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

Brian J. Harvey[a,1], Daniel C. Donato[b], and Monica G. Turner[a,1]

[a]Department of Zoology, University of Wisconsin–Madison, Madison, WI 53706; and [b]Washington State Department of Natural Resources, Olympia, WA 98504

Contributed by Monica G. Turner, June 17, 2014 (sent for review April 2, 2014; reviewed by F. Stuart Chapin III and Thomas T. Veblen)

Widespread tree mortality caused by outbreaks of native bark beetles (Circulionidae: Scolytinae) in recent decades 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 across a spectrum of prefire beetle outbreak severity, primarily from mountain pine beetle (*Dendroctonus ponderosae*). We found that recent (2001–2010) 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 y 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 y 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.

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

Natural disturbances (e.g., wildfires, floods, storms, insect outbreaks) play a central role in structuring ecosystems worldwide (1, 2), 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) (3, 4). Understanding these potential interactions and their consequences is critical for conserving and managing ecosystems in a period of increasing climate-driven disturbance activity (5, 6). Widespread outbreaks of native bark beetles (Circulionidae: Scolytinae) during the last decade have caused extensive tree mortality over tens of millions of hectares of conifer forests in North America (7, 8) and Eurasia (9, 10). Forest fire activity (occurrence, area burned) has also increased in these regions during this time (11), 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 (12, 13).

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*) (8). Severe MPB outbreaks can result in up to 90% mortality of tree basal area (14–18), 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) (14–17) 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) (19). Increases in dead and flammable fuels in postoutbreak forests can influence fire behavior (e.g., energy release and spread rate, see ref. 12 for a recent review) and present operational challenges for wildland firefighting (20, 21). However, less is known about whether wildfires that burn postoutbreak forests are more ecologically severe and have important consequences for ecosystem function compared with forests unaffected by recent outbreaks, despite heightened concern among scientists and forest managers (12, 13).

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 (19). 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 (22–24). 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 (22, 24) have lacked controls (i.e., stands of similar structure that

Significance

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 (2001–2010) 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.

Author contributions: B.J.H., D.C.D., and M.G.T. designed research; B.J.H. performed research; B.J.H. analyzed data; and B.J.H., D.C.D., and M.G.T. wrote the paper.

Reviewers: F.S.C., University of Alaska Fairbanks; and T.T.V., University of Colorado, Boulder.

The authors declare no conflict of interest.

[1]To whom correspondence may be addressed. Email: bjharvey@wisc.edu or turnermg@wisc.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1411346111/-/DCSupplemental.

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 (19). Recent case studies near Yellowstone National Park have begun to assess single fires using detailed field data on outbreak and fire severity (25), 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 (26–28). 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 nonforest (13). 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 (12).

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 (Fig. S1 and Table S1). The study fires included variation in prefire beetle-outbreak severity [0–84% 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 (8). 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 postoutbreak stage (0–2 y after beetle attack, ∼50% retention of largely red needles on beetle-killed trees) (12, 14, 15), considered to be most vulnerable to increased crown fire because canopy fuels are drier and more flammable (21, 29). Three fires burned forests where most attacked stands were in the gray postoutbreak stage (3–10 y after beetle attack, <5% needle retention on beetle-killed trees, most beetle-killed trees still standing) (12, 14, 15). Gray-stage forests are considered less vulnerable to increased crown fire because canopy fuels are substantially reduced (14–16, 30), although increased surface fuels from needle and branch fall could increase surface fire severity (15–17). Portions of fires burned during moderate (low temperature and wind and high relative humidity) or extreme (high temperature and wind and 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*) (25, 31), 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 before fire) using general linear mixed models that accounted for topography and burning conditions. To test whether 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 on higher slope positions (Table S8)–effects that are common in forests unaffected by beetle outbreaks (32–35). In red-stage stands, measures of fire severity were unrelated to prefire outbreak severity under moderate burning conditions (Fig. 1 *A–H* and 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. 1 *A–H* and 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. 1 *I–P* and 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. 1 *I–P* and 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 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 (26). The percentage of stand basal area with deep charring into tree crowns was correlated with char height (r_s = 0.77), and although also negatively related to postfire lodgepole pine seedling density (Fig. 2*B*), 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 (14–16), 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) (24, 25). 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

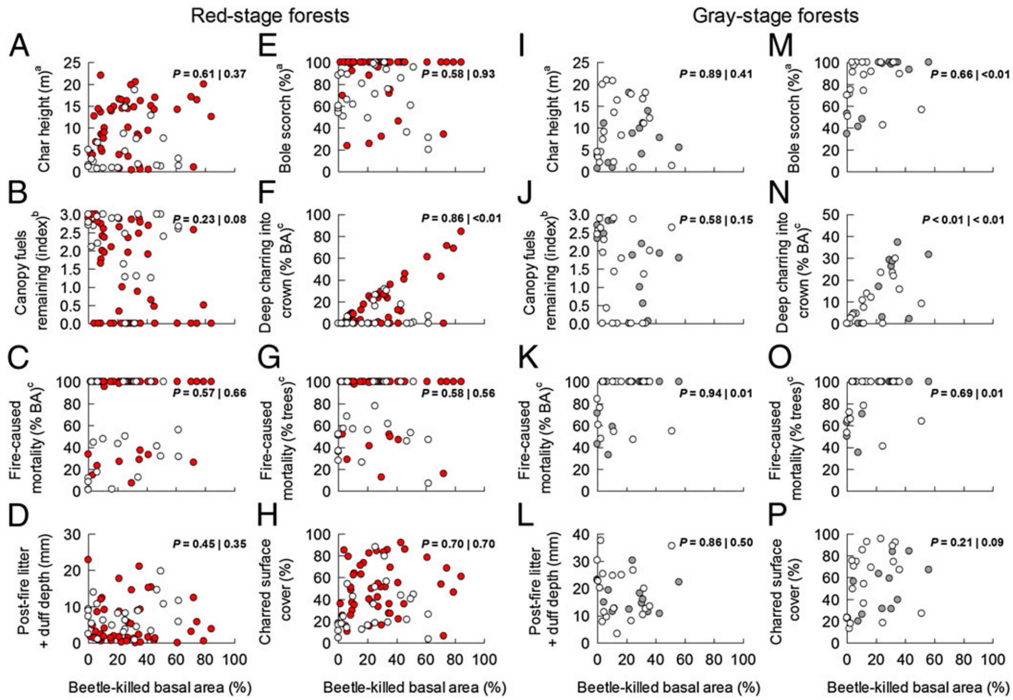

Fig. 1. Scatterplots of canopy and surface fire severity measures against beetle-killed basal area in red-stage ($n = 72$; *A–H*) and gray-stage ($n = 33$; *I–P*) forests. White circles show plots that burned during moderate burning conditions, and red (red-stage) and gray (gray-stage) circles show plots 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 codominant 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.

burned in red-stage stands under extreme conditions. This effect is not surprising, because dead wood chars more easily than live trees (36), 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 (15, 30). 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 (14, 15, 21, 29) and increased flammability of needles in recently attacked trees (21, 29), 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. 1*B*). 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

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

No. of plots present	Outbreak stage	Fire severity class	Postfire seedlings per hectare: Minimum to maximum	Mean	Median	Correlation with beetle outbreak severity in lodgepole pine only: r_s	df*	*P*
37 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.

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

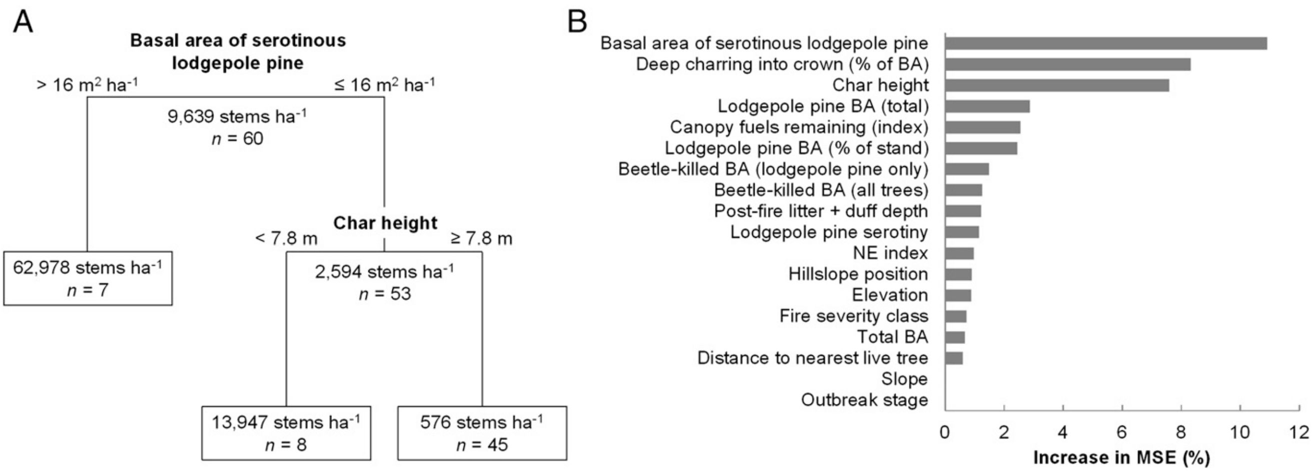

Fig. 2. Regression tree (*A*) and random forest (*B*) results indicating important variables explaining variability in postfire lodgepole pine seedling establishment. The model explained 28% of variance in lodgepole pine seedling density.

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 (25), spruce beetle (*Dendroctonus rufipennis*) outbreaks in subalpine forests (37), and Douglas-fir beetle (*Dendroctonus pseudotsugae*) outbreaks in lower-montane forests (31). However, some modeling studies suggest increased surface fire-line intensity with higher MPB outbreak severity in gray-stage stands under extreme conditions (15, 30), which is consistent with our findings. Redistribution of some coarse fuels to the forest floor from beetle-killed trees in gray-stage stands (15–17) 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 y of beetle infestation (12, 14–17), 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 (0–56% beetle-killed basal area) than the red-stage stands we studied or gray-stage stands measured elsewhere (14, 15, 25). 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 postoutbreak stages, fire severity was mostly unaffected by recent outbreak severity, which is consistent with models that predict similar fireline intensity between postoutbreak (red and gray stages) and unaffected lodgepole pine stands under moderate burning conditions (15, 30). Our results may also reflect the fire regime in many conifer forests of the Northern Rockies that are adapted to infrequent, stand-replacing fires (27, 38) that occur primarily under extreme rather than moderate burning conditions (35, 39).

Other studies of fire in areas of high outbreak severity (but lacking reference forests unaffected by MPB) have reported that recent postoutbreak forests can burn at high severity (24), 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 (25), 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 (38–40), 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 (41, 42), 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 1 y of fire (26).

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 (43) and considerably lower than well-studied lodgepole pine forests that burned in either 1988 or 2008 (25, 26, 44, 45). 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 (46); Table S10]. Conversely, the 2012 water year that followed our study fires had high drought stress [2012 water-year deficit was 20% above average (46); 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 nonserotinous (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 nonserotinous 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 (31). Because seedlings from other conifers and nonserotinous lodgepole pines can establish over a protracted postfire period (27), our postfire seedling trends for these species may not be indicative of stand regeneration over the longer term. How recent prefire beetle outbreaks in nonserotinous conifers [e.g., whitebark pine, subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), nonserotinous lodgepole pine] can alter postfire regeneration is not known.

Our field data across multiple wildfires provide 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 postoutbreak forests. Fire behavior and firefighter safety are key aspects of postoutbreak forest management that require further study (20). 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 (47) 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) (24) or in later stages of postoutbreak forests (e.g., >10 y after infestation) when most or all beetle-killed trees have fallen to the ground (14, 15, 17, 30). 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 (48, 49); thus, field studies in fires burning through later postoutbreak 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 postoutbreak wildfires.

Bark beetle outbreaks and wildfire occurrence are both predicted to increase with continued climate warming in North America (7, 46) and worldwide (11). 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 (15, 16, 30). Nonetheless, in serotinous lodgepole pine forests (which constitute a significant portion of beetle-killed forests in North America) (8), postfire forest resilience may not be 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 (38, 45, 50–52).

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 5 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 the 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

$$\text{Fire severity} \sim \text{burning conditions} + \text{slope position} + \text{beetle-killed basal area}(\%) \times \text{burning conditions}$$

Burning conditions is a categorical variable (moderate, extreme) representing the approximate weather at the time each plot burned (*SI Text* and 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 whether 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 (53–55). These methods are effective in uncovering hierarchical and nonlinear relationships among variables and are robust to any distribution (53–55). 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 (55). 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. 44 and 56), 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.

ECOLOGY

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 overfitting, minimizing cross-validated error by removing splits that exceeded the complexity parameter (55).

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) (26) and beetle outbreak stage. We used Spearman's rank correlation tests within each fire severity class because of highly skewed (nonnormal 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 $\pm$ SE unless noted otherwise.

ACKNOWLEDGMENTS. We thank T. Butusov and Z. Osterholz for help with fieldwork and R. Andrus, C. Naficy, and B. Hawkes for informative conversations regarding fire severity variables. A. Ives, J. Williams, and J. Orrock provided helpful reviews on earlier drafts of the manuscript. Funding was provided by Joint Fire Science Program Grants 12-3-01-3 and 09-1-06-3 and the National Park Service/George Melendez Wright Climate Change Fellowship.

1. Pickett ST, White PS (1985) *The Ecology of Natural Disturbance and Patch Dynamics* (Academic, Orlando, FL).
2. Attiwill PM (1994) The disturbance of forest ecosystems: The ecological basis for conservative management. *For Ecol Manag* 63(2-3):247–300.
3. Walker B, Hollin CS, Carpenter SR, Kinzig A (2004) Resilience, adaptability and transformability in social-ecological systems. *Ecol Soc* 9(2):5.
4. Paine RT, Tegner MJ, Johnson EA (1998) Compounded perturbations yield ecological surprises. *Ecosystems* 1(6):535–545.
5. Turner MG (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91(10):2833–2849.
6. Fleishman E, et al. (2011) Top 40 priorities for science to inform US conservation and management policy. *Bioscience* 61(4):290–300.
7. Bentz BJ, et al. (2010) Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *Bioscience* 60(8):602–613.
8. Raffa KF, et al. (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* 58(6):501–517.
9. Wermelinger B (2004) Ecology and management of the spruce bark beetle Ips typographus—a review of recent research. *For Ecol Manag* 202(1-3):67–82.
10. Schelhaas MJ, Nabuurs GJ, Schuck A (2003) Natural disturbances in the European forests in the 19th and 20th centuries. *Glob Change Biol* 9(11):1620–1633.
11. Flannigan MD, Krawchuk MA, de Groot WJ, Wotton BM, Gowman LM (2009) Implications of changing climate for global wildland fire. *Int J Wildland Fire* 18(5):483–507.
12. Hicke JA, Johnson MC, Hayes JL, Preisler HK (2012) Effects of bark beetle-caused tree mortality on wildfire. *For Ecol Manag* 271:81–90.
13. Association for Fire Ecology (2013) The merits of prescribed fire outweigh potential carbon emission effects. Available at http://fireecology.org/wp-content/uploads/AFEs-Prescribed-Fire-Position-Paper-2013.pdf. Accessed June 26, 2014.
14. 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(1):3–24.
15. Schoennagel T, Veblen TT, Negron JF, Smith JM (2012) Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. *PLoS ONE* 7(1):e30002.
16. Klutsch JG, Battaglia MA, West DR, Costello SL, Negrón JF (2011) Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in North-Central Colorado. *West J Appl For* 26(3):101–109.
17. Page WG, Jenkins MJ (2007) Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. *For Sci* 53(4):507–518.
18. Diskin M, Rocca ME, Nelson KN, Aoki CF, Romme WH (2011) Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. *Can J Res* 41(4):782–792.
19. Keeley JE (2009) Fire intensity, fire severity and burn severity: A brief review and suggested usage. *Int J Wildland Fire* 18(1):116–126.
20. Jenkins MJ, Page WG, Hebertson EG, Alexander ME (2012) Fuels and fire behavior dynamics in bark beetle-attacked forests in Western North America and implications for fire management. *For Ecol Manag* 275:23–34.
21. Page WG, Jenkins MJ, Alexander ME (2014) Crown fire potential in lodgepole pine forests during the red stage of mountain pine beetle attack. *Forestry* 87(3):347–361.
22. Lynch HJ, Renkin RA, Crabtree RL, Moorcroft PR (2006) The influence of previous mountain pine beetle (Dendroctonus ponderosae) activity on the 1988 Yellowstone fires. *Ecosystems* 9(8):1318–1327.
23. Kulakowski D, Jarvis D (2011) The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: A look at the past century. *For Ecol Manag* 262(9):1686–1696.
24. Prichard SJ, Kennedy MC (2014) Fuel treatments and landform modify landscape patterns of burn severity in an extreme fire event. *Ecol Appl* 24(3):571–590.
25. 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*, in press.
26. Turner MG, Romme WH, Gardner RH, Hargrove WW (1997) Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol Monogr* 67(4):411–433.
27. Kipfmueller KF, Kupfer JA (2005) Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness Area. *Ann Assoc Am Geogr* 95(3):495–510.
28. Veblen TT (1986) Age and size structure of subalpine forests in the Colorado Front Range. *Bull Torrey Bot Club* 113(3):225–240.
29. Jolly WM, et al. (2012) Relationships between moisture, chemistry, and ignition of Pinus contorta needles during the early stages of mountain pine beetle attack. *For Ecol Manag* 269:52–59.
30. Page W, Jenkins MJ (2007) Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. *For Sci* 53(6):662–674.
31. Harvey BJ, Donato DC, Romme WH, Turner MG (2013) Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. *Ecology* 94(11):2475–2486.
32. Holden ZA, Morgan P, Evans JS (2009) A predictive model of burn severity based on 20-year satellite-inferred burn severity data in a large southwestern US wilderness area. *For Ecol Manag* 258(11):2399–2406.
33. Thompson JR, Spies TA (2009) Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. *For Ecol Manag* 258(7):1684–1694.
34. Collins BM, et al. (2009) Interactions among wildland fires in a long-established Sierra Nevada natural fire area. *Ecosystems* 12:114–128.
35. Bessie WC, Johnson EA (1995) The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology* 76(3):747–762.
36. Donato DC, Campbell JL, Fontaine JB, Law BE (2009) Quantifying char in postfire woody detritus inventories. *Fire Ecol* 5(2):104–115.
37. Kulakowski D, Veblen TT (2007) Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology* 88(3):759–769.
38. Kipfmueller KF, Baker WL (2000) A fire history of a subalpine forest in south-eastern Wyoming, USA. *J Biogeogr* 27(1):71–85.
39. Schoennagel T, Veblen TT, Romme WH (2004) The interaction of fire, fuels, and climate across Rocky Mountain forests. *Bioscience* 54(7):661–676.
40. Romme W, et al. (2011) Twenty years after the 1988 Yellowstone fires: lessons about disturbance and ecosystems. *Ecosystems* 14(7):1196–1215.
41. Teste FP, Lieffers VJ, Landhäusser SM (2011) Viability of forest floor and canopy seed banks in Pinus contorta var. latifolia (Pinaceae) forests after a mountain pine beetle outbreak. *Am J Bot* 98(4):630–637.
42. Aoki CF, Romme WH, Rocca ME (2011) Lodgepole pine seed germination following tree death from mountain pine beetle attack in Colorado, USA. *Am Midl Nat* 165(2): 446–451.
43. Lotan JF, Critchfield WB (1990) Silvics of North America. Volume 1. Conifers. *Agricultural Handbook*, eds Burns RM, Honkala BH (US Department of Agriculture, Forest Service, Washington, DC), pp 302–315.
44. 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(1):21–36.
45. Schoennagel T, Turner MG, Romme WH (2003) The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. *Ecology* 84(11):2967–2978.
46. Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG (2011) Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proc Natl Acad Sci USA* 108(32):13165–13170.
47. Wulder M, Dymond C, White J, Leckie D, Carroll A (2006) Surveying mountain pine beetle damage of forests: A review of remote sensing opportunities. *For Ecol Manag* 221(1-3):27–41.
48. Buma B, Wessman CA (2012) Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. *For Ecol Manag* 266:25–33.
49. Kulakowski D, Matthews C, Jarvis D, Veblen TT (2013) Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (Populus tremuloides). *J Veg Sci* 24(1):168–176.
50. Romme WH, Despain DG (1989) Historical perspective on the Yellowstone Fires of 1988. *Bioscience* 39(10):695–699.
51. Barrett S (1994) Fire Regimes on Andesitic Mountain Terrain in Northeastern Yellowstone-National-Park, Wyoming. *Int J Wildland Fire* 4(2):65–76.
52. Barrett SW, Arno SF, Key CH (1991) Fire regimes of Western larch - lodgepole pine forests in Glacier National Park, Montana. *Can J For Res-Rev Can Rech For* 21(12): 1711–1720.
53. Breiman L, Friedman J, Stone CJ, Olshen RA (1984) *Classification and Regression Trees* (Chapman and Hall/CRC, Boca Raton, FL), 1st Ed.
54. De'ath G, Fabricius KE (2000) Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology* 81(11):3178–3192.
55. Maindonald J, Braun WJ (2010) *Data Analysis and Graphics Using R: An Example-Based Approach* (Cambridge Univ Press, Cambridge, UK), 3rd Ed.
56. Tinker DB, Romme WH, Hargrove WW, Gardner RH, Turner MG (1994) Landscape-scale heterogeneity in lodgepole pine serotiny. *Can J Res* 24(5):897–903.

Supporting Information

Harvey et al. 10.1073/pnas.1411346111

SI Text

Study Area. The study area comprised recent (2011) lightning-ignited wildfires in upper-montane and subalpine forests in the Northern Rockies (Fig. S1), located in five different National Forests in areas accessible by road (Table S1). Prefire 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 postoutbreak 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 (1)—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 1,000 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) (2). Each fire contained between 5 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 ref. 3) 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, nonforest, 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, prefire beetle outbreak severity, and fire severity in a 30-m-diameter circular plot (0.07 ha) divided into four quadrants (northeast, southeast, southwest, northwest; Tables S1–S7).

Pre- and Postfire 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 prefire sapling (trees < 1.4 m that established prefire) occurring in 3-m belt transects along the main axes of the circular plot (north, east, south, and west). In plots that burned as stand-replacing fire (i.e., all prefire live trees were killed by fire), postfire seedlings (trees that germinated postfire) were recorded in 2-m belt transects along the main axes of the plot. Slope (°), aspect (°), and geographic coordinates were measured at plot center.

Prefire Beetle Outbreak Severity. Prefire beetle outbreak severity was quantified following methods outlined in refs. 2 and 4, 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 (5). Each tree was assigned to one of five categories: (*i*) predisturbance snag, (*ii*) killed by bark beetles before fire, (*iii*) green attack at time of fire, (*iv*) live at the time of fire, or (*v*) 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 codominant 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 (Tables S6 and S7). 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, <5% of needle-bearing branches remaining; 1, needle-bearing branches remain, but <5% of needles remaining; 2, >5% but <50% of needles remaining; and 3, >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 postoutbreak live trees and basal area that were killed by fire was used to measure fire severity on the residual canopy after the outbreak. Surface fire severity was measured by recording the depth of postfire litter + duff (i.e., the soil O horizon) to the nearest mm at every 3 m along the main axis of the plot (20 pts/plot) and by recording the percent cover of charred surface (mineral soil, litter, woody debris), using the point intercept method (Tables S6 and S7). 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 (°), and aspect (Northeast Index) (6). To characterize local relative elevation, we calculated a slope position by rescaling elevation for each plot from 0 (bottom of slope) to 1 (ridge top) (4).

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 (7–9) to divide each fire into periods of moderate or extreme burning conditions. Extreme burning conditions were assigned to portions of fires that burned during conditions 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 S4). 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).

1. Meddens AJH, Hicke JA, Ferguson CA (2012) Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecol Appl* 22(7):1876–1891.
2. 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*, in press.
3. Turner MG, Romme WH, Gardner RH, Hargrove WW (1997) Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol Monogr* 67(4):411–433.
4. Harvey BJ, Donato DC, Romme WH, Turner MG (2013) Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. *Ecology* 94(11):2475–2486.
5. 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.
6. Beers TW, Dress PE, Wensel LC (1966) Notes and observations: Aspect transformation in site productivity research. *J For* 64(10):691–692.
7. Collins BM, Kelly M, Wagtendonk JW, Stephens SL (2007) Spatial patterns of large natural fires in Sierra Nevada wilderness areas. *Landscape Ecol* 22:545–557.
8. Thompson JR, Spies TA (2009) Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. *For Ecol Manag* 258(7):1684–1694.
9. Prichard SJ, Kennedy MC (2014) Fuel treatments and landform modify landscape patterns of burn severity in an extreme fire event. *Ecol Appl* 24(3):571–590.

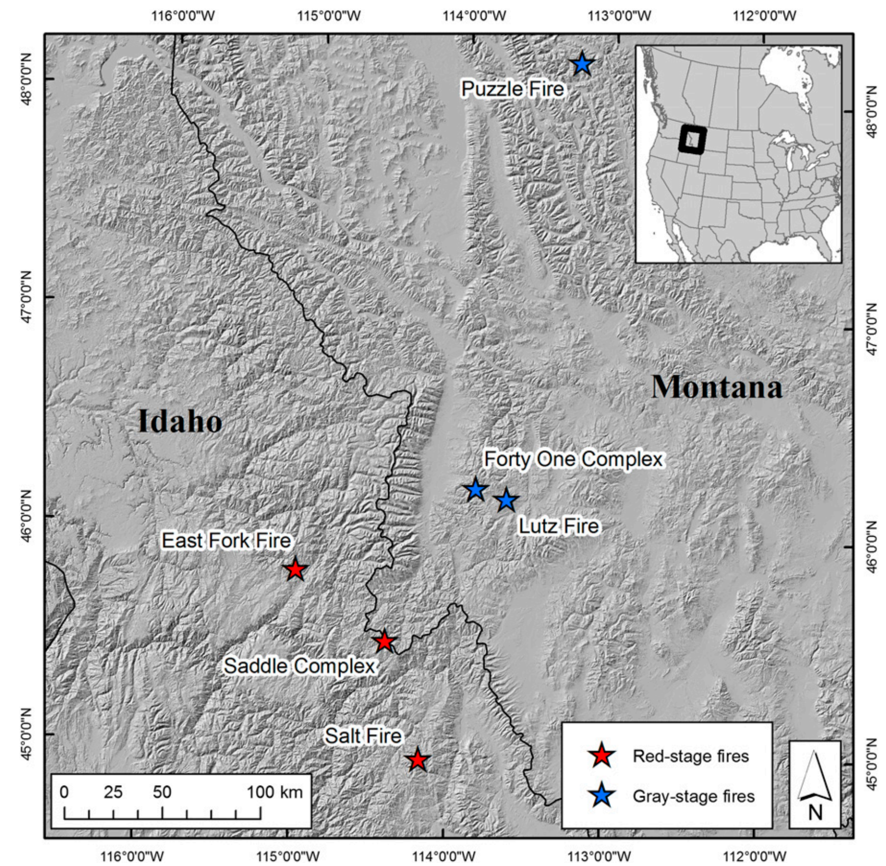

Fig. S1. Study area and location of fires in the Northern Rocky Mountains. All study fires burned in 2011.

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

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

*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 postfire tree regeneration analyses.

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

ABLA, *Abies lasiocarpa* (subalpine fir); BA, basal area; DFB, *Dendroctonus pseudotsugae* (Douglas-fir beetle); MPB, *Dendroctonus ponderosae*; NA, not applicable; PIAL, *Pinus albicaulis* (whitebark pine); 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, $n = 33$
Preoutbreak		
Live basal area, m^2/ha	35.8 (1.7)	42.1 (2.3)
Live stems, ha^{-1}	1,587 (115)	1,762 (122)
Dead basal area, m^2/ha	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)
Prefire (but postoutbreak)		
Beetle-killed basal area, m^2/ha	10.4 (1.2)	8.4 (1.4)
Beetle-killed basal area, %	26 (2)	19 (3)
Range, %	0–84	0–56
Beetle-killed snags, ha^{-1}	213 (25)	118 (19)
Prefire serotiny, %	30 (4)	23 (6)
Postfire		
Fire-killed basal area, m^2/ha	19.1 (1.6)	28.9 (2.3)
Fire-killed basal area, % of postoutbreak live basal area	75 (4)	86 (4)
Live basal area, m^2/ha	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

Preoutbreak 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*)

Fire name (start to end dates)	Burning conditions	No. of plots	Weather conditions and fire growth					
			Temperature, °C	RH, %	Wind speed, m/s	No. of days	Area burned, ha	Percentage of fire burned
Salt Fire	Moderate	9	16.6	22.6	2.6	21	3,821	38
(8/25–10/2)*	Extreme	21	21.3	14.9	3.2	17	6,177	62
Saddle Fire	Moderate	11	16.0	37.3	2.9	36	5,299	39
(8/18–9/30)†	Extreme	19	22.7	16.9	3.1	6	8,233	61
East Fork Fire	Moderate	4	20.3	38.7	1.1	10	1,717	42
(8/22–9/11)‡	Extreme	8	28.5	18.5	1.2	17	2,372	58
Lutz Fire	Moderate	2	20.7	31.4	1.4	29	1,100	75
(8/6–9/15)§	Extreme	3	24.4	18.4	1.5	8	359	25
Forty-one Complex	Moderate	10	17.1	37.3	1.5	20	2,707	59
(9/3–9/29)§	Extreme	6	23.7	17.1	1.5	7	1,881	41
Puzzle Creek Fire	Moderate	8	21.7	34.0	2.5	3	432	78
(9/9–9/13)¶	Extreme	4	25.8	19.9	2.3	2	123	22

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

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

†Hells Half Saddle (Idaho) RAWS located 16 km northwest of the Saddle Fire.

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

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

¶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: Red-stage forests	Percentage of trees sampled: Gray-stage forests
Predisturbance snag: killed before outbreak or fire; timing and cause of death unknown	Dead at time of sampling Highly weathered/decayed sapwood, most branches and bark missing No evidence of bark beetle activity (pre- or postfire)		0.5	1.8
Killed by bark beetles before fire				
Visible cambium	Dead at time of sampling, no needles in canopy Dry cambial tissue *Dendroctonus* exit holes on the outer bark Fully excavated (but vacated) adult and larval *Dendroctonus* or *Dryocoetes* galleries on the vascular cambium (>50% of bole circumference or remaining visible cambium)	1–3	8.8	3.2
No visible cambium*	Dead at time of sampling, no needles in canopy No available cambium visible due to excessive charring >15 cm dbh	1–3	4.2	3.2
Green-attack at time of fire	Dead at time of sampling, no needles in canopy Partially completed galleries with adult beetles charred under bark Or meeting all of the criteria for "killed by bark beetles prior to fire (visible cambium)" but containing needles in the canopy and located in a plot with partially completed galleries/charred beetles	2, 5	0.3	0.0
Live at the time of fire				
Killed by fire	Dead at time of sampling Charred bark, branches, or outer sapwood No evidence of bark beetle activity (no exit holes on outer bark, no galleries under bark) Not a highly decayed or well-weathered snag		67.5	75.4
Killed by bark beetles after fire	Alive or dead at the time of sampling Clear signs of postfire beetle activity [boring dust (which would have been consumed by fire), resin bleeding] or fully developed galleries but moist cambial tissue and/or any detectable level of needles in the canopy (which would still be present given needle-drop period of 2–3 y)	2, 4	0.1	0.5
Surviving tree	Alive at the time of sampling 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

Table adapted from ref. 5.

*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. 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(1):21–36.
2. 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, Canada), pp 3–66.
3. 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(1):3–24.
4. Powell EN, Townsend PA, Raffa KF (2011) Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. *Ecol Monogr* 82(1):69–84.
5. 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*, in press.

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*	8.6	8.2	0.3–22.0	9.3	8.7	0.7–20.9
Bole scorch, percentage of circumference*	84	100	20–100	84	97	35–100
Canopy fuels remaining, index†	1.7	2.1	0–3.0	1.6	1.9	0–2.9
Deep charring into crown, percentage of basal area‡	14	7	0–84	11	5	0–37
Surface						
Postfire 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, %‡	81	100	7–100	87	100	35–100
Fire-killed basal area, %‡	75	100	1–100	86	100	33–100

*Calculated from average of 20 unbroken codominant canopy trees per plot.
†Calculated from average of the subset of 20 sampled trees that were alive at the time of fire.
‡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*	7.6	4.8	0.7–20.9	†	9.8	9.9	0.3–22.0
Bole scorch, percentage of circumference*,‡	77	87	20–100	§	88	100	24–100
Canopy fuels remaining, index¶	1.9	2.4	0–3.0	§	1.5	1.9	0–3.0
Deep charring into crown, percentage of basal area‡,‖	8	3	0–32	§	17	9	0–84
Surface							
Postfire 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, %‡,‖	76	89	7–100	§	88	100	12–100
Fire-killed basal area, %‡,‖	69	92	1–100	§	86	100	7–100

*Calculated from average of 20 unbroken codominant canopy trees per plot.
†Significant difference between moderate and extreme conditions (Welch's *t* test, $P < 0.10$).
‡Statistical tests conducted on logit-transformed percentage to bound responses between 0% and 100%.
§Significant difference between moderate and extreme conditions (Welch's *t* test, $P < 0.05$).
¶Calculated from average of the subset of 20 sampled trees that were alive at the time of fire.
‖Calculated from all trees in the plot.

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*	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, %*,†	**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‡	**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†,§	**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†,§	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†,§	**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, %†	**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*	**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, %*,†	**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‡	**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†,§	**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†,§	**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**

Table S8. Cont.

Response	Predictor	β	SE	*t*	*P*
Tree mortality, % of trees, trees alive at time of fire†,§	**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, %†	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*	**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, %*,†	**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‡	**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†,§	**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†,§	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†,§	**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, %†	**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).

*Calculated from average of 20 unbroken codominant canopy trees per plot.

†Logit-transformed percentage to bound responses between 0% and 100%.

‡Calculated from average of the subset of 20 sampled trees that were alive at the time of fire.

§Calculated from all trees in the plot.

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

Tree species and no. of plots present	Outbreak stage	Fire severity class	Postfire seedlings per hectare: Minimum–maximum	Mean	Median	Correlation with beetle outbreak severity in conspecific trees only: r_s	df*	P
Subalpine fir								
20 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†	0	0	0	NA	NA	NA
Engelmann spruce								
8 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†	0–175	58	0	NA	NA	NA
	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†	0	0	0	NA	NA	NA
Douglas-fir								
3 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†	0	0	0	NA	NA	NA
	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†	0	0	0	NA	NA	NA
	Gray stage	All classes combined†	0	0	0	NA	NA	NA
		Severe surface†	0	0	0	NA	NA	NA
		Crown†	0	0	0	NA	NA	NA
Whitebark pine								
1 of 32 plots	All stages combined	All classes combined	0–397	12	0	−0.08	30	0.67
		Severe surface†	0	0	0	NA	NA	NA
		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†	0	0	0	NA	NA	NA
		Crown	0–397	50	0	−0.27	6	0.52
	Gray stage	All classes combined†	0	0	0	NA	NA	NA
		Severe surface†	0	0	0	NA	NA	NA
		Crown†	0	0	0	NA	NA	NA

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. Plots where the tree species was not present prefire were excluded before analysis. NA, not applicable.

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

†No test was possible (NA) 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 to 2012, averaged across all 1/8° grid cells that cover the Northern Rockies Ecoregion (n = 2,191 grid cells)

Water year	Annual water year moisture deficit (mm)	Percent of 1984 to 2012 average (+/−)	SDs from 1984 to 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

Higher values indicate 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, ref. 1.

1. Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG (2011) Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proc Natl Acad Sci USA* 108(32):13165–13170.