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

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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.

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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

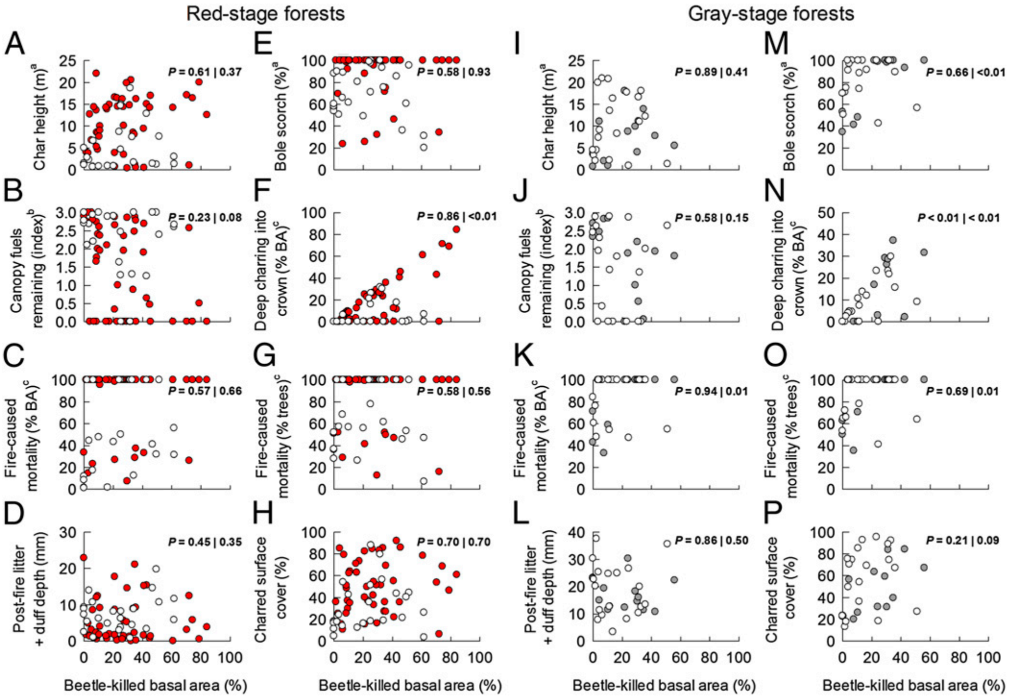

Fig. 1. Scatterplots of canopy and surface fire severity measures against beetle-killed basal area in red-stage ($n = 72$; *A–H*) and gray-stage ($n = 33$; *I–P*) forests. White circles show plots that burned during moderate burning conditions, and red (red-stage) and gray (gray-stage) circles show plots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

			Postfire 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*	*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.

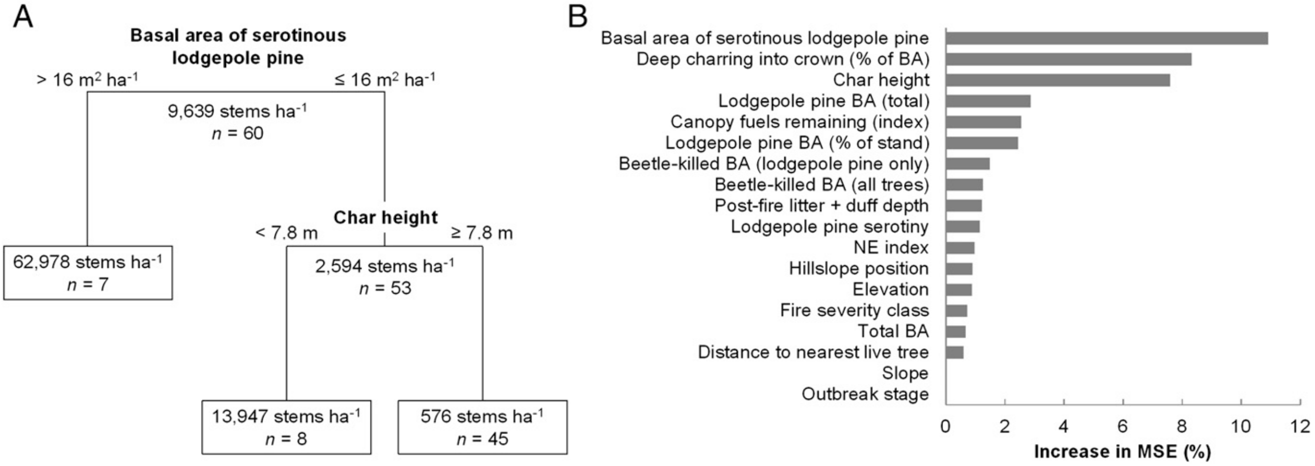

Fig. 2. Regression tree (*A*) and random forest (*B*) results indicating important variables explaining variability in postfire lodgepole pine seedling establishment. The model explained 28% of variance in lodgepole pine seedling density.

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.

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 ± SE unless noted otherwise.

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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* 24(7):1608–1625.
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.