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RESEARCH PAPER

What explains landscape patterns of tree mortality caused by bark beetle outbreaks in Greater Yellowstone?

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ABSTRACT

Aim Bark beetle outbreaks have recently affected extensive areas of western North American forests, and factors explaining landscape patterns of tree mortality are poorly understood. The objective of this study was to determine the relative importance of stand structure, topography, soil characteristics, landscape context (the characteristics of the landscape surrounding the focal stand) and beetle pressure (the abundance of local beetle population eruptions around the focal stand a few years before the outbreak) to explain landscape patterns of tree mortality during outbreaks of three species: the mountain pine beetle, which attacks lodgepole pine and whitebark pine; the spruce beetle, which feeds on Engelmann spruce; and the Douglas-fir beetle, which attacks Douglas-fir. A second objective was to identify common variables that explain tree mortality among beetle–tree host pairings during outbreaks.

Location Greater Yellowstone ecosystem, Wyoming, USA.

Methods We used field surveys to quantify stand structure, soil characteristics and topography at the plot level in susceptible stands of each forest type showing different severities of infestation (0–98% mortality; $n = 129$ plots). We then used forest cover and beetle infestation maps derived from remote sensing to develop landscape context and beetle pressure metrics at different spatial scales. Plot-level and landscape-level variables were used to explain outbreak severity.

Results Engelmann spruce and Douglas-fir mortality were best predicted using landscape-level variables alone. Lodgepole pine mortality was best predicted by both landscape-level and plot-level variables. Whitebark pine mortality was best – although poorly – predicted by plot-level variables. Models including landscape context and beetle pressure were much better at predicting outbreak severity than models that only included plot-level measures, except for whitebark pine.

Main conclusions Landscape-level variables, particularly beetle pressure, were the most consistent predictors of subsequent outbreak severity within susceptible stands of all four host species. These results may help forest managers identify vulnerable locations during ongoing outbreaks.

Keywords

Douglas-fir, Douglas-fir beetle, Engelmann spruce, insect outbreak, landscape ecology, lodgepole pine, mountain pine beetle, Rocky Mountains, spruce beetle, whitebark pine.

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INTRODUCTION

Bark beetles are ubiquitous agents of disturbance in western North American forests. Native bark beetles of the genus *Dendroctonus* (henceforth 'bark beetles' refers to tree-killing species within this genus) are particularly important because they kill healthy trees over extensive areas during episodic outbreaks. The most extensive bark beetle outbreaks recorded in recent history

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have occurred in the last 10 years and have affected more than 47 million hectares across the North American Rocky Mountains (Raffa *et al.*, 2008). These outbreaks have significant ecological effects on forest succession (Klutsch *et al.*, 2009), fuel dynamics (Simard *et al.*, 2011), nitrogen (Griffin *et al.*, 2011) and carbon cycling (Kurz *et al.*, 2008), as well as substantial socioeconomic impacts (Abbott *et al.*, 2009). Bark beetles generally target larger trees of their host species within stands, at least during outbreaks. At subcontinental and multi-decadal scales, recurrence of beetle outbreaks is mainly driven by climate, forest structure, tree physiology and their interactions (Raffa *et al.*, 2008; Fauria & Johnson, 2009). Over the course of an outbreak, local and landscape factors influence the amount and distribution of tree mortality, resulting in a mosaic of undisturbed and beetle-killed forest stands across the landscape. With climate warming, bark beetle reproduction is increasing and the range of some species is expanding in latitude and elevation (Bentz *et al.*, 2010; Logan *et al.*, 2010). Understanding the factors that are associated with increased severity of outbreaks is thus critical to predict future patterns of forest structure, function and composition, and socioeconomic impacts.

Many susceptibility and risk-rating systems have been developed to predict the likelihood of bark beetle disturbance at the stand scale (reviewed in Shore *et al.*, 2000). Risk of insect-caused mortality is the product of stand susceptibility, i.e. the attributes of a stand that increase the probability of tree mortality, and of beetle pressure, i.e. the abundance of beetle populations near the focal stand one or a few years before the outbreak (Shore & Safranyik, 1992; Bentz *et al.*, 1993). The most common variables explaining susceptibility to bark beetles are related to the quantity (stand basal area, abundance of large-diameter trees, etc.) and quality (e.g. site index) of host trees, and to their level of physiological stress (stem density, soil characteristics, etc.) (Shore & Safranyik, 1992; Reynolds & Holsten, 1994; Negrón, 1998; Perkins & Roberts, 2003). These empirical models typically have good predictive power at the stand scale once beetle density is known, but have had less success when applied to the landscape (Dymond *et al.*, 2006; Nelson *et al.*, 2006; Robertson *et al.*, 2008), suggesting that additional factors may drive bark beetle population dynamics at that scale.

Between outbreak episodes, bark beetles are present at low densities across the landscape, but under certain conditions local populations of some species erupt from epicentres and coalesce into outbreaks across susceptible forests. During an outbreak, infestations are initially concentrated in some areas of the landscape and show a high spatial and temporal autocorrelation pattern typical of contagious processes (Aukema *et al.*, 2006; Aukema *et al.*, 2008). Not all stands of the suitable host species and susceptible age classes are heavily infested, suggesting not only heterogeneity in defensive ability among trees (Raffa & Berryman, 1982), but also that some landscape or other characteristics may facilitate expansion of local beetle populations. Landscape composition (i.e. the proportion of different cover types) and configuration (i.e. the spatial arrangement of the different cover types) can affect the severity and frequency of insect defoliator outbreaks, for example (Roland, 1993; Cappuccino *et al.*, 1998; Campbell *et al.*, 2008). This is particularly true for bark beetles, which interact with their tree hosts across multiple spatial scales (Raffa *et al.*, 2008). For example, mortality of host trees in a stand is first driven by stand and tree characteristics, but may be later influenced by landscape attributes. Therefore, although stand-level factors might be important to explain the onset of local eruptions, landscape factors are possibly more important once a regional outbreak has begun (Raffa *et al.*, 2008).

The goal of this study was to explain the patterns of mortality of susceptible host trees caused during outbreaks of three species of bark beetles across the Greater Yellowstone ecosystem (Wyoming, USA). We performed field sampling to measure variables within plots (stand scale), and GIS analyses to measure landscape-level variables around each plot. These outbreaks occurred concurrently across the landscape, yet the bark beetle species are host specific at the level of plant genus: the mountain pine beetle (*Dendroctonus ponderosae*) feeds on lodgepole pine (*Pinus contorta* var. *latifolia*) and whitebark pine (*Pinus albicaulis*), the spruce beetle (*Dendroctonus rufipennis*) attacks Engelmann spruce (*Picea engelmannii*) and the Douglas-fir beetle (*Dendroctonus pseudotsugae*) feeds on Douglas-fir (*Pseudotsuga menziesii*). All beetles are native and have been historically associated with their current host. However, whitebark pine, a high-elevation species, historically was less exposed to the mountain pine beetle because of unsuitable thermal conditions, a transition that has been attributed to global warming (Logan *et al.*, 2010). Risk rating systems have been developed for each of these host tree species individually, but to our knowledge no study has yet compared multiple bark beetle–host tree systems in the same landscape and at the same time. Identifying variables that drive beetle-caused tree mortality across the beetle species studied could give insights into the epidemiology of these closely related species and could help improve current strategies of outbreak control.

Here we capitalize on the co-occurrence of outbreak populations of all three species of beetles, thereby controlling for differences between places and time, to address the following questions: (1) What is the relative importance of stand structure, topography, soil, landscape context and beetle pressure variables in explaining tree mortality patterns of an ongoing outbreak? (2) Are there common variables that explain tree mortality across the different species of bark beetles and host trees? Here, *landscape context* refers to the characteristics of the landscape (e.g. composition and configuration of forest types) surrounding the focal stand (Fig. 1), and *beetle pressure* is defined as the abundance of local bark beetle population eruptions around the focal stand a few years before the outbreak.

If outbreak-level beetle population dynamics dominated, we expected that landscape context and beetle pressure variables would have greater explanatory power than plot-level variables because once beetle populations are at epidemic levels across the landscape, stand and tree characteristics exert less influence on population dynamics (Wallin & Raffa, 2004). Specific expectations for measured variables describing plot and beetle population characteristics are summarized in Table 1. In particular, we

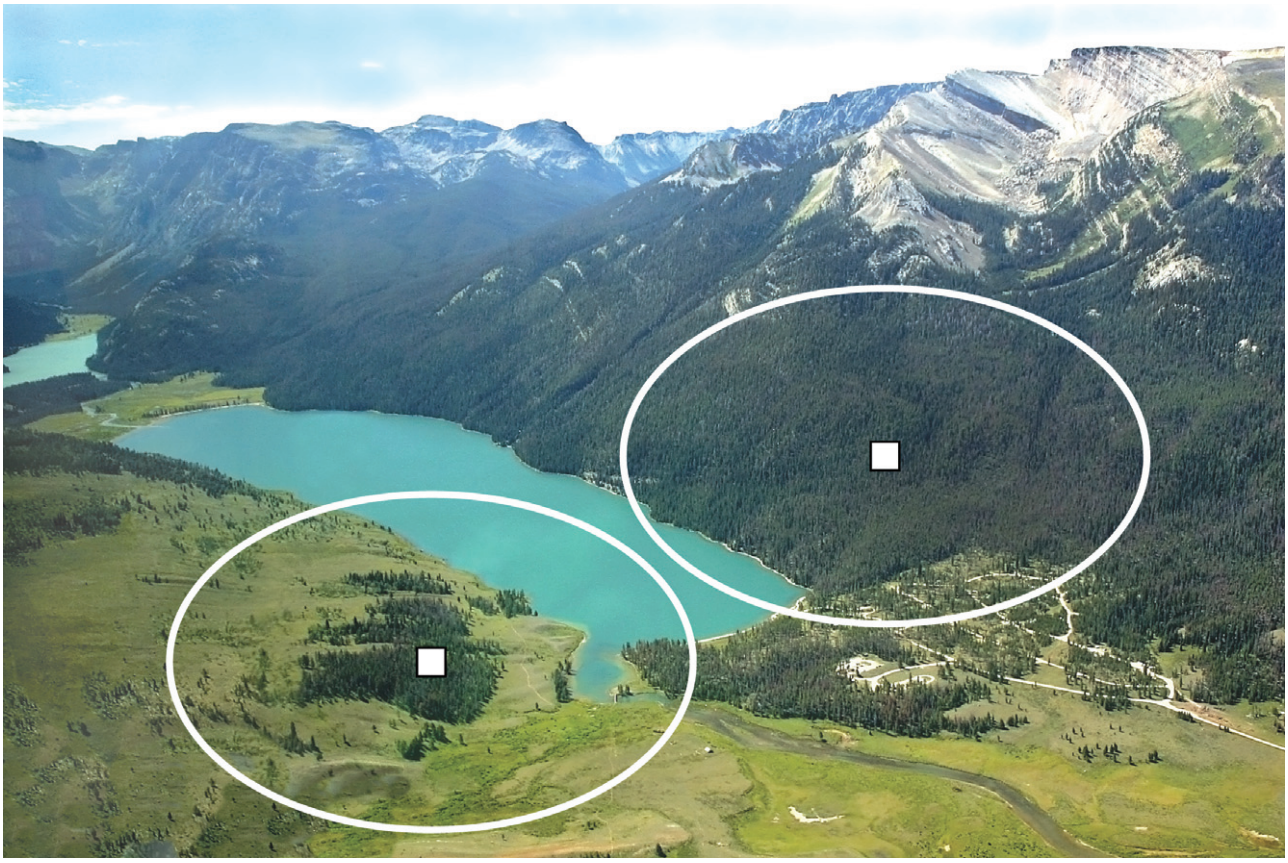

Figure 1 Landscape context, i.e. the characteristics of the landscape surrounding the focal stand, and beetle pressure, i.e. the abundance of local bark beetle population eruptions around the focal stand a few years before the outbreak, are landscape-level factors that can influence stand-level processes. Stands that are very similar at the plot scale (squares) may thus have very different landscape contexts (area in circles).

expected that distance to local eruptions in previous years would be negatively related to current mortality and that this effect would be the same across tree hosts because all three beetle species are closely related biologically.

METHODS

Study area

The Greater Yellowstone ecosystem covers an area of 80,000 km^2 in Wyoming, Idaho and Montana, and includes Yellowstone and Grand Teton national parks and several national forests (Fig. 2). Conifer forests dominate the landscape and show distinct zonation of forest types with elevation (Despain, 1990). Lodgepole pine grows on most xeric and nutrient-poor substrates at mid-elevation (between 2000 and 2600 m) where it forms both pioneer and late-successional stages. On more mesic sites, pioneer cohorts of lodgepole pine are succeeded by Engelmann spruce and subalpine fir (*Abies lasiocarpa*), and also by whitebark pine which also forms monospecific stands at the tree line (about 3000 m in elevation). Douglas-fir is typically found at lower elevations (< 2300 m) and on dry slopes. The climate is characterized by cold, long winters and dry summers. Mean annual temperature (Old Faithful weather station, 1971–2000) is 0.9 °C (mean monthly temperatures for January and July are respectively −10.7 °C and 13.7 °C) and mean annual precipitation is 620 mm (Western Regional Climate Center, 2007).

Fire is a major natural disturbance in the conifer forests of Greater Yellowstone. Lodgepole pine and Engelmann spruce forests are under a stand-replacing crown fire regime with an average fire return interval of 100–300 years (Romme & Despain, 1989), whereas Douglas-fir and whitebark pine forests are characterized by mixed-severity fire regimes (Baker *et al.*, 2007; Larson *et al.*, 2009). Native bark beetles are also important components of subalpine forest dynamics and undergo episodic outbreaks every 20–40 years at the landscape scale (Raffa *et al.*, 2008; Axelson *et al.*, 2009). In Greater Yellowstone, mountain pine beetle outbreaks have been documented in the 1920s and 1930s and in the late 1960s to early 1980s (Romme *et al.*, 1986; Furniss & Renkin, 2003; Lynch *et al.*, 2006); the current outbreak started in the early 2000s (USDA Forest Service, 2008).

Plot selection and field sampling

Field sampling focused on landscapes where bark beetles were generally present, i.e. landscapes that had localized pockets of

Table 1 List of explanatory variables available for the 2006 and 2007 sampling years and for the different forest types. Variables in bold were evaluated at different spatial scales, i.e. within 250-m, 500-m, 1-km and 2-km radius circular buffers around each plot (see text for further explanations). The rationale for including these variables in the analysis is provided.

Variables	Scale of measurement	Dataset			Expected relationships
		2006 (PICO, PIAL, PIEN, PSME)*	2007 (PICO)	2007 (PIAL, PIEN, PSME)	
Stand structure	Plot				
Pre-outbreak host relative basal area (%)†		Yes	Yes	Yes	Stands with a greater proportion of host species may be more susceptible to bark beetles
Per cent basal area in large trees (%)‡		Yes	Yes	–	Stands with a greater proportion of large trees may be more susceptible because larger trees have thicker phloem and are preferred by bark beetles
Stand post-fire age		Yes	Yes	–	Older stands may be more susceptible to beetles
Topography	Plot				
Elevation (m)		Yes	Yes	Yes	Tree mortality may decrease with elevation because colder temperatures at higher elevation may reduce the development rate of bark beetles and increase winter mortality; alternatively, trees growing in lower-elevation sites may be more water stressed and therefore more susceptible to bark beetles
Slope (%)		Yes	Yes	Yes	Trees may be more water stressed on steep slopes and therefore more susceptible to bark beetles
South-west-ness		Yes	Yes	Yes	Trees may be more water stressed on south-west-facing slopes and therefore more susceptible to bark beetles; also, trees growing on south-west-facing slopes may have a higher phloem temperature, which increases winter survival and development rate in the summer
Mineral soil	Plot				
Texture (sand-silt-clay) (%)		Yes	Yes	–	Trees growing on coarse-textured soils may be more water stressed and therefore more susceptible to bark beetles
Organic matter content (%)		Yes	Yes	–	Trees growing on soils with low organic matter content may be more water stressed and therefore more susceptible to bark beetles
pH (pH units)		Yes	Yes	–	Trees growing on acidic soils may have reduced growth rates because of lower nutrient availability and may be more susceptible to bark beetles
Total nitrogen (%)		Yes	Yes	–	Trees growing on nitrogen-poor soils may be less vigorous and therefore more susceptible to bark beetles
Exchangeable cations (p.p.m.)		Yes	Yes	–	Trees growing on nutrient-poor soils may be less vigorous and therefore more susceptible to bark beetles
Landscape context	Landscape				
Forest cover (%)		Yes	Yes	Yes	A greater amount of suitable habitat may increase bark beetle survival and probability of mass attack
Edge density (m ha^{-1})		Yes	Yes	Yes	More connected forest habitat may facilitate bark beetle coalescence and spread
Bark beetle pressure	Landscape				
Per cent forest beetle-killed (%)		Yes	Yes	Yes	A greater amount of local eruptions early in the outbreak may increase probability of attack in later stages of the outbreak
Distance to closest local eruption (m)		Yes	Yes	Yes	A stand that is closer to local eruptions early in the outbreak may be more likely to be attacked in the later stages of the outbreak

*PICO, lodgepole pine; PIAL, whitebark pine; PIEN, Engelmann spruce; PSME, Douglas-fir.

†Sum of the basal area of live trees at time of sampling and of dead trees with bark beetle galleries.

‡Pre-outbreak basal area of host trees with a diameter at breast height (d.b.h.) > threshold d.b.h., relative to pre-outbreak basal area of all trees with a d.b.h. > 7.5 cm. Threshold d.b.h. is species specific: lodgepole pine and whitebark pine, 20 cm; Engelmann spruce, 30 cm; Douglas-fir, 25 cm.

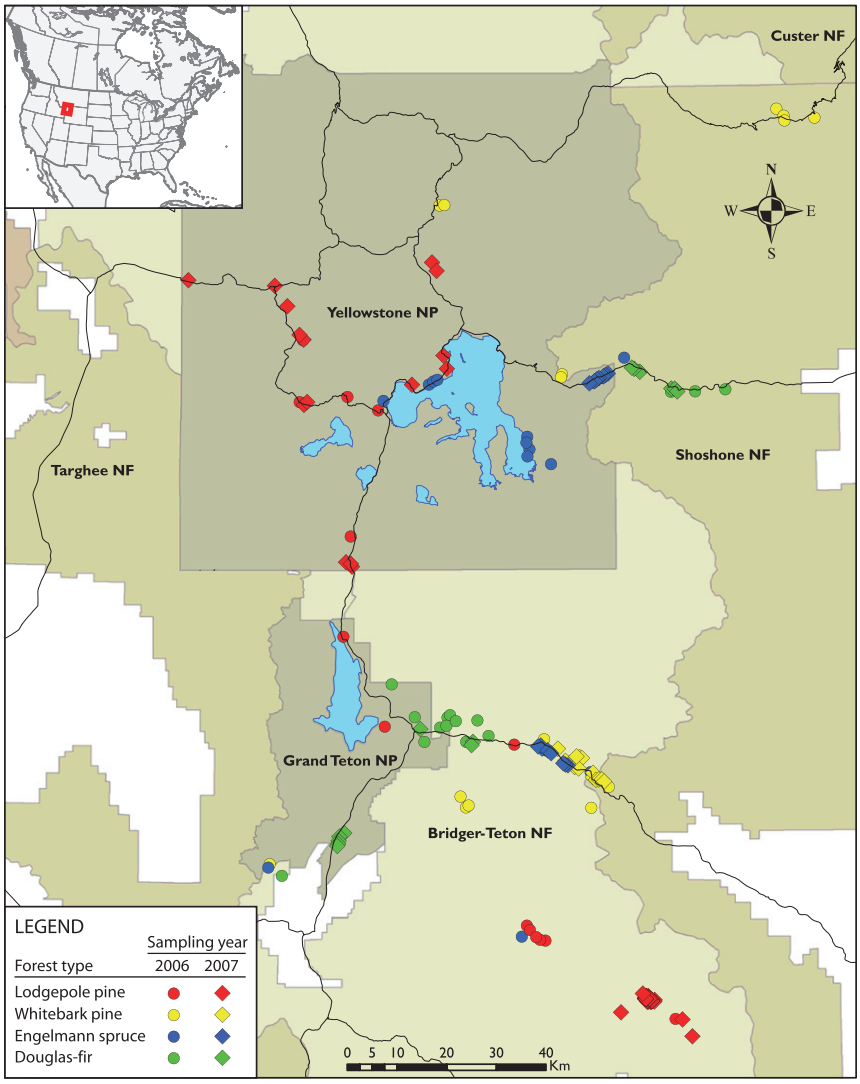

Figure 2 Location of the 129 sampling plots in Greater Yellowstone. NP, national park; NF, national forest.

infestation. Within these landscapes, we sampled specific locations that were attacked, and others that were not. We used US Forest Service Insect and Disease Aerial Detection Survey maps (USDA Forest Service, 2008), vegetation maps and field reconnaissance to select stands of varying degrees of beetle infestation throughout Greater Yellowstone, including undisturbed stands. Because it is well known that only relatively large-diameter trees are suitable for bark beetle development (Schmid & Frye, 1977; Shore & Safranyik, 1992), and because our objective was to identify variables that explain tree mortality in susceptible stands during outbreaks, we only selected stands dominated by host trees older than 100 years and with a diameter at breast height (d.b.h.) > 20 cm. In addition, beetle-infested stands had to show recent signs (i.e. about 1–5 years post-infestation) of beetle activity, i.e. red-needle or bare trees with fine twigs still attached to dead branches, along with presence of pitch tubes, boring dust and J-shaped ovipositional galleries (Safranyik & Carroll, 2006). Semi-variance analysis of Landsat satellite imagery performed on all bands except the thermal band, and on the ratio of bands 5 to 4, determined that pixel reflectance values were independent at distances greater than 500 m. We thus located the sampling plots at least 500 m from each other to reduce spatial autocorrelation in our data.

Field sampling was conducted during the summers of 2006 and 2007 using slightly different designs (Table 1). In 2006, we selected eight forest stands with low beetle disturbance (median basal area beetle-killed = 1.7%; range = 0–27.6%) and eight stands with severe mortality (median basal area beetle-killed = 73.5%; range = 42.3–97.8%) for each tree host species (lodgepole pine, whitebark pine, Engelmann spruce and Douglas-fir; $n = 16$ stands per tree host species, total $n = 64$ stands). In this study, a stand is defined as an area $\geq$ 4 ha that is relatively homogeneous in terms of post-fire age, structure, topography and species composition (overstorey and understorey); 'plot' is defined as the location in the stand where the measurements were taken. At each stand, we randomly placed a plot and recorded its location using a Trimble GeoExplorer 3 GPS (50–400 readings per plot, yielding a horizontal precision < 2 m for 97% of the plots after differential correction), slope (on a 50-m basis) and aspect. At each plot, two 100-m long and 4-m wide

transects (total area 800 m^2) placed in a cross pattern were used to describe tree attributes. For each standing tree rooted in the transects that had a d.b.h. > 7.5 cm, we recorded its species, d.b.h. and status [live, dead beetle-killed (using the criteria described above), or dead from other causes]. We recorded the same information (except tree d.b.h.) in five prism points (metric, basal area factor 2), one at the centre of the plot and one at each end of the transects. Increment cores were taken on 10 dominant host trees at 30 cm from the ground to get the oldest tree age possible without hindering the sampling of the cores. The cores were brought to the laboratory, mounted, polished (320 grit) and cross-dated under a dissecting microscope (40× magnification) using standard dendrochronological techniques (Stokes & Smiley, 1968). Samples of the mineral soil (to 15 cm depth) were collected at each of the five prism points and composited. Soil samples were sent to the University of Wisconsin Soil and Plant Analysis Lab (Madison, WI) to determine their pH, total N, exchangeable Ca, Mg and K, available P, and organic matter content following the University of Wisconsin – Madison Soil Testing Laboratory methods (University of Wisconsin – Madison, 2010). Exchangeable cation capacity was calculated as the sum of the exchangeable cations. Soil texture was determined using the Bouyoucos hydrometer technique (McKeague, 1976).

After the 2006 season it was clear that a greater sample size would be needed. Therefore, in 2007 we used data from lodgepole pine stands ($n = 23$) that were sampled for a different study (Simard *et al.*, 2011), and sampled additional stands of whitebark pine ($n = 14$), Engelmann spruce ($n = 15$) and Douglas-fir ($n = 13$). All stands sampled in 2007 represented a continuum of tree mortality, in contrast with the 2006 sampling that was concentrated on low- and high-severity mortality. In the lodgepole pine plots, all the variables that were sampled in 2006 were also collected, but in three 200-m^2 plots separated by 25 m (total area: 600 m^2). The other three forest cover types were sampled less intensively than the 2006 stands because of time constraints. In these stands, only site conditions (slope, aspect and elevation) and tree characteristics were recorded (Table 1). At each plot, tree characteristics (same variables as in the 2006 prism points) were recorded in three prism points (factor 2, metric) arranged in a triangular fashion and separated by 30 m. Sampling of increment cores and soil, and measurement of tree d.b.h. in linear transects were the most time-consuming tasks in the field and were thus not done in 2007 in the whitebark pine, Engelmann spruce and Douglas-fir stands. This unbalanced design was taken into account in subsequent statistical analyses (see Statistical Analyses).

From these field data, we computed the live and beetle-killed basal area for each plot using the prism point data. Pre-outbreak host basal area was computed as the sum of live and beetle-killed basal area of host trees. Pre-outbreak host relative basal area was calculated as the proportion of pre-outbreak host basal area relative to pre-outbreak basal area of all tree species × 100 and thus represents the relative abundance of host trees before the outbreak. Per cent basal area in large trees was calculated as the pre-outbreak basal area of host trees above a certain d.b.h. threshold relative to the pre-outbreak basal area of all trees in the plot with a d.b.h. > 7.5 cm × 100. The d.b.h. threshold values were 20 cm for lodgepole pine (Amman *et al.*, 1977) and whitebark pine (Perkins & Roberts, 2003), 30 cm for Engelmann spruce (Holsten *et al.*, 1999) and 25 cm for Douglas-fir (Negrón, 1998); this variable was calculated from the transect data only because tree d.b.h. was not noted in the prism points. Per cent host basal area beetle-killed was calculated as the proportion of host tree basal area beetle-killed relative to pre-outbreak basal area of host trees × 100.

Aspect was transformed to a south-west-ness index by taking the cosine of the difference between the aspect measured in the field and 225° (Beers *et al.*, 1966). This index ranges from −1 (north-east) and 1 (south-west) and expresses the contrast in sun exposure and dryness between these two aspects. Post-fire stand age was estimated by using the age of the oldest tree sampled.

Landscape-level variables: landscape context and bark beetle pressure

Most *Dendroctonus* have effective dispersal distances of only a few kilometres (Safranyik *et al.*, 1992, 1995; Turchin & Thoeny, 1993). Adults disperse from the trees in which they developed, land on trees largely in response to visual cues, and reject trees that are previously killed or particularly well defended. As they enter the bark, they emit pheromones that attract flying beetles of both sexes, and these aggregations rapidly exhaust host defences (Raffa & Berryman, 1983). This attraction declines exponentially with distance from its source, and the effective range is estimated to be tens of metres (Johnson & Coster, 1978; Byers *et al.*, 1989; Sullivan & Mori, 2009). Because of these spatiotemporal dynamics, the abundance of host trees in neighbouring stands and the connectivity of surrounding suitable habitat are important for local eruptions to contribute to outbreaks across the landscape (Aukema *et al.*, 2006; Raffa *et al.*, 2008; Robertson *et al.*, 2009). To characterize the landscape at multiple spatial scales around each plot (Fig. 1), we computed two landscape context indices (proportion of conifer forest and the forest–non-forest edge density; see below) and two beetle pressure variables (per cent forest beetle-killed and distance to the closest local infestation) in 250-m, 500-m, 1-km and 2-km radius buffers around each plot (Table 1). These buffers represent the range of effective dispersal of the beetles (Safranyik *et al.*, 1992, 1995; Turchin & Thoeny, 1993). In this study, beetle pressure is defined as the abundance of local bark beetle population eruptions around the focal stand a few years before the outbreak (here, 2003 and 2004).

For each plot and buffer size, we first computed the two landscape context variables using the 2001 National Land Cover Database (NLCD; Homer *et al.*, 2004), which is derived from 30-m pixel Landsat imagery taken around 2001: (1) the proportion of conifer forest, and (2) the forest–non-forest edge density. Edge density is a measure of fragmentation of a cover type and is calculated by dividing the total length of edge between two or more cover types (here, conifer forest versus all other cover

types) by the sampled area (McGarigal & Marks, 1995). Because the NLCD was derived from 2001 imagery, these variables thus represent forest conditions before the outbreak.

For beetle pressure variables, we used bark beetle disturbance maps that were developed for the study area and derived from remote sensing data. Briefly, the maps were generated using a change detection approach (Rogan *et al.*, 2002), differencing pre-outbreak (1999) and outbreak (2003, 2004 and 2007) Landsat imagery after transforming the images' reflectance values to the moisture stress index (Landsat band 5/band 4), a vegetation index sensitive to vegetation biomass (Rock *et al.*, 1986). The 2007 map was validated with field data and yielded an R^2 of 0.77 with a root-mean-square error of prediction of 14% basal area beetle-killed. To characterize tree mortality patterns in the early stages of the outbreak, we only used the maps for 2003 and 2004. During these years, only some small and scattered pockets of tree mortality were apparent in the landscape. We transformed these continuous maps of mortality to binary maps (beetle-killed versus undisturbed) using a threshold of 10% basal area beetle-killed. From these two maps (2003 and 2004), we first calculated the per cent forest beetle-killed, which is the percentage of pixels classified as beetle-killed for each buffer size (250-m, 500-m, 1-km and 2-km radius) around each plot. Second, we determined distance to the closest local eruption for 2003 and 2004 by identifying the smallest buffer size that contained at least four pixels (0.36 ha) classified as beetle-killed. Therefore, three of the landscape-level variables were calculated for different buffer sizes (proportion of conifer forest; forest–non-forest edge density; and per cent forest beetle-killed) whereas the fourth one (distance to closest local infestation) yielded a single value per site (Table 1). Additional details about the remote sensing analyses and the landscape-level variables can be found in Appendix S1 in Supporting Information.

Statistical analyses

To compare the relative importance of plot-level and landscape-level variables in explaining beetle-caused tree mortality, we analysed the data in three ways using the statistical software SAS/STAT (SAS Institute Inc, 2003). First, we used the variables that were common to all plots, therefore using only a subset of the plots (Table 1). Second, we analysed the effect of landscape context, beetle pressure and topography alone using the data from all sampled plots. Third, we only used the plot-level variables, i.e. stand structure and soil. This approach resulted in three regression models for each forest type; for all models, the response variable describing beetle-caused tree mortality was per cent host basal area beetle-killed (see Plot Selection and Field Sampling).

To identify and remove inter-correlated explanatory variables, we first calculated a correlation matrix between all pairs of variables. For each pair of correlated variables ($|r| > 0.4$), we retained the one that had the strongest correlation with per cent host basal area beetle-killed, and repeated the process until all inter-correlated explanatory variables were removed. To reduce the number of variables used in model selection, we also removed all explanatory variables that were weakly correlated ($r < 0.25$) with the response variable. For landscape context and beetle pressure variables that were calculated at multiple spatial scales, we first selected the scale (buffer size) that was best correlated with the response variable before entering the variable in the correlation matrix.

Model selection was done in two steps. First, the best 10 models with up to five variables were identified, based on the models' R^2_{adj} (PROC REG, BEST option). Because this model selection option only takes into account the overall fit of the model and not the level of significance of individual variables in the models, we performed a second step where we tested each model individually using a linear model approach (PROC GLM). Non-significant ($\alpha > 0.05$) variables were removed from each model in a backward selection process. Finally, we tested for the presence of spatial autocorrelation in the residuals of the regression models using correlograms and the software GS+ (Gamma Design Software, 2004). None of the regression model residuals were spatially autocorrelated (results not shown and not discussed hereafter).

RESULTS

In total, 129 plots were sampled in 2006 and 2007 across the Greater Yellowstone ecosystem (Fig. 2), representing a range of bark beetle-caused mortality of tree host basal area of 0–79% in lodgepole pine, 0–90% in whitebark pine, 0–98% in Engelmann spruce and 0–89% in Douglas-fir (see Appendix S2). Sampling year was not a significant variable in any of the regression models, suggesting that the differences in sampling designs between sampling years were inconsequential.

Lodgepole pine mortality

Using variables that were common to all plots (Table 1), lodgepole pine mortality decreased with distance from the nearest local infestation in 2004 and increased with per cent basal area in large trees ($R^2_{adj} = 0.63$; Table 2). With only the landscape context, beetle pressure and topographic variables, lodgepole pine mortality also decreased with distance from the nearest local infestation in 2004 but increased with elevation ($R^2_{adj} = 0.59$; Table 3). When only plot-level variables (stand structure and soil characteristics) were used, lodgepole pine mortality increased with per cent basal area in large trees ($R^2_{adj} = 0.40$; Table 4).

Whitebark pine mortality

In the model using variables that were common to all plots, whitebark pine mortality increased with pre-outbreak host relative basal area ($R^2_{adj} = 0.25$; Table 2). Per cent forest beetle-killed in 2004 within a radius of 1 km was only marginally significant ($P = 0.0683$) in this model, but was positively related to tree mortality in the model based on landscape context, beetle pressure and topographic variables ($R^2_{adj} = 0.12$; Table 3). In the model using plot-level measurements (stand structure and soil

Table 2 Results of the best linear models explaining per cent host basal area beetle-killed in a subset of plots for which all variables were measured (see Table 1). The '+' and '–' symbols before the explanatory variables represent the direction of the relationship.

	Model statistics				Explanatory variables			
Bark beetle – host tree	*N*	R^2_{adj}	*F*	*P*	Source	d.f.	*F*	*P*
Mountain pine beetle – lodgepole pine	38	0.63	32.82	< 0.0001	– Distance to BB 2004*	1	22.71	< 0.0001
					+ %BA in large trees	1	27.71	< 0.0001
Mountain pine beetle – whitebark pine	16	0.25	5.94	0.0287	+ Pre-outbreak host BA	1	5.94	0.0287
Spruce beetle – Engelmann spruce	16	0.66	29.99	< 0.0001	+ %BK 2003 – 500 m†	1	29.99	< 0.0001
Douglas-fir beetle – Douglas-fir	16	0.52	9.23	0.0032	+ Forest cover – 500 m‡	1	7.34	0.0179
					+ %BK 2003 – 2 km†	1	5.00	0.0435

BA = basal area.
*Distance to closest local bark beetle (BB) eruption in 2004.
†Proportion of area beetle-killed (BK) in 2003 within a radius of 500 m or 2 km.
‡Forest cover within a radius of 500 m.

Table 3 Results of the best linear models explaining per cent host basal area beetle-killed using landscape context, beetle pressure and topographic variables. The '+' and '–' symbols before the explanatory variables represent the direction of the relationship.

	Model statistics				Explanatory variables			
Bark beetle – host tree	*N*	R^2_{adj}	*F*	*P*	Source	d.f.	*F*	*P*
Mountain pine beetle – lodgepole pine	38	0.59	27.93	< 0.0001	– Distance to BB 2004*	1	25.24	< 0.0001
					+ Elevation	1	21.62	< 0.0001
Mountain pine beetle – whitebark pine	30	0.12	4.96	0.0342	+ %BK 2004 – 1 km†	1	4.96	0.0342
Spruce beetle – Engelmann spruce	31	0.62	25.44	< 0.0001	+ %BK 2003 – 500 m†	1	15.66	0.0005
					– Elevation	1	22.30	< 0.0001
Douglas-fir beetle – Douglas-fir	29	0.67	29.51	< 0.0001	+ Forest cover – 500 m‡	1	21.21	< 0.0001
					+ %BK 2003 – 2 km†	1	18.85	0.0002

*Distance to closest local bark beetle (BB) eruption in 2004.
†Proportion of area beetle-killed in 2003 or 2004 within a radius of 500 m, 1 km, or 2 km.
‡Percent forest cover within a radius of 500 m.

Table 4 Results of the best linear models explaining per cent host basal area beetle-killed using stand structure and soil variables in a subset of plots for which these variables were measured (see Table 1). The '+' and '–' symbols before the explanatory variables represent the direction of the relationship.

	Model statistics				Explanatory variables			
Bark beetle – host tree	*N*	R^2_{adj}	*F*	*P*	Source	d.f.	*F*	*P*
Mountain pine beetle – lodgepole pine	39	0.40	26.84	< 0.0001	+ %BA in large trees	1	26.84	< 0.0001
Mountain pine beetle – whitebark pine	16	0.25	5.94	0.0287	+ Pre-outbreak host BA	1	5.94	0.0287
Spruce beetle – Engelmann spruce	16	0.22	5.28	0.0375	+ Total nitrogen	1	5.28	0.0375
Douglas-fir beetle – Douglas-fir	16	0.28	6.96	0.0195	+ Pre-outbreak host BA	1	6.96	0.0195

BA = basal area.

characteristics) alone, whitebark pine mortality increased with pre-outbreak host relative basal area (R^2_{adj} = 0.25; Table 4).

Engelmann spruce mortality

In the all-variable model, spruce mortality increased with per cent forest beetle-killed in 2003 within a radius of 500 m (Table 2; R^2_{adj} = 0.66). In the model using landscape context, beetle pressure and topographic variables, spruce mortality increased with per cent forest beetle-killed in 2003 within a radius of 500 m and decreased with elevation (Table 3; R^2_{adj} = 0.62). In the model that used stand structure and soil characteristics variables, tree mortality increased with total nitrogen (R^2_{adj} = 0.22; Table 4).

Douglas-fir mortality

For the model using variables common to all plots ($R^2_{adj} = 0.52$; Table 2), and the one using landscape context, beetle pressure and topographic variables ($R^2_{adj} = 0.67$; Table 3), Douglas-fir mortality increased with per cent forest cover within a radius of 500 m and with per cent forest beetle-killed in 2003 within a radius of 2 km. Using stand structure and soil characteristics variables only, tree mortality increased with pre-outbreak host relative basal area ($R^2_{adj} = 0.28$; Table 4).

DISCUSSION

For three of the four tree host–bark beetle pairings (lodgepole pine, Engelmann spruce and Douglas-fir), beetle pressure, i.e. either proximity to initial (2003 and 2004) eruptions or the amount of beetle-killed forest in the surrounding landscape a few years before the outbreak (2003 and 2004), was a key predictor of subsequent mortality when all variables were used – for whitebark pine, the amount of beetle-killed forest in the surrounding landscape was only marginally significant ($P = 0.0683$). Similarly, for the models based on landscape context, beetle pressure and topographic variables only (Table 3), mortality of all host tree species included a measure of beetle pressure. For Douglas-fir, the percentage of coniferous forest surrounding the stands also predicted tree mortality, which suggests that the abundance of forest habitat in the landscape was important for supporting bark beetle outbreak and perhaps facilitating dispersal. However, edge density was not significant in any of the models that included landscape context variables, suggesting that this measure of habitat configuration and connectivity was relatively unimportant.

In general, models that included landscape context, beetle pressure and topographic variables (Tables 2 & 3) were much better at predicting the severity of bark beetle outbreaks ($R^2_{adj} = 0.59–0.67$ for lodgepole pine, Engelmann spruce and Douglas-fir) than the models that only included the plot-level variables (stand structure and soil characteristics; $R^2_{adj} = 0.22–0.40$), except for whitebark pine (see below). Models that used plot-level variables included descriptors of the abundance (pre-outbreak host basal area for whitebark pine and Douglas-fir) or average size (per cent basal area in large trees for lodgepole pine) of host trees (Tables 2 & 4). The absence of many plot-level variables in the models that used variables that were common to all plots (Table 2) may be due to the fact that only susceptible stands were sampled (i.e. stands with an abundance of large-diameter host trees).

These results are in agreement with current understanding of bark beetle population dynamics. Because these three bark beetle species typically feed and reproduce in live trees, successful reproduction of bark beetles at endemic (i.e. non-epidemic) levels is contingent on the presence of weakened or stressed host trees, which have compromised defence mechanisms. Successful colonization of a tree by bark beetles depends on the inter-play between beetle attack rate and tree defence, and subsequent reproduction is largely influenced by predation, competition with other insects and weather (Raffa *et al.*, 2008). Under endemic conditions, tree attributes such as tree vigour and size, and stand attributes such as density are critical for determining the outcome of bark beetle attack (Raffa & Berryman, 1983). However, when favourable environmental conditions (e.g. warm temperature, drought, etc.) increase the success rate of beetle attacks and populations reach a critical size, bark beetles can successfully mass-attack host trees irrespective of their vigour, age or size, and local infestations may develop (Wallin & Raffa, 2004; Raffa *et al.*, 2008). The transition from local eruptions to regional outbreaks may then be affected by landscape-level factors. In this study, beetle-killed stands were sampled when the outbreaks were well under way (2006–07), i.e. at a time when landscape factors may have had a greater influence on beetle activity than local factors. This is particularly true for the spruce beetle and the Douglas-fir beetle, which began to erupt one year earlier (2003) than the mountain pine beetle (2004), and whose impact was only explained by variables characterizing the surrounding landscape (Table 2). However, beetle pressure in the first years of the outbreak was a significant variable explaining tree mortality across all beetle species, suggesting that once an outbreak has begun, the best predictor of beetle-caused tree mortality in one place is the presence of nearby local infestations in previous years (Aukema *et al.*, 2006, 2008). The importance of beetle pressure in the models emphasizes the importance of beetle dispersal, a process about which very little is known.

Models for whitebark pine generally had the least explanatory power ($R^2_{adj} = 0.12–0.25$) and contrary to all the other tree host–beetle pairings studied, did not include landscape-level variables when all variables were considered (Table 2). This contrasting pattern may be linked to the interaction between the unique biogeography of whitebark pine and climate change. Whitebark pine is a high-elevation species that historically has not been continually exposed to mountain pine beetle outbreaks because prolonged low (<40 °C) winter temperature can kill overwintering larvae and because cool summer temperatures delay the insects' development rate. It has been proposed that whitebark pine may be relatively naïve to the mountain pine beetle and that the unprecedented levels of tree mortality sustained during the current outbreak may be caused by climate warming (Bentz *et al.*, 2010; Logan *et al.*, 2010). This hypothesis, however, remains to be tested.

CONCLUSION

The co-occurrence of outbreaks of three species of bark beetles on four host tree species in Greater Yellowstone allowed us to study the effects of landscape- and plot-level variables on the distribution of bark beetle impact during an ongoing outbreak, while controlling for differences between places and time. We conclude that in stands susceptible to bark beetle outbreaks (most trees older than 100 years and with a d.b.h. > 20 cm), variables describing forest habitat and beetle pressure in the surrounding landscape were much better than the selected plot-level measurements at explaining spatial patterns of beetle-caused tree mortality in stands of lodgepole pine, Engelmann

spruce and Douglas-fir. However, these variables were marginal predictors of whitebark pine mortality. It should be noted, however, that the overall lower predictive power of plot-level variables might be partly explained by the fact that the data were collected in susceptible stands only (i.e. stands established more than 100 years ago and having large host trees), and because the stands were sampled when the outbreaks were well under way, a time when landscape factors may override local factors. These results highlight the importance of landscape-level factors and positive feedback exerted by beetles once their populations have reached outbreak proportions.

In addition to giving insight into the epidemiology and biogeography of these bark beetle species, the results from this study may facilitate management responses to ongoing outbreaks by allowing short-term prediction of tree mortality. Our finding that good prediction of beetle-caused tree mortality can be achieved using GIS- and remote sensing-based data alone indicates that, once local infestations have occurred, only a few key pieces of information such as beetle pressure are needed. This in turn suggests that field and possibly aerial detection surveys, which are time- and resource-consuming, should be concentrated during the onset of outbreaks, but may be less required during large outbreaks. As the severity and extent of bark beetle outbreaks keep increasing, the improvement of current management tools will become more important.

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REFERENCES

Abbott, B., Stennes, B. & van Kooten, G.C. (2009) Mountain pine beetle, global markets, and the British Columbia forest economy. *Canadian Journal of Forest Research*, **39**, 1313–1321.

Amman, G.D., McGregor, M.D., Cahill, D.B. & Klein, W.H. (1977) *Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains*. USDA Forest Service General Technical Report INT-36. USDA Forest Service, Ogden, UT.

Aukema, B.H., Carroll, A.L., Zhu, J., Raffa, K.F., Sickley, T.A. & Taylor, S.W. (2006) Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. *Ecography*, **29**, 427–441.

Aukema, B.H., Carroll, A.L., Zheng, Y., Zhu, J., Raffa, K.F., Moore, R.D., Stahl, K. & Taylor, S.W. (2008) Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. *Ecography*, **31**, 348–358.

Axelson, J.N., Alfaro, R.I. & Hawkes, B.C. (2009) Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. *Forest Ecology and Management*, **257**, 1874–1882.

Baker, W.L., Veblen, T.T. & Sherriff, R.L. (2007) Fire, fuels and restoration of ponderosa pine–Douglas fir forests in the Rocky Mountains, USA. *Journal of Biogeography*, **34**, 251–269.

Beers, T.W., Dress, P.E. & Wensel, L.C. (1966) Aspect transformation in site productivity research. *Journal of Forestry*, **64**, 691–692.

Bentz, B.J., Amman, G.D. & Logan, J.A. (1993) A critical assessment of risk classification systems for the mountain pine beetle. *Forest Ecology and Management*, **61**, 349–366.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F. & Seybold, S.J. (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience*, **60**, 602–613.

Byers, J.A., Anderbrant, O. & Löfqvist, J. (1989) Effective attraction radius – a method for comparing species attractants and determining densities of flying insects. *Journal of Chemical Ecology*, **15**, 749–765.

Campbell, E.M., MacLean, D.A. & Bergeron, Y. (2008) The severity of budworm-caused growth reductions in balsam fir/spruce stands varies with the hardwood content of surrounding forest landscapes. *Forest Science*, **54**, 195–205.

Cappuccino, N., Lavertu, D., Bergeron, Y. & Régnière, J. (1998) Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia*, **114**, 236–242.

Despain, D.G. (1990) *Yellowstone vegetation. Consequences of environment and history in a natural setting*. Roberts Rinehart Publishers, Boulder, CO.

Dymond, C.C., Wulder, M.A., Shore, T.L., Nelson, T., Boots, B. & Riel, B.G. (2006) Evaluation of risk assessment of mountain pine beetle infestations. *Western Journal of Applied Forestry*, **21**, 5–13.

Fauria, M.M. & Johnson, E.A. (2009) Large-scale climatic patterns and area affected by mountain pine beetle in British Columbia, Canada. *Journal of Geophysical Research – Biogeosciences*, **114**, G01012.

Furniss, M.M. & Renkin, R. (2003) Forest entomology in Yellowstone National Park, 1923–1957: a time of discovery and learning to let live. *American Entomologist*, **49**, 198–209.

Gamma Design Software (2004) *GS+: Geostatistics for the environmental sciences. Version 7*. Gamma Design Software, Plainwell, MI.

Griffin, J.M., Turner, M.G. & Simard, M. (2011) Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. *Forest Ecology and Management*, **261**, 1077–1089.

Holsten, E.H., Thier, R.W. & Gibson, K.E. (1999) *The spruce beetle*. USDA Forestry Service, Forest Insect and Disease Leaflet 127. USDA Forestry Service, Washington, D.C.

Homer, C., Huang, C.Q., Yang, L.M., Wylie, B. & Coan, M. (2004) Development of a 2001 national land-cover database for the United States. *Photogrammetric Engineering and Remote Sensing*, **70**, 829–840.

Johnson, P.C. & Coster, J.E. (1978) Probability of attack by southern pine beetle in relation to distance from an attractive host tree. *Forest Science*, **24**, 574–580.

Klutsch, J.G., Negrón, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J. & Caissie, R. (2009) Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *Forest Ecology and Management*, **258**, 641–649.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T. & Safranyik, L. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature*, **452**, 987–990.

Larson, E.R., Van De Gevel, S.L. & Grissino-Mayer, H.D. (2009) Variability in fire regimes of high-elevation whitebark pine communities, western Montana, USA. *Ecoscience*, **16**, 282–298.

Logan, J.A., Macfarlane, W.W. & Willcox, L. (2010) Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone ecosystem. *Ecological Applications*, **20**, 895–902.

Lynch, H.J., Renkin, R.A., Crabtree, R.L. & Moorcroft, P.R. (2006) The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. *Ecosystems*, **9**, 1318–1327.

McGarigal, K. & Marks, B. (1995) *FRAGSTATS: spatial analysis program for quantifying landscape structure*. USDA Forest Service General Technical Report PNW-GTR-351. USDA Forest Service, Portland, OR.

McKeague, J.A. (1976) *Manual on soil sampling and methods of analysis*. Canadian Society of Soil Sciences, Ottawa, ON.

Negrón, J.F. (1998) Probability of infestation and extent of mortality associated with the Douglas fir beetle in the Colorado Front Range. *Forest Ecology and Management*, **107**, 71–85.

Nelson, T., Boots, B., Wulder, M.A., Shore, T., Safranyik, L. & Ebata, T. (2006) Rating the susceptibility of forests to mountain pine beetle infestations: the impact of data. *Canadian Journal of Forest Research*, **36**, 2815–2825.

Perkins, D.L. & Roberts, D.W. (2003) Predictive models of whitebark pine mortality from mountain pine beetle. *Forest Ecology and Management*, **174**, 495–510.

Raffa, K.F. & Berryman, A.A. (1982) Physiological differences between lodgepole pines resistant and susceptible to the mountain pine-beetle (Coleoptera, Scolytidae) and associated microorganisms. *Environmental Entomology*, **11**, 486–492.

Raffa, K.F. & Berryman, A.A. (1983) The role of host plant-resistance in the colonization behavior and ecology of bark beetles (Coleoptera, Scolytidae). *Ecological Monographs*, **53**, 27–49.

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

Reynolds, K.M. & Holsten, E.H. (1994) Relative importance of risk factors for spruce beetle outbreaks. *Canadian Journal of Forest Research*, **24**, 2089–2095.

Robertson, C., Wulder, M.A., Nelson, T.A. & White, J.C. (2008) Risk rating for mountain pine beetle infestation of lodgepole pine forests over large areas with ordinal regression modelling. *Forest Ecology and Management*, **256**, 900–912.

Robertson, C., Nelson, T.A., Jelinski, D.E., Wulder, M.A. & Boots, B. (2009) Spatial-temporal analysis of species range expansion: the case of the mountain pine beetle, *Dendroctonus ponderosae*. *Journal of Biogeography*, **36**, 1446–1458.

Rock, B.N., Vogelmann, J.E., Williams, D.L., Vogelmann, A.F. & Hoshizaki, T. (1986) Remote detection of forest damage. *BioScience*, **36**, 439–445.

Rogan, J., Franklin, J. & Roberts, D.A. (2002) A comparison of methods for monitoring multitemporal vegetation change using Thematic Mapper imagery. *Remote Sensing of Environment*, **80**, 143–156.

Roland, J. (1993) Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia*, **93**, 25–30.

Romme, W.H. & Despain, D.G. (1989) Historical perspective on the Yellowstone fires of 1988. *BioScience*, **39**, 695–699.

Romme, W.H., Knight, D.H. & Yavitt, J.B. (1986) Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? *The American Naturalist*, **127**, 484–494.

Safranyik, L. & Carroll, A.L. (2006) The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine* (ed. by L. Safranyik and W.R. Wilson), pp. 3–66. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC.

Safranyik, L., Linton, D.A., Silversides, R. & McMullen, L.H. (1992) Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. *Journal of Applied Entomology–Zeitschrift für Angewandte Entomologie*, **113**, 441–450.

Safranyik, L., Shore, T.L., Linton, D.A. & Taylor, S.P. (1995) Dispersal of the spruce beetle, *Dendroctonus rufipennis* Kirby (Col., Scolytidae) from an experimental log deck. *Journal of Applied Entomology–Zeitschrift für Angewandte Entomologie*, **119**, 335–340.

SAS Institute Inc (2003) *SAS/STAT Statistical Software, v. 9.1*. SAS Publishing, Cary, NC.

Schmid, J.M. & Frye, R.H. (1977) *Spruce beetle in the Rockies*. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-49. USDA Forest Service, Fort Collins, CO.

Shore, T.L. & Safranyik, L. (1992) *Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands*. Natural Resources Canada, Canada, Pacific and Yukon Region, Information Report BC-X-336. Natural Resources Canada, Canada, Pacific and Yukon Region, Victoria, BC.

Shore, T.L., Safranyik, L. & Lemieux, J.P. (2000) Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. *Canadian Journal of Forest Research*, **30**, 44–49.

Simard, M., Romme, W.H., Griffin, J.M. & Turner, M.G. (2011) Do mountain pinebeetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecological Monographs*, **81**, 3–24.

Stokes, M.A. & Smiley, T.L. (1968) *An introduction to tree-ring dating*. University of Chicago Press, Chicago, IL.

Sullivan, B.T. & Mori, K. (2009) Spatial displacement of release point can enhance activity of an attractant pheromone synergist of a bark beetle. *Journal of Chemical Ecology*, **35**, 1222–1233.

Turchin, P. & Thoeny, W.T. (1993) Quantifying dispersal of southern pine beetles with mark–recapture experiments and a diffusion model. *Ecological Applications*, **3**, 187–198.

University of Wisconsin – Madison (2010) UW Soil Testing Labs. Madison, WI. Available at: http://uwlab.soils.wisc.edu/ (accessed 1 October 2007).

USDA Forest Service (2008) *Forest insect and disease aerial survey. Regions 1, 2, and 4*. Available at: www.fs.usda.gov/r1 (regions 1 and 4); www.fs.usda.gov/r2 (region 2) (accessed 4 August 2008).

Wallin, K.F. & Raffa, K.F. (2004) Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. *Ecological Monographs*, **74**, 101–116.

Western Regional Climate Center (2007) *National Climatic Data Center 1971–2000 monthly normals, Old Faithful, Wyoming*. Available at: http://www.wrcc.dri.edu/ (accessed 8 April 2007).

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methods used to create bark beetle disturbance maps and landscape-level variables.

Appendix S2 Descriptive statistics of the explanatory variables used in the analyses.

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