# Causes and consequences of spatial patterns of fire severity in Northern Rocky Mountain forests: the role of disturbance interactions and changing climate

By

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## Abstract

Causes and consequences of spatial patterns of fire severity in Northern Rocky Mountain forests: the role of disturbance interactions and changing climate

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Bark beetle outbreaks have affected fire-prone forests across North America in recent decades, raising concern about whether outbreaks increase fire severity and/or reduce postfire tree regeneration. Wildfire activity has also increased over this period, but little is known about whether spatial patterns of fire severity are changing, and/or how spatial patterns of fire and warming climate affect postfire tree establishment. In this dissertation, I investigated relationships between beetle outbreaks, wildfire, climate, and postfire tree regeneration in the US Northern Rocky Mountains. I tested whether prefire beetle outbreaks affected fire severity and/or postfire tree regeneration, using field plots distributed region-wide. I field-validated satellite maps of fire severity, and tested whether spatial patterns of fire severity changed over the period 1984-2010. I also used extensive field surveys to test the effect of postfire drought severity and distance to seed source on tree establishment following stand-replacing fires.

Effects of beetle outbreak severity on fire severity were minimal, regardless of the interval between outbreaks and fires. Fire severity was instead largely driven by topography and extreme weather conditions. Effects of beetle outbreaks on postfire tree regeneration depended on regeneration mechanisms of dominant host trees. For tree species that retain a persistent seedbank in serotinous cones on live and dead trees, postfire tree regeneration was not affected by prefire beetle outbreak severity. However, for tree species that lack a persistent seedbank, postfire tree regeneration decreased with greater prefire beetle outbreak severity. Most metrics of spatial heterogeneity of fire severity were affected by fire size and the proportion of fires burning as stand replacing, but few metrics changed over time from 1984 to 2010. The proportion of fires burning as stand replacing increased from 0.22 to 0.27 over this time period, and further increases may cause rapid shifts in the configuration of burn severity.  Postfire tree regeneration for tree species that currently dominate subalpine forests was substantially reduced toward the interior of stand-replacing patches (i.e., far from seed sources) and in fires that were followed by severe drought. Overall, this research provides insight into disturbance dynamics in fire-prone forests and informs forest management and policy concerns.

## Introduction

Interacting disturbances and changing disturbance regimes present critical challenges for understanding and managing ecosystems. Species may be well-adapted to a particular disturbance regime - characterized by the frequency, size, severity, and spatial configuration of disturbance events (Pickett and White 1985, Turner et al. 1998). However, changes to one or more of the regime components can lead a loss of resilience [the capacity to tolerate disturbance without shifting to a different state (Walker et al. 2004)] and result in unexpected shifts in ecosystems (Paine et al. 1998). Understanding how drivers contribute to disturbance patterns and how systems respond to heterogeneity are necessary to anticipate future ecosystem dynamics (Turner 2010, Turner et al. 2013) and respond to resource management challenges (Fleishman et al. 2011).

These challenges are especially prominent in western North America, where warming climate is increasing the frequency and extent of wildfires and bark beetle outbreaks (genus: *Dendroctonus*) (Westerling et al. 2006, Raffa et al. 2008). Both are natural disturbances in western forests, but the dynamics of each may be changing in important ways. Bark beetle outbreaks are forecasted to expand in the coming century, shifting toward higher latitudes and elevations (Bentz et al. 2010). Future fire regimes will likely be characterized by more frequent and larger fires, with potential for fire regimes to move outside the paleoecological range of variability by the end of the 21st century (Westerling et al. 2011).

Whereas fire and bark beetle outbreaks have received much attention individually, less is known about how they interact. Modeling studies have begun to address this challenge (e.g., Simard et al. 2011, Schoennagel et al. 2012, Hicke et al. 2012), but a key limitation is a lack of empirical data showing what actually occurs when beetle-killed forests burn. These disturbances may be *linked* (Simard et al. 2011), such that bark beetle outbreaks alter the probability of occurrence or severity (the effects of fire on an ecosystem) of a subsequent fire. Alternatively, they may be *compound* (Paine et al. 1998) if synergistic effects of sequential disturbances on postfire succession result in ecosystem transitions to a qualitatively different state (Buma and Wessman 2011). Climate is a major driver of fire (Swetnam and Betancourt 1990, Westerling et al. 2006, Flannigan et al. 2009) and insect outbreaks (Logan et al. 2003, Raffa et al. 2008, Bentz et al. 2010) - and both disturbances can, in turn, have strong feedbacks to climate (Schimel et al. 2001, Kurz et al. 2008, Hicke et al. 2012a). If ecosystem changes are strong enough in direction or magnitude, they may result in transitions into “no-analogue communities” (Williams and Jackson 2007) or alternative stable states (Scheffer et al. 2001).

Ecologists have begun to study how the frequency, extent, and severity of disturbances may change, but consideration has not yet been given to how changing spatial patterns of disturbance severity may alter forested landscapes. The proportion of fires burning at high severity in the Northern Rockies region has not increased over the period 1984-2006 (Dillon et al. 2011), but intra-regional trends in fire severity have not been explored. Further, even if the proportion of fires burning at high severity remains constant, differing configurations of burn severity could influence resilience by affecting distance to seed sources (Turner et al. 1997, Donato et al. 2009). Tree species in the Northern Rockies may differ in their responses to changing burn severity patterns, but so far these relationships are unexplored.

Initial postfire succession is sensitive to changes in disturbance regimes and sets the long term trajectory for forest development in western North American conifer forests. Post-disturbance successional pathways may differ with post-disturbance climate (Savage et al. 2013), the interval between successive disturbances (Paine et al. 1998, Schoennagel et al. 2003, Johnstone and Chapin III 2006, Brown and Johnstone 2012), disturbance severity (Turner et al. 1999, Johnstone et al. 2010, Barrett et al. 2011), residual biotic legacies (often related to disturbance severity and species characteristics) (Tinker et al. 1994), or species interactions (Stuart et al. 1993, Franklin and Bergman 2011, Harvey and Holzman 2014). Initial postfire forest stand structure can vary widely and persist for centuries (Kashian et al. 2004, 2005), driving patterns in terrestrial carbon and nutrient flux (Turner et al. 2004, Smithwick et al. 2005). High-magnitude changes to one or more components of a disturbance regime can cause tree regeneration to fail, decreasing resilience and making forest ecosystems vulnerable to transitions to non-forest (Kasischke et al. 2010). Understanding when and where these transitions are likely is a major challenge for landscape ecologists and managers.

The Northern Rockies is an ideal region to study postfire successional trajectories driven by changes in fire regimes or disturbance interactions, as it has experienced recent increases in bark beetle outbreaks (Simard et al. 2012), fire activity (Westerling et al. 2006, Morgan et al. 2008), and climate warming (Westerling et al. 2006, 2011). The Northern Rockies region follows that established by Westerling et al. (2011), stretching from northwestern Wyoming to the US/Canada border at the northern tip of Idaho. Forests are conifer-dominated and vary compositionally with elevation, moisture, and latitude (Baker 2009). High-elevation forests are typically dominated by non-serotinous lodgepole pine (*Pinus contorta* var. *latifolia*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*). Mid- to low-elevation forests are dominated by serotinous lodgepole pine, ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and limber pine (*Pinus flexilis*). Higher latitude mesic forests in the study area are composed of grand fir (*Abies grandis*), Douglas-fir, western larch (*Larix occidentalis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Occasional woodlands of quaking aspen (*Populus tremuloides*) and juniper (*Juniperus* spp) also occur, generally at lower elevations. Historical fire regimes range from low-frequency, high-severity (stand-replacing) regimes in higher elevation and mesic forests to more frequent, mixed-severity regimes in lower elevation forests (Arno 1980, Baker 2009). Two focal regions within the US Northern Rocky Mountains - Glacier National Park (48° 46’ N, 114° 00’ W) and the Greater Yellowstone Ecosystem (GYE) (44° 10’ N, 110° 15’ W) comprise over 75,000 km$^2$ of mountainous conifer forest. Most land within each region is federally protected and managed as wilderness (Glacier, Yellowstone, and Grand Teton National Parks; surrounding National Forests).

This dissertation addresses implications of interacting disturbances and changing disturbance regimes for Northern Rocky Mountain forests. Chapters I, II, and III examine how fire and bark beetle outbreaks potentially interact in linked or compound ways to alter successional trajectories. Using detailed field measurements collected in three burned areas within the GYE, I empirically test relationships between bark beetle outbreak severity, fire severity, and postfire tree reestablishment in two contrasting conifer forests (subalpine forests dominated by lodgepole pine – Chapter I; and mid-montane forests dominated by Douglas-fir – Chapter II). I then use spatially extensive field data throughout the Northern Rockies ecoregion to test the broader consistency of relationships found in the GYE. These chapters fill an important void in disturbance ecology research where modeling studies have left off. In Chapter IV, I use field data and remote sensing analysis to characterize and tests for trends in the spatial heterogeneity of burn severity between 1984 and 2010 in the Northern Rockies. Statistical relationships are developed between spatial heterogeneity of burn severity and top-down (climate, topography) and bottom –up (vegetation) drivers to examine potential shifts in controls of disturbance regimes. Finally, in Chapter V, I examine the relationship between burn configuration pattern, postfire climate, and postfire tree establishment for different tree species of the Northern Rockies.

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# Chapter 1 - Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions

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## Abstract

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

In the green-attack / red stage, several canopy fire-severity measures increased with pre-fire outbreak severity under moderate burning conditions. Under extreme conditions, few fire-severity measures were related to pre-fire outbreak severity, and effect sizes were of marginal biological significance. The percentage of tree stems and basal area killed by fire increased with more green-attack vs. red-stage trees (i.e., the earliest stages of outbreak). In the gray stage, by contrast, most fire-severity measures declined with increasing outbreak severity under moderate conditions, and fire severity was unrelated to outbreak severity under extreme burning conditions. Post-fire lodgepole pine seedling regeneration was unrelated to pre-fire outbreak severity in either post-outbreak stage, but increased with pre-fire serotiny. Results suggest bark beetle outbreaks can affect fire severity in subalpine forests under moderate burning conditions, but have little effect on fire severity under extreme burning conditions when most large wildfires occur in this system. Thus, beetle outbreak severity was moderately linked to fire severity, but the strength and direction of the linkage depended on both endogenous (outbreak stage) and exogenous (fire weather) factors. Closely-timed beetle outbreak and fire did not impart compound effects on tree regeneration, suggesting the presence of a canopy seedbank may enhance resilience to their combined effects.

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

## Introduction

Severe natural disturbances have shaped Rocky Mountain forest landscapes for centuries or more (e.g., Kulakowski et al. 2003). While ecosystem response to individual disturbances is well-understood in many forests, interactions between disturbances present challenging questions for scientists and managers (Turner 2010). Recent outbreaks of native bark beetle species (genus: *Dendroctonus*) have caused extensive tree mortality over tens of millions of hectares of conifer forest in western North America (Raffa et al. 2008, Meddens et al. 2012), raising concern about the potential for severe wildfire following outbreaks (Hicke et al. 2012). Fuel profiles and fire models suggest fire behavior may be affected by pre-fire outbreaks (see Hicke et al. 2012 and Jenkins et al. 2012 for recent reviews), but field measures of fire severity (i.e., effects on the ecosystem) in post-outbreak forests are lacking. Outbreaks can also affect seed sources (e.g. Teste et al. 2011a, 2011b) in ways that may alter post-fire tree regeneration patterns (Harvey et al. 2013), but different regeneration mechanisms among tree species may lead to contrasting outcomes. Empirical data from fires that burn through post-outbreak stands are needed to assess the effects of outbreak severity and time since outbreak on fire severity, and the joint effects of outbreak severity and fire severity on post-fire trajectories.

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

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

In addition to linked interactions between outbreaks and fire, compound disturbance effects (Paine et al. 1998) may result if beetle outbreaks alter ecosystem response to subsequent fire, and post-fire regeneration mechanisms are likely key in determining outcomes. Beetles can indirectly reduce seed availability by killing large seed-producing trees (Bjorklund and Lindgren 2009), which can drive variability in post-fire seedling establishment in forests that lack a seedbank (Harvey et al. 2013). Adaptations such as serotinous cones may buffer compound disturbance effects if seedbanks remain viable after tree death (Teste et al. 2011a, 2011b, Aoki et al. 2011), but outcomes have not been tested empirically following beetle outbreaks and subsequent fire.

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

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

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

## Methods

### *Study area*

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

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

The Red Rock Complex Fire burned in 2011 through forest stands that were in the gray post-outbreak stage (Fig. 1C). Mountain pine beetle outbreaks began in 2003 in isolated study area locations, with widespread tree mortality peaking between 2005 and 2009 based on ADS data (Appendix A). Subalpine fir mortality attributed to outbreaks of western balsam bark beetle (*Dryocoetes confusus*) and Armillaria root disease (*Armillaria spp.*) was also reported from 2002-2009 in ADS maps and accounted for 31% of the tree mortality mapped in ADS surveys and 23% of tree mortality from our field data. No new tree mortality was reported in the study area in 2010 or 2011 in ADS maps, meaning that stands were 3-9 yr post-outbreak at the time of the 2011 Red Rock Complex Fire. The Red Rock Complex Fire was composed of the Red Rock and the Gray Hills Fires, ignited by lightning on August 20 and September 4, respectively. The Red Rock Complex Fire was managed for wildland fire use and was extinguished by snow and rain on October 2 after burning 4,761 ha in total; no suppression or management burning occurred in the study area (Dale Deiter, BTNF District Ranger, pers. comm.).

### *Sampling design*

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

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

### *Pre-fire beetle outbreak severity*

Pre-fire beetle outbreak severity was quantified following methods outlined in Harvey et al. (2013), by removing the bark on every tree taller than 1.4 m (19,012 individual trees) and recording evidence (or absence of evidence) of *Dendroctonus* activity (Safranyik and Carroll 2007). Each tree was assigned to one of five categories: (1) pre-disturbance snag, (2) killed by bark beetles prior to fire, (3) green attack at time of fire, (4) live at the time of fire, or (5) unknown (Table 1, Appendix B). By cross-referencing with ancillary information for each fire (e.g., aerial photos at the time of fire and ADS maps), beetle-killed trees were assigned as green-attack or red stage in the New Fork Lakes Fire and gray stage in the Red Rock Complex Fire. Classification of trees was informed by discussions with forest entomology experts (Ken Raffa, University of Wisconsin; Ken Gibson, USFS). Our measure of beetle-killed basal area (percentage of stand basal area) includes all pre-fire tree mortality that occurred during recent beetle outbreaks within each fire. The majority of this mortality is from mountain pine beetle, but tree mortality also includes other mortality agents such as western balsam bark beetle and Armillaria root disease for subalpine fir, and spruce beetle (*Dendroctonus rufipennis*) for Engelmann spruce, which was unavoidable in sampling subalpine forests that contain varying proportions of non-pine tree species.

### *Fire severity*

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

### *Topography and burning conditions*

A 10-m digital elevation model (DEM) was used in ArcGIS 10.1 to generate the following topographic variables for each plot center: elevation (m), slope (º), aspect (NE Index, [Beers et al., 1966]), and topographic curvature (the second derivative of the elevation surface [Zevenbergen and Thorne, 1987]). To capture local elevation effects, we calculated a slope position by re-scaling elevation for each plot from 0 (bottom of slope) to 1 (ridge top) (Harvey et al. 2013).

We used daily burn progression maps provided by the BTNF to divide each fire into two burning conditions based on weather conditions and fire growth using established methods (e.g., Thompson and Spies, 2009; Harvey et al. 2013). Moderate burning conditions occurred during periods of relatively low temperature and winds, high humidity, and modest fire growth; extreme burning conditions were during periods of relatively high temperatures and winds, low humidity, and rapid fire growth (Table 2). One exception to these trends was the wind speed during the New Fork Lakes Fire; average wind speed at the nearest remote automated weather station (RAWS) was higher during the moderate conditions (Table 2).

### *Statistical analysis*

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

Fire severity ~ Burning conditions X beetle-killed basal area (Eq. 1)

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

Stands in the New Fork Lakes Fire contained varying percentage of trees in the green-attack or red stage of outbreak; therefore we also tested for an effect of the percentage of beetle-killed basal area in the red stage (red-stage basal area / [green-attack + red-stage basal area]) on each of the fire severity variables. We performed this test using a second regression model on each fire-severity metric with the following form:

$$\text{Fire severity} \sim \text{Percentage red stage} \qquad \text{(Eq. 2)}$$

where the percentage red stage term was treated as a fixed effect. In this test, a positive relationship would indicate that red-stage trees were more related to increased fire severity, a negative relationship would indicate that green-attack trees were more related to increased fire severity, and no significant relationship would indicate that red-stage and green-attack trees were equally related (or equally unrelated) to fire severity. We were unable to account for burning conditions in these models because only one plot in the moderate burning conditions contained trees in the green-attack stage; therefore we tested for the effect of red stage: green-attack by pooling all plots in the New Fork Lakes Fire. Plot-level fire-severity metrics were highly correlated with each other in both fires (Appendix C); nonetheless, we report results for all measures because they represent different components of the ecosystem and may be of interest to managers individually.

To test if beetle outbreaks and wildfire produced compound disturbance effects on post-fire seedling establishment, we regressed post-fire lodgepole pine seedling establishment against beetle-killed basal area after accounting for other variables (fire severity, seed source, serotiny, topography) known to affect post-fire tree regeneration. Fire severity was represented by a fire severity class (light surface, severe surface, crown) that was assigned in the field to each plot following established protocols for the region (Turner et al. 1997). Potential seed source was represented by lodgepole pine basal area ha$^{-1}$. Pre-fire serotiny was represented by the percentage of lodgepole pine trees bearing serotinous cones (following methods in Tinker et al. 1994). Topographic variables were statistically unrelated to post-fire seedling density and therefore were not included in models. The model for post-fire lodgepole pine seedling density took the following form:

Post-fire lodgepole pine seedling density ~ fire severity class + pre-fire lodgepole pine basal area ha$^{-1}$ + pre-fire serotiny + beetle-killed basal area + ( pre-fire serotiny X beetle-killed basal area) (Eq. 3)

where all terms were treated as fixed effects. We included the interaction term to see if any effects of beetle-killed basal area on post-fire seedling density changed with levels of pre-fire serotiny. Because of very sparse post-fire tree regeneration in the Red Rock Complex Fire (only 7 out of 43 plots contained seedlings), we were unable to build the full regression model because degrees of freedom were limited. Therefore, we tested for compound disturbance interactions between fire severity and outbreak severity by using a Spearman rank correlation test between post-fire seedling density and pre-fire outbreak severity overall and within each fire-severity class.

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

All statistical analyses were performed in the R statistical software (version 2.12, R Foundation for Statistical Computing, Vienna, AT). Generalized least squares models used the function ‘gls’ in the nlme package in R (Pinheiro et al. 2013); generalized linear mixed models used the function ‘glmmPQL’ in the MASS package for R (Venables and Ripley 2002). Results are means ± 1 SE unless noted. For all analyses, we do not perform family-wide-adjustments and we set $\alpha = 0.10$ to reduce the chance of Type II error and not miss potentially meaningful and management-relevant effects. That is, we wanted to maximize the ability to detect any ecologically important effect of beetle outbreak severity on fire severity or tree regeneration because of its relevance for forest management.

## Results

### *Forest stand and disturbance characteristics*

Because of the later stage of outbreak in the Red Rock Complex Fire, the percentage of beetle-killed basal area was greater than in the New Fork Lakes Fire, which was in early outbreak stages. However, both fires included plots spanning low (<< 5% of basal area) to high (> 70% of basal area) levels of beetle-caused mortality (Table 3). Both fires included plots that encompassed a wide range of fire severity, and fire-severity metrics were similar across fires (Tables 3 and 4).

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

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

Under moderate burning conditions, char height, bole scorch, and the percentage of trees that were killed by fire increased with outbreak severity (Fig. 2A, D, E; Table 5), reaching levels typically recorded under extreme burning conditions in forests with or without pre-fire beetle outbreaks. The percentage of tree basal area killed by fire and both surface fire-severity metrics were unrelated to pre-fire outbreak severity (Fig. 2B, C, F; Table 5). Very few plots that burned under moderate conditions had high outbreak severity, lowering confidence in trends when ~50% of the basal area was beetle killed (Fig. 2). When we removed the one plot at ~50% beetle-killed basal area, all tests were non-significant ($P > 0.10$) under moderate conditions. However, these trends are likely biologically significant as there is no reason to believe this point is an outlier; beetle severity and fire severity measures were well within the observed trends under all burning conditions. Rather, this is related to the small number of plots ($n = 25$) that burned under moderate conditions.

Under extreme burning conditions, fire-severity metrics were either unrelated to, or showed modest increases, with higher outbreak severity; however effect sizes decreased relative to moderate burning conditions and were of marginal biological significance (Fig. 2G-L, Table 5). Bole scorch, the percentage of trees and tree basal area killed by fire, and charred surface cover were unrelated to outbreak severity. Char height increased and post-fire litter + duff depth decreased (indicating higher fire severity) with higher levels of outbreak severity. However, these effect sizes were slight (e.g., char height increasing from ~12 m to ~16 m; post-fire litter + duff decreasing from ~11 mm to ~2 mm; Fig. 2G, I).

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

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

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

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

Post-fire conifer regeneration was variable within each fire, but mean seedling densities differed by two orders of magnitude between the two fires. Post-fire tree seedling density was high in the New Fork Lakes Fire (mean 111,860 $ha^{-1}$, median 23,000 $ha^{-1}$, range 0 to 1,320,000 $ha^{-1}$, Table 3). Lodgepole pine made up 99.6% of all post-fire tree seedlings, and all were one or two years old at the time of sampling. Post-fire tree seedling density was much lower in the Red Rock Complex Fire (mean 1,928 $ha^{-1}$, median 0 $ha^{-1}$, range 0 to 639,179 $ha^{-1}$). Lodgepole pine made up 98.2% of seedlings in all but two of the plots, which had seedling densities > 100,000 $ha^{-1}$ and were dominated by Engelmann spruce. All seedlings in the Red Rock Complex Fire were in the cotyledon stage at the time of sampling. In both fires, post-fire seedling density differed with fire severity, with seedling density highest in plots that burned as severe-surface fire (Table 7). Seedling density was also positively related to pre-outbreak lodgepole pine basal area ($r_s = 0.47$, $P < 0.001$ and $r_s = 0.44$, $P = 0.003$ for the New Fork Lakes Fire and Red Rock Complex Fire, respectively) and pre-fire serotiny ($r_s = 0.47$, $P < 0.001$ and $r_s = 0.42$, $P = 0.005$, respectively).

When fire burned through the green-attack / red-stage outbreak (New Fork Lakes Fire) and after controlling for the effects of covariates (fire severity, pre-outbreak lodgepole pine basal area, and pre-fire serotiny), there was no evidence of compound disturbance effects from pre-fire outbreak followed by fire. Post-fire lodgepole pine seedling density was not related to pre-fire outbreak severity, which did not interact with serotiny (Fig. 4A, Table 8). Post-fire lodgepole pine seedling density was also unrelated to pre-fire beetle outbreak severity when no other covariates were included in the model ($t = 0.12$, $P = 0.91$, model not shown). When fire burned in gray-stage / post-outbreak stands (Red Rock Complex Fire), we also found no evidence of compound disturbance effects on post-fire tree seedling density. Non-parametric (Spearman's rank) tests revealed no relationship between post-fire lodgepole pine seedling density and pre-fire beetle outbreak severity overall ($r_s = -0.07$, $P = 0.65$) or within burn-severity classes (all $P > 0.10$) (Fig. 4B).

## Discussion

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

### *Fire severity in different post-outbreak stages*

*Green-attack / red stage* – Changes to canopy fire severity in green-attack / red-stage outbreaks under moderate burning conditions were consistent with many predictions based on studies of fuel properties and fire simulation modeling (Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012), and we also detected a modest effect of green-attack trees during the earliest stages of an outbreak. Stands in the early stages of an outbreak are a mixture of un-attacked (live), green-attack (dying), and red (dead) trees (Fig. 1B) – each with different tree-level physiological responses to beetle attack. Xylem conductivity rapidly deteriorates within days to weeks of mountain pine beetle infestation, mainly because of blue stain fungus (*Ophiostoma clavigerum*) transmitted by attacking beetles (Miller et al. 1986, Yamaoka et al. 1990, Edburg et al. 2012). Impaired xylem function causes concomitant decreases in canopy transpiration and leaf water potential (Hubbard et al. 2013), increasing needle flammability before the crown changes color and needles begin to drop (Jolly et al. 2012a). Therefore, during the first year of an outbreak (during the green-attack stage, but prior to the classic red stage), there can be a brief period of increased canopy flammability without an accompanying decrease in canopy bulk density (Jolly et al. 2012b). The fire-severity responses we measured in stands with ongoing beetle attack were consistent with fire behavior simulations early in outbreaks where beetle-killed trees retain their needles and a large percentage of tree crowns are fading from green to red (Schoennagel et al. 2012, Hoffman et al. 2012). As a stand progresses to the late-red stage when there are no more green–attack trees and red trees have lost a significant portion of their needles, canopy bulk density is substantially reduced and crown fire potential decreases (Klutsch et al. 2011, Simard et al. 2011). The decline in trees killed by fire and tree basal area killed by fire with an increasing relative percentage of red-stage to green-attack trees supports this expectation; however we also show that red stage and green-attack trees were of similar importance for other metrics. Thus our results suggest modest increases in fire severity in the earliest stages of the outbreak, before canopy bulk density declines, and provide support for the hypothesis that green-attack trees contribute to increased canopy-fire severity. This observation may also help to explain some of the differences in expectations among different studies (Hicke et al. 2012) and can inform modeling studies that do not currently discriminate between green-attack and red-stage trees in early outbreak stands.

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

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

Surface-fire severity was largely unrelated to pre-fire outbreak severity in the gray stage. These findings are consistent with modeling studies, given the minimal pre-fire snagfall in our study stands. Simulation studies of surface fire behavior in gray-stage stands have produced variable projections, in part because fuel profiles vary. Fuel bed depth and fine and coarse surface fuels in gray-stage stands range from no change (Simard et al. 2011) to moderate increases (Schoennagel et al. 2012) or increases up to 2-3X from undisturbed stands (Page and Jenkins 2007a). The rate of snagfall is also critical in differences among projections (Klutsch et al. 2011). Studies with greater increases in surface fuels predict increased heat release and spread rate in the gray stage (Page and Jenkins 2007b, Klutsch et al. 2011, Schoennagel et al. 2012), whereas studies with negligible changes to fuels predict no change to surface fire characteristics (Simard et al. 2011). Beetle outbreak in the Red Rock Complex Fire occurred 3-9 yr before fire (Appendix A), so most beetle-killed trees were still standing at the time of fire (Fig. 1C). Although needles had fallen from the canopy, decomposition rates can keep pace with fine fuel inputs, yielding little change to surface fuels (Simard et al. 2012, Donato et al. 2013a). This is likely why surface fire-severity was largely unaffected by beetle outbreak severity in our study area. Decades after outbreaks, heavy accumulation of coarse fuels from downed trees may have a greater affect on subsequent fire severity (Jenkins et al. 2008, Schoennagel et al. 2012).

### *Comparisons with other studies*

Our detailed field data collected following actual fires fill a knowledge gap in understanding beetle-fire interactions (Hicke et al. 2012), but direct comparisons to many previous studies are challenging because of differences in questions and/or approaches. Therefore, we interpret our results in the context of previous retrospective and modeling studies, but do not make direct comparisons among qualitatively different response variables.

Fire behavior simulation studies can help inform the interpretation of our results; however, predicted fire behavior is not directly comparable to post-fire measures of fire severity. Therefore, we cannot explicitly examine responses such as heat intensity, flame height, rate of spread, or resistance to control that may be of concern to operational fire management or suppression efforts (e.g., Jenkins et al. 2012). For example, our char height measurements are limited by tree height in some cases and do not represent actual flame heights. Our study tested for effects on fire severity across a range of pre-fire outbreak severity, including stands unaffected by recent outbreaks which effectively served as a control. However, our study focused on stands that did burn, meaning we cannot directly compare our results to studies that examine the probability that beetle-affected stands will burn relative to unaffected stands (see Bebi et al. 2003, Bigler et al. 2005, Lynch et al. 2006, Kulakowski and Jarvis 2011).

Consistent with our study, other retrospective studies report little evidence for effects of pre-fire outbreak severity on subsequent fire severity in the red or gray stage. Few empirical studies have assessed fire severity in the very early outbreak stages when green-attack trees are present, possibly because the early-attack and red stages are short-lived (Hicke et al. 2012) and relatively few fires have burned in forests at that stage. In red-stage subalpine forests in Colorado and mixed-conifer forests in California, pre-fire outbreaks were unrelated to satellite measures of fire severity (Kulakowski and Veblen 2007, Bond et al. 2009). Field measures of fire severity were also unrelated to outbreak severity under any burning conditions in gray-stage lower-montane Douglas-fir forests, where fire severity was largely driven by topography (Harvey et al. 2013). Comparisons with studies that have not quantified disturbance severity (Bebi et al. 2003, Bigler et al. 2005, Lynch et al. 2006) and/or controlled for burning conditions (e.g. Turner et al. 1999) remain difficult.

### *Compound disturbance interactions: serotiny as a buffer?*

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

Harvey unpublished data), driving variation in early post-fire tree establishment (Harvey et al. 2013, Côté et al. 2013).

### *Implications for post-outbreak management of stands*

For the few fire-severity measures that were related to pre-fire outbreak severity, our results suggest that post-outbreak fuel treatments would need to be applied in the first year of active bark beetle infestation or immediately thereafter to be effective at reducing fire severity. There is a very short window of time in the green-attack / red stage when some measures of fire severity under moderate conditions may increase to levels commonly observed under extreme burning conditions. This effect diminishes once needles have begun to drop in the mid-to-late red stage (Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012). Such an early response to beetle outbreak would be challenging because many tree crowns would still be in the green-attack phase (Fig. 1B), remaining undetected by visual surveys for at least another year (Dodds et al. 2006, Meddens et al. 2012). By the time abundant red crowns are visible, and subsequent planning procedures for treatments are implemented (commonly ≥2 yr on public lands; Collins et al. 2012, Griffin et al. 2013, Donato et al. 2013b), the potential for severe fire may already be declining; thus, treatments would occur in late-red/early-gray stands of already-reduced fire potentials. This situation presents a challenge in applying timely and effective post-outbreak fuel treatments.

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

Most large fires in Rocky Mountain subalpine forests occur during extreme burning conditions and severe drought (Schoennagel et al. 2004). Predictions of fire behavior show minimal effects of pre-fire outbreaks under extreme burning conditions (Simard et al. 2011, Schoennagel et al. 2012), and we observed fire-severity responses consistent with this expected fire behavior. For example, the biological significance of effects in extreme burning conditions are marginal, as the range of these responses across the spectrum of outbreak severity represent minor changes within already stand-replacing fire. Further, although we accounted for moderate and extreme burning conditions within each fire, both fires occurred in relatively mild fire years in Greater Yellowstone (Westerling et al. 2011). During years of severe drought, pre-fire outbreaks may have even less of a biological effect on fire severity, which may further reduce the effectiveness of fuel treatments. Comparisons of beetle-fire relationships in multiple fires across broad regions and/or under different climate conditions remain a research priority.

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

## Conclusion

We found the severity of recent wildfires to be moderately linked to pre-fire bark beetle outbreaks in lodgepole pine forests of Greater Yellowstone. For the fire-severity measures that were related to pre-fire outbreak severity, the strength and direction of interactions changed with burning conditions (i.e., weather) and the interval between beetle outbreaks and fire. Our results reveal a brief period where some measures of fire severity increase with outbreak severity in the green-attack / red stage, and suggest an influence of green-attack trees driving some of these trends. This is followed by decreases in fire severity in the gray post-outbreak stage when snags remain standing. However, the biologically significant effects of pre-fire bark beetle outbreak severity on subsequent fire severity were mainly manifest under moderate burning conditions and were reduced and/or undetectable under extreme burning conditions, which is when most large wildfires occur in Rocky Mountain subalpine forests. We also found that serotinous lodgepole pine forests were resilient to compound disturbance effects if beetle outbreaks were followed by fire within ~ 10 years. As post-outbreak forests in western North America transition into the gray stage, our findings help to identify when management actions may or may not be warranted to reduce future fire severity and/or improve post-fire tree establishment in serotinous lodgepole pine forests.

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Appendices:

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

**Appendix B.** Photographs of bark beetle outbreak severity measurements.

**Appendix C.** Correlation among fire severity measurements.

## TABLES

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

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

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

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

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

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

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

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

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

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

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

**Table 5.** General linear model results testing for effects of beetle outbreak severity on subsequent fire severity. Burning conditions and beetle-killed basal area terms were included as fixed effects. Burning conditions is a categorical variable with each burning condition as a different model intercept. BC = burning conditions; BA = basal area; Beetle-killed BA: Moderate BC = beetle effect under moderate burning conditions; Beetle-killed BA: Extreme BC = beetle effect under extreme burning conditions.

| Response | Predictor | *β* | SE | *t* | *P* |
|---|---|---|---|---|---|
| **Green-attack / red stage** | | | | | |
| (New Fork Lakes Fire) | | | | | |
| **Char height (m)**[†1] | Moderate BC (intercept) | 6.10 | 2.09 | 2.92 | <0.01 |
| | Extreme BC (intercept) | 11.96 | 1.30 | 9.20 | <0.01 |
| | Beetle-killed BA: Moderate BC | 27.70 | 11.95 | 2.32 | 0.02 |
| | Beetle-killed BA: Extreme BC | 6.22 | 3.60 | 1.72 | 0.09 |
| **Bole scorch (%)**[†2] | Moderate BC (intercept) | 1.67 | 0.37 | 4.54 | <0.01 |
| | Extreme BC (intercept) | 2.71 | 0.23 | 11.98 | <0.01 |
| | Beetle-killed BA: Moderate BC | 4.29 | 1.88 | 2.28 | 0.02 |
| | Beetle-killed BA: Extreme BC | 0.91 | 0.57 | 1.59 | 0.11 |
| **Tree mortality (% BA)**[†2] | Moderate BC (intercept) | 3.32 | 0.18 | 18.08 | <0.01 |
| | Extreme BC (intercept) | 3.40 | 0.11 | 29.63 | <0.01 |
| | Beetle-killed BA: Moderate BC | 1.70 | 1.11 | 1.53 | 0.13 |
| | Beetle-killed BA: Extreme BC | 0.48 | 0.33 | 1.46 | 0.15 |
| **Tree mortality (% trees)**[†2] | Moderate BC (intercept) | 3.05 | 0.21 | 14.46 | <0.01 |
| | Extreme BC (intercept) | 3.38 | 0.13 | 25.49 | <0.01 |
| | Beetle-killed BA: Moderate BC | 2.51 | 1.36 | 1.85 | 0.07 |
| | Beetle-killed BA: Extreme BC | 0.54 | 0.40 | 1.36 | 0.18 |
| **Litter + duff depth (mm)**[†1] | Moderate BC (intercept) | 14.28 | 2.12 | 6.73 | <0.01 |
| | Extreme BC (intercept) | 10.62 | 1.36 | 7.82 | <0.01 |
| | Beetle-killed BA: Moderate BC | -24.98 | 15.29 | -1.63 | 0.11 |
| | Beetle-killed BA: Extreme BC | -7.90 | 4.56 | -1.73 | 0.09 |
| **Charred surface cover (%)**[†2] | Moderate BC (intercept) | -1.31 | 0.44 | -2.99 | <0.01 |
| | Extreme BC (intercept) | -0.79 | 0.28 | 2.88 | <0.01 |
| | Beetle-killed BA: Moderate BC | 3.52 | 2.87 | 1.23 | 0.22 |
| | Beetle-killed BA: Extreme BC | 1.22 | 0.86 | 1.43 | 0.16 |
| **Gray stage / post outbreak** | | | | | |
| (Red Rock Complex Fire) | | | | | |
| **Char height (m)**[1] | Moderate BC (intercept) | 12.93 | 3.28 | 3.94 | <0.01 |

| | | | | | |
|---|---|---|---|---|---|
| | Extreme BC (intercept) | 9.23 | 1.76 | 5.24 | <0.01 |
| | Beetle-killed BA: Moderate BC | -13.37 | 6.94 | -1.93 | 0.06 |
| | Beetle-killed BA: Extreme BC | 5.20 | 4.70 | 1.11 | 0.28 |
| **Bole scorch (%)**[2] | Moderate BC (intercept) | 4.15 | 0.92 | 4.50 | <0.01 |
| | Extreme BC (intercept) | 2.19 | 0.49 | 4.44 | <0.01 |
| | Beetle-killed BA: Moderate BC | -5.85 | 1.95 | -3.00 | <0.01 |
| | Beetle-killed BA: Extreme BC | 2.06 | 1.32 | 1.56 | 0.13 |
| **Tree mortality (% BA)**[2] | Moderate BC (intercept) | 4.83 | 1.14 | 4.26 | <0.01 |
| | Extreme BC (intercept) | 2.32 | 0.61 | 3.81 | <0.01 |
| | Beetle-killed BA: Moderate BC | -6.90 | 2.40 | -2.88 | <0.01 |
| | Beetle-killed BA: Extreme BC | 2.00 | 1.63 | 1.23 | 0.23 |
| **Tree mortality (% trees)**[2] | Moderate BC (intercept) | 4.37 | 1.06 | 4.11 | <0.01 |
| | Extreme BC (intercept) | 2.42 | 0.27 | 4.24 | <0.01 |
| | Beetle-killed BA: Moderate BC | -6.49 | 2.25 | -2.89 | <0.01 |
| | Beetle-killed BA: Extreme BC | 1.92 | 1.52 | 1.27 | 0.21 |
| **Litter + duff depth (mm)**[1] | Moderate BC (intercept) | 0.28 | 2.53 | 0.11 | 0.91 |
| | Extreme BC (intercept) | 3.37 | 1.36 | 2.49 | 0.02 |
| | Beetle-killed BA: Moderate BC | 12.57 | 5.35 | 2.35 | 0.02 |
| | Beetle-killed BA: Extreme BC | -2.85 | 3.63 | -0.79 | 0.44 |
| **Charred surface cover (%)**[2] | Moderate BC (intercept) | 1.53 | 1.38 | 1.11 | 0.28 |
| | Extreme BC (intercept) | 0.10 | 0.74 | 0.14 | 0.89 |
| | Beetle-killed BA: Moderate BC | -4.25 | 2.92 | -1.46 | 0.15 |
| | Beetle-killed BA: Extreme BC | 2.10 | 1.98 | 1.06 | 0.29 |

[†] Spatial regression accounting for spatial autocorrelation, using *gls*

[1] General linear model (no transform)

[2] General linear model (logit transform for percentage variables)

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

| Response | Predictor | *β* | SE | *t* | *P* |
|---|---|---|---|---|---|
| **Char height (m)**†1 | Intercept | 13.75 | 1.95 | 7.04 | <0.01 |
| | Percentage red stage | -2.41 | 1.94 | -1.24 | 0.22 |
| **Bole scorch (%)**†2 | Intercept | 2.98 | 0.36 | 8.88 | <0.01 |
| | Percentage red stage | -0.45 | 0.30 | -1.48 | 0.14 |
| **Tree mortality (% BA)**†2 | Intercept | 3.68 | 0.17 | 21.28 | <0.01 |
| | Percentage red stage | -0.29 | 0.16 | -1.79 | 0.08 |
| **Tree mortality (% trees)**†2 | Intercept | 3.69 | 1.20 | 18.70 | <0.01 |
| | Percentage red stage | -0.37 | 0.19 | -1.94 | 0.06 |
| **Litter + duff depth (mm)**†1 | Intercept | 7.70 | 2.27 | 3.39 | <0.01 |
| | Percentage red stage | 2.94 | 2.41 | 1.22 | 0.23 |
| **Charred surface cover (%)**†2 | Intercept | -0.42 | 0.42 | -1.01 | 0.31 |
| | Percentage red stage | -0.39 | 0.44 | -0.90 | 0.37 |

[†] Spatial regression accounting for spatial autocorrelation, using *gls*

[1] General linear model (no transform)

[2] General linear model (logit transform for percentage variables)

**Table 7:** Post-fire lodgepole pine seedling regeneration density within each fire severity class in the New Fork Lakes fire and the Red Rock Complex Fire.

| Fire name<br>Fire-severity class | Post-fire lodgepole pine seedlings ha$^{-1}$<br>Mean | (SE) | Median |
|---|---|---|---|
| New Fork Lakes Fire | | | |
| Light-surface (*n* = 15) | 68,533 | (15,060) | 58,000 |
| Severe-surface (*n* = 40) | 241,400 | (49,339) | 116,000 |
| Crown (*n* = 45) | 11,156 | (1,756) | 8,000 |
| Red Rock Complex Fire | | | |
| Light-surface (*n* = 14) | 6 | (6) | 0 |
| Severe-surface (*n* = 13) | 2,449 | (1,288) | 0 |
| Crown (*n* = 16) | 5 | (5) | 0 |

**Table 8.** Generalized linear model testing the relationship between post-fire lodgepole pine regeneration and pre-fire beetle outbreak severity in the New Fork Lakes Fire, while accounting for fire severity, potential seed source, and pre-fire serotiny. BA = basal area (%).

| Response | Predictor | $\beta$ | SE | $t$ | $P$ |
|---|---|---|---|---|---|
| **Post-fire lodgepole pine seedlings / ha** †1 | Light-surface fire (intercept) | 7.84 | 0.57 | 13.69 | <0.01 |
| | Severe-surface fire (intercept) | 8.63 | 0.57 | 15.24 | <0.01 |
| | Crown fire (intercept) | 6.26 | 0.69 | 9.07 | <0.01 |
| | Lodgepole pine BA $ha^{-1}$ | 0.09 | 0.01 | 6.77 | <0.01 |
| | Pre-fire serotiny (% of trees) | 0.95 | 0.46 | 2.07 | 0.04 |
| | Beetle-killed BA | -0.13 | 1.49 | -0.09 | 0.93 |
| | Pre-fire serotiny X beetle-killed BA | 1.70 | 2.17 | 0.18 | 0.44 |

† Spatial regression accounting for spatial autocorrelation, using *glmmPQL*

[1] Generalized linear model (Poisson distribution with log-link for count data)

## Figure Legends

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

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

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

**Figure 4.** Post-fire lodgepole pine seedlings $ha^{-1}$ vs. pre-fire beetle outbreak severity in each fire-severity class for the green-attack / red stage (New Fork Lakes Fire) (A) and the gray stage / post outbreak (Red Rock Complex Fire) (B). Post-fire lodgepole pine seedling denstiy was unrelated ($P > 0.10$) to pre-fire outbreak severity in both fires.

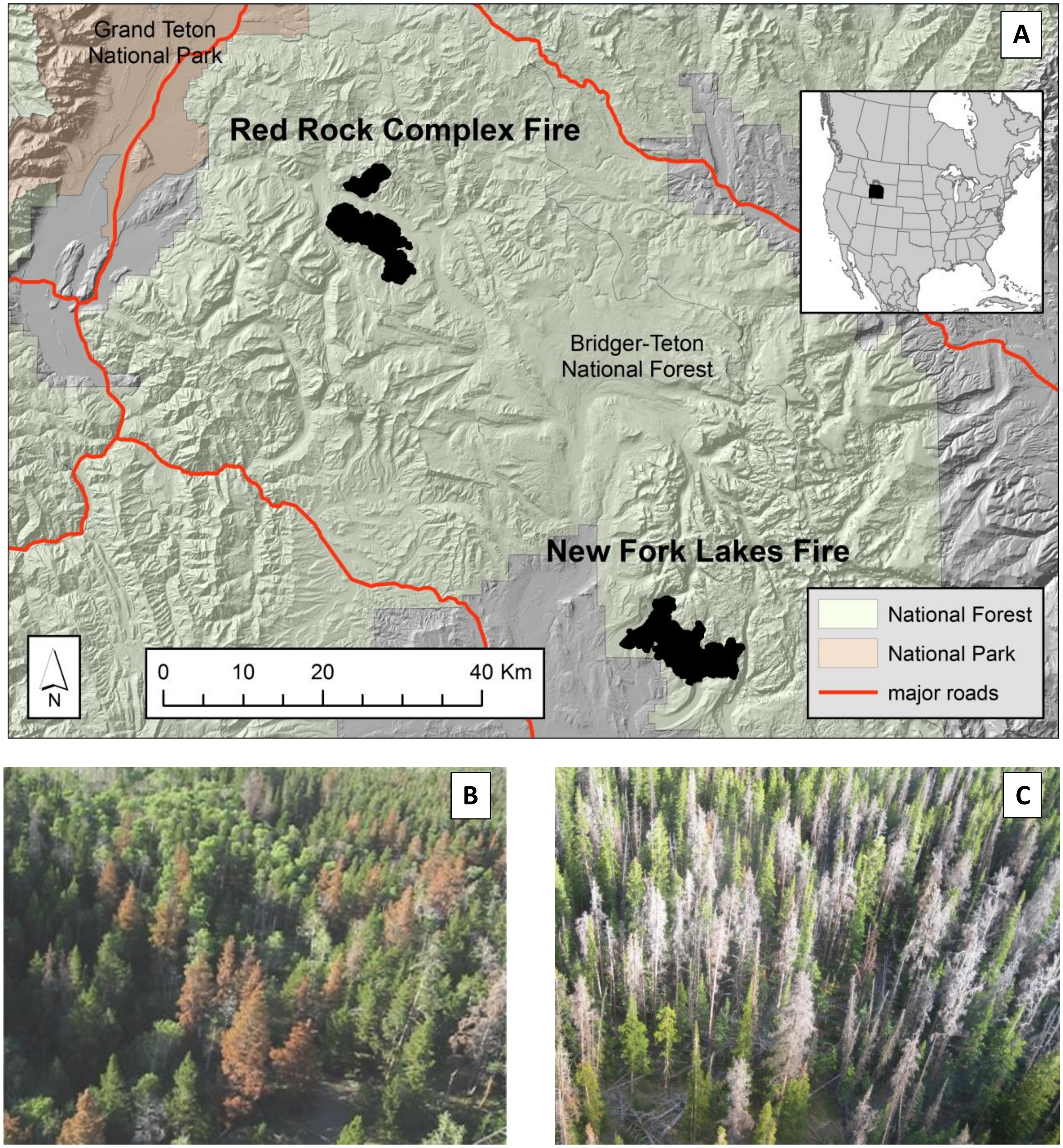
A
Grand Teton National Park
Red Rock Complex Fire
Bridger-Teton National Forest
New Fork Lakes Fire
National Forest
National Park
major roads
0
10
20
40 Km
N
B
C

**Figure 1**

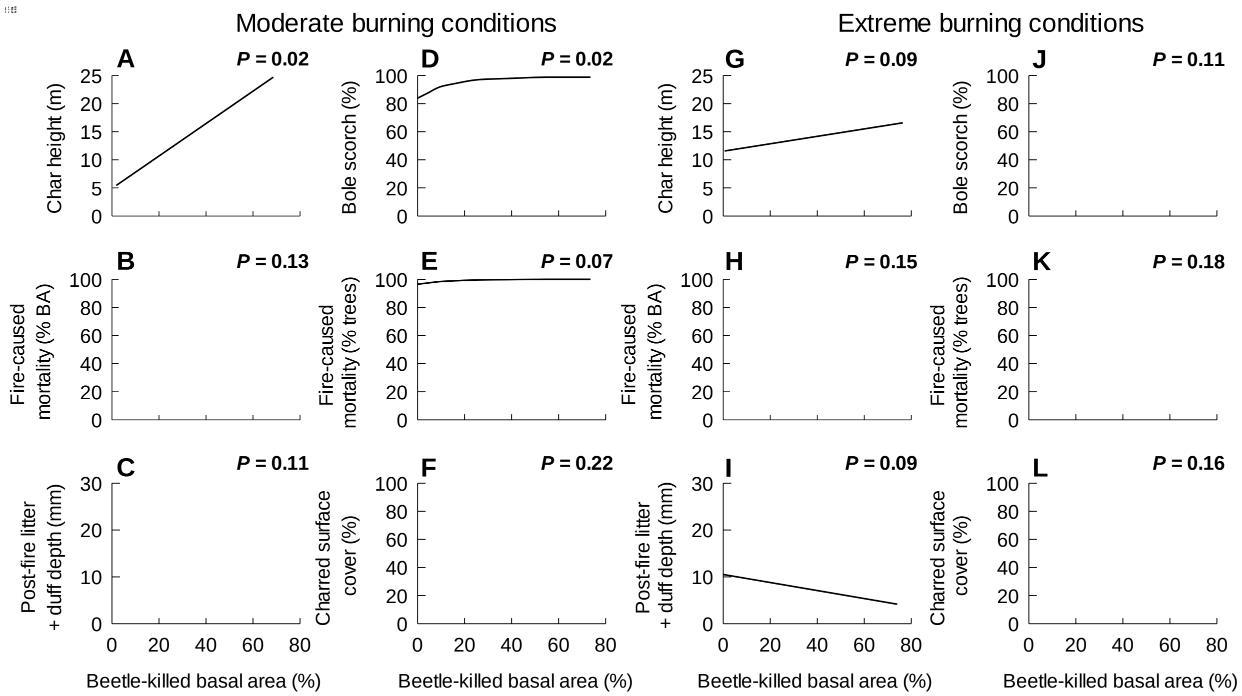
Moderate burning conditions
Extreme burning conditions
A
P = 0.02
Char height (m)
D
P = 0.02
Bole scorch (%)
G
P = 0.09
Char height (m)
J
P = 0.11
Bole scorch (%)
B
P = 0.13
Fire-caused mortality (% BA)
E
P = 0.07
Fire-caused mortality (% trees)
H
P = 0.15
Fire-caused mortality (% BA)
K
P = 0.18
Fire-caused mortality (% trees)
C
P = 0.11
Post-fire litter + duff depth (mm)
F
P = 0.22
Charred surface cover (%)
I
P = 0.09
Post-fire litter + duff depth (mm)
L
P = 0.16
Charred surface cover (%)
0
20
40
60
80
Beetle-killed basal area (%)

**Figure 2**

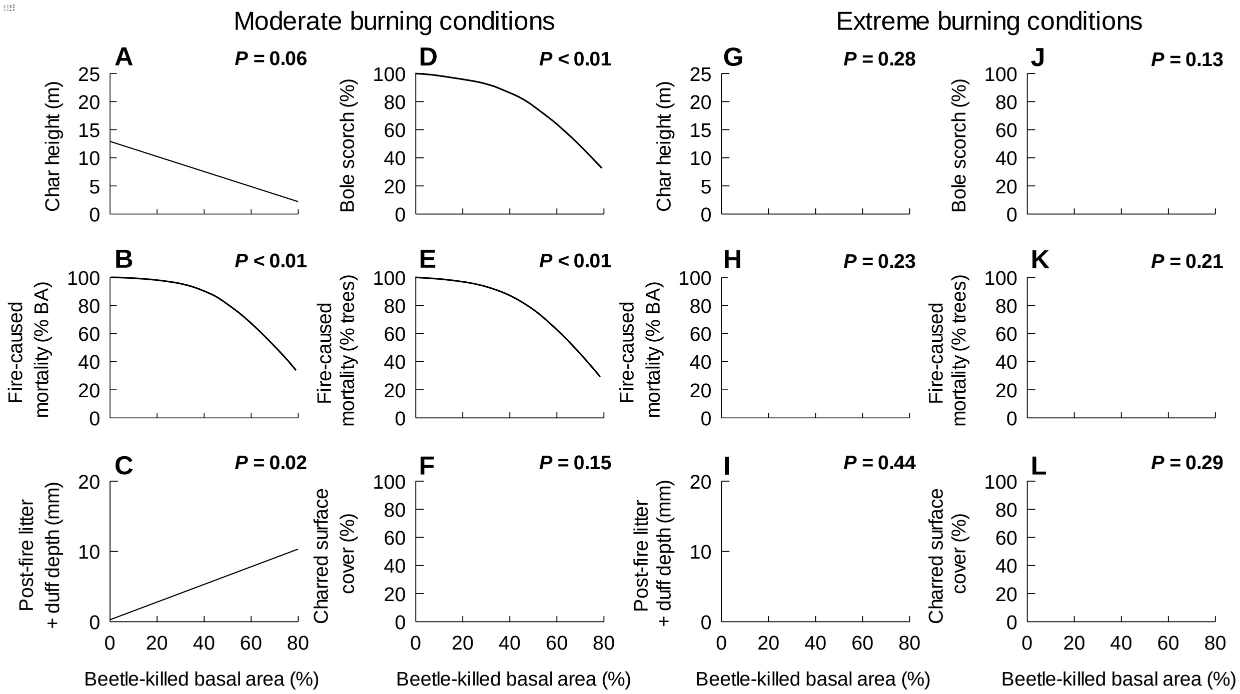
Moderate burning conditions
Extreme burning conditions
A
P = 0.06
Char height (m)
25
20
15
10
5
0
D
P < 0.01
Bole scorch (%)
100
80
60
40
20
0
G
P = 0.28
Char height (m)
J
P = 0.13
Bole scorch (%)
B
P < 0.01
Fire-caused mortality (% BA)
E
P < 0.01
Fire-caused mortality (% trees)
H
P = 0.23
Fire-caused mortality (% BA)
K
P = 0.21
Fire-caused mortality (% trees)
C
P = 0.02
Post-fire litter + duff depth (mm)
20
10
0
F
P = 0.15
Charred surface cover (%)
I
P = 0.44
Post-fire litter + duff depth (mm)
L
P = 0.29
Charred surface cover (%)
0
20
40
60
80
Beetle-killed basal area (%)

**Figure 3**

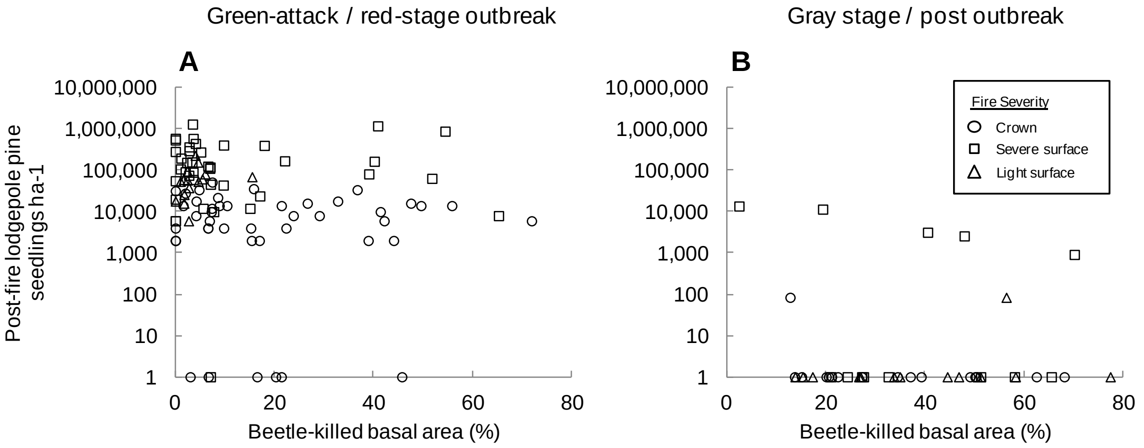
Green-attack / red-stage outbreak
Gray stage / post outbreak
A
B
Post-fire lodgepole pine seedlings ha-1
10,000,000
1,000,000
100,000
10,000
1,000
100
10
1
0
20
40
60
80
Beetle-killed basal area (%)
Fire Severity
○ Crown
□ Severe surface
△ Light surface

**Figure 4**

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

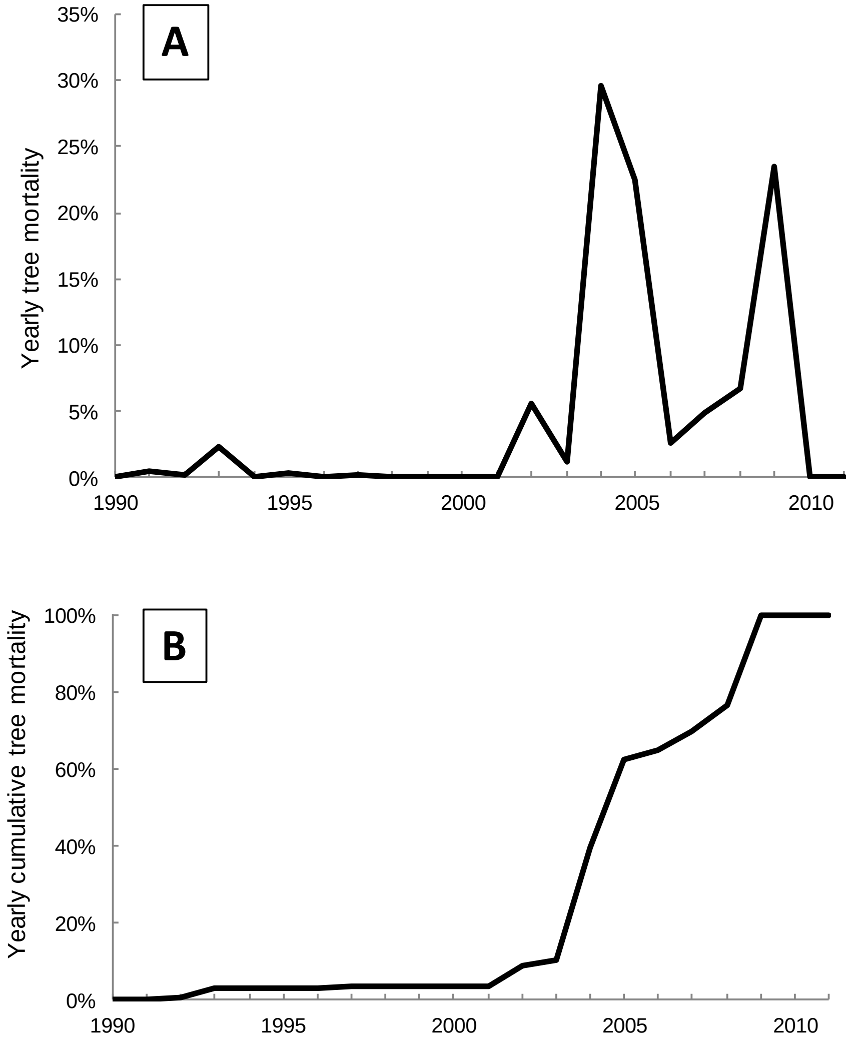

**Figure A1:** Time series of yearly (A) and yearly cumulative (B) tree mortality attributed to the mountain pine beetle beetle outbreak (69% of total mortality) and western balsam bark beetle (*Dryocoetes confusus*) and Armillaria root disease (31% of total mortality) in the area of the Red Rock Complex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

**Appendix B.** Photographs of bark beetle outbreak severity measurements

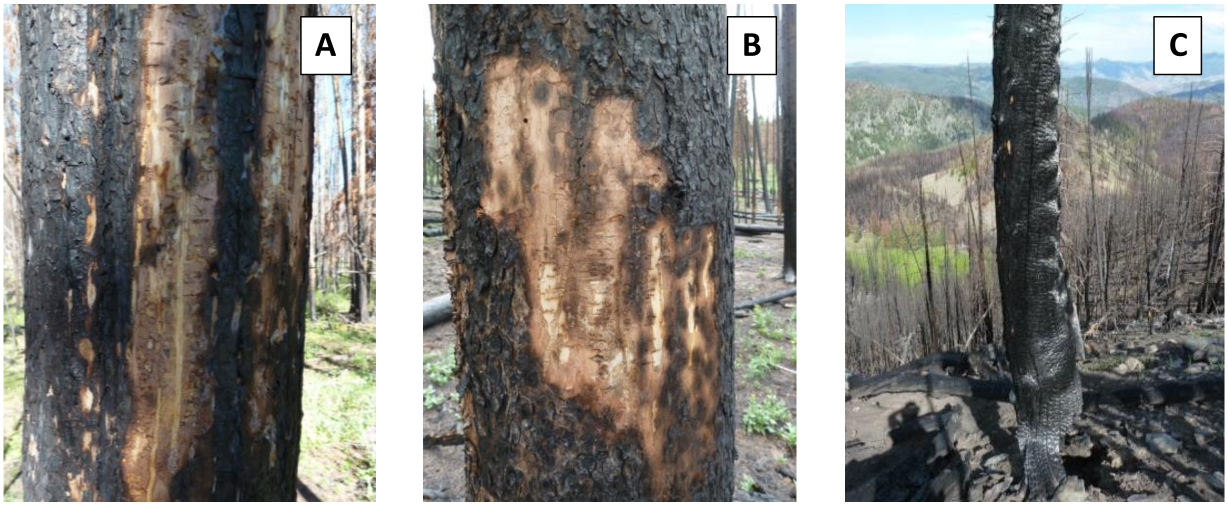

**Figure B1:** Photographs of general bole condition of trees classified as 'killed by bark beetles prior to fire' when galleries were visible on cambium (A-B), and 'killed by bark beetles prior to fire' when no cambium was visible but tree was obviously dead prior to fire (C) (Table 1). Photo credit: B.J. Harvey.

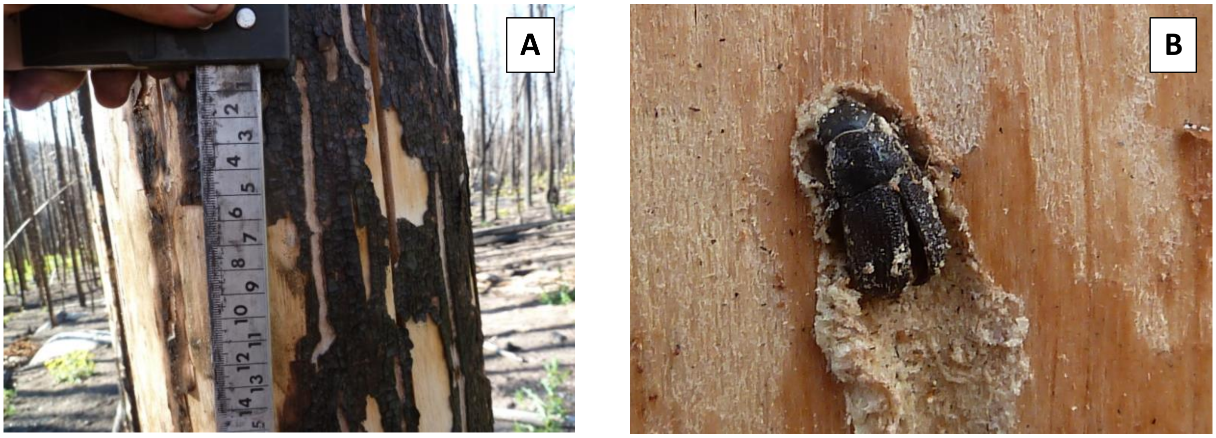

**Figure B2:** Photographs of general bole condition of trees that were classified as ‘green attack at time of fire’ with partially constructed adult galleries but no larval galleries (A); these trees often contained dead female mountain pine beetles underneath charred bark at the top end of galleries (B) (Table 1). Photo credit: B.J. Harvey.

**Figure B3:** Photographs of general bole condition (A-B) and crown condition (C) of trees with fully developed *Dendroctonus* galleries, but retaining needles in the canopy, classified as ‘live at the time of fire’ but attacked by beetles post-fire if there was no evidence of ‘green attack at the time of fire’ in the plot. If there was evidence of ‘green attack at the time of fire’ in the plot, trees were assigned to the ‘green attack at time of fire’ class (Table 1). Photo credit: B.J. Harvey.

**Figure B4:** Photographs of bole condition of trees classified as ‘live at the time of fire’ if there was no evidence of pre-fire galleries on sapwood (A), or fresh pitch tubes and boring dust on the outer bark (B-C) (Table 1). Photo credit: B.J. Harvey.

## **Appendix C.** Correlation among fire severity measurements

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

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

**Table C2**: Spearman rank correlations ($r_s$) among fire severity response variables in the Red Rock Complex Fire (gray / post-outbreak stage). $P < 0.001$ for all correlations. Relative difference normalized burn ratio (RdNBR) values were explored as a potential fire severity response variable, but timing of pre-fire images confounded beetle and fire effects in the fire severity index; thus RdNBR was excluded from analysis.

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

# Chapter 2 - Influence of recent bark beetle outbreak on fire severity and post-fire tree regeneration in montane Douglas-fir forests

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## Abstract

Understanding how disturbances interact to shape ecosystems is a key challenge in ecology. In forests of western North America, the degree to which recent bark beetle outbreaks and subsequent fires may be linked (e.g. outbreak severity affects fire severity) and/or whether these two disturbances produce compound effects on post-fire succession is of widespread interest. These interactions remain unresolved, largely because field data from actual wildfires following beetle outbreaks are lacking. We studied the 2008 Gunbarrel Fire, which burned 27,200 ha in Douglas-fir (*Pseudotsuga menziesii*) forests that experienced a bark beetle outbreak 4-13 years pre-fire (“gray stage,” after trees have died and needles have dropped), to determine whether outbreak severity influenced subsequent fire severity and post-fire tree regeneration. In 85 sample plots we recorded pre-fire stand structure and outbreak severity; multiple measures of canopy and forest-floor fire severity; and post-fire tree seedling density. Pre-fire outbreak severity was not related to any measure of fire severity except for mean bole scorch, which declined slightly with increasing outbreak severity. Instead, fire severity varied with topography and burning conditions (proxy for weather at time of fire). Post-fire Douglas-fir regeneration was low, with tree seedlings absent in 65% of plots. Tree seedlings were abundant in plots of low fire severity that also had experienced low outbreak severity (mean = 1,690 ha$^{-1}$), suggesting a dual filter on tree regeneration. Although bark beetles and fire collectively reduced live basal area to < 5% and increased snag density to > 2,000% of pre-outbreak levels, the lack of relationship between beetle outbreak and fire severity suggests these disturbances were not linked. Nonetheless, effects on post-fire tree regeneration suggest compound disturbance interactions that contribute to the structural heterogeneity characteristic of mid/lower montane forests.

**Keywords:** disturbance interactions, compound disturbance, fire ecology, Douglas-fir beetle,

Rocky Mountains, *Dendroctonus pseudotsugae*, *Pseudotsuga menziesii*, Greater Yellowstone

## Introduction

Understanding disturbance interactions, such as when the occurrence or severity of one disturbance influences the occurrence or severity of another (i.e., linked disturbances, Simard et al. 2011) is vital to anticipating future ecosystem dynamics and resource management challenges (Turner 2010). Recent bark beetle (Curculionidae: Scolytinae) epidemics have led to extensive tree mortality in forests of western North America (Raffa et al. 2008), raising pressing questions about how beetle outbreaks may influence subsequent fire activity (e.g., Hicke et al. 2012). Of greatest interest is whether post-outbreak wildfires will be more severe than those in undisturbed forests, an issue unresolved by studies to date. Retrospective analyses suggest relatively modest effects of pre-fire beetle outbreak on the occurrence of fire (e.g., Bebi et al. 2003, Lynch et al. 2006, Kulakowski et al. 2003, Kulakowski and Veblen 2007, Kulakowski and Jarvis 2011). However, previous studies have not tested the relationship between the severity of both beetle outbreaks and fire, and they lack field data needed to examine different fire effects (e.g. canopy vs. surface fire) (Hicke et al. 2012). Recent field studies have documented key changes in fuels as beetle outbreaks progress (e.g., Klutsch et al. 2011, Simard et al. 2011, Hoffman et al. 2012, Schoennagel et al. 2012, Jolly et al. 2012a, Donato et al. 2013), but projections of fire activity in response to these changes have differed markedly among studies and catalyzed spirited debate (e.g., Moran and Cochrane 2012, Jolly et al. 2012b, Simard et al. 2012). Empirical evidence that might resolve alternative expectations and provide insight into differences among forest types has been lacking (Hicke et al. 2012). Fires that have burned following recent beetle outbreaks in forests now provide opportunities for field studies to address these uncertainties empirically.

In addition to the potential for linked disturbance interactions, two disturbances that occur in close succession may interact to alter ecosystem response to the second disturbance, even if the second disturbance is not affected by the first (i.e., compound disturbances, Paine et al. 1998). For example, an abnormally short interval between fires can lead to substantial reductions in tree regeneration if the fire-free interval is less than the time required for trees to produce seed (e.g., Brown and Johnstone 2012). Especially in forest types that lack a persistent seed bank (e.g., non-serotinous conifers), beetle outbreaks followed by fire could exhibit compound disturbance effects if the outbreak substantially reduced seed supply. Bark beetles are more likely to kill large, cone-producing trees (Bjorklund and Lindgren 2009), and reduced propagule abundance in areas of high-severity beetle outbreaks could limit post-fire tree regeneration. Such compound disturbance effects could drive variability in post-fire succession and have long-term effects on forest structure and function, but this has not yet been explored.

While prior research on beetle-fire interactions has focused on high-elevation subalpine forests with crown-fire regimes, surprisingly little is known about mid/lower montane forests which cover ~30% of the US Rocky Mountains (Baker 2009). Key differences in stand structure, fire regimes, and regeneration mechanisms among forest types may lead to different disturbance interaction outcomes. Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests are a primary component of mid/lower montane forest ecosystems, occurring on moderate to steep slopes between ~1,850-2,500 m (Despain 1991, Barrett 1994). Stands range from dense closed-canopy forests to open woodlands (Despain 1991, Donato et al. 2013) and the fire regime is mixed-severity, including patches of surface and crown fire (Arno 1980, Barrett 1994, Baker 2009). Interior Douglas-fir is slow-growing, long-lived, and non-serotinous (lacking a seedbank).

Thick bark on mature trees insulates against surface fire, and seed dispersal from surviving trees onto exposed mineral soil leads to recruitment pulses after fire (Knight 1996, Baker 2009). Extensive areas of mid/lower montane forests were affected by Douglas-fir beetle (*Dendroctonus pseudotsugae*) outbreaks that peaked by 2005 (Meddens et al. 2012), but the potential effects of these outbreaks on fire severity and post-fire trajectories are unknown (Hicke et al. 2012).

Wildfires have recently burned some post-outbreak forests, providing ideal opportunities to evaluate the potential for linked or compound disturbance interactions between bark beetle outbreaks and fire. We studied the Gunbarrel Fire, which burned > 27,000 ha of gray-stage post-outbreak Douglas-fir forests in Greater Yellowstone (Wyoming, USA) in 2008, to address two research questions. (1) *How does severity of the recent bark beetle outbreak influence subsequent fire severity?* Because the fire occurred in the gray post-outbreak stage, in which needles had recently been shed from beetle-killed trees, we expected measures of canopy fire severity to either decline with increasing beetle-outbreak severity because of the reduced canopy fuel load or to be unrelated to beetle-outbreak severity (Donato et al. 2013). However, we expected measures of forest-floor fire severity to increase with beetle-outbreak severity because of accumulation of surface fuel and increased surface winds and temperatures beneath more open canopies (Jenkins et al. 2008, Hicke et al. 2012). We also expected that topography and/or burning conditions (i.e. weather) could over-ride beetle outbreak effects, such that outbreak severity would have less effect on fire severity in steep terrain or during extreme burning conditions. (2) *How does bark-beetle outbreak severity interact with fire severity to influence early post-fire Douglas-fir regeneration?* We expected post-fire Douglas-fir regeneration to decline with increasing beetle-outbreak severity because seed source would be reduced.

## Methods

### *Study area*

The study area is in the Absaroka Wilderness on the Shoshone National Forest (SNF), situated on the eastern edge of Greater Yellowstone (44º 30' N, 109º 45' E) and is typical of coniferous mid/lower montane forests in the Middle Rocky Mountain ecoregion (Omernik 1987) (Appendix A). Topography is variable and steep; with elevation ranging from 1,900-2,700 m in several drainages oriented approximately N-S and emptying into the Shoshone River. Slopes in study plots ranged from 2-43º (mean 22º) across all aspects. Mean daily temperatures range from -12 ºC in January to 22 ºC in July, with an annual mean precipitation of 69 cm falling primarily as winter snow and spring rain (www.prism.oregonstate.edu). Soils are well drained and derived from volcanic (andesitic) and metamorphic substrates. Forests are typical of the sloped perimeter of the Yellowstone Plateau, composed of pure Douglas-fir stands in middle elevations with assemblages including limber pine (*Pinus flexilis)* and Rocky Mountain juniper (*Juniperus scopulorum*) at lower elevations and lodgepole pine (*Pinus contorta* var. *latifolia*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) at higher elevations.

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

### *Sampling design*

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

Data were collected on stand structure, pre-fire beetle outbreak severity, and fire severity in a 30-m diameter circle plot (0.07 ha) divided into four quadrants (NE, SE, SW, NW). Stand structure was measured by recording the condition (live or dead), species, diameter at breast height (dbh) to the nearest 0.5 cm, and height of every tree taller than 1.4 m in the plot. We also recorded the species, height, and branch-whorl count for each live or dead pre-fire sapling (trees < 1.4 m that established pre-fire; ≥ 3 branch whorls) occurring in 3-m belt transects, and post-fire seedling (trees that germinated post-fire; < 3 branch whorls) in 2-m belt transects along the main axes of the circle-plot (N, E, S, W). GPS coordinates and distance to the nearest live seed-bearing tree were measured at plot center; the latter with a TruPulse 360 laser range finder.

### *Pre-fire beetle outbreak severity*

Pre-fire beetle outbreak severity was quantified by removing bark on every tree taller than 1.4 m and recording evidence of *Dendroctonus* activity (5,914 individual trees). The thick bark on Douglas-fir trees enabled us to sample well-preserved vascular cambium on most trees

(99.75% of basal area and 98.5% of trees). Trees were recorded as ‘killed by bark beetles prior to fire’ if they met all the following criteria: dead at time of sampling, presence of exit holes on outer bark, dry cambial tissue, fully excavated (but vacated) adult and larval galleries on the vascular cambium ( > 50% of bole circumference or remaining visible cambium), and no needles retained in the canopy. Dead trees with no evidence of pre-fire beetle activity or clear evidence of post-fire beetle activity were assumed to have been ‘live at the time of fire.’ Further details and validation of outbreak-severity methods are explained in Appendix B.

### *Fire severity*

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

### *Topography and burning conditions*

We used a 10-m digital elevation model in ArcGIS 10.1 to generate topographic variables based on each plot center: elevation (m), slope (°), aspect (NE Index, [Beers et al. 1966]), and topographic curvature (the 2nd derivative of the elevation surface [Zevenbergen and Thorne 1987]). Because absolute elevation in the study area spans > 1,000 m over 40 horizontal km, we calculated 'slope position' for each plot by re-scaling elevation in each drainage from 0 (drainage outlet to Shoshone River) to 1 (ridge top) to capture local elevational effects on fire severity. Reliable local (plot-scale) weather data were not available as plots were 3-37 km from the nearest weather station. Therefore, we followed methods of Thompson and Spies (2009), using a daily burn progression map provided by the SNF to divide the fire into two periods of burning conditions based on weather conditions and mapped fire growth during different periods. Plots in each drainage were assigned to a burn period based on the date when the majority of the drainage burned. *Moderate* burning conditions (40 plots) were during a period of relatively low temperatures and winds, high humidity, and modest fire growth. *Extreme* burning conditions (45 plots) were during a period of relatively high temperatures and winds, low humidity, and rapid fire growth (Appendix D). We confirmed there was no confounding relationship between beetle-killed basal area and moderate or extreme burning conditions ($t = 1.05$, $P = 0.30$, Welch's t-test).

### *Statistical analysis*

To test if fire severity was linked to pre-fire beetle outbreak severity, we used several analytical approaches before and after accounting for other variables known to influence wildfire. First, we tested for differences in pre-fire beetle-killed basal area (%) among integrative fire-severity classes overall and during different burning conditions using a one-way ANOVA. Second, we performed a Spearman's rank correlation test between each quantitative metric of fire severity and beetle-killed basal area in all plots regardless of burning conditions ($n = 85$), and separately for plots that burned during moderate ($n = 40$) and extreme ($n = 45$) burning conditions. Third, for fire-severity variables (RdNBR, char height, post-fire litter + duff depth, and charred surface cover) that met assumptions of parametric tests after transformation, we used mixed-effects linear models to test for effects of beetle outbreak severity while controlling for topography, burning conditions, and drainage (the latter to account for spatial grouping of plots). Preliminary stepwise variable selection (using BIC) among topographic (elevation, slope, aspect, topographic curvature, slope position) and stand structure (live and dead basal area and stem density) variables resulted in slope position as the only variable retained for all models. A term for burning conditions (moderate or extreme) was also included and beetle-killed basal area was included to test the main effect of outbreak severity. Interaction terms were also included to test whether effects of slope position and/or beetle outbreaks varied by burning conditions. In sum, final models contained burning condition, slope position, beetle-killed basal area, slope position

* burning condition, and beetle-killed basal area * burning condition as fixed effects, and drainage as a random effect. All regression models were assessed for heterogeneity of residuals, normality of errors, multicolinearity among explanatory variables, and overly influential data points (Cook's Distance value > 0.5); no violations were detected. Model residuals were tested for spatial autocorrelation using semivariograms; none was detected.

To test if beetle outbreaks and fire interacted to produce compound effects on post-fire Douglas-fir seedling density (stems ha$^{-1}$), we performed two analyses. First, to assess the relative importance of beetle outbreak severity as an explanatory variable for post-fire seedling establishment among other variables (topography, fire severity, seed source) known to affect post-fire tree regeneration, we used a combination of random forests and regression trees. These methods are effective in uncovering hierarchical and non-linear relationships among variables, and are robust to any distribution (Breiman et al 1984, De'ath and Fabricius 2000, Maindonald and Braun 2010). Random forests provide a list ranking the importance of explanatory variables from a large number of potential trees, and are a useful tool in combination with classical regression trees which are more interpretable for complex relationships among variables (Maindonald and Braun 2010). A full tree was built by adding the following candidate predictor variables: total (live and dead) pre-fire basal area ha$^{-1}$, total (live and dead) pre-fire Douglas-fir basal area ha$^{-1}$, elevation, slope, aspect, topographic curvature, slope position, drainage, fire-severity class, distance to seed source, and beetle-killed basal area. Ten runs of 1,000 trees were independently grown using random forests, and the increase in mean square error for exclusion of each variable was averaged across runs, providing a rank list of variable importance. Variables with a positive increase (i.e. variables that improved model fit) were added to the full regression tree. The regression tree was then trimmed to avoid over-fitting, minimizing cross-validated error by removing splits exceeding the complexity parameter (Maindonald and Braun 2010).

Second, post-fire Douglas-fir seedling density (stems ha$^{-1}$) was regressed against beetle-killed basal area within each fire severity class (which can affect post-fire tree seedling density, Turner et al. 1999). We used Spearman's rank correlation tests within each fire severity class, but 90% of plots that burned as crown or severe-surface fire had no post-fire seedlings. In light-surface fire plots, post-fire Douglas-fir seedling density was regressed against beetle-killed basal with a generalized linear model (negative binomial error structure; log-link). Because advance (pre-fire) regeneration can also be important to post-fire trajectories, we additionally tested relationships between advance regeneration, post-fire seedling density, and outbreak severity.

All statistical analyses were performed in the R statistical software (version 2.11.1, R Foundation for Statistical Computing, Vienna, AT). Results are means ± 1 SE unless noted. For all analyses, we set $\alpha = 0.10$ to reduce the chance of Type II error and not miss potentially meaningful relationships among variables.

## Results

### *Effects of bark beetles and fire on stand structure*

Pre-outbreak live basal area and stem density was 41.2 ± 1.6 m$^2$ ha$^{-1}$ and 948 ± 34 stems ha$^{-1}$, respectively, dominated by Douglas-fir (87 ± 2% of basal area; 71 ± 3% of live stems), with understory vegetation composed of tree saplings, woody shrubs, herbs, and graminoids. Beetle-kill ranged from 0-91% (mean 59%) of total basal area and was composed almost entirely (> 97%) of Douglas-fir trees killed by the Douglas-fir beetle. The Douglas-fir beetle outbreak reduced live basal area and live stem density (Fig. 1A, B); reduced mean live tree size (Fig. 1C);

and increased the number of standing dead trees (Fig. 1D). The Gunbarrel Fire further reduced live basal area and live stem density (Fig. 1A, B); and increased the number of standing and down dead trees (Fig. 1D, E). Bark beetles and subsequent fire collectively reduced live basal area to < 5% and increased snag density to > 2,000% of pre-disturbance levels, with consistent effects across levels of outbreak severity (Appendix E).

### *Effects of bark beetle outbreak on fire severity*

Our sampling design captured a wide range of fire severity for integrative, surrogate, canopy, and forest-floor measures. Of the 85 sample stands, 31 burned as crown fire, 31 as severe-surface fire, and 23 as light-surface fire; classes were statistically distinct for quantitative fire-severity measures (Table C2). RdNBR ranged from 21-1935 (mean 670). Canopy fire severity was variable: mean char height ranged from 0.7-23.1 m (mean 12.9 m); mean bole scorch spanned 38-100% (mean 92%) of bole circumference; tree mortality ranged from 15-100% (mean 90%); and fire-killed basal area ranged from 7-100% (mean 87%). Forest-floor fire severity was variable: post-fire litter + duff depth ranged from 0.4-32.2 mm (mean 8.34 mm); and charred surface cover ranged from 4-50% (mean 24%).

When considering univariate relationships between integrative or surrogate fire-severity metrics and outbreak severity, beetle-killed basal area did not differ among fire-severity classes ($F_{2,82} = 1.69$, $P = 0.19$) and was not correlated with RdNBR (Fig. 2A). Beetle outbreak severity was also not correlated ($P > 0.10$) with three of four measures of canopy fire severity (Fig. 2B,D,E) or either measure of forest-floor fire severity (Fig. 2F-G). Mean bole scorch decreased slightly with increasing beetle outbreak severity ($r_s = -0.18$, $P = 0.09$; Fig. 2C). Correlations remained non-significant after accounting for burning conditions (Fig. 2, inset table). Beetle-killed basal area also did not differ among fire severity classes under either moderate ($F_{2,37}$ = 1.11, $P = 0.34$) or extreme ($F_{2,42}$ = 1.55, $P = 0.22$) burning conditions. After accounting for burning conditions and slope position in regression analyses, RdNBR, char height, litter + duff depth, and charred surface cover (the variables that met parametric assumptions) were still unrelated to outbreak severity (Table 1). Fire severity was instead associated with slope position and burning conditions (i.e., weather); severity increased with higher slope positions during moderate burning conditions but not during extreme burning conditions (Table 1, Appendix F).

### *Effects of bark beetle outbreak on post-fire tree regeneration*

Post-fire Douglas-fir regeneration (seedlings that germinated post-fire; < 3 branch whorls) was variable, ranging from 0-4,750 seedlings ha$^{-1}$ (mean 215 ha$^{-1}$, median 0 ha$^{-1}$) and composing 88% of all post-fire tree seedlings. The post-fire seedling distribution was characterized by positive skew; 65% of plots had no seedlings (90% of severe-surface or crown fire plots).

Fire-severity class and beetle-killed basal area were the two highest ranked explanatory variables in the random forests analysis, and were the two variables retained after trimming the regression tree to reduce over-fitting (Fig. 3). In areas of crown or severe-surface fire, post-fire Douglas-fir seedling density was low (mean 13 stems ha$^{-1}$, median 0 stems ha$^{-1}$) and unrelated to pre-fire beetle outbreak severity ($P > 0.10$; Fig. 3A). Seedling density was high (mean 757 ha$^{-1}$, median 167 ha$^{-1}$) in areas of light-surface fire, and exceeded pre-fire stem density if outbreak severity and fire severity were low (Fig 3B). However, seedling density was low if outbreak severity was high in areas of light surface fire (Fig. 3B); density declined with increasing pre-fire outbreak severity in light-surface fire plots ($r_s = -0.48$, $P = 0.02$; Fig. 3A, Appendix G).

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

## Discussion

The lack of relationship between beetle-outbreak severity and subsequent fire severity indicates that these disturbances were not linked. However, they did interact to produce compound disturbance effects on post-fire tree regeneration, contributing to the structural heterogeneity characteristic of mid/lower montane forest ecosystems. Pre-fire Douglas-fir beetle outbreak had no detectable effect on surrogate, integrative, canopy, or forest-floor measures of fire severity, except for a slight reduction in bole scorch associated with increasing outbreak severity. Instead, fire severity varied with burning conditions (reflective of weather at the time of burning) and slope position. Bark beetle outbreaks preconditioned the forest response to low-severity fire such that tree regeneration was low if pre-fire outbreak severity was high. Given the extent of recent beetle outbreaks in western North America now in the gray stage, these results suggest implications for post-outbreak trajectories in other mid/lower montane ecosystems.

### *Beetle outbreaks and fire severity*

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

Our detailed field measurements of canopy and forest-floor fire severity allow for inferences into underlying mechanisms through comparison with fuel profile data in other studies, and evaluation of several standing hypotheses about beetle outbreaks and fire. We hypothesized either no relationship or a reduction in canopy fire severity with increasing pre-fire beetle outbreak severity, and this expectation was supported. Our findings largely match predictions from fuel profiles in gray-stage mid/lower montane forests, where canopy fuels are reduced relative to unaffected stands (Hoffman, et al. 2012, Donato et al. 2013). Canopy cover is inherently irregular in mid/lower montane forests, and beetle-induced changes increase this within-stand patchiness in a system that is already very heterogeneous (Donato et al. 2013). Our findings differed from gray-stage expectations in higher-elevation subalpine forests with more contiguous canopy fuels where the likelihood of severe crown fire is predicted to substantially decrease after needles fall from beetle-killed trees (DeRose and Long 2009, Klutsch et al. 2011, Simard et al. 2011). Expectations of increased forest-floor fire severity in the gray stage were not supported, as beetle-outbreak severity was unrelated to post-fire litter + duff and charred surface cover across burning conditions (i.e., weather) and slope position. Although measures of post-fire litter + duff depth potentially varied as a function of pre-fire litter + duff depth, this cannot be assessed post-fire. However, post-fire litter + duff depth was consistently correlated with other measures of fire severity (Table C1), indicating that our post-fire data were a reliable measure of fire effects rather than pre-fire conditions. An increase in surface fuel combined with a decrease in wind resistance from opening of the canopy has been hypothesized to increase forest-floor fire severity in most forest types (Jenkins et al. 2008, Klutsch et al. 2011, Hicke et al. 2012, Hoffman, et al. 2012, Schoennagel et al. 2012). While chronosequence studies in Douglas-fir forests show no difference (Donato et al. 2013) or slight increases (Jenkins et al. 2008) in coarse surface fuels from unaffected to gray-stage stands, slower snag-fall in mid/lower montane forests than subalpine forests (Donato et al., in press) may delay coarse surface fuel accumulation and thus delay beetle-induced increases in forest-floor fire-severity.

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

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

### *Beetles, fire and post-fire tree regeneration*

Although pre-fire beetle outbreak severity and fire severity were unrelated to one another (i.e., not linked), the combined disturbances interacted to influence post-fire tree regeneration, supporting expectations for compound disturbance effects (Paine et al. 1998). In the absence of fire, Douglas-fir regeneration after high-severity beetle outbreak can be as high as 1,900 stems ha$^{-1}$ (D. Donato, unpub. data). In the absence of severe beetle outbreaks, post-fire Douglas-fir seedling density can also be high, exceeding stand-replacement when fire severity is low (Fig. 3B). However, our data suggest that the beetle outbreak preconditioned the post-fire response to lower-severity fire through a reduction in the *in situ* seed source by killing large, seed-producing trees. These effects were manifest prior to the fire through a reduction in pre-fire advance regeneration following the beetle outbreak and continued post-fire through a reduction in postfire seedling establishment, ultimately resulting in a negative relationship between total Douglas-fir regeneration (all live trees < 1.4 m that established pre- or post-fire) and beetle outbreak severity ($r_s$ = -0.37, $P$ = 0.09). Our data are from early in post-fire succession (three years after fire), but these initial patterns are likely indicative of longer term trends. In nearby areas, post-fire Douglas-fir seedling density three years following the 1988 Yellowstone fires was highly correlated with density 24 years after the fires ($R^2$ = 0.87, $P$ < 0.001, D. Donato, unpub. data). Seed is generally available where surviving mature trees are present, as yearly cone crop failures in Douglas-fir are rare (Roeser 1942). However, > 50% of our study plots with no post-fire regeneration were > 150 m from the nearest mature live tree. Thus, patterns of early post-fire regeneration driven by compound beetle-fire disturbances likely promote persistent heterogeneity in stand structure - a defining characteristic of mid/lower montane ecosystems.

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

## Conclusion

Beetle outbreaks and fire are both expected to increase as climate warms (Bentz et al. 2010, Westerling et al. 2011), increasing the probability that they will overlap in time and space and heightening the need to understand how multiple disturbances interact to shape forest ecosystems. Using empirical field data from mid/lower montane forests in Greater Yellowstone, we found no evidence of pre-fire (gray-stage) bark beetle outbreaks in Douglas-fir forests affecting subsequent fire severity. Instead, fire severity varied largely with burning conditions (reflective of weather at time of burning) and slope position. Beetle outbreaks and fire interacted to affect post-fire tree regeneration, such that seedling density was uniformly low when fire severity was high, but was limited by beetle outbreak severity when fire severity was low. Although beetle outbreaks and subsequent fire were not linked disturbances, they produced compound effects that contribute to heterogeneity characteristic of mid/lower montane forests.

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**Appendix A.** Study area and recent Douglas-fir beetle outbreak history.

**Appendix B.** Supplemental information on beetle outbreak severity measurements

**Appendix C.** Supplemental information on fire severity measurements

**Appendix D.** Burning conditions as a proxy for weather at time of burning

**Appendix E.** Variability in stand structure impacts from bark beetle outbreak

**Appendix F.** Effects of slope position on fire severity during different burning conditions

**Appendix G.** Generalized linear model for post-fire Douglas-fir seedling density

**Table 1.** Results of mixed-effects linear models testing for effects of beetle outbreak severity on subsequent fire severity. Drainage basin was included as a random variable. Burning condition, slope position, beetle-killed basal area, and interaction terms were included as fixed effects. Burning conditions was a categorical variable with moderate burning conditions as the model intercept. Models were only run for fire-severity response variables that satisfied parametric statistics assumptions after transformation (if needed). BC = burning conditions, RdNBR = Relative differenced Normalized Burn Ratio.

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

# Figure Legends

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

**Figure 2.** Metrics of fire severity vs. beetle-killed basal area (%) during moderate and extreme burning conditions. Inset table shows Spearman rank correlations ($r_s$) and *P*-value for each fire severity response variable and beetle-killed basal area (%).

**Figure 3.** (A) Post-fire Douglas-fir seedling density (stems $ha^{-1}$) vs. beetle-killed basal area (%) by fire-severity class. Spearman rank correlations ($r_s$) were only significant in light surface fire ($r_s = -0.48$, $P = 0.02$). (B) Final pruned regression tree model for post-fire Douglas-fir seedling density (stems $ha^{-1}$), showing significant predictor variables in order of importance based on variance explained. Each node and terminal node for the regression tree shows the mean seedling density for that node and the number of plots in that group.

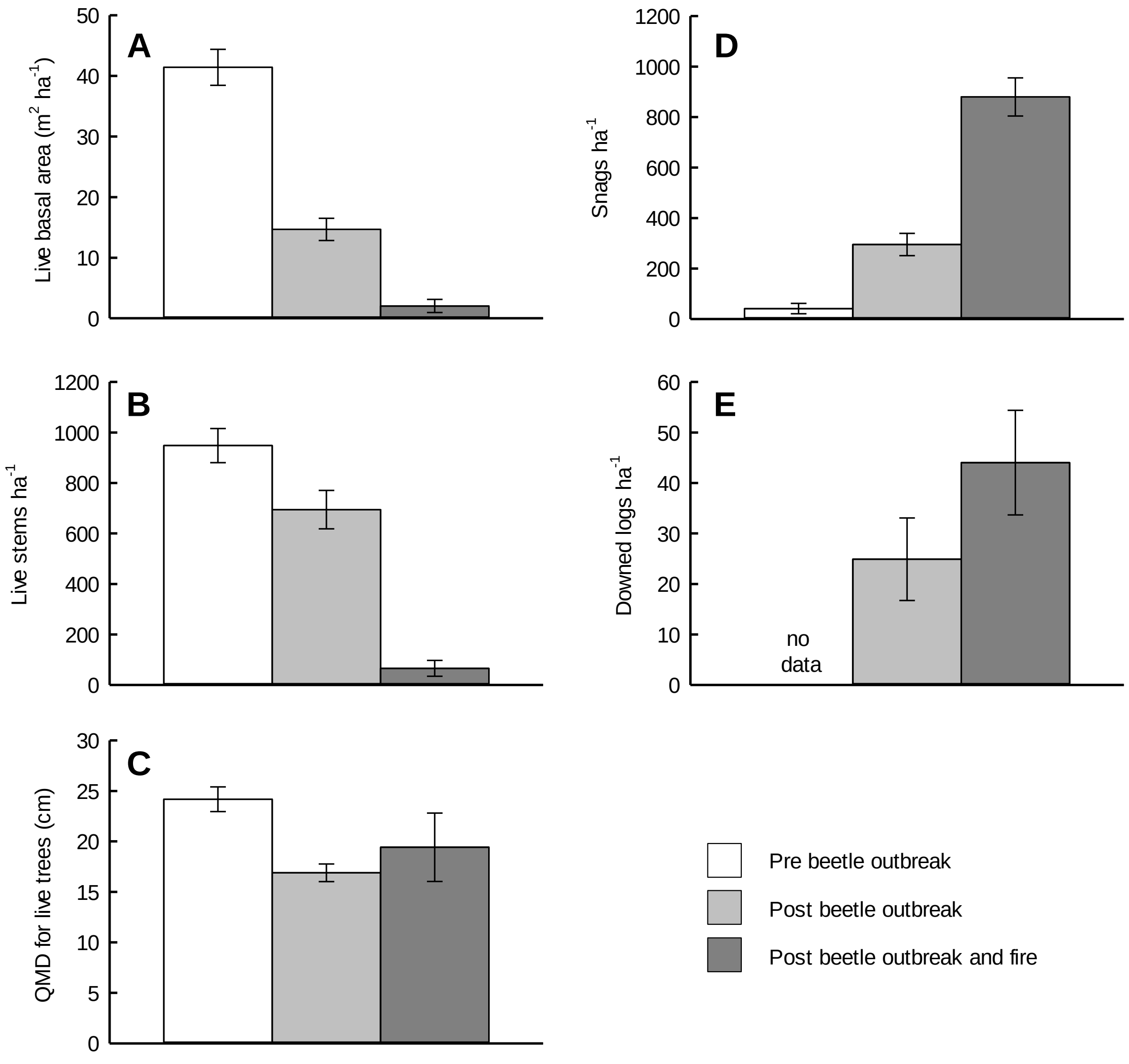
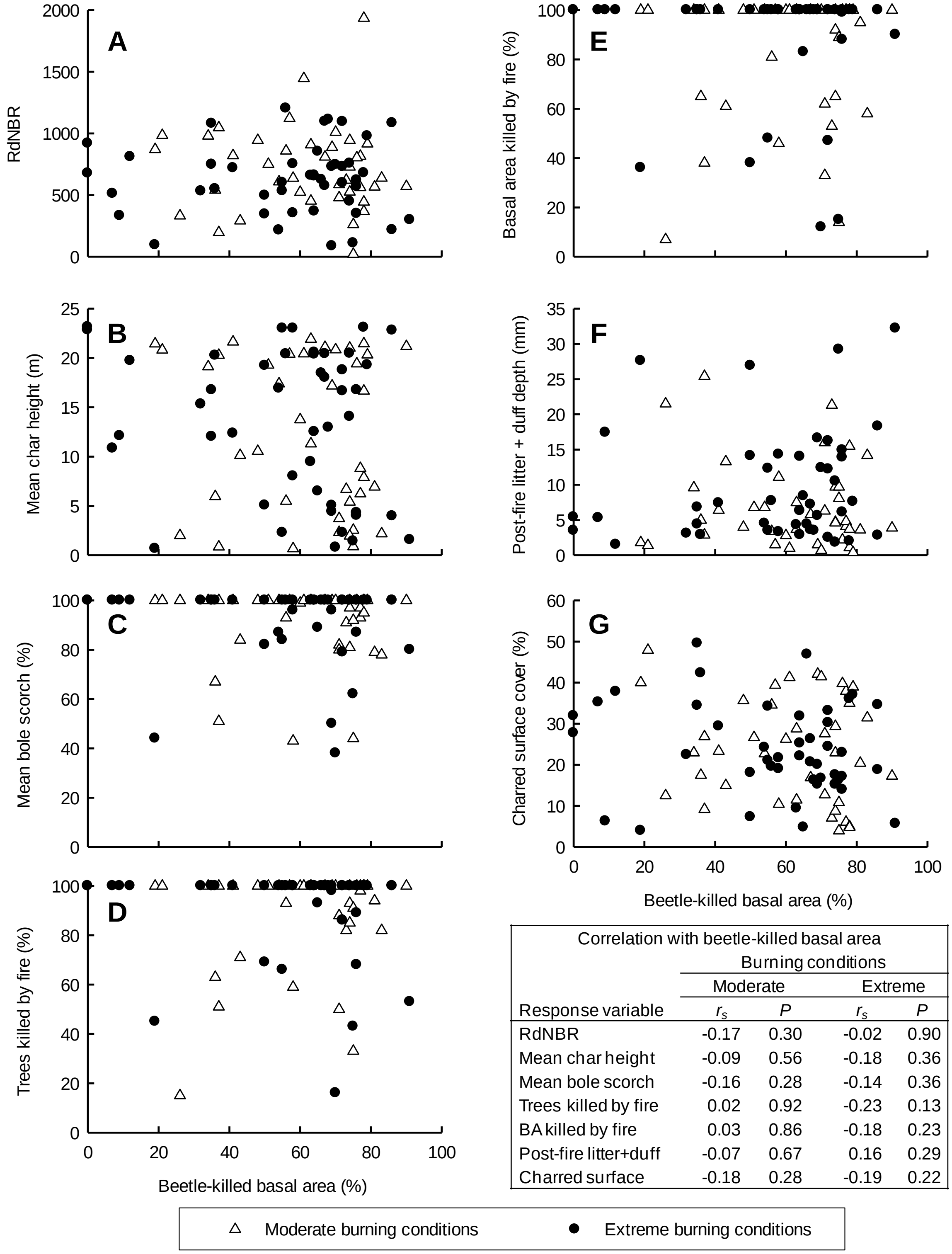

A
Live basal area ($m^2$ $ha^{-1}$)
0
10
20
30
40
50
B
Live stems $ha^{-1}$
0
200
400
600
800
1000
1200
C
QMD for live trees (cm)
0
5
10
15
20
25
30
D
Snags $ha^{-1}$
0
200
400
600
800
1000
1200
E
Downed logs $ha^{-1}$
0
10
20
30
40
50
60
no data
Pre beetle outbreak
Post beetle outbreak
Post beetle outbreak and fire

**Figure 1**



Correlation with beetle-killed basal area

| Response variable | Moderate $r_s$ | Moderate $P$ | Extreme $r_s$ | Extreme $P$ |
|---|---|---|---|---|
| RdNBR | -0.17 | 0.30 | -0.02 | 0.90 |
| Mean char height | -0.09 | 0.56 | -0.18 | 0.36 |
| Mean bole scorch | -0.16 | 0.28 | -0.14 | 0.36 |
| Trees killed by fire | 0.02 | 0.92 | -0.23 | 0.13 |
| BA killed by fire | 0.03 | 0.86 | -0.18 | 0.23 |
| Post-fire litter+duff | -0.07 | 0.67 | 0.16 | 0.29 |
| Charred surface | -0.18 | 0.28 | -0.19 | 0.22 |

**Figure 2**

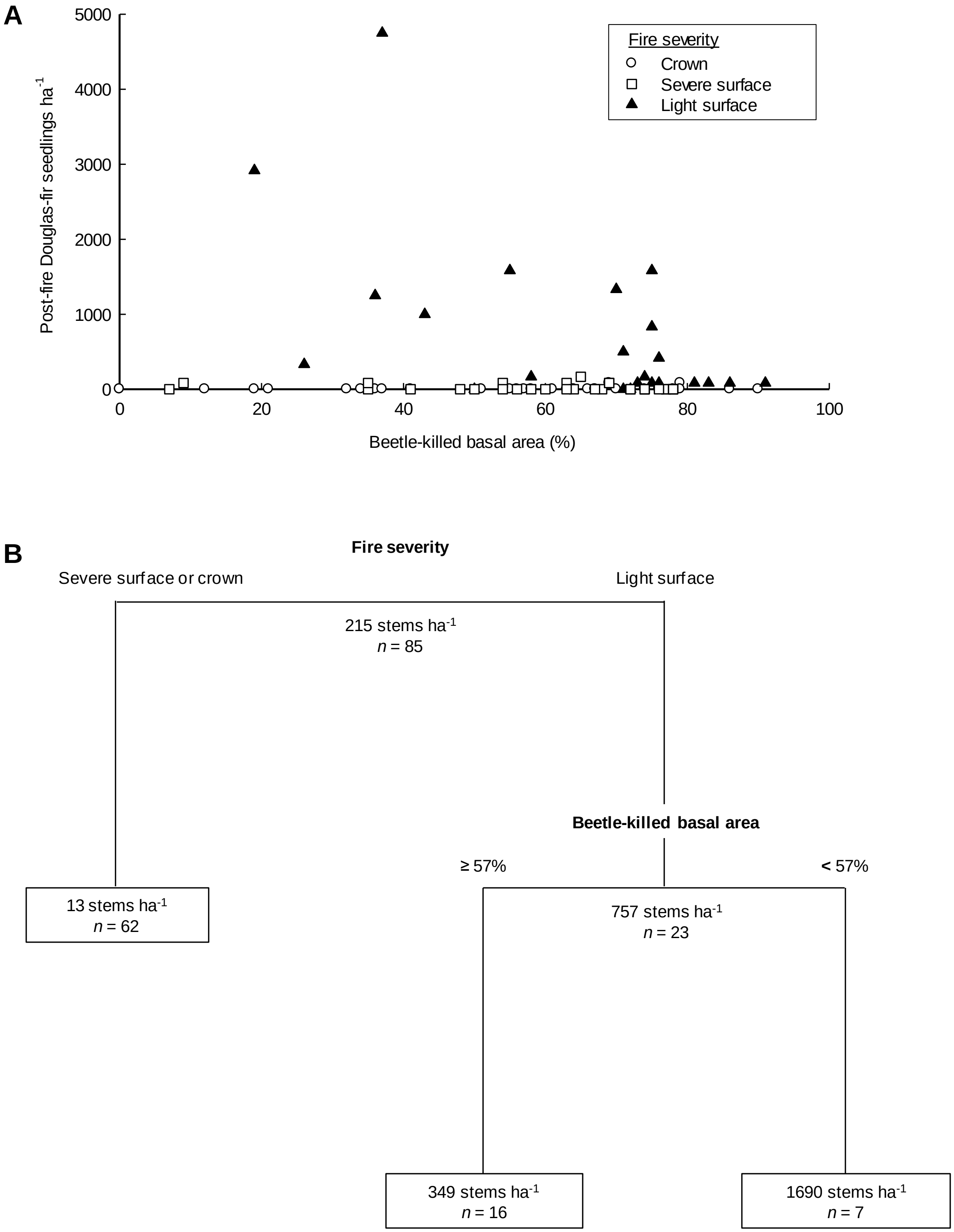

A
5000
4000
3000
2000
1000
0
Post-fire Douglas-fir seedlings ha$^{-1}$
0
20
40
60
80
100
Beetle-killed basal area (%)
Fire severity
○ Crown
□ Severe surface
▲ Light surface
B
Fire severity
Severe surface or crown
Light surface
215 stems ha$^{-1}$
$n$ = 85
13 stems ha$^{-1}$
$n$ = 62
Beetle-killed basal area
≥ 57%
< 57%
757 stems ha$^{-1}$
$n$ = 23
349 stems ha$^{-1}$
$n$ = 16
1690 stems ha$^{-1}$
$n$ = 7

Figure 3

**Appendix A**. Study area and recent Douglas-fir beetle outbreak history

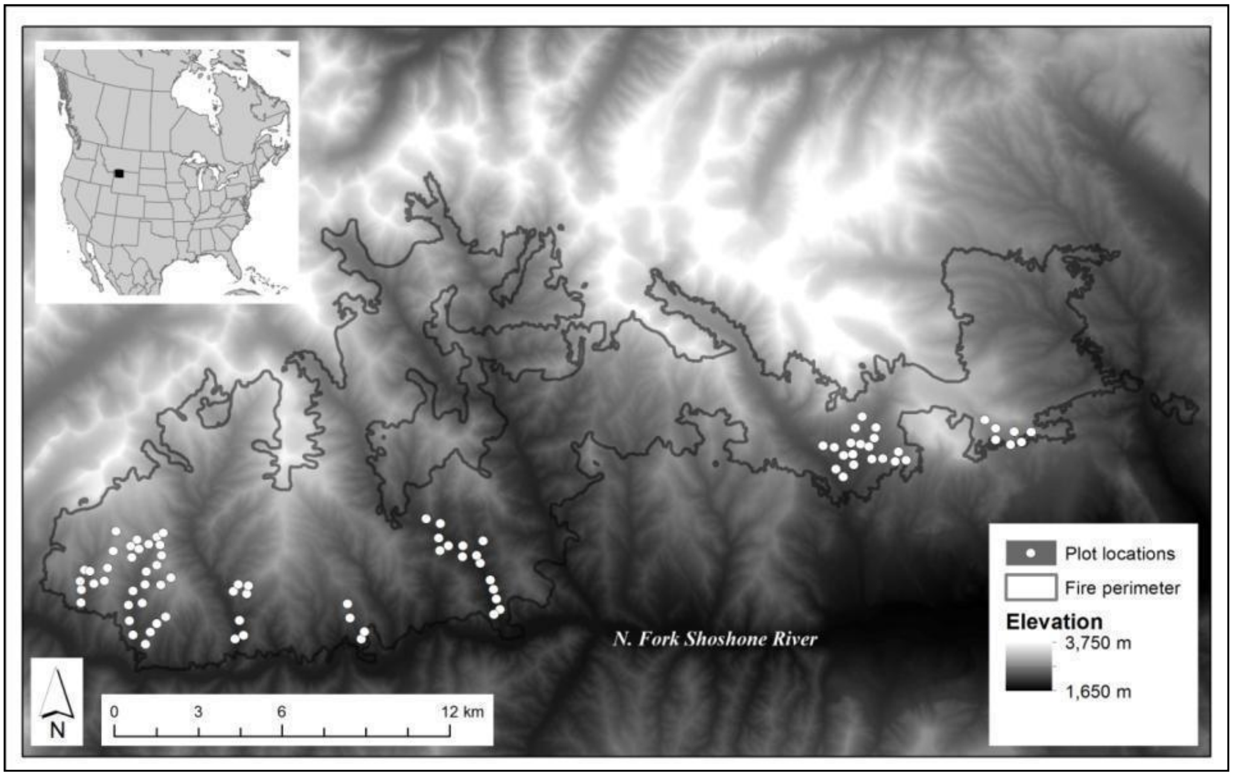


**Figure A1:** Map of the study area, plot locations, and regional context (inset). The Gunbarrel Fire burned on the Shoshone National Forest, Wyoming (USA) during summer 2008.

### *Recent Douglas-fir beetle outbreak history*

Douglas-fir mortality from the Douglas-fir beetle was first recorded from USDA aerial detection surveys (ADS) in and around the study stands in 1995. By the year 2000, 27% of the eventual beetle-caused tree mortality had occurred and at the peak of the outbreak (trees infested in 2001 and mapped as dead in 2002), 71% of the eventual beetle-caused tree mortality had occurred. As the outbreak subsided by 2005, 95% of the cumulative mortality had occurred, meaning 95% of beetle-killed trees were actively infested in 2004 or earlier (Figure A2). Trends were similar throughout the entire Gunbarrel Fire area. As trees killed by the Douglas-fir beetle can take up to one year for the canopy to change color (Belluschi and Johnson 1969), observed mortality (typically red-stage crowns visible from an aircraft) detected in ADS is likely from infestation the year before the mapping flight (Dodds et al. 2006, Meddens et al.2012). As the red stage typically lasts 2-3 years (Belluschi and Johnson 1969, Donato et al. 2013), only a very small percentage of trees (<< 5%; similar to background mortality levels in uninfested stands) would have been in the red stage at the time of the fire, and essentially all were in the gray stage. Pre-fire photos of the area within and surrounding the 2008 Gunbarrel Fire further illustrate the gray-stage condition of the forest prior to the fire (Figures A3-4).

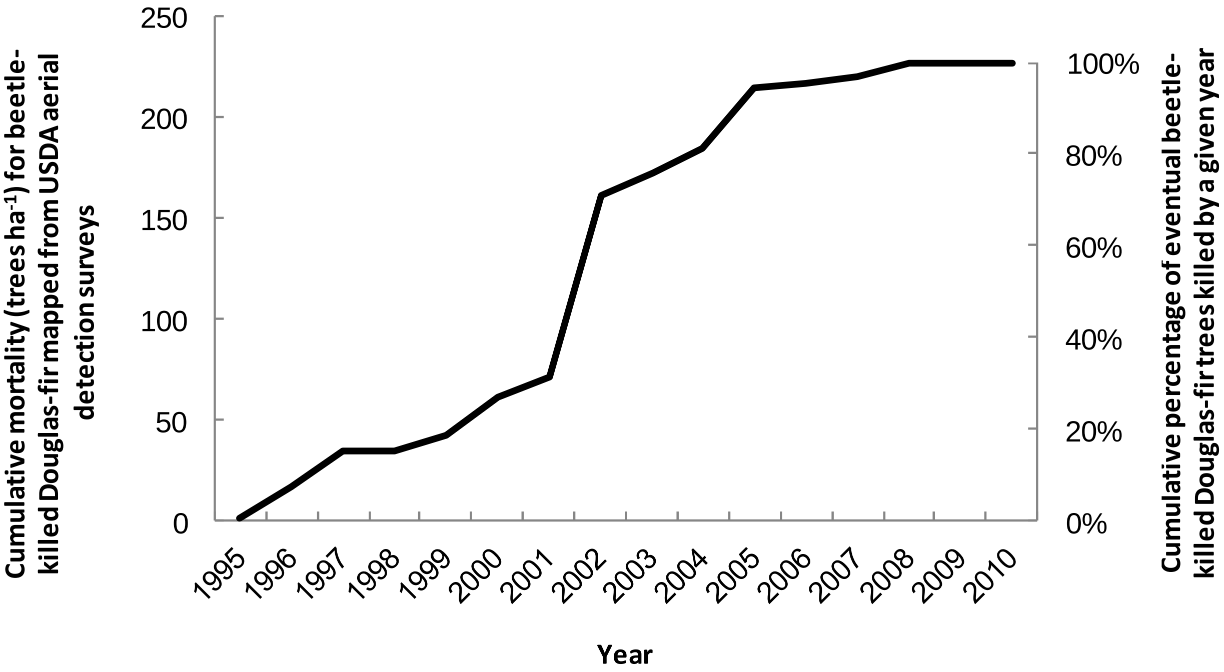


**Figure A2:** Cumulative yearly tree mortality attributed to the Douglas-fir beetle outbreak in the study stands, using USDA aerial detection survey data (http://www.fs.usda.gov) for each plot location. This illustrates that nearly all new mortality attributed to Douglas-fir beetle had ceased by 2005, three years prior to the Gunbarrel Fire. NOTE: Yearly cumulative mortality does not represent the percentage of all trees in a stand, but rather the cumulative percentage of the trees *eventually* killed by Douglas-fir beetles during the recent outbreak that were dead by a given year (i.e., 100% of the mortality caused by Douglas-fir beetle equated to a mean of 228 trees ha$^{-1}$, or 24% of all trees in study stands). Trends followed a similar temporal pattern for the entire Gunbarrel Fire area.

**Figure A3:** View of the Libby Creek drainage (the western-most drainage burned in the Gunbarrel Fire and sampled in this study) in 2007, one year before the 2008 Gunbarrel Fire. Trees in foreground are beetle-killed Douglas-fir trees in the gray stage; no current outbreak or red-stage trees are visible. Photo credit: Linda McCoy, former owner of Crossed Sabres Ranch, Cody, WY.

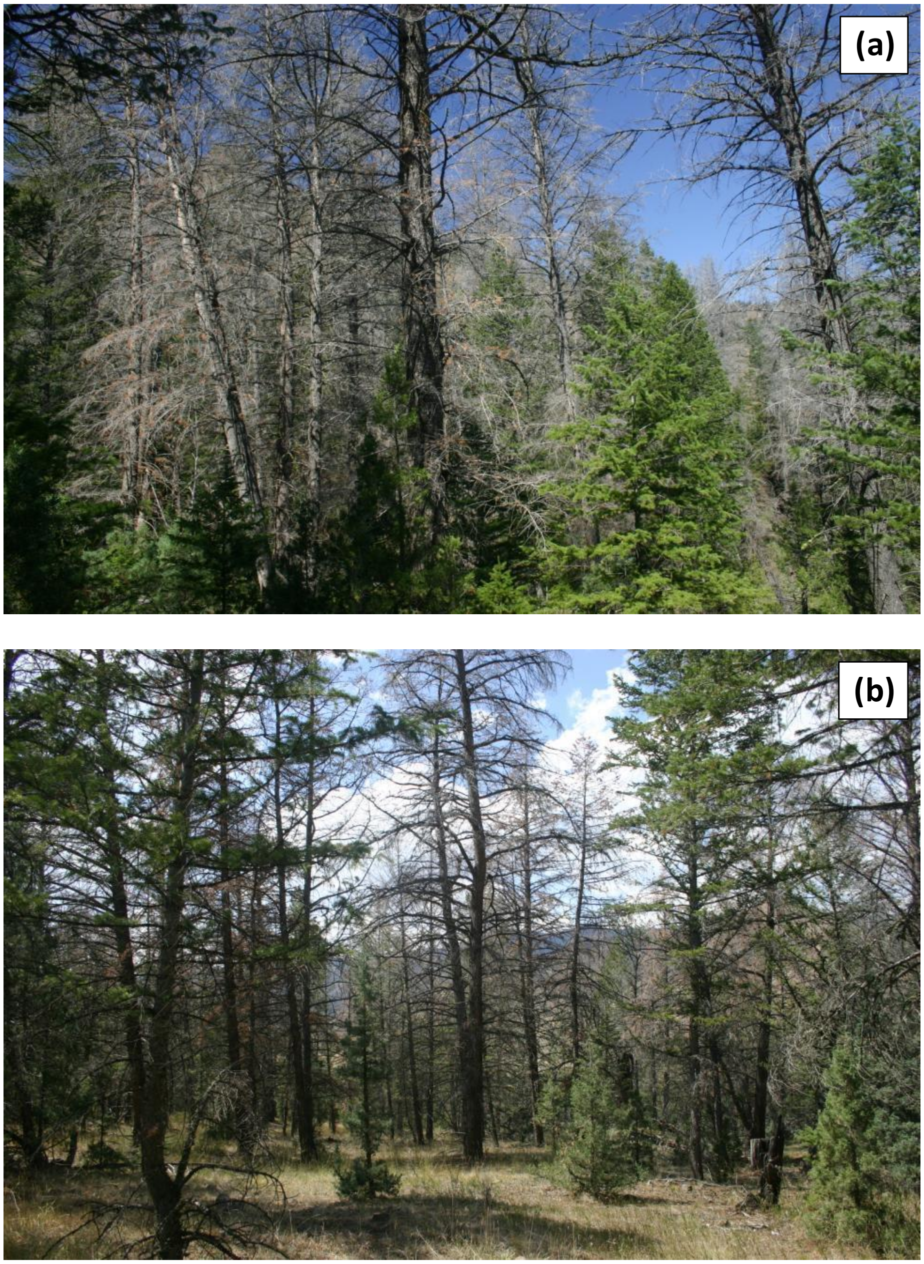


**Figure A4:** General stand-level outbreak conditions nearby the study area in 2006 (two years before the fire). Photos were taken from study plots measured for Douglas-fir outbreak severity in 2006, located 670 m (a) and 700 m (b) south of the eventual fire perimeter (Simard et al. 2012). Dead trees are beetle-killed Douglas-fir trees in the gray stage; no current outbreak or red-stage trees are visible. Photo credits: Martin Simard.

**References:**

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

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## **Appendix B.** Supplemental information on beetle outbreak severity measurements

### *Field measurements of beetle outbreak severity*

Pre-fire bark beetle outbreak severity was measured by assigning trees in each plot into four distinct categories: ‘live at the time of fire’, ‘killed by bark beetles prior to fire’, ‘pre-disturbance snag’, or ‘unknown’ (Table B1). Trees categorized as ‘live at the time of fire’ could be either dead or alive at the time of sampling. If dead, trees were categorized as ‘live at the time of fire’ if they had no evidence of pre-fire bark beetle activity (exit holes on outer bark, galleries under bark) and were not a highly decayed or well-weathered snag that indicated death prior to both disturbances (Figure B1). These individuals accounted for 70% of trees. The ‘live at the time of fire’ category also included live or dead trees that had obvious signs of post-fire beetle activity (boring dust [which would have been consumed by fire if beetle activity was pre-fire], resin bleeding) or had fully developed galleries but moist cambial tissue and/or any detectable level of needles in the canopy (Figure B1) – these individuals accounted for <1% of trees. For a tree to be categorized as ‘killed by bark beetles prior to fire’ it must have met all of the following criteria: dead at the time of sampling, presence of exit holes on the outer bark, dry cambial tissue, fully excavated (but vacated) adult and larval *Dendroctonus* galleries on the vascular cambium (> 50% of bole circumference or remaining visible cambium), and no needles in the canopy (Figure B2). These individuals accounted for 24% of trees. Dead trees with well-weathered sapwood and no evidence of pre-fire bark beetle activity were categorized as ‘pre-disturbance snags’, meaning they were most likely dead prior to the onset of the Douglas-fir beetle outbreak. These individuals accounted for 4% of trees. Severely burned dead trees with no visible cambium were categorized as ‘unknown,’ accounting for 1.5% of trees.

Douglas-fir beetles can sometimes attack fire-injured trees following light-surface fire (Parker et al. 2006), potentially leading to false-positive designation of trees as ‘killed by beetles prior to fire’ when in fact they were killed by beetles during or after fire. Several lines of evidence show this situation to be very unlikely given our sampling protocol. First, for potential beetle attack at the time of fire, a key factor is that Douglas-fir beetle tree infestation occurs in the late spring or early summer (Schmitz and Gibson 1996). Therefore active beetle infestation in 2008 would have occurred before the Gunbarrel Fire, meaning that some burned trees would exhibit partially completed galleries and beetles charred under the bark (as we have observed in a related beetle-fire study at another site; Harvey et al. unpublished data). We saw no evidence of such partial galleries on any tree. Second, regarding potential post-fire beetle attack, for trees to be successfully attacked by beetles following fire there must be a suitably high beetle population nearby the burned forest and the fire must occur close to the time of the next beetle flight (DeNitto et al. 2000). Because the beetle outbreak had subsided >3 years before the fire (Appendix A), the local beetle population would have been low. As the Gunbarrel Fire was in late July and August, it occurred after the 2008 beetle flight and ~ 9 months before the 2009 beetle flight. Combined, these circumstances make the possibility unlikely that there was substantial post-fire beetle attack in the year following the fire. Also, any such trees would likely still retain some needles in the canopy at the time of sampling. Needles from Douglas-fir trees begin to fall one year following attack from Douglas-fir beetle and continue to fall (and thus some are retained in the canopy) for 2 or more years following attack (Schmitz and Gibson 1996, Donato et al. 2013). Therefore, we conservatively categorized dead trees as ‘live at the time of fire’ if they exhibited beetle galleries but retained a detectable level of needles in the canopy at the time of sampling (accounting for < 1% of trees), as needles would be absent at the time of sampling if the tree were killed by bark beetles prior to fire, but present on the tree if it were killed by beetles at some point after the fire (Ken Gibson, pers. comm.).

*Supplemental validation and cross-check of field measures of beetle outbreak severity*

We performed a dendrochronological analysis to further test that trees classified as ‘killed by beetles prior to fire’ were indeed dead prior to fire and in the gray stage. Cross-sectional wedges were collected from a random sample of 10 dead trees field-classified as “beetle-killed prior to fire” (averaging 115 visible years per wedge cross-section; range 32-425) and a master chronosequence was built from cores collected from 27 live Douglas-fir trees (averaging 109 visible years per core; range 60-201). By manual cross-dating with skeleton plotting (Speer 2012), we used consistently reliable marker years with anomalously narrow growth rings (years with region-wide severe moisture deficit: 1988, 1994, 2000, and 2001, Westerling et al. 2011) to find the best cross-dated match between all trees (live and dead). Cross-dating the 10 trees field-classified as ‘killed by beetles prior to fire” with the live trees indicated that all died between 2002 and 2004. The most frequent year of death was 2002 (n=5), followed by 2003 (n = 4) and 2004 (n = 1). This matches the temporal trend in the aerial detection surveys (ADS), which show the peak of tree mortality in 2002 (Appendix A) and confirms the accuracy of our field measures of outbreak severity.

Finally, to cross-check the sensitivity of our analysis, results, and conclusions to any potential error in field classification of beetle-killed trees, we repeated all statistical analyses using measures of beetle outbreak severity from pre-fire ADS data, providing a second (albeit less quantitative and precise) measure of outbreak severity recorded independently from our field measures. ADS data can underestimate the magnitude of outbreak severity (Meddens et al. 2012) and are known to contain spatial error (Johnson and Ross 2008), two important reasons why they are not relied on as a primary source of information for fine-scale beetle outbreak severity. However, for purposes of our sensitivity analysis, we assume these errors to contain no bias that would make relative comparisons across space (e.g., plot to plot) problematic for a valid cross-check of our findings based on field data. In our sensitivity analysis, we substituted the cumulative number of trees per hectare that were beetle-killed between 1994 and 2008 on the ADS maps for our field measure, and then repeated all correlation and regression analyses with each fire-severity response variable. There was no qualitative difference between these results and our original analysis (i.e., all effects remained the same; there was no beetle effect on fire severity before or after accounting for burning conditions and slope position). This cross-check using ADS data as substitute of our field measures of beetle outbreak severity corroborates our findings and conclusions from our main analysis using our detailed quantitative field data.

**Table B1:** Evidence and criteria used to classify each tree in a plot into one of four categories: 'live at the time of fire', 'killed by bark beetles prior to fire', 'pre-disturbance snag', or 'unknown.'

| Field classification | Likely time of death | Likely cause of death | Evidence | Percent of all trees sampled |
|---|---|---|---|---|
| 'Pre-disturbance snag' | Prior to both disturbances | Unknown | dead at time of sampling<br>highly weathered/decayed sapwood<br>most branches and bark missing<br>no evidence of bark beetle activity (pre- or post-fire) | 4% |
| 'Killed by bark beetles prior to fire' | Pre-fire | Bark beetle attack | dead at time of sampling<br>*Dendroctonus* exit holes on the outer bark<br>dry cambial tissue<br>fully excavated (but vacated) adult and larval *Dendroctonus* galleries on the vascular cambium (> 50% of bole circumference or remaining visible cambium)<br>no needles in the canopy<br>Relevant references: Schmitz and Gibson 1996; Donato et al. 2013; Ken Gibson, pers. comm. | 24% |
| 'Live at time of fire' | Gunbarrel Fire | Fire | dead at time of sampling<br>charred bark, branches, or outer sapwood<br>no evidence of bark beetle activity (no exit holes on outer bark, no galleries under bark)<br>not a highly-decayed or well-weathered snag | 63% |
| 'Live at time of fire' | Beetle attack at time of fire | Fire | dead at time of sampling<br>partially completed galleries with adult beetles charred under the bark<br>Relevant references: Schmitz | 0% |

| | | | | |
|---|---|---|---|---|
| | | | and Gibson 1996; Harvey et al. unpublished data | |
| 'Live at time of fire' | Beetle attack post-fire | Bark beetle attack | alive or dead at the time of sampling<br>clear signs of post-fire beetle activity (boring dust [which would have been consumed by fire], resin bleeding) or fully developed galleries but moist cambial tissue and/or any detectable level of needles in the canopy (which would still be present given needle-drop period of 2-3 yrs)<br>Relevant references: DeNitto et al. 2000; Schmitz and Gibson 1996; Donato et al. 2013; Ken Gibson, pers. comm. | <1% |
| 'Live at time of fire' | Currently live | n/a | alive at the time of sampling<br>green foliage, no sign of *Dendroctonus* beetle activity | 7.0% |
| 'Unknown' | unknown | unknown | none available - excessive charring, etc. | 1.5% |

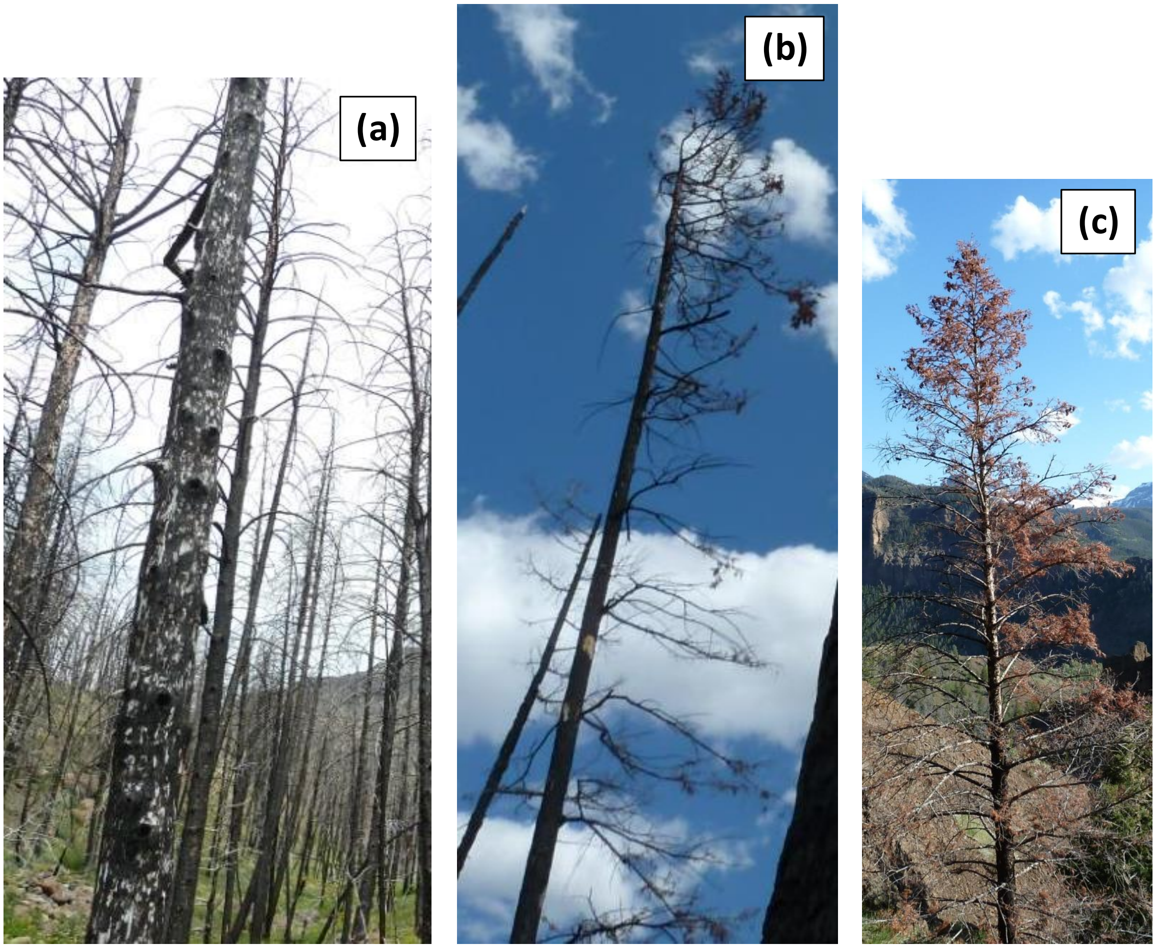

**Figure B1:** Photographs of general bole condition (a) and crown condition (b and c) of example trees that were dead at the time of sampling and classified as ‘live at the time of fire.’ Photo credits: B.J. Harvey.

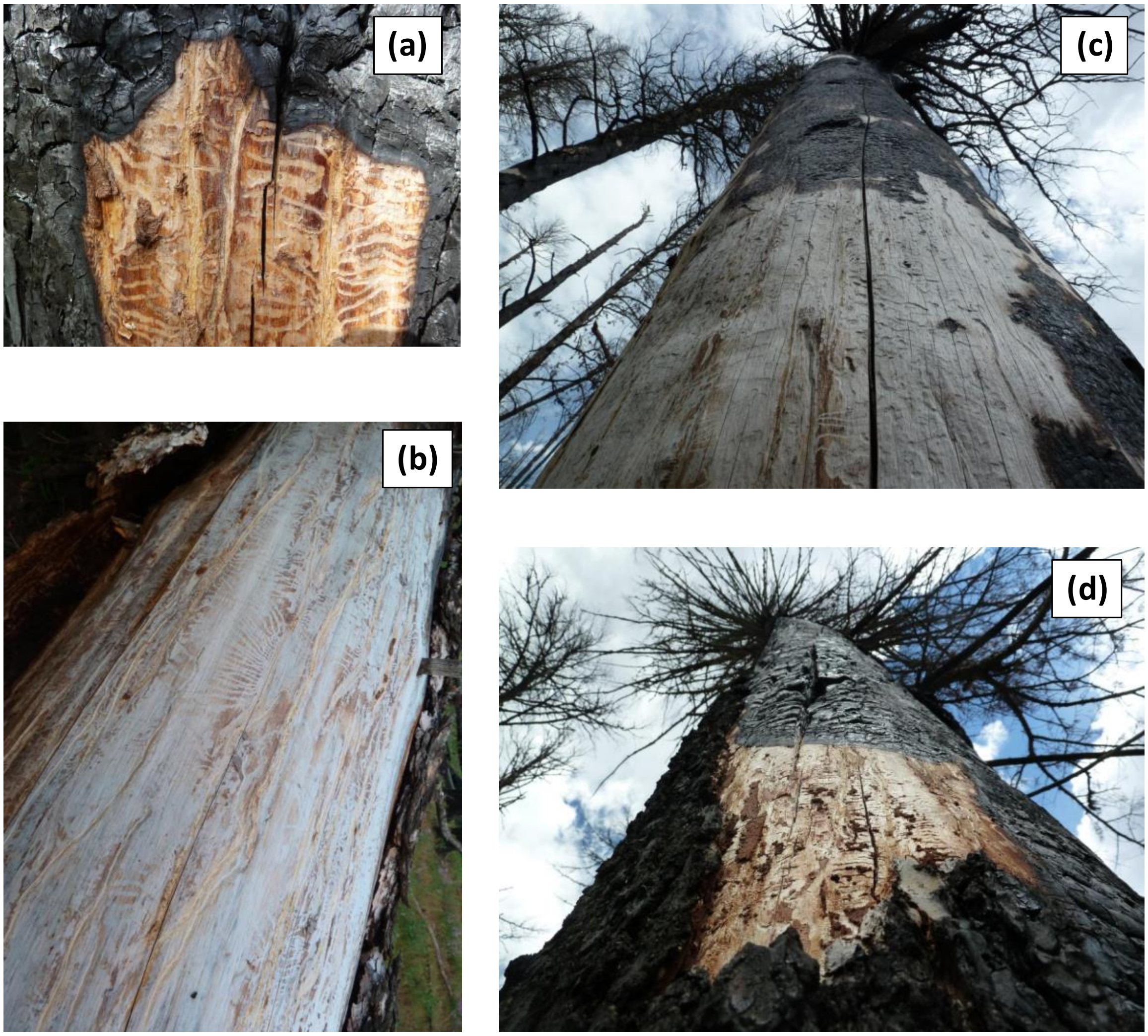

**Figure B2:** Photographs of general bole condition (a and b), and bole and crown condition (c-d) of example trees that were classified as ‘killed by bark beetles prior to fire.’ Photo credits: B.J. Harvey.

**References:**

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

## **Appendix C.** Supplemental information on fire severity measurements

### *Surrogate measurements of fire severity*

We also quantified fire severity for each plot from a satellite-derived index of fire severity - the Relative differenced Normalized Burn Ratio (RdNBR) downloaded from the Monitoring Trends in Burn Severity website (www.mtbs.gov). This commonly used, surrogate metric provides a reliable measure of fire severity by generating an index of change from pre- to post-fire based on reflectance in Landsat TM bands 4 and 7, which represent chlorophyll content and moisture in vegetation/soils, respectively (Miller and Thode 2007). Lower RdNBR values represent less pre- to post-fire change in live green vegetation, moisture content, and soil conditions (i.e., less-severe fire), whereas higher RdNBR values represent more change (i.e., more-severe fire). A single RdNBR value was extracted for each plot in ArcGIS 10.1 based on the pixel encompassing the plot center.

We attempted to reduce the potential redundancy of many response variables through a factor analysis; however this procedure did not produce interpretable synthetic variables. While RdNBR is, in a sense, a synthetic variable that should broadly represent important metrics of fire severity (Miller et al. 2009), we found modest Spearman rank correlations between RdNBR and other metrics of fire severity (Table C1). Therefore, we present analyses for RdNBR and field fire severity metrics.

**Table C1**: Spearman rank correlations ($r_s$) between fire severity response variables used to test for effects of beetle-killed basal area on fire severity. All correlations are significant ($P < 0.001$).

| | RdNBR | Litter + duff depth (mm) | Charred surface cover (%) | Mean char height (m) | Mean bole scorch (%) | Basal area killed by fire (%) | Trees killed by fire (%) |
|---|---|---|---|---|---|---|---|
| RdNBR | 1.00 | -0.57 | 0.58 | 0.49 | 0.46 | 0.47 | 0.41 |
| Litter + duff depth (mm) | | 1.00 | -0.62 | -0.64 | -0.52 | -0.59 | -0.57 |
| Charred surface cover (%) | | | 1.00 | 0.45 | 0.44 | 0.45 | 0.44 |
| Mean char height (m) | | | | 1.00 | 0.77 | 0.79 | 0.76 |
| Mean bole scorch (%) | | | | | 1.00 | 0.83 | 0.80 |
| Basal area killed by fire (%) | | | | | | 1.00 | 0.97 |
| Trees killed by fire (%) | | | | | | | 1.00 |

### *Quantitative field measurements of fire severity across fire severity classes*

Soil charring (if present) was measured to the nearest mm at every 3 m along the main axis of the plot (20 points per plot), but was excluded from analysis due to the potential confounding effects of erosion/deposition that may have occurred between the time of fire and sampling. We recorded whether there was deep charring (charring into the sapwood) on the bole of the tree using the following four categories: no deep char (0), deep char on < 50% of the bole circumference (1), deep char on > 50% of the bole circumference but only on the lower portion of the bole (not into the crown) (2), and deep char on > 50% of the bole circumference and into the crown (3). Charring scores were averaged across all trees in a plot. Fire-severity classes were defined following (Turner et al. 1999): ‘light surface fire’ – fire is not stand-replacing with some surviving canopy trees; ‘severe surface fire’ – fire is stand-replacing (100% overstory mortality) but canopy-tree needles are not consumed in fire; ‘crown fire’ – fire is stand-replacing, canopy-tree needles are consumed by fire, mineral soil is exposed, and char heights reach top of tree boles. Fire severity classes were statistically distinct for quantitative measures of fire effects (Table C2).

**Table C2:** Differences in quantitative fire severity metrics across fire-severity classes. Values are means (SE). Significant differences among classes for each variable (Tukey's HSD test, $P < 0.05$) are denoted using subscript letters ($^{a,b,c}$).

| | Fire-severity class | | | | | |
|---|---|---|---|---|---|---|
| Fire severity metric | Light surface<br>$n = 23$ | | Severe surface<br>$n = 31$ | | Crown<br>$n = 31$ | |
| Mean char height (m) | $3.3^a$ | (0.5) | $12.4^b$ | (0.9) | $20.6^c$ | (0.3) |
| Mean deep char level (trees) (0-3) | $0.15^a$ | (0.03) | $0.47^b$ | (0.06) | $0.81^c$ | (0.09) |
| Litter + duff depth (mm) | $15.8^a$ | (1.7) | $7.3^b$ | (0.9) | $3.8^c$ | (0.4) |
| Charred surface cover (%) | $16^a$ | (2) | $22^b$ | (2) | $31^c$ | (2) |

## References:

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# **Appendix D.** Burning conditions as a proxy for weather at time of burning

The Gunbarrel Fire spanned 40 km (E-W) by 20 km (N-S) in steep mountainous terrain, making weather measurements from the nearest remote automated weather station (RAWS) impractical for estimating local plot-scale weather. Therefore, we divided the fire into two burn periods following established protocols (Thompson and Spies 2009), using a daily fire progression map provided by the Shoshone National Forest District and regional weather from the Eagle, WY RAWS (3-37 km west of study stands). Modest fire growth (accounting for 34% of the total area burned) occurred during the periods Jul. 27-28, Aug. 5-19, and Aug. 22-30. Plots in drainages that burned mainly during these days ($n = 40$) were assigned “moderate burning conditions,” as this period was characterized by relatively low temperatures and winds, and high humidity (Table D1). Rapid fire growth (accounting for 66% of the total area burned) occurred during the periods Jul. 29 – Aug. 4 and Aug. 20-21. Plots in drainages that burned mainly on these days ($n = 45$) were assigned “extreme burning conditions,” as this period was characterized by relatively high temperatures and winds, and low humidity (Table D1).

## References:

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

**Table D1:** Regional weather information for the moderate and extreme burning condition periods in the Gunbarrel Fire. Weather data were downloaded from the Eagle, WY remote automated weather station (RAWS), located 3-37 km west of plot locations (www.raws.dri.edu).

| Burning Conditions | days | Hectares | % of fire | Temp. (ºC) | Rel. Hum. (%) | Wind speed (m/s) |
|---|---|---|---|---|---|---|
| Moderate | 26 | 8,553 | 34 | 22.0 | 22.6 | 4.2 |
| Extreme | 9 | 16,308 | 66 | 23.7 | 17.7 | 5.9 |

## **Appendix E.** Variability in stand structure impacts from bark beetle outbreak

Pre -disturbance stand structure was re-constructed using criteria in Table B1. Downed logs prior to beetle outbreak were not quantified because of decay over > 10 years before sampling and possible combustion of some downed logs in the fire. Conceivably, loss to decay and combustion could also be important for estimating post-outbreak, pre-fire downed log abundance; however such loss was likely not significant. Gray-stage post-outbreak stands contain very few fallen beetle-killed trees that would have been downed logs prior to fire (Donato et al. 2013). Second, even when the beetle-killed Douglas-fir trees fall, they most often fall in pieces, with the lower ~2-3 m of the bole remaining standing (Donato et al. 2013). In the few cases where plots contained beetle-killed trees that had broken and fallen, the lower (standing) portion of the bole was recorded and measured at breast height. There was also a lack of field evidence of “ghost logs” (i.e. logs entirely consumed in the fire and leaving a scar on the ground). In sum, this suggests that our methods accurately captured any beetle-killed trees that were down at the time of fire.

### **References:**

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

**Table E1: S**tand structure characteristics in all plots (*n* =85) across different levels of bark beetle outbreak severity. Values are means (SE). The bark beetle outbreak occurred from 1994 to 2005 and peaked in 2001-2002; the post-outbreak fire occurred in 2008; stands were sampled in 2011 – 3 years post-fire. PSME = Douglas-fir.

| | | Beetle outbreak severity class | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Stand structure variable | Disturbance condition | Background (0-10% trees) *n* = 17 | | Low (11-20% trees) *n* = 16 | | Moderate (21-40% trees) *n* = 33 | | High (40-70% trees) *n* = 19 | |
| Beetle-killed basal area (%) | Post-outbreak | 26 | (4) | 57 | (4) | 66 | (2) | 77 | (2) |
| Live basal area (m$^2$ ha$^{-1}$) | Pre-outbreak | 32.2 | (3.2) | 37.0 | (2.8) | 44.1 | (2.3) | 48.9 | (3.0) |
| | Post-outbreak | 22.9 | (2.6) | 14.8 | (1.5) | 13.5 | (1.3) | 9.4 | (1.0) |
| | Post-outbreak and fire | 2.6 | (1.8) | 1.6 | (0.9) | 2.3 | (1.0) | 1.6 | (0.7) |
| Live basal area (% PSME) | Pre-outbreak | 78% | (4%) | 85% | (3%) | 89% | (2%) | 97% | (1%) |
| | Post-outbreak | 70% | (6%) | 68% | (7%) | 73% | (4%) | 85% | (5%) |
| | Post-outbreak and fire | 61% | (22%) | 96% | (4%) | 88% | (8%) | 96% | (3%) |
| Live tree density (stems | Pre-outbreak | 1197 | (88) | 930 | (60) | 954 | (48) | 732 | (58) |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| ha$^{-1}$) | Post-outbreak | 1134 | (87) | 760 | (51) | 653 | (39) | 319 | (33) |
| | Post-outbreak and fire | 104 | (56) | 73 | (35) | 59 | (23) | 38 | (16) |
| Live tree density (% PSME) | Pre-outbreak | 58% | (7%) | 61% | (6%) | 70% | (4%) | 93% | (2%) |
| | Post-outbreak | 55% | (8%) | 54% | (8%) | 61% | (5%) | 86% | (5%) |
| | Post-outbreak and fire | 55% | (21%) | 87% | (10%) | 80% | (8%) | 95% | (3%) |
| Live QMD (cm) | Pre-outbreak | 18.8 | (1.2) | 22.6 | (0.8) | 24.4 | (0.6) | 30.0 | (1.4) |
| | Post-outbreak | 16.2 | (1.2) | 15.8 | (0.8) | 16.1 | (0.6) | 19.8 | (1.0) |
| | Post-outbreak and fire | 12.9 | (5.0) | 16.5 | (5.6) | 20.4 | (2.2) | 23.1 | (3.3) |
| Snag density (snags ha$^{-1}$) | Pre-outbreak | 27 | (11) | 13 | (5) | 61 | (25) | 43 | (12) |
| | Post-outbreak | 92 | (13) | 184 | (21) | 362 | (36) | 456 | (40) |
| | Post-outbreak and fire | 1096 | (110) | 840 | (64) | 905 | (55) | 677 | (68) |
| Downed logs (logs ha$^{-1}$) | Pre-outbreak | n.d. | (n.d.) | n.d. | (n.d.) | n.d. | (n.d.) | n.d. | (n.d.) |
| | Post-outbreak | 11 | (3) | 19 | (10) | 23 | (5) | 46 | (13) |
| | Post- | 25 | (6) | 31 | (14) | 51 | (7) | 60 | (14) |

outbreak
and fire

**Appendix F.** Effects of slope position on fire severity during different burning conditions

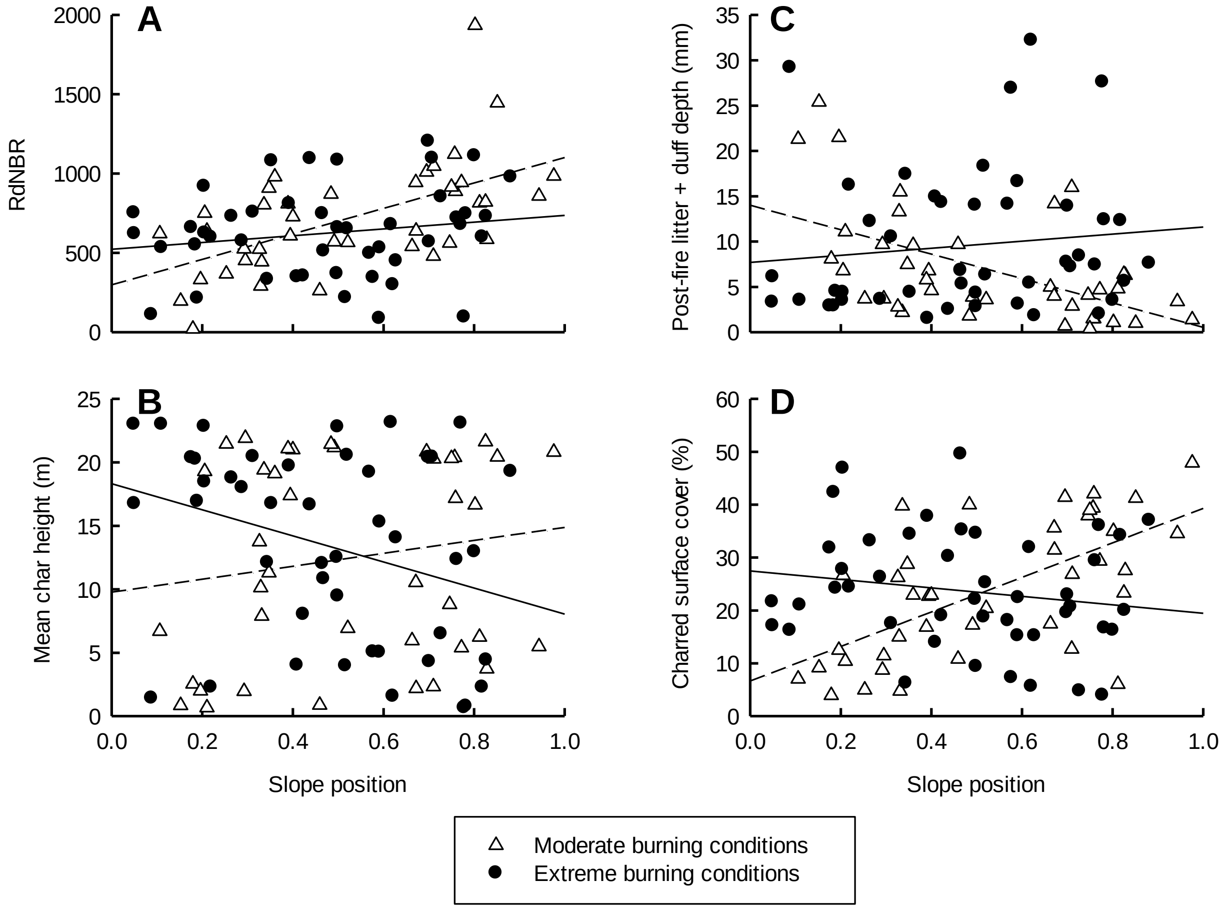

**Figure F1.** Metrics of fire severity vs. slope position for response variables that met parametric test assumptions and were included in multiple linear regression models (Table 1). Regression slopes for fire severity vs. slope position are denoted with dashed lines (moderate burning conditions) and solid lines (extreme burning conditions) to illustrate interaction effects of burning conditions and topography.

## **Appendix G.** Generalized linear model for post-fire Douglas-fir seedling density

**Table G1.** Results of generalized linear model regressing post-fire Douglas-fir seedling density against pre-fire beetle-killed basal area in light-surface fire plots using a negative binomial error structure with a log-link. Plots that burned as severe-surface or crown fire were excluded from this analysis because post-fire seedling density was very low with little variation in these categories (mean 13 stems $ha^{-1}$, median 0 stems $ha^{-1}$) and unrelated to pre-fire beetle outbreak severity ($P > 0.10$; Fig. 4A).

| Response | Predictor | $\beta$ | SE | $z$ | $P$ |
|---|---|---|---|---|---|
| **Post-fire Douglas-fir seedling density (stems ha$^{-1}$)** | (Intercept) | 9.05 | 1.08 | 8.42 | <0.01 |
| | Beetle-killed basal area | -4.31 | 1.61 | -2.68 | <0.01 |

# Chapter 3 - Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies

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Abstract:

Widespread tree mortality caused by outbreaks of native bark beetles (Circulionidae: Scolytinae) over the past decade has raised concern among scientists and forest managers about whether beetle outbreaks fuel more ecologically severe forest fires and impair postfire resilience. To investigate this question, we collected extensive field data following multiple fires that burned subalpine forests in 2011 throughout the Northern Rocky Mountains (USA) across a spectrum of prefire beetle outbreak severity, primarily from mountain pine beetle (*Dendroctonus ponderosae*). We found that recent (2001 to 2010) beetle outbreak severity was unrelated to most field measures of subsequent fire severity, which was instead driven primarily by extreme burning conditions (weather) and topography. In the red stage (0-2 years following beetle outbreak), fire severity was largely unaffected by prefire outbreak severity with few effects detected only under extreme burning conditions. In the gray stage (3-10 years following beetle outbreak), fire severity was largely unaffected by prefire outbreak severity under moderate conditions, but several measures related to surface fire severity increased with outbreak severity under extreme conditions. Initial postfire tree regeneration of the primary beetle host tree [lodgepole pine (*Pinus contorta* var. *latifolia*)] was not directly affected by prefire outbreak severity, but was instead driven by the presence of a canopy seedbank and by fire severity. Recent beetle outbreaks in subalpine forests affected few measures of wildfire severity, and did not hinder the ability of lodgepole pine forests to regenerate after fire, suggesting that resilience in subalpine forests is not necessarily impaired by recent mountain pine beetle outbreaks.

Keywords: disturbance interactions | forest resilience | fire ecology | serotiny | conifer forest

Significance Statement:

Understanding how multiple disturbances may interact to affect ecosystems is important for ecosystem management as climate-driven disturbance activity increases. Recent severe bark beetle (Circulionidae: Scolytinae) outbreaks have led to widespread concern about the potential for increased wildfire severity and decreased postfire forest resilience throughout the northern hemisphere. Using extensive field data collected in multiple recent (occurring in 2011) wildfires throughout the Northern Rocky Mountains (United States), we found that recent (2001 to 2010) prefire mountain pine beetle *(Dendroctonus ponderosae*) outbreak severity affected few measures of wildfire severity and was not directly related to postfire tree seedling establishment, suggesting that subalpine forests dominated by serotinous lodgepole pine (*Pinus contorta* var. *latifolia*) may be resilient to these two combined disturbances.

Natural disturbances (e.g., wildfires, floods, storms, insect outbreaks) play a central role in structuring ecosystems worldwide (Pickett and White 1985, Attiwill 1994), but multiple disturbances can potentially interact in synergistic (i.e., compound) ways that alter ecosystem resilience (the capacity to tolerate disturbance without shifting to a different state (Paine et al. 1998, Walker et al. 2004)). Understanding these potential interactions and their consequences is critical for conserving and managing ecosystems in a period of increasing climate-driven disturbance activity (Turner 2010, Fleishman et al. 2011). Widespread outbreaks of native bark beetles (Circulionidae: Scolytinae) during the past decade have caused extensive tree mortality over tens of millions of hectares of conifer forests in North America (Raffa et al. 2008, Bentz et al. 2010) and Eurasia (Schelhaas et al. 2003, Wermelinger 2004). Forest fire activity (occurrence, area burned) has also increased in these regions during this time (Flannigan et al. 2009), and concern has grown about whether the recent pulse of beetle-killed trees will increase the ecological severity of subsequent wildfires and/or decrease postfire forest resilience (Hicke et al. 2012, Association for Fire Ecology 2013).

Most tree mortality in the recent North American beetle outbreaks is attributable to mountain pine beetles (*Dendroctonus ponderosae*, MPB), primarily attacking lodgepole pine (*Pinus contorta* var. *latifolia*) (Raffa et al. 2008). Severe MPB outbreaks can result in up to 90% mortality of tree basal area (Page and Jenkins 2007a, Klutsch et al. 2011, Simard et al. 2011, Diskin et al. 2011, Schoennagel et al. 2012), which could compromise postfire resilience by increasing the severity of subsequent wildfires, decreasing seed sources (thus diminishing postfire tree regeneration), or both.

Tree mortality caused by MPB outbreaks alters the fuel structure of forests (i.e., the quantity, quality, and distribution of biomass (Page and Jenkins 2007a, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012)) in ways that could affect fire severity (defined as the degree of short-term ecological change caused by a fire, typically measured by the proportion of biomass lost, or vegetation killed by fire (Keeley 2009)). Increases in dead and flammable fuels in post-outbreak forests can influence fire behavior (e.g., energy release and spread rate, see (Hicke et al. 2012) for a recent review) and present operational challenges for wildland firefighting (Jenkins et al. 2012, Page et al. 2014). However, less is known about whether wildfires that burn post-outbreak forests are more ecologically severe and have important consequences for ecosystem function compared to forests unaffected by recent outbreaks, despite heightened concern among scientists and forest managers (Hicke et al. 2012, Association for Fire Ecology 2013).

In contrast to studies of fire behavior, studies of fire severity use retrospective (i.e., postfire) data, as ecological effects of fire (e.g., vegetation mortality, biomass loss) manifest after the fire has ended (Keeley 2009). Studies that have evaluated effects of MPB outbreaks on fire severity have typically compared the presence (or absence) of either disturbance or used remotely sensed indices of disturbance severity (Lynch et al. 2006, Kulakowski and Jarvis 2011, Prichard and Kennedy 2014). Most studies have not assessed wildfire severity across the spectrum of beetle outbreak severity (amount of basal area or trees killed by beetles), limiting the ability to detect complex disturbance interactions. Other studies (Lynch et al. 2006, Prichard and Kennedy 2014) have lacked controls (i.e., stands of similar structure that were unaffected by recent prefire outbreaks and burned under similar conditions), making it difficult to separate effects of beetle outbreaks from other factors that affect fire severity, such as topography, weather, fuels, and prefire vegetation adaptations to fire (Keeley 2009). Recent case studies near Yellowstone National Park (USA) have begun to assess single fires using detailed field data on outbreak and fire severity (Harvey et al. in press), but consistent trends across many fire events remain untested.

By killing large mature trees in a forest stand, MPB outbreaks may also limit the availability of key seed sources that would otherwise contribute to postfire tree establishment, therefore reducing forest resilience. For example, lodgepole pine is adapted to high-severity wildfires by storing seeds in serotinous (i.e., closed) cones until heat from fire opens the cones, leading to abundant postfire tree regeneration soon after fires (Veblen 1986, Turner et al. 1997, Kipfmueller and Kupfer 2005). If forests do not regenerate naturally following wildfire in areas where prefire trees are killed by MPB outbreaks, postfire planting or seeding may be needed to recover carbon stocks and prevent transitions to non-forest (Association for Fire Ecology 2013). Regional-scale field measures of prefire outbreak severity, wildfire severity, and postfire response are needed in wildfires that occurred in recent beetle-affected forests to resolve key uncertainties and contribute to more general understanding of disturbance interactions (Hicke et al. 2012).

In this study, we used field data to ask whether recent bark-beetle outbreaks affected wildfire severity (canopy, forest floor, and tree mortality) (*Methods* and *SI Text*) or initial postfire tree regeneration in six wildfires that burned a total of > 30,000 ha during summer 2011 in the Northern Rocky Mountains (United States) (Fig. S1 and Table S1). The study fires included variation in prefire beetle-outbreak severity (0 to 84% of tree basal area killed by bark beetles, primarily MPB-attacked lodgepole pine and to a lesser degree whitebark pine (*Pinus albicaulis*), Tables S2 and S3), typical of the range observed in many North American forests (Raffa et al. 2008). Such variation allowed us to assess fire severity across the spectrum of recent prefire outbreak severity, including stands unaffected by the recent outbreaks (effectively serving as a control). Three fires burned forests where most attacked stands were in the red post-outbreak stage (0-2 years after beetle attack, ~ 50% retention of largely red needles on beetle-killed trees (Simard et al. 2011, Schoennagel et al. 2012, Hicke et al. 2012)), considered to be most vulnerable to increased crown fire because canopy fuels are drier and more flammable (Jolly et al. 2012, Page et al. 2014). Three fires burned forests where most attacked stands were in the gray post-outbreak stage (3-10 years after beetle attack, < 5% needle retention on beetle-killed trees, most beetle-killed trees still standing (Simard et al. 2011, Schoennagel et al. 2012, Hicke et al. 2012)). Gray-stage forests are considered less vulnerable to increased crown fire because canopy fuels are substantially reduced (Page and Jenkins 2007b, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012), although increased surface fuels from needle- and branch-fall could increase surface-fire severity (Page and Jenkins 2007a, Klutsch et al. 2011, Schoennagel et al. 2012). Portions of fires burned during moderate (low temperature and wind, high relative humidity) or extreme (high temperature and wind, low relative humidity) weather conditions, and across a range of slope positions, allowing us to test for effects of MPB outbreaks while accounting for other factors known to affect fire severity (Table S4, and *SI Text*).

Using established protocols (Tables S3-S7 and *SI Text*) (Harvey et al. in press, 2013), we sampled burned areas in 2012 (1 y after fire). We reconstructed prefire forest structure and outbreak severity, and measured fire severity in 0.07-ha plots (*n* = 105). In plots (*n* = 70) of stand-replacing fire (i.e., all live prefire trees were killed by fire), we also measured postfire tree seedling establishment. To test whether prefire beetle outbreaks affected fire severity, we regressed eight field measures of fire severity [char height, bole scorch, fine fuels (needles and small branches) remaining in the canopy for trees that were alive at the time of fire, percentage of tree basal area with deep charring into the crown and < 5% of branches remaining, tree mortality (basal area and number of trees), postfire litter + duff depth, and charred surface cover] against prefire outbreak severity (percentage of stand basal area killed by bark beetles prior to fire) using general linear mixed models that accounted for topography and burning conditions. To test if the compound effects of beetle outbreaks and fire reduced postfire regeneration (thus decreasing resilience) in areas of stand-replacing fire, we used nonparametric analyses (random forests and regression trees, Spearman's rank correlations) to assess the relationship between prefire outbreak severity and postfire lodgepole pine seedling density. Because our field study captured wide natural variability across stands, we considered $P < 0.05$ as strong evidence of effects and $P < 0.10$ as suggestive/moderate evidence of effects in all models and statistical tests. See *Methods* and *SI Text* for further details on field measurements and analyses.

## Results

Fire severity in our study fires was driven primarily by burning conditions and slope position, with almost all measures of fire severity increasing under extreme burning conditions (Table S7) and nearly half increasing with higher slope positions (Table S8) - effects that are common in forests unaffected by beetle outbreaks (Bessie and Johnson 1995, Collins et al. 2009, Thompson and Spies 2009, Holden et al. 2009). In red stage stands, measures of fire severity were unrelated to prefire outbreak severity under moderate burning conditions (Fig. 1, Table S8).

Under extreme burning conditions, one measure of fire severity (the percentage of basal area with deeply charred boles and crowns) increased with outbreak severity, and a decrease in fine canopy fuels remaining on trees that were alive at the time of fire was suggested (Fig. 1A-H, Table S8).

In gray stage stands, measures of fire severity were unrelated to outbreak severity under moderate burning conditions, except for an increase in the percentage of basal area with deeply charred boles and crowns (Fig. 1I-P, Table S8). Under extreme burning conditions, four of eight measures of fire severity [bole scorch, deep charring of boles and crowns, fire-caused tree mortality (basal area and number of stems)] increased with outbreak severity, and an increase in charred surface cover was suggested; other measures of fire severity were unrelated to prefire outbreak severity (Fig. 1I-P, Table S8).

We did not find direct evidence that prefire MPB outbreaks negatively affected forest resilience via reduced early postfire tree regeneration, regardless of whether we controlled for fire severity (Table 1). Lodgepole pine composed 78% of all postfire tree seedlings (present in 37 out of 60 plots that contained lodgepole pine prefire), and seedling density was unrelated to prefire MPB outbreak severity overall, and within each combination of fire-severity class (crown or severe surface) and outbreak stage (red or gray). We found statistically significant, ecologically relevant patterns in the data for other variables, implying our statistical power to detect possible effects of beetle outbreaks was high. Specifically, we found that postfire lodgepole pine regeneration was driven primarily by the prevalence of lodgepole pine trees with serotinous cones, which provide a canopy seedbank, and by char height (an index of fire severity) (Fig. 2), similar to findings in forests without prefire beetle outbreaks (Turner et al.

1997). The percentage of stand basal area with deep charring into tree crowns was correlated with char height ($r_s = 0.77$), and while also negatively related to postfire lodgepole pine seedling density (Fig. 2B), was not selected by the regression tree. Postfire seedling density of other conifers was low, but also unrelated to prefire beetle outbreak severity (Table S9).

## Discussion

Fire severity in our study fires was driven primarily by burning conditions and topography. However, we detected several effects of prefire outbreak severity, and some effects were counter to expectations. Most surprising was that recent outbreaks were largely unrelated to fire severity in the red stage during moderate conditions, when changes to canopy fuels are expected to have a greater influence on wildfire (Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012), or during extreme conditions. Fire severity has been shown to increase with outbreak severity under moderate conditions in forests with ongoing beetle attack (i.e., mix of red stage trees and trees in the green attack stage in which needles on attacked trees dry out but have not all turned red or dropped from the canopy) (Harvey et al. in press, Prichard and Kennedy 2014). The only significant effect we detected was an increase in the percent of basal area with deep charring on the boles and into the crowns when fires burned in red stage stands under extreme conditions. This effect is not surprising, because dead wood chars more easily than live trees (Donato et al. 2009), and stands with more dead trees before fire (whether generated by beetle-kill or other causes) have more charred snags following fire. That this effect was only detected under extreme conditions is consistent with the importance of hot, dry, windy conditions for sustaining fire in large-diameter dead fuels from beetle-killed trees (Page and Jenkins 2007b, Schoennagel et al. 2012). Our data also suggested a decline in canopy fuels remaining after fire with increasing outbreak severity, which could reflect the intermix of red and green canopy fuels (Simard et al. 2011, Schoennagel et al. 2012, Jolly et al. 2012, Page et al. 2014) and increased flammability of needles in recently attacked trees (Jolly et al. 2012, Page et al. 2014) possibly leading to greater consumption of nearby needles on trees that were live at the time of fire. However, support for this effect was moderate (Fig 1B). Aside from these two effects detected during extreme burning conditions, fire severity was unrelated to outbreak severity in red stage forests.

Also surprising was our finding that outbreak effects on fire severity in gray stage stands were manifest primarily under extreme burning conditions: four of eight fire-severity measures increased (and one was suggestive) with prefire outbreak severity, indicating that the greater abundance of dead trees and surface fuels in gray-stage stands can influence fire effects. The abundance of deeply charred snags again increased steadily with outbreak severity, as expected. Percent bole scorch and the percentage of trees and basal area killed by fire also increased with outbreak severity, although these measures contained less variability over the range of fire severity as plots were most commonly at 100%. Prior retrospective studies have found that fire severity was unrelated to gray stage MPB outbreak in lodgepole pine (Harvey et al. in press), spruce beetle (*Dendroctonus rufipennis*) outbreaks in subalpine forests (Kulakowski and Veblen 2007) and Douglas-fir beetle (*Dendroctonus pseudotsugae*) outbreaks in lower-montane forests (Harvey et al. 2013). However, some modeling studies suggest increased surface fireline intensity with higher MPB outbreak severity in gray stage stands under extreme conditions (Page and Jenkins 2007b, Schoennagel et al. 2012), which is consistent with our findings. Redistribution of some coarse fuels to the forest floor from beetle-killed trees in gray stage stands (Page and Jenkins 2007a, Klutsch et al. 2011, Schoennagel et al. 2012) can increase potential for smoldering combustion and surface heating, which may lead to greater bole scorch (without an increase in char height) and an increase in the percentage of live trees that are killed by fire when outbreak severity is high. That these effects were detected under extreme rather than moderate burning conditions again suggests the importance of weather conditions for sustaining fire in coarse dead fuels. Our data also suggest that charred surface cover may increase with outbreak severity. Branch fall from beetle-killed trees begins to accumulate on the forest floor and herbaceous vegetation increases within 3-5 years of beetle infestation (Page and Jenkins 2007a, Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012, Hicke et al. 2012), which could increase the amount of charred material on the forest floor. We note that the gray-stage stands we studied had lower MPB-outbreak severity (0 to 56% beetle-killed basal area) than the red-stage stands we studied or gray-stage stands measured elsewhere (Harvey et al. in press, Simard et al. 2011, Schoennagel et al. 2012). Thus, results for forests in areas of greater outbreak severity may be different from what we observed. Further study is needed across multiple fires in gray stage stands with higher beetle-outbreak severity.

Under moderate burning conditions in both post-outbreak stages, fire severity was mostly unaffected by recent outbreak severity, which is consistent with models that predict similar fireline intensity between post-outbreak (red and gray stage) and unaffected lodgepole pine stands under moderate burning conditions (Page and Jenkins 2007b, Schoennagel et al. 2012). Our results may also reflect the fire regime in many conifer forests of the Northern Rockies that are adapted to infrequent, stand-replacing fires (Kipfmueller and Baker 2000, Kipfmueller and

Kupfer 2005) that occur primarily under extreme rather than moderate burning conditions (Bessie and Johnson 1995, Schoennagel et al. 2004).

Other studies of fire in areas of high outbreak severity (but lacking reference forests unaffected by MPB) have reported that recent post-outbreak forests can burn at high severity (Prichard and Kennedy 2014), and our results support these findings. However, testing for a true effect of beetle outbreak requires comparison with similar reference forests (with no prior outbreak) that burned in the same conditions. Our study provides such an evaluation because we included stands with and without recent high-severity MPB outbreaks. This comparison showed that fire severity was driven primarily by weather and topography, with MPB outbreaks affecting a minority of fire severity measures, primarily under extreme conditions. These findings build on those from single fires near Yellowstone National Park (Harvey et al. in press), and with inclusion of additional response variables, broaden understanding of relationships between beetle outbreaks and subsequent wildfire severity across the Northern Rockies region. Because stand-replacing fires occur regularly in subalpine forests unaffected by recent beetle-outbreaks without a loss of system resilience (e.g., 38, 39), the differences in fire severity we detected may not substantively change postfire ecosystem structure and function.

We found no direct effect of outbreak severity on initial postfire regeneration of lodgepole pine. Rather, the most important factor explaining postfire lodgepole pine seedling density was the prevalence of mature prefire lodgepole pine trees bearing serotinous cones. Thus, serotiny may be a key mechanism of forest resilience to beetle outbreaks and subsequent wildfire, provided that cones remain on burned trees and are not consumed in fire. Viable lodgepole pine seeds can remain in serotinous cones stored in the canopy long after tree death

(Aoki et al. 2011, Teste et al. 2011), and our results suggest that beetle-killed serotinous lodgepole pines may contribute to early postfire tree regeneration if fire severity is moderate. However, the decline in postfire seedling density with increased char height (and abundance of trees that were deeply charred into the crown with < 5% of branches remaining) suggests that beetle-killed serotinous lodgepole pine trees may provide little seed source under extreme burning conditions. Thus, compound (i.e., synergistic) effects from outbreaks and fire on tree regeneration may be possible following high-severity fires in stands where most lodgepole pine trees are dead at the time of fire. Postfire seedling density was substantially lower in gray stage stands overall, irrespective of outbreak severity (Table 1 and Table S3), which suggests possible depletion of the serotinous seedbank as cones deteriorate, are removed by seed predators, or are more likely to be consumed by fire. Lower regeneration also could have resulted from fewer prefire lodgepole pine trees in gray than in red stage stands. Our seedling data are from early in postfire succession, but they likely indicate longer-term trends because the vast majority of postfire serotinous lodgepole pine recruitment occurs within one year of fire (Turner et al. 1997).

Although not affected by the prefire MPB outbreak, the overall low initial postfire lodgepole pine seedling densities in this study may have been affected by warm/dry postfire climate. Across all fires, median postfire tree seedling densities were below prefire stand density and adequate stocking levels for managed forests (Lotan and Critchfield 1990), and considerably lower than well-studied lodgepole pine forests that burned in either 1988 or 2008 (Harvey et al. in press, Turner et al. 1997, 1999, Schoennagel et al. 2003). There was little drought stress in the Northern Rockies immediately following 1998 or 2008 (1989 and 2009 water-year deficits were at or below average (Westerling et al. 2011), Table S10). Conversely, the 2012 water year that followed our study fires had high drought stress (2012 water-year deficit was 20% above average (Westerling et al. 2011), Table S10), conditions that can reduce seedling establishment. This suggests that although MPB outbreaks and wildfire did not necessarily interact to produce compound effects on postfire lodgepole pine regeneration, climate is an important driver of all three (MPB outbreaks, wildfire activity, and postfire tree regeneration).

Postfire regeneration of non-serotinous (and mostly non-beetle killed) tree species was unaffected by prefire beetle outbreaks in our study (Table S9). However, if the primary beetle host tree species is non-serotinous and therefore cannot retain a seedbank after tree death (e.g., Douglas-fir (*Pseudotsuga menziesii*)), postfire tree regeneration can decrease if prefire outbreaks are severe (Harvey et al. 2013). Because seedlings from other conifers and non-serotinous lodgepole pines can establish over a protracted postfire period (Kipfmueller and Kupfer 2005), our postfire seedling trends for these species may not be indicative of stand regeneration over the longer term. How recent prefire beetle outbreaks in non-serotinous conifers (e.g., whitebark pine, subalpine fir (*Abies lasiocarpa)*, Engelmann spruce (*Picea engelmannii*), non-serotinous lodgepole pine) can alter postfire regeneration is not known.

Our field data across multiple wildfires provide new insight into relationships between recent beetle outbreaks, wildfire severity, and postfire regeneration; however, several important questions remain. First, although fire severity relates to some aspects of fire behavior, our data cannot address operational fire management concerns (e.g., firefighter safety, suppression effort needed, resistance to control) in post-outbreak forests. Fire behavior and firefighter safety are key aspects of post-outbreak forest management that require further study (Jenkins et al. 2012). Second, forest stands impacted by beetle outbreaks simultaneously can contain trees in various stages of outbreak (i.e., green attack, red, and gray), particularly in the earliest outbreak stages. At present, aerial detection survey maps are the best available information to determine prefire outbreak stage. Finer resolution data from aerial or satellite imagery (Wulder et al. 2006), or detailed prefire field measurements may aid in assigning beetle outbreak stage to individual trees or patches of trees rather than the whole fire. Third, fire severity and postfire tree regeneration outcomes may differ in forests with more uniformly high outbreak severity (e.g., consistently > 50% tree mortality) (Prichard and Kennedy 2014), or in later stages of post-outbreak forests (e.g., > 10 yrs after infestation) when most or all beetle-killed trees have fallen to the ground (Page and Jenkins 2007a, 2007b, Simard et al. 2011, Schoennagel et al. 2012). Many fallen beetle-killed trees could substantially increase surface fuels and redistribute serotinous cones to the forest floor in ways similar to wind-driven blowdown events (Buma and Wessman 2012, Kulakowski et al. 2013); thus field studies in fires burning through later post-outbreak stages are needed. Consistent information on older (pre-2000) outbreaks was unavailable for our study fires; therefore, whether older outbreaks may have influenced fire severity or postfire tree regeneration is unknown, and was beyond the scope of our study. Results may also differ among other forest types. Field studies in other conifer forests that have experienced severe beetle outbreaks and subsequent fire (e.g., whitebark pine, Engelmann spruce, ponderosa pine [*Pinus ponderosa*]) are needed, as fuel structures, fire regimes, and regeneration mechanisms can vary widely across these systems. Finally, outcomes may differ for other ecosystem responses such as coarse wood consumption or carbon dynamics in post-outbreak wildfires.

Bark beetle outbreaks and wildfire occurrence are both predicted to increase with continued climate warming in North America (Bentz et al. 2010, Westerling et al. 2011) and worldwide (Flannigan et al. 2009). The effects of each may be individually severe, but we found recent MPB outbreaks affected few measures of subsequent wildfire severity in subalpine forests in multiple wildfires across a large (~50,000 km$^2$) region of the Northern US Rockies. However, we found evidence for increased bole scorching and fire-caused mortality of live trees when gray stage forests burned under extreme burning conditions, consistent with modeled predictions of increases in surface fireline intensity (Page and Jenkins 2007b, Klutsch et al. 2011, Schoennagel et al. 2012). Nonetheless, in serotinous lodgepole pine forests (which constitute a significant portion of beetle-killed forests in North America (Raffa et al. 2008)), postfire forest resilience may not necessarily impaired by recent MPB outbreaks if there is a canopy seed source that is not consumed in the fire.

## Methods

**Study area and sampling design.** Upper-montane and subalpine forests of the region comprise a mix of conifer species, but are generally dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) with lesser components of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), whitebark pine (*Pinus albicaulis*), and Douglas-fir (*Pseudotsuga menziesii*) (Tables S1-S3). Fire regimes are characterized by infrequent fires that vary in severity, but generally include large patches of stand-replacing fire (Romme and Despain 1989, Barrett et al. 1991, Barrett 1994, Kipfmueller and Baker 2000, Schoennagel et al. 2003).

Study fires were all ignited by lightning and were located in five different National Forests (Table S1). See *SI Text* and Tables S2 and S3 for prefire forest composition and characterization of bark beetle outbreak stage at the time of the fire. We sampled between five and 30 circular plots (0.07 ha) in each fire, and plots were equally distributed among three fire-severity classes and separated by at least 400 m. In each plot, we recorded stand structure, prefire beetle outbreak severity, and fire severity; postfire tree seedling density was recorded in plots that burned as stand-replacing fire. See *SI Text* for details.

**Statistical models of fire severity.** To test whether fire severity was linked to prefire outbreak severity, we regressed each fire-severity metric against prefire beetle-killed basal area while accounting for other variables known to influence fire severity. Stepwise variable selection (using Bayesian information criteria) among topographic (elevation, slope, aspect, slope position) and stand structure (live and dead basal area and stem density) resulted in slope position being retained in models of fire severity. Therefore, the final models followed the structure:

Fire severity ~ burning conditions + slope position + beetle-killed basal area (%) × burning conditions

Burning conditions is a categorical variable (moderate, extreme) representing the approximate weather at the time each plot burned (*see SI Text*, Table S4); therefore model results are displayed with one intercept term for each burning condition and one slope term for the effect of beetle-killed basal area under each burning condition. Fire name was included and treated as a random effect to account for differences among fires. Treating fire as a fixed effect did not qualitatively change any model results. General linear mixed models (R package, nlme, www.r-project.org) were used for each response variable. Percentage response variables were logit-transformed (to bound responses between 0% and 100%) before analysis.

**Statistical models of postfire tree seedling density.** To test if MPB outbreaks and fire interacted to produce compound effects on postfire lodgepole pine seedling density (stems per hectare), we performed two analyses.

First, to assess the relative importance of MPB outbreak severity as an explanatory variable for postfire seedling establishment among other variables (topography, fire severity, seed source) known to affect postfire tree regeneration, we used a combination of Random Forests and regression trees (Breiman et al. 1984, De'ath and Fabricius 2000, Maindonald and Braun 2010). These methods are effective in uncovering hierarchical and non-linear relationships among variables, and are robust to any distribution (Breiman et al. 1984, De'ath and Fabricius 2000, Maindonald and Braun 2010). Random forest models provide a list ranking the importance of explanatory variables from a large number of potential trees, and are a useful tool in combination with classical regression trees, which are more interpretable for complex relationships among variables (Maindonald and Braun 2010). A full tree was built by adding the following candidate predictor variables: total (live and dead) prefire basal area per hectare, total (live and dead) prefire lodgepole pine basal area per hectare, the percentage of lodgepole pine trees bearing serotinous cones [estimating prefire serotiny using methods outlined in refs. (Tinker et al. 1994, Turner et al. 1999)], the basal area of lodgepole pine trees bearing serotinous cones, elevation, slope, aspect, slope position, fire-severity class, char height, the percentage of stand basal area with deep charring into the crown and <5% of branches remaining, fine fuels (needles and small branches) remaining in the canopy for trees that were alive at the time of fire, postfire litter + duff depth, distance to seed source (unburned living tree), beetle outbreak stage, total basal area killed by bark beetles, and MPB-killed basal area. Ten runs of 1,000 trees were independently grown using Random Forests, and the increase in mean square error for exclusion of each variable was averaged across runs, providing a rank list of variable importance. Variables with a positive increase (i.e., variables that improved model fit) were added to the full regression tree. The regression tree was then trimmed to avoid over-fitting, minimizing cross-validated error by removing splits that exceeded the complexity parameter (Maindonald and Braun 2010).

Second, postfire tree seedling density (stems per hectare) was regressed against beetle-killed basal area overall and within each combination of each fire-severity class (which can affect postfire tree seedling density (Turner et al. 1997)) and beetle outbreak stage. We used Spearman's rank correlation tests within each fire-severity class because of highly skewed (non-normal with many zeros) distributions in postfire seedling densities and violations of parametric model assumptions; we were unable to fit these data to general or generalized linear models. Analyses on postfire tree seedling densities were performed for lodgepole pine (accounting for 78% percent of postfire seedlings) and other conifers separately, as they have different fire adaptations (e.g., serotinous seedbanking vs. wind-dispersal). All regeneration models were conducted only on plots where the postfire tree seedling species was present in the plot prefire.

All statistical analyses were performed in the R statistical software (version 2.12, R Foundation for Statistical Computing). Results are means ± 1 SE unless noted otherwise.

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## Figure Legends

Figure 1. Scatterplots of canopy and surface fire-severity measures against beetle-killed basal area in red-stage (*n* = 72, A-H) and gray-stage (*n* = 33, I-P) forests. White circles show plots that burned during moderate burning conditions and red (red stage) and gray (gray stage) circles show plots that burned in extreme burning conditions. *P* values are reported for the main effect of beetle-killed basal area on each fire severity metric from general linear mixed models (Table S8). *P* values for beetle outbreak effects under each burning condition are separated by a vertical line (e.g., *P* = moderate | extreme). [a]calculated from average of 20 unbroken co-dominant canopy trees per plot that were alive or dead at the time of fire; [b]calculated from average of the subset of 20 sampled trees that were alive at the time of fire; [c]calculated from all trees in the plot.

Figure 2. Regression tree (A) and random forest (B) results indicating important variables explaining variability in postfire lodgepole pine seedling establishment. The model explained 28% of variance in lodgepole pine seedling density.

**Table 1.** Overall postfire lodgepole pine seedling density in each outbreak stage and fire severity class combination

| | | | Post-fire seedlings per hectare | | | Correlation with beetle outbreak severity in lodgepole pine only | | |
|---|---|---|---|---|---|---|---|---|
| No. of plots present | Outbreak stage | Fire severity class | Minimum to maximum | Mean | Median | $r_s$ | df[a] | $P$ |
| 37 out of 60 plots | All stages combined | All classes combined | 0 - 158,819 | 9,639 | 261 | -0.16 | 58 | 0.23 |
| | | Severe surface | 0 - 158,819 | 17,648 | 871 | -0.15 | 30 | 0.42 |
| | | Crown | 0 - 3,286 | 485 | 89 | 0.01 | 26 | 0.96 |
| | Red stage | All classes combined | 0 - 158,819 | 12,434 | 181 | -0.18 | 43 | 0.23 |
| | | Severe surface | 0 - 158,819 | 22,971 | 871 | -0.16 | 22 | 0.44 |
| | | Crown | 0 - 3,286 | 391 | 86 | 0.06 | 19 | 0.78 |
| | Gray stage | All classes combined | 0 - 6,063 | 1,255 | 771 | -0.11 | 13 | 0.70 |
| | | Severe surface | 0 - 6,063 | 1,682 | 645 | -0.09 | 6 | 0.83 |
| | | Crown | 0 - 1,792 | 767 | 771 | -0.17 | 5 | 0.72 |

Spearman rank correlations ($r_s$) testing the relationship between postfire lodgepole pine seedling density and prefire MPB outbreak severity (percentage of lodgepole pine basal area killed by MPB). Tests were conducted across all outbreak stages and fire severity classes, and individually in each combination of outbreak stage and fire severity class. Plots where lodgepole pine was not present prefire were excluded before analysis.

[a] Based on the number of plots in each combination of fire severity class and outbreak stage.

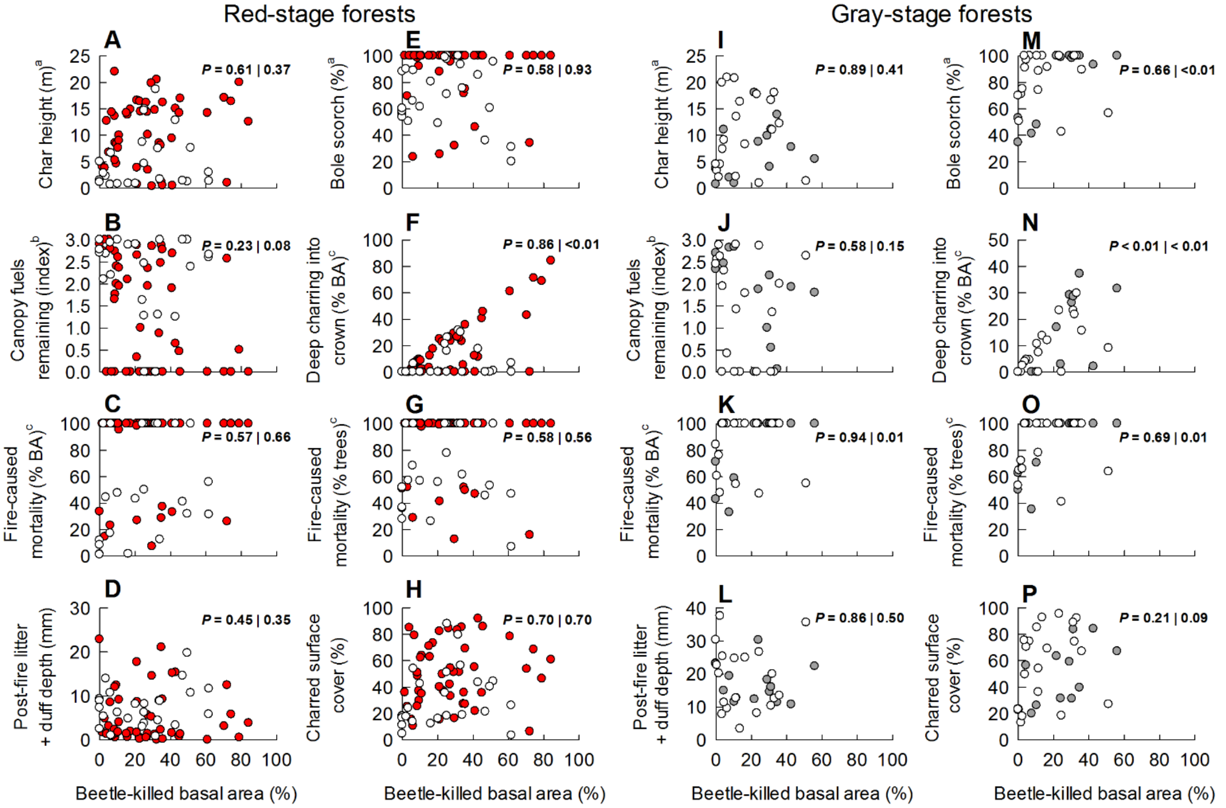
Red-stage forests
Gray-stage forests
A
P = 0.61 | 0.37
Char height (m)a
E
P = 0.58 | 0.93
Bole scorch (%)a
I
P = 0.89 | 0.41
Char height (m)a
M
P = 0.66 | <0.01
Bole scorch (%)a
B
P = 0.23 | 0.08
Canopy fuels remaining (index)b
F
P = 0.86 | <0.01
Deep charring into crown (% BA)c
J
P = 0.58 | 0.15
Canopy fuels remaining (index)b
N
P < 0.01 | < 0.01
Deep charring into crown (% BA)c
C
P = 0.57 | 0.66
Fire-caused mortality (% BA)c
G
P = 0.58 | 0.56
Fire-caused mortality (% trees)c
K
P = 0.94 | 0.01
Fire-caused mortality (% BA)c
O
P = 0.69 | 0.01
Fire-caused mortality (% trees)c
D
P = 0.45 | 0.35
Post-fire litter + duff depth (mm)
H
P = 0.70 | 0.70
Charred surface cover (%)
L
P = 0.86 | 0.50
Post-fire litter + duff depth (mm)
P
P = 0.21 | 0.09
Charred surface cover (%)
0 20 40 60 80 100
Beetle-killed basal area (%)

Figure 1.

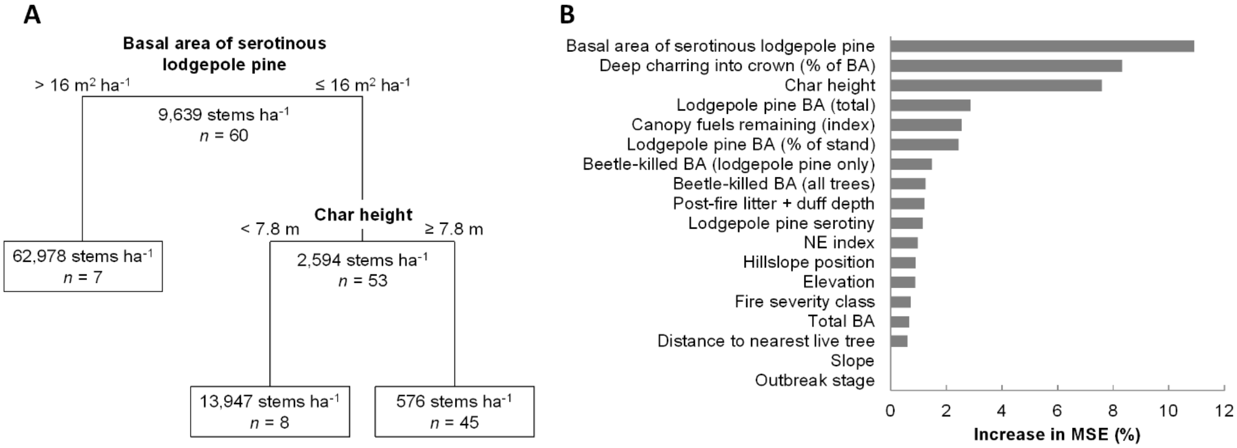
A
Basal area of serotinous lodgepole pine
> 16 m² ha⁻¹
≤ 16 m² ha⁻¹
9,639 stems ha⁻¹
n = 60
62,978 stems ha⁻¹
n = 7
Char height
< 7.8 m
≥ 7.8 m
2,594 stems ha⁻¹
n = 53
13,947 stems ha⁻¹
n = 8
576 stems ha⁻¹
n = 45
B
Basal area of serotinous lodgepole pine
Deep charring into crown (% of BA)
Char height
Lodgepole pine BA (total)
Canopy fuels remaining (index)
Lodgepole pine BA (% of stand)
Beetle-killed BA (lodgepole pine only)
Beetle-killed BA (all trees)
Post-fire litter + duff depth
Lodgepole pine serotiny
NE index
Hillslope position
Elevation
Fire severity class
Total BA
Distance to nearest live tree
Slope
Outbreak stage
0
2
4
6
8
10
12
Increase in MSE (%)

Figure 2.

## Supplemental Information

**Study area.** The study area comprised recent (2011) lightning-ignited wildfires in upper-montane and subalpine forests in the Northern Rockies, USA (Fig. S1) located in five different National Forests in areas accessible by road (Table S1). Pre-fire forest stands were dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) and subalpine-fir (*Abies lasiocarpa*) (collectively constituting 65% of total basal area), and included whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*), Engelmann spruce (*Picea engelmannii*), and Douglas-fir (*Pseudotsuga menziesii*) (Table S2). Based on US Department of Agriculture (USDA) aerial detection survey (ADS) maps produced each year between 2000 and 2011, we assigned each fire to a post-outbreak stage of beetle infestation. Although ADS data have important limitations in fine-scale spatial accuracy, they are suitable for identifying specific years in which outbreak activity occurred and/or peaked at the scale of the wildfire perimeter (Meddens et al. 2012) – the only purpose for which we used those data. Fires in which the majority of bark beetle outbreak within the fire perimeter occurred between 2000 and 2008 were categorized as gray-stage outbreak, whereas fires in which the majority of bark beetle outbreak within the fire perimeter occurred between 2009 and 2011 were categorized as red-stage outbreak (see main text for descriptions of stages). Outbreaks were composed mostly of mountain pine beetle (MPB) (87.7% of beetle-killed basal area), but included Douglas-fir beetle (6.8% of beetle-killed basal area), western balsam bark beetle (3.1% of beetle-killed basal area), and spruce beetle (0.3% of beetle-killed basal area) depending on stand composition. All fires were sampled in 2012.

**Sampling design.** Plots in each fire were located between 100 and 1000 m from roads and trails for accessibility, and separated by a minimum distance of 400 m to reduce spatial autocorrelation (analysis from 100 plots from a fire that burned in 2008 showed fire severity metrics to be spatially correlated at distances up to 395 m (Harvey et al. in press)). Each fire contained between five and 30 plots, depending on accessible area, and plots within a fire were equally distributed among three fire-severity classes (light-surface fire, severe-surface fire, and crown fire, defined in (Turner et al. 1997)) using field observations. Plots were systematically situated in each fire from a random start location > 100 m from the fire perimeter. Plots were established at 400 m intervals or further if necessary to avoid areas not meeting study criteria (rock outcrops, non-forest, etc.) until 30 plots or all accessible areas were sampled. Plot-center locations were randomized within 10 m of each systematic point location to avoid bias. In each plot, data were collected on stand structure, pre-fire beetle outbreak severity, and fire severity in a 30-m diameter circular plot (0.07 ha) divided into four quadrants (NE, SE, SW, NW) (Tables S1, S3- S5).

**Pre- and post-fire stand structure.** Stand structure was measured by recording the condition (live or dead), species, diameter at breast height (dbh) to the nearest 0.5 cm, and height of every tree taller than 1.4 m in the plot. We also recorded the species and height for every live or dead pre-fire sapling (trees < 1.4 m that established pre-fire) occurring in 3-m belt transects along the main axes of the circular plot (N, E, S, W). In plots that burned as stand-replacing fire (i.e., all pre-fire live trees were killed by fire), post-fire seedlings (trees that germinated post-fire) were recorded in 2-m belt transects along the main axes of the plot. Slope (º), aspect (º), and geographic coordinates were measured at plot center.

**Pre-fire beetle outbreak severity.** Pre-fire beetle outbreak severity was quantified following methods outlined in (Harvey et al. in press, 2013), by removing the bark on every tree taller than 1.4 m (12,568 individual trees) and recording evidence (or absence of evidence) of *Dendroctonus* or *Dryocoetes* activity (Safranyik and Carroll 2007). Each tree was assigned to one of five categories: (a) pre-disturbance snag, (b) killed by bark beetles prior to fire, (c) green attack at time of fire, (d) live at the time of fire, or (e) unknown (Table S5). By cross-referencing with ADS maps, beetle-killed trees within each fire were assigned as red-stage or gray-stage at the time of fire (Table S1). Information on older outbreaks (pre-2000) was not available, and outbreaks were passed the green-attack stage (year of attack) by the time of fire. Classification of trees was informed by consultations with forest entomology experts.

**Fire severity.** Canopy fire severity was measured on five randomly selected unbroken co-dominant canopy trees in each quadrant (maximum of 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 tree (Table S5). From a subset of these 20 trees that were alive at the time of fire, we also recorded a categorical assessment of postfire needles and fine branches remaining in the canopy with four classes: 0 – less than 5% of needle bearing branches remaining; 1 – needle bearing branches remain, but less than 5% of needles remaining; 2 – greater than 5% but less than 50% of needles remaining; and 3 – greater than 50% of needles remaining. For every tree in a plot, we recorded the level of deep charring (through the cambium and into the sapwood) on the bole and into the crown with three classes: 0 – no deep charring on the tree; 1 – deep char on the lower bole, but not into the crown; and 2 – deep charring into the crown and <5% of branches remaining. Fire-caused tree mortality was recorded by classifying every fire-damaged tree > 1.4 m tall in the plot that was alive at the time of fire but dead at the time of sampling as killed by fire. The percentage of post-outbreak live trees and basal area that were killed by fire was used to measure fire severity on the residual canopy after the outbreak. Surface fire severity was measured by recording the depth of post-fire litter + duff (i.e., the soil O horizon) to the nearest mm at every 3 m along the main axis of the plot (20 pts / plot) and by recording the percent cover of charred surface (mineral soil, litter, woody debris), using the point intercept method (Table S5). Points were spaced at 10-cm intervals along the main axis of the plot (480 per plot).

**Topography.** A 10-m digital elevation model (DEM) was used in ArcGIS 10.1 to generate the following topographic variables for each plot center: elevation (m), slope (º), and aspect (NE Index (Beers et al. 1966)). To characterize local relative elevation, we calculated a slope position by re-scaling elevation for each plot from 0 (bottom of slope) to 1 (ridge top) (Harvey et al. 2013).

**Burning conditions.** We used daily burn progression maps provided by the National Forest Service, weather data from the nearest Remote Automated Weather Station (RAWS), and weather thresholds shown to affect fire severity in North American conifer forests (Collins et al. 2007, Thompson and Spies 2009, Prichard and Kennedy 2014) to divide each fire into periods of moderate or extreme burning conditions. Extreme burning conditions were assigned to portions of fires characterized by temperatures > 27˚C, relative humidity < 20% and temperatures > 20 ˚C, or maximum wind speeds > 10 m/s with relative humidity < 20% regardless of temperature; these conditions accounted for the majority of area burned in these fires (Table S3). Portions of fires that burned under all other conditions (temperatures < 27˚C, relative humidity > 20%, or maximum wind speeds > 10 m/s with relative humidity > 20%) were assigned moderate burning conditions. All fires contained plots in both moderate and extreme conditions. In total, 44 plots burned under moderate burning conditions and 61 plots burned under extreme burning conditions (Table S4).

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## SI Figure Legends

Figure S1. Study area and location of fires in the Northern Rocky Mountains (USA). All study fires burned in 2011.

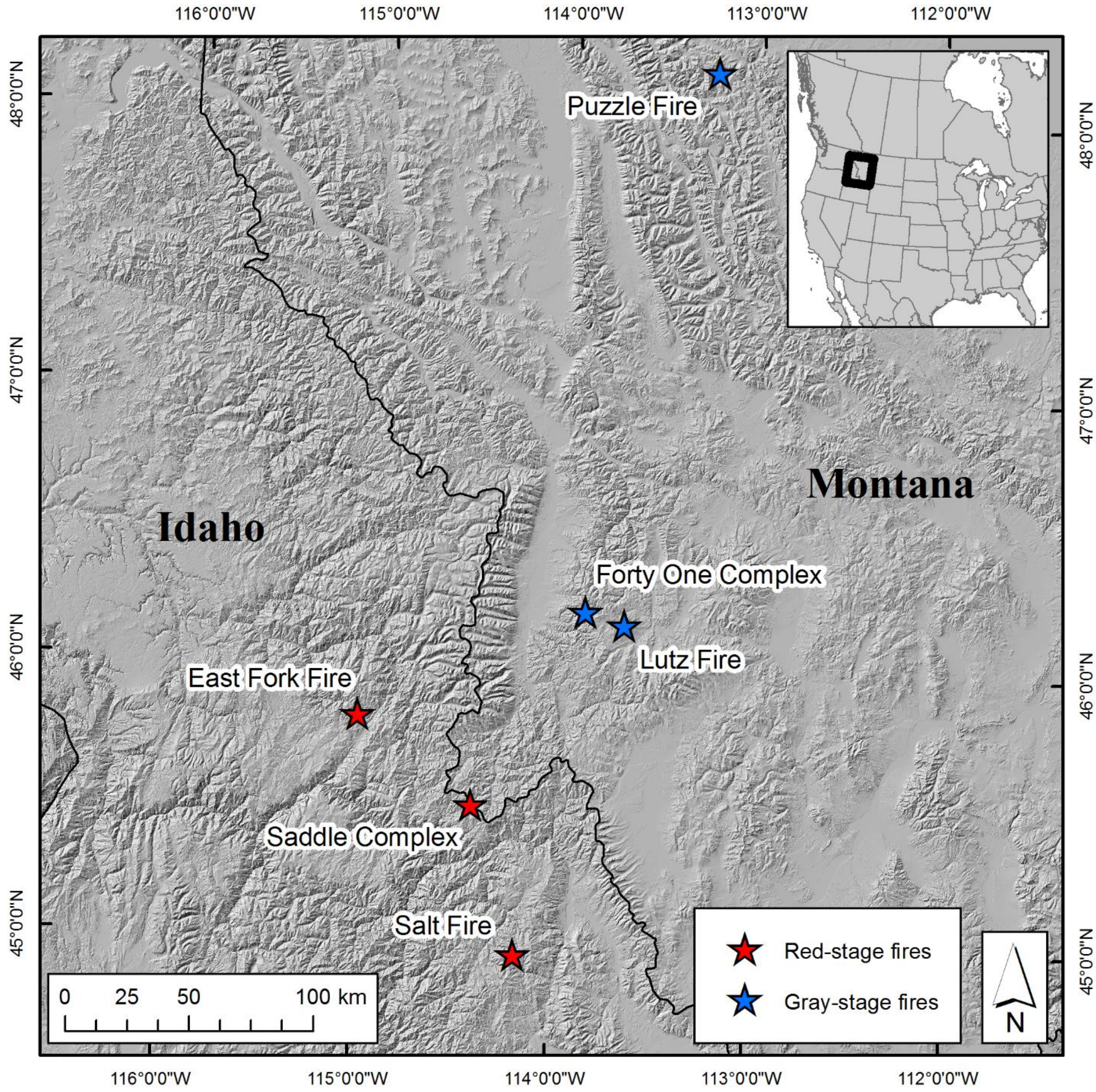
116°0'0"W
115°0'0"W
114°0'0"W
113°0'0"W
112°0'0"W
48°0'0"N
47°0'0"N
46°0'0"N
45°0'0"N
Puzzle Fire
Montana
Idaho
Forty One Complex
Lutz Fire
East Fork Fire
Saddle Complex
Salt Fire
Red-stage fires
Gray-stage fires
0
25
50
100 km
N

Figure S1.

**Table S1.** Characteristics of each fire sampled in this study (all fires occurred in 2011).

| Fire name | Location | Fire size, ha | Percentage of fire[a,b] | No. of plots sampled[a] |
|---|---|---|---|---|
| Salt Fire | Salmon-Challis National Forest, Idaho (44º 58’ N, 114º 12’ W) | 9,031 | (42,21,37) | 30 (*10*,*10*,10) |
| Saddle Fire | Salmon-Challis National Forest, Idaho (45º 31’ N, 114º 27’ W) | 12,497 | (66,18,16) | 30 (*10*,*10*,10) |
| East Fork Fire | Nez Perce National Forest, Idaho (45º 50’ N, 115º 01’ W) | 3,520 | (45,34,21) | 12 (*4*,*4*,4,) |
| Lutz Fire | Beaverhead-Deerlodge National Forest, Montana (46º 11’ N, 113º 39’ W) | 970 | (28,29,43) | 5 (*2*,*2*,1) |
| Forty-one Complex | Bitterroot National Forest, Montana (46º 15’ N, 113º 51’ W) | 5,131 | (47,31,22) | 16 (*5*,*6*,5) |
| Puzzle Creek Fire | Flathead National Forest, Montana (48º 12’ N, 113º 15’ W) | 603 | (19,48,33) | 12 (*4*,*4*,4) |

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[a] The three numbers in parentheses represent crown, severe surface, and light surface fire, respectively. Plots in italics were stand-replacing fire and used in the post-fire tree regeneration analyses.

[b] Percentage of each fire burning as crown, severe surface, and light surface fire was estimated using classified burn severity maps available from the Monitoring Trends in Burn Severity website: Salt Fire (http://fsgeodata.net/MTBS_Uploads/data/2011/maps/ID4498311423620110825_map.pdf), Saddle Fire (http://fsgeodata.net/MTBS_Uploads/data/2011/maps/ID4551711451120110818_map.pdf), East Fortk Fire http://fsgeodata.net/MTBS_Uploads/data/2011/maps/ID4583511503020110805_map.pdf), Lutz Fire (http://fsgeodata.net/MTBS_Uploads/data/2011/maps/MT4620711367720110806_map.pdf), Forty-One Complex (http://fsgeodata.net/MTBS_Uploads/data/2011/maps/MT4622211394220110828_map.pdf), Puzzle Fire (http://fsgeodata.net/MTBS_Uploads/data/2011/maps/MT4820911323720110909_map.pdf). Total fire size was also determined from these maps.

**Table S2.** Tree species (live, preoutbreak) and beetle outbreak characteristics of stands sampled in each fire in this study.

| | Tree species composition, percentage of total BA | | | | | | | | Beetle outbreak composition by beetle species, percentage of total beetle-killed BA (year of peak mortality) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fire name | ABLA | PIAL | PICO | PIEN | PIPO | PSME | Unknown / Other | Total percent beetle-killed BA (median) | MPB | DFB | WBBB | SB | Unknown | Outbreak stage at time of fire |
| Salt Fire | 37 | 19 | 32 | 11 | 0 | <1 | <1 | 3 to 84<br>(31) | 97<br>(2010) | 0 | 1<br>(2004) | 0 | 2 | Red |
| Saddle Fire | 2 | 0 | 52 | 1 | 9 | 36 | 0 | 0 to 79<br>(15) | 69<br>(2009) | 29<br>(2005) | 0 | 0 | 2 | Red |
| East Fork Fire | 17 | 0 | 62 | 6 | 0 | 13 | 2 | 0 to 52<br>(23) | 89<br>(2010) | 10<br>(2003) | 1<br>(unk) | <1 | 1 | Red |
| Lutz Fire | 20 | 3 | 72 | 5 | 0 | 0 | 0 | 10 to 30<br>(14) | 100<br>(2005) | 0 | 0 | 0 | 0 | Gray |
| Forty-one Complex | 50 | 17 | 14 | 14 | 0 | 5 | <1 | 0 to 43<br>(10) | 93<br>(2005) | 3<br>(2005) | 3 | 0 | 1 | Gray |
| Puzzle Creek Fire | 57 | 19 | <1 | 22 | 0 | 1 | 1 | 0 to 56<br>(24) | 74<br>(2004) | 3<br>(2001) | 16<br>(2009) | 3<br>(2009) | 4 | Gray |
| **Total** | **32** | **12** | **33** | **10** | **2** | **10** | **1** | **0 to 84**<br>(23) | **88**<br>n/a | **7**<br>n/a | **3**<br>n/a | **<1**<br>n/a | **2**<br>n | **n/a** |

ABLA, *Abies lasiocarpa* (subalpine fir); BA, basal area; DFB, *Dendroctonus pseudotsugae* (Douglas-fir beetle); MPB, *Dendroctonus ponderosae* (MPB); PIAL, *Pinus albicaulis* (whitebark pine); n/a, not applicable; PICO, *Pinus contorta* var. *latifolia* (lodgepole pine); PIEN, *Picea engelmannii* (Engelmann spruce); PIPO, *Pinus ponderosa* (ponderosa pine); PSME, *Pseudotsuga menziesii* (Douglas-fir); SB, *Dendroctonus rufipennis* (spruce beetle); WBBB, *Dryocoetes confusus* (western balsam bark beetle).

**Table S3.** Stand structure characteristics for red stage and gray stage forests: Preoutbreak, prefire, and postfire, measured in each 30-m diameter circle plot (707 $m^2$).

| Stand structure variable | Red stage forests, *n* = 72 | | Gray stage forests, *n* = 33 | |
|---|---|---|---|---|
| Pre-outbreak | | | | |
| Live basal area ($m^2$ $ha^{-1}$) | 35.8 | (1.7) | 42.1 | (2.3) |
| Live stems $ha^{-1}$ | 1,587 | (115) | 1,762 | (122) |
| Dead basal area ($m^2$ $ha^{-1}$) | 0.6 | (0.1) | 1.7 | (0.5) |
| Snags $ha^{-1}$ | 46 | (8) | 63 | (21) |
| | | | | |
| Basal area by species (%) | | | | |
| Lodgepole pine | 46 | (4) | 19 | (5) |
| Subalpine fir | 18 | (2) | 49 | (4) |
| Engelmann spruce | 5 | (2) | 14 | (3) |
| Whitebark/limber pine | 7 | (2) | 15 | (4) |
| Douglas-fir | 18 | (4) | 2 | (2) |
| Other / unknown | 5 | (2) | 1 | (0) |
| | | | | |
| Pre-fire (but post-outbreak) | | | | |
| Beetle-killed basal area ($m^2$ $ha^{-1}$) | 10.4 | (1.2) | 8.4 | (1.4) |
| Beetle-killed basal area (%) | 26 | (2) | 19 | (3) |
| Range (%) | 0 to 84 | | 0 to 56 | |
| | | | | |
| Beetle-killed snags $ha^{-1}$ | 213 | (25) | 118 | (19) |
| Pre-fire serotiny (%) | 30 | (4) | 23 | (6) |
| | | | | |
| Post-fire | | | | |
| Fire-killed basal area ($m^2$ $ha^{-1}$) | 19.1 | (1.6) | 28.9 | (2.3) |
| Fire-killed basal area (% of post-outbreak live basal area) | 75 | (4) | 86 | (4) |
| Live basal area ($m^2$ $ha^{-1}$) | 6.0 | (1.2) | 4.8 | (1.4) |
| Live stems $ha^{-1}$ | 267 | (60) | 268 | (93) |
| Lodgepole pine seedlings $ha^{-1}$ | 11,657 | (4,632) | 856 | (331) |
| Median seedlings $ha^{-1}$ | 93 | | 0 | |
| Other conifer seedlings $ha^{-1}$ | 2,614 | (1,500) | 95 | (41) |
| Median seedlings $ha^{-1}$ | 0 | | 0 | |

Pre-outbreak basal area by species refers to trees that were alive at the time of the outbreak. Values are means (SEs are in parentheses) unless otherwise noted.

**Table S4.** Differences in weather conditions for moderate or extreme burning conditions within each fire, using threshold cutoffs (see *Burning Conditions)*. Summed total area burned (hectares in moderate + extreme burning conditions) for each fire may differ from total area burned in Table S1 because of differences in US Forest Service daily burn progression map totals and MTBS burn severity map totals.

| | | | Weather conditions and fire growth | | | | | |
|---|---|---|---|---|---|---|---|---|
| Fire name (start to end dates) | Burning conditions | No. of plots | Temperature, °C | RH, % | Wind speed, m/s | No. of days | Area burned, ha | Percentage of fire burned |
| Salt Fire (8/25 - 10/2)[a] | Moderate | 9 | 16.6 | 22.6 | 2.6 | 21 | 3821 | 38 |
| | Extreme | 21 | 21.3 | 14.9 | 3.2 | 17 | 6177 | 62 |
| Saddle Fire (8/18 - 9/30)[b] | Moderate | 11 | 16.0 | 37.3 | 2.9 | 36 | 5299 | 39 |
| | Extreme | 19 | 22.7 | 16.9 | 3.1 | 6 | 8233 | 61 |
| East Fork Fire (8/22 - 9/11)[c] | Moderate | 4 | 20.3 | 38.7 | 1.1 | 10 | 1717 | 42 |
| | Extreme | 8 | 28.5 | 18.5 | 1.2 | 17 | 2372 | 58 |
| Lutz Fire (8/6 - 9/15)[d] | Moderate | 2 | 20.7 | 31.4 | 1.4 | 29 | 1100 | 75 |
| | Extreme | 3 | 24.4 | 18.4 | 1.5 | 8 | 359 | 25 |
| Forty-one Complex (9/3 - 9/29)[d] | Moderate | 10 | 17.1 | 37.3 | 1.5 | 20 | 2707 | 59 |
| | Extreme | 6 | 23.7 | 17.1 | 1.5 | 7 | 1881 | 41 |
| Puzzle Creek Fire (9/9 - 9/13)[e] | Moderate | 8 | 21.7 | 34.0 | 2.5 | 3 | 432 | 78 |
| | Extreme | 4 | 25.8 | 19.9 | 2.3 | 2 | 123 | 22 |

Footnotes for each fire indicate the nearest RAWS used to assign weather data. RH, relative humidity.

[a] Red Rock Peak (Idaho) RAWS located 18 km west of the Salt Fire.

[b] Hells Half Saddle (Idaho) RAWS located 16 km northwest of the Saddle Fire.

[c] Red River (Idaho) RAWS located 25 km southwest of the East Fork Fire.

[d] Gird Point (Montana) RAWS located 17 km west of the Lutz Fire, within the perimeter of the Forty-One Complex Fire.

[e] Fielding (Montana) RAWS located 15 km northwest of the Puzzle Creek Fire.

**Table S5:** Evidence and criteria used to classify each tree into one of five categories for reconstructing prefire beetle outbreak severity.

| Tree classification | Tree characteristics | Refs. | Percentage of trees sampled<br>Red stage forests | <br>Gray stage forests |
|---|---|---|---|---|
| **Predisturbance snag:** killed before outbreak or fire; timing and cause of death unknown | Dead at time of sampling<br>Highly weathered/decayed sapwood, most branches and bark missing<br>No evidence of bark beetle activity (pre- or post-fire) | | 0.5 | 1.8 |
| **Killed by bark beetles prior to fire** | | | | |
| Visible cambium | Dead at time of sampling, no needles in canopy<br>Dry cambial tissue<br>*Dendroctonus* exit holes on the outer bark<br>Fully excavated (but vacated) adult and larval *Dendroctonus* or *Dryocoetes* galleries on the vascular cambium (> 50% of bole circumference or remaining visible cambium) | (2-4) | 8.8 | 3.2 |
| No visible cambium[a] | Dead at time of sampling, no needles in canopy<br>No available cambium visible due to excessive charring<br>> 15 cm dbh | (2-4) | 4.2 | 3.2 |
| **Green-attack at time of fire** | Dead at time of sampling, no needles in canopy<br>Partially completed galleries with adult beetles charred under bark<br>Or meeting all the criteria for “killed by bark beetles prior to fire (visible cambium)” but containing needles in the canopy and located in a plot with partially completed galleries / charred beetles | (3) | 0.3 | 0.0 |
| **Live at the time of fire** | | | | |
| Killed by fire | Dead at time of sampling<br>Charred bark, branches, or outer sapwood<br>No evidence of bark beetle activity (no exit holes on outer bark, no galleries under bark)<br>Not a highly-decayed or well-weathered snag | | 67.5 | 75.4 |
| Killed by bark beetles after fire | Alive or dead at the time of sampling<br>Clear signs of post-fire beetle activity [boring dust (which | (3, 5) | 0.1 | 0.5 |

| | | | |
|---|---|---|---|
| | would have been consumed by fire), resin bleeding] or fully developed galleries but moist cambial tissue and/or any detectable level of needles in the canopy (which would still be present given needle-drop period of 2 to 3 y) | | |
| Surviving tree | Alive at the time of sampling<br>Green foliage, no sign of *Dendroctonus* beetle activity | 16.2 | 14.2 |
| **Unknown** | Deep charring on a tree < 15 cm dbh. | 2.4 | 1.6 |

This table is adapted from ref. 1.

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

1. Harvey BJ, Donato DC, Romme WH, Turner MG (2014) Fire severity and tree regeneration following bark beetle outbreaks: The role of outbreak stage and burning conditions. Ecol Appl, 10.1890/13-1851.1.
2. Turner MG, Gardner RH, Romme WH (1999) Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. Int J Wildland Fire 9:21–36.
3. Safranyik L, Carroll AL (2007) The Mountain Pine Beetle: A Synthesis of Biology, Management and Impacts on Lodgepole Pine, eds Safranyik L, Wilson B (Pacific Forestry Centre, Victoria, BC, Canada), pp 3–66.
4. Simard M, Romme WH, Griffin JM, Turner MG (2011) Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol Monogr 81:3–24.
5. Powell EN, Townsend PA, Raffa KF (2011) Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. Ecological Monographs 82:69–84.

**Table S6.** Plot-level measures of fire severity in red and gray stage forests, averaged across each outbreak stage.

| | Red-stage forests | | | Gray-stage forests | | |
|---|---|---|---|---|---|---|
| Fire-severity metric | Mean | Median | Range | Mean | Median | Range |
| Canopy | | | | | | |
| Char height, m[a] | 8.6 | 8.2 | 0.3-22.0 | 9.3 | 8.7 | 0.7-20.9 |
| Bole scorch, percentage of circumference[a] | 84 | 100 | 20-100 | 84 | 97 | 35-100 |
| Canopy fuels remaining, index[b] | 1.7 | 2.1 | 0-3.0 | 1.6 | 1.9 | 0-2.9 |
| Deep charring into crown, percentage of basal area[c] | 14 | 7 | 0-84 | 11 | 5 | 0-37 |
| Surface | | | | | | |
| Post-fire litter + duff depth, mm | 6.0 | 4.2 | 0.0-22.8 | 18.1 | 16.0 | 3.4-37.5 |
| Charred surface cover, % | 43 | 41 | 3-92 | 53 | 56 | 13-95 |
| Tree mortality | | | | | | |
| Fire-killed tree mortality, %[c] | 81 | 100 | 7-100 | 87 | 100 | 35-100 |
| Fire-killed basal area, %[c] | 75 | 100 | 1-100 | 86 | 100 | 33-100 |

[a] calculated from average of 20 unbroken co-dominant canopy trees per plot.
[b] calculated from average of the subset of 20 sampled trees that were alive at the time of fire.
[c] calculated from all trees in the plot.

**Table S7.** Plot-level measures of fire severity in forests that burned under moderate or extreme burning conditions.

| | Moderate burning conditions | | | | Extreme burning conditions | | |
|---|---|---|---|---|---|---|---|
| Fire-severity metric | Mean | Median | Range | *P* | Mean | Median | Range |
| Canopy | | | | | | | |
| Char height, m[a] | 7.6 | 4.8 | 0.7-20.9 | * | 9.8 | 9.9 | 0.3-22.0 |
| Bole scorch, percentage of circumference[a, d] | 77 | 87 | 20-100 | ** | 88 | 100 | 24-100 |
| Canopy fuels remaining, index[b] | 1.9 | 2.4 | 0-3.0 | ** | 1.5 | 1.9 | 0-3.0 |
| Deep charring into crown, percentage of basal area[c, d] | 8 | 3 | 0-32 | ** | 17 | 9 | 0-84 |
| Surface | | | | | | | |
| Post-fire litter + duff depth, mm | 12.4 | 9.9 | 0.8-37.5 | ** | 7.8 | 4.9 | 0.0-30.2 |
| Charred surface cover, % | 43 | 38 | 3-95 | | 49 | 49 | 6-92 |
| Tree mortality | | | | | | | |
| Fire-killed tree mortality, %[c, d] | 76 | 89 | 7-100 | ** | 88 | 100 | 12-100 |
| Fire-killed basal area, %[c, d] | 69 | 92 | 1-100 | ** | 86 | 100 | 7-100 |

*Significant difference between moderate and extreme conditions (Welch's t-test, $P < 0.10$).

**Significant difference between moderate and extreme conditions (Welch's t-test, $P < 0.05$).

[a] calculated from average of 20 unbroken co-dominant canopy trees per plot.

[b] calculated from average of the subset of 20 sampled trees that were alive at the time of fire.

[c] calculated from all trees in the plot.

[d] Statistical tests conducted on logit-transformed percentage to bound responses between 0% and 100%.

**Table S8.** General linear mixed models testing the effects of beetle outbreak severity (expressed as the percentage of tree BA that was beetle-killed) on canopy- and surface-fire severity.

| Response | Predictor | *β* | SE | *t* | *P* |
|---|---|---|---|---|---|
| **Red stage forests** | | | | | |
| **Char height, m**[a] | Moderate BC (intercept) | 2.19 | 1.93 | 1.38 | 0.26 |
| | **Extreme BC (intercept)** | **4.31** | **1.79** | **2.41** | **0.02** |
| | **Slope position** | **9.21** | **2.55** | **3.61** | **<0.01** |
| | Beetle-killed BA: Moderate BC | -3.27 | 6.34 | -0.52 | 0.61 |
| | Beetle-killed BA: Extreme BC | 3.47 | 3.85 | 0.90 | 0.37 |
| **Bole scorch, %**[a,d] | **Moderate BC (intercept)** | **1.13** | **0.54** | **2.09** | **0.04** |
| | **Extreme BC (intercept)** | **2.43** | **0.50** | **4.86** | **<0.01** |
| | Slope position | 0.75 | 0.69 | 1.09 | 0.28 |
| | Beetle-killed BA: Moderate BC | -0.95 | 1.72 | -0.55 | 0.58 |
| | Beetle-killed BA: Extreme BC | 0.09 | 1.04 | 0.08 | 0.93 |
| **Canopy fuels remaining, Index**[b] | **Moderate BC (intercept)** | **2.70** | **0.32** | **8.55** | **<0.01** |
| | **Extreme BC (intercept)** | **2.75** | **0.30** | **9.21** | **<0.01** |
| | **Slope position** | **-1.90** | **0.45** | **-4.23** | **<0.01** |
| | Beetle-killed BA: Moderate BC | 1.34 | 1.11 | 1.22 | 0.23 |
| | **Beetle-killed BA: Extreme BC** | **-1.20** | **0.68** | **-1.76** | **0.08** |
| **Deep charring into crown, percentage of BA**[c,d] | **Moderate BC (intercept)** | **-3.44** | **0.35** | **-9.93** | **<0.01** |
| | **Extreme BC (intercept)** | **-3.76** | **0.33** | **-11.47** | **<0.01** |
| | **Slope position** | **1.49** | **0.49** | **3.03** | **<0.01** |
| | Beetle-killed BA: Moderate BC | -0.21 | 1.21 | -0.17 | 0.86 |
| | **Beetle-killed BA: Extreme BC** | **3.44** | **0.75** | **4.60** | **<0.01** |
| **Tree mortality, % of BA,** BA alive at time of fire[c,d] | Moderate BC (intercept) | -0.58 | 0.68 | -0.85 | 0.40 |
| | **Extreme BC (intercept)** | **1.76** | **0.64** | **2.73** | **<0.01** |
| | **Slope position** | **2.09** | **0.97** | **2.17** | **0.03** |
| | Beetle-killed BA: Moderate BC | 1.37 | 2.38 | 0.57 | 0.57 |
| | Beetle-killed BA: Extreme BC | -0.65 | 1.47 | -0.44 | 0.66 |
| **Tree mortality, % of trees,** trees alive at time of fire[c,d] | **Moderate BC (intercept)** | **0.99** | **0.58** | **1.71** | **0.09** |
| | **Extreme BC (intercept)** | **2.28** | **0.55** | **4.15** | **<0.01** |
| | **Slope position** | **1.42** | **0.82** | **1.72** | **0.09** |
| | Beetle-killed BA: Moderate BC | -1.12 | 2.03 | -0.55 | 0.58 |
| | Beetle-killed BA: Extreme BC | -0.73 | 1.25 | -0.58 | 0.56 |
| **Litter + duff depth, mm** | **Moderate BC (intercept)** | **9.02** | **3.54** | **2.54** | **0.01** |
| | **Extreme BC (intercept)** | **7.24** | **3.48** | **2.08** | **0.04** |
| | Slope position | -2.21 | 1.98 | -1.12 | 0.27 |
| | Beetle-killed BA: Moderate BC | 3.76 | 4.97 | 0.76 | 0.45 |
| | Beetle-killed BA: Extreme BC | 2.77 | 2.95 | 0.94 | 0.35 |
| **Charred surface cover, %**[a] | **Moderate BC (intercept)** | **-1.15** | **0.46** | **-2.49** | **0.02** |
| | Extreme BC (intercept) | -0.62 | 0.43 | -1.43 | 0.16 |
| | **Slope position** | **1.07** | **0.53** | **2.01** | **0.05** |
| | Beetle-killed BA: Moderate BC | -0.51 | 1.33 | -0.39 | 0.70 |
| | Beetle-killed BA: Extreme BC | 0.31 | 0.80 | 0.39 | 0.70 |
| **Gray stage forests** | | | | | |
| **Char height, m**[a] | **Moderate BC (intercept)** | **9.29** | **3.15** | **2.95** | **<0.01** |
| | Extreme BC (intercept) | 3.67 | 5.25 | 0.70 | 0.49 |
| | Slope position | 2.18 | 6.16 | 0.35 | 0.73 |
| | Beetle-killed BA: Moderate BC | 1.60 | 11.06 | 0.14 | 0.89 |
| | Beetle-killed BA: Extreme BC | 9.55 | 11.30 | 0.85 | 0.41 |
| **Bole scorch, %**[a,d] | **Moderate BC (intercept)** | **2.17** | **0.68** | **3.20** | **<0.01** |
| | Extreme BC (intercept) | 0.87 | 1.13 | 0.77 | 0.45 |

| | | | | | |
|---|---|---|---|---|---|
| | Slope position | -0.33 | 1.33 | -0.25 | 0.80 |
| | Beetle-killed BA: Moderate BC | 1.06 | 2.39 | 0.44 | 0.66 |
| | **Beetle-killed BA: Extreme BC** | **7.30** | **2.44** | **2.99** | **<0.01** |
| **Canopy fuels remaining, Index[b]** | **Moderate BC (intercept)** | **1.75** | **0.53** | **3.33** | **<0.01** |
| | **Extreme BC (intercept)** | **2.51** | **0.88** | **2.85** | **<0.01** |
| | Slope position | -0.18 | 1.03 | -0.17 | 0.86 |
| | Beetle-killed BA: Moderate BC | -1.05 | 1.85 | -0.57 | 0.58 |
| | Beetle-killed BA: Extreme BC | -2.81 | 1.89 | -1.48 | 0.15 |
| **Deep charring into crown, percentage of BA[c,d]** | **Moderate BC (intercept)** | **-2.98** | **0.40** | **-7.39** | **<0.01** |
| | **Extreme BC (intercept)** | **-3.27** | **0.67** | **-4.86** | **<0.01** |
| | Slope position | -0.23 | 0.79 | -0.29 | 0.78 |
| | **Beetle-killed BA: Moderate BC** | **4.40** | **1.42** | **3.11** | **<0.01** |
| | **Beetle-killed BA: Extreme BC** | **5.51** | **1.45** | **3.80** | **<0.01** |
| **Tree mortality, % of BA,** BA alive at time of fire[c,d] | **Moderate BC (intercept)** | **2.04** | **0.73** | **2.81** | **<0.01** |
| | Extreme BC (intercept) | 0.22 | 1.22 | 0.18 | 0.86 |
| | Slope position | 1.04 | 1.43 | 0.73 | 0.47 |
| | Beetle-killed BA: Moderate BC | 0.18 | 2.56 | 0.07 | 0.94 |
| | **Beetle-killed BA: Extreme BC** | **6.85** | **2.62** | **2.62** | **0.01** |
| **Tree mortality, % of trees,** trees alive at time of fire[c,d] | **Moderate BC (intercept)** | **2.20** | **0.71** | **3.11** | **<0.01** |
| | Extreme BC (intercept) | 0.70 | 1.18 | 0.59 | 0.56 |
| | Slope position | 0.45 | 1.39 | 0.32 | 0.75 |
| | Beetle-killed BA: Moderate BC | 1.00 | 2.49 | 0.40 | 0.69 |
| | **Beetle-killed BA: Extreme BC** | **6.89** | **2.54** | **2.71** | **0.01** |
| **Litter + duff depth, mm** | **Moderate BC (intercept)** | **21.38** | **4.49** | **4.76** | **<0.01** |
| | **Extreme BC (intercept)** | **26.25** | **6.62** | **3.97** | **<0.01** |
| | Slope position | -8.74 | 7.42 | -1.18 | 0.25 |
| | Beetle-killed BA: Moderate BC | 2.32 | 12.89 | 0.18 | 0.86 |
| | Beetle-killed BA: Extreme BC | -9.15 | 13.31 | -0.69 | 0.50 |
| **Charred surface cover, %[a]** | Moderate BC (intercept) | -0.17 | 0.61 | -0.28 | 0.78 |
| | Extreme BC (intercept) | -1.28 | 1.02 | -1.25 | 0.22 |
| | Slope position | 0.35 | 1.20 | 0.29 | 0.77 |
| | Beetle-killed BA: Moderate BC | 2.76 | 2.15 | 1.28 | 0.21 |
| | **Beetle-killed BA: Extreme BC** | **3.91** | **2.20** | **1.78** | **0.09** |
| **All forests (stages combined)** | | | | | |
| **Char height, m[a]** | **Moderate BC (intercept)** | **5.68** | **1.51** | **3.77** | **<0.01** |
| | **Extreme BC (intercept)** | **4.09** | **1.74** | **2.36** | **0.02** |
| | **Slope position** | **7.02** | **2.37** | **2.96** | **<0.01** |
| | Beetle-killed BA: Moderate BC | -5.21 | 5.50 | -0.95 | 0.35 |
| | Beetle-killed BA: Extreme BC | 5.52 | 3.91 | 1.41 | 0.16 |
| **Bole scorch, %[a,d]** | **Moderate BC (intercept)** | **1.72** | **0.39** | **4.44** | **<0.01** |
| | **Extreme BC (intercept)** | **2.20** | **0.45** | **4.94** | **<0.01** |
| | Slope position | 0.33 | 0.60 | 0.55 | 0.58 |
| | Beetle-killed BA: Moderate BC | -1.03 | 1.39 | -0.74 | 0.46 |
| | Beetle-killed BA: Extreme BC | 1.26 | 0.98 | 1.28 | 0.20 |
| **Canopy fuels remaining, Index[b]** | **Moderate BC (intercept)** | **2.35** | **0.26** | **9.11** | **<0.01** |
| | **Extreme BC (intercept)** | **2.75** | **0.30** | **9.28** | **<0.01** |
| | **Slope position** | **-1.45** | **0.41** | **-3.56** | **<0.01** |
| | Beetle-killed BA: Moderate BC | 0.91 | 0.94 | 0.97 | 0.34 |
| | **Beetle-killed BA: Extreme BC** | **-1.66** | **0.67** | **-2.49** | **0.01** |
| **Deep charring into crown, percentage of BA[c,d]** | **Moderate BC (intercept)** | **-3.30** | **0.25** | **-12.97** | **<0.01** |
| | **Extreme BC (intercept)** | **-3.71** | **0.29** | **-12.64** | **<0.01** |
| | **Slope position** | **1.09** | **0.40** | **2.72** | **<0.01** |
| | Beetle-killed BA: Moderate BC | 0.90 | 0.93 | 0.97 | 0.34 |

| | | | | | |
|---|---|---|---|---|---|
| | **Beetle-killed BA: Extreme BC** | **3.88** | **0.66** | **5.88** | **<0.01** |
| **Tree mortality, % of BA,** BA alive at time of fire[c,d] | Moderate BC (intercept) | 0.66 | 0.50 | 1.31 | 0.19 |
| | **Extreme BC (intercept)** | **1.32** | **0.58** | **2.27** | **0.03** |
| | **Slope position** | **2.10** | **0.79** | **2.64** | **<0.01** |
| | Beetle-killed BA: Moderate BC | -0.36 | 1.84 | -0.20 | 0.85 |
| | Beetle-killed BA: Extreme BC | 0.47 | 1.31 | 0.36 | 0.72 |
| **Tree mortality, % of trees,** trees alive at time of fire[c,d] | **Moderate BC (intercept)** | **1.60** | **0.43** | **3.68** | **<0.01** |
| | **Extreme BC (intercept)** | **1.95** | **0.50** | **3.90** | **<0.01** |
| | **Slope position** | **1.22** | **0.68** | **1.78** | **0.08** |
| | Beetle-killed BA: Moderate BC | -1.20 | 1.58 | -0.76 | 0.45 |
| | Beetle-killed BA: Extreme BC | 0.48 | 1.12 | 0.42 | 0.67 |
| **Litter + duff depth, mm** | **Moderate BC (intercept)** | **14.04** | **3.26** | **4.30** | **<0.01** |
| | **Extreme BC (intercept)** | **13.41** | **3.39** | **3.96** | **<0.01** |
| | Slope position | -2.80 | 2.30 | -1.22 | 0.23 |
| | Beetle-killed BA: Moderate BC | 2.84 | 5.23 | 0.54 | 0.59 |
| | Beetle-killed BA: Extreme BC | 0.54 | 3.54 | 0.15 | 0.88 |
| **Charred surface cover, %[a]** | **Moderate BC (intercept)** | **-0.63** | **0.35** | **-1.79** | **0.08** |
| | **Extreme BC (intercept)** | **-0.68** | **0.40** | **-1.69** | **0.09** |
| | Slope position | 0.82 | 0.51 | 1.61 | 0.11 |
| | Beetle-killed BA: Moderate BC | -0.03 | 1.16 | -0.03 | 0.98 |
| | Beetle-killed BA: Extreme BC | 0.99 | 0.81 | 1.23 | 0.22 |

Burning conditions, slope position, and prefire beetle outbreak severity were included as fixed effects. Fire name (effects not shown) was included as a random effect. Burning conditions is a categorical variable with each burning conditions as a different model intercept. Significant ($P < 0.10$) terms in models are in bold. The beetle-killed BA is the beetle outbreak severity, expressed as the percentage of tree BA that was beetle-killed before fire. “Beetle-killed BA: moderate BC” is the beetle effect under moderate burning conditions and “beetle-killed BA: extreme BC” is the beetle effect under extreme burning conditions. BC, burning conditions; Slope position, local elevation for each plot rescaled from 0 (bottom of slope) to 1 (ridge top).

[a] calculated from average of 20 unbroken co-dominant canopy trees per plot.

[b] calculated from average of the subset of 20 sampled trees that were alive at the time of fire.

[c] calculated from all trees in the plot.

[d] Logit-transformed percentage to bound responses between 0% and 100%.

**Table S9.** Overall postfire conifer seedling density in each outbreak stage and fire severity class combination.

| Tree species<br>**No. of plots present** | Outbreak stage | Fire severity class | Post-fire seedlings per hectare | | | Correlation with beetle outbreak severity in conspecific trees only | | |
|---|---|---|---|---|---|---|---|---|
| | | | min - max | mean | median | $r_s$ | df[a] | *P* |
| **Subalpine fir** | | | | | | | | |
| **20 out of 59 plots** | All stages combined | All classes combined | 0 - 26,704 | 908 | 0 | -0.03 | 57 | 0.84 |
| | | Severe surface | 0 - 26,704 | 1,783 | 130 | -0.08 | 28 | 0.68 |
| | | Crown | 0 - 88 | 3 | 0 | -0.08 | 27 | 0.70 |
| | Red stage | All classes combined | 0 - 26,704 | 1,401 | 0 | 0.02 | 35 | 0.91 |
| | | Severe surface | 0 - 26,704 | 2,875 | 257 | -0.07 | 16 | 0.79 |
| | | Crown | 0 - 88 | 5 | 0 | -0.06 | 17 | 0.82 |
| | Gray stage | All classes combined | 0 - 586 | 79 | 0 | -0.29 | 20 | 0.19 |
| | | Severe surface | 0 - 586 | 144 | 85 | -0.49 | 10 | 0.11 |
| | | Crown[b] | 0 | 0 | 0 | n/a | n/a | n/a |
| **Engelmann spruce** | | | | | | | | |
| **8 out of 31 plots** | All stages combined | All classes combined | 0 – 59,319 | 2,349 | 0 | -0.06 | 29 | 0.73 |
| | | Severe surface | 0 – 59,319 | 3,158 | 0 | -0.06 | 21 | 0.78 |
| | | Crown | 0 - 175 | 22 | 0 | -0.16 | 6 | 0.70 |
| | Red stage | All classes combined | 0 – 59,319 | 4,258 | 0 | -0.08 | 14 | 0.76 |
| | | Severe surface | 0 – 59,319 | 5,560 | 0 | -0.10 | 11 | 0.74 |
| | | Crown[b] | 0 - 175 | 58 | 0 | n/a | n/a | n/a |
| | Gray stage | All classes combined | 0 - 179 | 24 | 0 | -0.14 | 13 | 0.61 |
| | | Severe surface | 0 - 179 | 35 | 0 | -0.17 | 8 | 0.65 |
| | | Crown[b] | 0 | 0 | 0 | n/a | n/a | n/a |
| **Douglas-fir** | | | | | | | | |
| **3 out of 26 plots** | All stages combined | All classes combined | 0 - 187 | 17 | 0 | -0.18 | 24 | 0.37 |
| | | Severe surface | 0 - 187 | 35 | 0 | -0.20 | 11 | 0.51 |
| | | Crown[b] | 0 | 0 | 0 | n/a | n/a | n/a |
| | Red stage | All classes combined | 0 - 187 | 20 | 0 | -0.18 | 21 | 0.41 |
| | | Severe surface | 0 - 187 | 38 | 0 | -0.18 | 10 | 0.57 |
| | | Crown[b] | 0 | 0 | 0 | n/a | n/a | n/a |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Gray stage | All classes combined[b] | 0 | 0 | 0 | n/a | n/a | n/a |
| | | Severe surface[b] | 0 | 0 | 0 | n/a | n/a | n/a |
| | | Crown[b] | 0 | 0 | 0 | n/a | n/a | n/a |
| **Whitebark pine** | | | | | | | | |
| **1 out of 32 plots** | All stages combined | All classes combined | 0 - 397 | 12 | 0 | -0.08 | 30 | 0.67 |
| | | Severe surface[b] | 0 | 0 | 0 | n/a | n/a | n/a |
| | | Crown | 0 - 397 | 25 | 0 | -0.24 | 14 | 0.37 |
| | Red stage | All classes combined | 0 - 397 | 26 | 0 | -0.12 | 13 | 0.67 |
| | | Severe surface[b] | 0 | 0 | 0 | n/a | n/a | n/a |
| | | Crown | 0 - 397 | 50 | 0 | -0.27 | 6 | 0.52 |
| | Gray stage | All classes combined[b] | 0 | 0 | 0 | n/a | n/a | n/a |
| | | Severe surface[b] | 0 | 0 | 0 | n/a | n/a | n/a |
| | | Crown[b] | 0 | 0 | 0 | n/a | n/a | n/a |

Spearman rank correlations (rs) testing the relationship between postfire conifer seedling density and prefire beetle outbreak severity (percentage of conspecific tree BA killed by bark beetles). Tests were conducted across all outbreak stages and fire severity classes, and individually in each combination of outbreak stage and fire severity class. Engelmann spruce accounted for 16% subalpine fir 6%, and Douglas-fir, and whitebark pine <1% of all postfire seedlings. n/a, not applicable. Plots where the tree species was not present prefire were excluded before analysis.

[a] Based on the number of plots in each combination of fire severity class and outbreak stage.

[b] No test was possible (n/a) because there were no tree seedlings present in stands of this outbreak stage and fire severity combination, regardless of beetle outbreak severity, or there were too few plots (fewer than 2) in the category to perform a test.

**Table S10.** Annual water year moisture deficit (Potential evapotranspiration - actual evapotranspiration, in mm) from 1984 – 2012, averaged across all 1/8-degree grid cells that cover the Northern Rockies Ecoregion (*n* = 2,191 grid cells). Higher values indicated greater moisture deficit (more drought stress), whereas lower values indicate higher moisture availability and lesser moisture deficit (drought stress). Percent of average is computed from the average (437 mm) between 1984 and 2012. Data source: (Westerling et al. 2011).

| Water Year | Annual water year moisture deficit (mm) | Percent of 1984-2012 average (+ / - ) | Standard deviations from 1984-2012 average (+ / - ) |
|---|---|---|---|
| 1984 | 332 | -24 | -1.28 |
| 1985 | 452 | +3 | +0.18 |
| 1986 | 364 | -17 | -0.90 |
| 1987 | 482 | +10 | +0.55 |
| 1988 | 605 | +38 | +2.05 |
| 1989 | 439 | +0 | +0.02 |
| 1990 | 460 | +5 | +0.27 |
| 1991 | 423 | -3 | -0.18 |
| 1992 | 515 | +18 | +0.95 |
| 1993 | 306 | -30 | -1.60 |
| 1994 | 558 | +28 | +1.48 |
| 1995 | 318 | -27 | -1.45 |
| 1996 | 371 | -15 | -0.81 |
| 1997 | 291 | -33 | -1.78 |
| 1998 | 344 | -21 | -1.14 |
| 1999 | 385 | -12 | -0.64 |
| 2000 | 539 | +23 | +1.24 |
| 2001 | 540 | +24 | +1.26 |
| 2002 | 455 | +4 | +0.22 |
| 2003 | 507 | +16 | +0.85 |
| 2004 | 422 | -3 | -0.19 |
| 2005 | 409 | -6 | -0.34 |
| 2006 | 439 | +1 | +0.02 |
| 2007 | 535 | +22 | +1.19 |
| 2008 | 424 | -3 | -0.16 |
| 2009 | 427 | -2 | -0.12 |
| 2010 | 371 | -15 | -0.81 |
| 2011 | 441 | +1 | +0.05 |
| 2012 | 524 | +20 | +1.06 |

# Chapter 4 - Spatial heterogeneity of burn severity in forests of the Northern Rocky Mountains (1984-2010)

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## Abstract

Context: Wildfires produce tremendous heterogeneity in burn severity that governs forest-landscape structure and function. Climate change is increasing wildfire frequency and area burned, but little is known about the controls on spatial heterogeneity of burn severity and/or whether heterogeneity is changing during a period of increased fire activity.

Objectives: In this study, I developed a field-validated burn severity atlas to characterize spatial heterogeneity of burn severity at two spatial extents (ecoregion and fire). Focusing on stand-replacing (SR) forest fire, I asked the following questions: 1) How does spatial heterogeneity vary by forest type? 2) What are the dominant controls of spatial heterogeneity in burn severity? 3) Is spatial heterogeneity and/or the primary drivers of heterogeneity changing over time?

Methods: The study includes all forest fires between the years 1984 and 2010 in the US Northern Rocky Mountains. I used linear regression and Random Forests, respectively, to test for trends in spatial heterogeneity of burn severity over time and for shifts in the drivers of those trends.

Results: Calibration with extensive field data allowed reliable mapping of SR fire (e.g., $R^2$ =0.62 for canopy tree mortality). Subalpine forests exhibited more SR fire, and larger, simpler shaped SR-fire patches than mid-montane forests. Most metrics of spatial heterogeneity of SR were affected by fire size and proportion SR, but few changed over time. Climate was most important for driving spatial heterogeneity of burn severity in subalpine forests, whereas topography and climate were of more equal importance in mid-montane forests. Differences between analysis extents (ecoregion, fire) yielded similar results.

Conclusions: Findings demonstrate quantifiable differences among forest types in the spatial patterns and drivers of wildfire severity. The importance of climate variables in driving fire size and proportion SR, combined with strong control of fire size and proportion SR on spatial heterogeneity of burn severity suggests that future fire patterns will change substantially in coming decades with potentially widespread consequences for forest landscape heterogeneity.

Keywords: Forest fires, burn severity, RdNBR, stand-replacing fire, conifer forest, climate change.

## Introduction

Natural disturbances promote heterogeneity in ecosystems worldwide (Turner and Dale 1998). Fire is the dominant disturbance in many forest ecosystems, with even very large wildfires producing complex spatial mosaics of varying burn severity (Keane et al 2008). Within fires, patches of severely burned (or stand replacing, SR) area vary in size, shape, and arrangement; and spatial heterogeneity of burn severity is widely recognized as an important driver of postfire forest structure and resilience (Schoennagel et al 2008). Following a fire, the mosaic of burned and unburned forest influences vegetation succession (Turner et al 1994; Turner et al 1997; Donato et al 2009; Haire and McGarigal 2010), carbon storage (Turner et al 2004; Kashian et al 2006; Meigs et al 2011), and wildlife habitat (Boyce et al 2003) for decades to centuries (Kashian et al 2005) - ultimately governing delivery of myriad ecosystem services (Turner et al 2013). Climate warming is causing observed and predicted increases in fire frequency and area burned in many fire-prone regions (Westerling et al 2006; Flannigan et al 2009; Westerling et al 2011), but little is known about whether spatial heterogeneity of burn severity is, or should be expected to, change under periods of increasing fire activity.

Spatial heterogeneity of burn severity refers to the composition and configuration of fire severity [defined as the degree of ecological change caused by a fire, typically measured by the amount of vegetation killed by fire (Keeley 2009)]. Widespread availability of satellite data from the Landsat TM project and developments in satellite indices of burn severity (Lentile et al 2006) now allow for spatially detailed (30-m resolution), wall-to-wall mapping of fire-severity mosaics. Combined with heightened interest spurred by recent increases in wildfire activity, availability of satellite data has catalyzed research of fire severity patterns (e.g., Miller et al

2008; Miller et al 2011; Thode et al 2011; Dillon et al 2011; Miller and Safford 2012; Hanson and Odion 2014). Most research has focused on the *composition* of fire severity (e.g,, the proportion of different fire-severity classes within fires), whereas the spatial *configuration* of fire severity (e.g., average patch size and shape for high-severity fire) has received less attention (but see Cansler and McKenzie 2014). To build a solid understanding of spatial heterogeneity of burn severity requires tracking metrics over space and time, and testing relationships between patterns and potential drivers.

Spatial heterogeneity of burn severity may be driven by a combination of top-down (e.g., climate) and bottom-up (e.g., topography and vegetation/fuels) controls, in ways similar to fire size and the proportion SR. For example, the occurrence of large wildfires is driven by short- and long-term climate conditions that pre-condition live and dead biomass (i.e., fuels) (Westerling et al 2006; Littell et al 2009; Westerling et al 2011). Vegetation (via flammability or continuity) and topography (via direct barriers or indirectly through effects on vegetation) can further promote or constrain fire spread (e.g., Flatley et al 2010). Fire severity may respond similarly to drivers, but direct tests of these relationships are lacking. Proportion at high severity is affected by climate and topography at regional scales (e.g., Dillon et al 2011), but research examining the configuration of burn severity has been conducted mostly in isolated fire events (e.g., Collins and Stephens 2010). Further, the influence of top-down vs. bottom-up drivers of spatial heterogeneity of burn severity may vary in different forest types (Cansler and McKenzie 2014), and similar to controls of fire size, may be non-stationary through time (Parisien et al 2011).

Alternatively, spatial heterogeneity of burn severity may be controlled tightly by landscape (i.e., fire) size and proportion SR, such that variability can be explained primarily by these two measures (and thus indirectly by top-down vs. bottom-up drivers), rather than directly by climate, topography, and vegetation. The proportion of a landscape occupied by a focal cover type can impose strong constraints for metrics of spatial configuration, with configuration metrics sometimes exhibiting threshold-like behavior once a critical proportion cover is reached (Gustafson and Parker 1992). If spatial heterogeneity of burn severity is tightly controlled by burned area and proportion SR, simple predictions of future fire activity (occurrence and size) will lend valuable insight into future burn severity configuration. The ability to detect trends in spatial heterogeneity of burn severity may also depend on the landscape extent in which analyses are conducted (Turner et al 2001). For example, patterns detected within the perimeter of individual fires (i.e, fire extent) may be different than patterns emerging at a regional scale where all fires are combined (i.e., ecoregion extent). Nearly all studies that have examined fire severity patterns do so at a single extent (most commonly individual fires), but whether the ability to detect trends differ by analysis extent has not been tested.

The Northern Rockies (NR) ecoregion is a large fire-prone forested region with sharp increases in fire activity in recent decades (Westerling et al 2006; Morgan et al 2008). Within the NR, forest types (i.e., fuel structures) and topographic context settings vary considerably, with the patterns and controls over spatial heterogeneity of burn severity likely context-dependent - similar to other regions (e.g., Cansler and McKenzie 2014). Fire activity in the NR is predicted to increase substantially over the next century (Westerling et al 2011), and understanding how this projected increase in fire activity will affect forest heterogeneity is critical for ecosystem management and conservation planning (Turner et al 2013).

In this study, I examine patterns and drivers of spatial heterogeneity in burn severity in forests of the Northern Rocky Mountains. First, I developed a field-calibrated fire-severity atlas of all large fires (> 250 ha) occurring between 1984 and 2010 in the Northern Rockies ecoregion, testing the relationship between a commonly used fire-severity index and several field measures of fire severity. Using fire severity maps classified into SR and less than SR fire I asked the following research questions about spatial heterogeneity in burn severity: 1) How does spatial heterogeneity of burn severity vary by dominant forest types (subalpine, mid-montane) within the NR ecoregion? 2) What are the dominant controls on spatial heterogeneity of burn severity for each forest type? 3) Is spatial heterogeneity of burn severity and/or the dominant drivers of spatial heterogeneity in burn severity changing over time (1984-2010)? For each of these questions, I tested if patterns or relationships differed by the landscape extent (NR ecoregion, or individual fire) of analysis. I expected spatial heterogeneity of burn severity to differ by forest type, corresponding to well-documented differences in fire regimes between forest types (Baker 2009). I expected the drivers of spatial heterogeneity of burn severity to differ by forest type, corresponding to different controls on fire activity (Schoennagel et al 2004). If spatial heterogeneity of burn severity is driven by the same variables as fire activity, I expected heterogeneity to decrease over time - characterized by an increase in larger, simpler shaped SR fire patches with more core area as fires become more dominated by SR fire. Finally, I expect trends to differ by analysis extent such that trends will be stronger at the ecoregion extent, as opposed to the fire extent where each fire (regardless of size) is weighted the same.

## Methods

### Study area

The Northern Rockies ecoregion encompasses EPA level III ecoregions 15, 16, 17, and 41, stretching from northwestern Wyoming to northeastern Washington through eastern Idaho and western Montana (Figure 1). The ecoregion is over 30 million hectares (ha), of which 22,400,343 ha (74%) is forest or woodland. Subalpine forests occupy the highest elevations (~1,500 to 3,000 m) and are dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta* var. *latifolia*), and whitebark pine (*Pinus albicaulis*). Subalpine forests account for 44.9% of the total forested area in the ecoregion (Appendix 1), and are characterized by infrequent, high-severity wildfires (Schoennagel et al 2004; Baker 2009). Mid-montane forests are situated at intermediate elevations (~750 to 2,500 m) and are dominated by Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), western larch (*Larix occidentalis*), ponderosa pine (*Pinus ponderosa*), limber pine (*Pinus flexilis*), and quaking aspen (*Populus tremuloides*). Mid-montane forests account for 52.7% of the total forested area in the ecoregion (Appendix 1), and the historical fire regime is mixed severity (Schoennagel et al 2004; Baker 2009). Low-montane forests and woodlands (~500 to 1,500 m elevation) are dominated by ponderosa pine, limber pine, and western juniper (*Juniperus occidentalis*), account for 2.5% of the total forested area in the ecoregion (Appendix 1), and area typified by a high-frequency but low-severity fire regime (Schoennagel et al 2004; Baker 2009).

### Field measures of fire severity

I used existing field data from 371 forest stands in nine different fires that burned in 2008 or 2011 in representative portions of the study region (Harvey et al 2013; Harvey et al 2014a; Harvey et al 2014b). Field data covered a wide range of topographic conditions, forest stand structure, and tree species composition that is broadly representative of the dominant forest types of the Northern Rockies (Appendix 2). Data from each plot included five measures of canopy-tree fire severity [tree mortality by basal area, tree mortality by number of trees, absolute char height (m), char height as % of tree height, % of bole circumference that was scorched), two measures of surface fire severity [postfire litter + duff depth (mm), % charred surface cover] (Harvey et al 2013; Harvey et al 2014a; Harvey et al 2014b), and one stand-level categorical measure of fire severity (unburned, light surface, severe surface, and crown) (Turner et al 1994) (Appendix 3).

### Satellite measures of fire severity

Satellite fire severity data at 30-m resolution were acquired from the Monitoring Trends in Burn Severity database (Eidenshink *et al.*, 2007; www.mtbs.gov) for all fires that occurred between 1984 and 2010 and had a perimeter within (or that at least partially intersected with) the boundary of the study area (Figure 1). Fires were retained for analysis if they met the following conditions: >50% of the area within the fire perimeter was forest vegetation; fire size was ≥ 250 ha; and the fire was not a prescribed fire. Fires were excluded from the study if either the pre or postfire satellite image was obstructed by the scanner line correction (SLC) failure on the Landsat 7 satellite, as analysis of spatial patterns was not possible because large swaths of data were missing. After excluding fires that met these conditions (68 fires, 455,177 total ha), the final dataset contained 668 fires. I used the Relative differenced Normalized Burn Ratio (RdNBR) as the satellite measure of burn severity; RdNBR accounts for differences in prefire vegetation biomass among locations and is therefore best suited for regional studies across different forest types (Miller and Thode 2007; Dillon et al 2011; Cansler and McKenzie 2014). By comparing differences between the near- and mid-infrared reflectance values in pre and postfire Landsat satellite images, RdNBR generates a continuous index of burn severity across an entire burned landscape. Higher values of RdNBR equate to greater burn severity; however the strength of relationships between RdNBR and field measures of burn severity can vary by region (Cansler and McKenzie 2012).

### Calibrating and validating RdNBR to field measures of fire severity

The RdNBR values were extracted for the location of each of the 371 field plots from burn severity maps. I compared linear, exponential, and logistic models by regressing each of the field measures of fire severity against RdNBR. I used 1,000 permutations of 60% (calibration) / 40% (validation) splits of the 371 field plots, with 60/40 splits stratified within each of the nine fires where field data were collected. Models with the highest calibration and validation $R^2$ values and the lowest calibration and validation root mean square error (RMSE) values were selected as the best model for each fire-severity variable.

### Generating classified maps of stand-replacing fire

I applied the formula from the best model for percent tree basal area killed by fire to determine the level of RdNBR which corresponds to SR fire, which I define as 90-95% (midpoint = 92.5%) basal area killed by fire. After reclassifying each map, a 3x3 majority filter was applied to minimize the influence of single-pixel patches, with the final result a binary map of SR fire and less than SR fire.

### Assigning vegetation, topography, and climate data to each fire

Each fire was assigned a single forest type based on the forest type (subalpine, mid montane, low montane, Appendix 1) that comprised the greatest number of cells within the fire perimeter. Forest types were based on the 30-m resolution environmental site potential (ESP) maps provided by the LANDFIRE vegetation mapping project, aggregated into three groups (Appendix 1). The ESP was chosen rather than existing vegetation because ESP is constant through time based on biophysical variables, whereas existing vegetation is influenced by fires that occurred in the study area.

Two topographic variables were extracted for each fire: mean elevation (m); and topographic complexity, which is the ratio of the total surface area within the perimeter of a fire to the flat planar area of a fire, where higher ratios of surface area to planar area indicate greater topographic complexity (Jenness 2004). Topographic data were extracted from a 30-m resolution digital elevation model, and a single value for each variable was assigned per fire.

Climate data for each fire were extracted by taking the area-weighted average value for each climate variable within each fire perimeter from an existing 12 x 12 km gridded hydroclimatic dataset for the region (Westerling et al 2011). Variables were among those with established relationships with fire frequency and area burned (Westerling et al 2006; Morgan et al 2008; Littell et al 2009; Westerling et al 2011) and included: maximum and average temperature (°C) the month when the fire started; average temperature (°C) the two months preceding the fire; total monthly precipitation (mm) the month when the fire started; total monthly precipitation (mm) the two months preceding the fire; peak snow water equivalent (kg/m$^2$) the winter preceding the fire, moisture deficit (mm) the month when the fire started; average moisture deficit (mm) the two months preceding the fire; cumulative moisture deficit (mm) for the water year (Oct. – Sept.) for the month when the fire started, and the total moisture deficit (mm) for the water year one year prior to the fire start. Because climate data were monthly resolution and fire start dates varied throughout the month when fires started, I included the month after the fire start date for the 'month when the fire started' variables. I included the month of the fire and preceding two months for the 'two months preceding the fire' variables. To standardize climate variables across fire locations, I re-scaled the values for each window of time to ± SD from the average over the 30-year period (1981-2010).

### Calculating landscape metrics of spatial heterogeneity of burn severity

For the ecoregion extent, a landscape was considered to be the entire area burned within the ecoregion. For each year, landscapes were generated using all burned area, burned area in subalpine forests, and burned area in mid-montane forests [*n* = 81 total landscapes (27 years for each of three forest groups)]. For the fire extent, a landscape was considered to be the interior of each burn perimeter of each fire (*n* = 668 total landscapes, one for each fire; 295 fires in mid montane, 353 fires in subalpine). All analyses that grouped landscapes by forest type excluded low-montane forests because of the small sample size (*n* = 20 fires). Landscapes at each extent were classified by burn severity (SR, not SR), and spatial heterogeneity of burn severity was characterized using seven metrics. In addition to the total area and proportion of the landscape that was SR, I calculated the SR area-weighted mean patch size and the SR area-weighed mean edge:area to provide a measure of patch size and shape complexity, respectively. Area-weighted means were chosen over arithmetic means because area-weighted means more accurately represent the 'average' cell in a landscape by weighting larger patches more, as a randomly selected cell in a landscape would have a higher probability of coming from a large patch. I also calculated the SR largest patch index, which represents a simple measure of dominance or aggregation, by quantifying the percentage of the landscape comprised by the largest SR patch. Finally, I calculated the total core area and the proportion of a landscape that was made up of core area (defined as locations within SR patches that are ≥ 150m from the edge of the patch). This distance was selected because it exceeds the probable dispersal distance for ~90% of seeds from most wind-dispersed NR conifers (Greene and Johnson 1996). Spatial pattern metrics were calculated in FRAGSTATS v4 (McGarigal et al 2012) and in R (R Development Core Team 2012). All patches were defined using the 8-neighbor rule.

### Analyses of trends in burn severity patterns

To compare spatial heterogeneity of burn severity between forest types, I compared means and standard errors for each metric at each landscape extent. To test the relationship between each metric of spatial heterogeneity of burn severity vs. area burned and proportion SR, I used Correlation (Spearman's rho) analysis. To test for trends in spatial metrics of burn severity over time (1984-2010), I used linear regression (with year as the term of interest) in models that contained burned area and/or proportion SR if those terms were significantly related to the response variable. All area measures (area burned, fire size, patch size, core area) were $\log_{10}$ transformed and all percent/proportion data were logit transformed prior to analysis.

### Analysis of drivers of burn severity patterns

Random Forests were used to rank the importance of topographic, vegetation, and climate variables for explaining variability in spatial heterogeneity of burn severity at the fire extent. Fire size and proportion SR were also included as predictor variables. For each metric, 1,000 regression trees were independently grown using random subsets of the predictor variables in the r-package ‘RandomForests.’ The increase in mean square error (IMSE) for each predictor variable when it was left out of the tree model was used to rank variable importance. For comparison across model runs for each response variable, predictor variable IMSE values were re-scaled as a percent of the total IMSE for all the variables summed. Analyses were conducted for all fires overall, and separately for fires occurring in subalpine and mid-montane forests. To test if the importance of drivers of spatial heterogeneity of burn severity have changed over time for each forest type (subalpine and mid-montane), separate Random Forest models were run separately for the early (1984-1997) and late (1998-2010) halves of the study period. For interpretability in comparison across time periods, percent IMSE values were aggregated into topography (elevation and SAR), vegetation (forest type), and climate (all climate variables) factors to illustrate if the amount of variability explained by each factor is changing over time. Analyses of predictor variables for spatial heterogeneity of burn severity were not conducted at the ecoregion extent because of unavailability of data at the appropriate scale.

## Results

### Field-validated fire severity atlas

Relationships between field measures of burn severity and RdNBR ranged from $R^2$ = 0.29 to 0.68, and $R^2$ values were similar between the calibration and validation datasets (Table 1, Figure 2). RMSE values ranged from 17 to 23%. Relationships were generally better for canopy-tree related measures than for forest floor measures. The cutoff for SR fire (90-95% of basal area killed by fire equated to an RdNBR value of 675 (Figure 2).

### Spatial heterogeneity in burn severity

From 1984 to 2010, a total of 668 named forest fires larger than 250 ha occurred in the NR ecoregion, burning 3,366,328 ha in total and accounting for ~15% of the total forested area in the Northern Rockies (Figure 1). Of this total burned area, 34% (1,152,636 ha) burned as SR fire, accounting for ~5% of the total forested area in the Northern Rockies. Of the total area burned, 9% (286,506 ha) was core area within SR patches and was greater than 150m from the nearest SR patch edge, accounting for ~1% of the total forested area in the Northern Rockies. Individual patches of SR fire ranged from less than 1 ha to over 25,000 ha. More than half of all patches were smaller than 0.5 ha, and more than two thirds were smaller than 1 ha; however, the summed area burned as SR fire in patches smaller than 1 ha accounted for only 1.7% of the total area in SR fire (Figure 3A). Greater than 75% of the total area of SR fire was in patches larger than100 ha, and nearly 50% was in patches larger than 1,000 ha (Figure 3A). Years with more total area burned had a greater proportion of the SR fire in larger patches. The within-year minimum patch size at which 50% of the total SR fire was captured increased with within-year area burned ($r_s = 0.44$, $P = 0.03$).

At the ecoregion extent, the total area burned, and amount and configuration of SR fire were all highly variable from year to year (Table 2). There were no fires recorded in 1993 and only one fire recorded in 1995. In contrast, 1988 had the most total area burned (944,454 ha), total SR area (373,189 ha), and total SR core area (109,964 ha). At the extent of individual fires, area burned varied by three orders of magnitude and the amount and configuration of SR fire was highly variable (Table 3).

Differences between forest types were detected at both the ecoregion- and fire- extents. At both extents, subalpine forests were characterized by more total area burned and more area burned as SR fire (both total area and percent of burned area) than mid-montane forests (Tables 2, 3). SR-fire patches in subalpine forests were larger and simpler shaped than in mid-montane forests, resulting in a greater largest patch index and more SR core area (total, and percent of burned area) (Tables 2, 3).

### Effects of fire size and proportion SR on spatial heterogeneity of burn severity

Area burned (or fire size) and proportion SR were strongly related to most metrics of spatial heterogeneity of burn severity at both landscape extents, but their relative importance differed by metric. The relationship between Proportion SR and area burned / fire size was variable, and only at the fire extent did proportion SR increase with burned area (Figures 4A, 5A). At both extents, SR patch complexity and SR proportion core area were most strongly affected by proportion SR, whereas SR patch size was affected by both area burned and proportion SR (Figures 4 and 5). The main differences among analysis extents were for SR largest patch index and total SR core area. At the ecoregion extent, total SR core area was most strongly related with area burned and the SR largest patch index was affected by both area burned and proportion SR (Figure 4). At the fire extent, SR largest patch index was most strongly related with proportion SR and total SR core area was affected by both area burned and proportion SR (Figure 5).

### Top-down vs. bottom-up controls on spatial heterogeneity of burn severity

Across forest types, nearly all of the explained variability in fire size was driven by climate (Figure 6A), whereas proportion SR was driven primarily by topography and forest type (Figure 6B). For fires in each forest type, climate remained the strongest driver of fire size (Figures 7A, 8A), but drivers of proportion SR differed. Climate variables explained most variation in proportion SR for subalpine forests, whereas topographic variables explained most variation for mid-montane forests. Across and within forest types, other metrics of spatial heterogeneity of burn severity were tightly controlled by fire size and proportion such that other variables provided little explanatory power once fire size and proportion SR were taken into account (Figures 6-8).

### Trends in patterns and drivers over time

At the ecoregion extent, the distribution of area burned in different patch sizes was variable from year to year, but the within-year minimum patch size at which 50% of the total SR fire was captured (777 ha) did not change over time ($r_s = -0.17$, $P = 0.42$, Figure 3B). Area burned and proportion SR did not change over time overall or for either forest type, although an increase in proportion SR was suggested for mid-montane forests (Figure 9). At the fire extent, area burned (fire size) did not change over time, but proportion SR increased from 0.22 to 0.27 across all forest types (Figure 10). The relatively flat trend in subalpine forests and near significant trend in mid-montane forests suggests that the greatest increase in proportion SR occurred in mid-montane forests. Trends over time were not detected for other metrics of spatial heterogeneity of burn severity at either scale, except for a slight decrease in patch shape complexity for subalpine forests at the ecoregion scale (Appendix 4).

Across time, the relative importance of climate and topography for explaining variability in spatial heterogeneity of burn severity shifted, although trends differed by forest type (Figure 11). For subalpine forests, the relative importance of climate variables decreased over time and the relative importance of topography variables increased for all metrics except patch shape complexity, which showed the opposite trend (Figure 11). In contrast, for mid-montane forests, most metrics showed an increase in the relative amount of variability explained by climate and a decrease in the amount explained by topography; SR largest patch index and SR proportion core area were exceptions to this trend (Figure 11). For both forest types, climate was the dominant driver of fire size in both time periods, although little total variance was explained for mid-montane forests (Figure 11).

## Discussion

### RdNBR and field measures of burn severity

This study produced the first quantitative assessment of how RdNBR relates to a wide range of fire-severity field measures across the NR ecoregion, and each relationship may be important for different ecological processes and/or management goals. Overall, the models indicate that RdNBR works best for field measures that relate to canopy tree mortality (actual tree mortality, bole scorch, and fire-severity classes based primarily on effects to canopy trees). RdNBR worked less well for char height, which may be related to the fact that bole scorch is tightly correlated with tree mortality (McHugh and Kolb 2003). RdNBR had a poor relationship with postfire litter + duff depth, with $R^2$ values similar to those reported elsewhere (Hudak et al 2007). In contrast, the relationship with charred surface cover was higher than expected from other studies (Hudak et al 2007) and almost as high as canopy-tree $R^2$ values. The difference between these two forest-floor measures is possibly because charred surface-cover is a direct byproduct of fire, whereas postfire litter + duff depth could be influenced by prefire litter + duff depth. That canopy fire-severity measures were more closely related to RdNBR than forest-floor measures is not surprising given that satellite sensors have a relatively unobstructed view of the canopy relative to the forest floor (Hudak et al 2007). These models relating RdNBR to field measures of fire severity will be useful for other researchers and managers in the NR region, and the approach can be applied in other systems. Accuracy for SR fire was within the range of other studies (see Cansler and McKenzie 2012 for a review), and employing bootstrapped model runs of training and validation splits ensures robust relationships with known accuracy. Maps of SR vs. non-SR fire using the threshold identified in this study can be applied to other analyses aimed at projecting postfire forest succession and/or ecosystem processes across the NR ecoregion.

Calibrating satellite indices of fire severity to ecologically meaningful variables has been a challenge for regional studies of fire severity (Miller et al 2009; Cansler and McKenzie 2012). A common approach uses the Composite Burn Index (CBI) (Key and Benson 2005) as a semi-quantitative index of field-calibrated fire severity. This approach has advantages of speed and simplicity: CBI is easily and rapidly collected in the field, allowing for extensive spatial coverage, and aggregates components of fire severity to a single number. However, disaggregating CBI-calibrated fire-severity maps into components of fire severity is challenging. Different components of a forest stand (or other vegetation structure) may project different spectral signals to satellite sensors. By quantitatively capturing different components of fire severity (e.g., canopy trees, understory ground cover), field measures and models relating to RdNBR can characterize burn severity in ways that are unique to each component within a forest. Future research could prioritize linking different field measures of fire severity (e.g., CBI, quantitative measures) to build extensive and compatible data archives of fire severity field sites for consistent region-wide mapping.

### Spatial heterogeneity of burn severity varies by forest type

This is the first study to quantitatively characterize multiple landscape metrics of SR fire across space and time for an entire ecoregion. In doing so, we identify important differences in spatial heterogeneity of burn severity among forest types than can serve as a valuable baseline for tracking future changes in fire severity patterns. For example, the data in Tables 1 and 2 present quantitative descriptions of fire severity patterns that highlight clear differences in fire regimes previously described qualitatively (e.g., Schoennagel et al 2004; Baker 2009). This study demonstrates that subalpine forests in the NR are characterized by more SR fire that is spatially aggregated in larger and simpler shaped patches than mid-montane forests, and the numbers provided can help in identify when a particular fire is inside or outside the range of what would be considered ‘normal’ for this forest type. There are well-documented adaptations to such fire patterns in subalpine forests, including light, wind-dispersed seeds and aerial seedbanks (i.e, serotinous cones) that enable capacity for rapid postfire tree establishment in large patches of SR fire (Harvey et al in prep; Turner et al 1997; McKenzie and Tinker 2012). This study also demonstrates that SR fire constitutes a substantial portion of contemporary mixed-severity fire regimes in mid-montane forests (Halofsky et al 2011; Perry et al 2011) at both the individual fire and ecoregion extent. The fire adaptations (e.g., thick bark, heavier seeds) of dominant trees in mid-montane forests are better suited to fire patterns characterized by smaller SR patches with more complex shapes (i.e., more edge), but these species can also rapidly colonize SR patches if burned areas are within dispersal distances from surviving trees (Harvey et al in prep). Approaches that combine dendroecological data, historical photographs, and/or modeled fire behavior can reconstruct spatial dynamics of fire regimes prior to the availability of satellite data (i.e., pre-1984), and aide in placing these contemporary fire patterns in a historical context (e.g., Hessburg et al 2007; Sherriff et al 2014).

## Controls of spatial heterogeneity of burn severity and changes over time

The lack of strong temporal trends detected in this study (Figures 9, 10) could be due to the short period of time (<30 yrs) over which satellite fire severity data are available. However, the increase in proportion SR across all forest types is reflective of expected future trends. Spatial heterogeneity of burn severity in our study was strongly controlled by fire size and proportion SR, elevating the importance of understanding the controls of these two key components of fire regimes in different forest types. Analyzing fires separately for subalpine and mid-montane forests allowed detection of relationships not evident at the ecoregion scale (Dillon et al 2011). For example, fire size and proportion SR were both strongly driven by climate for subalpine forests. In mid-montane forests, however, fire size was mostly explained by climate, whereas proportion SR was more strongly related to topography. These differences support the understanding that climate can override local topographic or vegetation controls on fire occurrence and severity in subalpine forests (Turner and Romme 1994; Bessie and Johnson 1995; Haire et al 2013), whereas more complex topography exerts control over fire size and severity in mid- and low-elevation forests (Perry et al 2011; Cansler and McKenzie 2014). They also suggest differences in how fires in each of these forest types may respond to future climate change. One of the key climate variables responsible for fire size in mid-montane forests and fire size and proportion SR in subalpine forests was water-year cumulative moisture deficit, which is predicted to increase substantially over the next century (Westerling et al 2011). This suggests that fire size and proportion SR are likely to increase in subalpine forests, and spatial heterogeneity of burn severity will respond accordingly (i.e., large, simple-shaped SR patches with high SR core area). In mid-montane forests, constraints on proportion SR imposed by topography may moderate changes to spatial heterogeneity of burn severity such that spatial patterns may not change as drastically with fire size.

Differences among forest types in top-down vs. bottom-up controls over time (Figure 11) provide support for dynamic, non-stationary fire-environment relationships (Parisien et al 2011), and may be an indication of subtle shifts in the controls on fire regimes in the NR that are already underway. The increase over time in the relative importance of topographic variables (Figure 9) may indicate that climate is becoming less limiting as the frequency of severe-drought years increases (Westerling et al 2011). Alternatively, mid-montane forests that were historically limited by a mixture of top-down and bottom-up controls (Perry et al 2011) may be headed toward more top-down control imposed by a warming climate. Monitoring the relationship between spatial heterogeneity of burn severity and the relative importance of drivers as climate change continues is a key research priority. Although not examined in this study, increasing fire frequency may also eventually lead to limits on burnable fuel, highlighting the importance of understanding how multiple fires in quick succession (i.e., “reburns”) may interact (Thompson et al 2007; Collins et al 2009; Holden et al 2010; Parks et al 2014). Eventually, fuel limitation may become the strongest driver of regional burn severity patterns.

### Analysis extent and spatial heterogeneity of burn severity

Scale has a strong influence on pattern detectability and inference (Levin 1995), and analysis extent is particularly influential on spatial patterns (Turner et al 2001). Contrary to expectations, however, there were few differences in patterns for spatial heterogeneity of burn severity between the ecoregion and fire extents. Most relationships between burned area and proportion SR vs. spatial heterogeneity of burn severity did not differ in direction or strength between scales (Figures 4 and 5). The main difference between analysis extents was for trends over time. Similar to Dillon et al. (2011), I found no evidence for an increase in the yearly total area burned or proportion of SR fire at the scale of the NR ecoregion. However, analyses at the fire scale revealed that individual fires, are, on average, burning with a greater percent at SR fire.

### Management implications and future research priorities

As a result of the complex mosaic of burn severity generated in the NR ecoregion between 1984 and 2010, more than 90% of the area burned as SR fire (and more than 98% of the total NR forested area) exists within 150 m of less-severe fire (i.e., where surviving prefire trees will provide a seed source). This heterogeneity is critical for the maintenance of myriad ecosystem services supplied by forests (Turner et al 2013), and it is important that fire and forest management activities do no homogenize burn landscapes through activities such as burnouts of unburned tree islands or widening of fire perimeters along edges (Stephens et al 2013). Preserving heterogeneity wherever possible will become even more pressing as a warming climate continues to increase fire activity (Westerling et al 2011) - especially if the relationships between spatial heterogeneity of burn severity and fire size/proportion SR presented here remain strong in the future.

The collective understanding of and ability to detect changes in spatial heterogeneity of burn severity can be improved by further research in several key directions. First, it is important to note that the satellite record of wildfires covers a ~30-year record of ecosystem change, and measuring longer trajectories of change remains difficult. The value of high spatial and spectral detail in this ~30-year record should not be understated, as it is nearly impossible to acquire this level of detail in historical records or future projections. Research that integrates detailed contemporary understanding of spatial heterogeneity with past data (Hessburg et al 2007; Williams and Baker 2012; Sherriff et al 2014) is a key frontier, and incorporating this understanding into modeling projections of future fire activity is needed. Second, examining burn severity patterns from the perspective of the forest landscape remaining after the fire (rather than from the perspective of the fire itself) may provide more ecologically meaningful metrics of forest ecosystem resilience. As an illustrative example, most fire severity studies (including this one) assume that the edges of burned patches are characterized by vegetation that will aide in re-seeding within the burned patch. Other cover types (e.g., rock, bare ground, non-forest vegetation), however, may actually occupy some edges. In such cases, postfire forest resilience may be overestimated from burn severity mosaics alone. Future research that attributes burn patch edges in automated ways can improve this situation. Finally, analyses of spatial patterns of burn severity can only be conducted with images where no portion of the image is obstructed. Approximately 9% of the total fires mapped between 2003 and 2011 were affected by swaths of ‘no data’ due to the SLC problem on the Landsat 7 satellite, and were therefore excluded from analyses. The launch of Landsat 8 in 2013 alleviates this problem into the future, but algorithms that can fill in gaps of no data by using multiple images simultaneously may help partially recover some of the missing data from 2003-2011

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## Tables

Table 1. Models relating each fire severity metric to RdNBR. Best models for each fires severity metric were selected based on the highest $R^2$ and lowest RMSE. Plots of each model run and raw data points are in Figure 2.

| Fire severity metric | Form | Model | $R^2_{cal}$ | $R^2_{val}$ | $RMSE_{cal}$ | $RMSE_{val}$ |
|---|---|---|---|---|---|---|
| Basal area killed by fire (%) | Logistic | $y = \frac{1}{(1 + e^{0.0066(288-RdNBR)})}$ | 0.62 | 0.60 | 22% | 22% |
| Trees killed by fire (%) | Logistic | $y = \frac{1}{(1 + e^{0.0064(259-RdNBR)})}$ | 0.63 | 0.62 | 20% | 20% |
| Char height (m) | Linear | $y = 0.19 + 0.0134(RdNBR)$ | 0.50 | 0.49 | 23% | 23% |
| Char height (% of tree height) | Logistic | $y = \frac{1}{(1 + e^{0.003(854-RdNBR)})}$ | 0.55 | 0.55 | 21% | 22% |
| Bole scorch (%) | Logistic | $y = \frac{1}{(1 + e^{0.0054(253-RdNBR)})}$ | 0.60 | 0.59 | 20% | 20% |
| Postfire litter + duff depth (mm) | Linear | $y = 18.1 \pm 0.0121(RdNBR)$ | 0.30 | 0.29 | 18% | 18% |
| Charred surface cover (%) | Exponential | $y = 0.1029(e^{0.0015*RdNBR})$ | 0.57 | 0.57 | 17% | 17% |
| Fire severity class (0,1,2,3) | Linear | $y = 0.4825 + 0.002(RdNBR)$ | 0.68 | 0.67 | 18% | 18% |

Table 2. Summary statistics for the ecoregion extent. Values are means (SE) from all years (*n* =27).

| | | | Total (all forest types combined) | | |
|---|---|---|---|---|---|
| | Mid-montane | Subalpine | Min – max | Mean (SE) | Median |
| Yearly area burned (ha) | 51,896 (18,651) | 71,319 (31,496) | 0 – 944,545 | 124,731 (42,072) | 34,962 |
| Stand-replacing fire | | | | | |
| Total area (ha) | 13,116 (5,449) | 29,203 (12,973) | 0 – 373,189 | 42,690 (15,706) | 9,982 |
| Percent of burned area (%) | 22 (2) | 41 (2) | 1 – 47 | 31 (2) | 34 |
| Mean patch size (area wtd., ha) | 866 (278) | 1,643 (365) | 0 – 7,578 | 1,468 (332) | 772 |
| Edge:area (area wtd., m/ha) | 211 (21) | 128 (6) | 93 – 600 | 165 (19) | 141 |
| Largest patch index (%) | 7 (1) | 12 (2) | | | |
| Core area, total (ha) | 2,783 (1,326) | 8,867 (4,319) | 0 – 109,964 | 10,611 (4,443) | 2,438 |
| Core area, percent of fire (%) | 4 (1) | 10 (1) | 0.0 – 17.1 | 6.9 (0.8) | 6.7 |

Table 3. Summary statistics for the fire extent. Values are means (SE) from all fire events (*n* =668).

| | | | Total (all forest types combined) | | |
|---|---|---|---|---|---|
| | Mid-montane | Subalpine | Min – max | Mean (SE) | Median |
| Number of fires | 295 | 353 | n/a | n/a | n/a |
| Total area burned | 1,400,428 | 1,923,740 | n/a | n/a | n/a |
| Fire size, mean (ha) | 4,747 (661) | 5,450 (1,064) | 260 – 229,048 | 5,039 (634) | |
| Fire size, median (ha) | 1,343 | 1,316 | | | 1,312 |
| Stand-replacing fire | | | | | |
| Total area (ha) | 1,200 (204) | 2,234 (436) | 0 – 113,393 | 1,726 (248) | 344 |
| Percent of burned area (%) | 20 (1) | 38 (1) | 0 – 83 | 29 (1) | 28 |
| Mean patch size (area wtd., ha) | 354 (70) | 677 (83) | 0 – 14,652 | 517 (54) | 106 |
| Edge:area (area wtd., m/ha) | 302 (13) | 174 (4) | 44 – 1,333 | 239 (7) | 190 |
| Largest patch index (%) | 12 (1) | 24 (1) | 0 – 82 | 18 (1) | 11 |
| Core area, total (ha) | 245 (55) | 603 (148) | 0 – 44,277 | 429 (82) | 28 |
| Core area, percent of fire (%) | 3.31 (0.35) | 7.12 (0.43) | 0.00 – 43.40 | 5.25 (0.29) | 1.96 |

# Figures

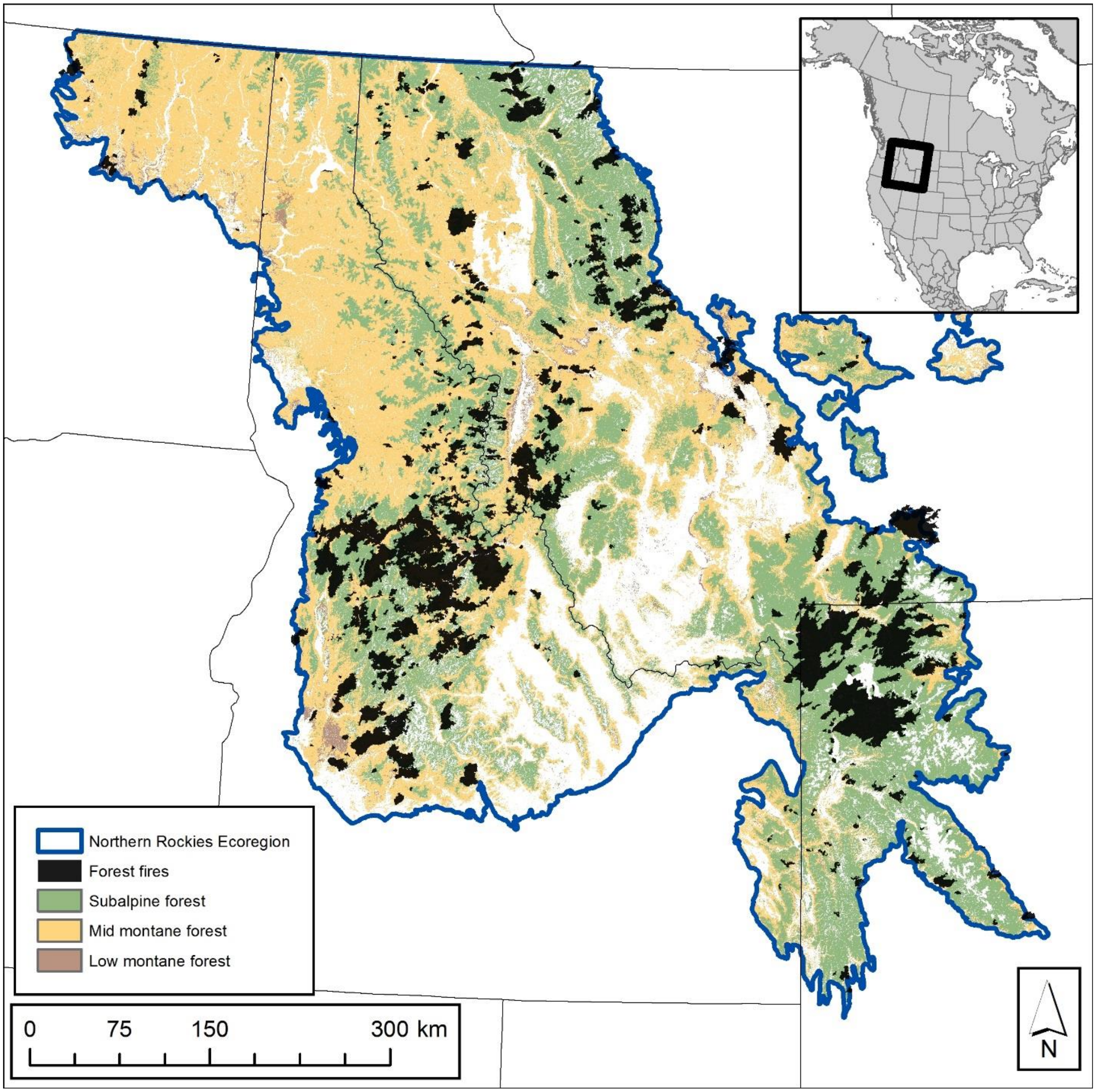


Figure 1. Northern Rockies study area with all forest fires that were included in this study.

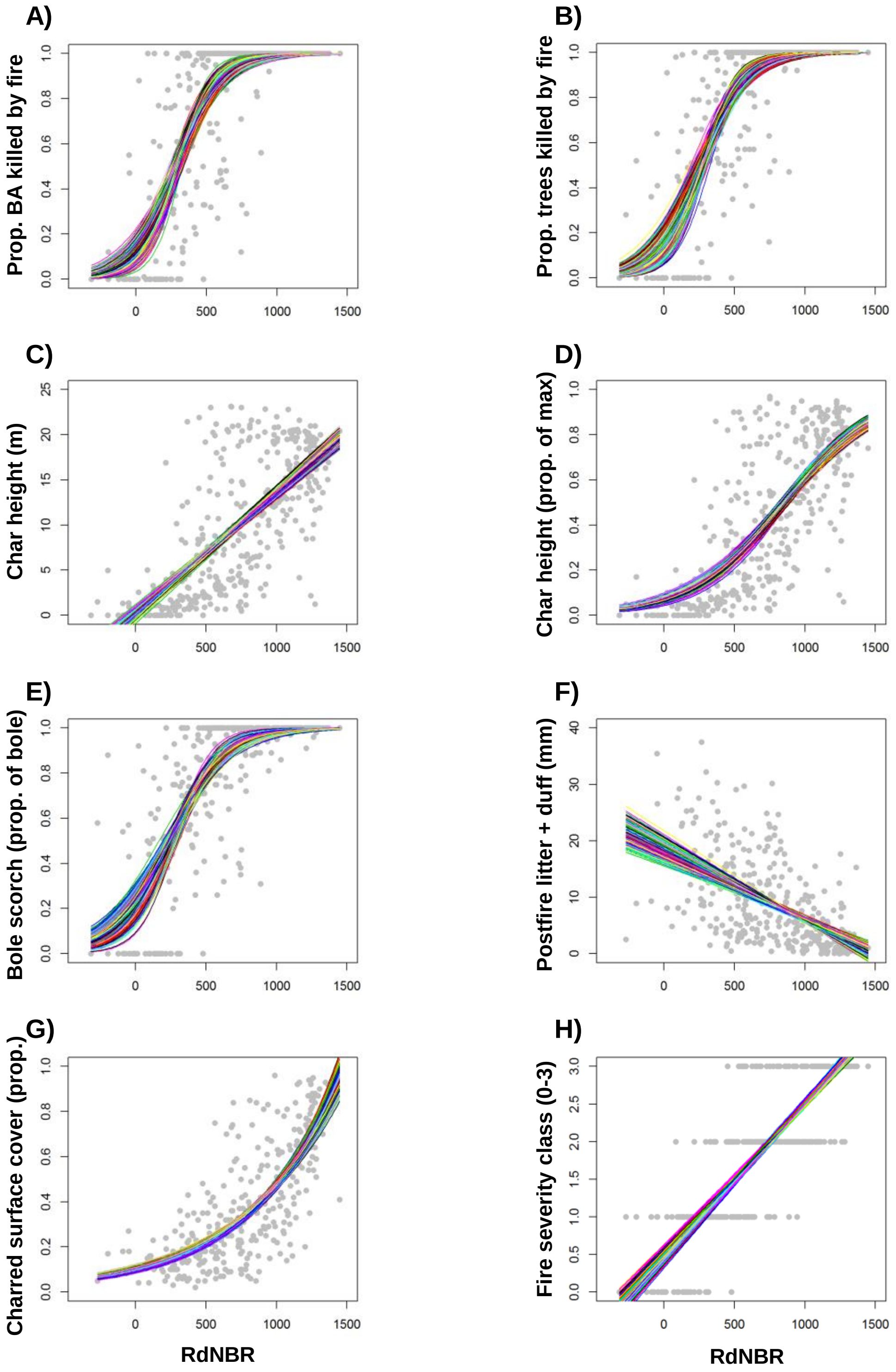


Figure 2. Scatterplots of each fire severity metric vs. RdNBR, with each of the 1,000 model runs for the best model (linear, exponential, or logistic) overlaid. See Table 1 for model outputs.

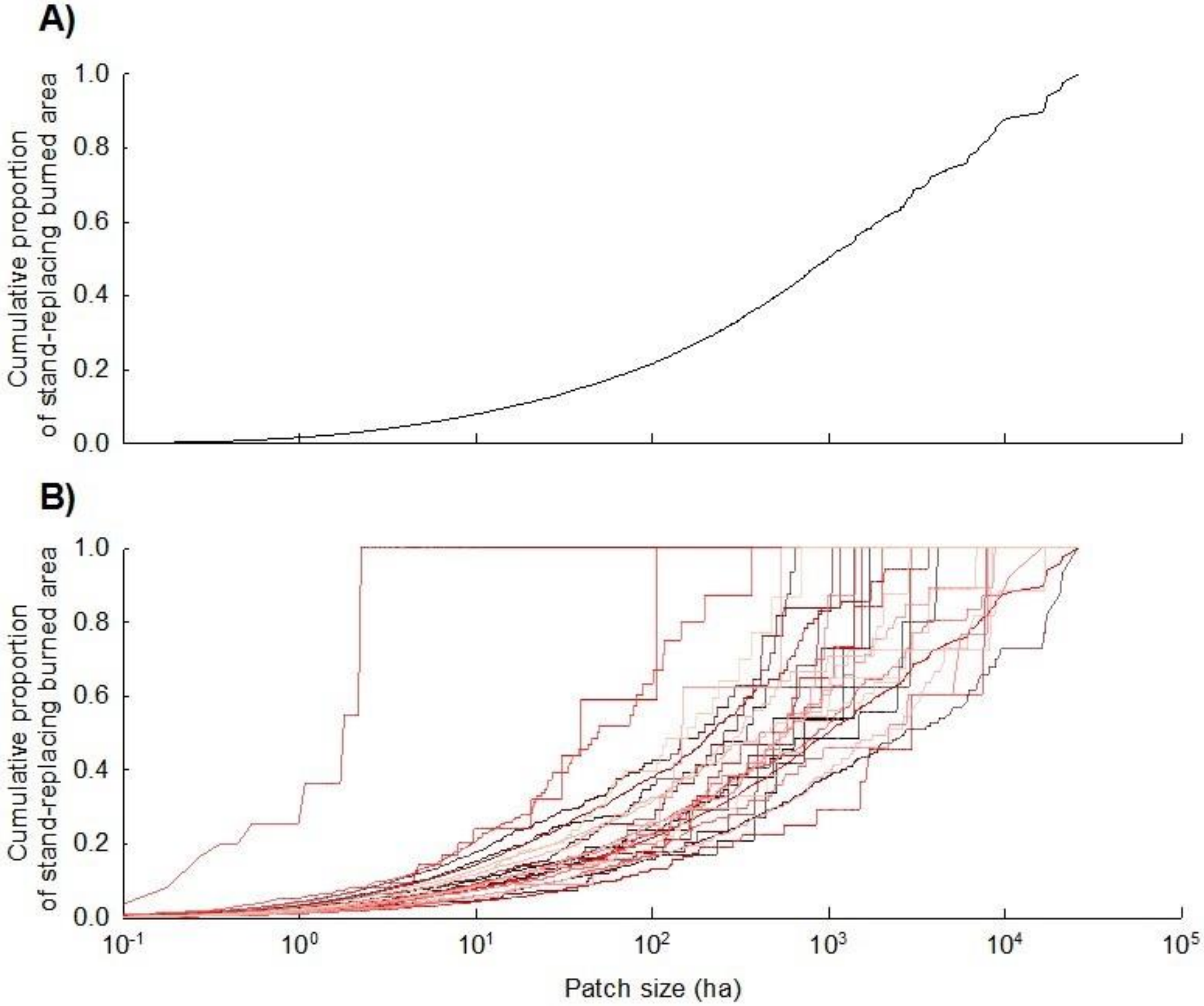


Figure 3. Cumulative frequency distribution of stand-replacing burned area (y-axis) with increasing patch size (x-axis) in all years combined (A) and each year separately (B). Colors in (B) grade from dark red (1984) to light red (2010). X-axis is log scale.

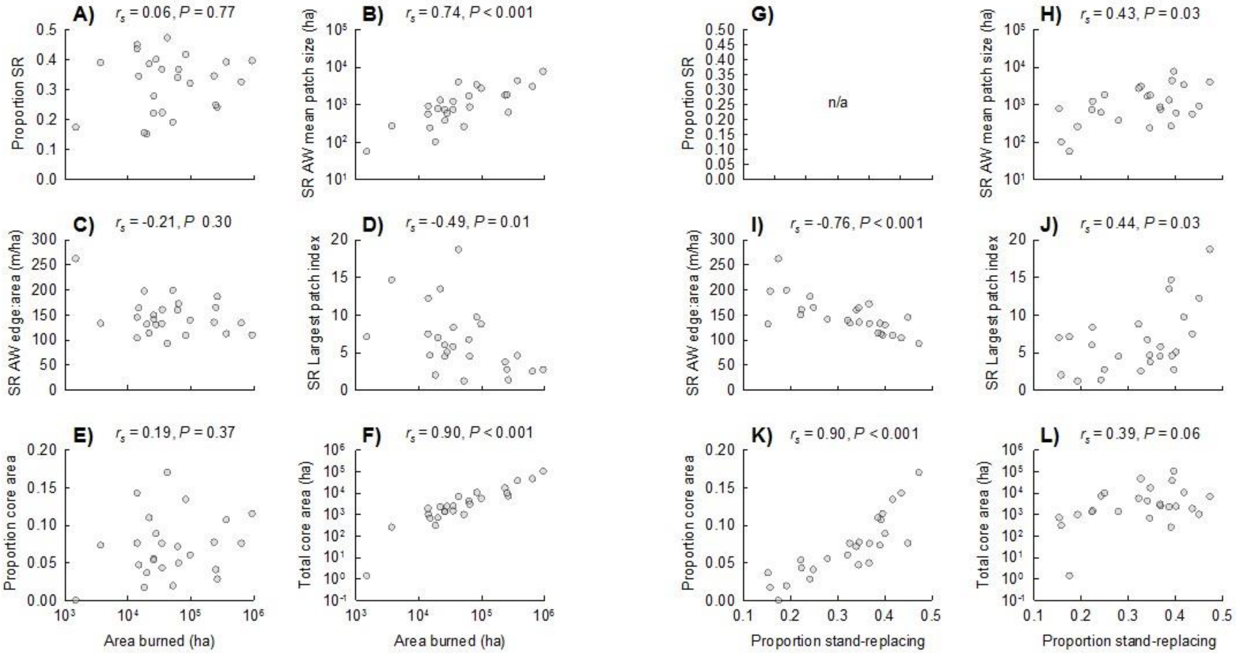


Figure 4. Scatterplots, Spearman’s rho coefficients, and *P*-values for each landscape metric of burn severity and area burned (A-F) and proportion of area burned that was stand-replacing (G-L) at the ecoregion extent. Each point represents one year (from 1984 to 2010).

n/a = not applicable because x- and y-variable are the same.
SR = Stand replacing; AW = area-weighted
Axes representing area measures are on a $\log_{10}$ scale.

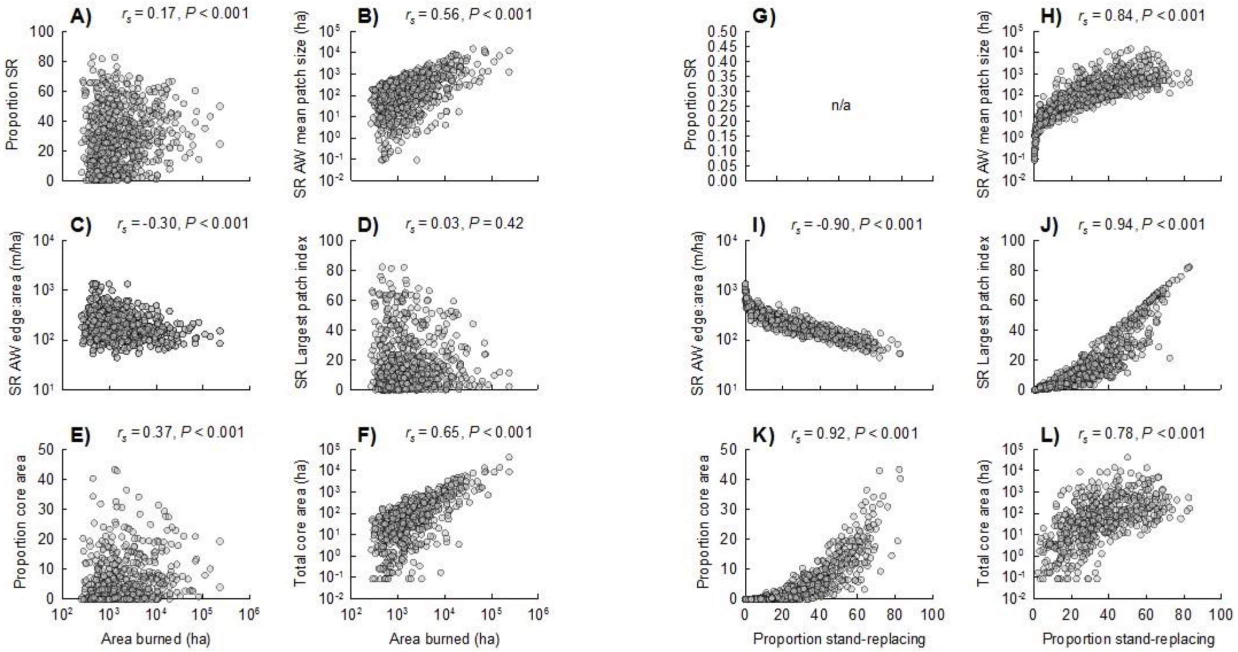


Figure 5. Scatterplots, Spearman's rho coefficients, and *P*-values for each landscape metric of burn severity and area burned (A-F) and proportion of area burned that was stand-replacing (G-L) at the fire extent. Each point represents one wildfire.

n/a = not applicable because x- and y-variable are the same.
SR = Stand replacing; AW = area-weighted
Axes representing area measures are on a $\log_{10}$ scale.

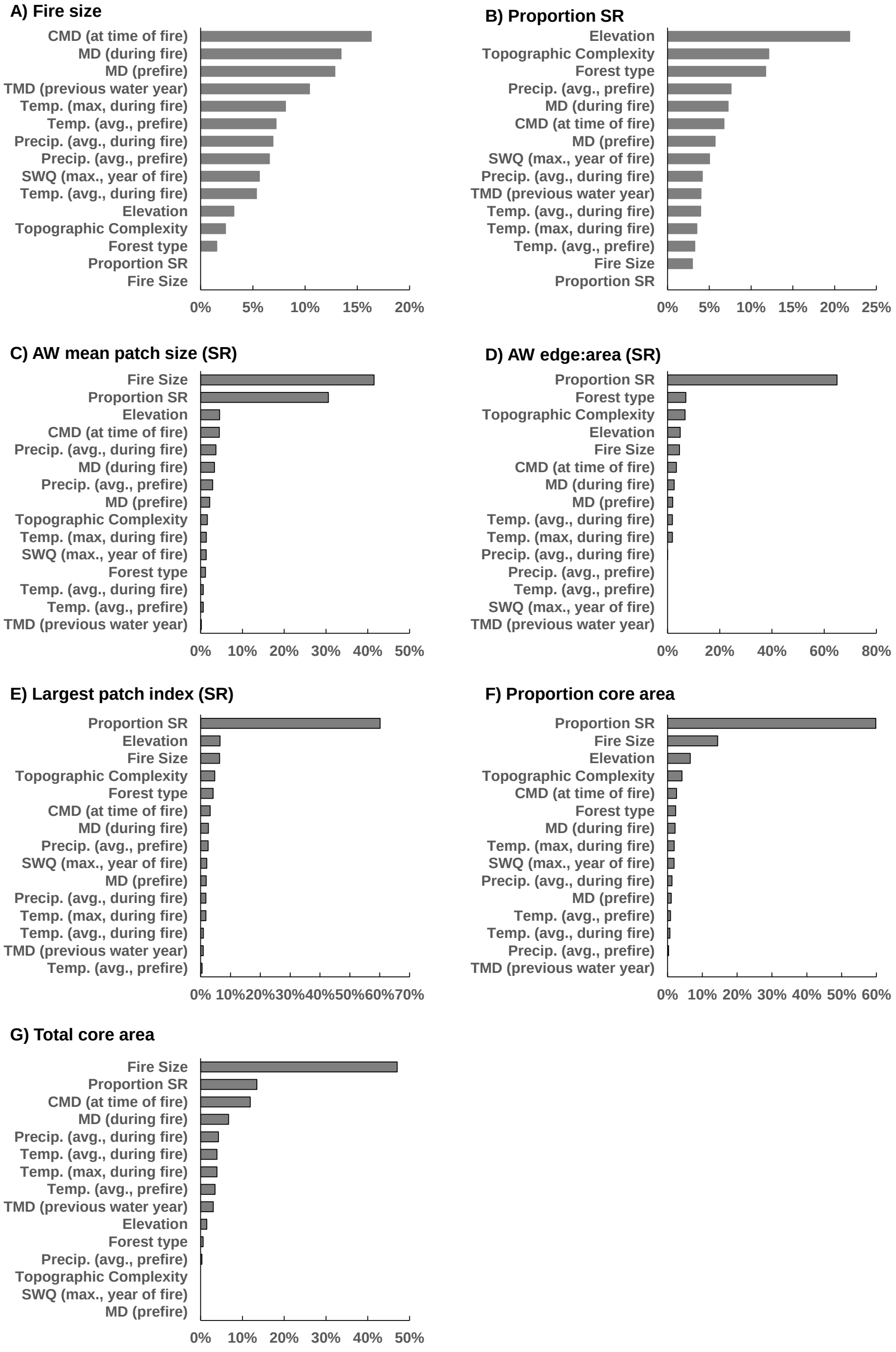


Figure 6. Random Forest results for all forest fires, indicating percent of total explained variance in each landscape metric attributed to each explanatory variable. Total explained variance was 24% (A), 36% (B), 63% (C), 72% (D), 84% (E), 78% (F), and 46% (G).

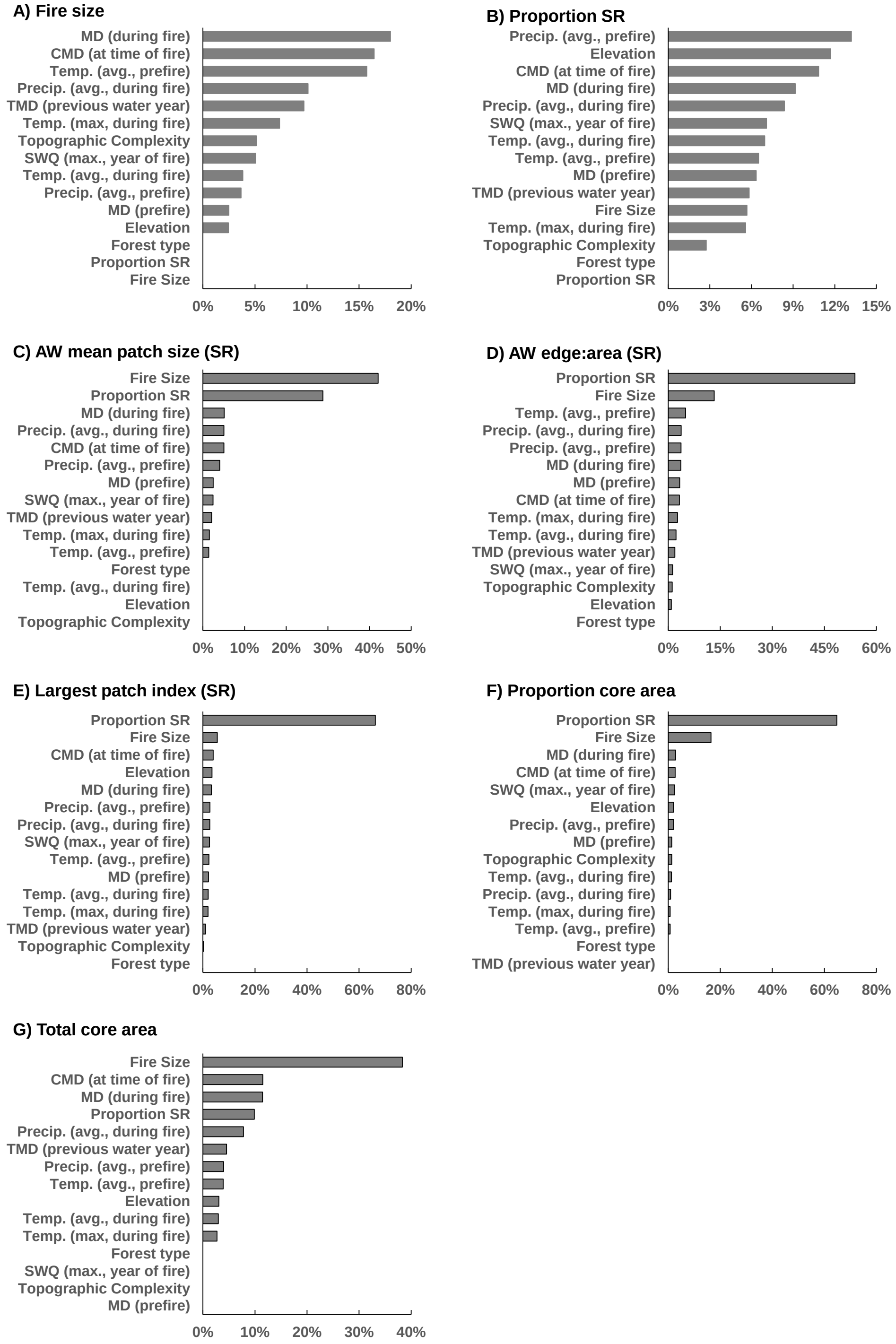


Figure 7. Random Forest results for subalpine forest fires, indicating percent of total explained variance in each landscape metric attributed to each explanatory variable. Total explained variance was 24% (A), 14% (B), 64% (C), 78% (D), 79% (E), 76% (F), and 49% (G).

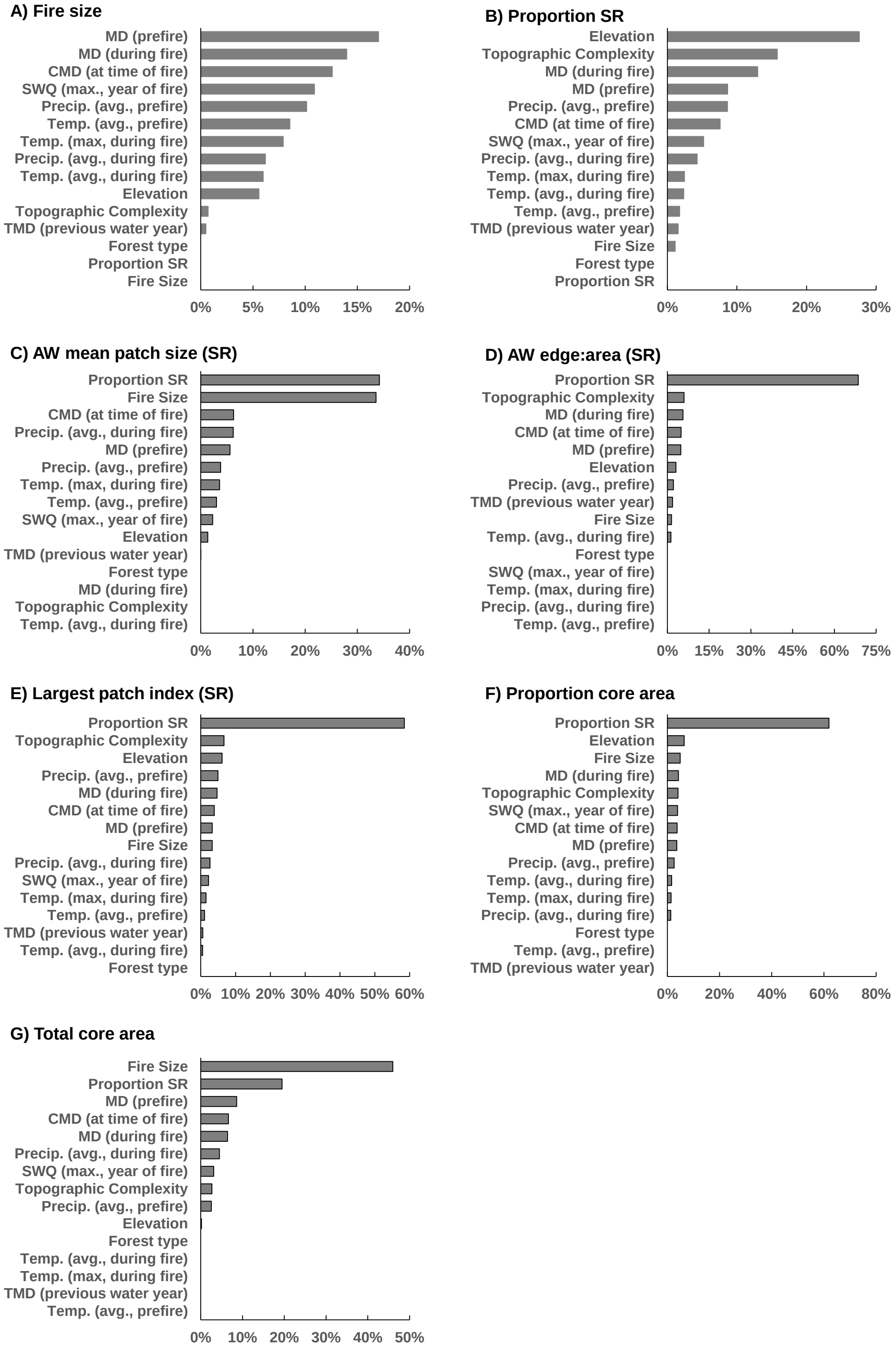


Figure 8. Random Forest results for mid-montane forest fires, indicating percent of total explained variance in each landscape metric attributed to each explanatory variable. Total explained variance was 3% (A), 24% (B), 29% (C), 64% (D), 84% (E), 73% (F), and 43% (G).

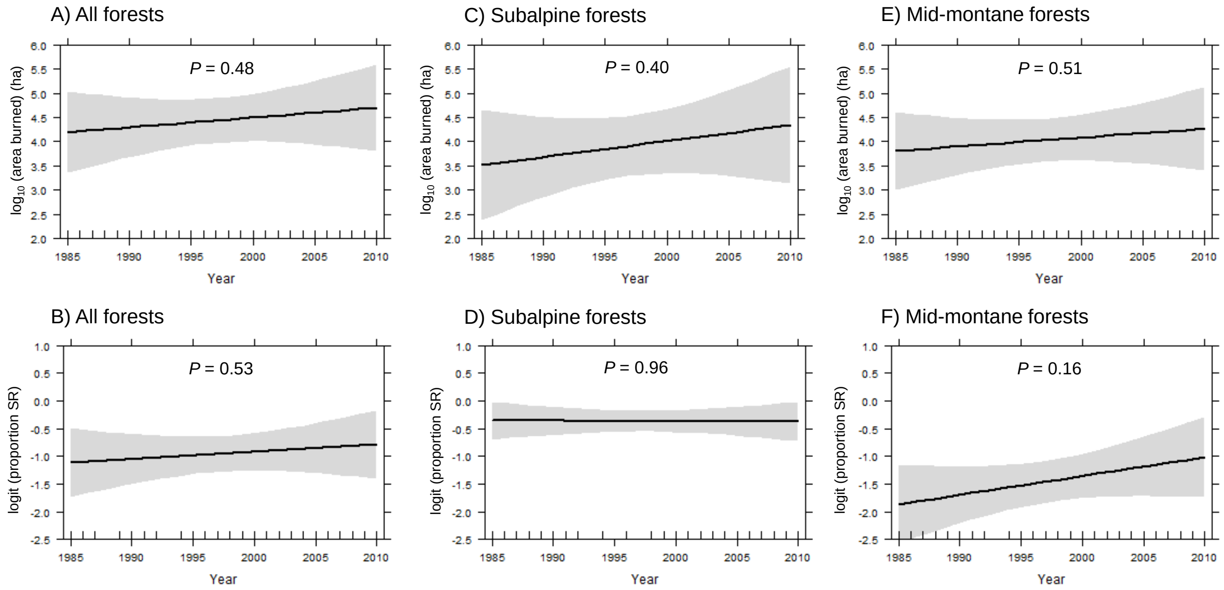
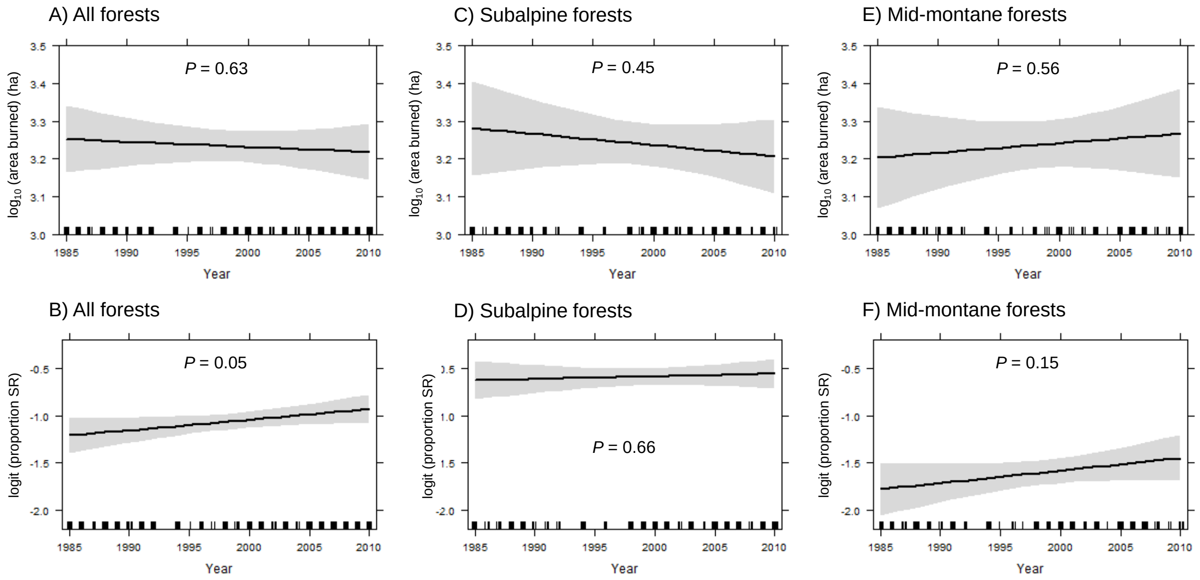


Figure 9. Total area burned and proportion SR over time at the ecoregion extent. For proportion SR (B, D, F), lines represent effects holding total area burned at the mean value.


A) All forests

C) Subalpine forests

E) Mid-montane forests

B) All forests

D) Subalpine forests

F) Mid-montane forests

Figure 10. Total area burned and proportion SR over time at the fire extent. For proportion SR (B, D, F), lines represent effects holding total area burned (i.e., fire size) at the mean value.

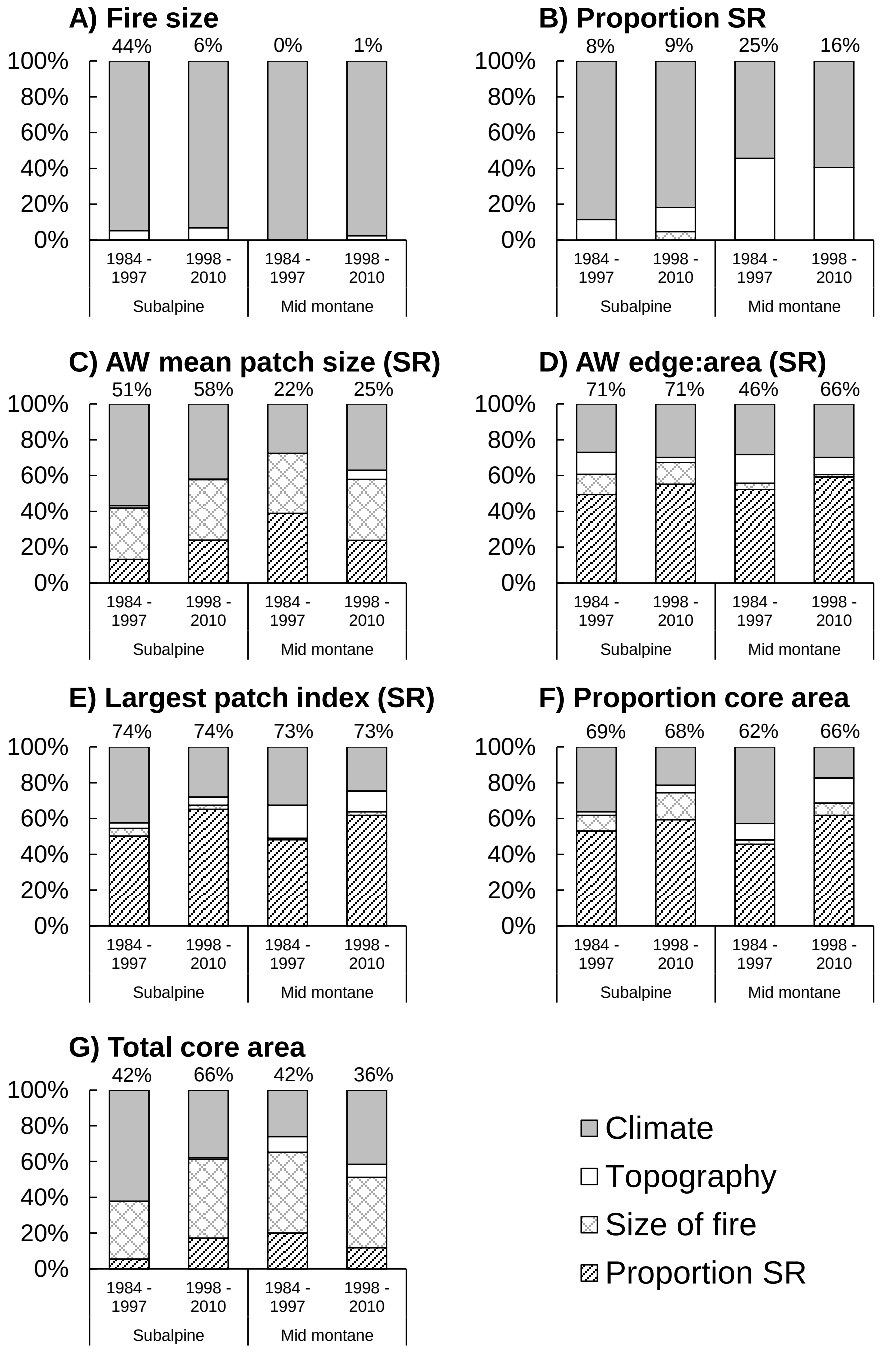


Figure 11. Relative contribution of climate, topography, fire size (where appropriate), and proportion stand-replacing (where appropriate) variables in Random Forests models explaining variation in each landscape metric. Subalpine forests had 111 fires (1,089,823 ha) between 1984 and 1997 and 242 fires (833,917 ha) between 1984 and 1997, whereas mid-montane had 104 (390,306 ha) and 191 (1,010,122 ha), respectively. Numbers at the top of bars shows the percent of total variation explained by Random Forest models.

## Appendices

Appendix 1. Forest types in the Northern Rockies, grouped by LANDFIRE Environmental Site Potential (ESP) code.

| Forest type LANDFIRE Environmental Site Potential vegetation name (code) | Total hectares | % of forest type area | % of all NR forested area |
|---|---|---|---|
| Subalpine | 10,050,715 | 100.0 | 44.9 |
| Rocky Mountain subalpine dry-mesic spruce-fir forest and woodland (1055) | 5,290,887 | 52.6 | 23.6 |
| Rocky Mountain subalpine mesic-wet spruce-fir forest and woodland (1056) | 4,122,409 | 41.0 | 18.4 |
| Northern Rocky Mountain subalpine woodland and parkland (1046) | 306,943 | 3.1 | 1.4 |
| Rocky Mountain poor-site lodgepole pine forest (1167) | 165,248 | 1.6 | 0.7 |
| Northern Rocky Mountain conifer swamp (1161) | 164,283 | 1.6 | 0.7 |
| All others | 944 | 0.0 | 0.0 |
| Mid-montane | 11,799,616 | 100.0 | 52.7 |
| Northern Rocky Mountain dry-mesic montane mixed conifer forest (1045) | 6,923,091 | 58.7 | 30.9 |
| Middle Rocky Mountain montane Douglas-fir forest and woodland (1166) | 2,768,546 | 23.5 | 12.4 |
| Northern Rocky Mountain mesic montane mixed conifer forest (1047) | 1,835,814 | 15.6 | 8.2 |
| Rocky Mountain aspen forest and woodland (1011) | 270,441 | 2.3 | 1.2 |
| All others | 1,724 | 0.0 | 0.0 |
| Low-montane | 550,012 | 100.0 | 2.5 |
| Northern Rocky Mountain ponderosa pine woodland and savanna (1053) | 410,038 | 74.6 | 1.8 |
| Rocky Mountain foothill limber pine-juniper woodland (1049) | 71,788 | 13.1 | 0.3 |
| Inter-mountain basins aspen-mixed conifer forest and woodland (1061) | 38,278 | 7.0 | 0.2 |
| Southern Rocky Mountain ponderosa pine woodland (1054) | 22,088 | 4.0 | 0.1 |
| All others | 7,821 | 1.4 | 0.0 |

Appendix 2. Descriptive statistics of physical setting, prefire stand structure, and prefire tree species composition from the 371 plots used to calibrate and validate RdNBR.

| Variable | Min-max | Mean | Median |
|---|---|---|---|
| Physical setting | | | |
| Latitude (decimal deg.) | 43.08 – 48.22 | 44.51 | 44.49 |
| Longitude (decimal deg.) | -115.03 - -109.43 | -111.52 | -110.29 |
| Elevation (m) | 1735 – 2788 | 2382 | 2472 |
| Slope (deg.) | 1 – 37 | 15 | 13 |
| Solar radiation input (WH/m$^2$) | 376,134 – 718,349 | 598,221 | 613,786 |
| Prefire stand structure | | | |
| Basal area (m$^2$/ha) | 12.9 – 86.3 | 37.0 | 35.5 |
| Stand density (stems/ha) | 141 – 5,829 | 1,594 | 1,471 |
| Large trees only (>10 cm dbh) | 141 – 2,122 | 834 | 785 |
| Quadratic mean diameter (cm) | 8.6 – 43.0 | 18.7 | 17.1 |
| Maximum tree height (m) | 15.2 – 33.2 | 23.3 | 23.1 |
| Prefire stand composition (% of tree BA) | | | |
| Douglas-fir (*Pseudotsuga menziesii*) | 0 – 100 | 26 | 0 |
| Engelmann spruce (*Picea engelmannii*) | 0 – 73 | 5 | 0 |
| grand fir (*Abies grandis*) | 0 – 23 | <1 | 0 |
| limber pine (*Pinus flexilis*) | 0 – 76 | 2 | 0 |
| lodgepole pine (*Pinus contorta*) | 0 – 100 | 48 | 45 |
| *Pinus* sp. (unk. beyond genus) | 0 – 28 | <1 | 0 |
| ponderosa pine (*Pinus ponderosa*) | 0 – 75 | <1 | 0 |
| quaking aspen (*Populus tremuloides*) | 0 – 1 | <1 | 0 |
| *Salix* sp. (unk. beyond genus) | 0 – 5 | <1 | 0 |
| subalpine fir (*Abies lasiocarpa*) | 0 – 88 | 13 | 0 |
| Rocky Mountain juniper (*Juniperus scopulorum*) | 0 – 33 | <1 | 0 |
| Unknown | 0 – 32 | 1 | 0 |
| whitebark pine (*Pinus albicaulis*) | 0 – 72 | 3 | 0 |

Appendix 3. Descriptive statistics of RdNBR and field measures of fire severity from the 371 plots used to calibrate RdNBR.

| Fire severity metric | Description | Min-max | Mean | Median |
|---|---|---|---|---|
| RdNBR | Relative differenced Normalized Burn Ratio. Satellite index of burn severity from Landsat TM bands 4 and 7 (Miller and Thode 2007). | -314 - 1447 | 704 | 730 |
| Basal area killed by fire (%) | The percentage of tree basal area per plot that was alive at the time of fire and killed by the fire. | 0 - 100 | 79 | 100 |
| Trees killed by fire (%) | The percentage of trees per plot that were alive at the time of fire and killed by the fire. | 0 - 100 | 80 | 100 |
| Char height (m) | Average height of charring from randomly selected dominant canopy trees (20/plot) that were alive at the time of fire. | 0 - 23.1 | 9.5 | 8.7 |
| Char height (% of tree height) | Average percent of total tree height that was charred from randomly selected dominant canopy trees (20/plot) that were alive at the time of fire. | 0 - 100 | 41 | 38 |
| Bole scorching (% of circumference) | Average percent of tree bole circumference that was charred from randomly selected dominant canopy trees (20/plot) that were alive at the time of fire. | 0 - 100 | 79 | 99 |
| Postfire litter + duff depth (mm) | Average depth of postfire litter + duff (i.e., soil "O" horizon) taken from 20 points > 3 m apart along the main plot axis (N-S,E-W). | 0 - 37.5 | 8.8 | 6.2 |
| Charred surface cover (%) | Average percent of charred ground cover in plots, taken from 480-500 points > 10 cm apart along the main plot axis (N-S,E-W). | 2 - 96 | 39 | 33 |
| Fire severity class | | Number of plots | | |
| Unburned (0) | No evidence of any fire effects | 38 | | |
| Light surface (1) | Some canopy tree mortality from fire, but most canopy trees remain living with green needles. Patchy evidence of surface fire. | 87 | | |
| Severe surface (2) | 100% canopy tree mortality, but needles on canopy trees were not | 120 | | |

| | | |
|---|---|---|
| | consumed in fire. Prefire soil "O" horizon consumed, but needles from dead trees cover soil postfire. | |
| Crown (3) | 100% canopy tree mortality, with needles of canopy trees consumed in fire. Soil is charred and exposed, with no litter cover. | 126 |

Appendix 4. Temporal trends in spatial patterns of burn severity at each analysis extent Regression models included area burned (or fire size) and proportion SR when appropriate. Results indicate whether the beta coefficient for the term ‘year’ in each model was significantly different from zero.

| | Ecoregion extent | | | Fire extent | | |
|---|---|---|---|---|---|---|
| Forest type | Overall | Subalpine | Mid montane | Overall | Subalpine | Mid montane |
| SR proportion | - | - | - | ^ | - | - |
| SR patch size | - | - | - | - | - | - |
| SR patch shape | - | v | - | - | - | - |
| SR LPI | - | - | - | - | - | - |
| Proportion core | - | - | - | - | - | - |
| Total core area | - | - | - | - | - | - |

^ coefficient was significantly greater than zero, indicating an increase over time.
v coefficient was significantly less than zero, indicating an increase over time.
- coefficient was not significantly different from zero, indicating no change over time.
n.a. Not applicable; no test was possible because of type of data.

# Chapter 5 - High and dry: Postfire drought and large stand-replacing burn patches reduce postfire tree regeneration in subalpine forests

Running head: Drought and postfire forest regeneration

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Keywords: wildfire, forest resilience, conifer seedlings, *Pinaceae*, succession, climate change, Greater Yellowstone Ecosystem, Glacier National Park, Rocky Mountains

Abstract:

Wildfire shapes forests worldwide, but a warming climate may alter postfire forest tree regeneration by changing fire severity patterns (therefore increasing distance to seed sources in larger burned patches) and causing greater drought stress on postfire tree seedlings. Such effects may be most pronounced in high-elevation or high-latitude forests adapted to reproduce quickly following stand-replacing fires. We examined postfire tree regeneration in stand-replacing burn patches in upper-montane and subalpine forests of the US Northern Rockies using field data from 184 plots in which recent forest fires were followed by varying postfire climate conditions. We characterized temporal patterns of postfire tree establishment, then asked how postfire tree establishment varied with (a) postfire drought severity and (b) distance to seed source in patches of stand-replacing fire. We tested for effects on total postfire tree establishment (all species) and on species that varied in strategies of postfire regeneration. Postfire tree seedling establishment varied substantially, and establishment of most species peaked by 3-5 yr postfire. Total postfire tree seedling establishment declined sharply with greater postfire drought severity, but was unrelated to distance to seed source. Total postfire tree establishment also was greater on cooler/wetter aspects, which may provide local refugia during regional postfire droughts. Effects of postfire drought and distance to postfire seed source varied among species. For higher-elevation conifers that dominate present-day subalpine and upper montane forests (*Pinus contorta*, *Picea engelmannii*, and *Abies lasiocarpa*), postfire seedling establishment declined sharply with increasing drought severity and distance to seed source. For lower montane species (*Pseudotsuga menziesii*, *Populus tremuloides*) or species with protracted postfire establishment (*Pinus albicaulis*), postfire tree establishment was not related to distance to seed source, and

these species were not affected by drought severity. Our findings suggest that, if changes in seasonal drought and wildfire patterns manifest as projected under future climate change, postfire establishment of species that currently characterize upper-montane and subalpine forests could be substantially reduced. These reductions are unlikely to be offset by modest gains from other tree species currently in warmer/drier elevations below the subalpine zone, potentially resulting in reduced extent and increased patchiness of these high-elevation forests.

## Introduction

Wildfires shape forest ecosystems by structuring dominant vegetation patterns and ecosystem function at multiple scales (Turner *et al.*, 2004; Schoennagel *et al.*, 2008), and regulating delivery of myriad forest-related ecosystem services (Adams, 2013; Turner *et al.*, 2013). Dominant tree species in many high-elevation (i.e., subalpine) and high-latitude (i.e., boreal) forest ecosystems are adapted to severe, or stand-replacing fires wherein nearly all prefire trees are killed by fire (Johnstone *et al.*, 2004, 2010a; Schoennagel *et al.*, 2004; Baker, 2009). In such systems, postfire resilience [the capacity to tolerate fire without shifting to an alternative ecosystem-state (adopted from Walker *et al.*, 2004)] depends on successful and abundant early-postfire tree regeneration that drives forest structure (Kashian *et al.*, 2005) and function (Kashian *et al.*, 2006) for centuries or more. Climate change has serious potential to compromise postfire forest resilience by altering fire activity (Westerling *et al.*, 2006) and/or increasing drought stress on postfire tree seedlings (Johnstone *et al.*, 2010b; Williams *et al.*, 2012) - presenting daunting challenges for forest management and policy (Stephens *et al.*, 2013). To better forecast climate change-induced impacts on these extensive forest biomes, robust empirical field data from actual wildfires are needed to test whether changes in postfire tree regeneration are already occurring, and when/where they might be expected to continue in the future.

Two key mechanisms governing postfire regeneration in forests with stand-replacing fire regimes are seed delivery and seedling establishment in recently burned areas. Assuming a sufficient seed supply, seed delivery into stand-replacing patches depends on both patch size and seed-dispersal traits of dominant trees. Large wildfires often contain remarkable heterogeneity in burn severity, leaving most stand-replacing burned area situated within several hundred meters of a surviving seed source (e.g., Turner *et al.*, 1994; Donato *et al.*, 2009). Experiments have demonstrated potential dispersal distances for many conifer species (e.g., Greene *et al.*, 1999), but how actual postfire tree establishment patterns vary as a function of distance to the edge of stand-replacing patches has received less attention (but see Donato *et al.*, 2009) and may vary among species. Once seeds arrive in a stand-replacing burned patch, successful germination and tree establishment are governed by climate conditions and local site factors (e.g., topographic setting, competition). Drought stress is a leading cause of tree mortality (Williams *et al.*, 2012), and young seedlings are particularly vulnerable to prolonged drought. Subalpine and boreal forests demonstrate enormous capacity for resilience when large, severe fires are followed by suitable climate conditions [e.g., the 1988 Yellowstone Fires (Turner *et al.*, 1997; Romme *et al.*, 2011) or 20th Century boreal forest fires (Johnstone *et al.*, 2004)], but how tree regeneration is affected when large fires are followed by drought is less clear. Tests of the effects of postfire climate on tree establishment have generally been limited to simulation modeling studies (Savage *et al.*, 2013; Azpeleta Tarancón *et al.*, 2014) or single fire events where topographic gradients are used as a proxy for climate (e.g., Dodson & Root, 2013). Until recently, there have been limited opportunities to test the coupled effects of postfire climate and distance to seed source on postfire tree establishment across multiple burned landscapes.

Upper montane and subalpine forests of the US Northern Rocky Mountains provide a natural laboratory to test the effects of fire size and climate on postfire tree regeneration. Since the mid-1980s, the region has experienced disproportionate increases in wildfire activity relative to other regions in the western US (Westerling *et al.*, 2006; Morgan *et al.*, 2008), and postfire climate conditions following recent large fire years have varied substantially (Westerling *et al.*, 2011).

Regional fire regimes are generally characterized by infrequent, stand-replacing fires (Arno, 1980; Romme & Despain, 1989; Barrett *et al.*, 1991; Barrett, 1994; Kipfmueller & Baker, 2000; Schoennagel *et al.*, 2003), and since 1984 over one million ha of forest (~5% of the total forested area in the Northern Rockies) have burned as stand-replacing fire (Harvey, in prep). Most upper montane and subalpine forests in the region are designated as wilderness, so postfire tree regeneration patterns are largely not confounded by management or prior land-use. Further, this large region shares many tree genera and species with most other subalpine and boreal forest biomes, making trends applicable to extensive forests worldwide.

Variability in fire-related traits (Agee, 1993; Baker, 2009) (Table 1) among tree species in this biome may drive contrasting responses to distances to postfire seed sources and postfire climate conditions, but the net effects on overall postfire tree regeneration are not known. Thin-barked conifers are readily killed by fire, but can rapidly colonize burned areas from seeds that arrive within a few years of fire. Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are classified as fire "avoiders" because they rely on wind-dispersed seeds from surviving trees outside a burned patch. Lodgepole pine (*Pinus contorta* var. *latifolia*) can produce seed in non-serotinous cones that rely on wind dispersal, or serotinous cones that require heat for seed release; the level of serotiny typically decreases with increasing elevation and fire-return interval (Tinker *et al.*, 1994; Schoennagel *et al.*, 2003). Lodgepole pine is classified as a fire "evader" where serotiny is high and a fire "invader" where serotiny is low. Whitebark pine (*Pinus albicaulis*) relies on pre and postfire seed dispersal via birds into burned patches – also making this species a fire "invader," although establishment is typically later than early invaders such as lodgepole pine. Thick bark allows conifers such as western larch (*Larix occidentalis*) and

Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) to sometimes survive fire ("resistors") but also re-seed into severely burned areas ("invader" behavior). Quaking aspen (*Populus tremuloides*) is the dominant angiosperm in subalpine forests, and can re-sprout from extensive root networks following fire - making it a fire "endurer." Aspen can also be an effective fire "invader" with extremely light-weight seeds that can disperse long distances into burned patches. Shade tolerance varies among all of these species, with less shade-tolerant species typically establishing earliest after fire.

In this study, we quantified postfire tree establishment in stand-replacing patches of 11 different fires that occurred between 1994 and 2003 across the US Northern Rocky Mountains, to examine the temporal and spatial patterns of regeneration under varying postfire climate conditions. Specifically, we asked: (1) What are the temporal patterns of early postfire conifer regeneration, and do patterns differ by species? 2) How is postfire tree establishment in stand-replacing patches affected by two key factors expected to increase with changing climate: postfire drought severity and distance to postfire seed source? 3) How do effects of postfire drought severity and distance to postfire seed source vary among fire-related traits? We also tested the effects of other local factors (e.g., biotic interactions) on postfire tree establishment. We expected most tree species to establish within ~10 years of fire, but species with low shade-tolerance or rapid dispersal-capacity to establish earlier than shade-tolerant species or those relying on irregular seed dispersal. Postfire tree establishment for all species was expected to decrease with increasing postfire drought severity, but particularly so for species that establish earlier after fire (and are therefore more vulnerable to postfire drought). We expected postfire tree establishment to decrease toward the interior of stand-replacing patches for fire avoiders, resisters, and invaders, but not for fire evaders or endurers that can retain strong on-site propagules. Understanding these responses to dominant drivers will help forecast future subalpine and boreal forest resilience under expected climate change.

## Methods and materials

### *Study area*

The study area is composed of two focal regions in the US Northern Rocky Mountains - Glacier National Park (hereafter, “Glacier”) (48° 46’ N, 114° 00’ W) and the Greater Yellowstone Ecosystem (hereafter, “Greater Yellowstone”) (44° 10’ N, 110° 15’ W), which together comprise over 75,000 $km^2$ of mountainous conifer forest. Most land is federally protected and managed as wilderness (Glacier, Yellowstone, and Grand Teton National Parks; and portions of surrounding National Forests). The climate in both regions is characterized by cool summers (~20°C average daily July temperature) and cold winters (~-15°C average daily January temperature), with most precipitation falling as winter snow and spring rain. Greater Yellowstone is warmer and drier than Glacier, resulting in a 21% greater water-year cumulative moisture deficit (CMD) from 1983-2012 in our Greater Yellowstone study fires (source: Westerling *et al.*, 2011).

Upper montane and subalpine forests occupy mountain slopes and plateaus from ~1,000 to 2,000 m elevation in Glacier and from ~2,000 to 3,000 m elevation in Greater Yellowstone; lower elevations in Glacier are a result of the ~4 ½° increase in latitude compared to Greater Yellowstone (Figure 1). Forests are largely dominated by Engelmann spruce, subalpine fir, and lodgepole pine, and correspond to the *Abies lasiocarpa* Series as described by Arno (1980). The highest elevations toward the upper treeline include whitebark pine, whereas the lowest elevations include western larch and Douglas-fir. At all elevations occasional stands of quaking aspen can occur. Fire regimes are characterized by infrequent (150 to 300-yr interval), stand-replacing wildfires that are primarily driven by prolonged periods of warm, dry, windy conditions (Arno, 1980; Romme & Despain, 1989; Barrett *et al.*, 1991; Barrett, 1994; Kipfmueller & Baker, 2000; Schoennagel *et al.*, 2004), and are often followed by abundant but variable postfire tree regeneration (e.g., Romme *et al.*, 2011).

All forests that we sampled were mature stands prefire (i.e., no evidence of recent prefire disturbance) with mean basal area of ~35 $m^2$ $ha^{-1}$ and stand density of ~450 large (≥15 cm dbh) trees $ha^{-1}$. Stands were primarily dominated by subalpine fir, Engelmann spruce, and lodgepole pine (Table 2). Western larch was present prefire in nearly half of the Glacier plots (but does not occur in Greater Yellowstone), and stands had minor prefire components of Douglas-fir and whitebark pine in Glacier and Greater Yellowstone, respectively. In our study plots, prefire lodgepole pine serotiny was greater in Glacier, because the study fires in Greater Yellowstone occurred at high elevations where lodgepole pine serotiny is very low (Schoennagel *et al.*, 2003) (Table 2).

### *Study design*

Sample plots in each study area were located in patches of stand-replacing fire in wildfires that burned in 1994, 1999, 2000, or 2003 (Figure 1). These years represent large fire years occurring since the availability of satellite-derived burn severity maps, and they cover a wide range of regional and local postfire climate conditions (cool and wet to warm and dry). For fires that occurred in each of these years, we identified candidate stand-replacing-fire patches that were ≥

4 ha in size and contained prefire subalpine forest as indicated on National Park Service vegetation maps. Patches were delineated using satellite-derived burn severity maps (Harvey, in prep) and high-resolution aerial photographs provided by the National Park Service. Stand-replacing patches were defined as areas with >90% canopy tree mortality from fire (although mortality was most often 100%) and patch edges were defined by areas where >25% of the prefire canopy trees survived the fire (although canopy-tree survival was most often >75%). From a random starting point (to account for varying wind directions) along the perimeter of each stand-replacing patch, sample plots were situated along transects that started at the edge and continued into the interior at an angle perpendicular to the patch edge. Plots were located at progressively longer distances from the edge of the stand-replacing burn patch, at 15-, 45-, 90-, 150-, 350-, 550-, 750-, and 1,000- m, depending on patch size (one patch in Greater Yellowstone was large enough to fit a plot at 1,250 m from the edge; no patches in Glacier were large enough to fit plot distances > 750 m from the edge). For each transect, we also included one control (unburned) plot 15-m away from the edge of the stand-replacing patch and aligned with the transect azimuth. Multiple transects within the same fire were separated by a minimum distance of 350 m and oriented in perpendicular angles. In total, we sampled 78 postfire plots (14 transects, seven fires) and 14 control plots in Glacier, and 106 postfire plots (18 transects, four fires) and 18 control plots in Greater Yellowstone. The number of transects per fire varied based on the area available for sampling within each fire.

### *Field data collection*

Each sample plot was a 30-m diameter circle (707 $m^2$) in which we collected data on postfire tree regeneration, prefire stand-structure, postfire ground cover, and physical site characteristics. We recorded every tree seedling established postfire in variable-sized subplots according to the density of postfire trees. Default subplot size was four 2 x 15 m rectangular plots (120 $m^2$ total area) situated along the cardinal-direction axes of the plot. Subplot size was objectively decreased to four 0.5 x 15 m belt plots (30 $m^2$ total area) or increased to the entire plot (707 $m^2$ total area) if > 200 or < 10 trees were captured in the default subplot size, respectively. For each tree stem in the subplots, we recorded the species, height (cm), approximate age [yr, by counting the number of bud scars on the main stem and adjusting by +0.8 yr (Urza & Sibold, 2013)], and any evidence of animal browsing or mechanical damage.

To characterize prefire stand structure, we recorded the number of standing or down (but standing prefire) prefire trees (> 15 cm dbh) for each species that were rooted in the plot. If prefire lodgepole pine trees were present, we noted any evidence of serotinous cones [e.g., partially closed or highly reflexed cones on burned and/or fallen prefire logs, (Tinker *et al.*, 1994)]. Distance to the nearest live, prefire, seed-bearing tree was measured from plot center with a TruePulse laser rangefinder. Postfire ground cover was recorded in eight 0.25-m circle subplots (two in each plot quadrant) where we recorded percent cover of wood, litter, bryophyte, soil, and rock to the nearest 5%. In the same eight 0.25-m circle subplots we also recorded postfire vegetation cover for major plant forms (forb, graminoid, shrub) to the nearest 5%. We recorded plot coordinates (UTM NAD83 Zone 12N), elevation (m), slope (deg), and aspect (compass azimuth) from plot center.

For each control (unburned edge) plot, we measured stand basal area ($m^2$ $ha^{-1}$) per species using a basal area prism (basal area factor 2) from plot-center, and recorded presence of cones on mature trees. If lodgepole pine was present, we scored each plot for percent serotiny based on up to 12 trees nearest the plot center following established methods (Tinker *et al.*, 1994). Field sampling was conducted from June to August 2013.

### *Postfire climate data*

Monthly climate data during the period 1983 to 2012 were extracted for each plot from an existing 12 × 12 km gridded dataset for the region (Westerling *et al.*, 2011). To characterize drought severity during the early postfire period, we used average water-year (Oct. – Sept) CMD (mm) for years 0-3 postfire in each plot. To account for among-site variation in climate settings, we standardized drought severity for each plot by re-scaling CMD values for the 3-yr postfire time window to ± standard deviations (SDs) of the 1983-2012 average for each plot location.

### *Statistical analyses*

The number of postfire tree seedlings for each species that established each year (based on bud scars) in each plot were standardized to seedlings ha$^{-1}$. To characterize temporal patterns of seedling establishment for each species, we plotted the annual number of seedlings established ha$^{-1}$ averaged across all plots within in each region (Glacier and Greater Yellowstone). Temporal trends in quaking aspen establishment were not analyzed because of low confidence in relationships between bud scars and age.

To test for the effect of postfire drought severity and distance to the nearest seed source on postfire tree establishment, we used generalized linear regression models with a log-link (family = quasi-Poisson) to account for over-dispersed count data. The response variable was the normalized rate of seedling establishment (seedlings ha$^{-1}$ yr$^{-1}$) to account for varying time-since-fire captured by our study design. This was calculated by dividing the total number of seedlings ha$^{-1}$ in each plot by the years since stand-replacing fire (ranging from 10 to 19 yr). The unit of analysis was the plot ($n$ = 184). To test the effect of postfire drought severity, we included a term that characterized the 3-yr postfire drought severity as ± SDs from the 1983-2012 average for each plot location. We also included a term for region (Glacier vs. Greater Yellowstone) and topographic aspect (NE, or topographic moisture index), to account for macro- and micro-climate, respectively. To test the effect of distance to seed source, we used one of two terms in the model: distance to the edge of the stand-replacing burn patch, or distance to the nearest prefire live seed-bearing tree (surviving within a burn patch). Whichever term was correlated (using Spearman's *rho*) more strongly with postfire seedling establishment was selected for the model. Models were constructed to also account for other factors that can affect postfire tree regeneration. These terms included fire severity, presence of tree species prefire (as a proxy for local seed supply from nearby surviving trees), slope, and biotic interactions (Table 3).

We generated one model for all postfire tree seedlings across all species, and separate models for each species. Models for each species excluded plots in fires where < 25% of the plots in that fire contained the species prefire. Quaking aspen was an exception to this rule, as it was relatively abundant postfire but occurred in one plot prefire. In all models, we considered $P < 0.05$ as significant support for effects. All models were assessed for fit using diagnostic residual plots, and outliers and/or overly influential points (i.e., Cook's Distance > 1.0) were removed from final models. All statistical analyses were conducted in R (R Development Core Team, 2012) using the 'glm' function in the 'stats' package.

## Results

Ninety-eight percent of plots contained postfire tree seedlings, and normalized establishment rates ranged from 0 to 33,067 seedlings ha$^{-1}$ yr$^{-1}$. Tree establishment rates spanned four orders of magnitude in each region. Mean and median annual seedling establishment rates were one and two orders of magnitude higher, respectively, in Glacier than Greater Yellowstone (Table 4, Figures 4-7, 10). By ten years after fire in Glacier, there was an average of a 105-fold increase in the number of pre to postfire trees per plot (i.e., the number of postfire seedlings compared to the number of prefire stems >15 cm dbh), and postfire seedling density exceeded prefire stem density in 95% (74/78) of plots. Engelmann spruce was the most abundant postfire tree, followed by lodgepole pine, western larch, and Douglas-fir. In Greater Yellowstone, there was an average of a 5-fold increase in the number of pre to postfire trees per plot by ten years after fire, and postfire seedling density exceeded prefire stem density in 53% (56/106) of plots. Lodgepole pine was most abundant, followed by Engelmann spruce, quaking aspen, and whitebark pine. In both regions, postfire subalpine fir establishment was relatively sparse, despite being the most abundant prefire tree.

### *Temporal patterns of postfire tree establishment*

Temporal seedling establishment patterns varied by species. Lodgepole pine (evader/invader) establishment was characterized by a distinct pulse of seedlings in the year of the fire, followed by protracted establishment ~3-5 years postfire (Figure 2A, F). Establishment of avoiders (Engelmann spruce and subalpine fir) and resister/invaders (western larch and Douglas-fir) began immediately postfire and peaked by ~4-6 years after fire in Glacier (Figure 2B-E). Establishment peaks for avoiders and invaders (whitebark pine) were generally later and less pronounced in Greater Yellowstone (Figure 2G-I).

### *Effects of postfire drought severity and distance to postfire seed source*

Postfire drought severity had a strong negative effect on overall postfire tree establishment (Tables 5 and 6, Figure 3). Among tree species with early postfire establishment, negative effects of postfire drought severity were detected for evaders (serotinous lodgepole pine), invaders (non-serotinous lodgepole pine), avoiders (Engelmann spruce and subalpine fir) (Tables 5 and 6, Figure 4) and resister/invaders (western larch) (Figure 5). In contrast, postfire establishment for Douglas-fir, quaking aspen, and whitebark pine was unrelated to postfire drought severity (Tables 5 and 6, Figure 5). Overall postfire tree establishment was unrelated to distance to postfire seed source, but effects for individual species were variable (Tables 5 and 6, Figures 3-5). Postfire tree establishment declined with increasing distance to seed source for early postfire invaders (non-serotinous lodgepole pine) and fire avoiders (Engelmann spruce and subalpine fir), but not for fire evaders (serotinous lodgepole pine), fire resister/invaders (western larch, Douglas-fir), or fire endurers/invaders with capacity for re-sprouting or long-distance dispersal (quaking aspen and whitebark pine).

### *Other factors affecting postfire seedling establishment*

Effects of other factors on postfire tree establishment varied among species (Tables 5 and 6, Figures S1-S8). Overall tree establishment decreased with greater fire severity (Tables 5 and 6, Figure 3), but postfire quaking aspen regeneration increased with fire severity (Figure S7). For most species, establishment increased with local prefire presence or abundance of the tree species. Postfire seedling establishment was greater on cooler/wetter (i.e., more northeast) aspects for all trees combined (Figure 3), and for serotinous lodgepole pine, Engelmann spruce, western larch, and whitebark pine (Figures 4 and 5). Greater abundance of postfire shrubs was associated with increased Engelmann spruce and whitebark pine establishment, but had little association with other species (Figures S1-S8). Effects of slope were variable among species (Table 5 and 6, Figures S1-S8).

## Discussion

### *Rapid postfire tree establishment and initial floristics*

Postfire regeneration was characterized by rapid tree establishment, co-occurrence of shade-intolerant and -tolerant tree species, and wide variability in postfire tree seedling densities. Our results demonstrate relatively synchronous early postfire establishment of fire evaders, invaders, avoiders, and resisters – covering a range of shade tolerances and seed weights. These results support findings following large fires in subalpine forests of the US Northern Rockies (Turner *et al.*, 1999; Kipfmueller & Kupfer, 2005; McKenzie & Tinker, 2012) and boreal forests in Canada (Johnstone *et al.*, 2004). The primary exception to the pattern of early postfire establishment was whitebark pine, which often exhibits delayed germination from soil seedbanks that are deposited by Clark's nutcracker (*Nucifraga columbiana*) (Tomback *et al.*, 2001). Overall, however, greater than 95% of tree seedlings across all species established within 10 yr of fire, with establishment dates for most species peaking ~2-4 yr postfire. Continued establishment may occur after our sampling [as has been observed in Douglas-fir forests in the Pacific Northwest US (see Freund *et al.*, 2014)], but our data support one aspect of precocious complexity in forest structure (Donato *et al.*, 2012) in that early- and late-successional dominants (e.g., lodgepole pine and subalpine fir) are present immediately after a disturbance.

### *Postfire drought severity negatively affects postfire tree establishment*

The strongest and most consistent factor affecting postfire tree establishment rates was climate. At the broadest scale, median postfire tree establishment decreased by two orders of magnitude from Glacier to Greater Yellowstone, corresponding to an increase in moisture deficit (drought stress) from Glacier to Greater Yellowstone. This trend was detected for all species together and for each species individually (three species were not compared among regions because they only occurred prefire in our plots for one region). Postfire drought severity (0-3 years postfire) had consistently-strong negative effects on all species combined and for species that currently dominate upper montane and subalpine forests (lodgepole pine, Engelmann spruce, and subalpine fir). That these species are early postfire colonizers likely places them at the greatest risk of seedling mortality from postfire drought stress. For example, postfire lodgepole pine establishment decreased more sharply with postfire drought severity where serotiny was high (fire evader) than where serotiny was absent (fire invader). Western larch (fire resister/invader), which abuts the lower-elevations of subalpine forests in Glacier (Arno, 1980) and also established rapidly after fire (Figure 2), was negatively affected by postfire drought severity.

Three tree species that were unrelated to postfire drought were likely unaffected because of either drought avoidance or tolerance. For whitebark pine (fire invader), the lack of negative effect from postfire drought stress is likely because of protracted postfire tree establishment compared to the other fire invaders (e.g., non-serotinous lodgepole pine), resulting in most seedling establishment occurring after the postfire drought period. Douglas-fir trees have greater drought tolerance compared to upper-montane and subalpine conifers (Piñol & Sala, 2000), and our results suggest this may also apply to seedlings because postfire Douglas-fir establishment occurred over a similar period as other conifers that responded negatively to greater drought severity. Quaking aspen was also unaffected by postfire drought severity in our study. Throughout its range, mature quaking aspens are vulnerable to extended and/or repeated droughts, and are generally expected to decline under future climate scenarios (Anderegg *et al.*, 2013). However, quaking aspen is extremely widespread and well adapted to disturbance (Shinneman *et al.*, 2013). The dual regenerative strategies of quaking aspen (re-sprouting and long-distance seed dispersal) suggest that aspen might be able to utilize energy reserves from underground roots to tolerate postfire drought stress, or continually establish over a protracted postfire period to avoid postfire drought stress.

Microclimate (mediated through topographic aspect) also affected postfire tree regeneration. Regeneration for most species was greatest on northeast-facing topographic aspects that experience cooler/moister microclimates than other topographic positions (Tables 5 and 6, Figures 3-5). Greater microsite moisture has been shown to increase germination success (Tomback *et al.*, 2001), and our results suggest that northeast aspects may provide important refugia to buffer against severe postfire drought conditions. Similar findings have been reported for postfire tree regeneration in boreal forests (Johnstone *et al.*, 2010b).

### *Effect of distance to postfire seed source varies among fire-regenerative strategies*

The effect of distance to postfire seed source (edge of stand-replacing patch or individual live prefire tree) differed among species, and effects were strongest for fire avoiders (Engelmann spruce and subalpine fir). Engelmann spruce and subalpine fir are easily killed by fire, and possess light-weight seeds positioned high in the canopy that facilitate wind dispersal into burned areas from outside stand-replacing patches (Greene & Johnson, 1996). Lodgepole pine establishment also decreased with distance to postfire seed source in areas where prefire serotiny was not observed (thus lodgepole pine was a fire invader), but not in areas where prefire serotiny was observed (thus lodgepole pine was a fire evader). These findings support patterns observed following the 1988 Yellowstone Fires, where the level of prefire serotiny dictated the importance of distance to postfire seed source (Turner *et al.*, 1997, 2004).

Distance to postfire seed source was not important for fire resisters/invaders, endurers, or invaders with heavy-weight seeds. Neither Douglas-fir nor western larch postfire establishment were affected by distance to postfire seed source. Both species rely partially on wind-dispersal of seeds from trees outside a burned patch, but thick bark and pruning of lower branches allows mature trees to often survive fire and reseed locally, similar to ponderosa pine found at lower elevations (Bonnet *et al.*, 2005; Haire & McGarigal, 2010). The lack of significant effect of distance to surviving seed source for either species could be from the capacity for long-distance dispersal (Donato *et al.*, 2009), or an on-site seed source throughout the interior of stand-replacing patches that could have occurred from trees that were damaged and/or killed by fire, but not burned to the extent that cones in the canopy were consumed (Larson & Franklin, 2005). Quaking aspen establishment was not affected by distance to postfire seed source, largely supporting findings in the Southern US Rocky Mountains (Coop *et al.*, 2010) and in Yellowstone National Park (Turner *et al.*, 2003). Postfire aspen seedlings have been recorded up to 15 km away from prefire mature trees (Turner *et al.*, 2003), and such enormous capacity for long-distance dispersal as a fire invader provides a plausible mechanism for our observed data. Aspen establishment may also have been related to proximity to prefire aspen clones and therefore be from vegetative reproduction (re-sprouting) as a fire endurer. Finally, we did not detect a significant effect of distance to postfire seed source for whitebark pine. This is likely because heavy-weight seeds of this fire invader are dispersed primarily by Clark's nutcracker (Tomback *et al.*, 2001), and dispersal by birds can be farther and less predictable than wind dispersal.

### *Local fire severity and postfire tree regeneration*

For all tree species combined, postfire tree establishment decreased with greater fire severity in the plot. Variations in fire severity within areas of stand-replacing fire can have strong effects on postfire seedling establishment (Turner *et al.*, 1999; Harvey *et al.*, 2014a, 2014b); greater fire severity can consume more cones/seeds on trees that would have otherwise provided a local seed source (Alexander & Cruz, 2012) and/or alter postfire soil conditions in ways that limit conifer seedling establishment (Shenoy *et al.*, 2011). Quaking aspen was the only species for which postfire establishment increased with fire severity, supporting findings that suggest this species establishes well on severely burned sites (Turner *et al.*, 2003; Wan *et al.*, 2014) and may expand its current distribution with increased fire activity.

### *Other factors affecting postfire tree regeneration*

As expected, postfire tree regeneration increased for most species with the presence or abundance of the tree species prefire (a proxy for local seed source). Competition with early successional shrubs can limit seedling survival for conifers with low shade-tolerance (Nagel & Taylor, 2005; Harvey & Holzman, 2014), but our results suggest evidence of facilitative interactions between some conifer seedlings and shrubs. For both Engelmann spruce and whitebark pine, co-occurring shrubs were primarily in the *Ceanothus* genus and were > 2-3 × the height of the postfire tree seedlings (Harvey, unpublished data). The positive effect of shrubs could be a response to increased shade and decreased moisture stress in the microclimate created underneath shrubs, or increased nutrient availability because *Ceanothus* is a nitrogen-fixing genus. For whitebark pine, shrubs may also provide protective cover for Clark's nutcrackers, which may facilitate deposition of seed caches underneath shrubs (Tomback *et al.*, 2001). Effects of slope were variable; slope was the only predictor variable where the direction of the effect varied by species. Slopes for our sites were concentrated on slopes < 20 degrees, and trends may have been driven by a few plots on steeper slopes rather than reflecting any biologically meaningful mechanisms.

### *Implications and expectations for future fire activity, postfire climate, and forest resilience*

In the broader context of established fire-climate relationships and climate-model predictions, our findings lend insight into likely future patterns of postfire forest resilience in the Northern Rockies and similar systems. With continued increases in regional warming, fire frequency and area burned will likely both increase over the next century, with future average fire-seasons matching or exceeding the largest fire years in the historical record (Westerling *et al.*, 2011). The amount of stand-replacing fire increases proportionally (~30 to 40%) with the amount of area burned, and the proportion of stand-replacing fire within any given fire has been increasing since 1984 (Harvey, in prep). Therefore, future years will likely experience a substantial increase in area burned as stand-replacing fire, potentially resulting in larger stand-replacing patches with greater distances to postfire seed sources. Postfire climate conditions are also expected to become warmer and drier over the next century, as average water-year CMD is predicted to be between +2.0 and +3.0 SD of the current 30-yr mean by the year 2050 (Westerling *et al.*, 2011).

For comparison, during the most extreme and extended postfire drought in our study period (2000 - 2003) the 3-yr postfire mean CMD ranged from +0.7 to +1.1 SD. Together, these factors strongly suggest that large fire years (with large expanses of stand-replacing fire) followed by droughts at least as severe as those experienced in recent decades will become a regular occurrence in the Northern Rockies over the next century.

If these expected conditions occur, our data suggest that future forest resilience may be substantially altered. The strong negative relationship between postfire tree establishment and postfire drought severity for tree species that currently dominate subalpine forests (lodgepole pine, Engelmann spruce, subalpine fir) suggests that these species may be particularly challenged by future conditions. Fire avoiders (subalpine fir and Engelmann spruce) are the most drought-sensitive among subalpine trees (Piñol & Sala, 2000), and these species also exhibited the greatest reductions with increasing distance to stand-replacing patch-edge among all the species in our study. Both species also require several decades before cones are produced on young trees, leaving the potential for reduced seed availability, reduced seed delivery, and lower seedling survival under future climate-fire scenarios. Fire evaders and invaders with early cone development (lodgepole pine and western larch) may fare better. These species possess capacity for development of both serotinous and non-serotinous cones on trees < 10 yr old (Scher, 2002; Turner *et al.*, 2007). In some cases, precocious cone development may provide enough seed supply to allow these two species to capitalize on predicted increases in fire frequency (Westerling *et al.*, 2011). However, western larch is highly drought sensitive (Piñol & Sala, 2000), which may lead to failed postfire tree regeneration even if seed were available. Increased fire frequency may also select for greater prevalence of serotiny in lodgepole pine, which may decrease establishment by requiring that fire years are followed by suitable climate conditions (Buma *et al.*, 2013). Our findings support this hypothesis, as areas with greater serotiny were associated with stronger drought-driven decreases in postfire lodgepole pine seedling establishment than areas with lower serotiny.

Future postfire tree establishment may increase for species presently situated on either end of the elevation bounds of the upper montane / subalpine forest zone. Slow-reproducing treeline pioneer species' such as whitebark pine may benefit from a protracted establishment period that can provide a buffer against postfire drought by increasing the likelihood of overlap of seed arrival/germination during favorable conditions. Also, long-distance dispersal from animals may assist in finding suitable microsites. However, the future of whitebark pine is uncertain because of introduced pathogens and novel insect infestations (Logan *et al.*, 2010), and how those factors may affect postfire regeneration is unknown. Quaking aspen may benefit from increased fire frequency (Kulakowski *et al.*, 2013), owing to extremely light seeds that can disperse via wind over several km (Turner *et al.*, 2003) and the ability to resprout from underground root structures. In our study, quaking aspen was also the only species to respond positively to increased fire severity in stand-replacing patches (Table 6). However, whether young postfire aspen are more or less sensitive to drought compared to adult trees (Anderegg *et al.*, 2013) is unknown, and requires further study to know how well aspen seedlings may persist once established. Fire resister/invaders with moderate drought tolerance (Douglas-fir) may benefit from predicted increases in fire frequency if mature trees can persist and are not killed by severe fire. Provided suitable dispersal into burned areas, Douglas-fir likely stands the best chance of increased postfire establishment in the upper montane / subalpine zone because of lower drought sensitivity compared to other trees (Piñol & Sala, 2000).

Our findings suggest that sharp decreases in establishment for the current dominant species in these forests (e.g., lodgepole pine, Engelmann spruce, subalpine fir) may greatly outweigh the potential for increased establishment of other species (e.g., Douglas-fir, quaking aspen). For example, if our models for overall tree regeneration are extended to match expected postfire climate conditions by mid-21st Century (drought severity between +2.0 and +3.0 SD of our study period, but holding all other variables in our models constant at their means), postfire tree establishment would decrease to between 22 and 108 seedlings $ha^{-1}$ $yr^{-1}$ in Glacier and between 47 and 78 seedlings $ha^{-1}$ $yr^{-1}$ in Greater Yellowstone. Such postfire establishment rates would be less than 2% (Glacier) and 33% (Greater Yellowstone) of contemporary rates we observed, and less than 0.3% of rates observed after the 1988 Yellowstone Fires (Turner *et al.*, 2004). Estimates based on our empirical data are conservative, as other drivers will likely also change (e.g., greater fire severity, increasing distance to seed sources), and trends could be nonlinear (Scheffer *et al.*, 2012). Warm/dry periods during the Holocene (~12,000 years ago to present) were associated with increased drought severity and fire activity throughout the Northern Rockies, and many areas of lodgepole pine forests were converted to Douglas-fir woodlands (Whitlock *et al.*, 2003). Although some locations experienced more severe Holocene climate warming than we have observed in recent decades (Whitlock *et al.*, 2003), the magnitude of drought severity and fire activity expected for the 21st century far exceeds that in the paleo record (Westerling *et al.*, 2011). If future fire patterns are such that patch size substantially limits seed delivery and fires are followed by climate conditions that lead to extensive seedling mortality, forest regeneration could eventually fail.

Our study suggests several key directions for future research. First, differences among our two focal study regions demonstrate that Greater Yellowstone may be closer to a ‘tipping point’ for postfire tree regeneration, and regional climate may play a role. Nearly half the plots in Greater Yellowstone had yet to attain postfire tree densities that equal prefire densities (compared to just 5% of plots in Glacier). Transitions are more likely to occur in warmer, drier environments closer to the edge of species range boundaries (Bell *et al.*, 2014) and studies that focus on the edge of species ranges may be able to detect stronger trends, or more quickly detect ecosystem state shifts. Second, research that experimentally manipulates moisture conditions to test the specific drought tolerance of tree seedlings may provide empirical support for patterns we observed, eventually building mechanistic models of thresholds in forest resilience. Combined with modeling of the probabilistic occurrence of large fire years followed by prolonged (~3-4 yr) drought, these insights can provide quantitative assessments of when postfire tree recruitment may occur and when it may be reduced/absent. Finally, as climate trends continue, the relative influence of microsite factors (e.g., topography, nurse logs and shrubs) may become important to buffer tree seedlings from harsh drought conditions. Continued monitoring of postfire forest regeneration following ‘natural experiments’ and experimental studies (e.g., using seed traps to test dispersal) is needed to better understand and predict when changes in forest resilience will lead to transitions to non-forest ecosystems.

Overall, our findings suggest that climate change could have substantial impacts on postfire forest resilience over extensive high-elevation and high-latitude forested areas. Mechanisms we evaluated are general to crown-fire regimes in forests throughout the northern hemisphere that share similar taxa (Turner & Romme, 1994). Fire-prone subalpine and boreal forests are among the most extensive biomes worldwide, and evidence is already accumulating in support of changing extent and patterns of fire in these systems (Westerling *et al.*, 2011; de Groot *et al.*, 2013). Our findings are consistent with mechanisms that could lead to future decreases in postfire resilience, reductions in extent, and increased patchiness of high-elevation and high-latitude forests.

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Supporting information.

Figure S1. Modeled effects of each predictor variable on postfire serotinous lodgepole pine regeneration (seedlings $ha^{-1}$ $yr^{-1}$).

Figure S2. Modeled effects of each predictor variable on postfire non-serotinous lodgepole pine regeneration (seedlings $ha^{-1}$ $yr^{-1}$).

Figure S3. Modeled effects of each predictor variable on postfire Engelmann spruce regeneration (seedlings $ha^{-1}$ $yr^{-1}$).

Figure S4. Modeled effects of each predictor variable on postfire subalpine fir regeneration (seedlings $ha^{-1}$ $yr^{-1}$).

Figure S5. Modeled effects of each predictor variable on postfire western larch regeneration (seedlings $ha^{-1}$ $yr^{-1}$).

Figure S6. Modeled effects of each predictor variable on postfire Douglas-fir regeneration (seedlings $ha^{-1}$ $yr^{-1}$).

Figure S7. Modeled effects of each predictor variable on postfire quaking aspen regeneration (seedlings $ha^{-1}$ $yr^{-1}$).

Figure S8. Modeled effects of each predictor variable on postfire whitebark pine regeneration (seedlings $ha^{-1}$ $yr^{-1}$).

Tables

Table 1. Fire-regeneration strategy and fire-related traits for common tree species in upper montane and subalpine forests of the US Northern Rockies.

| | | | Important fire-related traits[2,3] | | | |
|---|---|---|---|---|---|---|
| Scientific name | Common name | Fire-regeneration strategy[1] | Bark thickness | Seed dispersal | Seed weight | Shade tolerance |
| *Pinus contorta* | lodgepole pine (serotinous) | evader | thin | aerial seedbank | medium | very low |
| *Pinus contorta* | lodgepole pine (non-serotinous) | invader | thin | wind | medium | very low |
| *Picea engelmannii* | Engelmann spruce | avoider | thin | wind | medium | moderate |
| *Abies lasiocarpa* | subalpine fir | avoider | thin | wind | heavy | very high |
| *Pseudotsuga menziesii* | Douglas-fir | resister/ invader | thick | wind | medium | moderate |
| *Larix Occidentalis* | western larch | resister/ invader | thick | wind | light | very low |
| *Populus tremuloides* | quaking aspen | endurer/ invader | thin | re-sprouting /wind | very light | low |
| *Pinus albicaulis* | whitebark pine | invader | thin | animal | very heavy | moderate |

[1] Agee JK (1993) *Fire Ecology of Pacific Northwest Forests*. Island Press.

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Table 2. Topographic setting and prefire stand structure of the stand-replacing burn patch plots in Glacier and Greater Yellowstone.

| | Glacier (*n* = 78) | | | | Greater Yellowstone (*n* = 106) | | | |
|---|---|---|---|---|---|---|---|---|
| Variable | Min - max | Median | Mean (SE) | Freq. | Min - max | Median | Mean (SE) | Freq. |
| Topographic conditions | | | | | | | | |
| Elevation (m) | 1,119 - 1,847 | 1,246 | 1,350 (26) | | 2,065 - 2,687 | 2,503 | 2,407 (20) | |
| Slope (deg) | 0 - 24 | 6 | 7 (1) | | 0 - 47 | 5 | 7 (1) | |
| NE Index (0-2) | 0.0 -2.0 | 0.9 | 0.9 (0.1) | | 0.0 - 2.0 | 0.3 | 0.7 (0.1) | |
| Prefire stand structure | | | | | | | | |
| Basal area (m$^2$ ha$^{-1}$)[a] | 18 - 62 | 31 | 33 (1) | | 16 -50 | 36 | 36 (1) | |
| Tree density (≥ 15 cm, stems ha$^{-1}$)[b] | 142 - 1,075 | 403 | 472 (25) | | 14 - 962 | 403 | 422 (15) | |
| % of stems (≥ 15 cm)[b] | | | | | | | | |
| lodgepole pine | 0 - 38 | 4 | 7 (1) | 60% | 0 - 100 | 19 | 30 (3) | 75% |
| subalpine fir | 0 - 92 | 23 | 28 (2) | 90% | 0 - 100 | 39 | 40 (3) | 90% |
| Engelmann spruce | 8 - 100 | 42 | 42 (2) | 99% | 0 - 96 | 14 | 20 (2) | 77% |
| western larch | 0 - 40 | 0 | 4 (1) | 44% | 0 - 0 | 0 | 0 (0) | 0% |
| Douglas-fir | 0 - 53 | 3 | 8 (1) | 55% | 0 - 38 | 0 | 1 (0) | 8% |
| whitebark pine | 0 - 0 | 0 | 0 (0) | 0% | 0 - 90 | 0 | 5 (1) | 29% |
| unknown | 0 - 68 | 3 | 11 (2) | n/a | 0 - 45 | 0 | 4 (1) | n/a |
| Prefire lodgepole pine serotiny (% of trees) | 25 - 100 | 100 | 86 (11) | n/a | 0 - 50 | 0 | 15 (5) | n/a |

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[a] basal area was measured in the control (unburned) plots outside the stand-replacing burn patches.

[b] Tree stems (≥ 15 cm) were recorded in each postfire plot, and included stems that had fallen since fire.

Table 3. Predictor variables included in models of postfire tree regeneration.

| **Factor**<br>*Variable*<br>Measurement | Description (units, data range) |
|---|---|
| **Climate** | |
| *Region* | |
| Glacier or Greater Yellowstone | Region where plot is located, reflecting a cooler/wetter region (Glacier) with a 30-yr mean of 210 mm CMD or a warmer/drier region (Greater Yellowstone) with a 30-yr mean of 255 mm CMD. |
| *Postfire drought severity* | |
| Cumulative moisture deficit | Water-year (Oct.-Sept.) cumulative moisture deficit averaged across 1-, 2-, and 3-yr postfire (± SD from the 30-yr mean from 1983-2012, -1.27 to 1.11). |
| *Local microclimate* | |
| Topographic aspect | Cosine-transformed aspect reflecting similarity of plot aspect to Northeast, which is the coolest/wettest aspect (Beers *et al.*, 1966) (index with 0.0 = SW and 2.0 = NE, 0.0 to 2.0) |
| **Fire** | |
| *Distance to postfire seed source* | |
| Distance to live prefire tree | Distance from plot center to the nearest prefire live seed-bearing tree (m, 5 to 750) |
| Distance to patch edge | Distance from plot center to the nearest edge of the stand-replacing burn patch (m, 15 to 1,250) |
| *Fire severity* | |
| RdNBR | Satellite index of fire severity for the plot, using the relative differenced normalized burn ratio (RdNBR) (Miller & Thode, 2007) (320 to 1,475) |
| **Local factors** | |
| *Seed supply* | |
| Presence prefire | Presence of the postfire tree species in the plot prior to the fire (yes, no) |
| Stems prefire | Prefire stems (> 15 cm dbh) in the plot for the postfire tree species (prop. of total stems, 0.00 to 1.00) |
| *Local topography* | |
| Slope | Slope measured from plot center (degrees, 0 to 47) |
| *Biotic interactions* | |
| Shrub cover | Cover of shrubs averaged from eight 0.25 $m^2$ subplots within each plot (proportion of total cover, 0.00 to 0.74) |

Table 4. Postfire tree regeneration (postfire seedlings $ha^{-1}$ $yr^{-1}$) in the stand-replacing burn patch plots.

| | Glacier (*n* = 78) | | | | Greater Yellowstone (*n* = 106) | | | |
|---|---|---|---|---|---|---|---|---|
| Tree species | Min-max | Median | Mean (SE) | Freq. | Min-max | Median | Mean (SE) | Freq. |
| All tree species combined | 3 - 33,067 | 1,055 | 4,454 (819) | 100% | 0 - 2,035 | 45 | 232 (39) | 96% |
| lodgepole pine | 0 - 8,400 | 170 | 570 (147) | 74% | 0 - 1,800 | 26 | 192 (34) | 92% |
| subalpine fir | 0 - 933 | 0 | 50 (16) | 38% | 0 - 167 | 0 | 6 (2) | 36% |
| Engelmann spruce | 0 - 27,733 | 251 | 3,177 (706) | 81% | 0 - 632 | 0 | 13 (7) | 37% |
| western larch | 0 - 4,133 | 37 | 357 (83) | 77% | 0 - 0 | 0 | 0 (0) | 0% |
| Douglas-fir | 0 - 2,933 | 6 | 241 (61) | 41% | 0 - 6 | 0 | 0 (0) | 8% |
| whitebark pine | 0 - 267 | 0 | 6 (4) | 5% | 0 - 176 | 0 | 8 (2) | 43% |
| quaking aspen | 0 - 1,067 | 0 | 44 (15) | 32% | 0 - 359 | 0 | 13 (4) | 36% |

Table 5. Generalized linear models testing the effects of explanatory variables on postfire tree regeneration rates (seedlings yr$^{-1}$ ha$^{-1}$) for all trees combined, and each species separately. Terms in **bold** were significant at $P$ < 0.05.

| Species | Predictor variables | $\beta$ | SE | *t* | *P* |
|---|---|---|---|---|---|
| total trees<br>(all species) | **Region (Greater Yellowstone)** | **-2.75** | **0.43** | **-6.40** | **<0.01** |
| | **Drought severity (± SD)** | **-1.32** | **0.25** | **-5.19** | **<0.01** |
| | **Topographic aspect (NE Index)** | **0.50** | **0.16** | **3.19** | **<0.01** |
| | Distance to seed source (m)[a] | 0.00 | 0.00 | 0.20 | 0.84 |
| | **Fire severity (RdNBR)** | **-0.00** | **0.00** | **-4.12** | **<0.01** |
| | Prefire trees (stems ha$^{-1}$) | -0.00 | 0.00 | -0.16 | 0.87 |
| | **Slope (deg.)** | **0.04** | **0.02** | **2.13** | **0.03** |
| | Shrub cover (prop.) | -0.22 | 0.89 | -0.25 | 0.81 |
| lodgepole pine<br>(serotinous) | **Region (Greater Yellowstone)** | **-1.90** | **0.68** | **-2.78** | **<0.01** |
| | **Drought severity (± SD)** | **-0.92** | **0.35** | **-2.62** | **0.01** |
| | **Topographic aspect (NE Index)** | **0.59** | **0.22** | **2.64** | **0.01** |
| | Distance to seed source (m)[b] | -0.00 | 0.00 | -0.10 | 0.92 |
| | Fire severity (RdNBR) | -0.00 | 0.00 | -0.54 | 0.59 |
| | **Prefire trees (relative density)** | **2.46** | **1.10** | **2.24** | **0.03** |
| | **Slope (deg.)** | **0.09** | **0.03** | **3.50** | **<0.01** |
| | Shrub cover (prop.) | -0.84 | 1.89 | -0.44 | 0.66 |
| lodgepole pine<br>(non serotinous) | Region (Greater Yellowstone) | -0.61 | 0.35 | -1.75 | 0.08 |
| | **Drought severity (± SD)** | **-0.61** | **0.23** | **-2.67** | **<0.01** |
| | Topographic aspect (NE Index) | -0.21 | 0.24 | -0.85 | 0.39 |
| | **Distance to seed source (m)[b]** | **-0.00** | **0.00** | **-1.96** | **0.05** |
| | Fire severity (RdNBR) | 0.00 | 0.00 | 0.19 | 0.85 |
| | **Prefire trees (relative density)** | **1.71** | **0.17** | **3.51** | **<0.01** |
| | **Slope (deg.)** | **-0.08** | **0.35** | **-2.38** | **0.02** |
| | Shrub cover (prop.) | 0.12 | 1.04 | 0.12 | 0.91 |
| Engelmann spruce | **Region (Greater Yellowstone)** | **-4.43** | **1.06** | **-4.18** | **<0.01** |
| | **Drought severity (± SD)** | **-1.86** | **0.24** | **-7.90** | **<0.01** |
| | **Topographic aspect (NE Index)** | **0.66** | **0.14** | **4.80** | **<0.01** |
| | **Distance to seed source (m)[b]** | **-0.03** | **0.00** | **-5.76** | **<0.01** |
| | Fire severity (RdNBR) | -0.00 | 0.00 | -1.44 | 0.15 |
| | **Prefire trees (relative density)** | **4.69** | **0.68** | **6.89** | **<0.01** |
| | Slope (deg.) | -0.01 | 0.02 | -0.79 | 0.43 |
| | **Shrub cover (prop.)** | **2.01** | **0.96** | **2.10** | **0.04** |
| subalpine fir | **Region (Greater Yellowstone)** | **-2.39** | **0.50** | **-4.83** | **<0.01** |
| | **Drought severity (± SD)** | **-1.41** | **0.31** | **-4.63** | **<0.01** |

| | | | | | |
|---|---|---|---|---|---|
| | Topographic aspect (NE Index) | -0.06 | 0.20 | -0.30 | 0.77 |
| | **Distance to seed source (m)[b]** | **-0.02** | **0.01** | **-2.73** | **<0.01** |
| | Fire severity (RdNBR) | -0.00 | 0.00 | -0.92 | 0.36 |
| | Prefire trees (relative density) | 1.48 | 0.77 | 1.93 | 0.06 |
| | Slope (deg.) | 0.00 | 0.03 | 0.03 | 0.98 |
| | Shrub cover (prop.) | 0.30 | 1.22 | 0.24 | 0.81 |
| western larch[c] | **Drought severity (± SD)** | **-1.36** | **0.32** | **-4.25** | **<0.01** |
| | **Topographic aspect (NE Index)** | **0.93** | **0.28** | **3.39** | **<0.01** |
| | Distance to seed source (m)[b] | -0.01 | 0.01 | -1.59 | 0.12 |
| | Fire severity (RdNBR) | -0.00 | 0.00 | -1.16 | 0.25 |
| | Prefire trees (relative density) | 2.03 | 1.96 | 1.04 | 0.30 |
| | **Slope (deg.)** | **0.11** | **0.03** | **3.86** | **<0.01** |
| | Shrub cover (prop.) | 0.33 | 1.50 | 0.22 | 0.83 |
| Douglas-fir[c] | Drought severity (± SD) | -1.94 | 16.2 | -0.12 | 0.91 |
| | Topographic aspect (NE Index) | 0.57 | 9.41 | 0.06 | 0.95 |
| | Distance to seed source (m)[b] | -0.03 | 0.33 | -0.08 | 0.94 |
| | Fire severity (RdNBR) | 0.00 | 0.05 | 0.02 | 0.98 |
| | Prefire trees (relative density) | 4.92 | 56.9 | 0.09 | 0.93 |
| | Slope (deg.) | 0.12 | 1.02 | 0.12 | 0.90 |
| | Shrub cover (prop.) | -5.12 | 76.3 | -0.07 | 0.95 |
| quaking aspen[d] | Region (Greater Yellowstone) | -0.91 | 0.51 | -1.79 | 0.08 |
| | Drought severity (± SD) | 0.52 | 0.40 | 1.29 | 0.20 |
| | Topographic aspect (NE Index) | -0.12 | 0.31 | -0.37 | 0.71 |
| | Distance to seed source (m)[a] | -0.00 | 0.00 | -0.53 | 0.60 |
| | **Fire severity (RdNBR)** | **0.00** | **0.00** | **2.07** | **0.04** |
| | Slope (deg.) | -0.03 | 0.04 | -0.71 | 0.48 |
| | Shrub cover (prop.) | -0.28 | 1.56 | -0.18 | 0.86 |
| whitebark pine[c] | Drought severity (± SD) | -0.98 | 0.68 | -1.45 | 0.16 |
| | **Topographic aspect (NE Index)** | **1.29** | **0.44** | **2.96** | **<0.01** |
| | Distance to seed source (m)[a] | 0.00 | 0.00 | 1.08 | 0.29 |
| | Fire severity (RdNBR) | -0.00 | 0.00 | -1.19 | 0.24 |
| | **Prefire trees (relative density)** | **7.88** | **1.89** | **4.17** | **<0.01** |
| | Slope (deg.) | -0.07 | 0.04 | -1.77 | 0.09 |
| | **Shrub cover (prop.)** | **5.54** | **2.30** | **2.41** | **0.02** |

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[a] distance (m) to the edge of the stand-replacing burn patch

[b] distance (m) to the nearest prefire live seed-bearing tree

[c] region term not in model because tree species was only in plots in a single region prior to fire

[d] prefire trees term not in model because tree species was only in one plot prefire

Table 6. Summary of effects on postfire tree regeneration, overall, and for each tree species. Effects are noted for terms with $P < 0.05$ in models summarized in Table 5.

| | | Climate | | | Fire | | Local factors | | |
|---|---|---|---|---|---|---|---|---|---|
| Tree species | Fire-regenerative strategy[1] | Region (GYE) | Drought severity | NE Index | Distance to seed source | Fire severity | Prefire trees | Slope | Shrub cover |
| all species combined | all | - | - | + | | - | | + | |
| lodgepole pine (serot.) | evader | - | - | + | | | + | + | |
| lodgepole pine (non serot.) | invader | | - | | - | | + | - | |
| Engelmann spruce | avoider | - | - | + | - | | + | | + |
| subalpine fir | avoider | - | - | | - | | | | |
| western larch | resister/invader | n/a | - | + | | | | + | |
| Douglas-fir | resister/invader | n/a | | | | | | | |
| quaking aspen | endurer/invader | | | | | + | n/a | | |
| whitebark pine | invader | n/a | | + | | | + | | + |

[1] Agee JK (1993) *Fire Ecology of Pacific Northwest Forests*. Island Press, 513 pp.

n/a: term not tested in model; see methods and results.

GYE = Greater Yellowstone

Figure legends:

Figure 1. Study area map. A) Location of US Northern Rockies in North America. B) Location of each study area within the Northern Rockies Ecoregion (outlined in blue). C) The Glacier study area with Glacier NP highlighted in green and each study fire shaded in black. D) The Greater Yellowstone study area with Yellowstone NP and Grand Teton NP highlighted in green and each study fire shaded in black. Years of fire occurrence are in parentheses in C) and D).

Figure 2. Temporal trends of postfire tree establishment (seedlings ha$^{-1}$ in each postfire year) for each species in each study region.

Figure 3. Modeled effects of each predictor variable on postfire tree regeneration rates for all species (total tree seedlings ha$^{-1}$ yr$^{-1}$). Plots depict the effect of each variable holding all other variables in the model constant at their mean. See Table 5 for full model results.

Figure 4. Modeled effects of the focal fire (distance to seed source) and climate variables on postfire tree regeneration rates (seedlings ha$^{-1}$ yr$^{-1}$) for the most dominant prefire subalpine forest species (lodgepole pine, Engelmann spruce, subalpine fir). Plots depict the effect of each variable holding all other variables in the model constant at their mean. See Table 5 for full model results.

Figure 5. Modeled effects of the focal fire (distance to seed source) and climate variables on postfire tree regeneration rates (seedlings ha$^{-1}$ yr$^{-1}$) for less dominant prefire subalpine forest species (western larch, Douglas-fir, quaking aspen, whitebark pine). Plots depict the effect of each variable holding all other variables in the model constant at their mean. See Table 5 for full model results.

Figures

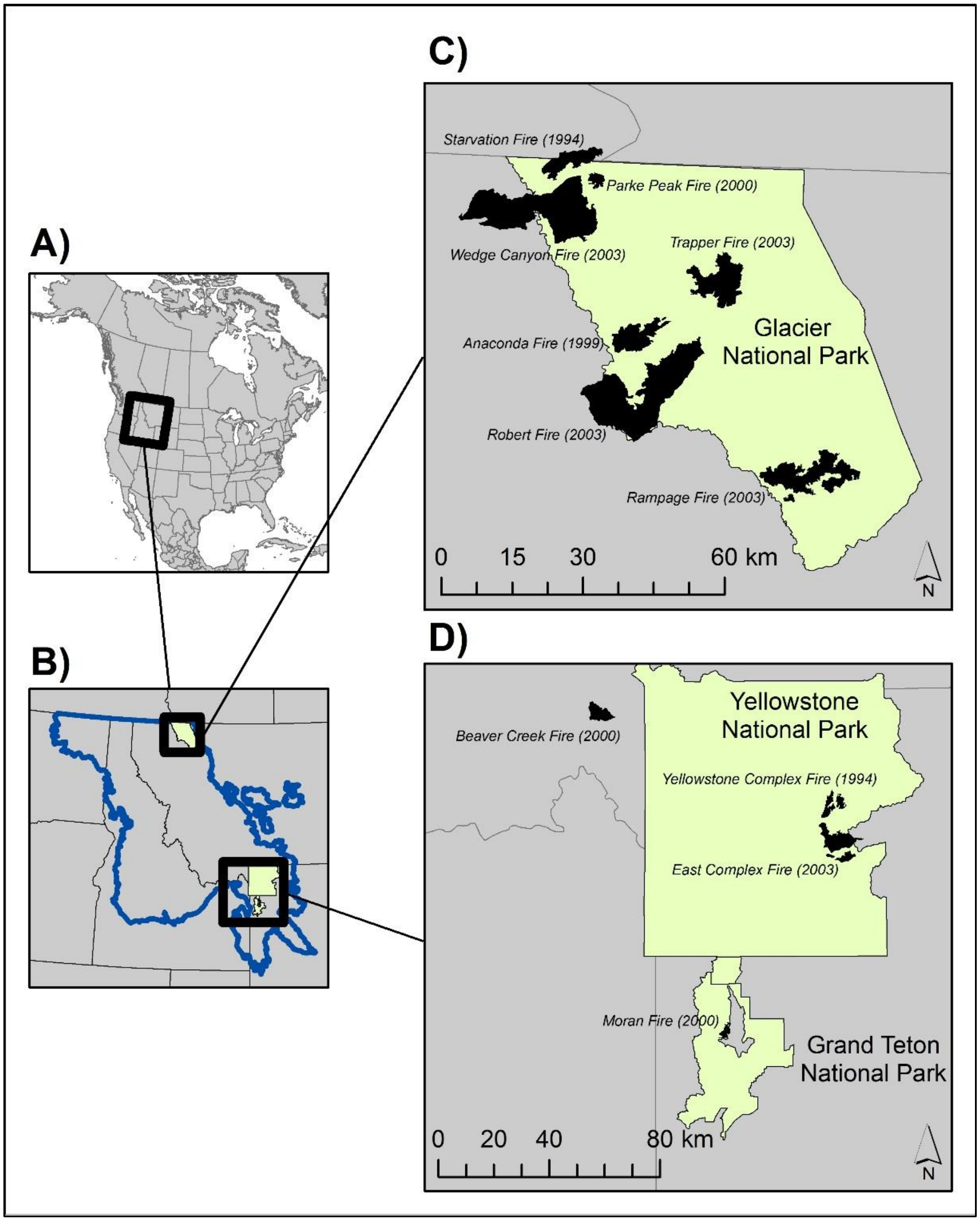

Figure 1.

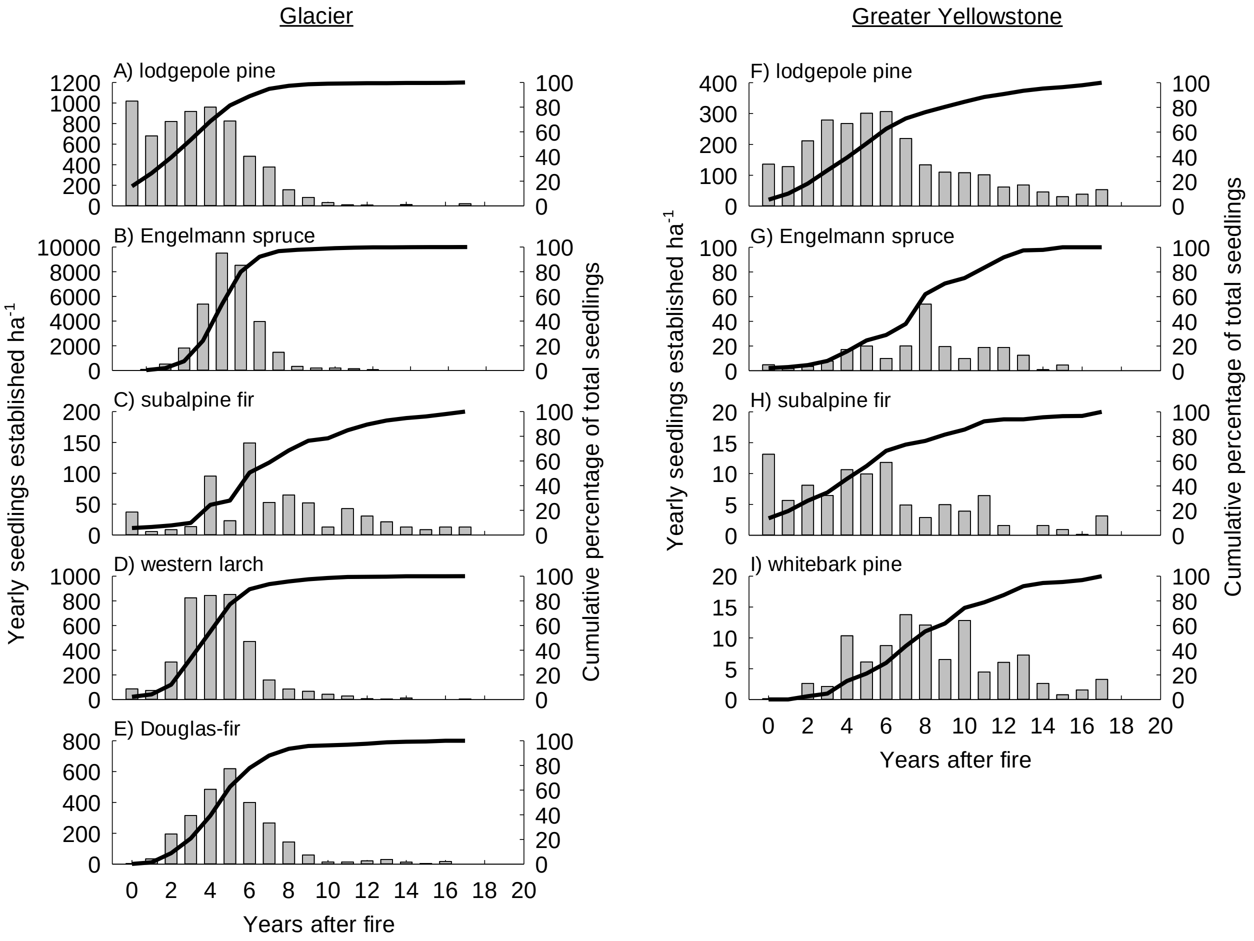
Glacier
Greater Yellowstone
A) lodgepole pine
B) Engelmann spruce
C) subalpine fir
D) western larch
E) Douglas-fir
F) lodgepole pine
G) Engelmann spruce
H) subalpine fir
I) whitebark pine
Yearly seedlings established ha$^{-1}$
Cumulative percentage of total seedlings
Years after fire
0
2
4
6
8
10
12
14
16
18
20
1200
1000
800
600
400
200
10000
8000
6000
4000
2000
150
100
50
400
300
15
5

Figure 2.

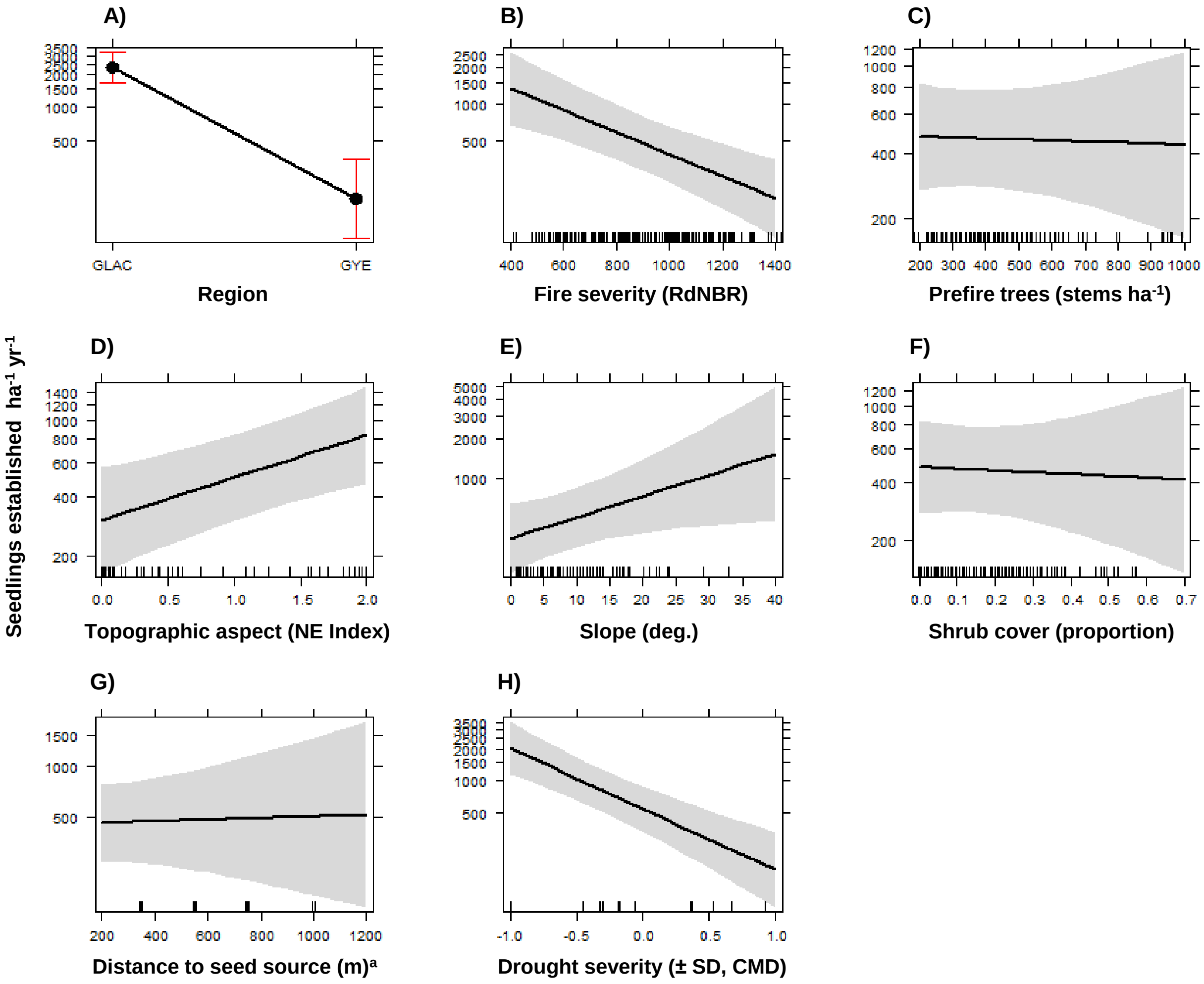
Seedlings established ha$^{-1}$ yr$^{-1}$
A)
3500
3000
2500
2000
1500
1000
500
GLAC
GYE
Region
B)
2500
2000
1500
1000
500
400
600
800
1000
1200
1400
Fire severity (RdNBR)
C)
1200
1000
800
600
400
200
200
300
400
500
600
700
800
900
1000
Prefire trees (stems ha$^{-1}$)
D)
1400
1200
1000
800
600
400
200
0.0
0.5
1.0
1.5
2.0
Topographic aspect (NE Index)
E)
5000
4000
3000
2000
1000
0
5
10
15
20
25
30
35
40
Slope (deg.)
F)
1200
1000
800
600
400
200
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Shrub cover (proportion)
G)
1500
1000
500
200
400
600
800
1000
1200
Distance to seed source (m)$^{a}$
H)
3500
3000
2500
2000
1500
1000
500
-1.0
-0.5
0.0
0.5
1.0
Drought severity (± SD, CMD)

Figure 3.

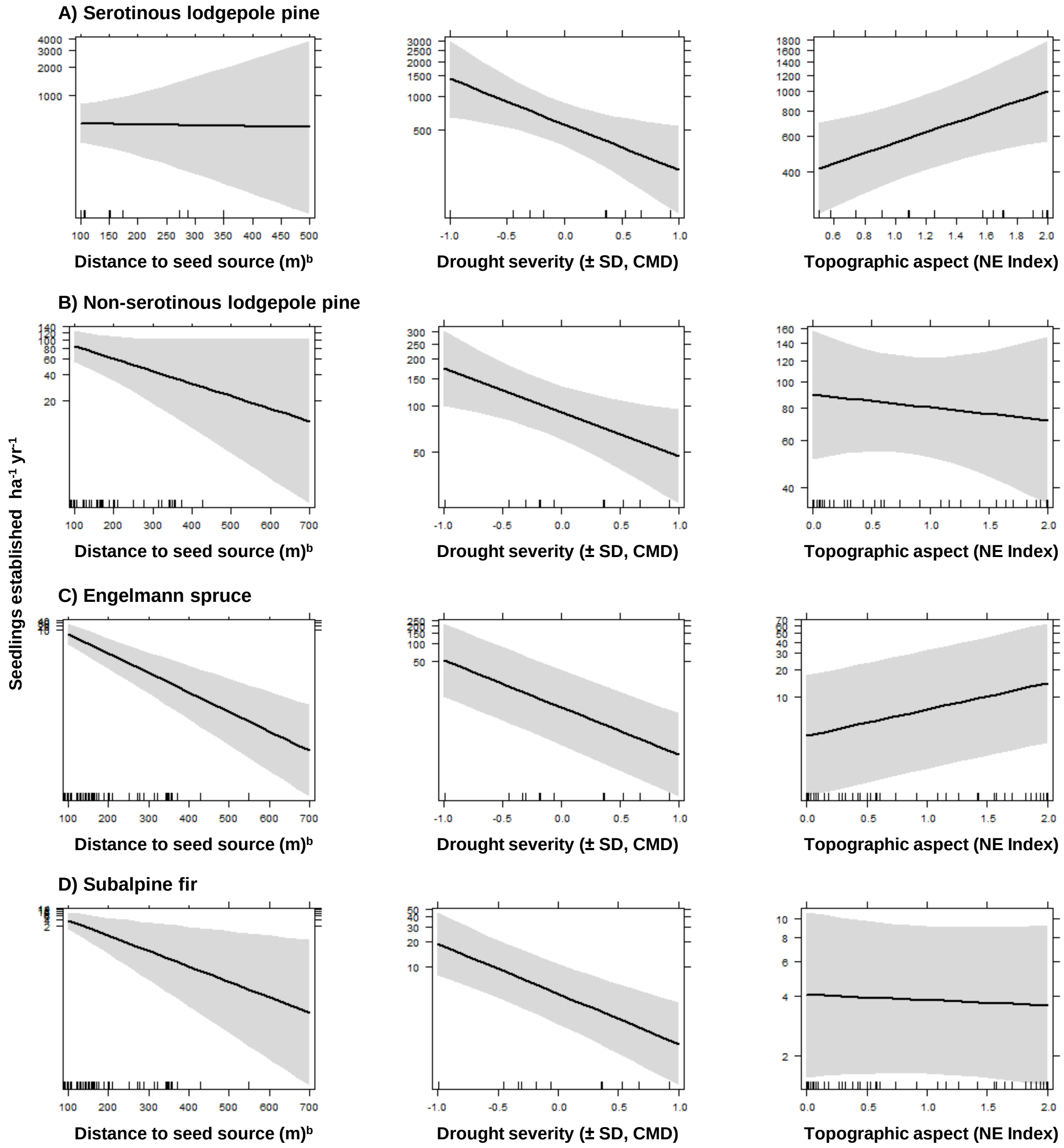
A) Serotinous lodgepole pine
B) Non-serotinous lodgepole pine
C) Engelmann spruce
D) Subalpine fir
Seedlings established ha-1 yr-1
Distance to seed source (m)b
Drought severity (± SD, CMD)
Topographic aspect (NE Index)
4000
3000
2000
1000
100
150
200
250
300
350
400
450
500
3000
2500
2000
1500
1000
500
-1.0
-0.5
0.0
0.5
1.0
1800
1600
1400
1200
1000
800
600
400
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
140
120
100
80
60
40
20
600
700
300
250
200
150
100
50
160
140
120
100
80
60
40
1.5
70
10
8
6
4
2

Figure 4.

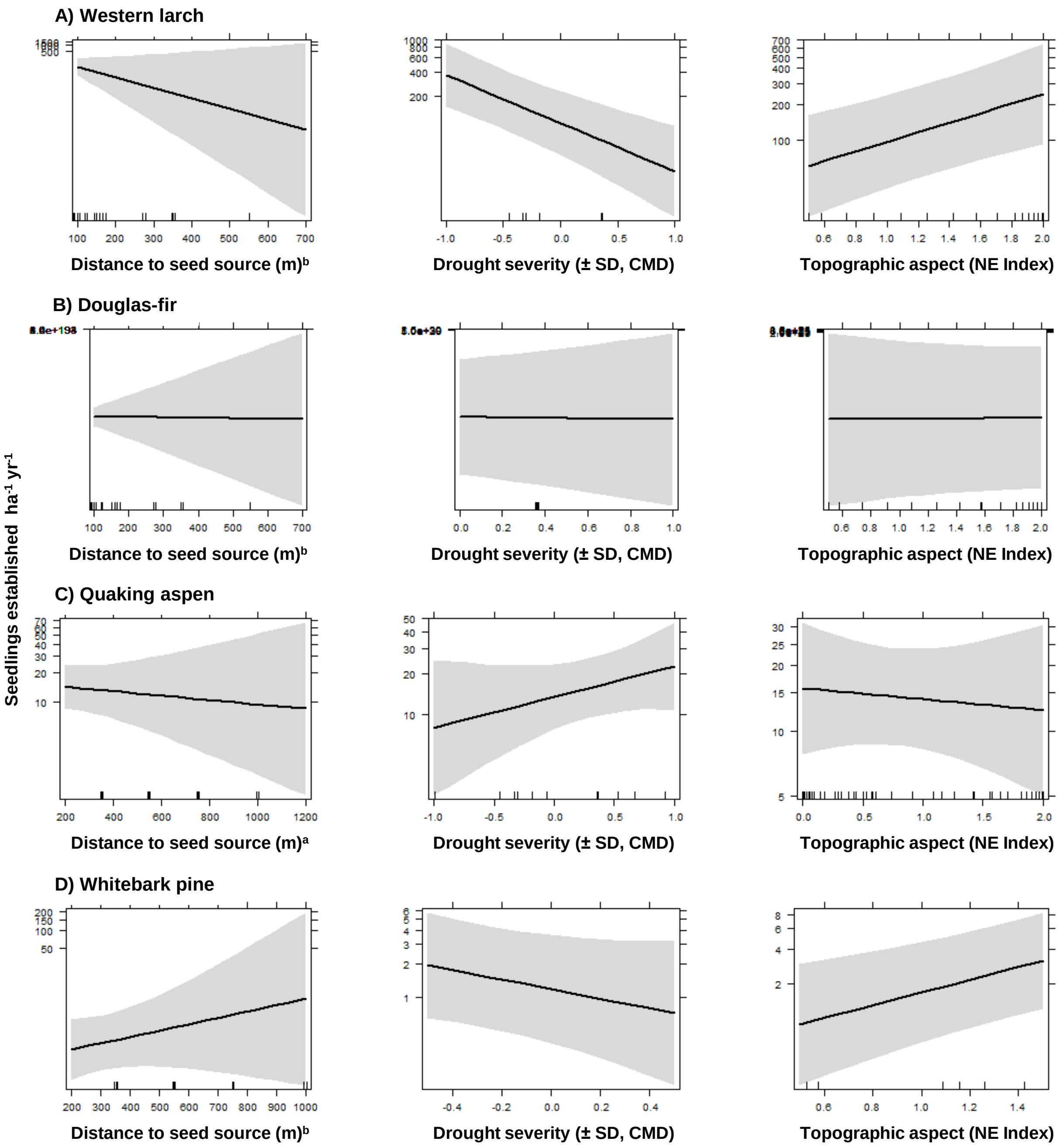
Seedlings established ha-1 yr-1
A) Western larch
500
100 200 300 400 500 600 700
Distance to seed source (m)b
1000 800 600 400 200
-1.0 -0.5 0.0 0.5 1.0
Drought severity (± SD, CMD)
700 600 500 400 300 200 100
0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0
Topographic aspect (NE Index)
B) Douglas-fir
100 200 300 400 500 600 700
Distance to seed source (m)b
0.0 0.2 0.4 0.6 0.8 1.0
Drought severity (± SD, CMD)
0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0
Topographic aspect (NE Index)
C) Quaking aspen
70 60 50 40 30 20 10
200 400 600 800 1000 1200
Distance to seed source (m)a
50 40 30 20 10
-1.0 -0.5 0.0 0.5 1.0
Drought severity (± SD, CMD)
30 25 20 15 10 5
0.0 0.5 1.0 1.5 2.0
Topographic aspect (NE Index)
D) Whitebark pine
200 150 100 50
200 300 400 500 600 700 800 900 1000
Distance to seed source (m)b
6 5 4 3 2 1
-0.4 -0.2 0.0 0.2 0.4
Drought severity (± SD, CMD)
8 6 4 2
0.6 0.8 1.0 1.2 1.4
Topographic aspect (NE Index)

Figure 5.

Supporting information.

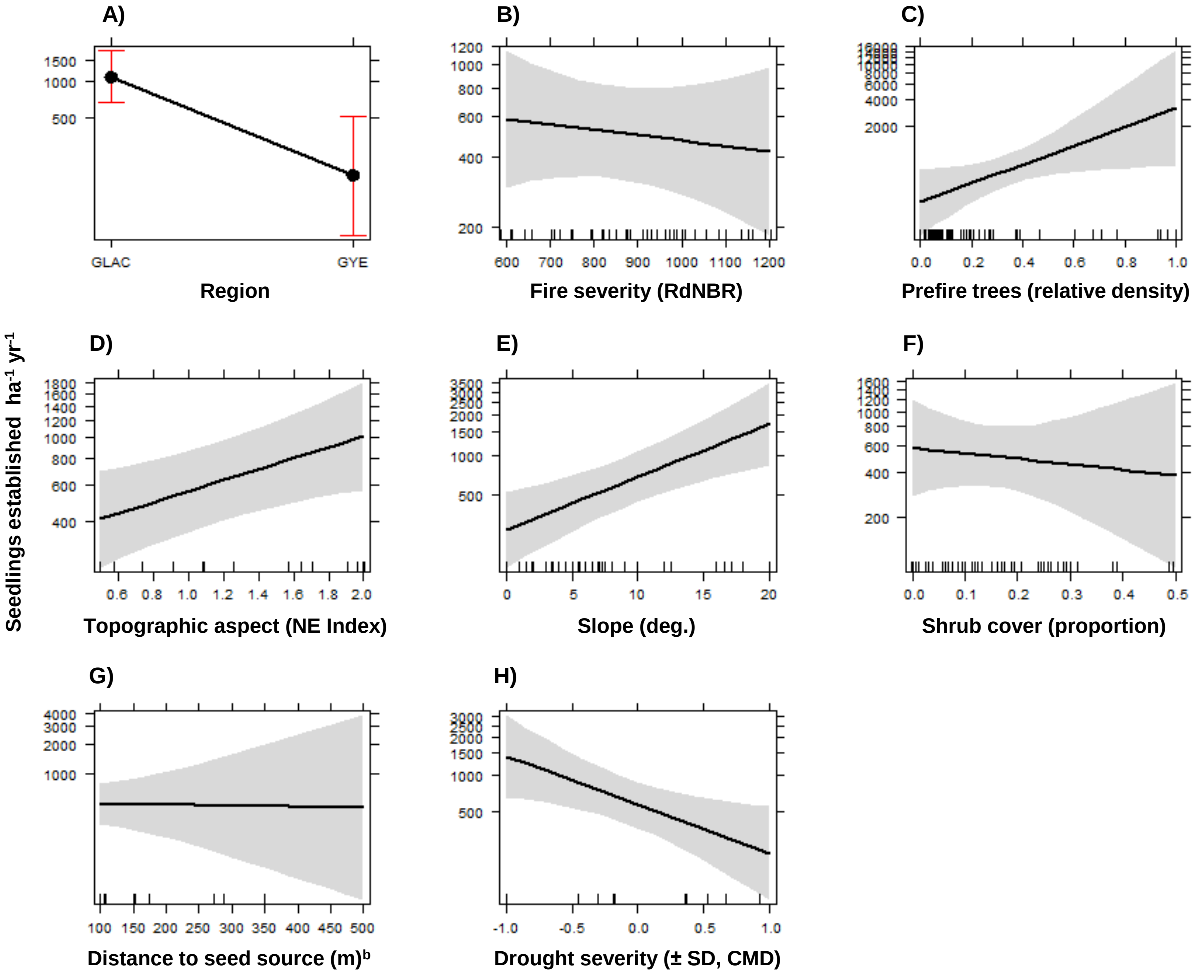

Figure S1. Modeled effects of each predictor variable on postfire serotinous lodgepole pine regeneration (seedlings ha$^{-1}$ yr$^{-1}$).

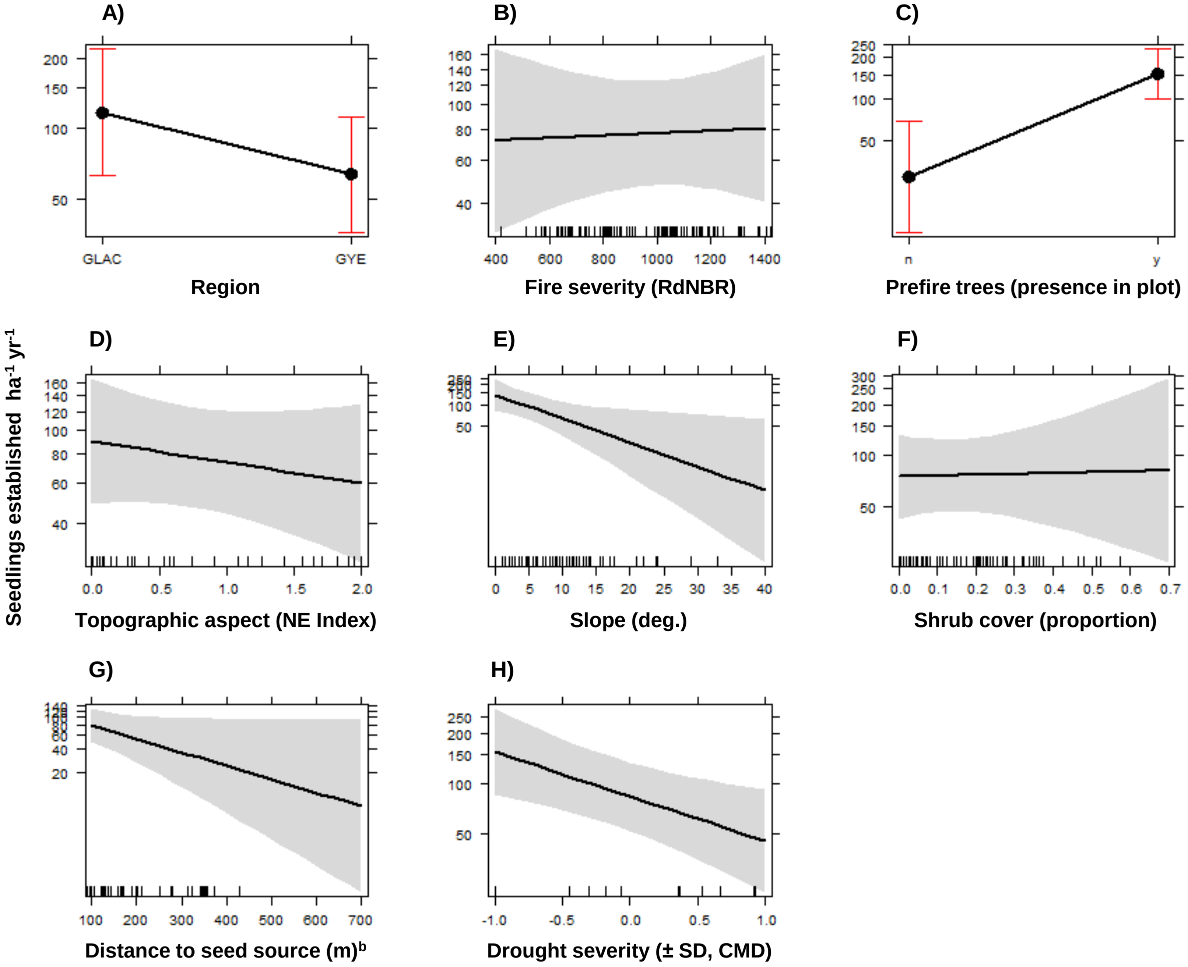

Figure S2. Modeled effects of each predictor variable on postfire non-serotinous lodgepole pine regeneration (seedlings ha$^{-1}$ yr$^{-1}$).

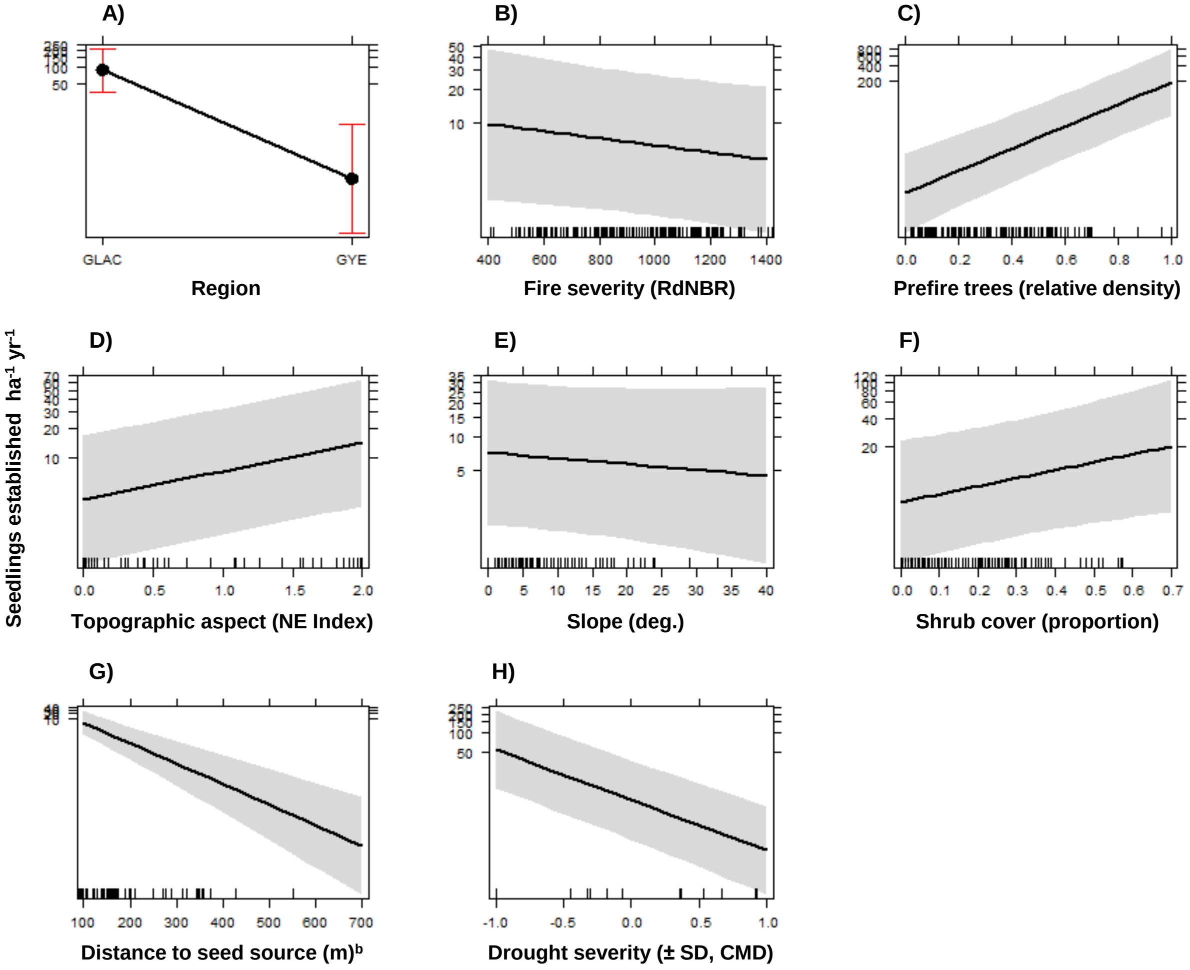

Figure S3. Modeled effects of each predictor variable on postfire Engelmann spruce regeneration (seedlings $ha^{-1}$ $yr^{-1}$).

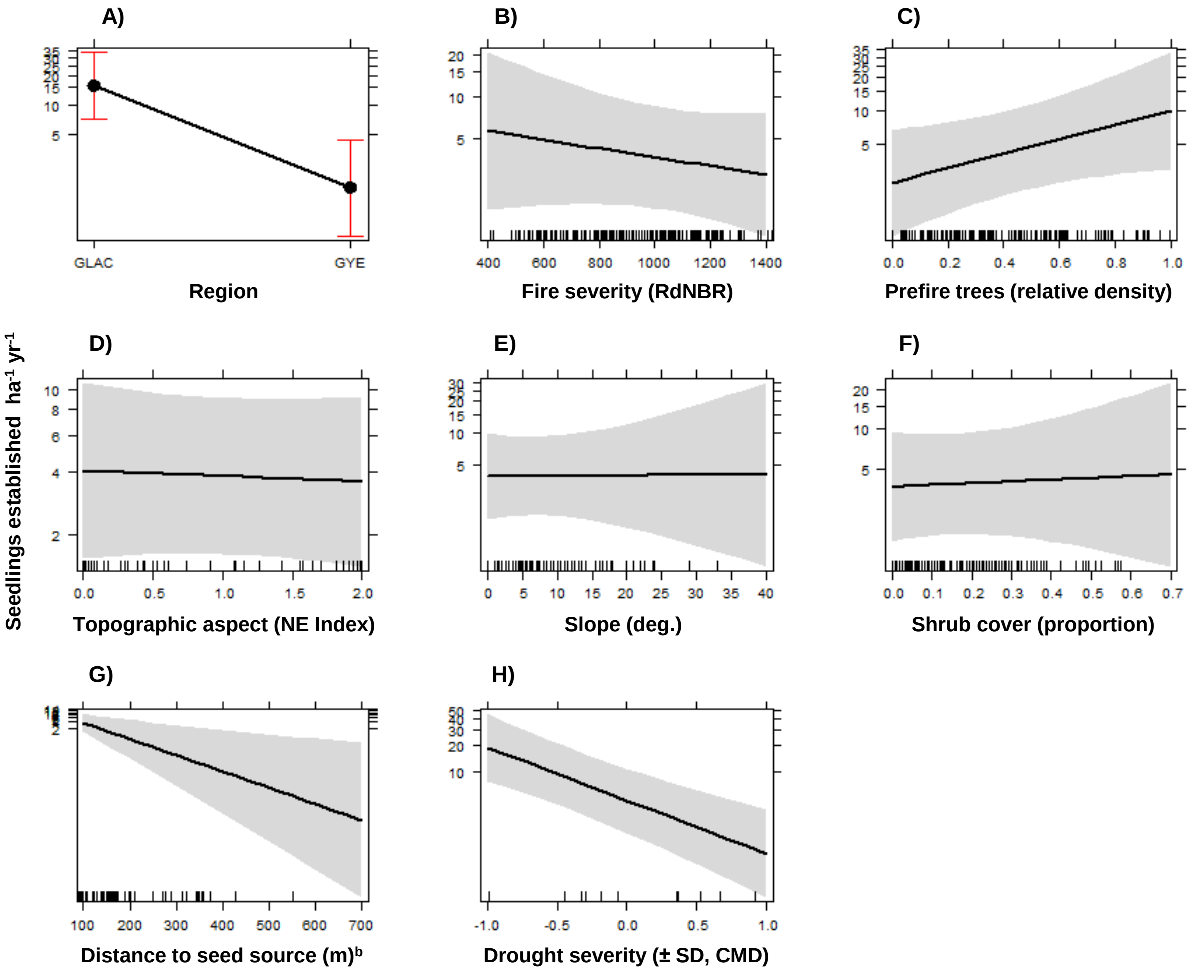

Figure S4. Modeled effects of each predictor variable on postfire subalpine fir regeneration (seedlings ha$^{-1}$ yr$^{-1}$).

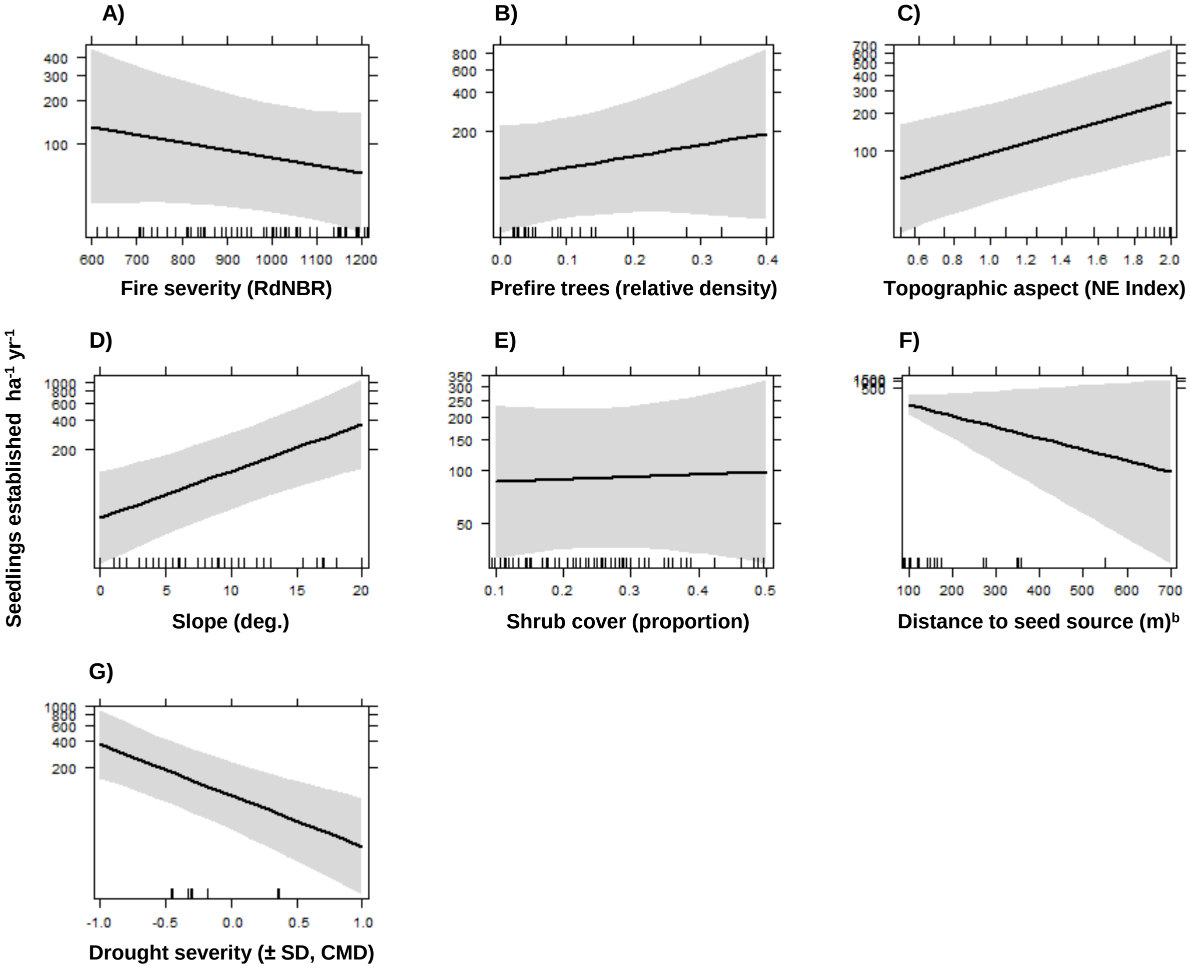

Figure S5. Modeled effects of each predictor variable on postfire western larch regeneration (seedlings ha$^{-1}$ yr$^{-1}$).

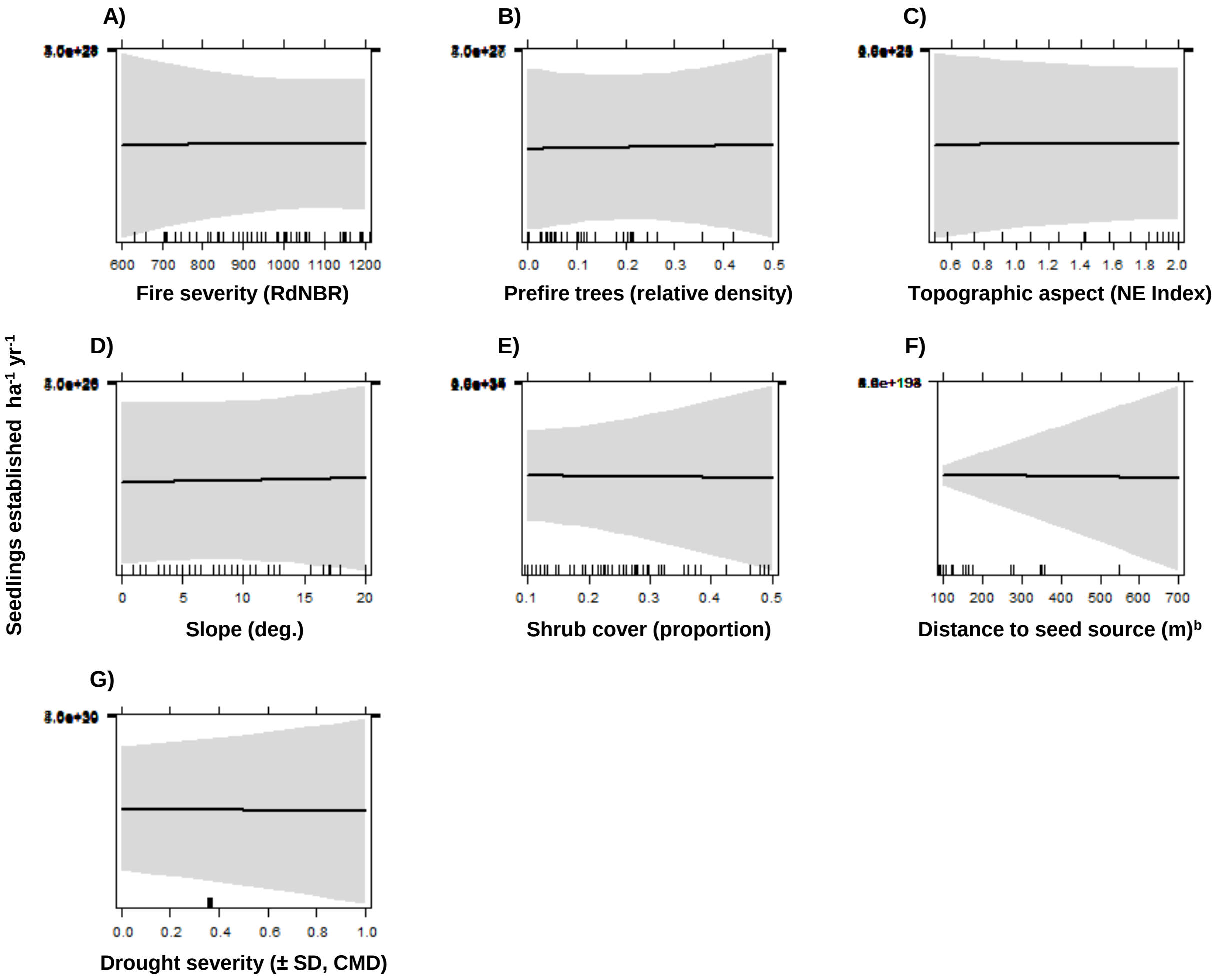

Figure S6. Modeled effects of each predictor variable on postfire Douglas-fir regeneration (seedlings ha$^{-1}$ yr$^{-1}$).

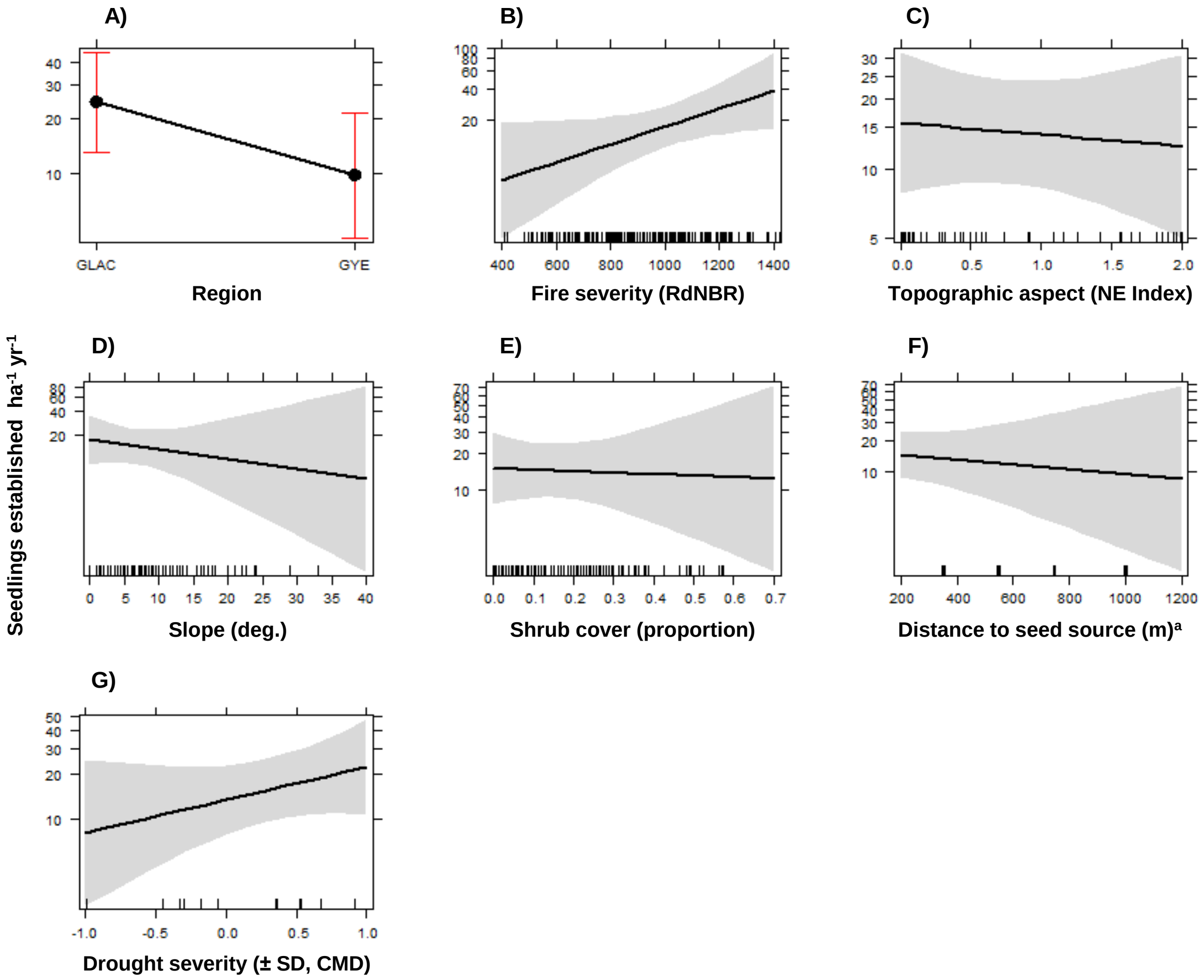

Figure S7. Modeled effects of each predictor variable on postfire quaking aspen regeneration (seedlings ha$^{-1}$ yr$^{-1}$).

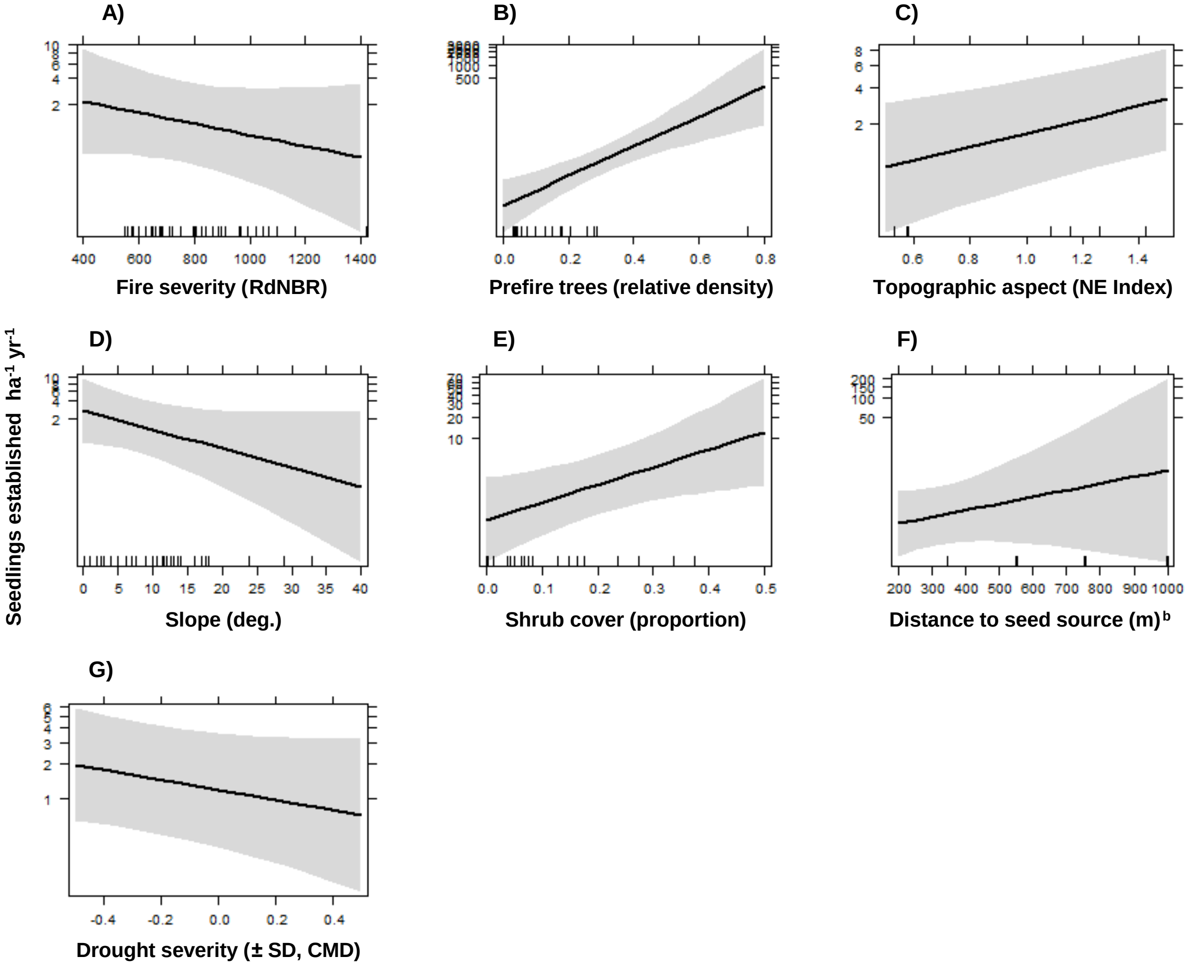

Figure S8. Modeled effects of each predictor variable on postfire whitebark pine regeneration (seedlings ha$^{-1}$ yr$^{-1}$).

## Dissertation conclusions

Overall, this research provides insight into contemporary disturbance dynamics in the Northern Rocky Mountains, which can be used to inform forest management and anticipate likely changes under future climate change and increased disturbance activity. Understanding the direct and indirect effects of climate change on ecosystem resilience is a key priority for basic and applied research (Turner 2010, Fleishman et al. 2011). Several key findings related to these priorities are summarized below:

**1. Fire severity in subalpine and mid-montane forests of the Northern Rocky Mountains is driven primarily by climate, weather, and topography; fire severity is less affected by prior disturbances such as insect outbreaks.** Despite widespread concern that bark beetle outbreaks lead to unprecedented increases in wildfire severity, results from Chapters I-III demonstrated minimal effects of these prefire disturbances on subsequent fire severity. Instead, fire severity increased substantially with extreme weather (e.g., hot, dry, windy conditions) and with slope position at the scale of individual fires. Similar controls on fire severity patterns were also detected in Chapter IV at the regional scale - across all wildfires that burned in the Northern Rockies between 1984 and 2010. Across scales (Chapters I-IV), the relative influence of topography on fire severity was stronger in mid-elevation forests, whereas climate (and weather) was the dominant control on fire severity for subalpine forests. These findings suggest future climate conditions in the Northern Rockies will likely continue to shape fire severity patterns, and projected increases in warming and drying may lead to substantial increases in forest fire severity.

**2. The capacity for bark beetle outbreaks and subsequent wildfires to produce compound effects on forest regeneration depends on the dominant tree species.** By killing large, seed-producing trees, bark beetle outbreaks can affect postfire tree regeneration. However, a key finding in Chapters I-III was that this relationship hinges on the adaptations and reproductive mechanisms of the beetle-host tree. In non-seedbanking species such as Douglas-fir, severe beetle outbreaks substantially reduced subsequent postfire regeneration because the seed source is depleted from seed-producing trees as soon as they are killed. In contrast, severe beetle outbreaks did not alter subsequent postfire tree regeneration in serotinous lodgepole pine forests, because serotinous trees (live and dead) maintain a multi-year seedbank in closed cones that is released after fire. These results broaden understanding of context-dependent disturbance interactions, and illustrate cases when forests can be resilient to two successive disturbances.

**3. Climate change in the Northern Rockies will likely indirectly affect forest resilience by increasing the total and relative amount of fires that are stand replacing, and directly affect forest resilience by causing drought stress on postfire tree seedlings.** Relationships between spatial heterogeneity of burn severity, fire size, and proportion stand-replacing (SR) fire described in Chapter IV suggest that climate-driven increases fire activity are likely to substantially increase the amount, and alter the configuration of SR fire in the Northern Rockies. Specifically, larger fires with a greater proportion of SR fire such as those predicted for the region (Westerling et al. 2011) will likely be characterized by larger, simpler shaped patches of SR fire with more total area far from seed sources. These changes, combined with the direct effects of climate change, will alter postfire tree regeneration patterns if large fires are followed by subsequent drought (Chapter V). Drought-adapted and easily dispersed tree species will likely increase in abundance under future fire-climate scenarios, whereas drought-sensitive trees with limited dispersal (or that rely on in situ seedbanks) will likely decrease in abundance. The net effects of these outcomes will govern future forest resilience, with potential shifts to non-forest likely under climate conditions projected for the mid-21st century.

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