

Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests

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Abstract. Understanding how disturbances interact to shape ecosystems is a key challenge in ecology. In forests of western North America, the degree to which recent bark beetle outbreaks and subsequent fires may be linked (e.g., outbreak severity affects fire severity) and/or whether these two disturbances produce compound effects on postfire succession is of widespread interest. These interactions remain unresolved, largely because field data from actual wildfires following beetle outbreaks are lacking. We studied the 2008 Gunbarrel Fire, which burned 27 200 ha in Douglas-fir (*Pseudotsuga menziesii*) forests that experienced a bark beetle outbreak 4–13 years prefire (“gray stage,” after trees have died and needles have dropped), to determine whether outbreak severity influenced subsequent fire severity and postfire tree regeneration. In 85 sample plots we recorded prefire stand structure and outbreak severity; multiple measures of canopy and forest-floor fire severity; and postfire tree seedling density. Prefire outbreak severity was not related to any measure of fire severity except for mean bole scorch, which declined slightly with increasing outbreak severity. Instead, fire severity varied with topography and burning conditions (proxy for weather at time of fire). Postfire Douglas-fir regeneration was low, with tree seedlings absent in 65% of plots. Tree seedlings were abundant in plots of low fire severity that also had experienced low outbreak severity (mean = 1690 seedlings/ha), suggesting a dual filter on tree regeneration. Although bark beetles and fire collectively reduced live basal area to <5% and increased snag density to >2000% of pre-outbreak levels, the lack of relationship between beetle outbreak and fire severity suggests that these disturbances were not linked. Nonetheless, effects on postfire tree regeneration suggest compound disturbance interactions that contribute to the structural heterogeneity characteristic of mid/lower montane forests.

Key words: compound disturbance; *Dendroctonus pseudotsugae*; disturbance interactions; Douglas-fir beetle; fire ecology; Greater Yellowstone; *Pseudotsuga menziesii*; Rocky Mountains, USA.

INTRODUCTION

Understanding disturbance interactions, such as when the occurrence or severity of one disturbance influences the occurrence or severity of another (i.e., linked disturbances [Simard et al. 2011]) is vital to anticipating future ecosystem dynamics and resource management challenges (Turner 2010). Recent bark beetle (Curculionidae: Scolytinae) epidemics have led to extensive tree mortality in forests of western North America (Raffa et al. 2008), raising pressing questions about how beetle outbreaks may influence subsequent fire activity (e.g., Hicke et al. 2012). Of greatest interest is whether post-outbreak wildfires will be more severe than those in undisturbed forests, an issue unresolved by studies to date. Retrospective analyses suggest relatively modest effects of prefire beetle outbreak on the occurrence of fire (e.g., Bebi et al. 2003, Kulakowski et al. 2003, Lynch et al. 2006, Kulakowski and Veblen 2007, Kulakowski and Jarvis 2011). However, previous studies have not

tested the relationship between the severity of both beetle outbreaks and fire, and they lack field data needed to examine different fire effects (e.g., canopy vs. surface fire [Hicke et al. 2012]). Recent field studies have documented key changes in fuels as beetle outbreaks progress (e.g., Klutsch et al. 2011, Simard et al. 2011, Hoffman et al. 2012, Jolly et al. 2012a, Schoennagel et al. 2012, Donato et al. 2013a), but projections of fire activity in response to these changes have differed markedly among studies and catalyzed spirited debate (e.g., Jolly et al. 2012b, Moran and Cochrane 2012, Simard et al. 2012). Empirical evidence that might resolve alternative expectations and provide insight into differences among forest types has been lacking (Hicke et al. 2012). Fires that have burned following recent beetle outbreaks in forests now provide opportunities for field studies to address these uncertainties empirically.

In addition to the potential for linked disturbance interactions, two disturbances that occur in close succession may interact to alter ecosystem response to the second disturbance, even if the second disturbance is not affected by the first (i.e., compound disturbances

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[Paine et al. 1998]). For example, an abnormally short interval between fires can lead to substantial reductions in tree regeneration if the fire-free interval is less than the time required for trees to produce seed (e.g., Brown and Johnstone 2012). Especially in forest types that lack a persistent seed bank (e.g., nonserotinous conifers), beetle outbreaks followed by fire could exhibit compound disturbance effects if the outbreak substantially reduced seed supply. Bark beetles are more likely to kill large, cone-producing trees (Bjorklund and Lindgren 2009), and reduced propagule abundance in areas of high-severity beetle outbreaks could limit postfire tree regeneration. Such compound disturbance effects could drive variability in postfire succession and have long-term effects on forest structure and function, but this has not yet been explored.

While prior research on beetle–fire interactions has focused on high-elevation subalpine forests with crown-fire regimes, surprisingly little is known about mid/lower montane forests that cover ~30% of the U.S. Rocky Mountains (Baker 2009). Key differences in stand structure, fire regimes, and regeneration mechanisms among forest types may lead to different disturbance interaction outcomes. Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests are a primary component of mid/lower montane forest ecosystems, occurring on moderate to steep slopes between ~1850 and 2500 m (Despain 1991, Barrett 1994). Stands range from dense closed-canopy forests to open woodlands (Despain 1991, Donato et al. 2013a), and the fire regime is mixed severity, including patches of surface and crown fire (Arno 1980, Barrett 1994, Baker 2009). Interior Douglas-fir is slow-growing, long-lived, and nonserotinous (lacking a seedbank). Thick bark on mature trees insulates against surface fire, and seed dispersal from surviving trees onto exposed mineral soil leads to recruitment pulses after fire (Knight 1996, Baker 2009). Extensive areas of mid/lower montane forests were affected by Douglas-fir beetle (*Dendroctonus pseudotsugae*) outbreaks that peaked by 2005 (Meddens et al. 2012), but the potential effects of these outbreaks on fire severity and postfire trajectories are unknown (Hicke et al. 2012).

Wildfires have recently burned some post-outbreak forests, providing ideal opportunities to evaluate the potential for linked or compound disturbance interactions between bark beetle outbreaks and fire. We studied the Gunbarrel Fire, which burned >27 000 ha of gray-stage post-outbreak Douglas-fir forests in Greater Yellowstone (Wyoming, USA) in 2008, to address two research questions. (1) How does severity of the recent bark beetle outbreak influence subsequent fire severity? Because the fire occurred in the gray post-outbreak stage, in which needles had recently been shed from beetle-killed trees, we expected measures of canopy fire severity to either decline with increasing beetle-outbreak severity because of the reduced canopy fuel load or to be unrelated to beetle outbreak severity

(Donato et al. 2013a). However, we expected measures of forest-floor fire severity to increase with beetle outbreak severity because of accumulation of surface fuel and increased surface winds and temperatures beneath more open canopies (Jenkins et al. 2008, Hicke et al. 2012). We also expected that topography and/or burning conditions (i.e., weather) could override beetle outbreak effects, such that outbreak severity would have less effect on fire severity in steep terrain or during extreme burning conditions. (2) How does bark beetle outbreak severity interact with fire severity to influence early postfire Douglas-fir regeneration? We expected postfire Douglas-fir regeneration to decline with increasing beetle outbreak severity because seed source would be reduced.

METHODS

Study area

The study area is in the Absaroka Wilderness on the Shoshone National Forest (SNF), situated on the eastern edge of Greater Yellowstone (44°30' N, 109°45' E) and is typical of coniferous mid/lower montane forests in the Middle Rocky Mountain ecoregion (Omernik 1987) (Appendix A; see Plate 1). Topography is variable and steep; with elevation ranging from 1900 to 2700 m in several drainages oriented approximately north–south and emptying into the Shoshone River. Slopes in study plots ranged from 2° to 43° (mean 22°) across all aspects. Mean daily temperatures range from –12°C in January to 22°C in July, with an annual mean precipitation of 69 cm falling primarily as winter snow and spring rain (data available online).⁴ Soils are well drained and derived from volcanic (andesitic) and metamorphic substrates. Forests are typical of the sloped perimeter of the Yellowstone Plateau, composed of pure Douglas-fir stands in middle elevations with assemblages including limber pine (*Pinus flexilis*) and Rocky Mountain juniper (*Juniperus scopulorum*) at lower elevations and lodgepole pine (*Pinus contorta* var. *latifolia*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) at higher elevations.

Douglas-fir beetle outbreaks began in isolated study area locations in 1995 and peaked by 2001–2002 (Appendix A). By 2008 (4–13 years post-outbreak), stands were in the gray stage commonly described in the literature (no new beetle attack occurring, <50% needle retention on beetle-killed trees) (Hicke et al. 2012, Donato et al. 2013a). The 2008 Gunbarrel Fire was lightning ignited on 27 July and managed for wildland fire use (no management activity in the study area) until 30 August, burning 27 200 ha in total. No other recent disturbance (fire, blowdown, insect outbreak) in the study plots was indicated by field evidence or agency records.

⁴ www.prism.oregonstate.edu

Sampling design

Study plots ($n = 85$) were distributed throughout seven drainages that burned in the Gunbarrel Fire (spanning 35 km) in Douglas-fir dominated stands (>50% of basal area) with variable prefire beetle outbreak severity. Plots were stratified by fire severity so that we sampled areas at low, moderate, and high severity in each drainage. From a random start ~ 1 km from the fire perimeter in each drainage, plots were situated systematically along a series of elevational contours with a separation distance of 400 m or farther if necessary to sample the next available stand meeting the study criteria (avoiding rock outcrops, non-Douglas-fir forest types, etc.) until all the suitable area in each drainage was sampled. Field sampling occurred in July–August 2011.

Data were collected on stand structure, prefire beetle outbreak severity, and fire severity in a 30 m diameter circle plot (0.07 ha) divided into four quadrants (northeast, southeast, southwest, northwest). 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, height, and branch-whorl count for each live or dead prefire sapling (trees <1.4 m that established prefire; ≥ 3 branch whorls) occurring in 3-m belt transects, and postfire seedling (trees that germinated postfire; <3 branch whorls) in 2-m belt transects along the main axes of the circle plot (north, east, south, west). GPS coordinates and distance to the nearest live seed-bearing tree were measured at plot center; the latter with a TruPulse 360 laser range finder (Laser Technology, Inc., Centennial, Colorado, USA).

Prefire beetle outbreak severity

Prefire beetle outbreak severity was quantified by removing bark on every tree taller than 1.4 m and recording evidence of *Dendroctonus* activity (5914 individual trees). The thick bark on Douglas-fir trees enabled us to sample well-preserved vascular cambium on most trees (99.75% of basal area and 98.5% of trees). Trees were recorded as “killed by bark beetles prior to fire” if they met all the following criteria: dead at time of sampling, presence of exit holes on outer bark, dry cambial tissue, fully excavated (but vacated) adult and larval galleries on the vascular cambium (>50% of bole circumference or remaining visible cambium), and no needles retained in the canopy. Dead trees with no evidence of prefire beetle activity or clear evidence of postfire beetle activity were assumed to have been “live at the time of fire.” Further details and validation of outbreak severity methods are explained in Appendix B.

Fire severity

Because a variety of different fire effects may be informative, fire severity was quantified with surrogate (satellite), integrative (multiple strata), canopy (trees),

and forest floor (ground layer vegetation and soil) metrics of fire effects using remotely sensed and field data. Surrogate fire severity was measured remotely using the Relative differenced Normalized Burn Ratio (RdNBR), which is commonly used to assess variation in fire severity (Miller et al. 2009). Because RdNBR controls for prefire differences in live biomass, it provides an index of relative rather than absolute change, making it well suited for assessing fire severity when prior disturbances such as beetle outbreaks have decreased live biomass (J. Miller, *personal communication*). Data were downloaded from the Monitoring Trends in Burn Severity web site (*available online*)⁵ and extracted for each plot center location (Appendix C). An integrative fire severity class (light surface, severe surface, crown) was also assigned to each plot in the field following established protocols for the region (Appendix C and Turner et al. 1999). Canopy fire severity was recorded on five randomly selected codominant canopy trees >30 cm dbh in each quadrant (20 trees per plot). On the main bole of each selected tree, we recorded the maximum percentage of scorching around the circumference and the maximum char height to the nearest 0.5 m. Tree mortality from fire (basal area and number of trees) was quantified by classifying every fire-damaged tree taller than 1.4 m in the plot that was alive at the time of fire (no evidence of disease, insect infestation, or mechanical wounding) but dead at the time of sampling as “killed by fire.” Forest floor fire severity was measured by recording the percentage cover of charred surface (mineral soil, litter, woody debris) using the point intercept method at 10-cm intervals along the main axes of the circle plot (480 points per plot) and by recording the depth of postfire litter + duff (in millimeters) at every 3 m along the main axis of the plot (20 points per plot).

Topography and burning conditions

We used a 10-m digital elevation model in ArcGIS 10.1 to generate topographic variables based on each plot center: elevation (meters), slope (degrees), aspect (Northeast Index, [Beers et al. 1966]), and topographic curvature (the second derivative of the elevation surface [Zevenbergen and Thorne 1987]). Because absolute elevation in the study area spans >1000 m over 40 horizontal km, we calculated slope position for each plot by rescaling elevation in each drainage from 0 (drainage outlet to Shoshone River) to 1 (ridge top) to capture local elevational effects on fire severity.

Reliable local (plot scale) weather data were not available as plots were 3–37 km from the nearest weather station. Therefore, we followed methods of Thompson and Spies (2009), using a daily burn progression map provided by the SNF to divide the fire into two periods of burning conditions based on weather

⁵ www.mtbs.gov

conditions and mapped fire growth during different periods. Plots in each drainage were assigned to a burn period based on the date when the majority of the drainage burned. *Moderate* burning conditions (40 plots) were during a period of relatively low temperatures and winds, high humidity, and modest fire growth. *Extreme* burning conditions (45 plots) were during a period of relatively high temperatures and winds, low humidity, and rapid fire growth (Appendix D). We confirmed there was no confounding relationship between beetle-killed basal area and moderate or extreme burning conditions ($t = 1.05$, $P = 0.30$, Welch's t test).

Statistical analysis

To test if fire severity was linked to prefire beetle outbreak severity, we used several analytical approaches before and after accounting for other variables known to influence wildfire. First, we tested for differences in prefire beetle-killed basal area (percentage) among integrative fire severity classes overall and during different burning conditions using a one-way ANOVA. Second, we performed a Spearman's rank correlation test between each quantitative metric of fire severity and beetle-killed basal area in all plots regardless of burning conditions ($n = 85$), and separately for plots that burned during moderate ($n = 40$) and extreme ($n = 45$) burning conditions. Third, for fire severity variables (RdNBR, char height, postfire litter + duff depth, and charred surface cover) that met assumptions of parametric tests after transformation, we used mixed-effects linear models to test for effects of beetle outbreak severity while controlling for topography, burning conditions, and drainage (the latter to account for spatial grouping of plots). Preliminary stepwise variable selection (using BIC) among topographic (elevation, slope, aspect, topographic curvature, slope position) and stand structure (live and dead basal area and stem density) variables resulted in slope position as the only variable retained for all models. A term for burning conditions (moderate or extreme) was also included and beetle-killed basal area was included to test the main effect of outbreak severity. Interaction terms were also included to test whether effects of slope position and/or beetle outbreaks varied by burning conditions. In sum, final models contained burning condition, slope position, beetle-killed basal area, slope position \times burning condition, and beetle-killed basal area \times burning condition as fixed effects, and drainage as a random effect. All regression models were assessed for heterogeneity of residuals, normality of errors, multicollinearity among explanatory variables, and overly influential data points (Cook's distance value >0.5); no violations were detected. Model residuals were tested for spatial autocorrelation using semivariograms; none was detected.

To test if beetle outbreaks and fire interacted to produce compound effects on postfire Douglas-fir seedling density (measured as stems per hectare), we

performed two analyses. First, to assess the relative importance of beetle outbreak severity as an explanatory variable for postfire seedling establishment among other variables (topography, fire severity, seed source) known to affect postfire tree regeneration, we used a combination of random forests and regression trees. These methods are effective in uncovering hierarchical and nonlinear relationships among variables, and are robust to any distribution (Breiman et al. 1984, De'ath and Fabricius 2000, Maindonald and Braun 2010). Random forests provide a list ranking the importance of explanatory variables from a large number of potential trees, and are a useful tool in combination with classical regression trees which are more interpretable for complex relationships among variables (Maindonald and Braun 2010). A full tree was built by adding the following candidate predictor variables: total (live and dead) prefire basal area per hectare, total (live and dead) prefire Douglas-fir basal area per hectare, elevation, slope, aspect, topographic curvature, slope position, drainage, fire severity class, distance to seed source, and beetle-killed basal area. Ten runs of 1000 trees were independently grown using random forests, and the increase in mean square error for exclusion of each variable was averaged across runs, providing a rank list of variable importance. Variables with a positive increase (i.e., variables that improved model fit) were added to the full regression tree. The regression tree was then trimmed to avoid over-fitting, minimizing cross-validated error by removing splits exceeding the complexity parameter (Maindonald and Braun 2010).

Second, postfire Douglas-fir seedling density (stems per hectare) was regressed against beetle-killed basal area within each fire severity class (which can affect postfire tree seedling density [Turner et al. 1999]). We used Spearman's rank correlation tests within each fire severity class, but 90% of plots that burned as crown or severe surface fire had no postfire seedlings. In light surface fire plots, postfire Douglas-fir seedling density was regressed against beetle-killed basal area with a generalized linear model (negative binomial error structure; log-link). Because advance (prefire) regeneration can also be important to postfire trajectories, we additionally tested relationships between advance regeneration, postfire seedling density, and outbreak severity.

All statistical analyses were performed in the R statistical software (R Development Core Team 2010). Results are means \pm 1 SE unless noted. For all analyses, we set $\alpha = 0.10$ to reduce the chance of Type II error and not miss potentially meaningful relationships among variables.

RESULTS

Effects of bark beetles and fire on stand structure

Pre-outbreak live basal area and stem density was 41.2 ± 1.6 m²/ha and 948 ± 34 stems/ha, respectively, dominated by Douglas-fir ($87\% \pm 2\%$ of basal area; $71\% \pm 3\%$ of live stems), with understory vegetation

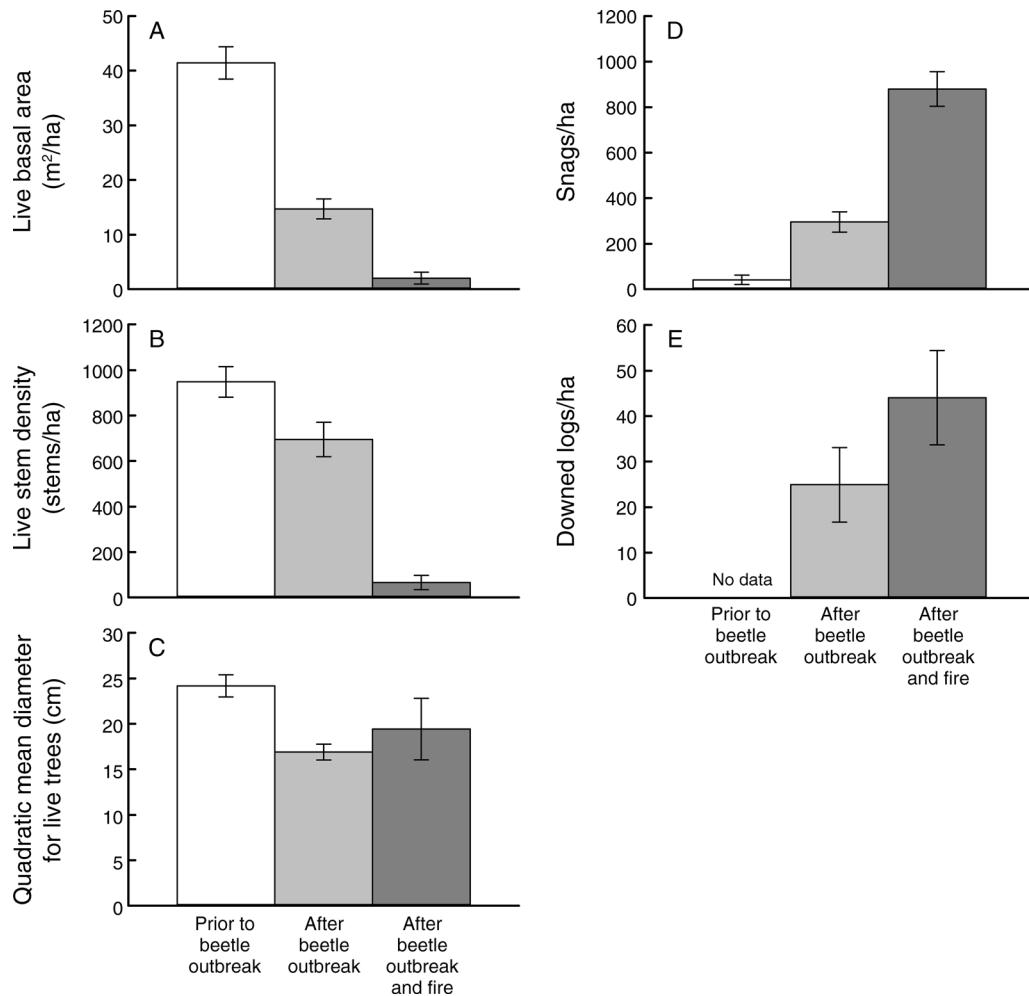


FIG. 1. Stand structure characteristics in all plots ($n=85$) prior to the bark beetle outbreak, after the bark beetle outbreak, and postfire. Pre-outbreak values were reconstructed by assigning all trees killed by the fire and any trees with evidence of recent prefire beetle mortality as alive prior to beetle outbreak (Appendix B). Downed logs prior to beetle outbreak were not estimated because of decay over more than 10 years before sampling and possible combustion of some downed logs in the fire. Values are means and 95% confidence intervals.

composed of tree saplings, woody shrubs, herbs, and graminoids. Beetle kill ranged from 0% to 91% (mean 59%) of total basal area and was composed almost entirely (>97%) of Douglas-fir trees killed by the Douglas-fir beetle. The Douglas-fir beetle outbreak reduced live basal area and live stem density (Fig. 1A, B); reduced mean live tree size (Fig. 1C); and increased the number of standing dead trees (Fig. 1D). The Gunbarrel Fire further reduced live basal area and live stem density (Fig. 1A, B); and increased the number of standing and down dead trees (Fig. 1D, E). Bark beetles and subsequent fire collectively reduced live basal area to <5% and increased snag density to >2000% of predisturbance levels, with consistent effects across levels of outbreak severity (Appendix E).

Effects of bark beetle outbreak on fire severity

Our sampling design captured a wide range of fire severity for integrative, surrogate, canopy, and forest-floor measures. Of the 85 sample stands, 31 burned as crown fire, 31 as severe surface fire, and 23 as light surface fire; classes were statistically distinct for quantitative fire severity measures (Appendix C: Table C2). RdNBR ranged from 21 to 1935 (mean 670). Canopy fire severity was variable: mean char height ranged from 0.7 to 23.1 m (mean 12.9 m); mean bole scorch spanned 38–100% (mean 92%) of bole circumference; tree mortality ranged from 15% to 100% (mean 90%); and fire-killed basal area ranged from 7% to 100% (mean 87%). Forest-floor fire severity was variable: postfire litter + duff depth ranged from 0.4 to 32.2 mm (mean 8.3 mm), and charred surface cover ranged from 4% to 50% (mean 24%).

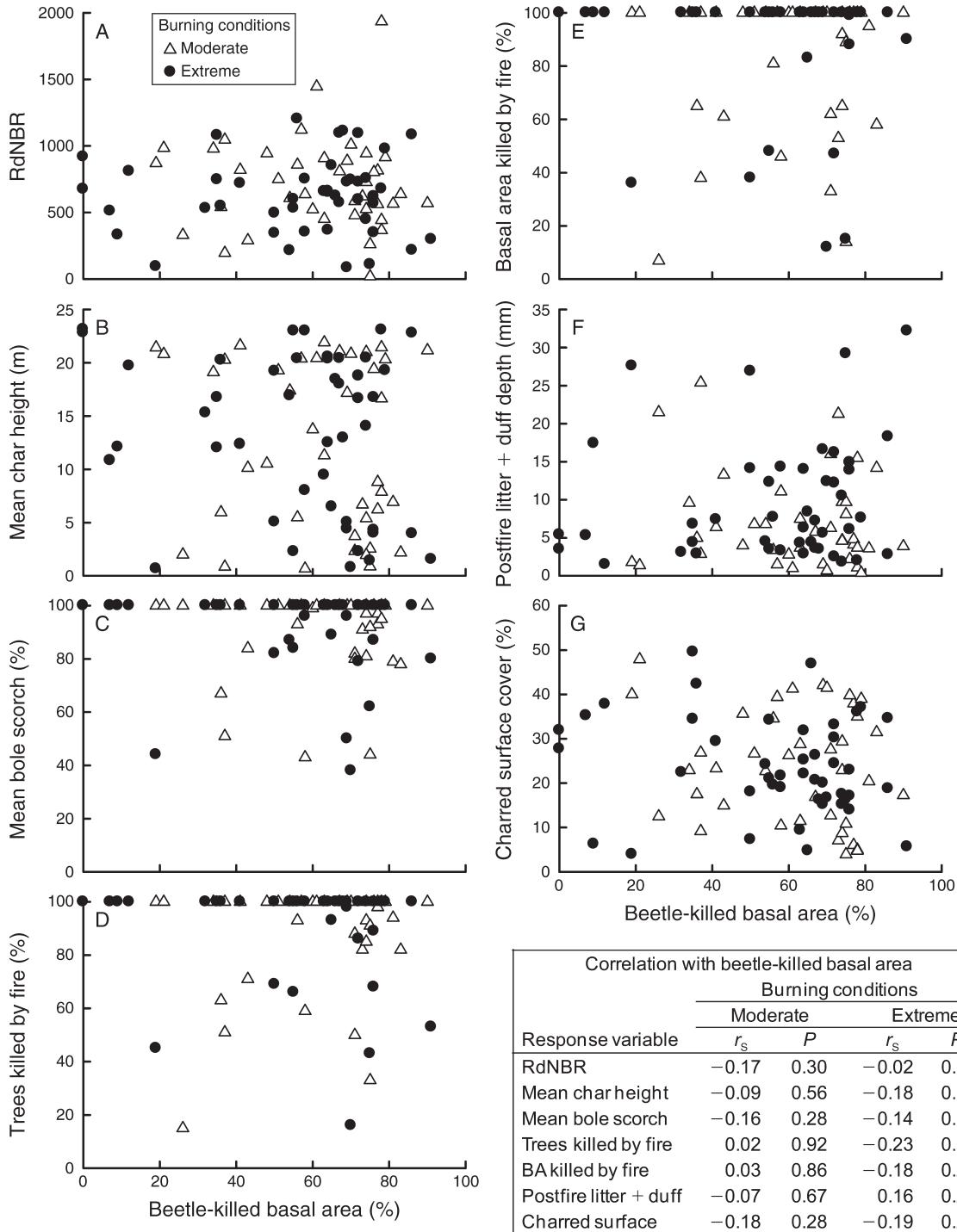


FIG. 2. Metrics of fire severity vs. percentage beetle-killed basal area during moderate and extreme burning conditions. The inset table shows Spearman rank correlations (r_s) and P values for each fire severity response variable and beetle-killed basal area. RdNBR stands for Relative differenced Normalized Burn Ratio (see *Methods: Fire severity*).

When considering univariate relationships between integrative or surrogate fire severity metrics and outbreak severity, beetle-killed basal area did not differ among fire severity classes ($F_{2,82} = 1.69$, $P = 0.19$), and was not correlated with RdNBR (Fig. 2A). Beetle

outbreak severity was also not correlated ($P > 0.10$) with three of four measures of canopy fire severity (Fig. 2B, D, E) or either measure of forest-floor fire severity (Fig. 2F, G). Mean bole scorch decreased slightly with increasing beetle outbreak severity ($r_s = -0.18$, $P = 0.09$;

TABLE 1. Results of mixed-effects linear models testing for effects of beetle outbreak severity on subsequent fire severity.

Response (transformation)	Predictor	β	SE	t	P
RdNBR (no transformation)	Moderate BC (intercept)	402.4	190.0	2.12	0.04
	Extreme BC	125.8	238.6	0.53	0.62
	Slope position	769.4	181.4	4.24	<0.01
	Beetle-killed basal area	-176.7	251.7	-0.70	0.48
	Extreme BC \times slope position	-575.0	256.1	-2.24	0.03
	Extreme BC \times beetle-killed basal area	159.8	310.9	0.51	0.61
Mean char height (m) (no transformation)	Moderate BC (intercept)	14.37	5.01	2.87	<0.01
	Extreme BC	5.65	6.29	0.90	0.41
	Slope position	4.45	4.78	0.93	0.35
	Beetle-killed basal area	-7.77	6.63	-1.17	0.25
	Extreme BC \times slope position	-13.93	6.75	-2.06	0.04
	Extreme BC \times beetle-killed basal area	3.22	8.19	0.39	0.70
Litter + duff depth (mm) (natural log)	Moderate BC (intercept)	2.90	0.53	5.49	<0.01
	Extreme BC	-1.47	0.66	-2.24	0.08
	Slope position	-2.17	0.51	-4.23	<0.01
	Beetle-killed basal area	-0.30	0.71	-0.42	0.67
	Extreme BC \times slope position	2.69	0.73	3.70	<0.01
	Extreme BC \times beetle-killed basal area	0.82	0.87	0.94	0.35
Charred surface cover (%) (arcsine square-root)	Moderate BC (intercept)	14.29	7.02	2.04	0.05
	Extreme BC	18.02	8.72	2.07	0.09
	Slope position	33.93	6.92	4.90	<0.01
	Beetle-killed basal area	-12.81	9.41	-1.36	0.18
	Extreme BC \times slope position	-41.47	9.79	-4.24	<0.01
	Extreme BC \times beetle-killed basal area	4.58	11.68	0.39	0.70

Notes: The drainage basin was included as a random variable. Burning conditions (BC), slope position, beetle-killed basal area, and interaction terms were included as fixed effects. "Burning conditions" was a categorical variable, with moderate burning conditions as the model intercept. Models were only run for fire severity response variables that satisfied parametric statistics assumptions after transformation (if needed). RdNBR stands for Relative differenced Normalized Burn Ratio.

Fig. 2C). Correlations remained nonsignificant after accounting for burning conditions (Fig. 2, inset table). Beetle-killed basal area also did not differ among fire severity classes under either moderate ($F_{2,37} = 1.11$, $P = 0.34$) or extreme ($F_{2,42} = 1.55$, $P = 0.22$) burning conditions. After accounting for burning conditions and slope position in regression analyses, RdNBR, char height, litter + duff depth, and charred surface cover (the variables that met parametric assumptions) were still unrelated to outbreak severity (Table 1). Fire severity was instead associated with slope position and burning conditions (i.e., weather); severity increased with higher slope positions during moderate burning conditions but not during extreme burning conditions (Table 1, Appendix F).

Effects of bark beetle outbreak on postfire tree regeneration

Postfire Douglas-fir regeneration (seedlings that germinated postfire; <3 branch whorls) was variable, ranging from 0 to 4750 seedlings/ha (mean 215 seedlings/ha, median 0 seedlings/ha) and composing 88% of all postfire tree seedlings. The postfire seedling distribution was characterized by positive skew; 65% of plots had no seedlings (90% of severe-surface or crown fire plots).

Fire severity class and beetle-killed basal area were the two highest ranked explanatory variables in the random forests analysis, and were the two variables retained

after trimming the regression tree to reduce over-fitting (Fig. 3). In areas of crown or severe surface fire, postfire Douglas-fir seedling density was low (mean 13 stems/ha, median 0 stems/ha) and unrelated to prefire beetle outbreak severity ($P > 0.10$; Fig. 3A). Seedling density was high (mean 757 seedlings/ha, median 167 seedlings/ha) in areas of light surface fire, and exceeded prefire stem density if outbreak severity and fire severity were low (Fig. 3B). However, seedling density was low if outbreak severity was high in areas of light surface fire (Fig. 3B); density declined with increasing prefire outbreak severity in light surface fire plots ($r_S = -0.48$, $P = 0.02$; Fig. 3A; Appendix G).

Prefire advance regeneration density (saplings <1.4 m; ≥ 3 branch whorls) was positively correlated with postfire seedling density ($r_S = 0.42$, $P < 0.05$), and similar to postfire seedlings, was negatively correlated with prefire outbreak severity ($r_S = -0.37$, $P = 0.08$). Most advance regeneration (82% of saplings) was composed of Douglas-fir, and >75% established in the period 2003–2008, before the fire but after the peak beetle outbreak.

DISCUSSION

The lack of relationship between beetle outbreak severity and subsequent fire severity indicates that these disturbances were not linked. However, they did interact to produce compound disturbance effects on postfire tree regeneration, contributing to the structural hetero-

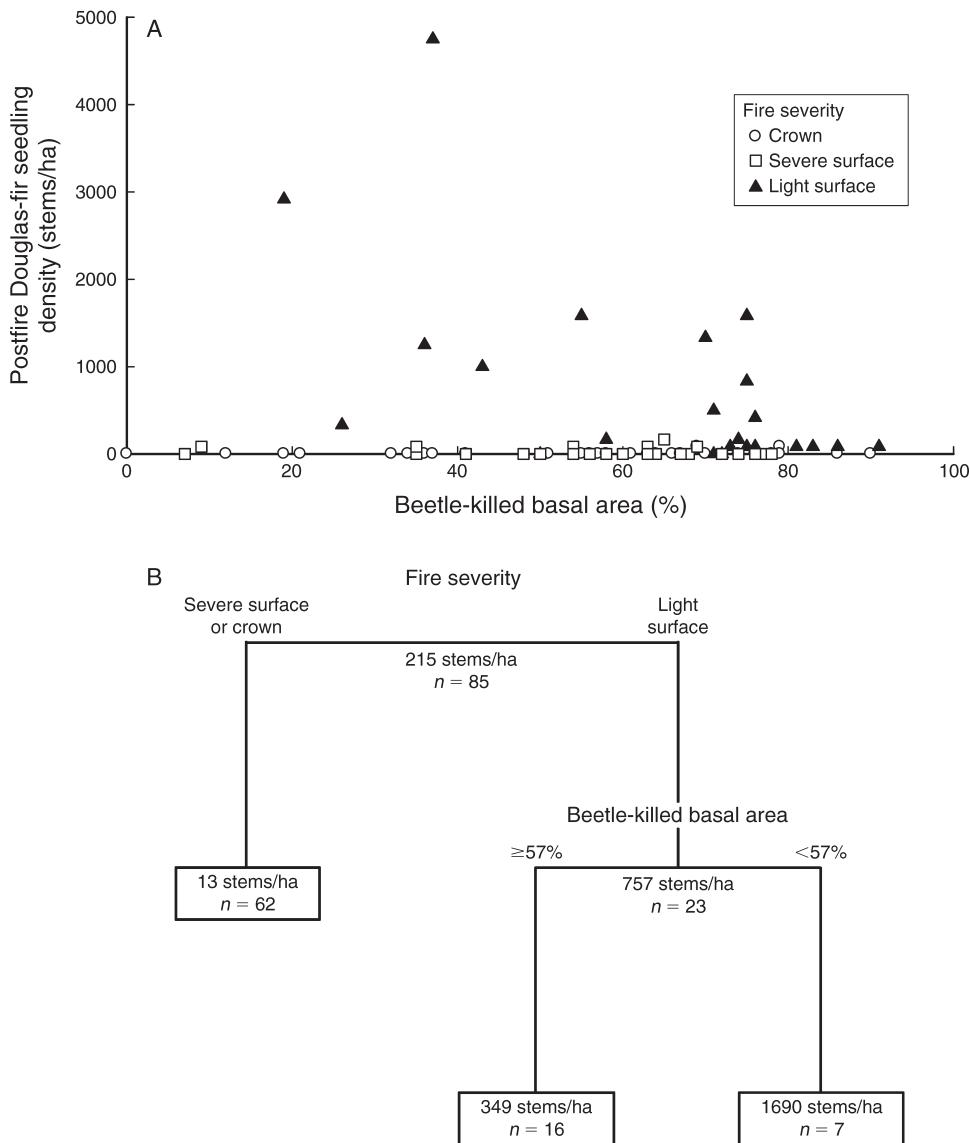


FIG. 3. (A) Postfire Douglas-fir seedling density vs. percentage beetle-killed basal area by fire-severity class. Spearman rank correlations (r_s) were only significant in light surface fire ($r_s = -0.48$, $P = 0.02$). (B) Final pruned regression tree model for postfire Douglas-fir seedling density (stems/ha), showing significant predictor variables in order of importance based on variance explained. Each node and terminal node for the regression tree shows the mean seedling density for that node and the number of plots in that group.

geneity characteristic of mid/lower montane forest ecosystems. Prefire Douglas-fir beetle outbreak had no detectable effect on surrogate, integrative, canopy, or forest-floor measures of fire severity, except for a slight reduction in bole scorch associated with increasing outbreak severity. Instead, fire severity varied with burning conditions (reflective of weather at the time of burning) and slope position. Bark beetle outbreaks preconditioned the forest response to low-severity fire such that tree regeneration was low if prefire outbreak severity was high. Given the extent of recent beetle outbreaks in western North America now in the gray

stage, these results suggest implications for post-outbreak trajectories in other mid/lower montane ecosystems.

Beetle outbreaks and fire severity

Our finding of no linked relationship between beetle outbreak severity and surrogate and integrative measures of fire severity were consistent with most, but not all, retrospective studies in subalpine forests. We found no evidence that surrogate measures of fire severity (RdNBR) varied with beetle-killed basal area, indicating similar pre- to postfire changes in live biomass across



PLATE 1. Mixture of beetle-killed, fire-killed, and living trees three years after the Gunbarrel Fire, in the Absaroka Wilderness, Greater Yellowstone, USA. Photo credit: B. J. Harvey.

levels of outbreak severity (Appendix E). These results are consistent with hypotheses of no effect based on other retrospective studies that used satellite indices of fire severity in montane forests in California (Bond et al. 2009) and subalpine forests in Colorado (Kulakowski and Veblen 2007). While Bigler et al. (2005) reported a slight increase in high-severity fire in subalpine forest stands where beetle outbreaks occurred decades before fire, they did not quantify beetle outbreak severity and the effect was small relative to topography. We also found no field evidence that integrative fire severity classes were affected by beetle outbreak severity under moderate or extreme burning conditions. These results differed from field measures in lodgepole pine forests burned in the 1988 Yellowstone Fires (Turner et al. 1999), where plots in which >50% of the trees had evidence of mountain pine beetle (*Dendroctonus ponderosae*) outbreak within the prior 20 years were more likely to have burned as a crown fire. Incongruence between findings could indicate differences between subalpine and mid/lower montane forests, in the spatial resolution of field sampling, or in the interval between the two disturbances.

Our detailed field measurements of canopy and forest-floor fire severity allow for inferences into underlying mechanisms through comparison with fuel profile data in other studies, and evaluation of several standing hypotheses about beetle outbreaks and fire. We hypothesized either no relationship or a reduction in canopy fire severity with increasing prefire beetle outbreak severity, and this expectation was supported. Our findings largely match predictions from fuel profiles in gray-stage mid/lower montane forests, where canopy fuels are reduced relative to unaffected stands (Hoffman et al. 2012, Donato et al. 2013a). Canopy cover is inherently irregular in mid/lower montane forests, and beetle-induced changes increase this within-stand patchiness in a system that is already very heterogeneous (Donato et al. 2013a). Our findings differed from gray-stage expectations in higher-elevation subalpine forests with more contiguous canopy fuels where the likelihood of severe crown fire is predicted to substantially decrease after needles fall from beetle-killed trees (DeRose and Long 2009, Klutsch et al. 2011, Simard et al. 2011). Expectations of increased forest-floor fire severity in the gray stage were not supported, as beetle outbreak

severity was unrelated to postfire litter + duff and charred surface cover across burning conditions (i.e., weather) and slope position. Although measures of postfire litter + duff depth potentially varied as a function of prefire litter + duff depth, this cannot be assessed postfire. However, postfire litter + duff depth was consistently correlated with other measures of fire severity (Appendix C: Table C1), indicating that our postfire data were a reliable measure of fire effects rather than prefire conditions. An increase in surface fuel combined with a decrease in wind resistance from opening of the canopy has been hypothesized to increase forest-floor fire severity in most forest types (Jenkins et al. 2008, Klutsch et al. 2011, Hicke et al. 2012, Hoffman et al. 2012, Schoennagel et al. 2012). While chronosequence studies in Douglas-fir forests show no difference (Donato et al. 2013a) or slight increases (Jenkins et al. 2008) in coarse surface fuels from unaffected to gray-stage stands, slower snag-fall in mid/lower montane forests than subalpine forests (Donato et al. 2013b) may delay coarse surface fuel accumulation and thus delay beetle-induced increases in forest-floor fire severity.

Our study measured fire severity in gray-stage post-outbreak forests, and it is possible that results may differ in other post-outbreak stages. In particular, fire severity in the red stage (1–3 years post-outbreak, >50% of dead needles remaining in the canopy) is of heightened concern (Hicke et al. 2012) because of higher foliar ignitability (Jolly et al. 2012a). However, our findings may apply to extensive areas of post-outbreak mid/lower montane forest because recent outbreaks of most North American bark beetle species peaked between 2004 and 2007 (Meddens et al. 2012) and forests have now transitioned to the gray stage, which lasts ~15–20 years (Hicke et al. 2012). After the gray stage (>20 years post-outbreak), the probability of burning (Lynch et al. 2006) or severe fire (Bigler et al. 2005) may increase, and coarse fuel accumulation from snag-fall may lead to higher forest-floor fire severity (Donato et al. 2013a). Field studies following fires in other post-outbreak stages and forest types remain a research priority.

Our data show that fire severity was unaffected by recent beetle outbreaks; however our analysis did not capture real-time fire behavior (e.g., flame length, fireline intensity, rate of spread) that is important for operational fire management (e.g., suppression efforts) in post-outbreak stands. Thus, real-time fire behavior in post-outbreak stands remains understudied.

Beetles, fire, and postfire tree regeneration

Although prefire beetle outbreak severity and fire severity were unrelated to one another (i.e., not linked), the combined disturbances interacted to influence postfire tree regeneration, supporting expectations for compound disturbance effects (Paine et al. 1998). In the absence of fire, Douglas-fir regeneration after high-severity beetle outbreak can be as high as 1900 stems/ha (D. Donato, *unpublished data*). In the absence of severe

beetle outbreaks, postfire Douglas-fir seedling density can also be high, exceeding stand replacement when fire severity is low (Fig. 3B). However, our data suggest that the beetle outbreak preconditioned the postfire response to lower-severity fire through a reduction in the in situ seed source by killing large, seed-producing trees. These effects were manifest prior to the fire through a reduction in prefire advance regeneration following the beetle outbreak and continued postfire through a reduction in postfire seedling establishment, ultimately resulting in a negative relationship between total Douglas-fir regeneration (all live trees <1.4 m that established pre- or postfire) and beetle outbreak severity ($r_s = -0.37$, $P = 0.09$). Our data are from early in postfire succession (three years after fire), but these initial patterns are likely indicative of longer-term trends. In nearby areas, postfire Douglas-fir seedling density three years following the 1988 Yellowstone fires was highly correlated with density 24 years after the fires ($R^2 = 0.87$, $P < 0.001$; D. Donato, *unpublished data*). Seed is generally available where surviving mature trees are present, as yearly cone crop failures in Douglas-fir are rare (Roeser 1942). However, >50% of our study plots with no postfire regeneration were >150 m from the nearest mature live tree. Thus, patterns of early postfire regeneration driven by compound beetle–fire disturbances likely promote persistent heterogeneity in stand structure, a defining characteristic of mid/lower montane ecosystems.

Compound disturbance effects have also been observed following other sequential disturbances, including blowdown followed by fire (Buma and Wessman 2011), and spruce beetle outbreak followed by fire (Kulakowski et al. 2013). Although serotinous conifers can experience compound effects following successive fires (Brown and Johnstone 2012), such species may buffer a forest from compound beetle outbreak–fire effects on tree regeneration because a persistent canopy seedbank can remain viable up to 25 years after tree death (Aoki et al. 2011, Teste et al. 2011). The interaction between regenerative mechanisms (e.g., seedbanking, resprouting) and beetle–fire relationships remains an important focus of future research.

CONCLUSION

Beetle outbreaks and fire are both expected to increase as climate warms (Bentz et al. 2010, Westerling et al. 2011), increasing the probability that they will overlap in time and space and heightening the need to understand how multiple disturbances interact to shape forest ecosystems. Using empirical field data from mid/lower montane forests in Greater Yellowstone, we found no evidence of prefire (gray-stage) bark beetle outbreaks in Douglas-fir forests affecting subsequent fire severity. Instead, fire severity varied largely with burning conditions (reflective of weather at time of burning) and slope position. Beetle outbreaks and fire interacted to affect postfire tree regeneration, such that seedling

density was uniformly low when fire severity was high, but was limited by beetle outbreak severity when fire severity was low. Although beetle outbreaks and subsequent fire were not linked disturbances, they produced compound effects that contribute to heterogeneity characteristic of mid/lower montane forests.

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SUPPLEMENTAL MATERIAL

Appendix A

Study area and recent Douglas-fir beetle outbreak history ([Ecological Archives E094-227-A1](#)).

Appendix B

Information on beetle outbreak severity measurements ([Ecological Archives E094-227-A2](#)).

Appendix C

Information on fire severity measurements ([Ecological Archives E094-227-A3](#)).

Appendix D

Burning conditions as a proxy for weather at time of burning ([Ecological Archives E094-227-A4](#)).

Appendix E

Variability in stand structure impacts from bark beetle outbreak ([Ecological Archives E094-227-A5](#)).

Appendix F

Effects of slope position on fire severity during different burning conditions ([Ecological Archives E094-227-A6](#)).

Appendix G

Generalized linear model for postfire Douglas-fir seedling density ([Ecological Archives E094-227-A7](#)).