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Warming increased bark beetle-induced tree mortality by 30% during an extreme drought in California

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Abstract

Quantifying the responses of forest disturbances to climate warming is critical to our understanding of carbon cycles and energy balances of the Earth system. The impact of warming on bark beetle outbreaks is complex as multiple drivers of these events may respond differently to warming. Using a novel model of bark beetle biology and host tree interactions, we assessed how contemporary warming affected western pine beetle (*Dendroctonus brevicomis*) populations and mortality of its host, ponderosa pine (*Pinus ponderosa*), during an extreme drought in the Sierra Nevada, California, United States. When compared with the field data, our model captured the western pine beetle flight timing and rates of ponderosa pine mortality observed during the drought. In assessing the influence of temperature on western pine beetles, we found that contemporary warming increased the development rate of the western pine beetle and decreased the overwinter mortality rate of western pine beetle larvae leading to increased population growth during periods of lowered tree defense. We attribute a 29.9% (95% CI: 29.4%–30.2%) increase in ponderosa pine mortality during drought directly to increases in western pine beetle voltinism (i.e., associated with increased development rates of western pine beetle) and, to a much lesser extent, reductions in overwintering mortality. These findings, along with other studies, suggest each degree (°C) increase in temperature may have increased the number of ponderosa pine killed by upwards of 35%–40% °C^{-1} if the effects of compromised tree defenses

(15%–20%) and increased western pine beetle populations (20%) are additive. Due to the warming ability to considerably increase mortality through the mechanism of bark beetle populations, models need to consider climate's influence on both host tree stress and the bark beetle population dynamics when determining future levels of tree mortality.

KEYWORDS
bark beetles, climate impacts, drought, forest dynamics, modeling, tree mortality

1 | INTRODUCTION

Tree mortality has increased rapidly across the Western United States in recent decades (Fettig et al., 2021; Hicke et al., 2016) and represents a large potential release of carbon to the atmosphere (7–25 Tg C year^{-1}) that needs to be considered in the projections of future carbon emissions (Hicke et al., 2013). Disturbance regimes of forests have likely already changed due to warming climate (resulting in increased area burned by fire, increased wind severity, more extensive droughts, and outbreaks of certain insects), and thus have reduced forest resilience and the ability to provide continued ecosystem services (Seidl et al., 2016). Forests experiencing altered disturbance regimes may shift into chronic disequilibrium, preventing the ecosystem from returning to its prior state (McDowell et al., 2020; Serra-Diaz et al., 2015). The resulting losses from productivity shifts may cause forests to act as carbon sources to the atmosphere for decades (Dore et al., 2008). However, intensified disturbances may lead to the replacement of susceptible tree species with those more adapted to current and future climates, leading to increases or decreases in the productivity of forests long term (Reyer et al., 2017). Therefore, a mechanistic understanding of interactions among climate, forests, and disturbances is necessary to plan forest management actions and to forecast the effects of climate change on biological systems.

Bark beetles are a major cause of mature tree mortality in many conifer forests worldwide, with up to 2% of bark beetle species capable of landscape-level outbreaks (Bentz & Jönsson, 2015; Raffa et al., 2008). Many of these are what are termed “aggressive” bark beetles, those that can kill live hosts. During the outbreaks, aggressive bark beetles kill host trees through synchronized mass attacks, mediated by aggregation pheromones, by chewing through the bark to feed and reproduce in the subcortical layer (Raffa et al., 2008). Under most conditions, host tree defenses constrain bark beetle populations at endemic levels, but conditions such as drought facilitate bark beetle attacks on better-defended and larger-diameter hosts (Boone et al., 2011). Such hosts yield exponentially more bark beetle offspring, resulting in positive feedbacks that lead to more widespread bark beetle outbreaks (Raffa et al., 2008). Outbreaks collapse when bark beetles exhaust susceptible host pools, or when acutely cold temperatures or predators and parasitoids collapse bark beetle populations (Sambaraju et al., 2012; Wermelinger, 2002).

Understanding interactions among climate, forests, and disturbances are crucial to global vegetation dynamics as climate change is expected to increase tree mortality attributed to bark beetles in mid-latitude conifer forests over the next century (Weed et al., 2013). Quantifying bark beetle outbreaks and their sensitivity to climate becomes increasingly important as bark beetles spread to higher latitudes and new locations (Weed et al., 2013). Climate change may disrupt bark beetle and host interactions, changing rates of host tree mortality through several mechanisms. First, warming may reduce the time required for bark beetles to develop from eggs to adults and reduce levels of overwintering mortality; these dynamics may increase their population success and thus increase tree mortality (Bentz et al., 2010). Second, increased drought frequency and intensity under climate change may alter interactions among bark beetles and hosts (Williams et al., 2015). Regional drought often acts as a catalyst for bark beetle outbreaks, as water-stressed trees have lower rates of growth and carbon assimilation, which may compromise host defenses (Kolb et al., 2016) and result in large amounts of tree mortality over short periods of time (Fettig, 2019).

Many challenges exist in attempting to model these interactions. First, warming temperatures can have complex effects on bark beetle populations. While warming may aid in host procurement by increasing voltinism (the number of generations within a year; Bentz et al., 2010; Raffa et al., 2015), warmer temperatures can also result in maladaptive life cycles in which the bark beetle's flight synchrony is disrupted, or crucial life stages become misaligned with seasonal temperatures (Bentz et al., 2010; Lombardo et al., 2018). Second, modeling the transition from endemic to epidemic stages of bark beetle populations in a manner that captures both high-severity outbreaks and recovery of tree host populations post-outbreak is difficult (Huang et al., 2020; Raffa et al., 2008). This is because dynamics between host and beetle populations are highly nonlinear and small uncertainties in initial condition or parameterizations can cause a large difference in the timing of the transition from the endemic stage to the epidemic stage (Raffa et al., 2008). Finally, interactions between bark beetles and tree hosts can be altered by changing climatic conditions, affecting both bark beetle population dynamics (development and mortality) and host tree defenses. For example, warming can exacerbate the effects of drought, further compromising host tree defenses, and increasing beetle attack success (Franceschi et al., 2005; Kolb et al., 2016).

Vegetation models often assume that bark beetle attacks are contained within background mortality or arise from the plant vulnerability under stressed conditions (Fisher et al., 2015; Huang et al., 2020). These models may miss the timing and severity of tree mortality, as each measure (tree host defense and bark beetle populations) responds to climate differently with highly non-linear interactions. Accurate forecasts of bark beetle-induced tree mortality should, therefore, account for the influence of climate on both populations of bark beetles and the defenses of host trees (Anderegg et al., 2015). Much work has been done to forecast bark-beetle-induced tree mortality using models that simulate the temperature-dependent development and mortality of bark beetles (Bentz & Jönsson, 2015). These models can capture beetle population responses to climate and allow for forecasting of annual and decadal fluctuations in bark beetle populations under future climates. The PHENIPS model of the European spruce beetle (*Ips typographus* (L.)) (Baier et al., 2007) has been shown to effectively capture bark beetle flight and development. This model has been used to estimate the number of beetle generations annually in various efforts to assess the response of beetle-caused tree mortality to warming and drought (Netherer et al., 2019; Seidl et al., 2007, 2017). PHENIPS relies on the cumulative sum of degree days since April 1st to track the development stage and the number of European spruce beetle generations. Tree mortality and damage are calculated as a function of the number of beetle generations (Seidl et al., 2007). Bark beetles develop as a cohort within a given host, and all disperse once the conditions necessary for development and flight are met. However, treating bark beetles as a single cohort may fail to capture the phenological asynchrony that can occur within host trees or at the landscape scale which may lead to diminished attack (Lombardo et al., 2018). Furthermore, treating a whole generation as synchronous may fail to capture the effects of temperature on the mortality and development of various life stages of the bark beetles. Individual-based models of the development of mountain pine beetle (*Dendroctonus ponderosae*) have illustrated that non-linear effects of temperature on the development of different life stages can mediate bark beetle population success (Régnière et al., 2012). This work suggests the need for life-stage-specific phenological details and overwinter mortality rates (Régnière et al., 2012). However, individual-based models often are too computationally intensive to be applied at larger scales. Integral projection models used for stochastic rate simulation can simulate a population's advancement through the crucial stages of development with associated variability at a reasonable computational cost (Goodsman et al., 2018; Powell & Bentz, 2009). As far as we know, however, no models have accurately incorporated this level of bark beetle phenology and mortality with stress-dependent host defense into a single model (Huang et al., 2020).

In order to quantify the impact of climate warming on bark beetle population dynamics and the resulting tree mortality, we tested the contribution of two mechanisms influenced by warming temperature (voltinism and overwintering mortality) on levels of host ponderosa pine (PP, *Pinus ponderosa)* mortality in the Sierra Nevada resulting from western pine beetle outbreaks (WPB, *Dendroctonus brevicomis*) during the 2012–2015 drought in California. We developed a model of bark beetles' development and interactions among climate, and host defense, comparing historical and contemporary temperature cases and host tree mortality when tree stress was held constant. Specifically, we aimed to test two hypotheses: (H1) higher contemporary temperatures increased WPB-induced tree mortality during the drought; (H2) the higher tree host mortality results primarily from shorter WPB generation times (increased voltinism) and not overwintering mortality, as the winter temperatures are not low enough to cause significant mortality of overwintering WPB.

2 | METHODS

2.1 | Study area

Our study area encompasses the Eldorado, Stanislaus, Sierra, and Sequoia National Forests, Kings Canyon, Sequoia, and Yosemite National Parks, and areas of the Sierra Nevada among them in California, United States (Figure 1). To differentiate the spatial variability in climate conditions, the total study area was divided into North and South regions along 37.5° latitude (approximately the midpoint) and two elevation bands, determined by the 90th percentile of the host PP range as estimated from the USDA Forest Service Forest Inventory and Analysis Program (hereafter FIA, Bechtold & Patterson, 2015; Figure 1). These are hence referred to as the four sub-regions.

This area is classified as Sierra Nevada mixed conifer consisting of predominantly of PP, sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), canyon live oak (*Quercus chrysolepsis*), California black oak (*Quercus kellogii*), and white fir (*Abies concolor*). PP is found at elevations from 400 m, representing the lowest elevations of the mixed conifer forests of the western slope of the Sierra Nevada, up to 2200 m. The Stanislaus Tuolumne Experimental Forest (located near the center of our study area, at an elevation of 1590–1950 m) receives, on average, 940 mm of precipitation more than half falling as winter snow (Adams et al., 2004). Precipitation is seasonal, generally with an extended dry period during the summer (June–September) and cool, moist winters typical of a Mediterranean climate type. Air temperatures range from −7 to 7°C during January and 6 to 27°C in July.

During 2012–2015, an extreme drought initiated bark beetle-caused tree mortality throughout the study area. This drought was among the strongest on record for California and has in part been attributed to climate warming characterized by elevated potential evapotranspiration (Williams et al., 2015). While tree mortality was widespread throughout the central and southern Sierra Nevada, it was not uniform either spatially or by tree species and tree size (Fettig et al., 2019). PP suffered the highest levels of mortality, primarily due to the multivoltine (multiple generations year^{-1}) WPB, for which PP is the only host in the region. In some areas, mortality of PP exceeded 90%, with

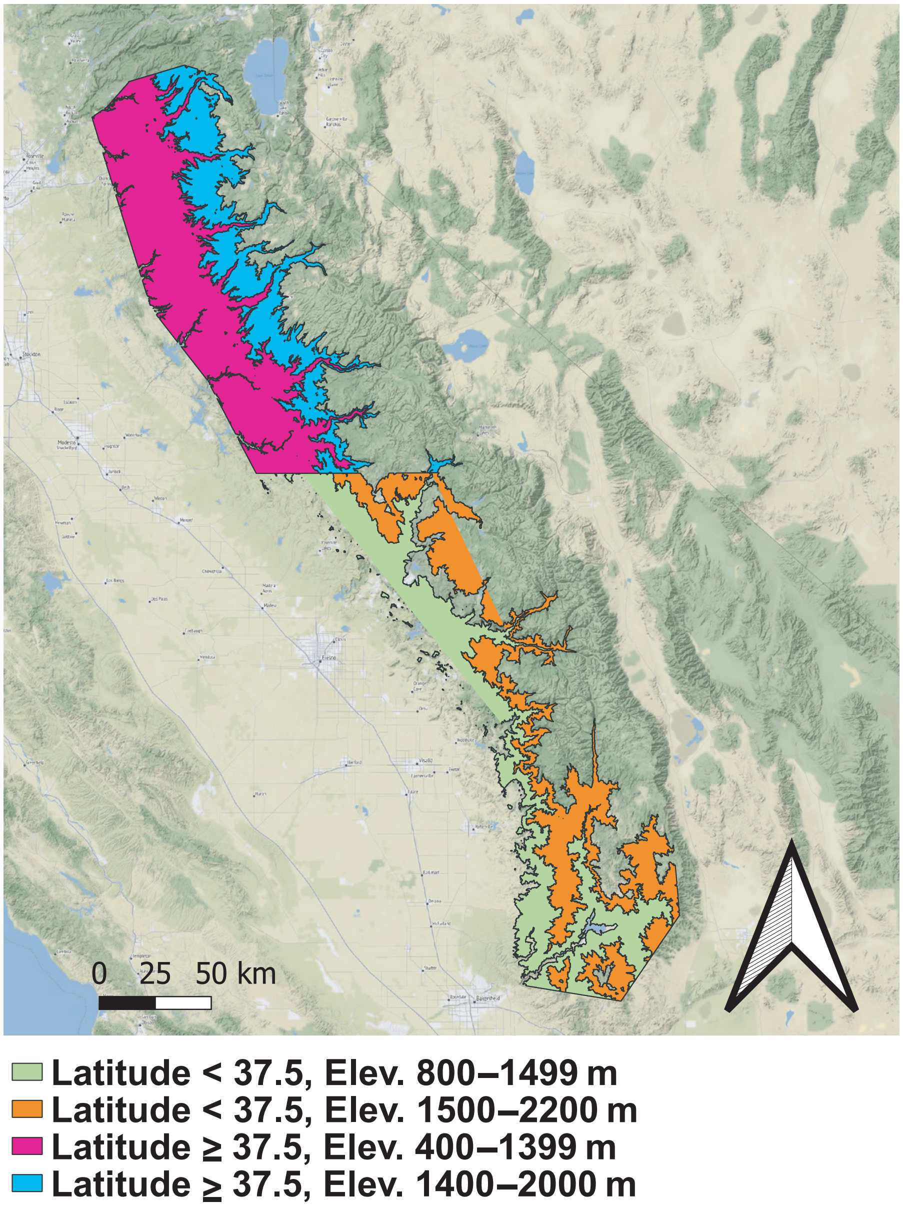


FIGURE 1 Study area: California, United States. These four sub-regions (represented by different colors) were used in the calculation of climate, vegetation, and tree mortality variables

greater mortality observed in larger PP size classes (>31.8 cm dbh, diameter at 1.37 m in height; Fettig et al., 2019).

2.2 | Model description

We constructed a combined model of bark beetle phenology, population dynamics, and attack on trees to test the contribution of warming on WPB outbreaks (Figure 2, Sup. 1). As an overview of the process, the first aspect of this is insect mortality and phenology model (IMAP) which uses the daily minimum and maximum temperature to calculate sub-cortical temperatures and calculates WPB growth based on the vital rates of five development stages (Goodsman et al., 2018). It further calculates WPB behaviors such as oviposition and flight initiation for a WPB population. We parameterized IMAP using the published phenology of WPB and validated its performance against field data on flight timing and observations of WPB biology (Table S1, Sup. 2). We incorporated IMAP into the tree death and insect attack model (TDIA). The TDIA accounts for the number of bark beetles in flight, the number and size of hosts available, and the drought state during a daily time step to determine the likelihood of tree death. When bark beetles successfully kill a tree host through the attack, a proportional number of new egg-laying adult WPB are introduced into the IMAP beetle population model. The TDIA was parameterized based on the field data of tree stand age structure and composition (and tree mortality), along with the measured drought surrogates, and validated against the FIA record of tree mortality. Lastly, we ran the combined IMAP/TDIA model under contemporary and historical temperatures to understand how an increase in temperature impacted WPB development and the ultimate level of host tree mortality.

The WPB life cycle includes eight stages: egg, four larval instars, pupa, teneral adult, and finally adult (see Miller & Keen, 1960 and the

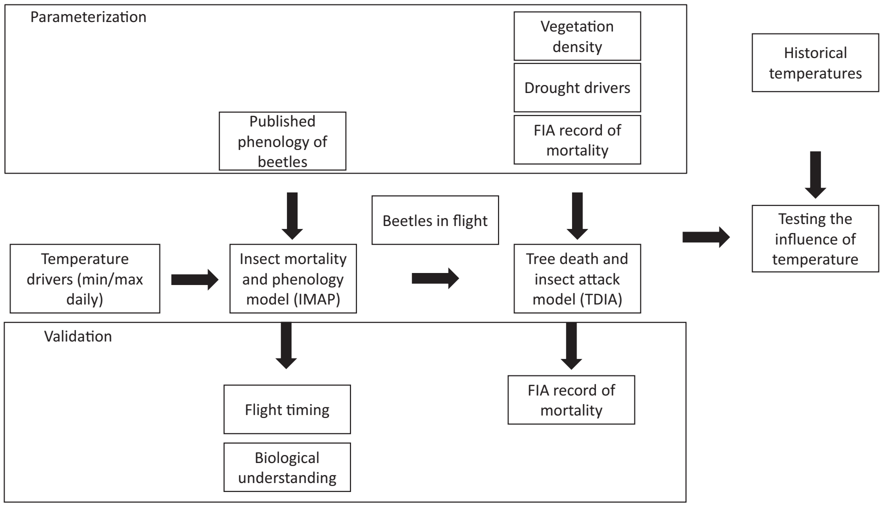


FIGURE 2 Overview of the model structure, parameterization, and validation

references therein). As adults, WPB aggregate and mass attack; if successful, adults oviposit in egg galleries constructed in the phloem (inner bark). Once the eggs hatch, emerging larvae feed outward toward the outer bark. In the later larval stages, particular temperature thresholds are necessary to begin pupation (the transformation into adults). Before emerging as adults, the bark beetle's exoskeleton hardens in the teneral adult stage. Under bark temperature plays a role in determining the rate of development, while external temperatures play a role in the timing of emergence and flight synchrony (Gaylord et al., 2008; Miller & Keen, 1960).

2.3 | Insect mortality and phenology model (IMAP)

In order to accommodate the difference between air and under bark (phloem) temperature, we use a statistical model to estimate phloem temperature from air temperature (minimum and maximum daily; see Sup. 3.2). The statistical model is based on previous phloem temperature models (Lewis, 2011; Powell & Bentz, 2009), interpolating between the maximum and minimum temperature using a sine curve and then corrects for the difference between mean air temperature and mean phloem temperature. Specifically,

$$T_i = \beta_{0j} + \beta_{1j}\left(\mu_t + \left(\frac{\Delta_t \sin\left(\theta_j\right)}{2}\right)\right), \tag{1}$$

where θ_j is the discretized circular angle in radians, which can be one of seven regularly spaced values in the set $\{-\frac{\pi}{2}, -\frac{\pi}{4}, \ldots, \pi, \frac{5\pi}{4}\}$ following the cycle from daily minimum to daily maximum, Δ_t is the daily temperature range, and μ_t is the mean daily temperature. The constants β_{0j} and β_{1j} are regression parameters relating phloem and air temperature at time j. This function considers the period between the minimum and maximum temperatures of the first day and then the maximum temperature of the first day and minimum temperature of the next day, generating eight three-hour periods for which the daily median rate of development is calculated. The median rate of development for WPB (R_i) is calculated based on a temperature and stage-dependent rate equation (Hilbert & Logan, 1983) as follows:

$$R_i = R_{0i}\left(\frac{(T - T_{0i})^2}{(T - T_{0i})^2 + k_i}\right) - e^{\frac{T_{mi} - (T - T_{0i})}{d_i}}, \tag{2}$$

where R_{0i} is a parameter scaling the development rate at temperature (T) for development state i. The minimum development temperature (°C) in the stage is T_0, the maximum survivable temperature at a given stage is T_m. The parameters k_i and d_i are estimated shape parameters. The stochastic rate, r_j, at a specific time step j, t_j, is assumed to follow a lognormal distribution with median rate, $R_i(T(t_j))$, given in Equation (2) as follows,

$$p\left(r_j;\mu_j,\sigma_s^2\right) = \frac{1}{r_j\sqrt{2\pi\sigma_s^2}} e^{\frac{-\left(\ln\left(r_j\right)-\mu_j\right)^2}{2\sigma_s^2}}, \tag{3}$$

where

$$\mu_j = \ln\left(R_i\left[T\left(t_j\right)\right]\Delta t\right),$$

σ_s^2 is the scale parameter in the lognormal, $T(t_j)$ is the temperature during the time step, and the aging increment for a particular individual during the time interval is $r_j\,\Delta t$. The distribution of developmental ages across individuals at the next time step is updated based on the distribution of rates at the current time step (Equation 3) and the current distribution of developmental ages using convolution.

Overwintering mortality of WPB larvae is based on the coldest winter temperature (°C) for a given year. The surviving larvae (S_L) are calculated as follows,

$$S_L = \frac{n_l}{1 + e^{\frac{-(T_{min}+\alpha)}{\beta}}}, \tag{4}$$

where n_l is the number of larvae, α and β are parameters fit to empirical data, and $T_{\min}$ is the minimum winter temperature(°C). Overwintering mortality for the other WPB life stages is defined as threshold temperatures below which a proportion of the population is removed.

After WPB reaches adulthood, a proportion of the adult population takes flight at each time step, based on the daily maximum temperature. The proportion of the population to take flight (P_f) was determined by a nonlinear function (McCambridge, 1971) defined as,

$$P_f = x_0 + x_1 T + x_2 T^2, \tag{5}$$

where T is the maximum daily temperature (°C), P_f is the proportion of the WPB population to initiate flight and $0 \leq P_f \leq 1$, P_f is zero when below and above-set breakpoints for minimum and maximum flight temperature and x_0, x_1, x_2 are estimated from empirical data. See Goodsman et al. (2018) for a more detailed description of IMAP.

2.4 | Tree defense and insect attack model

The tree defense and insect attack (TDIA) model determines attack success rate based on host tree density for different host tree size classes, the attack preference of WPB for host tree size classes, and the impact of drought stress and tree size on host defense. We divided PP into two size classes (10–31.8 and >31.8 cm dbh) due to WPB's preference for colonizing larger PP (Fettig et al., 2019; Stephenson et al., 2019), and based on data (see Section S2.3) that showed clear differences in mortality between these two size classes of PP. We did not consider PP <10 cm dbh as they generally would not serve as hosts for WPB (Fettig et al., 2019; Miller & Keen, 1960). The WPB that successfully colonize PP becomes the parents in the next generation within the IMAP model. WPB that do not successfully colonize a PP die.

Once WPB reaches flight, as estimated by IMAP, their likelihood of a successful attack is calculated based on the density of PP, the amount of drought stress experienced by PP, and the density of WPB in flight at a given time. If we begin with the mean expected number of successful attacks per PP (a_t) as follows,

$$a_t = \frac{k b_i}{N_t}, \tag{6}$$

where b_i is the density of WPB in flight (beetles/ha) attracted to a given PP host class and N_t is the potential number of hosts (PP/ha) in each host size class. The approach for calculating b_i is discussed below in Equations (12–14). We assume a spatially implicit representation of dispersal efficiency to determine the fraction of the WPB population that can successfully attack susceptible PP. Specifically, the term k represents the aggregation efficiency of WPB to attack PP, accounting for some amount of WPB loss during dispersal and aggregation.

Given the expected number of WPB attacks per PP (a_t), the resulting rate of tree mortality, $F(\varphi; a_t)$, is calculated as follows

$$F(\varphi; a_t) = \frac{a_t}{\varphi}, \tag{7}$$

where φ is the critical number of attacking WPB needed to overcome a single PP's defenses and $0 \leq F(\varphi; a_t) \leq 1$. The remaining PP host density is calculated as follows,

$$N_{t+1} = N_t \left(1 - F(\varphi; a_t)\right). \tag{8}$$

The resulting WPB parents (P_{t+1}) from this attack for each PP size class are represented as follows,

$$P_{t+1} = \varphi N_t F(\varphi; a_t). \tag{9}$$

The resulting parents of each PP size class are combined and used in the IMAP model to initiate the next WPB generation.

As stated in Equation (7), φ is the critical number of attacking WPB needed to overcome a single PP's defense. As φ increases, the probability of PP survival increases, and the WPB in flight becomes ineffective in reproducing. We related φ and the influence of drought and PP size as a logarithmic equation

$$\log(\varphi) = \beta_0 + \beta_1 C_t + \beta_2 S, \tag{10}$$

where β_0 represents a baseline number of WPB needed to kill a PP; β_1 reflects the influence of drought on stress C_t; and β_2 reflects the influence of the PP size class (S) (binary 1 or 0). Parameterization of Equation (10) is described further in Sup. 3.9.

The influence of drought on PP stress, C_t, for each time step is the 4-year standard precipitation index calculated as

$$C_t = \frac{p_{(4\text{ year sum})} - \mu_{\text{normal}}}{\sigma_{\text{normal}}}, \tag{11}$$

where μ_{normal} and σ_{normal} are the mean and standard deviation of the 4-year rolling sum of precipitation (cm) for the period of 1995–2005, calculated for each site and $p_{(4\text{ year sum})}$ is the sum of precipitation (cm) in the previous 4 years. See Sup. 2.1 for more information.

We included a sub-model to calculate the number of WPB drawn to each PP size class. We found further evidence for this decision in our tree mortality data (Sup. 2.3). Before the drought, the mortality rate of large PP to insects or drought was about half that of small PP to insects or drought; however, during the drought, the mortality rate of large PP was ~2.6 times that of small PP (Figure S3). To accommodate this, we calculated the proportion of WPB that attack the larger(preferred) PP size class (H) as

$$H = F(\varphi; a_t)^{\rho}, \tag{12}$$

where $F(\varphi; a_t)$ is the rate of mortality (in the proportion of host trees), if all WPB were to attack the preferred size class, ρ is an estimated parameter, and $0 \leq H \leq 1$.

The number of WPB that attack the larger PP size class is calculated as follows,

$$b_p = H b_{fl}, \tag{13}$$

where b_{fl} is the total number of WPB in flight. The number of WPB that attack the smaller host size class (less preferred) is calculated as follows

$$b_s = b_{fl} - b_p. \tag{14}$$

These are used as b_i for each size class in Equation (6).

2.5 | Data description

Daily climate drivers (precipitation (cm), minimum temperature (°C), and maximum temperature (°C)) were gathered for each study area from DAYMET (Thornton et al., 2014) for 2001–2018, with the first 5 years used to initialize the model (Sup. 2.1). Initial tree density (2005–2006) and tree mortality data (2007–2018) used for model initialization and calibration were derived from FIA plots within our study areas (Sup. 2.2). PP density per plot was aggregated to represent the density at a given diameter class in each patch using the plot level adjustment factors and was then scaled to a per hectare basis. Data from 2005 to 2006 were used to calculate the initial conditions for the stands in 2006, using the mean density (Sup. 2.2).

To calculate the tree mortality, we isolated the host species and only kept entries for which mortality was linked to insects or drought (Figure S2). We included both mortality that was classified as drought or insect as the FIA dataset does not specify mortality attributed to WPB. Without a clear method of attribution in individual plot-level data, it was necessary to attribute all PP mortality to WPB, which may overestimate the total amount of WPB mortality. Fettig et al. (2019) determined that 89.8% of large PP (>31.8 cm) and 77.0% of smaller host PP (10–31.8 cm) were killed by WPB. We observed a very similar pattern in the FIA-based mortality data to those of the more extensively censused plots of Fettig et al. (2019) in Sup. 2.2. Given WPB is not known to colonize trees after death like other bark beetles, we assumed that all PP colonized by WPB were not killed prior to the attack (Fettig et al., 2019; Miller & Keen, 1960). While there were other bark beetle species killing during the drought event, a vast majority of PP mortality throughout the region during the drought was attributed to WPB (Fettig et al., 2019).

2.6 | Model calibration

To parameterize the IMAP model, we synthesized the data found in Miller and Keen (1960). This seminal work provides summaries of many studies conducted by the USDA Forest Service and others on the ecology and management of WPB (Sup. 3). The data presented provide estimates of the development rates for eggs, larvae, late larvae, pupae, teneral adults, and adults under various temperatures (Sup. 3.4, 5). Miller and Keen (1960) also provide mortality thresholds for different life stages of WPB and average population statistics on background brood mortality necessary for simulation.

We used a Markov Chain Monte-Carlo sampler to parameterize TDIA against the observed tree mortality ($N = 45{,}000$ model runs) (Sup. 3.10). We used a multivariate lognormal proposed distribution based on a pre-model sampling run. For the TDIA parameters (k, β_0, β_1, β_2, ρ), estimates of mortality were determined using the attack model and biological parameters. Within the attack model, k determines the aggregation effectiveness of the WPB to PP (Equation 6). β_0, β_1, β_2 determines the defenses of trees in relation to drought (β_1) and tree size class (β_2; Equation 10). The parameter ρ determines the relative influence of the size class preference (Equation 12). Parameter values that resulted in less than biologically feasible WPB successful attack numbers were also removed (<500 WPB attacking the larger host size class). A range was provided for the parameters of the initial population of endemic WPB, calculated from the survival rates and flight records.

2.7 | Model validation

We validated the WPB rate of development and flight initiation by comparing modeled runs with field capture data. We compared IMAP projections against WPB flight data for a research site (Eldorado National Forest) containing multiple traps within our study area (Hayes et al., 2009). The model was run using the minimum and maximum daily temperature drivers for the area and time surveyed and we compared the relative flight for the period in which capture data were available. Model runs for flight validation were started the previous fall (Oct 15th) to account for overwintering development.

For validation of the TDIA model, we tested how well the underlying model captured the dynamics using leave-one-site cross-validation. We fit the model four times removing one sub-region from each. Next, for each, we predicted the sub-region that had been removed and assessed the accuracy of the predictions.

2.8 | Hypothesis testing

To test the contribution of climate warming to PP mortality caused by WPB, we removed the amount of climate warming observed over the last century and held precipitation at observed levels. We measured climate warming by finding the difference in the monthly means between our study period (2001–2018) and historical conditions (1895–1945) for both the maximum and minimum daily temperature (Sup. 4.1, 4.2). The mean for both maximum and minimum daily temperature was subtracted from the observed maximum and minimum daily temperature for each month.

This new climate driver was then used to test H1 by comparing PP mortality between historical and contemporary temperature simulations. We further ran simulations wherein either the development rate of WPB, or the overwinter mortality, was changed to historical conditions. To test H2, we compared these runs against the contemporary simulations to understand the relative contribution of each mechanism. The 95% confidence interval of all simulation runs was used to determine the WPB-induced PP mortality difference between scenarios. We additionally analyzed the mean development rate under each climate driver, and the number of mortality events for different life stages of the WPB population (Sup. 4.3, 4.4).

3 | RESULTS

3.1 | Model calibration

The final acceptance rate for the Mark Chain Monte-Carlo sampler was 25.4% and the greatest autocorrelation was in the β_0, which remained above 0.1 for approximately 100 samples. We thinned the resulting chain to every 100 samples to account for autocorrelation. The model correctly simulated the temporal pattern of the WPB outbreak at the regional scale, remaining in the endemic stage (<1 PP killed ha^{-1}) before the drought, the building stage (1–5 PP killed ha^{-1}) at the beginning of the drought, and the epidemic stage (>10 PP killed ha^{-1}) after 3 years of drought (Figure S14). The predicted mortality was able to explain 73% of the variance in the observed mortality data (Figure S14). The estimated values for each parameter and the 95% confidence interval were used in the scenario simulations (Table 1). These parameters produced tree defense values for φ that are ~300–63,000 for the smaller size class and ~550–104,000 for the larger size class (Figure S13) and with mortality occurring commonly within the expected range of beetles necessary to kill a tree (Miller & Keen, 1960).

3.2 | Model validation

Our phenology and flight model captures the general timing of annual flight when tested over three separate years using a Kolmogorov–Smirnov test. Only one of the traps in any of the years tested was determined to be significantly different ($p > .05$ for all other traps tested). Comparing the mean observed rate suggests we fail to reject the null hypothesis that the simulated and observed data are similarly distributed (Figure 3). This suggests a good correspondence between model flight timing and data collected in the field (Hayes et al., 2009).

In validating the TDIA model using leave-one-site cross-validation, we found the model captured 91.28 of the variability in the resulting PP population at any time step and captured 70.59% of the variability in the amount of PP mortality at any time step (Figure S15). While this is lower than the initial parameterization runs ($R^2 = .71$ vs. $R^2 = .73$), it seems the underlying method is consistent even with single sub-regions not included in the calibration, and that the model is capturing the underlying interaction between PP stress and WPB populations well.

TABLE 1 Parameter values and confidence intervals estimated for the TDIA model

Parameter	Median (95% CI)
k	0.2009 (0.1971–0.2052)
β_0	10.03 (10.00–10.15)
β_1	1.545 (1.527–1.550)
β_2	0.506 (0.500–0.523)
Initial population	840 (726–870)
ρ	0.051 (0.049–0.053)

3.3 | Impact of warming on WPB population dynamics

Warmer contemporary temperatures increased WPB voltinism as simulated through the mean rate of development across the four sub-regions. During the drought period, voltinism increased an average of 1.46 generations per sub-region (~0.36 generations year^{-1}) when comparing contemporary and historical temperatures (Figure 4a). At the same time, warmer contemporary temperatures slightly reduced overwintering mortality (Figure 4b). Under contemporary temperatures, overwintering mortality rates of larvae averaged 2.67% compared to 3.33% for historical temperatures (Figure 4b). These two mechanisms resulted in an increase in WPB flight per year during the years of peak PP mortality (Figure 4c). During the contemporary climate simulations, the number of WPB reaching flight was 35.1% higher at the initiation of the drought and remained elevated (37.4%–45.4%) during the drought years when compared to the historical simulations (Figure 4c).

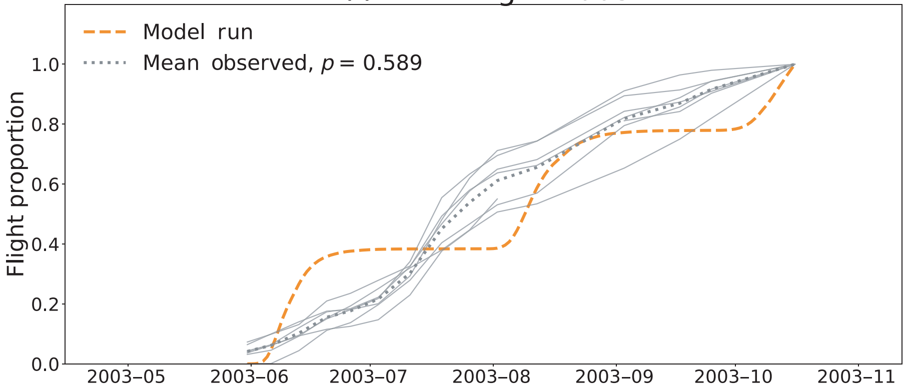
3.4 | Impact of warming on levels of WPB-caused tree mortality

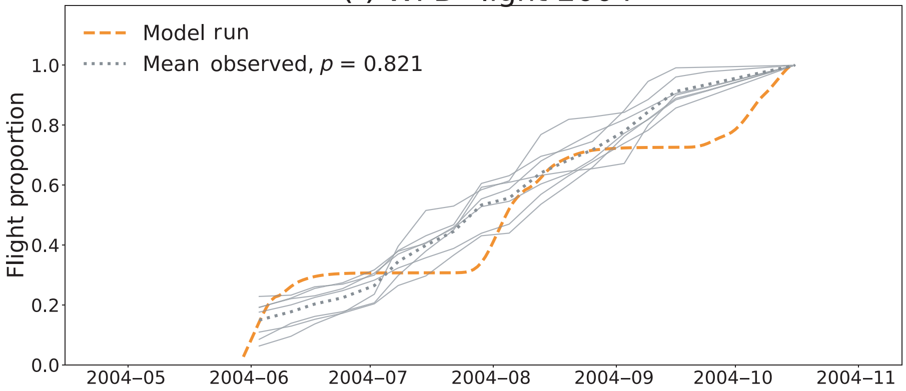
PP mortality resulting from WPB attacks increased 29.9% (95% CI [29.4%–30.2%]) under warmer contemporary temperatures when compared to historical temperatures during the same period (Figure 5). The largest increase in PP mortality aligns with the years where PP mortality was highest, an increase of 5.86 trees ha^{-1} during peak mortality. Due to the preference of WPB for colonizing large-diameter PP (>31.8 cm dbh), this equates to a loss of ~45.6% of PP biomass (Sup. 4.5). This result supports our proposed H1. Simulations isolating the mechanisms (WPB development and overwinter mortality) that could increase PP mortality showed distinct effects (Figure 6). Reductions in overwintering mortality slightly increased PP mortality (6.4%), while increases in voltinism increased PP mortality by 26.9%. This result supports our proposed H2.

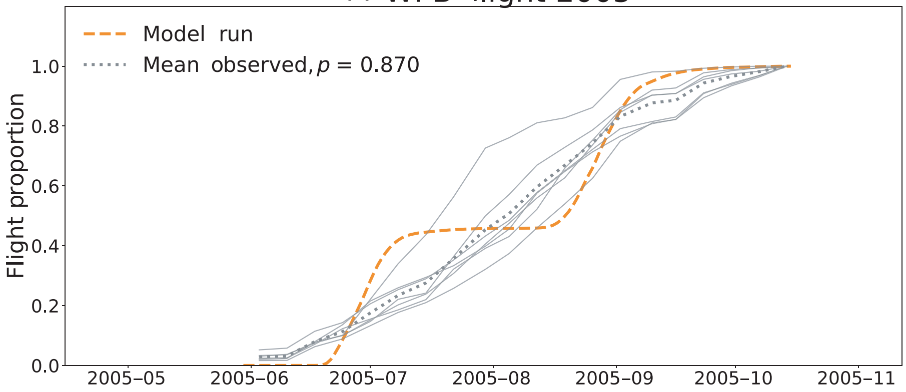
4 | DISCUSSION

In our study, contemporary warming increased positive feedbacks between WPB populations and drought-stressed hosts contributing to the high levels of PP mortality observed during the drought period (Figure 5). This affirms H1, that higher contemporary

FIGURE 3 Comparison of proportion of western pine beetle (WPB) flight per time step of modeled runs against field data from Hayes et al. (2009) for 3 years (a) 2003, (b) 2004, and (c) 2005. Each plot was sampled approximately every 7 days. Models were run from the previous fall (Oct. 15th) to account for the development of the prior overwintering generation. Solid grey lines represent individual traps


(a) WPB flight 2003


(b) WPB flight 2004


(c) WPB flight 2005

temperatures increased WPB-induced tree mortality during the drought. In our simulation, the WPB outbreak began following multiple years of drought as tree defenses weakened and the number of WPB required to kill individual PP decreased. Warmer contemporary temperatures led to an increase in WPB population during this period (through the mechanisms of increased voltinism and decreased overwintering mortality; Figure 4), ultimately leading to ~30% higher PP mortality than under historical temperatures. As WPB attack efficiency decreased, due to the absence of drought and loss of most of the suitable tree hosts, WPB populations returned to endemic levels (Figure 4).

The difference between the two mechanisms (increased voltinism and decreased overwintering mortality) suggests that the increasing development rate played a greater role in increasing host mortality. This affirms H2, that higher PP mortality mainly results from shorter WPB generation times, as the winter temperatures are normally not critically low enough to limit WPB populations in the Sierra Nevada. The increase in WPB voltinism accounted for a large majority of the increase in PP mortality, though a slight reduction in levels of overwintering mortality of WPB larvae was observed (Figures 4 and 6). Further, our results suggest that only minor increases in the voltinism (~0.36 generations year^{-1}) can substantially increase the population levels of multivoltine species, such as WPB. Of note, both projections of WPB voltinism (historically and contemporary) are within the range reported for WPB in the Sierra Nevada (i.e., 2–4 generations year^{-1}, Miller & Keen, 1960). In our simulations, neither the contemporary nor the cooler historical winter temperatures were sufficiently cold to collapse WPB populations. This reflects our understanding of WPB population dynamics in the Sierra Nevada, where historically, only rarely did high levels of

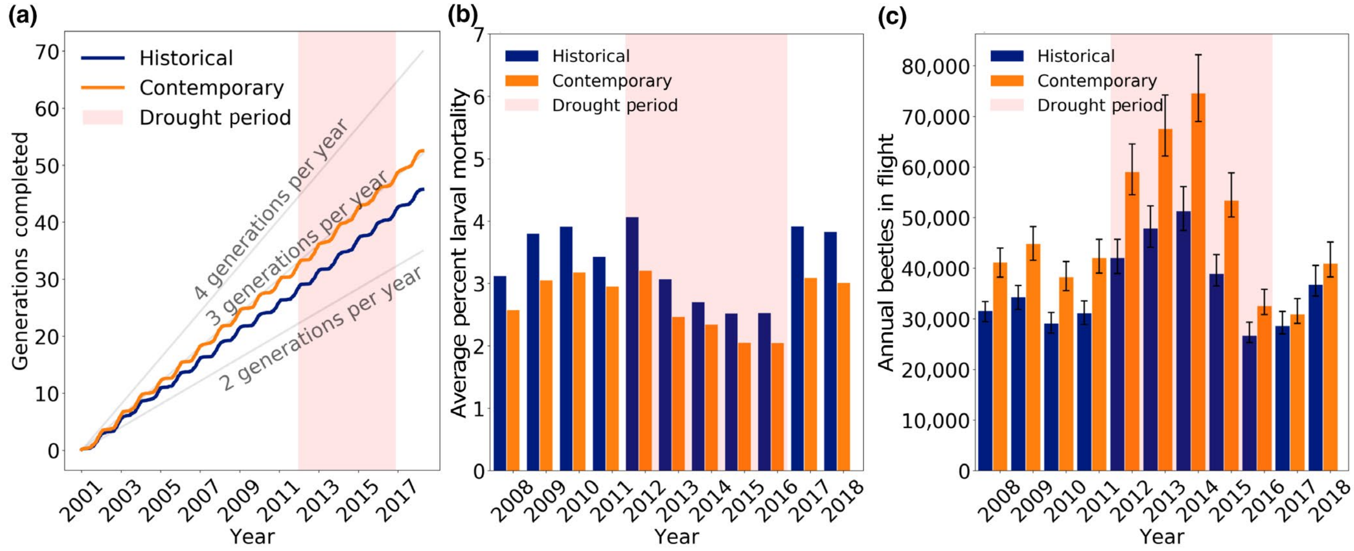


FIGURE 4 Mechanisms of warming influence on western pine beetle (WPB). (a) Cumulative number of WPB generations completed in the simulation under historical and contemporary climate. (b) Expected annual mean larval mortality rate under historical and contemporary climate. (c) Mean number of WPB in flight under historical and contemporary climate. Drought period refers to the overlapping years of meteorological drought (2012–2015) and lagged PP responses (2014–2016). Error bars represent the 95% confidence interval

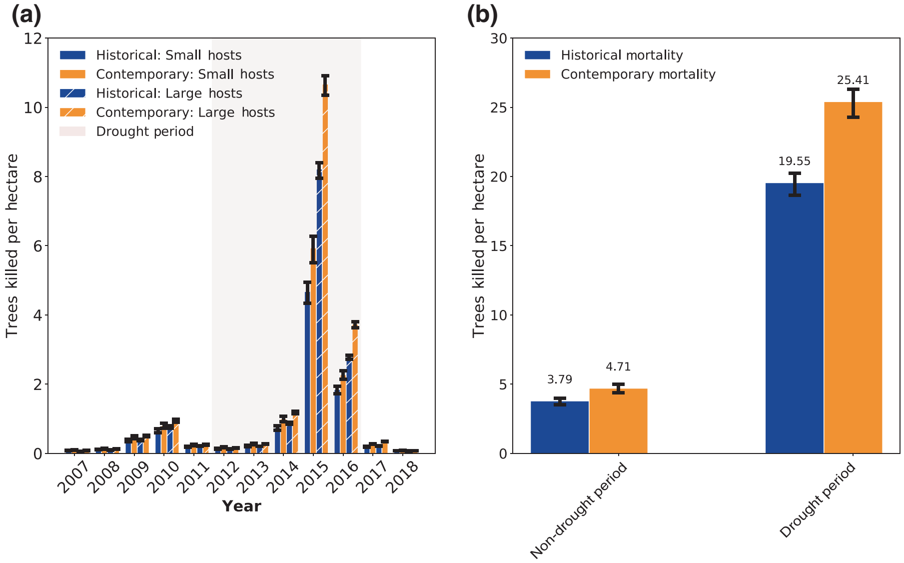


FIGURE 5 Impacts of warming on mortality of ponderosa pine (PP) attributed to western pine beetle (WPB) during drought; (a) simulated PP mortality under contemporary and historical temperatures for small hosts (10–31.8 cm dbh) and large hosts (>31.8 cm dbh); and (b) simulated PP mortality under contemporary and historical temperatures for the drought and non-drought periods. Drought years refer to the overlapping years of meteorological drought (2012–2015) and lagged PP responses (2014–2016). Error bars represent the 95% confidence interval

overwintering mortality occur (Keen & Furniss, 1937; Miller & Keen, 1960).

Over the next century, tree mortality from bark beetles will become increasingly important to forest dynamics (Bentz et al., 2010; Buotte et al., 2017). Bark beetle outbreaks have increased over the past two decades leading to tree mortality across ~4.3 million hectares in the United States. (Hicke et al., 2020; Raffa et al., 2008) and are threatening the suitability of some forests (Fettig et al., 2021). Many, though not all, of these outbreaks, appear to be driven by warming temperatures, drought, and elevated host stress, trends likely to increase across the next century (Weed et al., 2013). Our results suggest that warming and drought each had unique effects on levels of PP mortality during the extreme drought event in the Sierra Nevada. We find that each degree (°C) of mean annual warming across the study area led to an increase in the number of PP killed by WPB by ~20% solely through the effect of warming on WPB populations (study region mean annual temperature increase of 1.4°C). Similar results could occur in areas where bark beetle species have yet to hit their developmental maxima (Deutsch et al., 2008). A study of the same tree mortality event (Goulden & Bales, 2019) focused on the separate mechanism of tree moisture-stress (mediated by evapotranspiration) found warming to increase tree mortality by ~15%–20% $°C^{-1}$. This suggests that each degree (°C) increase in temperature may have increased the number of PP killed by upwards of 35%–40% $°C^{-1}$ if the effects of compromised tree defenses (15%–20%) and increased bark beetle (WPB) populations (20%) are additive. There is a possibility that some portion of the increase would be host trees susceptible to both conditions (thus, not additive), however, given the nonlinear

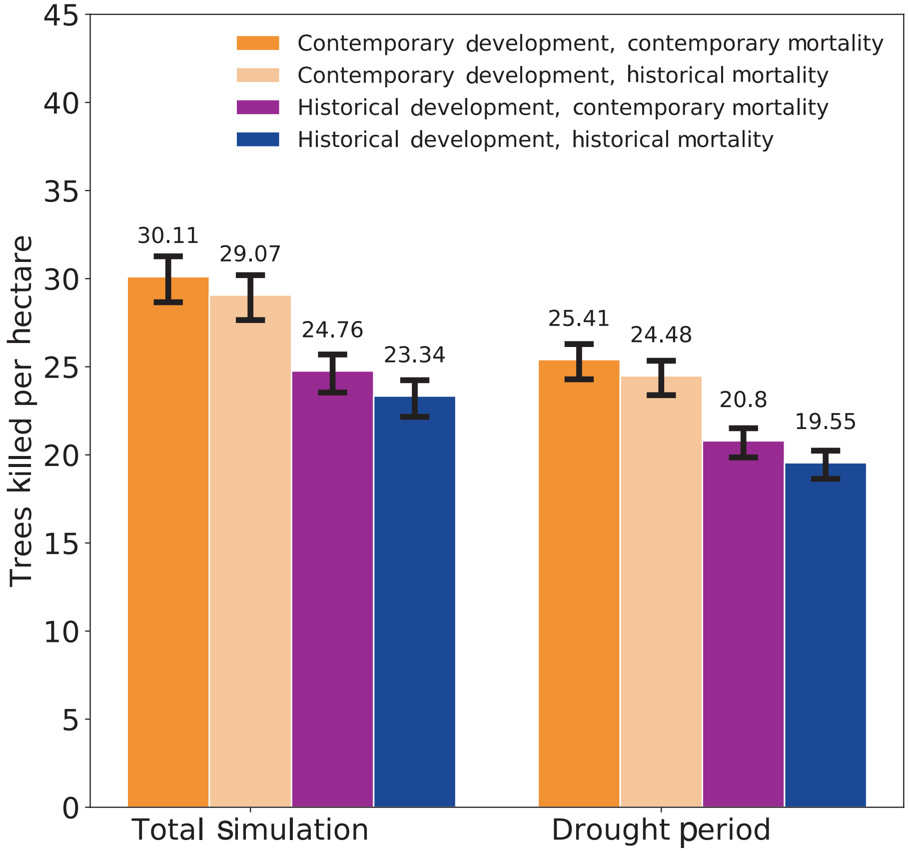


FIGURE 6 The relative influences of separate mechanisms of WPB response to warming on ultimate PP mortality. The number of PP killed per hectare under four simulations, with altered climate drivers impacting WPB development and overwintering mortality. Drought period refers to the overlapping years of meteorological drought (2012–2015) and lagged PP responses (2014–2016). Error bars represent the 95% confidence interval

effect drought has on initiating bark beetle mortality events there is a further possibility these effects would create a greater than additive feedback. However, further study would be necessary to determine that effect. Of note, WPB was not the only bark beetle species causing significant levels of tree mortality during the drought period, though it alone was implicated in most of the PP mortality (Fettig et al., 2019). Mountain pine beetle (*Dendroctonus ponderosae*), for example, killed many sugar pine (*Pinus lambertiana*) during the drought. While tree mortality attributed to bark beetles is an inherent part of many coniferous forests, massive bark beetle attacks of the magnitude observed in the Sierra Nevada can fundamentally shift the ecological function and structure of these forests (Fettig et al., 2019; Stephens et al., 2018). Further, species-specific mortality can facilitate forest-type conversion (Fettig et al., 2019; Stephens et al., 2018).

Our results suggest an increase in future bark beetle disturbance due to increased voltinism. Similar simulations of *Ips typographus* bark beetles in the forests of Austria found that the land area disturbed by bark beetles is projected to increase 684% under warming of 4°C (Seidl et al., 2017). Similar increases in voltinism were modeled for the behavior of spruce beetle (*Dendroctonus rufipennis*) in Colorado, moving from primarily semi-voltine (less than one generation a year) to univoltine (one generation a year; Temperli et al., 2013). While increases in temperature may increase the severity and frequency of outbreaks, this may dampen subsequent outbreaks by severely reducing hosts (Foster et al., 2018).

Our study provides a framework to connect the unique relationships among drought, vegetation dynamics, and resulting tree mortality for individual host and beetle relationships (Restaino et al., 2019). Models of future change that consider only changes in tree physiology in response to climate or consider insect mortality as included in background mortality will misrepresent the mortality on the landscape, as both beetle populations and tree moisture stress mediate host mortality levels (Anderegg et al., 2015). McDowell and Allen (2015), posit that tall conifers with isohydric traits are increasingly susceptible to increased drought stress; this may be further compounded when these trees are the preferred hosts of bark beetles. As these species are required to close their stoma earlier during the drought, their ability to continually defend themselves against bark beetle attacks will decrease. This type of dual susceptibility illustrates the importance of accounting for both the pressure of attacking beetle populations and the response of host defenses to the climate.

Our model represents a step forward for mechanistic simulation of bark beetle populations and the mortality they inflict in tree hosts. Previous beetle-caused tree mortality models simulated the phenology of beetles as a uniform cohort often at a uniform rate, calculating the necessary thermal units need to finish as cohort or to initiate flight (Seidl et al., 2007; Temperli et al., 2013). We feel the inclusion of the stage-dependent temperature response is crucial to determine the temperature response of the beetles to warming, as much of their successes are determined by the synchrony of crucial life states and not just the accumulation of thermal units (Bentz & Jönsson, 2015; Logan & Powell, 2001; Powell & Logan, 2005).

While our model advances understanding of mechanistic insect disturbances, there are several avenues for improvement. Dynamics that affect host defenses such as tree host proportion, evaporative demand, and the role of non-structural carbon, which we here have simplified to a regional drought index (4-year SPI), all determine host stress (Goulden & Bales, 2019; Huang et al., 2020; Koontz et al., 2019; Madakumbura et al., 2020). The inclusion of additional host defense dynamics would likely improve the model's performance in situations where drought is not the dominant driver of host defenses and where there are varied levels of defense for multiple hosts. The beetle attack is often the critical last step in the mortality of conifers; however, as seen in-field data from Fettig et al. (2019), occasionally severely weakened larger trees are capable of defending themselves against bark beetle attack.

Several bark beetle phenology models have been incorporated within vegetation demography models to better capture the response of trees to nutrient limitation, forest and host density, and drought measures (soil moisture, vapor pressure deficit, precipitation, etc.; Foster et al., 2018; Seidl & Rammer, 2017; Temperli et al., 2013). Many of these use a statistical or hazard ranking system to simulate tree defense (Foster et al., 2018; Seidl & Rammer, 2017), while others use a fixed number of bark beetles necessary to kill a tree (Fahse & Heurich, 2011; Goodsman et al., 2017). We feel that these approaches are best synthesized through an understanding of the beetle pressure necessary to kill a tree, as informed by the stress that the tree is experiencing. This approach provides the opportunity to directly relate bark beetle pressure to measures of host tree stress already utilized with tree physiology models such as carbon starvation or loss of hydraulic conductance (McDowell et al., 2013). Including further bark beetle dynamics could also improve the ability to track outbreaks. Incorporating finer-scale host and bark beetle densities and beetle migration would improve our understanding of the emergent properties of outbreaks (Anderegg et al., 2015). The inclusion of density- (both of host and bark beetle) specific aggregation has been a predictive measure of bark beetle attack (Powell & Bentz, 2014), and range of aggregation pheromones can help to inform the migration of bark beetles both to aggregate at tree hosts and deter additional bark beetles when populations within a host are too high (Fahse & Heurich, 2011). We did not include the presence of antagonists within our model owing to limited data on antagonists in the study area and because they are believed to play a minor role when compared to host susceptibility in the WPB and PP system (Bellows, 1998). However, it has been shown to be an important component in the *Ips typographus* system and the inclusion of a more mechanistic density-dependent mortality of bark beetles would likely improve the model (Fahse & Heurich, 2011).

Data on beetle processes and history of outbreaks is often a limiting factor in beetle model development. A limited number of bark beetle phenological models are available due to limitations in our understanding of the ecology of most bark beetle species (Bentz & Jönsson, 2015). Additionally, quantifying the indirect effects of climate on the host tree physiology, host tree distribution, and the community of organisms that interact during a bark beetle's life cycle may be necessary (Bentz et al., 2010). We included tree mortality attributed to drought or insects in our calibration data, owing to the uncertainty of attribution in the sampling method by the FIA. This data overall aligned with the more intensive attribution gathered from Fettig et al. (2019) and is likely a conservative estimate of PP mortality (Sup. 2.2). However, the uncertainty of FIA attribution may overestimate the amount of mortality attributed to WPB. This may explain the model's difficulty in accurately capturing mortality within the smaller tree host size class for the years immediately during the drought (Figure S14), as these may be records of host trees succumbing to other causes of death.

Given the projections of future drought globally, the resilience of many forests will likely decline without intervention to reduce insect outbreaks (Pokhrel et al., 2021; Seidl, 2014; Seidl et al., 2017). A wide array of tools and tactics are available to reduce the severity and extent of bark beetle infestations when applied properly at appropriate spatial and temporal scales (Fettig & Hilszczański, 2015; Fettig et al., 2007). Efforts to decrease susceptibility of forest stands focus on reducing tree densities and increasing tree species and stand age diversities, while landscape management focuses on configuration and composition of susceptible stands to foster greater disaggregation of hosts to prevent broad-scale impacts (Honkaniemi et al., 2020). Reducing tree density is also a prevalent management prescription to mitigate more extensive fire disturbance, although, fire prevention management focuses primarily on the understory, while bark beetle prevention would require removing hosts in the overstory (Agee & Skinner, 2005). Limiting the impact of bark beetles through the increased harvesting of conifers in some systems may prove ineffective as overall risk increases under a warming climate and this may have deleterious effects on carbon storage and biodiversity (Zimová et al., 2020). As seen in the 2012–2015 Sierra Nevada, the conditions presented by extreme droughts may introduce higher-level regulation into the bark beetle-host system, with high levels of mortality even under much lower host densities (Koontz et al., 2019). Concerted management to mitigate both wildfires and bark beetle outbreaks may require allowing both disturbances to occur, which will create the condition that prevents them from rising to such extreme intensities (Hessburg et al., 2019). Prioritization of management responses will become increasingly important due to constraints imposed by limitations in resources, infrastructure, and markets, among other factors. For example, tree populations at the lower margins of elevational and latitudinal constraints are likely to experience higher levels of mortality (as demonstrated for PP during this extreme drought event, Fettig et al., 2019), and thus these areas likely justify increased surveillance and management.

5 | CONCLUSION

Capturing bark beetle population dynamics is crucial to determining host tree mortality under drought. We created a framework to examine tree mortality in response to temperature by including beetle phenology, beetle overwintering mortality, and host stress. We found that contemporary warming increased the development rate of WPB and decreased the overwintering mortality rate of WPB larvae leading to increased population growth during periods of lowered tree defense. Furthermore, warming enhanced the feedback between drought and WPB populations and increased PP mortality in the 2012–2015 Sierra Nevada drought. Due to the insect- and host-specific nature of herbivory, process-based models need to include climate dynamics affecting both participants to accurately predict tree mortality levels.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

Z.R., C.X., and R.C. designed the study, with input from P.B., C.F., M.G., C.K., L.K., L.M., B.A, J.P., L.M., C.F., Z.R., C.X., and D.G. designed the biological western pine beetle model and the beetle attack and host defense model. Z.R., C.X., and D.G. designed the computational framework. C.F., and L.M. provided field data on beetle-induced tree mortality and beetle flight. J.P. provided data on phloem temperature. A.H., G.M., and M.G. provided input into climate data and attribution methods. Z.R., and C.X. conducted the simulations. Z.R. analyzed model outputs, with input from other authors. All authors aided in interpreting the results and contributed to the manuscript.

DATA AVAILABILITY STATEMENT

Data for this analysis or code to run simulations that support the findings of this study are available from the corresponding author upon reasonable request. Data and code will be available in the online repository prior to the publication at https://github.com/ZacharyRobbins/IMAP_TDIA_Warming.

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