Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions

Brian J. Harvey [1a], Daniel C. Donato[1], William H. Romme[2], Monica G. Turner[1]

[1]University of Wisconsin – Madison
[2]Colorado State University
[a]Corresponding author; e-mail: bjharvey@wisc.edu

Abstract

The degree to which recent bark beetle (*Dendroctonus ponderosae*) outbreaks may influence fire severity and post-fire tree regeneration is of heightened interest to resource managers throughout western North America, but empirical data on actual fire effects are lacking. Outcomes may depend on burning conditions (i.e., weather at the time of fire), outbreak severity, or the interval between outbreaks and subsequent fire. We studied recent fires that burned through green-attack / red-stage (outbreaks < 3 yr before fire) and gray-stage (outbreaks 3-15 yr before fire) in subalpine forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) in Greater Yellowstone, Wyoming, USA, to determine if fire severity was linked to pre-fire beetle outbreak severity and whether these two disturbances produced compound ecological effects on post-fire tree regeneration. With field data from 143 post-fire plots that burned under different conditions, we assessed canopy and surface fire-severity as well as post-fire tree seedling density against reconstructed pre-fire outbreak severity.

Under moderate burning conditions, fire severity in green-attack / red-stage forests increased with pre-fire beetle outbreak severity and with greater relative proportions of green-attack vs. red-stage trees (i.e., the earliest stages of outbreak), whereas fire severity in gray-stage forests declined with pre-fire outbreak severity. Under extreme burning conditions, fire severity and pre-fire outbreak severity were only weakly associated in green-attack / red-stage forests and unrelated in the gray stage. Post-fire lodgepole pine seedling regeneration was unrelated to pre-fire outbreak severity in either post-outbreak stage, but increased with pre-fire serotiny. Results suggest mountain pine beetle outbreaks lead to a brief period of increased potential for severe fire at the earliest phase of the outbreak (i.e., with green-attack trees), largely under moderate burning conditions, followed by a protracted period of diminished potential for severe fires during the gray stage. Thus, beetle outbreak severity was linked to fire severity, but the magnitude direction of the linkage depended on both endogenous (outbreak stage) and exogenous (fire weather) factors. Closely-timed beetle outbreak and fire did not impart compound effects on tree regeneration, suggesting the presence of a canopy seedbank may enhance resilience to their combined effects.

Keywords: disturbance interactions, compound disturbance, *Dendroctonus ponderosae*, mountain pine beetle, *Pinus contorta*, lodgepole pine, subalpine forest, fire ecology, Greater Yellowstone Ecosystem, Rocky Mountains, USA.

Introduction

Severe natural disturbances have shaped Rocky Mountain forest landscapes for centuries or more (e.g., Kulakowski et al. 2003). While ecosystem response to individual disturbances is well-understood in many forests, interactions between disturbances present challenging questions for scientists and managers (Turner 2010). Recent outbreaks of native bark beetle species (genus: *Dendroctonus*) have caused extensive tree mortality over tens of millions of hectares of conifer forest in western North America (Raffa et al. 2008, Meddens et al. 2012), raising concern about the potential for severe fire following outbreaks (Hicke et al. 2012). Fuel profiles and fire models suggest fire behavior may be affected by pre-fire outbreaks (see Hicke et al. 2012 and Jenkins et al. 2012 for recent reviews), but field measures of fire severity (i.e., effects on the ecosystem) in post-outbreak forests are lacking. Outbreaks can also affect seed sources (e.g. Teste et al. 2011a, 2011b) in ways that may alter post-fire tree regeneration patterns (Harvey et al. in press), but different regeneration mechanism among tree species may lead to contrasting outcomes. Empirical data from fires that burn through post-outbreak stands are needed to assess the effects of outbreak severity and time since outbreak on fire severity, and the joint effects of outbreak severity and fire severity on post-fire trajectories.

Bark beetle outbreaks and fire may be linked disturbances, in that fire severity may be affected by pre-fire outbreaks. Linkages between disturbances may change with outbreak severity (e.g., the proportion of beetle-killed basal area or trees), time since outbreak, and/or under different burning conditions (i.e., weather). Following initiation of a bark beetle outbreak, forest stands transition predictably through several stages (e.g., Page and Jenkins 2007a, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012, Donato et al. 2013a). In the early stages of an outbreak, infested stands are a mixture of green-attack trees (< 1 yr after infestation by adult beetles but prior to successful emergence of pupae, ~ 100% retention of largely green needles on infested trees) and red-stage trees (1-2 yr after infestation, ~ 50% retention of largely red needles on beetle-killed trees). Stands next transition to the gray stage (3-15 yr after infestation, no new beetle attack occurring, << 50% needle retention on beetle-killed trees) and then the silver stage (25-30 yr post-outbreak, most beetle-killed trees fallen down). High uncertainty exists for predicted fire behavior in the transient early outbreak stages (Simard et al. 2011, Schoennagel et al. 2012, Hoffman et al. 2012), where studies to date have not considered the influence of green-attack trees, which can exhibit rapid increases in foliar flammability (Jolly et al. 2012a). Most fire simulation studies agree that crown-fire potential decreases in gray and silver stands but report equivocal changes to surface-fire behavior (Page and Jenkins 2007b, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012, Hicke et al. 2012, Donato et al. 2013a). Across simulation studies, the effects of outbreaks on fire potentials are greatest under moderate weather and diminish under extreme weather.

Fire simulation modeling is instructive for understanding potential fire behavior (e.g., fire intensity, rate of spread, energy output) and addressing operational concerns (e.g., fire suppression or firefighter safety), but it does not directly address the ecological effects of fire in post-outbreak forests. Although fire severity and behavior are related, fire effects are most appropriately measured with empirical post-fire data and cannot be predicted from fire behavior alone. Prior retrospective studies have mainly relied on remote measures (e.g., satellite or aerial records) that detect coarse-scale disturbance occurrence or severity (e.g. Lynch et al. 2006), or do not account for burning conditions when evaluating disturbance severity (Kulakowski and Veblen 2007, Bond et al. 2009). Field data may uncover fire-severity responses that are undetectable with remote data, but field measures of outbreak and fire severity under different burning conditions are lacking (Hicke et al. 2012).

In addition to linked interactions between outbreaks and fire, compound disturbance effects (Paine et al. 1998) may result if beetle outbreaks alter ecosystem response to subsequent fire, and post-fire regeneration mechanisms are likely key in determining outcomes. Beetles can indirectly reduce seed availability by killing large seed-producing trees (Bjorklund and Lindgren 2009), which can lead to decreases in post-fire seedling establishment in forests that lack a seedbank (Harvey et al. in press). Adaptations such as serotinous cones may buffer compound disturbance effects if seedbanks remain viable after tree death (Teste et al. 2011a, 2011b, Aoki et al. 2011), but outcomes have not been tested empirically following beetle outbreaks and subsequent fire.

The ability to directly address linked and compound interactions between beetle outbreaks and fire has been limited by a lack of spatially explicit field data to characterize the severity of both disturbances. High-elevation subalpine forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) make up over 15% of the forested area of the Rocky Mountains (Baker 2009) and have experienced widespread recent mountain pine beetle (*Dendroctonus ponderosae*) outbreaks (Raffa et al. 2008, Meddens et al. 2012). Recent fires have burned through beetle-outbreak impacted stands, presenting an excellent opportunity to empirically evaluate how disturbances interact in linked or compound ways in this widespread forest type.

We collected field data following recent wildfires that burned through different outbreak/post-outbreak stages under contrasting burning conditions in subalpine forests of the Greater Yellowstone Ecosystem (GYE) to test for disturbance interactions across a range of contexts. Specifically, we asked: (1) What is the effect of recent bark beetle outbreaks on subsequent fire severity, and do any effects differ with time since outbreak and/or under different burning conditions (i.e., in what ways are these disturbances linked)? (2) How does pre-fire outbreak severity affect post-fire lodgepole pine seedling establishment (i.e., do these disturbances produce compound effects)?

Canopy fire severity was expected to increase with pre-fire outbreak severity in the green-attack / red stage due to greater needle flammability without concomitant loss of needles from beetle-killed trees (Jolly et al. 2012a); no change to surface fire severity was expected because surface fuels are little-changed from unattacked stands (Simard et al. 2011, Schoennagel et al. 2012, but see Page and Jenkins 2007a). In the gray post-outbreak stage, canopy fire severity was expected to decline with higher pre-fire outbreak severity because of lower available canopy fuel once needles are shed from beetle-killed trees, whereas surface fire severity was expected to increase with pre-fire outbreak severity due to accumulation of fine fuels (Page and Jenkins 2007a, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012). In both post-outbreak stages, effects were expected to be lessened under extreme burning conditions when weather could override beetle-induced changes to fuels. Because beetle-killed lodgepole pine can maintain a viable aerial seedbank (Aoki et al. 2011, Teste et al. 2011b), high-levels of serotiny were expected to buffer against compound disturbance effects, such that post-fire seedling density would not vary with pre-fire outbreak severity.

Methods

Study area

The study areas were in the Gros Ventre Wilderness and the Bridger Wilderness on the Bridger-Teton National Forest (BTNF), located in the southern portion of the GYE (43º 20’ N, 110º 08’ E) (Figure 1A). Mean daily temperatures range from -18 ºC in January to 22 ºC in July, and annual mean precipitation is 60 cm (www.prism.oregonstate.edu). Soils are well drained, fine-loamy, and derived from sedimentary and metamorphic substrates (heavily glaciated Typic Dystrocryepts and Haplocryalfs [Munn and Arneson 1998]). Forests are dominated by lodgepole pine (constituting > 50% of basal area), but depending on topography and elevation stands often include whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Lodgepole pine-dominated subalpine forests of Greater Yellowstone are characterized by stand-replacing crown fires with fire-return intervals of 150 to 300 years (Romme and Despain 1989, Schoennagel et al. 2003, Higuera et al. 2011) which are often followed by high but spatially variable post-fire seedling densities (Turner et al. 1999).

The New Fork Lakes Fire burned in 2008 through forest stands that were in the green-attack / red stage (Fig. 1B). Mountain pine beetle outbreaks were first recorded in isolated locations in the study area in 2006 and 2007 in USDA aerial detection survey (ADS) maps. Aerial surveys in 2008 were flown after the New Fork Lakes Fire (therefore there is no available record of new beetle-induced tree mortality in 2008), but aerial photos taken during the fire by USFS personnel indicated many trees in the red stage at the time of the fire (Fig. 1B). Field evidence also indicated there was active infestation occurring at the time of the fire, with many trees in the green-attack stage. The New Fork Lakes Fire was started when a campfire escaped containment on July 29 and continued until August 30, burning 6,106 ha in total. Fire management included active ignitions (i.e., burnouts) along the southwestern perimeter of the fire to protect structures during a period of steady southwest winds (Steve Markason, USFS Helitack Supervisor, pers. comm.). No suppression activities occurred in the study area.

The Red Rock Complex Fire burned in 2011 through forest stands that were in the gray post-outbreak stage (Fig. 1C). Mountain pine beetle outbreaks began in 2003 in isolated study area locations, with widespread tree mortality peaking between 2005 and 2009 based on ADS data (Appendix A). Subalpine fir mortality attributed to outbreaks of western balsam bark beetle (*Dryocoetes confusus*) and Armillaria root disease (*Armillaria spp.*) was also reported from 2002-2009 in ADS maps. No new tree mortality was reported in the study area in 2010 or 2011 in ADS maps, meaning that stands were 3-9 yr post-outbreak at the time of the 2011 Red Rock Complex Fire. The Red Rock Complex Fire was composed of the Red Rock and the Gray Hills Fires, ignited by lightning on August 20 and September 4, respectively. The Red Rock Complex Fire was managed for wildland fire use and was extinguished by snow and rain on October 2 after burning 4,761 ha in total; no suppression or management burning occurred in the study area (Dale Deiter, BTNF District Ranger, pers. comm.).

Sampling design

In both fires, study plots were distributed in subalpine forests dominated by lodgepole pine with variable pre-fire mountain pine beetle outbreak severity. Plots were systematically situated in each fire, but the exact process differed slightly due to different configurations of suitable sample areas. Plots in the New Fork Lakes Fire (n = 100) were arranged in a grid in the western 1/3 of the fire, after field reconnaissance indicated that was the only portion of the fire where lodgepole pine was consistently > 50% of the basal area. From a random start location, plots were separated by a minimum distance of 100 m or further if necessary to avoid areas not meeting the study criteria (rock outcrops, non-forest, etc.) until all the suitable area was sampled. Plots in the Red Rock Complex Fire (n = 43) were distributed throughout the fire in areas that were dominated by lodgepole pine based on USFS vegetation maps. From a minimum distance of 100 m within the fire perimeter at each of 10 accessible locations along the fire perimeter, plots were situated along a transect perpendicular to the fire perimeter and separated by a minimum of 400 m or further if necessary to the next available stand meeting study criteria until all the suitable area was sampled. Minimum spacing between plots was increased to 400 m in the Red Rock Complex Fire because preliminary analyses of the New Fork Lakes Fire data indicated that response variables were spatially correlated at distances up to 395 m (further addressed in statistical analysis). Plot center locations were randomized within 10 m of each grid/transect location to avoid bias. Field sampling occurred in 2010 (New Fork Lakes Fire) and 2012 (Red Rock Complex Fire), two and one years following fire, respectively.

In each plot, data were collected on stand structure, pre-fire beetle outbreak severity, and fire severity in a 30-m diameter circular plot (0.07 ha) divided into four quadrats (NE, SE, SW, NW). Stand structure was measured by recording the condition (live or dead), species, diameter at breast height (dbh) to the nearest 0.5 cm, and height of every tree taller than 1.4 m in the plot. We also recorded the species and height for every live or dead pre-fire sapling (trees < 1.4 m that established pre-fire) occurring in 3-m belt transects along the main axes of the circle plot (N, E, S, W). In the New Fork Lakes Fire, post-fire seedlings (trees that germinated post-fire) were recorded in 20-0.25 m^2 quadrats placed every 3 m along the main axes of the plot. Because post-fire tree seedling density was sparse in the Red Rock Complex Fire, sample area was increased and post-fire seedlings were recorded in 3-m belt transects along the main axes of the plot. Slope (º), aspect (º), and geographic coordinates were measured at plot center.

Pre-fire beetle outbreak severity

Pre-fire beetle outbreak severity was quantified following methods outlined in Harvey et al. (in press), by removing the bark on every tree taller than 1.4 m (19,012 individual trees) and recording evidence (or absence of evidence) of *Dendroctonus* activity (Safranyik and Carroll 2007). Each tree was assigned to one of five categories: (1) pre-disturbance snag, (2) killed by bark beetles prior to fire, (3) green attack at time of fire, (4) live at the time of fire, or (5) unknown (Table 1, Appendix B). By cross-referencing with ancillary information for each fire (e.g., aerial photos at the time of fire and ADS maps), beetle-killed trees were assigned as green-attack or red-stage in the New Fork Lakes Fire and gray-stage in the Red Rock Complex Fire. Classification of trees was informed by discussions with forest entomology experts (Ken Raffa, University of Wisconsin; Ken Gibson, USFS).

Fire severity

We quantified fire severity in each plot using field measures of fire effects in multiple strata. Canopy fire severity was measured on five randomly selected co-dominant canopy trees in each quadrant (20 trees per plot) by recording the maximum char height to the nearest 0.5 m and the maximum percentage of scorching around the circumference on the main bole of each selected tree. Fire-caused tree mortality was recorded by classifying every fire-damaged tree > 1.4 m in the plot that was alive at the time of fire but dead at the time of sampling as killed by fire. The percentage of post-outbreak live trees and basal area that were killed by fire was used to measure fire severity on the residual canopy after the outbreak. Surface fire severity was measured by recording the depth of post-fire litter + duff (i.e., the soil O horizon) to the nearest mm at every 3 m along the main axis of the plot (20 pts / plot) and by recording the percent cover of charred surface (mineral soil, litter, woody debris), using the point intercept method. Points were arranged in 5 x 5 grids contained within a 0.5 m x 0.5 m sample frame at every 3 m along the main axis of the plot in the New Fork Lakes Fire (500 pts / plot) and were spaced at 10-cm intervals along the main axis of the plot in the Red Rock Complex Fire (480 pts / plot).

Topography and burning conditions

A 10-m digital elevation model (DEM) was used in ArcGIS 10.1 to generate the following topographic variables for each plot center: elevation (m), slope (º), aspect (NE Index, [Beers et al., 1966]), and topographic curvature (the second derivative of the elevation surface [Zevenbergen and Thorne, 1987]). To capture local elevation effects, we calculated a slope position by re-scaling elevation for each plot from 0 (bottom of slope) to 1 (ridge top) (Harvey et al, in press).

We used daily burn progression maps provided by the BTNF to divide the fire into two burning conditions based on weather conditions and fire growth using established methods (e.g., Thompson and Spies, 2009; Harvey et al., in press). Moderate burning conditions occurred during periods of relatively low temperature and winds, high humidity, and modest fire growth; extreme burning conditions were during periods of relatively high temperatures and winds, low humidity, and rapid fire growth (Table 2). One exception to these trends was the wind speed during the New Fork Lakes Fire; average wind speed at the nearest remote automated weather station (RAWS) was higher during the moderate conditions (Table 1).

Statistical analysis

To test whether fire severity was linked to pre-fire outbreak severity, we regressed canopy and surface fire-severity variables against pre-fire beetle-killed basal area while controlling for other variables known to influence wildfire. Fire-severity response variables were transformed to conform to linear model assumptions when necessary (e.g., arcsine square root transform of percent cover data), and regression models were only run on variables that had distributions not violating model assumptions before or after transformation. This resulted in two canopy fire severity measures (char height and bole scorch) and two surface fire severity measures (post-fire litter + duff depth and charred surface cover). Stepwise variable selection (using BIC) among topographic (elevation, slope, aspect, topographic curvature, slope position) and stand structure (live and dead basal area and stem density) variables did not result in any additional variables being retained in models of fire severity. Therefore, the final models contained burning condition, beetle-killed basal area, and burning condition * beetle-killed basal area as fixed effects. For variables that did not meet assumptions of parametric tests before or after possible transformations (the percentage of post-outbreak live basal area and trees killed by fire), we used Spearman rank correlation tests between beetle-killed basal area and fire response variables to evaluate effects.

Because stands in the New Fork Lakes Fire contained varying proportions of trees in the green-attack or red stage of outbreak, we also tested for an effect of the proportion of beetle-killed basal area in the red stage (red-stage basal area / [green-attack + red-stage basal area]) on each of the fire severity variables, using a second regression model for each response variable. In this test, a positive relationship would indicate that red-stage trees were more related to increased fire severity, a negative relationship would indicate that green-attack trees were more related to increased fire severity, and no significant relationship would indicate that red-stage and green-attack trees were equally related to fire severity.

To test if beetle outbreaks and wildfire produced compound disturbance effects on post-fire seedling establishment, we regressed post-fire lodgepole pine seedling establishment against beetle-killed basal area after accounting for other variables (fire severity, seed source, serotiny, topography) known to affect post-fire tree regeneration. Fire severity was represented by a fire severity class (light surface, severe surface, crown) that was assigned in the field to each plot following established protocols for the region (Turner et al. 1997). Potential seed source was represented by lodgepole pine basal area ha^{-1}. Pre-fire serotiny was represented by the percentage of lodgepole pine trees bearing serotinous cones (following methods in Tinker et al. 1994). Stepwise variable selection (using BIC) revealed that topographic variables were not correlated with post-fire seedling density and therefore were not included in models. Final models for post-fire lodgepole pine seedling density included fire severity class, lodgepole pine basal area, pre-fire serotiny, beetle-killed basal area, and pre-fire serotiny * beetle-killed basal area. We included the interaction term to see if any effects of beetle-killed basal area on post-fire seedling density changed with levels of pre-fire serotiny. Because of very sparse post-fire tree regeneration in the Red Rock Complex Fire (only 7 out of 43 plots contained seedlings), we were unable to build the full regression model because degrees of freedom were limited. Therefore, we tested for compound disturbance interactions between fire severity and outbreak severity by using a Spearman rank correlation test between post-fire seedling density and pre-fire outbreak severity overall and within each fire-severity class.

Generalized least squares (GLS) models were used to account for spatial autocorrelation among plots in the New Fork Lakes Fire, after estimating parameters from empirical variograms (Crawley 2007). The modeled variogram was a spherical correlation structure with a mean range of 303 m across fire-severity response variables (min 210 m, max 395 m) and a range of 216 m for post-fire lodgepole pine seedling density; the nugget was approximately zero and was not modeled. Generalized linear models (e.g., negative binomial) can be useful for count data such as seedling density, but to our knowledge there currently exists no negative binomial model that can simultaneously account for spatial autocorrelation structure in the data. Therefore, we used GLS models and transformed post-fire seedling data prior to analysis (natural log + 1) to meet model assumptions. Variograms indicated no spatial structure in model residuals from ordinary least squares (OLS) models in the Red Rock Complex Fire; OLS models were used for analyses.

All statistical analyses were performed in the R statistical software (version 2.12, R Foundation for Statistical Computing, Vienna, AT). Results are means ± 1 SE unless noted. For all analyses, we set α = 0.10 to reduce the chance of Type II error and not miss potentially meaningful effects. That is, we wanted to maximize the ability to detect any ecologically important effect of beetle outbreak severity on fire severity or tree regeneration because of its relevance for forest management.

Results

Forest stand and disturbance characteristics

Because of the later stage of outbreak in the Red Rock Complex Fire, the percentage of beetle-killed basal area was greater than in the New Fork Lakes Fire, which was in early outbreak stages. However, both fires included plots spanning low (<< 5% of basal area) to high (> 70% of basal area) levels of beetle-caused mortality (Table 3). Both fires included plots that encompassed a wide range of fire severity, and fire-severity metrics were similar across fires (Tables 3 and 4). Plot-level fire-severity metrics were highly correlated with each other in both fires (Appendix C); nonetheless, we report results for all measures because they represent different components of the ecosystem and may be of interest to managers individually.

Linked disturbances? Effects of pre-fire beetle outbreak severity on fire severity

Green-attack / red-stage outbreak - Several fire-severity metrics increased with pre-fire beetle outbreak severity when fire occurred early in the green-attack / red stage, but effects were generally most pronounced under moderate rather than extreme burning conditions.

Under moderate burning conditions, char height and bole scorch increased with outbreak severity (Fig. 2A-B, Appendix D), reaching levels typically recorded under extreme burning conditions in forests with or without pre-fire beetle outbreaks. Post-fire litter + duff depth decreased (indicating increased fire severity) with increasing pre-fire outbreak severity (Fig. 2C, Appendix D), but charred surface cover was unrelated (Fig. 2D, Appendix D). The proportion of post-outbreak live basal area and trees that were killed by fire was less related to outbreak severity ($r_s = 0.25$, $P = 0.24$ for basal area, $r_s = 0.35$, $P = 0.09$ for trees). Fire severity also varied with the relative proportion of green-attack vs. red-stage trees in early-outbreak stands. Three fire-severity metrics (char height, bole scorch, reduced litter + duff depth) increased as the relative proportion of trees in the green-attack stage increased; charred surface cover showed no relationship (Appendix D). Very few plots that burned under moderate conditions had high outbreak severity, making the confidence interval around these trends fairly wide when ~50% of the basal area was beetle killed (Fig. 2A-C). We were unable to test for statistical outliers in this case because standard methods (e.g., Cook's distance) do not exist for GLS models. When we removed the one plot at ~50% beetle-killed basal area, all tests were non-significant ($P > 0.10$) under moderate conditions. However, these trends are likely biologically significant as there is no reason to believe this point is an outlier; beetle severity and fire severity measures were well within the observed trends under all burning conditions. Rather, this is related to the small number of plots ($n = 25$) that burned under moderate conditions.

Under extreme burning conditions, most relationships between fire severity metrics and outbreak severity became either non-significant (bole scorch) or decreased in effect size (char height, post-fire litter + duff depth) (Fig. 2, Appendix D). The proportion of post-outbreak live basal area and trees killed by fire increased with outbreak severity ($r_s = 0.47$, $P < 0.01$, and $r_s = 0.48$, $P < 0.01$, respectively). Fire-severity metrics were unrelated to the relative proportion of green-attack vs. red-stage trees during extreme burning conditions (Appendix D).

Gray stage / post outbreak - Several fire-severity metrics declined with pre-fire outbreak severity when fire occurred in the gray stage during moderate burning conditions, but were unrelated to outbreak severity during extreme burning conditions.

Under moderate burning conditions, char height and bole scorch both decreased with higher pre-fire outbreak severity (Fig. 3A-B, Appendix D). Post-fire litter + duff depth increased (indicating decreased fire severity) with higher pre-fire beetle outbreak severity, but charred surface cover was unrelated (Fig 3C-D, Appendix D). Fire-caused tree mortality (proportion of post-outbreak live basal area and trees killed by fire) declined with higher pre-fire beetle outbreak severity (r_s = -0.55, P = 0.04 for basal area; r_s = -0.45, P = 0.10 for trees). Under extreme burning conditions, no fire-severity metrics were related to pre-fire outbreak severity (Fig 3E-H, Appendix D).

Compound disturbances? Effects of outbreak severity on post-fire tree seedling density

Post-fire conifer regeneration was variable within each fire, but mean seedling densities differed by two orders of magnitude between the two fires. Post-fire tree seedling density was high in the New Fork Lakes Fire (mean 111,860 ha^{-1}, median 23,000 ha^{-1}, range 0 to 1,320,000 ha^{-1}, Table 3). Lodgepole pine made up 99.6% of all post-fire tree seedlings, and all were one or two years old at the time of sampling. Post-fire tree seedling density was much lower in the Red Rock Complex Fire (mean 1,928 ha^{-1}, median 0 ha^{-1}, range 0 to 639,179 ha^{-1}). Lodgepole pine made up 98.2% of seedlings in all but two of the plots, which had seedling densities > 100,000 ha^{-1} and were dominated by Engelmann spruce. All seedlings in the Red Rock Complex Fire were in the cotyledon stage at the time of sampling. In both fires, post-fire seedling density differed with fire severity, with seedling density highest in plots that burned as severe-surface fire (Fig. 4A-B). Seedling density was also positively related to pre-outbreak lodgepole pine basal area (r_s = 0.47, P < 0.001 and r_s = 0.44, P = 0.003 for the New Fork Lakes Fire and Red Rock Complex Fire, respectively) and pre-fire serotiny (r_s = 0.47, P < 0.001 and r_s = 0.42, P = 0.005, respectively).

When fire burned through the green-attack / red-stage outbreak (New Fork Lakes Fire) and after controlling for the effects of covariates (fire severity, pre-outbreak lodgepole pine basal area, and pre-fire serotiny), there was no evidence of compound disturbance effects from pre-fire outbreak followed by fire. Post-fire lodgepole pine seedling density was not related to pre-fire outbreak severity ($t = 0.40$, $P = 0.69$), which did not interact with serotiny ($t = -0.28$, $P = 0.78$) in the GLS model. Post-fire lodgepole pine seedling density was also unrelated to pre-fire beetle outbreak severity when no other covariates were included in the model ($t = -1.11$, $P = 0.27$) (Fig. 4C). When fire burned in gray-stage / post-outbreak stands (Red Rock Complex Fire), we also found no evidence of compound disturbance effects on post-fire tree seedling density. Non-parametric (Spearman's rank) tests revealed no relationship between post-fire lodgepole pine seedling density and pre-fire beetle outbreak severity overall ($r_s = -0.07$, $P = 0.65$) or within any burn-severity classes (all $P > 0.10$) (Fig. 4D).

Discussion

Pre-fire beetle outbreak severity was associated with fire severity in subalpine forests of Greater Yellowstone, indicating that these disturbances were linked. However, the magnitude and even the direction of the relationship between outbreak severity and fire severity changed with time since outbreak, and effects were contingent upon burning conditions. Under moderate burning conditions, several measures of fire severity increased with outbreak severity in the green-attack / red stage but decreased with outbreak severity in the gray stage. Under extreme burning conditions (which is when most large wildfires in subalpine forests occur), most relationships between fire severity and pre-fire beetle outbreak severity were weak or non-significant in both outbreak stages. Despite these links between disturbances, post-fire seedling densities suggested that beetle outbreaks and subsequent fire do not produce compound disturbance effects in serotinous lodgepole pine forests. Our results highlight the importance of understanding beetle outbreak effects on wildfire in the context of other drivers (e.g., burning conditions), and illustrate that effects can change with time since outbreak. Further, they suggest that serotiny can provide resilience against potential compound disturbance effects from beetle outbreaks and fire.

Our detailed field data collected following actual fires fill a knowledge gap in understanding beetle-fire interactions (Hicke et al. 2012), but direct comparisons to previous studies are challenging because of differences in questions and/or approaches. Because fire behavior and fire severity (the effects to the ecosystem) are related, fire simulation studies can help inform the interpretation of our results. However, predicted fire behavior is not directly comparable to post-fire measures of fire severity. Therefore, we cannot explicitly examine responses such as heat intensity, flame height, rate of spread, or resistance to control that may be of concern to operational fire management or suppression efforts (e.g., Jenkins et al. 2012). For example, our char height measurements are limited by tree height in some cases and do not represent actual flame heights. Because our study focused on post-outbreak stands that did burn, we cannot directly compare our results to studies that examine the probability that beetle-affected stands will burn relative to unaffected stands (Bebi et al. 2003,Bigler et al. 2005, Lynch et al. 2006, Kulakowski and Jarvis 2011). Therefore, we interpret our results in the context of previous retrospective and modeling studies, but do not make direct comparisons among qualitatively different response variables.

Fire severity in different post-outbreak stages

Green-attack / red stage – Changes to canopy fire severity in green-attack / red-stage outbreaks under moderate burning conditions were consistent with many predictions based on studies of fuel properties and fire simulation modeling (Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012), but we detected an important effect of green-attack trees during the earliest stages of an outbreak. Stands in the early stages of an outbreak are a mixture of un-attacked (live), green-attack (dying), and red (dead) trees (Fig. 1B) – each with different tree-level physiological responses to beetle attack. Xylem conductivity rapidly deteriorates within days to weeks of mountain pine beetle infestation, mainly because of blue stain fungus (*Ophiostoma clavigerum*) transmitted by attacking beetles (Miller et al. 1986, Yamaoka et al. 1990, Edburg et al. 2012). Impaired xylem function causes concomitant decreases in canopy transpiration and leaf water potential (Hubbard et al. 2013), increasing needle flammability before the crown changes color and needles begin to drop (Jolly et al. 2012a). Therefore, during the first year of an outbreak (prior to the classic red stage), there is a brief period of increased canopy flammability without an accompanying decrease in canopy bulk density (Jolly et al. 2012b). The fire-severity responses we measured in stands with ongoing beetle attack were consistent with fire behavior simulations in early red-stage stands where beetle-killed trees retain their needles and a large proportion of tree crowns are fading from green to red (Schoennagel et al. 2012, Hoffman et al. 2012). As a stand progresses to the late-red stage when there are no more green–attack trees and red trees have lost a significant portion of their needles, canopy bulk density is substantially reduced and crown fire potential decreases (Klutsch et al. 2011, Simard et al. 2011). Our data are also consistent with this expectation, as fire severity declined as the proportion of red-stage: green-attack trees increased. Thus our results suggest an increase in fire severity in the earliest stages of the outbreak, before canopy bulk density declines, and support the hypothesis that green-attack trees increase canopy-fire severity. This observation may also help to explain some of the differences in expectations among different studies (Hicke et al.

2012) and can inform modeling studies that do not currently discriminate between green-attack and red-stage trees in early outbreak stands.

Relationships between surface-fire severity and outbreak severity in green-attack / red-stage stands were less straightforward than those for canopy-fire severity. Red-stage increases in fine surface fuels have been reported in some cases but not others, and predictions of surface fire behavior vary (Page and Jenkins 2007a, Page and Jenkins 2007b, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012). These disparities may be from differences in timing of fuels data collection; surface fuels and within-stand weather conditions (e.g., wind speeds) should only change after needle-drop has begun later in the red stage. In the early outbreak stages that burned in the New Fork Lakes Fire, there was presumably little change to surface fuels in stands with high outbreak severity because green-attack or early red-stage trees had not dropped needles. The increases in forest-floor fire severity we report may therefore be from carryover effects from canopy fire severity rather than from changes to surface fuels.

Gray stage / post outbreak– Decreased canopy fire severity in the gray stage under moderate burning conditions is consistent with predictions from fire simulation studies (reviewed in Hicke et al. 2012). Canopy bulk density is reduced by ~ 50% in the gray stage relative to undisturbed stands (Page and Jenkins 2007a, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012). This reduction is expected to decrease active crown fire potential (Klutsch et al. 2011, Simard et al. 2011) unless beetle-killed trees have started to fall, which can increase wind penetration through stands (Schoennagel et al. 2012). In the gray stage stands we measured, nearly all beetle-killed trees were still standing. Increased potential for passive crown fire (i.e., torching) has been predicted in some studies (Page and Jenkins 2007b, Schoennagel et al. 2012) but not others (Simard et al. 2011). Although it is often impossible to differentiate between passive and active crown fire behavior with post-fire data, our findings indicate overall gray-stage reductions in canopy fire severity if burning conditions are moderate, and no effect if burning conditions are extreme.

Surface-fire severity was largely unrelated to pre-fire outbreak severity in the gray stage. These findings are consistent with modeling studies, given the minimal pre-fire snagfall in our study stands. Simulation studies of surface fire behavior in gray stage stands have produced variable projections, in part because fuel profiles vary. Fuel bed depth and fine and coarse surface fuels in gray-stage stands range from no change (Simard et al. 2011) to moderate increases (Schoennagel et al. 2012) or increases up to 2-3X from undisturbed stands (Page and Jenkins 2007a). The rate of snagfall is also critical in differences among projections (Klutsch et al. 2011). Studies with greater increases in surface fuels predict increased heat release and spread rate in the gray stage (Page and Jenkins 2007b, Klutsch et al. 2011, Schoennagel et al. 2012), whereas studies with negligible changes to fuels predict no change to surface fire characteristics (Simard et al. 2011). Beetle outbreak in the Red Rock Complex Fire occurred 3-9 yr before fire (Appendix A), so most beetle-killed trees were still standing at the time of fire (Fig. 1C). Although needles had fallen from the canopy, decomposition rates can keep pace with fine fuel inputs, yielding little change to surface fuels (Simard et al. 2012). This is likely why surface fire-severity was largely unaffected by beetle outbreak severity in our study area. Decades after outbreaks, heavy accumulation of coarse fuels from downed trees may affect subsequent fire severity (Jenkins et al. 2008, Schoennagel et al. 2012).

Comparisons with other retrospective studies

Consistent with our study, other retrospective studies report little evidence for effects of pre-fire outbreak severity on subsequent fire severity in the red or gray stage. Few empirical studies have assessed fire severity in the very early outbreak stages, possibly because the early-attack and red stages are short-lived (Hicke et al. 2012) and relatively few fires have burned in forests at that stage. In red-stage subalpine forests in Colorado and mixed-conifer forests in California, pre-fire outbreaks were unrelated to satellite measures of fire severity (Kulakowski and Veblen 2007, Bond et al. 2009). Field measures of fire severity were also unrelated to outbreak severity under any burning conditions in gray-stage lower-montane Douglas-fir forests, where fire severity was largely driven by topography (Harvey et al. in press). Comparisons with studies that have not quantified disturbance severity (Bebi et al. 2003, Bigler et al. 2005, Lynch et al. 2006) and/or controlled for burning conditions (e.g. Turner et al. 1999) remain difficult.

Compound disturbance interactions: serotiny as a buffer?

Pre-fire beetle outbreaks and subsequent fire did not produce compound disturbance effects (Paine et al. 1998) on tree regeneration for serotinous lodgepole pine. Post-fire seedling density is largely driven by pre-fire serotiny along with fire severity in Rocky Mountain lodgepole pine forests (Turner et al. 1997, 1999, Schoennagel et al. 2003), and pre-fire outbreak severity does not appear to alter this relationship. In the early stages of a bark beetle outbreak, serotiny may maintain resilience to subsequent fire by sustaining a viable seedbank after tree death (Aoki et al. 2011, Teste et al. 2011a). Decreased post-fire seedling density in serotinous gray-stage stands, compared with serotinous green-attack / red-stage stands, suggests the seedbank declines as time since outbreak increases, and cones fall to the forest floor (Teste et al. 2011a) where seeds can be consumed by animals or destroyed by fire (Buma and Wessman 2011, Kulakowski et al. 2013). In the five gray-stage plots (of the seven with seedlings) that had high pre-fire serotiny (> 15%), there was a strong decrease in post-fire lodgepole pine seedling density with increasing pre-fire outbreak severity (r^2 = 0.91, P = 0.03). However, our interpretations are limited by differences in the time between fire and data collection and/or post-fire climate conditions. We sampled one year after the Red Rock Fire (vs. two years after the New Fork Fire), which is unlikely to change estimates in areas of crown fire but may underestimate postfire seedling density in areas of lower fire severity, which may recruit during the second year postfire (Turner et al. 1999). Growing conditions in 2009 following the New Fork Lakes Fire were slightly wet (water-year moisture deficit was 11% below average), whereas 2012 following the Red Rock Fire Complex was very dry (water-year moisture deficit was 28 % above average), which could have reduced seedling establishment (data source: Westerling et al. 2011). In any case, serotinous lodgepole pine forests may be resilient to compound disturbance effects from successive beetle outbreaks and fire so long as cone-bearing trees are still standing. This contrasts with non-serotinous species where seed source is substantially reduced following severe bark beetle or defoliator outbreaks (Simard and Payette 2005, B.J. Harvey unpublished data), leading to reductions in early post-fire tree establishment (Harvey et al. in press, Côté et al. 2013).

Implications for post-outbreak management of stands

Our results suggest that post-outbreak fuel treatments would need to be applied in the first year of active bark beetle infestation or immediately thereafter to be effective at reducing fire severity. There is a very short window of time in the green-attack / red stage when fire severity under moderate conditions may increase to levels commonly observed under extreme burning conditions. This effect diminishes once needles have begun to drop in the red stage (Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012). Such an early response to beetle outbreak would be very challenging because many tree canopies would still be in the green-attack phase (Fig. 1B), remaining undetected by visual surveys for at least another year

(Dodds et al. 2006, Meddens et al. 2012). By the time the red crowns of beetle-killed trees are detected in ADS surveys, the potential for severe fire may already be declining. Even if aerial detection of green-attack trees was possible, the time required for ADS data to be collected and relayed to managers, regulatory procedures to be approved, and mobilization of logging equipment is commonly > 2 yr on accessible public lands (Collins et al. 2012, Griffin et al. 2013, Donato et al. 2013b). Thus, treatments would likely not be applied until stands are transitioning from the late-red to the early-gray stage, when fire potentials decline. This situation presents a challenge in applying timely and effective post-outbreak fuel treatments.

Following peak tree mortality from 2007 to 2009 (Raffa et al. 2008, Meddens et al. 2012), gray-stage stands now account for the largest proportion of beetle-affected forest in western North America. Our results suggest that management treatments may not be necessary to reduce fire severity in gray-stage / post-outbreak stands (i.e., no more necessary than in unattacked forests), and treated stands would require post-harvest slash treatment to avoid unintentional increases in surface-fire potential (Collins et al. 2012, Griffin et al. 2013). In later stages (> 20 yr post-outbreak), simulation models have predicted that accumulation of coarse fuel could increase surface-fire severity in untreated stands (Collins et al. 2012, Griffin et al. 2013, Donato et al. 2013b); empirical data are needed to test these predictions.

Most large fires in Rocky Mountain subalpine forests occur during extreme burning conditions and severe drought (Schoennagel et al. 2004). Predictions of fire behavior show minimal effects of pre-fire outbreaks under extreme burning conditions (Simard et al. 2011, Schoennagel et al. 2012), and we observed fire-severity responses consistent with this expected fire behavior. However, although we accounted for moderate and extreme burning conditions within each fire, both fires occurred in relatively mild fire years in Greater Yellowstone (B.J.

Harvey, unpublished data). During years of severe drought, pre-fire outbreaks may have even less of an effect on fire severity, which would reduce the effectiveness of fuel treatments. Comparisons of beetle-fire relationships across years with different climate conditions remain a research priority.

With respect to tree regeneration, our data suggest several important management implications. First, if the interval between beetle outbreak and subsequent fire is short (less than about 10 years) in serotinous lodgepole pine stands, *in situ* seed supply is likely to be adequate for stand regeneration. Thus, active measures such as post-fire seeding may not be needed, unless other species (e.g., aspen) respond more quickly and potentially outcompete lodgepole pine (depending on management objectives for stand composition). In gray-stage stands, further research is required because we were unable to determine the factors responsible for low tree regeneration. Moreover, we sampled one, not two years after fire, and seedling density can increase substantially in year two in areas of less-severe fire (Turner et al. 1997). Reduced fire severity in gray-stage stands can enhance survival of pre-fire advance regeneration, diminishing the importance of post-fire seedling establishment. There may be a window of time in the gray and silver stages when seed supply remains low until post-outbreak trees produce cones and restore a canopy seedbank. These dynamics need further study.

Conclusion

We found the severity of recent wildfires to be linked to pre-fire bark beetle outbreaks in lodgepole pine forests of Greater Yellowstone, although the strength and direction of these interactions changed with burning conditions (i.e., weather) and the interval between beetle outbreaks and fire. Our results suggest a brief period where fire severity increases with outbreak severity in the transient green-attack / red stage, and the data reveal a strong influence of green-attack trees. This is followed by a decrease in fire severity in the protracted gray post-outbreak stage. However, the effects of pre-fire bark beetle outbreak severity on subsequent fire severity were mainly manifest under moderate burning conditions and were reduced and/or undetectable under extreme burning conditions, which is when most large wildfires occur in Rocky Mountain subalpine forests. We also found that serotinous lodgepole pine forests were resilient to compound disturbance effects if beetle outbreaks were followed by fire within ~ 10 years. As post-outbreak forests in western North America transition into the gray stage, our findings help to identify when management actions may be effective – as well as when they may not be needed - to reduce future fire severity and/or improve post-fire tree establishment in serotinous lodgepole pine forests.

Acknowledgements

We thank N. Labonte, S. Armstrong, A. Meiritz, Z. Osterholz, D. Guerrero-Harvey, C. Harvey, and M. Harvey for fieldwork assistance. M. Simard, J. Griffin, K. Raffa, J. Williams, P. Townsend, R. Renkin, D. Abendroth, and D. Dieter provided valuable input on study design, analysis and interpretation. Yellowstone NP and the Bridger-Teton NF provided housing and logistical support. Funding was provided by the Joint Fire Sciences Program grant 09-1-06-3.

References

Aoki, C. F., W. H. Romme, and M. E. Rocca. 2011. Lodgepole pine seed germination following tree death from mountain pine beetle attack in Colorado, USA. The American Midland Naturalist 165:446–451.

Baker, W. L. 2009. Fire ecology in Rocky Mountain landscapes, 1st edition. Island Press, Washington, D.C.

Bebi, P., D. Kulakowski, and T. Veblen. 2003. Interactions between fire and spruce beetles in a subalpine rocky mountain forest landscape. Ecology 84:362–371.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Notes and observations: aspect transformation in site productivity research. Journal of Forestry 64:691–692.

Bigler, C., D. Kulakowski, and T. T. Veblen. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. Ecology 86:3018–3029.

Bjorklund, N., and B. S. Lindgren. 2009. Diameter of lodgepole pine and mortality caused by the mountain pine beetle: factors that influence their relationship and applicability for susceptibility rating. Canadian journal of forest research 39:908–916.

Bond, M. L., D. E. Lee, C. M. Bradley, and C. T. Hanson. 2009. Influence of pre-fire tree mortality on fire severity in conifer forests of the San Bernardino Mountains, California. Open Forest Science Journal 2:41–47.

Buma, B., and C. A. Wessman. 2011. Disturbance interactions can impact resilience mechanisms of forests. Ecosphere 2:1–13.

Collins, B. J., C. C. Rhoades, M. A. Battaglia, and R. M. Hubbard. 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. Forest Ecology and Management 284:260–268.

Côté, D., F. Girard, F. Hébert, S. Bouchard, R. Gagnon, and D. Lord. 2013. Is the closed-crown boreal forest resilient after successive stand disturbances? A quantitative demonstration from a case study. Journal of Vegetation Science 24:664–674.

Crawley, M. J. 2007. The R Book, 1st edition. Wiley, West Sussex, UK.

Dodds, K. J., S. L. Garman, and D. W. Ross. 2006. Landscape analyses of Douglas-fir beetle populations in northern Idaho. Forest Ecology and Management 231:119–130.

Donato, D. C., B. J. Harvey, W. H. Romme, M. Simard, and M. G. Turner. 2013a. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. Ecological Applications 23:3–20.

Donato, D. C., M. Simard, W. H. Romme, B. J. Harvey, and M. G. Turner. 2013b. Evaluating post-outbreak management effects on future fuel profiles and stand structure in bark beetle-impacted forests of Greater Yellowstone. Forest Ecology and Management 303:160–174.

Edburg, S. L., J. A. Hicke, P. D. Brooks, E. G. Pendall, B. E. Ewers, U. Norton, D. Gochis, E. D. Gutmann, and A. J. Meddens. 2012. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. Frontiers in Ecology and the Environment 10:416–424.

Griffin, J. M., M. Simard, and M. G. Turner. 2013. Salvage harvest effects on advance tree regeneration, soil nitrogen, and fuels following mountain pine beetle outbreak in lodgepole pine. Forest Ecology and Management 291:228–239.

Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. in press. Influence of recent bark beetle outbreak on fire severity and post-fire tree regeneration in montane Douglas-fir forests. Ecology.

Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management 271:81–90.

Higuera, P. E., C. Whitlock, and J. A. Gage. 2011. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. Holocene 21:327–341.

Hoffman, C., P. Morgan, W. Mell, R. Parsons, E. K. Strand, and S. Cook. 2012. Numerical simulation of crown fire hazard immediately after bark beetle-caused mortality in lodgepole pine forests. Forest Science 58:178–188.

Hubbard, R. M., C. C. Rhoades, K. Elder, and J. Negron. 2013. Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. Forest Ecology and Management 289:312–317.

Jenkins, M. J., E. Hebertson, W. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. Forest Ecology and Management 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. Forest Ecology and Management 275:23–34.

Jolly, W. M., R. A. Parsons, A. M. Hadlow, G. M. Cohn, S. S. McAllister, J. B. Popp, R. M. Hubbard, and J. F. Negron. 2012a. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. Forest Ecology and Management 269:52–59.

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

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. Western Journal of Applied Forestry 26:101–109.

Kulakowski, D., and D. Jarvis. 2011. The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: A look at the past century. Forest Ecology and Management 262:1686–1696.

Kulakowski, D., C. Matthews, D. Jarvis, and T. T. Veblen. 2013. Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (*Populus tremuloides*). Journal of Vegetation Science 24:168–176.

Kulakowski, D., and T. T. Veblen. 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88:759–769.

Kulakowski, D., T. T. Veblen, and P. Bebi. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. Journal of Biogeography 30:1445–1456.

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.

Meddens, A. J. H., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecological Applications 22:1876–1891.

Miller, R. H., H. S. Whitney, and A. A. Berryman. 1986. Effects of induced translocation stress and bark beetle attack (*Dendroctonus ponderosae*) on heat pulse velocity and the dynamic wound response of lodgepole pine (*Pinus contorta* var. *latifolia*). Canadian Journal of Botany 64:2669–2674.

Munn, L. C., and C. S. Arneson. 1998. Soils of Wyoming: A digital statewide map at 1:500,000-scale. University of Wyoming, Laramie, WY.

Page, W. G., and M. J. Jenkins. 2007a. Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. Forest Science 53:507–518.

Page, W., and M. J. Jenkins. 2007b. Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. Forest Science 53:662–674.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1:535–545.

Powell, E. N., P. A. Townsend, and K. F. Raffa. 2011. Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. Ecological Monographs 82:69–84.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58:501–517.

Romme, W. H., and D. G. Despain. 1989. Historical perspective on the Yellowstone Fires of 1988. BioScience 39:695–699.

Safranyik, L., and A. L. Carroll. 2007. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. Pages 3–66 *in* L. Safranyik and B. Wilson, editors. The mountain pine beetle: a synthesis of biology, management and impacts on lodgepole pine.

Schoennagel, T., M. G. Turner, and W. H. Romme. 2003. The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. Ecology 84:2967–2978.

Schoennagel, T., T. T. Veblen, J. F. Negron, 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.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. BioScience 54:661.

Simard, M., and S. Payette. 2005. Reduction of black spruce seed bank by spruce budworm infestation compromises postfire stand regeneration. Canadian Journal of Forest Research

35:1686–1696.

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? Ecological Monographs 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? Reply. Ecology 93:946–950.

Teste, F. P., V. J. Lieffers, and S. M. Landhäusser. 2011a. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecological Applications 21:150–162.

Teste, F. P., V. J. Lieffers, and S. M. Landhäusser. 2011b. Viability of forest floor and canopy seed banks in *Pinus contorta* var. *latifolia* (Pinaceae) forests after a mountain pine beetle outbreak. American Journal of Botany 98:630–637.

Thompson, J. R., and T. A. Spies. 2009. Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. Forest Ecology and Management 258:1684–1694.

Tinker, D. B., W. H. Romme, W. W. Hargrove, R. H. Gardner, and M. G. Turner. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Canadian Journal of Forest Research 24:897–903.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Turner, M. G., R. H. Gardner, and W. H. Romme. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. International Journal of Wildland Fire 9:21–36.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67:411–433.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences 108:13165 –13170.

Yamaoka, Y., R. H. Swanson, and Y. Hiratsuka. 1990. Inoculation of lodgepole pine with four blue-stain fungi associated with mountain pine beetle, monitored by a heat pulse velocity (HPV) instrument. Canadian Journal of Forest Research 20:31–36.

Zevenbergen, L. W., and C. R. Thorne. 1987. Quantitative analysis of land surface topography. Earth Surface Processes and Landforms 12:47–56.

TABLES

Table 1: Evidence and criteria used to classify each tree into one of five categories for reconstructing pre-fire beetle outbreak severity. See Appendix B for photos of trees. Stands in the New Fork Lakes Fire (NFLF) were in the green-attack / red stage and stands in the Red Rock Complex Fire (RRCF) were in the gray post-outbreak stage.

		% of trees sampled	
Tree classification	Tree characteristics	NFLF	RRCF
Pre-disturbance snag (killed before outbreak or fire; timing and cause of death unknown)	• dead at time of sampling • highly weathered/decayed sapwood, most branches and bark missing • no evidence of bark beetle activity (pre- or post-fire)	1.7	1.0
Killed by bark beetles prior to fire	Visible cambium: • dead at time of sampling, no needles in canopy • dry cambial tissue • *Dendroctonus* exit holes on the outer bark • fully excavated (but vacated) adult and larval *Dendroctonus* galleries on the vascular cambium (> 50% of bole circumference or remaining visible cambium)	2.3	6.8
	No visible cambium [a]: • dead at time of sampling, no needles in canopy • no available cambium visible due to excessive charring • > 15 cm dbh Relevant references: Turner et al. 1999, Safranyik and Carroll 2007, Simard et al. 2011, Ken Gibson, pers. comm.	1.0	9.3
Green-attack at time of fire	• dead at time of sampling, no needles in canopy • partially completed galleries with adult beetles charred under bark	2.1	0.0

	• OR meeting all the criteria for “killed by bark beetles prior to fire (visible cambium)” but containing needles in the canopy and located in a plot with partially completed galleries / charred beetles Relevant references: Safranyik and Carroll 2007, Ken Gibson and Ken Raffa, pers. comm.		
Live at the time of fire			
Killed by fire	• dead at time of sampling • charred bark, branches, or outer sapwood • no evidence of bark beetle activity (no exit holes on outer bark, no galleries under bark) • not a highly-decayed or well-weathered snag	81.7	72.0
Killed by bark beetles after fire	• alive or dead at the time of sampling • clear signs of post-fire beetle activity (boring dust [which would have been consumed by fire], resin bleeding) or fully developed galleries but moist cambial tissue and/or any detectable level of needles in the canopy (which would still be present given needle-drop period of 2-3 yrs) Relevant references: Safranyik and Carroll 2007, Powell et al. 2011, Ken Gibson, pers. comm.	9.1	0.1
Surviving tree	• alive at the time of sampling • green foliage, no sign of *Dendroctonus* beetle activity	2.8	10.9
Unknown	• deep charring on a tree < 15 cm dbh.	0.3	0.0

[a] Trees in this category were added to the ‘killed by bark beetles prior to fire’ category for all analyses because they were dead prior to the fire based on charring characteristics and most likely killed by bark beetles based on tree size and outbreak history in area.

Table 2: Regional weather information for the moderate and extreme burning condition periods in the New Fork Lakes Fire (green attack / red stage) and the Red Rock Complex Fire (gray stage / post outbreak). Weather data were downloaded from the Half Moon, WY remote automated weather station (RAWS) (~25 km southeast of plot locations) for the New Fork Lakes Fire, and the Grand Teton, WY RAWS (~35 km northwest of plot locations) for the Red Rock Complex Fire. Values are means of the daily average conditions during the active burning hours (10:00-18:00) in each burning period. Data source: www.raws.dri.edu.

Burning Conditions	Duration (days)	Area burned (ha)	Total % of fire area	Temp. (ºC)	Rel. Hum. (%)	Wind speed (km/h)
New Fork Lakes Fire[a]						
Moderate	3	1,271	16	23.9	17.9	15.8
Extreme	1	1,115	14	27.2	13.3	11.9
Red Rock Complex Fire						
Moderate	41	2,008	42	20.5	30.4	11.9
Extreme	3	2,753	58	24.9	20.1	14.0

[a] data for the New Fork Lakes Fire do not cover the entire area of the fire because plots are restricted to the western 1/3 of the fire; thus moderate and extreme burning conditions are characterized for this portion of the fire only.

Table 3. Stand structure characteristics for each study area pre-outbreak, pre-fire, and post-fire. Pre-fire beetle-killed basal area and snags is composed of the sum of red stage and green attack in the New Fork Lakes Fire and is gray stage in the Red Rock Complex Fire. Values are means (SE).

Stand structure variable	New Fork Lakes Fire		Red Rock Complex Fire	
Pre-outbreak				
Live basal area (m^2 ha^{-1})	29.5	(0.6)	39.2	(1.5)
Live stems ha^{-1}	1,836	(76)	1,893	(131)
Lodgepole pine basal area (%)	96	(<1)	52	(4)
Pre-fire				
Beetle-killed basal area (m^2 ha^{-1})	4.0	(0.5)	14.6	(1.3)
Beetle-killed basal area (%)	13.9	(1.7)	36.9	(2.8)
Range	0.0 to 71.9		2.4 to 77.5	
Beetle-killed snags ha^{-1}	101	(12)	267	(23)
Pre-fire serotiny (%)	45.2	(2.2)	23.5	(4.0)
Post-fire				
Fire-killed basal area (m^2 ha^{-1})	22.7	(1.0)	34.0	(1.9)
Fire-killed basal area (% of post-outbreak live basal area)	77.1	(0.3)	86.2	(3.8)
Live basal area (m^2 ha^{-1})	0.5	(0.2)	3.1	(1.1)
Live stems ha^{-1}	52	(18)	209	(54)
Lodgepole pine seedlings ha^{-1}	111,860	(22,489)	744	(416)
Median	23,000		0	
Conifer seedlings ha^{-1} (all spp.)	112,280	(22,479)	1,928	(1,521)
Median	23,000		0	

Table 4. Plot-level measures of fire severity in the New Fork Lakes Fire (green attack / red stage) and the Red Rock Complex Fire (gray stage / post outbreak).

	Green attack / red stage (New Fork Lakes Fire)			Gray stage (Red Rock Complex Fire)		
Fire severity metric	Mean	Median	Range	Mean	Median	Range
Canopy						
Char height (m)	11.5	11.9	0.7 to 21.6	9.6	9.7	0.6 to 17.2
Bole scorch (% of circumference)	90	100	38 to 100	87	97	25 to 100
Surface						
Post-fire litter + duff depth (mm)	10.2	9.0	0.0 to 29.7	3.6	2.2	0.0 to 12.8
Charred surface cover (%)	41	36	5 to 94	53	44	5 to 99
Other						
Fire-killed tree mortality (%)	88	99	20 to 100	86	100	28 to 100
Fire-killed basal area (%)	77	98	3 to 100	86	100	20 to 100

Figure Legends

Figure 1. (A) Location of the New Fork Lakes Fire and the Red Rock Complex Fire on the Bridger-Teton National Forest in Greater Yellowstone (Wyoming, USA). Aerial photos illustrate stand structure and the green-attack / red stage for the New Fork Lakes Fire (B) and the gray stage / post outbreak for the Red Rock Complex Fire (C). Post-fire field data indicated that many trees with green crowns in the New Fork Lakes Fire (A) were in the 'green attack' stage of beetle infestation at the time of the fire. Photos were taken from helicopters flying over each fire (at the time of fire) in the area where post-fire field plots were subsequently located. Photo credits: Steve Markason and Dale Deiter (USFS).

Figure 2. Fire severity vs. outbreak severity for fires burning under moderate and extreme burning conditions in lodgepole pine forests in the green attack / red stage of mountain pine beetle outbreak (New Fork Lakes Fire). Plots illustrate effects from models in Appendix D. Solid lines are generalized least squares (GLS) regression lines for significant ($P < 0.10$) relationships; dashed lines are 95% confidence intervals on regression slopes. Non-significant relationships are denoted with "n.s."

Figure 3. Fire severity vs. outbreak severity for fires burning under moderate and extreme burning conditions in lodgepole pine forests in the gray stage / post outbreak phase of mountain pine beetle outbreak (Red Rock Complex Fire). Plots illustrate effects from models in Appendix D. Solid lines are ordinary least squares (OLS) regression lines for significant ($P < 0.10$) relationships; dashed lines are 95% confidence intervals on regression slopes. Non-significant relationships are denoted with "n.s."

Figure 4. Post-fire lodgepole line seedlings ha^{-1} in each fire severity class (light surface, severe surface, crown) for the green attack / red stage (New Fork Lakes Fire) (A) and the gray stage / post outbreak (Red Rock Complex Fire) (B). Values are means with ± 95% confidence intervals. Scatterplots showing post-fire lodgepole pine seedlings ha^{-1} and pre-fire beetle outbreak severity in each fire severity class for green attack / red stage (C) and gray stage / post outbreak (D).

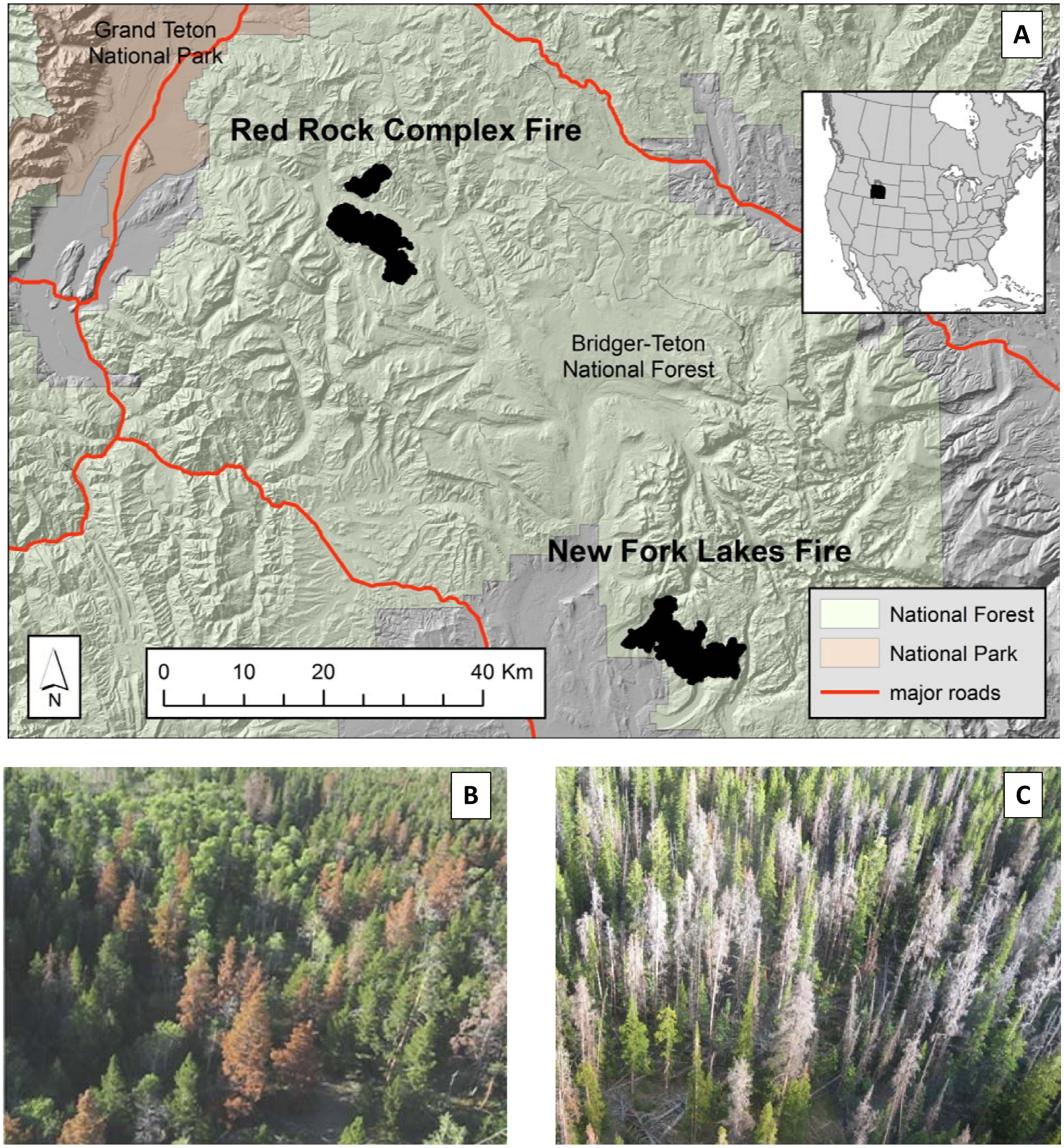
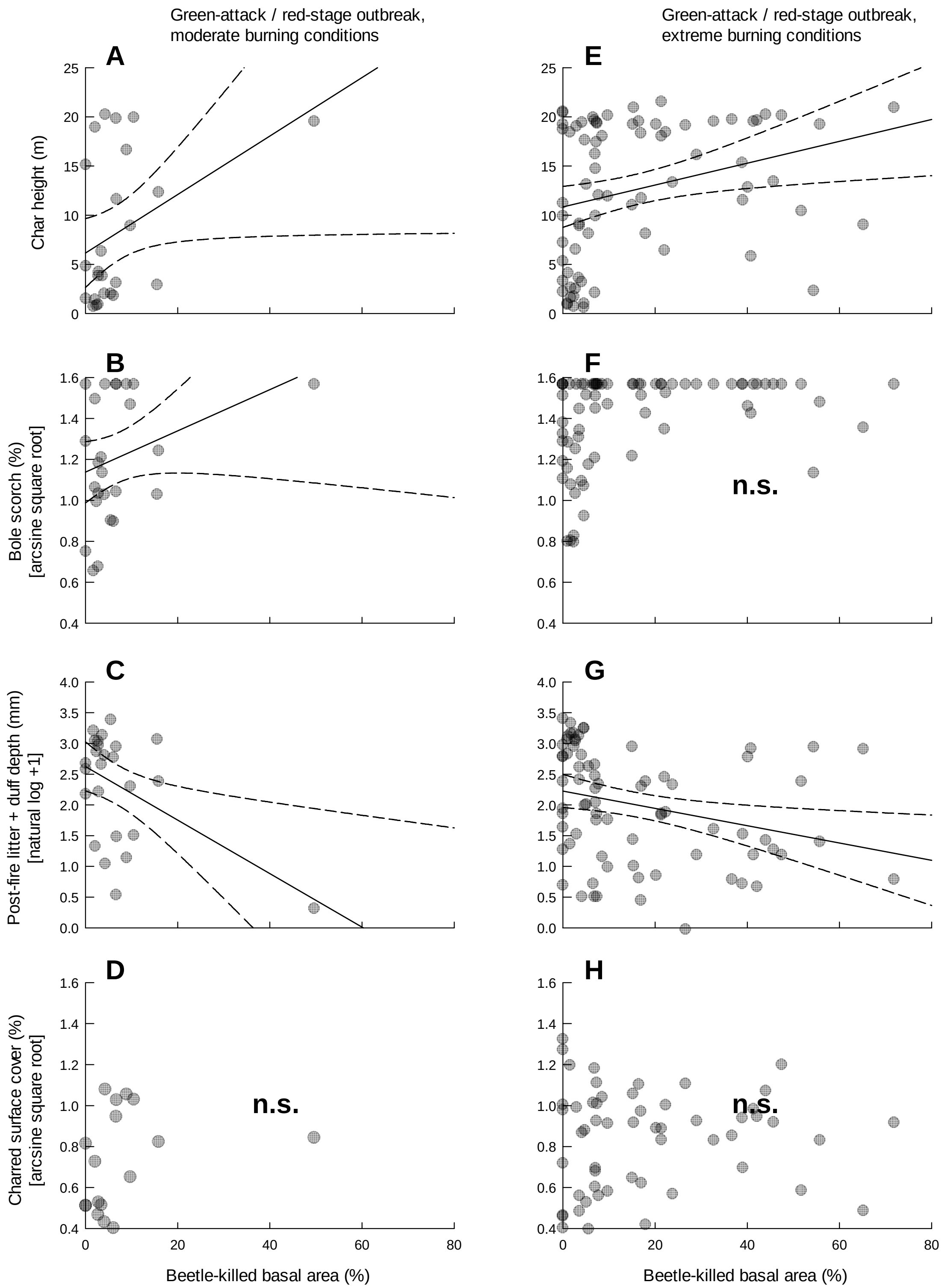

A
Grand Teton
National Park
Red Rock Complex Fire
Bridger-Teton
National Forest
New Fork Lakes Fire
National Forest
National Park
major roads
N
0
10
20
40 Km
B
C

Figure 1



796

797 **Figure 2**

798

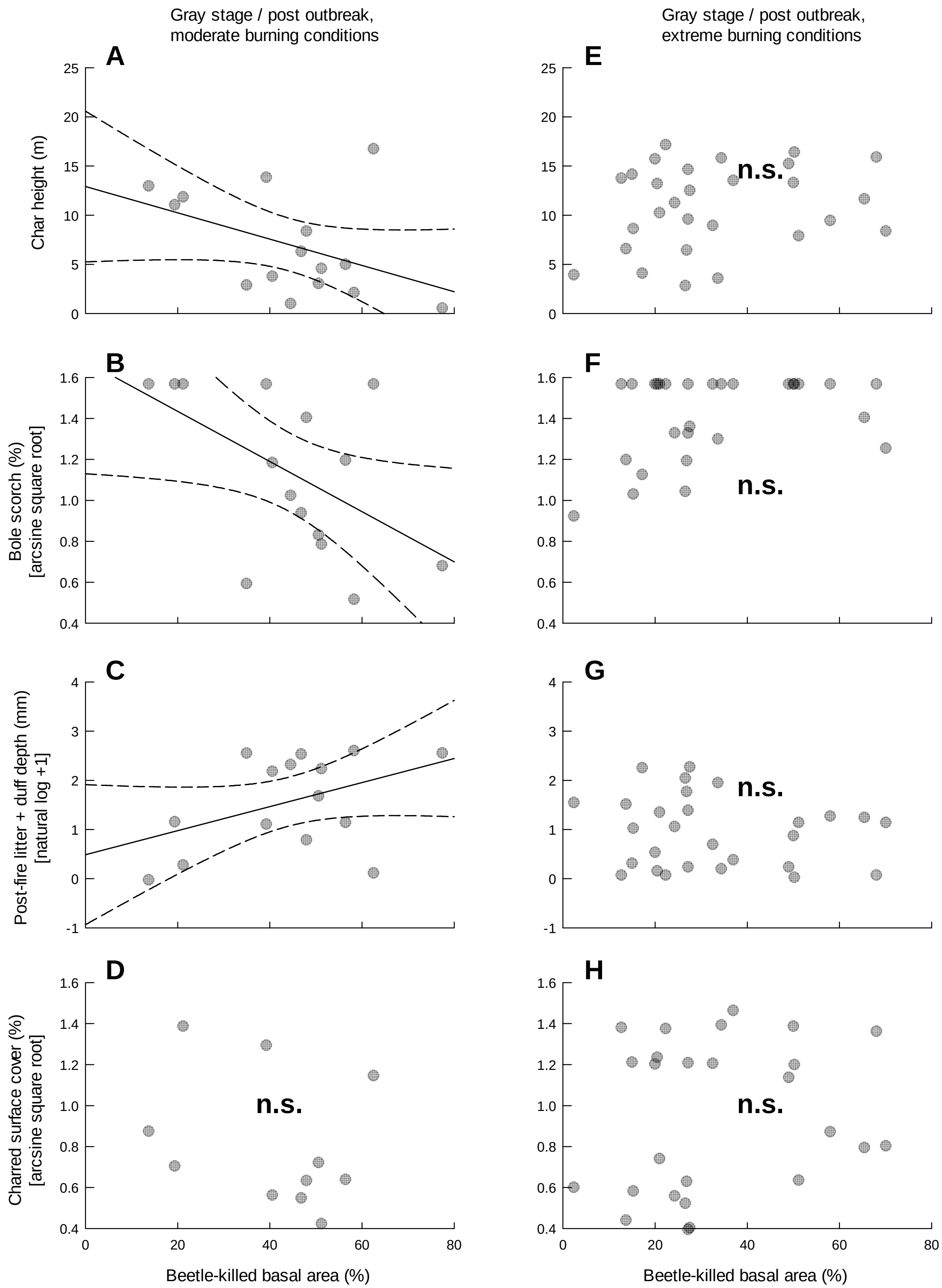

Gray stage / post outbreak,
moderate burning conditions
Gray stage / post outbreak,
extreme burning conditions
A
E
B
F
C
G
D
H
Char height (m)
Bole scorch (%)
[arcsine square root]
Post-fire litter + duff depth (mm)
[natural log +1]
Charred surface cover (%)
[arcsine square root]
n.s.
n.s.
n.s.
n.s.
n.s.
Beetle-killed basal area (%)
Beetle-killed basal area (%)

Figure 3

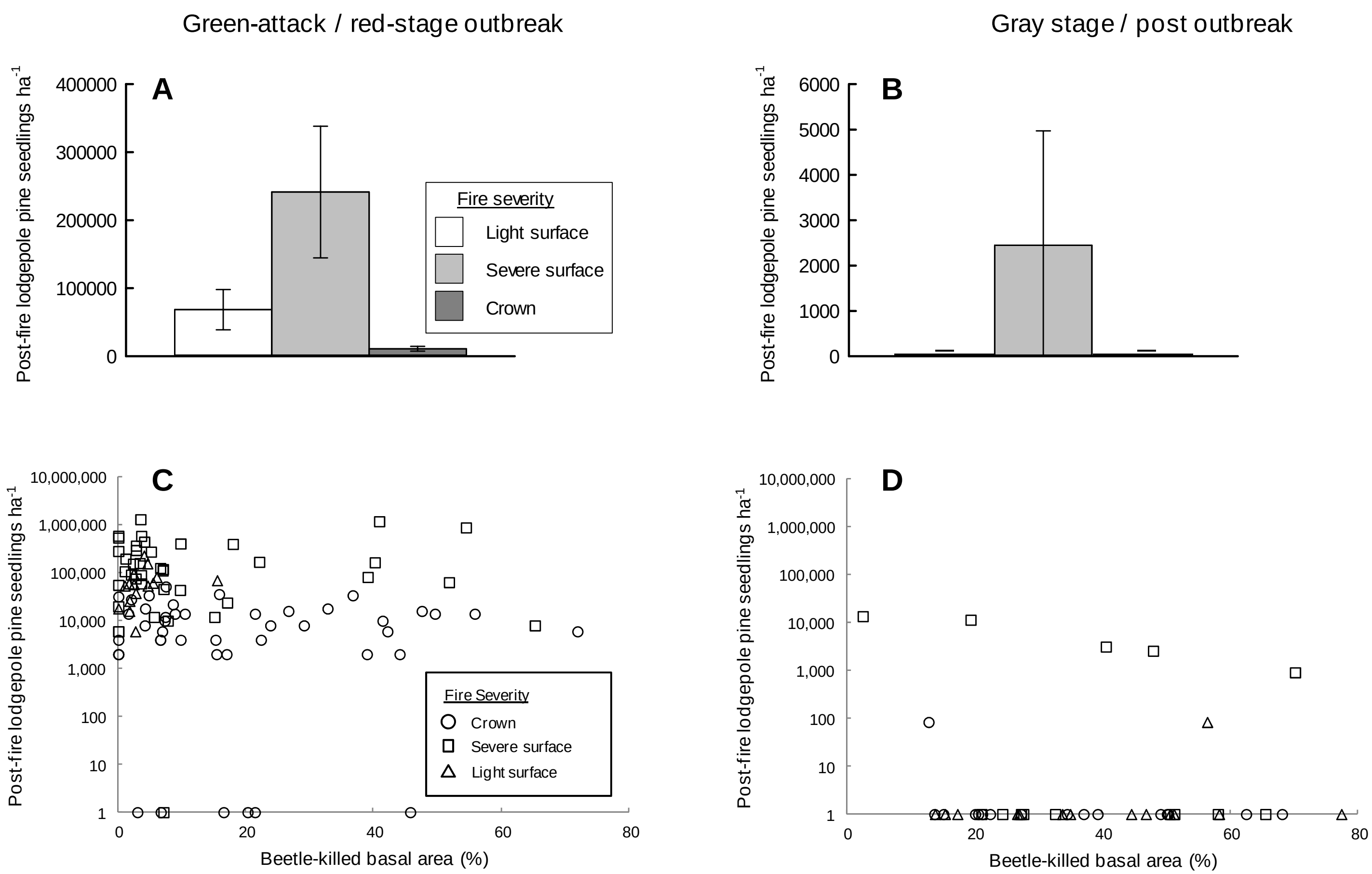

Green-attack / red-stage outbreak
Gray stage / post outbreak
A
B
C
D
Post-fire lodgepole pine seedlings ha-1
400000
300000
200000
100000
0
6000
5000
4000
3000
2000
1000
Fire severity
Light surface
Severe surface
Crown
10,000,000
1,000,000
100,000
10,000
1,000
100
10
1
Fire Severity
Crown
Severe surface
Light surface
0
20
40
60
80
Beetle-killed basal area (%)

Figure 4

Appendix A. Time series of bark-beetle attributed tree mortality in the Red Rock Complex Fire

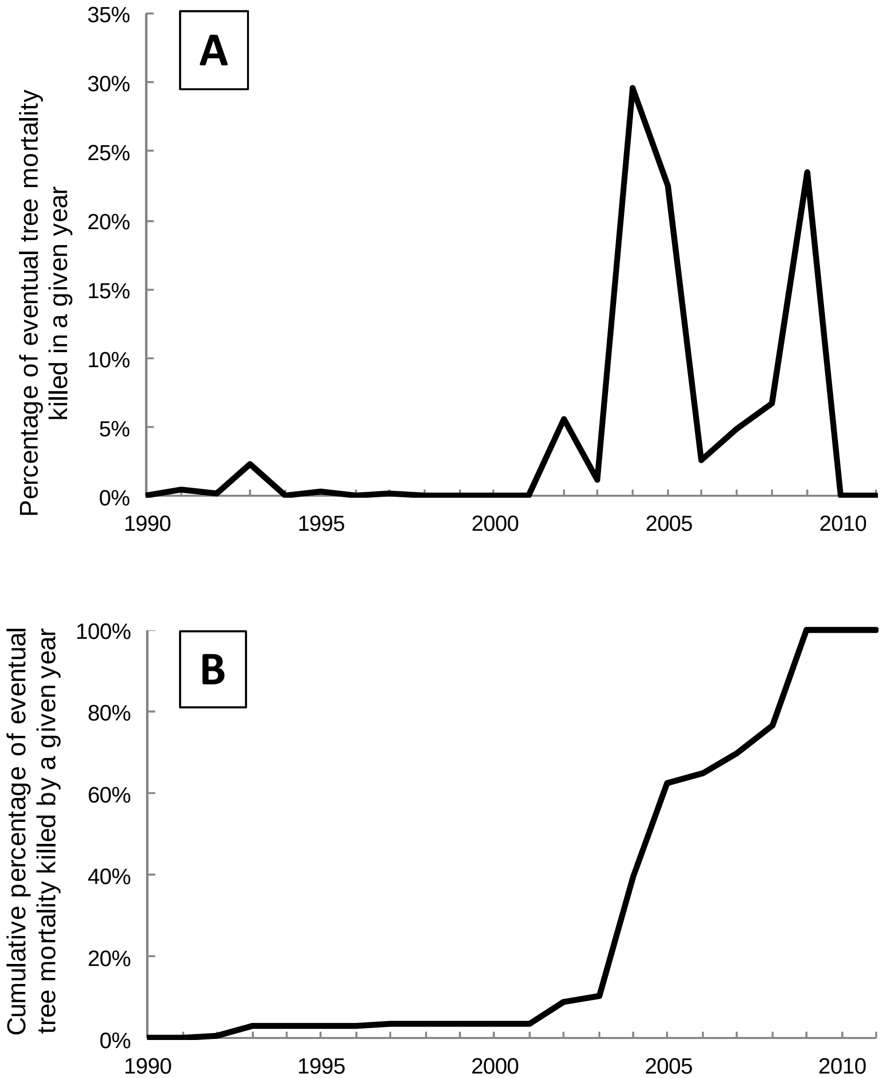


Figure A1: Time series of annual (A) and cumulative (B) tree mortality attributed to the mountain pine beetle beetle outbreak (69% of total mortality) and western balsam bark beetle (*Dryocoetes confusus*) and Armillaria root disease (31% of total mortality) in the area of the Red Rock Complex Fire. Data are calculated from USDA aerial detection surveys (http://www.fs.usda.gov). NOTE: Yearly cumulative mortality does not represent the percentage of all trees, but rather the cumulative percentage of all trees eventually killed during the recent outbreak that died by a given year.

Appendix B. Photographs of bark beetle outbreak severity measurements

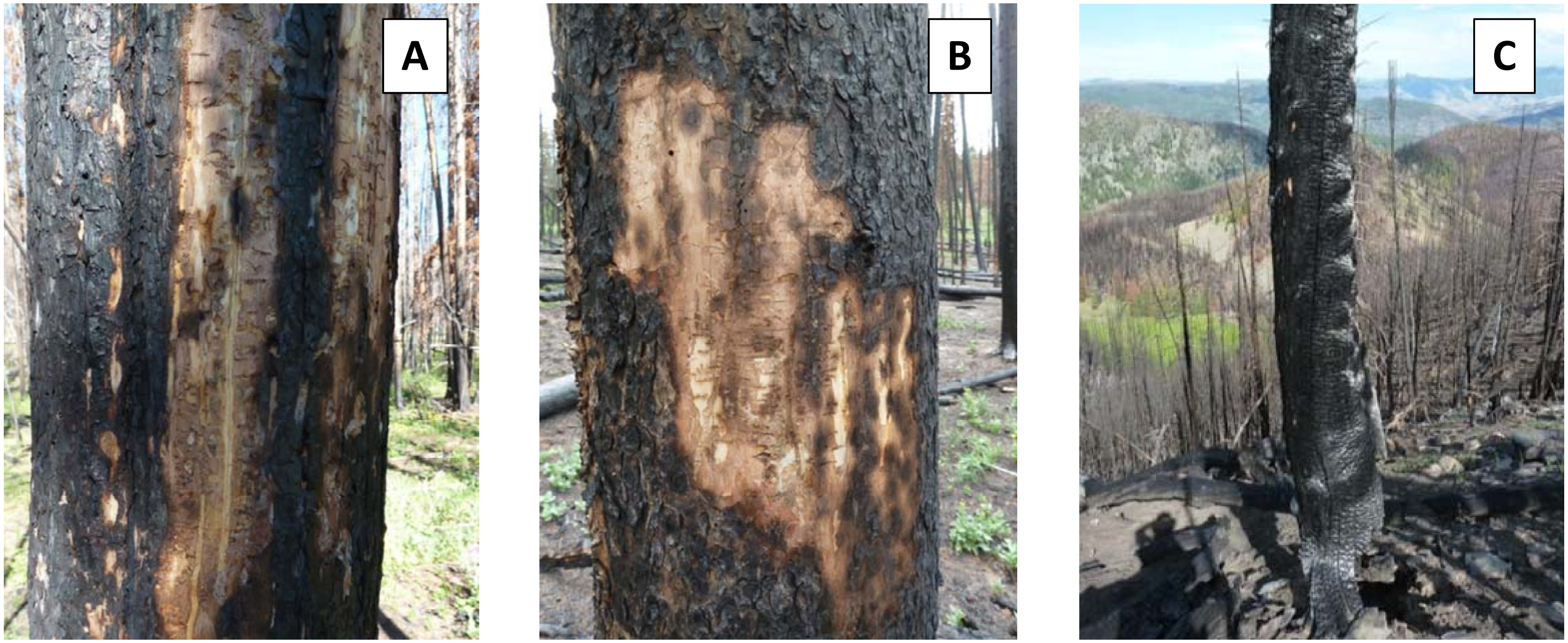


Figure B1: Photographs of general bole condition of trees classified as ‘killed by bark beetles prior to fire’ when galleries were visible on cambium (A-B), and ‘likely killed by bark beetles prior to fire’ when no sapwood was visible but tree was obviously dead prior to fire (C). Photo credit: B.J. Harvey.

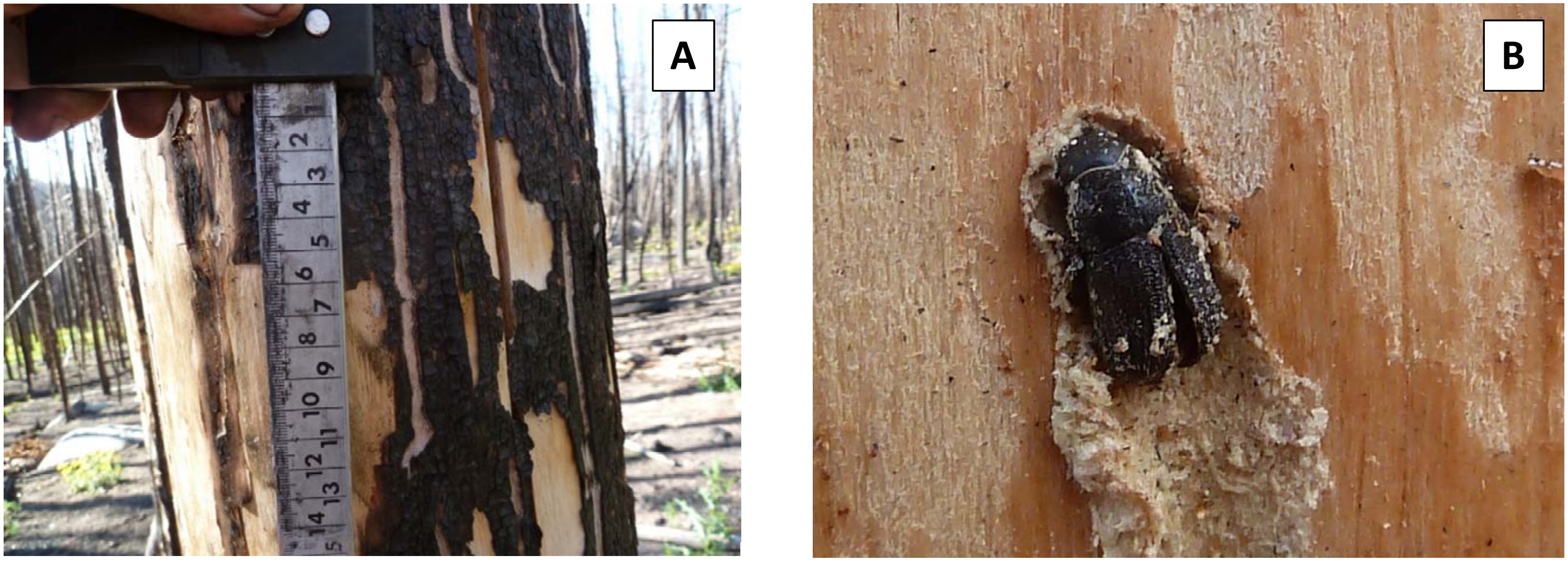


Figure B2: Photographs of general bole condition of trees that were classified as ‘green attack at time of fire’ with partially constructed adult galleries but no larval galleries (A); these trees often contained dead female mountain pine beetles charred underneath the bark at the top end of galleries (B). Photo credit: B.J. Harvey.

Figure B3: Photographs of general bole condition (A-B) and crown condition (C) of trees with fully developed *Dendroctonus* galleries, but retaining needles in the canopy, classified as ‘live at the time of fire’ but attacked by beetles post-fire if there was no evidence of ‘green attack at the time of fire’ in the plot. If there was evidence of ‘green attack at the time of fire’ in the plot, trees were assigned to the ‘green attack at time of fire’ class. Photo credit: B.J. Harvey.

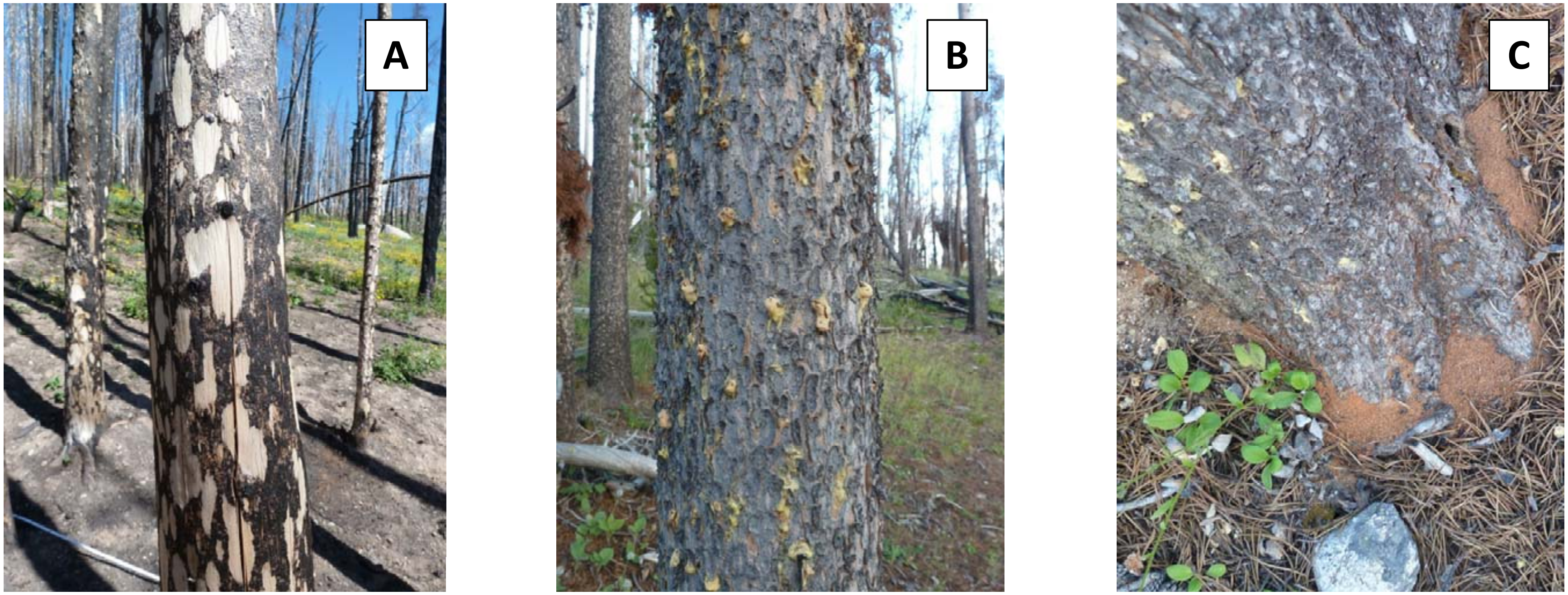


Figure B4: Photographs of bole condition of trees classified as ‘live at the time of fire’ if there was no evidence of pre-fire galleries on sapwood (A), or fresh pitch tubes and boring dust on the outer bark (B-C). Photo credit: B.J. Harvey.

Appendix C. Correlation among fire severity measurements

Table C1: Spearman rank correlations (r_s) among fire severity response variables in the New Fork Lakes Fire (green-attack / red stage). $P < 0.001$ for all correlations. Relative difference normalized burn ratio (RdNBR) values were explored as a potential fire severity response variable, but timing of pre-fire images confounded beetle and fire effects in the fire severity index; thus RdNBR was excluded from analysis.

	RdNBR	Char height (m)	Bole scorch (%)	Post-outbreak live basal area killed by fire (%)	Post-outbreak live trees killed by fire (%)	Post-fire litter +duff depth (mm)	Charred surface cover (%)
RdNBR	1.00	0.86	0.89	0.77	0.78	-0.85	0.85
Char height (m)		1.00	0.91	0.81	0.83	-0.88	0.87
Bole scorch (%)			1.00	0.79	0.80	-0.86	0.86
Post-outbreak live basal area killed by fire (%)				1.00	0.99	-0.78	0.77
Post-outbreak live trees killed by fire (%)					1.00	-0.79	0.79
Post-fire litter +duff depth (mm)						1.00	-0.88
Charred surface cover (%)							1.00

Table C1: Spearman rank correlations (r_s) among fire severity response variables in the Red Rock Complex Fire (gray / post-outbreak stage). $P < 0.001$ for all correlations. Relative difference normalized burn ratio (RdNBR) values were explored as a potential fire severity response variable, but timing of pre-fire images confounded beetle and fire effects in the fire severity index; thus RdNBR was excluded from analysis.

	RdNBR	Char height (m)	Bole scorch (%)	Post-outbreak live basal area killed by fire (%)	Post-outbreak live trees killed by fire (%)	Post-fire litter +duff depth (mm)	Charred surface cover (%)
RdNBR	1.00	0.84	0.78	0.78	0.77	-0.78	0.83
Char height (m)		1.00	0.86	0.79	0.78	-0.86	0.81
Bole scorch (%)			1.00	0.84	0.86	-0.83	0.83
Post-outbreak live basal area killed by fire (%)				1.00	0.99	-0.74	0.75
Post-outbreak live trees killed by fire (%)					1.00	-0.75	0.75
Post-fire litter +duff depth (mm)						1.00	-0.85
Charred surface cover (%)							1.00

Appendix D. Fire-severity model outputs

Table D1. Results of linear models testing for effects of beetle outbreak severity on subsequent fire severity. Burning condition and beetle-killed basal area terms were included as fixed effects. Burning conditions was a categorical variable with moderate burning conditions as the model intercept. Models were only run for fire-severity response variables that satisfied parametric statistics assumptions after transformation (if needed). Models for New Fork Lakes Fire are generalized least squares (GLS) models with a spherical correlation structure to account for spatial correlation among plots (see methods); models for Red Rock Complex Fire are ordinary least squares (OLS) models. BC = burning conditions.

Response (transformation)	Predictor	β	SE	t	P
<u>**New Fork Lakes Fire**</u>					
Char height (m)	Moderate BC (intercept)	6.10	2.10	2.90	<0.01
(*no transformation*)	Extreme BC	5.91	2.46	2.41	0.02
	Beetle-killed basal area	27.57	11.92	2.31	0.03
	Extreme BC * beetle-killed basal area	-21.63	12.43	-1.74	0.09
Bole scorch (%)	Moderate BC (intercept)	1.17	0.07	16.03	<0.01
(*arcsine – square root*)	Extreme BC	0.21	0.08	2.52	0.01
	Beetle-killed basal area	0.93	0.37	2.51	0.01
	Extreme BC * beetle-killed basal area	-0.76	0.39	-1.95	0.05

Litter + duff depth (mm)	Moderate BC (intercept)	2.62	0.22	12.18	<0.01
(*natural log [1 mm added]*)	Extreme BC	-0.46	0.26	-1.79	0.08
	Beetle-killed basal area	-4.30	1.75	-2.46	0.02
	Extreme BC * beetle-killed basal area	3.14	1.82	1.72	0.09
Charred surface cover (%)	Moderate BC (intercept)	0.55	0.09	6.30	<0.01
(*arcsine – square root*)	Extreme BC	0.12	0.10	1.15	0.25
	Beetle-killed basal area	0.72	0.58	1.23	0.22
	Extreme BC * beetle-killed basal area	-0.47	0.61	-0.77	0.44
Red Rock Complex Fire					
Char height (m)	Moderate BC (intercept)	12.93	3.28	3.94	<0.01
(*no transformation*)	Extreme BC	-3.69	3.72	-0.99	0.33
	Beetle-killed basal area	13.37	6.94	-1.93	0.06
	Extreme BC * beetle-killed basal area	18.57	8.38	2.22	0.03
Bole scorch (%)	Moderate BC (intercept)	1.68	0.19	8.92	<0.01
(*arcsine – square root*)	Extreme BC	-0.39	0.24	-1.85	0.07
	Beetle-killed basal area	-1.22	0.40	-3.08	<0.01
	Extreme BC * beetle-killed basal area	1.63	0.48	3.38	<0.01
Litter + duff depth (mm)	Moderate BC (intercept)	0.49	0.58	0.84	0.41
(*natural log [1 mm added]*)	Extreme BC	0.69	0.66	1.06	0.30

	Beetle-killed basal area	2.44	1.22	2.00	0.05
	Extreme BC * beetle-killed basal area	-3.05	1.48	-2.07	0.05
Charred surface cover (%)	Moderate BC (intercept)	1.06	0.27	3.90	<0.01
(*arcsine – square root*)	Extreme BC	-0.29	0.31	-0.93	0.36
	Beetle-killed basal area	-0.82	0.57	-1.43	0.16
	Extreme BC * beetle-killed basal area	1.26	0.69	1.83	0.08

Table D2. Results of linear models testing for relationship between fire severity and the proportion of beetle-killed basal area in the red stage (red stage BA / [green attack + red stage BA]) in the New Fork Lakes Fire. Burning condition and proportion (red or down) terms were included as fixed effects. Burning conditions is a categorical variable. Shown in the table is the slope of the proportion term (red) under each burning condition. Models were only run for fire-severity response variables that satisfied parametric statistics assumptions after transformation (if needed). Models are generalized least squares (GLS) models with a spherical correlation structure to account for spatial correlation among plots (see methods). BC = burning conditions.

Response (transformation)	Predictor	β	SE	t	P
Char height (m)	Prop. red stage in moderate BC	-10.71	6.02	-1.78	0.08
(*no transformation*)	Prop. red stage in extreme BC	-0.77	1.98	-0.39	0.70
Bole scorch (%)	Prop. red stage in moderate BC	-0.38	0.18	-2.04	0.04
(*arcsine – square root*)	Prop. red stage in extreme BC	-0.04	0.06	-0.71	0.48
Litter + duff depth (mm)	Prop. red stage in moderate BC	2.03	0.90	2.26	0.03
(*natural log [1 mm added]*)	Prop. red stage in extreme BC	0.14	0.30	0.16	0.65
Charred surface cover (%)	Prop. red stage in moderate BC	-0.22	0.29	-0.76	0.45
(*arcsine – square root*)	Prop. red stage in extreme BC	-0.06	0.09	-0.61	0.54