

Geographically variable response of *Dendroctonus ponderosae* to winter warming in the western United States

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Abstract

Context Milder winters have contributed to recent outbreaks of *Dendroctonus ponderosae* in Canada, but have not been evaluated as a factor permitting concurrent outbreaks across its large range (ca. 1500 × 1500 km) in the western United States (US).

Objectives We examined the trend in minimum air temperatures in *D. ponderosae* habitats across the western US and assessed whether warming winters explained the occurrence of outbreaks using physiological and population models.

Methods We used climate data to analyze the history of minimum air temperatures and reconstruct physiological effects of cold on *D. ponderosae*. We evaluated

relations between winter temperatures and beetle abundance using aerial detection survey data.

Results Extreme winter temperatures have warmed by about 4 °C since 1960 across the western US. At the broadest scale, *D. ponderosae* population dynamics between 1997 and 2010 were unrelated to variation in minimum temperatures, but relations between cold and *D. ponderosae* dynamics varied among regions. In the 11 coldest ecoregions, lethal winter temperatures have become less frequent since the 1980s and beetle-caused tree mortality increased—consistent with the climatic release hypothesis. However, in the 12 warmer regions, recent epidemics cannot be attributed to warming winters because earlier winters were not cold enough to kill *D. ponderosae*.

Conclusions There has been pronounced warming of winter temperatures throughout the western US, and this has reduced previous constraints on *D. ponderosae* abundance in some regions. However, other considerations are necessary to understand the broad extent of recent *D. ponderosae* epidemics in the western US.

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Introduction

The abundance of many organisms important to natural resource management is influenced by

mortality from winter temperature (Bentz and Mullins 1999; Sæther et al. 2002; Crozier 2004; Altwegg et al. 2005; Altwegg et al. 2006). Thus a climatic trend of warming winters could influence features of population dynamics such as the probability of outbreaks and extinctions (Thomas et al. 2004). For example, range expansion and increased abundance of some damaging forest insects in Europe and North America have been permitted by warming winters over the past two decades (Battisti et al. 2005; Tran et al. 2007; Sambaraju et al. 2012). Given the apparent links between recent warming and pest outbreaks, and the expectation for continued warming (Donat et al. 2013; Fischer et al. 2013), there is a need to better understand trends in the specific climate variables that affect physiological processes important to the abundance of tree-killing forest insects.

Bark beetles are the most important disturbance agents of North American forests having killed trees on millions of forest hectares during the past two decades (Aukema et al. 2006; Meddens et al. 2012). The ramifications of the extensive tree mortality caused by these beetles are immense and persistent (Weed et al. 2013). Among bark beetles, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has been the most damaging (Aukema et al. 2006; Safranyik and Carroll 2006; Raffa et al. 2008). Meddens et al. (2012) estimated that 63 and 94 % of total bark beetle-caused tree mortality from 1997 to 2010 in the US and Canada was caused by *D. ponderosae*, respectively. Dramatic population increases of tree-killing bark beetles are believed to be the result of positive feedbacks that enable beetles to overcome host tree defenses through mass-attacks and thereby transition small local infestations to outbreak status (Raffa et al. 2008; Martinson et al. 2013). Key factors that strengthen positive feedbacks include behavioral plasticity of beetles (Boone et al. 2011) and weather effects on insect survival, developmental rate, seasonal rhythms of tree attacks, and tree defenses (Régnière and Bentz 2007; Powell and Bentz 2009). Once populations attain outbreak status, negative feedback due to host tree depletion and weather influence beetle population fluctuations (Berryman 1976; Safranyik and Linton 1991; Safranyik and Carroll 2006; MacQuarrie and Cooke 2011). The initiation and progression of recent *D. ponderosae* outbreaks, for example, have been empirically correlated with prior infestation size and negative

deviations in precipitation and/or various metrics of temperature (Aukema et al. 2006; Hicke et al. 2006; Campbell et al. 2007; Macias Fauria and Johnson 2009; Chapman et al. 2012; Preisler et al. 2012).

Cold is one dimension of climate that can influence *D. ponderosae* population success (Safranyik 1978; Cole 1981; Safranyik and Linton 1991, 1998). Larvae, the usual overwintering stage, can survive to about -40°C by supercooling to avoid freezing (Bentz and Mullins 1999). However, less extreme temperatures, such as rapid drops in temperature during late fall or early spring, can also cause mortality when larvae are not fully cold-hardened (Safranyik and Linton 1991; Régnière and Bentz 2007). These demographic effects can be so strong in some areas that populations remain at low density for decades if there are intermittent beetle-killing cold bouts (Evenden and Gibson 1940; Safranyik and Linton 1991; Bentz et al. 2010). However, the frequency of extreme cold events may be changing in ways that are relevant to *D. ponderosae* (Macias Fauria and Johnson 2009; Donat et al. 2013). Warming winters, for example, are among the climatic factors that have permitted greater population success of mountain pine beetles in high elevation pine habitats (Logan and Powell 2001; Logan et al. 2010; Bentz et al. 2011a) and range expansion into northern British Columbia and Alberta, Canada (Carroll et al. 2004; Cudmore et al. 2010; Safranyik et al. 2010; de la Giroday et al. 2012; Sambaraju et al. 2012).

While it is clear that milder winters have been extremely consequential to *D. ponderosae* near the margins of its poleward and altitudinal distributions, the importance of winter cold in permitting outbreaks and on annual growth rates of outbreaking populations has not been investigated across a broad extent of its historical range in the western US. Large mortality events due to winter cold can push populations back to endemic levels (i.e., halt outbreaks) and diminish positive feedback (Safranyik and Linton 1991; Martinson et al. 2013). A reduction in the frequency of extremely cold winters over time then could favor positive feedback and not only permit outbreaks, but also prolong them especially in regions historically subjected to very cold winters. In this study we evaluated the temporal and spatial trend in extreme minimum temperatures across the western US using the extensive climate monitoring network of the US National Oceanic and Atmospheric Association (NOAA). We then tested whether amelioration of

winter cold could provide a general explanation for the occurrence of *D. ponderosae* outbreaks in the western US and whether annual growth rates of outbreaking populations were affected by winter cold.

Methods

Study organism

Dendroctonus ponderosae is a tree-killing bark beetle with a broad distributional range extending north from Baja California Norte, Mexico to British Columbia and western Alberta, Canada and east from the Pacific coast of North America to South Dakota in the United States. This beetle can reproduce in at least 22 species of *Pinus*, but lodgepole pine (*P. contorta* Douglas ex Louden var. *latifolia* Engelm. ex S. Watson) is the most common host (Safranyik and Carroll 2006). Beetles must attack trees en masse to overcome host defense (Safranyik and Carroll 2006). Attacking adults are commonly active for a brief period in July and August that varies with temperature and across its geographic range. Successfully attacking beetles bore through the outer bark and into the phloem, where they mate and oviposit. Development rate and activity of *D. ponderosae* are strongly temperature-dependent (Bentz et al. 2001). Beetles complete their life cycle in one or two years depending on location and annual temperature patterns (Bentz et al. 2014). The overwintering life stage varies depending on attack timing and temperature, but larvae are the most common overwintering stage. Pupation and molting to adults occurs during the following spring/early summer (Amman 1973). During the winter beetles arrest feeding and synthesize cryoprotectants that permit them to survive temperatures approaching -40°C via supercooling (Somme 1964; Safranyik and Linton 1998; Bentz and Mullins 1999). The larvae are the most cold-tolerant life stage, followed by adults, pupae, and eggs (Somme 1964; Amman 1973; Bentz and Mullins 1999; Lester and Irwin 2012).

Estimation of *D. ponderosae* abundance and study area

Multiple spatially explicit datasets were combined to test for effects of minimum winter temperatures on interannual changes in host tree mortality from *D.*

ponderosae. Host tree mortality, a proxy for beetle abundance, was estimated from annual surveys conducted by the USDA Forest Service's Forest Health Protection Aerial Detection Survey (ADS) program. Tree needles turn red the summer following *D. ponderosae* attack (Edburg et al. 2012), and observers in fixed-wing aircrafts record the area and number of "red" pine trees killed by *D. ponderosa* annually. Damage observed in year t reflects trees that were killed by *D. ponderosae* during the previous growing season, in year $t-1$ (Meddens et al. 2012). ADS data from 1997 to 2011, corresponding to the trees killed by *D. ponderosae* from 1996 to 2010, were obtained from the USFS Forest Health Technology Enterprise Team in Fort Collins, Colorado. Damage data were provided in spatial polygonal format and included data on pine tree species attacked, forest type, and an estimated number of trees killed by *D. ponderosae*.

We stratified our analyses into 23 ecoregions (Fig. 1) that generally followed the Level III ecoregion classifications recognized by the US Environmental Protection Agency (Omernik 2004). *Pinus* host distribution throughout the western US was extracted from a larger forest cover dataset (250-m raster with the distribution of 141 forest types across the contiguous US; Ruefenacht et al. 2008). Ecoregions containing forests impacted by *D. ponderosae* were extracted from the original ecological region dataset by overlaying the ADS data. Some modifications to the ecoregion boundaries were made so that their boundaries closely approximated the geographic extent of interbreeding populations of *D. ponderosae*. Relatively large ecoregions (e.g., Coast Range, Middle Rockies, North Rockies, and Southern Rockies) were subdivided into separate regions based upon the underlying pine forest distribution and topographic features (e.g., river canyons, deserts, and mountains) known to affect movement of *D. ponderosae* populations (Mock et al. 2007; Chen and Walton 2011; Gayathri Samarasekera et al. 2012). For example, we created five subregions from the Ecoregion Level III classification of "Middle Rockies" to correspond to geographically distinct, forested areas (i.e., Black Hills, Big Horn mountains, Central mountains, Yellowstone Ecosystem, and the western Montana mountains) (Fig. 1). Subregions were created for similar reasons within the Coast Range, North Rockies, and Southern Rockies (Fig. 1). In some instances ADS data extended into ecoregions

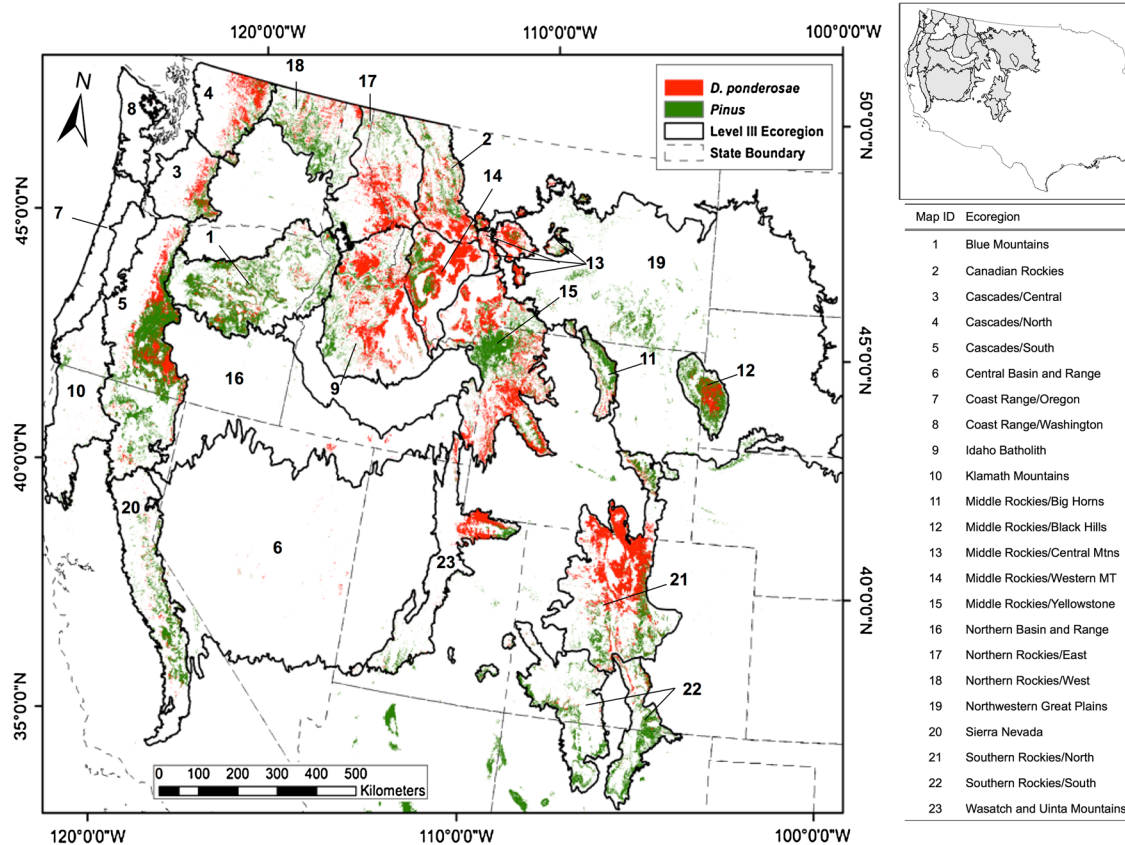


Fig. 1 Cumulative area of pine mortality due to *D. ponderosae* from 1996 to 2010 across western United States (*red*) documented during USFS Aerial Detection Surveys. Distribution of *Pinus* (*green*) extracted from forest types of the US

(Ruefenacht et al. 2008). Level III Ecoregion boundaries accessed from US Environmental Protection Agency (US EPA 2011)

containing only marginal forest habitat (e.g., Columbia and Colorado Plateaus, Northwestern Glaciated Plains, and Wyoming Basin) but adjacent to regions containing the majority of contiguous pine forest and ADS damage in that area. Instead of allocating ADS data to these marginal ecoregions we modified the boundaries so that ADS and pine data were spatially associated with ecoregions containing the majority of pine forest. All GIS processing was conducted using ArcMap 10 (ESRI, Redlands, CA).

Once the geographic boundaries of populations were finalized the annual number of pine trees killed within each ecoregion from 1996 to 2010 was generated using the following methods. ADS data were merged into one spatial layer and each ADS damage polygon was assigned to each ecoregion based on its geographic location. We then summed the number of killed trees recorded in each polygon per year for each

ecoregion. Time series were then standardized to permit comparisons among ecoregions by dividing the number of annual trees killed by the actual forest area flown during ADS in each year (Appendix 1, Online Supplementary Material). Our GIS processing resulted in 34 population time series of varying length (1–15 years of observed mortality). We restricted our study area to consider only those ecoregions with greater than 10 years of continuous pine mortality resulting in a dataset of pine mortality recorded from 23 regions with observations spanning an average of 14.8 ± 0.5 years (mean \pm SD, range 10–15) (Table S1; Fig. S1, Online Supplementary Material).

Time trend in minimum winter air temperatures

We tested for a long-term trend in minimum winter air temperatures across the study region because cold

snaps are thought to induce the greatest mortality of *D. ponderosae* (Safranyik and Linton 1998). We also evaluated the time trend in the frequency of winter air temperatures dropping below -40°C , which is thought to induce 100 % beetle mortality (Safranyik and Linton 1991). Daily temperature data from 1960 to 2011 were downloaded from all available weather stations across the study region using the NOAA National Climatic Distribution Center's online acquisition system (<http://www.ncdc.noaa.gov>). We chose 1960 as a starting point because this allowed us to include many stations and still have a relatively long time series; also, 1960 was a match with parallel analyses that have been conducted in the southeastern US (Tran et al. 2007). From this database we selected weather stations based upon their geographic location and whether stations had been recording air temperatures for at least 45 consecutive years since 1960. When possible, stations geographically located within the range of elevation where *D. ponderosae* impact was documented in each ecoregion were selected. This range of elevation was determined by extracting values from the GTOPO30 digital elevation model (30-arc seconds, US Geological Survey) at the geometric centroid of each ADS damage polygon. In many ecoregions it was difficult to locate stations meeting both criteria because of the scarcity of stations in these areas recording air temperatures >44 years. In these regions we selected stations located near forests that had continuous temperature records for at least 45 years. We located 630 weather stations using these selection criteria (Table 1; Fig. S2, Online Supplementary Material). We considered temperature data available at higher elevations from Snow Telemetry (SNOTEL) stations (USDA Natural Resources Conservation Service), but air temperature records only date back to the 1970s and were incomplete for many stations.

The minimum temperature was defined as the coldest night from August 1st in calendar year $t - 1$ to July 31st in year t , corresponding to the typical generational period of *D. ponderosae*. We refer to this period hereafter as a 'beetle year'. This metric was extracted for each beetle year from each station's time series of daily maximum and minimum temperatures. We then calculated annual deviations in minimum temperature (residual values) in each beetle year from the long-term mean minimum temperature from 1960 to 2011 observed at each station. The temporal trend in

minimum temperature was evaluated by regressing the residual of minimum temperature against year using a linear mixed modeling framework. We used Akaike information criteria (AICc) to compare models without a random effect to models including two random effect structures (random-intercept and random-slope and intercept) (Zuur et al. 2009). The information content was higher for the random-intercept model including weather station as the random effect. We then tested for differences in warming with respect to ecoregions and due to station elevation, latitude, and longitude. We first estimated the slope of minimum air temperature vs. year for each of the 630 weather stations since 1960. We tested for variation in slopes (rate of warming) among ecoregions using ANOVA. Variation in the rate of warming with respect to geographic location and physical variables was assessed across the study area by fitting all possible regression models including station longitude, latitude, elevation, and their two-way interactions as predictors. The best model was selected by evaluation of AICc (Burnham and Anderson 2002).

Influence of minimum winter air temperature on population dynamics of *D. ponderosae*

The influence of winter cold on *D. ponderosae* dynamics was tested by examining the relationship between minimum air temperatures and interannual *D. ponderosae* growth rates. Tree mortality data were used as a proxy for *D. ponderosae* abundance (Aukema et al. 2008; Preisler et al. 2012). Then per capita growth rates (R_t) were calculated for each of the 23 population time series using the expression:

$$R_t = \ln(N_{t+1} + 1) - \ln(N_t + 1) \quad (1)$$

where N_{t+1} and N_t represent the abundances of *D. ponderosae* (no. dead trees) within the current (t) and following year ($t + 1$), respectively. Bark beetle populations are notable for fluctuating between low and high abundance steady states. Positive feedback enables beetles to transition to high abundance whereas negative feedback processes tend to stabilize populations around one or the other local equilibria (Raffa and Berryman 1986; Martinson et al. 2013). We therefore expected endogenous feedback to affect *D. ponderosae*, as is generally detected in similar time series of other bark beetle species (Økland and Berryman 2004; Friedenberget al. 2008). A discrete

Table 1 Summary weather station data and estimated regression coefficients describing the annual rate of minimum air temperature warming from 1960 to 2011 in each ecoregion

Ecoregion	No. Stations ^a	Elevation (m) ^b Mean ± SD	Years of data	Min. air temp. (°C) ^c		°C year ⁻¹ ± SE
				Min.	Max.	
Blue Mountains	29	938 ± 245	50.9 ± 2.1	-44.4	5.0	0.09 ± 0.01**
Canadian Rockies	12	1180 ± 205	50.8 ± 2.2	-45.6	-8.3	0.07 ± 0.01**
Cascades/Central	10	549 ± 455	50.5 ± 2.6	-41.1	-1.7	0.05 ± 0.01**
Cascades/North	16	473 ± 309	50.6 ± 2.0	-38.3	0.0	0.09 ± 0.01**
Cascades/South	40	906 ± 520	51.7 ± 0.9	-36.7	0.6	0.07 ± 0.01**
Central Basin and Range	92	1520 ± 252	50.8 ± 2.0	-41.7	-2.2	0.06 ± 0.004**
Coast Range/OR	10	39 ± 58	50.6 ± 2.3	-24.4	-0.6	0.04 ± 0.01*
Coast Range/WA	9	54 ± 50	50.3 ± 2.8	-16.7	-1.1	0.04 ± 0.01*
Idaho Batholith	28	1353 ± 373	51.0 ± 2.0	-45.0	-5.6	0.09 ± 0.01**
Klamath Mountains	19	449 ± 281	51.0 ± 1.7	-28.9	0.6	0.05 ± 0.01**
Middle Rockies/Big Horns	2	1964 ± 705	50.0 ± 2.8	-42.8	-16.7	0.02 ± 0.03 ^{ns}
Middle Rockies/Black Hills	13	1306 ± 237	51.5 ± 1.5	-43.9	-12.2	0.07 ± 0.01**
Middle Rockies/Central Mtns	3	1435 ± 304	50.0 ± 2.6	-41.7	2.2	0.09 ± 0.02**
Middle Rockies/W MT	16	1543 ± 246	51.1 ± 1.8	-46.7	-0.6	0.07 ± 0.01**
Middle Rockies/Yellowstone	24	1795 ± 292	51.3 ± 1.9	-47.8	9.4	0.08 ± 0.01**
Northern Basin and Range	27	1335 ± 249	50.6 ± 2.2	-46.1	-5.0	0.09 ± 0.01**
Northern Rockies/East	28	817 ± 190	50.8 ± 2.0	-42.2	-4.4	0.10 ± 0.01**
Northern Rockies/West	10	651 ± 116	51.6 ± 1.3	-38.3	-6.7	0.10 ± 0.01**
Northwestern Great Plains	138	951 ± 289	51.1 ± 1.8	-47.8	1.7	0.06 ± 0.003**
Sierra Nevada	25	1343 ± 478	51.2 ± 1.6	-41.7	1.1	0.05 ± 0.01**
Southern Rockies/North	29	2418 ± 442	50.4 ± 2.3	-49.4	-15.6	0.07 ± 0.01**
Southern Rockies/South	25	2376 ± 240	51.6 ± 1.2	-45.6	-12.2	0.10 ± 0.01**
Wasatch and Uinta Mountains	25	1862 ± 323	51.3 ± 1.3	-46.7	-1.1	0.08 ± 0.01**
Total	630	1233 ± 619	51.0 ± 1.9	-41.0 ± 7.9	-3.2 ± 6.4	0.07 ± 0.02

** $P < 0.01$, * $P < 0.05$, ns: not significantly different from zero

^a NOAA stations and their metadata accessed from (<http://www.ncdc.noaa.gov>)

^b Elevation of weather stations

^c Minimum and maximum reported values of extreme minimum air temperatures from 1960 to 2011

model of population dynamics (Eq. 2) was fit to the data to explore the influence of endogenous effects and minimum air temperature on per capita growth rates of *D. ponderosae* (Royama 1992; Berryman 2003):

$$R_t = \beta_0 + \beta_1 \cdot N_t + \beta_2 \cdot N_{t-1} + \varepsilon_t \quad (2)$$

where N_t and N_{t-1} equal current and previous abundance, β_i 's equal the estimated model coefficients corresponding to the intercept and strength of feedbacks, and ε_t represents exogenous (density-independent) effects; e.g., due to climate and estimation error. A positive or negative value of β_1 or β_2 would indicate

the presence of positive or negative feedback, respectively. Because ADS mainly detect bark beetles when they are abundant (domain of epidemic abundance), we expected a priori that *D. ponderosae* populations would be primarily affected by first order, negative feedback (e.g., resource depletion; Økland and Berryman 2004; Martinson et al. 2013). A linear mixed modeling framework was used to estimate parameters of the above model similar to the approach for analysis of minimum air temperatures. Nonstationary time series were linearly detrended prior to model fitting. AICc model selection favored a final model of density

dependence that included ecoregion as a random effect.

After fitting the model as described above, the demographic effect of winter cold on *D. ponderosae* population dynamics was assessed through correlation of density-adjusted model residuals (ϵ_t) with annual minimum air temperatures in each ecoregion. Average annual minimum air temperatures were calculated within each ecoregion by first interpolating daily temperatures at 100 random points within pine forested areas in each ecoregion from 1996 to 2010. Locations were randomly generated within each ecoregion from the pine raster using the function ‘genrandpnts’ in the software Geospatial Modeling Environment version 0.7.1.0 (Beyer 2012) and were confirmed to overlap closely with ADS data (Fig. S3, Online Supplementary Material). Temperature interpolation was implemented in the software BioSIM (Régnière and St-Amant 2007) based on the method of Régnière (1996), which estimates temperatures while accounting for climatic gradients due to topography and geographic location. BioSIM uses the same database of geographically indexed NOAA weather station data that was used to evaluate long-term trends in minimum air temperature above, but only includes daily data back to 1980. The extreme minimum air temperature within each beetle year was extracted from all locations and averaged for each ecoregion from 1996 to 2010. We hypothesized that the influence of minimum air temperature may vary across the distribution of beetle population growth rates so quantile regression was used to evaluate the influence of average minimum air temperature at each decile of beetle population growth. Lastly, geographic variation in the influence of winter cold on beetle growth rates was examined by modeling the relationship between minimum air temperature and growth rates within each ecoregion.

Relating cold-induced mortality to population dynamics of *D. ponderosae*

The importance of minimum air temperatures on *D. ponderosae* dynamics was also examined by comparing how well physiological effects of winter cold on larval mortality explain fluctuations of *D. ponderosae* abundance. We estimated the physiological effects of winter cold using a previously published process-based model that predicts daily survival of *D.*

ponderosae cohorts by estimating seasonal changes in cold tolerance (Régnière and Bentz 2007). Beetles avoid freezing by supercooling and the capacity for supercooling depends upon the type and amount of cryoprotectants in the hemolymph (Somme 1982). The supercooling point (SCP), the temperature at which tissue crystallization and death occurs (Lee 2010), changes in *D. ponderosae* with season and recent temperatures (Bentz and Mullins 1999).

The cold tolerance model that we employed (Régnière and Bentz 2007) had been parameterized using hourly phloem temperatures and data from frequent measurements of larval SCP taken between the fall and spring from field populations that were exposed to natural fluctuations in temperature (Bentz and Mullins 1999). The model recognizes three qualitative states [(1) non-cold hardened feeding state (summer); (2) variable cold tolerance depending on recent temperatures (fall and spring); and (3) fully cold-hardened (winter)] and estimates the frequency distribution of SCPs for larvae as a function of temperature throughout the lifecycle. Thus,

$$p(\text{survival})_t = \min\left(p(\text{survival})_{t-1}, \sum_i \frac{p_i}{1 + e^{-(T_t - \alpha_i)/\beta_i}}\right), \quad (3)$$

where T_t is the minimum daily temperature on day t , p_i is the probability of survival in each state i , α_i is the median of the SCP distribution of state i , and β_i is the spread parameter for the SCP distribution in state i (further details in Régnière and Bentz 2007). Estimates of overwintering survival from this model are in close accordance with a range of laboratory (Safranyik and Linton 1998) and field observations (Régnière and Bentz 2007).

The cold tolerance model was run in BioSIM to predict the physiological effect of winter temperatures in each of our study ecoregions from 1980 to 2011. We began simulations in 1980 to assess temporal patterns of winter temperature and expected physiological effects prior to and coincident when tree mortality data were available. Overwintering survival of *D. ponderosae* was estimated from air temperatures interpolated at the same 100 random locations as mentioned above in each ecoregion (Fig. S3, Online Supplementary Material). Prior to estimating physiological effects, interpolated air temperatures were converted to phloem temperatures following Bolstad et al. (1997) to account for thermal buffering by the bark. Model

outputs (absolute minimum phloem temperature, expected probability of winter survival, and minimum LT_{50} [i.e., median SCP or 50 % mortality]) were summarized for each ecoregion by averaging across the 100 locations in each beetle year. Raw survival data were modeled as a function of minimum phloem temperature using a loess smoother (span 0.6).

We assessed spatio-temporal changes in the historical importance of minimum winter air temperature, and its influence on the overwintering biology of *D. ponderosae*, by comparing average model predictions between the periods 1980–1990 and 1991–2011 for each ecoregion (Fig. S4, Online Supplementary Material). For both time periods, we calculated the average minimum phloem temperature and survival for each ecoregion. We used these estimates then to calculate the average amount of winter warming that occurred between the two periods in each ecoregion and the associated influence on survival:

$$I_i = S_{1991-2011} / S_{1980-1990}, \quad (4)$$

where $S_{1980-1990}$ and $S_{1991-2011}$ denote the average predicted survival from 1980–1990 and 1991–2011 in each ecoregion (i), respectively. Equation 4 is interpretable as an index of demographic release analogous to the index of generational mortality or k -value used in key-factor analysis (Morris 1959; Varley et al. 1973).

Results

Time trend in minimum winter air temperatures

There was a significant regional warming trend in minimum air temperature from 1960 to 2011 of about 3.6 °C (Fig. 2). The slope of this relationship averaged 0.07 ± 0.02 °C/yr (mean \pm SE; $P < 0.001$; range -0.11 – 0.38) across all ecoregions, and the majority of ecoregions (22 of 23) demonstrated a significant warming trend (Table 1). The rate of warming varied significantly among ecoregions (one-way ANOVA $F_{22,607} = 3.50$; $P < 0.001$), but was similar among most regions (Table 1). Notable exceptions were that warming in Southern Rockies/South was significantly greater than in Coast/OR, Sierra Nevada, and NW Great Plains, and warming in the Northern Rockies/East was greater than NW Great Plains and Sierra Nevada (Table 1).

The majority of weather stations (605 stations or 96 %) demonstrated a positive warming trend since 1960, but regression coefficients were only significantly different from zero for 39 % of stations (Table S2, Online Supplementary Material). Only one station displayed a significant cooling trend during this time period (Libby 30 SSE, MT). Across all ecoregions, the slope of this relationship tended to increase in a northwesterly direction and with elevation in a westward direction. Each of the five parameters in the model was significant ($P < 0.001$) but the model explained only 6 % of the variation in slopes (Table S3, Online Supplementary Material).

Influence of minimum air temperature on *D. ponderosae* population dynamics

The aerial detection survey (ADS) indicated that pine tree mortality from *D. ponderosae* during 1997 to 2011 ranged from 1 tree to 21 million trees ecoregion⁻¹ year⁻¹ with the greatest mortality affecting forests of the Rocky Mountains (Fig. 1; Table S1, Online Supplementary Material). Forty-two percent of total *D. ponderosae*-caused pine mortality across the western US was reported in ID Batholith and the Middle Rockies. Pine mortality was lowest within the Coast Range, NW Great Plains, and Central Basin and Range representing 0.04 % of cumulative mortality across the western US (Table S1, Online Supplementary Material). Most of the mortality from *D. ponderosae* was to lodgepole (*P. contorta*) and ponderosa pines (*P. ponderosa* Engelm.). However, ADS data also indicated mortality of limber pine (*P. flexilis* James), Rocky Mountain bristlecone (*P. aristata* Engelm.), sugar (*P. lambertiana* Doug.), western white (*P. monticola* Douglas ex Don), and whitebark (*P. albicaulis* Engelm.) pines. *D. ponderosae* activity was recorded at elevations from 182 to 2853 m asl (Table S1, Online Supplementary Material).

Per capita growth rates of *D. ponderosae* during the study period, based on number of trees killed, averaged -0.02 ± 0.01 (mean \pm SE, range -1.2 to 1.1 , $n = 288$) trees killed in year _{$t+1$} per tree killed in year _{t} . As hypothesized, the dominant endogenous effect was first order negative feedback. Of the four models considered, the top ranked model indicated direct density dependence (N_t) ($F_{1,263} = 16.9$; $P < 0.001$) and a weak, but positive influence from delayed density dependence (N_{t-1}) ($F_{1,263} = 18.1$;

Fig. 2 Minimum air temperatures have warmed $0.07 \pm 0.02 \text{ }^\circ\text{C year}^{-1}$ ($P < 0.001$, $n = 52$ years) or about $3.6 \text{ }^\circ\text{C}$ since 1960 in regions affected by *D. ponderosae* (from 550 to 630 weather stations). Points are mean \pm SE residual values from the long-term station mean minimum winter temperature. *Inset* Proportion of weather stations reporting temperatures from 1960 to 2011 below $-40 \text{ }^\circ\text{C}$ that can induce 100 % beetle mortality (Safranyik and Carroll 2006)

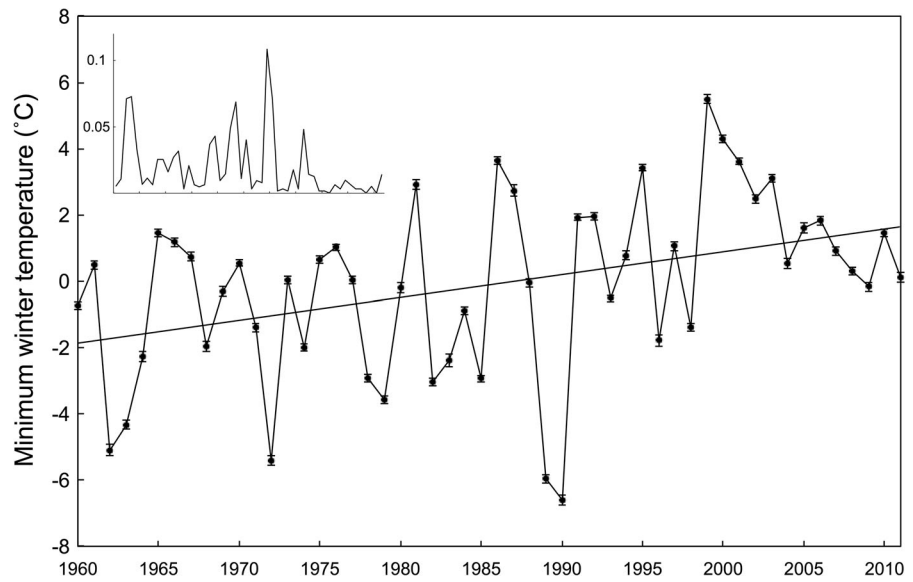


Table 2 Model selection results showing estimated regression coefficients of alternative models describing density-dependence of *Dendroctonus ponderosae*

Model rank	Intercept	N_t	N_{t-1}	Model R^2	df	logLik	AICc	Δ AICc
1	0.09	-0.35	0.26	0.11	5	-97.6	205.5	0.0
2	0.57	-0.45		0.05	4	-107.7	223.6	18.1
3	0.04		-0.05	0.01	4	-113.0	234.2	28.7
4	-0.02			0	3	-114.3	234.8	29.3

$P < 0.001$) (Table 2). The three alternative models provided poor fits to *D. ponderosae* dynamics and were not considered plausible models (Δ AICc > 2) (Table 2).

Interannual *D. ponderosae* growth rates across the western US adjusted for population density (ϵ_t) were not related to interannual variation in minimum winter air temperatures (OLS regression: $F_{1,264} = 0.03$; $P = 0.856$) and quantile regression indicated that this relationship was not significant for any decile of population growth (Fig. 3; Table 3). Average population growth was generally negative in regions/years subjected to the coldest winters ($< -30 \text{ }^\circ\text{C}$). For example, population growth rates (ϵ_t) averaged -0.12 ± 0.01 (mean \pm SE, $n = 13$) and -0.01 ± 0.06 ($n = 42$) during winters when temperatures dropped below $-35 \text{ }^\circ\text{C}$ and were between -35 and $-30 \text{ }^\circ\text{C}$, respectively. Growth rates were generally positive (0.05 ± 0.04 , $n = 69$) during moderately (-25 to $-30 \text{ }^\circ\text{C}$) cold winters but negative (-0.08 ± 0.05 , $n = 32$) in areas where minimum temperatures remained above $-10 \text{ }^\circ\text{C}$.

There was modest spatial heterogeneity in the relationship between population growth rates (ϵ_t) and minimum winter temperature (Table 4). The slope of this relationship averaged 0.03 ± 0.01 growth rate/ $^\circ\text{C}$ (range -0.04 to 0.10) across all ecoregions and was not significantly different from zero for the majority (17 of 23) of ecoregions (Table 4). There was, however, a significant and positive correlation between population growth rate and minimum air temperature in the Central, North, and South Cascades, Northern Rockies/East, Southern Rockies/South, and in Western Montana within the Middle Rockies. A marginally significant relationship was found in the Northern Rockies/West and Middle Rockies/Yellowstone (Table 4).

Relating cold-induced mortality to *D. ponderosae* population growth

Estimated average annual survival of *D. ponderosae* from 1980 to 2011 varied from 0.08 to 0.99 and was related closely to the coldest night of the year (Fig. 4

Fig. 3 Relationship between *D. ponderosae* population growth rates and minimum winter air temperature across the western US. Points signify interannual changes in beetle abundance in study area as measured by pine mortality documented during USFS Aerial Detection Surveys 1997 to 2011. Lines are linear fits for each decile of beetle population growth

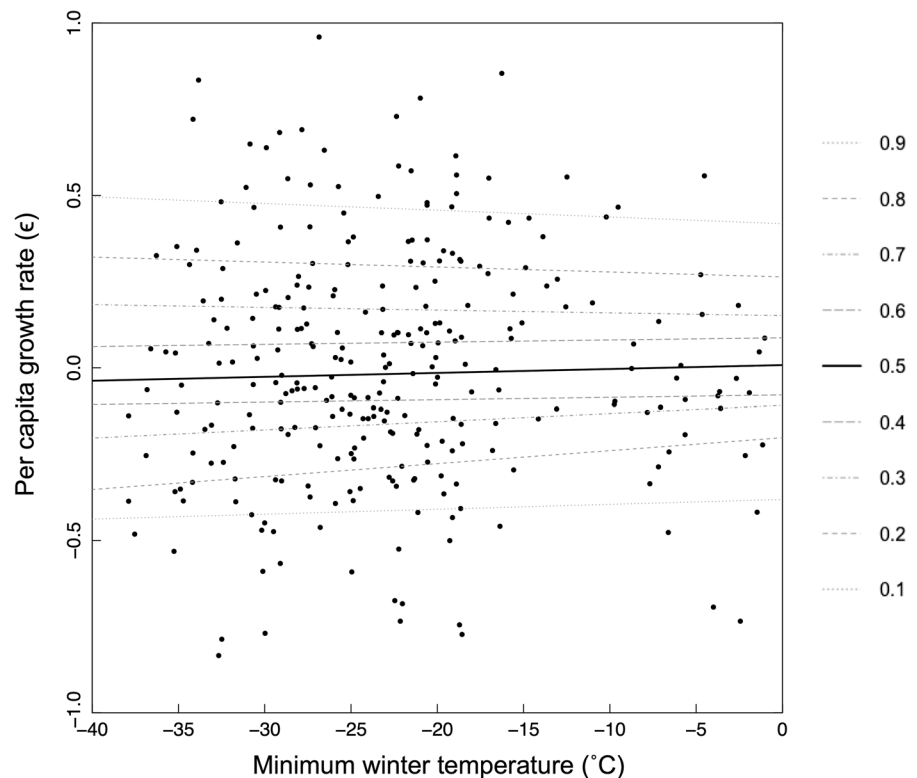


Table 3 Coefficients from decile regression models evaluating the relationship between minimum winter air temperature and *Dendroctonus ponderosae* population growth rates fit to data in Fig. 3

Decile	Slope	Intercept
10	0.001 ± 0.004 ^{ns}	-0.38 ± 0.10**
20	0.004 ± 0.003 ^{ns}	-0.230 ± 0.07**
30	0.002 ± 0.002 ^{ns}	-0.11 ± 0.05*
40	0.001 ± 0.002 ^{ns}	-0.08 ± 0.05 ^{ns}
50	0.001 ± 0.002 ^{ns}	0.01 ± 0.06 ^{ns}
60	0.006 ± 0.003 ^{ns}	0.09 ± 0.07 ^{ns}
70	-0.001 ± 0.003 ^{ns}	0.15 ± 0.07*
80	-0.001 ± 0.004 ^{ns}	0.26 ± 0.10**
90	-0.001 ± 0.006 ^{ns}	0.41 ± 0.12**

** $P < 0.01$, * $P < 0.05$, ns: not significantly different from zero

and Table S4, Online Supplementary Material). The model predicted that across all ecoregions, sites with extreme phloem temperatures approaching $-25\text{ }^{\circ}\text{C}$ would experience about 50 % larval mortality (Fig. 4). The model estimated an expected average

survival of 0.18 ± 0.06 ($n = 15$, mean \pm SD) for populations subjected to extreme temperatures below $-35\text{ }^{\circ}\text{C}$. Predicted survival of populations exposed to minimum temperatures above $-10\text{ }^{\circ}\text{C}$ averaged 0.98 ± 0.01 ($n = 94$) (Fig. 4).

There was notable geographical and temporal variation in the influence of cold temperature on larval survival. Two general patterns emerged among ecoregions related to the historical influence of winter cold on larval survival and the temporal trend in warming: (1) ecoregions that have warmed but have never been cold enough to cause considerable mortality and (2) ecoregions where the frequency of extreme winter temperature events important to larval survival have declined. Winter temperatures in the Coast, Klamath, and Sierra Nevada mountain ranges historically were not cold enough to cause appreciable mortality (estimated winter survival averaged 0.96 ± 0.05). Since 1980, minimum phloem temperatures in these regions averaged $-7.7 \pm 5.6\text{ }^{\circ}\text{C}$, about $16\text{ }^{\circ}\text{C}$ above the predicted SCP ($-23.0 \pm 2.2\text{ }^{\circ}\text{C}$) (Table S4, Online Supplementary Material). Conversely, in other ecoregions such as the Middle

Table 4 Regression coefficients for each ecoregion describing the relationship between minimum winter air temperature and the density-independent component of *Dendroctonus ponderosae* growth rates (ϵ_t)

Ecoregion	Model R^2	Intercept		Minimum winter temperature ($^{\circ}\text{C}$)	
		Mean \pm SE	P	Mean \pm SE	P
Blue Mountains	0.05	0.5 \pm 0.5	0.284	0.03 \pm 0.02	0.230
Canadian Rockies	0.05	-0.7 \pm 1.0	0.546	-0.02 \pm 0.03	0.518
Cascades/Central	0.60	1.6 \pm 0.4	0.001	0.1 \pm 0.02	0.001
Cascades/North	0.25	1.6 \pm 0.6	0.035	0.07 \pm 0.03	0.046
Cascades/South	0.43	1.1 \pm 0.4	0.010	0.06 \pm 0.02	0.009
Central Basin and Range	0.01	0.8 \pm 0.9	0.384	0.04 \pm 0.04	0.374
Coast Range/Oregon	0.01	-0.2 \pm 0.1	0.115	-0.03 \pm 0.03	0.308
Coast Range/Washington	0.10	-0.5 \pm 0.5	0.398	-0.05 \pm 0.08	0.571
Idaho Batholith	0.03	2.0 \pm 1.6	0.234	0.06 \pm 0.05	0.256
Klamath Mountains	0.06	-0.2 \pm 0.2	0.485	-0.02 \pm 0.03	0.564
Middle Rockies/Big Horns	0.05	0.7 \pm 1.1	0.544	0.03 \pm 0.04	0.523
Middle Rockies/Black Hills	0.06	1.4 \pm 1.0	0.197	0.05 \pm 0.04	0.215
Middle Rockies/Central Mtns	0.08	0.9 \pm 1.5	0.586	0.03 \pm 0.05	0.590
Middle Rockies/Western MT	0.47	3.0 \pm 0.9	0.006	0.09 \pm 0.03	0.006
Middle Rockies/Yellowstone	0.19	2.3 \pm 1.2	0.077	0.07 \pm 0.03	0.078
Northern Basin and Range	0.06	0.7 \pm 1.2	0.601	0.03 \pm 0.06	0.607
Northern Rockies/East	0.49	1.4 \pm 0.4	0.003	0.05 \pm 0.01	0.005
Northern Rockies/West	0.18	0.8 \pm 0.4	0.083	0.04 \pm 0.02	0.081
Northwestern Great Plains	0.06	-1.4 \pm 1.9	0.478	-0.04 \pm 0.07	0.516
Sierra Nevada	0.08	-0.5 \pm 1.6	0.766	-0.02 \pm 0.08	0.789
Southern Rockies/North	0.05	-0.5 \pm 1.0	0.591	-0.02 \pm 0.04	0.542
Southern Rockies/South	0.28	1.5 \pm 0.7	0.044	0.07 \pm 0.03	0.036
Wasatch and Uinta Mtns	0.03	2.0 \pm 1.7	0.263	0.09 \pm 0.08	0.267

Rockies, historical minimum winter temperatures commonly approached or exceeded predicted SCPs (Fig. S4, Online Supplementary Material).

In the majority of ecoregions the influence of winter cold on predicted larval survival varied spatially due to the timing, degree, and frequency of cold events approaching or exceeding the SCP (Fig. S4, Online Supplementary Material). Prior to the 1990s, winter temperatures in the Blue Mountains, Idaho Batholith, and southern Rockies/North approached or dropped below the predicted SCP of beetles, but cold events were rare during the period when population growth rates were estimated (1996–2010). There was also a diminishing frequency of cold events in all of the other ecoregions, but in some ecoregions winter temperatures caused significant mortality during the period when growth rates were estimated. For

example, in the Middle Rockies estimated survival averaged 0.42 ± 0.08 after cold snaps in the 1998 and 2005 beetle years when winter temperatures averaged -29.5 ± 1.7 $^{\circ}\text{C}$.

The model predicted an overall proportional increase in annual survival (demographic release, I) of 1.18 ± 0.16 (range 1.04–1.71) due to 3.8 ± 1.6 $^{\circ}\text{C}$ of warming between the periods 1980–1990 and 1991–2011 (Fig. 4, Fig. S4, Online Supplementary Material). However, there was notable spatial variation in the degree of warming and its expected effects on *D. ponderosae* survival (Fig. 5) between these periods due to the nonlinear relationship between expected survival and minimum phloem temperature (Fig. 4). Populations inhabiting areas with the coldest temperatures [e.g., Middle Rockies/Western MT (14), Middle Rockies/Yellowstone (15), Middle Rockies/

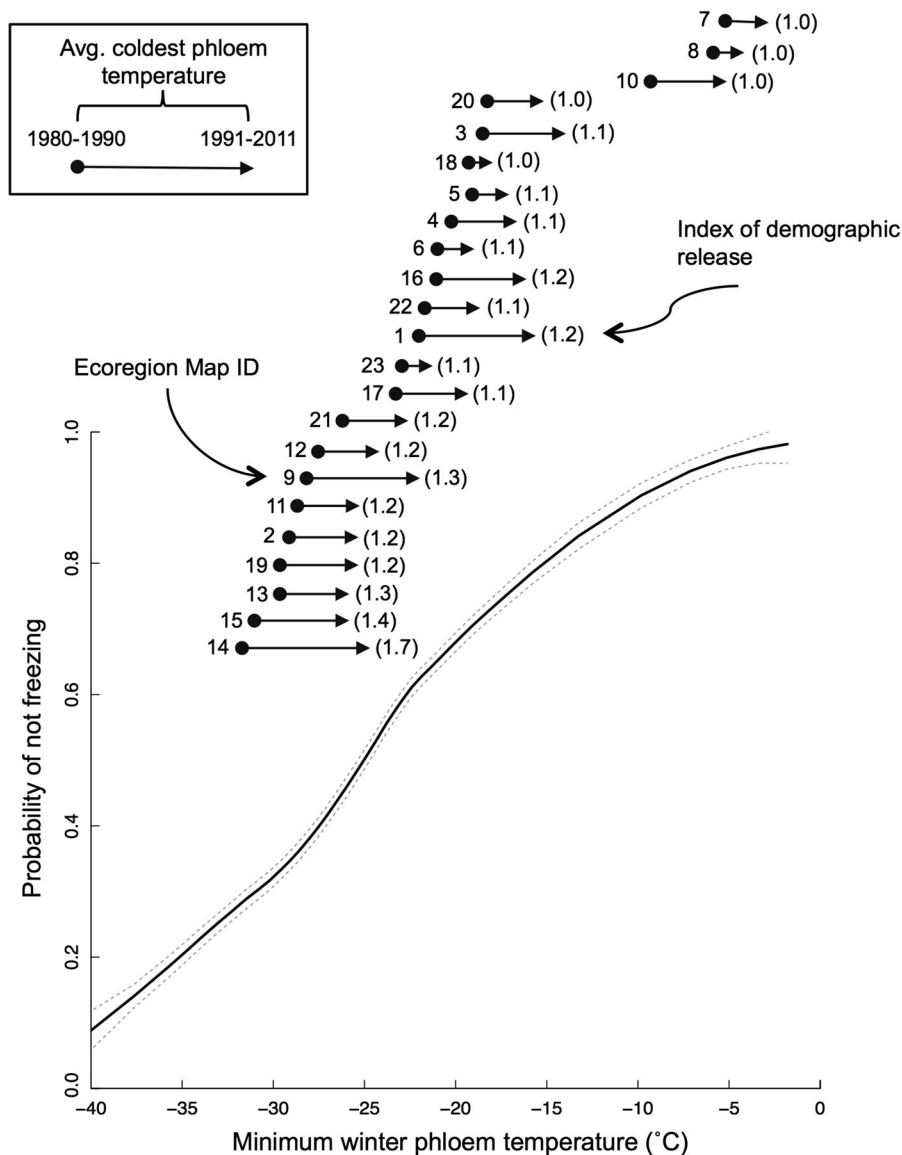


Fig. 4 The demographic effect of warming on *D. ponderosae* varies across its geographical distribution due to the nonlinearity in survival with respect to winter temperature. *Solid line* Expected survival ($\pm 95\%$ CI) of *D. ponderosae* as a function of minimum phloem temperature using the cold tolerance model (Régnière and Bentz 2007). *Points* to the left of *arrows* denote historical minimum phloem temperature of each ecoregion during 1980–1990 and correspond to values on the x-axis. *Numbers* to the left of the *points* refer to ecoregion codes in Fig. 1. *Arrow length* denotes the amount of warming (corresponding to the values on the x-axis) in each ecoregion between the periods 1980–1990 to 1991–2011. The *parenthetical values*

indicate the demographic release (I , Eq. 4) associated with warming for each ecoregion (i.e., the proportional increase in expected survival). For example, ecoregion 14 had the lowest minimum temperatures during 1980–1990, warmed the most (-32 to -24 °C), and experienced the greatest demographic release from warming (expected winter survival almost doubled; $I = 1.7$). At the other extreme, ecoregion 7 was predicted to experience no demographic release ($I = 1.0$) because it began with warm winters that would rarely produce mortality (average minimum = -5 °C during 1980–1990), and also warmed relatively little (-2.5 °C)

Central Mtns (13), and Idaho Batholith (9)] experienced the largest predicted demographic release (I) per 1 °C of warming between these periods (Figs. 4, 5).

Conversely, populations located along the decelerating portion of the response function [e.g., Coast Range/Oregon (7), Coast Range/Washington (8), and

Klamath Mountains (10)] were predicted to experience only subtle increases in survival per 1 °C of warming (Fig. 4).

Discussion

Cold temperature is of demonstrable importance to the survival of *D. ponderosae* and many other plants and animals (Bale et al. 2002; Daly et al. 2012). Since 1960 the coldest night of the year within *D. ponderosae* habitats in the western US has warmed by about 4 °C, which is a very large change relative to more frequently analyzed metrics of climatic temperatures (e.g., mean annual temperature, Christensen et al. 2007); 4 °C is also almost identical to estimates for the same period for the southeastern US (Tran et al. 2007). We have been unable to find comparable estimates for

other continents. Others have noted warming of average winter temperatures (Alward et al. 1999; Luterbacher et al. 2004; Vose et al. 2005), but examination of trends in minimum annual temperatures are rare (but see Edgell 1994; Jung et al. 2002; Macias Fauria and Johnson 2009). It would be useful to know if patterns in the US are representative of other mid to high latitude ecosystems because winter warming has broad relevance to biodiversity and natural resource management (Keen and Furniss 1937; Coulson et al. 2001; Sæther et al. 2002; Crozier 2004; Altwegg et al. 2006). Some notable emerging threats to forest health management are associated with the diminishing likelihood of winter kill of pest insects due to climate change (Weed et al. 2013). For example, winter warming has permitted northward range expansion of the southern pine beetle *D. frontalis* (Zimmermann) in the mid-Atlantic region

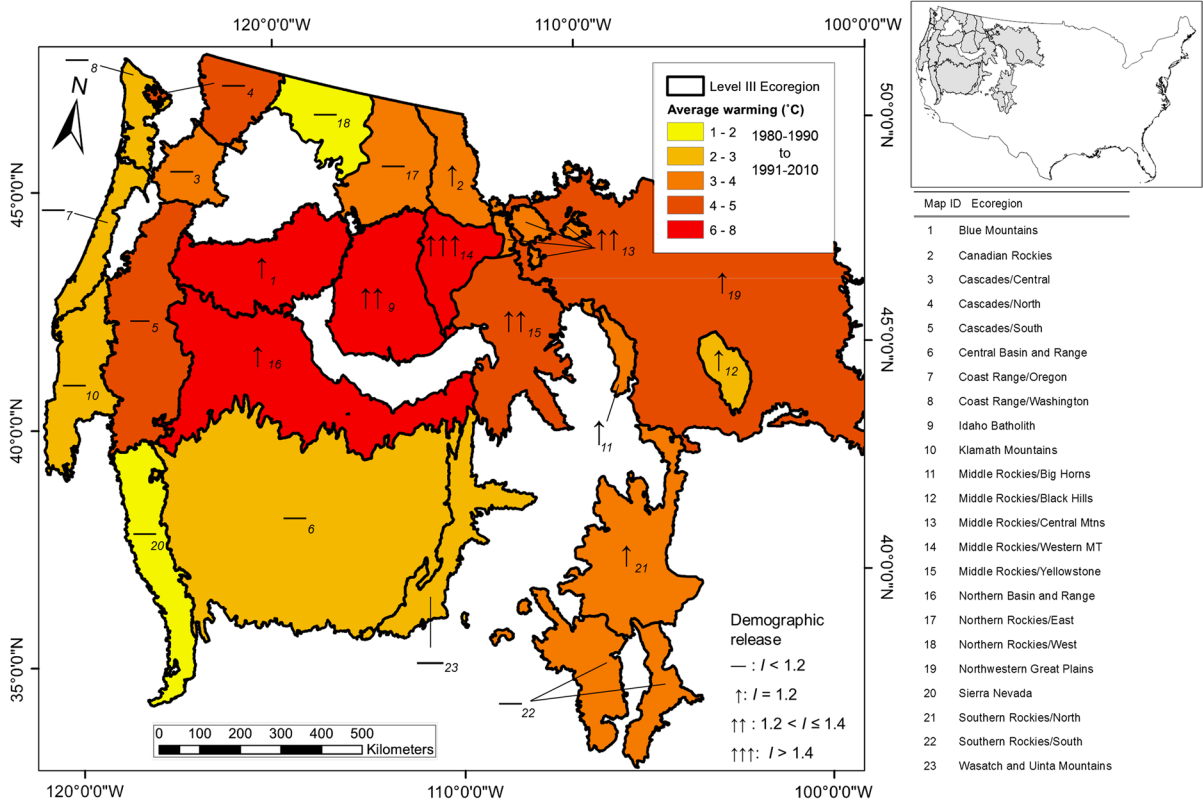


Fig. 5 Geographical variation in the extent of winter warming and associated change in expected survival to *D. ponderosae* (demographic release, *I*) predicted from the cold tolerance model (Régnière and Bentz 2007) between the periods 1980–1990 to 1991–2011 (yellow to red). Modest to high levels

of demographic release ($I \geq 1.2$) associated with winter warming permitted *D. ponderosae* impacts in some ecoregions (arrows), but not in others where the effects of warming were minor ($I < 1.2$, -). Subscript values denote ecoregion map ID codes

of the US (Tran et al. 2007) and of *D. ponderosae* in Canada (Sambaraju et al. 2012), the hemlock woolly adelgid in the northeastern US (Paradis et al. 2008), and at least three species of defoliating Lepidoptera in Europe (Battisti et al. 2005; Jepsen et al. 2008).

The hypothesis that warming winters provide a general explanation for the spatially extensive epidemic of *D. ponderosae* in the western US was supported by the climatic trend (Fig. 2). We then assessed demographic effects to *D. ponderosae* associated with amelioration of winter cold. Our results suggest that broad-scale annual fluctuations between 1996 and 2010 of outbreaking populations have been generally unrelated to variation in extreme minimum winter temperatures (Fig. 3). We did, however, find significant relationships between minimum winter temperature and interannual changes in beetle abundance in some ecoregions that are in good agreement with the independent predictions based on physiology (Fig. 4). Cold temperatures are most likely to influence beetle abundance in regions/years where minimum temperatures average less than -20°C , and sometimes reach -30°C or colder. It is notable that our records of beetle abundance, though spatially extensive, were only from 1996 to 2010 and it was possible that recent epidemics were permitted by warming that occurred before 1996 since climatic amelioration has been occurring for decades (Fig. 2). This is especially true because increases in winter survival are not expected to cause bark beetle outbreaks, but merely to permit them when other circumstances lead to population growth (Tran et al. 2007; Raffa et al. 2008).

Since winter warming has been occurring prior to 1996 we reconstructed expected patterns of winter mortality for each ecoregion back to 1980 using climate records and the physiological model of cold tolerance. This analysis revealed two general patterns with respect to warming and demographic release to *D. ponderosae*. Winter temperatures during the 1980s were more likely than recent times to drop below the lower lethal temperatures of *D. ponderosae* in the Blue Mountains, Canadian Rockies, Idaho Batholith, Middle Rockies/Bighorns, Middle Rockies/Black Hills, Middle Rockies/Central Mountains, Middle Rockies/Western MT, Middle Rockies/Yellowstone, Northern Basin and Range, Northwestern Great Plains, and Southern Rockies/North. In these ecoregions, however, the extent of winter cold amelioration and

associated demographic release varied spatially ($I = 1.2\text{--}1.7$) (Figs. 4, 5). Consistent with the hypothesis of climatic release, the majority of these ecoregions experienced generally rising levels of tree mortality from *D. ponderosae* during 1996 to 2010 (Fig. S1, Online Supplementary Material).

However, physiological reconstruction of historical patterns in winter mortality identified twelve other ecoregions where climatic release from warming minimum winter temperatures seems unlikely as an explanation for recent *D. ponderosae*-caused tree mortality. In these ecoregions, winters dating back to 1980 were never cold enough to drop below the predicted lower lethal temperatures of *D. ponderosae* (Fig. S4, Online Supplementary Material). Hence demographic release associated with warming in these regions did not occur or was relatively small ($I < 1.2$) (Fig. 5). These included mainly coastal and southern ecoregions (Central Basin and Range, Central, Southern and North Cascades, Klamath Mountains, Coast Range/OR, Coast Range/WA, Northern Rockies/East, Northern Rockies/West, Sierra Nevada, Southern Rockies/South, Wasatch and Uinta Mountains). Of these, forests within the Cascades and Wasatch and Uinta Mountains have been experiencing extensive and generally increasing tree mortality from *D. ponderosae*, the Coast Range has been experiencing significant sustained tree mortality, and the Klamath Mountains and Sierra Nevada have been experiencing modest but growing tree mortality (Fig. S1, Online Supplementary Material). These cases contribute to the general pattern of high and generally increasing tree mortality from *D. ponderosae*, but it is unlikely that tree mortality from *D. ponderosae* in these ecoregions was permitted by reduced mortality due to winter cold. In these regions historical winter temperatures rarely dropped to levels that would have caused high winter mortality. The concordance of patterns in *D. ponderosae* impacts across ecoregions where amelioration of winter mortality is and is not a plausible explanation suggest geographic variability in the role of cold temperature on population growth, and highlight that alternative factors also play a role.

The complementary approaches used in this study suggest caution is needed when interpreting the results of correlations between demographic rates and climatic metrics. For example, a positive correlation between minimum temperatures and growth rates was observed in four ecoregions where the physiological

model predicted winter cold to be of minor historical importance to *D. ponderosae* (Central, North, and South Cascades and Southern Rockies/South). Moreover, growth rates were estimated during a period when winters had already warmed well beyond temperatures where sustained cold-induced mortality was likely. Hence these correlations cannot plausibly implicate warming winters in permitting outbreaks in these regions and may simply be spurious or reflect the influence of some other temperature-mediated process important to *D. ponderosae* fitness (Jenkins et al. 2001; Powell and Bentz 2014).

Broad scale synchrony in the abundance of *D. ponderosae* (Aukema et al. 2006, 2008; Chapman et al. 2012) suggests that regionally correlated factors are putative drivers of beetle outbreaks (Moran 1953). Climatic variation in general is a theoretically attractive candidate for driving population fluctuations that are broader than the dispersal capabilities of individuals (Liebhold et al. 2004), and effects of extreme cold on survival is one possible mechanism by which climate might affect *D. ponderosae*. Other candidates include warming year-round temperatures that influence generation time and adult emergence synchrony (Bentz et al. 2014) and drought effects that can weaken tree defenses (Safranyik and Carroll 2006; Chapman et al. 2012; Preisler et al. 2012). However, it is unlikely that any single climatic metric can explain the recent epidemic of *D. ponderosae* across the western US because the region encompasses high spatial variability in climate as evidenced by the tremendous range in baseline climate prior to the epidemic. Moreover, plasticity and genetic variability in temperature-dependent development traits (Bentz et al. 2011b) allow differential population response to changing temperatures across the range of this insect within the western US (Bentz et al. 2014).

The overall relation between winter mortality and *D. ponderosae* abundance in western North America is similar to that for the congener *D. frontalis* in eastern North America (Tran et al. 2007). Both species exhibit dramatic fluctuations in abundance, and in colder habitats release from the constraint of winter mortality can favor population growth. On both sides of the continent, amelioration of winter temperatures by about 4 °C over the last 50 years is permitting epidemics of both species in northern forests that were previously shielded by cold temperatures that enforced distribution limits (Weed et al. 2013). Once

released, however, and in warmer parts of their distributions, population growth is mainly attributable to factors other than winter mortality.

Several factors important to *Dendroctonus* population success were not considered in our study (e.g., suppression management, natural enemies, and mutualistic fungi on which the beetle larvae depend). Foremost among these are forest structure and composition that have been influenced by a history of disturbance regimes (Peet 2000; Kinloch 2003) and management practices across the study area. Mature, even-aged, monospecific stands of lodgepole and ponderosa pines are naturally susceptible to *D. ponderosae* (Raffa et al. 2008; Fettig et al. 2014). High frequency in the landscape of stands susceptible to *D. ponderosae* can promote landscape-scale epidemics because it favors successful dispersal and aggregation by beetles (Safranyik and Carroll 2006; Bone et al. 2013; Fettig et al. 2014). Lodgepole and ponderosa pine stands throughout much of our study area are a frequent consequence of clear-cut logging and wildfires (Axelson et al. 2009), which were both widespread during the early 1900s (Peet 2000). Active fire suppression since then has resulted in more of those stands surviving into the 1990s than would have otherwise been the case (Taylor and Carroll 2004; Raffa et al. 2008).

Our results add to evidence that global climate change can have predictably different effects on insect populations across their geographical range (Robinet and Roques 2010; Buckley and Kingsolver 2012). The inherently strong nonlinearity in survival with respect to minimum winter temperature is a general mechanism by which uniform warming can generate strong demographic effects on poleward and high elevation populations while being of little consequence elsewhere in the distribution of the same species. Of course winter survival is only one of several traits affected by temperature that can influence abundance. Climatic effects on the seasonal progression of life stages can also vary geographically, both due to differential climatic forcing and to evolved differences in development as a function of temperature (Bentz et al. 2014; Valtonen et al. 2014). The very general tendency for warming temperatures to accelerate development probably works to the benefit of many insect populations at mid to high latitudes (Frazier et al. 2006), but the same warming may be detrimental to populations at southern latitudes because survival

under heat, like survival under cold, is inherently nonlinear (Deutsch et al. 2008; Mora et al. 2013). Understanding the processes that yield geographic patterns in population responses to climate change is crucial for anticipating and mitigating impacts on biodiversity and natural resource management.

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