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Fuel Loads and Simulated Fire Behavior in "Old-Stage" Beetle-Infested Ponderosa Pine of the Colorado Plateau

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Recent bark beetle outbreaks in western North America have led to concerns regarding changes in fuel profiles and associated changes in fire behavior. Data are lacking for a range of infestation severities and time since outbreak, especially for relatively arid cover types. We surveyed fuel loads and simulated fire behavior for ponderosa pine stands of the Colorado Plateau 15–20 years after bark beetle infestation (i.e., "old-stage"). Increasing infestation severity resulted in reduced canopy bulk density, canopy base height, canopy cover, and litter loads whereas woody fuel loads were increased, especially among larger size classes. Using the Fire and Fuels Extension of the Forest Vegetation Simulator, torching index was predicted to decrease with infestation severity whereas crowning index was predicted to increase. Under modeled severe weather conditions, increasing infestation severity was predicted to shift the predominant fire type from surface fire to passive crown fire, whereas the probability of active crown fire was not significantly influenced by old-stage bark beetle-caused tree mortality. We also estimated snagfall rates of infested trees and found that the median time from infestation to snagfall was 9–12 years, with larger trees taking longer to fall.

Keywords: bark beetles, fire hazard, snagfall rates

Bark beetle outbreaks are known to modify fuel complexes of affected conifer ecosystems in western North America (Hicke et al. 2012, Jenkins et al. 2012, Jenkins et al. 2014), and there have been concerns regarding possible associated changes in fire behavior. Outbreaks can modify fuels and microclimates in complex ways that vary with space and time since disturbance, and the impact on fire behavior may also be correspondingly complex (Simard et al. 2011). Typically, not all host trees are killed during outbreaks, and, among those that are, the timing of infestation is spread out over several years (Hansen 2014). Surface fuel loads, by size class, will vary with time. For example, litter accumulates as needles fall from killed trees 3–5 years after infestation, but most of that material will decompose just a few years later. Conversely, snagfall may be drawn out over years to decades and downed logs typically persist on the forest floor for decades (Hansen 2014). Surviving secondary stand structure and recruited seedlings may serve as ladder fuels that promote torching as the postoutbreak stand develops (Simard et al. 2011). These changes in bark beetle-affected stands are associated with phases of stand structure and fuel loads known as "red-stage," "gray-stage," and "old-stage" (Simard et al. 2011, Hicke et al. 2012, Jenkins et al. 2012).

A red-stage pine stand will contain a mix of recently-attacked trees with fallen, fading, yellow, or red-colored needles, currently attacked trees with green needles, and uninfested green-needled trees (Jenkins et al. 2008). Large-diameter overstory trees are preferred by most *Dendroctonus* species (Coleoptera: Curculionidae, sf. Scolytinae), and their death results in drying of needles and woody materials as well as changes in the foliar terpenoid profile, affecting

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flammability and, especially, ignitability (Page et al. 2012, 2014, Jenkins et al. 2014). Observational evidence suggests that rates of crown fire spread in red-stage stands are 2–3 times higher than in uninfested stands (Page et al. 2014), although predictions using fire behavior models vary. Some model results indicate that the red stage is associated with a heightened probability of active crown fire (Page and Jenkins 2007a, Schoennagel et al. 2012), whereas others predict that the red stage is more likely to be associated with passive fires (torching of single crowns or groups of crowns) or even surface fires, depending on wind speeds and fuel moisture levels (Klutsch et al. 2011, Simard et al. 2011).

Within 3–5 years, needles from infested trees fall to the ground along with fine branches, increasing surface fuel loads as canopy bulk density (CBD) is reduced (Page and Jenkins 2007b). Crown fire hazard is thought to decrease during this gray stage because of the reduction in canopy fuels and gaps between surviving trees (Page and Jenkins 2007a, Klutsch et al. 2011, Hicke et al. 2012). Potential fire behavior is confounded, however, by modification of the physical environment via increased within-stand wind speeds and increased solar insolation, a result of canopy cover reductions (Jenkins et al. 2014).

After a few years to decades, the snags fall to the ground during the old stage, substantially increasing surface fuel loads of coarse woody debris (CWD) (i.e., ≥7.6 cm diameter). Meanwhile, relatively rapid decomposition of fine fuels (i.e., litter and woody fuels <0.6 cm diameter) on the forest floor combined with decreased litterfall due to the reduced live overstory may reduce surface loads of fine fuels even as snagfall proceeds (Jenkins et al. 2008, Simard et al. 2012, Hansen 2014). Further modification of surface and aerial fuels may result from the beetle-caused release of the secondary stand structure (i.e., surviving over- and understory trees), recruitment of seedlings into canopy gaps, and increases in shrubs, herbs, and grasses (Hansen 2014). Although these changes increase torching potential in the old-stage stand (Hicke et al. 2012), compared with that of the preoutbreak stand, the potential for increased active crown fire is offset by the discontinuity in canopy fuels (Page and Jenkins 2007a) and reduced CBD (Jenkins et al. 2008). This is supported by the modeling of Simard et al. (2011) for all but the highest wind speeds at which point crown fires were predicted regardless of beetle history. Modeling by Schoennagel et al. (2012), however, indicates that ignition of CWD (1,000-hour fuels) results in increased surface fireline intensities. Combined with the increased within-stand wind speeds resulting from more open canopies, their simulations indicated an increased hazard of active crown fire despite the relatively low CBD.

The widespread use of operational fire behavior models for research purposes reflects the impracticality of conducting controlled experiments regarding wildland fire. Nevertheless, the contradictory results of fire behavior models when applied to bark beetle-infested stands point to model weaknesses for use in these applications. Fire behavior simulations of red-stage stands are particularly controversial because the operational models poorly handle the issue of reduced foliar moisture content among infested trees (Jolly et al. 2012, Moran and Cochrane 2012, Page et al. 2014). This confounding issue, however, has little, if any, influence in old-stage stands where most snags have fallen and associated fine fuels (foliage and small branches) are mostly decomposed.

Regardless of modeling limitations, time since the initiation of bark beetle-caused tree mortality can result in significant variability among multiple fuel profile characters that must be considered in efforts to understand bark beetle-caused impacts on potential fire behavior. The postoutbreak changes in fuel profiles outlined above have been documented in several conifer types including ponderosa (*Pinus ponderosa* Douglas ex Laws.) (Hoffman et al. 2012) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) (Page and Jenkins 2007b, Klutsch et al. 2009, Simard et al. 2011, Schoennagel et al. 2012). For example, in a survey of Arizona ponderosa pine measured ~5 years postoutbreak, beetle-affected plots had significantly greater litter depth and surface woody fuel loads in all size classes than uninfested plots (Hoffman et al. 2012). In addition, infested lodgepole pine stands in Utah, measured ~20 years postoutbreak, had significantly greater surface woody fuel loads among larger size classes, especially 1,000-hour fuels, compared with uninfested stands; 1-hour fuels and litter/duff were not significantly different, presumably due to decomposition (Page and Jenkins 2007b). Nevertheless, Hicke et al. (2012) identified a knowledge gap regarding the influence of a range of outbreak severities and time since attack on fire behavior, particularly for relatively arid types such as ponderosa pine.

We have periodically remeasured permanent plots established on the Colorado Plateau in ponderosa pine type that experienced a substantial bark beetle outbreak ca. 1992–1996 (US Department of Agriculture [USDA] Forest Service 1996). A suite of bark beetles were found in infested pines including mountain pine beetle (*Dendroctonus ponderosae* Hopkins), round-headed pine beetle (*Dendroctonus adjunctus* Blandford), western pine beetle (*Dendroctonus brevicomis* LeConte), larger Mexican pine beetle (*Dendroctonus approximatus* Dietz), red turpentine beetle (*Dendroctonus valens* LeConte), and pine engraver beetles (*Ips pini* Say; *Ips knausi* Swaine). These plots were installed in 1995–1996 to analyze factors that influence the transition from endemic to epidemic beetle population phases and to parameterize a stand-level, bark beetle risk rating model (Chojnacky et al. 2000). In 2012, we remeasured these plots and added Brown's planar intercept transect sampling (Brown 1971) to the over- and understory plot data. Fuel loads of these stands with varying bark beetle intensity were characterized, and these data were used in the Fire and Fuels Extension of the Forest Vegetation Simulator (FFE-FVS) (Dixon 2002, Reinhardt and Crookston 2003, Rebain 2010) to estimate fire behavior in old-stage ponderosa pine stands. Our objectives were to characterize changes to fuel profiles 15–20 years after bark beetle-caused tree mortality and to model bark beetle-related changes in potential fire behavior of old-stage stands such as flame length, rate of spread, and crown fire hazard. In addition, the temporal nature of our data set allowed us to investigate snagfall rates for beetle-killed trees.

Methods

Tree Data and Surface Fuel Measurements

Nine hundred permanent plots were established at 45 ponderosa pine-dominated sites in southern Utah, northern Arizona, and southwestern Colorado during 1995–1996 (Chojnacky et al. 2000) (Figure 1). These sites were located in the vicinity of contemporaneous bark beetle-caused mortality using USDA Forest Service, Forest Health Protection aerial detection survey maps[1] and represented a range of bark beetle severity, from mostly uninfested to widespread beetle-caused mortality of mature pines. Two parallel transects were established at each site, 80 m apart, each with 10 contiguous 405 m^2 circular plots (11.4 m radius). This sampling scheme was intended to capture spatiotemporal variation in bark beetle-caused mortality. Standard forest metrics were taken for all standing trees ≥7.6 cm

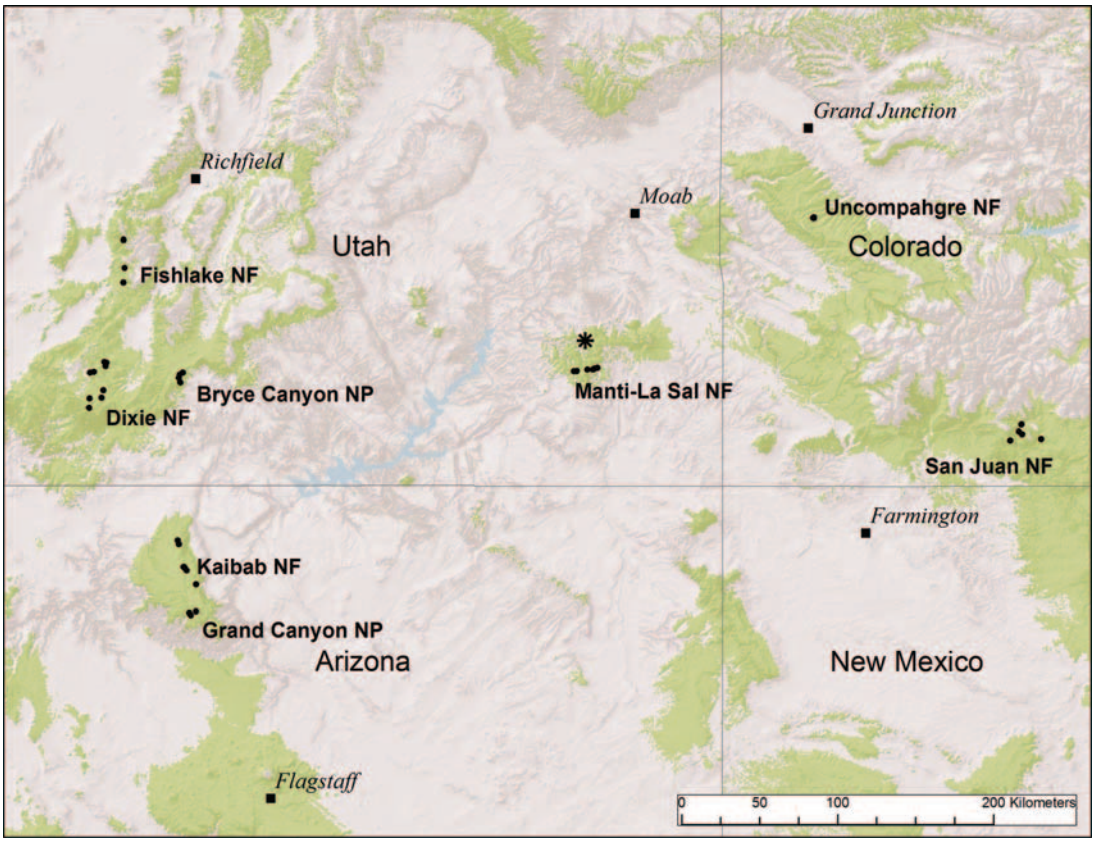

Figure 1. Site locations (20 plots at each site, subsampled during 2012 for surface fuels) in ponderosa pine type (green polygons) of the Colorado Plateau of the southwest United States. The asterisk is the North Long Point remote automated weather station site, used to estimate "severe" weather and fuel moisture conditions. See Appendix A for site descriptions. NF, National Forest; NP, National Park.

dbh including species, dbh, Keen tree class (Keen 1943), and crown ratio. At each plot, 2–5 ponderosa pines were subsampled for age, total height, and crown base height. Year of attack was estimated for all bark beetle-infested stems, and beetle species were identified by egg gallery patterns and sizes (Chojnacky et al. 2000). Plot centers were identified with plastic stakes or rebar, and all pines were marked with metal tags facing plot center. Stems <7.6 cm dbh were measured with a single 13.5 m^2 circular plot (2.1 m radius) centered on each 405 m^2 overstory plot. Preoutbreak stand structure was estimated by recoding recent beetle-killed trees as live (i.e., trees killed since 1991). Plots were checked for new beetle infestations and ingrowth (previously small trees attaining 7.6 cm dbh) in 1998–2000 (all plots), 2001–2002 (Utah and Arizona plots), 2004 (Utah plots), and 2006–2007 (all plots). Since establishment, five sites have been logged and two others had some, but not all, plots cut (these were among the most heavily infested plots). In 2012, we resurveyed the intact plots (Appendix A). All trees ≥7.6 cm dbh were remeasured for diameter and two to five ponderosa pines at each plot were remeasured for total height and crown base height. Beetle-caused mortality subsequent to the previous visit was recorded by bark beetle species and estimated year of attack. Understory trees were again measured with a 13.5 m^2 circular plot. Fire history records for each site were obtained from geographic information system (GIS) database managers from each respective national forest and national park.

During the 2012 resurveys, we selected a subset of plots at each site for surface fuel quantification. To maximize the range of infestation severity sampled, we conducted a stratified subsample based on the infested basal area (BA) at each plot. Plots were assigned to one of three strata according to infested BA (0, 0.01–0.37, or >0.37 m^2 $plot^{-1}$), and we randomly selected up to five plots in each stratum for line transect sampling when available. Thus, each 20-plot site had 5–15 plots sampled for surface fuels, totaling 321 of the original 900 plots. Only data from these 321 plots are used here. Surface fuels were measured with line transects, based on FIREMON protocols (Fire Effects Monitoring and Inventory System) (Lutes et al. 2006). From each plot center, three transects extended radially 11.4 m slope distance (the overstory plot edge was 11.4 m *horizontal* distance), at 0, 120, and 240° azimuth. The slope was measured for each transect. One thousand-hour fuels (≥7.6 cm diameter) were sampled for diameter and decay class along the full transect length. One hundred-hour fuels (2.5–7.6 cm diameter) were sampled at the distal 4.6 m segment of each transect, whereas 1-hour (0–0.6 cm) and 10-hour fuels (0.6–2.5 cm) were sampled at the distal 1.8 m segment. At the distal end of each transect, we sampled live and dead woody plant cover, live and dead herbaceous plant cover, and the forest floor using FIREMON protocols (Lutes et al. 2006). Plot canopy cover was measured using a densitometer (GRS, Arcata, CA) at plot center and at 3.7, 7.3, and 11.0 m from plot center on each cardinal direction. Line transect data were entered into FIREMON (version 2.1.2) to summarize surface fuel loads. Tree data from the over- and understory plots were also entered into the FIREMON database. FIREMON Analysis Tools (FMAT, version 2.10) was used to create input files for the fire simulation model FFE-FVS. Plot-level CBD and canopy base height (CBH) were calculated in FFE-FVS based on the field data.

Table 1. Fuel models most commonly picked by FFE-FVS logic rules using a dynamic approach and their proportional frequency relative to the total number of plots.

Fuel model 1	Proportion	Fuel model 2	Proportion
SB2	0.293	SB3	0.247
TL6	0.250	SB2	0.174
SB3	0.088	TL6	0.110
GS2	0.085	TL5	0.101
Timber	0.073	SH2	0.076
SH2	0.073	Brush	0.064
TL9	0.064	GS2	0.040
GS1	0.030	SH1	0.036
SH1	0.012	SB1	0.036
TU1	0.009	GS1	0.030

The total number of plots is 321. Fuel models 1 and 2 are weighted differently. Model 1 has a weighting of >50%, and model 2 has a weighting of <50% (actual weightings are different for each plot). See Scott and Burgan (2005) for fuel model descriptions (e.g., SB2 is a slash-blowdown fuel type model).

FFE-FVS, by default, uses conifers >1.8 m tall to calculate CBD and CBH. Because beetle-created canopy gaps could encourage seedling recruitment (Hansen 2014), we modified this to include seedlings down to 0.3 m tall and included all tree species in the calculations. Compared with the default settings, this approach increased the probability that FFE-FVS would predict torching and crown fire behavior for bark beetle-infested stands.

Fire Behavior

FFE is an extension of the widely used growth and yield simulation model, FVS (Dixon 2002, Reinhardt and Crookston 2003, Rebain 2010). The base FVS model can be used to simulate stand development and FFE adds fuel dynamics and potential fire behavior. We used the model to simulate fire behavior for the stand conditions measured in 2012, 15–20 years postoutbreak, but did not simulate tree growth. FFE-FVS computes a variety of fire behavior parameters including flame length, indices of crown fire hazard, and fire type (Rebain 2010). Surface fire behavior depends on factors such as slope, fuel quantities, and environmental factors and, in FFE-FVS, is calculated using the methods of Rothermel (1972) and Albini (1976). FFE-FVS reports surface flame length and total flame length; the latter includes any crown fire activity. Using input aerial and surface fuels, FFE-FVS computes torching index (the 6.1 m wind speed predicted to initiate a crown fire) and crowning index (the 6.1 m wind speed predicted to sustain an active crown fire) based on rules developed by Scott and Reinhardt (2001); lower values for these indices indicate greater crown fire hazard. Predictions of fire type are based on an algorithm comparing the user-defined wind speed with the torching and crowning indices. There are four possible fire types: surface (crowns do not burn), passive (individual trees or groups of trees torch), conditional-crown (surface fire from an adjacent stand will continue as a surface fire; crown fire from an adjacent stand will continue as a crown fire), and active-crown (fire moves through tree crowns, burning all crowns and killing all trees).

Potential fire behavior was modeled in separate FFE-FVS (FVS version 0979; version date July 15, 2013) simulations using either custom fuel models, wherein empirical fuel loads were directly used to predict fire behavior, or a dynamic approach, wherein FFE-FVS logic rules selected from a combination of 2 of 53 possible fuel models (Johnson et al. 2011) (Table 1). Custom fuel models better represent empirical fuel loads but, unlike the 53 defined fuel models, are uncalibrated (Noonan-Wright et al. 2013). We present the results from each so that the reader may infer additional information. All simulations were based on the Utah FVS variant (Keyser and Dixon 2008). Historic weather conditions and fuel moisture data were obtained from a remote automated weather station (RAWS), North Long Point, Utah (37.84′ N, 109.84′ W, 2,645 m), with observations from 1998 to 2013. This station is in ponderosa pine type and is centrally located to our sites at an elevation ~120 m higher than the average of our sites. The 90th percentile weather conditions (air temperature 26° C; 1-minute sustained wind gust of 32 km/hour at 6.1 m) and 10th percentile fuel moistures (2, 3, 4, and 7%, respectively, for 1-, 10-, 100-, and 1,000-hour fuel classes) were calculated from the record (May–September each year) using FireFamily Plus (version 4.1; Bradshaw and McCormick 2000). We chose the 90th percentile to be consistent with Klutsch et al. (2011) who used FFE-FVS to simulate fire behavior in bark beetle-infested lodgepole pine stands. All reported results are from simulations using these "severe" conditions. In FFE-FVS, midflame wind speeds are adjusted using a correction factor derived from canopy closure (Rebain 2010) and can thus account for bark beetle-caused alterations of the within-stand environment. In addition to the standard FFE-FVS output, surface rates of spread and reaction intensities were calculated for each plot.

Snagfall Rate

For the snagfall rate data, each stem killed by bark beetles during the 1990s outbreak (343 total stems among the intact sites) was tracked through the subsequent surveys to estimate the number of years to snagfall (trees killed after the initial outbreak were examined for snagfall during each resurvey but not used in this analysis). Because the survey interval ranged from 2 to 6 years at each site, we assumed that the year of snagfall was the midpoint between when the snag was last observed standing and when it was first observed on the ground. Although, for any given stem, this could result in an error as great as 3 years, these errors were assumed to average out over the data set (i.e., hypothetically, for each tree that fell the year after we surveyed, another fell the year before we surveyed).

Statistical Analyses

Generalized linear mixed models (PROC GLIMMIX; SAS Institute, Inc., Cary, NC) (Littell et al. 2006) were used to detect differences in observed fuel loads and predicted potential fire behavior as a function of bark beetle-caused pine mortality. Tree density and BA of pine mortality were grouped into four intervals by infestation year: pre-1991, 1991–1997, 1998–2004, or 2004–2011 (Figure 2). We tested infested stem counts and infested BA, from the 1991–1997 outbreak, as explanatory variables for predicting stand structure, fuel loads, and potential fire behavior. For each response variable, we report the best fitting of these two predictor variables, as judged by Akaike's Information Criterion (AIC). Covariates included infested BA and stem counts from other infestation intervals (e.g., 1998–2004), elevation, slope, aspect, and preoutbreak plot characteristics such as total BA, live BA, BA by species, BA by group (pines, nonpine conifers, and hardwoods), and stem density. We also included time, in years, since the last documented fire. For most sites, fire records only extend to ca. 1960 and sites without record of fire were coded as 50 years. Site within national forest/park was used as a random variable. Although the sites were not randomly selected from a population of possible locations, we needed to account for this potential source of variance yet we were not interested in its effects. Denominator degrees of freedom were specified as the

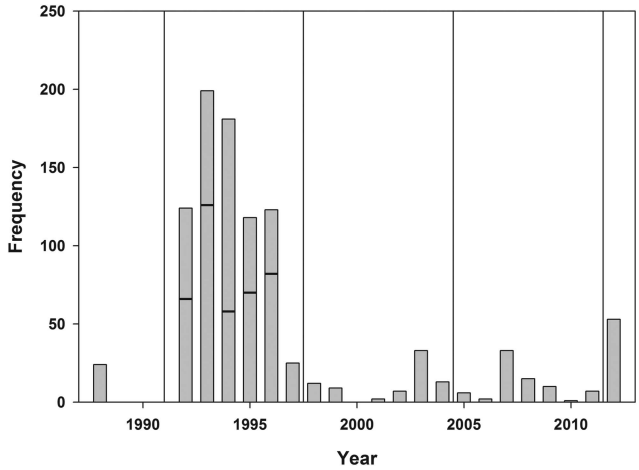

Figure 2. The total number of bark beetle-killed stems, by infestation year, for all plots in all sites (i.e., 900 plots of 405 m^2 each). The vertical lines indicate the temporal groupings used in the analyses (see Methods). The horizontal lines in the bars for 1992–1996 indicate stems lost in salvage logging operations; stems above the lines were cut, and affected plots were not used in our analyses. Stems estimated to have been infested before 1991 are classified, arbitrarily, as 1988. The stems infested in 2012 were not used in the analyses because they were still "green" at the time of the 2012 surveys.

Kenward-Roger type. We specified a log-normal model a posteriori based on residual diagnostics. Model residuals were tested for spatial dependence using Moran's I test (spdep package, R statistical software, R Project for Statistical Computing; Bivand 2002); we did not detect evidence of spatial dependence and the results of those tests are not shown.

For the categorical fire type data, we used a multinomial logistic regression model (PROC LOGISTIC, generalized logit link function; SAS Institute, Inc.). In these models, one level of the response variable is chosen as a reference, and comparisons are made among other response levels by covariable parameter estimates and their associated test statistics. Because these models do not allow random effects, we included plot latitude and longitude and their second-order terms and interactions as covariates in lieu of site within forest.

Results

Plot and Fuelbed Characteristics

Total BA (all species, live and dead), live ponderosa pine BA, CBD, and canopy cover were significantly and inversely related to the density of stems infested 1991–1997 (Figure 3; see Appendix B for model results and parameter estimates). Because plots with greater preoutbreak BA tended to incur greater beetle-caused mortality (Garza 2015), postoutbreak ponderosa pine BA was similar among infested and uninfested plots (Figure 4). Ponderosa pine quadratic mean diameter (QMD) and CBH were significantly and inversely related to BA infested 1991–1997. The densities of live trees (≥7.6 cm dbh) and seedlings (trees <1.5 m tall) were significantly and positively related to the density of stems infested 1991–1997. The densities of saplings (trees ≥1.5 m tall but <7.6 cm dbh) and snags were not significantly related to density or BA of stems infested 1991–1997 (results not shown). Snag density, however, was significantly and positively related to the density of stems infested 2005–2011 ($F_{1,\,138.7}$=4.94, P = 0.0279). No other bark beetle-related covariates were significant for any of these response variables.

Surface Fuel Loads

Litter depth (Figure 5) and litter loads (Table 2) were significantly and inversely related to the density of stems infested 1991–1997 (see Appendix B for model results and parameter estimates), whereas duff loads were not correlated with any beetle-related variable (density of stems infested 1991–1997: $F_{1,\,305.5}$=1.27, P = 0.2609). Assuming 250 infested stems ha^{-1}, the models predict that infested plots had ~25% less litter depth and mass than uninfested plots (Figure 5; Table 2). All diameter classes of woody fuels were significantly and positively related to the density of stems infested (1991–1997) or BA infested (1991–1997) with increasingly greater differences among the larger size classes (Table 2). Combined 1-, 10-, and 100-hour fuel classes, which are used in the surface fire behavior models along with forest floor loads, were also significantly and positively related to the density of stems infested 1991–1997 (Figure 5). None of the other beetle-related covariates were significant in any model except pre-1991 infested stem density, which was inversely correlated with 1-hour fuel loads.

Potential Fire Behavior

Ponderosa pine BA infested during the 1990s outbreak was marginally significant as a predictor variable, with a positive relationship, for surface flame length using custom fuel models ($F_{1,\,306.4}$ = 3.37, P = 0.0672); beetle-related variables were not significant in models using data from dynamically selected fuel models (ponderosa pine BA infested in 1991–1997: $F_{1,\,315.7}$ = 2.53, P = 0.1129) (Figure 6; see Appendix C for model results and parameter estimates). Total flame length was significantly and inversely related to the density of stems infested 1991–1997 using either custom or dynamically selected fuel models; the density of stems infested 2005–2011 was a significant covariate, also with an inverse relationship.

Torching index was significantly and inversely related to BA infested 1991–1997, concomitant with decreasing canopy base height, using simulations based on either custom or dynamically selected fuel models (i.e., higher hazard of torching with increasing infestation severity). Crowning index, in contrast, was significantly and positively related to the density of stems infested 1991–1997 for both fuel models (i.e., lower crown fire hazard with increasing infestation severity). Surface fire rate of spread was significantly and positively related to BA infested 1991–1997 using simulations based on either custom or dynamically selected fuel models. The density of stems infested 1991–1997 was marginally significant as a predictor of reaction intensity, with an inverse relationship, for simulations using dynamically selected fuel models but was not significant using custom fuel model simulations (custom: $F_{1,\,306.9}$ = 2.20, P = 0.1393; dynamic: $F_{1,\,310.1}$ = 3.84, P = 0.0509). Smoke potential (i.e., emissions of PM2.5, particulates with known human health consequences) was significantly and positively related to BA infested 1991–1997 using either custom or dynamically selected fuel models (custom: $F_{1,\,306.2}$ = 18.79, P < 0.0001; dynamic: $F_{1,\,305.1}$ = 21.25, P < 0.0001; relationship not graphically shown).

Fire type was significantly related to BA infested 1991–1997 using either custom or dynamically selected fuel models (custom: Wald χ^2 = 10.74, df = 3, P = 0.0132; dynamic: Wald χ^2 = 13.49, df = 3, P = 0.0037). In both cases, the probability of passive fire increased, whereas the probability of surface fire decreased as a function of increasing infestation severity, a reflection of the decreasing canopy base heights (Figure 7). Parameter estimates for conditional crown and active crown fires were not significant, indicating that their probabilities are not influenced by infestation for the "severe"

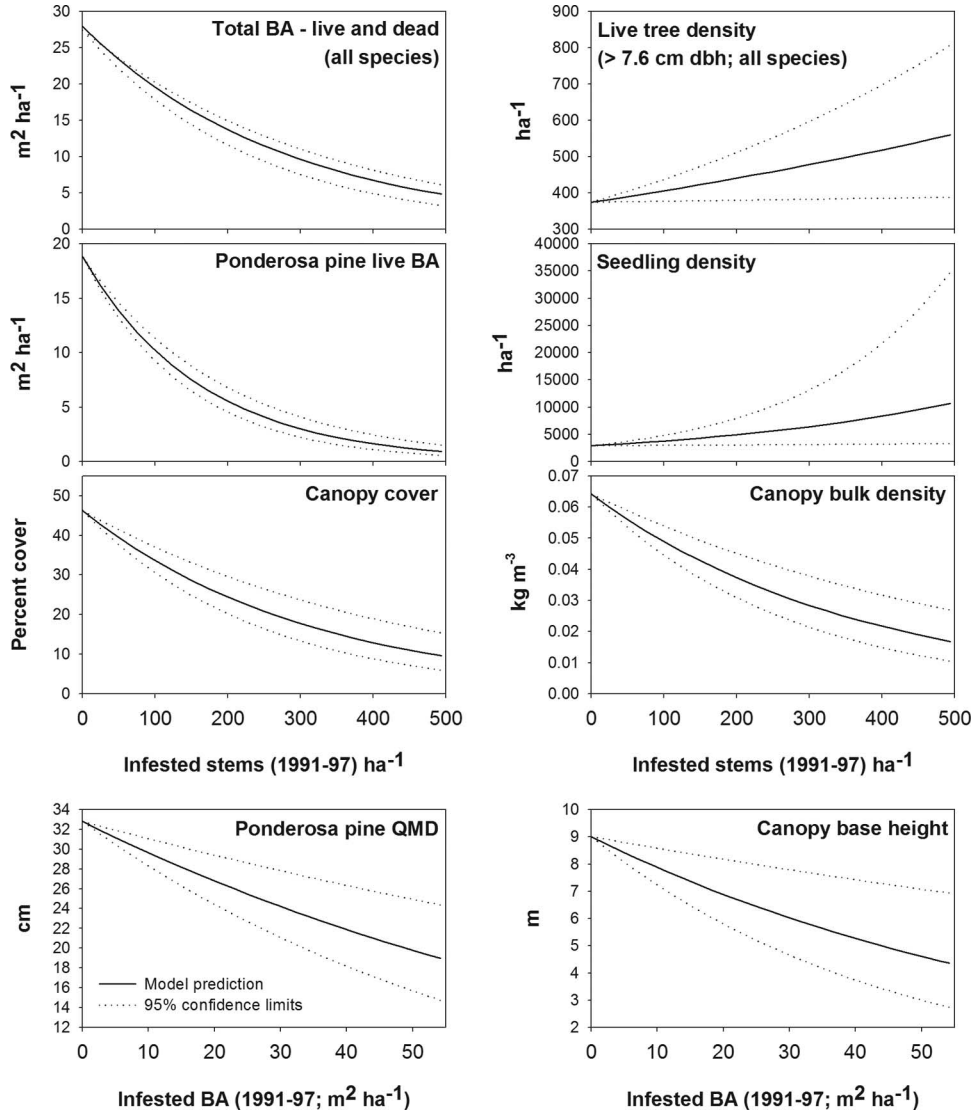

Figure 3. Predicted postoutbreak stand structure and fuelbed characteristics 15–20 years postoutbreak as a function of bark beetle infestation severity. These traces were created by using equations and parameters derived from observed data (Appendix B). Covariate values for the equations are the median values in our data set (Appendix D). All graphs were produced by holding the covariates constant while varying the infestation severity, i.e., stems or BA killed during the 1990s outbreak. Changing the covariate values modifies the scale, but not the character, of the relationships between the response and explanatory variables. Note that the 95% confidence limits regard the parameter estimate for infestation severity.

weather and fuel moisture conditions used in the simulations (model results not shown).

Significant Covariates

For most fuel load type/size classes, significant covariates commonly included preoutbreak total BA, live BA, and ponderosa pine BA; the correlations generally were positive. Time since the last fire was significant and positively correlated to most fuel load type/size classes (none of these were stand-replacing fires). Regarding potential fire behavior, common significant covariates included preoutbreak live BA, total stem density (≥7.6 cm dbh), and sapling density, generally with positive relationships (except for crown fire hazard indices for which higher values indicate lower hazard). Again, time since the last fire was significant and positively correlated with more severe fire behavior (e.g., greater flame lengths and reaction intensity plus reduced torching and crowning indices).

Snagfall Rates

About 8% of 343 infested stems fell within 5 years of infestation, including three that were estimated to fall 2.5 years after infestation (Figure 8). About 5% of the beetle-killed stems were still standing during the 2012 surveys; these were infested 17–20 years earlier. Larger diameter trees tended to fall later than smaller trees. For infested stems <50 cm dbh, the 50th percentile stem fell 9.5–10 years postinfestation, whereas the 50th percentile stem >50 cm dbh fell about 12 years postinfestation. Most of the snags still standing during the 2012 surveys were >50 cm dbh.

Discussion

Stand Structure and Fuel Loads

Bark beetle infestations modified stand structure and surface fuels in old-stage ponderosa pine plots (i.e., 15–20 years postinfestation) consistent with previous descriptions. *Dendroctonus* spp. generally infest larger diameter trees, reducing BA and QMD (Hansen

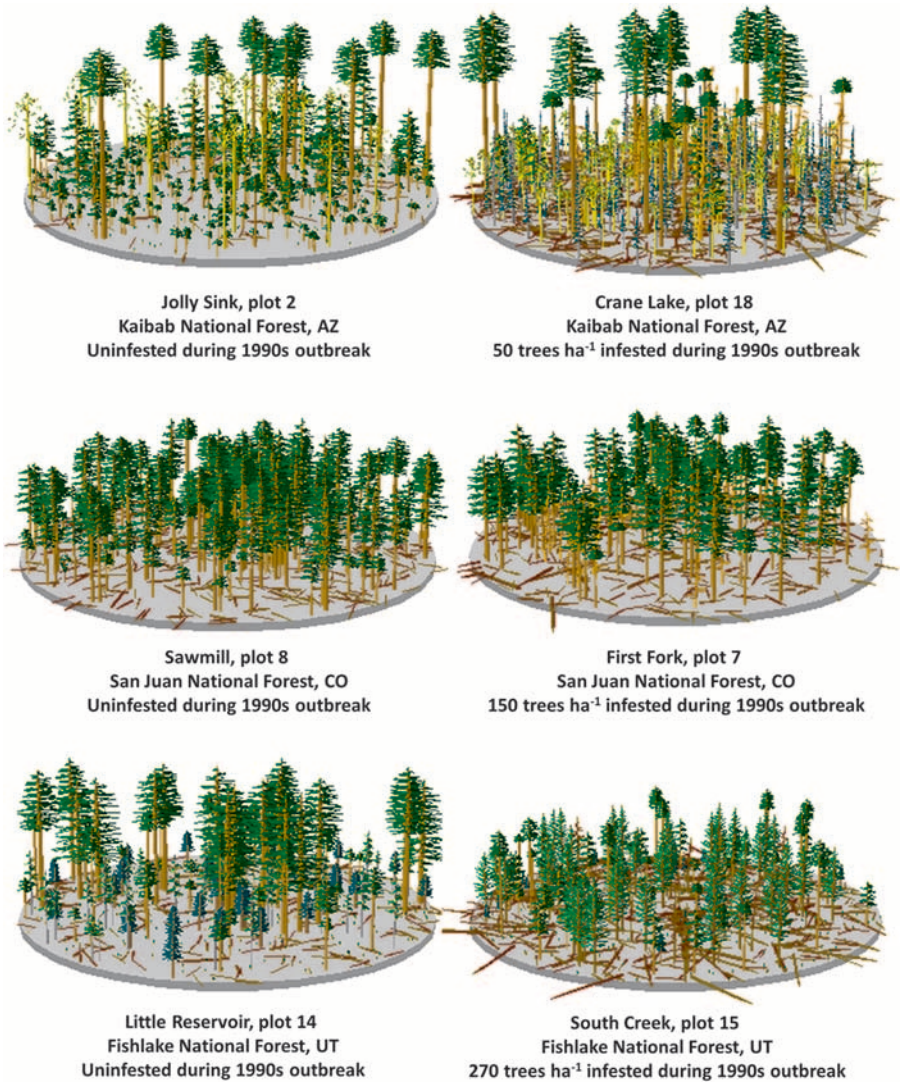

Figure 4. FVS-Stand Visualization System depictions of 2012 stand conditions at three undisturbed plots (left column) and three plots with varying amounts of trees infested during the 1990s outbreak (right column). Out of 321 plots, these were selected to best represent "typical" conditions based on least squares differences comparing plot parameters (e.g., preoutbreak stem density, ponderosa pine BA, QMD, and others) to median values from the population of 321 plots.

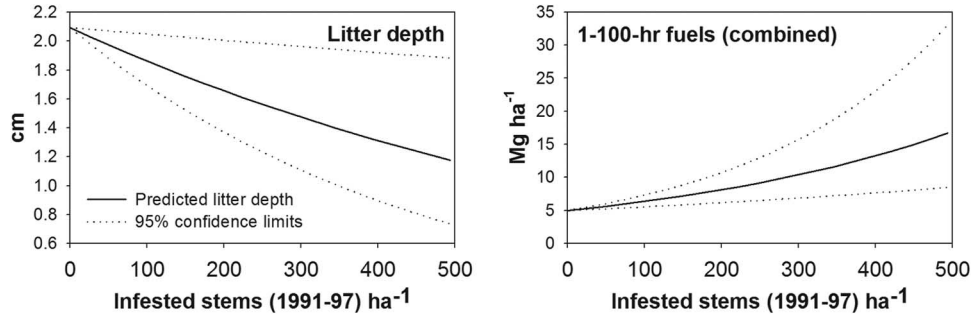

Figure 5. Predicted litter depth and combined 1-, 10-, and 100-hour surface fuel loads 15–20 years postoutbreak as a function of bark beetle infestation severity. These traces were created by using the equations given in Appendix B. Covariate values for the equations are the median values in our data set (Appendix D). All graphs were produced by holding the covariates constant while varying the infestation severity, i.e., stems killed during the 1990s outbreak. Changing the covariate values modifies the scale, but not the character, of the relationships between the response and explanatory variables. Note that the 95% confidence limits regard the parameter estimate for infestation severity.

2014), and this effect was observed among our plots (Figure 3). Interestingly, live tree density (stems ≥7.6 cm dbh) was increased as a function of infestation severity, suggesting that ingrowth (stems <7.6 cm dbh in the original surveys that exceeded that threshold in later surveys) more than replaced the density of the infested trees. Seedling density also increased as a function of infestation severity, a result of recruitment into canopy gaps. The lowered CBHs as a function of infestation severity reflect seedling recruitment as well as

Table 2. Fuel loads by size class as a function of infested trees per ha.

Fuel class	Fuel loads			
	Undisturbed	10th percentile (25 ha^{-1})	50th percentile (50 ha^{-1})	90th percentile (250 ha^{-1})
	(Mg ha^{-1})			
Litter	9.21	8.94	8.69	6.78
1-hr[a]	0.22	0.25	0.27	0.36
10-hr	1.97	2.08	2.17	3.22
100-hr	3.02	3.29	3.56	6.79
1,000-hr sound	10.71	12.34	14.18	43.68
1,000-hr rotten	6.34	6.85	7.41	13.78

These values were calculated using the equations given in Appendix B. Covariate values for the equations were the median values in our data set (Appendix D). Thus, we held the covariates constant while varying the infestation severity, i.e., stems or BA killed during the 1990s outbreak. Changing the covariate values modifies the scale but not the character of the relationships between the response and explanatory variables. Infested stem density percentile values were derived from our data set among plots with at least one infested stem.

[a]1-hour fuels calculated using infested ponderosa pine BA (1991–1997); 10th percentile, 15 m^2 ha^{-1}; 50th percentile, 6.9 m^2 ha^{-1}; 90th percentile, 23.6 m^2 ha^{-1}.

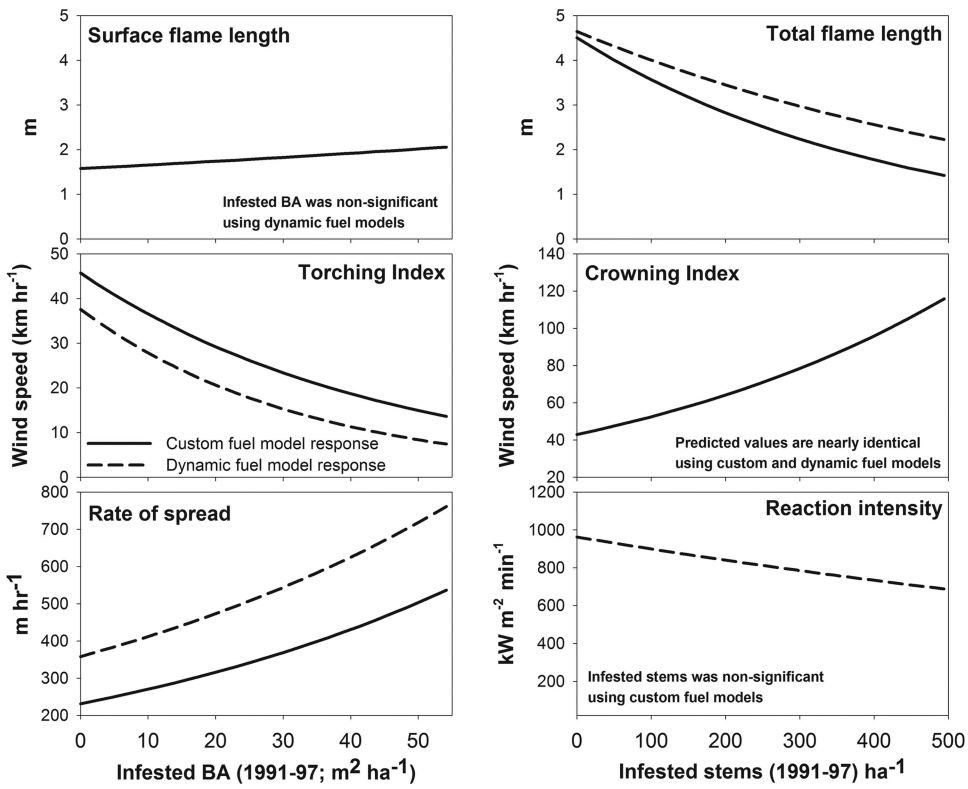

Figure 6. Predicted fire behavior of bark beetle-infested ponderosa pine type 15–20 years postoutbreak, using custom or dynamically selected fuel models, as a function of infestation severity. These traces were created by using the equations given in Appendix C. Covariate values for the equations are the median values in our data set (Appendix D). All graphs were produced by holding the covariates constant while varying the infestation severity, i.e., stems or BA killed during the 1990s outbreak. Changing the covariate values modifies the scale, but not the character, of the relationships between the response and explanatory variables. Note that the relationship for surface flame length was marginally significant using custom fuel models ($F_{1,\ 306.4} = 3.37$, $P = 0.0672$) and nonsignificant using dynamically selected fuel models.

the growth of advance regeneration released by the bark beetle-caused deaths of canopy trees and suggest increased torching hazard. The infestation-related decreases in CBD and canopy cover reflect the loss of high-volume crowns associated with host size classes preferred by bark beetles. These responses in CBH and CBD are aligned with expectations based on previous observations in lodgepole pine (Jenkins et al. 2008, Hicke et al. 2012) and suggest reduced crown fire hazard in old-stage stands. Because the median interval from bark beetle infestation to snagfall was ~10 years, snag density in 2012 was not related to stems or BA killed between 1991 and 1997. Snag density *was* related to infestation severity, however, during the 6-year interval before the 2012 measurements.

Surface fuels in the old-stage plots were also modified. Litter depth and litter loads were reduced as a function of infestation severity (Figure 5; Table 2). This was expected because, although there may be a pulse of litterfall in the immediate aftermath of an infestation (<5 years) (Page and Jenkins 2007b, Simard et al. 2011, Hoffman et al. 2012), this material typically decomposes quickly (Simard et al. 2012, Hansen 2014). Moreover, ongoing litterfall is reduced in old-stage stands because of a reduction in live crown

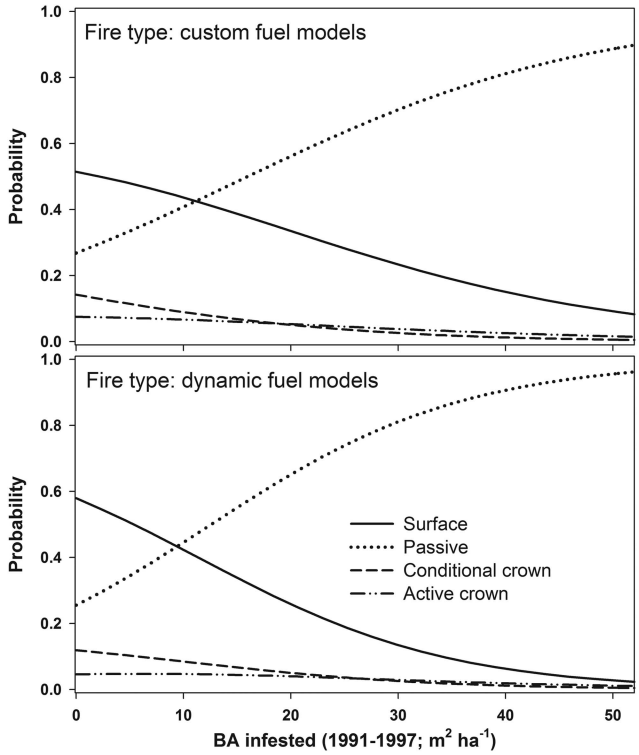

Figure 7. Predicted fire type 15–20 years postoutbreak as a function of infestation severity. Predictions are from FFE-FVS simulations, using custom and dynamically selected fuel models, based on "severe" weather and fuel conditions (see Methods). The parameter estimates for conditional and active crown fires were not significant in multinomial logistic regression models, indicating that these fire types are not influenced by infestation severity for these weather and fuel moisture conditions. Traces were created by using the equations given by a multinomial logistic regression model (not shown). Covariate values for the equations are the median values in our data set (Appendix D). All graphs were produced by holding the covariates constant while varying BA killed during the 1990s outbreak.

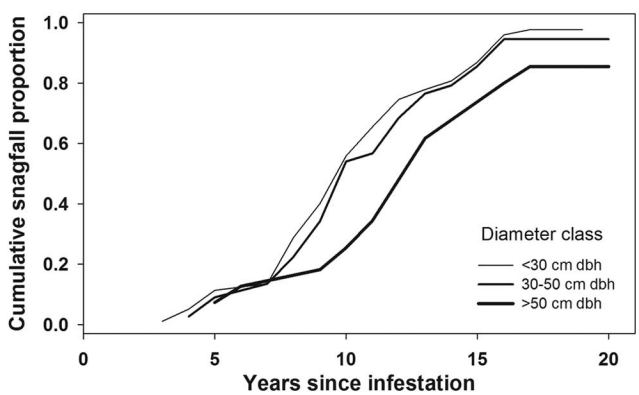

Figure 8. Cumulative proportions of snagfall (relative to total infested stems), by diameter class, as a function of years since bark beetle infestation (<30 cm dbh, *n* = 177; 30–50 cm dbh, *n* = 111; >50 cm dbh, *n* = 55).

volume, and recovery may take decades (Hansen 2014). For example, Simard et al. (2011) measured a 36-year postoutbreak chronosequence in lodgepole pine of the Greater Yellowstone area and found, relative to uninfested stands, litter depth increases of 60% in red-stage stands and declines of 45–50% between 2 and 35 years postoutbreak. In contrast, litter loads in Utah lodgepole pine stands measured ~20 years postoutbreak were not significantly different from those in uninfested stands (Page and Jenkins 2007b), possibly due to accelerated growth of residual trees and resulting litterfall (Hansen 2014).

Although litter loads were reduced as a function of infestation severity in our old-stage plots, loads of all size classes of woody fuels increased with infestation severity, with greater differences among increasing material size classes. Assuming 250 infested stems ha^{-1} and median values for covariates, our generalized linear mixed models predict that loads of 1-, 10-, 100-, and 1,000-hour fuels will be increased by 54, 62, 224, and 407%, respectively, compared with those for uninfested stands (using the equations in Appendix B and covariate values in Appendix D; Table 2). These results are comparable to those from other investigators although direct comparisons among studies are confounded by differences in preoutbreak stand conditions, infestation severity, host species, and climate. Page and Jenkins (2007a), for example, found significant differences among larger fuel classes in old-stage (~20 years postoutbreak) lodgepole pine with increases of 124, 112, and 679%, respectively for 10-, 100-, and 1,000-hour fuels, and Simard et al. (2011) found that 1,000-hour fuel loads tripled by 35 years postoutbreak compared with those in red-stage stands, although 1- and 10-hour fuels decreased by that time. The only published ponderosa pine data are from gray-stage (5 years postoutbreak) stands (Hoffman et al. 2012), and comparisons to our results are further confounded in that those stands were infested by *Ips* spp., which attack smaller diameter trees that are subsequently prone to relatively rapid snagfall. Nevertheless, beetle-infested stands had significantly greater surface woody fuel loads among all size classes, especially 1,000-hour fuels (Hoffman et al. 2012).

Increases in 1,000-hour fuels in old-stage stands have consequences beyond changes in potential fire behavior. Although there are ecological benefits to CWD, these fuels may cause substantial soil heating during fires (Brown et al. 2003). Moreover, decayed wood is a receptive bed for spot fires, and CWD creates challenges in accessing remote fires as well as increased difficulty in constructing and holding firelines (Page et al. 2013). Firefighter safety may also be compromised by weakened snags, reduced availability of escape routes, and the need for larger safety zones.

Another important factor regarding the impact of bark beetles on fuels is the spatiotemporal variability in beetle-caused mortality. Notably, the density of beetle-killed trees decreases as a function of increasing spatial scales (Hansen 2014). For example, Klenner and Arsenault (2009) measured ponderosa pine stands in British Columbia with mortality rates as high as 95% among stems >30 cm dbh yet only ~1% of three forest districts were classified as having >50% mortality. This pattern is captured in data from our plots purposely located in the vicinity of beetle activity. For example, the two most heavily infested sites averaged 133 and 178 infested trees ha^{-1} but with considerable plot-to-plot variance, ranging from 25 to 790 infested trees ha^{-1} in one site and from 74 to 494 infested trees ha^{-1} in the other (both sites were salvage logged after the 1995–1996 surveys and were not included in our 2012 analyses). That is, the influence of bark beetle-caused tree mortality greatly varies even within a stand. Therefore, we expect beetle-influenced fuel loads and fire behavior to vary even at the *substand* scale for the ponderosa pine type we surveyed.

Simulated Fire Behavior

FFE-FVS-simulated fire behavior in old-stage stands as a function of infestation severity generally follows expectations, given the above observed changes in fuel profiles. Surface flame length was increased (custom fuel models) or not affected (dynamically selected fuel models) by increasing infestation severity (Figure 6). Although combined 1-, 10-, and 100-hour fuel classes increased with infestation severity, this was offset by decreased litter loads (Figure 5), and litter is a primary carrier of fire among many fuel models (Scott and Burgan 2005). Total flame length had an inverse relationship with infestation severity using either fuel model selection method. This reflects the reduced crown fire hazard as a function of diminished CBD with the beetle-caused loss of live overstory trees.

The FFE-FVS simulations indicated that torching index was reduced (i.e., increased crown fire hazard) as infestation severity increased due to lower canopy base heights in the old-stage plots where overstory pines were removed and saplings and seedlings increased. Similar model prediction was found in old-stage Greater Yellowstone Area lodgepole pine where increased saplings created ladder fuels, allowing some stands to experience torching in the absence of wind (Simard et al. 2011). This phenomenon is less likely, however, among our ponderosa pine sites because recruitment was less dense compared with that of old-stage lodgepole pine stands. That is, our infested plots averaged <100 ponderosa pine saplings per ha compared with 1,000–4,000 lodgepole pine saplings per ha among old-stage stands elsewhere in the Rocky Mountains (Simard et al. 2011, Hansen 2014). Crowning index was predicted to increase with increasing infestation severity, concomitant with decreasing canopy bulk density. Rate of spread was also predicted to increase as a function of infestation severity. With increasing infestation severity, the simulations predicted increasing probability of passive fire in old-stage stands commensurate with declining probability of surface fire (Figure 7). These old-stage changes in fire behavior are generally in alignment with the predictions for lodgepole pine outlined by Page and Jenkins (2007b), Jenkins et al. (2008), Simard et al. (2011), and Hicke et al. (2012). Modeling by Page and Jenkins (2007b) indicated that rate of spread was mostly affected by the increased midflame wind speeds, due to loss of canopy sheltering. Associated drying of surface fuels had a minimal effect on rate of spread, and changes in surface fuel loads did not modify rate of spread. We did not examine FFE-FVS behavior to gauge the relative importance of midflame wind speeds and fuel loads on rates of spread.

The fire behavior parameter from our study that contrasts results from other studies is reaction intensity, a measure of the energy released by combustion per unit area per unit time. Our FFE-FVS results, using dynamically selected but not custom fuel models (Figure 6), indicate declining heat release with increasing infestation severity, apparently driven more by declining litter loads than increasing woody fuel loads. Modeling by Page and Jenkins (2007b) and Schoennagel et al. (2012), however, found significantly greater fireline intensities[2] among old-stage lodgepole pine stands than among uninfested stands. The reason for this difference is that FFE-FVS does not include 1,000-hour fuels (the most substantially modified fuel class among old-stage stands) in its algorithms (Rebain 2010). Page and Jenkins (2007b) and Schoennagel et al. (2012), however, explicitly included these fuels by using a hybrid of BehavePlus and the First Order Fire Effects Model; the latter is intended for prediction of secondary fire effects such as tree mortality, fuel consumption, and soil heating (Lutes 2013). Page and Jenkins' (2007b) simulations indicated that fires in old-stage stands released twice the heat of uninfested stands, which reduced torching indices in the former. Nevertheless, active crown fire hazard was reduced (i.e., increased crowning index) in old-stage stands because of reduced CBD and enlarged canopy gaps. Schoennagel et al.'s (2012) modeling, wherein the litter depth of old-stage stands did not significantly differ from those of uninfested stands, indicated that increased 1,000-hour fuels in old-stage stands will increase fireline intensity to such a magnitude that active crown fire hazard also increased despite the reduction in CBD. Consider, however, that fuel moisture in 1,000-hour fuels (by definition, slow to change) will substantially affect the contribution of these fuels to fire severity (Jenkins et al. 2008).

The issue of 1,000-hour fuel exclusion is not unique to FFE-FVS. All of the most commonly used US operational fire behavior models (e.g., BehavePlus, NEXUS, FFE-FVS, FlamMap, FSim, FETM, and FARSITE) are based on the surface fire behavior and crown fire initiation models of Rothermel (1972) and Van Wagner (1977) that do not include 1,000-hour fuels in their parameter calculations (Jenkins et al. 2012, Schoennagel et al. 2012). Depending on fire duration, these fuels are thought to increase the potential for crown fire initiation (i.e., torching), contribute to fire severity, increase smoke production, and affect soil heating (Brown et al. 2003, Jenkins et al. 2008, Hoffman et al. 2013). In our opinion, however, the alternative modeling methods of Page and Jenkins (2007b) and Schoennagel et al. (2012) are unconventional and difficult to replicate. Moreover, it is uncertain to what degree, if any, such approaches may improve simulations. For example, assuming that litter loads drive a surface fire and that these fine fuels are relatively reduced among old-stage stands (Table 2; Figure 5), the duration of the flaming front may be insufficient to ignite the larger surface fuels, depending on fuel moistures. Even if ignited, beetle-caused loads of 1,000-hour fuels will probably contribute to localized, intense fire behavior but not necessarily active crown fire (Page et al. 2013).

In addition to the modeling problems associated with foliar moisture content of red-stage stands, predictions for bark beetle-impacted stands of all stages are limited by assumptions of the Rothermel (1972) rate-of-spread equation as well as the crown fire transition and propagation equations of Van Wagner (1977) and Scott and Reinhardt (2001). These equations are the basis of all fire simulation models, including FFE-FVS and BehavePlus, and predictions from these models will be limited by the assumptions of the underlying equations, which are dubious even under ideal conditions (Cruz and Alexander 2010). These assumptions may be further stretched when applied to stands, beetle-affected or otherwise, which are spatially and temporally variable with respect to surviving, killed, and recruited trees (Jenkins et al. 2012, Hoffman et al. 2013, Page et al. 2014). Spatial heterogeneity of aerial fuels (i.e., trees), however, may decrease active and passive crown fire propagation, which suggests that operational model results may be conservative when applied to beetle-impacted stands (Simard et al. 2012). Regardless, operational fire simulation models are the only way to estimate potential fire behavior. These models are simplifications of complex systems and, thus, have inherent limitations (Cruz and Alexander 2010). Nevertheless, these models represent the best, currently available science for understanding the effects of fuel modifications on fire behavior. Managers and researchers recognize the limitations of the models but have also gained an understanding of

model robustness and are comfortable interpreting simulation output. Simulation models such as FFE-FVS are the best decision support tools for informing managers of the potential consequences of fuelbed changes after natural disturbances (e.g., blowdown and bark beetle infestation) and fuel management operations (fuel treatments and prescribed fire). Physics-based models may eventually address the deficiencies of operational models, but these have had limited field validation (Jenkins et al. 2014, Page et al. 2014), require highly detailed input data, and are computationally intensive. Our use of FFE-FVS was intended to show the potential fire behavior consequences in beetle-infested stands, contrasting differences among undisturbed ponderosa pine stands and old-stage stands with varying outbreak severities. We advise the reader to consider *relative*, rather than absolute, differences in simulated fire behavior as a function of beetle-caused mortality levels.

Postoutbreak, postfire empirical data are best suited for assessing bark beetle-related effects on fire severity. Such data have been collected for red- and gray-stage, but not old-stage, lodgepole pine type in the northern US Rocky Mountains (Harvey et al. 2014). Weather and topography were found to be the most important factors explaining fire severity (defined with field measures such as char height and bole scorch), whereas bark beetle outbreak severity was not correlated with most fire severity metrics, especially under moderate fire weather conditions. Under extreme weather conditions, gray-stage stands (most beetle-infested snags still standing) did indicate a positive, significant correlation between outbreak severity and fire severity for four of eight fire severity metrics (Harvey et al. 2014). The effect of gray- and old-stage infested lodgepole pine stands on fire *occurrence* was investigated after the 1988 Yellowstone National Park wildfires (Lynch et al. 2006). Although weather and aspect were found to be the primary factors driving the burn pattern, old-stage stands were found to be 11% more likely to burn than uninfested stands; gray-stage stands were not correlated with the burn pattern. That is, old-stage fuel profiles significantly influenced fire behavior but not to a substantial degree.

Snagfall Rates

We found that the median interval from infestation to snagfall was 10 years.[3] The interval was dependent on diameter with larger trees remaining standing for longer intervals (Figure 8), presumably because of additional decay-resistant heartwood (Chambers and Mast 2014). The infested pines in our plots were killed by *Dendroctonus* species between 1991 and 1997 and ~5% of 343 infested trees remained standing in 2012; most of these were >50 cm dbh. In comparison, Hoffman et al. (2012) reported that 48% of bark beetle-infested ponderosa pine had fallen by 5 years postoutbreak in an Arizona study, although the majority of the trees were killed by *Ips* species, which often attack smaller diameter trees. Elsewhere in Arizona, Chambers and Mast (2014) found that 99% of *Ips*-infested pines remained standing after 3 years, but ~80% had fallen by 7 years after infestation with smaller diameter trees among the factors affecting snagfall rate. Our results are similar to results of other studies that examined snagfall rates of ponderosa pine killed by *Dendroctonus* species, including in Colorado (Schmid et al. 1985), northeast California (Landram et al. 2002), and northern California and southern Oregon (Keen 1955). In general, the snagfall rate is negligible the first 5 years and then rapid 5–15 years postoutbreak with slower rates in larger trees.

Summary

We found that bark beetle infestations in old-stage ponderosa pine plots modified stand structure similar to previous descriptions for ponderosa and lodgepole pine (Hansen 2014). Pine BA, QMD, and CBD were reduced, reflecting the loss of large-diameter host trees. CBH was lower among infested plots after the loss of large host trees combined with recruitment of seedlings and growth of surviving secondary stand structure. Likewise, surface fuel loads were modified in ways previously described or proposed for old-stage lodgepole pine stands (Page and Jenkins 2007b, Jenkins et al. 2008, Simard et al. 2011, Hicke et al. 2012). Woody fuel loads were greatly increased, especially in the 1,000-hour class, whereas litter loads were reduced due to decomposition of needles from the killed trees combined with reduced litterfall from the surviving secondary stand structure.

These beetle-caused changes in the fuel profile of old-stage ponderosa pine affected many aspects of FFE-FVS simulated fire behavior similar to that described for old-stage lodgepole pine (Page and Jenkins 2007a, Jenkins et al. 2008, Simard et al. 2011, Hicke et al. 2012). Surface flame length (using custom fuel models), torching potential, and rate of spread were all increased as a function of infestation severity, whereas the probability of active crown fire was decreased. In contrast with two previous lodgepole pine studies (Page and Jenkins 2007a, Schoennagel et al. 2012), however, our simulations in old-stage ponderosa pine predict declining heat release with increasing infestation severity (using dynamically selected, but not custom, fuel models). Fire behavior models based on Rothermel's equations, including FFE-FVS, exclude 1,000-hour fuels, which will greatly influence total energy released by combustion. Excluding or including this fuel type can significantly influence predictions of torching potential, depending on whether the surface fire is of sufficient duration to ignite these fuels. Conflicting simulation results suggest opportunities for further research and development of fire behavior models appropriate for beetle-influenced stands. Such models need to address the heightened flammability and ignitibility of red-stage stands, the spatial and temporal variability of bark beetle-influenced fuels, and the contribution of 1,000-hour fuels to fire spread and torching.

Although the relative influence of bark beetle-caused tree mortality on fuel characteristics of old-stage stands may be less important than other factors affecting fire behavior and occurrence such as past disturbance, stand structure, topography, weather, and vegetation type (Hicke et al. 2012, Harvey et al. 2014), our data show that the impacts are significant. We expect that old-stage ponderosa pine stands will burn differently than uninfested stands with some fire behavior parameters becoming more severe due to heightened within-canopy wind speeds, lowered CBHs, and heavy loads of downed woody material. We expect other types of fire behavior to be moderated due to reduced litter loads, lowered CBD, and widened canopy gaps. Spatiotemporal variability of tree mortality due to bark beetles, which can be substantial even at the substand scale, should be considered when assessing potential modifications to fuel complexes and fire behavior. Because bark beetle-killed tree density (i.e., infested trees per unit area) decreases with increasing spatial scales, for example, the influence of bark beetles on fuels and fire behavior at the landscape scale should decline relative to effects at the stand scale.

Endnotes

1. See www.fs.usda.gov/detail/r1/forest-grasslandhealth/?cid=stelprdb5410518 for more information.
2. "Reaction intensity" and "fireline intensity" are not directly comparable but trends can be compared.
3. Using the default snagfall rate in FFE-FVS results in ~50%, by biomass, snagfall after 8 years, we found that invoking the SNAGFALL keyword and setting the rate-of-fall correction factor to 0.8 for ponderosa pine would result in ~50% snagfall after 10 years. Note that the MPB extension in FVS can be used for lodgepole but not ponderosa pine.

Literature Cited

ALBINI, F.A. 1976. *Estimating wildfire behavior and effects.* USDA For. Serv., Gen. Tech. Rep. INT-GTR-30, Intermountain Forest and Range Experiment Station, Ogden, UT. 92 p.

BIVAND, R. 2002. Spatial econometric functions in R: Classes and methods. *J. Geog. Syst.* 4:405–421.

BRADSHAW, L.S., AND E. MCCORMICK. 2000. *FireFamily Plus user's guide.* Available online at http://firelab.org/sites/default/files/images/downloads/FFP-4_1_Draft_Users_Guide_0.pdf; last accessed Dec. 30, 2014.

BROWN, J.K. 1971. A planar intersect method for sampling fuel volume and surface area. *For. Sci.* 17:96–102.

BROWN, J.K., E.D. REINHARDT, AND K.A. KRAMER. 2003. *Coarse woody debris: Managing benefits and fire hazard in the recovering forest.* USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-10, Rocky Mountain Research Station, Fort Collins, CO. 20 p.

CHAMBERS, C.L., AND J.N. MAST. 2014. Snag dynamics and cavity excavation after bark beetle outbreaks in southwestern ponderosa pine forests. *For. Sci.* 60(4):713–723.

CHOJNACKY, D.C., B.J. BENTZ, AND J.A. LOGAN. 2000. *Mountain pine beetle attack in ponderosa pine: Comparing methods for rating susceptibility.* USDA For. Serv., Rep. RMRS-RP-26, Rocky Mountain Research Station, Fort Collins, CO. 10 p.

CRUZ, M.G., AND M.E. ALEXANDER. 2010. Assessing crown fire potential in coniferous forests of western North America: A critique of current approaches and recent simulation studies. *Int. J. Wildl. Fire* 19: 377–398.

DIXON, G.E. 2002. *Essential FVS: A user's guide to the Forest Vegetation Simulator.* USDA For. Serv., Intern. Rep., Forest Management Service Center, Fort Collins, CO. 219 p.

GARZA, C.A. 2015. *Modeling endemic bark beetle populations in southwestern ponderosa pine*. Texas A&M University, Master's thesis, College Station, TX. 98 p.

HANSEN, E.M. 2014. Forest development and carbon dynamics following mountain pine beetle outbreaks. *For. Sci.* 60(3):476–488.

HARVEY, B.J., D.C. DONATO, AND M.G. TURNER. 2014. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. *Proc. Natl. Acad. Sci. USA* 111(42):15120–15125.

HICKE, J.A., M.C. JOHNSON, J.L. HAYES, AND H.K. PREISLER. 2012. Effects of bark beetle-caused tree mortality on wildfire. *For. Ecol. Manage.* 271:81–90.

HOFFMAN, C.M., P. MORGAN, W. MELL, R. PARSONS, E. STRAND, AND S. COOK. 2013. Surface fire intensity influences simulated crown fire behavior in lodgepole pine forests with recent mountain pine beetle-caused tree mortality. *For. Sci.* 59(4):390–399.

HOFFMAN, C.M., C. HULL SIEG, J.D. MCMILLIN, AND P.Z. FULÉ. 2012. Fuel loadings 5 years after a bark beetle outbreak in south-western USA ponderosa pine forests. *Int. J. Wildl. Fire* 21(3):306–312.

JENKINS, M.J., E. HEBERTSON, W.G. PAGE, AND C.A. JORGENSEN. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *For. Ecol. Manage.* 254:16–34.

JENKINS, M.J., W.G. PAGE, E.G. HEBERTSON, AND M.E. ALEXANDER. 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in Western North America and implications for fire management. *For. Ecol. Manage.* 275:23–34.

JENKINS, M.J., J.B. RUNYON, C.J. FETTIG, W.G. PAGE, AND B.J. BENTZ. 2014. Interactions among the mountain pine beetle, fires, and fuels. *For. Sci.* 60(3):489–501.

JOHNSON, M.C., M.C. KENNEDY, AND D.L. PETERSON. 2011. Simulating fuel treatment effects in dry forests of the western United States: Testing the principles of a fire-safe forest. *Can. J. For. Res.* 41(5):1018–1030.

JOLLY, W.M., R. PARSONS, J.M. VARNER, B.W. BUTLER, K.C. RYAN, AND C.L. GUCKER. 2012. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Comment. *Ecology* 93:941–946.

KEEN, F.P. 1943. Ponderosa pine tree classes redefined. *J. For.* 41(4): 249–253.

KEEN, F.P. 1955. The rate of natural falling of beetle-killed ponderosa pine snags. *J. For.* 53:720–723.

KEYSER, C.E., AND G.E. DIXON. 2008. *Utah (UT) variant overview—Forest Vegetation Simulator.* USDA For. Serv., Intern. Rep., Forest Management Service Center, Fort Collins, CO. 45 p.

KLENNER, W., AND A. ARSENAULT. 2009. Ponderosa pine mortality during a severe bark beetle (Coleoptera: Curculionidae, Scolytinae) outbreak in southern British Columbia and implications for wildlife habitat management. *For. Ecol. Manage.* 258:S5–S14.

KLUTSCH, J.G., M.A. BATTAGLIA, D.R. WEST, S.L. COSTELLO, AND J.F. NEGRÓN. 2011. Evaluating potential fire behavior in lodgepole pine dominated forests after a mountain pine beetle epidemic in north-central Colorado. *West. J. Appl. For.* 26:101–109.

KLUTSCH, J.G., J.F. NEGRÓN, S.L. COSTELLO, C.C. RHOADES, D.R. WEST, J. POPP, AND R. CAISSIE. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *For. Ecol. Manage.* 258:641–649.

LANDRAM, F.M., W.F. LAUDENSLAYER JR., AND T. ATZET. 2002. Demography of snags in eastside pine forests of California. P. 605–620 in *Proc. of the Ecology and management of dead wood in western forests, 1999 November 2–4, Reno, NV*, Laudenslayer, W.F. Jr., P.J. Shea, B.E. Valentine, C.P. Weatherspoon, and T.E. Lisle (tech. coords.). USDA For. Serv., Gen. Tech. Rep. PSW-GTR-181, Pacific Southwest Research Station, Berkeley, CA.

LITTELL, R.C., G.A. MILLIKEN, W.W. STROUP, R.D. WOLFINGER, AND O. SCHABENBERGER. 2006. *SAS system for mixed models*, 2nd ed. SAS Institute, Inc., Cary, NC. 814 p.

LUTES, D.C. 2013. *FOFEM 6.0 user guide.* Available online at http://firelab.org/sites/default/files/images/downloads/FOFEM6_Help_May12014.pdf; last accessed Dec. 30, 2014.

LUTES, D.C., R.E. KEANE, J.F. CARATTI, C.H. KEY, N.C. BENSON, S. SUTHERLAND, AND L.J. GANGI. 2006. *FIREMON: The Fire Effects Monitoring and Inventory System.* USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-164-CD, Rocky Mountain Research Station, Fort Collins, CO. 1 CD.

LYNCH, H.J., R.A. RENKIN, R.L. CRABTREE, AND P.R. MOORCROFT. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. *Ecosystems* 9: 1318–1327.

MORAN, C.J., AND M.A. COCHRANE. 2012. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Comment. *Ecology* 93:939–941.

NOONAN-WRIGHT, E.K., N.M. VAILLANT, AND A.L. REINER. 2013. The effectiveness and limitations of fuel modeling using the Fire and Fuels Extension to the Forest Vegetation Simulator. *For. Sci.* 60(2):231–240.

PAGE, W.G., M.E. ALEXANDER, AND M.J. JENKINS. 2013. Wildfire's resistance to control in mountain pine beetle-attacked lodgepole pine forests. *For. Chron.* 89(6):783–794.

Page, W.G., and M.J. Jenkins. 2007a. Predicted fire behavior in selected mountain pine beetle infested lodgepole pine. *For. Sci.* 53:662–674.

Page, W.G., and M.J. Jenkins. 2007b. Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the Intermountain Region. *For. Sci.* 53:507–518.

Page, W.G., M.J. Jenkins, and J.B. Runyon. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. *Can. J. For. Res.* 42:1631–1647.

Page, W.G., M.J. Jenkins, and M.E. Alexander. 2014. Crown fire potential in lodgepole pine forests during the red stage of mountain pine beetle attack. *Forestry* 87(3):347–361.

Rebain, S.A. (comp.). 2010. *The fire and fuels extension to the forest vegetation simulator: Updated model documentation.* USDA For. Serv., Intern. Rep., Forest Management Service Center, Fort Collins, CO. 409 p. Available online at www.fs.fed.us/fmsc/ftp/fvs/docs/gtr/FFEguide.pdf; last accessed Apr. 17, 2014.

Reinhardt, E.D., and N.L. Crookston (tech. eds.). 2003. *The Fire and Fuels Extension to the Forest Vegetation Simulator.* USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-116, Rocky Mountain Research Station, Fort Collins, CO. 209 p.

Rothermel, R.C. 1972. *A mathematical model for predicting fire spread in wildland fuels.* USDA For. Serv., Res. Pap. INT-RP-115, Intermountain Forest and Range Experiment Station, Ogden, UT. 40 p.

Schmid, J.M., S.A. Mata, and W.F. McCambridge. 1985. *Natural falling of beetle-killed ponderosa pine*, vol. 454. USDA For. Serv., Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 3 p.

Schoennagel, T., T.T. Veblen, J.F. Negrón, and J.M. Smith. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. *PLoS One* 7:e30002.

Scott, J.H., and R.E. Burgan. 2005. *Standard fire behavior fuel models: A comprehensive set for use with Rothermel's surface fire spread model.* USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-153, Rocky Mountain Research Station, Fort Collins, CO. 72 p.

Scott, J., and E.D. Reinhardt. 2001. *Assessing crown fire potential by linking models of surface and crown fire behavior.* USDA For. Serv., Res. Pap. RMRS-RP-29, Rocky Mountain Research Station, Fort Collins, CO. 59 p.

Simard, M., W.H. Romme, J.M. Griffin, and M.G. Turner. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Reply. *Ecol. Monogr.* 81:3–24.

Simard, M., W.H. Romme, J.M. Griffin, and M.G. Turner. 2012. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecology* 93:946–950.

USDA Forest Service. 1996. *Forest insect and disease conditions in the United States 1995.* Forest Health Protection, Washington, DC. 83 p.

Van Wagner, C.E. 1977. Conditions for the start and spread of crown fire. *Can. J. For. Res.* 7:23–34.

Appendices
Appendix A: Site Characteristics

Site name (no. of plots sampled)	Live PP BA (m^2 ha^{-1})	PP QMD (cm)	Infested PP (ha^{-1})	Other species BA (m^2 ha^{-1})[a]	Surface fuels (Mg ha^{-1})[b]
Bryce Canyon National Park, Utah					
Dave's Hollow (10)	16.9 (10.4)	24.8 (8.5)	7.4 (11.9)	0.0	32.3 (24.7)
Fairyland (8)	12.1 (5.9)	30.1 (12.5)	9.3 (18.4)	0.0	23.3 (29.0)
Horse Corrals (8)	12.6 (7.3)	27.5 (9.3)	3.1 (8.7)	0.0	21.7 (9.2)
Paria View (5)	11.6 (9.1)	27.9 (8.3)	0.0	1.0 (1.3)	25.6 (17.8
Dixie National Forest, Utah					
Blue Spring Mountain (12)	16.1 (16.5)	22.2 (6.0)	103.0 (107.4)	15.7 (8.1)	96.3 (58.9)
Bowers Flat (13)	22.8 (12.9)	38.7 (30.6)	131.2 (168.9)	1.3 (2.7)	62.7 (26.9)
Cooper Knoll (7)	26.3 (5.9)	26.1 (3.0)	3.5 (9.3)	0.5 (0.8)	41.3 (17.8)
Rock Canyon (5)	11.6 (5.5)	41.4 (6.6)	0.0	0.0	25.2 (7.3)
Strawberry Knolls (7)	25.4 (11.3)	35.3 (5.2)	42.4 (101.6)	0.0	54.1 (32.7)
Strawberry Point (10)	12.9 (7.8)	31.0 (10.1)	12.4 (26.7)	14.7 (13.5)	63.3 (41.4)
The Pass (6)	21.5 (7.0)	31.1 (2.9)	0.0	8.1 (6.3)	63.3 (29.3)
Willis Creek (6)	12.6 (6.0)	26.2 (5.3)	16.5 (40.4)	17.6 (8.7)	56.8 (26.3)
Yellowjacket (10)	43.2 (9.2)	19.7 (1.5)	12.4 (21.0)	8.6 (4.5)	69.9 (23.6)
Fishlake National Forest, Utah					
Indian Creek (3)	29.7 (23.3)	53.2 (9.5)	8.2 (14.3)	1.4 (1.4)	14.0 (4.0)
Little Reservoir (6)	18.0 (8.2)	34.9 (5.4)	4.1 (10.1)	5.7 (10.4)	52.3 (48.4)
South Creek (15)	11.4 (7.7)	26.7 (8.9)	95.5 (115.5)	9.5 (8.6)	111 (23.8)
Manti-La Sal National Forest, Utah					
Butts Canyon No. 1 (7)	34.9 (7.9)	39.6 (5.0)	24.7 (62.4)	0.1 (0.2)	54.0 (23.4)
Butts Canyon No. 2 (10)	26.1 (8.0)	43.2 (4.3)	17.3 (23.4)	0.0 (0.1)	47.6 (20.6)
Corrals (6)	31.0 (19.3)	38.6 (9.8)	12.4 (30.2)	0.0	21.2 (11.2)
Kigalia (8)	16.6 (12.4)	34.9 (9.2)	9.3 (18.4)	9.7 (7.0)	80.0 (88.9)
Peavine (8)	16.2 (11.4)	45.8 (18.1)	9.3 (12.8)	0.3 (0.4)	50.0 (48.0)
Twin Springs (5)	29.3 (6.9)	32.5 (4.8)	0.0	0.0	60.7 (35.8)
Grand Canyon National Park, Arizona					
Basin No. 1 (8)	24.2 (10.9)	49.9 (15.5)	21.6 (40.6)	10.0 (12.2)	76.7 (27.3)
Basin No. 2 (15)	24.5 (20.1)	71.7 (107.0)	14.8 (20.5)	13.2 (9.2)	72.5 (33.8)
Robber's Roost (15)	19.5 (13.5)	87.4 (100.0)	26.4 (35.5)	17.4 (10.3)	112 (51.1)
Kaibab National Forest, Arizona					
Crane Lake West (7)	18.1 (4.8)	30.8 (10.1)	10.6 (19.4)	8.0 (10.9)	53.6 (35.8)
Crane Lake (8)	14.2 (16.2)	30.4 (15.5)	18.5 (25.6)	8.4 (7.3)	76.3 (25.5)
Dog Lake (6)	12.2 (8.0)	50.1 (10.0)	8.2 (20.2)	39.5 (11.6)	76.5 (33.1)
Jolly Sink No. 1 (5)	29.2 (15.5)	34.7 (14.4)	0.0	0.6 (1.2)	33.0 (17.4)
Jolly Sink No. 2 (4)	21.0 (8.4)	59.1 (19.5)	0.0	1.5 (3.0)	36.3 (20.0)
Pleasant Valley (10)	23.7 (10.3)	23.3 (8.6)	51.9 (89.8)	5.9 (9.1)	80.8 (67.7)
Telephone Hill (8)	36.9 (23.8)	36.4 (12.8)	27.8 (59.7)	4.1 (6.5)	53.3 (43.5)
San Juan National Forest, Colorado					
Coffee Creek (10)	25.9 (12.1)	54.9 (9.7)	0.0	1.2 (1.2)	59.8 (31.0)
First Fork (11)	25.9 (7.8)	45.2 (7.9)	22.5 (44.8)	0.1 (0.1)	21.8 (14.2)
First Notch (8)	9.9 (4.1)	32.2 (4.8)	9.3 (12.8)	0.9 (1.2)	39.7 (23.7)
Horse Creek (2)	20.4 (19.7)	53.7 (18.2)	0.0	5.6 (3.8)	40.2 (20.8)
Sawmill (8)	29.9 (11.9)	32.8 (7.3)	0.0	1.1 (1.4)	36.1 (20.1)
Uncompahgre National Forest, Colorado					
Haley Draw No. 1 (7)	28.1 (14.4)	32.9 (8.5)	3.5 (9.3)	5.8 (14.3)	48.6 (25.6)
Haley Draw No. 2 (7)	25.1 (9.6)	38.2 (15.4)	38.8 (92.3)	3.0 (5.1)	69.8 (45.0)
Haley Draw No. 3 (7)	24.7 (10.0)	48.5 (11.6)	10.6 (19.4)	2.7 (1.6)	72.2 (35.5)

Values are means (SD); 2012 conditions. All BA values only include live stems.
[a]Nonpine species were white fir, subalpine fir, Douglas-fir, blue spruce, quaking aspen, juniper, and gambel oak.
[b]Surface fuels include litter, duff, and all downed woody materials.

Appendix B: Fuelbed Model Results and Parameter Estimates and Fit

Note: all models are log scale.

Total BA: 2012 (m^2 ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 311.1} = 119.58$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	2.5255	0.06295	18.48	40.12	<0.0001	2.3935	2.6575
Preoutbreak total BA	0.02820	0.001587	296.1	17.77	<0.0001	0.02508	0.03132
Preoutbreak conifer BA	−0.01244	0.003258	239	−3.82	0.0002	−0.01886	−0.00602
PP stems infested 1991–1997	−0.00355	0.000325	311.1	−10.94	<0.0001	−0.00419	−0.00291

Live BA, all species: 2012 (m^2 ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 308.2} = 152.27$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* Value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	2.2684	0.09328	58.91	24.32	<0.0001	2.0818	2.4551
Preoutbreak live PP BA	0.01174	0.003057	301.8	3.84	0.0002	0.005723	0.01776
Preoutbreak live BA	0.01408	0.003198	285	4.40	<0.0001	0.007788	0.02038
Time since fire	0.005619	0.001936	39.01	2.90	0.0061	0.001703	0.009534
Preoutbreak stems ≥7.6 cm	0.000209	0.000091	314.4	2.29	0.0225	0.000030	0.000389
PP stems infested 1991–1997	−0.00439	0.000356	308.2	−12.34	<0.0001	−0.00509	−0.00369

Live BA, ponderosa pine: 2012 (m^2 ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 308.9} = 141.33$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	1.9194	0.1174	72.98	16.35	<0.0001	1.6854	2.1533
Preoutbreak live BA	−0.01832	0.004460	248.4	−4.11	<0.0001	−0.02710	−0.00953
Preoutbreak live PP BA	0.05683	0.004324	275.3	13.14	<0.0001	0.04832	0.06534
Preoutbreak stems ≥7.6 cm	0.000275	0.000130	297.9	2.12	0.0349	0.000020	0.000531
Time since fire	0.005139	0.002325	42.99	2.21	0.0325	0.000450	0.009827
PP stems infested 1991–1997	−0.00612	0.000515	308.9	−11.89	<0.0001	−0.00713	−0.00511

Canopy base height: 2012 (m); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 301.7} = 9.49$, $P = 0.0023$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	4.5782	1.3468	24.88	3.40	0.0023	1.8038	7.3526
Preoutbreak live PP BA	0.01195	0.002739	306	4.36	<0.0001	0.006562	0.01734
Preoutbreak live PP stems	−0.00076	0.000169	310	−4.52	<0.0001	−0.00110	−0.00043
Preoutbreak gambel oak BA	−0.1962	0.03970	299.6	−4.94	<0.0001	−0.2743	−0.1181
Preoutbreak sapling density	−0.00014	0.000029	291.1	−4.69	<0.0001	−0.00020	−0.00008
Elevation	−0.00123	0.000542	24.68	−2.27	0.0320	−0.00235	−0.00011
PP BA infested 1991–1997	−0.01342	0.004354	301.7	−3.08	0.0023	−0.02198	−0.00485

Ponderosa pine QMD: 2012 (cm); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 309.6} = 18.33$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	2.6774	0.05912	42.58	45.29	<0.0001	2.5581	2.7967
Preoutbreak live PP QMD	0.02539	0.001528	129.7	16.62	<0.0001	0.02237	0.02842
PP BA infested 1991–1997	−0.01011	0.002362	309.6	−4.28	<0.0001	−0.01476	−0.00546

Live tree density ≥7.6 cm dbh: 2012 (ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 290.9} = 33.76$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	0.4334	1.3819	35.65	0.31	0.7557	−2.3703	3.2370
Preoutbreak stems ≥7.6 cm	0.000824	0.000120	308.5	6.85	<0.0001	0.000587	0.001061
Preoutbreak live PP stems	0.000677	0.000172	307.4	3.94	0.0001	0.000339	0.001015
Elevation	0.001935	0.000557	36.32	3.47	0.0013	0.000806	0.003064
PP stems infested 1991–1997	−0.00263	0.000453	290.9	−5.81	<0.0001	−0.00353	−0.00174

Seedling density: 2012 (<7.6 cm dbh and >1.5 m tall; ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 155.8} = 4.80$, $P = 0.0300$.

Parameter	Estimate	SE	*df*	*t* Value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	8.2077	0.1765	76.31	46.50	<0.0001	7.8562	8.5593
Preoutbreak live PP stems	−0.00107	0.000443	165.9	−2.42	0.0164	−0.00195	−0.00020
Preoutbreak seedling density	0.000063	8.209E−6	162.7	7.73	<0.0001	0.000047	0.000080
PP stems infested 1991–1997	0.002646	0.001208	155.8	2.19	0.0300	0.000260	0.005033

Canopy bulk density: 2012 (kg m^{-3}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 301.8} = 31.81$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	−3.7619	0.1754	22.37	−21.45	<0.0001	−4.1253	−3.3986
Preoutbreak live BA	0.01223	0.002485	307.3	4.92	<0.0001	0.007342	0.01712
Preoutbreak stems ≥7.6 cm	0.000696	0.000131	305.9	5.30	<0.0001	0.000437	0.000954
Preoutbreak hardwood BA	−0.01908	0.006971	304.3	−2.74	0.0066	−0.03279	−0.00536
Time since fire	0.007411	0.003148	34.89	2.35	0.0243	0.001019	0.01380
Preoutbreak sapling density	0.000172	0.000030	289.1	5.72	<0.0001	0.000113	0.000231
PP stems infested 1991–1997	−0.00271	0.000481	301.8	−5.64	<0.0001	−0.00366	−0.00177

Canopy cover: 2012 (%); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 300.5} = 43.08$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	1.2361	0.8609	36.7	1.44	0.1595	−0.5087	2.9809
Preoutbreak total BA	0.01068	0.002387	279.4	4.47	<0.0001	0.005982	0.01538
Preoutbreak stems ≥7.6 cm	0.000489	0.000123	294	3.96	<0.0001	0.000246	0.000731
Preoutbreak aspen BA	−0.01947	0.006619	300.4	−2.94	0.0035	−0.03249	−0.00644
Elevation	0.000823	0.000350	38.11	2.35	0.0239	0.000115	0.001531
Preoutbreak nonpine conifer	−0.01475	0.004502	207.3	−3.28	0.0012	−0.02363	−0.00588
PP stems infested 1991–1997	−0.00319	0.000486	300.5	−6.56	<0.0001	−0.00415	−0.00223

Litter depth: 2012 (cm); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 306.9} = 5.79$, $P = 0.0167$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	0.09555	0.1444	33.9	0.66	0.5127	−0.1979	0.3890
Preoutbreak total BA	0.005822	0.002359	261.4	2.47	0.0142	0.001176	0.01047
Preoutbreak live PP stems	0.000356	0.000162	303.9	2.19	0.0290	0.000037	0.000674
Preoutbreak juniper BA	−0.1433	0.04799	304.6	−2.99	0.0030	−0.2377	−0.04890
Time since last fire	0.007948	0.002792	34.51	2.85	0.0074	0.002276	0.01362
PP stems infested 1991–1997	−0.00117	0.000484	306.9	−2.41	0.0167	−0.00212	−0.00021

Litter mass: 2012 (Mg ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 306.6} = 6.14$, $P = 0.0137$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	1.5886	0.1429	33.63	11.12	<0.0001	1.2981	1.8791
Preoutbreak total BA	0.006015	0.002318	263.2	2.59	0.0100	0.001450	0.01058
Preoutbreak live PP stems	0.000334	0.000159	304.9	2.10	0.0365	0.000021	0.000648
Preoutbreak juniper BA	−0.1436	0.04712	304.6	−3.05	0.0025	−0.2364	−0.05091
Time since last fire	0.007708	0.002769	35.09	2.78	0.0086	0.002087	0.01333
PP stems infested 1991–1997	−0.00118	0.000475	306.6	−2.48	0.0137	−0.00211	−0.00024

1-hour woody fuels: 2012 (Mg ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 298.5} = 9.56$, $P = 0.0022$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	−2.4512	0.1933	27.46	−12.68	<0.0001	−2.8475	−2.0549
Preoutbreak total BA	0.04948	0.005498	218.9	9.00	<0.0001	0.03865	0.06032
Preoutbreak live PP BA	−0.05160	0.005812	254.8	−8.88	<0.0001	−0.06305	−0.04016
Preoutbreak hardwood BA	−0.03262	0.009699	277.4	−3.36	0.0009	−0.05172	−0.01353
Time since last fire	0.01204	0.003877	36.47	3.11	0.0037	0.004185	0.01990
PP stems infested before 1991	−0.01488	0.005759	288.7	−2.58	0.0103	−0.02621	−0.00355
PP BA infested 1991–1997	0.01872	0.006052	298.5	3.09	0.0022	0.006806	0.03062

10-hour woody fuels: 2012 (Mg ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 306.4} = 11.10$, $P = 0.0010$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	0.4231	0.1286	18.18	3.29	0.0040	0.1531	0.6931
Preoutbreak live BA (all spp.)	0.009346	0.002988	307.2	3.13	0.0019	0.003467	0.01523
Preoutbreak conifer BA	0.01498	0.005859	213.6	2.56	0.0113	0.003430	0.02653
PP stems infested 1991–1997	0.002003	0.000601	306.4	3.33	0.0010	0.000820	0.003185

100-hour woody fuels: 2012 (Mg ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 279.1} = 23.70$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	0.5179	0.1408	67.91	3.68	0.0005	0.2369	0.7988
Preoutbreak live BA	0.02509	0.004705	150.4	5.33	<0.0001	0.01579	0.03439
Preoutbreak live PP BA	−0.02638	0.005022	209.9	−5.25	<0.0001	−0.03628	−0.01648
Time since last fire	0.008610	0.002802	43.29	3.07	0.0037	0.002959	0.01426
PP stems infested 1991–1997	0.003271	0.000672	279.1	4.87	<0.0001	0.001948	0.004593

1,000-hour sound woody fuels: 2012 (Mg ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 216.9} = 31.54$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	2.0061	0.1753	130.3	11.44	<0.0001	1.6592	2.3529
Preoutbreak live BA (all spp.)	0.01332	0.005173	173.2	2.57	0.0109	0.003105	0.02353
PP stems infested 1991–1997	0.005680	0.001011	216.9	5.62	<0.0001	0.003686	0.007673

1,000-hour rotten woody fuels: 2012 (Mg ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 165.8} = 4.95$, $P = 0.0275$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	2.0600	0.2383	105.1	8.65	<0.0001	1.5875	2.5324
Preoutbreak total BA	0.02555	0.009794	65.58	2.61	0.0112	0.005996	0.04511
Preoutbreak live PP BA	−0.02499	0.01039	126.6	−2.41	0.0176	−0.04555	−0.00444
Preoutbreak live stems	−0.00099	0.000386	125.3	−2.55	0.0118	−0.00175	−0.00022
PP stems infested 1991–1997	0.003135	0.001409	165.8	2.22	0.0275	0.000352	0.005917

1- to 100-hour combined fuels: 2012 (Mg ha^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 312.6} = 12.23$, $P = 0.0005$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	0.8460	0.1786	32.76	4.74	<0.0001	0.4824	1.2096
Preoutbreak total BA	0.01097	0.003440	270.7	3.19	0.0016	0.004195	0.01774
Time since last fire	0.008915	0.003618	37.33	2.46	0.0184	0.001587	0.01624
Preoutbreak conifer BA	0.01710	0.006705	185	2.55	0.0116	0.003871	0.03033
PP stems infested 1991–1997	0.002452	0.000701	312.6	3.50	0.0005	0.001073	0.003832

Appendix C: Fire Behavior Model Results and Parameter Estimates and Fit

Note: all models are log scale.

Custom fuel models: surface flame lengths (m); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 306.4} = 3.37$, $P = 0.0672$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	0.2039	0.08595	28.31	2.37	0.0247	0.02798	0.3799
Preoutbreak stems ≥7.6 cm	0.001235	0.000479	286.8	2.58	0.0104	0.000293	0.002178
Preoutbreak live stems	−0.00132	0.000502	291.3	−2.63	0.0089	−0.00231	−0.00033
Preoutbreak juniper BA	−0.1016	0.03120	305	−3.26	0.0012	−0.1630	−0.04026
Time since last fire	0.003494	0.001561	31.44	2.24	0.0325	0.000311	0.006676
Preoutbreak seedling density	8.881E−6	2.723E−6	191.9	3.26	0.0013	3.511E−6	0.000014
Slope	0.008226	0.002049	44.36	4.01	0.0002	0.004097	0.01235
PP BA infested 1991–1997	0.004895	0.002665	306.4	1.84	0.0672	−0.00035	0.01014

Dynamically-selected fuel models: surface flame lengths (m); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 315.7} = 2.53$, $P = 0.1129$.

Parameter estimates are not shown.

Custom fuel models: total flame lengths (m); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 303.1} = 8.04$, $P = 0.0049$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	0.08816	0.2813	23.64	0.31	0.7568	−0.4930	0.6693
Preoutbreak live BA (all spp.)	0.009219	0.004234	307.5	2.18	0.0302	0.000887	0.01755
Preoutbreak stems ≥7.6 cm	0.000835	0.000198	303.1	4.22	<0.0001	0.000445	0.001224
Time since last fire	0.01583	0.005261	36.16	3.01	0.0048	0.005157	0.02650
PP stems infested 2005–2011	−0.00866	0.002926	283.5	−2.96	0.0033	−0.01442	−0.00290
Preoutbreak sapling density	0.000171	0.000052	290.5	3.30	0.0011	0.000069	0.000272
PP stems infested 1991–1997	−0.00233	0.000821	303.1	−2.84	0.0049	−0.00395	−0.00071

Dynamically-selected fuel models: total flame lengths (m); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 303.5} = 4.21$, $P = 0.0411$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	−5.9157	2.1738	28.54	−2.72	0.0110	−10.3648	−1.4665
Preoutbreak live BA (all spp.)	0.008280	0.003756	303.3	2.20	0.0282	0.000889	0.01567
Preoutbreak stems ≥7.6 cm	0.000703	0.000178	308.9	3.95	<0.0001	0.000352	0.001053
Slope	0.01501	0.005727	101	2.62	0.0101	0.003649	0.02637
Elevation	0.002681	0.000876	28.77	3.06	0.0048	0.000888	0.004474
Preoutbreak sapling density	0.000171	0.000046	291.1	3.73	0.0002	0.000081	0.000262
PP stems infested 2005–2011	−0.00660	0.002597	285.6	−2.54	0.0116	−0.01171	−0.00149
PP stems infested 1991–1997	−0.00149	0.000728	303.5	−2.05	0.0411	−0.00292	−0.00006

Custom fuel models: torching index wind speed (km hour^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 293.4} = 8.23$, $P = 0.0044$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	4.5127	0.1807	65.56	24.97	<0.0001	4.1518	4.8736
Preoutbreak live PP BA	0.01862	0.004347	282.9	4.28	<0.0001	0.01007	0.02718
Preoutbreak stems ≥7.6 cm	−0.00079	0.000202	244.5	−3.94	0.0001	−0.00119	−0.00040
Preoutbreak hardwood BA	0.03412	0.01202	274.9	2.84	0.0049	0.01046	0.05777
Time since last fire	−0.01423	0.003461	34.2	−4.11	0.0002	−0.02126	−0.00720
PP BA infested 1991–1997	−0.02236	0.007793	293.4	−2.87	0.0044	−0.03770	−0.00702

Dynamically selected fuel models: torching index wind speed (km hour^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 294.9} = 14.95$, $P = 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	4.1888	0.1883	67.04	22.25	<0.0001	3.8130	4.5646
Preoutbreak live PP BA	0.02099	0.004462	277.8	4.70	<0.0001	0.01220	0.02977
Preoutbreak stems ≥7.6 cm	−0.00086	0.000204	238.5	−4.21	<0.0001	−0.00126	−0.00046
Preoutbreak aspen BA	0.03290	0.01230	267.6	2.67	0.0079	0.008679	0.05712
Time since last fire	−0.00987	0.003443	35.52	−2.87	0.0069	−0.01686	−0.00289
Slope	−0.01085	0.005316	57.97	−2.04	0.0457	−0.02150	−0.00021
Preoutbreak sapling density	−0.00011	0.000053	286.5	−2.08	0.0384	−0.00021	−5.91E−6
PP BA infested 1991–1997	−0.03007	0.007777	294.9	−3.87	0.0001	−0.04538	−0.01477

Custom fuel models: crowning index wind speed (km hour^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\ 301.5} = 31.50$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	4.5204	0.1299	22.81	34.80	<0.0001	4.2516	4.7892
Preoutbreak live BA (all spp.)	−0.00879	0.001852	307	−4.75	<0.0001	−0.01243	−0.00514
Preoutbreak stems ≥7.6 cm	−0.00053	0.000098	306.5	−5.45	<0.0001	−0.00073	−0.00034
Preoutbreak hardwood BA	0.01522	0.005197	304.7	2.93	0.0037	0.004991	0.02544
Time since last fire	−0.00563	0.002363	35.33	−2.38	0.0226	−0.01043	−0.00084
Preoutbreak sapling density	−0.00013	0.000022	289	−5.74	<0.0001	−0.00017	−0.00008
PP stems infested 1991–1997	0.002010	0.000358	301.5	5.61	<0.0001	0.001305	0.002715

Dynamically-selected fuel models: Crowning index wind speed (km hour^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\,300.4} = 31.40$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	4.5170	0.1319	22.48	34.23	<0.0001	4.2437	4.7904
Preoutbreak live BA (all spp.)	−0.00868	0.001849	306.2	−4.70	<0.0001	−0.01232	−0.00504
Preoutbreak stems ≥7.6 cm	−0.00053	0.000098	306.9	−5.44	<0.0001	−0.00073	−0.00034
Preoutbreak hardwood BA	0.01527	0.005194	305.2	2.94	0.0035	0.005046	0.02549
Time since last fire	−0.00556	0.002406	34.28	−2.31	0.0269	−0.01045	−0.00068
Preoutbreak sapling density	−0.00013	0.000022	287.7	−5.73	<0.0001	−0.00017	−0.00008
PP stems infested 1991–1997	0.002004	0.000358	300.4	5.60	<0.0001	0.001300	0.002708

Custom fuel models: reaction intensity (MJ m^{-2} min^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\,306.9} = 2.20$, $P = 0.1393$.

Parameter estimates are not shown.

Dynamically selected fuel models: reaction intensity (kW m^{-2} min^{-1})
Significant bark beetle-related fixed-effect test statistic: $F_{1,\,310.1} = 3.84$, $P = 0.0509$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	6.3998	0.1069	26.49	59.89	<0.0001	6.1803	6.6192
Preoutbreak total BA (all spp.)	0.005541	0.001623	291.9	3.41	0.0007	0.002347	0.008734
Preoutbreak juniper BA	−0.09671	0.03445	309.5	−2.81	0.0053	−0.1645	−0.02892
Time since last fire	0.006227	0.002087	36.53	2.98	0.0051	0.001996	0.01046
Preoutbreak seedling density	9.72E−6	3.112E−6	254.9	3.12	0.0020	3.592E−6	0.000016
PP stems infested 1991–1997	−0.00068	0.000347	310.1	−1.96	0.0509	−0.00136	2.792E−6

Custom fuel models: rate of spread (m hour^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\,303.9} = 19.58$, $P < 0.0001$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	5.5867	0.09525	25.37	58.65	<0.0001	5.3907	5.7827
Preoutbreak live BA (all spp.)	−0.01001	0.002026	308.6	−4.94	<0.0001	−0.01400	−0.00603
Preoutbreak juniper BA	−0.1250	0.03825	306.6	−3.27	0.0012	−0.2003	−0.04978
Slope	0.01341	0.002655	60.18	5.05	<0.0001	0.008101	0.01872
Preoutbreak sapling density	−0.00007	0.000024	301.9	−3.06	0.0024	−0.00012	−0.00003
Preoutbreak seedling density	7.442E−6	3.336E−6	209.8	2.23	0.0268	8.651E−7	0.000014
Preoutbreak conifer BA	0.009956	0.003697	164.9	2.69	0.0078	0.002656	0.01726
PP BA infested 1991–1997	0.01551	0.003505	303.9	4.42	<0.0001	0.008611	0.02241

Dynamically selected fuel models: rate of spread (m hour^{-1}); significant bark beetle-related fixed-effect test statistic: $F_{1,\,313.3} = 8.38$, $P = 0.0041$.

Parameter	Estimate	SE	*df*	*t* value	Prob. (*t*)	95th percentile Lower	95th percentile Upper
Intercept	6.0513	0.09375	88.64	64.55	<0.0001	5.8650	6.2376
Preoutbreak live BA (all spp.)	−0.01103	0.002473	262.5	−4.46	<0.0001	−0.01590	−0.00616
Slope	0.01326	0.003230	43.03	4.10	0.0002	0.006742	0.01977
Preoutbreak sapling density	−0.00010	0.000034	310.7	−2.83	0.0050	−0.00016	−0.00003
PP BA infested 1991–1997	0.01392	0.004809	313.3	2.89	0.0041	0.004458	0.02338

Appendix D

Covariate medians, from 321 field plots, used in equations from Appendices B and C to produce Figures 3 and 5–7 and Table 2.

Covariate (units)	Median	Mean	Range
Preoutbreak total BA—all species (m^2 ha^{-1})	28.5	30.1	2.3–92.8
Preoutbreak live BA—all species (m^2 ha^{-1})	27.5	28.6	2.3–92.8
Preoutbreak live PP BA (m^2 ha^{-1})	20.1	21.7	0.0–79.5
Preoutbreak stems ≥7.6 cm dbh (ha^{-1})	444.8	517.9	24.7–1,902.7
Preoutbreak live PP stems ≥7.6 cm dbh (ha^{-1})	222.4	277.5	0–1,260.2
Preoutbreak gambel oak BA (m^2 ha^{-1})	0.0	0.2	0–10.3
Preoutbreak PP QMD (cm)	32.0	35.3	8.1–83.3
Preoutbreak sapling density (all spp.; ha^{-1})	0.0	394.9	0–7,413.0
Preoutbreak seedling density (all spp.; ha^{-1})	0.0	3,796.7	0–61,527.9
Preoutbreak live hardwood[a] BA (m^2 ha^{-1})	0.0	2.4	0–38.2
Preoutbreak live aspen BA (m^2 ha^{-1})	0.0	2.2	0–38.2
Preoutbreak live juniper BA (m^2 ha^{-1})	0.0	0.2	0–6.9
Preoutbreak nonpine conifer[b] BA (m^2 ha^{-1})	0.0	3.8	0–60.4
PP stems infested before 1991 (ha^{-1})	0.0	1.7	0–49.4
PP stems infested 2005–2011 (ha^{-1})	0.0	3.0	0–247.1
Time since last fire (yr)	50.0	38.1	0–50.0[c]
Elevation (m)	2,522	2,492	2,195–2,773
Slope (%)	10	14.6	0–70

[a]Hardwoods are quaking aspen, gambel oak, and mountain mahogany.
[b]Nonpine conifers were white fir, subalpine fir, Douglas-fir, and blue spruce.
[c]Plots without fire history were coded as 50; records for most sites go back to ca. 1960.