ADVANCING EARTH AND SPACE SCIENCE

JAMES | Journal of Advances in Modeling Earth Systems®

RESEARCH ARTICLE
10.1029/2022MS003073

Bark Beetle Effects on Fire Regimes Depend on Underlying Fuel Modifications in Semiarid Systems

Jianning Ren[1,2], Erin J. Hanan[2], Jeffrey A. Hicke[3], Crystal A. Kolden[4], John T. Abatzoglou[4], Christina (Naomi) L. Tague[5], Ryan R. Bart[6], Maureen C. Kennedy[7], Mingliang Liu[1], and Jennifer C. Adam[1]

[1]Department of Civil and Environmental Engineering, Washington State University, Pullman, WA, USA, [2]Department of Natural Resources and Environmental Science, University of Nevada, Reno, Reno, NV, USA, [3]Department of Geography, University of Idaho, Moscow, ID, USA, [4]Management of Complex Systems, University of California, Merced, Merced, CA, USA, [5]Bren School of Environmental Science & Management, University of California, Santa Barbara, Santa Barbara, CA, USA, [6]Sierra Nevada Research Institute, University of California, Merced, Merced, CA, USA, [7]Division of Sciences and Mathematics, School of Interdisciplinary Arts and Sciences, University of Washington, Tacoma, Tacoma, WA, USA

Key Points:

- Five years after beetle outbreak, fire probability decreased due to reduced vegetation productivity and fuel loading
- Six to fifteen years after outbreak, fire probability increased due to more fuel loading from snag-fall
- Fifteen years after outbreak, fire probability decreased due to lower fuel aridity when mortality level was higher than 50%

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

J. C. Adam,
jcadam@wsu.edu

Citation:

Ren, J., Hanan, E. J., Hicke, J. A., Kolden, C. A., Abatzoglou, J. T., (Naomi) Tague, C. L., et al. (2023). Bark beetle effects on fire regimes depend on underlying fuel modifications in semiarid systems. *Journal of Advances in Modeling Earth Systems*, *15*, e2022MS003073. https://doi.org/10.1029/2022MS003073

Received 8 MAR 2022
Accepted 11 JAN 2023

Author Contributions:

Conceptualization: Jianning Ren, Erin J. Hanan, Jeffrey A. Hicke, Jennifer C. Adam
Data curation: Jianning Ren, John T. Abatzoglou, Christina (Naomi) L. Tague, Mingliang Liu
Formal analysis: Jianning Ren, Erin J. Hanan, Crystal A. Kolden, Christina (Naomi) L. Tague, Jennifer C. Adam
Funding acquisition: Erin J. Hanan, Crystal A. Kolden, Jennifer C. Adam

Abstract

Although natural disturbances such as wildfire, extreme weather events, and insect outbreaks play a key role in structuring ecosystems and watersheds worldwide, climate change has intensified many disturbance regimes, which can have compounding negative effects on ecosystem processes and services. Recent studies have highlighted the need to understand whether wildfire increases or decreases after large-scale beetle outbreaks. However, observational studies have produced mixed results. To address this, we applied a coupled ecohydrologic-fire regime-beetle effects model (RHESSys-WMFire-Beetle) in a semiarid watershed in the western US. We found that in the red phase (0–5 years post-outbreak), surface fire extent, burn probability, and surface and crown fire severity all decreased. In the gray phase (6–15 years post-outbreak), both surface fire extent and surface and crown fire severity increased with increasing mortality. However, fire probability reached a plateau during high mortality levels (>50% in terms of carbon removed). In the old phase (one to several decades post-outbreak), fire extent and severity still increased in all mortality levels. However, fire probability increased during low to medium mortality (≤50%) but decreased during high mortality levels (>50%). Wildfire responses also depended on the fire regime. In fuel-limited locations, fire probability increased with increasing fuel loads, whereas in fuel-abundant (flammability-limited) systems, fire probability decreased due to decreases in fuel aridity from reduced plant water demand. This modeling framework can improve our understanding of the mechanisms driving wildfire responses and aid managers in predicting when and where fire hazards will increase.

Plain Language Summary

Bark beetle outbreaks have impacted millions of hectares of forest in western North America. Beetle-caused tree mortality can increase or decrease wildfire hazards by altering surface fuel loading and decreasing leaf moisture. Previous studies have observed increases in fire following beetle attacks. However, others have found no change or a decrease. Such discrepancies can result from several interacting factors, such as how much time has passed since an outbreak, the level of tree mortality, and pre-outbreak fuel conditions. To examine how these factors influence surface and crown fire characteristics in a semiarid watershed, we used a model that simulates interactions among hydrology, vegetation, beetle effects, and fire. We found that in the first 5 years after attack, surface fire probability and extent decreased due to decreases in plant productivity and fuel loading. Surface and crown fire severity had similar responses as surface fire extent. Following that, fire responses were a function of two counteracting forces: increases in fuel loading from delayed needle- and snag-fall and wetter fuels from reduced plant water demand. The dominant force depended on fuel conditions. In fuel-limited locations, fire increased with more fuel loads, whereas in fuel-abundant locations, fire normally decreased due to wetter fuels. This research provides a practical tool for managers to better predict when and where fire hazards will increase.

1. Introduction

Bark beetle outbreaks and wildfire are significant agents of change in North American forests (Hicke et al., 2012, 2016). In recent decades, these compounding disturbances have increased significantly and affected millions of hectares of forest (Hicke et al., 2016; Littell et al., 2009; Raffa et al., 2008; Seidl et al., 2020). While

Investigation: Jianning Ren, Erin J. Hanan, Jennifer C. Adam
Methodology: Jianning Ren, Erin J. Hanan, Jeffrey A. Hicke, Crystal A. Kolden, John T. Abatzoglou, Christina (Naomi) L. Tague, Ryan R. Bart, Maureen C. Kennedy, Mingliang Liu, Jennifer C. Adam
Project Administration: Erin J. Hanan, Crystal A. Kolden, Jennifer C. Adam
Resources: Jianning Ren, Erin J. Hanan, Crystal A. Kolden, John T. Abatzoglou, Ryan R. Bart, Maureen C. Kennedy, Mingliang Liu, Jennifer C. Adam
Software: Jianning Ren, Erin J. Hanan, Jeffrey A. Hicke, Crystal A. Kolden, Christina (Naomi) L. Tague, Ryan R. Bart, Maureen C. Kennedy, Mingliang Liu, Jennifer C. Adam
Supervision: Erin J. Hanan, Jeffrey A. Hicke, Crystal A. Kolden, John T. Abatzoglou, Christina (Naomi) L. Tague, Maureen C. Kennedy, Mingliang Liu, Jennifer C. Adam
Validation: Jianning Ren, Erin J. Hanan, Jeffrey A. Hicke, John T. Abatzoglou, Christina (Naomi) L. Tague, Ryan R. Bart, Maureen C. Kennedy, Jennifer C. Adam
Visualization: Jianning Ren, Erin J. Hanan, Jennifer C. Adam
Writing – original draft: Jianning Ren, Erin J. Hanan, Jennifer C. Adam
Writing – review & editing: Jianning Ren, Erin J. Hanan, Jeffrey A. Hicke, Crystal A. Kolden, John T. Abatzoglou, Christina (Naomi) L. Tague, Ryan R. Bart, Mingliang Liu, Jennifer C. Adam

climate change is expected to continue to increase the severity and frequency of these disturbances, it is less clear how they will interact with one another (Bennett et al., 2018). Bark beetle outbreaks can change fuel conditions and corresponding wildfire characteristics by altering ecohydrological processes and forest fuel structure (Goeking & Tarboton, 2020; Wayman & Safford, 2021). However, the direction of ecohydrological responses to beetle outbreaks can vary over space and time within watersheds (Ren et al., 2021), which can in turn influence fuel loading, fuel moisture, and fire regimes. Therefore, understanding and managing fire risk in landscapes that are prone to these compounding disturbances requires understanding how fuel conditions change over space and time.

There are three phases of tree response to beetle outbreaks: the red phase, gray phase, and old phase. The "red phase" occurs 0–5 years after beetle outbreak, during which foliar moisture content decreases and some conifer species' needles turn red (Hicke et al., 2012; Jolly, Parsons, Hadlow, et al., 2012). The "gray phase" occurs 6–15 years after beetle outbreak, when dead foliage falls to the ground but snags remain standing (Halofsky et al., 2020). The "old phase" occurs one or more decades after beetle outbreak, when snags fall to ground and understory vegetation cover increases (Hicke et al., 2012; Mitchell & Preisler, 1998). While classifying these discrete phases is helpful for understanding post-outbreak processes, their length can vary among tree species, and because beetles can attack trees for multiple years, a mix of different phases can occur in a single stand (Hicke et al., 2012).

Like other ecohydrological processes, fuel conditions and wildfire respond differently to the three phases of beetle outbreak. Hicke et al. (2012) developed a conceptual framework that describes how beetle-caused tree mortality affects wildfire behavior (Figure 1). During the red phase, dead foliage is still in the canopy, thus dead surface fuels remain unchanged, but canopy foliage dries and becomes more flammable. Consequently, surface fire hazard (e.g., the probability of fire and fire severity) remains unchanged but crown fire potential increases. In the gray phase, needle-fall increases dead surface fuel loading and reduces canopy bulk density. As a result, surface fire hazard and severity increase but crown fire potential decreases. In the old phase, as dead snags fall to the ground and understory vegetation cover increases, surface fire hazard and severity remains elevated, while crown fire potential may further decrease with decreasing canopy bulk density.

While the conceptual framework outlined above is useful for understanding temporal wildfire responses to beetle outbreaks, several uncertainties still remain (Halofsky et al., 2020; Hicke et al., 2012). For example, in the gray and old phases, many field observations (Bebi et al., 2003; Berg et al., 2006; Lynch et al., 2006) and modeling studies (Ager et al., 2007; Lundquist, 2007; Meigs et al., 2016) have documented decreases or no change of fire probability and fire severity, while others have found increases (Bigler et al., 2005; Turner et al., 1999; Wayman & Safford, 2021). These increases in crown fire severity during the gray phase may have occurred because once the canopy opened, more radiation was able to penetrate, and competition for resources decreased. This can promote rapid understory growth and tree regeneration (Hicke et al., 2012; Mikkelson et al., 2013), which can in turn increase ladder fuels (Collins et al., 2010; Klutsch et al., 2011; Lynch et al., 2006). Decreases in fire severity may occur because there is less live vegetation after beetle outbreak (Meigs et al., 2016), but this relationship may be complicated by other factors, such as fire weather, local fuel gradients, mixed beetle-caused mortality, and difficulties in sampling (Ager et al., 2007; Berg et al., 2006; Hicke et al., 2012; Lundquist, 2007).

Fire responses to beetle outbreaks can also vary along fuel gradients and with fire weather. For example, logs from beetle outbreaks have promoted fire spread in fuel-limited lodgepole pine forest (Gara et al., 1985). However, in cooler more flammability-limited forests, increases in wind speed and higher surface temperatures from opening of the canopy increase fire probability more often than changes fuel loading (Cooper et al., 2017; Hicke et al., 2012; Page & Jenkins, 2007; Simard et al., 2011).

Because the factors influencing wildfire responses to beetle outbreaks can interact in complex ways, it is difficult to characterize mechanistic relationships among them using observational studies and/or controlled experiments, which are often constrained by data limitations and difficulty in controlling the confounding variables that occur in the field (Hicke et al., 2012). Simulation models complement and help address the limitations of observational studies and/or controlled experiments by allowing us to characterize how fuels and fire behavior vary in response to a range of outbreak severities (i.e., beetle-caused tree mortality; Ren et al., 2022) and site-specific environmental conditions during different phases of beetle outbreaks (Bond et al., 2009; Hicke et al., 2012; McCarley et al., 2017).

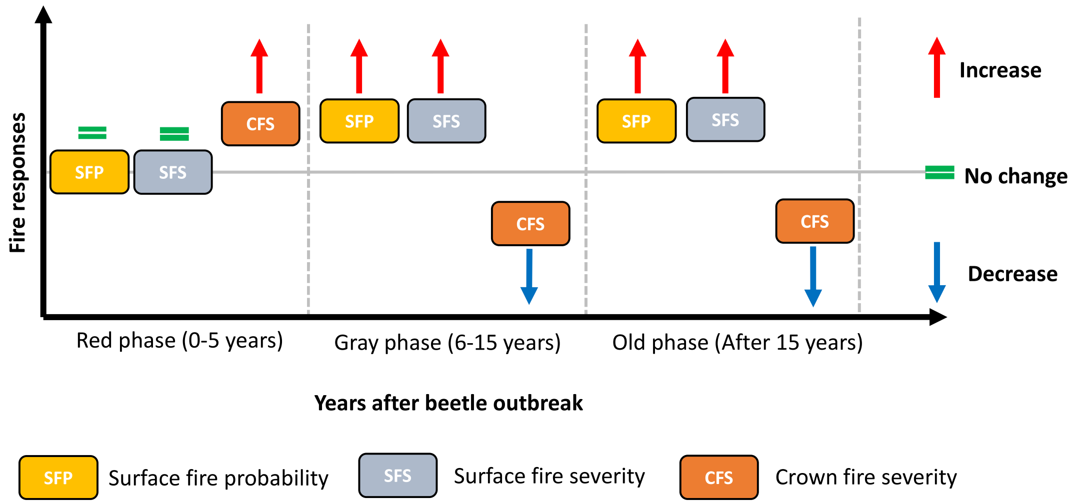

Figure 1. Conceptual framework of wildfire responses to beetle outbreaks adapted from Hicke et al. (2012). The mechanisms depicted here are summarized in Table S1 in Supporting Information S1.

The overarching objective of this paper is to understand how fuels and wildfire regimes respond to beetle-caused tree mortality across a range of environmental conditions and post-outbreak time periods. Specifically, we asked the following questions.

1. How do wildfire characteristics (surface fire extent and probability, and surface and crown fire severity) respond to beetle outbreaks during different phases of outbreak (i.e., the red phase, gray phase, and old phase)?
2. How does the degree of beetle-caused tree mortality (i.e., the percentage of biomass removed) influence post-outbreak wildfire characteristics?
3. How do pre-outbreak fuel conditions (i.e., fuel loading and fuel aridity) affect wildfire regimes after beetle outbreaks?

2. Methods

2.1. Study Area

Trail Creek is a 167-km^2 sub-catchment of the Big Wood River basin, located in Blaine County (Idaho, US) between the Salmon-Challis National Forest and Sawtooth National Forest (43.44°N, 114.19°W; Figure 2). Trail Creek experiences cold, wet winters and warm, dry summers. The mean annual precipitation is around 900 mm, of which 60% falls as snow (Frenzel, 1989). The daily average temperature ranges from −28°C in winter to 24°C in summer. Trail Creek has a strong elevation gradient, ranging from 1760 to 3478 m, which also coincides with gradients in aridity and vegetation cover. Lower to middle elevations are arid and covered by sagebrush, riparian species, and grass; middle to higher elevations are relatively humid and are covered by Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta varlatifolia*), subalpine fir (*Abies lasiocarpa*), and mixed shrub and herbaceous vegetation (Buhidar, 2001). There are no records of large wildfires (>400 ha) occurring in Trail Creek over the last 40 years (MTBS, Eidenshink et al., 2007). According to LANDFIRE, Trail Creek has distinct fire regimes in the northern (high elevation) and the southern (low elevation) portions of the watershed. The northern part of the basin is flammability limited with an approximate 200-year FRI (Table 1; Rollins, 2009) and the southern part of the basin is fuel-limited, with a 35-year fire return interval (FRI). Some transitional areas experience a mixed severity fire regime with 35 to 200-year FRIs. An aridity gradient, defined as the ratio of average annual potential evapotranspiration (PET) to average annual precipitation (P) over a 38-year period (1980–2018), generally overlaps with these fire regime groups (Figure 2a, Table 1).

2.2. Model Descriptions

2.2.1. Ecohydrological Model

We used a coupled ecohydrologic-fire regime-beetle effects model (RHESSys-WMFire-Beetle) to understand the effect of beetle-caused mortality on fire regimes. This framework couples the Regional Hydro-ecologic

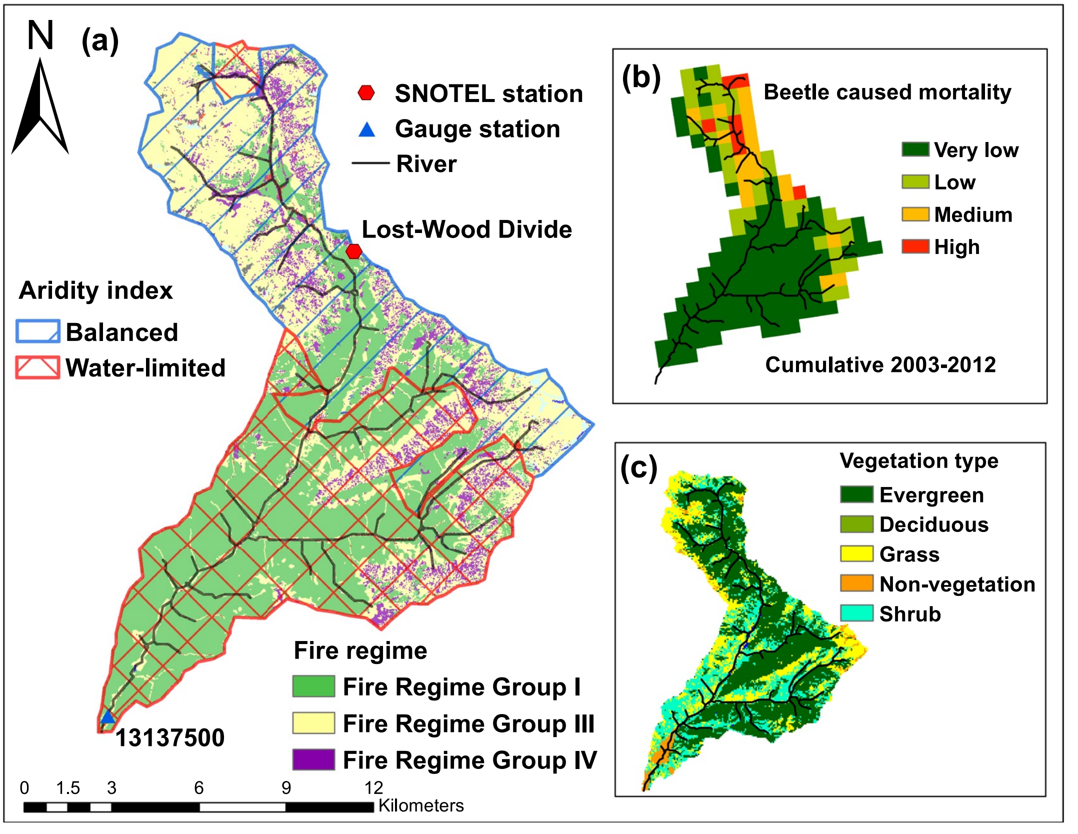

Figure 2. Study site—Trail Creek located in Idaho, US, is a sub-catchment of the Big Wood River basin. Panel (a) shows fire regimes based on LANDFIRE (Rollins, 2009). The outlined diamond grid and diagonal stripes show different zones according to an aridity index (i.e., annual mean potential evapotranspiration [PET]/precipitation (P)) calculated from historical 38-year meteorological data: PET/$P > 2$ is water-limited, PET/$P < 0.8$ is energy-limited, PET/P between 0.8 and 2 is balanced. Panel (b) shows beetle caused tree mortality from 2003 to 2012 (Meddens et al., 2012) overlapped with topography (elevations range from 1,760 to 3,478 m). Panel (c) shows land cover (Dewitz, 2019). Evergreen and deciduous are forested areas.

Simulation System (RHESSys) with models for fire spread (WMFire; Kennedy et al., 2017), fire effects (Bart et al., 2020), and beetle effects (Ren et al., 2021). RHESSys is a distributed, process-based land surface model that simulates how climate and land use changes influence biogeochemical cycling and hydrology (Tague & Band, 2004). It has been widely tested and applied in mountainous watersheds across the Pacific Northwest, western North America, and globally (e.g., Garcia & Tague, 2015; Hanan et al., 2017, 2018, 2021; Lin et al., 2019; Ren et al., 2021; Son & Tague, 2019; Tague & Peng, 2013). A more detailed description of the RHESSys model can be found in Text S1 in Supporting Information S1 and papers by Garcia et al. (2016), Tague and Band (2004), and Tague et al. (2013).

2.2.2. Fire Spread and Fire Effect Models

WMFire is a stochastic fire spread model that has been coupled with RHESSys (Kennedy et al., 2017). The coupled model has previously been tested and applied in the Western US and can reproduce expected fire regimes

Table 1
Fire Regime Groups (Rollins, 2009) and Corresponding Characteristics for Figure 2

Fire regime group	Fire characteristics
Fire Regime Group I	≤35-year fire return interval (FRI), low and mixed severity
Fire Regime Group III	35 to 200-year FRI, low and mixed severity
Fire Regime Group IV	>200-year FRI, any severity

(Hanan et al., 2021; Kennedy et al., 2017, 2021; Ren et al., 2022). It calculates the probability of fire spread (P_s) over time and space based on dead surface fuel loading (i.e., litter carbon), fuel aridity (i.e., relative deficit; 1 – evapotranspiration/PET), wind speed and direction, and topographic slope, which are outputs from RHESSys. WMFire then produces maps of P_s over randomized ignitions and stochastic spread to produce fire size distributions over time. A fire effects model connects fire spread to fire severity, which in turn modifies RHESSys litter and vegetation state variables (Bart et al., 2020). Fire effects include vegetation mortality and consumption of vegetation, litter, and coarse woody debris (CWD). Crown fire severity is simulated as a function of surface fuels and understory consumed and canopy height structure. Consequently, these simulated fire effects can influence the post fire hydrologic and biogeochemical fluxes and their interactions with vegetation and fuel recovery (Hanan et al., 2021). WMFire is a stochastic model and requires approximately 200 replicate simulations to model a representative fire regime (Kennedy, 2019).

2.2.3. Beetle Effects Model

Ren et al. (2021) also coupled a beetle effects model with RHESSys-WMFire (i.e., RHESSys-WMFire-Beetle; modified from Edburg et al., 2011). This model includes a dead foliage pool (i.e., red needles that remain on trees) and a snag pool (i.e., standing dead tree stems) as additional carbon (C) and nitrogen (N) stores in RHESSys. After beetle-kill, leaf C and N are immediately moved from the leaf into the dead foliage pools and they remain on the canopy for one or more years, per user input (here we used 1 year; Edburg et al., 2011; Meddens et al., 2012). After a year, dead foliage C and N are transferred from the canopy to litter C and N stores using an exponential decay rate (we prescribe a half-life of 2 years). Similarly, stem C and N remain in the snag pool for several years (here we prescribe 5 years) and are then transferred into a CWD pool with an exponential decay rate (here we prescribe a half-life of 10 years from snag pool to CWD). In the beetle effects model, we calculate two leaf area indices (LAIs): Total LAI includes both the dead foliage and live leaves in the canopy, while Live LAI only includes the live leaves. Total LAI can affect how the canopy intercepts precipitation and radiation (Ren et al., 2021). The overstory canopy height is calculated as a function of both live stem C and snag C. In this study, we assume the same beetle–caused mortality level for all evergreen patches across a landscape. Also, when fire spreads from the ground to the overstory canopy, it consumes the same fractions of snags and dead foliage as stems and live leaves.

2.3. Input Data

We used US Geologic Survey National Elevation Dataset (NED, Gesch et al., 2018) at 10-m resolution to calculate slope and aspect across Trail Creek, and then delineate basin and sub-basin boundaries using the GRASS GIS tool r.watershed. We aggregated topographic data to generate patches with a resolution of 100-m. We used vegetation cover categories (including evergreen, deciduous, shrub, grass, and unvegetated; i.e., bare ground or urban) from the National Land Cover Database (NLCD 2016; Dewitz, 2019) and soil texture (i.e., sandy loam and loam) from the spatially continuous probability soils map (POLARIS, Chaney et al., 2016). In total, our model setup included 72 sub-basins and 16,705 patches, of which, 49.6% were evergreen, 24.9% were shrub, 22.1% were grass, 0.3% were deciduous, and 3.1% were not vegetated (Figure 2).

We acquired meteorological inputs, including maximum and minimum temperatures, precipitation, relative humidity, radiation, and wind speed, from high-resolution (1/24th degree or ∼4-km) gridMET data sets for the years 1979–2017 (Abatzoglou, 2013). Then, to extend the gridMET record back for the years 1900–1978, we used ERA-20C daily reanalysis data (spanning 1900–2010), which is interpolated to match the gridMET resolution (Poli et al., 2016). The resulting daily data (1900–1978) was bias corrected to match the gridMET for each month based on the overlapping period for the two data sets (1979–2010) as described in Hanan et al. (2021). We further bias corrected the 1900–1978 data with PRISM (Daly et al., 1994).

2.4. Simulation Experiments

To examine how beetle-caused tree mortality affects fire regimes (specifically fire extent, burn probability, and fire severity), we ran a series of model simulations spanning the years 1910–1990 using the coupled RHESSys-WMFire-Beetle. In each scenario, we prescribed different mortality levels on 1 September 1915, and then simulated 75 years following the outbreak. Consequently, the simulation period captured three phases after beetle outbreak, but ended prior to significant 21st century climate change effects on fuel conditions (Hanan

Table 2
Description of Simulation Scenarios

	Scenarios	Beetle effects model	Fire spread and effects model	Number of simulations
Fire scenarios	Control (no beetle outbreak)	off	on	200
	Mortality (10%–90%)	on	on	200 for each mortality level
No-fire scenarios	Control (no beetle outbreak)	off	off	1
	Mortality (10%–90%)	on	off	One for each mortality level

Note. The beetle-caused mortality scenarios were for increments of 10% between 10% and 90% mortality.

et al., 2022; Tang & Riley, 2020). This enabled our research to focus on how beetle outbreaks affect wildfire and excluded any confounding effects of climate change. We defined the pre-outbreak phase as the period before beetle outbreaks (1910–1914), the red phase as 0–5 years post-outbreak (1915–1920), the gray phase as 6–15 years post-outbreak (1921–1930), and old phase as 16–75 years post-outbreak (1931–1990).

We prescribed nine beetle-caused mortality levels ranging from 10% to 90% biomass removal (in 10% increments) and applied each level uniformly to all evergreen patches (Figure 2c). We also included a no-mortality scenario as a control run, resulting in 10 total fire "on" scenarios (Table 2).

The modeled differences in fire characteristics between mortality scenarios and the control run represent the fire responses to beetle outbreaks. To better understand the fire severity responses to beetle outbreak, we also ran an additional 10 fire "off" scenarios (i.e., one for each mortality level) and examined the differences in C pools between the fire and no fire scenarios. We considered surface and crown fire severity to be the net C loss caused by fire in the litter and overstory pools, respectively.

We used fire extent (mean fire size) and burn probability (P_{burn}) as key metrics of fire responses. The mean fire size was calculated as the mean number of patches burned per fire. For each 100-m patch, the P_{burn} of surface fire was calculated as:

$$p_{\text{burn}} = \frac{\text{number of time burned across all simulations}}{\text{number of simulation years} * \text{number of simulations}} \tag{1}$$

To compare our simulation results with literature, we selected a set of model outputs as surrogates for fuel and fire characteristics (Table 3). We used litter C and overstory leaf C to represent dead surface fuel and canopy fuel dynamics, respectively. For fire characteristics, we focused on the probability of surface fire occurrence (represented as P_{burn}), surface fire severity (represented as litter C lost), and crown fire severity (represented as canopy C lost). Because WMFire only simulates fire starts at the surface, we did not include the probability of crown fire occurrence in our analysis.

Table 3
Definitions of Fuel and Fire Characteristics Potentially Affected by Bark Beetle-Caused Tree Mortality (Modified From Hicke et al., 2012)

Category	Characteristics	Model output	Definition
Canopy fuels	Canopy fuel loads	Overstory leaf C	Mass of fuel in canopy
Dead surface fuels	Fine fuel loads	Litter C	Litter; dead surface fuels <1'' in diameter
Fire	Surface fire extent	Mean fire size	Number of patches burned per fire
	Probability of surface fire occurrence	Burn probability (P_{burn})	Probability that fire occurs
	Surface fire frequency	P_{burn}	Standardized fire frequency for different phases
	Surface fire severity	Net litter C loss	Effects of fire on ecosystem properties (changes in surface fine fuel loading)
	Crown fire severity	Overstory tree canopy leaf C loss	Effects of fire on ecosystem properties (changes in canopy fuel loading)

Note. The model output column is the corresponding model output for different fuel and fire characteristics.

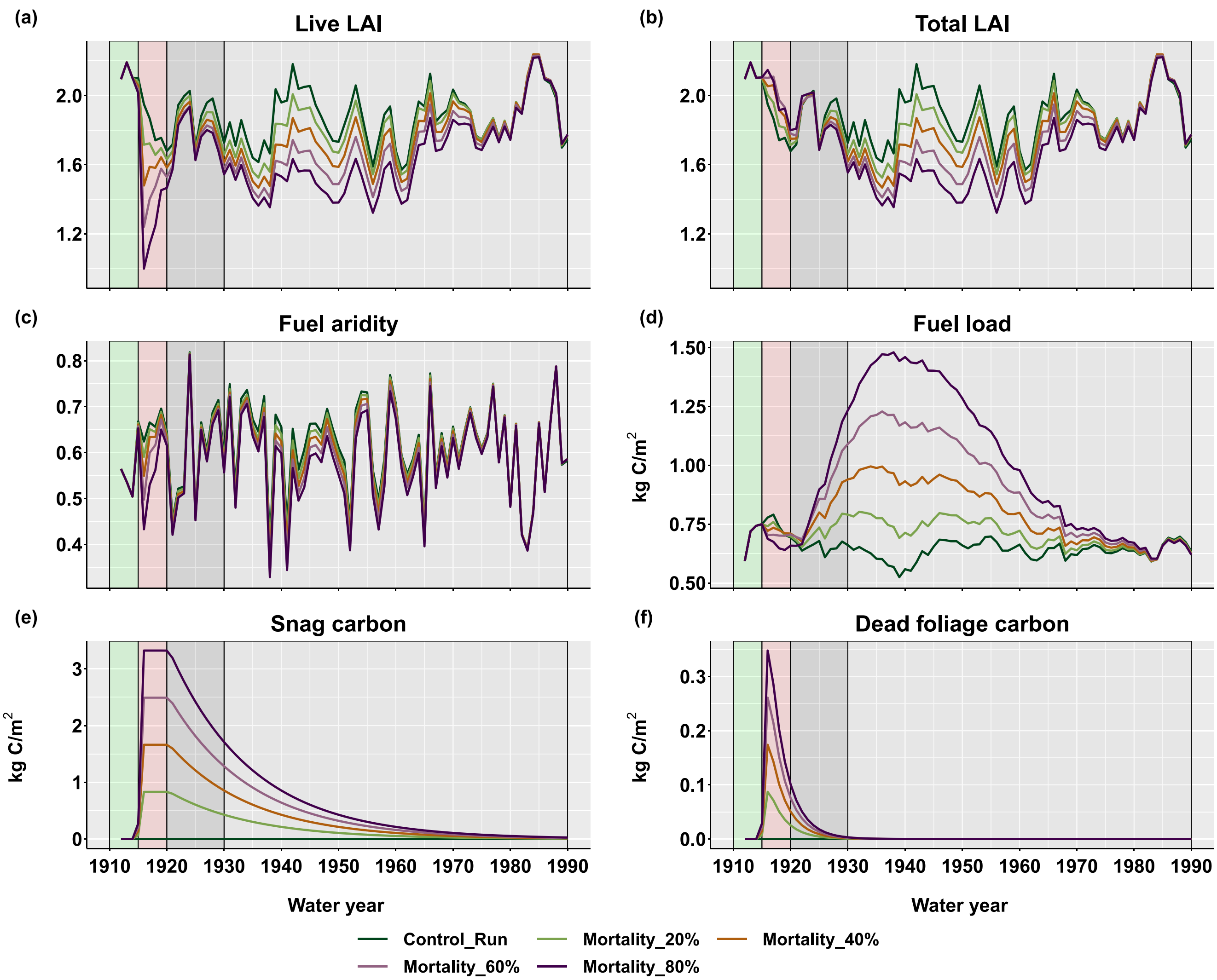

Figure 3. Basin-scale vegetation responses to beetle outbreaks. The background color corresponds to the 4 phases of beetle outbreaks: pre-outbreak (before 1915), red (1915–1920), gray (1921–1930), and old (1931–1990) phases. Fuel load is represented as the modeled litter C pool, fuel aridity is calculated as 1—ET/PET, ET is evapotranspiration and PET is potential is evapotranspiration.

3. Results

3.1. Basin-Scale Vegetation and Fuel Responses to Beetle-Caused Tree Mortality in the Absence of Fire

During the *red phase* (1915–1920), more than 50% of dead foliage fell to the ground and snags remained standing as prescribed by the beetle effects model (Figures 3e and 3f). However, litter C remained lower than in the control run because beetle kill reduced plant productivity and litter accumulation, and a large portion of carbon remained locked up in the dead foliage and snag pools in the first few years after beetle outbreak. The live leaf area index (Live LAI) was smaller in the mortality than in the control (no-mortality) simulations but exhibited greater productivity than the control run in the first 5 years after beetle outbreak (Figure 3a). Fuel aridity decreased compared to the control run, due to lower Live LAI in all beetle-caused mortality scenarios (low Live LAI reduced PET, thereby reducing fuel water deficit; Figure 3c). Unlike Live LAI, Total LAI (which includes live leaves and dead canopy foliage) increased in the red phase because beetle-caused mortality increased growth in understory plants, while dead foliage also remained in the canopy (Figure 3b).

In the *gray phase* (1921–1930), snags started falling to the ground and no dead foliage remained on the canopy (Figures 3e and 3f). The dead surface fuel load (i.e., the litter) was higher in the nine beetle-caused mortality scenarios than in the control run and increased with outbreak severity (Figure 3d). Fuel aridity did not differ

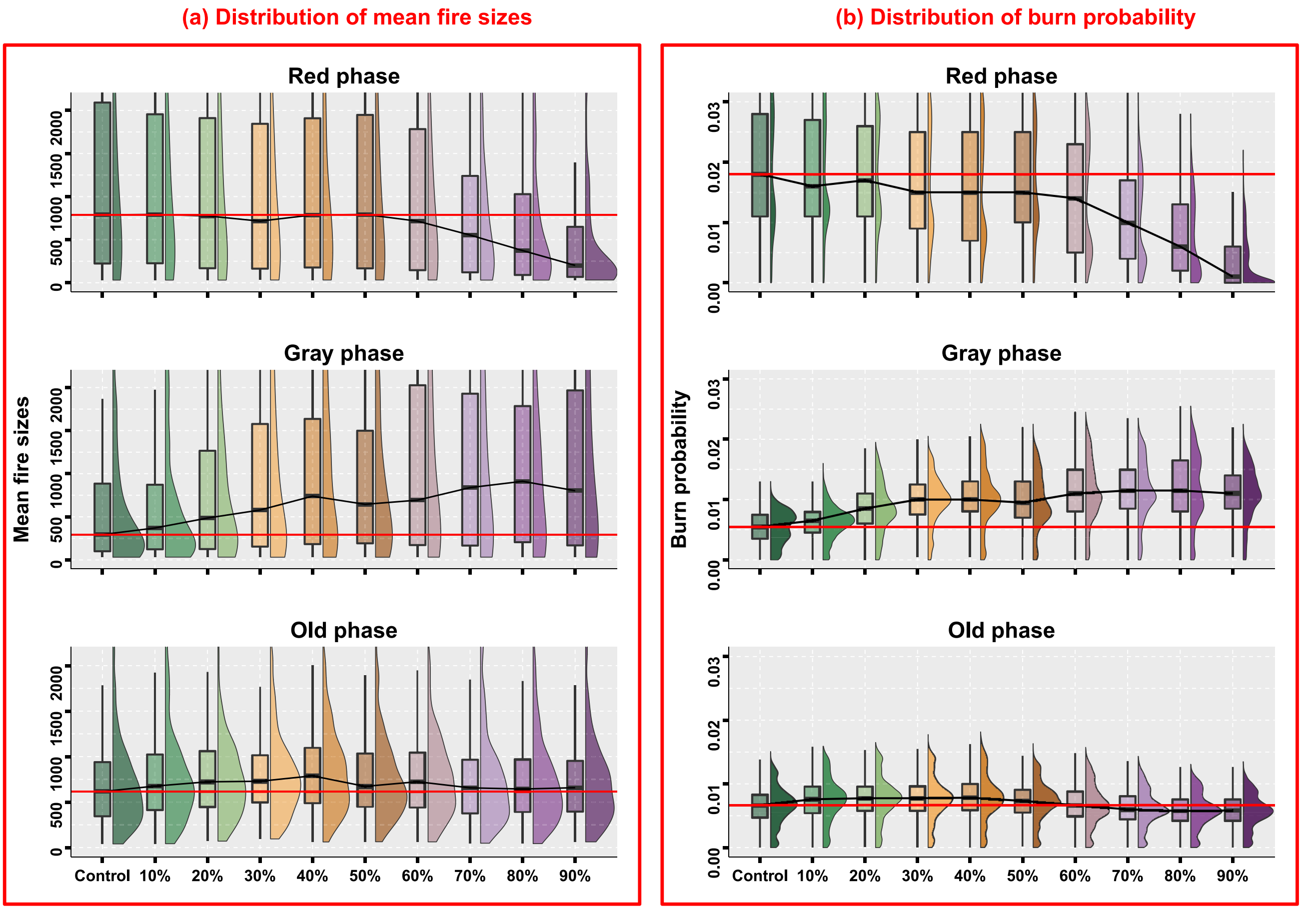

Figure 4. (a) Distribution of mean fire sizes (number of patches burned) for each phase, distributions were calculated from 200 replicate simulations for each scenario. (b) Distribution of burn probability for each phase, distributions were calculated for all patches across the basin for each scenario. Box plots show 25th, median, 75th percentile, the red line is the median value of the control run, and the black line connects the median for each mortality scenario. Low beetle-caused mortality is 10%–20%, medium mortality is 20%–50%, and high mortality is >50%.

between the mortality scenarios and the control run because differences in evapotranspiration (ET) were much smaller between mortality scenarios and control run (Figures 3a and 3c).

In the old phase (1931–1990), all snags fell to the ground as CWD and vegetation slowly recovered. The modeled fuel loading was still higher than in the control run and peaked around 25 years after beetle outbreak (i.e., in 1940) due to snag-fall and CWD decay (Figure 3d). Fuel aridity was lower than in the control run due to reduced water consumption from slowly recovering vegetation (Figure 3c). At the end of the old phase, there was no more litter than in the control run. Live LAI and fuel aridity also caught up to levels observed in the control run (Figures 3c and 3d).

3.2. Fire Extent and Probability Characteristics

Fire extent and probability responded similarly with some discrepancies in each outbreak phase. In the *red phase*, fire extent decreased or did not change (Figure 4a). At low to medium beetle-caused mortality (≤50%), there were no obvious changes in the distribution of fire extent compared to the control run. At high beetle-caused mortality (>50%), fire extent decreased with increasing mortality (Figure 4a). Conversely, fire probability decreased even in the low mortality scenario and decreased more with increasing mortality in medium to high mortality scenarios (Figure 4b). The decreases in fire extent and probability mainly occurred in response to decreases in fuel loading caused by lower tree productivity (Figure 3d).

In the *gray phase*, fire extent and probability both generally increased with mortality (Figure 4). However, fire probability increases plateaued at a 60% mortality (Figure 4b). Above 60% mortality, median fire probability remained elevated while the occurrence of large fires continued to increase (i.e., the distribution of fire extent shifted to have a longer tail toward larger fires). In fuel-limited systems, increases in fuel loading (due to red needle- and snag-fall) can lead to larger fires. However, once fuel loads are no longer limiting, fire probability will stop responding to fuel loading and will instead respond more to changes in fuel aridity (Figure S2 in Supporting Information S1). In higher mortality scenarios (>50%), we found that fuel aridity did not differ from the control run during the gray phase, nor did fire probability (Figure 3c).

In the *old phase*, fire extent and probability exhibited a different response to beetle-caused mortality (Figure 4, old phase). Under low to medium mortality ≤50%) fire extent increased relative to the control run, and the magnitude increased with greater mortality (Figure 4a). Under high mortality (>50%), fire extent slightly increased, and the magnitude was similar among different mortality scenarios. Fire probability had similar responses in low and medium mortality scenarios but showed a decreasing trend in high mortality scenarios. These shifts in fire probability occurred because increases in fuel loading from snag- and needle-fall and decreases in fuel aridity from reduced plant water demand had competing effects and the dominant effects differed among different levels of mortality. This will be further discussed in Section 4.1. The spatial patterning of fire probability (P_{burn}) responses to mortality during the three phases are described in Text S3 in Supporting Information S1.

3.3. Fire Severity

Surface fire severity responded differently during different outbreak phases (Figure 5). *In the red phase*, for the control run (i.e., the no outbreak scenario), surface fire severity was driven by single large fire events (Figure S4 in Supporting Information S1, 1917 fire). Following low and medium beetle-caused mortality (≤50%), fire severity decreased slightly compared to the control (no beetle outbreak) scenario, but the decreases did not change with mortality level (Figure 5). Following high mortality (>50%) scenarios, fire severity decreased substantially in response to decreases in fuel loading (Figure 3d). *In the gray phase*, during medium to high mortality (>20%), fire severity increased with increasing mortality, especially for the second half of the gray phase (Figure S4 in Supporting Information S1 and Figure 5) due to increases in fuel loading that were driven by dead foliage and snag-fall (Figure 3d). *In the old phase*, with low to medium mortality (≤50%), surface fire was more severe and the severity increased with higher mortality (Figure 5; Figure S4 in Supporting Information S1, median, 95th percentile, and maximum fire severity were all further away from the top green line; i.e., the no fire scenario). With high mortality (>50%), fire severity reached an upper limit and stopped increasing with higher mortality. However, in some extreme events, surface fire severity increased with increasing mortality and could sometimes even reduce surface fuel loads back to their pre-outbreak levels (e.g., Figure 5 old phase and Figure S4 in Supporting Information S1 mortality 90% scenario).

Overstory leaf C (both live leaf and dead foliage) loss caused by fire can be a metric of crown fire severity. In general, crown fire responded similarly to beetle-caused mortality as did surface fires (Figure 6 and Figure S5 in Supporting Information S1). However, the timing of severe crown fires exhibited some unique patterns (Figure 6). First, the increases in crown fire severity were more evident after around 25 years post-outbreak (i.e., after 1940; Figure 6a, illustrated by the difference between the dashed line and solid lines). This is around the time when fuel loading peaked, and canopy height was low (Figure3d and Figure S6 in Supporting Information S1). This occurred because snag-fall and increasing litter loads enabled fire to spread to the overstory more easily.

Second, in high mortality scenarios, extreme fire events consumed 60%–70% of canopy C, which is characteristic of a high severity/stand replacing fire (Figure 6b, illustrated by the decrease in the distance of the lighter orange band from the top). In high mortality scenarios, fire can be more severe even if it is less frequent (Figure 4b). Stand replacing fires only occurred when there was an increase in dead surface fuel loading (caused by snag-fall). Once fuel loading dropped back to the level observed in the control run, the likelihood of severe fire decreased back to that which was observed before outbreak (Figure 3d).

4. Discussion

Understanding and managing fire risk in landscapes that are vulnerable to bark beetle outbreaks requires examining how fuel conditions change over space and time. We examined how the extent of mortality, pre-outbreak fuel conditions, and time since outbreak can influence fire regimes using a novel ecohydrologic-fire regime-beetle effects model (RHESSys-WMFire-Beetle) in a semiarid watershed in the western US. We found that fire extent

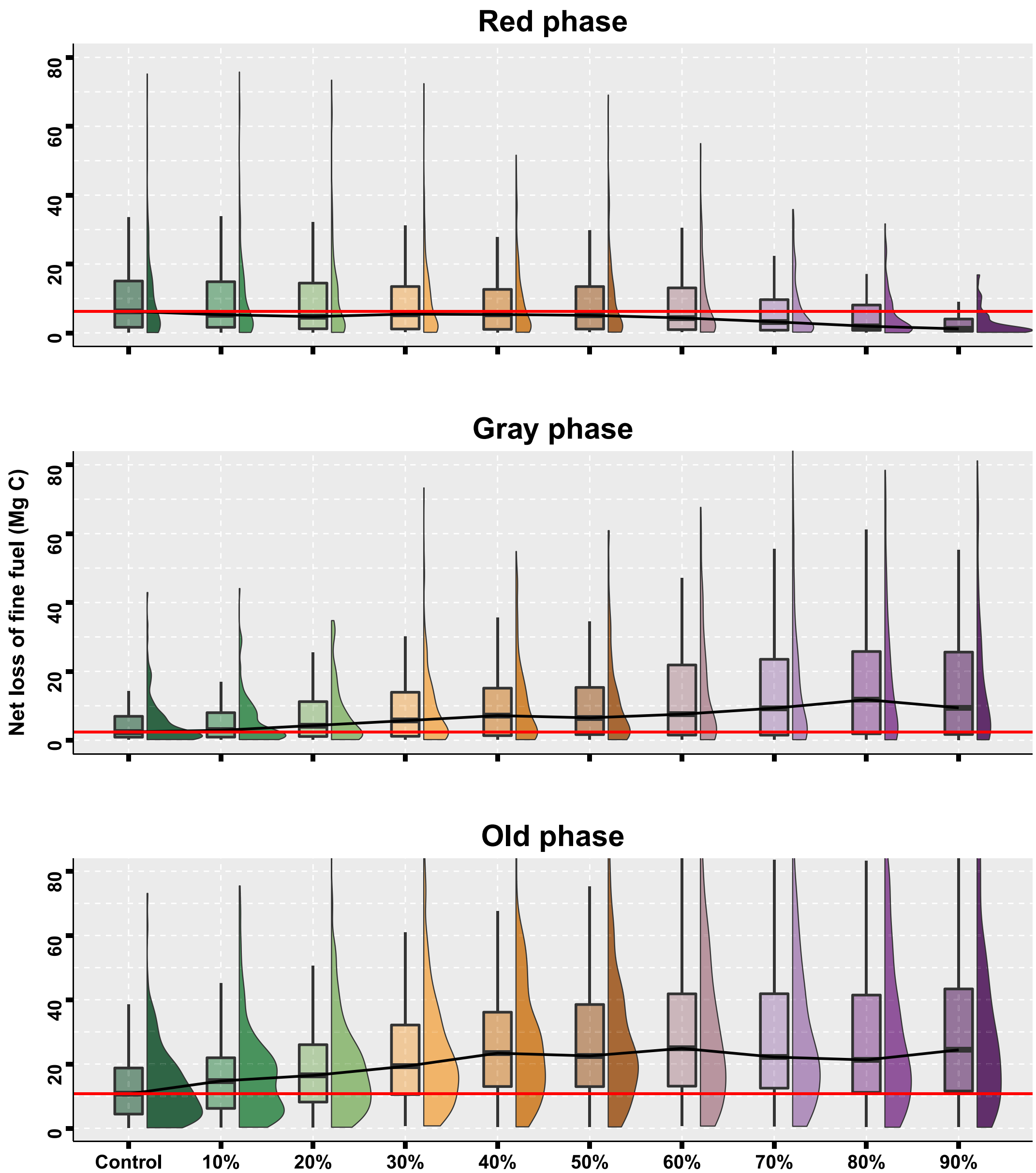

Figure 5. Distribution of surface fire severity for each phase. Distributions come from 200 simulation replicates for each scenario. Box plots show 25th, median, and 75th percentile values for fine fuel C loss. The red line is the median value for the control run; the black line connects the median line for each scenario. Low beetle-caused mortality is 10%–20%; medium mortality is 30%–50%; and high mortality is larger than 50%.

and probability decreased in the red phase, increased in the gray phase, and had different responses in the old phase contingent on the level of beetle-caused tree mortality.

The influence of time after outbreak on fire depended on how fuel loading and fuel aridity changed in response to vegetation growth dynamics, snag-fall, and litter-fall from dead foliage. There was a complex, non-linear relationship between mortality level and fire responses during the gray and old phases. Following low to medium mortality (≤50%), surface fire probability increased. Following high mortality (>50%), fire probability reached a plateau in the gray phase but started decreasing in the old phase. Vegetation regrowth played an important role in driving fuel conditions and fire probability. In the old phase, the slow recovery of overstory vegetation led to less water consumption and lower fuel aridity, which decreased fire probability in high mortality scenarios. Our findings provide insight into beetle wildfire interactions for mixed conifer forests in the inland northwestern US,

10.1029/2022MS003073

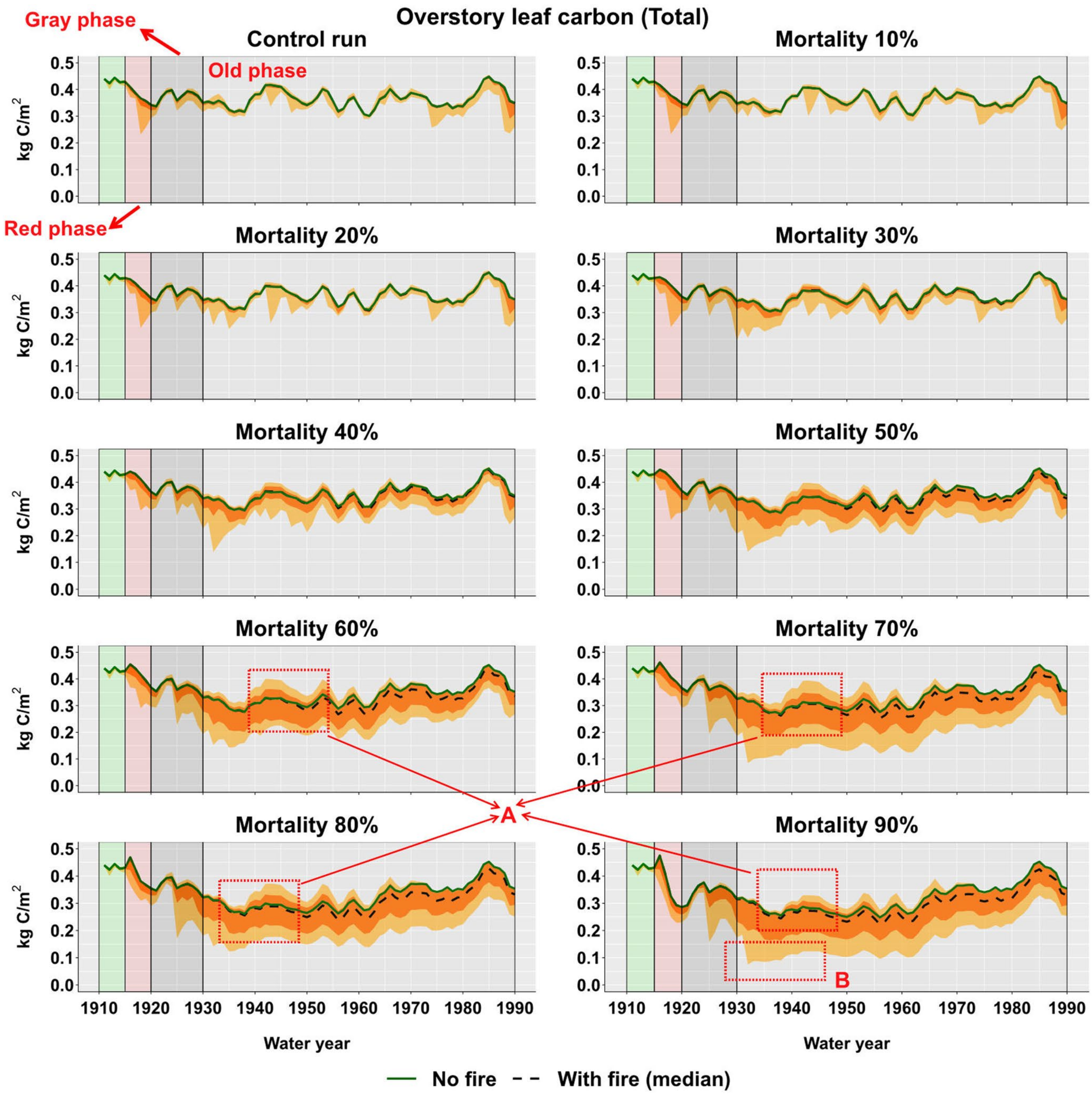

Figure 6. Distribution of leaf C for the 200 fire simulations and the no fire scenario (all means include both live leaf and dead foliage killed by beetle outbreaks. The dashed line is the median total leaf C for the fire scenarios; and the solid green line is the no fire scenario. Light orange shading shows the maximum and minimum total leaf C, dark orange shows the 5th and 95th percentile total leaf C. The differences between the no-fire scenario (green line) and fire scenarios (other lines) can be a surrogate for cumulative fire severity. Label A shows the increases in crown fire severity was more evident after around 25 years post-outbreak. Label B shows the extreme fire events can consume more than 60% of canopy leaf C. See Figure S5 in Supporting Information S1 for detailed canopy fire severity results.

however, additional analyses are needed to examine how these complex relationships play out in other forest types and climate regions.

4.1. Effects of Pre-Outbreak Fuel Conditions on Wildfire Responses

Fuel loading and fuel aridity can compound or counteract one another to drive fire probability and behavior. In locations that were fuel-limited prior to outbreak, fire probability increased in response to increasing fuel loading

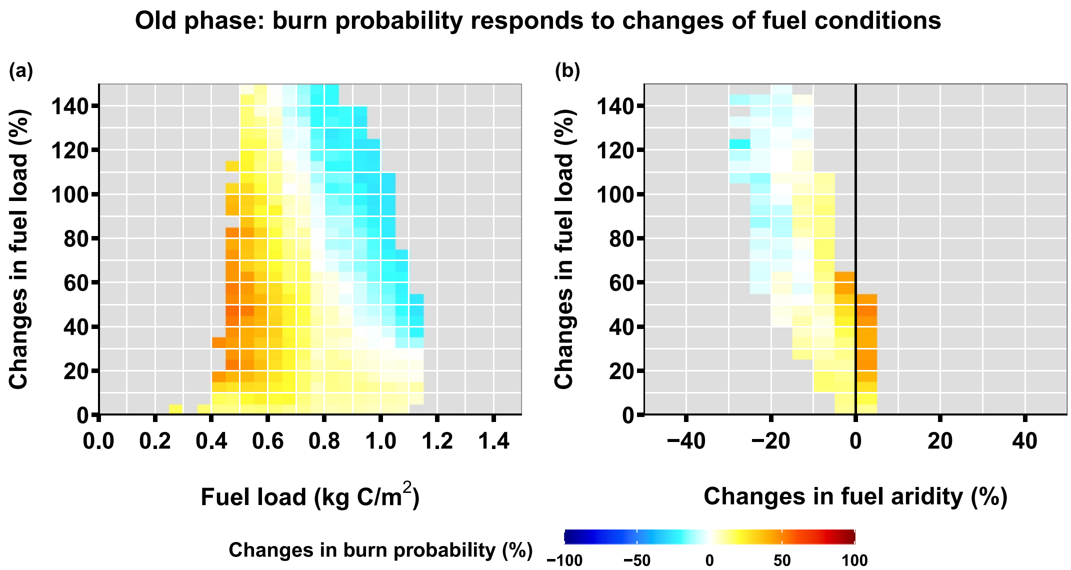

Figure 7. The response of burn probability to fuel load, the relative change in fuel load, and the relative change in fuel aridity during the old phase in the evergreen forest-dominated area (the changes are calculated as the outbreak scenario minus the control scenario). We merged all beetle outbreak scenarios together and binned the data at every 5% or 0.05 kg C/m^2. Bins with less than 100 samples are removed. The change in burn probability for each bin is the median value. The black line divides fuel aridity into "increasing" and "decreasing" zones.

from beetle-caused tree mortality (Figure 7a). However, in areas that were less fuel-limited, increases in fuel loading and decreases in fuel aridity had opposite effects on P_{burn} and whether there was a net increase or decrease depended on the phase of outbreak. For example, once there was enough fuel from snag-fall in the old phase, P_{burn} only responded to changes in fuel aridity, and fire regimes shifted from fuel-limited to flammability-limited. However, fuel aridity changes were relatively small and slow compared to changes in fuel loading (Figure 7b). Similarly, Kaufmann et al. (2008) found changes in fuel aridity after beetle outbreaks play an important role in driving fire hazard. Beetle-caused mortality can increase fuel loading in semiarid systems, thus shifting fire regimes from fuel-limited to flammability-limited (e.g., in the old phase).

In this study, fire regime shifts from fuel-to flammability-limited only lasted through the old phase when there was more fuel loading in mortality scenarios. During the old phase, fuel first accumulated due to snag-fall then decreased back to baseline levels (Figure 3d). Fire regimes also returned to baseline with these declines in fuel loading. However, one limitation of these findings is that our model does not simulate vegetation type conversion. In the natural world, fire- and beetle-caused mortality can promote the growth of fire-tolerant species (Bart, 2016; Goforth & Minnich, 2008). For example, after high tree mortality, grasses and shrubs located in lower elevations may begin to displace higher elevation evergreen forests. These type conversions may eventually result in a more fuel-limited fire regime.

4.2. The Effects of Tree Mortality on Fire Responses

The extent of beetle-caused mortality played an important role in post-outbreak fire responses, although mortality effects varied among phases. Mortality level affects fuel loading and fuel aridity by altering vegetation productivity and turnover, increasing dead fuels, and transforming canopy structure. We found that surface fire probability and severity only responded to beetle outbreaks when mortality was higher than 10% and stopped increasing at around 50% during the old phase. Similarly, based on field observations in mixed-conifer forests in the Sierra Nevada, Wayman and Safford (2021) reported that fire severity increased most substantially when beetle-caused mortality surpassed 15% and was below 30%–40%. In this study, fire severity may have stopped increasing with mortality above 50% because plant water demand decreased, leading to decreases in fuel aridity. Although we also found an upper limit (~50%) where median fire probability and fire severity no longer increased with increasing mortality, the occurrence of extremely severe fires may continue to increase in some cases (e.g., Figure S4 in Supporting Information S1, old phase). Based on reconstructed disturbance history, Kulakowski et al. (2003) also found a

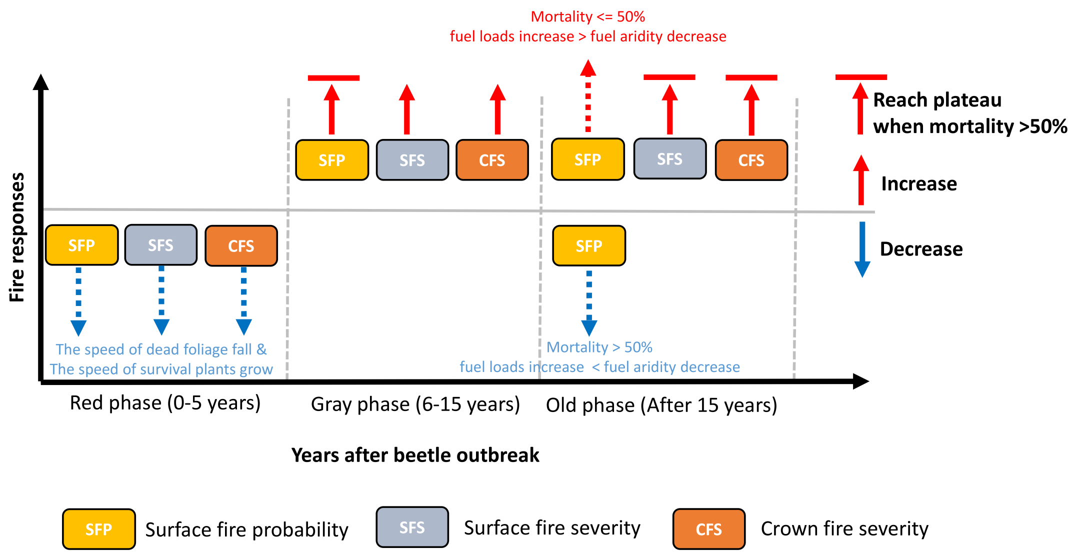

Figure 8. Revised conceptual model showing fire responses to beetle outbreaks from our research. The mechanisms depicted here are described in Table S1 in Supporting Information S1. The dashed arrows are used to indicate that the fire responses are uncertain and depend on the dominant mechanisms. In the red phase, fire responses depend on the speed of dead foliage-fall and the rate at which surviving plants grow. In the old phase, surface fire probability changes depend on competing effects of increasing fuel loading and decreasing fuel aridity after beetle outbreaks. When mortality is less than 50%, increases in fuel loading dominate over decreases in fuel aridity and cause an increase in surface fire probability. The opposite is true when mortality is larger than 50%.

decrease in low-severity fire due to higher moisture on the forest floor following beetle outbreaks. These findings highlight the utility of modeling studies that can capture the full range of possible fire responses (including extreme fires) to beetle outbreaks, while field studies are limited by the number of observations.

We also found that fire probability responses to beetle-caused mortality are different during different phases after outbreak (Figure 4b). There was a negative relationship between them in the red phase (i.e., higher mortality reduced fire probability), a positive relationship with a plateau in the gray phase, but mixed responses in the old phase. The negative relationships in both the red phase and the old phase occurred for different reasons. In the red phase, decreases in fire probability that occurred with increasing mortality were caused by reductions in fuel loading. In the old phase, when mortality was above 50%, fire probability decreased with increasing mortality in locations that were not limited by fuel loading but by fuel aridity. Like the mechanisms driving decreases in fire severity, this occurred because increasing mortality in these locations decreased fuel aridity. Such mechanisms may also explain decreases in fire activity observed in other flammability-limited landscapes (e.g., Bebi et al., 2003; Kulakowski et al., 2003).

In high mortality scenarios, fuel aridity was an important factor constraining the effects of beetle outbreak on fire probability and fire severity. For example, in the old phases, surface fire severity remained elevated even after fire probability decreased (Figure 8). This occurred because high mortality increased fuel moisture, which may have limited the probability of fire, but once weather conditions were suitable for fire to spread, increased fuel loads led to higher fuel consumption. These tradeoffs may explain some of the contradictory relationships between beetle outbreaks and fire in recent field observations. When mortality is moderate, its effects on fuel moisture do not dominate over increases in fuel loading—thus increasing fire severity (Metz et al., 2011; Prichard & Kennedy, 2014). However, when mortality is high, reductions in fuel aridity can reduce fire probability, leading to decreases in fire occurrence, even though there is more fuel available and under the right circumstances, the likelihood of a severe fire may increase (Kulakowski et al., 2003).

Other field observations have found no correlation between beetle-caused mortality and fire severity, therefore claiming wildfire is mostly driven by other factors such as forest structure and fire weather. For example, Harvey et al. (2013) found that mid/lower montane forests became even more heterogeneous following beetle outbreaks, which decreased fuel continuity and likely decreased the probability of fire. In southwestern Colorado, Andrus et al. (2016) found that fire weather and topography outstripped the effects of beetle outbreaks in driving fire severity. While our study focuses on a single semiarid watershed in the inland northwestern US, future research is needed to test our modeling framework in other watersheds to cover broader climate and ecological gradients.

4.3. The Effects of Beetle Outbreak Phases on the Fire Responses

The effects of beetle outbreaks on fire probability and severity vary among the red, gray, and old phases following attack. In the conceptual framework developed by Hicke et al. (2012; Figure 1), surface fire probability does not change in the red phase and increases in the gray and old phases due to increases in surface fuel loading. Additionally, crown fire severity is hypothesized to increase in the red phase but decrease in the gray and old phases due to changes in canopy fuel loading and leaf moisture. Here we refine and expand this conceptual framework using results from our process-based modeling study (Figure 8 and Table S1 in Supporting Information S1).

We found that in our semiarid watershed, during the *red phase*, surface fire probability and severity had opposite responses than those hypothesized by Hicke et al. (2012). For example, their framework suggests that beetle outbreaks do not increase surface fire probability or fire severity during the red phase because they do not substantially change dead surface fuel loading (Figure 1; Bebi et al., 2003; Berg et al., 2006; Bond et al., 2009; Hicke et al., 2012). However, we found that modeled surface fire probability and severity decreased during the red phase because beetle outbreaks reduced vegetation productivity and dead foliage initially lingered in the canopy, leading to an initial decrease in surface fuels. Our results are corroborated by field studies that have found fire severity can decrease during the red phase in the U.S. Pacific Northwest, due to decreases in live vegetation (Meigs et al., 2016). Turner et al. (1999) also found a decrease in crown fire severity due to less fuel mass and heterogeneous fuel distribution. However, other studies have found no link between beetle outbreaks and wildfire severity due to other drivers dominating, such as topography, local weather, and forest type (Bebi et al., 2003; Bond et al., 2009; Harvey et al., 2013).

Our modeling study further extends the Hicke et al. (2012) conceptual framework by accounting for the effects of surviving vegetation on fuel accumulation during the red phase. However, these modeling results only reflect one possible outcome because surface fuel loading responds to both vegetation productivity and the rate of litterfall. In our model, litterfall from dead foliage is controlled by two parameters: *delay time* and *rate of dead foliage fall*. If the delay time is shorter and dead foliage fall is faster than typical leaf phenology in the no outbreak scenario, litter loading may increase, thereby increasing fire probability. Furthermore, the relatively short length of the red phase ($\leq$5 years) and the fact that beetles can attack trees for multiple years (leading to a mixture of phases in a given location) increases the uncertainty surrounding fire responses (Jolly, Parsons, Varner, et al., 2012; Jolly, Parsons, Hadlow, et al., 2012).

In the *old phase*, changes in surface fuel aridity can cause discrepancies between our model study and the conceptual framework. Although we found that surface fire probability increased when mortality was lower than 50%, it decreased when mortality was higher. The differences at high mortality may have occurred because the Hicke et al. (2012) conceptual framework only considered the effects of increases in surface fuel loading and did not consider the possible effects of decreases in fuel aridity. We found that in high mortality scenarios, fire probability decreased because decreases in fuel aridity dominated over increases in fuel loading. Similarly, Kulakowski et al. (2003) reconstructed historical disturbance data in Colorado and concluded that surface fire probability can decrease after beetle outbreaks due to increases in fuel moisture.

We found that the largest differences between our model and the Hicke et al. (2012) conceptual model occurred with crown fire severity. Crown fire severity is driven in large part by changes in leaf moisture and surface fire probability, which can counteract one another. In their conceptual framework, Hicke et al. (2012) suggested that in the red phase, crown fire severity increases due to decreases in leaf moisture (Figure 1). However, our model did not account for how changes in dead leaf moisture influence fire propagation to the canopy. Instead, we found that crown fire severity decreased due to decreases in surface fire probability (Figure 8). Future modeling work should account for changes in dead leaf moisture after beetle outbreaks and examine how decreases in leaf moisture and decreases in surface fire probability compete to influence crown fire severity.

In the old and gray phases, Hicke et al. (2012) suggested that decreases in crown fire severity occurred because decreases in canopy fuel dominated over increases in surface fire probability. However, we found the opposite to be true—there was a net increase in canopy fire severity caused by increases in surface fire probability and the effects of lower overstory canopy height due to snag-fall, which dominated over decreases in canopy fuel.

Similarly, Turner et al. (1999) found crown fire severity could increase when the connection between ground and canopy fuels increased. Thus, the conceptual framework should be expanded to consider canopy fuel structure when predicting crown fire responses to beetle outbreaks.

4.4. Study Limitations and Future Directions

One limitation of our study is that we assumed beetle-caused mortality was uniform across all forested areas. In reality, beetles preferentially attack older trees (Edburg et al., 2011). We expect that because older trees have more biomass and corresponding litter production, older stands will be less fuel-limited (i.e., more flammability-limited). After beetle outbreaks, the fire regime will be shifted to flammability-limited due to higher fuel loading from the red needle- and snag-fall in the gray and old phases. As a result, beetle preference for older trees may temper increases in the probability of fire occurrence but could also likely increase fire severity once a successful ignition occurs. A related factor that should be considered is fuel connectivity. If beetles preferentially attack older trees, spatial fuel heterogeneity may increase across the watershed thereby reducing connectivity and fire size (Harvey et al., 2013). Further research is needed to test how age relationships modify wildfire responses.

Another limitation of our modeling study is that RHESSys-WMFire-Beetle does not include the effects of beetle outbreaks on land surface temperatures. Recent studies have found that summer surface temperatures increase after outbreaks due to decreases in ET and associated cooling and more radiation reaching the ground when the canopy opens (Bright et al., 2013; Cooper et al., 2017). These temperature increases can in turn increase fuel aridity and decrease fuel loading (by increasing decomposition rates). Under these circumstances, wildfire responses would likely depend on location. In flammability-limited areas, the higher temperature may curtail decreases in fuel aridity, thus increasing the probability of fire. In fuel-limited areas, the higher temperatures may reduce fuel loading, thus reducing fire probability. Moreover, increases in land surface temperature can also promote more arid microclimates and increase wind speed, leading to higher fire probability across all regions (Hicke et al., 2012; Page & Jenkins, 2007). These multiple influences can compete or compound one another in driving fire responses, and therefore should also be considered in future research and applications.

Finally, we note that, as with all models, our predictions reflect both strengths and limitations of our current understanding of the primary controls on post-beetle hydrology, ecosystem carbon cycling and fire. While previous applications of RHESSys-WMFire-Beetle have demonstrated reasonable correspondences with multiple observed measures (such as post-disturbance regrowth, fire return intervals), uncertainty in key parameters (such rate of dead foliage fall) means that results should be interpreted as "best guesses." We note that high computation cost of running a coupled ecosystem-fire model mean that we cannot fully evaluate the impact of parameter uncertainties. Nonetheless, we argue that these results offer a valuable, mechanistic explanation for observed temporal and spatial variation in beetle outbreak effects and provide insight into how we might expect fire risk to evolve given a range of beetle-caused mortalities.

5. Conclusion

Our research shows that the impacts of beetle outbreaks on fire probability and fire severity are conditioned by mortality level, phase, and pre-outbreak fuel conditions. To our knowledge, this is the first time that a modeling approach has been used to examine how the coupling among fire, vegetation, and fuels evolve over time following beetle outbreaks. Our results also highlight the importance of how fuel loading and fuel aridity vary within watersheds. In fuel-abundant locations, fire probability may decrease following an outbreak, while in fuel-limited locations, fire probability can increase post-outbreak with increases in fuel loading (e.g., in the old phase). The complex interactions among mortality, local conditions, and time since an outbreak make the prediction of fire response difficult. Our novel coupled modeling framework can be applied to different watersheds to help project fire hazard following beetle outbreaks. This can support long-term management that aims to increase forest resilience and decrease vulnerability to fire.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data sets used to run simulations for this study can be found in the Open Science Forum: https://doi.org/10.17605/OSF.IO/HWMXP (Ren et al., 2022a), and the model code can be found on Zenodo: https://doi.org/10.5281/zenodo.5156688 (Ren et al., 2022b).

Acknowledgments
This project is supported by National Science Foundation of United States under award DMS-1520873 and DEB-1916658. Tung Nguyen and William Burke have helped to set up the RHESSys model. We also thank Nicholas Engdahl and Jan Boll for providing valuable suggestions on the manuscript. We are grateful to the editor and three anonymous reviewers who helped improve the quality of this paper.

References

Abatzoglou, J. T. (2013). Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology*, *33*(1), 121–131. https://doi.org/10.1002/joc.3413

Ager, A. A., McMahan, A., Hayes, J. L., & Smith, E. L. (2007). Modeling the effects of thinning on bark beetle impacts and wildfire potential in the Blue Mountains of eastern Oregon. *Landscape and Urban Planning*, *80*(3), 301–311. https://doi.org/10.1016/j.landurbplan.2006.10.010

Andrus, R. A., Veblen, T. T., Harvey, B. J., & Hart, S. J. (2016). Fire severity unaffected by spruce beetle outbreak in spruce-fir forests in southwestern Colorado. *Ecological Applications*, *26*, 700–711. A Publication of the Ecological Society of America. https://doi.org/10.1890/15-1121

Bart, R. R. (2016). A regional estimate of postfire streamflow change in California. *Water Resources Research*, *52*(2), 1465–1478. https://doi.org/10.1002/2014WR016553

Bart, R. R., Kennedy, M. C., Tague, C. L., & McKenzie, D. (2020). Integrating fire effects on vegetation carbon cycling within an ecohydrologic model. *Ecological Modelling*, *416*, 108880. https://doi.org/10.1016/j.ecolmodel.2019.108880

Bebi, P., Kulakowski, D., & Veblen, T. T. (2003). Interactions between fire and spruce beetles in a subalpine rocky mountain forest landscape. *Ecology*, *84*(2), 362–371. https://doi.org/10.1890/0012-9658(2003)084[0362:IBFASB]2.0.CO;2

Bennett, K. E., Bohn, T. J., Solander, K., McDowell, N. G., Xu, C., Vivoni, E., & Middleton, R. S. (2018). Climate-driven disturbances in the San Juan River sub-basin of the Colorado river. *Hydrology and Earth System Sciences*, *22*(1), 709–725. https://doi.org/10.5194/hess-22-709-2018

Berg, E. E., David Henry, J., 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

Bigler, C., Kulakowski, D., & Veblen, T. T. (2005). Multiple disturbance interactions and drought influence fire severity in Rocky Mountain Subalpine Forests. *Ecology*, *86*(11), 3018–3029. https://doi.org/10.1890/05-0011

Bond, L. M., Lee, E. D., Bradley, M. C., & Hanson, T. C. (2009). Influence of pre-fire tree mortality on fire severity in conifer forests of the San Bernardino Mountains, California. *The Open Forest Science Journal*, *2*(1), 41–47. https://doi.org/10.2174/1874398600902010041

Bright, B. C., Hicke, J. A., & Meddens, A. J. H. (2013). Effects of bark beetle-caused tree mortality on biogeochemical and biogeophysical MODIS products. *Journal of Geophysical Research: Biogeosciences*, *118*(3), 974–982. https://doi.org/10.1002/jgrg.20078

Buhidar, B. B. (2001). *The Big Wood River watershed management plan*. Idaho Department of Environmental Quality, Twin Falls Regional Office.

Chaney, N. W., Wood, E. F., McBratney, A. B., Hempel, J. W., Nauman, T. W., Brungard, C. W., & Odgers, N. P. (2016). POLARIS: A 30-meter probabilistic soil series map of the contiguous United States. *Geoderma*, *274*, 54–67. https://doi.org/10.1016/j.geoderma.2016.03.025

Collins, B. J., Rhoades, C. C., Underhill, J., & Hubbard, R. M. (2010). Post-harvest seedling recruitment following mountain pine beetle infestation of Colorado lodgepole pine stands: A comparison using historic survey records. *Canadian Journal of Forest Research*, *40*(12), 2452–2456. https://doi.org/10.1139/x10-172

Cooper, L. A., Ballantyne, A. P., Holden, Z. A., & Landguth, E. L. (2017). Disturbance impacts on land surface temperature and gross primary productivity in the Western United States. *Journal of Geophysical Research: Biogeosciences*, *122*(4), 930–946. https://doi.org/10.1002/2016JG003622

Daly, C., Neilson, R. P., & Phillips, D. L. (1994). A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology*, *33*(2), 140–158. https://doi.org/10.1175/1520-0450(1994)033<0140:ASTMFM>2.0.CO;2

Dewitz, J. (2019). *National Land Cover Database (NLCD) 2016 products*. U.S. Geological Survey Data Release. https://doi.org/10.5066/P96HHBIE

Edburg, S. L., Hicke, J. A., Lawrence, D. M., & Thornton, P. E. (2011). Simulating coupled carbon and nitrogen dynamics following mountain pine beetle outbreaks in the Western United States. *Journal of Geophysical Research*, *116*(G4), G04033. https://doi.org/10.1029/2011JG001786

Eidenshink, J. C., Schwind, B., Brewer, K., Zhu, Z.-L., Quayle, B., & Howard, S. M. (2007). A project for monitoring trends in burn severity. *Fire Ecology*, *3*(1), 3–21. https://doi.org/10.4996/fireecology.0301003

Frenzel, S. A. (1989). *Water resources of the upper Big Wood River basin, Idaho*. US Geological Survey.

Gara, R. I., Littke, W. R., Agee, J. K., Geiszler, D. R., Stuart, J. D., & Driver, C. H. (1985). Influence of fires, Fungi and mountain pine beetles on development of a lodgepole pine forest in south-central Oregon. *The Bark Beetles, Fuels, and Fire Bibliography*, *12*.

Garcia, E. S., & Tague, C. L. (2015). Subsurface storage capacity influences climate–evapotranspiration interactions in three Western United States catchments. *Hydrology and Earth System Sciences*, *19*(12), 4845–4858. https://doi.org/10.5194/hess-19-4845-2015

Garcia, E. S., Tague, C. L., & Choate, J. S. (2016). Uncertainty in carbon allocation strategy and ecophysiological parameterization influences on carbon and streamflow estimates for two Western US forested watersheds. *Ecological Modelling*, *342*, 19–33. https://doi.org/10.1016/j.ecolmodel.2016.09.021

Gesch, D. B., Evans, G. A., Oimoen, M. J., & Arundel, S. (2018). *The National Elevation Dataset* (pp. 83–110). American Society for Photogrammetry and Remote Sensing. Retrieved from http://pubs.er.usgs.gov/publication/70201572

Goeking, S. A., & Tarboton, D. G. (2020). Forests and water yield: A synthesis of disturbance effects on streamflow and snowpack in Western coniferous forests. *Journal of Forestry*, *118*(2), 172–192. https://doi.org/10.1093/jofore/fvz069

Goforth, B. R., & Minnich, R. A. (2008). Densification, stand-replacement wildfire, and extirpation of mixed conifer forest in Cuyamaca Rancho State Park, southern California. *Forest Ecology and Management*, *256*(1), 36–45. https://doi.org/10.1016/j.foreco.2008.03.032

Halofsky, J. E., Peterson, D. L., & Harvey, B. J. (2020). Changing wildfire, changing forests: The effects of climate change on fire regimes and vegetation in the Pacific northwest, USA. *Fire Ecology*, *16*(1), 4. https://doi.org/10.1186/s42408-019-0062-8

Hanan, E. J., Kennedy, M. C., Ren, J., Johnson, M. C., & Smith, A. M. (2022). Missing climate feedbacks in fire models: Limitations and uncertainties in fuel loadings and the role of decomposition in fine fuel accumulation. *Journal of Advances in Modeling Earth Systems*, *14*(3), e2021MS002818. https://doi.org/10.1029/2021MS002818

Hanan, E. J., Ren, J., Tague, C. L., Kolden, C. A., Abatzoglou, J. T., Bart, R. R., et al. (2021). How climate change and fire exclusion drive wildfire regimes at actionable scales. *Environmental Research Letters*, *16*(2), 024051. https://doi.org/10.1088/1748-9326/abd78e

Hanan, E. J., Tague, C., Choate, J., Liu, M., Kolden, C., & Adam, J. (2018). Accounting for disturbance history in models: Using remote sensing to constrain carbon and nitrogen pool spin-up. *Ecological Applications*, *28*, 1197–1214. A Publication of the Ecological Society of America. https://doi.org/10.1002/eap.1718

Hanan, E. J., Tague, C., Schimel, J. P., & Schimel, J. P. (2017). Nitrogen cycling and export in California chaparral: The role of climate in shaping ecosystem responses to fire. *Ecological Monographs*, *87*(1), 76–90. https://doi.org/10.1002/ecm.1234

Harvey, B. J., Donato, D. C., Romme, W. H., & Turner, M. G. (2013). Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. *Ecology*, *94*(11), 2475–2486. https://doi.org/10.1890/13-0188.1

Hicke, J. A., Johnson, M. C., Hayes, J. L., & Preisler, H. K. (2012). Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management*, *271*, 81–90. https://doi.org/10.1016/j.foreco.2012.02.005

Hicke, J. A., Meddens, A. J. H., & 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

Jolly, W. M., Parsons, R., Varner, J. M., Butler, B. W., Ryan, K. C., & Gucker, C. L. (2012). Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecology*, *93*(4), 941–946.

Jolly, W. M., Parsons, R. A., Hadlow, A. M., Cohn, G. M., McAllister, S. S., Popp, J. B., et al. (2012). Relationships between moisture, chemistry, and ignition of Pinus contorta needles during the early stages of mountain pine beetle attack. *Forest Ecology and Management*, *269*, 52–59. https://doi.org/10.1016/j.foreco.2011.12.022

Kaufmann, M. R., Aplet, G. H., Babler, M. G., Baker, W. L., Bentz, B., Harrington, M., et al. (2008). *The status of our scientific understanding of lodgepole pine and mountain pine beetles - A focus on forest ecology and fire behavior* (p. 13). The Nature Conservancy. GFI Technical Report 2008-2. Retrieved from https://www.fs.usda.gov/treesearch/pubs/40895

Kennedy, M. C. (2019). Experimental design principles to choose the number of Monte Carlo replicates for stochastic ecological models. *Ecological Modelling*, *394*, 11–17. https://doi.org/10.1016/j.ecolmodel.2018.12.022

Kennedy, M. C., Bart, R. R., Tague, C. L., & Choate, J. S. (2021). Does hot and dry equal more wildfire? Contrasting short- and long-term climate effects on fire in the Sierra Nevada, CA. *Ecosphere*, *12*(7), e03657. https://doi.org/10.1002/ecs2.3657

Kennedy, M. C., McKenzie, D., Tague, C., & Dugger, A. L. (2017). Balancing uncertainty and complexity to incorporate fire spread in an eco-hydrological model. *International Journal of Wildland Fire*, *26*(8), 706. https://doi.org/10.1071/WF16169

Klutsch, J. G., Battaglia, M. A., West, D. R., Costello, S. L., & Negrón, J. F. (2011). Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in North-Central Colorado. *Western Journal of Applied Forestry*, *26*(3), 101–109. https://doi.org/10.1093/wjaf/26.3.101

Kulakowski, D., Veblen, T. T., & Bebi, P. (2003). Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. *Journal of Biogeography*, *30*(9), 1445–1456. https://doi.org/10.1046/j.1365-2699.2003.00912.x

Lin, L., Band, L. E., Vose, J. M., Hwang, T., Miniat, C. F., & Bolstad, P. V. (2019). Ecosystem processes at the watershed scale: Influence of flowpath patterns of canopy ecophysiology on emergent catchment water and carbon cycling. *Ecohydrology*, *0*(0), e2093. https://doi.org/10.1002/eco.2093

Littell, J. S., McKenzie, D., Peterson, D. L., & Westerling, A. L. (2009). Climate and wildfire area burned in Western U.S. ecoprovinces, 1916–2003. *Ecological Applications*, *19*(4), 1003–1021. https://doi.org/10.1890/07-1183.1

Lundquist, J. E. (2007). The relative influence of diseases and other small-scale disturbances on fuel loading in the Black Hills. *Plant Disease*, *91*(2), 147–152. https://doi.org/10.1094/PDIS-91-2-0147

Lynch, H. J., Renkin, R. A., Crabtree, R. L., & Moorcroft, P. R. (2006). The influence of previous mountain pine beetle (dendroctonus ponderosae) activity on the 1988 Yellowstone Fires. *Ecosystems*, *9*(8), 1318–1327. https://doi.org/10.1007/s10021-006-0173-3

McCarley, T. R., Kolden, C. A., Vaillant, N. M., Hudak, A. T., Smith, A. M. S., & Kreitler, J. (2017). Landscape-scale quantification of fire-induced change in canopy cover following mountain pine beetle outbreak and timber harvest. *Forest Ecology and Management*, *391*, 164–175. https://doi.org/10.1016/j.foreco.2017.02.015

Meddens, A., A Hicke, J., & A Ferguson, C. (2012). Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the Western United States. *Ecological Applications*, *22*, 1876–91. A Publication of the Ecological Society of America. https://doi.org/10.2307/41723101

Meigs, G. W., Zald, H. S. J., Campbell, J. L., Keeton, W. S., & Kennedy, R. E. (2016). Do insect outbreaks reduce the severity of subsequent forest fires? *Environmental Research Letters*, *11*(4), 045008. https://doi.org/10.1088/1748-9326/11/4/045008

Metz, M. R., Frangioso, K. M., Meentemeyer, R. K., & Rizzo, D. M. (2011). Interacting disturbances: Wildfire severity affected by stage of forest disease invasion. *Ecological Applications*, *21*(2), 313–320. https://doi.org/10.1890/10-0419.1

Mikkelson, K. M., Bearup, L. A., Maxwell, R. M., Stednick, J. D., McCray, J. E., & Sharp, J. O. (2013). Bark beetle infestation impacts on nutrient cycling, water quality and interdependent hydrological effects. *Biogeochemistry*, *115*(1), 1–21. https://doi.org/10.1007/s10533-013-9875-8

Mitchell, R. G., & Preisler, H. K. (1998). Fall rate of lodgepole pine killed by the mountain pine beetle in central Oregon. *Western Journal of Applied Forestry*, *13*(1), 23–26. https://doi.org/10.1093/wjaf/13.1.23

Page, W. G., & Jenkins, M. J. (2007). Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. *Forest Science*, *53*(4), 507–518. https://doi.org/10.1093/forestscience/53.4.507

Poli, P., Hersbach, H., Dee, D. P., Berrisford, P., Simmons, A. J., Vitart, F., et al. (2016). ERA-20C: An atmospheric reanalysis of the twentieth century. *Journal of Climate*, *29*(11), 4083–4097. https://doi.org/10.1175/JCLI-D-15-0556.1

Prichard, S. J., & Kennedy, M. C. (2014). Fuel treatments and landform modify landscape patterns of burn severity in an extreme fire event. *Ecological Applications*, *24*(3), 571–590. https://doi.org/10.1890/13-0343.1

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

Ren, J., Adam, J. C., Hicke, J. A., Hanan, E. J., Tague, C. L., Liu, M., et al. (2021). How does water yield respond to mountain pine beetle infestation in a semiarid forest? *Hydrology and Earth System Sciences*, *25*(9), 4681–4699. https://doi.org/10.5194/hess-25-4681-2021

Ren, J., Hanan, E. J., Abatzoglou, J. T., Kolden, C. A., Tague, C., Naomi, L., et al. (2022). Projecting future fire regimes in a semiarid watershed of the inland northwestern United States: Interactions among climate change, vegetation productivity, and fuel dynamics. *Earth's Future*, *10*(3), e2021EF002518. https://doi.org/10.1029/2021EF002518

Ren, J., Hanan, E. J., Hicke, J. A., Kolden, C. A., Abatzoglou, J. T., Tague, C. L., et al. (2022a). Code for Bark beetle effects on fire regimes depend on underlying fuel modifications in semiarid systems (Version 7.1.2) [Software]. Zenodo. https://doi.org/10.5281/zenodo.5156688

Ren, J., Hanan, E. J., Hicke, J. A., Kolden, C. A., Abatzoglou, J. T., Tague, C. L., et al. (2022b). Data for Bark beetle effects on fire regimes depend on underlying fuel modifications in semiarid systems [Dataset]. Open Science Forum. https://doi.org/10.17605/OSF.IO/HWMXP

10.1029/2022MS003073

Rollins, M. G. (2009). LANDFIRE: A nationally consistent vegetation, wildland fire, and fuel assessment. *International Journal of Wildland Fire*, *18*(3), 235–249. https://doi.org/10.1071/WF08088

Seidl, R., Honkaniemi, J., Aakala, T., Aleinikov, A., Angelstam, P., Bouchard, M., et al. (2020). Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. *Ecography*, *43*(7), 967–978. https://doi.org/10.1111/ecog.04995

Simard, M., Romme, W. H., Griffin, J. M., & Turner, M. G. (2011). Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecological Monographs*, *81*(1), 3–24. https://doi.org/10.1890/10-1176.1

Son, K., & Tague, C. (2019). Hydrologic responses to climate warming for a snow-dominated watershed and a transient snow watershed in the California Sierra. *Ecohydrology*, *12*(1), e2053. https://doi.org/10.1002/eco.2053

Tague, C., & Peng, H. (2013). The sensitivity of forest water use to the timing of precipitation and snowmelt recharge in the California Sierra: Implications for a warming climate. *Journal of Geophysical Research: Biogeosciences*, *118*(2), 875–887. https://doi.org/10.1002/jgrg.20073

Tague, C. L., & Band, L. E. (2004). RHESSys: Regional Hydro-ecologic simulation system—An object-oriented approach to spatially distributed modeling of carbon, water, and nutrient cycling. *Earth Interactions*, *8*(19), 1–42. https://doi.org/10.1175/1087-3562(2004)8<1:RRHSSO>2.0.CO;2

Tague, C. L., McDowell, N. G., & Allen, C. D. (2013). An integrated model of environmental effects on growth, carbohydrate Balance, and mortality of Pinus ponderosa forests in the southern rocky Mountains. *PLoS One*, *8*(11), e80286. https://doi.org/10.1371/journal.pone.0080286

Tang, J., & Riley, W. J. (2020). Linear two-pool models are insufficient to infer soil organic matter decomposition temperature sensitivity from incubations. *Biogeochemistry*, *149*(3), 251–261. https://doi.org/10.1007/s10533-020-00678-3

Turner, M. G., Romme, W. H., & Gardner, R. H. (1999). Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire*, *9*(1), 21–36. https://doi.org/10.1071/wf99003

Wayman, R. B., & Safford, H. D. (2021). Recent bark beetle outbreaks influence wildfire severity in mixed-conifer forests of the Sierra Nevada, California, USA. *Ecological Applications*, *31*(3). https://doi.org/10.1002/eap.2287