Forest Ecology and Management 545 (2023) 121307

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Factors associated with bark beetle infestations of Colorado Plateau ponderosa pine using repeatedly-measured field plots

E. Matthew Hansen [a,*], Barbara J. Bentz [b], James C. Vandygriff [c], Chris Garza [d]

[a] Rocky Mountain Research Station, 860 N 1200 E, Logan, UT 84321, USA
[b] Rocky Mountain Research Station, 860 N 1200 E, Logan, UT 84321, USA
[c] Rocky Mountain Research Station (retired), 860 N 1200 E, Logan, UT 84321, USA
[d] Siglo Group, 1306 E Cesar Chavez St, Austin, TX 78702, USA

ARTICLE INFO

Keywords:
Bark beetles
Ponderosa pine
Colorado Plateau
Drought
Mountain pine beetle
Risk rating

ABSTRACT

Decades of research have brought increasing focus to the biotic and abiotic factors associated with bark beetle infestation of North American conifers. Information is lacking, however, regarding beetle-caused mortality for ponderosa pine of the Colorado Plateau. From 1995 to 2019, we installed and periodically remeasured permanent plots in this forest type with a goal of identifying factors related to infestation probability including tree and stand characters, and abiotic factors such as temperature and precipitation. Forty-eight sites were distributed throughout the Colorado Plateau, each with two transects of 10 contiguous ~ 0.04 ha circular plots. Stand and tree conditions were measured or interpolated for each year from plot establishment in 1995 until the final measurements in 2019. Temperature, precipitation, and other abiotic conditions were estimated from Daymet interpolations. We used a generalized linear mixed model to identify significant explanatory variables resulting in the best accuracy of predicting stem-level bark beetle-caused pine mortality. Tree and stand conditions were found related to the probability of infestation. Pines >15.2 cm dbh were more likely to become infested compared to pines below that threshold; no relationship was found above that breakpoint. Similarly, stems 80–180 years old had elevated probability of infestation compared to stems < 80 years; stems > 180 years were intermediate. Pines with poor crown vigor (low crown volume, suppressed or intermediate canopy position) were more likely to become infested compared to pines with good crown vigor (high crown volume, dominant or open grown canopy position). Pine basal area (BA), a surrogate for intra-species competition, was positively related to probability of infestation. Pine BA infested the previous year, a surrogate for beetle population size, was also positively related to probability of infestation. Several drought- and precipitation-related variables resulted in similar model accuracy. Best model fit among these, by a slight margin, was contemporaneous climate water deficit (CWD), a measure of plant water stress, summed from April-August. Increasing CWD was associated with increased probability of infestation. Finally, counts of days above 16 °C the previous year were negatively related to infestation probability. That is, relatively warm weather during the previous year was associated with reduced beetle success, possibly because it can result in fractional beetle life cycles that disrupt synchronized attacks on new hosts or leave overwintering brood in less cold hardy life stages.

1. Introduction

Bark beetles are a major disturbance agent in coniferous forests of western North America, playing important roles in ecosystem processes and functioning such as carbon and nutrient cycling (Hansen 2014). During the three decades ending in 2012 in the western U.S., tree mortality due to bark beetles in the genus *Dendroctonus* (Coleoptera: Curculionidae, Scolytinae) occurred on 6.6 million ha, exceeding the canopy area killed by wildfire over the same interval (Hicke et al. 2016). Changes in climate have contributed to recent bark beetle success and widespread host mortality in some areas, directly via temperatures favorable for insect survival and development, and indirectly via environmental stressors that compromise host tree defenses (Weed et al. 2015; Kolb et al. 2016; Fettig et al. 2019; Stephenson et al. 2019).

* Corresponding author.
E-mail addresses: earl.hansen@usda.gov (E. Matthew Hansen), barbara.bentz@usda.gov (B.J. Bentz), jvandygr@gmail.com (J.C. Vandygriff), cgarza@siglogroup.com (C. Garza).

https://doi.org/10.1016/j.foreco.2023.121307
Received 15 June 2023; Received in revised form 24 July 2023; Accepted 26 July 2023
Available online 2 August 2023

Weather, however, is one of several factors concurrently needed to result in bark beetle outbreaks including availability of susceptible host trees and extant beetle populations (Raffa et al. 2008). Decades of research in some conifer systems has contributed to an understanding of stand conditions and weather favorable for bark beetle population success (Bentz et al. 2019, Bentz et al. 2021). These efforts have informed management options for resource managers to reduce stand susceptibility and promote long-term resiliency to large-scale tree mortality events in high value areas (Fettig et al. 2014). Tree, stand, and environmental factors associated with bark beetle infestations, however, are undocumented for southwestern ponderosa pine (Pinus ponderosa Douglas ex Lawson & C. Lawson) and a previous attempt at stand risk rating (Munson and Anhold 1995) was extrapolated from other regions. Recent genetic analyses support three separate species previously recognized as *P. ponderosa*. The geographic boundaries of the two new species, *P. brachyptera* and *P. scopulorum*, overlap within the Colorado Plateau (Willyard et al. 2021). Without detailed plot-level information, we retain the use of *P. ponderosa*.

Host tree factors known to be important for *Dendroctonus* bark beetle population growth include high proportions of large diameter host trees that are a suitable size for high levels of offspring production. The propensity for bark beetles to infest large diameter trees in dense stands was noted over 100 years ago (Hopkins 1910) and this relationship has been subsequently investigated in multiple host tree systems (e.g., Massey and Wygant 1954; Cole and Amman 1980; Negrón 1998). In lodgepole pine (*Pinus contorta*) systems, for example, mountain pine beetle (MPB, *D. ponderosae* Hopkins) preferentially attacks the largest diameter trees, and most surviving pines in post-outbreak stands come from intermediate and suppressed crown classes (Hansen 2014). Unlike in lodgepole pine systems, many larger diameter ponderosa pines are not attacked during bark beetle outbreaks. Although some studies found a positive relationship between diameter and probability of infestation (Negrón et al. 2008; Klenner and Arsenault 2009), others found little relation beyond about 20 cm dbh (McCambridge 1982; Olsen et al. 1996). The role of tree size in stand susceptibility to bark beetles varies depending on the location, density, and age classes of stands (Sartwell and Stevens 1975; Negrón and Popp 2004; Schmid and Mata 2005). In addition to tree size, stands with the highest basal area of host trees have the greatest likelihood of bark beetle-caused mortality (Fettig et al. 2014).

Environmental factors associated with increased bark beetle-caused mortality in conifer systems include drought and warm temperatures (Negrón et al. 2009; Santos and Whitham 2010; Chapman et al. 2012; Egan et al. 2016; Hart et al. 2017), the combination of which has been coined "hotter droughts" (Millar and Stephenson 2015). Water stress can compromise the amount and type of tree defenses used against insect attacks, although tree responses can be complex (McDowell et al. 2008; Anderegg et al. 2015). Kolb et al. (2019) found that experimental water stress predisposed ponderosa pines to bark beetle attack, although the main effect was a reduction in induced resin flow, rather than changes in terpene composition. Drought is a landscape-level effect that provides abundant stressed hosts that can more easily be colonized, increasing the likelihood of a beetle outbreak (Raffa et al. 2008). A recent hot drought in central and southern California, estimated to be the most severe in 1000 years (Robeson 2015), was associated with the death of $>$ 100 million trees, in part due to bark beetle attacks on water-stressed trees (Fettig et al. 2019; Koontz et al. 2021).

In addition to the indirect effects of water stress on host trees, warm temperatures can directly influence bark beetle population success by reducing cold temperature-related mortality (Régnière and Bentz 2007) and altering the timing of life cycle events including generation length (Hansen and Bentz 2003; Bentz et al. 2021). Reduced generation length can lead to accelerated bark beetle population growth, in turn causing increased tree mortality per year. For example, empirical evidence linked the regionalized spruce beetle (*D. rufipennis* Kirby) outbreaks in Alaska during the 1990s with runs of unusually warm summer temperatures that resulted in univoltine (one generation per year) rather than the typical semivoltine brood (one generation per two years) (Berg et al. 2006). Recent MPB-caused mortality of high-elevation five-needle pines in the northern U.S. Rocky Mountains was similarly influenced by warm conditions that promoted the univoltine cycle over the semivoltine cycle (Bentz et al. 2014). For multivoltine (two or more generations per year) bark beetle species such as *Ips* spp. and western pine beetle (*D. brevicomis* LeConte), warm temperatures might increase the number of full or partial generations per year and, therefore, accelerate host mortality particularly during drought (Robbins et al. 2022; Bentz et al. 2023). The influence of warm temperatures on MPB success, however, is more nuanced. MPB has a strong tendency to develop on the univoltine cycle regardless of geographic region, elevation, or year-to-year weather variations (Bentz et al. 2014). The prevalence of univoltinism across such divergent conditions is a result of locally-adapted lifestage-specific developmental rates, a facultative prepupal diapause, and reproductive diapause in variants at southerly latitudes (Bentz and Hansen 2017; Bentz et al. 2021; Hansen unpublished data). These MPB traits constrain the possibility of a bivoltine life cycle (Bentz and Powell 2014; Soderberg et al. 2020; Bentz et al. 2021). Excessive warming outside the bounds of adaptation for univoltinism more likely leads to fractional voltinism wherein a generation is completed in less than one year but fewer than two generations occur per year as was observed at a warm southern California site (Bentz et al. 2014). This outcome may be seasonally maladaptive for important traits such as synchronized emergence needed to overwhelm host defenses and the timing of optimal life stages for overwintering (Powell and Logan 2005). Therefore, although climate warming can result in accelerated bark beetle population growth and concomitant host mortality, for some species and conditions, warming might lead to local population collapses. In the latter case, it could be said that there is a range of temperatures associated with the univoltine cycle and weather warmer or colder than that reduces the probability of beetle success.

Bark beetle population size has been correlated with host tree mortality in several systems including MPB in lodgepole pine and spruce beetle in spruce (Reynolds and Holsten 1994; Hansen et al. 2006; Safranyik and Carroll 2006; Preisler et al. 2012). In these systems, very large population density can result in self-amplifying population outbreaks wherein widespread host mortality continues despite environmental conditions returning to levels less favorable for bark beetle success (Raffa et al. 2008). In contrast, a widespread pinyon ips (*Ips confusus* LeConte) outbreak in the southwestern U.S. that was associated with a regional drought in 2001–2003 ended after precipitation returned to more typical levels (Kleinman et al. 2012).

Our goal was to investigate the probability of bark beetle-caused mortality in ponderosa pine of the Colorado Plateau as a function of tree and stand characters, drought, temperature, and extant bark beetle population size. We initiated permanent plots, predominately in areas with endemic or incipient-epidemic bark beetle population levels, across the Colorado Plateau during 1995–96. The plots were remeasured every 2–7 years though 2019 (Chojnacky et al. 2000; Hansen et al. 2015). This long-term dataset enabled us to associate bark beetle infestations with changes in biotic and abiotic conditions at the tree and stand level.

2. Materials and methods

2.1. Field data

Permanent plots were installed across the Colorado Plateau at 45 sites in Utah, Arizona, and Colorado during 1995 and 1996 (Chojnacky et al. 2000). Three additional sites were measured during 2019 (Fig. 1, Table 1). Site selection was from areas with: 1) ponderosa pine as the major component (generally $>$ 50% of stand composition and avoiding stands with younger, small, or sparse ponderosa pine); 2) current bark beetle activity in or near the site (identified by aerial detection survey maps; some sites were intentionally installed in uninfested stands to

Fig. 1. Locations of the 45 sites installed during 1995–96 across the Colorado Plateau to monitor bark beetle activity in ponderosa pine type and to identify the factors associated with infestations. Three additional sites were installed 2019 on the Dolores Ranger District, San Juan National Forest, Colorado to augment the population of infested stems in the dataset. Each site has two parallel transects of 10 contiguous ~ 0.04 ha (1/10th acre) fixed radius plots with 100% survey of stems > 7.6 cm dbh. The green polygons depict the distribution of ponderosa pine. RD = Ranger District; NP = National Park.

represent endemic conditions); 3) road access within ~ 0.5 km; and 4) no evidence of vegetation management within the previous ~ 40 years. During plot establishment, field crews subjectively rated 15 of the original 45 sites as having endemic beetle conditions, 20 had increasing conditions, six had epidemic conditions, and four were rated as post-epidemic. Plot locations within sites were randomized by azimuth and distance from a reference point. Each site consisted of two parallel pairs of 10 contiguous ~ 0.04 ha (1/10 acre) circular plots (Chojnacky et al. 2000). The two transects were spaced at 80 m. At two sites, the parallel transect configuration was modified to fit within the local stand boundaries.

At each plot, all trees > 7.6 cm dbh were identified by species, measured for dbh, assessed for status (live, beetle-attacked, or other mortality), and classified using Keen's age and crown vigor classes (Keen 1943). For bark beetle-attacked trees, bark was removed to identify species by collecting adults and/or observing the species-unique egg gallery pattern. Year of attack was estimated by presence/absence and maturity of brood, relative sapwood moisture under the bark, and host needle color and retention (Chojnacky et al. 2000). These characters are unfailing for current and 1-year old attacks, becoming more variable and, therefore, less accurate with time. We consider estimates beyond 3-years old to be unreliable and such trees were classified as "older" beetle-caused mortality. The sites were visited every 2–7 years thereafter (Table 1). We updated the status of each tree during each visit and, for recently infested pines, identified bark beetle species and estimated year of attack. Additionally, ingrowth was added to the dataset, i.e., trees that attained 7.6 cm dbh since the previous visit. During 2012, we updated all variables (status, dbh, Keen crown vigor class, etc.) and added fuel load transects (Hansen et al. 2015). Final visits occurred during 2019 including remeasurement of all pine diameters. That year, we also installed three new sites northwest of Dolores, Colorado where a significant, ongoing bark beetle outbreak presented an opportunity to augment the dataset with additional infested trees. This decision was made because infested trees were poorly represented in the original dataset.

2.2. Building the dataset

From the field-collected data, we developed a dataset that included tree-level estimates of stem and stand conditions plus environmental variables for each year from three years before the first measurements until the final measurements. Observations in this dataset only included ponderosa pine although some plot-level variables, such as total basal area (BA; m^2 ha^{-1}), included all species (in descending order of total abundance: white fir, *Abies concolor*; Gambel oak, *Quercus gambelii*; quaking aspen, *Populus tremuloides*; blue spruce, *Picea pungens*; Douglas-

Table 1
Location, elevation, installation year, and remeasurement years of sites.

Site	Latitude (°N)	Longitude (°W)	Elevation (m)	Installation and remeasurement years
Bryce National Park, Utah				
Dave's Hollow	37.64	112.18	2418	1995, 1998, 2002, 2004, 2012
Fairyland Point	37.65	112.16	2377	1995, 1998, 2002, 2004, 2012
Horse Corrals	37.62	112.18	2438	1995, 1998, 2002, 2004, 2012
Paria View	37.60	112.17	2461	1995, 1998, 2002, 2004, 2012
Cedar City Ranger District, Dixie National Forest, Utah				
Blue Spring Mountain	37.66	112.69	2778	1996, 1998, 2002, 2004, 2006, 2012, 2019
Bower's Flat	37.55	112.62	2515	1995, 1998, 2002, 2004, 2006, 2012, 2019
Cooper Knoll	37.71	112.60	2511	1995, 1999, 2002, 2004, 2006, 2012, 2019
Dry Valley	37.65	112.68	2623	1996, 1998 (site cut after 1998)
Duck Creek	37.53	112.65	2561	1995, 1998, 2002, 2004, 2006, 2012, 2019
Rock Canyon	37.69	112.60	2519	1996, 1999, 2002, 2004, 2006, 2012, 2019
Strawberry Knolls	37.51	112.63	2498	1995, 1999, 2002, 2004, 2006, 2012, 2019
Strawberry Point	37.45	112.70	2622	1996, 1998, 2002, 2004, 2006, 2012, 2019
The Pass	37.72	112.61	2568	1996, 1999, 2002, 2004, 2006, 2012, 2019
Tommy Creek #1	37.62	112.68	2701	1995 (site cut after 1995)
Tommy Creek #2	37.61	112.66	2509	1995 (site cut after 1995)
Willis Creek	37.51	112.69	2684	1996, 1998, 2002, 2004, 2006, 2012, 2019
Yellowjacket Spring	37.66	112.67	2649	1995, 1999, 2002, 2004, 2006, 2012, 2019
Beaver Ranger District, Fishlake National Forest, Utah				
Indian Creek	38.42	112.50	2378	1996, 1998, 2001, 2004, 2006, 2012, 2019
Little Reservoir	38.26	112.49	2247	1996, 1998, 2001, 2004, 2006, 2012, 2019
South Creek	38.17	112.50	2316	1996, 1998, 2001, 2004, 2006, 2012, 2019
Grand Canyon National Park, Arizona				
Robber's Roost Spring	36.28	112.08	2612	1996, 1998, 2002, 2007, 2012
The Basin #1	36.27	112.12	2558	1996, 1998, 2002, 2007, 2012
The Basin #2	36.25	112.11	2514	1996, 1998, 2002, 2007, 2012
North Kaibab Ranger District, Kaibab National Forest, Arizona				
Crane Lake	36.53	112.14	2621	1995, 1999, 2002, 2007, 2012
Crane Lake West	36.53	112.15	2621	1995, 1999, 2002, 2007, 2012
Dog Lake	36.43	112.08	2684	1995, 1999, 2002, 2007, 2012
Jolly Sink	36.69	112.19	2462	1995, 1999, 2002, 2007, 2012
Jolly Sink #2	36.66	112.18	2534	1995, 1999, 2002, 2007, 2012
Pleasant Valley	36.51	112.13	2644	1995, 1999, 2002, 2007, 2012
Telephone Hill	36.53	112.15	2621	1995, 1999, 2002, 2007, 2012
Monticello Ranger District, Manti-LaSal National Forest, Utah				
Butts	37.68	109.78	2440	1996, 1998, 2002, 2004, 2006, 2012, 2019
Butts 2	37.67	109.79	2480	1996, 1999, 2002, 2004, 2006, 2012, 2019
Corrals	37.68	109.77	2438	1996, 1999, 2002, 2004, 2006, 2012, 2019
Hammond	37.68	109.79	2464	1996, 1998, 2002, 2004, 2006, 2012, 2019
Kigalia	37.67	109.83	2560	1996, 1998, 2002, 2004, 2006, 2012, 2019
Peavine	37.66	109.88	2560	1996, 1999, 2002, 2004, 2006, 2012, 2019
Twin Springs	37.66	109.90	2533	1996, 1999, 2002, 2004, 2006, 2012, 2019
Dolores Ranger District, San Juan National Forest, Colorado				
Doe Canyon	37.72	108.67	2438	2019
Glade Mountain	37.71	108.67	2435	2019
Peeled Pine	37.76	108.70	2493	2019
Pagosa Ranger District, San Juan National Forest, Colorado				
Coffee Creek	37.32	107.34	2332	1995, 1999, 2002, 2006, 2012, 2019
First Fork	37.36	107.32	2267	1995, 1999, 2002, 2006, 2012, 2019
First Notch	37.26	107.38	2487	1995, 1999, 2002, 2006, 2012, 2019
Horse Creek	37.30	107.32	2457	1995, 1999, 2002, 2006, 2012, 2019
Sawmill Reservoir	37.27	107.21	2439	1995, 1999, 2002, 2006, 2012, 2019
Ouray Ranger District, Uncompahgre National Forest, Colorado				
Haley Draw	38.55	108.52	2613	1996, 2000, 2007, 2012

(*continued on next page*)

Table 1 (*continued*)

Site	Latitude (°N)	Longitude (°W)	Elevation (m)	Installation and remeasurement years
Haley Draw 2	38.54	108.52	2448	1996, 2000, 2007, 2012
Haley Draw 3	38.55	108.52	2569	1996, 2000, 2007, 2012

fir, *Pseudotsuga menziesii*; juniper; *Juniperus* spp.; limber pine, *Pinus flexilis*; subalpine fir, *Abies lasiocarpa*; mountain mahogany, *Cercocarpus* spp.; and Engelmann spruce, *Picea engelmannii*). To estimate tree diameter at each time step, average annual diameter growth for each stem was first estimated by dividing dbh increment from the first to last measurement by the number of years between measurements. Then, the dbh for any given year was estimated by taking the dbh at the final measurement and subtracting the average annual increment times the number of years between that final measurement and the year of the estimate. We added diameter class as an explanatory variable because small pines are typically not attacked by *Dendroctunus* species and some studies found no linear relationship between attack rates and ponderosa pine dbh beyond ~ 20 cm (McCambridge 1982; Olsen et al. 1996).

Live trees were assumed to be live throughout the study, whereas bark beetle-infested trees were removed from the dataset the year after attack. Trees estimated to have been infested > 3 years before measurements were not used in analyses because of low confidence in year-of-attack estimates. Keen crown vigor class was assumed to be stable from plot installation until the 2012 remeasurements; few trees changed classes at that time. Keen's "age class 4" is defined, in part, as trees older than 300 years. Few trees in our plots were measured or estimated at that age, so we collapsed these into age class 3 during analyses (180–300 years).

Plot level data were calculated for each year including BA, stand density index (SDI), and stem counts for live ponderosa pine only and for all live stems. We also calculated the proportion of ponderosa pine among the live trees by BA and stem counts. Further, we calculated the average live ponderosa pine dbh, the average dbh of pines > 20 cm dbh, and the maximum ponderosa pine dbh at each plot. Each of these were also calculated at the site level (i.e., summed or averaged over the 20 plots). Many of the tree-, plot-, and site-level variables we investigated are analogs of variables found significantly related to infestation probability by Garza (2015), Stevens (1980), and Chojnacky et al. (2000).

Stem counts and basal area of pines infested the previous year were used as surrogates for beetle population size and these were calculated at the plot and site level. In preliminary analyses we used aerial detection survey (ADS) data as a surrogate for beetle population size but these proved unworkable. In addition to spatial, temporal, and species errors that can be problematic to ADS (Coleman et al. 2018), US Forest Service-Forest Health Protection reporting was modified over the years of this project. For example, older data were reported as group-wise polygons with stem counts while newer data were reported as larger polygons with estimates of stems per acre. Additionally, the three Forest Service Regions within the footprint of this study adopted different standards through time and, perhaps most critically, flight coverage was not available for all years at our sites.

Environmental variables were derived from Daymet data (https://daymet.ornl.gov/). These are daily weather data interpolated from ground observations, gridded at 1 × 1 km resolution. Data for the continental U.S. are available starting from 1980 and include daily minimum and maximum temperature, precipitation, and vapor pressure. From these data we computed a suite of climate variables considered influential to bark beetle success or host stress including analogs of variables found important in studies such as Bentz et al. (2010) and Preisler et al. (2012). Temperature variables included: 1) average temperatures computed at annual, seasonal, and monthly resolutions; 2) average and extreme minimum winter temperatures (Régnière and Bentz 2007); 3) annual, seasonal, and monthly degree-day accumulations above various threshold values found important for prepupal diapause development or aversion (Bentz and Hansen 2017, Bentz et al. 2021); and 4) annual, seasonal, and monthly counts of days the maximum temperature exceeded these same threshold values (Table 2). Heat load index, a function of slope, aspect, and latitude, was calculated for each plot (McCune and Keon 2002). For many of these variables we also calculated time lags up to five years before the year of interest.

Similarly, average and accumulated precipitation was computed for annual, seasonal, and monthly intervals. These also included time lags as well as accumulated values up to five years before the observed year. Finally, we calculated climatic water deficit (CWD) which reflects available water as a function of precipitation, temperature, aspect, slope, and actual evapotranspiration (Stephenson 1990, Lutz et al. 2010). CWD was calculated twice, once using daily Daymet data at a 1 km × 1 km resolution and once using monthly modeled 800 m × 800 m PRISM data (PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu). CWD was calculated for multiple intervals: monthly (e.g., August), seasonal (e.g., May-August), annual, and coincident with an approximate MPB generation ($August_{n-1}$ – $August_n$). The final dataset includes over 200 explanatory variables measured or calculated for each observation including tree characters, plot- and site-level stand conditions, precipitation, drought, temperature, and beetle pressure (Table 2).

2.3. Analyses

The dataset has 229,544 observations for 13,150 ponderosa pines; the average record for each stem spans about 17.4 years. Only 1,236 of these were beetle-killed, however, which confounded analyses. We planned to use generalized linear mixed models (PROC GLIMMIX, SAS Institute, Inc., Cary, NC, USA; Littell et al. 2006) which can account for autocorrelation of residuals with annually repeated measurements (i.e., response error distribution specified as autoregressive lag 1) but the covariance matrices for this size dataset far outstripped our computing resources. We also explored classification trees but these were not appropriate for such a large dataset wherein one response class is represented in < 1% of observations. Plot- and site-level responses were also tested during preliminary analyses.

Instead, we returned to generalized linear mixed models but with a subset of the dataset for which the covariance matrices could be computed. This smaller dataset came from observations at plots with epidemic and collapsing beetle populations to maximize any signal from tree, stand, and environmental conditions associated with those converse outcomes of beetle-caused mortality or survival. The model used tree-level binary response (live or infested) with AR(1) response error distribution. Infested stems were identified from sites with at least two infested trees per year (i.e., 2 + trees per 20 plots per year). Counts or BA of pines infested the previous year, surrogates for beetle population size, were consistently important in preliminary analyses but these data are not available for the first year of data at any given site. For example, sites established in 1995 are assumed to have satisfactory estimates of infestation date as early as 1992, so 1992 is the first record available. But observations estimated as infested during 1992 lack data for previous year infestation and, therefore, cannot be used in models if this beetle population surrogate is included. After applying these restrictions, the dataset had 851 observations of beetle-infested trees.

For the live tree population, we focused on trees from sites with "collapsing" beetle activity. These were identified from sites with no infested stems during year *n* and with at least 3 trees infested during year *n-1*. That is, the site had a source of beetles during year *n* yet conditions were apparently not favorable for new attacks. There were 7,514 observations of a live tree meeting these conditions. Although this population of live trees may represent environmental drivers of collapsing beetle populations, it may fail to capture the effects of stand conditions

Table 2
Names and definitions of explanatory variables tested in models predicting probability of tree-and plot-level bark beetle-caused pine mortality.

Variable name	Definition
Tree variables	
Keen_age	Keen age class
Keen_crn	Keen crown class
Dbh	Diameter at breast height
D_Class	Diameter class
BA	Basal area
Dbhsr	Square-root dbh
Plot variables	
plot_pine_ba	BA of plot-level live pine
plot_pine_sdi	Stand density index (SDI) of plot-level level pine
plot_pines	Plot-level live pine stem count
totalBA	Plot-level live BA, all species
totalSDI	Plot-level live SDI, all species
total_stems	Plot-level live tree stem count
propBA_plot	Plot-level pine proportion of live BA
prop_stems_plot	Plot-level pine proportion of live stem count
max_pine_dbh	Plot-level largest pine
mean_pine_dbh	Plot-level average pine dbh
mean_big_pine_dbh	Plot-level average of pines > 20 cm dbh
Site variables	
site_pine_ba	Site-level live pine BA
site_pine_sdi	Site-level live pine SDI
site_pines	Site-level live pine stem count
totalBAsite	Site-level all species live BA
totalSDIsite	Site-level all species live SDI
site_stems	Site-level all species live stem count
propBAsite	Site-level pine proportion live BA
prop_stems_site	Site-level pine proportion live stem count
max_pine_dbh_site	Site-level largest pine
mean_pine_dbh_site	Site-level average pine dbh
mean_big_pine_dbh_site	Site-level average dbh of pines > 8″
Beetle population surrogates	
beetle_ba_site	Site-level BA of pines infested the previous year
beetle_trees_site	Site-level stem count of pines infested the previous year
Precipitation variables	
prcp_sumApr_Aug	Total April-August precipitation (mm) for current year
prcp_sumJune_Aug	Total June-August precipitation for current year
prcp_sumAugust	August precipitation for current year
cum_prec	Total water year precipitation of current and previous year
cum3_prec	Total water year precipitation of current and previous 2 years
cum4_prec	Total water year precipitation of current and previous 3 years
cum5_prec	Total water year precipitation of current and previous 4 years
prev_prec	Total water year precipitation of previous year
current_prec	Total water year precipitation of current year
current_swe	Total snow water equivalent for current water year
cum_JunAug_prec	Total June-August precipitation for current and previous year
prev_JunAug_prec	June-August precipitation for previous year
ann_avg_prec	Long-term average precipitation (mm; water-year)
prism_ppt_Aug	PRISM-estimated current August precipitation
prism_cwd_Aug	PRISM-calculated cumulative water deficit for August of current year
prism_ppt_Jul	PRISM-estimated current July precipitation
prism_cwd_Jul	PRISM-calculated cumulative water deficit for July of current year
prism_ppt_JA	PRISM-calculated precipitation for July-August of current year
prism_cwd_JA	PRISM-calculated cumulative water deficit for July-August of current year
prism_ppt_JJA	PRISM-calculated precipitation for June-August of current year
prism_cwd_JJA	PRISM-calculated cumulative water deficit for June-August of current year
prism_ppt_MJJA	PRISM-calculated precipitation for May-August of current year
prism_cwd_MJJA	PRISM-calculated cumulative water deficit for May-August of current year
prism_ppt_AA	PRISM-calculated precipitation for April-August of current year
prism_cwd_AA	PRISM-calculated cumulative water deficit for April-August of current year
prism_ppt_MA	PRISM-calculated precipitation for March-August of current year
prism_cwd_MA	PRISM-calculated cumulative water deficit for March-August of current year
prism_ppt_annual	PRISM-calculated precipitation for current year
prism_cwd_annual	PRISM-calculated cumulative water deficit for current year
prism_ppt_SO	PRISM-calculated precipitation for September-October of previous year
prism_cwd_SO	PRISM-calculated cumulative water deficit for September-October of previous year
Daymet_cwd_Aug	Daymet-calculated cumulative water deficit for August of current year
Daymet_ppt_Jul	Daymet-estimated current July precipitation
Daymet_cwd_Jul	Daymet-calculated cumulative water deficit for July of current year
Daymet_ppt_JA	Daymet-calculated precipitation for July-August of current year
Daymet_cwd_JA	Daymet-calculated cumulative water deficit for July-August of current year
Daymet_ppt_JJA	Daymet-calculated precipitation for June-August of current year
Daymet_cwd_JJA	Daymet-calculated cumulative water deficit for June-August of current year
Daymet_ppt_MJJA	Daymet -calculated precipitation for May-August of current year
Daymet_cwd_MJJA	Daymet-calculated cumulative water deficit for May-August of current year
Daymet_ppt_AA	Daymet-calculated precipitation for April-August of current year
Daymet_cwd_AA	Daymet-calculated cumulative water deficit for April-August of current year
Daymet_ppt_MA	Daymet-calculated precipitation for March-August of current year
Daymet_cwd_MA	Daymet-calculated cumulative water deficit for March-August of current year
Daymet_ppt_annual	Daymet-calculated precipitation for current year
Daymet_CWD_annual	Daymet-calculated cumulative water deficit for current year
Daymet_ppt_SO	Daymet-calculated precipitation for September-October of previous year
Daymet_cwd_SO	Daymet-calculated cumulative water deficit for September-October of previous year
Temperature variables	
tmax_avgApr_Aug	Average daily maximum temperature April-August for current year
tmin_avgApr_Aug	Average daily minimum temperature April-August for current year
tmin_minDec_Feb	Coldest overnight low of current year winter
winter_temp	Average Dec-Feb temperature for current year
deviation	Current year average daily maximum April-August minus long term site average
devL1	Previous year average daily maximum April-August minus long term site average
devL2	Two-year lag average daily maximum April-August minus long term site average
devL3	Three-year lag average daily maximum April-August minus long term site average
global_dev	Current year average daily maximum April-August minus long term average of all sites
glob_devL1	Previous year average daily maximum April-August minus long term average of all sites
glob_devL2	Two-year lag average daily maximum April-August minus long term average of all sites
glob_devL3	Three-year lag average daily maximum April-August minus long term average of all sites
summer_temp	Average June-August temperature for current year
summer_L1	Average June-August temperature for previous year
summer_L2	Average June-August temperature for two year lag
summer_L3	Average June-August temperature for three year lag

(*continued on next page*)

Table 2 (*continued*)

Variable name	Definition
august_temp	Average August temperature for current year
avg_ann_temp_current	Average annual temperature for current year
avg_temp_Aug	Average August temperature for current year
avg_ann_max	Long-term (30 year) average daily maximum
avg_ann_min	Long-term average daily minimum
avg_Aug_max	Long-term average August daily maximum temperature
avg_aug_min	Long-term average August daily minimum temperature
avg_min_temp_winter	Long-term average daily minimum Dec-Feb
ann_temp	Long-term average annual temperature
aug_temp	Long-term average August temperature
DD15_Tmax	Degree-days > 15 °C for current year, April-August
DD16_Tmax	Degree-days > 16 °C for current year, April-August
DD17_Tmax	Degree-days > 17 °C for current year, April-August
DD18_Tmax	Degree-days > 18 °C for current year, April-August
DD19_Tmax	Degree-days > 19 °C for current year, April-August
DD20_Tmax	Degree-days > 20 °C for current year, April-August
DD21_Tmax	Degree-days > 21 °C for current year, April-August
DD22_Tmax	Degree-days > 22 °C for current year, April-August
DD23_Tmax	Degree-days > 23 °C for current year, April-August
DD24_Tmax	Degree-days > 24 °C for current year, April-August
DD25_Tmax	Degree-days > 25 °C for current year, April-August
DD15P1	Degree-days > 15 °C for previous year, April-August
DD15P2	Degree-days > 15 °C for year n-2, April-August
DD15P3	Degree-days > 15 °C for year n-3, April-August
DD16P1	Degree-days > 16 °C for previous year, April-August
DD16P2	Degree-days > 16 °C for year n-2, April-August
DD16P3	Degree-days > 16 °C for year n-3, April-August
DD17P1	Degree-days > 17 °C for previous year, April-August
DD17P2	Degree-days > 17 °C for year n-2, April-August
DD17P3	Degree-days > 17 °C for year n-3, April-August
DD18P1	Degree-days > 18 °C for previous year, April-August
DD18P2	Degree-days > 18 °C for year n-2, April-August
DD18P3	Degree-days > 18 °C for year n-3, April-August
DD19P1	Degree-days > 19 °C for previous year, April-August
DD19P2	Degree-days > 19 °C for year n-2, April-August
DD19P3	Degree-days > 19 °C for year n-3, April-August
DD20P1	Degree-days > 20 °C for previous year, April-August
DD20P2	Degree-days > 20 °C for year n-2, April-August
DD20P3	Degree-days > 20 °C for year n-3, April-August
DD21P1	Degree-days > 21 °C for previous year, April-August
DD21P2	Degree-days > 21 °C for year n-2, April-August
DD21P3	Degree-days > 21 °C for year n-3, April-August
DD22P1	Degree-days > 22 °C for previous year, April-August
DD22P2	Degree-days > 22 °C for year n-2, April-August
DD22P3	Degree-days > 22 °C for year n-3, April-August
DD23P1	Degree-days > 23 °C for previous year, April-August
DD23P2	Degree-days > 23 °C for year n-2, April-August
DD23P3	Degree-days > 23 °C for year n-3, April-August
DD24P1	Degree-days > 24 °C for previous year, April-August
DD24P2	Degree-days > 24 °C for year n-2, April-August
DD24P3	Degree-days > 24 °C for year n-3, April-August
DD25P1	Degree-days > 25 °C for previous year, April-August
DD25P2	Degree-days > 25 °C for year n-2, April-August
DD25P3	Degree-days > 25 °C for year n-3, April-August
Count15A_A	Counts of days > 15 °C, August year n-1 through August of current year
Count16A_A	Counts of days > 15 °C, August year n-1 through August of current year
Count17A_A	Counts of days > 15 °C, August year n-1 through August of current year
Count18A_A	Counts of days > 15 °C, August year n-1 through August of current year
Count19A_A	Counts of days > 15 °C, August year n-1 through August of current year
Count20A_A	Counts of days > 15 °C, August year n-1 through August of current year
Count21A_A	Counts of days > 15 °C, August year n-1 through August of current year
Count22A_A	Counts of days > 15 °C, August year n-1 through August of current year
Count23A_A	Counts of days > 15 °C, August year n-1 through August of current year
Count24A_A	Counts of days > 15 °C, August year n-1 through August of current year

Table 2 (*continued*)

Variable name	Definition
Count25A_A	Counts of days > 15 °C, August year n-1 through August of current year
Count15P1	Counts of days > 15 °C for previous year
Count15P2	Counts of days > 15 °C for year n-2
Count15P3	Counts of days > 15 °C for year n-3
Count16P1	Counts of days > 16 °C for previous year
Count16P2	Counts of days > 16 °C for year n-2
Count16P3	Counts of days > 16 °C for year n-3
Count17P1	Counts of days > 17 °C for previous year
Count17P2	Counts of days > 17 °C for year n-2
Count17P3	Counts of days > 17 °C for year n-3
Count18P1	Counts of days > 18 °C for previous year
Count18P2	Counts of days > 18 °C for year n-2
Count18P3	Counts of days > 18 °C for year n-3
Count19P1	Counts of days > 19 °C for previous year
Count19P2	Counts of days > 19 °C for year n-2
Count19P3	Counts of days > 19 °C for year n-3
Count20P1	Counts of days > 20 °C for previous year
Count20P2	Counts of days > 20 °C for year n-2
Count20P3	Counts of days > 20 °C for year n-3
Count21P1	Counts of days > 21 °C for previous year
Count21P2	Counts of days > 21 °C for year n-2
Count21P3	Counts of days > 21 °C for year n-3
Count22P1	Counts of days > 22 °C for previous year
Count22P2	Counts of days > 22 °C for year n-2
Count22P3	Counts of days > 22 °C for year n-3
Count23P1	Counts of days > 23 °C for previous year
Count23P2	Counts of days > 23 °C for year n-2
Count23P3	Counts of days > 23 °C for year n-3
Count24P1	Counts of days > 24 °C for previous year
Count24P2	Counts of days > 24 °C for year n-2
Count24P3	Counts of days > 24 °C for year n-3
Count25P1	Counts of days > 25 °C for previous year
Count25P2	Counts of days > 25 °C for year n-2
Count25P3	Counts of days > 25 °C for year n-3
DDlt15	Daily maxima degree-days < 15 °C for previous September-November
DD_TminLT15	Daily minima degree-days < 15 °C for previous September-November
Dlt15	Count of daily maxima < 15 °C for previous September-November
DDlt15P1	Count of daily maxima < 15 °C for year n-2 September-November
DDlt15P2	Count of daily maxima < 15 °C for year n-3 September-November
DDlt15P3	Count of daily maxima < 15 °C for year n-4 September-November
HLI	Heat load index
Prism_temp_Aug	PRISM-estimated average temperature for August of current year
Prism_temp_Jul	PRISM-estimated average temperature for July of current year
Prism_temp_JA	PRISM-estimated average temperature for July-August of current year
prism_temp_JJA	PRISM-estimated average temperature for June-August of current year
prism_temp_MJJA	PRISM-estimated average temperature for May-August of current year
prism_temp_AA	PRISM-estimated average temperature for April-August of current year
prism_temp_MA	PRISM-estimated average temperature for March-August of current year
prism_temp_annual	PRISM-estimated average temperature for current year
prism_temp_SO	PRISM-estimated average temperature for September-October of previous year
Daymet_temp_Jul	Daymet-estimated average temperature for July of current year
Daymet_temp_JA	Daymet-estimated average temperature for July-August of current year
Daymet_temp_JJA	Daymet-estimated average temperature for June-August of current year
Daymet_temp_MJJA	Daymet-estimated average temperature for May-August of current year
Daymet_temp_AA	Daymet-estimated average temperature for April-August of current year

(*continued on next page*)

Table 2 (*continued*)

Variable name	Definition
Daymet_temp_MA	Daymet-estimated average temperature for March-August of current year
Daymet_temp_annual	Daymet-estimated average temperature for current year
Daymet_temp_SO	Daymet-estimated average temperature for September-October of previous year

on infestation probability. That is, beetle outbreak and collapse occurred under correlated stand conditions. Therefore, we added a third population of trees to the dataset, live trees from sites *without* current or previous infestations. This group has about 167,000 observations. Again, this is far too many observations for our computing resources, so we generated a random sample matching that of the collapsing-live group, 7,514 (PROC SURVEYSELECT, random sample without replacement). Thus, this dataset has 15,879 observations (i.e., 851 + 7514 + 7514).

We used the dataset with 15,879 observations in a logistic model to accommodate the binomial response (0 = live, 1 = infested) with fixed (e.g., temperature, precipitation, beetle pressure, tree and stand characters) and random (e.g., site, plot, and year) effects. Year within stem (by plot by site) was specified as a random effect and the response error distribution specified as AR(1) to account for temporal autocorrelation of residuals. These models output pseudo-AIC, which are not appropriate for comparing model fit among model iterations. Instead, we compared model iterations using confusion matrices for each iteration (i.e., a different suite of explanatory variables), focusing on balanced accuracy, i.e., the average accuracy of live and infested classes. With > 200 explanatory variables, millions of combinations are possible. During exploratory analyses we made histograms of live and infested tree classes as a function of each explanatory variable and visually selected factors that appeared likely to be predictive in statistical models (Fig. 2). Two- and three-way interactions were also tested for significance. Henceforth, we refer to this as the "discovery model" and it includes only significant explanatory variables ($\alpha < 0.05$) that resulted in the highest confusion matrix balanced accuracy. With > 15,000 observations in the discovery model, small *p*-values are possible even among predictor variables that have small ecological effects. To inform size effects, we requested the odds ratios in the GLIMMIX model statement.

We recognized that different random samples of live trees without previous infestation (i.e., 7,665/167,000) would result in different parameter estimates, if not different significant explanatory variables. To ensure variable consistency among different random samples, we compared 100 iterations of the discovery model using datasets with differing random samples from the live-without-previous-infestation population. All explanatory variables in the discovery model were significant for all 100 iterations. Parameter estimates for the "final model" were determined using bootstrap methods and included calculation of 99% confidence limits. This was done by generating 5,000 random samples of 750 from each of the infested, collapsing-live, and live-without-previous-infestation populations so that each would be equally represented. All 48 sites were represented in the 5,000 iterations. During this final step, we also conducted a leave-one-out-cross-validation (LOOCV) to remove the bias of each observation being predicted by the model (Rushing et al. 2015). Finally, we averaged the odds ratios for each variable over the 5,000 bootstrap samples.

3. Results

Several bark beetle species were identified from infested trees at our study sites. MPB was common, typically associated with roundheaded pine beetle (*D. adjunctus* Blandford) and/or southwestern pine beetle (*D. barberi* Hopkins). Note that *D. barberi* was recently reinstated and removed from synonymy with western pine beetle, *D. brevicomis* LeConte (Valerio-Mendoza et al. 2019). The three sites added in September 2019 included plots with current MPB attacks, galleries < 15 cm long and with few or no eggs, but we found no evidence of other bark beetle species at that time. Yet, most stems infested during 2018 or earlier had evidence of MPB and roundheaded pine beetle. As an aside, we returned to this area again in September 2020 and September 2022 and found the same condition – fresh MPB attacks but without evidence of other *Dendroctonus* spp. despite previous year attacked pines with evidence of MPB and roundheaded pine beetle. This anecdote suggests that MPB is the primary mortality agent in this mixed bark beetle system. Because roundheaded pine beetle has an attack peak during October (Chansler 1967), we surmise that MPB initiates attacks of pine in areas that have both species present. Some sites in Arizona also had evidence of the larger Mexican pine beetle (*D. approximatus* Erichson). We consider these four species the primary mortality agents in our plots. We also commonly found evidence of pine engraver beetles (*Ips pini* Say, *I. knausi* Swaine) and, occasionally, red turpentine beetles (*D. valens* LeConte) near the root collar of trees infested by other bark beetle

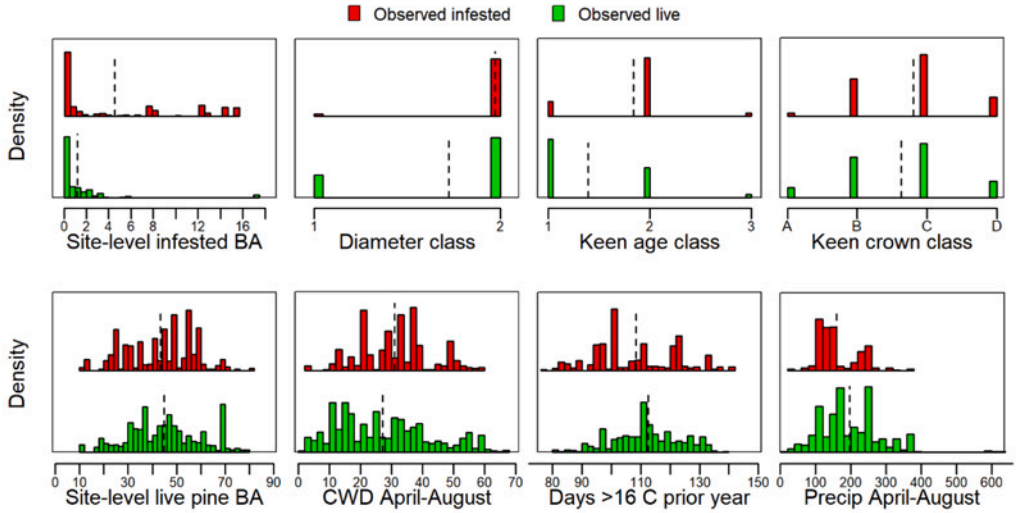

Fig. 2. Examples of histograms used to visually detect explanatory variables for inclusion in a generalized linear mixed model predicting the probability of bark beetle infestation of ponderosa pine. Dashed lines are mean values of the observed infested and live classes.

species.

The discovery model found multiple explanatory variables that were significantly related to the probability of tree-level infestation. For the best fitting final model, judged by balanced accuracy of confusion matrices, these included: a) tree diameter-, age-, and crown vigor-class; b) site-level live pine BA; c) site-level pine BA infested the previous year; d) the number of days exceeding 16 °C during the previous calendar year (*n*-1); and e) contemporaneous CWD summed from April through August (Table 3). Each of these variables had notable odds ratios, albeit to varying degrees. Among the categorical explanatory variables, diameter class had the greatest difference in probability of infestation among the levels of that variable, with pines in diameter class 2 (>15.2 cm) over 9 times as likely to be infested compared to pines in diameter class 1 (Fig. 3). Pines in Keen age class 2 (80–180 years) were over 5 times more likely to be infested compared to pines in age class 1 (<80 years) whereas pines in age class 3 (>180 years) were about 3.5 times more likely to be infested compared to pines in age class 1. Pines in Keen crown class A were the least likely to be infested whereas pines in crown class D were nearly 8 times more likely to be infested than those in crown class A. Among the continuous explanatory variables, counts of days exceeding a threshold of 16 °C during the previous calendar year had the greatest range in probability of infestation over the observed range of that variable. The odds ratio for Count16Previous at 77 days was estimated as 6.726 and 0.218 for Count16Previous at 140 days (Fig. 4). This suggests that when Count16Previous = 140 days the likelihood of being infested is 30.85 times less than when Count16Previous = 77 (6.726/0.218). Site-level BA infested the previous year also had a pronounced difference in odds ratio over the observed range of that value and higher values resulted in higher probability of being infested. The odds ratio at Beetle_BA_Site = 0 was 0.818 and 11.101 at Beetle_BA_Site = 17.35. Therefore, the maximum observed Beetle_BA_Site value was 13.57 times more likely to be infested relative to pines at sites without trees infested the previous year. In contrast, there was only a 2.3-fold change in odds ratio over the observed range of site-level live pine BA (odds ratio at Site_Pine_BA = 10.879 is 0.668, odds ratio at Site_Pine_BA = 81.879 is 1.550) (Fig. 4). CWD April-August had a similar likelihood difference across the range of that variable.

For the final model, the equation for logit-scale probability of infestation using mean parameter estimates of the 5,000 LOOCV bootstrap iterations is (Table 4):

$$\text{Logit} = -1.0724 + 0.1505*\text{Beetle\_BA\_Site} + 2.2049*\text{D\_Class2} + 1.6519*\text{Keen\_Age2} + 1.2513*\text{Keen\_Age3} + 1.0239*\text{Keen\_CrownB} + 1.2515*\text{Keen\_CrownC} + 2.0416*\text{Keen\_CrownD} + 0.0188*\text{Daymet\_CWD\_AA} + 0.0119*\text{Site\_Pine\_BA} - 0.0473*\text{Count16Previous} \quad [1].$$

Where Beetle_BA_Site is site-level pine BA infested the previous year; D_Class2 = 1 if dbh class is 2 (>15.2 cm), 0 otherwise; Keen_Age2 = 1 if Keen age class is 2 (80–180 years), 0 otherwise; Keen_Age3 = 1 if Keen age class is 3 (>180 years), 0 otherwise; Keen_CrownB = 1 if Keen crown class is "B", 0 otherwise; Keen_CrownC = 1 if Keen crown class is "C", 0 otherwise; Keen_CrownD = 1 if Keen crown class is "D", 0 otherwise; Daymet_CWD_AA is Daymet-based climatic water deficit from April-August; Site_Pine_BA is site-level live pine BA (i.e., summed over twenty 0.04 ha plots); and Count16Previous is a count of days exceeding a threshold of 16 °C during the previous calendar year. The logit-scale predictions can be transformed into probability of infestation using:

$P_{Inf} = 1/(1 + e^{-\text{logit}})$ [2].

Using $P_{Inf} < 0.5$ as "live" and $P_{Inf} \geq 0.5$ as "infested", the leave-one-out-cross-validation confusion matrix is:

	Actual Infested	Actual Live
Predicted Infested	1100	450
Predicted Live	582	2868

Model accuracy is 65.4% for infested trees and 86.4% for live trees; balanced accuracy is 75.9%. That is, 34.6% of infested pines had $P_{Inf} < 0.5$ and 13.6% of live pines had $P_{Inf} > 0.5$ (Fig. 5).

Table 3
Tree, stand, and environmental variables significantly related to the probability of bark beetle infestation in ponderosa pine of the Colorado Plateau. These values are from one of 100 iterations of a GLIMMIX model using a subset of data from selected from observations of infested, collapsing-live, and live without previous infestation populations ("Discovery model"; see Methods). This dataset had 15,879 observations. The other iterations had the same population size. Test values slightly varied among the iterations but these variables were significant for each iteration (α = 0.05).

	Num	Den		
Variable	DF	DF	F Value	Pr > F
Beetle_BA_Site	1	6273	512.48	<0.0001
D_Class	1	211	94.71	<0.0001
Keen_Age	2	9224	132.45	<0.0001
Keen_Crown	3	9224	27.50	<0.0001
Daymet_CWD_AA	1	6273	77.87	<0.0001
Site_Pine_BA	1	6273	16.76	<0.0001
Count16Previous	1	6273	212.92	<0.0001

"Beetle_BA_Site" is site-level infested BA (m^2 ha^{-1}) for the previous year; "D_Class" is dbh class (1 = < 15.2 cm, 2 ≥ 15.2 cm); "Keen_Age" is Keen age class (1 = <80 years, 2 = 80–180 years, 3 = >180 years); "Keen_Crown" is Keen crown-vigor class (A, B, C, D; A is a full, robust, open-grown or dominant crown and D is a sparse, narrow, suppressed or intermediate crown); "Daymet_CWD_AA" is the contemporaneous Daymet-based annual climatic water deficit summed from April-August; "Site_Pine_BA" is site-level basal area for pines only; and "Count16Previous" is a count of days exceeding a threshold of 16 °C during the previous calendar year.

4. Discussion

The explanatory variables in our final model represent categories of factors considered important in initiating and sustaining bark beetle outbreaks. Factors associated with bark beetle infestation of Colorado Plateau ponderosa pine between 1995 and 2019 included precipitation and water stress, temperatures influencing bark beetle developmental success, host tree suitability and susceptibility, and extant or previous year beetle population size (Raffa et al. 2008; Preisler et al. 2012). Given the complexity of interacting factors contributing to infestation, we consider model fit to be good.

As hypothesized, several drought and precipitation variables were found significantly related to infestation probability, although a single measure did not emerge from our analyses as being clearly superior to others. High values of summed April through August climatic water deficit (Daymet_CWD_AA), which indicate high plant water stress, were associated with a higher probability of infestation. Although Daymet_CWD_AA had the highest confusion matrix balanced accuracy, accuracy of several other drought and precipitation-related variables were within 1% of that of Daymet_CWD_AA. The relationship between drought stress and infestation probability has been noted in other western U.S. bark beetle-conifer systems including *Ips* species in ponderosa and piñon pines (Negrón et al. 2009; Gaylord et al. 2013; McNichol et al. 2022) and western pine beetle in ponderosa pine in California (Koontz et al. 2021) and Arizona (Kolb et al. 2016). Drought is a landscape-level effect that increases susceptible host abundance (Raffa et al. 2008). Although many of our sites have increasing trends in annual CWD since 1980 and this variable was positively related to the probability of infestation at the stem-level, most sites had no apparent uptick in mortality during the region-wide dry years from 2000 to 2003 (Fig. 6). In contrast, that drought event has been associated with widespread beetle- and drought-caused mortality in piñon pine of the Colorado Plateau (Santos and Whitham 2010). MPB population buildup was also associated with the 2000–2003 drought in Colorado lodgepole pine but not ponderosa pine, potentially due to differences in forest composition and age structure between the species (Chapman et al. 2012). Perhaps related to our finding that precipitation variables were

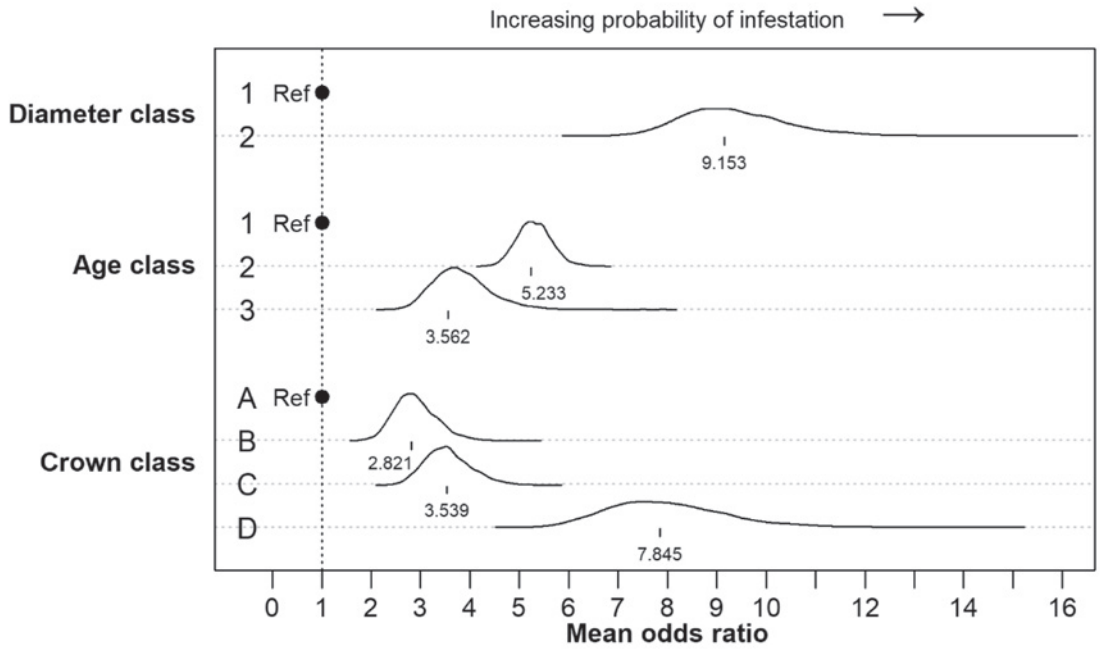

Fig. 3. Mean odds ratios for categorical explanatory variables in the final model with distribution of odds ratios for each of the 5,000 bootstrap iterations using subsets of the data (leave-one-out cross validation). For each categorical variable, the level with the lowest odds ratio was assigned as the reference (Ref) and odds ratios of other levels are in relation to that reference. Observations with larger odds ratios are more likely to be infested.

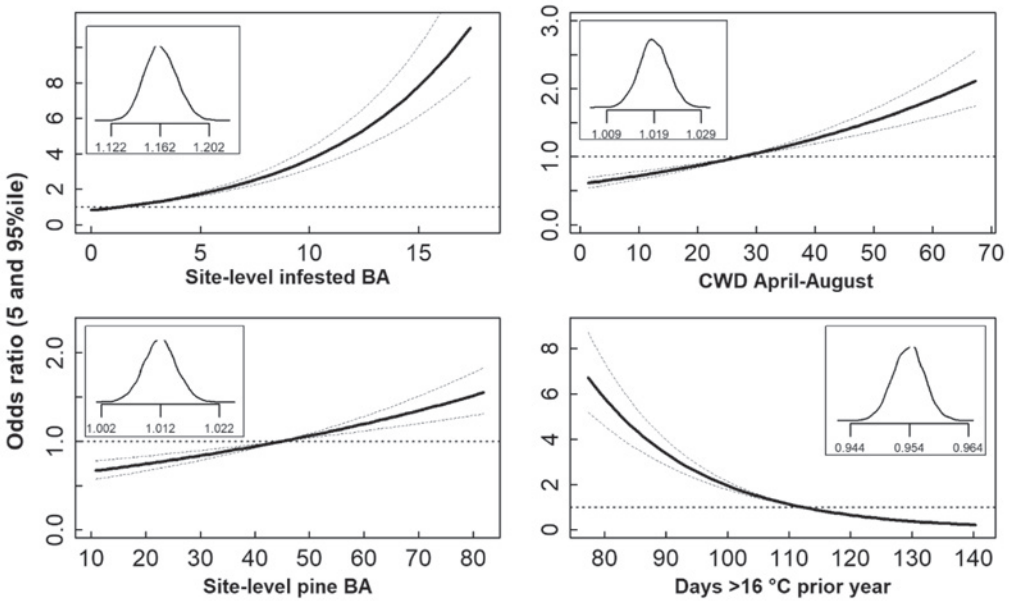

Fig. 4. Odds ratios for the continuous variables found best-fitting in the final model. The plots are scaled such that the odds ratio is 1 at the mean observed value of that variable with the change in odds ratio, relative to the mean value, depicted across the range of values in our dataset. Ratios $>$ 1 indicate increasing probability of infestation whereas and ratios $<$ 1 indicate decreasing probability. The inset plots depict the bootstrap odds ratio distributions for each variable (the mean value depicted at the midpoint is the estimated change in odds over one unit change in the explanatory variable, i.e., there is a 1.162 increase in the odds ratio at Site-level infested BA = 6 compared to that at Site-level infested BA = 5). The faint dotted lines show the odds ratios for the 5th and 95th percentile bootstrap runs (i.e., these are not the 90% confidence intervals which would not be visible at this scale given the sample size of 5,000 resulting in miniscule standard deviations).

negatively related to infestation probability, a study of radial growth of southwestern U.S. conifer species as a function of temperature and precipitation found ponderosa pine to maximally benefit from warm season (July-September) precipitation (Truettner et al. 2018). This suggests that ponderosa pine defenses against bark beetle attack might be enhanced by current year precipitation, especially from spring through summer, despite antecedent drought conditions.

We found no significant relationship between infestation probability and winter temperatures that could cause widespread bark beetle mortality. This might be the result of the lack of lethal winter temperatures during the interval of our measurements. For example, Bentz and Mullins (1999) estimate a mean super cooling point of −26.9 °C for 4th instar MPB larvae sampled during January from southern Utah but few of our plots experienced temperatures approaching this level after 1990 (Fig. 7). The final model (i.e., best fitting) includes only one temperature variable, Count16Previous, a count of days exceeding a threshold of 16 °C during the previous calendar year. Higher values of Count16-Previous (i.e., warmer temperatures) were associated with a lower probability of infestation. This result conceivably reflects that "too much" warm weather can result in fractional voltinism, such as one full

Table 4
Log-scale mean parameter estimates of significant explanatory variables displayed in Table 3, with 99% confidence intervals. These values were calculated from 5,000 iterations of bootstrap methods wherein 750 samples were randomly selected from each of infested, collapsing-live, and live without previous infestation populations (see Methods). These mean parameter estimates define the "final model" (Eq. 1).

Effect	Mean	Standard deviation	0.5 %ile	95.5 %ile
Intercept	−1.0724	0.3723	−1.0860	−1.0588
Beetle_BA_Site	0.1505	0.0112	0.1501	0.1509
Dbh_Class 2 (>15.2 cm)	2.2049	0.1353	2.1999	2.2098
Keen_Age 2 (80–180 years)	1.6519	0.0778	1.6490	1.6547
Keen_Age 3 (>180 years)	1.2513	0.1943	1.2442	1.2584
Keen_Crown (B)	1.0239	0.1614	1.0181	1.0298
Keen_Crown (C)	1.2515	0.1576	1.2457	1.2572
Keen_Crown (D)	2.0416	0.1908	2.0346	2.0485
Daymet_CWD_AA	0.0188	0.0030	0.0187	0.0189
Site_Pine_BA	0.0119	0.0027	0.0118	0.0120
Count16Previous	−0.0473	0.0028	−0.0474	−0.0472

and a second partial generation within one year, which can be maladaptive. This was observed at a warm *Pinus monophylla* site in southern California where voltinism faster than univoltinism, but not bivoltinism, occurred and the endemic population collapsed (Bentz et. al. 2014). MPB uses locally-adapted developmental rates, prepupal diapause, and reproductive (i.e., adult) diapause to maintain univoltinism over its wide-ranging geographic and elevational distribution although remarkably warm or cool conditions can result in generation times less than or greater than one year (Bentz et al. 2014; Bentz et al. 2021). Although there are no published MPB field phenology studies in ponderosa pine, the propensity to the univoltine cycle has been observed in at least six pine species (Bentz et al. 2014; Soderberg et al. 2020). Fractional voltinism is considered maladaptive because it can result in cold-intolerant lifestages with the onset of winter and can disrupt synchronized emergence needed to overwhelm host defenses (Powell and Logan 2005). We speculate that high values of Count16Previous reflects maladaptive voltinism and subsequently lower infestation probability the following year similar to the results found by Preisler et al. (2012). Further study is needed to confirm that MPB from the region of this study can develop on a fractional life cycle.

During outbreaks, bark beetles commonly attack large diameter hosts with thick phloem (i.e., food resources). Such trees are typically the most vigorous and highly defended and are generally attacked only when there are sufficient conspecifics to overwhelm host defenses (Raffa et al. 2008). During the time period of our study most sites had relatively low levels of infested pine (i.e., endemic bark beetle populations). Under endemic conditions, bark beetles are typically found in smaller diameter hosts and these trees are often suppressed or otherwise stressed (Smith et al. 2011; Bleiker et al. 2014). This dynamic might contribute to the variance observed in MPB-ponderosa pine systems regarding susceptibility as a function of host diameter. Negrón et al. (2008) and Klenner and Arsenault (2009) found positive relationships between ponderosa pine diameter and infestation probability whereas McCambridge (1982) and Olsen et al. (1996) found little relation beyond about 20 cm dbh. Our results are similar to the latter in that we found little overall relationship between dbh and infestation probability but did find a significant effect by diameter class with a breakpoint of 15.2 cm. Trees>15.2 cm dbh were significantly more likely to be infested than trees smaller than that threshold but we found no further gains in model fit by increasing the breakpoint or adding diameter classes (e.g., >30 and 75 cm dbh).

Both elements of Keen's (1943) ponderosa pine tree classes were significant in our model. Not surprisingly, the youngest age class (<80 years) had the lowest probability of infestation. Younger pines are likely to be smaller, with less phloem resources, and generally more vigorous and capable of resisting beetle attack. As trees increase in size and age, phloem resources also increase, and we found that age class 2 (80–180 years) had the highest probability of infestation (Table 4, Fig. 3). Trees in age class 3 (>180 years) had intermediate odds of infestation, potentially due to the oldest pines having the thickest bark which conceivably acts as a physical barrier to beetle attacks. Crown-vigor

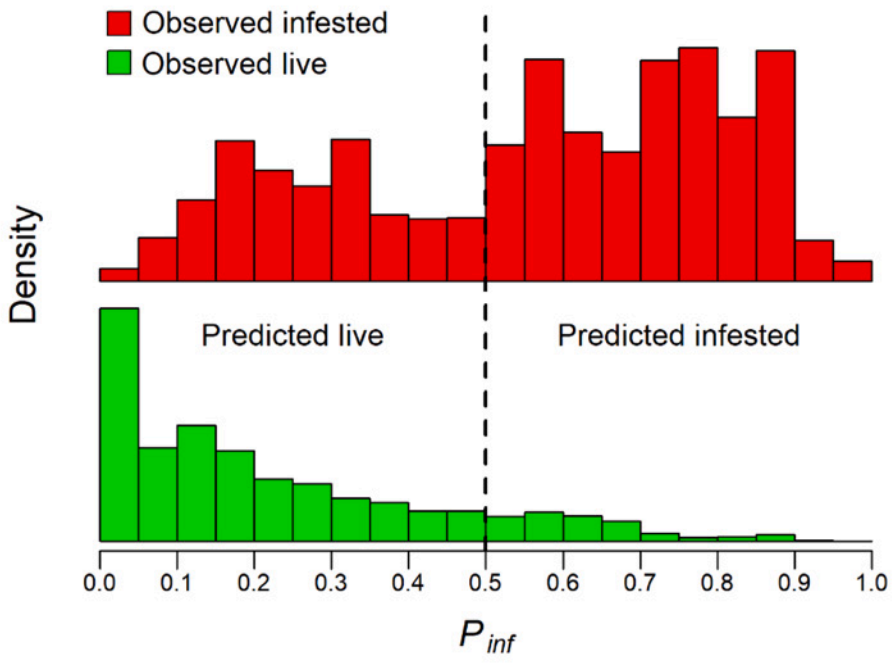

Fig. 5. Histograms of model-predicted probability (P_{Inf}) of infestation for infested (top panel) and live (bottom panel) classes as observed. These predictions are from 5,000 bootstrap samples wherein one observation was iteratively left out of the model building step and the resulting parameter estimates were used to predict the omitted observation (leave-one-out-cross-validation).

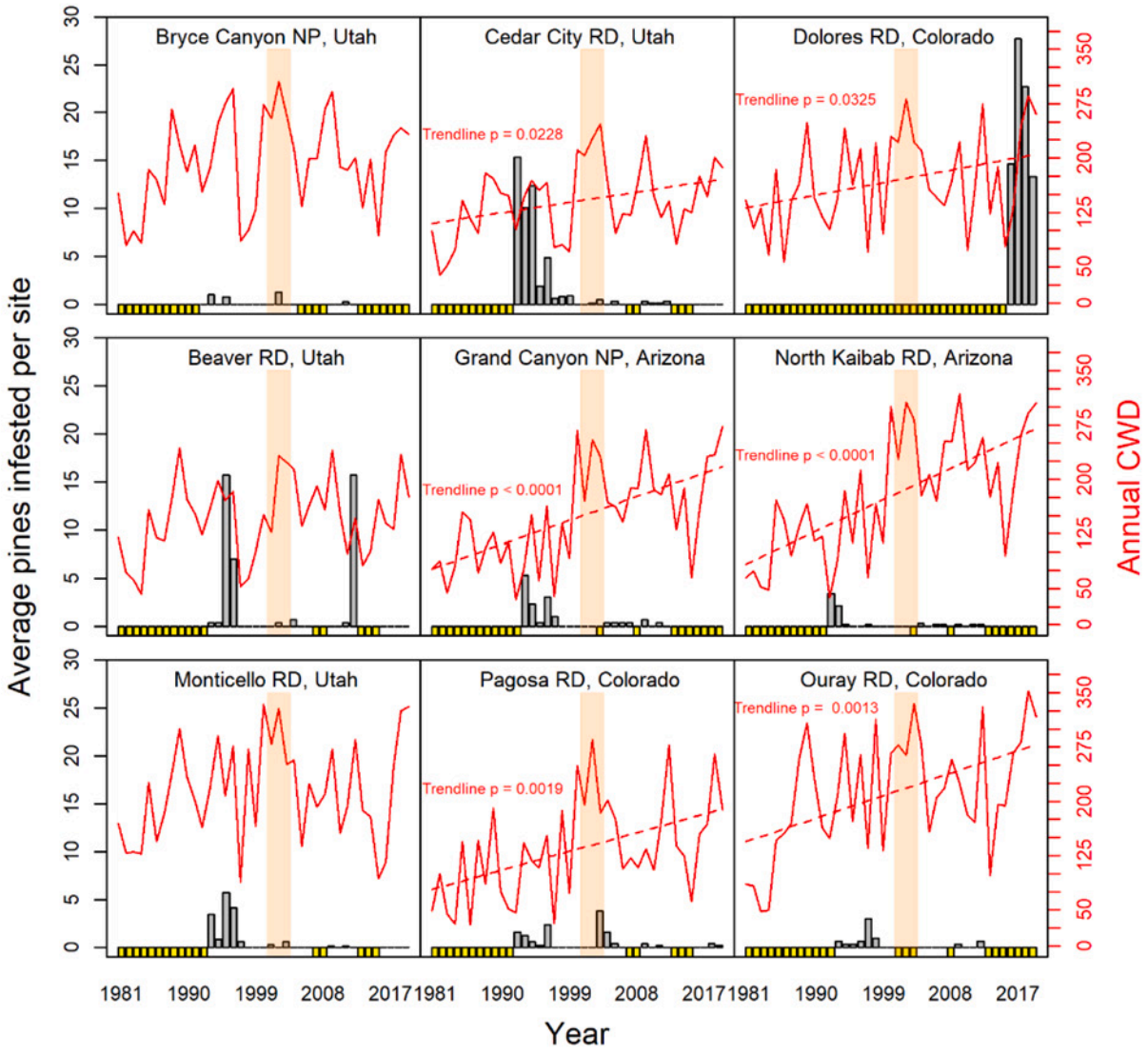

Fig. 6. Average numbers of ponderosa pines infested per site per year by Ranger District (RD) or National Park (NP) (Y1 axis) and annual climatic water deficit (CWD) averaged over those sites (Y2 axis). The yellow bars indicate years lacking infested pine data. Trendlines in CWD through time are only shown if significant ($\alpha = 0.05$). The highlighted bars indicate the region-wide drought in the southwest U.S. from 2001–2003.

class was also significantly related to the probability of infestation with less vigorous pines (class D) more likely to be infested, i.e., those with less crown volume[1]. It might be considered that Keen's crown-vigor classes reflect competition; class "A" trees have relatively little competition for sun, water, and nutrients whereas class "D" trees are in high competition with neighboring trees. In an Oregon study, less vigorous ponderosa pines, measured as wood production per unit leaf area, were also found to be more likely to be infested by MPB (Larsson et al. 1983). Relatedly, site-level live pine BA was positively related to infestation probability and provided slightly better model fit than pine SDI. Similar relationships between greater stand density and greater likelihood of infestation probability have been found in many other bark beetle-conifer systems including ponderosa pine (Stevens 1980; Larsson et al. 1983; Oliver 1995; Chojnacky et al. 2000).

Extant beetle population size is a key factor in occurrence of host mortality for other *Dendroctonus* systems (Reynolds and Holsten 1994; Safranyik and Carroll 2006) and we found counts or BA of stems infested the previous year to be consistently significant in exploratory models, with a positive relationship to infestation probability. Our final model found previously infested BA to have a slightly better balanced accuracy in the confusion matrices compared to counts of infested stems. BA better represents the surface area (i.e., bark beetle habitat) from which new brood will emerge. The odds ratio for this variable indicates that its effect becomes increasing influential at the upper extremes of its observed range, i.e., very high levels of infested BA from the previous year are associated with considerably higher odds of infestation (Fig. 4). We hoped to include spatially explicit variables of beetle pressure but this proved unworkable beyond the plot-level because of varying densities of nearby sampled area. For example, mid-transect plots had adjacent plots either side plus additional nearby plots on the parallel transect whereas plots on transect ends had only one adjacent plot and most plots on the other transect were further away. Meanwhile, site-level infested BA consistently resulted in better model fit than plot-level infested BA. This could be an artifact of plot-to-plot variability of

[1] Crown-vigor class "A" is defined as >55% live crown ratio with a wide crown, long and dense needles, large dbh relative to age, and open grown or dominant canopy position. In contrast, class "D" is defined as <10 crown ratio with a narrow crown, sparse needles, small dbh relative to age, and intermediate or suppressed canopy position (Keen 1943). "B" and "C" trees are intermediate in these characters.

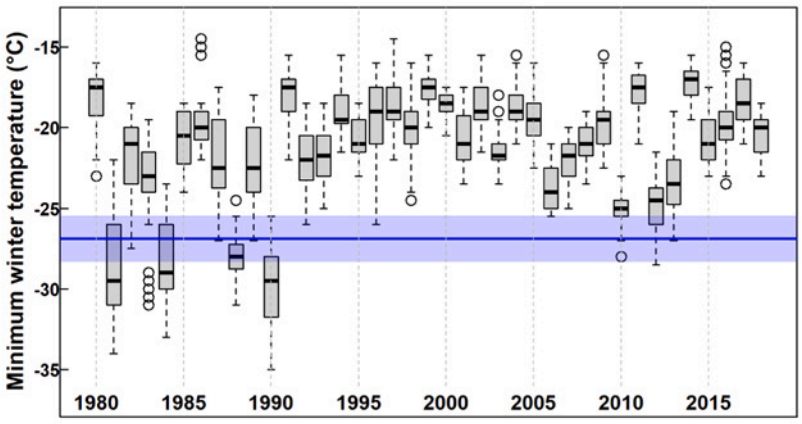

Fig. 7. Boxplots of extreme winter (December-February) minimum temperatures, estimated by Daymet, at our 48 sites from 1980 to 2019. The blue line indicates the estimated supercooling point (LD50) for 4th instar mountain pine beetle larvae sampled during January in southern Utah with a 90% confidence interval (Bentz and Mullins 1999).

infestations whereas the aggregated site-level metric yields a better measure of beetle pressure in the local area. Certain meteorological conditions can disperse large numbers of bark beetles tens of kilometers above the canopy (de la Giroday et al. 2011; Evenden et al. 2014). Most bark beetle dispersal, however, occurs over short distances (i.e., <100 m from the natal host) (Safranyik et al. 1992; Kautz et al. 2011; Powell and Bentz 2014), and new attacks generally occur near old ones (Wermelinger 2004; Robertson et al. 2007).

Although overall model fit was good, there were errors associated with infested stems that had low predicted probability of infestation (Fig. 5, top histogram). We suspect the most substantial weakness of our dataset is lack of information regarding nearby beetle activity outside of our plots. Among the 5,000 LOOCV iterations, there were 345 observations of infested stems with $P_{Inf} < 0.3$. One-hundred eighty-seven of these were in the least susceptible Keen age class 1 (i.e., <80 years old). Of those, 117 were in sites with pines infested the previous year suggesting "spillover" from nearby pines in more susceptible age-, size-, and crown-classes. Given that our surrogate for extant beetle population size was limited to the twenty ~ 0.04 ha plots, we suspect unmeasured beetle pressure from nearby areas challenged our plot trees that otherwise had factors associated with low probability of infestation.

Our results reveal tree and stand characters plus environmental factors associated with heightened susceptibility to bark beetle infestation for ponderosa pine of the Colorado Plateau. Although multiple *Dendroctonus* species were found infesting trees in our study, MPB was the most abundant and was a common species among all sites. Factors identified in our analyses align with those of previous studies that investigated tree mortality due to MPB and other *Dendroctonus* species. Our analyses, however, showed a high degree of complex interactions among variables as they related to the probability of infestation, perhaps due to the long-term and extensive number of trees included. Any single variable had low predictive power, whereas multiple variables that concurrently surpassed threshold values heightened the probability of bark beetle infestation (Raffa et al. 2008). We hypothesized warm temperatures would have a positive influence on bark beetle population growth, and therefore tree mortality. Instead, more days with temperatures > 16C was related to lower infestation probability, highlighting how adaptations in bark beetles may limit unconstrained increases in population growth as climate warms. Although we found that high water stress resulted in a higher probability of infestation, most of our sites did not display the pattern of drought-induced tree mortality caused by *Ips* species in the same region during the same period (Kleinman et al. 2012). Our results, therefore, also highlight potential differences among bark beetle species and host trees in the role of drought in population outbreaks and associated tree mortality.

CRediT authorship contribution statement

E. Matthew Hansen: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Funding acquisition. **Barbara J. Bentz:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition. **James C. Vandygriff:** Investigation, Data curation, Writing – review & editing. **Chris Garza:** Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Funding for this project was provided by the Rocky Mountain Research Station and Forest Health Protection (Special Technology Development Project R3-95-01 and Evaluation Monitoring Program INT-EM-F-12-02). Thanks to the many who were involved in the original study design including John Anhold, Tom Eager, Patrice Janiga, Jesse Logan, Roy Mask, Steve Munson, Lynn Rasmussen, Sheri Smith, and Jill Wilson. L. Scott Baggett provided statistical advice and review. And thanks to those who assisted with plot establishment and remeasurements including Creed Clayton, Christa Blakely, Bridget Kobe Clayton, Mark Wagner, Ryan Bracewell, Ben Meyerson, Sharon Parkes, Jason Neumann, Christopher Scott, Al Dymerski, John Pratt, and José Rivera Meléndez. We also thank Robert Coulson, Diana Doan-Crider, Andrew Birt, Mort Kothman, and Daniel Goldberg for their logistical support and assistance with preliminary data analyses. We are grateful to two anonymous reviewers whose comments improved this manuscript. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

References

Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J. D., Stephenson, N.L., Tague, C., Zeppel, M., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. New Phytologist 208 (3), 674–683.

Bentz, B.J., E.M. Hansen, M. Davenport, M. and D. Soderberg. 2021. Complexities in predicting mountain pine beetle and spruce beetle response to climate change. In *Bark Beetle Management, Ecology, and Climate Change* (pp. 31-54). Academic Press. https://doi.org/10.1016/B978-0-12-822145-7.00013-1.

B.J. Bentz D.R. Cluck B.M. Bulaon S.L. Smith Western pine beetle voltinism in a changing California climate 2023 In press Agriculture and Forest Entomology 10.1111/afe.12586.

Bentz, B.J., Hansen, E.M., 2017. Evidence for a prepupal diapause in the mountain pine beetle (*Dendroctonus ponderosae*). Environmental Entomology 47 (1), 175–183. https://doi.org/10.1093/ee/nvx192.

Bentz, B.J., Mullins, D.E., 1999. Ecology of mountain pine beetle (Coleoptera: Scolytidae) cold hardening in the intermountain west. Environmental Entomology 28 (4), 577–587. https://doi.org/10.1093/ee/28.4.577.

Bentz, B.J., Powell, J.A., 2014. Mountain pine beetle seasonal timing and constraints to bivoltinism: (A comment on Mitton and Ferrenberg, "Mountain pine beetle develops an unprecedented summer generation in response to climate warming"). The American Naturalist 184 (6), 787–796. https://doi.org/10.1086/678405.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60 (8), 602–613.

Bentz, B.J., Jönsson, A.M., Schroeder, M., Weed, A., Wilcke, R.A.I., Larsson, K., 2019. *Ips typographus* and *Dendroctonus ponderosae* models project thermal suitability for intra- and inter-continental establishment in a changing climate. Frontiers in Forests and Global Change 2, 1. https://doi.org/10.3389/ffgc.2019.00001.

Bentz, B., Vandygriff, J., Jensen, C., Coleman, T., Maloney, P., Smith, S., Grady, A., Schen-Langenheim, G., 2014. Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients in the western United States. Forest Science 60 (3), 434–449.

Berg, E.E., Henry, J.D., Fastie, C.L., De Volder, A.D., Matsuoka, S.M., 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. Forest Ecology and Management 227 (3), 219–232. https://doi.org/10.1016/j.foreco.2006.02.038.

Bleiker, K., O'Brien, M., Smith, G., Carroll, A., 2014. Characterisation of attacks made by the mountain pine beetle (Coleoptera: Curculionidae) during its endemic population phase. The Canadian Entomologist 146 (3), 271–284. https://doi.org/10.4039/tce.2013.71.

Chansler, J.F., 1967. Biology and life history of *Dendroctonus adjunctus* (Coleoptera: Scolytidae). Annals of the Entomological Society of America 60 (4), 760–767. https://doi.org/10.1093/aesa/60.4.760.

Chapman, T.B., Veblen, T.T., Schoennagel, T., 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology 93 (10), 2175–2185. https://doi.org/10.1890/11-1055.1.

Chojnacky, D.C., Bentz, B.J., Logan, J.A., 2000. Mountain pine beetle attack in ponderosa pine: Comparing methods for rating susceptibility. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, p. 10 p.. RMRS-RP-26.

Cole, W. and G. Amman. 1980. Mountain pine beetle dynamics in lodgepole pine forests, Part 1: course of an infestation. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-89, 56 pp.

Coleman, T.W., Graves, A.D., Heath, Z., Flowers, R.W., Hanavan, R.P., Cluck, D.R., Ryerson, D., 2018. Accuracy of aerial detection surveys for mapping insect and disease disturbances in the United States. Forest Ecology and Management 430, 321–336. https://doi.org/10.1016/j.foreco.2018.08.020.

de la Giroday, H.-M., Carroll, A.L., Lindgren, B.S., Aukema, B.H., 2011. Incoming! Association of landscape features with dispersing mountain pine beetle populations during a range expansion event in western Canada. Landscape Ecology 26 (8), 1097–1110.

Egan, J.M., Sloughter, J.M., Cardoso, T., Trainor, P., Wu, K., Safford, H., Fournier, D., 2016. Multi-temporal ecological analysis of Jeffrey pine beetle outbreak dynamics within the Lake Tahoe Basin. Population Ecology 58 (3), 441–462. https://doi.org/10.1007/s10144-016-0545-2.

Evenden, M.L., Whitehouse, C.M., Sykes, J., 2014. Factors influencing flight capacity of the mountain pine beetle (Coleoptera: Curculionidae: Scolytinae). Environmental Entomology 43 (1), 187–196. https://doi.org/10.1603/EN13244.

Fettig, C.J., Gibson, K.E., Munson, A.S., Negrón, J.F., 2014. Cultural practices for prevention and mitigation of mountain pine beetle infestations. Forest Science 60 (3), 450–463. https://doi.org/10.5849/forsci.13-032.

Fettig, C.J., Mortenson, L.A., Bulaon, B.M., Foulk, P.B., 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, US. Forest Ecology and Management 432, 164–178. https://doi.org/10.1016/j.foreco.2018.09.006.

Garza, C., 2015. Modeling Endemic Bark Beetle Populations in Southwestern Ponderosa Pine Forests. Texas A&M University. Master's thesis).

Gaylord, M.L., Kolb, T.E., Pockman, W.T., Plaut, J.A., Yepez, E.A., Macalady, A.K., Pangle, R.E., McDowell, N.G., 2013. Drought predisposes piñon–juniper woodlands to insect attacks and mortality. New Phytologist 198 (2), 567–578.

Hansen, E.M., 2014. Forest development and carbon dynamics after mountain pine beetle outbreaks. Forest Science 60 (3), 476–488. https://doi.org/10.5849/forsci.13-039.

Hansen, E.M., Bentz, B.J., 2003. Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). The Canadian Entomologist 135 (5), 697–712. https://doi.org/10.4039/n02-109.

Hansen, E.M., Bentz, B.J., Munson, A.S., Vandygriff, J.C., Turner, D.L., 2006. Evaluation of funnel traps for estimating tree mortality and associated population phase of spruce beetle in Utah. Canadian Journal of Forest Research 36 (10), 2574–2584. https://doi.org/10.1139/x06-141.

Hansen, E.M., Johnson, M.C., Bentz, B.J., Vandygriff, J.C., Munson, A.S., 2015. Fuel loads and simulated fire behavior in "old-stage" beetle-infested Ponderosa Pine of the Colorado Plateau. Forest Science 61 (4), 644–664. https://doi.org/10.5849/forsci.14-081.

Hart, S.J., Veblen, T.T., Schneider, D., Molotch, N.P., 2017. Summer and winter drought drive the initiation and spread of spruce beetle outbreak. Ecology 98 (10), 2698–2707. https://doi.org/10.1002/ecy.1963.

Hicke, J.A., Meddens, A.J., Kolden, C.A., 2016. Recent tree mortality in the western United States from bark beetles and forest fires. Forest Science 62 (2), 141–153. https://doi.org/10.5849/forsci.15-086.

Hopkins, A.D., 1910. Insects which kill forest trees: Character and extent of their depredations and methods of control, No. 125. US Government Printing Office.

Kautz, M., Dworschak, K., Gruppe, A., Schopf, R., 2011. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. Forest Ecology and Management 262, 598–608. https://doi.org/10.1016/j.foreco.2011.04.023.

Keen, F.P., 1943. Ponderosa pine tree classes redefined. Journal of Forestry 41 (4), 249–253. https://doi.org/10.1093/jof/41.4.249.

Kleinman, S.J., DeGomez, T.E., Snider, G.B., Williams, K.E., 2012. Large-scale pinyon ips (*Ips confusus*) outbreak in southwestern United States tied with elevation and land cover. Journal of Forestry 110 (4), 194–200. https://doi.org/10.5849/jof.11-060.

Klenner, W., Arsenault, A., 2009. Ponderosa pine mortality during a severe bark beetle (Coleoptera: Curculionidae, Scolytinae) outbreak in southern British Columbia and implications for wildlife habitat management. Forest Ecology and Management 258, S5–S14. https://doi.org/10.1016/j.foreco.2009.08.035.

Kolb, T.E., C.J. Fettig, M.P. Ayres, B.J. Bentz, J.A. Hicke, R. Mathiasen, J.E. Stewart, J.E., and A.S. Weed. 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. *Forest Ecology and Management* 380: 321-334. https://doi.org/10.1016/j.foreco.2016.04.051.

Kolb, T., K. Keefover-Ring, S.J. Burr, R. Hofstetter, M. Gaylord, M. and K.F. Raffa. 2019. Drought-mediated changes in tree physiological processes weaken tree defenses to bark beetle attack. *Journal of Chemical Ecology* 45(10): 888-900. https://doi.org/10.1007/s10886-019-01105-0.

Koontz, M.J., A.M. Latimer, L.A. Mortenson, C.J. Fettig, C.J. and M.P. North. 2021. Cross-scale interaction of host tree size and climatic water deficit governs bark beetle-induced tree mortality. *Nature Communications* 12(1): 1-13. https://doi.org/10.1038/s41467-020-20455-y.

Larsson, S., Oren, R., Waring, R.H., Barrett, J.W., 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. Forest Science 29 (2), 395–402. https://doi.org/10.1093/forestscience/29.2.395.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Schabenberger, O., 2006. SAS System for Mixed Models, 2nd ed. SAS Institute Inc, Cary, North Carolina, United States.

Lutz, J.A., Van Wagtendonk, J.W., Franklin, J.F., 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. Journal of Biogeography 37 (5), 936–950. https://doi.org/10.1111/j.1365-2699.2009.02268.x.

Massey, C.L., Wygant, N.D., 1954. Biology and control of the Engelmann spruce beetle in Colorado, No. 944. US Department of Agriculture.

McCambridge, W.F. 1982. *Ponderosa pine mortality resulting from a mountain pine beetle outbreak* (Vol. 235). Rocky Mountain Forest and Range Experiment Station, Forest Service, US Department of Agriculture.

McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13, 603–606. https://doi.org/10.1111/j.1654-1103.2002.tb02087.x.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New phytologist 178 (4), 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x.

McNichol, B.H., Clarke, S.R., Faccoli, M., Montes, C.R., Nowak, J.T., Reeve, J.D., Gandhi, K.J., 2022. Relationships between drought, coniferous tree physiology, and Ips bark beetles under climatic changes. In: Bark beetle management, ecology, and climate change. Academic Press, pp. 153–194. https://doi.org/10.1016/B978-0-12-822145-7.00004-0.

Millar, C.I., Stephenson, N.L., 2015. Temperate forest health in an era of emerging megadisturbance. Science 349 (6250), 823–826. https://doi.org/10.1126/science.aaa9933.

Munson, S. and J. Anhold. 1995. Site risk rating for mountain pine beetle in ponderosa pine. *As cited in Chojnacky, DC, BJ Bentz, and JA Logan* (2000).

Negrón, J.F., 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. Forest Ecology and Management 107, 71–85. https://doi.org/10.1016/S0378-1127(97)00319-8.

Negrón, J.F., Popp, J.B., 2004. Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. Forest Ecology and Management 191 (1–3), 17–27. https://doi.org/10.1016/j.foreco.2003.10.026.

Negrón, J.F., Allen, K., Cook, B., Withrow, J.R., 2008. Susceptibility of ponderosa pine, *Pinus ponderosa* (Dougl. ex Laws.), to mountain pine beetle, *Dendroctonus ponderosae* Hopkins, attack in uneven-aged stands in the Black Hills of South Dakota and

Wyoming USA. Forest Ecology and Management 254 (2), 327–334. https://doi.org/10.1016/j.foreco.2007.08.018.
Negrón, J.F., McMillin, J.D., Anhold, J.A., Coulson, D., 2009. Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona, USA. Forest Ecology and Management 257 (4), 1353–1362. https://doi.org/10.1016/j.foreco.2008.12.002.
Oliver, W.W. 1995. Is self-thinning in ponderosa pine ruled by *Dendroctonus* bark beetles? *In* Proceedings of the 1995 National Silviculture, Workshop, **GTR-RM-267**. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, C.O., pp., 213–218.
Olsen, W.K., Schmid, J.M., Mata, S.A., 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. Forest Science 42 (3), 310–327. https://doi.org/10.1093/forestscience/42.3.310.
Powell, J.A., Bentz, B.J., 2014. Phenology and density-dependent dispersal predict patterns of mountain pine beetle impact. Ecological Modeling 273, 173–185. https://doi.org/10.1016/j.ecolmodel.2013.10.034.
Powell, J.A., Logan, J.A., 2005. Insect seasonality: circle map analysis of temperature-driven life cycles. Theoretical Population Biology 67 (3), 161–179. https://doi.org/10.1016/j.tpb.2004.10.001.
Preisler, H.K., Hicke, J.A., Ager, A.A., Hayes, J.L., 2012. Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. Ecology 93 (11), 2421–2434. https://doi.org/10.1890/11-1412.1.
Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58 (6), 501–517. https://doi.org/10.1641/B580607.
Régnière, J., Bentz, B., 2007. Modeling cold tolerance in the mountain pine beetle, *Dendroctonus ponderosae*. Journal of Insect Physiology 53 (6), 559–572. https://doi.org/10.1016/j.jinsphys.2007.02.007.
Reynolds, K.M., Holsten, E.H., 1994. Relative importance of risk factors for spruce beetle outbreaks. Canadian Journal of Forest Research 24 (10), 2089–2095. https://doi.org/10.1139/x94-268.
Robbins, Z.J., Xu, C., Aukema, B.H., Buotte, P.C., Chitra-Tarak, R., Fettig, C.J., Goulden, M.L., Goodsman, D.W., Hall, A.D., Koven, C.D., Kueppers, L.M., Madakumbura, G.D., Mortenson, L.A., Powell, J.A., Scheller, R.M., 2022. Warming increased bark beetle-induced tree mortality by 30% during an extreme drought in California. Global Change Biology 28 (2), 509–523.
Robertson, C., Nelson, T.A., Boots, B., 2007. Mountain pine beetle dispersal: The spatial–temporal interaction of infestations. Forest Science 53 (3), 395–405. https://doi.org/10.1093/forestscience/53.3.395.
Robeson, S.M., 2015. Revisiting the recent California drought as an extreme value. Geophysical Research Letters 42 (16), 6771–6779. https://doi.org/10.1002/2015GL064593.
Rushing, C., Bulusu, A., Hurwitz, H.I., Nixon, A.B., Pang, H., 2015. A leave-one-out cross-validation SAS macro for the identification of markers associated with survival. Computers in Biology and Medicine 57, 123–129. https://doi.org/10.1016/j.compbiomed.2014.11.015.
Safranyik, L. and A.L. Carroll. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *The mountain pine beetle: a synthesis of biology, management and impacts on lodgepole pine*. Victoria, BC, Canada: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, pp. 3–66.
Safranyik, L., Linton, D.A., Silversides, R., McMullen, L.H., 1992. Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. Journal of Applied Entomology 113, 441–450. https://doi.org/10.1111/j.1439-0418.1992.tb00687.x.
Santos, M.J., Whitham, T.G., 2010. Predictors of *Ips confusus* outbreaks during a record drought in southwestern USA: implications for monitoring and management. Environmental Management 45 (2), 239–249. https://doi.org/10.1007/s00267-009-9413-6.
Sartwell, C., Stevens, R.E., 1975. Mountain pine beetle in ponderosa pine–prospects for silvicultural control in second-growth stands. Journal of Forestry 73 (3), 136–140. https://doi.org/10.1093/jof/73.3.136.
Schmid, J.M., and S.A. Mata. 2005. Mountain pine beetle-caused tree mortality in partially cut plots surrounded by unmanaged stands. Research Paper RMRS-RP-54, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO. 11 p.
Smith, G.D., Carroll, A.L., Lindgren, B.S., 2011. Facilitation in bark beetles: endemic mountain pine beetle gets a helping hand. Agricultural and Forest Entomology 13, 37–43. https://doi.org/10.1111/j.1461-9563.2010.00499.x.
Soderberg, D.N., Mock, K.E., Hofstetter, R.W., Bentz, B.J., 2020. Translocation experiment reveals capacity for mountain pine beetle persistence under climate warming. Ecological Monographs 91 (1), e01437.
Stephenson, N.L., 1990. Climatic control of vegetation distribution: the role of the water balance. The American Naturalist 135 (5), 649–670. https://doi.org/10.1086/285067.
Stephenson, N.L., Das, A.J., Ampersee, N.J., Bulaon, B.M., Yee, J.L., Edwards, D., 2019. Which trees die during drought? The key role of insect host-tree selection. Journal of Ecology 107 (5), 2383–2401.
Stevens, R.E. 1980. *Risk rating guide for mountain pine beetle in Black Hills ponderosa pine* (Vol. 385). US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.
Truettner, C., Anderegg, W.R.L., Biondi, F., Koch, G.W., Ogle, K., Schwalm, C., Litvak, M. E., Shaw, J.D., Ziaco, E., 2018. Conifer radial growth response to recent seasonal warming and drought from the southwestern USA. Forest Ecology and Management 418, 55–62.
Valerio-Mendoza, O., García-Román, J., Becerril, M., Armendáriz-Toledano, F., Cuéllar-Rodríguez, G., Negrón, J.F., Sullivan, B.T., Zúñiga, G., 2019. Cryptic species discrimination in western pine beetle, *Dendroctonus brevicomis* LeConte (Curculionidae: Scolytinae), based on morphological characters and geometric morphometrics. Insects 10 (11), 377. https://doi.org/10.3390/insects10110377.
Weed, A.S., Bentz, B.J., Ayres, M.P., Holmes, T.P., 2015. Geographically variable response of *Dendroctonus ponderosae* to winter warming in the western United States. Landscape Ecology 30 (6), 1075–1093.
Wermelinger, B., 2004. Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. Forest Ecology and Management 202 (1–3), 67–82. https://doi.org/10.1016/j.foreco.2004.07.018.
Willyard, A., Gernandt, D.S., López-Reyesand, A., Potter, K.M., 2021. Mitochondrial phylogeography of the ponderosa pines: widespread gene capture, interspecific sharing, and two unique lineages. Tree Genetics & Genomes 17 (6), 47. https://doi.org/10.1007/s11295-021-01529-4.