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Fire severity unaffected by spruce beetle outbreak in spruce-fir forests in southwestern Colorado

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Abstract. Recent large and severe outbreaks of native bark beetles have raised concern among the general public and land managers about potential for amplified fire activity in western North America. To date, the majority of studies examining bark beetle outbreaks and subsequent fire severity in the U.S. Rocky Mountains have focused on outbreaks of mountain pine beetle (MPB; *Dendroctonus ponderosae*) in lodgepole pine (*Pinus contorta*) forests, but few studies, particularly field studies, have addressed the effects of the severity of spruce beetle (*Dendroctonus rufipennis* Kirby) infestation on subsequent fire severity in subalpine Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests. In Colorado, the annual area infested by spruce beetle outbreaks is rapidly rising, while MPB outbreaks are subsiding; therefore understanding this relationship is of growing importance. We collected extensive field data in subalpine forests in the eastern San Juan Mountains, southwestern Colorado, USA, to investigate whether a gray-stage (<5 yr from outbreak to time of fire) spruce beetle infestation affected fire severity. Contrary to the expectation that bark beetle infestation alters subsequent fire severity, correlation and multivariate generalized linear regression analysis revealed no influence of pre-fire spruce beetle severity on nearly all field or remotely sensed measurements of fire severity. Findings were consistent across moderate and extreme burning conditions. In comparison to severity of the pre-fire beetle outbreak, we found that topography, pre-outbreak basal area, and weather conditions exerted a stronger effect on fire severity. Our finding that beetle infestation did not alter fire severity is consistent with previous retrospective studies examining fire activity following other bark beetle outbreaks and reiterates the overriding influence of climate that creates conditions conducive to large, high-severity fires in the subalpine zone of Colorado. Both bark beetle outbreaks and wildfires have increased autonomously due to recent climate variability, but this study does not support the expectation that post-beetle outbreak forests will alter fire severity, a result that has important implications for management and policy decisions.

Key words: Dendroctonus rufipennis; *disturbance interactions; fire ecology; Rocky Mountains; San Juan Mountains; subalpine zone; wildfire.*

Introduction

Widespread tree mortality from recent bark beetle outbreaks across western North American forests (Raffa et al. 2008, Meddens et al. 2012) has raised concern among the general public, land managers, and scientists about periods of amplified fire activity (Hicke et al. 2012, Jenkins et al. 2012). Results from fire models and anecdotal evidence from firefighters suggests that changes to forest fuel structure and composition from beetle outbreaks, particularly in areas of severe infestation (>90% of tree basal area), may promote periods of elevated fire behavior and uncertain ecological implications for post-fire forest ecosystems. A beetle outbreak has the potential to alter the probability, extent, or severity of a subsequent wildfire (linked disturbances; sensu Simard et al. 2011), but the necessary conditions of a beetle outbreak (e.g., severity and time since outbreak) that elevate fire activity remain disputed. Bark beetle outbreaks followed by fire may also act synergistically to produce nonlinear or unpredictable changes in ecosystem structure and function (compound disturbances; sensu Paine et al. 1998), which has important consequences for post-fire regeneration and resilience of subalpine forests in the Rocky Mountains (Kulakowski et al. 2013, Harvey et al. 2014*a*). Alternatively, wildfire may be independent of bark beetle outbreaks, or the effects of other biophysical factors may override a potential interaction between the two disturbances (Harvey et al. 2013). One such overriding factor is climate, which has been independently linked to increases in bark beetle infestation from warming temperatures (Hebertson and Jenkins 2008, Bentz et al. 2010, Hart et al. 2014) and increased area burned from increased drought severity (Dennison

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et al. 2014). In this context, management and policy decisions need to be informed by a better understanding of the nature and magnitude of any effects of prior bark beetle outbreaks on subsequent fire activity.

To date, the majority of studies examining links between bark beetle outbreaks and subsequent fire activity in the U.S. Rocky Mountains have focused on outbreaks of mountain pine beetle (MPB; *Dendroctonus ponderosae*), which have infested >71000 km^2 of primarily lodgepole pine (*Pinus contorta)* forest between 2000 and 2013 in the western USA (Hicke et al. 2012, Hart et al. 2015). Currently, the MPB outbreaks are subsiding, but recent outbreaks of spruce beetle (*Dendroctonus rufipennis* Kirby) in Colorado have affected over half a million hectares of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forest (Colorado State Forest Service 2014). Initiating in ca. 2001, the total area affected has increased abruptly since 2009, and in 2014 alone, over 100000 new hectares were affected (Appendix S1). Thus, the potential linkage of fire activity to previous spruce beetle outbreak is of increasing concern among the general public and policy makers in Colorado (Finley 2013, Colorado State Forest Service 2014).

Stand-scale fire behavior modeling and retrospective studies suggest complex influences of spruce beetle outbreaks on fire behavior (intensity, type, flame length; Jenkins et al. 2008, DeRose and Long 2009) and fire severity (ecological effects; Kulakowski and Veblen 2007). Using fuel inputs from chronosequence measurements of bark beetle outbreaks, fire behavior modeling studies predict periods of amplified fire behavior (active crown fire, rate of spread, flame length, and fireline intensity), primarily in the early stages of an outbreak, that track changes to fuel profiles (continuity, flammability, structure; see Hicke et al. 2012 for review). However, expectations vary with infestation severity and simulated weather conditions (Jenkins et al. 2008, DeRose and Long 2009). Following tree death from spruce beetle, foliar moisture and flammability remain highly variable, but a decrease in foliar moisture and changes to foliar chemistry in the yellow stage (needles retained and yellow-colored, fine-fuel intact) promote needle flammability and increase crown fire probability for a brief period prior to needle drop (<14 months after trees are attacked; Page et al. 2014). The pulse of yellow needles (1–2 yr post-attack) to the forest floor initiates the gray stage (2–10 yr post-attack; Hansen et al. 2010). During the gray stage, fire behavior models predict decreased probability of canopy fire from reduced canopy bulk density (CBD) and canopy fuel continuity, and increased surface fire intensity from the accumulation of canopy fuel on the forest floor (Jenkins et al. 2008, DeRose and Long 2009). During the old stage (>10 yr post-attack), surface fire intensity continues to escalate with increased surface fuel loading and the probability of crown fire returns when understory vegetation (e.g., shrubs and tree regeneration) creates ladder fuels to the forest canopy (Hicke et al. 2012). Despite the limitations of fire models (sensu Coen 2005, Jolly et al. 2012, Alexander and Cruz 2013), these predictions offer insight for fire suppression operations and scientific inquiry about periods of elevated fire behavior (Jenkins et al. 2008, DeRose and Long 2009), but do not necessarily translate to predictions of post-fire ecological effects across topographically and biologically complex landscapes, or long-term implications for forest regeneration and resilience.

Though retrospective studies in spruce-fir forests of Colorado address fundamentally different questions than fire behavior modeling results, case studies using overlay analysis of remotely sensed spatial datasets of beetle infestation and fire have not supported hypothesized increases in fire frequency (Bebi et al. 2003), extent (Bigler et al. 2005), or severity (Bigler et al. 2005, Kulakowski and Veblen 2007). Instead, topography, climatic conditions and short-term weather (hot, dry, windy weather) conducive to fire spread, and pre-outbreak fuel loads commonly lead to high-severity fire irrespective of beetle activity (Veblen et al. 1994, Bigler et al. 2005, Kulakowski and Veblen 2007). The incongruence between fire modeling studies and case studies is a likely result of covarying factors (e.g., spruce beetle outbreak and forest structure) in case studies, differences in spatial scale (stand vs. landscape scale), and/or the mechanistic limitations of existing fire models, which cannot incorporate fine-scale heterogeneity in fuel profiles or weather. Further, the case studies examining the effect of spruce beetle severity on fire severity were limited by the accuracy and spatial resolution of the remotely derived beetle and fire severity datasets, which lacked robust field quantification of beetle or fire severity. These limitations highlight the need for research that uses field methods to quantify the severity of both the pre-fire bark beetle outbreak and post-wildfire effects on the forest, while controlling for potentially confounding factors. This can be done by including stands with high outbreak severity and similar uninfested stands that serve as a control (Harvey et al. 2013).

During extreme drought in 2012–2013, lightning ignited the West Fork Complex fires (West Fork, Papoose, and Windy Pass Fires; 2013), East Fork fire (2013), and Little Sands fire (2012), which collectively burned 60000 ha of gray-stage spruce beetle infested forest (<5 yr from outbreak to time of fire; Appendix S1; Colorado State Forest Service 2014) in the eastern San Juan Mountains, southwestern Colorado (Fig. 1). The rare overlap of two climate-driven forest disturbances provides a unique opportunity to conduct an empirical field study that quantifies the influence of a gray-stage spruce beetle infestation on fire severity. Specifically, we seek to address the following question: After controlling for abiotic and biotic factors known to affect fire severity, how did spruce beetle infestation influence the severity of the 2012–2013 fire events in the spruce-fir forests in southwestern Colorado?

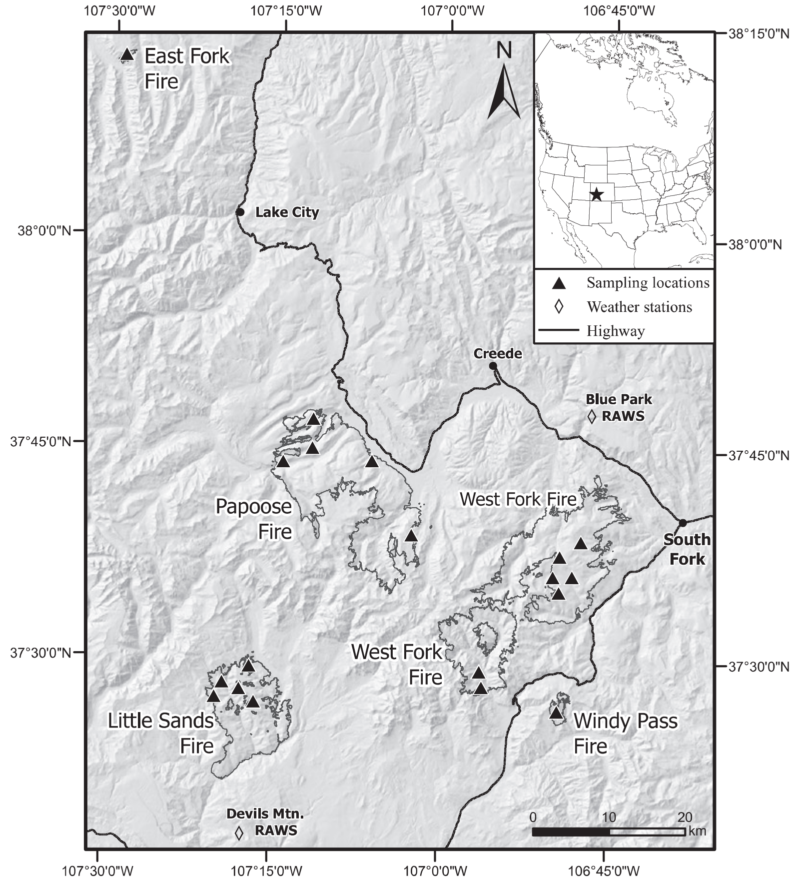

Fig. 1. Location of the five subalpine fires studied and the two weather stations (RAWS, Remote Automatic Weather Stations) used to assess burning conditions in the southern Colorado Rocky Mountains, USA. All fires burned in the summer of 2013 with the exception of the Little Sands Fire that burned in 2012. The insets display the location of the study area in North America and Colorado.

Methods

Study area

The study fires (West Fork Complex fires, Little Sands fire, and East Fork fire) burned in three National Forests (Rio Grande, San Juan, and Uncompaghre) in the southern Colorado Rocky Mountains (37°30′ N, 107°00′ W; Fig. 1). The elevation ranged from the lower extent of spruce-fir forest (2500 m) to tree line (3500 m) across steep mountainous terrain (plot slope mean, 25°; range, 0–62°). The mountains and basins in the study area are composed of Precambrian rocks and more recent alluvial sediments, which were built and eroded by a variety of geologic processes (Romme et al. 2009). Late spring snowpack and summer monsoon rains maintain a cool and moist climate in the subalpine zone (Romme et al. 2009). From 1981 to 2010, annual mean precipitation was 85 cm and mean annual temperatures ranged from −7° to 13°C in the eastern San Juan Mountains (PRISM 2014). Subalpine forests in the area are composed of Engelmann spruce, subalpine fir, and aspen (*Populus tremuloides*). The lower extent of the study area in the upper montane zone includes mixed conifer forests of Douglas fir (*Psuedotsuga menziesii*) and white fir (*Abies concolor*). Lodgepole pine is uncommon in this region of the Rocky Mountains (Peet 2000).

The spruce beetle outbreak in the eastern San Juan Mountains initiated around 2001 and reached an epidemic level in 2008 (Appendix S1). The area around the West Fork Complex fires was severely infested by spruce beetle (mean plot basal area infested, 58%; range, 9–95%), while beetle infestation in the Little Sands and East Fork fire was minimal (mean plot basal area infested, 8%; range, 0–60%). By the time of the fires in 2012–13, the beetle-killed Engelmann spruce had been dead for approximately 5 yr; therefore they had lost a majority of their needles, but retained most fine branches and bark (gray stage). All five fires were lightning ignited and burned 60000 ha (Appendix S2) within remote areas of three National Forests, primarily during extreme fire weather conditions. Consequently, suppression efforts were limited. We restricted sampling to areas without evidence of active suppression, which was determined by evidence of fireline and recent chainsaw activity.

Sampling design

Plots (n = 143) were stratified across a range of spruce beetle infestation and fire severities within spruce-fir dominated stands. Starting from a random location >100 m from the fire perimeter, plots were systematically spaced by at least 400 m to reduce the influence of spatial autocorrelation and randomly located in a suitable site (e.g., >80% spruce-fir basal area and no rock outcrops or meadow). In smaller fires (Windy Pass and East Fork Fire), a 400 m grid was aligned within the fire perimeter to maximize potential sampling locations. Within each 20 × 20 m plot (0.04 ha), data were collected on pre- and post-fire stand structure and composition, severity of pre-fire beetle effects on tree mortality (percentage of total basal area killed), and fire severity. Sampling was conducted from June to August 2014 (1 yr after the West Fork Complex and East Fork Fire, and 2 yr after the Little Sands Fire).

Determining the effects of spruce beetle and fire on stand structure

We assessed stand structure and composition by recording tree species, tree status (live or dead), diameter at breast height (dbh) to the nearest centimeter, canopy position, and height (m) of the five tallest trees. Aspect (°), slope (°), elevation (m), and geographic position (UTMs) were recorded at plot center. We computed basal area, tree stems per hectare (stems/ha), and quadratic mean diameter (Curtis and Marshall 2000) from the plot data.

Pre-fire beetle outbreak severity assessment

Following the methods outlined in Harvey et al. (2014*a*), pre-fire spruce beetle outbreak severity was measured by removing the bark on dead trees >4 cm (7186 trees) (1.4 m) to examine the cambium for evidence of *Dendroctonous* activity. Seedlings and saplings <4 cm dbh and other understory vegetation was fully consumed in most plots and thus could not be reliably measured. Each tree was classified as (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 (Appendix S3). Trees classified as "killed by spruce beetle prior to fire" were divided into two categories: (1) visible cambium (20.9% of total trees) and (2) no visible cambium (10.3% of total trees). Those trees with no visible cambium were excessively charred, but we classified them as "killed by spruce beetle prior to fire" if they were spruce and the dbh was greater than the minimum size class attacked in adjacent unburned areas (typically 10–15 cm dbh). The spruce beetle was responsible for a majority of the tree mortality, but other potential mortality agents included other bark beetles (e.g., *Ips*, *Dryocoetes*), climate, and tree competition (Romme et al. 2009). We computed spruce beetle-caused tree mortality (percentage of basal area) by dividing the basal area of the trees classified as "killed by spruce beetle prior to fire" by the total basal area in a plot.

Fire severity assessment

Field and remotely sensed assessments of fire severity measured fire effects from the forest floor and the canopy. For each tree >4 cm dbh we recorded: char height to the nearest 0.5 m, percentage of the tree charred (10% classes), maximum percentage of charring around the circumference of the main bole (10% classes), and the percentage of the bole with fine fuel (<1 cm) and needles still attached (10% classes). Trees were classified as "killed by fire" if they were alive at time of fire, dead at time of sampling, and had no evidence of forest pathogens or wounds (Appendix S2). We computed fire-caused tree mortality (percentage of basal area and stems per hectare) from only those trees alive at time of fire. Trees retaining a significant portion (>75%) of their green needles post-fire and without post-fire beetle activity were classified as "live." We measured forest floor fire severity by dividing each plot into quadrants and estimating the percentage of forest floor charred within each quadrant to the nearest 10%. We did not sample other measures of surface fire severity (e.g., litter and duff loss), because precipitation events had significantly altered immediate post-fire characteristics at time of sampling (1–2 yr post-fire). To compare field measures to remote measures of fire severity, we extracted the relative differenced Normalized Burn Ratio (RdNBR) value at plot center; downloaded from Monitoring Trends in Burn Severity website (MTBS 2013) for each plot in the West Fork Complex and Little Sands fires. RdNBR data were not available for the East Fork fire. RdNBR is a measure of pre- and post-fire-caused change to live green biomass, moisture content, and soil characteristics; it is commonly used as a remote measure of fire severity by the USDA (Miller et al. 2009).

Topography and solar radiation

Differences in solar radiation and available moisture created by topographic variables (e.g., aspect, slope, and curvature) can influence fuel characteristics and fire activity (Holden et al. 2009). We derived and extracted the following topographic and radiation variables at plot center from a 30 m digital elevation model in ArcGIS 10.2: aspect (Northeast Index; Beers et al. 1966), topographic curvature (the second derivative of elevation; Zevenbergen and Thorne 1987), slope position, annual solar radiation (McCune and Keon 2002), and heat load index (McCune and Keon 2002). Slope position is a relative measure of elevation from 0 (toe of slope) to 1 (ridge top) that is preferable to raw elevation because it accounts for the relative position of a location on the slope, which is most mechanistically linked with fire. Both annual solar radiation and heat load index rescale aspect to measure incident radiation along a north-south axis and relative temperature along a northeast (coolest slope)-southwest axis (warmest slope), respectively.

Assessing weather conditions

We used maps of daily fire progression from the Geospatial Multi-Agency Coordination Group (GeoMAC; USGS 2013) and daily averaged weather data (collected hourly) during the burning period (10:00–17:00 h) from the nearest Remote Automated Weather Station (RAWS; *data available online*)[4] to classify each day of fire growth as occurring under moderate (55 plots) or extreme burning conditions (85 plots; Collins et al. 2006, Thompson and Spies 2009). Temperature, relative humidity, and average wind speed thresholds for moderate and extreme conditions (Appendix S2) were determined by natural breaks that coincided with days of large fire growth and thresholds from previous studies (Prichard and Kennedy 2014, Harvey et al. 2014*b*). Days where the temperature and wind speed exceeded the threshold and the relative humidity fell below the threshold were classified as extreme burning conditions. All other days were classified as having burned under moderate conditions. Moderate and extreme burning conditions had similar average temperature, but extreme burning conditions had considerably lower average relative humidity, higher average wind speeds, and higher average wind gusts for all fires (Appendix S3).

Testing the effects of burning conditions on fire severity

To assess the influence of burning conditions on fire severity within the spruce-fir cover type, burning conditions were overlaid with remotely sensed estimates of fire severity to examine (1) mean RdNBR by burning condition and (2) the percentage of area burned at low, moderate, and high fire severity (thresholds from Miller et al. 2009). Prior to overlay analysis, we intersected the area of spruce-fir forest (USDA 2012) that burned with the burning conditions spatial dataset to delineate spruce-fir areas that burned under moderate and extreme conditions. This dataset was overlaid with the raw and classified RdNBR dataset to calculate descriptive statistics of fire severity for each burning condition class. Specifically, for each burning condition class, we calculated the mean RdNBR value, standard deviation, and percentage of the combined fire area that burned at low, moderate, and high severity by burning condition (Miller et al. 2009). Since our overlay analyses assessed the entire population and not a sample, differences between descriptive statistics were viewed as real and no inferential statistics were necessary.

[4] http://www.raws.dri.edu/

Testing the effects of pre-fire spruce beetle outbreak severity on fire severity

We used two analytical approaches to assess the relative influence of pre-fire beetle outbreak severity (percentage of total basal area killed by beetle) on fire severity: (1) Spearman's rank correlations and (2) multivariate generalized linear regression modeling. The Spearman's rank correlation tested the bivariate relationship, while the multivariate generalized linear regression models tested the relationship in the context of other drivers known to influence fire severity.

Using a Spearman's rank correlation, we tested beetle-killed basal area against each quantitative measure of fire severity (char height, m; fire-killed stems, %; fire-killed basal area, %; surface charred; %; fine fuel remaining, %) for all plots. To minimize the chances of not detecting an ecologically significant effect of the severity of beetle outbreak (measured as percentage of basal area killed by beetles) on fire severity that was actually present (Type II error), we set the α to 0.10. Spearman correlations used the function "cor" in the "stats" package in R (R Core Team 2014).

To assess the relative importance of each variable in determining fire severity, we used a multivariate generalized linear modeling approach. Whereas other studies examining links between bark beetle outbreaks and fire have used mixed-effects models to control for site variation (Harvey et al. 2013), we found that local variability in fire effects (intraclass correlation coefficient = 0.02–0.16, P value from ANOVA test of drainage variable = 0.193–0.998; Smith et al. 2009) was not significantly different from the variability across the study area. Thus, multivariate generalized linear regression models were adopted to compare the influence of beetle outbreak severity to topography (slope position, topographic curvature, aspect, slope), solar radiation (incoming solar radiation, heat load index), and stand structure (combined live and dead basal area and stem density at time of fire) variables. All predictor variables were z-score transformed and fire severity response variables represented by a percentage were logit transformed. We selected the subset of biophysical variables that best related to fire severity using forward, backward, and stepwise model selection and the Bayesian information criterion (BIC). Variable selection removed beetle-killed basal area from all models, but we forced this variable into the final model to test its relative influence.

Though it was a significant predictor, burning condition was excluded from all models. Our sampling design captured a range of fire severity levels under both moderate and extreme conditions, which did not accurately represent the disproportionately high amount of high severity fire. Thus, using only our plot data, mean average and range of each fire severity metric was falsely similar under both burning conditions. Instead, the overlay analysis mentioned previously was used to examine the influence of burning conditions on fire

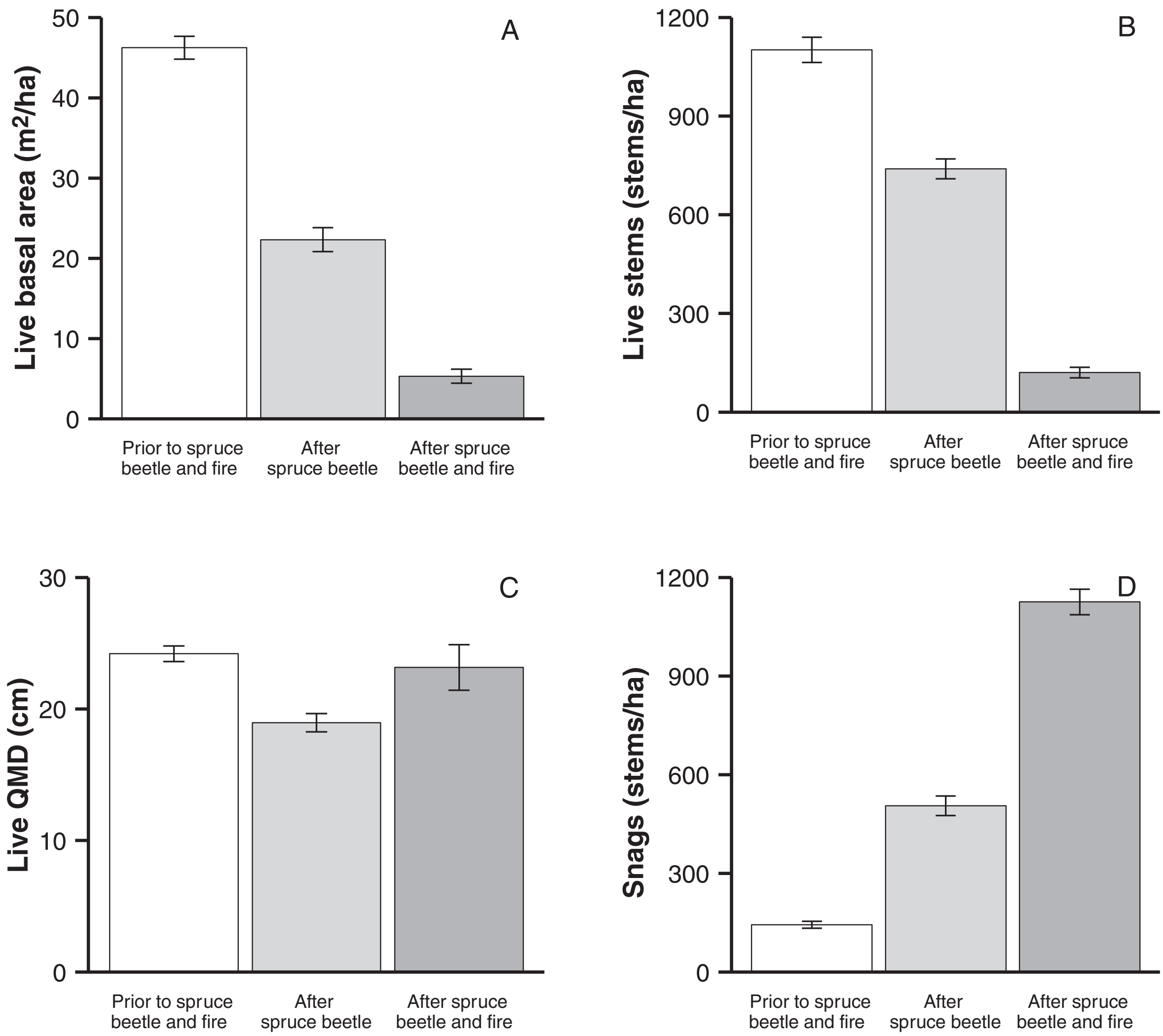

Fig. 2. Stand structure characteristics prior to spruce beetle outbreak and fire, after spruce beetle outbreak, and after spruce beetle outbreak and fire for all plots (n = 143). Pre-outbreak and pre-fire characteristics were reconstructed with the criteria presented in Appendix S2. All values are mean averages and 95% confidence intervals.

severity. Final models took the form basal area (combined live and dead at time of fire), slope position, and beetle-killed basal area. The multivariate generalized linear models used the function glm in the stats package in R (R Core Team 2014).

Results

Effect of spruce beetle and fire on stand structure

The spruce beetle outbreak reduced live basal area by more than 50% (Fig. 2A; Appendix S5), stem density by 33% (Fig. 2B, D), and mean live tree size by 22% (Fig. 2C). The severity of beetle-caused tree mortality ranged from 0 to 95% (mean 46%; Fig. 2) of total basal area at the plot level and was almost entirely composed of spruce beetle-killed Engelmann spruce (>99%). The remainder of the spruce beetle-attacked trees was subalpine fir. The fires further reduced live basal area by 66% and stem density by 83%, while increasing the density of snags (Fig. 2D), mean live tree size, and variance in mean live tree size (Fig. 2C).

Effects of burning conditions on fire severity

Over 90% of the area burned by all fires occurred during extreme burning conditions (Table 1; Appendix S3) and burned primarily at high severity (78% of hectares burned; Table 1). Examining only spruce-fir dominated stands (Table 1), moderate burning conditions resulted in lower fire severity (mean RdNBR = 785, SD = 401.8) than extreme burning conditions (mean RdNBR = 929, SD = 376.5), but both burning conditions produced a disproportionately high level of high severity fire. Low fire severity was evenly distributed under both burning conditions, but a higher percentage of moderate fire severity was represented under moderate burning conditions.

Table 1. Assessment of fire severity (RdNBR) and area burned by burning condition in spruce-fir forests in the West Fork Complex fires and Little Sands fires.

	Fire severity (RdNBR)		Area burned by fire severity class (ha)			Area burned overall	
Burning condition	Mean	SD	Low	Moderate	High	Total area burned (ha)	Percentage of area burned
Moderate	785	401.8	569 (21%)	367 (14%)	1726 (65%)	2666	9
Extreme	929	376.5	3251 (21%)	2180 (8%)	20299 (79%)	25 765	91

Note: SD is standard deviation.

Effects of pre-fire spruce beetle outbreak severity on fire severity

Using univariate correlation, we found the percentage of beetle-killed basal area was not correlated ($P > 0.10$) with char height (m), bole scorch (%), fine fuel remaining (%), surface charred (%), or RdNBR under extreme and moderate burning conditions, and fire-killed stems/ha (%) or fire-killed basal area (%) under extreme conditions (Table 2, Fig. 3A–E). Under moderate burning conditions, the percentage of beetle-killed basal area was positively correlated with the percentage of fire-killed stems ($rs = 0.231$, $P = 0.09$; Fig. 3F, Table 2*)* and fire-killed basal area ($rs = 0.275$, $P = 0.04$; Fig. 3G, Table 2).

In the multivariate generalized linear regression analysis, basal area (combined live and dead at time of fire) and slope position were the best predictors of fire severity; this was evidenced by higher magnitude beta coefficients for these two variables, significant *P* values, and consistent improvement of BIC across multiple fire severity metrics. Fire-killed stems/ha (%) and fire-killed basal area (%) increased on higher slope positions, whereas fire-killed stems/ha, bole scorch (%), surface charred (%), and RdNBR decreased with total basal area (combined live and dead, negative beta; Table 3). Fire severity metrics were not significantly related to beetle-killed basal area and had lower magnitude coefficients when compared to non-beetle related factors included in the models. All other predictor variables (e.g., combined live and dead stems/ha and annual solar radiation) considered in the models were consistently unrelated to fire severity.

Table 2. Spearman rank correlation (r_s) and *P* values for each fire severity response variable and percentage of basal area killed by spruce beetle in each plot across all fires.

	Burning conditions			
	Extreme ($n = 85$)		Moderate ($n = 55$)	
Fire Effect	r_s	P	r_s	P
Char height (m)	−0.03	0.768	0.04	0.763
Bole scorch (%)	−0.09	0.404	0.10	0.483
Fine fuel remaining (%)	0.06	0.613	−0.08	0.572
Surface charred (%)	0.09	0.434	0.06	0.677
Fire-killed stems/ha (%)	−0.06	0.562	0.23	0.090*
Fire-killed basal area (%)	−0.05	0.677	0.28	0.042**
RdNBR	0.14	0.270	0.09	0.611

Note: Range of beetle kill is 0–95% of total basal area. Significance levels indicated by ** $P < 0.05$; * $P < 0.1$.

Discussion

Contrary to the expectation that spruce beetle infestations alter subsequent fire severity (see Hicke et al. 2012 for a review), we found that pre-fire spruce beetle severity (<5 yr from outbreak to time of fire) had no effect on nearly all measures of fire severity, regardless of burning conditions, in five subalpine wildfires that burned 60000 ha in southwestern Colorado. The exceptions to this finding occurred in examining univariate relationships of fire-killed stems and fire-killed basal area where we found a marginal increase in fire severity with increasing beetle severity under moderate burning conditions. It is under moderate burning conditions that fire behavior models predict the strongest effects from beetle outbreaks on fire behavior (Simard et al. 2011, Schoennagel et al. 2012). Similar to the findings of previous case studies using remotely sensed measures of spruce beetle outbreaks and fire severity in spruce-fir forests (Kulakowski and Veblen 2007) and in other forest types (Bond et al. 2009), as well as field studies examining measures of bark beetle and fire severity in other forest types (e.g., Harvey et al. 2013, 2014*b*), fire severity in this study was more strongly related to topography, weather, and forest structure.

Effects of burning conditions on fire severity

Broad-scale climatic oscillations (strong La Niña and positive Atlantic Multidecadal Oscillation) that drive extreme drought in the southwest USA and short-term weather conditions necessary for initiation and development of large fire events (e.g., >5000 ha) in cool, moist subalpine forests (Buechling and Baker 2004, Sibold et al. 2006, Schoennagel et al. 2007) were present during the summers in which the fires burned and for the days of extreme fire growth (Appendix S2). Six consecutive days of warm, dry, and windy conditions produced extreme fire behavior (InciWeb 2013), which burned >34000 ha in the West Fork Complex, primarily at high severity. Lengthy, climate-driven, fire-free periods in the subalpine zone allow high levels of biomass to

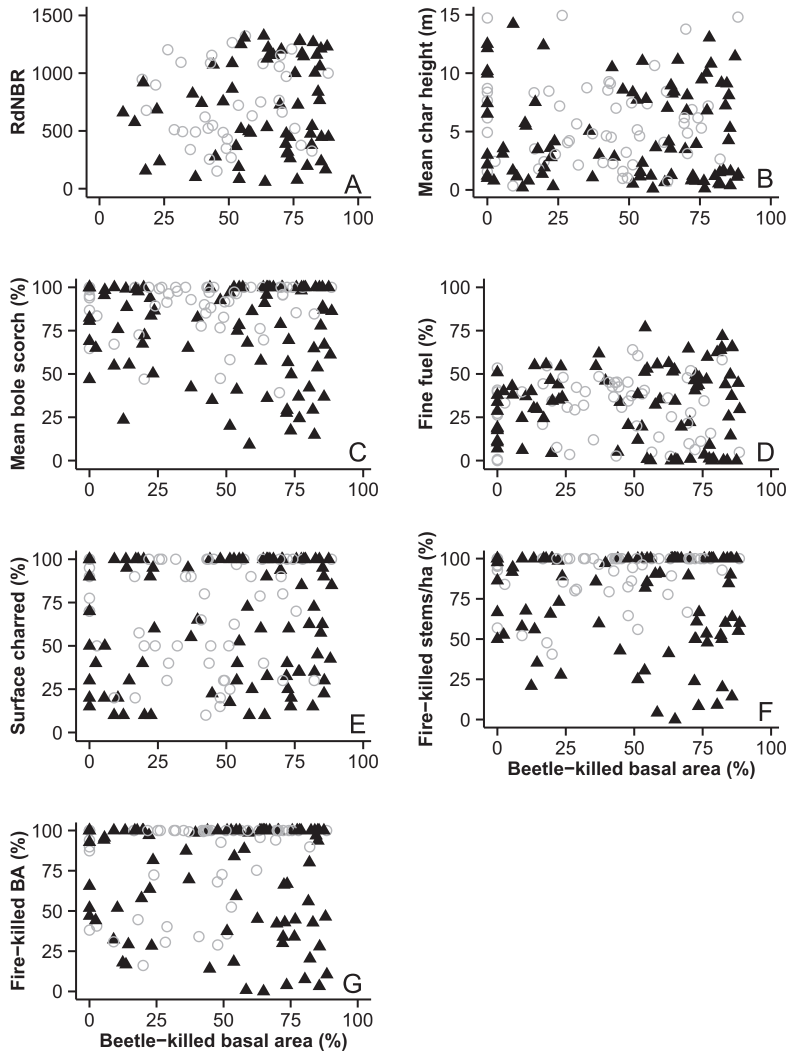

Fig. 3. (A–G) Fire severity measures plotted against spruce beetle killed basal area under moderate and extreme burning conditions (moderate, circle; extreme, triangle) in an early, gray-stage spruce beetle outbreak in subalpine, spruce-fir forests. RdNBR is relative differenced Normalized Burn Ratio. Percentage of fine fuel measures the remaining fine fuel (<1 cm) attached to the tree bole. BA is basal area.

accumulate, which promotes extensive, stand-replacing fires under extreme fire weather conditions (Schoennagel et al. 2007). Such conditions facilitated the burning of >90% of the burned area of which 79% burned at high severity (Table 1). However, moderate conditions also produced primarily high-severity fire (65%). Thus, we conclude that short-term weather conditions were an important factor in promoting daily fire growth and increasing fire severity, but given weather conditions conducive to burning, fire severity is uniformly high in mature spruce-fir forests.

Effects of pre-fire spruce beetle outbreak severity on fire severity

Consistent with a previous case study examining remotely sensed datasets of spruce beetle outbreaks and subsequent fire severity 2–3 yr after an outbreak in northern Colorado (Kulakowski and Veblen 2007), we found that RdNBR, a remote measure of canopy and surface fire severity, was not related to field measurements of pre-fire spruce beetle killed basal area. Further, RdNBR was correlated ($P < 0.02$; Appendix S4) to all field measures of fire severity; an important validation of the use of RdNBR to assess fire severity in beetle-affected forests. The current study further improves upon past research by recording fine-scale field measurements of fire severity to assess general expectations about the influence of a gray-stage spruce beetle outbreak on both canopy and surface fire severity.

In the current study in the gray-stage expected decreases in canopy fire severity across all infestation severities (Hicke et al. 2012) or only in severely attacked stands (DeRose and Long 2009) were not detected under

Table 3. Generalized linear regression results from the fire severity models (chosen with Bayesian information criterion) used to compare the beetle outbreak severity coefficient and significance to the following non-beetle related predictor variables: pre-fire total basal area (live and dead basal area of all species at time of fire) and slope position (relative position on slope from valley to ridgeline).

Response and predictor	Beta	SE	*t*	*P*	Pr(>|*t*|)
Fire-killed stems/ha (%)†					
Pre-fire total basal area	−0.65	0.21	−3.14	<0.01	***
Slope position	0.43	0.21	2.07	0.04	**
Beetle-killed basal area	−0.12	0.21	−0.57	0.57	…
Fire-killed basal area (%)†					
Slope position	0.53	0.24	2.18	0.03	**
Beetle-killed basal area	0.14	0.24	0.58	0.56	…
Char height (m)‡					
Pre-fire total basal area	−0.53	0.34	−1.58	0.12	…
Slope position	0.05	0.34	0.14	0.89	…
Beetle-killed basal area	−0.12	0.35	−0.35	0.73	…
Fine fuel remaining (%)†					
Pre-fire total basal area	0.05	0.14	0.38	0.70	…
Slope position	−0.04	0.14	−0.25	0.80	…
Beetle-killed basal area	−0.21	0.15	−1.46	0.15	…
Bole scorch (%)†					
Pre-fire total basal area	−0.56	0.19	−2.90	<0.01	***
Slope position	0.18	0.19	0.93	0.35	…
Beetle-killed basal area	−0.22	0.20	−1.11	0.27	…
Surface charred (%)†					
Pre-fire total basal area	−0.84	0.23	−3.66	<0.01	***
Slope position	0.13	0.23	0.57	0.57	…
Beetle-killed basal area	0.10	0.23	0.41	0.68	…
RdNBR‡					
Pre-fire total basal area	−0.19	0.10	−1.89	0.06	*
Slope position	−0.02	0.10	−0.21	0.83	…
Beetle-killed basal area	0.16	0.14	1.12	0.26	…

Notes: The fine fuel percentage is the percentage of the bole with fuel less than a quarter inch remaining. A positive beta indicates increased fire severity, while a negative beta decreases fire severity. Intercepts are not necessary for comparison. Significance levels are indicated by *** $P < 0.01$; ** $P < 0.05$; * $P < 0.1$.

†Logit transform for percentage variables.

‡No transform.

extreme burning conditions (Fig. 2A–G, Table 2). This suggests that extreme fire weather conditions, pre-outbreak stand attributes, and topographic factors negated any potential effects from the beetle outbreak. Five years after the outbreak, canopy bulk density (CBD) and vertical fuel continuity were likely still sufficient to char the entire bole and branches of stands of beetle-killed trees. The slight increase in canopy fire severity (fire-killed stems/ha and fire-killed basal area) with increasing beetle-killed basal area under moderate conditions (Fig. 2F, G, Table 2) represented a relatively small portion of the area burned (<10%; Table 1). However, these results support inferences from other field studies (Harvey et al. 2014*a*) and fire behavior modeling studies (Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012) that found or expected that effects of the beetle outbreak would be strongest during moderate weather conditions. This finding may be explained by several fuel-related mechanisms: (1) the added fine fuel on the forest floor or increase in understory biomass may have been sufficiently dry to elevate fire intensity in beetle-killed areas, (2) the added fine fuel may have increased fire duration, or (3) surface wind speeds may have increased fire intensity and type from decreased vegetative sheltering (Jenkins et al. 2008). In contrast to some other forest ecosystem types, canopy fire is not necessary to cause death of spruce and fir. Thin bark and shallow roots make both species particularly susceptible to severe injury or mortality from fire (Alexander 1987, Jenkins et al. 2014), which may be elevated by slight increases in fire intensity or duration from the added fine fuel. Because canopy fire is not a prerequisite for fire-caused tree death, comparing our measurements of fire-killed basal area and stems/ha to fire behavior modeling studies examining periods of elevated crown fire is difficult.

Counter to expectations of elevated surface fire severity with increased beetle outbreak severity (Jenkins et al. 2008, Hicke et al. 2012), we found that the likely contribution of canopy fuel to the forest floor and the understory response to the beetle outbreak did not alter surface fire severity. Jorgensen and Jenkins (2011) found significant decreases in canopy fuel between the endemic and epidemic (<5 yr post-spruce beetle outbreak) stages that significantly elevated litter and 100-h fuels and promoted understory growth of herbs and shrubs, but did not increase 1 and 10-h fuel surface fuel loads. Given existing high-fuel loads in mature stands of spruce-fir, we hypothesize that the additional surface fuel at this stage of a beetle outbreak and the understory response did not produce an ecologically significant difference in fire severity. The expected increase in surface fire severity may be evident later in the outbreak (old-stage) when more canopy fuel and snags fall to the forest floor; this needs further study.

Though spruce beetle outbreaks undoubtedly alter factors known to influence fire severity (e.g., fuel characteristics and post-outbreak forest structure), fire severity was best explained by topographic and pre-outbreak stand structure variables in this study (Table 3). Fire severity increased with slope position, a likely result of the upslope preheating effect, upslope winds during the burning period, and the cooler and wetter conditions of higher elevation stands that can produce more biomass (Bigler et al. 2005, Dillon et al. 2011). We also found that greater pre-outbreak basal area reduced fire severity. Sites with high basal area consisted of larger trees that had thicker bark and were presumably more resistant to fire-injury (Fig. 2C) and/or were in more mesic areas with an understory component less susceptible to fire spread. The dominant influence of extreme weather conditions, topography, and stand attributes shown in this study complements the findings of existing case studies in spruce-fir forests (e.g., Bigler et al. 2005) and field studies showing little to no influence of bark beetle severity on fire severity in Douglas fir forests of northern Wyoming (Harvey et al. 2013) and lodgepole pine forests across the northern Rocky Mountains (Harvey et al. 2014*b*). There are incongruences between case study findings and expectations of decreased canopy severity (DeRose and Long 2009) and elevated surface fire severity in the gray stage, inferred from fire-behavior models (Jenkins et al. 2008, Hicke et al. 2012). These incongruences may be a result of mechanistic (e.g., assigning the entire stand canopy to a particular mortality stage) and spatial limitations (e.g., modeling homogeneous stands rather than a complex landscape) of fire models (Coen 2005, Jolly et al. 2012, Alexander and Cruz 2013), as well as differences in time since outbreak, percentage of composition of spruce and fir, outbreak severity, and weather scenarios.

This study focused on the immediate ecological implications (e.g., number of trees killed and basal area killed) of fires that burned through a <5-yr old, severe spruce beetle outbreak. Findings may differ when fires occur earlier in an outbreak when a majority of the needles are still attached to beetle-killed trees or later in the gray to old stage when more fuel has fallen to the forest floor, and thus, empirical studies of fires in other stages are needed. This study did not address potential effects of the spruce beetle outbreak on real-time fire behavior (e.g., flame length, fireline intensity, or rate of spread); such studies are needed to help validate fire behavior models and address important operational issues in wildfire management and safety (Jenkins et al. 2012, Page et al. 2013).

Conclusion

Many beetle-affected forests in western North America are transitioning into the gray stage of attack and wildfire activity is increasing, but the ecological and land management implications of fire events in beetle-attacked forests are uncertain. We conducted the first field study that quantified the influence of spruce beetle severity on fire severity. This field-based analysis is a methodological improvement upon past studies relying on remotely sensed data, which may not capture the complex relationships between these two events. In agreement with the findings of post-beetle fire severity in other forest types, our results do not support the expectation that bark beetle outbreaks alter fire severity when the interval between spruce beetle outbreaks and fire is <5 yr. Instead, fire severity was driven by topography, weather, and stand structure, a result consistent with the understanding that fires in subalpine forests characteristically burn at high severity. Bark beetle infestation and fire activity have both autonomously increased in conjunction with recent warming and drought, and thus, will likely overlap more frequently in time and space. However, the currently available evidence indicates that neither area burned (Hart et al. 2015) nor severity of fires are being directly driven by increases in beetle-caused tree mortality.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1890/15-1121/suppinfo

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.1c2g1