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

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Abstract. The degree to which recent bark beetle (*Dendroctonus ponderosae*) outbreaks may influence fire severity and postfire 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 during fire), outbreak severity, or intervals between outbreaks and subsequent fire. We studied recent fires that burned through green-attack/red-stage (outbreaks <3 years before fire) and gray-stage (outbreaks 3–15 years before fire) subalpine forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) in Greater Yellowstone, Wyoming, USA, to determine if fire severity was linked to prefire beetle outbreak severity and whether these two disturbances produced compound ecological effects on postfire tree regeneration. With field data from 143 postfire plots that burned under different conditions, we assessed canopy and surface fire severity, and postfire tree seedling density against prefire outbreak severity.

In the green-attack/red stage, several canopy fire-severity measures increased with prefire outbreak severity under moderate burning conditions. Under extreme conditions, few fire-severity measures were related to prefire outbreak severity, and effect sizes were of marginal biological significance. The percentage of tree stems and basal area killed by fire increased with more green-attack vs. red-stage trees (i.e., the earliest stages of outbreak). In the gray stage, by contrast, most fire-severity measures declined with increasing outbreak severity under moderate conditions, and fire severity was unrelated to outbreak severity under extreme burning conditions. Postfire lodgepole pine seedling regeneration was unrelated to prefire outbreak severity in either post-outbreak stage, but increased with prefire serotiny. Results suggest bark beetle outbreaks can affect fire severity in subalpine forests under moderate burning conditions, but have little effect on fire severity under extreme burning conditions when most large wildfires occur in this system. Thus, beetle outbreak severity was moderately linked to fire severity, but the strength and 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.

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

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 wildfire following outbreaks (Hicke et al. 2012). Fuel profiles and fire models suggest fire behavior may be affected by prefire 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. 2011*a*, *b*) in ways that may alter postfire tree regeneration patterns (Harvey et al. 2013), but different regeneration mechanisms 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

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of outbreak severity and fire severity on postfire trajectories.

Bark beetle outbreaks and wildfire may be linked disturbances, in that fire severity may be affected by prefire outbreaks. Linkages between disturbances may change with outbreak severity (e.g., the percentage 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 2007*a*, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012, Donato et al. 2013*a*). In the early stages of an outbreak, infested stands are a mixture of green-attack trees ($<$1 year after infestation by adult beetles but prior to successful emergence of pupae, $\sim$100% retention of largely green needles on infested trees) and red-stage trees (1–2 years after infestation, $\sim$50% retention of largely red needles on beetle-killed trees). Stands next transition to the gray stage (3–15 years after infestation, no new beetle attack occurring, $\ll$50% needle retention on beetle-killed trees, most snags still standing) and then the silver (sometimes called "old outbreak") stage (25–30 years 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, Hoffman et al. 2012, Schoennagel 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. 2012*a*). Most fire simulation studies agree that the potential for crown fire decreases in gray and silver stands, but report equivocal changes to surface-fire behavior (Page and Jenkins 2007*b*, Klutsch et al. 2011, Simard et al. 2011, Hicke et al. 2012, Schoennagel et al. 2012, Donato et al. 2013*a*). Across simulation studies, the effects of outbreaks on fire potentials depend on 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. Fire effects are most appropriately measured with empirical postfire data and cannot be predicted from modeled 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 postfire 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 drive variability in postfire seedling establishment in forests that lack a seedbank (Harvey et al. 2013). Adaptations such as serotinous cones may buffer compound disturbance effects if seedbanks remain viable after tree death (Aoki et al. 2011, Teste et al. 2011*a*, *b*), but outcomes have not been tested empirically following beetle outbreaks and subsequent fire.

The ability to directly address linked interactions between beetle outbreaks and fire and potential compound effects resulting from their interactions 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 if/how disturbances interact or produce compound effects 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. Beetle-caused tree mortality varied within fires and included stands that were unaffected by the recent outbreaks, effectively serving as a control against which to compare beetle outbreak effects along a spectrum of outbreak severity. Specifically, we asked the following questions: (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 prefire outbreak severity affect postfire lodgepole pine seedling establishment (i.e., do these disturbances produce compound effects)?

Canopy fire severity was expected to increase with prefire 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. 2012*a*); no change to surface fire severity was expected because surface fuels are little changed from un-attacked stands (Simard et al. 2011, Schoennagel et al. 2012, but see Page and Jenkins 2007*a*). In the gray post-outbreak stage, canopy fire severity was expected to decline with higher prefire 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 prefire outbreak severity due to accumulation of fine fuels (Page and Jenkins 2007*a*, 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. 2011*b*), high levels of serotiny were expected to buffer against compound disturbance effects, such that postfire seedling density would not vary with prefire outbreak severity.

METHODS

Study area

The study fires 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 (43°20′ N, 110°08′ E; Fig. 1A). Mean daily temperatures range from −18°C in January to 22°C in July, and annual mean precipitation is 60 cm (PRISM climate data; *available online*).[4] 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 predominantly high, but spatially variable, postfire 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 USDA Forest Service (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 started when a campfire escaped containment on 29 July and continued until 30 August, burning 6106 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, *personal communication*). 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 and accounted for 31% of the tree mortality mapped in ADS surveys and 23% of tree mortality from our field data. No new tree mortality was reported in the study area in 2010 or 2011 in ADS maps, meaning that stands were 3–9 years 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 20 August and 4 September, respectively. The Red Rock Complex Fire was managed for wildland fire use and was extinguished by snow and rain on 2 October after burning 4761 ha in total; no suppression or management burning occurred in the study area (Dale Deiter, *personal communication*).

Sampling design

In both fires, study plots were distributed in subalpine forests dominated by lodgepole pine with variable prefire 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 ($n = 100$, sampled in 2010, two years after fire) were arranged in a grid in the western one-third of the fire, after field reconnaissance indicated that was the only portion of the fire where lodgepole pine was consistently >50% of the stand 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, and so on) until all the suitable area was sampled. Plots in the Red Rock Complex Fire ($n = 43$, sampled in 2012, one year after fire) 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 (collected two years prior) indicated that response variables were spatially correlated at distances up to 395 m (addressed further in statistical analysis). Plot center locations were random-

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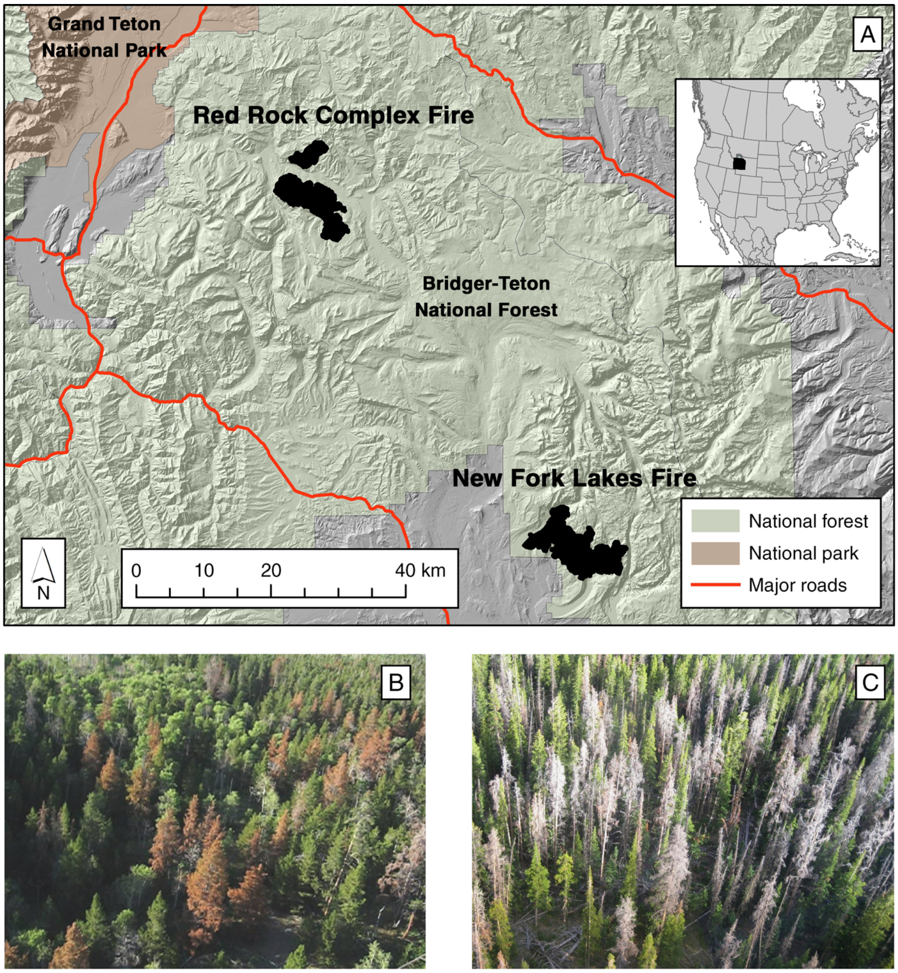

FIG. 1. (A) Location of the New Fork Lakes Fire and the Red Rock Complex Fire on the Bridger-Teton National Forest in Greater Yellowstone (Wyoming, USA). Aerial photos illustrate stand structure and (B) the green-attack/red stage for the New Fork Lakes Fire and (C) the gray post-outbreak/stage for the Red Rock Complex Fire. (B) Postfire field data indicated that many trees with green crowns in the New Fork Lakes Fire 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 postfire field plots were subsequently located. Photo credits: Steve Markason and Dale Deiter (USFS).

ized within 10 m of each grid/transect location to avoid bias.

In each plot, data were collected on stand structure, prefire 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 prefire sapling (trees $<$1.4 m that established prefire) occurring in 3-m belt transects along the main axes of the circle plot (N, E, S, W). In the New Fork Lakes Fire, postfire seedlings (trees that germinated postfire) were recorded in 20 0.25-m^2 quadrats placed every 3 m along the main axes of the plot. Because postfire tree seedling density was sparse in the Red Rock Complex Fire, sample area was increased and postfire seedlings were recorded in 3-m belt transects along the main axes of the plot. Slope (degrees), aspect (degrees), and geographic coordinates were measured at plot center.

Prefire beetle outbreak severity

Prefire beetle outbreak severity was quantified following methods outlined in Harvey et al. (2013), 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

TABLE 1. Evidence and criteria used to classify each tree into one of five categories for reconstructing prefire beetle outbreak severity.

Tree classification	Characteristics	Relevant references	Trees sampled (%) NFLF	Trees sampled (%) 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 postfire).		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).	1, 2, 3, 4	2.3	6.8
No visible cambium†	Dead at time of sampling, no needles in canopy, no available cambium visible due to excessive charring, >15 cm diameter at breast height (dbh).	1, 2, 3, 4	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, 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.	2, 4, 5	2.1	0.0
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 postfire 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 years).	2, 4, 6	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

Notes: 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. Both fires were located in the Bridger-Teton National Forest in Greater Yellowstone (Wyoming, USA; see Fig. 1). Relevant references are: 1, Turner et al. (1999); 2, Safranyik and Carroll (2007), 3, Simard et al. (2011); 4, Ken Gibson, *personal communication*; 5, Ken Raffa, *personal communication*; and 6, Powell et al. (2011).

† 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 the area.

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). Our measure of beetle-killed basal area (percentage of stand basal area) includes all prefire tree mortality that occurred during recent beetle outbreaks within each fire. The majority of this mortality is from mountain pine beetle, but tree mortality also includes other mortality agents

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).

Location and burning conditions	Duration (d)	Area burned (ha)	Total % of fire area	Temperature (°C)	Relative humidity (%)	Wind speed (km/h)
New Fork Lakes Fire†						
Moderate	3	1271	16	23.9	17.9	15.8
Extreme	1	1115	14	27.2	13.3	11.9
Red Rock Complex Fire						
Moderate	41	2008	42	20.5	30.4	11.9
Extreme	3	2753	58	24.9	20.1	14.0

Notes: Weather data were downloaded from the Half Moon, Wyoming, remote automated weather station (RAWS; ~25 km southeast of plot locations) for the New Fork Lakes Fire, and the Grand Teton, Wyoming, 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 was the RAWS USA climate archive (www.raws.dri.edu).

† Data for the New Fork Lakes Fire do not cover the entire area of the fire because plots were restricted to the western one-third of the fire; thus, moderate and extreme burning conditions are characterized for this portion of the fire only.

such as western balsam bark beetle and Armillaria root disease for subalpine fir, and spruce beetle (*Dendroctonus rufipennis*) for Engelmann spruce, which was unavoidable in sampling subalpine forests that contain varying proportions of non-pine tree species.

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 codominant 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 postfire litter + duff (i.e., the soil O horizon) to the nearest mm at every 3 m along the main axis of the plot (20 points/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 × 5 grids contained within a 0.5 × 0.5 m sample frame at every 3 m along the main axis of the plot in the New Fork Lakes Fire (500 points/plot) and were spaced at 10-cm intervals along the main axis of the plot in the Red Rock Complex Fire (480 points/plot).

Topography and burning conditions

A 10-m digital elevation model (DEM) was used in ArcGIS 10.1 (ESRI 2012) to generate the following topographic variables for each plot center: elevation (meters), slope (degrees), 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. 2013).

We used daily burn progression maps provided by the BTNF to divide each fire into two burning conditions based on weather conditions and fire growth using established methods (e.g., Thompson and Spies 2009, Harvey et al. 2013). 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 2).

Statistical analysis

To test whether fire severity was linked to prefire outbreak severity, we regressed canopy and surface fire-severity variables against prefire beetle-killed basal area under contrasting burning conditions. General linear models were used for response variables that conformed to linear model assumptions. Percentage data were logit-transformed to bound responses between 0% and 100%. Topographic (elevation, slope, aspect, topographic curvature, slope position) and stand structure (live and dead basal area and stem density) were statistically unrelated to fire severity, and were not included in fire-severity models. Therefore, models for each fire-severity response variable took the following form:

$$\text{Fire severity} \sim \text{burning conditions} \times \text{beetle-killed basal area} \qquad (1)$$

where burning conditions and beetle-killed basal area were treated as fixed effects. Because burning conditions is a categorical variable (moderate, extreme), model results are displayed with one intercept term for each burning condition and one slope term for the effect of beetle-killed basal area under each burning condition.

Stands in the New Fork Lakes Fire contained varying percentages of trees in the green-attack or red stage of outbreak; therefore, we also tested for an effect of the percentage 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. We performed this test using a second regression model on each fire-severity metric with the following form:

$$\text{Fire severity} \sim \text{percentage red stage} \qquad (2)$$

where the percentage red-stage term was treated as a fixed effect. 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 (or equally unrelated) to fire severity. We were unable to account for burning conditions in these models because only one plot in the moderate burning conditions contained trees in the green-attack stage; therefore, we tested for the effect of the percentage of red-stage trees relative to green-attack trees by pooling all plots in the New Fork Lakes Fire. 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.

To test if beetle outbreaks and wildfire produced compound disturbance effects on postfire seedling establishment, we regressed postfire lodgepole pine seedling establishment against beetle-killed basal area after accounting for other variables (fire severity, seed source, serotiny, topography) known to affect postfire 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 per hectare. Prefire serotiny was represented by the percentage of lodgepole pine trees bearing serotinous cones (following methods in Tinker et al. 1994). Topographic variables were statistically unrelated to postfire seedling density, and therefore were not included in models. The model for postfire lodgepole pine seedling density took the following form:

$$\begin{aligned}&\text{Postfire lodgepole pine seedling density}\\&\quad \sim \text{fire severity class}\\&\quad + \text{prefire lodgepole pine basal area/ha}\\&\quad + \text{prefire serotiny} + \text{beetle-killed basal area}\\&\quad + (\text{prefire serotiny} \times \text{beetle-killed basal area}) \qquad (3)\end{aligned}$$

where all terms were treated as fixed effects. We included the interaction term to see if any effects of beetle-killed basal area on postfire seedling density changed with levels of prefire serotiny. Because of very sparse postfire 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 postfire seedling density and prefire outbreak severity overall and within each fire-severity class.

Variograms indicated no spatial structure in model residuals in the Red Rock Complex Fire, permitting the use of general linear models; however, plots in the New Fork Lakes Fire were spatially correlated and required spatial regression models. To account for spatial autocorrelation, we included a random spatial autocorrelation effect using a spherical correlation structure using plot x–y coordinates. For fire-severity response variables, we used generalized least squares (GLS) models that included a spatial term. Seedling density was modeled with a generalized linear mixed model (Poisson family for count data with a log link) that included a spatial term.

All statistical analyses were performed in the R statistical software (version 2.12; R Development Core Team 2010). Generalized least squares models used the function "gls" in the nlme package in R (Pinheiro et al. 2013); generalized linear mixed models used the function "glmmPQL" in the MASS package for R (Venables and Ripley 2002). Results are means ± SE unless noted. For all analyses, we do not perform family-wide adjustments, and we set $\alpha = 0.10$ to reduce the chance of Type II error and not miss potentially meaningful and management-relevant 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 ($\ll$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).

Linked disturbances? Effects of prefire beetle outbreak severity on fire severity

Green-attack/red-stage outbreak.—Several fire-severity metrics increased with prefire outbreak severity when fire occurred in the green-attack/red stage, but effects

TABLE 3. Stand structure characteristics for each study area pre-outbreak, prefire, and postfire.

Stand structure variable	New Fork Lakes Fire	Red Rock Complex Fire
Pre-outbreak		
Live basal area (m^2/ha)	29.5 ± 0.6	39.2 ± 1.5
Live stems (no./ha)	1836 ± 76	1893 ± 131
Lodgepole pine basal area (%)	96 ± <1	52 ± 4
Prefire		
Beetle-killed basal area (m^2/ha)	4.0 ± 0.5	14.6 ± 1.3
Beetle-killed basal area (%)	13.9 ± 1.7	36.9 ± 2.8
Range of beetle-killed basal area (%)	0.0–71.9	2.4–77.5
Beetle-killed snags (no./ha)	101 ± 12	267 ± 23
Prefire serotiny (%)	45.2 ± 2.2	23.5 ± 4.0
Postfire		
Fire-killed basal area (m^2/ha)	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)	0.5 ± 0.2	3.1 ± 1.1
Live stems (no./ha)	52 ± 18	209 ± 54
Lodgepole pine seedlings (no./ha)	111 860 ± 22 489	744 ± 416
Median lodgepole pine seedlings (no./ha)	23 000	0
Conifer seedlings, all spp. (no./ha)	112 280 ± 22 479	1928 ± 1521
Median conifer seedlings, all spp. (no./ha)	23 000	0

Notes: Prefire 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).

were generally most pronounced under moderate rather than extreme burning conditions.

Under moderate burning conditions, char height, bole scorch, and the percentage of trees that were killed by fire increased with outbreak severity (Fig. 2A, D, E, Table 5), reaching levels typically recorded under extreme burning conditions in forests with or without prefire beetle outbreaks. The percentage of tree basal area killed by fire and both surface fire-severity metrics were unrelated to prefire outbreak severity (Fig. 2B, C, F, Table 5). Very few plots that burned under moderate conditions had high outbreak severity, lowering confidence in trends when ~50% of the basal area was beetle killed (Fig. 2). When we removed the one plot at ~50% beetle-killed basal area, all tests were nonsignificant ($P > 0.10$) 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, fire-severity metrics were either unrelated to, or showed modest increases, with higher outbreak severity; however, effect sizes decreased relative to moderate burning conditions and were of marginal biological significance (Fig. 2G–L, Table 5). Bole scorch, the percentage of trees and tree basal area killed by fire, and charred surface cover were unrelated to outbreak severity. Char height increased and postfire litter + duff depth decreased (indicating higher fire severity) with higher levels of outbreak severity. However, these effect sizes were slight (e.g., char height increasing from ~12 m to ~16 m; postfire litter + duff decreasing from ~11 mm to ~2 mm; Fig. 2G, I).

Fire severity also varied with the relative percentage of green-attack vs. red-stage trees. The percentage of

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).

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

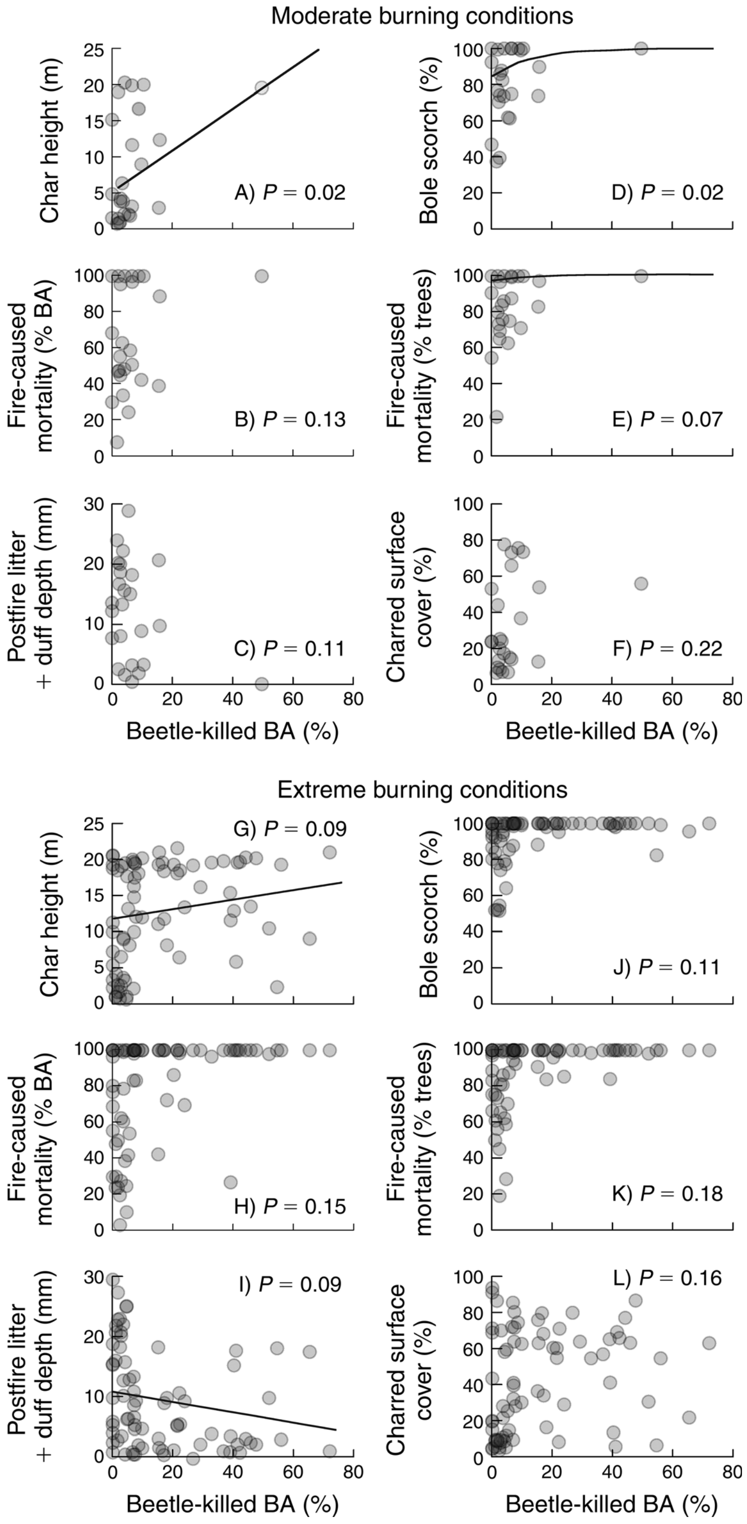

FIG. 2. Fire severity vs. outbreak severity for plots burning under moderate and extreme burning conditions in lodgepole pine forests in the green-attack/red stage of mountain pine beetle outbreak (New Fork Lakes Fire). Plots with lines illustrate significant ($P < 0.10$) effects from the models in Table 5. BA represents basal area.

TABLE 5. General linear model results testing for effects of beetle outbreak severity on subsequent fire severity.

Response and predictor	β	SE	*t*	*P*
Green-attack/red stage (New Fork Lakes Fire)				
Char height (m)†‡				
Moderate BC (intercept)	6.10	2.09	2.92	<0.01
Extreme BC (intercept)	11.96	1.30	9.20	<0.01
Beetle-killed BA: moderate BC	27.70	11.95	2.32	0.02
Beetle-killed BA: extreme BC	6.22	3.60	1.72	0.09
Bole scorch (%)†§				
Moderate BC (intercept)	1.67	0.37	4.54	<0.01
Extreme BC (intercept)	2.71	0.23	11.98	<0.01
Beetle-killed BA: moderate BC	4.29	1.88	2.28	0.02
Beetle-killed BA: extreme BC	0.91	0.57	1.59	0.11
Tree mortality (% BA)†§				
Moderate BC (intercept)	3.32	0.18	18.08	<0.01
Extreme BC (intercept)	3.40	0.11	29.63	<0.01
Beetle-killed BA: moderate BC	1.70	1.11	1.53	0.13
Beetle-killed BA: extreme BC	0.48	0.33	1.46	0.15
Tree mortality (% trees)†§				
Moderate BC (intercept)	3.05	0.21	14.46	<0.01
Extreme BC (intercept)	3.38	0.13	25.49	<0.01
Beetle-killed BA: moderate BC	2.51	1.36	1.85	0.07
Beetle-killed BA: extreme BC	0.54	0.40	1.36	0.18
Litter + duff depth (mm)†‡				
Moderate BC (intercept)	14.28	2.12	6.73	<0.01
Extreme BC (intercept)	10.62	1.36	7.82	<0.01
Beetle-killed BA: moderate BC	−24.98	15.29	−1.63	0.11
Beetle-killed BA: extreme BC	−7.90	4.56	−1.73	0.09
Charred surface cover (%)†§				
Moderate BC (intercept)	−1.31	0.44	−2.99	<0.01
Extreme BC (intercept)	−0.79	0.28	2.88	<0.01
Beetle-killed BA: moderate BC	3.52	2.87	1.23	0.22
Beetle-killed BA: extreme BC	1.22	0.86	1.43	0.16
Gray stage/post-outbreak (Red Rock Complex Fire)				
Char height (m)‡				
Moderate BC (intercept)	12.93	3.28	3.94	<0.01
Extreme BC (intercept)	9.23	1.76	5.24	<0.01
Beetle-killed BA: moderate BC	−13.37	6.94	−1.93	0.06
Beetle-killed BA: extreme BC	5.20	4.70	1.11	0.28
Bole scorch (%)§				
Moderate BC (intercept)	4.15	0.92	4.50	<0.01
Extreme BC (intercept)	2.19	0.49	4.44	<0.01
Beetle-killed BA: moderate BC	−5.85	1.95	−3.00	<0.01
Beetle-killed BA: extreme BC	2.06	1.32	1.56	0.13
Tree mortality (% BA)§				
Moderate BC (intercept)	4.83	1.14	4.26	<0.01
Extreme BC (intercept)	2.32	0.61	3.81	<0.01
Beetle-killed BA: moderate BC	−6.90	2.40	−2.88	<0.01
Beetle-killed BA: extreme BC	2.00	1.63	1.23	0.23
Tree mortality (% trees)§				
Moderate BC (intercept)	4.37	1.06	4.11	<0.01
Extreme BC (intercept)	2.42	0.27	4.24	<0.01
Beetle-killed BA: moderate BC	−6.49	2.25	−2.89	<0.01
Beetle-killed BA: extreme BC	1.92	1.52	1.27	0.21
Litter + duff depth (mm)‡				
Moderate BC (intercept)	0.28	2.53	0.11	0.91
Extreme BC (intercept)	3.37	1.36	2.49	0.02
Beetle-killed BA: moderate BC	12.57	5.35	2.35	0.02
Beetle-killed BA: extreme BC	−2.85	3.63	−0.79	0.44
Charred surface cover (%)§				
Moderate BC (intercept)	1.53	1.38	1.11	0.28
Extreme BC (intercept)	0.10	0.74	0.14	0.89
Beetle-killed BA: moderate BC	−4.25	2.92	−1.46	0.15
Beetle-killed BA: extreme BC	2.10	1.98	1.06	0.29

Notes: Burning conditions and beetle-killed basal area terms were included as fixed effects. Burning conditions is a categorical variable with each burning condition as a different model intercept. Abbreviations are: BC, burning conditions; BA, basal area; Beetle-killed BA: moderate BC, beetle effect under moderate burning conditions; and Beetle-killed BA: extreme BC, beetle effect under extreme burning conditions.

† Spatial regression accounting for spatial autocorrelation, using the function "gls" (Pinheiro et al. 2013).

‡ General linear model (no transformation).

§ General linear model (logit-transformed for percentage variables).

TABLE 6. General linear models testing for relationship between fire severity and the percentage of beetle-killed basal area in the red stage (red stage BA/[green-attack + red-stage BA]) in the New Fork Lakes Fire.

Response and predictor	β	SE	t	P
Char height (m)†‡				
Intercept	13.75	1.95	7.04	<0.01
Percentage red stage	−2.41	1.94	−1.24	0.22
Bole scorch (%)†§				
Intercept	2.98	0.36	8.88	<0.01
Percentage red stage	−0.45	0.30	−1.48	0.14
Tree mortality (% BA)†§				
Intercept	3.68	0.17	21.28	<0.01
Percentage red stage	−0.29	0.16	−1.79	0.08
Tree mortality (% trees)†§				
Intercept	3.69	1.20	18.70	<0.01
Percentage red stage	−0.37	0.19	−1.94	0.06
Litter + duff depth (mm)†‡				
Intercept	7.70	2.27	3.39	<0.01
Percentage red stage	2.94	2.41	1.22	0.23
Charred surface cover (%)†§				
Intercept	−0.42	0.42	−1.01	0.31
Percentage red stage	−0.39	0.44	−0.90	0.37

† Spatial regression accounting for spatial autocorrelation, using the function "gls" (Pinheiro et al. 2013).
‡ General linear model (no transformation).
§ General linear model (logit-transformed for percentage variables).

trees and tree basal area killed by fire increased with a higher relative percentage of trees in the green-attack stage, whereas green-attack and red-stage trees contributed equally to other measures of fire severity (Table 6).

Gray stage/post-outbreak.—Most fire-severity metrics declined with higher prefire outbreak severity when fire occurred in the gray stage during moderate burning conditions, but all were unrelated to outbreak severity during extreme conditions.

Under moderate burning conditions, all canopy fire-severity measures decreased and postfire litter + duff depth increased (indicating decreased fire severity) with higher prefire beetle outbreak severity (Fig. 3A–E, Table 5). Charred surface cover was unrelated to prefire outbreak severity (Fig. 3F, Table 5). Under extreme burning conditions, all fire-severity metrics were unrelated to prefire outbreak severity (Fig. 3G–L, Table 5).

Compound disturbances? Effects of outbreak severity on postfire tree seedling density

Postfire conifer regeneration was variable within each fire, but mean seedling densities differed by two orders of magnitude between the two fires. Postfire tree seedling density was high in the New Fork Lakes Fire (mean = 111 860 seedlings/ha, median = 23 000 seedlings/ha, range = 0–1 320 000 seedlings/ha; Table 3). Lodgepole pine made up 99.6% of all postfire tree seedlings, and all were one or two years old at the time of sampling. Postfire tree seedling density was much lower in the Red Rock Complex Fire (mean = 1928 seedlings/ha, median = 0 seedlings/ha, range = 0–639 179 seedlings/ha). Lodgepole pine made up 98.2% of seedlings in all but two of the plots, which had seedling densities >100 000 seedlings/ha 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, postfire seedling density differed with fire severity, with seedling density highest in plots that burned as severe-surface fire (Table 7). 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 prefire 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 prefire serotiny), there was no evidence of compound disturbance effects from prefire outbreak followed by fire. Postfire lodgepole pine seedling density was not related to prefire outbreak severity, which did not interact with serotiny (Fig. 4A, Table 8). Postfire lodgepole pine seedling density was also unrelated to prefire beetle outbreak severity when no other covariates were included in the model ($t = 0.12$, $P = 0.91$, model not shown). When fire burned in gray-stage/post-outbreak stands (Red Rock Complex Fire), we also found no evidence of compound disturbance effects on postfire tree seedling density. Nonparametric (Spearman's rank) tests revealed no relationship between postfire lodgepole pine seedling density and prefire beetle outbreak severity overall ($r_S = -0.07$, $P = 0.65$) or within burn-severity classes (all $P > 0.10$; Fig. 4B).

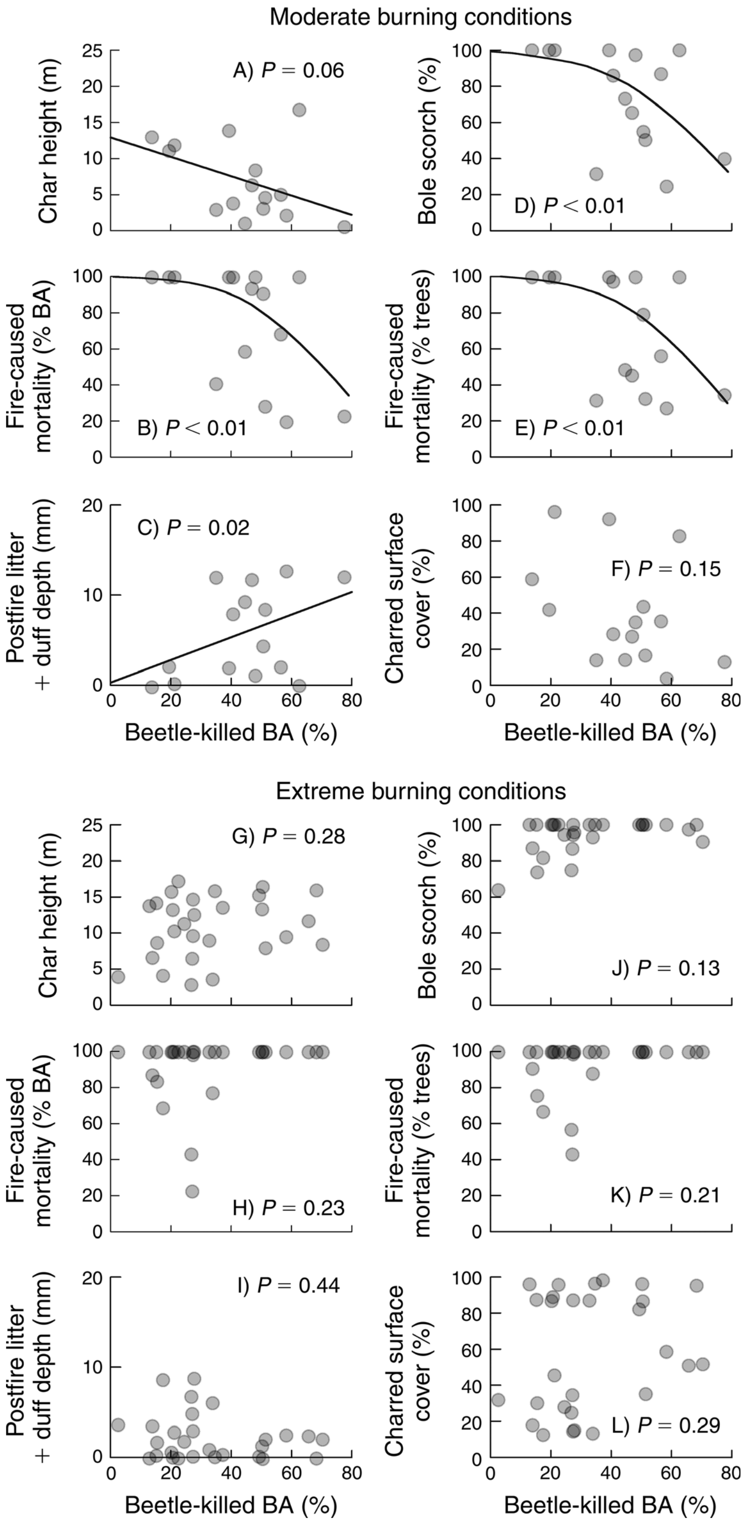

FIG. 3. Fire severity vs. outbreak severity for plots burning under moderate and extreme burning conditions in lodgepole pine forests in the gray-stage/post-outbreak phase of mountain pine beetle outbreak (Red Rock Complex Fire). Plots with lines illustrate significant ($P < 0.10$) effects from the models in Table 5. BA represents basal area.

TABLE 7. Postfire lodgepole pine seedling regeneration density within each fire-severity class in the New Fork Lakes fire and the Red Rock Complex Fire.

Fire name and fire-severity class	Postfire lodgepole pine seedlings (no./ha) Mean	SE	Median
New Fork Lakes Fire			
Light-surface ($n = 15$)	68 533	15 060	58 000
Severe-surface ($n = 40$)	241 400	49 339	116 000
Crown ($n = 45$)	11 156	1 756	8 000
Red Rock Complex Fire			
Light-surface ($n = 14$)	6	6	0
Severe-surface ($n = 13$)	2 449	1 288	0
Crown ($n = 16$)	5	5	0

DISCUSSION

Prefire beetle outbreak severity was associated with some measures of fire severity in subalpine forests of Greater Yellowstone, indicating that these disturbances were moderately linked. However, the strength and the direction of the relationship 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 when most large wildfires in subalpine forests occur, most relationships between fire severity and prefire beetle outbreak severity were weak (i.e., of marginal biological significance) or nonsignificant in both outbreak stages. Postfire seedling densities suggested that recent beetle outbreaks and subsequent fire do not produce compound disturbance effects in serotinous lodgepole pine forests. Our results show that most measures of wildfire severity are unrelated to prefire beetle outbreaks across a wide range of beetle-caused tree mortality, highlight the importance of understanding beetle outbreak effects on wildfire in the context of other drivers (e.g., burning conditions), and illustrate that any effects that are present can change with time since outbreak. Further, they suggest that serotiny can provide resilience against potential compound disturbance effects from beetle outbreaks and fire.

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), and we also detected a modest 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

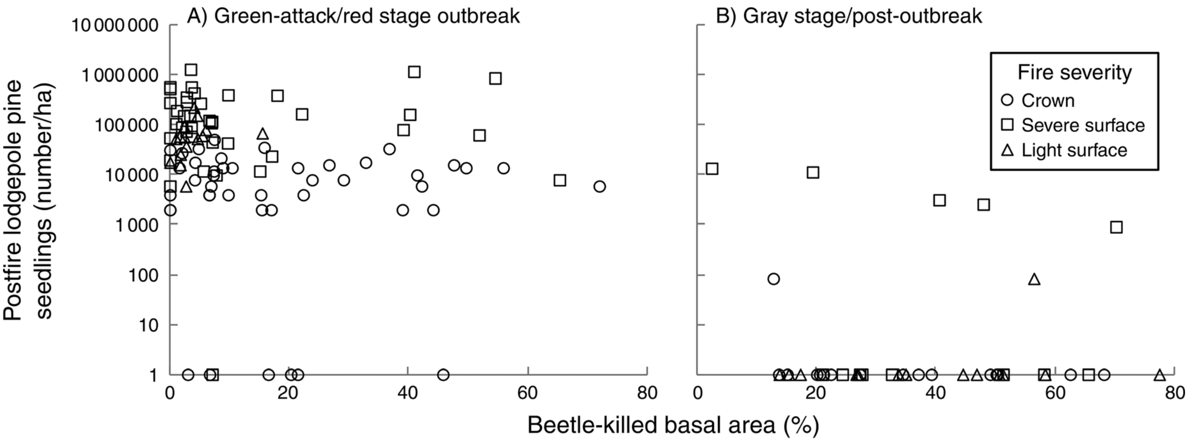

FIG. 4. Postfire lodgepole pine seedlings vs. prefire beetle outbreak severity in each fire-severity class for (A) the green-attack/red stage (New Fork Lakes Fire) and (B) the gray stage/post-outbreak (Red Rock Complex Fire). Postfire lodgepole pine seedling density was unrelated ($P > 0.10$) to prefire outbreak severity in both fires.

Table 8. Generalized linear model testing the relationship between postfire lodgepole pine regeneration and prefire beetle outbreak severity in the New Fork Lakes Fire, while accounting for fire severity, potential seed source, and prefire serotiny.

Response and predictor	β	SE	*t*	*P*
Postfire lodgepole pine seedlings (no./ha)†‡				
Light-surface fire (intercept)	7.84	0.57	13.69	<0.01
Severe-surface fire (intercept)	8.63	0.57	15.24	<0.01
Crown fire (intercept)	6.26	0.69	9.07	<0.01
Lodgepole pine BA/ha	0.09	0.01	6.77	<0.01
Prefire serotiny (% of trees)	0.95	0.46	2.07	0.04
Beetle-killed BA (%)	−0.13	1.49	−0.09	0.93
Prefire serotiny × beetle-killed BA	1.70	2.17	0.18	0.44

Note: BA represents basal area.

† Spatial regression accounting for spatial autocorrelation, using the function "glmmPQL" (Venables and Ripley 2002).

‡ Generalized linear model (Poisson distribution with log-link for count data).

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. 2012*a*). Therefore, during the first year of an outbreak (during the green-attack stage, but prior to the classic red stage), there can be a brief period of increased canopy flammability without an accompanying decrease in canopy bulk density (Jolly et al. 2012*b*). The fire-severity responses we measured in stands with ongoing beetle attack were consistent with fire behavior simulations early in outbreaks where beetle-killed trees retain their needles and a large percentage of tree crowns are fading from green to red (Hoffman et al. 2012, Schoennagel 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). The decline in trees killed by fire and tree basal area killed by fire with an increasing relative percentage of red-stage to green-attack trees supports this expectation; however, we also show that red-stage and green-attack trees were of similar importance for other metrics. Thus, our results suggest modest increases in fire severity in the earliest stages of the outbreak, before canopy bulk density declines, and provide support for the hypothesis that green-attack trees contribute to increased 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 2007*a*, *b*, 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, which aligns with our finding that three out of four measures of surface fire severity were unrelated to outbreak severity. The increase 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 2007*a*, 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 2007*b*, 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 postfire 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 prefire outbreak severity in the gray stage. These findings are consistent with modeling studies, given the minimal prefire 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 two to three times from undisturbed stands (Page and Jenkins 2007*a*). 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 2007*b*, 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 three to nine years 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, Donato et al. 2013*a*). 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 have a greater affect on subsequent fire severity (Jenkins et al. 2008, Schoennagel et al. 2012).

Comparisons with other studies

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 many previous studies are challenging because of differences in questions and/or approaches. 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 behavior simulation studies can help inform the interpretation of our results; however, predicted fire behavior is not directly comparable to postfire 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. Our study tested for effects on fire severity across a range of prefire outbreak severity, including stands unaffected by recent outbreaks which effectively served as a control. However, our study focused on stands that did burn, meaning we cannot directly compare our results to studies that examine the probability that beetle-affected stands will burn relative to unaffected stands (see Bebi et al. 2003, Bigler et al. 2005, Lynch et al. 2006, Kulakowski and Jarvis 2011).

Consistent with our study, other retrospective studies report little evidence for effects of prefire 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 when green-attack trees are present, 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, prefire 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. 2013). 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?

Prefire beetle outbreaks and subsequent fire did not produce compound disturbance effects (Paine et al. 1998) on tree regeneration for serotinous lodgepole pine. Postfire seedling density, as we found, is largely driven by prefire serotiny along with fire severity in Rocky Mountain lodgepole pine forests (Turner et al. 1997, 1999, Schoennagel et al. 2003), and prefire outbreak severity does not appear to alter this relationship. In the early stages of a bark beetle outbreak, serotiny may confer resilience to subsequent fire by sustaining a viable seedbank after tree death (Aoki et al. 2011, Teste et al. 2011*a*). Decreased postfire 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. 2011*a*) 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 prefire serotiny (>15%), there was a strong decrease in postfire lodgepole pine seedling density with increasing prefire 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 postfire 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 when burned. 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*), driving variation in early postfire tree establishment (Côté et al. 2013, Harvey et al. 2013).

Implications for post-outbreak management of stands

For the few fire-severity measures that were related to prefire outbreak severity, 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 some measures of 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 mid-to-late red stage (Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012). Such an early response to beetle outbreak would be challenging because many tree crowns 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 abundant red crowns are visible, and subsequent planning procedures for treatments are implemented (commonly $\geq$2 years on public lands; Collins et al. 2012, Donato et al. 2013*b*, Griffin et al. 2013), the potential for severe fire may already be declining; thus, treatments would occur in late-red/early-gray stands of already-reduced fire potentials. 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 there may not be an elevated need for management treatments to reduce fire severity in gray-stage/post-outbreak forests where beetle-killed trees remain standing (i.e., no more necessary than in un-attacked forests). In later stages ($>$20 years post-outbreak), simulation models have predicted that accumulation of coarse fuel could exceed target levels and increase surface-fire severity in untreated stands relative to treated stands (Collins et al. 2012, Griffin et al. 2013, Donato et al. 2013*b*); 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 effects of prefire outbreaks differing depending on burning conditions (Simard et al. 2011, Schoennagel et al. 2012), and we observed fire-severity responses consistent with this expected fire behavior. For example, the biological significance of effects in extreme burning conditions are marginal, as the range of these responses across the spectrum of outbreak severity represent minor changes within already stand-replacing fire. Further, although we accounted for moderate and extreme burning conditions within each fire, both fires occurred in relatively mild fire years in Greater Yellowstone (Westerling et al. 2011). During years of severe drought, prefire outbreaks may have even less of a biological effect on fire severity, which may further reduce the effectiveness of fuel treatments. Comparisons of beetle-fire relationships in multiple fires across broad regions and/or under 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 postfire 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 in year two in areas of less severe fire (Turner et al. 1997). Reduced fire severity in gray-stage stands can enhance survival of prefire advance regeneration, diminishing the importance of postfire seedling establishment. There may be a window of time in the gray and silver stages when seed supply remains low until surviving 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 moderately linked to prefire bark beetle outbreaks in lodgepole pine forests of Greater Yellowstone. For the fire-severity measures that were related to prefire outbreak severity, the strength and direction of interactions changed with burning conditions (i.e., weather) and the interval between beetle outbreaks and fire. Our results reveal a brief period where some measures of fire severity increase with outbreak severity in the green-attack/red stage, and suggest an influence of green-attack trees driving some of these trends. This is followed by decreases in fire severity in the gray post-outbreak stage when snags remain standing. However, the biologically significant effects of prefire 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 or may not be warranted to reduce future fire severity and/or improve postfire tree establishment in serotinous lodgepole pine forests.

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Supplemental Material

Appendix A

Time series of bark beetle-attributed tree mortality in the Red Rock Complex Fire (*Ecological Archives* A024-195-A1).

Appendix B

Photographs of bark beetle outbreak severity measurements (*Ecological Archives* A024-195-A2).

Appendix C

Correlation among fire-severity measurements (*Ecological Archives* A024-195-A3).