

Elevational shifts in thermal suitability for mountain pine beetle population growth in a changing climate

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Future forests are being shaped by changing climate and disturbances. Climate change is causing large-scale forest declines globally, in addition to distributional shifts of many tree species. Because environmental cues dictate insect seasonality and population success, climate change is also influencing tree-killing bark beetles. The mountain pine beetle, *Dendroctonus ponderosae*, is a major disturbance in *Pinus* forests of the western US. Using a mechanistic, phenology-based demographic model driven by downscaled daily temperature data, we describe recent and future spatial and temporal thermal suitability for mountain pine beetle population growth in a topographically complex region. Trends in model-predicted growth rates among Global Climate Models were similar and suggest that, relative to future trends, mountain pine beetle population growth within the past 60 years was most optimal at middle elevations and least optimal at the lowest and highest elevations. This trend aligns with observed mountain pine beetle-caused tree mortality that was greatest at middle elevations between 1997 and 2013, as estimated from Aerial Detection Surveys. However, thermal suitability for optimal phenological synchrony was predicted to shift in recent years, and by the end of the century, the best thermal habitats for mountain pine beetle will be at the lowest and highest elevations. Mechanistic demographic models are valuable tools for modelling future thermal regimes that may be both beneficial and maladaptive for mountain pine beetle population growth and subsequent tree mortality.

Keywords: bark beetle, climate change, *Dendroctonus ponderosae*, demographic model, phenology, vulnerability

Introduction

Future forests are being shaped by a changing climate. As precipitation and temperature patterns continue to change, the distribution of tree species (Hamann and Wang, 2006) and tree physiological responses (McDowell et al., 2011; Zeppel et al., 2011) will be significantly affected. Habitats with climatic conditions for growth are predicted to shift north for several species (Rehfeldt et al., 2006; McLane and Aitken, 2012), and water limitation, which can be amplified by warming temperatures, has already resulted in large-scale forest declines globally (Allen et al., 2010; Anderegg et al., 2015). In addition to the direct effects of climate, forests are shaped by disturbances that dictate composition and structure. Wildfire and bark beetle population outbreaks are two important disturbances in the western US that influence landscape-scale forest patterns, and are themselves influenced by climate.

Nearly 760 000 ha per year was affected by wildfire in the western US between 1980 and 2000, and these fires were significantly correlated with dry, warm conditions in the seasons leading up to and including the fire season (Littell et al., 2009).

Outbreaks of bark beetle species affected >5 million ha in the western US between 1997 and 2011 (Meddens et al., 2012) and were also driven by warm summer and winter temperatures (Preisler et al., 2012; Weed et al., 2015), in addition to water limitation that stressed host trees (Chapman et al., 2012; Gaylord et al., 2013; Hart et al., 2013). The significance of tree-killing disturbances in a changing climate is also reflected in their influence on forest carbon cycling. In the western US between 1997 and 2010, wildfire and bark beetles combined resulted in a carbon transfer similar to the amount in harvested trees, although the carbon in trees killed by bark beetles was estimated to exceed that of carbon in trees killed by wildfire (Hicke et al., 2013). Almost 65 per cent of all bark beetle-affected area was due to one species, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae) (foresthealth.fs.usda.gov).

Mountain pine beetle has a long evolutionary history with western North America *Pinus* trees (Sequeira et al., 2000; Mock et al., 2007; Brunelle et al., 2008; Bracewell et al., 2010). Females oviposit eggs in *Pinus* phloem, a tissue layer that is responsible for translocation of photosynthate, and larvae feed and develop through multiple lifestages to become adults. In most cases,

successful attack and larval feeding girdle the tree, resulting in tree death. Most *Pinus*, however, are not passive prey and instead have evolved a resinous defence mechanism that is triggered upon attack by native predators such as mountain pine beetle (Franceschi *et al.*, 2005). Overwhelming the induced defences of host trees, however, requires a large number of beetles attacking the tree in a relatively short amount of time (Raffa *et al.*, 2008). Two processes have evolved that increase the probability of ‘mass attack’ on a tree. The first is a sophisticated system whereby attacking adult beetles metabolize tree defensive compounds to produce and release pheromones that aggregate conspecifics to a tree (Raffa and Berryman, 1983). The second is temperature-driven physiological processes that synchronize development such that large numbers of beetles are ready to emerge from brood trees at a similar time and are therefore available to respond to aggregating pheromones produced by conspecifics (Logan and Bentz, 1999). Because emergence timing is mediated by temperature, temporal variability across elevations and years can occur (Bentz *et al.*, 2014; Chen *et al.*, 2015). Mountain pine beetle has also evolved associations with phytopathogenic fungi and bacteria that can play roles in mediating tree defence response, detoxifying tree terpenes and providing vital nutrients to developing larvae and adults (Raffa and Berryman, 1982; Bleiker and Six, 2007; Boone *et al.*, 2013). Clearly, the associations among mountain pine beetle, its microbial associates and host trees are complex and highly evolved, and temperature-dependent traits that promote seasonal synchrony are vital to these associations and subsequent population growth (Raffa *et al.*, 2008; Addison *et al.*, 2014).

Synchronized timing of adult emergence occurs as a result of temperature-dependent development thresholds and rates among life stages (Bentz *et al.*, 1991). These same rates and thresholds also dictate the amount of time required for development from an egg to adult emergence (i.e. a generation), which varies across habitats and among years (Reid, 1962; Bentz *et al.*, 2014). Emergence synchrony of a sufficient number of adults increases the probability of mass attacks on trees, and a shorter generation time allows the process to occur more often. At low-to-mid elevations, a generation is typically completed in 1 year (i.e. univoltine), and at higher elevations and in cold years, 2 years are required for a generation (i.e. semivoltine) (Reid, 1962; Amman, 1973). In recent years, warm growing season temperatures have allowed a mix of univoltine and semivoltine lifecycles at high elevations (Bentz *et al.*, 2014), and warming minimum temperatures have reduced the amount of direct beetle mortality due to cold temperatures (Weed *et al.*, 2015). At some locations, predicted increases in temperatures throughout the century could eventually result in development of more than a single generation in a year (i.e. bivoltine), a trait historically limited by relatively cool habitat temperatures (Bentz *et al.*, 2014) although proposed to have occurred at a 3020 m site in Colorado (Mitton and Ferrenberg, 2012; but see Bentz and Powell, 2014). In other locations, however, continued rapid warming could become maladaptive when environmental cues for phenological synchrony are no longer reliable (van Asch and Visser, 2007; Van Dyck *et al.*, 2015).

The influence of climate change on thermal suitability for mountain pine beetle was previously evaluated based on a phenology model driven by forecasted temperatures at a 45–50 km resolution (Hicke *et al.*, 2006; Bentz *et al.*, 2010; Safranyik *et al.*, 2010). Here, we use an enhanced demographic model (MPB-R), driven by downscaled daily temperatures from three Global

Climate Models (GCM) at a 4 km resolution, to predict mountain pine beetle population growth rates across a complex topography in the US northern Rocky Mountains. MPB-R is a previously developed model that connects temperature-dependent mountain pine beetle phenology with the concept of adult emergence synchrony and mass attack to predict annual population growth rates (Powell and Bentz, 2009, 2014). Low population growth rates are predicted when temperature regimes result in unsynchronized adult emergence or emergence outside the appropriate seasonal window. Conversely, temperatures that promote univoltine, well-timed and synchronized adult emergence result in high predicted growth rates. We acknowledge that MPB-R does not consider other factors influencing outbreak dynamics including forest composition and age (Fettig *et al.*, 2014), the effect of winter temperatures on mountain pine beetle survival (Régnière and Bentz, 2007), and the effect of summer temperatures on fungal associates (Addison *et al.*, 2014). Results described here only include the influence of year-round temperatures on mountain pine beetle generation time and the timing of adult emergence as it influences successfully mass attacked trees.

Methods

Study area

The study area in the Northern Rockies, US, is topographically complex and encompasses forested areas of northern and central Idaho, and western Montana and Wyoming (Figure 1). The area was further delineated by only including those locations containing pine species, the main hosts of mountain pine beetle. Pine presence in 1 km pixels throughout the study area was determined based on Blackard *et al.* (2008). Pine host species in the study area include ponderosa pine (*Pinus ponderosa* Laws.), western white pine (*P. monticola* Dougl.), limber pine (*P. flexilis* James), lodgepole pine (*P. contorta* Dougl.) and whitebark pine (*P. albicaulis* Engelm.), ranging in elevation from 300 to 3500 m (J. Shaw, personal communication). Based on the distribution of pine species along elevational gradients, the study area was divided into four elevation categories that reflect the thermal habitat for mountain pine beetle host tree species: Elevcat1 ≤ 1200 m, Elevcat2 = 1201–1800 m, Elevcat3 = 1801–2400 m, Elevcat4 ≥ 2400 m (Figure 2). Of the total area impacted by mountain pine beetle within the study area between 1997 and 2013, estimated from annual USDA Forest Service Aerial Detection Surveys (ADS) (foresthhealth.fs.usda.gov), the greatest percentage was within Elevcat3 (42.9 per cent) and least in Elevcat1 (1.4 per cent), followed by Elevcat4 (31.2 per cent) and Elevcat2 (24.5 per cent).

Mountain pine beetle demography model (MPB-R)

A cohort-based phenology model for mountain pine beetle that predicts life stage-specific developmental timing was previously developed using populations from central Idaho and northern Utah (Bentz *et al.*, 1991). Information on missing life stages in the original model was added by Logan and Bentz (1999), and additional experimental data were included in a new parameterization by Régnière *et al.* (2012). Hourly temperatures drive development through eight life stages (including oviposition) as a function of nonlinear rate curves with different lower and upper development thresholds and optima for each life stage, including log-normal variability in developmental times (Régnière *et al.*, 2012). Powell and Bentz (2009, 2014) built on this work and developed a demographic model (MPB-R) that connects the temperature-dependent mountain pine beetle phenology model with the concept of adult emergence synchrony and mass attacks on trees. The basic premise of MPB-R is that certain thermal regimes across the lifespan of a generation will result in a brood adult emergence distribution that produces ‘effective beetles’. Effective beetles are

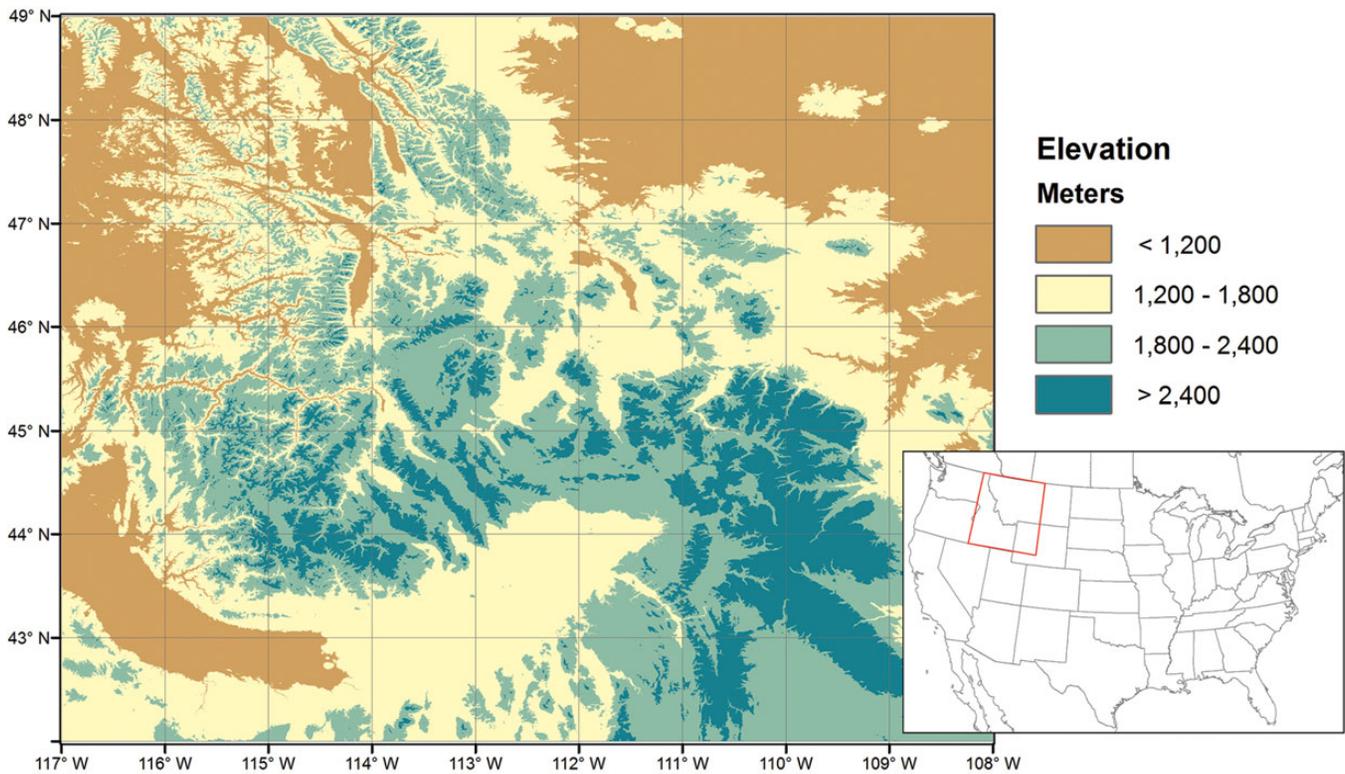


Figure 1 Elevation, partitioned by thermal habitat of *Pinus* species that are hosts to mountain pine beetle (see Figure 2), and location of the study area in the western US.

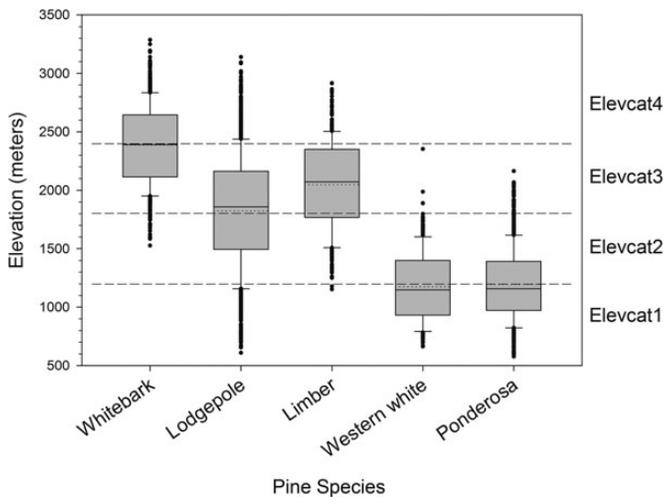


Figure 2 Pine species found within the study area as a function of elevation category: Elevcat1 \leq 1200 m, Elevcat2 = 1201–1800 m, Elevcat3 = 1801–2400 m and Elevcat4 \geq 2400 m; whitebark (*P. albicaulis*), lodgepole (*P. contorta*), limber (*P. flexilis*), western white (*P. monticola*) and ponderosa (*P. ponderosa*). Data from USDA Forest Service, Forest Inventory and Analyses (J. Shaw, personal communication). Boxplots display the median (solid line), mean (dotted line), 10th and 90th percentiles and all outliers.

those adults in an emergence distribution from a single tree that exceed a daily threshold to successfully attack non-stressed, vigorous host trees. Further, only adults that are predicted to emerge between 30 June and 1 September are considered due to seasonality constraints. Females

predicted to emerge outside of this seasonal window are assumed to lay eggs, which will result in cold-vulnerable life stages being present during winter, thereby leading to brood mortality (Reid and Gates, 1970).

As described in Powell and Bentz (2009), unknown parameters in MPB-R were determined from nonlinear regression between observed mountain pine beetle-caused tree mortality within the Sawtooth National Recreation Area (SNRA), Idaho, US estimated from ADS between 1994 and 2005, and model predictions using observed hourly air temperatures within mountain pine beetle infested stands. The total number of beetles laying eggs in an average tree, mean number of eggs laid per female, a multiplicative parameter adjusting developmental variance expressed in the field (likely to be higher than that expressed in controlled laboratory experiments), and the total emerging brood adults were parameters determined from the nonlinear regression (Powell and Bentz, 2009). Although the number of adults necessary to overwhelm a tree's defences will vary with tree size and physiological status, the model was parameterized using a constant attack threshold of 250 beetles per tree per day, estimated for a 20-cm DBH tree based on data in Raffa and Berryman (1983). The predicted population growth rate for a year is the product of the number of effective beetles per tree and a fitted parameter converting effective beetles to newly infested trees (Powell and Bentz, 2009). The model was initially fit using 2 metrics from ADS, ha and number of trees impacted by mountain pine beetle. Because variability was 50 per cent lower when ha impacted was used, model parameterization continued with this metric. MPB-R successfully described 92 per cent of observed variance in ADS estimated growth rates in the SNRA (Powell and Bentz, 2009) and over 90 per cent of observed variance in an evaluation study in mixed species stands of northern Washington, US (Powell and Bentz, 2014).

Previous research has shown that mountain pine beetle has locally adapted to varying environments across its range in the western US, and populations in the southwestern US have a different developmental response to temperature than populations in the northwestern US (Bentz et al., 2001,

2011; Bracewell *et al.*, 2013). The phenology parameters used in MPB-R are based on populations from Idaho and northern Utah, within the Northern Rockies study area region (Règnière *et al.*, 2012). Further, we do not expect differences in developmental timing due to host tree species that are growing within the same thermal regime (Bentz *et al.*, 2014, 2015). MPB-R is therefore valid for use in the mixed pine landscapes of our Northern Rockies study area.

MPB-R evaluation

To evaluate MPB-R predictions in the Northern Rockies study area, daily maximum and minimum temperature data were acquired from the Snowpack Telemetry network, Global Historical Climatology Network, and Remote Automatic Weather Stations network. All temperatures used were TopoWx-processed (Oyler *et al.*, 2014). The TopoWx process addresses limitations of existing temperature stations by applying comprehensive quality assurance measures as well as homogenization and infilling procedures that generate serially complete records for a given station (Oyler *et al.*, 2014). We chose weather stations within the study area that were also near mountain pine beetle-caused tree mortality between 1999 and 2013, as identified from ADS. Using flight path information from ADS, a buffer of at least 4 km surrounding a station must have been flown in consecutive years between 1999 and 2013 (Supplementary data, Figure S1). A 4-km buffer was chosen because that is the pixel size of the downscaled temperature data used for predicting future population growth (see below). Finally, we only used stations that met these criteria and also had <10 per cent of the temperatures between 1999 and 2013 infilled during the TopoWx processing. These restrictions reduced the number of weather stations that could be used in the model evaluation process but provide a conservative evaluation of MPB-R. Twelve stations across the study area fit our criteria (Supplementary data, Figure S1).

MPB-R is driven by hourly temperatures. To reduce the time required for each model run, hourly temperatures were derived from daily extrema using sinusoidal interpolation; rate curve integration was performed using Simpson's rule with five steps per day (quarter-day subintervals) (see Duncan, 2015). Predicted annual mountain pine beetle population growth between 1999 and 2013 was determined by running MPB-R using TopoWx-processed daily maximum and minimum temperatures from the selected stations within the study area (Supplementary data, Figure S1). We also used separate MPB-R runs to evaluate the potential for successful completion of two generations within a single year (i.e. bivoltine). To test for potential bivoltinism, for each starting day of attack between 31 May and 30 June in each year, MPB-R was run over sufficient time to complete two generations. If the time required for two generations was greater than 375 days, the required thermal energy for bivoltinism was considered unlikely. Developmental milestones for cold sensitive life stages (eggs and pupae) were also tracked, and minimum temperatures between milestones were checked for temperatures below the lethal threshold of -18°C (Reid and Gates, 1970; Amman and Cole, 1983). If temperatures were either too cold for the vulnerable lifestages or the required time to complete two generations was greater than 375 days, bivoltinism was considered thermally impossible.

We were interested in comparing MPB-R predictions of mountain pine beetle population growth trends with estimates of trends in beetle-caused tree mortality observed within the study area between 1999 and 2013. We estimated mountain pine beetle-caused tree mortality trends surrounding the 12 selected weather stations using annual estimates of beetle-caused tree mortality from ADS. Host tree mortality, a proxy for mountain pine beetle abundance, is detected annually by observers in fixed-wing aircrafts as the area and number of host trees with red needles. Pine needles turn red, on average, the summer following *D. ponderosae* attack. Therefore, impact observed in year t reflects trees that were killed during the previous growing season, in year $t - 1$. Although there is inherent variability in annual estimates of mountain pine beetle-caused tree mortality from aerially detected data, these data have been shown to be valuable in assessing factors that influence mountain pine beetle-caused tree mortality in the US and Canada (Aukema *et al.*,

2008; Chapman *et al.*, 2012; Preisler *et al.*, 2012; Chen *et al.*, 2015) and to analyse trends in mountain pine beetle population growth rates (Weed *et al.*, 2015). We calculated population growth for a year as the ratio of impacted area between years $t + 1$ and t for 4 km circular buffers around each weather station (Supplementary data, Figure S1). To evaluate whether the trend in predicted population growth (i.e. MPB-R) was consistent with the trend in estimated population growth (i.e. ADS), the cumulative distributions of predicted growth rates and observed beetle-caused tree mortality for each weather station were compared using linear regression analyses (SAS v 9.3).

Predicting future mountain pine beetle population growth rates using MPB-R

Daily maximum and minimum temperatures for projecting mountain pine beetle population growth in future climates were derived using the Multi-variate Adaptive Constructed Analogs (MACA) method (Abatzoglou and Brown, 2012) (www.climate.northwestknowledge.net/MACA). The MACA method is a statistical method for downscaling GCMs from a coarse resolution to a higher spatial resolution (i.e. 4 km). The GCMs used were coordinated by the Coupled Model Intercomparison Project Phase 5 (CMIP5). GCM outputs from historical experiments provided data for the years 1950–2005, and output for 2006 through 2100 were forced by the Representative Concentration Pathway 4.5 (RCP 4.5) and 8.5 (RCP 8.5) experiments. RCP 4.5 represents moderate action to mitigate climate change, and RCP 8.5 a future with no climate mitigation and high emissions. Although several GCM outputs are available, we used output from three GCMs that have been favourably ranked for ecological analyses in the western US (Rupp *et al.*, 2013). We acquired temperatures from the Canadian Earth System Model (CanESM2), the Community Climate System Model (CCSM4) and Centre National de Recherches Météorologiques (CNRM-CM5) using both the RCP 4.5 and RCP 8.5 emission scenarios. Daily temperatures predicted for 22 282 gridded MACA cells across the study area at elevations ranging from 291 to 3896 m with pine present, were used to drive MPB-R. As described above for MPB-R evaluation, hourly temperatures were derived from daily extrema using sinusoidal interpolation and rate curves were integrated using Simpson's rule with five steps per days (see Duncan, 2015).

Annual univoltine population growth for each of the 22 282 MACA cells was predicted by running MPB-R using daily temperatures for each year from 1950 to 2099. Because both temperature and host species vary by elevation, we report model results by elevation zone where host species are found (Figure 2). The mean and standard deviation of annual population growth for all stations within an elevation zone were calculated for each year. A locally weighted linear regression algorithm (lowess, The MathWorks, Inc.) was applied to the mean values from 1950 to 2100 to generate a trend line for each GCM by elevation category. We also checked if daily maximum and minimum temperatures for each year and each cell could produce bivoltine mountain pine beetle generations (see above). Our definition of strict bivoltinism requires median emergence of the second generation within 375 days of attack, and temperatures above -18°C when eggs and pupae are present. For each year, the mean and standard deviation of the number of sites with successful bivoltine potential was calculated. Similar to univoltine population growth values, a lowess smoothing algorithm was applied to the mean values from 1950 to 2099 to generate a trend line of bivoltine potential for each elevation category.

Results

Temperature trends

Downscaled climate data from the RCP 4.5 and RCP 8.5 emission scenarios showed a trend for increasing mean temperatures after ~ 1990 at all elevations. The temperature increase in future years based on both emission scenarios was greatest for the CanESM2 GCM (Figure 3). Across all GCMs, there was an approximate 3° – 4°C

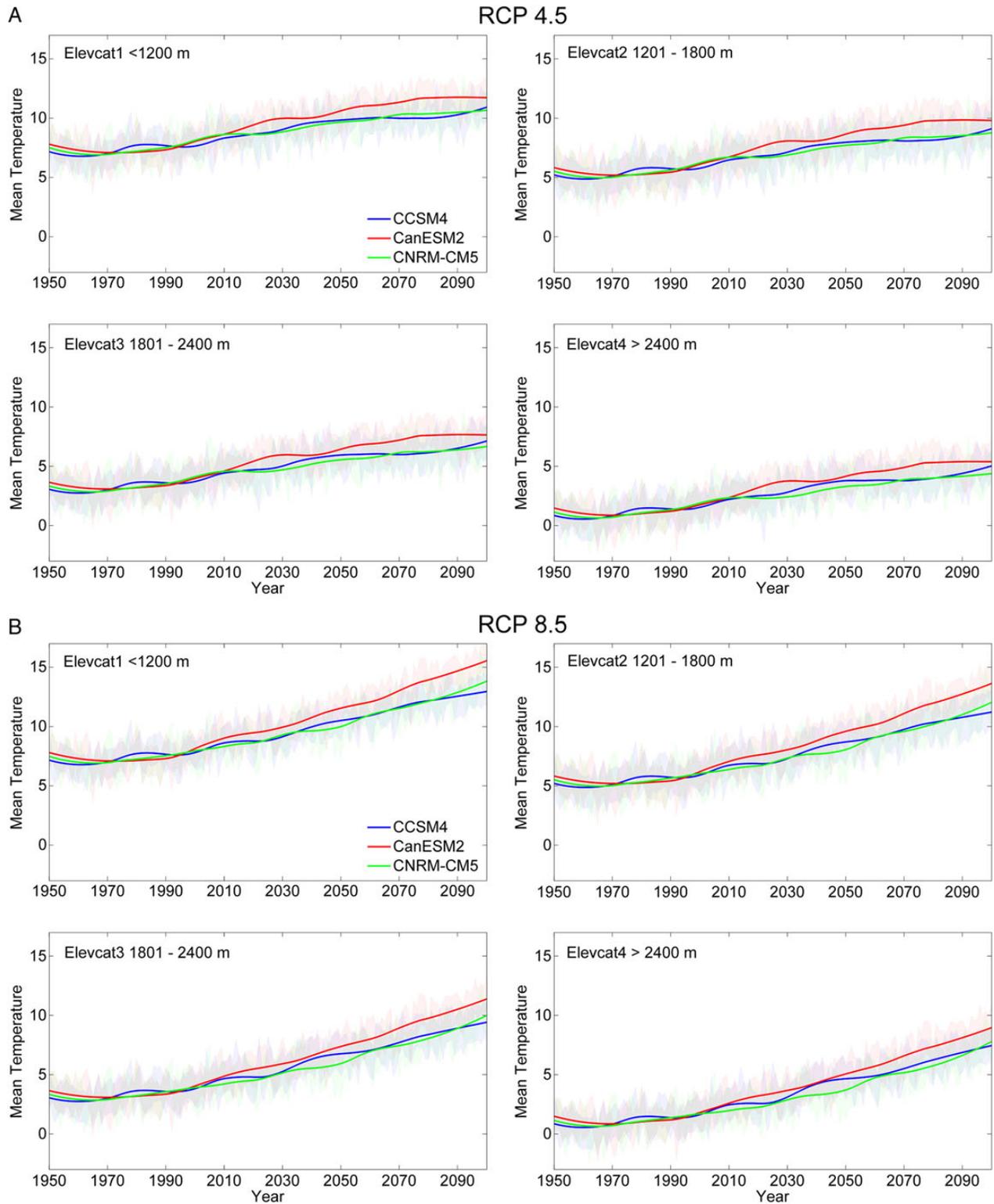


Figure 3 Mean annual predicted temperatures for each year between 1950 and 2100 within four elevation categories based on three GCMs (CCSM4, CanESM2 and CNRM-CM5) and a (A) moderate, RCP 4.5 and (B) no-action, RCP 8.5, emission scenario. Shown is the mean annual trend in temperature based on a lowest smoothing algorithm (lines) and standard deviation (shading) among cells within an elevation category. Mean annual predictions were calculated using 4472 cells containing *Pinus* in Elevcat1, 7194 cells in Elevcat2, 7105 cells in Elevcat3 and 3511 cells in Elevcat4.

increase in mean temperatures based on the RCP 4.5 scenario and a 6°–7°C increase using the RCP 8.5 scenario, depending on the GCM and elevation. Similarly, minimum and maximum annual temperatures also showed an increasing trend after 1990 (Supplementary data, Figures S3 and S4). A similar increasing trend between 1990 and 2100 was predicted for the four elevation categories, although across different temperature ranges. For example, mean annual temperatures at the highest elevations (Elevcat4) were predicted to increase from ~1° to 5°C based on the RCP 4.5 scenario and from 1° to 8°C based on the RCP 8.5 scenario. At the lowest elevations (Elevcat1), the predicted increase in mean temperature based on RCP 4.5 was from 8° in 1990 to 12°C in 2100, and 8° to 14–16°C based on the RCP 8.5 scenario. Based on both the RCP 4.5 and RCP 8.5 scenarios, by 2040 mean temperatures within an elevation category will have warmed such that mean temperatures are similar to temperatures in 2000 (during the recent outbreak) at the next lower elevation category. For example, by 2040 mean annual temperatures at Elevcat4 cells were predicted to be similar to mean annual temperatures in 2000 at Elevcat3 cells.

MPB-R evaluation

To evaluate MPB-R predictions within the study area, we ran the model for each year between 1999 and 2013 using daily maximum and minimum temperatures from selected weather stations (Supplementary data, Figure S1). Predicted cumulative population growth was compared with estimated observed cumulative population growth as determined from ADS-detected hectares impacted by mountain pine beetle. Although the magnitude of population growth within a 4-km buffer surrounding each weather station varied among stations and was often greater based on ADS-observed area values than model-predicted growth, the model-predicted increasing trends in impact through time were significant in explaining the observed increasing trends for all weather stations

Table 1 Linear regression statistics testing the relationship between observed mountain pine beetle-caused tree mortality, estimated from ADS and mountain pine beetle univoltine population growth predictions from MPB-R using temperature data from 12 weather stations within the study area (Supplementary data, Figure S1)

Name	Elevation (m)	Adj. R^2	F	Pr > F
Kellogg	725	0.75	36.99	<0.0001
Codon	1124	0.92	17.81	<0.0001
Nukols	1229	0	Not est.	Not est.
Humboldt Gulch	1296	0.91	119.94	<0.0001
Lindberg Lake	1325	0.73	33.44	0.0001
Mica	1373	0.71	30.72	0.0002
Kraft Creek	1453	0.69	27.38	0.0003
Lookout	1561	0.93	157.52	<0.0001
Sunset	1699	0.83	59.61	<0.0001
Crab Creek	2092	0.58	17.81	0.0014
White Elephant	2338	0.95	229.35	<0.0001
Evening Star	2755	0.89	95.96	<0.0001

Daily maximum and minimum temperatures from 1999 to 2013 from each station were used to run MPB-R after TopoWx processing (Oyler *et al.*, 2014). Zero univoltine population growth was predicted at the Nukols site.

except Nukols (Table 1, Supplementary data, Figure S2). Nukols and Kellogg were at the lowest elevations and predicted to have no or very low univoltine population growth in the 4-km buffer surrounding each temperature station. Although in some years an extra generation was predicted to be completed using temperature data from both stations, predicted median emergence of the second generation was >375 days past the initial attack date of the first generation, and therefore not strictly bivoltine or univoltine. An extra non-bivoltine generation every few years could have influenced observed population growth in these low elevation areas. Strict bivoltinism, however, was not predicted for any year between 1999 and 2013 at any of the evaluation sites (not shown). Moreover, it was not surprising that the relative magnitude of observed growth based on ADS data was greater than growth predicted using MPB-R. Predicted population growth using MPB-R was only influenced by temperature and mountain pine beetle-killed trees within a 4-km buffer surrounding the temperature site. In reality, beetles from outside the buffer could disperse into the buffer resulting in dramatic increases in population size. This dispersal of beetles and dramatic changes in population size are reflected in the ADS data, but not MPB-R predictions. Most importantly, however, MPB-R predicted the increasing trends in univoltine population growth between 1999 and 2013 within 4-km buffers surrounding each weather station.

Predicted future mountain pine beetle population growth rates

Predicted univoltine population growth through time varied by elevation and slightly different trends were predicted for each of the GCMs and emission scenarios (Figure 4). Based on the RCP 4.5 emission scenario, univoltine growth predicted using CanESM2 temperatures steadily declined from 1950 through 2010 with zero population growth predicted by 2100 at Elevcat1 cells ($N = 4472$) (Figure 4A). A similar trend was seen using the RCP 4.5 CCSM4 and CNRM-CM5 GCMs, although a slight increase in growth was predicted between 1950 and 1970. For Elevcat2 cells, growth remained stable from 1950 through 1990 and then declined continually until 2100 ($N = 7194$). At Elevcat3 cells, growth remained relatively high through 2030 and then declined ($N = 7105$) (Figure 4). CanESM2 GCM predicted warmer temperatures and hence a more rapid drop in growth was seen using temperatures based on this GCM. At the highest elevations (Elevcat4), univoltine population growth was relatively low initially, with a gradual increase beginning in the late 1980s ($N = 3511$). Population growth was predicted to remain high through the century for the CCSM4 and CNRM-CM5 GCMs. Again, warmer temperatures predicted by CanESM2 RCP 4.5 emission scenario resulted in a reduction in univoltine growth earlier in the century than the other 2 GCMS (Figures 4 and 5A).

The declining trend in predicted univoltine population growth using the RCP 8.5 scenario was similar to predictions from the RCP 4.5 scenario at Elevcat1 and Elevcat2 cells (Figure 4). However, for Elevcat3 and Elevcat4 cells, predictions using RCP 8.5 scenario temperatures resulted in a different trend in growth through time compared with results when RCP 4.5 temperatures were used. At Elevcat3 cells, predicted growth remained relatively high until 2030 and then dropped dramatically, eventually reaching 0 before the end of the century. At Elevcat4 cells, growth increased until 2040 and then continually declined through 2100 (Figures 4 and 5A).

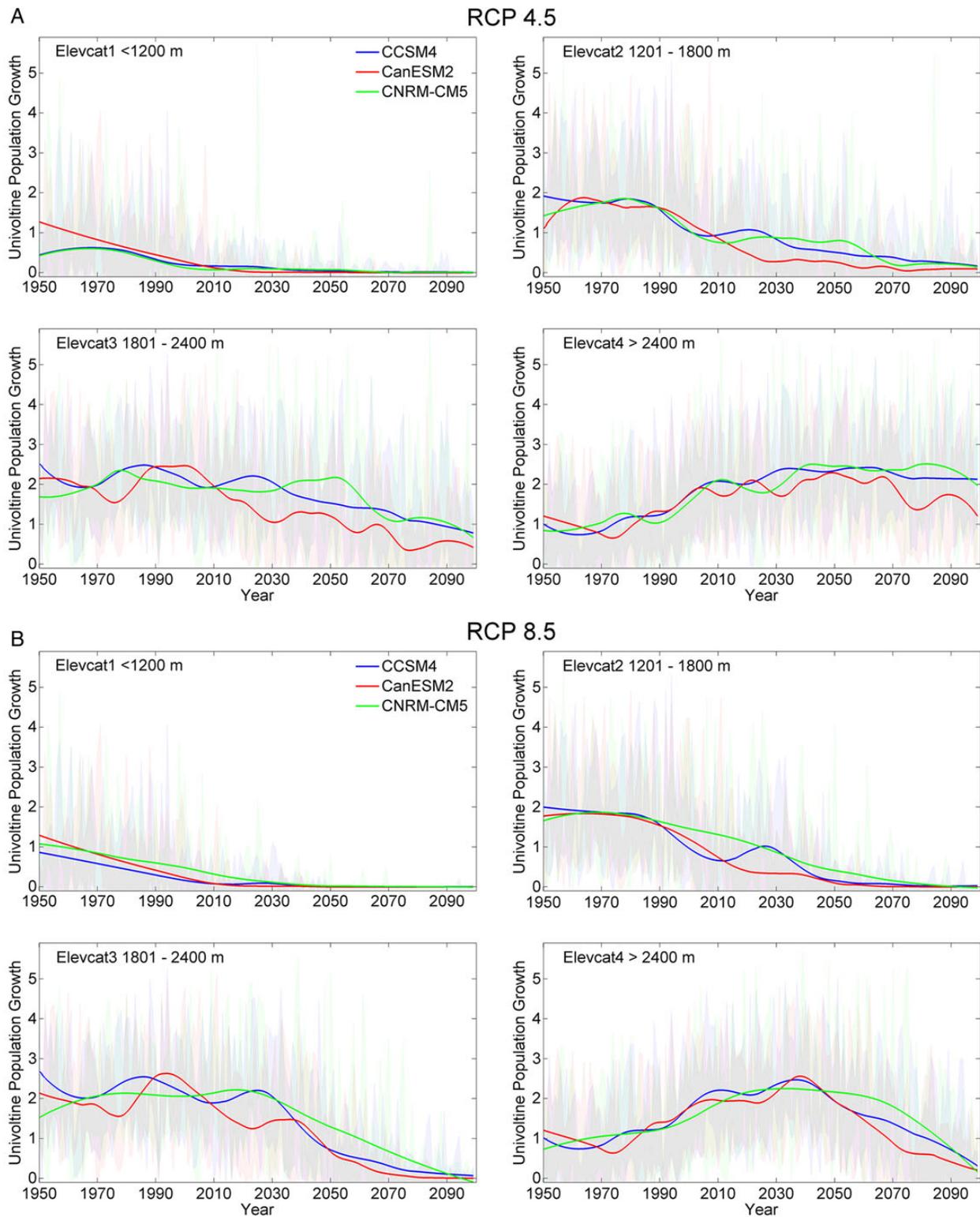


Figure 4 Predicted univoltine mountain pine beetle population growth rates using MPB-R and projected daily downscaled temperatures from three GCMs (CCSM4, CanESM2, CNRM-CM5) and a (A) moderate, RCP 4.5, and (B) no-action, RCP 8.5, emission scenario. Shown is the trend in mean annual growth based on a lowest smoothing algorithm (lines) and the standard deviation among MBP-R predictions within an elevation category (shading). Annual predictions from 1950 to 2100 were calculated for 4472 cells containing *Pinus* in Elevcat1, 7194 cells in Elevcat2, 7105 cells in Elevcat3 and 3511 cells in Elevcat4. Variability in model predictions among cells within an elevation zone was large and reflects the complex topography and variability in temperature, in addition to model sensitivity to temperature.

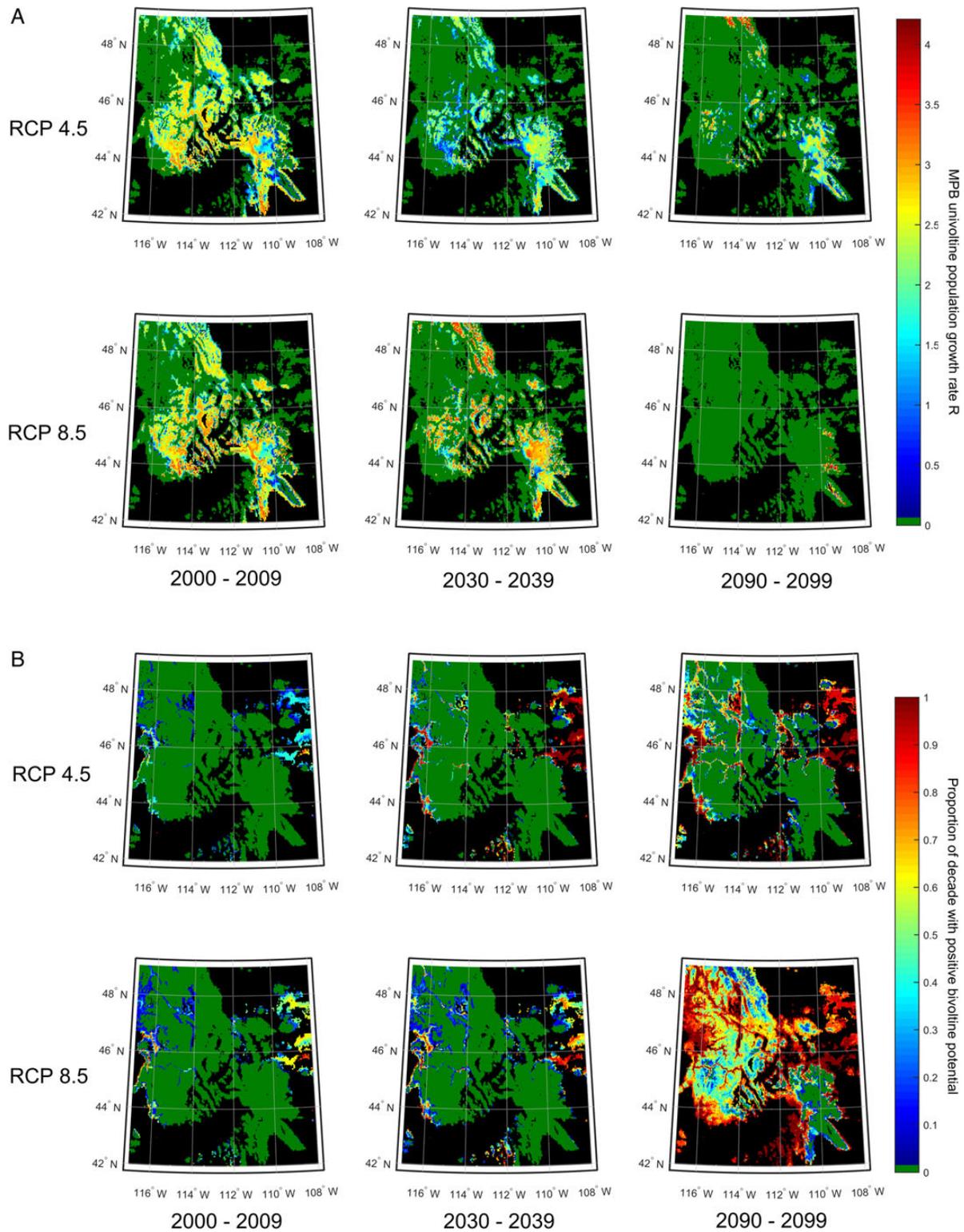


Figure 5 Maps of predicted mean decadal univoltine population growth (A), and the proportion of a decade with bivoltine population potential (B) across the study area where pines occur. Predictions are based on the CanESM2 GCM for the RCP 4.5 and RCP 8.5 emission scenarios.

Using temperatures from the RCP 4.5 scenario and CanESM2 GCM, the proportion of Elevcat1 cells predicted to have two generations in a single year between May/June_{yr} and May/June_{yr+1} was

very low in 1950, remained low until ~2000 and then increased continually until 2090 when 70 per cent of cells were predicted to be bivoltine (Figures 5B and 6). A similar trend was seen using

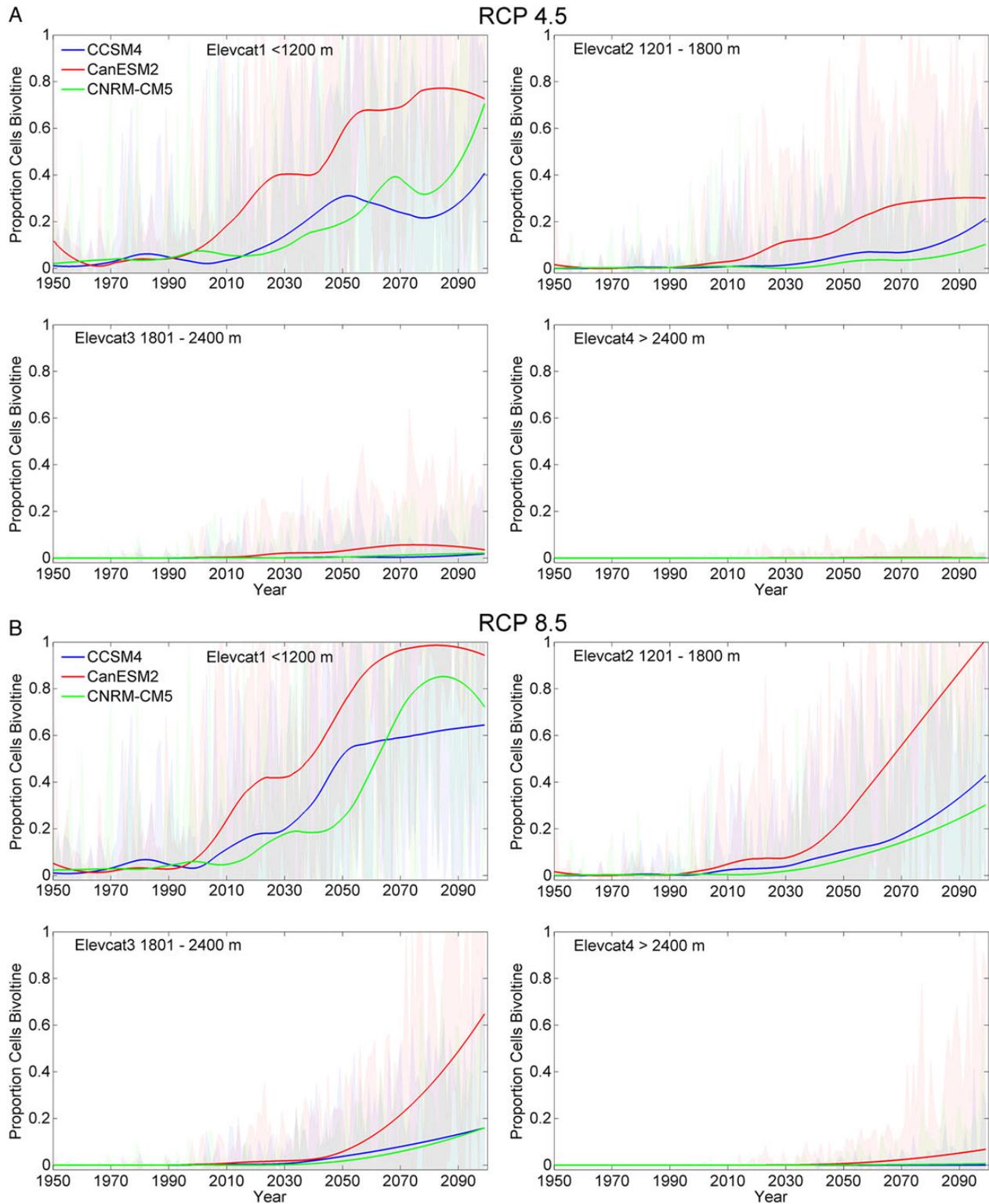


Figure 6 Mean annual proportion of cells within an elevation category where bivoltine mountain pine beetle population growth is predicted using MPB-R and projected daily downscaled temperatures from three GCMs (CCSM4, CanESM2, CNRM-CM5) and a (A) moderate, RCP 4.5, and (B) no-action, RCP 8.5, emission scenario. Shown is the trend in mean annual proportion based on a loess smoothing algorithm (lines) and the standard deviation among MBP-R predictions within an elevation category (shading). Annual predictions from 1950 to 2100 were calculated for 4472 cells containing *Pinus* in Elevcat1, 7194 cells in Elevcat2, 7105 cells in Elevcat3 and 3511 cells in Elevcat4. Variability in model predictions among cells within an elevation zone was large and reflects the complex topography and variability in temperature, in addition to model sensitivity to temperature.

the CCSM4 and CNRM-CM5 GCMs, although the increase in population growth started slightly later and the CCSM4 predictions were lower than those from CanESM2 and CNRM-CM5. At Elevcat2, using CanESM2 and RCP 4.5 scenario temperatures, the mean predicted proportion of cells with bivoltinism was 0 until ~2010 and then increased slowly through the rest of the century peaking at values between 10 per cent and 30 per cent depending on the GCM (Figure 6). Using RCP 4.5 temperatures, predicted mean bivoltinism among Elevcat3 cells was zero throughout the century for the CNRM-CM5 and CCSM4 GCMs and slightly above zero for the CanESM2 model. At the highest elevations (Elevcat4), mean proportion of cells with bivoltinism was zero throughout the 150 years. Temperatures from the RCP 8.5 scenario resulted in similar trends in predictions of proportion bivoltinism relative to RCP 4.5 temperatures, although the proportions by 2100 were greater (Figures 5B and 6).

Discussion

Downscaled climate projections suggest an increasing trend in annual mean, minimum and maximum temperatures from 1990 through 2100 across the study area. An increase over the next century in the predicted highest maximum and minimum temperatures is well documented across the western US (Abatzoglou and Barbero, 2014) and within the study area (Pederson *et al.*, 2010). Our goal was to use a previously developed demographic model of mountain pine beetle population growth, MPB-R, to evaluate how the predicted increasing temperatures would influence mountain pine beetle populations and outbreak potential. We first evaluated how well MPB-R predicted trends in population growth within the study area using observed temperatures from established weather stations to drive the model and mountain pine beetle impact within a 4 km buffer surrounding each station, estimated from ADS. Although the magnitude of impact in the area surrounding each weather station differed among stations, we found that MPB-R was significant in predicting the increasing trend in beetle-caused tree mortality observed during a recent outbreak between 1999 and 2013.

Forecasted downscaled temperatures suggest that across our four elevation categories, a similar increasing trend in mean temperatures will occur between 2010 and 2100. MPB-R predictions based on these downscaled climate data, however, suggest that mountain pine beetle population response to the increasing temperatures will differ across elevations within the study area. At the lowest elevations, where univoltine population growth rates and estimated beetle-caused tree mortality were also the lowest in recent years, forecasted mean annual temperatures approach 10°C by 2040. MPB-R predictions suggest a transition to bivoltinism at >50 per cent of low elevations sites in the next 25 years. Bivoltinism, defined here as two generations in <375 days when annual simulations are initiated between 1 May and 30 June, was considered to be thermally unlikely within the last century across the range of mountain pine beetle due to evolved developmental thresholds that restrict development during winter (Bentz and Powell, 2014; but see Mitton and Ferrenburg, 2012). At the highest elevations, bivoltine lifecycles were only predicted after 2070 when the warmest, no-action RCP8.5 scenario was used. The rarity of quantified bivoltinism within the past century in mountain pine beetle habitats suggest that as a potential no-analog or novel

outcome of changing temperatures the ramifications to mountain pine beetle population dynamics and pine forest ecosystems may also be novel. Pine species that grow at the lowest elevations, currently ponderosa and western white pine in our study area, are predicted to be most affected by future bivoltine mountain pine beetle populations.

At middle elevations, which were predicted to have the greatest univoltine mountain pine beetle population growth rates prior to 2000, temperatures were predicted to become maladaptive with associated declining univoltine population growth rates throughout the century. Further, as warming temperatures result in declining population growth at middle elevations, univoltine population growth rates were predicted to increase at the highest elevations. Refugia from persistent mountain pine beetle outbreaks in the last century were at the highest elevations where the coldest year-round temperatures occurred (MacFarlane *et al.*, 2013). MPB-R predicts an elevational shift in optimal thermal regimes for mountain pine beetle univoltine population growth rates from middle-to-high elevations as climate warms in coming decades, a result also found by Hicke *et al.* (2006). In fact, an increase in elevation of optimal thermal habitat for mountain pine beetle was evident at the highest elevations after 1990, coinciding with 31.2 per cent of all mountain pine beetle-caused tree mortality between 1997 and 2013 in this elevational zone. However, when forecasted temperatures from the warmest, no-action RCP-85 scenario were used to run MPB-R, even the highest elevations become too warm for strict univoltinism.

It is well documented that warming temperatures associated with climate change can result in both beneficial and maladaptive phenological shifts in insects (Bale *et al.*, 2002; Chown *et al.*, 2010; Valtonen *et al.*, 2014). In the case of the mountain pine beetle, the relative advantage of the climate change-induced phenological shift differs elevationally. MPB-R predicts population growth rate as a function of temperature effects on phenology that dictate adult emergence synchrony and generation time. Therefore, predictions of declining univoltine population growth rates at middle elevations in a changing climate suggest developmental traps (*sensu* Van Dyck *et al.*, 2015) that occur as a result of inaccurate or changed cues during development in new thermal regimes. For example, species that are typically cued by cooler fall temperatures to diapause but instead continue to develop in a warming climate could end up in a maladaptive developmental pathway with increased mortality and reduced population growth (Dworschak *et al.*, 2014; Van Dyck *et al.*, 2015). In mountain pine beetle, evolved developmental thresholds and rates that promote univoltine generations and synchronized adult emergence are predicted to become no longer viable in middle elevation thermal regimes. Without adaptation in rates and thresholds to the warming temperatures, the highest population growth will shift to the highest elevations where thermal regimes that promote synchronized and univoltine generations are predicted. Although it is clear that mountain pine beetle has locally adapted to climatic conditions across its broad range (Bentz *et al.*, 2011; Bracewell *et al.*, 2013), the capacity for adaptation to a rapidly changing climate remains unclear.

Mountain pine beetle host trees will also be influenced by a changing climate. Species distribution modelling predicts that the current climatic niche for trees will be disrupted in a changing climate, shifting distributions poleward and up in elevation (McLane and Aitken, 2012). In our study area, western white and ponderosa pine currently grow at the lowest elevations, and

lodgepole, limber and whitebark pine grow at middle to high elevations. Bioclimate envelope studies suggest that by 2100 whitebark pine is likely to experience the largest loss of suitable area (71–99 per cent) and the least area of newly suitable habitat (Chang *et al.*, 2014; Hansen and Phillips, 2015), although simulation modelling suggests that at least some whitebark pine will remain in upper subalpine landscapes (Keane *et al.*, In Press). Predicted trends for lodgepole pine are similar although less extreme. Ponderosa pine, however, was found to be less vulnerable to a loss of climate suitability due to availability of newly suitable habitat at slightly higher elevations (Hansen and Phillips, 2015). Throughout the century, the lowest and highest elevations become most thermally suitable for mountain pine beetle population growth. Pine hosts at the lowest elevations may be unavailable, however, if ponderosa and western white pines migrate up in elevation. Such a migration could be beneficial as they would move from elevations where bivoltinism is predicted to be the greatest into an elevational zone of relatively low predicted mountain pine beetle population growth. Conversely, although whitebark pine habitat suitability is predicted to decrease, upward migration of lodgepole and limber pine would retain suitable hosts at the highest elevations where thermal suitability for mountain pine beetle univoltine population growth is predicted to be most optimal.

National Forests in the US are required to take steps to incorporate climate change and potential adaptation into management and planning of future forests (Peterson *et al.*, 2011; adaptation-partners.org). To adequately predict future forest vulnerability to changing climate, integration of mechanistic demographic models that predict climate change influences on forest insects, such as MPB-R, with models of potential range shifts for associated tree species is needed.

Conclusions

The recent availability of daily downscaled temperature data at 4 km resolution allowed us to run a mechanistic model describing mountain pine beetle population growth to predict thermal suitability for population outbreaks in a future climate across a complex topography. A major benefit of physiological-based mechanistic models, relative to statistical models, is that predictions of biological behaviours that have not been quantified with field data are possible. For example, reduced mountain pine beetle univoltine population growth rates with warming temperatures were predicted at middle elevations, a result of disrupted phenological cues (*sensu* developmental traps), with a shift in optimal univoltine thermal regimes to the highest elevations. Moreover, bivoltinism, a trait not commonly observed for mountain pine beetle (Bentz and Powell, 2014) and therefore difficult to statistically forecast or quantify from field data, was predicted to occur at more than 50 per cent of sites at the lowest elevations where temperatures throughout the century warmed sufficiently. The capacity to estimate both beneficial and maladaptive future thermal regimes for mountain pine beetle is key to the development of management plans for future pine forests. Because our model only estimates thermal suitability for beetle population growth, one of many factors important to mountain pine beetle outbreak potential, integration with other factors including climate effects on host tree distribution and stand-level processes is needed.

We acknowledge uncertainty in downscaled GCM-based temperature predictions in addition to uncertainty in our model (MPB-R) predictions. One of the greatest uncertainties is our lack of understanding of potential adaptations in mountain pine beetle temperature-dependent traits, the traits driving our mechanistic model. Phenotypic plasticity in development traits, which we include in our model as variability among individuals, has allowed for recent population success in variable climates (Bentz *et al.*, 2011). Adaptation in thermal thresholds and rates of development, however, could dramatically influence the capacity for maintaining seasonality in ways that differ from our current understanding of appropriate seasonal windows for this insect. For example, our model predicts disrupted mountain pine beetle phenological cues at middle elevations, although rapid evolution of slower development rates or novel developmental thresholds could maintain univoltinism at middle elevations as temperatures warm. Understanding trait adaptations is an important area of future research, and mechanistic demographic models provide ideal tools for integrating adaptive capacity for predictive purposes (Yurk and Powell, 2009; Cobbold and Powell, 2011). When used with downscaled climate projections, demographic models can be used to incorporate important physiological processes that influence mountain pine beetle population growth and associated tree mortality into forest management planning.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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