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RESEARCH ARTICLE

FIRES FOLLOWING BARK BEETLES: FACTORS CONTROLLING SEVERITY AND DISTURBANCE INTERACTIONS IN PONDEROSA PINE

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ABSTRACT

Previous studies have suggested that bark beetles and fires can be interacting disturbances, whereby bark beetle–caused tree mortality can alter the risk and severity of subsequent wildland fires. However, there remains considerable uncertainty around the type and magnitude of the interaction between fires following bark beetle attacks, especially in drier forest types such as those dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson). We used a full factorial design across a range of factors thought to control bark beetle–fire interactions, including the temporal phase of the

RESUMEN

Estudios previos han sugerido que los escarabajos de la corteza y el fuego pueden ser disturbios interactivos, por lo que la mortalidad de árboles causada por estos escarabajos puede alterar el riesgo y la severidad de incendios subsecuentes. Sin embargo, una considerable incertidumbre persiste en torno al tipo y magnitud de la interacción entre los incendios que siguen al ataque de insectos, especialmente en tipos de bosques secos como los dominados por pino ponderosa (*Pinus ponderosa* Lawson & C. Lawson). Usamos un diseño factorial a través de un rango de factores que pensamos controlaban la interacción entre el escarabajo de la corteza y los incendios, incluyendo la fase temporal del estallido del insecto, el nivel outbreak, level of mortality, and wind speed. We used a three-dimensional physics-based model, HIGRAD/FIRETEC, to simulate fire behavior in fuel beds representative of 60 field plots across five national forests in northern Arizona, USA. The plots were dominated by ponderosa pine, and encompassed a gradient of bark beetle–caused mortality due to a mixture of both *Ips* and *Dendroctonus* species. Non-host species included two sprouting species, Gambel oak (*Quercus gambelii* Nutt.) and alligator juniper (*Juniperus deppeana* Steud.), as well as other junipers and pinyon pine (*Pinus edulis* Engelm.). The simulations explicitly accounted for the modifications of fuel mass and moisture distribution caused by bark beetle–caused mortality. We first analyzed the influence of the outbreak phase, level of mortality, and wind speed on the severity of a subsequent fire, expressed as a function of live and dead canopy fuel consumption. We then computed a metric based on canopy fuel loss to characterize whether bark beetles and fire are linked disturbances and, if they are, if the linkage is antagonistic (net bark beetle and fire severity being less than if the two disturbances occurred independently) or synergistic (greater combined effects than independent disturbances). Both the severity of a subsequent fire and whether bark beetles and fire are linked disturbances depended on the outbreak phase of the bark beetle mortality and attack severity, as well as the fire weather (here, wind). Greater fire severity and synergistic interactions were generally associated with the "red phase" (when dead needles remain on trees). In contrast, during the "gray phase" (when dead needles had fallen to the ground), fire

de mortalidad y la velocidad del viento. Para simular el comportamiento del fuego en camas de combustible en 60 parcelas representativas a lo largo de cinco bosques nacionales en el norte de Arizona, EEUU, usamos el modelo físico tridimensional HIGRAD/FIERETEC. Las parcelas estaban dominadas por pino ponderosa, y abarcaban un gradiente de mortalidad causado por escarabajos de diversas especies, tanto de los géneros *Ips* como de *Dendroctonus*. Las especies no hospedantes de estos escarabajos incluían a dos rebrotantes como el roble de Gambela (*Quercus gambelii* Nutt.) y el táscate (*Juniperus deppeana* Steud.), como así también otras especies de juníperos y de pino edulis (*Pinus edulis* Engelm.). Las simulaciones representaron explícitamente las modificaciones de la biomasa combustible y la distribución de humedad causada por la mortalidad inducida por estos escarabajos. Primeramente analizamos la influencia de la fase del estallido poblacional, el nivel de mortalidad, y la velocidad del viento, en la severidad de un incendio subsecuente, expresado en función del consumo de combustible vivo y muerto del dosel. Luego computamos una medida basada en la pérdida del combustible del dosel para caracterizar si los escarabajos de la corteza y el fuego son disturbios relacionados entre sí y, si lo son, si esa relación es antagónica (daño por el escarabajo y severidad del fuego son menores que cuando ambos disturbios ocurren independientemente), o sinérgica (mayores efectos combinados que si ocurriesen independientemente). Ambos, la severidad de un incendio subsecuente y si los escarabajos y el fuego son disturbios relacionados, dependen de la fase del estallido, de la mortalidad, y de la severidad del ataque, y también del entorno meteorológico del fuego, en este caso la velocidad del viento. Una mayor severidad e interacciones sinérgicas fueron generalmente asociadas con la fase "roja" (cuando las acículas muertas permanecen en los árboles). En contraste con esto, durante la fase "gris" (cuando las acículas han caído al suelo), severity was either similar to, or less than, green-phase fires and interactions were generally antagonistic, but included both synergistic and neutral interactions. The simulations also revealed that the magnitude of the linkage between these two disturbances was smaller for fires occurring during high wind conditions, especially in the red phase. This complexity might be a reason for the contrasted or controversial perception of bark beetle–fire interactions reported in the literature, since both fire severity and the type and magnitude of the linkage can vary strongly among studies. These results suggest that, for fires burning in the gray phase following moderate levels of mortality, bark beetle–caused mortality may buffer rather than exacerbate fire severity. However, for fires burning under high wind speeds, regardless of the outbreak phase or level of mortality, the near complete loss of canopy fuels may push this ecosystem into an alternative state dominated by sprouting species.

la severidad del fuego fue similar a, o menor que, las fases de fuego “verde” y las interacciones fueron generalmente antagónicas, pero incluyeron también interacciones sinérgicas y neutras. Las simulaciones también revelaron que la magnitud entre ambos disturbios fue menor durante la ocurrencia de vientos fuertes, especialmente en la fase roja. Esta complejidad podría ser una razón sobre la percepción controversial o contrastante de las interacciones entre estos escarabajos y el fuego reportados en la literatura, dado que ambos, la severidad y el tipo y magnitud de la relación, pueden variar fuertemente entre estudios. Estos resultados sugieren que, para incendios que queman en la fase gris seguidos de moderados niveles de mortalidad, la causa de mortalidad debida a los escarabajos puede atemperar, más que exacerbar, la severidad del fuego. Sin embargo, para incendios que queman bajo fuertes velocidades de viento, independientemente de la fase del estallido o el nivel de mortalidad, el casi completo consumo del dosel puede derivar este ecosistema a un estado alternativo dominado por especies rebrotantes.

Keywords: antagonism, canopy fuel consumption, *Dendroctonus,* fire severity, HIGRAD/FIRETEC, interacting disturbances, *Ips,* linked disturbances, *Pinus ponderosa,* synergism

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INTRODUCTION

Natural disturbances can have complex and sometimes unpredictable effects on ecosystems by changing their susceptibility to and severity of subsequent disturbances (Darling and Côté 2008, Metz *et al.* 2013). Recent droughts and favorable host conditions throughout western North America have led to widespread tree mortality due to bark beetles (Curculionidae: Scolytinae), raising concerns that high levels of tree mortality could trigger severe wildfires (Bentz *et al.* 2009). Ultimately, a major concern is that the interaction of the two disturbances reduces resiliency or pushes the ecosystem into an alternative state that is otherwise unlikely in the absence of the interaction (Gunderson *et al.* 2000). However, both the severity of a fire following bark beetle–caused mortality and the type and magnitude of bark beetle–wildfire interactions may depend upon a number of factors. These factors include the temporal phase of the outbreak, severity and rate of the mortality, the species-specific beetle–host combination, and the fire weather (see reviews in Jenkins *et al.* 2008, 2012, 2014; Hicke *et al.* 2012). How bark beetle–caused mortality alters the severity of a subsequent fire as well as the type and magnitude of the interaction between fires following bark beetle–caused mortality remains poorly understood across the gradient of these controlling factors, especially in dry forest types such as those dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson).

Although many studies have made inferences regarding the nature of bark beetle–fire interactions based on changes in fire severity, relatively few have directly assessed if these changes are due to an interaction between the two disturbances. The nature of the interaction between two disturbances is classified as either neutral or linked depending upon the combined impact of the two disturbances relative to the sum of the effects of the independent disturbances. If bark beetles and fire are linked disturbances, the linkage can be either synergistic, in which the combined severity is greater than the total severity of the two disturbances occurring independently, or antagonistic, in which the combined disturbance severity is lower than the severity if the disturbances occurred independently (Turner and Bratton 1987). If we define severity as the combined loss of canopy foliar mass due to the disturbances, then a synergistic bark beetle–fire interaction would result in greater foliar mass loss relative to the sum of independent bark beetle outbreaks and wildfires. In contrast, an antagonistic bark beetle–fire interaction would result in a net mass loss relative to the sum of the two disturbances occurring independently. Alternatively, if the two disturbances are not linked, they are considered neutral (also called additive), as mass loss of the combined disturbances is similar to the mass loss of the disturbances occurring independently (Turner and Bratton 1987).

Due to the difficulties in assessing disturbance interactions relative to the two disturbances occurring independently, most studies have inferred interactions based on comparisons of fire severity following bark beetle mortality relative to fire severity without bark beetles present. These previous studies have provided insights into some of the controlling factors on fire behavior in bark beetle–impacted fuels, foremost of which is the temporal phase of the outbreak. Many studies have categorized the time between the occurrence of the bark beetle outbreak and a wildland fire into distinct temporal phases that represent the major changes in the forest fuel complex following the outbreak (e.g., Hicke *et al*. 2012). The temporal sequence of interest in this paper begins with the green phase (unattacked), and progresses through red (red needles remain on dead trees), and then to the gray phase (dead needles have fallen to the ground). Previous studies have suggested that bark beetle–caused mortality influences the canopy fuel moisture in the red phase and canopy fuel continuity in the gray phase thus affecting the severity of a subsequent fire. Theoretical frameworks and some studies predict higher fire severity in the red phase and lower in the gray phase (Jenkins *et al.* 2008, Hicke *et al.* 2012, Prichard and Kennedy 2014, Meigs *et al.* 2016). However, other studies have suggested that fires during the gray phase may be more severe than fires in green-phase forests, or they may be less severe or have little effect on fire severity in either phase (Hoffman 2011; Simard *et al.* 2011; Donato *et al.* 2013; Harvey *et al.* 2014*a*, 2014*b*). These varying fuel effects across the temporal phases thus can potentially alter both the severity of a subsequent fire as well as type and magnitude of the bark beetle–fire interaction.

The lack of consistency is in part due to the effect of other controlling factors, including the severity and rate of bark beetle–caused mortality, specific bark beetle–host combinations, and fire weather. For example, several studies have suggested that the severity and rate of bark beetle–caused mortality plays a pivotal role in the severity of a subsequent fire (DeRose and

Long 2009; Hoffman *et al.* 2012*b;* Donato *et al.* 2013; Harvey *et al.* 2014*a,* 2014*b;* Hoffman *et al.* 2015). Thus, varying levels and rates of mortality may alter subsequent fire severity, whether the disturbances are linked or not, and even the type and magnitude of the interaction across different phases. Studies have also suggested that the effects of the severity of bark beetle–caused mortality on fire severity can be non-linear, whereby effects occur at some levels but not at others (e.g., DeRose and Long 2009, Hoffman 2011). Further, the effect of bark beetle−caused mortality severity on subsequent fire severity is likely to vary due to differences in pre-outbreak forest structures and beetle selection differences associated with various bark beetle−host combinations (Hicke *et al.* 2012). Finally, fire weather during a subsequent fire can alter the influence that bark beetle−caused mortality has on fire severity (Harvey *et al.* 2013, Hart *et al.* 2015, Andrus *et al.* 2016), and have the potential to alter both fire severity as well as the type and magnitude of the interaction. For example, high wind speeds can alter the heat transfer processes and decrease the relative effect of small-scale variations in the fuels complex on fire behavior and effects (Linn *et al.* 2013). However, few studies have explicitly evaluated the nature of bark beetle−fire interactions or the potential influence of other controlling factors.

The aim of this study was to quantify the influence of the temporal phase of the outbreak, level of mortality, and burning conditions on fire severity and to quantify the type and magnitude of the interaction of a fire following bark beetle–caused morality across these gradients. To meet our objective, we utilized field-based data (Hoffman *et al.* 2012*a*) to develop analogous mixed-species forests dominated by ponderosa pine that represent the range of tree mortality measured in the field. We then simulated fire behavior using a full factorial design that included a temporal sequence, with three levels of mortality and three open wind speeds using HIGRAD/FIRETEC, a three-dimensional detailed physics-based model. For each simulation, we assessed fire severity by quantifying dead, live, and total canopy fuel consumption. We then quantified the type and magnitude of the interaction, based on live fuel mortality, by adapting the metric of canopy mass loss that Metz *et al.* (2013) used to explore the interaction between an introduced pathogen and fire. The metric contrasts live canopy fuel loss due to the two disturbances occurring separately to canopy fuel loss due to a fire (foliage consumption) following bark beetle–caused mortality (foliage mortality). We hypothesized: 1) that fire severity (total canopy fuel consumption) would increase in the red phase and decrease in the gray phase, relative to the green phase, with increasing levels of mortality either increasing (red phase) or decreasing (gray phase) consumption. 2) The bark beetle−fire interaction would be synergistic during the red phase and antagonistic during the gray phase, with the magnitude of the interaction increasing with the level of mortality and decreasing with increasing wind speeds, since fine-scale effects of mortality levels would be overwhelmed at high wind speeds.

METHODS

HIGRAD/FIRETEC Simulation Fuel Beds Setup

To meet our overall objectives, we used HIGRAD/FIRETEC (hereafter referred to as FIRETEC), a coupled fire−atmospheric model (Linn 1997, Linn *et al.* 2002). FIRETEC captures essential physical phenomena that determine the behavior of a wildfire through the solution of a set of coupled partial differential equations that rely on a Large Eddy Simulation (LES) approach (Pimont *et al.* 2009, Dupuy *et al.* 2011). Since FIRETEC can account for spatially heterogeneous fuel and fuel moistures with ~2 m resolution, it has proved useful for exploring the effects of bark beetle–

caused tree mortality on fire behavior in other forest types (e.g., Linn *et al.* 2013, Hoffman *et al.* 2015). Further, the model has produced realistic simulations of historical fires (Bossert *et al.* 2000, Bradley 2002) and experimental field fires (Linn and Cunningham 2005, Pimont *et al.* 2009, Dupuy *et al.* 2011, Linn *et al.* 2012, Dupuy *et al.* 2014, Pimont *et al.* 2014). Most pertinently to this study, FIRETEC has reproduced moisture-sensitivity experimental results (Marino *et al.* 2012) and produced realistic simulations of canopy field experiments (Linn *et al.* 2012, Pimont *et al.* 2014), and crown fire rate-of-spread estimates in bark beetle–impacted fuels (Hoffman *et al.* 2016).

FIRETEC Simulation Fuel Beds Setup

We conducted all FIRETEC simulations using a consistent three-dimensional 400 m × 400 m × 615 m grid of computational domain with a horizontal resolution of 2 m and a vertical resolution that varied from ~1.5 m near the ground to ~3 m near the top of the canopy. We derived realistic fuel input for FIRETEC from individual tree data collected in 60 plots of ponderosa pine forests immediately following an abrupt and widespread bark beetle outbreak in 2001 to 2003 in Arizona, USA (Hoffman *et al.* 2012*a*). The mixed-species plots were composed of ~71 % ponderosa pine, with Gambel oak (*Quercus gambelii* Nutt.), several species of junipers (*Juniperus* spp. L.), pinyon pine (*Pinus edulis* Engelm.), and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) constituting the remaining 30 % of the trees (Table 1). Ponderosa pine mortality occurred across a range of tree diameters due to the multiple species of bark beetles, including *Ips* (*Ips lecontei* Swaine and *I. pini* Say) and *Dendroctonus* species (*D. brevicomis* LeConte, *D. adjunctus* Blandford, and *D. frontalis* Zimmerman) (USDA Forest Service 2004; Williams *et al.* 2008). We randomly distributed sampled trees within the computational domain following Ripley (1977), such that the analogous forest represented the plot-level averages in terms of density, species composition, canopy base height, and tree heights described by Hoffman *et al.* (2012*a;* Table 1). We distributed the biomass in each tree using a series of parabolic profiles similar to Linn *et al.* (2005), in which the tree crown dimensions were determined using a combination of field tree measurements, and an estimated canopy width following Bechtold (2004). Because larger diameter woody crown fuel components (>2 mm) are considered to contribute little to crown fires (Rothermel 1983), our simulated crowns only consisted of fine fuels <2 mm, such as needles and small twigs. We represented surface fuel load within the computational domain as a combination of fine dead down woody fuels from Hoffman *et al.* (2012*a*) and herbaceous loadings from Sabo *et al.* (2009). For all simulations, the litter fuel moisture was set at 3 % and herbaceous fine fuel moisture at 30 % to represent a very low dead fuel moisture scenario with mixed live and cured herbaceous layer similar to the D1L1 scenario in BehavePlus (Andrews 2009).

We ran a total of 21 simulations: three green phase to account for fire behavior in no-mortality stands (Figure 1A) at three wind speeds, plus nine red phase and nine gray phase to account for three levels of mortality and three wind speeds (see Table 2 for a summary of stand and fuel characteristics for simulations). To simulate different levels of bark beetle–caused mortality, we randomly selected to “kill” 20 %, 58 %, or all of the ponderosa pine trees in the simulated domain. These percentages represented the observed range and mean amount of mortality, and the random selection of “killed” trees is in agreement with field observations that documented mortality in all tree size classes (Hoffman *et al.* 2012*a*). This approach makes a simplifying assumption that the mortality was synchronous; in reality, the mortality occurred over two years (Negrón *et al.* 2009). We simulated each level

Table 1. Stand and fuel characteristics in Southwestern mixed-species stands dominated by ponderosa pine (host species) used for the design of fire simulation input. Mortality was attributed to both *Ips* and *Dendroctonus* bark beetles. Simulation mortality levels are based on the low, average, and high levels observed in 60 field plots (Hoffman *et al.* 2012*a*). DBH = diameter at breast height, HGT = tree height, and CBH = canopy base height.

	No mortality	20 % mortality	58 % mortality (mean)	100 % mortality
Total density (trees ha^{-1})	467	400 (live) 67 (dead) 467 (total)	273 (live) 194 (dead) 467 (total)	134 (live) 333 (dead) 467 (total)
Density *Pinus ponderosa* (trees ha^{-1})	333	266 (live) 67 (dead) 333 (total)	139 (live) 194 (dead) 333 (total)	0 (live) 333 (dead) 333 (total)
Host density (%)	71.3	66.5	50.9	0
Density non-host species[a] (trees ha^{-1})	134	134	134	134
Mean DBH (cm)	23.5	23.5	23.7	24.2
Mean HGT (m)	9.6	9.6	9.7	9.9
Mean CBH (m)	3.2	3.2	3.2	3.2
Crown width (m)	3.3	3.3	3.4	3.4
Foliar fuel load (kg m^{-2})	1.11 (live) 0.00 (dead) 1.11 (total)	0.96 (live) 0.15 (dead) 1.11 (total)	0.66 (live) 0.45 (dead) 1.11 (total)	0.34 (live) 0.76 (dead) 1.11 (total)
Canopy bulk density (kg m^{-3})[b]	0.171 (live) 0.000 (dead) 0.171 (total)	0.147 (live) 0.024 (dead) 0.171 (total)	0.101 (live) 0.07 (dead) 0.171 (total)	0.051 (live) 0.120 (dead) 0.171 (total)
Foliar live fuel moisture (%)	100	100	100	100
Foliar dead fuel moisture (%)	15	15	15	15
Canopy fuel moisture content (%)	100	88	66	41
Surface herbaceous fine fuel (kg m^{-2})	0.005	0.005	0.005	0.005
Herbaceous fuel moisture (%)	30	30	30	30
Dead fine fuel load (kg m^{-2})	0.91	0.91[c]	0.91[c]	0.91[c]
Litter depth (cm)	6.8	6.8[c]	6.8[c]	6.8[c]
Litter moisture (%)	3	3	3	3

[a] Non-host species included pinyon pine, Gambel oak, Douglas-fir, Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), Utah juniper (*J. osteosperma* [Torr.] Little), oneseed juniper (*J. monosperma* [Engelm.] Sarg.), and alligator juniper (*J. deppeana* Steud.).

[b] Canopy bulk density was estimated using load over depth method. The depth of the canopy layer was the difference between mean tree height and mean canopy base height.

[c] In gray phase–mortality domains, the mass of dead foliage was added to the surface fuel load, and the litter depth was increased to account for the addition of the dead foliage.

of mortality for both the red and the gray phases, to account for temporal changes in the fuel complex, by modifying fuel mass and moisture distribution in FIRETEC input data. For red-phase simulations, killed trees retained their entire pre-outbreak biomass, but with a reduced canopy fuel moisture of 15 %, which falls within the range for recently killed lodgepole pine needles (Jolly *et al.* 2012). For gray-phase simulations, the canopy biomass of killed trees was "transferred" from crowns to the surface fuel to mimic the fall of dead canopy fuel.

To account for the effects of burning conditions on disturbance interactions, we simulated each combination of mortality level and temporal phase at three different synoptic scale wind velocities: 10 m sec^{-1}, 20 m sec^{-1},

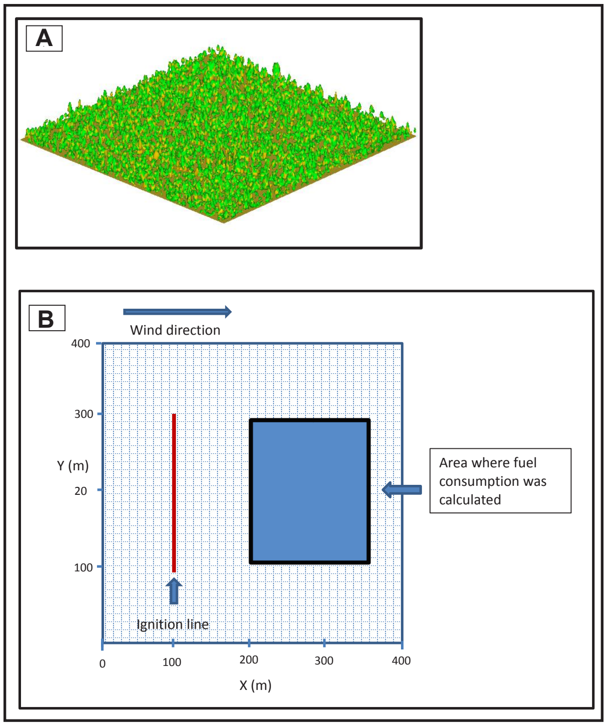

Figure 1. A) no-mortality fuel domain developed from field data showing arrangement of trees; B) top view of the 400 m × 400 m × 450 m fuel domain, showing ignition line, wind direction, and 178 m × 164 m area where fuel consumption was calculated.

and 40 m sec^{-1}, which we refer to as low, moderate, and high, respectively. To develop realistic turbulent wind fields for each simulation, we followed the approach outlined in Pimont *et al.* (2011) and Cassagne *et al.* (2011), with a flat topography under neutral atmospheric conditions. We used a 200-meter long fireline 100 m from the upwind boundary to initiate the fires.

Table 2. Summary of the 21 simulations used to model predicted fire behavior in mixed-species ponderosa pine stands. Mortality phases include before a bark beetle attack (green), when the cured needles remain on the trees (red), and when the dead needles have fallen to the ground (gray). Mortality levels were 0% (green), 20%, 58%, and 100% of ponderosa pine, and synoptic scale wind speeds were 10 m sec^{-1} (low), 20 m sec^{-1} (moderate), and 40 m sec^{-1} (high).

Simulation	Mortality phase	Mortality level	Wind speed
Green_low	green	none	low
Green_mod	green	none	moderate
Green_high	green	none	high
Red20_low	red	20%	low
Red20_mod	red	20%	moderate
Red20_high	red	20%	high
Red58_low	red	58%	low
Red58_mod	red	58%	moderate
Red58_high	red	58%	high
Red100_low	red	100%	low
Red100_mod	red	100%	moderate
Red100_high	red	100%	high
Gray20_low	gray	20%	low
Gray20_mod	gray	20%	moderate
Gray20_high	gray	20%	high
Gray58_low	gray	58%	low
Gray58_mod	gray	58%	moderate
Gray58_high	gray	58%	high
Gray100_low	gray	100%	low
Gray100_mod	gray	100%	moderate
Gray100_high	gray	100%	high

Data Generation and Analyses

To quantify fire severity, we estimated the fraction of total, live, and dead canopy fuel consumption in a 178 m × 160 m sampling located 100 m downwind of the ignition line (Figure 1B) within each simulation. We calculated the fraction of canopy fuel consumption for each ~4 m^2 cell by integrating the vertical column above each surface cell that had canopy above it and then dividing by the sum of the initial mass in each column. In addition, we qualitatively assessed fire type using definitions in Scott and Reinhardt (2001): surface fire = a fire spreading through surface fuels, torching = a crown fire in which individual or small groups of trees torch out, and active crown fire = a crown fire in which the entire fuel complex becomes involved.

To compare total fuel consumed across temporal phases, wind speeds, and levels of bark beetle–caused mortality severity, we used a spatially blocked bootstrapping approach following Lahiri (2003) and generated 10 000 bootstrap samples for each simulation by spatially rearranging trees in the simulation domain. For each bootstrap iteration, we then computed the pairwise differences in mean percent consumption between all pairs of treatment combinations (e.g., low wind green phase versus low wind, low mortality red phase) using Bonferroni-adjusted 95 % confidence intervals to maintain an experiment-wise $\alpha = 0.05$ (Dunn 1961). We identified significant differences at $\alpha = 0.05$ by adjusted confidence intervals ($\alpha = 0.008$ for each phase–wind set) for a given difference not including zero. Bootstrap computations and plots were generated using R version 3.2.0 (R development Core Team 2015).

To characterize the type and magnitude of the linkage between the two disturbances (bark beetles and fire), we adapted the approach used by Metz *et al.* (2013). These authors used the addition theorem of probability, whereby the expected joint fractional mortality of the two agents = $A + (B[1 - A])$, where A = fraction of canopy killed by agent A, and B = fraction of canopy killed by agent B. Significant departures above or below this value represented synergistic or antagonistic disturbance interactions, respectively.

We computed canopy mass losses corresponding to each disturbance sequence:

$$M_{\mathrm{b}} = \frac{m^{\mathrm{d}}}{m_0} \quad , \qquad (1)$$

$$M_{\mathrm{f}} = \frac{m_{\mathrm{c}}}{m_0} \quad , \qquad (2)$$

$$M_{\mathrm{bf}} = \frac{m^{\mathrm{d}} + m_{\mathrm{c}}^{\mathrm{l}}}{m_0} \quad . \qquad (3)$$

In the above equations, M_{b}, M_{f} and M_{bf} are the mass loss corresponding to beetle mortality alone, fire alone, and fire following beetle mortality, respectively. They are expressed as a fraction of the pre-disturbance canopy fuel mass m_{o}, before either bark beetle–caused mortality or canopy fuel consumption. Variables m^{d} and m_{c} are the canopy masses that were killed by bark beetle and consumed by the fire, respectively; $m_{\mathrm{c}}^{\mathrm{l}}$ is the canopy fuel mass that survived the beetle attack but was consumed by the fire. The definition of M_{bf} avoids a double counting of mass losses killed by beetle attack and later consumed by the fire within the canopy at the red stage.

$M_{\mathrm{b+f}}$ is the mass loss of the fire following bark beetle–caused mortality, assuming independent disturbances (Metz *et al.* 2013):

$$M_{\mathrm{b+f}} = M_{\mathrm{b}} + M_{\mathrm{f}}(1 - M_{\mathrm{b}}) \ . \qquad (4)$$

We developed a synergism index, *Syn,* to quantify the magnitude of the linkage between the two disturbances, as the degree of dampening of the second disturbance:

$$M_{\mathrm{bf}} = M_{\mathrm{b}} + (1 + Syn)M_{\mathrm{f}}(1 - M_{\mathrm{b}}) \ , \qquad (5)$$

or, equivalently,

$$Syn = \frac{M_{\mathrm{bf}} - M_{\mathrm{b}}}{(1 - M_{\mathrm{b}})M_{\mathrm{f}}} - 1 \quad . \qquad (6)$$

Combining the above equations leads to:

$$Syn = \frac{\frac{m_{\mathrm{c}}^{\mathrm{l}}}{m_0 - m^{\mathrm{d}}}}{\frac{m_{\mathrm{c}}}{m_0}} - 1 \quad , \qquad (7)$$

which expresses that the synergism index is the deviation of the ratios between live fuel consumption in beetle-attacked stands to fuel consumption in unattacked (green-phase) stands.

Syn = 0 corresponds to disturbances that are neutral or not linked as $M_{\mathrm{bf}} = M_{\mathrm{b+f}}$ and live fuels consumed in a fire after a beetle attack is similar to the amount consumed by fire in green-phase stands. *Syn* > 0 corresponds to synergistically linked disturbances. For example, if *Syn* = 0.5, the fire severity to the surviving trees would be increased by 50 %.

Syn < 0 corresponds to antagonistically linked disturbances. For example, if *Syn* = –0.5, the fire severity to surviving trees would be decreased by 50 %.

RESULTS

Total Canopy Fuel Consumption

Red phase. Fire severity (the percentage of total canopy fuel consumed) during the red phase increased with the level of mortality compared to the green phase, but the magnitude of the increase varied by wind speed (Figure 2A, B, C). At low wind speeds, consumption significantly increased with each increase in mortality level (Figure 2A). In the green phase under low winds, the fire was mainly confined to surface fuels with some torching (Figure 3a), and only 32 % of the total canopy fuels were consumed. With increasing levels of mortality under low winds, fire severity increased, transitioning to crown fires spreading unimpeded due to the continuity of dry fuel, and consuming twice as much canopy fuel in the 100 % mortality scenario compared to the green phase (Figure 3j). In contrast, at moderate and high wind speeds, the magnitude in differences in fuel consumption among mortality levels was small, and only at ≥58 % mor-

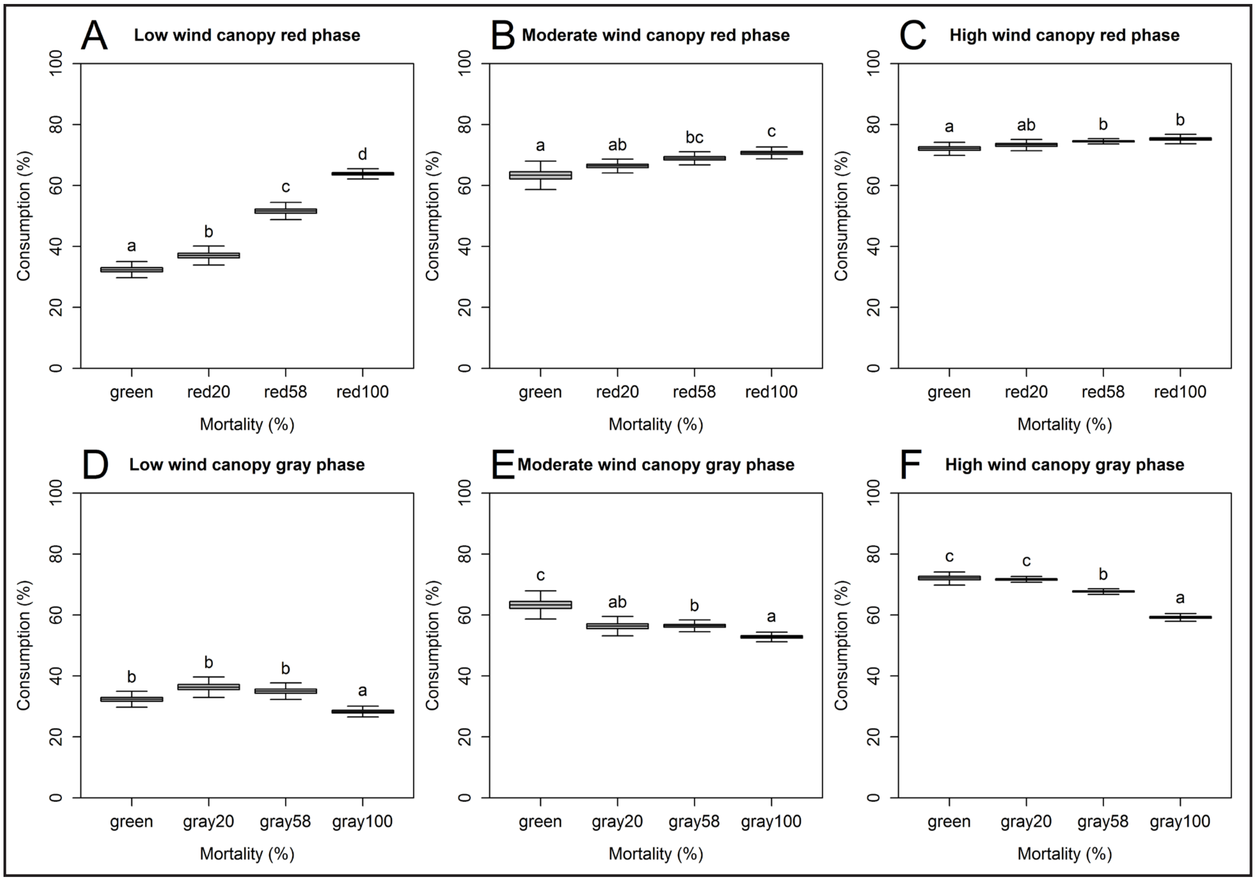

Figure 2. Percent canopy fuel consumption in the red phase (A through C) and gray phase (D through F), for low (A, D), moderate (B, E), and high wind (C, F) simulations. Boxes indicate 25th and 75th percentiles with medians (solid line); whiskers above and below boxes are calculated as 1.5 multiplied by the interquartile range. Letters above boxes indicate significant Bonferroni-adjusted differences among mortality levels within a given phase–wind speed.

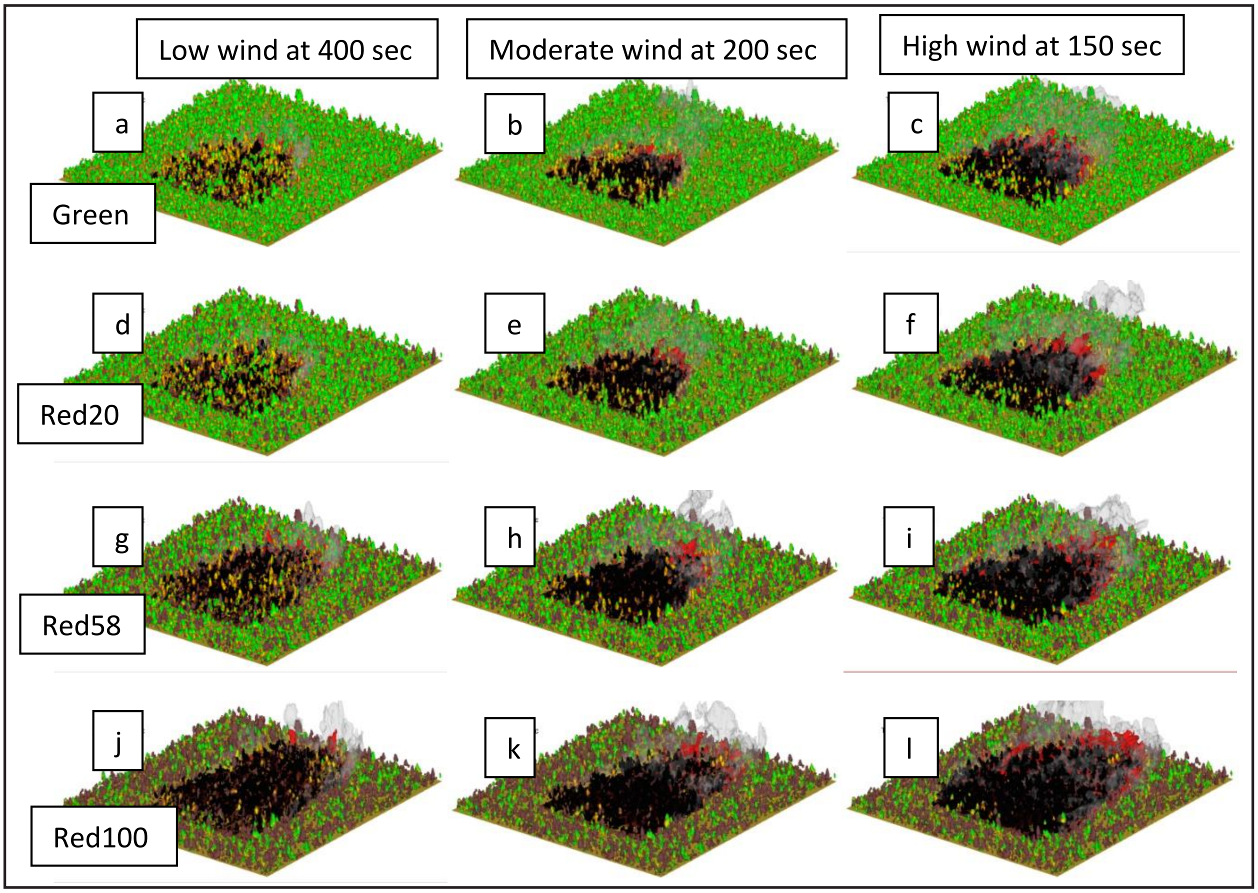

Figure 3. Simulations at 400 s after ignition for low wind speed (first column), at 200 s after ignition for moderate wind speed (second column), and at 150 s for high wind speed (third column). The first row is green phase, second row is red phase 20 % mortality (red20), third row is red phase 58 % mortality (red58), and fourth row is red phase 100 % mortality of all susceptible trees (red100). Colors on the horizontal ground plane indicate the bulk densities of the surface fuels. Live trees are green, dead trees are brown, and burned areas of the canopy are black. The orange, red, and gray isosurfaces indicate areas of hot gases.

tality was canopy fuel consumption significantly higher than in the green phase (Figure 2B, C). At moderate wind speed, the fires in all levels of mortality showed crowning behavior and high fuel consumption (Figure 3, second column). Fuel consumption under moderate wind averaged 63 % in green-phase stands, and increased to only 70 % with 100 % ponderosa pine mortality. Consistent with our hypothesis, at high winds, a large proportion (72 % to 75 %) of the canopy burned, regardless of the level of bark beetle–caused tree mortality, and the increases at greater mortality levels were <4 % (Figure 2C). Fires spread easily from tree to tree (active crown fire) under high winds, and crowning occurred in all scenarios (Figure 3, third column).

As expected, the percent consumption of canopy fuels was greater for the dead (red phase) than for the live (green-phase) canopy fuels (Figure 4). This was true at all wind speeds, but differences were greater in the low wind speed scenarios. In the 20 % mortality case under low wind conditions, the percent live canopy consumption (31.5 %) was almost equal to that of the green phase (30.0 %). This would suggest that the presence of torching dead trees did not strongly influence consumption of live fuels. However, dead canopy fuels were consumed nearly twice as much (62.2 %)

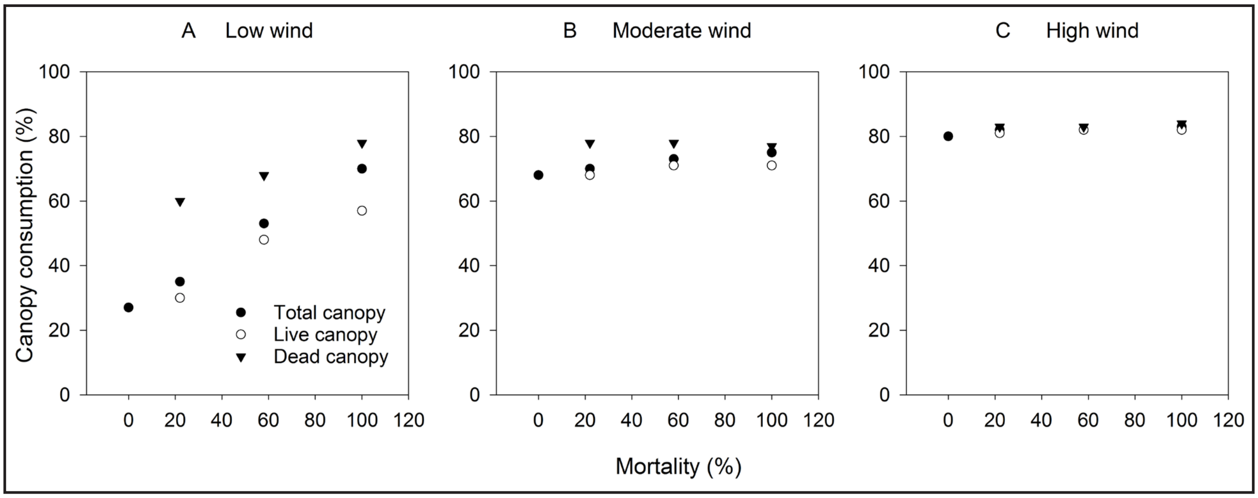

Figure 4. Percentage of live, dead, and total canopy fuel consumed during red-phase fires, by tree mortality level for (A) low, (B) moderate, and (C) high wind speeds.

as the live fuels. At 58 % mortality, percent live fuel consumption (47.1 %) was noticeably higher than in the green phase (30.0 %) due to the presence of torching dead trees, but the live fuel consumption was still much lower than dead fuel consumption (68.6 %). For the 100 % mortality case at low wind speed, the percent live and dead tree consumption was up to 58 % and 73.9 %, respectively. As bark beetle–caused mortality increased, and therefore the influence of the burning dead trees increased, burning of the remaining live trees increased as well, suggesting a tendency towards active crown fire instead of the predominantly torching behavior seen at 20 % mortality. We observed similar trends at moderate and high wind speeds, but the magnitude of the differences was smaller at higher wind speeds as the fires consumed more of the total canopy even in the green phase in active crown fires.

Gray phase. In contrast with our hypothesis, at low wind speeds, total canopy fuel consumption did not decrease with increasing levels of mortality until mortality reached 100 %. In fact, canopy consumption in the 20 % and 58 % mortality scenarios increased slightly, but not significantly, compared to the green phase (Figure 2D). Under low wind speed, canopy fuel consumption was 36.3 % in the 20 % mortality scenario or 12 % higher than consumption in the green phase. In contrast, with 100 % mortality, post-outbreak total canopy fuel consumed decreased by 12 % compared to the green phase. Fires burning under low wind speeds were characterized by torching and crowning in the green phase, 20 % mortality and 50 % mortality scenarios. At 100 % mortality in the gray phase, surface fire with some torching prevailed (Figure 5, first column).

In contrast to consumption under low winds, under moderate and high winds, there was some support of a pattern of decreasing consumption with increasing mortality levels, but the values were not always significantly lower than consumption in the green phase (Figure 2E, F). Simulated consumption at moderate wind speeds was lower at all levels of mortality (56.3 % less for 20 % mortality, 56.42 % less for 58 % mortality, and 52.8 % less for 100 % mortality) compared to 63.2 % consumption in the green-phase scenario. Under moderate winds and low mortality, the fire was able to bridge the mortality-caused discontinuities in the crowns to some degree (Figure 5, second column). Under high winds, fires in green phase (Figure 5c) and low-mor-

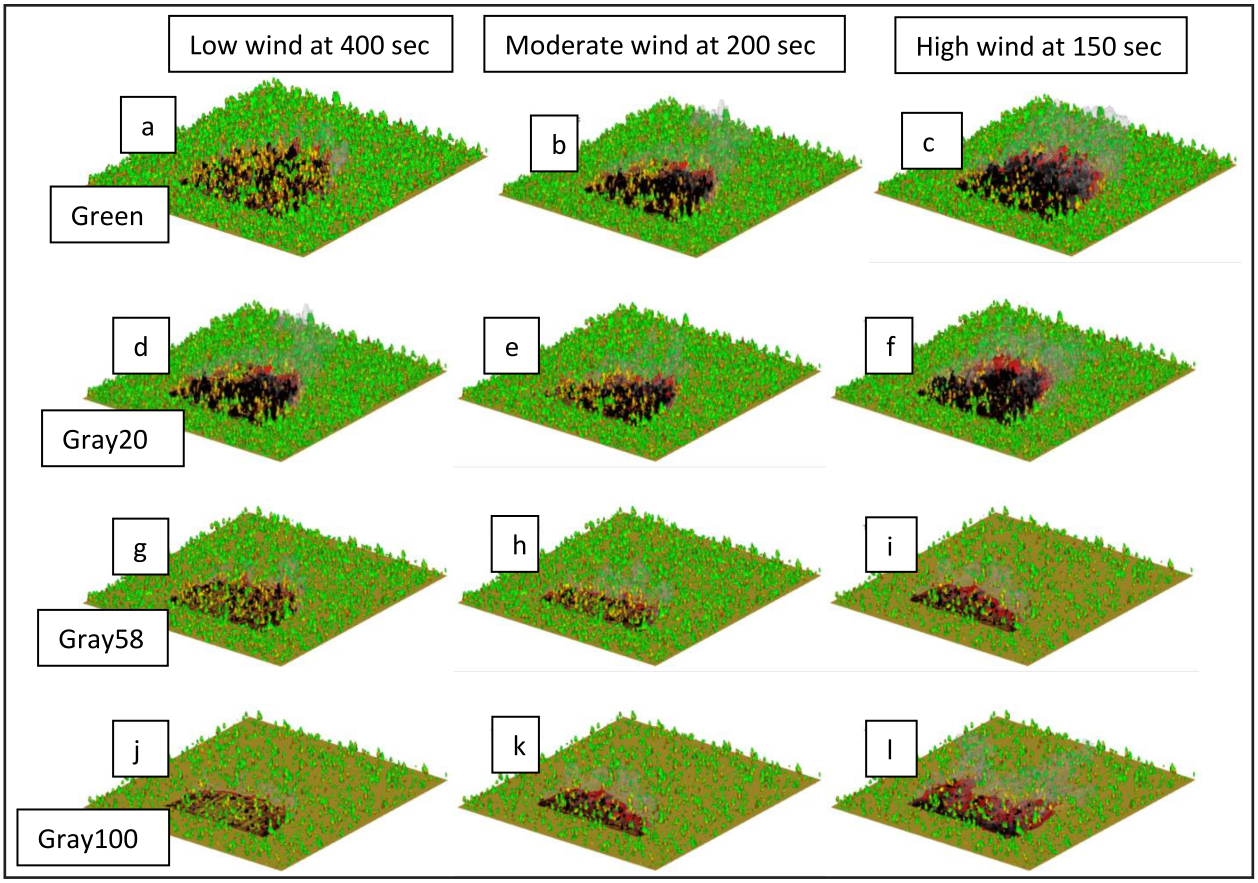

Figure 5. Simulations at 400 s after ignition for low wind speed (first column), at 200 s after ignition for moderate wind speed (second column), and at 150 s for high wind speed (third column). The first row is green phase, second row is gray phase 20 % mortality (gray20), third row is gray phase 58 % mortality (gray58), and fourth row is gray phase 100 % mortality (gray100). Colors on the horizontal ground plane indicate bulk densities of surface fuels. Live tree locations are green, dead tree locations are brown. Burned areas of the canopy are black. The orange, red, and gray isosurfaces indicate areas of hot gases.

tality gray phase (Figure 5f) readily spread from crown to crown; whereas in moderate-mortality (Figure 5i) and high-mortality (Figure 5l) gray-phase scenarios, fires spread mostly on the surface. In the high wind scenario, predicted crown consumption averaged 72.1 % in the green-phase scenario, was similar with 20 % mortality (71.6 %), and decreased monotonically with increasing levels of tree mortality.

Severity Indices and Synergism

During the red phase, the canopy mass loss from fires following bark beetle attacks (M_{bf}) increased with bark beetle–caused mortality levels and wind speed, as did the total fuel consumption as described above (Table 3). More interestingly, M_{bf} was equal to or greater than M_{b+f}, meaning that fires during the red phase following bark beetle attacks would result in more severe canopy loss compared to bark beetle attacks and fires occurring independently, leading to a positive synergism index (Table 4). The synergism index reached +0.53 for low wind red phase with 58 % mortality, indicating that the canopy loss was 53 % higher for surviving trees following bark beetle–caused mortality than for green-phase stands, revealing a strong synergy between

Table 3. Canopy mass loss after bark beetles alone (M_b), fire alone (M_f), the combination of bark beetles and fire (M_{bf}), and the combination of bark beetles and fire assuming disturbances were independent (M_{b+f}). Phases are green (no mortality), red, and gray with 20 %, 58 %, and 100 % bark beetle–caused mortality of ponderosa pine trees at low (10 m sec^{-1}), moderate (20 m sec^{-1}), and high (40 m sec^{-1}) wind speeds.

		Low wind speed			**Moderate wind speed**			**High wind speed**		
Phase	M_b	M_f	M_{bf}	M_{b+f}	M_f	M_{bf}	M_{b+f}	M_f	M_{bf}	M_{b+f}
Green	0.00	0.30			0.67			0.82		
Red20	0.14		0.41	0.40		0.74	0.72		0.85	0.84
Red58	0.40		0.68	0.58		0.85	0.80		0.90	0.89
Red100	0.69		0.87	0.79		0.92	0.90		0.95	0.94
Gray20	0.13		0.45	0.40		0.63	0.72		0.82	0.84
Gray58	0.39		0.56	0.58		0.73	0.80		0.85	0.89
Gray100	0.72		0.77	0.79		0.85	0.90		0.88	0.94

Table 4. Synergism indices, defined as the factor of increase of canopy mass loss required for the second disturbance agent (here, fire) to reach the same mass loss assuming independence or, equivalently, the deviation of the ratio between mass loss in surviving trees and mass loss in green-phase unattacked stands. If *Syn* = 0, the disturbances are neutral (N); values >0 indicate synergistic disturbances (+), and values <0 indicate antagonistic disturbances (–). Bolded values differ from zero by >0.05. Values <0.05 are neutral (N); degrees of synergism are denoted as: (+) for values >0.1, (++) for values >0.2, and (+++) for values >0.5. Degrees of antagonism are denoted as (–) for values <–0.1, (– –) for values <–0.2, and (– – –) for values <–0.5.

Phase	Low wind	Moderate wind	High wind
Red20	0.0194 (N)	0.0309 (N)	0.0082 (N)
Red58	**0.530 (+++)**	**0.0968 (+)**	0.0230 (N)
Red100	**0.890 (+++)**	**0.117 (+)**	0.0212 (N)
Gray20	**0.202 (++)**	**–0.130 (–)**	–0.0165 (N)
Gray58	**–0.0793 (–)**	**–0.169 (–)**	**–0.0758 (–)**
Gray100	**–0.338 (––)**	**–0.289 (––)**	**–0.269 (––)**

bark beetle attacks and fire in this scenario. The synergism was maximum (+0.89) at 100 % bark beetle–caused mortality of ponderosa pine trees and low wind speeds. That is, fires during the red phase following bark beetle–caused mortality would result in an 89 % increase of canopy loss compared to bark beetle–caused mortality and fires occurring independently. We observed similar effects for the moderate wind speed, but the synergism was less pronounced (10 % to 12 %). At high winds or for the lowest level of mortality (Red20, Table 4), the synergism was negligible, indicating a neutral linkage between the two disturbances in these conditions.

In the gray phase, increasing levels of mortality generally resulted in increasing levels of canopy mass losses at all wind speeds (Table 3). Yet, in all cases except the low wind 20 % mortality scenario, the combined effect of bark beetle attack and fire was less severe than the canopy losses when the disturbances occurred independently; that is, M_{bf} was equal to or less than M_{b+f}. Thus, all but two of the synergism indices for the gray phase showed antagonistic linkages between bark beetle attacks and fires (Table 4), suggesting that the bark beetle–caused tree mortality tended to decrease the severity of the subsequent fire on surviving trees by 8 % to 34 %, especially in stands with high mortality rates. The one synergistic effect ($M_{bf} > M_{b+f}$) occurred in low mortality scenarios under low wind, in which 45 % of the canopy fuel was consumed following bark beetle attack compared to 40 %, assuming the disturbances were independent. In this scenario, the disturbances were synergistic (+0.202, Table 4). The one gray-phase scenario with neutral linkage between disturbances was the low mortality level under high wind.

DISCUSSION

Although bark beetle attacks and fire are common disturbances in forest ecosystems, variability in initial conditions, the temporal phase, severity of bark beetle–caused mortality, and the fire weather can lead to different conclusions about the interaction of these two disturbances (Parker *et al.* 2006). Our design that controlled for initial conditions and incorporated a full-factorial range of three factors thought to control fire severity following bark beetle mortality provided insights into disturbance interactions and aids in explaining seemingly contrasting results among previous studies. Our work demonstrates the complex influences of bark beetle–caused mortality on the severity of subsequent fires, as well as on the nature and magnitude of interactions between bark beetle attacks and fires. Depending on the temporal phase of the bark beetle–caused mortality and attack severity, as well as fire weather (here, wind), bark beetle–caused mortality may or may not have significant effects on total fuel consumption, and our indices based on canopy loss show that bark beetle attacks and fire may or may not be linked disturbances. Notably, wind speed had a strong influence on the type and magnitude of the interaction between bark beetle attacks and fire, which was expected given the critical role wind speed has regarding crown fire initiation and propagation (Van Wagner 1977). Several previous retrospective studies have approximated burning conditions in bark beetle–impacted forests as moderate or severe using temperature and relative humidity ranges, but wind data were not available (e.g., Prichard and Kennedy 2014, Agne *et al.* 2016). Our results suggest that including ambient wind in burn condition estimates would likely improve our understanding of fire effects in bark beetle–impacted forest fuels.

As we hypothesized, during the red phase, regardless of the amount of bark beetle–caused tree mortality and wind speed, fire severity increased compared to fires in the green phase, and the level of amplification increased with increasing levels of tree mortality. We attributed the increase in fire severity during the red phase to the reduction in fuel moisture content that occurs when needles die. Lower fuel moisture levels during the red phase are critical to alter the threshold required for crown ignition (Jolly *et al.* 2012, Page *et al.* 2012, Giunta *et al.* 2016) and transition from the surface into the canopy. For example, dead red-phase lodgepole pine *(Pinus contorta* Douglas ex Loudon) needles averaged ~12 % moisture content compared to green needles that averaged ~109 % moisture content; and dead needles ignited up to four times faster than green needles in laboratory ignition tests (Jolly *et al.* 2012). At low wind speeds and low mortality levels, this effect results in the torching of dead trees, but has only minimal effect on consumption of live trees. At higher mortality levels, the abundance of burning dead trees begins to affect the burning of live trees, and the canopy begins to support some active crown fire activity even at low wind speeds. Simulations in lodgepole pine by Hoffman *et al.* (2012*b*) showed a similar increase in canopy fuel consumption, as did observations by Harvey *et al.* (2014*b*) in the earliest phases of a bark beetle outbreak in lodgepole pine in Wyoming, USA, and observations by Prichard and Kennedy (2014) following wildfires that burned through red-phase mortality in mixed conifer stands in Washington, USA. Here, we showed that this increase was not only due to fuel consumption of dead trees, but also due to fuel consumption of the live trees that survived the bark beetle outbreak, revealing the synergy between the two disturbances. Moderate and high wind speeds created scenarios that were progressively more conducive to crown fire spread even in the green phase, and the reduced fuel moisture was less important. Although the presence of dead foliage in the crowns increased fire severity at higher wind speeds, active crowning also occurred in green-phase stands under these wind speeds and thus the mortality had less influence. The implication is that, under dry conditions and high winds, the presence or even prevalence of red-phase bark beetle–caused tree mortality may have little or no effect on fire severity. These results are in agreement with a retrospective study (Bond *et al.* 2009) that found no evidence that recent bark beetle–caused mortality influenced fire severity in two wildfires in California, USA, mixed-conifer forests that burned under extreme fire weather caused by Santa Ana winds.

The increase in fire severity and synergism predicted in our study for red-phase stands under low- to moderate-wind speeds appears to contradict the conclusion by Harvey *et al.* (2014*a*) that fire severity in lodgepole pine stands was largely unaffected by pre-fire bark beetle–outbreak severity. The differences between the two studies could be because Harvey *et al.* studied a mid-red-phase lodgepole pine forest, with only ~50 % of the dead needles retained in the canopy, and our study addressed the early red phase, before any of the dead needles had fallen off the trees. In addition, Harvey *et al.* (2014*a*) studied mountain pine beetle-caused mortality that resulted in needle loss over multiple years, whereas the abrupt and widespread mortality that we studied in Southwestern ponderosa pine forests was incited by a "global change-type drought" (Breshears *et al.* 2009) that increased susceptibility to multiple *Ips* and *Dendroctonus* bark beetle species, killing trees within one to two years (Negrón *et al.* 2009). Finally, if the "moderate" and "extreme" burning conditions approximated by Harvey *et al.* (2014*a*) by relative humidity and temperature also included higher wind speeds, their results are in line with our simulations that suggested that increasing levels of mortality during the red phase under moderate- and high-wind speeds led to minor and sometimes non-significant increases in fire severity.

In partial support of our hypothesis, the gray-phase simulations suggested that, as dead needles fell to the ground, total canopy consumption generally decreased compared to green-phase scenarios, especially with moderate- or high-wind speeds and mortality levels above 20 %. This is in line with the assessment of Meigs *et al.* (2016) of remotely sensed fire severity in wildfires that burned through gray-phase insect-impacted forests in the Pacific Northwest. That is, after accounting for pre-fire biomass and topography, burn severity was generally lower in forests with higher pre-fire insect damage (Meigs *et al.* 2016). However, our simulations revealed one exception, at low levels of mortality and low wind speeds, whereby consumption did not decline until mortality reached 100 % under low winds and 58 % under high winds. We attributed these unexpected results to both the decline in the canopy fuels, which allows greater wind penetration that invigorates the fire, and to the slight increase in surface fuels, which enhanced the sustainability and continuity of the surface fire. Page and Jenkins (2007) speculated that increased wind penetration and increased surface fuels in the gray phase could facilitate surface fires transitioning into crown fires, and these simulations support that. Linn *et al.* (2012) found that the addition of dead needles during the gray phase provided greater surface fuel continuity, and therefore sustained simulated fire spread in patchy pinyon–juniper woodlands. The study by Hoffman (2011) in lodgepole pine forests found that simulated crown consumption was higher in stands experiencing between 20% and 55% mortality compared to green-phase stands, which they also attributed to the combination of increased wind penetration and surface fuels with adequate levels of crown continuity. Agne *et al.* (2016) also noted that high-severity fire was more prevalent in lodgepole pine stands with lower levels of mountain pine beetle-caused tree mortality during the gray phase that burned in an Oregon, USA, wildfire. In contrast, Andrus *et al.* (2016) reported higher fire-killed basal area with increasing beetle-killed basal area under moderate burning conditions during the gray phase in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)–subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) forests affected by spruce beetles *(Dendroctonus rufipennis* Kirby*)* in Colorado, USA, but noted that canopy fire is not necessary to kill thin-barked and shallow-rooted spruce and fir trees.

This study addressed a number of knowledge gaps raised in the review by Hicke *et al.* (2012), as well as several of the limitations of previous studies highlighted in the review by Page *et al.* (2014). First, our study explored the influence of bark beetle–caused mortality on fire severity in a lesser-studied, drier mixed-species forest type dominated by ponderosa pine, and the role of canopy fuel moisture on fire severity in red-phase stands, especially under less severe weather conditions. In addition, we used a design that ensured that bark beetle–impacted stands were similar to green-phase stands. Questions of how similar bark beetle–impacted stands were to green-phase stands often constrain the implications of observational studies. In response to the suggestion by both Hicke *et al.* (2012) and Page *et al.* (2014), we used a model that accounted for the complex spatial arrangement of crown fuels that included a mixture of varying levels of live and dead tree canopy fuels, and accounted for variable fuel moisture content of the affected trees. The fact that the model outputs for bark beetle–impacted lodgepole pine are in agreement with measured fire behavior (Hoffman *et al.* 2016) provides support for FIRETEC's usefulness in predicting fire dynamics in bark beetle–affected ponderosa pine fuels, but it is important to compare these simulation-based findings to emerging data sets in the future. In addition, bark beetle–caused mortality potentially affects other fire behavior attributes, such as rate of spread (ROS), flame length, and fireline intensity. It is evident from our simulations (see Figures 2 and 4) that bark beetle–caused mortality also effected fire ROS, so this is an area that warrants additional work.

Implications

Our results suggest that bark beetle and fire disturbances can be linked synergistically or antagonistically, and can also be neutral disturbances and, thus, either dampen, amplify, or have little effect on the ecological consequences, as noted by others (Turner 2010, Turner *et al.* 2013). Given increasing anthropogenic pressures (e.g., land use changes, human population growth, species introductions) and climate change, increased disturbance frequency, as well as interactions among disturbances, are likely consequences in the future (Seidl *et al.* 2014, Buma 2015, Foster *et al.* 2016). Although a relatively small proportion of fires have occurred in beetle-killed fuels in the western US over the last three decades (0.5% to 1.3%), there are recent examples of fires burning through forests with high levels of beetle-impacted fuels (Hicke *et al.* 2016). For example, 64% of the fuels burned in the High Park Fire in northern Colorado had previous bark beetle–caused mortality (Hicke *et al.* 2016). Further, 29% of the 277 large (>400 ha) fires in recent decades in the Pacific Northwest had over 10% previous insect damage (Meigs *et al.* 2016). Thus, future forest policy and management will require a stronger focus on how multiple disturbances might influence the capacity to sustain forest ecosystem services and carbon stocks (Seidl *et al.* 2016).

For some dry coniferous forests, such as those dominated by ponderosa pine and affected by a century of fire exclusion and past management practices, moderate levels of bark beetle–caused tree mortality may assist in moving forest densities closer in line with historical averages (Hoffman *et al.* 2012*a*), similar to the benefit of moderately burned areas of wildfires (e.g., Stevens-Rumann *et al.* 2012). Lower tree densities due to bark beetle–caused mortality is likely to enhance stand resistance to both *Ips* (Negron *et al.* 2009) and *Dendroctonus* beetles, partly due to host depletion (e.g., Temperli *et al.* 2015), but also due to increased vigor of remaining trees (Fettig *et al.* 2014). Our simulations suggest that bark beetle–induced mortality can also reduce the severity of subsequent fires. In areas with moderate levels of tree mortality, and especially for fires burning in the gray phase, native bark beetles could buffer rather than exacerbate subsequent fire severity. However, if these stands burn under high wind speeds, regardless of the outbreak phase or level of mortality, very little post-outbreak canopy fuels would remain. This is not surprising since no-mortality stands also support active crown fire with nearly the same overall consumption of canopy mass as the combined beetle-caused mortality and fire under high winds. Thus, fires burning under such high-wind conditions may push this mixed-species ecosystem into one at least temporarily dominated by non-pine sprouting species such as Gambel oak and alligator juniper. Such sprouter-dominated patches would tend to be resilient to subsequent fires, but whether ponderosa pine would eventually reestablish is uncertain (Savage and Mast 2005, Coppoletta *et al.* 2016).

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