowest precipitation) could be a result of those trees having thinner phloem that cannot support substantial brood development and hence a large beetle population (Amman 1969, Amman and Baker 1972, Cole 1975, Safranyik and Carroll 2006). However, the lack of a decline in the other regions suggests differences in growth response to drought across regions. Increases in mortality probability at the highest levels of precipitation in the NR and CR may be an indication of an interaction between whitebark pine mortality from mountain pine beetles and from white pine blister rust, a disease caused by the introduced pathogen *Cronartium ribicola* Fisch. (Bockino and Tinker 2012). White pine blister rust infection severity is higher in these two regions than the GYE (Keane et al. 2012) and tends to increase with precipitation (Bockino and Tinker 2012). We suggest further research is necessary to better understand the relationship between precipitation and tree defensive capabilities and the mechanisms of tree susceptibility due to drought stress in whitebark pine systems (e.g., Das et al. 2007).

2.5.4 Outbreak Characteristics

There were differences in the relative magnitude of the outbreaks across regions. The GYE experienced the most area with mortality, in both absolute area and relative to the area of whitebark pine, of all regions. Several factors likely contributed to this difference. Whitebark pine commonly occurs in pure stands in the GYE, but in the other regions it more often occurs in mixed stands (Arno and Hoff 1989, Weaver 2001) that contain tree species that are not host to mountain pine beetles (e.g., subalpine fir, *Abies lasiocarpa*). Additionally, previous whitebark pine mortality from white pine blister rust has been lower in the GYE (Greater Yellowstone Whitebark Pine Monitoring Working Group 2013) compared to the other regions (Keane et al. 2012). Therefore, beetles had a relatively larger food supply in the GYE. Finally, combined weather suitability for whitebark pine mortality was the highest for more consecutive years in the GYE than in the other regions.

2.5.5 Future Weather Suitability for Whitebark Pine Mortality

Reliable future estimates of weather suitability depend on a reliable statistical model of the probability of whitebark pine mortality. Fewer data are available for estimating the climate relationships at the edges of the observed range of explanatory variables, as evident in the wide standard errors in the log-odds plots at these values (Fig. 2.5). Predicting future weather suitability given these temperatures is more uncertain, particularly when the mean values of the log-odds plots are increasing or decreasing at the highest temperatures. Under RCP 8.5, projected average fall temperatures in the CR and Cascades are in the upper range of observed temperatures, where the log-odds begin to decline, and the standard errors are wide, in the first 30 years of this century. Projected April-August temperatures are in the range of high uncertainty in the CR and Cascades late in this century. We therefore have less confidence in the estimated seasonal temperature and combined future weather suitability in these two regions. In all regions we have the highest confidence in our estimates of increasing future weather suitability for whitebark pine mortality from the effects of increasing winter minimum temperature.

We clamped future temperatures to the range of observed temperatures in the model development dataset. For winter minimum temperature, whose effects plateau at higher temperatures, this clamping has little influence on estimated future weather suitability. Clamping does have an influence when the log-odds are increasing at the highest temperatures. However, this is generally the range for which we have the least confidence, and clamping future temperatures produces a conservative estimate of future weather suitability for whitebark pine mortality. Clamping did not greatly influence projected precipitation suitability because future projected values were usually within the range of observations.

Estimates of future weather suitability for whitebark pine mortality from beetle colonization depended on which weather influences were considered. Studies that estimate future weather effects should strive to separate individual components of weather effects in their system, and provide estimates of uncertainty for each.

2.5.6 Caveats

The definition of the distribution of whitebark pine potentially influenced our statistical model performance and goodness-of-fit. A range-wide distribution map of whitebark does not exist at 1-km or finer resolution, therefore either an over- or underestimate of unattacked whitebark pine was possible. In the course of model development in the GYE, we found that defining the distribution of whitebark pine from combined aerial detection survey and blister rust (R. Keane, pers.com.) data, as we did for the other three regions, resulted in a model with wider standard errors and lower R^2 than a model based on those grid cells that contained at least 10% whitebark pine according to the Landenberger (2008) distribution map (data not shown). The availability of a similar fine-resolution, range-wide distribution map may improve model fit and reduce variability in estimated weather effects in the other regions as well.

2.6 Conclusions

General patterns of weather influence on whitebark pine mortality from mountain pine beetles were consistent across geographic regions. Winter temperature was the most important weather influence on whitebark pine mortality from mountain pine beetles. The magnitude of its influence, however, varied geographically. The effects of other seasonal temperatures and drought stress also varied geographically in the outer portions of the observed ranges of temperature and precipitation. Questions about the reasons for these differences remain. Our understanding of weather influences on beetle outbreaks in whitebark pine forests would benefit from a more precise whitebark pine distribution map, research on beetle development rates across climatic gradients at high elevations, and research on the mechanisms of whitebark pine susceptibility due to drought stress.

Further work on this subject is necessary to fully understand the results and conclusions. Although the current research suggests geographic patterns of mechanisms, additional analyses that will be conducted in the near future will provide more confidence in the assessment of geographic variability in weather influences on whitebark pine mortality from mountain pine beetle colonization. A model with weather variables defined in terms of departures from the climatological normal could help inform the idea that regional differences in weather effects are a result of beetles in different regions evolving under unique temperature regimes. Modeling in terms of anomalies could also help identify if there are common temperature thresholds for beetle outbreaks to occur across regions. Including spatially explicit variables of climatological normals for each of the weather variables could further understanding of spatial patterns of whitebark pine mortality. Finally, because the same temperature variables were selected in each regional final model, one model with data from all regions could be developed and analyzed, allowing for different response curves by region.

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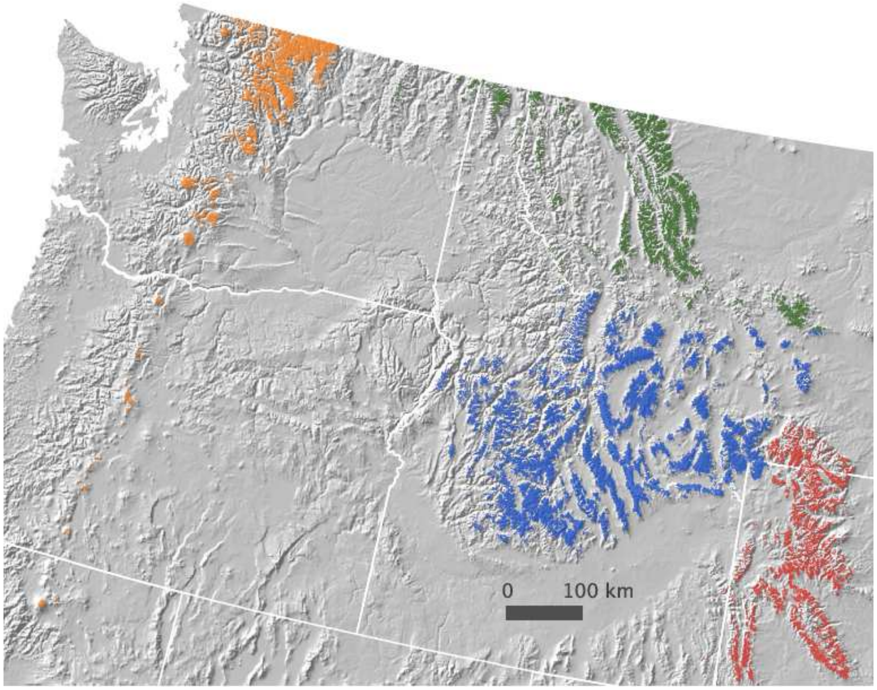


Figure 2.1. Geographic regions for developing models of the presence of whitebark pine mortality from mountain pine beetles in the western U.S.: Greater Yellowstone Ecosystem (red), Central Rockies (blue), Northern Rockies (green), and Cascades (orange).

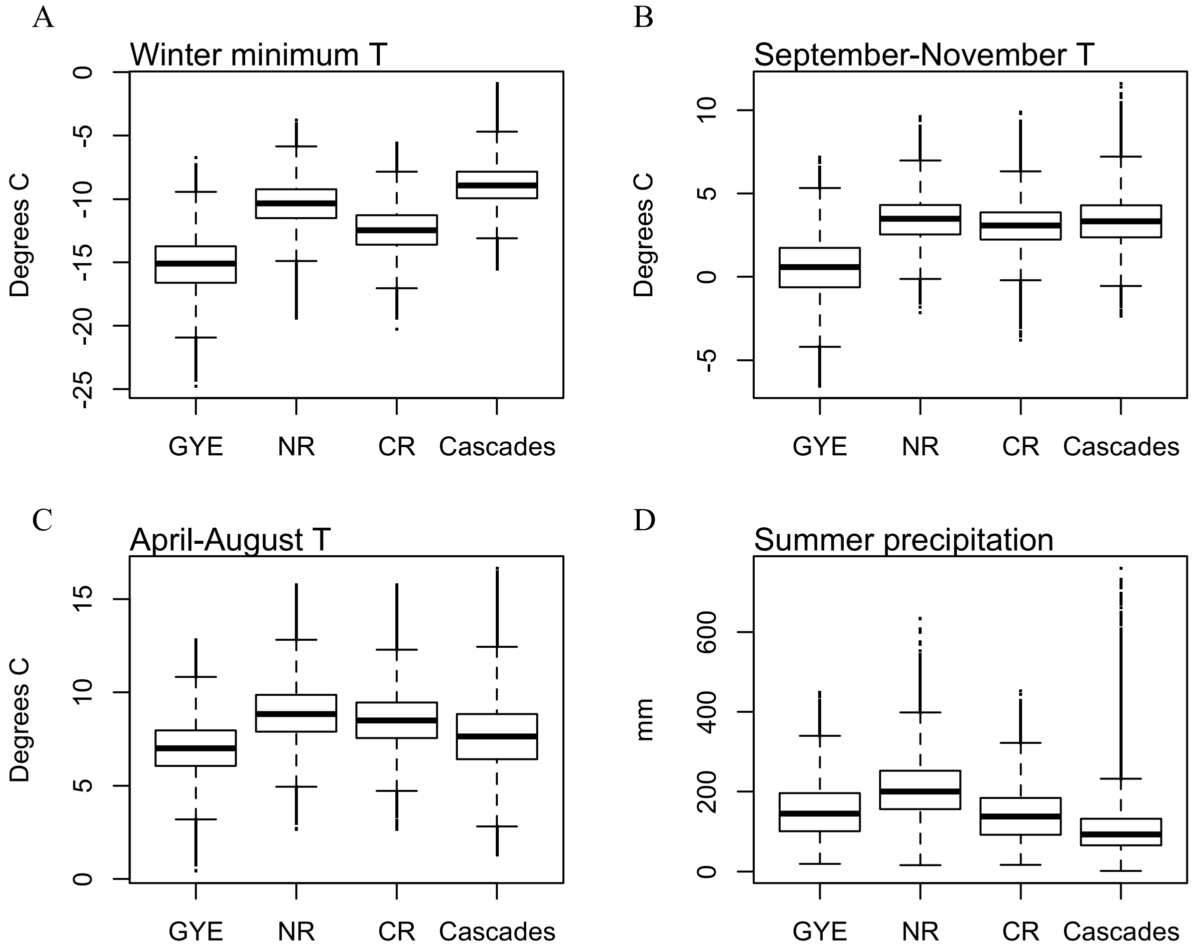


Figure 2.2. Distributions, from all 1-km pixels for each year during 1979-2009, of A) winter (coldest month) minimum temperature, B) average September-November temperature, C) average April-August temperature, and D) cumulative June-August precipitation in four regions within the range of whitebark pine in the western U.S. GYE = Greater Yellowstone Ecosystem, NR = Northern Rockies, CR = Central Rockies.

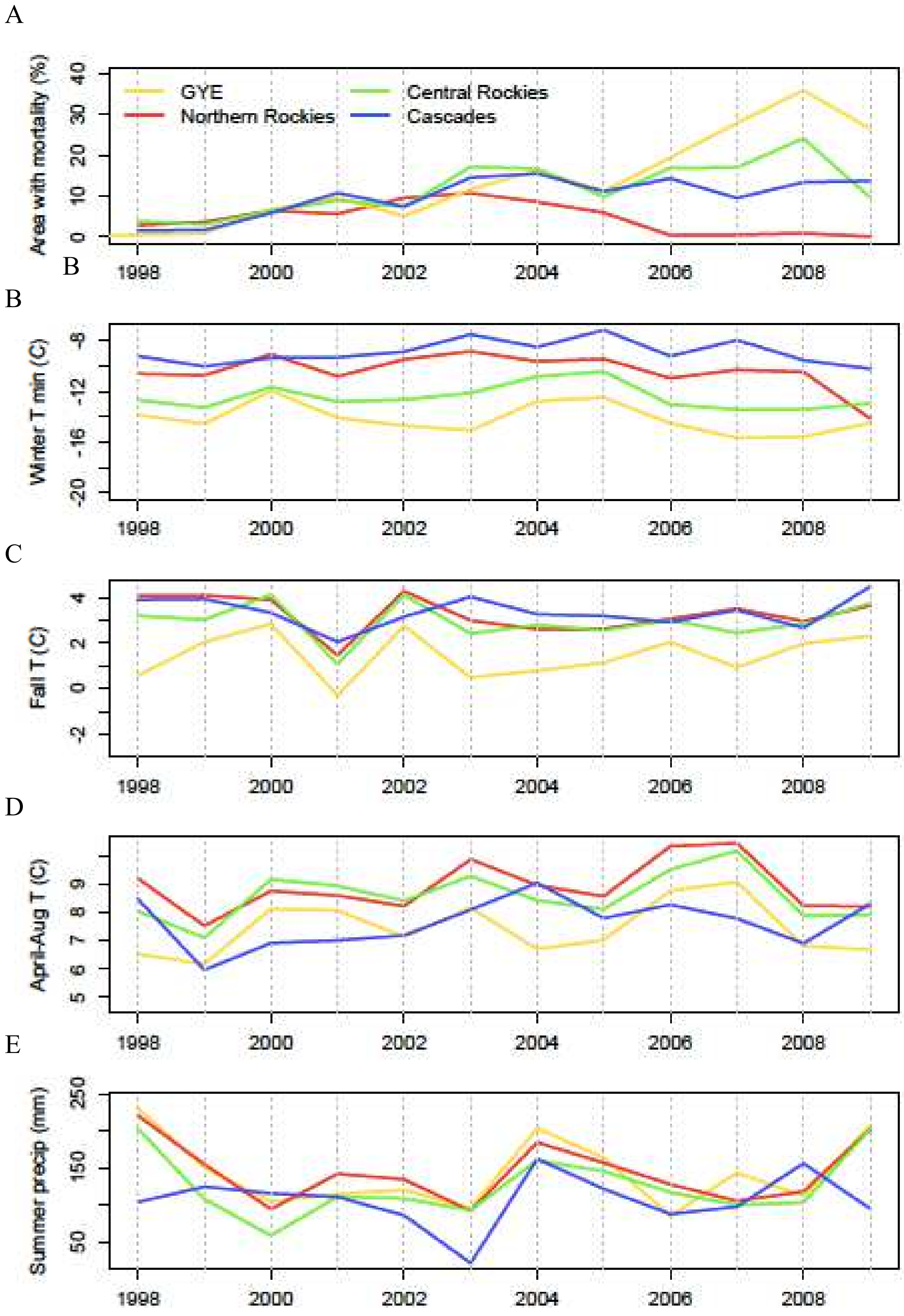
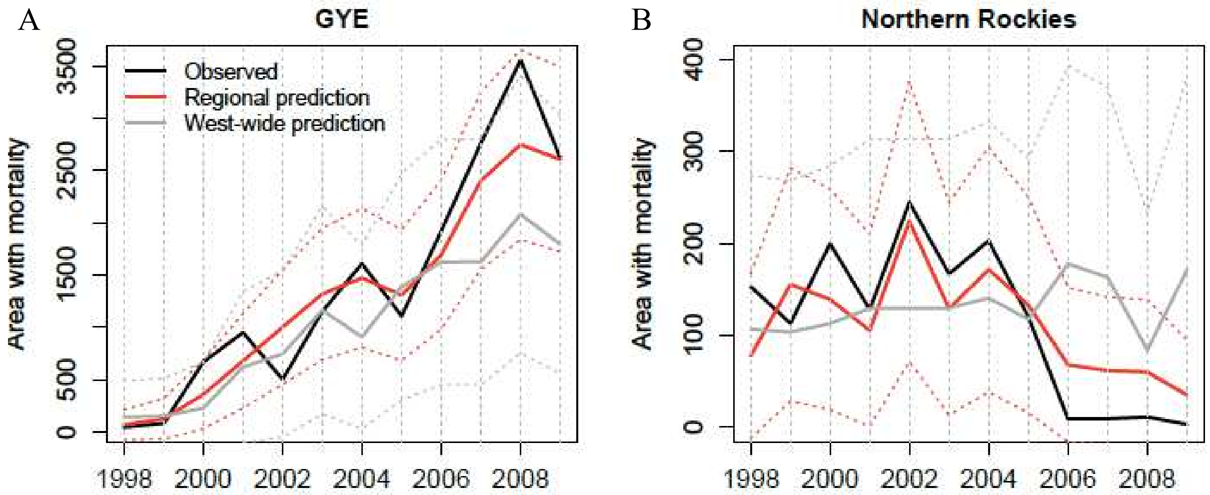
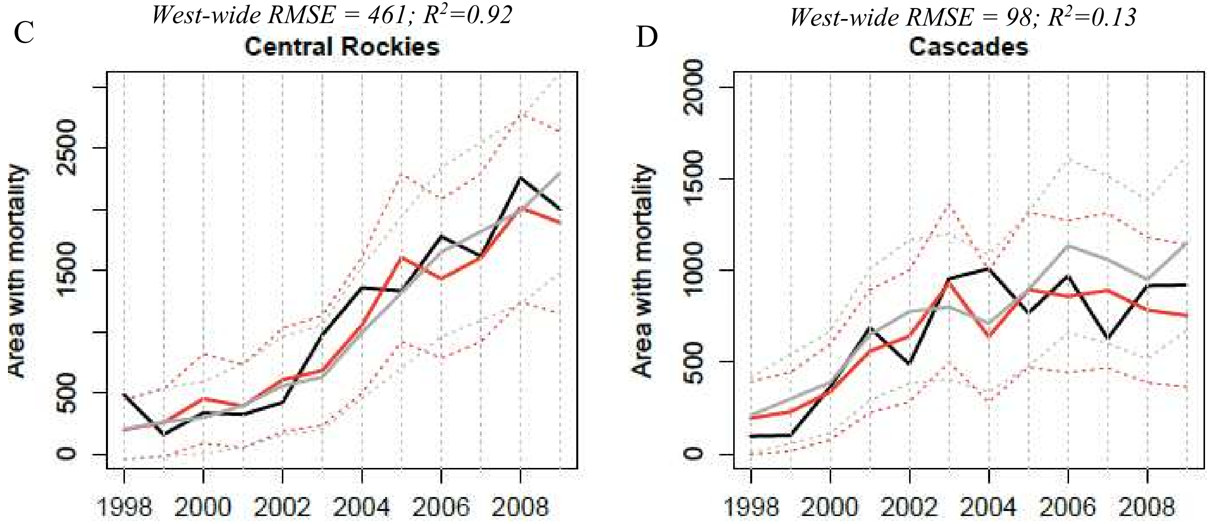


Figure 2.3. Spatially averaged time series for each region of A) percent of total whitebark pine area in each region with recorded mortality from mountain pine beetles, B) average winter (coldest month) minimum temperature, C) average September-November temperature, average April-August temperature, and E) cumulative June-August precipitation.



Regional RMSE = 243; R^2=0.96
West-wide RMSE = 461; R^2=0.92

Regional RMSE = 45; R^2=0.75
West-wide RMSE = 98; R^2=0.13



Regional RMSE = 220; R^2=0.91
West-wide RMSE = 221; R^2=0.90

Regional RMSE = 170; R^2=0.71
West-wide RMSE = 210; R^2=0.67

Figure 2.4. Observed (black lines) and predicted whitebark pine area with mortality from mountain pine beetles using separate regional models (red lines) and a west-wide model (gray lines). Predicted 95% CI (dotted lines) were calculated through yearly cross-validation.

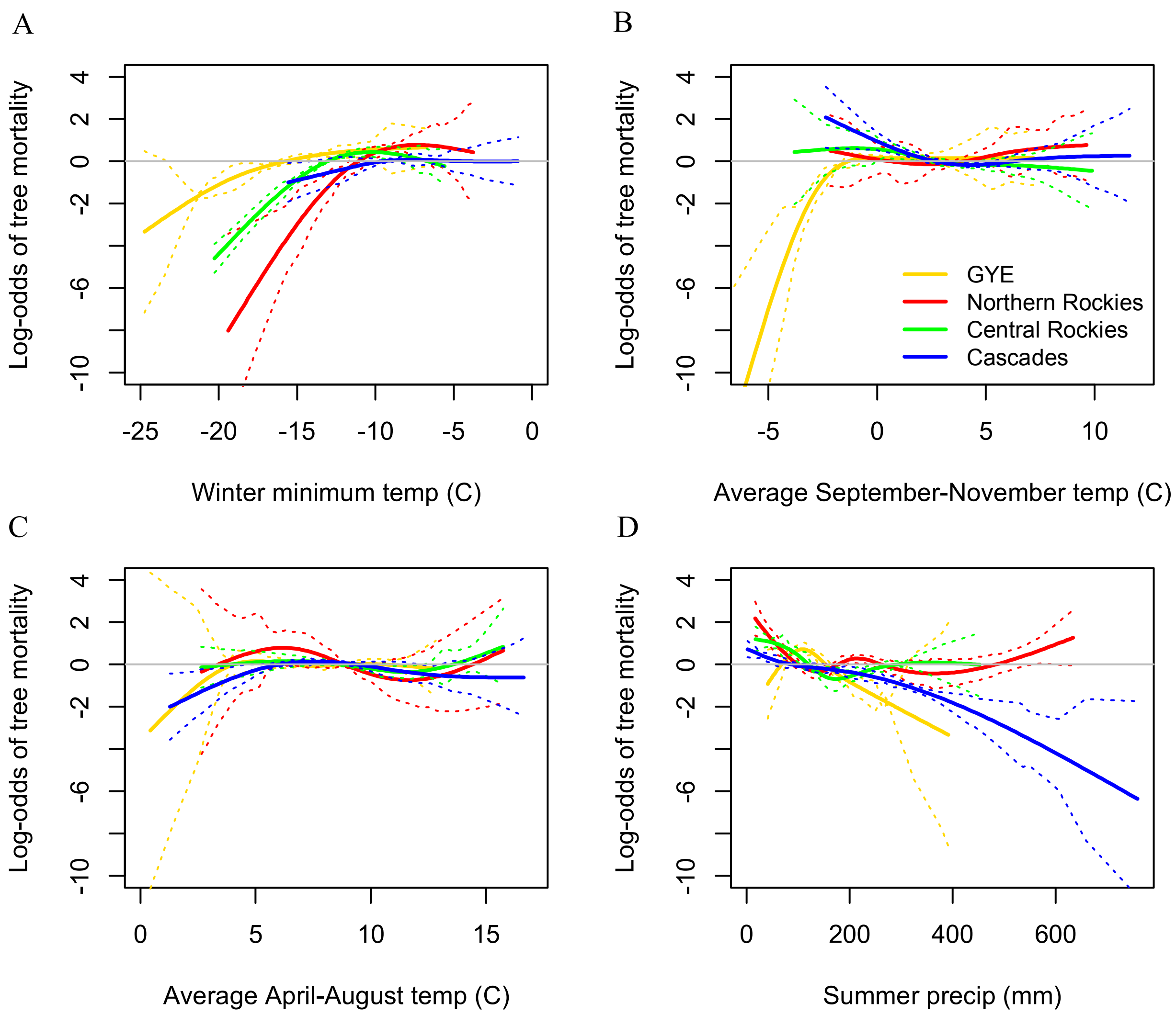


Figure 2.5. Log-odds of whitebark pine mortality from mountain pine beetle colonization due to the effects of A) winter (coldest month) minimum temperature, B) average September-November temperature, C) average April-August temperature and D) total summer (June-August) precipitation, from four regional statistical models developed independently. GYE = Greater Yellowstone Ecosystem. See Figure 2.1 for regional boundaries.

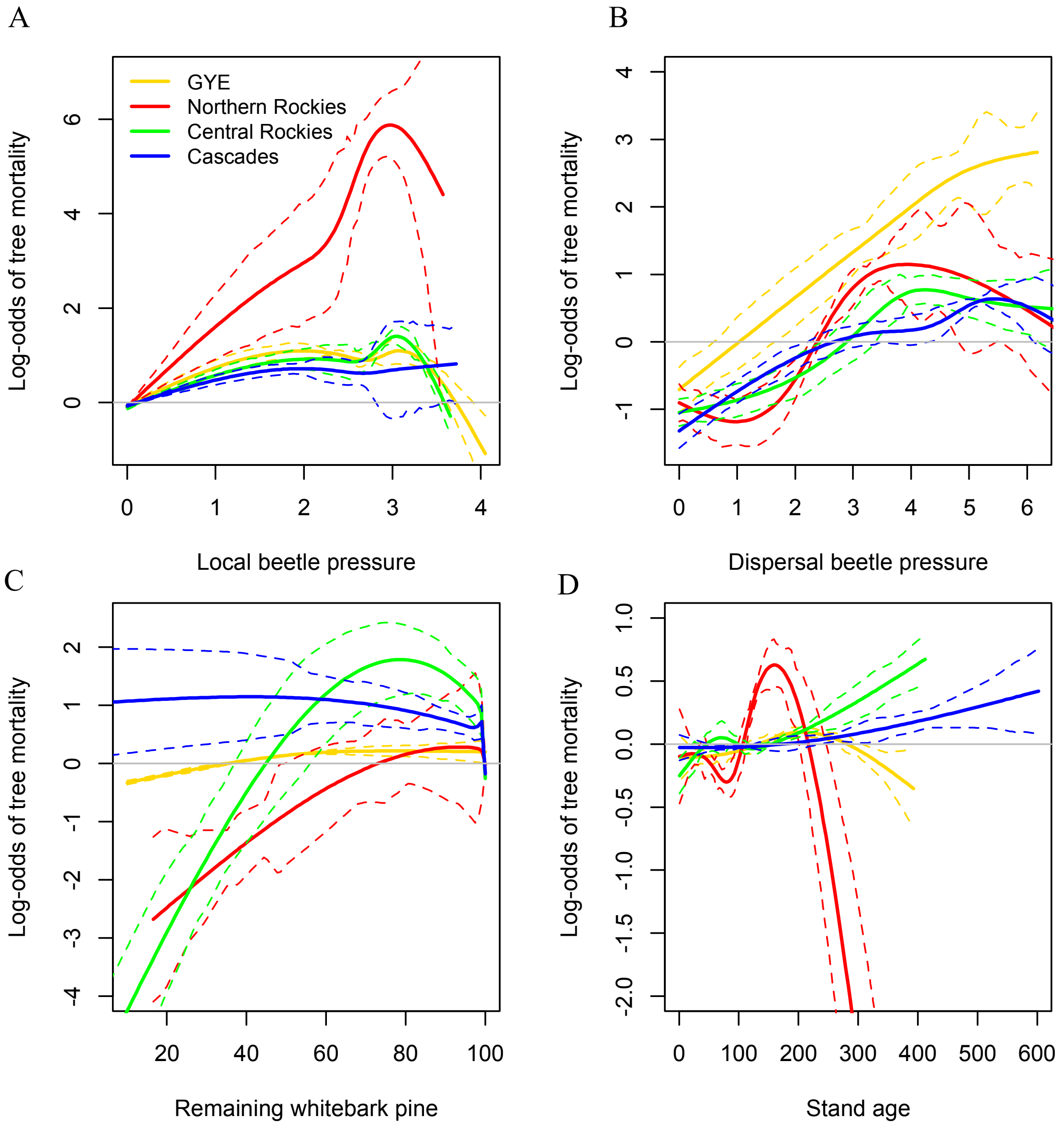
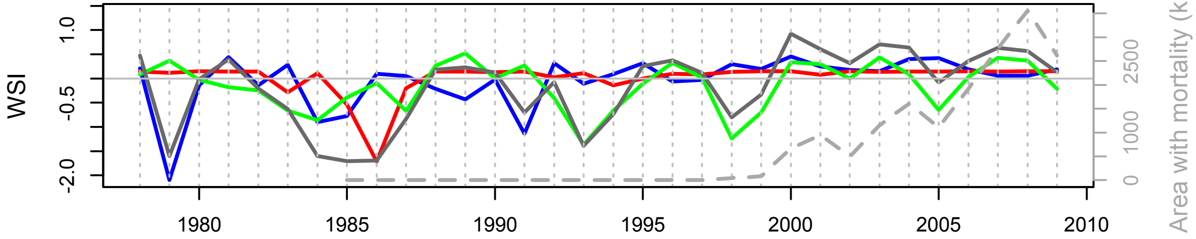
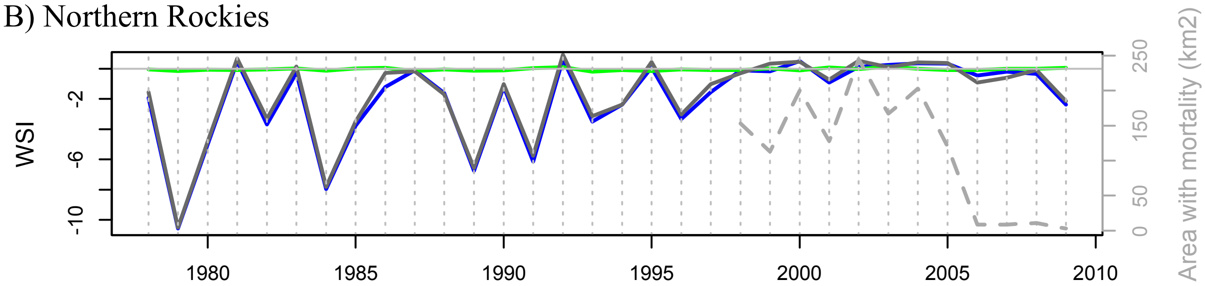


Figure 2.6. Log-odds of whitebark pine mortality from mountain pine beetles due to the effects of A) local beetle pressure, B) dispersal beetle pressure, C) remaining whitebark pine, and D) stand age based on four regional statistical models. GYE = Greater Yellowstone Ecosystem.

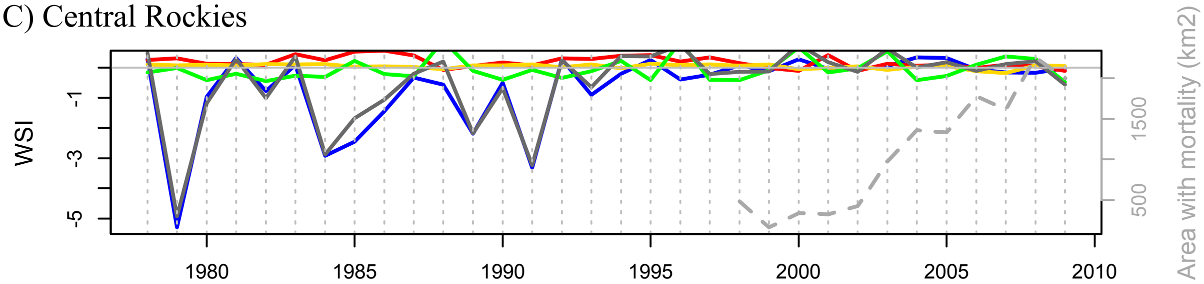
A) Greater Yellowstone Ecosystem



B) Northern Rockies



C) Central Rockies



D) Cascades

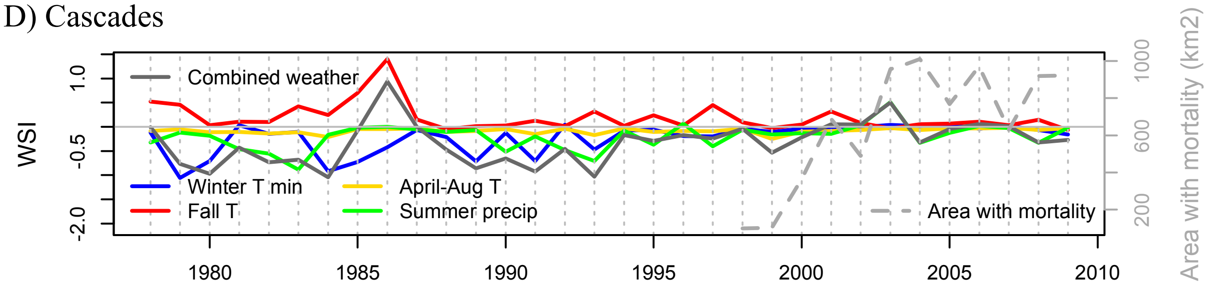


Figure 2.7. Individual and combined weather suitability indices for whitebark pine mortality from mountain pine beetles in the A) Greater Yellowstone Ecosystem, B) Northern Rockies, C) Central Rockies, and D) Cascades regions. Yearly values are spatially averaged over all grid cells in the region.

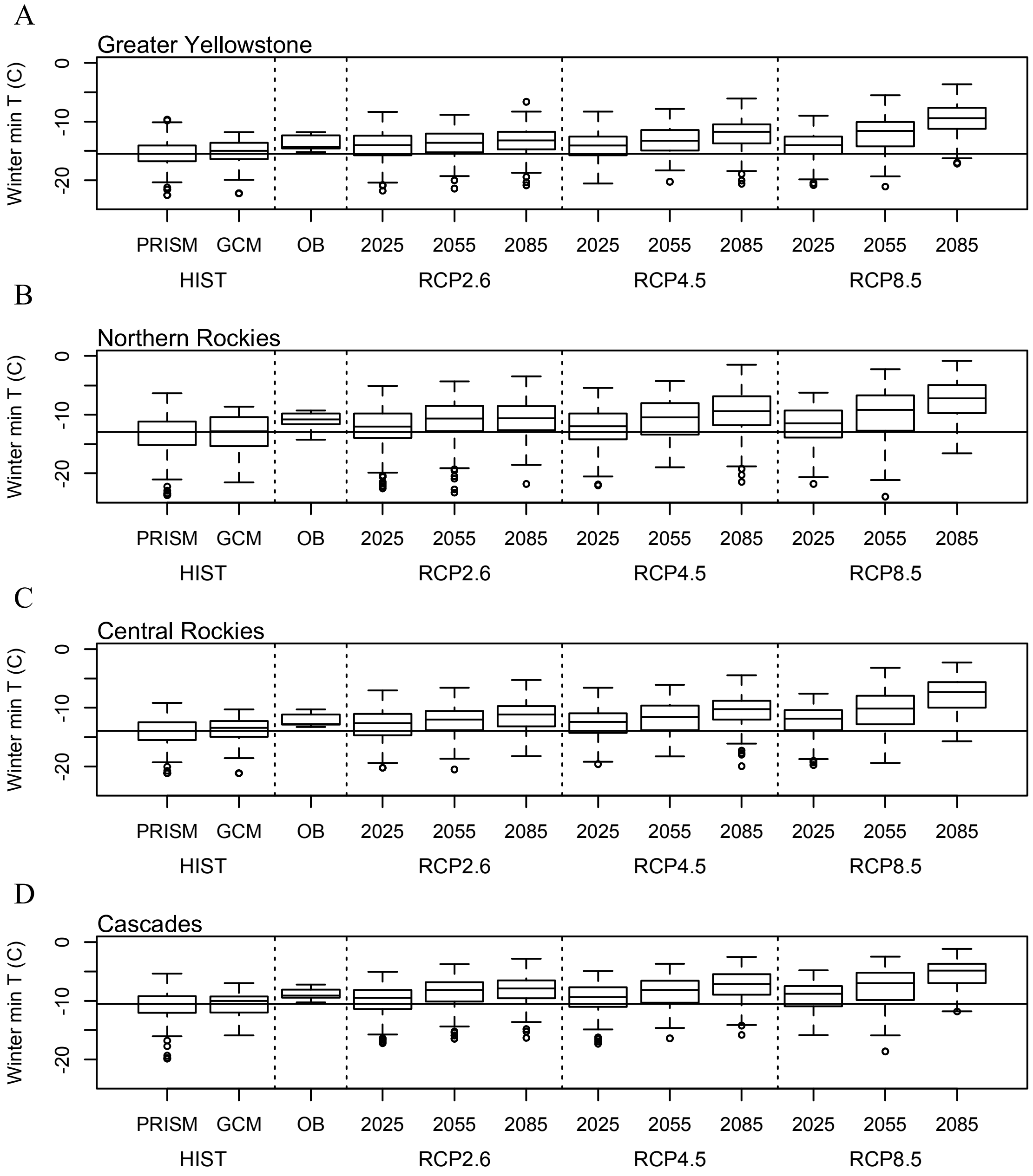


Figure 2.8. Historical and future winter minimum winter temperature data, spatially averaged over the range of whitebark pine, in the A) Greater Yellowstone Ecosystem, B) Northern Rockies, C) Central Rockies, and D) Cascade regions. “HIST” represents 1979-2009 values, showing both PRISM and hindcast general circulation model (GCM) data and “OB” represents PRISM data during the recent outbreak period (1997-2009). Distributions of GCM data are comprised of 300 data points: WSI estimates from the model applied to 10 GCM projections (Table 1.3) that were then spatially averaged over the region for each year. Horizontal black line marks the median value of the PRISM data during the historical period for each region.

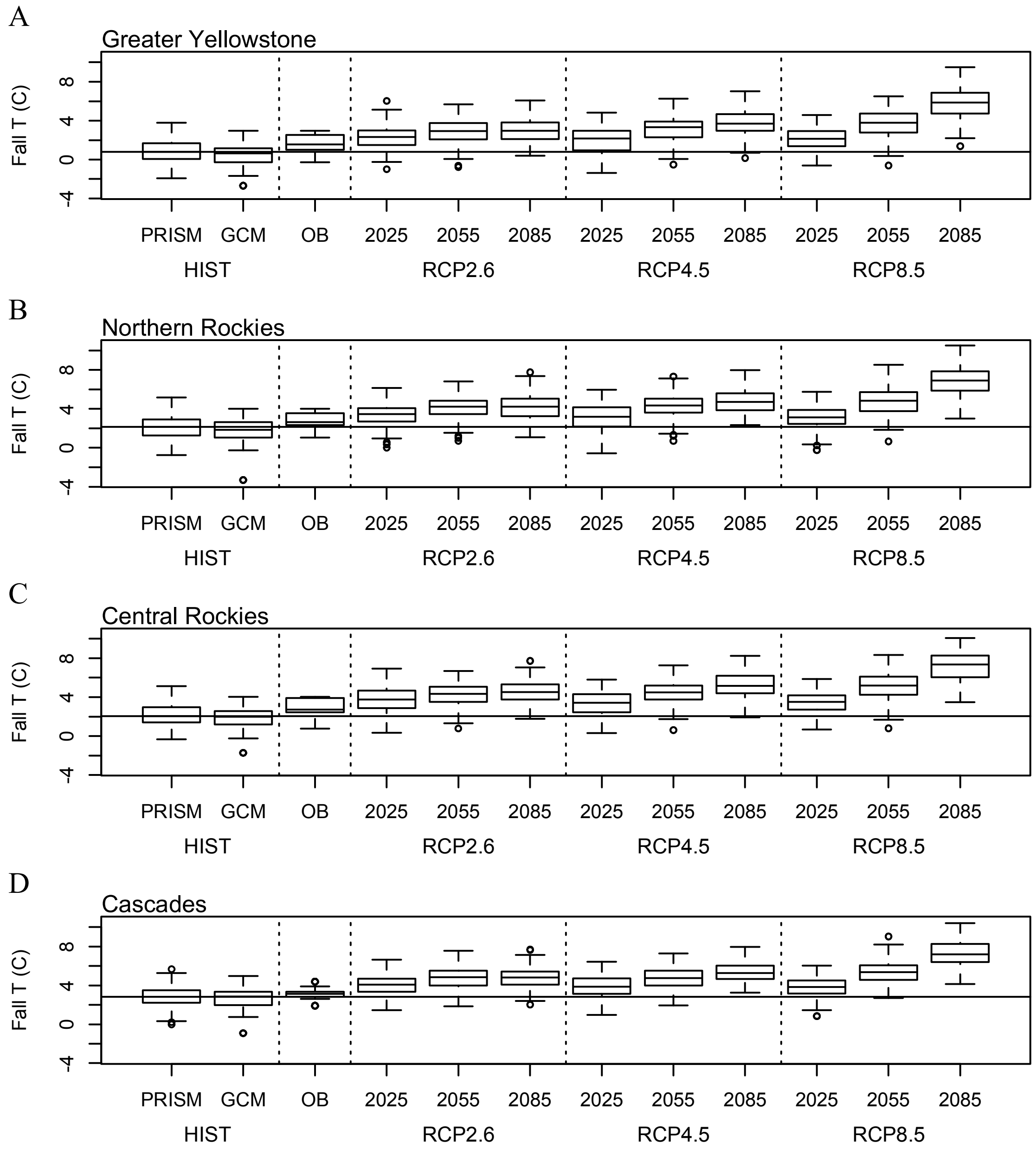


Figure 2.9. Historical and future average fall (September-November) temperature data, spatially averaged over the range of whitebark pine, in the A) Greater Yellowstone Ecosystem, B) Northern Rockies, C) Central Rockies, and D) Cascade regions. "HIST" represents 1979-2009 values, showing both PRISM and hindcast general circulation model (GCM) data and "OB" represents PRISM data during the recent outbreak period (1997-2009). Distributions of GCM data are comprised of 300 data points: WSI estimates from the model applied to 10 GCM projections (Table 1.3) that were then spatially averaged over the region for each year. Horizontal black line marks the median value of the PRISM data during the historical period for each region.

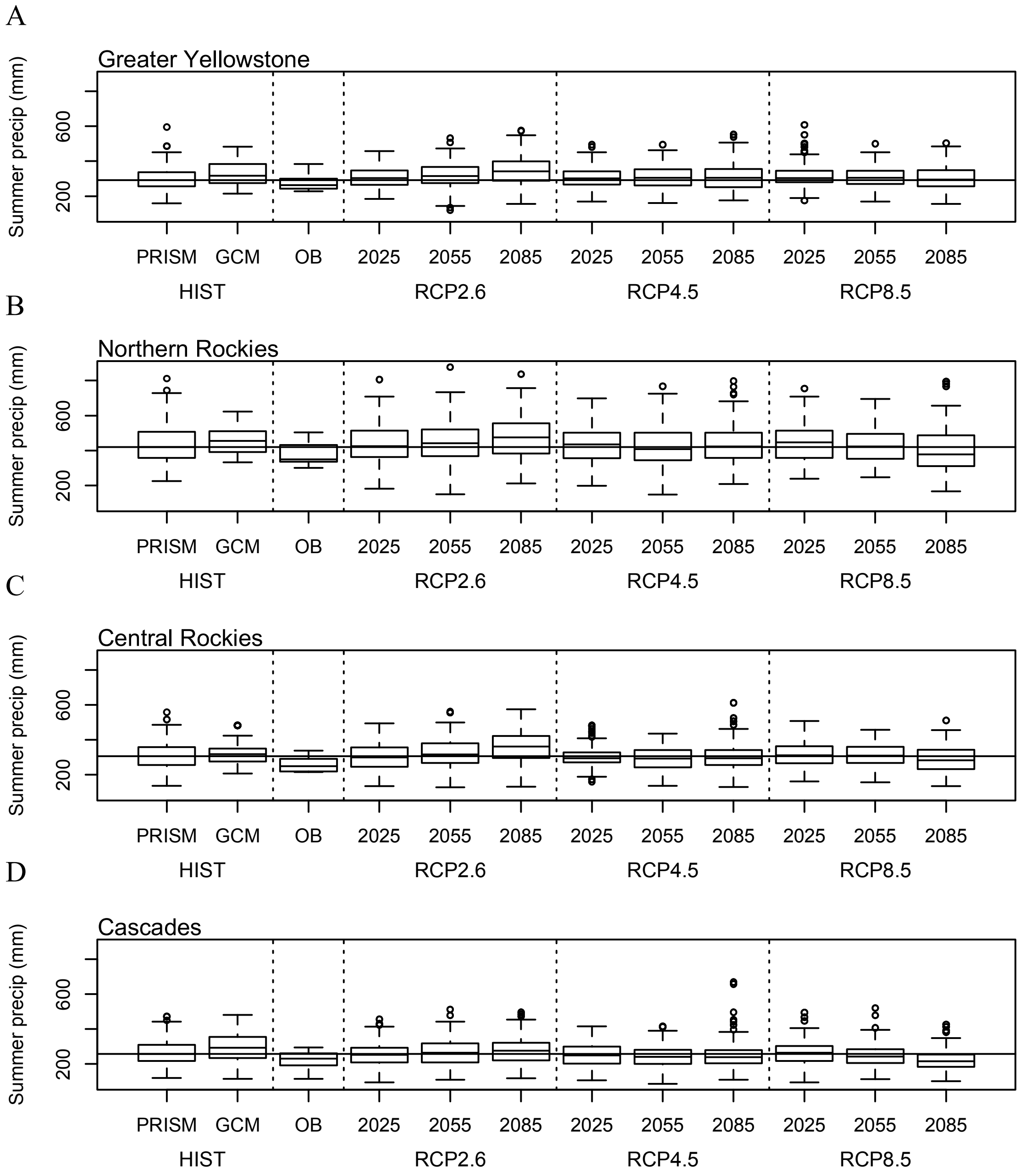


Figure 2.10. Historical and future total summer (June-August) precipitation data, spatially averaged over the range of whitebark pine, in the A) Greater Yellowstone Ecosystem, B) Northern Rockies, C) Central Rockies, and D) Cascade regions. "HIST" represents 1979-2009 values, showing both PRISM and hindcast general circulation model (GCM) data and "OB" represents PRISM data during the recent outbreak period (1997-2009). Distributions of GCM data are comprised of 300 data points: WSI estimates from the model applied to 10 GCM projections (Table 1.3) that were then spatially averaged over the region for each year. Horizontal black line marks the median value of the PRISM data during the historical period for each region.

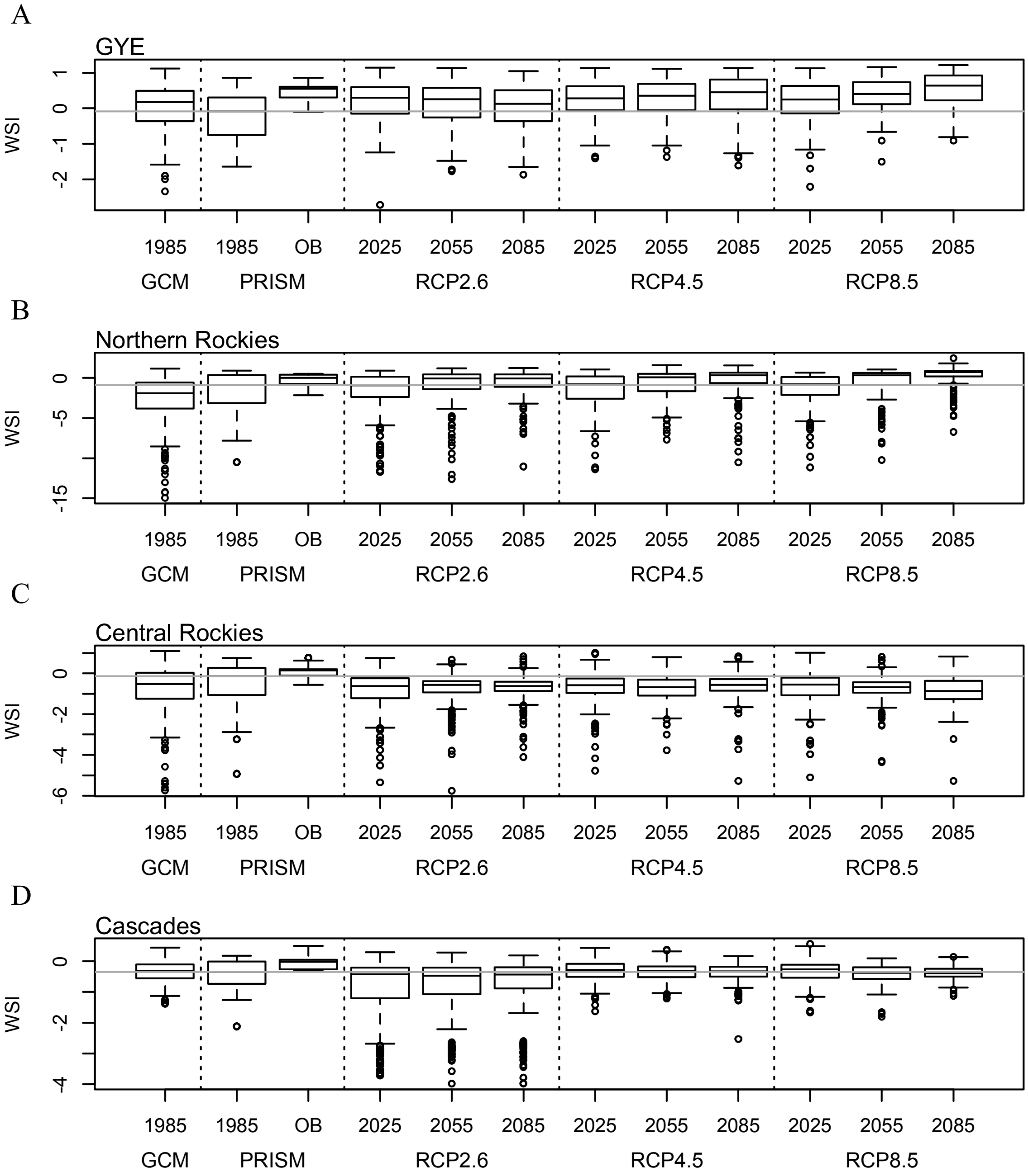


Figure 2.11. Distributions of combined weather suitability index (WSI) for whitebark pine mortality from mountain pine beetle attacks spatially averaged over each region for each year in A) the Greater Yellowstone Ecosystem, B) the Northern Rockies, C) the Central Rockies, and D) the Cascades. Numbers on the x-axis indicted the center of the 30-year period included in the distribution. "OB" indicated the period of the recent outbreak (1997-2009). Future suitability was estimated using 10 general circulation models (GCM) (Appendix A: Table A2) forced with low (RCP 2.6), medium (RCP 4.5) and high (RCP 8.5) emissions scenarios. Horizontal gray line marks median WSI during the 1985 period based on historical PRISM data. Distributions of GCM data are comprised of 300 data points: WSI

estimates from the model applied to 10 GCM projections (Table 1.3) that were then spatially averaged over the region for each year.

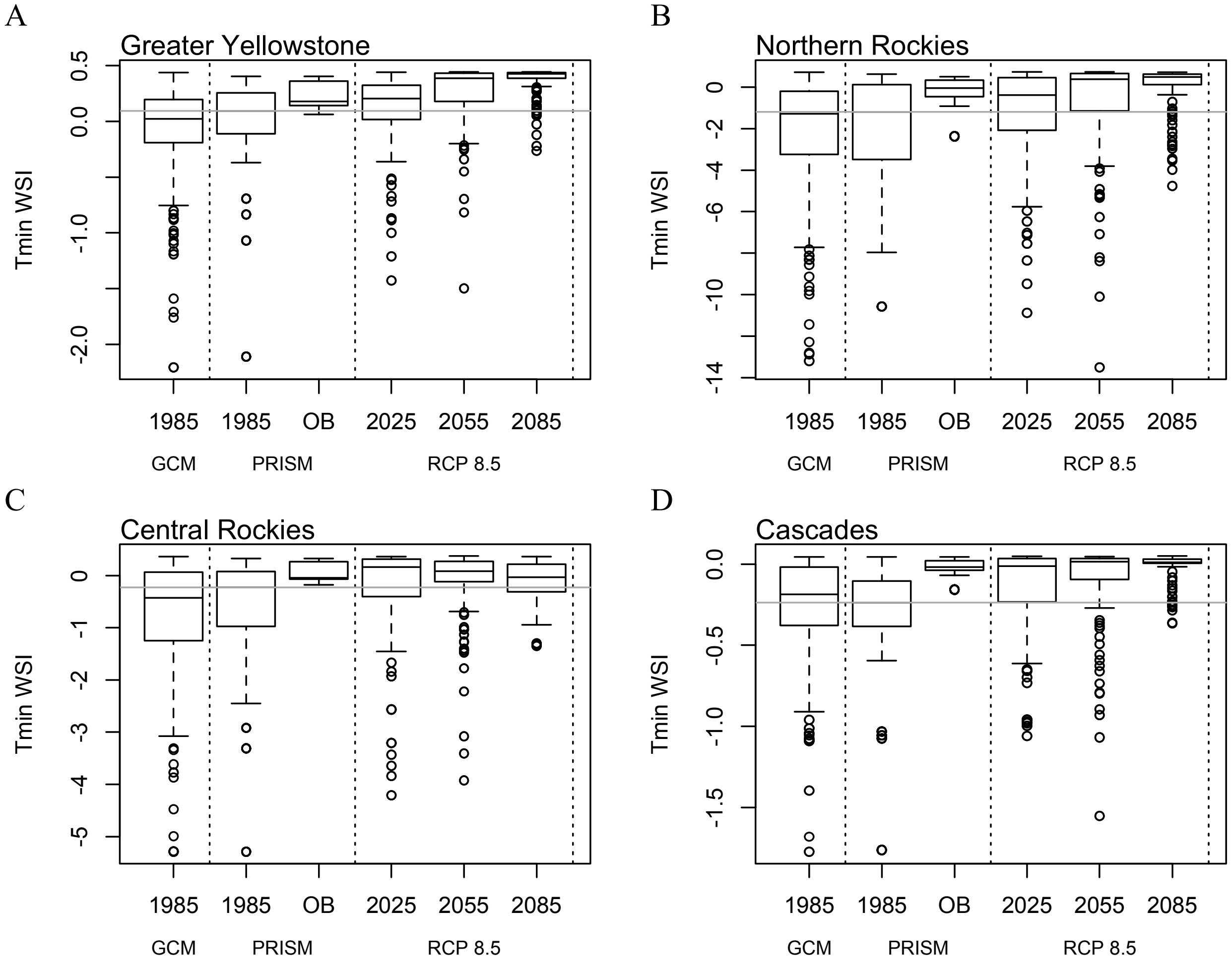


Figure 2.12. Suitability of minimum winter (coldest month) temperatures for whitebark pine mortality from mountain pine beetle colonization, spatially averaged over the range of whitebark pine, in the A) Greater Yellowstone Ecosystem, B) Northern Rockies, C) Central Rockies, and D) Cascades regions. Predictive models were applied to climate projections from 10 general circulation models (Appendix A: Table A2) forced with a high emissions scenario (RCP 8.5). Numeric labels indicate center of the 30-year period of each distribution of suitability values; "OB" indicates recent outbreak period (1997-2009). Distributions of GCM data are comprised of 300 data points: WSI estimates from the model applied to 10 GCM projections (Table 1.3) that were then spatially averaged over the region for each year.

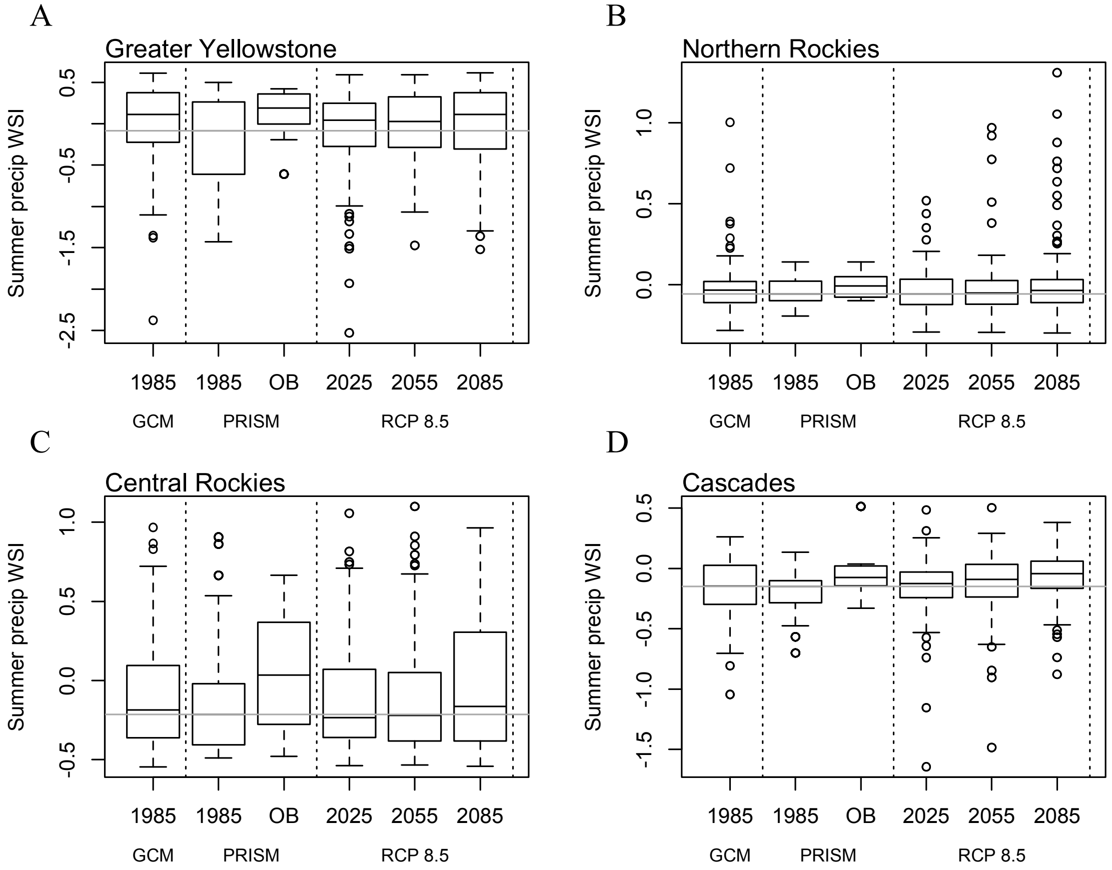


Figure 2.13. Suitability of total summer (June-August) precipitation for whitebark pine mortality from mountain pine beetle colonization, spatially averaged over the range of whitebark pine, in the A) Greater Yellowstone Ecosystem, B) Northern Rockies, C) Central Rockies, and D) Cascades regions. Predictive models were applied to climate projections from 10 general circulation models (Table 1.1) forced with a high emissions scenario (RCP 8.5). Numeric labels indicate center of the 30-year period of each distribution of suitability values, "OB" indicates recent outbreak period (1997-2009). Distributions of GCM data are comprised of 300 data points: WSI estimates from the model applied to 10 GCM projections (Table 1.3) that were then spatially averaged over the region for each year.

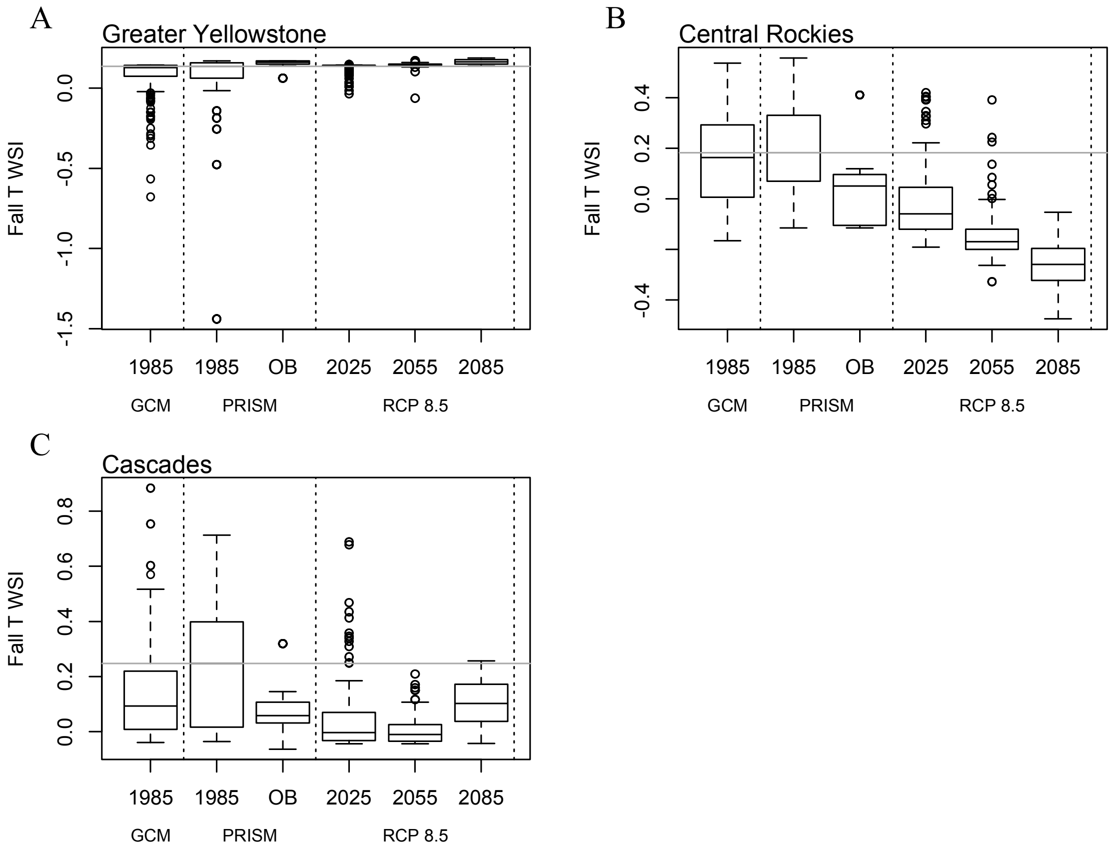


Figure 2.14. Suitability of average fall (September-November) temperatures for whitebark pine mortality from mountain pine beetle colonization, spatially averaged over the range of whitebark pine, in the A) Greater Yellowstone Ecosystem, B) Central Rockies, and C) Cascades regions. Predictive models were applied to climate projections from 10 general circulation models (Table 1.3) forced with a high emissions scenario (RCP 8.5). Numeric labels indicate center of the 30-year period of each distribution of suitability values, "OB" indicates recent outbreak period (1997-2009). Distributions of GCM data are comprised of 300 data points: WSI estimates from the model applied to 10 GCM projections (Table 1.3) that were then spatially averaged over the region for each year.

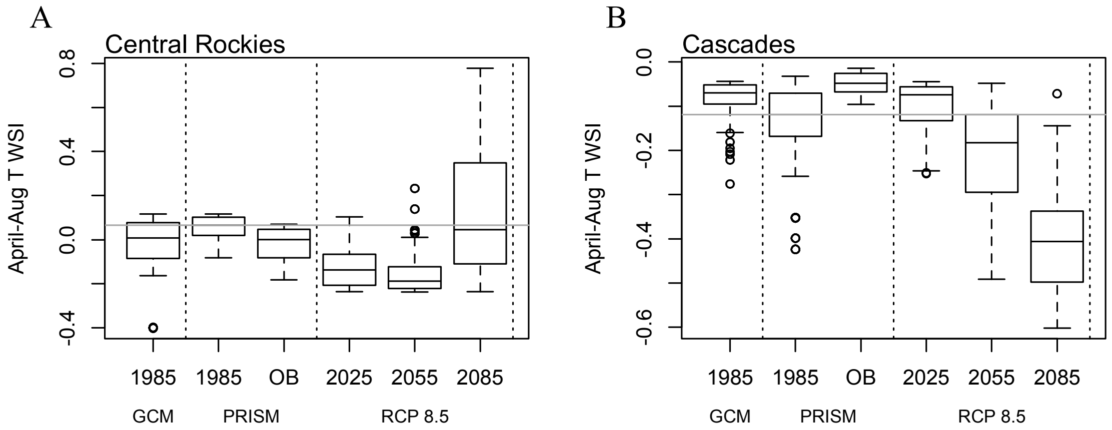


Figure 2.15. Suitability of average April-August temperatures for whitebark pine mortality from mountain pine beetle colonization, spatially averaged over the range of whitebark pine, in the A) Central Rockies, and B) Cascades regions. Predictive models were applied to climate projections from 10 general circulation models (Table 1.3) forced with a high emissions scenario (RCP 8.5). Numeric labels indicate center of the 30-year period of each distribution of suitability values, "OB" indicates recent outbreak period (1997-2009). Distributions of GCM data are comprised of 300 data points: WSI estimates from the model applied to 10 GCM projections (Table 1.3) that were then spatially averaged over the region for each year.

Chapter 3: Capturing Subregional Variability in Regional-scale Climate Change Vulnerability Assessments of Natural Resources[3]

3.1 Abstract

Climate change vulnerability assessments that encompass a wide range of climatological or ecological variability need to incorporate the potential for variability in species or resource vulnerability. Here we present and evaluate a framework for incorporating variability in vulnerability to climate change as implemented in the first regional-scale assessment led by the U. S. Forest Service. During the course of this assessment, five subregional workshops were held to capture variability in vulnerability and develop adaptation tactics. Our framework consisted of a questionnaire to address three objectives: 1) identify species, resources, or other information missing from the regional assessment; 2) describe subregional variability in exposure, sensitivity, and adaptive capacity; and 3) determine additional information needed to either assess vulnerability or develop adaptation options. This framework was used in six natural resource categories; in our results and discussion we focus on wildlife resources. Participants identified three habitat types and 13 species as important in subregions that were not included in the regional assessment. Participants also described multiple instances of subregional variability in exposure, sensitivity, and adaptive capacity. A better understanding of the mechanisms of climate influence on wildlife populations was

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[3] Buotte, P.C., D.L. Peterson, K.S. McKelvy, J.A. Hicke. 2015. Capturing Subregional Variability in Regional-scale Climate Change Vulnerability Assessments of Natural Resources. Global Environmental Change. In Preparation.

an information need common across all subregions. We provide recommendations, including a revised framework, for improving the process of capturing subregional variability in a regional vulnerability assessment. Our revised framework is structured around pathways of climate influence and population characteristics, each with separate rankings for exposure, sensitivity, and adaptive capacity. This structure allows for a quantitative ranking of species, pathways, exposure, sensitivity, and adaptive capacity. These rankings can be used to direct the development and implementation of future regional research and monitoring programs.

3.2 Introduction

Global mean annual temperature has increased by 0.8°C since 1880 (Walsh et al. 2014), and future warming is almost certain (IPCC 2013). Although historical precipitation trends vary spatially (IPCC 2013), declines in regional streamflows have been well documented (Rood et al. 2005, Luce and Holden 2009, Fu et al. 2010). Understanding how these temperature and precipitation changes will affect natural resources, and developing management plans that address these changes, is a primary focus of federal agencies, including the U.S. Forest Service (USFS) (USDA Forest Service 2008) and the U.S. National Park Service (NPS) (National Park Service 2010).

Developing such management plans requires projecting future climate conditions and understanding how climate can influence natural resources. Climate change vulnerability assessments (CCVAs) (Glick et al. 2011) provide a framework for achieving this understanding. CCVAs evaluate vulnerability of a resource or species in several steps, including 1) assessing future changes in climate ("exposure"); 2) determining the response of the resource or species to climate ("sensitivity"); and 3) documenting the ability of a species to minimize impacts through behavior changes, evolutionary adaptation, or physical relocation (“adaptive capacity”). Exposure and sensitivity together define potential impact; impact and adaptive capacity define vulnerability (Glick et al. 2011).

For the USFS, CCVAs fulfill several purposes. They provide a framework for synthesizing projections of future climate conditions, assessing known sensitivities of species or resources to direct and indirect effects of climate change, developing potential management strategies and tactics for adaptation to climate change, and monitoring the outcomes of those actions (Peterson et al. 2011). CCVAs can also help ensure that stated agency or organizational goals can continue to be met under changing climate conditions (Julius et al. 2008), and that they fulfill federally mandated requirements to address climate change impacts within the agency (USDA Forest Service 2008).

Across the United States, the USFS has to date conducted multiple CCVAs (Halofsky et al. 2011, Swanston et al. 2011, EcoAdapt 2014, Raymond et al. 2014). These assessments focused on relatively small regions and included one to four National Forests or National Parks (e.g., Olympic National Forest and Olympic National Park, WA (Halofsky et al. 2011); northern Wisconsin (Swanston et al. 2011); the Nez Perce-Clearwater National Forest, ID (EcoAdapt 2014); and the North Cascades Range, WA (Raymond et al. 2014).

An alternative to multiple CCVAs, each focused on a small area, is a larger, regional CCVA, which can include multiple land management agencies and cover many management units. Because of their extent, regional CCVAs can span a range of environments and habitats, include more species and populations, and involve potentially differing management objectives and priorities.

Conducting regional-scale CCVAs offers several advantages. A regional CCVA may provide a better match to the scale of species distributions and the scale at which ecological processes (e.g. dispersal) operate. Another advantage is the increased potential for collaboration across administrative boundaries, which rarely have ecological relevance. Collaborating across boundaries allows the development of local management options that are coordinated over a larger region (Joyce et al. 2008, Littell et al. 2010). For example, from a local perspective a species undergoing a range shift may look like extirpation, but from a regional perspective such change can be seen as a range expansion and an opportunity for collaboration (Stephenson and Millar 2012). Finally, organizing and conducting one regional CCVA may be more efficient than conducting multiple smaller CCVAs.

Despite these advantages, there are challenges to conducting regional CCVAs. One challenge is the number of species or resources that may be present within a larger region. Assessments cannot be conducted for all species or resources, so a subset must be chosen. Therefore, thoughtful selection is required to identify those species and resources to consider within the regional CCVA. Some species may be important and of interest across a region, and some may be important only in particular areas.

A second challenge is the potential for spatial variability in vulnerability to climate change within a region (e.g., O'Brien et al. 2004). Even if important species or resources are present across the region, the vulnerability of those species or resources may not be constant spatially. Subregional variability could result from variability in projected future climate (exposure). For example, if a regional assessment area includes subregions with both maritime and continental climates, or low and high elevations, then projected future climate conditions may be quite different between those two subregions. This difference would translate into different levels of exposure for a species that is common to both subregions. Other variability may result from species sensitivities to climate. Some species, like the mountain pine beetle (*Dendroctonous ponderosa* Hopkins*)*, are physiologically adapted to their local climatic conditions (Bentz et al. 2001), even though their distribution covers a much wider climatic range. Adaptive capacity of a species or resource might also vary among subregions. Adaptive capacity can depend on a number of factors, such as current landscape connectivity, population demographics and genetics, interactions with predators, competitors, or pathogens, and management objectives among agencies or stakeholders within the region. All of these factors are likely to vary across a large geographic region. Thus, capturing variability across subregions is an important component of a regional CCVA.

Regional CCVAs can provide a starting point for overcoming the difficulties in assessing vulnerability to climate change and developing a portfolio of management strategies coordinated across ecological and administrative boundaries. Comparing and contrasting climate change vulnerability across subregions can aid in developing adaptive monitoring and research programs (Lindenmayer and Likens 2009) based on hypotheses describing those pathways (Nichols and Williams 2006). Thus, regional CCVAs offer significant advantages for large land management agencies such as the USFS and NPS. However, there are important challenges of selecting appropriate species or resources and capturing subregional variability in vulnerability in regional CCVAs that are not present in CCVAs of smaller regions. These issues may lead to concerns about the quality and usefulness of regional CCVAs, yet to date no research has evaluated ways to address these concerns.

Several tools for assessing climate sensitivity or vulnerability have been developed, including the Climate Sensitivity Database (http://climatechangesensitivity.org), the NatureServe Climate Change Vulnerability Index (http://www.natureserve.org/conservation-tools/climate-change-vulnerability-index), and the System for Assessing Vulnerability of Species (SAVS) to climate change (Bagne et al. 2011). However, these tools do not always return the same vulnerability ranking for a given species (Lankford et al. 2014), and none are designed specifically for capturing subregional variability in vulnerability to climate change. Assessing vulnerability for wildlife species, here focusing on terrestrial endotherms, is particularly complex. Not only are some species directly physiologically sensitive to climate (Buckley et al. 2012), but there are also multiple indirect ways for climate to influence wildlife. Examples include species habitat associations, effects of disturbances on habitats, and interactions with other species. For many wildlife species, little is known about their direct or indirect sensitivity to climate change. Difficulties in assessing vulnerability are further compounded by a lack of modeling techniques that can adequately capture indirect effects.

In this paper, we present a framework for capturing subregional variability in climate change vulnerability in a regional CCVA. First, we describe the framework as implemented in the first regional CCVA conducted by the USFS and partner agencies and organizations. Second, we summarize the results of implementing the framework for wildlife resources, evaluate the evidence for subregional variability in vulnerability to climate change, and evaluate the ability of our framework to characterize subregional variability. Finally, we recommend how the process can be improved to capture subregional variability in regional CCVAs. Although we focus on wildlife vulnerability, we provide examples of how this approach can be applied to other natural resources as well.

3.3 Methods

3.3.1 The Regional CCVA

We developed a framework for capturing subregional variability vulnerability to climate change for the Northern Rockies Adaptation Partnership (NRAP), the first regional CCVA led by the USFS (http://adaptationpartners.org/nrap). NRAP was a collaborative effort among multiple federal and state agencies, nongovernmental organizations, universities, and Native American tribes. The two primary objectives of NRAP were to synthesize the best available scientific information to assess climate change vulnerability, and develop adaption options throughout the region. The NRAP geographic area covers 15 national forests and three national parks in the USFS Northern Region, which includes the northern panhandle portion of Idaho, all of Montana, portions of North and South Dakota, and the Greater Yellowstone Area in Wyoming and Idaho (Figure 1). Because this region encompasses a wide range of climatological, topographic, and ecological variability, five subregions were delineated: West, Central, East, Greater Yellowstone Area, (GYA) and Grassland (Figure 1).

The process of conducting the NRAP CCVA is shown in Figure 2. A regional level leadership team organized the assessment and compiled a first draft. The assessment covered eight resource categories (water resources, fisheries, wildlife, forested vegetation, non-forested vegetation, ecological disturbance, recreation, and ecosystem services), plus a section describing projected future climate conditions. Regional-level scientists and managers on each of the eight resource teams selected specific resources to be covered in each chapter.

Workshops were held in October-November 2014 with scientists and managers in each of the five subregions to 1) capture subregional information and variability in vulnerability to climate change not addressed in the regional vulnerability assessment, and 2) develop adaptation strategies (general) and tactics (on-the-ground actions) for responding to projected effects of climate change. At these workshops, chapter leads presented their draft assessments, and participants discussed distinctive features of their subregion compared to the rest of the region. Participants then divided into resource groups to evaluate subregional variability in climate change vulnerability and develop adaptation options. The regional leadership team reviewed and synthesized the information gathered from the workshops and provided subregional participants the opportunity to review the assessment before final publication.

3.3.2 Framework for Capturing Subregional Variability

We sought to capture subregional variability based on the expert opinions of subregional-level managers and scientists attending the workshops. Our framework consisted of questions (Appendix A) to capture: 1) species, resources, or other information missing from the regional assessment (Questions 1 & 2); 2) subregional variability in sensitivity (Questions 3 & 5), exposure (Question 4), and adaptive capacity (Question 5), and; 3) additional information needed to either assess vulnerability or develop adaptation options (Question 6). We expected participants would have read the draft CCVA and would consider all components of their resource area when answering the questions. In the results and discussion below, we focus on results from the wildlife resource group.

3.4 Results & Discussion

Over the five subregional workshops, there were four to nine participants in the wildlife resource group, excluding the discussion leader and note taker. The wildlife chapter lead author was the discussion leader at four of the five workshops, and the note taker was consistent at three of the five. In total, participants discussed 19 wildlife species (Table 1).

3.4.1 Information Missing from the Regional CCVA

At every workshop, wildlife resource participants recommended adding species important in their subregion that were not included in the draft regional assessment (Table 1). Whether to include a suggested new species was decided based on consensus of the workshop participants in each subregion. Added species tended to be those that were seen as sensitive to some aspect of climate and for which participants saw viable management options. Participants tended to think first in terms of climate change effects on habitat types, and then species that used those habitats. Three regionally important habitats (riparian, aspen, and mountain grasslands) were not represented in the regional assessment. Within these three habitats, participants added 13 species. In some subregions, species included in the regional assessment were not discussed, even though present in the subregion, because participants saw no viable management options, because that species had been discussed at a previous workshop, or because they were seen as lower priority in that subregion.

3.4.2 Evidence for Subregional Variability in Vulnerability to Climate Change

Synthesis of workshop discussions revealed that participants tended to organize their thoughts according to what we termed “pathways of climate influence”. Example pathways include physiological tolerance limits and habitat, covering habitat associations and previous habitat loss due to climate change and/or climatic variability. Participants discussed how these pathways could interact with population characteristics (e.g., location in the species' environmental niche, population genetics, and population size) to ultimately affect the future state of a population. We found this framework (Figure 3) to be a useful way of assimilating participant responses and characterizing subregional variability. Initially, it was sometimes difficult to categorize a response as belonging to sensitivity, exposure, or adaptive capacity. However, when we reviewed responses in terms of climate influence pathways (Figure 3), defining exposure, sensitivity, and adaptive capacity was more intuitive.

3.4.2.1 Pathways of Climate Influence

We identified two broad categories of climate influence pathways: direct and indirect (Figure 3). Direct pathways operate through species' physiological tolerance of temperature or moisture. More commonly discussed in workshops were indirect pathways, in which climate conditions affect a component of a species' environment, which in turn affects that species. The relative importance of pathways, as determined by the number of times a pathway was discussed in a subregion, divided by the sum of times all pathways were discussed, differed across subregions (Figure 4). Below we summarize workshop discussions of important pathways in each subregion.

Direct, physiological pathways were seldom discussed at the workshops (Figure 4). In two subregions, participants identified several species likely to have physiological limits, but stated that those limits were not known.

Indirect pathways of climate influence were more common, and evidence for subregional variability in indirect pathways was more abundant. Variability occurred in exposure, sensitivity, and adaptive capacity components of indirect pathways. To account for the indirect nature of these pathways, here we expand the definition of exposure from strictly changes in climate that directly influence an organism to include changes in other ecosystem components as a result of changes in climate.

Climate influence through effects on habitat was an important pathway in all subregions (Figure 4), but was not always expressed similarly. Species habitat associations differed across subregions. For example, in the GYA, ruffed grouse (*Bonasa umbellus*) preferred aspen habitat but were associated with a broader range of habitats in the Central subregion. Therefore, ruffed grouse were seen as more sensitive to climate effects, through effects on aspen, in the GYA than in the Central subregion. The importance of previous habitat loss, potentially due to recent warming, also differed across the subregions. In the Eastern subregion, there has been extensive lodgepole pine (*Pinus contorta* var. *latifolia*) mortality from mountain pine beetles, likely due to warmer winters (Bentz et al. 2010). Cavity nesting birds (e.g. pygmy nuthatch, *Sitta pygmaea*) were thought to be more sensitive to potential future habitat loss due to climate change, through increased tree mortality from mountain pine beetles, because they have already lost a substantial portion of their habitat. Therefore, exposure to climate influences through habitat loss was seen as higher in this subregion than in the others.

Climate effects can manifest through interspecific interactions. Participants in the Central subregion cited the example of flammulated owls (*Psiloscops flammeolus*) feeding on insects that depend on understory plant composition, and how that composition could be altered by increased abundance of invasive plants (e.g., Cheat grass, *Bromus tectorum*) in response to drier conditions or more frequent fires. Therefore, exposure to climate influences was higher for flammulated owls because dry forest habitats types, susceptible to species invasions, were more common.

Climate conditions can influence human population distribution and development. In the GYA and Central subregions, participants discussed the potential for increased human density and shifts in residential development into riparian areas in response to future climate. These changes could lead to reductions in available habitat and increases in wildlife-human conflicts. Changing demands for energy sources and the influence of energy development on wildlife habitat were discussed in the Central subregion. Participants saw increases in human population growth and development as increasing wildlife exposure to habitat loss and direct mortality.

Disease occurrence and transmission can be influenced by temperature and moisture conditions. Negative effects on wildlife populations from exposure to an increase in West Nile virus (*Flavivirus* sp.) occurrence and transmission due to climate change were discussed in three of the five subregions. The potential for increased exposure to diseases affecting bighorn sheep (*Ovis canadensis*) were discussed in the GYA.

Habitat connectivity allows for individuals and populations to track shifts in their habitat due to climate changes and is therefore an important component of species' adaptive capacity. Connectivity was a primary concern in four of the five subregions. Participants considered several scales of connectivity to be important: the ability for individuals to move through the landscape to meet their daily needs, the ability to complete seasonal migrations, and the ability to track potentially shifting habitat. The geographical composition of the subregion (e.g., island mountain ranges in the East subregion compared to more continuous mountainous terrain in the GYA) was an important influence on connectivity. Numerous indirect influences on each of those scales of connectivity were discussed. For example, habitat loss due to future increases in wildfires or human development can influence dispersal connectivity.

3.4.2.2 Wildlife Population Characteristics

Participants noted that the ultimate influence of direct and indirect climate influences could depend on current animal population characteristics. These characteristics included the position the population occupies in its environmental niche (e.g., at optimal conditions, or at marginal conditions), population size, and genetic diversity. Current population characteristics are a result of the culmination of past climate conditions, species evolution, and dispersal events (Jackson et al. 2009), that are likely unique to each population.

Species exist in different parts of their environmental niches in each subregion: some are in the middle, but some are on the climatic boundaries of their niche. Thus, similar exposure to climate change can lead to loss of habitat in one subregion but not another. For example, the West and Central subregions are at the junction of maritime and continental climates, and many species within these subregions are at the edges of their ranges. For example, participants in the Central subregion discussed how future climate change is expected to increase habitat suitability for fisher (*Martes pennanti*) such that fisher may expand their range into the subregion.

Participants also discussed the importance of population size and genetic structure in determining effects of climate change. Hypothetical examples of how a small population compared with a large population could be affected by direct and indirect pathways of climate influence were discussed, and genetically diverse populations were compared with genetically uniform populations. Few specific populations were cited because participants felt these characteristics were largely unknown.

3.4.2.3 Information Needs

A lack of information can prohibit identification of climate vulnerabilities. In most subregions, participants discussed the general lack of understanding of the specific mechanisms of direct climate sensitivity for many wildlife species, and agreed that a better understanding was essential for both assessing vulnerability and developing adaptation options. For example, the physiological mechanisms that limit the distribution of moose were cited as not understood. Participants also identified multiple indirect pathways they saw as particularly important but not well understood. The lack of understanding of climate influences on disease occurrence and transmission was discussed in three of the five subregions. The influences of changes in water supply, habitat distribution, vegetation phenology, community composition, species interactions, and human development on connectivity and dispersal ability were identified as poorly understood processes, but again, essential for assessing vulnerability and developing adaptation options. Finally, the need for coordinated monitoring of important wildlife resources was identified in three of the subregions.

3.4.3 Framework Evaluation

A primary result of working through our questionnaire was the identification of multiple species important in subregions that were not included in the regional draft assessment (Table 1). Vulnerability assessments for each of these additional species were included in the final NRAP assessment, which makes the product a more useful resource for users in all subregions.

The questionnaire and workshop discussions also elucidated subregional differences in pathways of climate change influence (Figure 4) and vulnerability. This information helped participants develop management tactics appropriate for each subregion. Another benefit of our questionnaire was the identification of common knowledge gaps across subregions. Discussions of the current lack of understanding of specific mechanisms of climate influence also helped identify research needs.

Although our framework allowed for open discussions, as originally intended, it limited our ability to make quantitative comparisons of the species importance and vulnerability across subregions. A common set of species and pathways was not evaluated in all subregions. Therefore, a lack of recorded information did not necessarily indicate a lack of importance. Species or pathways were excluded from discussion because 1) they were added at subsequent workshops, 2) participants decided to discuss only those species for which they could identify viable management actions, or 3) they had been discussed in a previous workshop.

3.5 Recommendations

We developed a set of recommendations for improving the process of capturing subregional variability in wildlife vulnerability to climate change. We believe these recommendations will provide a better balance between open discussion and consistent, quantitative measures of subregional variability in climate change vulnerability.

3.5.1 Developing the Species List

We recommend that an initial list of species to be covered in the assessment be sent to the subregions for review well in advance of the workshops. Species can be selected for assessment because 1) there is prior information on climate sensitivities (Raymond et al. 2014), (2) they represent critical habitat types (Decker and Fink 2014), (3) they are rare, endangered, hunted or otherwise important to people, or (4) there are viable management alternatives. These reasons may vary by subregion. Providing participants with an additional opportunity to comment on the species included before the workshops will ensure all subregions have the opportunity to discuss the same set of species. Not having to spend time adding to the species list will allow more time for discussing subregional vulnerabilities during the workshops.

3.5.2 Revised Framework for Capturing Subregional Variability

Information from workshop discussion was more easily structured in terms of potential pathways of climate influence on habitats and species, rather than strictly in terms of exposure, sensitivity, and adaptive capacity. An important element missing from our original framework was the ability to quantitatively rank species or the components of vulnerability. We therefore developed a revised framework for capturing subregional variability that is structured around potential pathways of climate influence and population characteristics (Figure 3) and that allows for quantitative rankings of vulnerability.

Our revised questionnaire (Appendix B) lists potential pathways of climate change and population characteristics, and asks for separate rankings for exposure, sensitivity, adaptive capacity, and information needed within each pathway. Additional space is provided for comments to capture information that does not fit within a ranking structure and to allow for open discussion. We recommend that the regional leadership team provide workshop participants with as complete a list of potential pathways as possible. Deciding on a final species list well in advance of the workshops (our first recommendation) would make this task easier. However, pathways or population characteristics will likely be added during workshops. We suggest including those in subsequent workshops, and if possible, having previous participants rank them as well. If that is not feasible, the regional leadership team could complete those rankings. To allow for quantitative comparisons across subregions, participants were asked to complete a questionnaire for each species in the assessment and to record if a species is not present or a pathway is not applicable in that subregion.

This framework is based on pathways and population characteristics important in the NRAP region. Figure 3 depicts the most common pathways and population characteristics discussed, but is not a comprehensive list of either. Depending on the species, a single pathway may be comprised of multiple additional pathways. For example, for a riparian species, the habitat pathway could include a pathway of altered hydrological dynamics due to changes in precipitation timing and quantity. For a forest species, the habitat pathway could include a disturbance pathway due to projected increases in fire or beetle outbreaks.

This structure allows for a quantitative ranking of species vulnerability across subregions. Separately ranking exposure, sensitivity, and adaptive capacity allows for a synthesis and ranking of the components of vulnerability across subregions. The species, pathway, and component rankings could then be mapped to provide a visual depiction of vulnerability across the region.

3.6. Conclusions

Regional CCVAs provide an opportunity to elicit and synthesize our understanding of climate change vulnerability across diverse subregions. However, when regional CCVA encompass a broad range of climatological and ecological variability, it may be difficult to produce a useful assessment unless subregional variability is considered. We found multiple instances of subregional variability in vulnerability to climate change across the NRAP region. Our experience in NRAP workshops suggests that a framework structured around pathways of climate influence and population characteristics is an intuitive way to capture subregional variability in a CCVA workshop setting.

Our framework can be applied to natural resources other than wildlife. For example, tree species may experience climate change effects through interspecific interactions. Changes in temperature and precipitation can alter tree species composition, thereby changing competitive interactions. An assessment of ecosystem services may include a pathway of climate influences on economics. Our revised framework does not necessarily include all of the important pathways of climate influence. Rather, specific pathways will vary by resource area and according to the ecological, climatological, social, and economic characteristics of the region.

This framework can be used as a foundation for designing future research and monitoring programs (Nichols and Williams 2006). Focal species must be selected for research and monitoring, and the rankings our framework provides would allow for an objective means of making those selections. Identifying and contrasting the importance of pathways of climate influence across subregions can suggest potential mechanisms of climate influence. Hypotheses can be developed to account for these mechanisms and management actions monitored to test those hypotheses. Based on the results of those tests, decisions can be made to continue with management actions, or develop new actions or hypotheses, creating an adaptive monitoring program (Lindenmayer and Likens 2009). The assessment of adaptive capacity across the region can inform initial decisions of where to conduct research or management.

Capturing the subregional variability in vulnerability to climate change within a regional CCVA will make the product more useful to managers and scientists across the region. The process of conducting regional CCVA will improve with repetition and with people sharing their experiences of what did and did not work well.

3.7 Acknowledgements

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Table 3.1. Species covered in the draft Northern Rockies Adaptation Partnership vulnerability assessment and discussed at subregional workshops. Note that not being discussed does not indicate absence from a subregion. See Figure 1 for subregional boundaries.

Habitat	Species	Regional Draft	West	Central	East	GYA	Grassland
Dry forest							
	pygmy nuthatch: *Sitta pygmaea*	X		X	X	X	
	flammulated owl: *Otus flammeolus*	X		X		X	
Riparian/wetland							
	Townsend's big-eared bat:			X	X	X	
	Corynorhinus townsendii			X	X	X	
	American beaver:			X		X	
	Castor canadensis					X	
	harlequin duck:					X	
	Histrionicus histrionicus			X		X	
	northern bog lemming:			X		X	
	Synaptomys borealis						
	Moose: *Alces alces*						
	boreal toad: *Bufo boreas*						
	Columbia spotted frog:						
	Rana luteiventris						
Aspen							
	cavity nesters			X	X	X	
	ruffed grouse: *Bonasa umbellus*					X	

Sagebrush grasslands						
greater sage-grouse:	X				X	X
Centrocercus urophasianus				X		
pygmy rabbit: *Brachylagus idahoensis*					X	
Brewer’s sparrow: *Spizella breweri*					X	
pronghorn *Antilocapra americana*						
Mountain grasslands						
mountain quail: *Oreortyx pictus*		X				
Mesic old-growth forest						
Fisher: *Martes pennanti*	X		X		X	
Snow-dependent species						
American pika: *Ochotona princeps*	X				X	
Canada lynx: *Lynx canadensis*	X		X		X	
Wolverine: *Gulo gulo*	X		X		X	

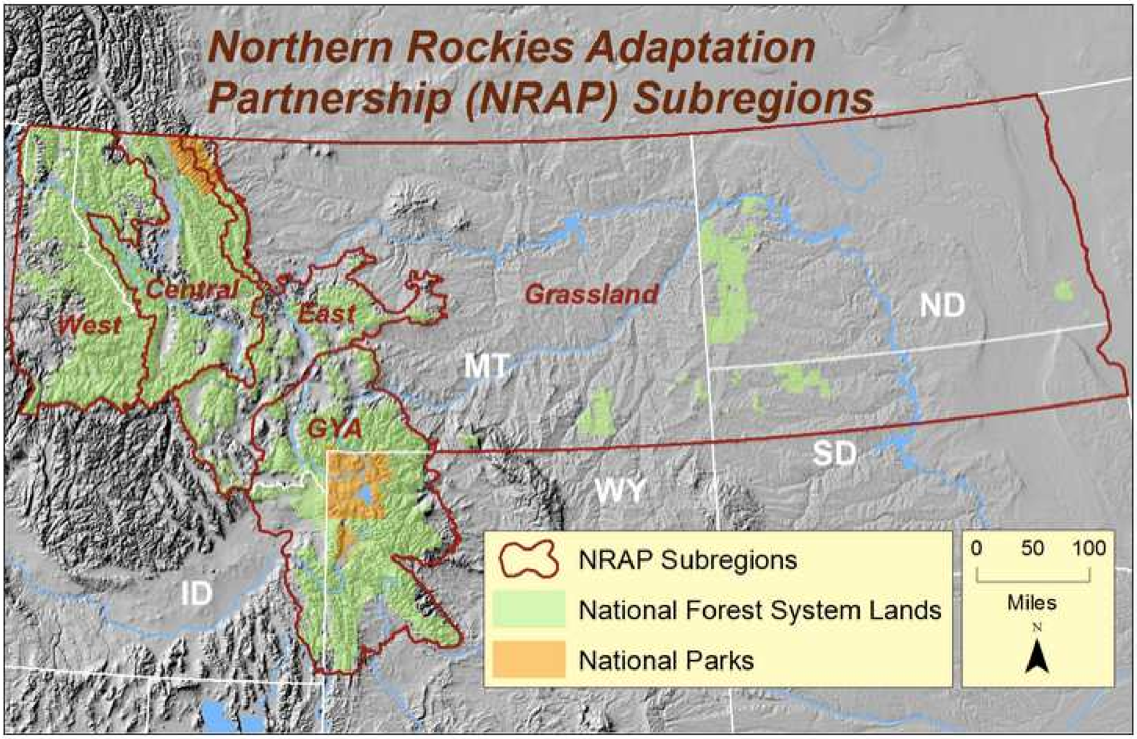


Figure 3.1. Regional and subregional boundaries of the Northern Rockies Adaptation Partnership. Figure credit: Northern Rockies Adaptation Partnership, http://adaptationpartners.org/NRAP.

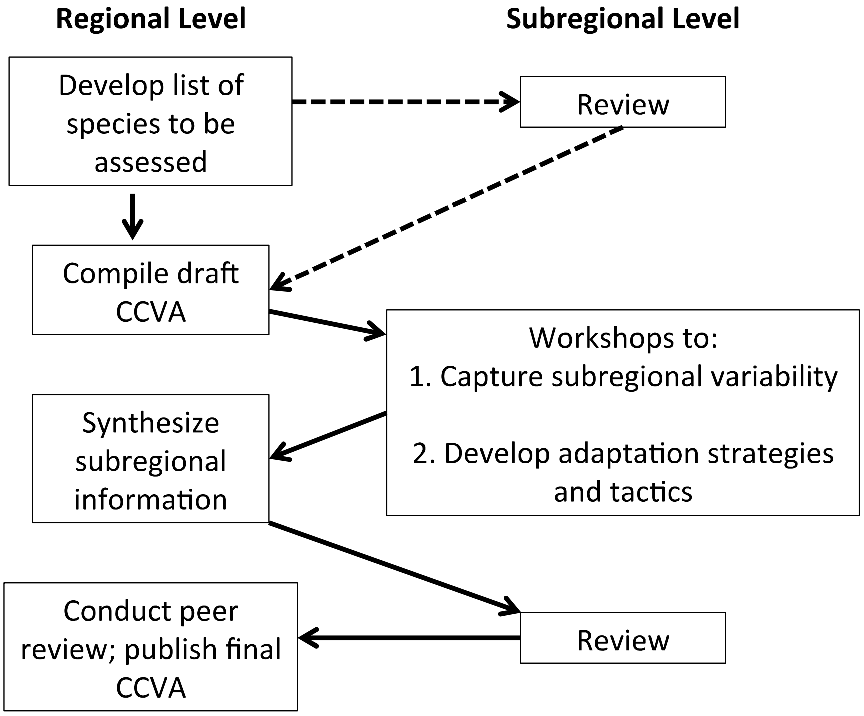
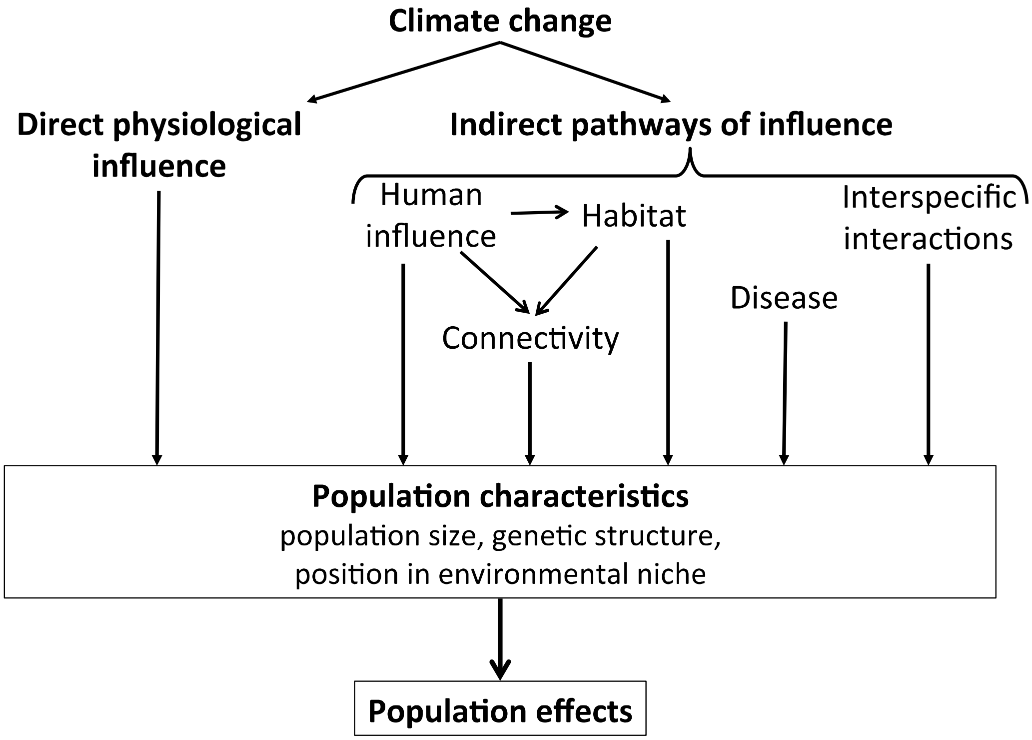


Figure 3.2. Conceptual diagram illustrating the process of conducting a regional climate change vulnerability assessment. Solid arrows indicate workflows that occurred during the Northern Rockies Adaptation Partnership. Dashed arrows indicate workflows we recommend for future assessments. Regional personnel conducted tasks on the left, and tasks on the right occurred in subregions. Regional personnel led workshops in which subregional personnel were participants.



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that were discussed in the Northern Rockies Adaptation Partnership. Pathways interact with population characteristics to produce effects on the population.

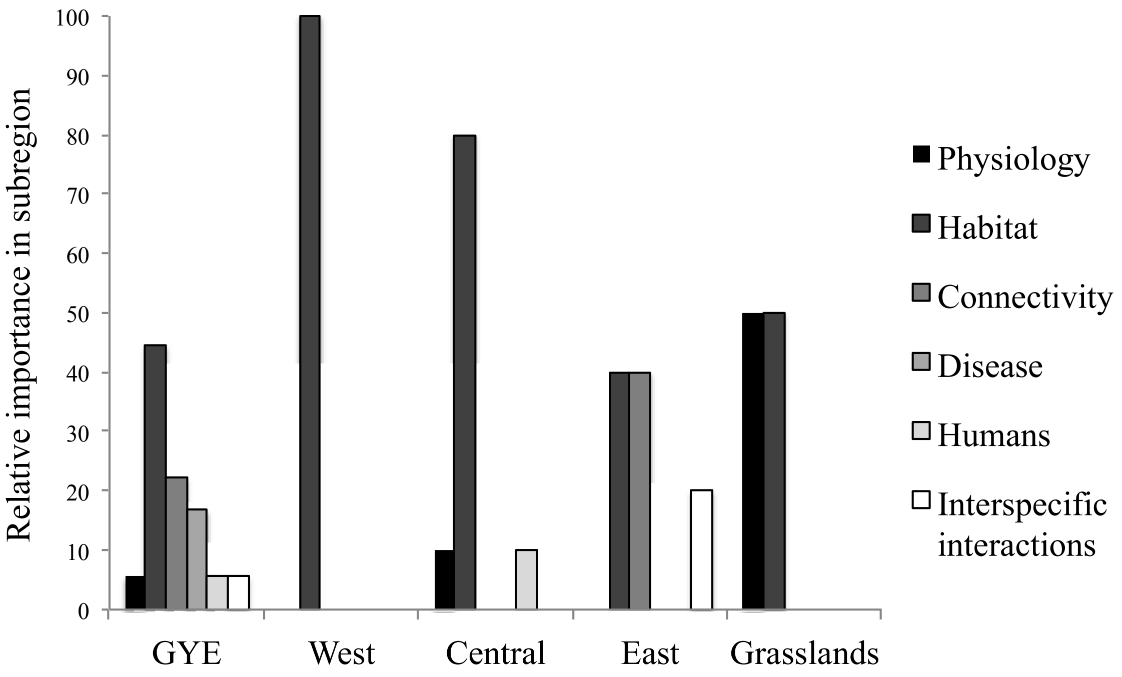

Figure 3.4. Relative importance of climate influence pathways across subregions of a regional climate change vulnerability assessment. Importance was calculated by dividing the number of times a pathway was discussed by the total number of times all pathways were discussed. See Figure 1 for subregional boundaries.

Chapter 4: Concluding Remarks

I found evidence for geographic variability in the vulnerability of natural resources to climate change. Both methods, statistical modeling and workshop participant questionnaires, helped identify variability.

Climate influences on whitebark pine mortality from mountain pine beetles varied across the range of whitebark pine. In all geographic regions, winter minimum temperature suitability was higher during the recent outbreaks than in years prior to the outbreaks. However, the magnitude of the effect of winter temperature varied across regions. The influence of September-November and April-August temperatures varied both in functional form and magnitude across regions. These differences led to differences in future weather suitability for whitebark pine mortality from mountain pine beetles across regions. Future weather suitability increased in the GYE and NR, but declined in the CR and Cascades. Geographic variability in vulnerability of wildlife populations to climate influences emerged from the subregional climate change vulnerability assessment workshops. My questionnaire, and associated workshop discussions, elucidated subregional differences in pathways of climate change influence and vulnerability. This information helped participants develop management tactics appropriate for each subregion. Another benefit of the questionnaire was the identification of common knowledge gaps across subregions.

Adaptive monitoring programs can provide a framework for developing and testing hypotheses about the effects of climate change. Understanding geographic variability in the vulnerability of natural resources to climate change can inform the design of adaptive management programs. Identifying and contrasting climate influences across geographic regions can suggest potential mechanisms of climate influence. Hypotheses can be developed to account for these mechanisms and management actions monitored to test those hypotheses. Based on the results of those tests decisions can be made to continue with management actions, or develop new actions or hypotheses.

I found geographic variability in the importance of summer precipitation in initiating the recent mountain pine beetle outbreaks in whitebark pine forests. This result suggests a theory that whitebark pine susceptibility to mountain pine beetle attack due to drought stress varies geographically. A hypothesis is that trees that are not drought stressed can allocate more resources to defense. Testable predictions are trees that lived were growing better than trees that died, and the pattern of live and dead trees varies geographically according to soil water holding capacity. If those predictions are upheld, management actions, such as protecting individual trees with chemical applications or thinning around healthy trees, can then focus on areas with the best growth conditions.

During subregional workshops to assess climate change vulnerability in the Northern Rockies Adaptation Partnership, habitat connectivity was identified as an important ecological function that varied geographically. Wolverine (*Gulo gulo*) is a species of concern in this region and ranges over vast areas. Habitat connectivity is therefore particularly important for wolverines. It was suggested that the island mountain ranges, unique to the Central subregion of the Northern Rockies, present unique connectivity challenges. This leads to the hypothesis that wolverine habitat is less well connected in the Central subregion than other subregions. A testable prediction is that wolverine genetic diversity is lower in this subregion than others. If true, this would indicate management strategies in the Central subregion should focus on identifying and enhancing corridors of connectivity between areas of wolverine habitat.

Humans are a foundation species: our influences extend from the global climate, to ecosystems, to populations, and to individuals. We have learned much about how our planetary system works and how our actions influence it at multiple scales. We have the responsibility to continue learning and implementing that knowledge so that future generations have ecologically, and socially, diverse and functional communities: so that our luck doesn’t run out on this planet.

Appendix 3.1.

Questionnaire for capturing subregional variability in vulnerability used during the Northern Rockies Adaptation Partnership workshops.

Resource / Ecosystem Component: ______________________________

1. Are there any sensitivities to climate not captured in the summary? If so, please describe.

2. Is new information or research needed, or does additional existing information need to be incorporated? If so, please describe.

3. Describe any geographic variation in sensitivity to climate, or adaptive capacity, that is not incorporated in the summary.

For example, do geographically distinct populations have different thermal tolerances?

4. Are there local features in your region that would alter the predicted climate trends?

For example, are there glaciers in the headwaters that will continue to influence stream temperatures in the near-term?

5. Are there places on the ground where the resource is more, or less, sensitive to climate change due to overlapping risks? Please think about non-climate stressors as well. If so, is mapping the combined sensitivities critical for developing adaptation strategies? Do these maps exist or need to be developed?

6. Are additional information or maps, either of sensitivity or exposure, critical for developing adaptation strategies?

Appendix 3.2.

Revised questionnaire for capturing subregional variability in wildlife vulnerability to climate change with example pathways.

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Species:

Subregion:

If species is neither present, nor expected to expand into this subregion, check here.

Rank each category of Sensitivity, Exposure, Adaptive Capacity, and Organizational Capacity as 1=low to 5=high, Unknown (U), or Not Applicable (NA).

Enter Information Needed, to either assess vulnerability or develop adaptation options, as Yes or No.

Adaptive Capacity is the species ability to tolerate, alleviate, or escape undesirable conditions.

Organizational Capacity is your organization's ability to influence conditions. E.g. does your organization have the legal, financial, etc. ability to manage for this species? Are there collaboratives in place that extend your management potential?

Sensitivity and *Exposure* examples are given for each pathway below.

Please provide specific comments where you can.

Physiological limits

Sensitivity: Does this species have upper or lower temperature thresholds? Direct water requirements (e.g. amphibians)?

Exposure: What is the expected change in temperature & precipitation?

	Sensitivity	Exposure	Adaptive Capacity	Organizational Capacity	Information Needed
Ranking					

Comments:

Indirect Climate Vulnerability Pathways

Habitat Association

Sensitivity: Habitat generalist or specialist?

Exposure: Projected changes in the distribution of all or some component of habitat.

	Sensitivity	Exposure	Adaptive Capacity	Organizational Capacity	Information Needed
Ranking					

Comments: