FINAL REPORT

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Bark beetles, fuels and future fire hazard in contrasting conifer forests of Greater Yellowstone

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ABSTRACT

The extent and severity of bark beetle (Curculionidae: Scolytinae) epidemics and the frequency of large, severe fires have reached unprecedented levels in recent decades, and these trends are expected to continue with ongoing climate change. Insects and fire have tremendous ecological and economic effects in western forests, yet their interactions are poorly understood. We combined field studies and simulation modeling to understand how bark beetle infestation and post-outbreak management affect fire hazard in two widespread but contrasting forest types, lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) in the Greater Yellowstone Ecosystem (GYE) in northwestern Wyoming. We directly addressed key bark-beetle research priorities identified by US Forest Service scientists for the western US, via three primary questions and several supplemental studies.

(1) How do effects of bark beetle outbreaks on fuel profiles and subsequent fire hazard differ between lodgepole pine and Douglas-fir forests? A 20-year "time-since-beetle-outbreak" chronosequence was sampled in Douglas-fir forests of the GYE to quantify changes in fuel profiles and to contrast these fuel profiles with those previously developed for lodgepole pine. The strongest effects of beetles in Douglas-fir were canopy thinning and increased spatial heterogeneity of fuels. Significant reductions were seen in available canopy fuel load and canopy bulk density, whereas effects on surface fuels were minor after accounting for pre-beetle variation in stand structure. Coarse fuel accumulation was lower in Douglas-fir forests (2x higher than in green stands) than reported for higher-elevation forest types like lodgepole pine (3-8x higher). Post-outbreak seedling regeneration was sparse in Douglas-fir stands, suggesting that beetle-caused reductions in stand densities will persist for a long time. **(2) How was the severity of recent fire in lodgepole pine and Douglas-fir forests affected by prior bark beetle infestation, and does the combination of beetle infestation and fire compromise forest recovery?** Field studies were conducted in recently burned forests that had been affected by beetle outbreaks prior to the fire. Fire severity in gray-stage Douglas-fir forests was related primarily to local topography and weather conditions at the time of burning; the effect of pre-fire beetle outbreak severity on fire severity was negligible. However, greater beetle-caused tree mortality was associated with lower post-fire tree seedling densities because of loss of the Douglas-fir seed source. Fire severity in lodgepole pine forests was greatest in stands having high proportions of trees in the green-attack stage (i.e., in the earliest phase of the outbreak), but fire severity decreased with increasing proportions of red and gray-stage trees. This is apparently the first documentation of the important influence of green-attack trees, which have very low foliar moisture and increased flammability, but retain crown bulk density. Effects were most pronounced under moderate burning conditions, with greatly diminished influence of beetle activity under extreme burning conditions. Post-fire lodgepole pine seedling densities were unrelated to pre-fire beetle outbreak severity. Unlike Douglas-fir, lodgepole pine forests appear resilient to the combined effects of beetles and fire because of the persistent seed bank within serotinous lodgepole pine cones. **(3) What post-beetle fuel treatments are likely to change the hazard of subsequent severe fire in lodgepole pine and Douglas-fir forests?** We initialized the FIRE AND FUELS EXTENSION TO THE FOREST VEGETATION SIMULATOR model for lodgepole pine and Douglas-fir with our field data, then used simulations to explore the effects of salvage, slash treatments, and other common forest management practices on future fire hazard. Across all simulated treatments in both lodgepole pine and Douglas-fir, the strongest projected effects

relative to untreated post-outbreak stands were reductions in coarse woody surface fuels and in well-decayed standing snags, and reduced biomass carbon storage. The reduction in coarse woody surface fuels suggests reduced heat release and less resistance to control in future fires. Treatment effects on fine fuels, both canopy and surface, were surprisingly minor or short-lived; convergence between treated and untreated stands was projected within about a decade.

Supplemental studies: In addition to the primary research objectives outlined above, we conducted three related studies that laid the groundwork for one of the primary objectives or complemented our field studies. We continued our efforts to develop new algorithms for mapping tree mortality in beetle-killed conifer forests at landscape scales and successfully mapped tree mortality in major forest types of the GYE. Second, we capitalized on our time-since beetle chronosequences to contrast nitrogen cycling in beetle-attacked lodgepole pine and Douglas-fir. Third, we conducted a field study of the effects of post-outbreak salvage harvest on fuels, tree regeneration, and nitrogen cycling in lodgepole pine forests, complementing our modeling study; litter and nitrogen dynamics exhibited some changes over time after beetle outbreak, but few differences were seen between salvaged and untreated stands.

Our research findings have implications for management of beetle outbreaks and fires in Rocky Mountain forests. Our intent is to help managers identify the kinds of actions that will likely be effective in reducing adverse impacts of beetles and fires, and also to identify actions that are sometimes suggested but that may be relatively ineffective. Two main messages emerge from our findings. (1) Impacts of beetles and fire are contingent on numerous factors, including the stage of the outbreak when fire occurs and the burning conditions at the time of the fire. (2) Timing and context of post-beetle-fire treatments are important. Some management actions may be effective if fire occurs at certain stages of beetle outbreak but ineffective at other stages, and different forest types and structural conditions typically require different management approaches. To date, the research supported by this grant has resulted in 10 papers published in refereed scientific journals, 5 additional papers submitted or in preparation for submission to refereed journals, parts or all of 3 Ph.D. dissertations, contributions to synthetic communications produced by JFSP, 9 formal conference presentations, a special session on post-disturbance fuels and fire modeling at the AFE Conference in Utah, and numerous informal presentations at field stations and other venues.

BACKGROUND AND PURPOSE

Recent increases in insect and fire activity throughout the western US have presented forest managers with formidable challenges. The extent and severity of bark beetle (Curculionidae: Scolytinae) epidemics reached unprecedented levels (Raffa et al. 2008), and the frequency of large, severe fires continues to increase (Westerling et al. 2006). These trends are expected to continue because climate change–especially warmer temperatures, earlier snowmelt and more severe summer droughts–is implicated for both disturbances. Insects and fire have tremendous ecological and economic effects in western forests, yet their interaction is poorly understood. Studies are beginning to provide insights into how fuels and projected fire behavior may change following bark beetle epidemics (e.g., Jenkins et al. 2008, Simard et al. 2011, Schoennagel et al. 2012, Hicke et al. 2012, Jenkins et al. 2012) and beginning to evaluate the efficacy of forest management practices (e.g., removal of beetle-killed trees or remaining small trees) designed to reduce future fire hazard (e.g, Collins et al. 2012). However, whether vulnerability to severe fire does or does not increase following bark beetle outbreaks remains unresolved, in part because empirical data on wildland fires that have burned through beetle-killed forests are scarce. Research has shown that time since beetle outbreak is critical for understanding the relationship between beetle outbreaks, stand structure, fuel dynamics and fire hazard, but again, rigorous empirical datasets are relatively few. In this study, we combined field studies and simulation modeling to understand how bark beetle infestation and post-outbreak management affect fire hazard in two widespread but contrasting forest types, lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*). Previous research on beetle outbreak effects on fire in lodgepole pine forests has been inconclusive, and few studies have examined Douglas-fir.

Lodgepole pine and Douglas-fir forests are key components of Rocky Mountain landscapes. Both experienced extensive and severe recent bark beetle outbreaks, yet important differences between these forest types (Keane 2008) suggest that post-beetle changes in fuel hazard may be distinct. We hypothesized that differences in fire regime, stand structure and regeneration potential would lead to important differences in fuel profiles, fire hazard and, in turn, the effectiveness of alternative mitigation strategies in lodgepole pine and Douglas-fir. We focused on changes in the fuel profiles over time, observed effects of bark-beetle-outbreak timing and severity on the severity of subsequent fires, and effectiveness of management strategies for addressing fuel hazards arising from insect outbreaks. We directly addressed key bark beetle research priorities identified by US Forest Service scientists for the western US (Negron et al. 2008). Our work addressed three primary questions.

Question 1: How do effects of bark beetle outbreaks on fuel profiles and subsequent fire hazard differ between lodgepole pine and Douglas-fir forests? Bark beetle outbreaks substantially alter stand structure and live and dead fuel characteristics. We are beginning to understand how fuels and potential fire behavior change over time following mountain pine beetle outbreaks in lodgepole pine forests, but little research has addressed interior Douglas-fir forests, which are extensive in the Rockies and often coincide with locations where residential development is increasing. Given differences in structure and dynamics of lodgepole pine and Douglas-fir forests, we predicted significant differences in post-beetle fuel dynamics and potential fire behavior (summarized in Table 1).

Table 1. *Summary of hypothesized effects of bark beetle attack on fuels and potential fire behavior in two contrasting forest types. Hypotheses for lodgepole pine reflect our prior time-since-beetle outbreak (TSB) data, published in Simard et al. (2011).*

Time since beetle attack (TSB, yrs)	Undamaged TSB = 0		Red attack TSB = 1-2		Gray attack TSB = 3-5		Old attack TSB = 20	
Forest type	PSME	PICO	PSME	PICO	PSME	PICO	PSME	PICO
Data availability	✱	✓	✱	✓	✱	✓	✱	✓
Fuel trends: CBD	(reference)		↓	⇩	↓	⇩	↓	⇩
CBH			-	-	-	-	-	⇩
Fine woody fuels (1-h)			-	-	-	-	-	-
Coarse woody fuels (1000-h)			-	-	-	-	↑	⇧
Grasses			↑	-	↑	-	↑	⇧
Fire behavior: Flame length†	(reference)		↑	-	↑	-	↑	-
Torching			-	-	-	-	↑	⇧
Active crowning			-	⇧	↓	⇩	↓	⇩
Soil heating			-	-	-	-	↑	⇧

Note: PSME: Douglas-fir; PICO: lodgepole pine; ✱: data to be obtained in the proposed study; ✓: data available from 2006 JFSP grant; CBD: Canopy Bulk Density; CBH: Canopy Base Height; †: Frontal flame length, influenced by the < ¼ inch (76 mm) compartment of surface fuels.

Question 2: How was the severity of recent fire in lodgepole pine and Douglas-fir forests affected by prior bark beetle infestation, and does the combination of beetle infestation and fire compromise forest recovery? The ability to address directly the effects of beetle infestation on fire severity has been limited by a lack of spatially explicit data to characterize the extent *and* severity of both disturbances and an absence of field studies of fire in beetle-killed forests. We hypothesized that fire severity would differ among recent beetle-damaged forests (1-2 years), older beetle-damaged forests (3-10 years) and undisturbed forests, following the hypotheses above (Table 1). Field studies evaluated fire severity in areas that burned in 2008 in Douglas-fir and lodgepole pine forests. We also evaluated postfire forest recovery/regeneration in areas of varying pre-fire beetle outbreak severity. We hypothesized that the effects of subsequent fire on regeneration will depend on beetle-damage severity, time since beetle outbreak and fire severity.
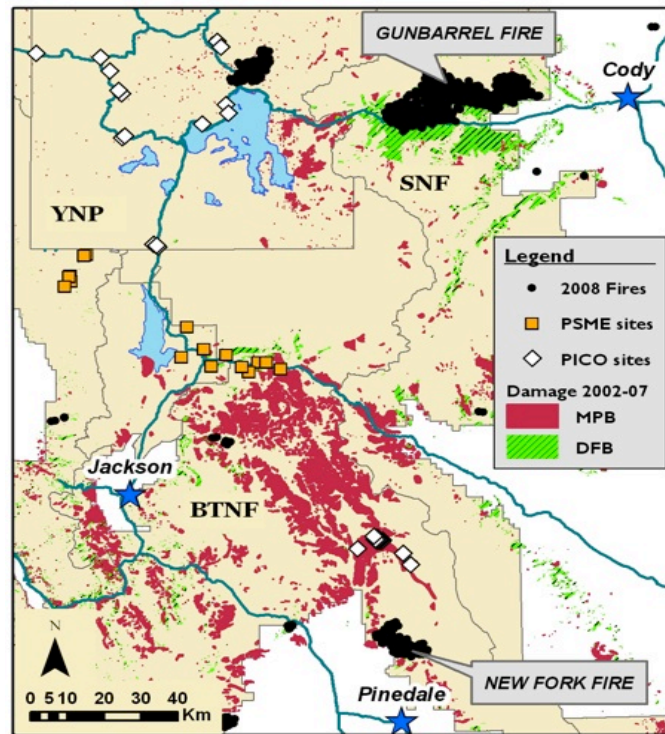
Question 3: What post-beetle fuel treatments are likely to change the hazard of subsequent severe fire in lodgepole pine and Douglas-fir forests? Given the potential for increased fire hazard following bark beetle outbreaks, forest managers would like options for treating beetle-killed stands proactively to reduce the likely damage from future wildfires. Harvest of beetle-killed trees (i.e., 'salvage') may be prescribed to reduce the amount of dead material in the forest canopy (to reduce crown fire spread potential) and to decrease the surface accumulation of woody fuels from natural snag-fall over time (to reduce surface fire intensity and resistance to control). The extent of recent beetle outbreaks has led to broadening application of these treatments, but few data have been available to inform post-outbreak management actions (see Lewis, 2009; Collins et al., 2011, 2012; Griffin et al., 2013). We evaluated how different post-harvest fuel treatments in beetle-affected stands could affect fuel profile dynamics and other characteristics of stand structure over the ensuing decades.

LOCATION AND STUDY DESCRIPTION

Location. Our studies were conducted in the Greater Yellowstone Ecosystem (GYE) in northwestern Wyoming (Fig. 1), where we built on >20 yrs of research and our recent studies (funded by JFSP) of bark beetles and fire in lodgepole pine. The study area includes Yellowstone (YNP) and Grand Teton National Parks and the Bridger-Teton (BTNF) and Shoshone (SNF) National Forests. The mountain pine beetle (MPB) and Douglas-fir beetle (DFB) were both active since 2002 in lodgepole pine and Douglas-fir, respectively, and significant area has burned recently in beetle-affected forests.

Study overview. To contrast fuel profiles and fire hazard between the two forest types (Question 1), a "time-since-beetle-outbreak" (TSB) chronosequence was sampled in Douglas-fir forests of the GYE to quantify fuel profiles from 0 to 20 yrs since the epidemic and to contrast these fuel profiles with those from lodgepole

Fig. 1. Study region in Greater Yellowstone depicting areas of bark beetle infestation and subsequent recent fire.

pine (Simard et al. 2011). In addition, we capitalized on the opportunity to contrast nitrogen cycling in beetle-attacked lodgepole pine and Douglas-fir. To determine how the behavior and severity of recent fires was affected by the bark beetle infestation (Question 2), field studies were conducted to determine how the actual spatial variation of fire severity across the landscape was related to severity and stage of the pre-fire beetle infestation. We also determined whether postfire tree regeneration was influenced by severity of the pre-fire beetle outbreak. Finally, to understand the potential effectiveness of alternative fuel treatments (Question 3), we initialized the FIRE AND FUELS EXTENSION TO THE FOREST VEGETATION SIMULATOR model (Reinhardt and Crookston 2003) for lodgepole pine and Douglas-fir with our field data. Simulations explored the effects of a wide range of common forest management practices (e.g., thinning, removal of beetle killed trees or remaining small trees, slash management, etc.) on future fire hazard. In addition, we conducted a complementary field study to evaluate effects of post-outbreak salvage harvest on fuels, tree regeneration, and nitrogen cycling in lodgepole pine. Lastly, we have continued our efforts to develop new algorithms for mapping tree mortality in beetle-killed conifer forests.

For each primary objective, we describe the study and summarize key findings. For published work, summaries are brief; greater detail is included for results that are not yet published.

Effects of bark beetle outbreak on fuel profiles in Douglas-fir forests

Study description. We studied canopy and surface fuels in interior Douglas-fir forests in Greater Yellowstone, Wyoming, USA, to determine how fuel characteristics varied with time since outbreak of the Douglas-fir beetle (*Dendroctonus pseudotsugae*) (Donato et al. 2013a). We established a TSB chronosequence of plots (*n* = 20) in Douglas-fir, similar to what we had done previously for lodgepole pine (Simard et al. 2011). We sampled five replicates of each stage: green (undisturbed); red stage (1-3 yr post-outbreak, with >50% of beetle-killed basal area retaining red needles and/or trees still being attacked); gray stage (4-14 yr post-outbreak, all beetle-killed trees with <<50% needle retention, most fine branches still intact, no new attack occurring); and silver stage (25-30 yr post-outbreak, beetle-killed trees deteriorating structurally, a.k.a. 'old-attack'). Dendrochronological analysis on 250 live-tree cores and 75 dead-tree samples was used to reconstruct initial stand conditions and verify that all classes were similar prior to outbreak, and to verify outbreak severity and timing of each TSB class (Johnson and Miyanishi 2008, Simard et al. 2011). In each 0.25-ha plot, we described the tree (DBH or height if < 1.4 m tall; live / dead; quantity of red needles; presence / absence beetle galleries and pitch tubes; crown base height) and understory (% cover and height in twenty 1-m^2 quadrats) layers. Surface fuels were sampled in ten 20-m transects using Brown's planar intercept method (Brown 1974). We produced vertical profiles of canopy bulk density for each plot, using field-measured crown base height, and crown fuel biomass estimated from DBH and allometric relationships (Brown 1978). These profiles were used to derive effective canopy bulk density and canopy base height following Scott and Reinhardt (2001). To assess effects of beetle outbreak on surface temperatures and relative humidities during summer (i.e., fire season), we deployed micrometeorological probes in three stands in each TSB class (iButton, Maxim Integrated Products, Dallas Semiconductor, Sunnyvale, California, USA).

Field data were used to generate a comprehensive fuel profile for each stand. These data provide very similar inference as common fire models, as they include the main variables that drive model outputs, plus others for which models cannot currently account. Chief among the model-driving responses are canopy bulk density (amount of fuel per unit volume of canopy, a determinant of mass flow rate and spread potential of crown fire), available canopy fuel load (potential energy available for release from crown fuels), canopy base height (vertical gap beneath the base of tree crowns, which affects the ability of fire to move vertically from the surface to the canopy), and surface fuel loads by size class and live/dead category (which affect fireline intensity, spread, and transition to crowns) (see Van Wagner 1977, Rothermel 1983, Cruz et al. 2003, Reinhardt and Crookston 2003, Reinhardt et al. 2006). Because current fire models have recognized shortcomings (Jenkins et al. 2008, Cruz and Alexander 2010, Klutsch et al. 2011, Hicke et al. 2012), we focused on fuel profiles, which contain more comprehensive and reliable information than fire models for this application. Our study represents one of the most detailed field assessments of post-disturbance fuels conducted to date, and it is the first to specifically compare disturbance effects to background variation in stand structure.

In addition to quantifying post-outbreak fuel profiles, we collected data on post-outbreak tree regeneration in TSB chronosequence in Douglas-fir (Donato et al. in preparation). In the GYE, Douglas-fir spans an exceptionally wide range of environmental conditions, from mesic closed-canopy stands to drier open parklands that form the lower elevation ecotone with non-forest

vegetation. We examined how post-outbreak forest structure and composition as well as regeneration abundance, timing, and growth varied with post-outbreak time in these two settings (mesic forest vs. dry parkland). A specific question was whether dry parklands may revert toward non-forest condition after a beetle outbreak because of limited regeneration on marginal forest sites, especially under the generally warmer climate of the past two decades.

Key findings. Douglas-fir beetle outbreak was associated with altered fuel profiles in Douglas-fir forests of Greater Yellowstone; however the magnitude and importance of these changes (and resulting stand structures) were comparable to the range of pre-outbreak stand conditions (Donato et al. 2013a). The strongest effects of beetles were canopy thinning and increased spatial heterogeneity of fuels over post-outbreak time, whereas effects on surface fuels were generally minor after accounting for background variation. Stand structure in each of the TSB classes reflected the partial and slow nature of Douglas-fir beetle outbreaks (Donato et al. 2013a). Outbreak severity ranged from 38-83% of pre-outbreak basal area and did not differ among red, gray, and silver classes (mean 59%, compared to the endemic level of 4% in green stands; Donato et al. 2013a). Live basal area declined with time since outbreak, but remained at 14 to 16 m^2 ha^{-1} in gray and silver stands. Live stems were as numerous as dead stems in all TSB classes, even in the overstory.

After accounting for pre-outbreak basal area, there were significant reductions in available canopy fuel load and canopy bulk density with increasing time since outbreak. Foliage biomass began declining in the red stage (8.0 Mg ha^{-1} versus 12.1 Mg ha^{-1} in green stands; Donato et al. 2013a). Total available canopy fuel load declined monotonically and was approximately halved by the silver stage (8.0 vs. 17.0 Mg ha^{-1} in green stands); however, the proportion dead was elevated in both the red and gray stages. Canopy bulk density declined by ~30% in post-outbreak stands compared to green stands (0.10 kg m^{-3}). Ranges in canopy fuels in undisturbed stands, associated with the xeric-mesic gradient, were comparable to beetle outbreak effects (Donato et al. 2013a).

After accounting for pre-existing variation in stand basal area, there were few significant changes in surface fuels associated with beetle outbreak, (Donato et al. 2013a). Most size classes of surface woody fuels showed no trend with time since outbreak, except that silver stands had comparatively low levels of 1-h fuels and high levels of 1000-h sound fuels. The only other significant response was herbaceous biomass, which was about 50% greater in the red stage.

Patterns of dead surface fuels in post-outbreak Douglas-fir suggested key differences from other ecosystems. As we hypothesized, coarse fuel accumulation was much lower in Douglas-fir forests (2x higher than in green stands) than that reported for higher-elevation forest types (3-8x higher; Page and Jenkins 2007a, Simard et al. 2011, Schoennagel et al. 2012).

Following bark beetle outbreak in Douglas-fir, limited new (post-outbreak) seedling regeneration was observed in either the mesic or xeric setting, even 20+ years after bark-beetle outbreak, with >80% of seedlings having established prior to outbreaks (Donato et al., in preparation). This advanced regeneration was abundant in mesic forest stands (median 1560 stems ha^{-1}) and sparse to absent in dry parklands (median 152 stems $ha^{-1)}$. These data suggest successional trajectories following beetle outbreaks in Rocky Mountain Douglas-fir forests are determined largely by the

extant understory, rather than new outbreak-stimulated regeneration. Thus, in mesic closed-canopy stands with abundant tree understories, succession is accelerated by the bark-beetle outbreak, and forests are likely to persist. In dry parklands, however, lack of a well-developed tree understory combined with an absence of seedling recruitment means that beetle-induced mortality shifts the system toward non-forest vegetation. Such potential tree-line shifts are consistent with hypotheses regarding directional changes or century-scale fluctuations in forest cover associated with climatic conditions, with bark beetles as the immediate catalyst of change (Donato et al., in preparation).

Effects of pre-fire beetle outbreak on fire severity and forest regeneration

Study description. We conducted field studies in fires that burned through post-outbreak forests to evaluate the effects of pre-fire beetle outbreaks on fire severity and post-fire tree regeneration. The Gunbarrel Fire (Shoshone National Forest) burned in summer 2008 through gray-stage Douglas-fir forests with variable levels of pre-fire outbreak severity (5-90% beetle-killed basal area). The New Fork Lakes fire and the Red Rock Complex Fire (Bridger-Teton National Forest) burned through green-attack / red stage and gray stage lodgepole pine forests, respectively; both fires had variable pre-fire outbreak severity (0-78% beetle-killed basal area). Portions of each of these fires burned under moderate (low winds and temperatures, high relative humidity) and extreme (high winds and temperatures, low relative humidity) burning conditions, allowing us to test for different effects of outbreak severity on fire severity under contrasting conditions. Sample plots ($n = 85$ for the Gunbarrel Fire, $n = 100$ for the New Fork Lakes fire, $n = 43$ for the Red Rock Complex Fire) were situated systematically throughout burned areas that covered the range of fire severity and pre-fire beetle outbreak severity in each fire.

In each study plot, we collected data on pre-fire stand structure and outbreak severity, fire severity, and post-fire tree seedling establishment in a 30 m diameter circle plot divided into 4 quadrants. 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 each live or dead pre-fire sapling (trees < 1.4 m that established pre-fire) in 3-m belt transects along the main N-S and E-W axis of the plot. Pre-fire beetle outbreak severity was quantified following methods outlined in Harvey et al. (in press), by removing the bark on every tree taller than 1.4 m (24,926 individual trees) and recording evidence (or absence of evidence) of *Dendroctonus* activity (Schmitz and Gibson 1996, Safranyik and Carroll 2007). Each tree was assigned to one of five distinct categories: 'pre-disturbance snag', 'killed by bark beetles prior to fire', 'green attack at time of fire', 'live at the time of fire', or 'unknown'. Canopy fire severity was measured on five randomly selected co-dominant canopy trees in each quadrant (20 trees per plot) by recording the maximum char height to the nearest 0.5 m and the maximum percentage of scorching around the circumference on the main bole of each selected tree. We also recorded the proportion of basal area and trees that were killed by fire. Surface fire severity was measured by recording the depth of post-fire litter + duff (mm) at every 3 m along the main axis of the plot (20 points per plot) and by recording the percent cover of charred surface (mineral soil, litter, woody debris), using the point intercept method at 480 points along the main axis of the plot. Post-fire tree seedlings (trees that germinated post-fire) were recorded in twenty 0.25-m^2 quadrats, four 2-m belt transects or four

3-m belt transects, depending on the density of seedlings; sampling area increased as density decreased. Data on abiotic conditions (e.g., slope, aspect, elevation, topographic curvature) were also collected in each plot.

To test if fire severity was linked to pre-fire outbreak severity, we used general linear models (or generalized linear models to account for spatial autocorrelation, when necessary). We regressed each fire severity measure against the proportion of basal area killed by beetles while accounting for burning conditions (moderate or extreme) and topography (local elevation). Non-parametric Spearman rank correlations were used for non-normally distributed response variables. We used several approaches to test if fire severity and outbreak severity produced compound effects on post-fire tree regeneration. If parametric assumptions were met, we used generalized linear models (accounting for spatial autocorrelation) to regress log-transformed seedling densities against pre-fire outbreak severity while accounting for pre-fire basal area (proxy for seed source), serotiny (for lodgepole pine), and fire severity. If parametric assumptions were not met, we used random forests, regression trees, and/or spearman rank correlation tests to test for effects of pre-fire outbreak severity on post-fire tree regeneration.

Key findings. The relationship between pre-fire outbreak severity and fire severity was complex, and varied by forest type, burning conditions, and outbreak stage. In gray-stage Douglas-fir forests, fire severity was unrelated to pre-fire outbreak severity under moderate and extreme burning conditions and was instead driven by topography when burning conditions were moderate (Harvey et al. in press). In lodgepole pine forests, fire severity was affected by pre-fire outbreak severity under moderate conditions, but the direction of effects differed with outbreak stage (Harvey et al. in review). Under extreme conditions, which is when most large fires in subalpine forests occur, effects of outbreak severity on fire severity decreased or became non-significant. The effect of outbreak severity on post-fire seedling establishment differed between lodgepole pine and Douglas-fir, presumably due to different regeneration mechanisms (e.g., serotinous vs. non-serotinous).

Gray-stage Douglas-fir forests. Canopy and forest floor measures of fire severity in gray-stage Douglas-fir forests were unrelated (all $P > 0.10$) to pre-fire outbreak severity under moderate and extreme burning conditions (Harvey et al. in press). One exception was the percentage of bole scorch, which declined slightly (indicating lower fire severity) with increasing outbreak severity. Fire severity was instead driven by topography; severity increased toward ridgetops and decreased toward valley bottoms. Effects of topography were stronger under moderate burning conditions than under extreme burning conditions. Three years following fire, overall Douglas-fir tree regeneration was low (tree seedlings were absent in 65% of plots) and most often occurred in light-surface fire plots (which contained surviving pre-fire trees). In plots that burned as light surface fire, seedling density declined with increasing pre-fire outbreak severity ($r_s = -0.48$, $P = 0.02$).

Green-attack / red-stage lodgepole pine forests. Under moderate burning conditions, many measures of fire severity increased with pre-fire outbreak severity to levels commonly experienced under extreme burning conditions. Char height, bole scorch, and tree mortality from fire increased; and litter and duff depth decreased (indicating higher fire severity) with outbreak severity (Fig. 2). Charred surface cover was unrelated to outbreak severity ($P > 0.10$). For each

of the significant relationships, fire severity increased with the relative proportion of green-attack to red-stage trees in a plot, indicating the importance of changes to foliar flammability before needles change color and are dropped. Under extreme burning conditions, relationships between pre-fire outbreak severity were weak or non-significant (Fig. 2). Pre-fire outbreak severity and fire severity did not combine to produce compound disturbance effects in green-attack / red-stage serotinous lodgepole pine forests. After controlling for the effects of covariates (fire severity, pre-outbreak lodgepole pine basal area, and pre-fire serotiny), post-fire lodgepole pine seedling density was not related to pre-fire outbreak severity ($t = 0.40$, $P = 0.69$), which did not interact with serotiny ($t = -0.28$, $P = 0.78$).

Gray-stage lodgepole pine forests. Under moderate burning conditions, fire severity declined with increased pre-fire outbreak severity. Char height, bole scorch, and tree mortality from fire decreased; and litter and duff depth increased (indicating lower fire severity) with outbreak severity (Fig. 3). Charred surface cover was unrelated to outbreak severity ($P > 0.10$). Under extreme burning conditions, all fire severity metrics were unrelated to pre-fire outbreak severity (Fig. 3). Only seven plots (of 43) contained post-fire seedlings, not providing enough degrees of freedom to include covariates in an OLS model with pre-fire beetle outbreak severity. Univariate tests revealed no relationship between post-fire lodgepole pine seedling density and pre-fire beetle outbreak severity overall ($r_s = -0.07$, $P = 0.65$) or within any burn-severity classes (all $P > 0.10$), indicating that pre-fire outbreak severity and fire severity do not combine to produce compound disturbance effects in gray-stage serotinous lodgepole pine forests.
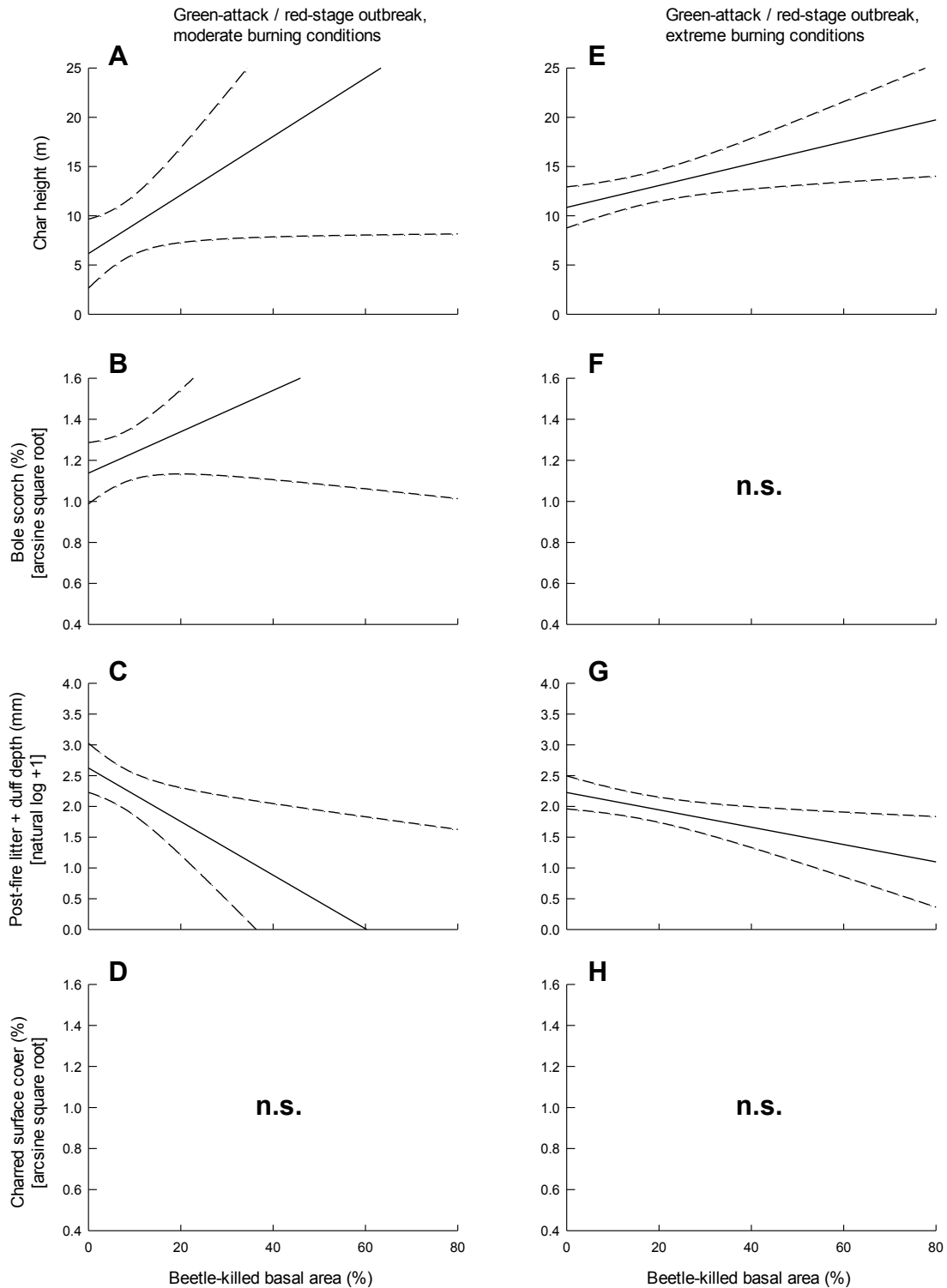
Fig. 2. *Fire severity vs. outbreak severity for fires burning under moderate and extreme burning conditions in lodgepole pine forests in the green attack / red stage of mountain pine beetle outbreak (New Fork Lakes Fire). Solid lines are generalized least squares (GLS) regression lines for significant relationships; dashed lines are 95% confidence intervals on regression slopes. Non-significant relationships are denoted with "n.s."*

Gray stage / post outbreak,
moderate burning conditions

Gray stage / post outbreak,
extreme burning conditions
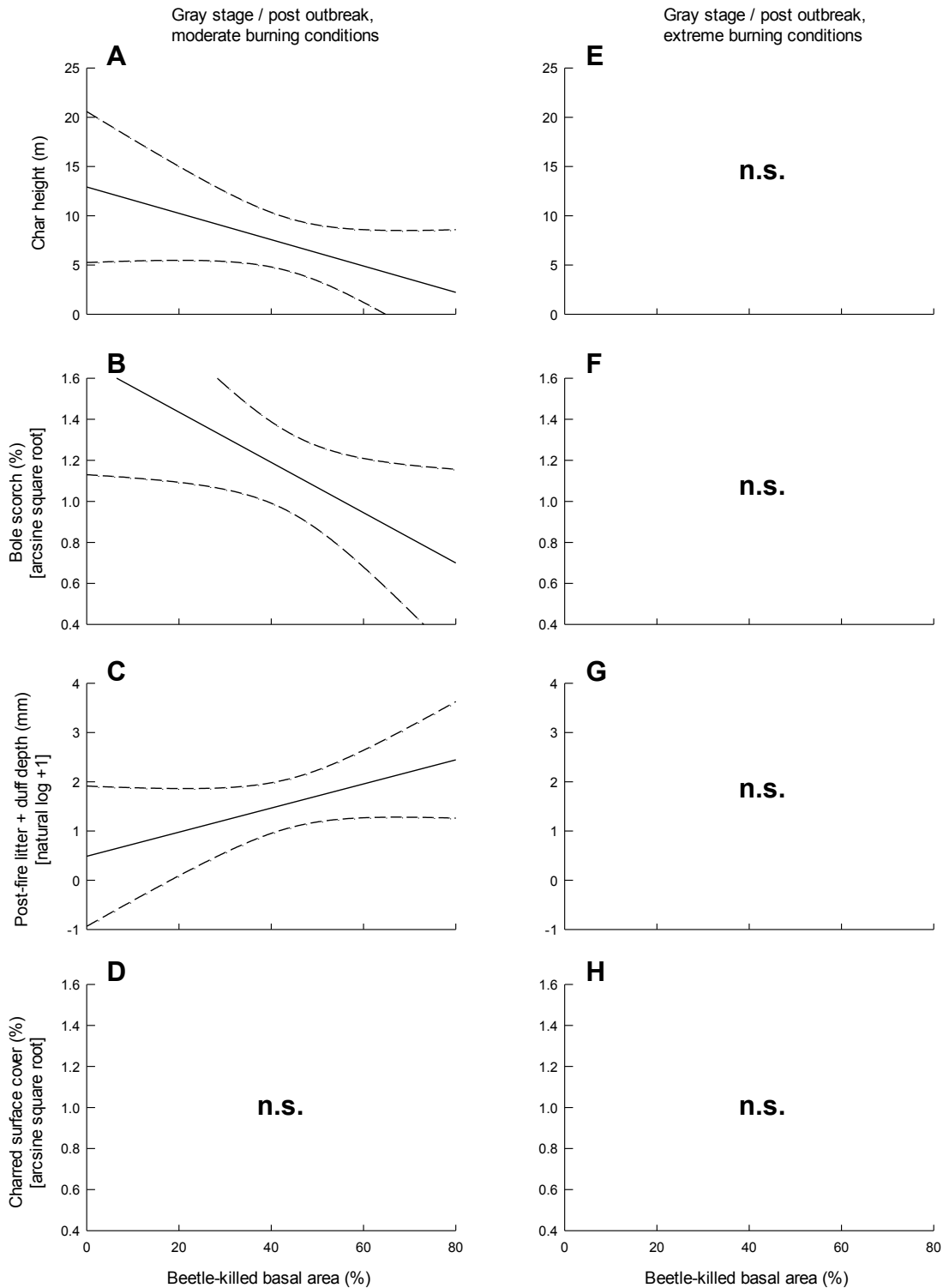
Fig. 3. *Fire severity vs. outbreak severity for fires burning under moderate and extreme burning conditions in lodgepole pine forests in the gray stage / post outbreak phase of mountain pine beetle outbreak (Red Rock Complex Fire). Solid lines are ordinary least squares (OLS) regression lines for significant relationships; dashed lines are 95% confidence intervals on regression slopes. Non-significant relationships are denoted with "n.s."*

Effects of post-outbreak forest management

Study description. We conducted a modeling study to evaluate the short- and long-term (0 to 50-yr) effects of common post-outbreak management treatments on fuel profiles and stand structures in lodgepole pine and Douglas-fir forests (Donato et al. 2013b). We used the FIRE AND FUELS EXTENSION TO THE FOREST VEGETATION SIMULATOR (FFE-FVS; Reinhardt and Crookston 2003) to simulate the effects of various post-beetle treatment scenarios on live and dead tree density, live and dead surface fuel loading, potential fire behavior and likely fire effects under a range of weather conditions, in lodgepole pine and Douglas-fir stands (Ager et al. 2007a, 2007b). We first evaluated the model by comparing 25-yr projections of 10 gray-stage stands, without management, to the empirical data collected in our time-since-beetle chronosequences. We then asked: (a) how different post-harvest fuel treatments compare in terms of fuel profile and stand structure development, and (b) how these comparisons potentially differ by forest type. Responses of interest included canopy fuel metrics, surface fuel loads, snag and live-tree dynamics, and carbon storage in live and dead tree biomass. Understanding relationships among dynamics of fuel profiles and other aspects of stand structure can inform prescriptions and tradeoffs involved in post-outbreak management. We simulated five commonly used management prescriptions (Table 2) and projected for 50 years after treatment.

Table 2. *Post-bark-beetle-outbreak management options simulated in this study using FVS (from Donato et al. 2013b).*

Treatment name	Treatment description[a]
Control	No trees harvested; no fuel treatments implemented
Slash in place	Beetle-killed trees harvested; branches and unmerchantable tops (slash) cut from boles and left in place, not piled
Prescribed burn	Beetle-killed trees harvested; branches and unmerchantable tops cut from boles, then burned over most of harvest unit area
Pile and burn	Beetle-killed trees harvested; branches and unmerchantable tops cut from boles, aggregated into piles and burned
Whole tree removal	Beetle-killed trees harvested; entire trees including branches and unmerchantable tops removed from site

[a]*For treatments with harvest of beetle-killed trees (slash-in-place, prescribed-burn, pile-and-burn, whole-tree-removal), cutting prescription included retention of 10% of snags left standing, and assumed a 15% cull rate (stems cut but left on site due to breakage/defect; adapted from Snell and Brown, 1980).*
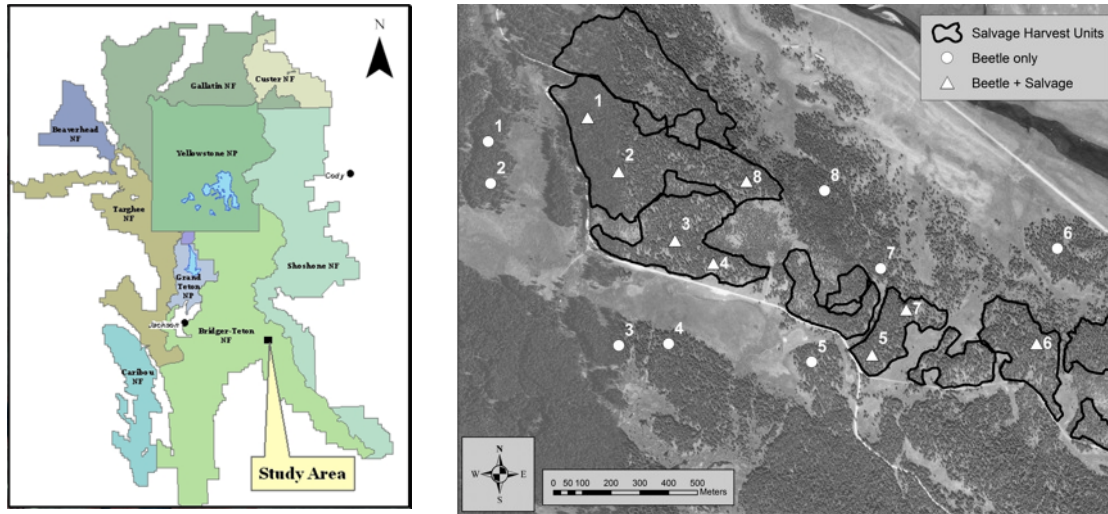
Figure 4. *Location of study sites in the Green River area of Bridger-Teton National Forest.*

In addition to the modeling study, we conducted a field study of post-outbreak salvage harvest in beetle-killed lodgepole pine on the Bridger-Teton National Forest (Fig. 4; Griffin et al. 2013). This was an opportunistic addition to our research program that capitalized on a planned timber sale, and this study was supported in part by supplemental funding from the USFS Western Wildlands Environmental Threat Assessment Center. Study sites were located in a 4-km² area of the Green River Lakes region in lodgepole pine forests that established following a fire in 1849. We used a paired and replicated before-after-control-impact (BACI) experimental design consisting of eight pairs of 50-m x 50-m plots located in beetle-killed forests. In each pair, one plot was harvested and a similar plot < 400 m away was unmanaged. A commercial operator conducted the salvage harvest in summer 2009 using a feller-buncher, with lop-and-scatter slash treatments in all harvested plots. The harvest prescription was to remove dead and dying (beetle-infested) lodgepole pine and stipulated that young growth (advance regeneration) should be protected throughout the harvest. We sampled vegetation, fuels, litter, soils and nitrogen availability following standard protocols (Griffin et al. 2013).

Key findings. Simulated consequences of post-outbreak stand management on fuels. Across all post-outbreak treatments that we simulated in lodgepole pine and Douglas-fir, the strongest projected effects relative to unharvested stands were reductions in coarse woody surface fuels (after 10-20 yr), fewer well-decayed standing snags (after 40 yr), and reduced biomass carbon storage (throughout all 50 years) (Donato et al. 2013b). The reduction in coarse woody surface fuels suggests reduced heat release and less resistance to control in future fires. Projected effects on fine fuels, both in the canopy and surface layers, were surprisingly minor or short-lived; natural fall and decay of fine material in unharvested stands led to the convergence of most fuel variables between treated and untreated stands within about a decade. Most follow-up treatment methods – whether unmerchantable tree parts were left in place, burned, piled, or removed entirely – had similar impacts on most aspects of fuel and stand structure in lodgepole pine and Douglas-fir forests. However, the prescribed burning treatment was distinct and generally had

the strongest effects, owing to greater consumption of forest floor mass and mortality of small trees, which had persistent influences on both the canopy and surface fuel layers.

Treatment effectiveness in reducing fuels was mirrored by reductions in biomass carbon storage and recruitment of well-decayed snags, illustrating common tradeoffs involved in fuel treatments (Donato et al. 2013b). All the simulated treatments reduced carbon storage (on-site live+dead tree biomass) relative to unharvested stands in both forest types, and these reductions were larger than those associated with the beetle outbreak itself. Our study stands experienced 40-80% basal area mortality, leaving a significant component of both large and small live trees, which continued growing after the outbreak.

Most simulated treatment effects were very similar across lodgepole pine and Douglas-fir forests. The main forest type differences were: (a) surface coarse wood, for which treatment effects were strongest in lodgepole pine because more rapid natural snag-fall in that type led to the highest coarse fuel loads in unharvested stands; (b) recruitment of advanced-decay snags in later years, which was absent in lodgepole pine but present in Douglas-fir; and (c) canopy base height and bulk density, which were respectively lower and higher (i.e., more conducive to crown fire) in lodgepole pine relative to Douglas-fir – in large part because of a dense regeneration layer in lodgepole pine forests that is often sparse or absent in Douglas-fir

Field study of post-outbreak salvage harvest in lodgepole pine. Post-outbreak timber harvest in beetle-killed lodgepole pine reduced advance regeneration by about 50% (from 3575 to 1688 stems ha^{-1}), with significant reductions in larger height classes (30 to 140 cm) but not in smaller (< 30 cm) height classes. Relative species density did not change, and harvested stands remained dominated by lodgepole pine. Several litter variables (total litter %N, total litter N pool) changed with time but did not respond to salvage harvest, and others (litter depth, %N of free needle litter) did not change over time or with salvage harvest. Following salvage harvest, soil temperatures at the litter-soil interface during early summer were about 2-3°C warmer in treated plots, but late-summer and winter temperatures did not differ with treatment. Effects of salvage harvesting on inorganic nitrogen availability was also minimal. Although resin-bag accumulated ammonium increased about threefold between 2007 and 2010 (as stands progressed through the green-attack and red stages) there was no effect of salvage harvest on seasonal or annual rates of resin-bag accumulated nitrate or ammonium (Griffin et al. 2013).

Post-outbreak timber harvest also substantially altered the amount and vertical distribution of fuels. Canopy fuels declined in all stands from 2007 to 2010 as beetle-killed trees shed their needles, but the decrease was greater in salvage-logged plots (–80%) than untreated plots (-30%); effective canopy bulk density followed a similar trend. Dead woody surface fuel loads in all size categories doubled in the treated plots following harvest, whereas these fuel loads did not change in the untreated plots (Griffin et al. 2013). Salvage harvest had no detectable effect on duff depth or dead fuel depth.

Remote sensing of bark beetle outbreak severity

Study description. Accurately assessing the spatial and temporal progression of tree mortality during a bark-beetle outbreak remains difficult. Townsend et al. (2012) introduced a general approach to map defoliation in broadleaf deciduous forests. We have developed a modification of that approach to map mortality in beetle-killed forests of the GYE. The Townsend et al. (2012) approach involved differencing pre- and during-disturbance Landsat images using the Normalized Difference Infrared Index (NDII, Hardisky et al. 1983), calculated for Landsat images as $(\rho_{B4} - \rho_{B5}) / (\rho_{B4} + \rho_{B5})$, where ρ is surface reflectance in Landsat bands 4 (B4, near infrared, NIR, 760-900 nm) and 5 (B5, shortwave infrared, SWIR, 1550-1750 nm). Extensive testing has shown that NDII (and similar indices employing both the NIR and SWIR) are best for detecting forest disturbance (Townsend et al. 2012).

In this study, our objectives were to map: (1) the year of start of for a beetle outbreak, (2) year of peak mortality, and (3) total percent mortality. We also wanted to map the spread of mortality across the landscape to produce year-by-year maps of percent mortality during the course of an outbreak. Finally, we used the Landsat record to map greenness recovery following the disturbance. These objectives distinguish our effort from other research focusing on the detection of red-attacked forests (Skakun et al. 2003), beetle-killed forests (beetle killed or not, e.g. Meddens et al. 2011), the timing of beetle attack (Goodwin et al. 2008), or identification of individual dead trees from hyperspatial imagery (Coops et al. 2006). Our research demonstrates the first generalized approach to accurately map proportional mortality as well as the timing of mortality over large areas.

Our Landsat model was calibrated to field data collected from 2006-2012 in the GYE, including 299 variable-radius plots representing 2800 to 5000 m^2 (a Landsat pixel covers 900m^2) in which we tallied tree species composition and mortality (Fig. S1). Field plots were established in all of the major forest types experiencing beetle disturbance, including lodgepole pine (*Pinus contorta*, PICO, affected by mountain pine beetle), whitebark pine (*P. albicaulis*, PIAL, also affected by mountain pine beetle), Engelmann spruce (*Picea engelmannii*, PIEN, affected by spruce beetle) and Douglas-fir (*Pseudotsuga menziesii*, PSME, affected by Douglas-fir beetle). Mortality of overstory trees ranged from 0-100% in our field data.

A chief consideration for mapping disturbance is the selection of appropriate images for implementing the change detection. That is, accurate detection of proportional mortality requires a "before" image with no mortality (or some modest level of mortality). To overcome this, most researchers employ a time series of images (e.g., LANDTRENDR of Kennedy et al. 2010, in which an image profile is used to detect beetle kill by Miegs et al. 2011). We follow a general profile approach, and to this end, we acquired all growing season (June-September) images for the Landsat period of record (including Landsat 5 and Landsat 7) for the area including the four Landsat footprints covering the GYE (Fig. S2). Each image was atmospherically corrected using the LEDAPS algorithm (Masek et al. 2008) and topographically normalized following Soenen et al. (2005). We then calculated NDII. To account for inter- and intra-annual variability in NDII, we then normalized each NDII image to its 80th percentile value for forested areas (determined using NLCD, Figs. S3-4), under the assumption that the 20% of forests with highest values of

NDII should be the least disturbed (i.e., undisturbed) forests in a scene, and hence represented a basis for detection of no-change (Townsend et al. 2012).

To further account for the high amount of variability in spectral reflectance across a year, we then created a single NDII image per year, calculated as the mean NDII across all growing season images in a year. Our mean NDII image used only mid-summer (July and August) images, where available, avoiding June and September images, which can show residual effects of high vegetation moisture content (June) or moisture stress (September). However, where clouds, shadows or SLC-off artifacts prevented calculation of mean NDII, we gap-filled using June/September NDII. Our approach has the benefit of creating a single, composite cloud/shadow- and missing-data-free NDII image per year using the best available data. We merged the annual mean NDII images for the four Landsat footprints into one composite image for each year of the time series.

To identify disturbances from the imagery, we first used an iterative moving-filter approach operating on a 3x3 pixel array centered on each pixel in the image time series to split the time series at each year and statistically test (using a Welch's t-test) whether NDII of the two halves of the data set (three years on either side of a time point) were significantly different in terms of both the mean and variance. To ensure that aberrant short dips in NDII were not interpreted as disturbances, we repeated the moving-window filter three times for each profile, each time omitting from none to two years of data from the center point. We flagged a profile as having a disturbance if the maximum p-value of all three moving-window filters was less than 0.05. Time series with no obvious breaks were flagged as undisturbed.

When a profile was flagged as disturbed (i.e., all three windowed comparisons had p-values < 0.05), we took the average of the years where the t-statistic attained a maximum for the three windowed comparisons and flagged this as the year of the initiation of the disturbance (Y_{start}).. The process is illustrated in Fig. S5 for disturbed locations and Fig. S6 for (relatively) undisturbed locations. We then fit a cubic curve to the NDII profile from one year prior to Y_{start} ($NDII_{start-1}$) through either ten years after Y_{start} ($NDII_{start+10}$) or the last year of the time series, whichever comes first. The lowest point on the NDII profile that occurs where the second derivative of the cubic curve is positive (the region where the cubic curve is concave) is identified as the year of maximum disturbance (Y_{peak}), i.e. the highest mortality unaccompanied by recovery in greenness through understory response or regeneration/release. We use the cubic curve to smooth issues with noise in the NDII profile and to avoid any false peaks that are observed after the first significant dip in the profile right after the start of the disturbance. We also identify a maximum pre-disturbance NDII, $NDII_{undist}$, as our value for a reference undisturbed NDII based on the NDII profile for the five years prior to Y_{start}. We compute a metric of greenness recovery for each years post Y_{peak} as proportional increase in NDII from $NDII_{undist}$, i.e. $R_Y = (NDII_Y - NDII_{min})/(NDII_{undist} - NDII_{min})$, where R_Y refers to proportional recovery of greenness from pre-disturbed conditions in year Y. Note that R_Y does not refer to recovery of live biomass (which would take decades or more), only to recovery of greenness detected from Landsat, and is probably best interpreted as a metric of understory response.

The assembled NDII time series were then integrated with the field data to estimate mortality as a function in the decline in NDII during the period between Y_{undist} and Y_{peak}. Note that while the

proportion of dead trees in the canopy may still be high in the years following Y_{peak}, the relationship between decline in NDII and mortality is obscured by the greenness recovery, R_Y (see increasing profiles in Figs. S4-5). We model mortality in any given year as a logistic fit (because mortality is a proportion between 0 and 1) of the difference between $NDII_{undist}$ and $NDII_Y$, where $NDII_Y$ is the NDII in the year that the plot was sampled. The model is only applied to field data collected in years spanning the window Y_{undist} onwards. Because forests vary widely in their openness, we also include $NDII_{undist}$ in the logistic model to account for variability in initial NDII among sites. Thus, proportional mortality in year Y is modeled as:

$$Mortality(\%)_Y = \frac{1}{1 + \exp{(\beta_0 + \beta_1 * [NDII_{undist} - NDII_Y] + \beta_2 * [NDII_{undist}])}}$$

We employed 1000 permutations using a 75%/25% split of the data for model calibration and validation. This allowed us to assess uncertainty in the model and report the range of model performance.

Final model parameters were:

$\beta_0 = 1.202 \pm 0.0830$ (1.S.D.)
$\beta_1 = -11.839 \pm 0.711$ (1.S.D.)
$\beta_2 = 5.880 \pm 0.460$ (1.S.D.)

Model performance was:

- Calibration $R^2 = 0.783$ (0.675 – 0.843) S.D. = 0.025
- Calibration RMSE = 0.081 (0.065 – 0.091) S.D. = 0.0035
- Validation $R^2 = 0.705$ (0.370 – 0.879) S.D. = 0.078
- Validation RMSE = 0.102 (0.073 – 0.132) S.D. = 0.0092
- Model-averaged $R^2 = 0.724$ (0.709 – 0.728) S.D. = 0.002
- Model-averaged RMSE = 0.099 (0.098 – 0.105) S.D. = 0.0008

Key findings. The results indicate a very strong fit between observed and predicted mortality, comparable with Townsend et al. (2012) and highly repeatable across divisions of the data (Fig. 5). The model performed equivalently for all four forest types, with no difference in residuals by year of sampling, and no significant difference in residuals by plot basal area (Table 3). Root mean square errors indicate that tree mortality can routinely be estimated accurately within 10%. The model exhibited a slight bias at low levels of mortality (low mortality was overpredicted), but this is an unavoidable consequence of the fact that plots with low or no mortality were not included in the model because we are unable to detect a significant change in NDII that would allow determination of $NDII_{undist}$ (see Fig. 5). The results (Table 3, Fig. 5) suggest that confidence in our estimation of proportional mortality starts at about 20% basal area of dead trees. Fig. S7 shows the mapped year of start of a mortality event, while Fig. S8 shows the year of peak mortality. The year of peak mortality aligns well with aerial detection survey maps (Fig S9). We used the results to map percent mortality for 1995-2012 (Figs. S10-S27), and peak mortality for any year (Fig. S28). The results show that the majority of the landscape has been

impacted by mortality events, with the bulk of the activity occurring 2001-2008. The maps we have developed (see Appendix) show mortality, regardless of disturbance type. Thus far, we have used ancillary maps to mask areas with mortality due to fire or logging.

Table 3. *Model validation for annual maps of tree mortality in the GYE derived from Landsat imager; results by species (top) and year of field sampling (bottom).*

	N	R^2	RMSE
Species			
PIEN	17	0.830	0.083
PICO	53	0.623	0.086
PSME	21	0.783	0.118
PIAL	36	0.710	0.109
Year			
2006	27	0.763	0.096
2007	54	0.750	0.093
2008	2	1.000	0.127
2009	21	0.565	0.101
2010	5	0.507	0.112
2011	4	0.030	0.122
2012	14	0.725	0.100
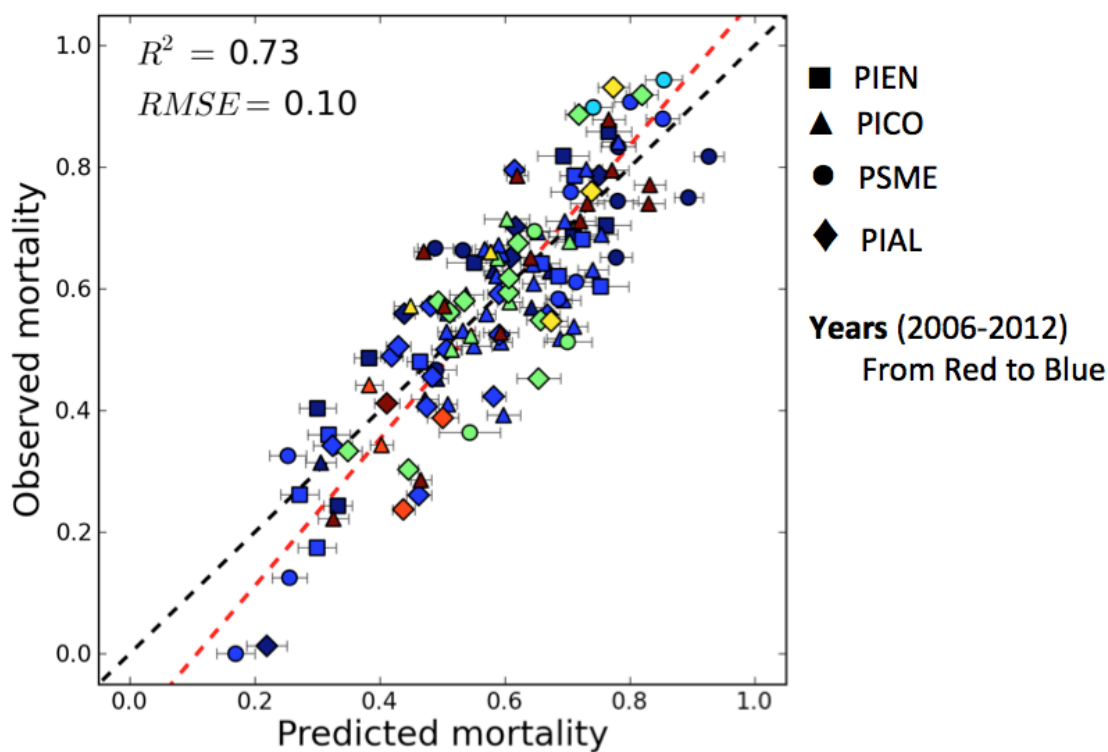
Fig. 5. *Model validation, predicted vs. observed tree mortality. Units are proportion of basal area killed. Results indicate good model skill and no model bias by year of field sampling or overstory canopy type.*

MANAGEMENT IMPLICATIONS

Fuels, potential fire behavior, and fire severity

Bark beetle outbreak effects on fuel profiles differed between lower montane Douglas-fir forests and higher-elevation lodgepole pine forests with stand-replacing fire regimes. Relatively low pre-outbreak tree density and canopy biomass, as well as slow regeneration dynamics, in Douglas-fir were among the most important differences from lodgepole pine. In Douglas-fir, canopy thinning associated with beetle-caused tree mortality resulted in very low canopy fuel mass and continuity, with little recovery up to three decades post-outbreak. Changes in surface fuels were comparatively minor.

Wildland fuels in Douglas-fir (or lower montane) forests should be managed in the context of wide background variation; bark beetle outbreaks are but one of many factors influencing fuel profiles and fire potentials. For most categories of both canopy and surface fuels, effect sizes of the beetle outbreak were similar or even less than the range associated with background variability. Beetles may alter the fuel profile within a given stand, but when viewed across stands, these effects were of similar magnitude to among-stand variation in the absence of beetle disturbance, suggesting little need for post-outbreak fuels treatment. Prioritization of treatments in Douglas-fir forests will benefit by considering which fuel components are uniquely affected by beetles (e.g., window of reduced canopy foliar moisture in initial outbreak stage), which components vary with similar magnitude in response to beetles and other drivers (e.g., canopy fuel load and bulk density), and which components seem to vary less with beetles than other drivers (e.g., most surface woody fuels). Treatments in beetle-affected landscapes could continue to address a variety of objectives rather than focusing singularly on beetle impacts. Treatments might best be targeted towards creating defensible space in the event of a subsequent fire in beetle-killed forest.

In Douglas-fir, any post-outbreak fuel management might be prioritized for denser stands in which crown fuels are more continuous, and coarse woody fuels are more abundant, rather than stands shifted to a sparse woodland/savanna condition that is unlikely to support significant crown fire activity. Our data in post-outbreak Douglas-fir stands suggest reduced fire potentials, particularly for crown fire after the red stages, although abundant coarse fuels in silver stands could increase burn residence time and heat release. Thus, there is reduced potential for both vertical (torching) and horizontal (spreading) crown fire propagation, all other factors equal, but greater potential for dense stands to support fire. Again, treatments might best be targeted towards creating defensible space around valuable infrastructure.

In lodgepole pine, the window of time in which salvage harvest could reduce post-outbreak canopy fuels compared to untreated stands is very early in the outbreak sequence and very short. Where canopy fuel metrics are of concern, our findings suggest that prompt post-outbreak management (i.e., in the green attack / red stage) is important for treatment efficacy (Donato et al. 2013b, Griffin et al., 2013). During the short window of time that lodgepole pine stands are in the green-attack / red stage, fire severity under moderate burning conditions may increase to levels commonly observed under extreme burning conditions. Harvest of dead trees conducted later (i.e., gray stage) may have little relevance to reducing crown fire potentials. That is, the

longer salvage harvest is delayed after beetle attack, the less effective the treatment will be because the stage is ephemeral, and available canopy fuels are progressively shed from beetle-killed trees. Management treatments would likely need to be applied during the year of active infestation or immediately thereafter to reduce fire severity in beetle-attacked lodgepole pine. However, management at this early stage of beetle outbreak is improbable because many tree canopies would still be green and remain undetected by visual surveys for at least one more year. By the time the red crowns are detected in ADS surveys, information is relayed to managers, regulatory procedures are approved, a sale goes through the bidding process, and logging equipment is mobilized, beetle-killed stands would likely have transitioned to the late-red or gray stage. Early management could be conducted in the immediate vicinity of vulnerable infrastructure. However, our findings do not support the efficacy of pre-emptive fuels treatments in areas remote from the wildland-urban interface because beetles and fires do not appear to be moving stands outside their historical range of variability, and the spatial extent of treatment needed to have a measureable effect on fire behavior at a landscape scale would be exorbitantly expensive and technically impossible.

In gray-stage stands of both lodgepole pine and Douglas-fir, management treatments are not needed to reduce canopy- or surface-fire severity. Our analyses of recent fires that burned through beetle-killed forests showed that no measures of fire severity increased with outbreak severity in the gray stage. Further, under extreme burning conditions (when most large fires occur in the Rocky Mountains and when variation in fuels are generally less influential on fire activity), pre-fire outbreak severity had no detectable effect on fire severity. In addition, simulated fuel profiles varied little between treated and untreated stands after the first decade, suggesting that salvage harvest would have little influence on post-outbreak fire behavior. In essence, natural fall and decay of fine material in unharvested stands led to similar post-outbreak fuel structure to treated stands within about a decade. This finding represents a key difference from operations in which all live and dead trees are removed, in which the result is similar to a clearcut and thus wholly different from untreated stands that retain mature trees (Collins et al., 2012). However, the main change we observed in fuel profiles following treatment – reduction in coarse woody surface fuels after 10-20 years – may result in reduced heat release and resistance to control in future fires (e.g., Monsanto and Agee, 2008; Collins et al., 2012). Harvest of beetle-killed trees and subsequent treatments altered the fuel profile and structure of outbreak-impacted stands, but overall effects were similar among treatments, suggesting flexibility in management options in post-outbreak forests (Donato et al. 2013b).

In some beetle-killed lodgepole pine forests, merchantable trees can be harvested without severely compromising potential tree regeneration and without large initial effects on soil N (Griffin et al. 2013). Impacts on other aspects of stand structure were also relatively minor (excepting soft snag recruitment and reductions in biomass carbon storage), harvest of beetle-killed trees for objectives other than fuel reduction (e.g., for timber or biomass-fuel production) potentially can leave post-outbreak ecosystems largely intact if live trees are not also felled.

Post-disturbance stand structure and tree regeneration

Differences between Douglas-fir and lodgepole pine dynamics suggest different emphases on their post-outbreak management. The FVS projections for unharvested stands suggest that large,

decayed snags begin to appear in Douglas-fir forests in a few decades after outbreak, while lodgepole pine snags fall much faster and are down before they matriculate into the decayed class (Donato et al. 2013b). In the short term, retention of new sound snags during management actions is important for providing post-disturbance wildlife habitat (Saab et al. 2007). In the longer term, because few soft snags are recruited in lodgepole pine stands regardless of management, prescriptions attempting to maintain snag structures well into the future may be most relevant to tree species that stand longer as snags, such as Douglas-fir (Donato et al. 2013b).

Managers should consider forest type and the interval between the two disturbances when anticipating tree regeneration after fires that burned through beetle-killed forests. If the interval between beetle outbreak and subsequent fire is less than about 10 years in serotinous lodgepole pine stands, *in situ* seed supply is likely to be adequate for stand regeneration. Active measures such as post-fire seeding may not be needed, unless other species (e.g., aspen) respond more quickly and potentially outcompete lodgepole pine. Our data cannot provide guidance if the interval between beetle outbreak is longer (e.g., gray stage) in lodgepole pine, as we were unable to determine the factors responsible for the sparse tree regeneration we observed. In beetle-killed Douglas-fir forests, postfire tree regeneration may be sharply reduced overall and limited to areas that are near live trees that can serve as a seed source. Douglas-fir forests are inherently variable in density and age structure, and postfire Douglas-fire recruitment occurs over many years (Donato et al., unpublished data). Thus, post-fire seeding may not be needed if maintaining variable stand structures across the landscape is a desired management target. However, if high-density, even-aged post-fire stands are the goal, forest managers may wish to consider postfire seeding to accelerate tree regeneration in burned areas that are far from live mature trees.

Field experiments tracked over the long term will provide the most robust information on the efficacy and tradeoffs associated with post-outbreak management practices. Modeling exercises are valuable in exploring potential consequences of post-outbreak management, but current limitations of fuel/fire models in heterogeneous post-disturbance environments indicate the need for field studies. Further, given known uncertainties in the models, reporting detailed fuel profiles to managers can actually carry more complete information on how fire potentials may be affected by beetle outbreaks.

RELATIONSHIP TO OTHER RECENT FINDINGS AND ONGOING WORK

The recent review by Hicke et al. (2012) offers the best current and objective synthesis of fire-bark beetle interactions. Their analysis is especially useful because of its emphasis on identifying areas where multiple studies agree and those where disagreement remains, and for the careful discussion of why different studies produce seemingly different results. Thus, we reference their synthesis to place our findings in the context of current understanding.

Most previous studies have addressed cool, moist forest types such as lodgepole pine and spruce (Hicke et al. 2012). Here, we provide some of the first empirical data on interior Douglas-fir forests, an important lower montane component of western forests. We quantified fuels using a rigorously validated and replicated time-since-beetle-outbreak chronosequence, and contrasted

post-outbreak fuel dynamics in this lower montane forest type with subalpine lodgepole pine forests. Our analyses included information on snagfall rates and microclimate, both identified as important research needs (Hicke et al. 2012).

Detailed field data on actual fires in beetle-killed forests have been notably absent from much of the discussion of fire-beetle interactions, as most studies have simulated fire behavior (Hicke et al. 2012). While fire behavior (e.g., heat intensity, flame height, rate of spread) is related to fire severity (i.e., effects on the ecosystem), real-time fire behavior cannot be measured with post-fire data. Further, data on fire behavior can inform operational fire management, whereas data on fire severity can inform longer-term forest management. By documenting fire severity across a range of pre-fire beetle outbreak severities in lodgepole pine and Douglas-fir, we address a key knowledge gap in understanding the ecological effects of these two disturbances (Hicke et al. 2012). We present extensive field data on canopy and surface fire severity and beetle-outbreak severity in current-attack to gray-stage lodgepole pine, and in gray-stage Douglas-fir. Our field-measured data provide the precise overlap of killed trees and burned area that Hicke et al. (2012) noted as critical for understanding the impacts of beetle outbreak on subsequent fire severity. Such data allow for stronger inference than can be obtained by using rapid survey protocols for fire severity such as satellite indices, or coarse measures of beetle outbreak severity using ADS data (e.g., Kulakowski and Veblen 2007, Bond et al. 2009). We further distinguished moderate from extreme burning conditions, which is important for knowing under what contexts pre-fire beetle outbreak severity can affect fire severity. Our findings that beetle-induced changes have less of an effect (or no effect) on fire severity under extreme burning conditions is consistent with modeling studies of fire behavior (e.g. Simard et al. 2011, Schoennagel et al. 2012). This is an important result, as most large fires occur under extreme weather and climate conditions in the Rocky Mountain forests (Schoennagel et al. 2004). Under moderate conditions, the data point toward a strong influence of trees that are in the green-attack stage. Again, this is consistent with modeling studies from stands where most needles on beetle-attacked trees were still in the canopy (Schoennagel et al. 2012). Our finding that fire severity decreased with a higher proportion of red-stage (relative to green-attack) beetle-killed trees is consistent with modeling studies of the late-red stage when more than half of the beetle-killed trees have dropped most of their needles (Simard et al. 2011). Thus, our data suggest the importance of further differentiating the earliest phases of a developing outbreak; fire in the full or late red stage is likely to have different effects than fire in the early green-attack stage. In gray stage forests, our data are largely consistent with expectations (Jenkins et al., 2008, Klutsch et al. 2011, Simard et al. 2011, Hicke et al. 2012, Jolly et al. 2012, Schoennagel et al. 2012, Donato et al. 2013a).

Relatively little work to date has directly assessed the consequences of post-bark-beetle-outbreak management practices on forest structure and function or future fire hazard (but see Collins et al. 2011, 2012). We simulated the consequences of several post-disturbance forest management practices that are common in the study region (Donato et al. 2013), and we also conducted an additional field study of post-outbreak salvage in beetle-killed lodgepole pine (Griffin et al. 2013). Our findings were generally consistent with those of other post-disturbance studies. Model simulations suggested minimal effects of harvesting beetle-killed trees on the canopy fuel metrics that drive crown fire behavior, and few differences among post-harvest treatments. This finding stems from a harvest prescription of only dead trees, and it does differ from operations that include concurrent removal of live trees (Collins et al. 2012). By the gray stage, beetle-killed

trees carry no needles – the primary contributor to canopy bulk density and base height (Cruz et al. 2003, Reinhardt and Crookston 2003, Reinhardt et al. 2006). Multiple studies have reported that crown fire potentials are already reduced in gray-stage forests, without management, due to needle drop that thins out canopy biomass relative to undisturbed stands (DeRose and Long 2009, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012). Our projections of coarse surface fuel increases over time without management, and the related decreases in treated stands, are of less magnitude than that reported by Collins et al. (2012), perhaps because of different mortality levels or initial stand densities between our study regions. Models of fire behavior in heterogenous forests, such as those affected by bark-beetle outbreak, have known limitations. Until fire models can more accurately represent the changes in fuel characteristics and heterogeneity at a scale that permits stand-to-landscape simulation of fire, a viable alternative is to focus on the fuels themselves, which are readily interpreted by many forest managers.

Results of our field study of post-outbreak salvage harvest (Griffin et al. 2013) were consistent with findings in other studies of post-disturbance salvage harvest. For example, we observed a net decline in total sapling density, consistent with other studies post-disturbance timber harvest (Jonasova and Prach 2004, Donato et al. 2006, Greene et al. 2006, Jonasova and Prach 2008, Keyser et al. 2009). Among other studies, the consequences of salvage harvest for tree composition vary considerably. We found evidence for a change in forest composition following salvage harvest, and successional trajectories were also unaltered by salvage harvest in loblolly pine (*Pinus taeda*) following an outbreak of the southern pine beetle (*Dendroctonus frontalis*) (Coleman et al. 2008). In contrast, a shift to subalpine fir appeared likely in post-outbreak lodgepole pine stands in Colorado that were untreated, whereas lodgepole pine dominance was maintained by post-outbreak salvage harvest (Collins et al. 2011). Consistent with our results, other studies have reported increased dead surface fuel loads following harvest (e.g., McIver and Ottmar 2007, Donato et al. 2006, McGinnis et al. 2010, Collins et al. 2012).

In conjunction with the stated goals of our project, our complementary studies provided new insights on tree regeneration following beetle outbreak and on ecosystem-level processes, such as nitrogen cycling, in post-outbreak lodgepole pine and Douglas-fir stands (Griffin et al. 2011, Griffin and Turner 2012). Our field studies found evidence of substantial nitrogen retention following bark beetle outbreak in lodgepole pine and in Douglas-fir, consistent with other recent studies (e.g., Rhoades et al. 2012). Understory vegetation and surviving trees respond rapidly to beetle-induced mortality of canopy trees, as evidenced by increase in cover and foliar nitrogen concentration.

Finally, we concur fully with Hicke et al. (2012) regarding the need for greater specificity in study questions, time since outbreak, and the fuels or fire characteristics that are reported when comparing among studies. In many cases, direct comparisons cannot be made among studies, and some of the apparent disagreement in the literature is attributable to "apples to oranges" comparison. Even comparisons of the same stage may lead to apparent differences in findings among – e.g., large surface fuels will differ substantially in gray-stage forests depending on whether beetle-killed trees have fallen yet or not. Furthermore, few studies provide rigorous validated of TSB chronosequences, which may contribute additional uncertainty in comparing results of different studies (Johnson and Miyanishi 2008).

FUTURE WORK NEEDED

Most remaining uncertainties about how changes in canopy fuels affect fire in beetle-killed forests focus on the red stage, and more empirical studies are needed to evaluate fire activity (behavior and severity) in beetle-killed forests relative to unattacked forest, while accounting simultaneously for other factors (e.g., weather, topography) known to affect fire. We especially encourage additional studies during the onset of beetle outbreak to further elucidate the role of green-attack trees. In particular, real-time monitoring of beetle-attacked trees from the green-attack to gray stage is important to resolve the net effects of reduced foliar moisture, increased flammability, concurrent canopy thinning, and the patchy spatial distribution of live and dead biomass on actual crown fire potentials. As most beetle-affected forests in western North America transition to later outbreak stages following peaks in tree mortality from 2007-2009 (Meddens et al. 2012), additional opportunities will arise to empirically study more fires occurring in the gray and silver stages. We underscore the importance of contrasting the behavior and severity of fire in post-outbreak forests (of varying severity) relative to unattacked forests burning under the same conditions. The issue remains not whether beetle-killed forests will burn (they will), but whether and how they may burn differently than would be expected under given conditions. Field studies of actual fires in beetle-killed stands, with and without management, will best elucidate the magnitude of these potential effects. Experimental fires either in beetle-killed forests or in which beetle-kill has been simulated may also be informative (e.g., Schroeder and Mooney 2012). Studies following the long-term post-fire successional trajectories of areas experiencing beetle outbreaks and fire are also needed to understand the consequences of the interval between bark-beetle outbreak and subsequent fire on various responses, including post-fire tree regeneration.

Models such as FVS are not predictions, but rather projections of a set of assumptions and of current understanding. Although we calibrated our projections by using field data, like any modeling exercise, this analysis carries several key uncertainties. Perhaps the most important uncertainty relates to FVS' treatment of spatial heterogeneity in stand and fuel structure, a crucial factor in any discontinuous forest environment (Pimont et al., 2009), and particularly in post-outbreak forests (Donato et al. 2013a). Again, field-based evaluations of real fires in beetle-killed forests under varying conditions are needed to resolve the differences in predictions among modeling study.

For the fate of live trees and other ecosystem responses, elucidating the effects of a wide range of live-tree retention prescriptions is an important next step in studies of post-outbreak management. For lodgepole pine in particular, windthrow can be an important factor in the decades following outbreak, associated with greater exposure in newly opened stands. The FVS model does not automatically adjust falling/breakage rates in this situation. Our projections validated well against field data from 30-year post-outbreak stands, suggesting this potential error was minimized; however wind exposure is site-specific and post-outbreak dynamics of remnant live trees may differ in other sites. This uncertainty is more important for prescriptions that retain live trees, and less so for common post-outbreak prescriptions in other regions that remove all stems, resembling a clearcut (e.g., Collins et al., 2012).

DELIVERABLES

(A) Deliverables crosswalk table from original research proposal, with current status.

Deliverable Type	Description	Delivery Dates	Status
Refereed publication	Contrasting effects of bark-beetle outbreak on fuel profiles and fire hazard in Douglas-fir (Q1 field data + modeling; postdoc A)	June 2011	**Completed.** Donato et al. 2013a
Refereed publication	Spatial variation in canopy, understory and large woody fuels following bark beetle attack (Q1 remote sensing; postdoc B)	August 2011	**Initial analyses completed.** Simard (2010) dissertation, Chapter 2
Refereed publication	*Effects of bark beetles on severity of recent fires in Douglas-fir and lodgepole pine forests (Q2 field data; new PhD student)	September 2011	**Completed.** Harvey et al. 2013
Refereed publication	*Effects of bark beetle infestation and fire on recovery of lodgepole pine and Douglas-fir forests (Q2 field data, new PhD student)	December 2011	**Completed.** Harvey et al., in review
Refereed publication	Relationship between fire severity and bark beetle infestation in the Greater Yellowstone (Q2 remote sensing; postdoc B)	December 2011	**In preparation.** Simard, Townsend, in prep.
Refereed publication	Effects of alternative fuel treatments on fire severity in lodgepole pine and Douglas-fir forests (Q3 FVS modeling; postdoc A)	June 2012	**Completed.** Donato et al. 2013b
PhD dissertation	Interactions between bark beetles and fire in contrasting conifer forests of Greater Yellowstone (new PhD student)	June 2012	**Completed.** Chapters for this project are done, but Harvey PhD will include other work in progress
Conference presentations	We have a strong record of presenting results at national meetings (e.g., Ecological Society of America, International Association for Wildland Fire, US-IALE) and anticipate 4-6 presentations.	2010-2012	**Completed.** See full listing below

Access to remote sensing products via web site	Remote sensing products will be made available through the Townsend Lab website, rs.forest.wisc.edu.	June 2012	**In preparation**. Townsend, in prep.
Presentations to regional managers	We will present our research to forest managers in the Rocky Mountain region in coordination with the national parks and forests in the GYE, and the USFS Rocky Mountain Region.	2011-12	**Completed.** See below, also contributions to JFSP Science Briefs.

*These were completed, but we included fire severity and postfire regeneration together in for each forest type, and submitted a separate paper for lodgepole pine and Douglas-fir.

(B) Additional deliverables, beyond those listed in the original proposal, resulting from this project.

Deliverable Type	Description	Status
Refereed publication	Development of a new method for surfacing the cross sections of large logs to prepare them for scanning and cross dating.	**Completed.** Donato and Timme 2012
Refereed publication	Analysis of how nitrogen cycling changes during bark beetle outbreak in lodgepole pine, using the same TSB chronosequence we studied previously	**Completed.** Griffin et al. 2011
Refereed publication	Comparison of post-outbreak nitrogen cycling in lodgepole pine and Douglas-fir	**Completed.** Griffin and Turner 2012
Refereed publication	Response to comments on our earlier work on consequences of bark beetle outbreak for fuels and fire behavior in lodgepole pine	**Completed.** Simard et al. 2012.
Refereed publication	Study of consequences of post-outbreak salvage harvest in lodgepole pine on fuel profiles, regeneration density and soil nitrogen;	**Completed.** Griffin et al. 2013
Refereed publication	Invited paper providing an opportunity to synthesize concepts regarding ecosystem services in forest landscapes.	**Completed.** Turner et al. 2013
Refereed publication	Manuscript on additional data collected to evaluate patterns and rates of tree regeneration following bark beetle outbreak in Douglas-fir forests of Greater Yellowstone.	**In preparation.** Donato et al., in prep.
Refereed publication	Manuscript describing field-measured fire severity and pre-fire beetle-outbreak severity in six recent fires in the Northern Rockies	**In preparation.** Harvey et al., in prep.

Publications

Donato D.C. and S.H. Timme. 2012. A method for surfacing large log cross-sections in preparation for scanning and cross-dating. Tree-Ring Research 68:115-119.

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

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

Griffin, J. M., M. G. Turner and M. Simard. 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. Submitted to Forest Ecology and Management 261:1077-1089.

Griffin, J. M. and M. G. Turner. 2012. Bark beetle outbreak induces similar changes to the nitrogen cycle in contrasting conifer forests. Oecologia 170:551-565.

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

Harvey, B. J., D. C. Donato, W. H. Romme and M. G. Turner. 2013. Influence of recent bark beetle outbreak on wildfire severity and post-fire tree regeneration in montane Douglas-fir forests. Ecology (In press).

Harvey, B. J., D. C. Donato, W. H. Romme and M. G. Turner. Disturbance interactions between mountain pine beetle outbreaks and wildfire change with outbreak stage and burning conditions. Submitted to Ecological Applications (In review).

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

Turner, M. G., D. C. Donato and W. H. Romme. 2013. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. Landscape Ecology 28:1081–1097.

Theses and Dissertations

Griffin, J. M. 2011. Bark beetle disturbance and nitrogen cycling in conifer forests of Greater Yellowstone. PhD Dissertation, University of Wisconsin-Madison.

Harvey, B. J. 2014 (expected). Causes and consequences of spatial patterns of fire severity in Northern Rocky Mountain forests: the role of disturbance interactions and changing climate. PhD Dissertation, University of Wisconsin-Madison. (Chapters related to this award have been completed.)

Simard, M. 2010. Bark beetle-fire-forest interactions in the Greater Yellowstone Ecosystem. PhD dissertation, University of Wisconsin, Madison. (Much of Simard's work was funded by an earlier JFSP award, but Chapter 2 includes analyses of post-disturbance recovery using remote sensing imagery, which was part of this award.)

Conference Presentations (chronological)

Griffin, J.M., M. Simard, and M.G. Turner. 2010. Ecological consequences of bark beetle disturbance in Greater Yellowstone. University of Wyoming – National Park Service Research Station Seminar Series. July 1, 2010. Grand Teton National Park, Moran, WY. (Invited)

Donato, D.C., M.G. Turner, B.J. Harvey, W.H. Romme and M. Simard, 2011. Bark beetle outbreaks & wildfire potential in Douglas-fir forests of Greater Yellowstone. Annual conference, US chapter of the International Association for Landscape Ecology, Portland, Oregon.

Donato, D.C., M. Simard, M.G. Turner, W.H. Romme, B.J. Harvey and J.M. Griffin. 2011. Comparing bark beetle (*Dendroctonus* spp.) impacts on fuels in lodgepole pine and Douglas-fir forests of Greater Yellowstone. North American Forest Insect Working Conference, Portland, Oregon.

Harvey, B.J., M.G. Turner, W.H. Romme, D.C. Donato, M. Simard and P.A. Townshend. 2011. Effects of recent mountain pine beetle infestation on fire severity and post-fire regeneration in a lodgepole pine forest of Greater Yellowstone. Annual conference, US chapter of the International Association for Landscape Ecology, Portland, Oregon.

Donato, D. C., M. G. Turner, W. H. Romme, B. J. Harvey. 2012. Disturbance at the edge: Douglas-fir beetle outbreaks and potential forest-grassland shifts near the lower tree line of Greater Yellowstone. Ecological Society of America Meeting, Portland, Oregon.

Donato, D. C., B. J. Harvey, W. H. Romme, M. Simard, M. G. Turner. 2012. Bark beetle effects on fuel profiles and wildfire severity in Douglas-fir forests of Greater Yellowstone. Association for Fire Ecology conference, Portland, Oregon.

Harvey, B. J., M. G. Turner, W. H. Romme, D. C. Donato. 2012. Douglas-fir beetle impacts on fire severity and postfire tree regeneration in lower montane forests of Greater Yellowstone. Ecological Society of America Meeting, Portland, Oregon.

Townsend, P. A., A. Singh, C. C. Kingdon, M. Simard and W. Fox. 2012. Change detection and insect disturbance: synthesis from five systems. ForestSat 2012, Corvallis, Oregon.

Harvey, B.J., D.C. Donato, W.H. Romme, and M.G. Turner. 2013. Field evidence of recent bark beetle outbreaks affecting fire severity in subalpine forests: the importance of time since outbreak and burning conditions. Ecological Society of America Meeting, Minneapolis, MN.

*Postdoctoral Associate Donato also co-organized a special session at the Association for Fire Ecology (AFE) conference in 2011 in Utah, focusing on post-disturbance fuels and fire modeling.

Outreach to Managers

We have been very active in presenting the results of our research at meetings that are well attended by forest managers throughout the West. Our presentations were well received and followed up by much discussion. Doctoral student Jake Griffin gave a public lecture during summer 2010 at the University of Wyoming-National Park Service Research Station seminar series. This lecture was attended by ~80 people, including National Park Service and US Forest Service personnel, students at the Teton Science School, and area residents. A local science writer also attended the talk and wrote an article describing our research results ("Researchers: beetles aren't bad for forest", written by Cory Hatch, JACKSON HOLE NEWS & GUIDE, July 7, 2010, page 7A). Postdoctoral Associate Dan Donato co-organized a special session on post-disturbance fuels and fire modeling at the AFE Conference in Utah, and he also presented at the North American Forest Insect Working Group conference. We have also contributed to several synthetic communications produced by JFSP, most notably the FIRE SCIENCE DIGEST (Issue 12, February 2012) produced by Gail Wells that nicely summarized the state of the science for fire-beetle interactions.

LITERATURE CITED

Ager, A. A., A. J. McMahan, L. Hayes and E. L. Smith. 2007a. Modeling the effects of thinning on bark beetle impacts and wildfire potential in the Blue Mountains of eastern Oregon. Landsc. Urban Plan. 80:301-311.

Ager, A. A., A. J., McMahan, J. J. Barrett and C. W. McHugh. 2007b. A simulation study of thinning and fuel treatments on a wildland-urban interface in eastern Oregon, USA. Landsc. Urban Plan. 80: 292-300.

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

Brown, J. K. 1974. Handbook for inventorying downed woody material. Gen. Tech. Rep. INT-16, USDA For. Serv., Interm. For. Rang. Exp. Stn, Ogden, UT.

Brown, J.K. 1978. Weight and density of crowns of Rocky Mountain conifers. Res. Pap. INT-197, USDA For. Serv., Interm. For. Range Exp. Stn, Ogden, UT.

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

Collins, B.J., C.C. Rhoades, R.M. Hubbard, and M.A. Battaglia. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. Forest Ecol. Manage. 261:2168-2175.

Coops, N. C., M. Johnson, M. A. Wulder, and J. C. White. 2006. Assessment of QuickBird high spatial resolution imagery to detect red attack damage due to mountain pine beetle infestation. Remote Sensing of Environment 103:67-80.

Cruz, M. G., and M. E. Alexander. 2010. Assessing crown fire potential in coniferous forests of western North America: a critique of current approaches and recent simulation studies. International Journal of Wildland Fire 19:377-398.

Cruz, M. G., M. E. Alexander, R. H. Wakimoto. 2003. Assessing canopy fuel stratum characteristics in crown fire prone fuel types of western North America. International Journal of Wildland Fire 12:39-50.

DeRose, R. J., and J. N. Long. 2009. Wildfire and spruce beetle outbreak: Simulation of interacting disturbances in the central Rocky Mountains. Ecoscience 16:28-38.

Donato, D.C., J.B. Fontaine, J.L. Campbell, W.D. Robinson, J.B. Kauffman, and B.E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science 311: 352-352.

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

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

Goodwin, N. R., N. C. Coops, M. A. Wulder, S. Gillanders, T. A. Schroeder, and T. Nelson. 2008. Estimation of insect infestation dynamics using a temporal sequence of Landsat data. Remote Sensing of Environment 112:3680-3689.

Greene, D.F., S. Gauthier, J. Noel, M. Rousseau, and Y. Bergeron. 2006. A field experiment to determine the effect of post-fire salvage on seedbeds and tree regeneration. Front. Ecol. Environ. 4:69-94.

Griffin, J. M., M. G. Turner, and M. Simard. 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. Submitted to Forest Ecology and Management 261:1077-1089.

Griffin, J. M., and M. G. Turner. 2012. Bark beetle outbreak induces similar changes to the nitrogen cycle in contrasting conifer forests. Oecologia 170:551-565.

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

Hardisky, M. A., V. Klemas, and R. M. Smart. 1983. The influence of soil-salinity, growth form, and leaf moisture on the spectral radiance of *Spartina alterniflora* canopies. Photogrammetric Engineering and Remote Sensing 49:77-83

Harvey, B. J., D. C. Donato, W. H. Romme and M. G. Turner. 2013. Influence of recent bark beetle outbreak on wildfire severity and post-fire tree regeneration in montane Douglas-fir forests. Ecology (In press).

Harvey, B. J., D. C. Donato, W. H. Romme and M. G. Turner. Disturbance interactions between mountain pine beetle outbreaks and wildfire change with outbreak stage and burning conditions. Submitted to Ecological Applications (In review).

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

Jenkins, M. J., E. Hebertson, W. G. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. Forest Ecol. Manage. 254:16-34.

Jenkins, M. J., W. G. Page, E. G. Hebertson, M. E. Alexander. 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in Western North America and implications for fire management. Forest Ecology and Management 275:23-34.

Johnson, E. A. and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters 11:419-431.

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

Jonasova, M. Prach, K., 2004. Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak. Ecol. Eng. 23, 15-27.

Jonasova, M. Prach, K., 2008. The influence of bark beetles outbreak vs. salvage logging on ground layer vegetation in Central European mountain spruce forests. Biol. Conserv. 141, 1525-1535.

Keane, R.E. 2008. Biophysical controls on surface fuel litterfall and decomposition in the northern Rocky Mountains, USA. Can. J. Forest Res. 38: 1431-1445.

Kennedy, R. E., Z. G. Yang, and W. B. Cohen. 2010. Detecting trends in forest disturbance and recovery using yearly Landsat time series: 1. LandTrendr - Temporal segmentation algorithms. Remote Sensing of Environment 114:2897-2910.

Keyser, T.L., F.W. Smith, and W.D. Shepperd. 2009. Short-term impact of post-fire salvage logging on regeneration, hazardous fuel accumulation, and understorey development in ponderosa pine forests of the Black Hills, SD, USA. Int. J. Wildland Fire 18: 451-458.

Klutsch, J. G., M. A. Battaglia, D. R. West, S. L. Costello, and J. F. Negron. 2011. Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in North-Central Colorado. Western Journal of Applied Forestry 26:101-109.

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

Lewis, D., 2009. Stand and landscape-level simulations of mountain pine beetle (*Dendroctonus ponderosae*) and salvage logging effects on live tree and deadwood habitats in south-central British Columbia, Canada. Forest Ecol. Manage. 258, S24-S35.

Masek, J. G., C. Q. Huang, R. Wolfe, W. Cohen, F. Hall, J. Kutler, and P. Nelson. 2008. North American forest disturbance mapped from a decadal Landsat record. Remote Sensing of Environment 112:2914-2926.

McGinnis, T.W., J.E. Keeley, S.L. Stephens, and G.B. Roller. 2010. Fuel buildup and potential fire behavior after stand-replacing fires, logging fire-killed trees and herbicide shrub removal in Sierra Nevada forests. Forest Ecol. Manage. 260:22-35.

Meddens, A. J. H., J. A. Hicke, and L. A. Vierling. 2011. Evaluating the potential of multispectral imagery to map multiple stages of tree mortality. Remote Sensing of Environment 115:1632-1642.

Meigs, G. W., R. E. Kennedy, and W. B. Cohen. 2011. A Landsat time series approach to characterize bark beetle and defoliator impacts on tree mortality and surface fuels in conifer forests. Remote Sensing of Environment 115:3707-3718.

Negron, J. F., B. J. Bentz, C. J. Fettig and others. 2008. US Forest Service bark beetle research in the western United State: looking toward the future. J. Forestry (Sept 2008):325-331

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

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

Pimont, F., J. Dupuy, R.R. Linn, and S. Supont. 2009. Validation of FIRETEC wind-flows over a canopy and a fuel-break. International Journal of Wildland Fire 18:775–790.

Pyne, S.J., P.L. Andrews, and R. D. Laven. 1996. Introduction to wildland fire, 2nd edition. Wiley, New York.

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

Reinhardt, E.D. and N. L. Crookston. 2003. The fire and fuels extension to the Forest Vegetation Simulator. Gen. Tech. Rep. RMRS-GTR-116, USDA Forest Service, Rocky Mtn Res. Stn, Ogden, UT.

Reinhardt, E., J. Scott, K. Gray, and R. Keane. 2006. Estimating canopy fuel characteristics in five conifer stands in the western United States using tree and stand measurements. Canadian Journal of Forest Research 36:2803-2814.

Rhoades, C. C., J. H. McCutchan, Jr., L. A. Cooper, D. Clow, T. M. Detmer, J. S. Briggs, J. D. Stednick, T. T. Veblen, R. M. Ertz, G. E. Likens, and W. M. Lewis, Jr. 2013.

Biogeochemistry of beetle-killed forests: explaining a weak nitrate response. PNAS www.pnas.org/cgi/doi/10.1073/pnas.1221029110

Rothermel, R. C. 1983. How to predict the spread and intensity of forest and range fires. General Technical Report INT-143, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.

Schmitz, R. F., and K. E. Gibson. 1996. Douglas-fir beetle. Forest Insect & Disease Leaflet 5, USDA Forest Service, Rocky Mountain Research Station, Ogden, UT, USA.

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

Schmitz, R., and K. Gibson. 1996. Douglas-Fir Beetle. USDA Forest Service, Forest insect and disease leaflet 5, 7.

Schoennagel, T., T. T. Veblen, J. Negrón, and J. M. Smith. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS ONE 7(1):e300002.

Schroeder, D., and C. Mooney. 2012. Fire behavior in simulated mountain pine beetle-killed stands. Final Report. FPInnovations, Wildfire Operations Research, 1176 Switzer Drive, Hinton AB T7V 1V3 Canada.

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

Skakun, R. S., M. A. Wulder, and S. E. Franklin. 2003. Sensitivity of the thematic mapper enhanced wetness difference index to detect mountain pine beetle red-attack damage. Remote Sensing of Environment 86:433-443.

Soenen, S. A., D. R. Peddle, and C. A. Coburn. 2005. SCS+C: A modified sun-canopy-sensor topographic correction in forested terrain. Ieee Transactions on Geoscience and Remote Sensing 43:2148-2159.

Snell, J.A.K., and J. K. Brown. 1980. Handbook for predicting residue weights of Pacific Northwest conifers. GTR-PNW-103, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland.

Townsend, P. A., A. Singh, J. R. Foster, N. J. Rehberg, C. C. Kingdon, K. N. Eshleman, and S. W. Seagle. 2012. A general Landsat model to predict canopy defoliation in broadleaf deciduous forests. Remote Sensing of Environment 119:255-265.

Van Wagner, C. E. 1977. Conditions for the start and spread of crown fire. Canadian Journal of Forest Research 7:23-24.

Westerling, A.L., H. G., Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313: 940-943.