

# Forest structure altered by mountain pine beetle outbreaks affects subsequent attack in a Wyoming lodgepole pine forest, USA

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**Abstract:** Extensive outbreaks of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) will alter the structure of many stands that will likely be attacked again before experiencing a stand-replacing fire. We examined a stand of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) in Grand Teton National Park currently experiencing a moderate-level outbreak and previously attacked by mountain pine beetle in the 1960s. Consistent with published studies, tree diameter was the main predictor of beetle attack on a given tree, large trees were preferentially attacked, and tree vigor, age, and cone production were unimportant variables for beetle attack at epidemic levels. Small trees killed in the stand were killed based mainly on their proximity to large trees and were likely spatially aggregated with large trees as a result of the previous outbreak. We concluded that the driving factors of beetle attack and their spatial patterns are consistent across outbreak severities but that stand structure altered by the previous outbreak had implications for the current outbreaks in the same location. This study should catalyze additional research that examines how beetle-altered stand structure affects future outbreaks — an important priority for predicting their impacts under climate change scenarios that project increases in outbreak frequency and extent.

**Résumé :** De vastes épidémies du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins) vont modifier la structure de plusieurs peuplements qui vont probablement être attaqués de nouveau avant d'être détruits par un feu qui entraîne le remplacement du peuplement. Nous avons étudié un peuplement de pin pin tordu latifolié (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) dans le parc national de Grand Teton qui subit présentement une épidémie moyennement sévère et qui a déjà été attaqué par le dendroctone du pin ponderosa dans les années 1960. Conformément aux études publiées, le diamètre des arbres était le principal prédicteur de l'attaque de l'insecte sur un arbre en particulier; l'insecte préfère les gros arbres et la vigueur de l'arbre, son âge et la production de cônes ne sont pas des variables importantes en lien avec l'attaque de l'insecte lors d'une épidémie. Les petits arbres qui ont été tués dans le peuplement l'ont été surtout parce qu'ils étaient situés à proximité de gros arbres et ils étaient probablement regroupés avec de gros arbres à cause de l'épidémie précédente. Nous arrivons à la conclusion que les facteurs qui sont à l'origine de l'attaque de l'insecte et leur répartition spatiale sont les mêmes pour différents niveaux de sévérité, mais que la structure du peuplement qui a été modifiée par une épidémie précédente avait des conséquences sur l'épidémie actuelle qui sévit au même endroit. Cette étude devrait susciter d'autres travaux de recherche pour déterminer comment la structure du peuplement qui est modifiée par l'insecte influence les épidémies futures — une importante priorité pour prédire leurs impacts dans l'optique de scénarios de changement climatique qui prévoient une augmentation de la fréquence et de l'étendue des épidémies.

[Traduit par la Rédaction]

## Introduction

Insect outbreaks are pervasive and significant disturbance agents that are important in shaping the structure of coniferous forests in western North America (Nigh et al. 2008; Axelsson et al. 2009; Klutsch et al. 2009; Vyse et al. 2009). Second only to wildfires as the largest source of tree mortality in this region (Samman and Logan 2000), insect infestations influence an average annual area in the United States of 20.4 million ha, resulting in losses of nearly \$1.5 billion (Dale et al. 2001). Several researchers have shown that the

annual extent of insect infestation in North America was comparable to the area burned by fire each year in the last decade (Leenhouts 1998; Kurz and Apps 1999; USDA Forest Service 2005).

Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex Watson) is perhaps the most widespread of all conifer species in western North America, ranging from the central Yukon Territory to southern Colorado and from near the Pacific coast in British Columbia to western South Dakota (Lotan and Critchfield 1990). Mature lodgepole pine trees are attacked and killed by mountain pine beetle (MPB) (*Dendroc-*

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*tonus ponderosae* Hopkins), an indigenous bark beetle but one of the most important insects causing widespread mortality in North America. Hicke and Jenkins (2008) estimated in 2008 that 46% of lodgepole pine forests in the western United States were highly susceptible to MPB attack. A current unprecedented MPB outbreak began in the late 1990s and had affected 10.1 million ha of lodgepole pine forest in British Columbia by 2007 (Westfall and Ebata 2008) and 800 000 ha in Colorado (Klutsch et al. 2009) alone.

The spatial pattern of beetle attack in pure lodgepole pine stands during MPB epidemics has been studied in detail. MPB preferentially attacks trees of larger diameter (Cole and Amman 1969; Safranyik et al. 1974), presumably because they afford a larger target for emerging and dispersing beetles to locate (Hynum and Berryman 1980). Burnell (1977) proposed that while MPB attacks trees in relation to their diameter, the distribution of host trees was well explained by a random model, and smaller trees were simply attacked once larger trees were depleted. Subsequent studies, however, showed that attack of small trees by MPB was better explained by their proximity to large trees (Mitchell and Preisler 1991; Preisler 1993; Preisler and Mitchell 1993). The relationship of MPB attack to large-diameter trees is considered robust (Björklund and Lindgren 2009), and MPB attack has been shown to be relatively independent of tree age except for the effect of age on tree size (Mitchell and Preisler 1991; Preisler and Mitchell 1993). Moreover, although trees of lower vigor or higher stress tend to be host trees at endemic levels of MPB (Fetting et al. 2007), few studies have shown definitively that tree vigor is an important determinant of MPB attack at epidemic levels (Amman et al. 1988; Preisler and Mitchell 1993; but see Waring and Pitman 1985).

Mortality associated with MPB outbreaks clearly affects lodgepole pine forest structure with implications not only for future stand dynamics but also for the potential of subsequent MPB attacks. First, outbreaks act to “thin” stands by reducing stand density, which theoretically releases residual pine in response to increased light and space resulting from canopy mortality (Romme et al. 1986). Field experiments with silvicultural thinning effects on MPB attack have shown that thinned forests are less attractive to insects, although little effect of tree density on the spatial pattern of host tree selection was found once MPB attack began (Preisler and Mitchell 1993). Second, MPB outbreaks release lodgepole pine tree regeneration (Nigh et al. 2008; Vyse et al. 2009) as well as increase the dominance of small-diameter trees (Klutsch et al. 2009). Finally, canopy tree mortality may also change species composition if stand composition was mixed prior to the outbreak or if post-outbreak establishment favors species other than lodgepole pine (Astrup et al. 2008; Axelson et al. 2009). Each of these effects theoretically reduces the susceptibility of an unmanaged stand to future MPB attack until the stand is regenerated by a stand-replacing fire (Axelson et al. 2009) and may also change the way future attacks proceed through the stand if a subsequent attack actually occurs.

A major gap in our understanding of the spatial dynamics of MPB attack in lodgepole pine forests is that most published studies were conducted in stands that did not experience previous insect outbreaks that may have altered stand structure to the extent that bark beetle behavior may be affected. More specifically, few studies have specified outbreak

severity (Björklund and Lindgren 2009) despite its wide variation across western North America (Lynch et al. 2006). MPB dynamics at “epidemic levels” may differ in an outbreak of low or moderate severity compared with high severity. The return interval for MPB outbreaks in a stand is approximately 20–55 years in the northern Rocky Mountains (Cole and Amman 1980; Alfaro et al. 2004; Taylor et al. 2006). Given a stand-replacing fire interval of 150–300 years (Lotan and Critchfield 1990), stand structure of areas attacked will be altered by beetles over large regions, outbreak severity will undoubtedly vary across the landscape, and areas previously attacked by MPB are likely to be attacked again. We therefore focus on the difference in MPB attack between lodgepole pine stands typically described in the literature (high-severity outbreak, not previously attacked) and stands likely to be widespread following the current unprecedented outbreak (low- to moderate-severity outbreak in a stand previously attacked by MPB). Specifically, we examined MPB dynamics in a lodgepole pine stand over three growing seasons to address the following questions: (i) what is the effect of previous MPB attacks on current stand structure and (ii) do the characteristics of attacked trees (diameter, age) differ from published studies when the outbreak is only of low to moderate severity?

## Methods

### Study area

The study site was a forest dominated by lodgepole pine in the central portion of Grand Teton National Park in northwestern Wyoming (43°45'N, 110°36'W). The sampled area was located on a flat, topographically uniform area approximately 0.5 km south of the Snake River on dry, coarse-textured, sandy, and gravelly alluvial soils at an elevation of 2090 m. Weather patterns in the area are continental, with 71% of the annual precipitation (59 cm) falling between November and May as snow at nearby Moran, Wyoming (Martner 1986).

The sampled stand is composed of about 1400 trees/ha, 85% of which are lodgepole pine ranging between 4.0 and 40.0 cm in diameter at breast height (DBH) (1.4 m). The stand contains a small, younger cohort of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and whitebark pine (*Pinus albicaulis* Engelm.) that represent 12% of the trees, mostly in subcanopy positions. Other tree species were rare (Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Englemann spruce (*Picea engelmannii* Parry ex Engelm.)), representing <1% of the live trees. Tree age dating suggests that the stand originated following a stand-replacing fire around 1879, creating a pure lodgepole pine stand of moderate density based on ranges published by Kashian et al. (2005) for the Greater Yellowstone Ecosystem. Mortality of lodgepole pine due to MPB in the stand began in the early 1950s, reaching its peak in the 1960s at moderate levels (40%–50%; Grand Teton National Park, unpublished data). In the current outbreak, light mortality due to MPB was first noticeable at the study site in 2005; observed cumulative mortality was 32% in 2008, 39% in 2009, and 44% in 2010, and additional mortality is expected in subsequent years. The current MPB outbreak is heavy elsewhere in western Wyoming (for example, mortality is >90% in forests approximately 120 km south of

the study site), but mortality has been relatively low in the Greater Yellowstone Ecosystem with no near-future projections of large changes in this trend.

### Field sampling

A 50 m × 50 m (0.25 ha or 2500 m<sup>2</sup>) permanent plot was randomly located within the ~5 ha stand chosen for sampling. All live and dead standing trees ≥4 cm DBH ( $n = 355$ ) were mapped by measuring and recording their  $X$ - and  $Y$ -coordinates to the nearest 0.1 m within the plot. Trees were measured and described in three consecutive field seasons in 2008–2010; trees were marked with an aluminum numbered tag at breast height in 2008 to ensure accurate re-measurements in 2009 and 2010. Information recorded for each tree included species, DBH, and crown position class (dominant, codominant, intermediate, overtopped; Oliver and Larsen 1990). The effects of MPB (or lack thereof) were recorded for each lodgepole pine tree; trees were classified as live, dead but not beetle killed, gray (attacked by MPB >5 years ago and killed), red (attacked by MPB 3–5 years ago and killed), yellow (attacked by MPB 1–2 years ago and near dead), or green (attacked by MPB in the last year, discernable by the presence of pitch tubes or other evidence). Evidence of MPB attack was easily identifiable based on the presence of exit holes in the bark, pitch tubes, and (or) distinctive J-shaped beetle galleries beneath the bark; the presence of J-shaped galleries is a reliable indicator of tree mortality due to MPB (Simard et al. 2011). In addition, an increment core was extracted at 30 cm above mineral soil from all stems ≥4 cm DBH for age determination. Increment cores were mounted and sanded per standard techniques (Stokes and Smiley 1968) and annual rings were counted beneath a dissecting scope. Tree ages are reported as ring counts plus an estimate of the number of years required to reach 30 cm (core height), determined by harvesting five trees <5 cm DBH at their base. Coarse woody debris was examined for galleries to ascertain whether tree death occurred due to MPB; if a fallen tree was determined to have been rooted in the plot and killed by MPB, it was tallied and measured at approximate DBH. Most beetle-killed trees from the current outbreak remained standing for the duration of this study; recently killed and fallen trees were easily discernible from trees killed in the 1960s by the presence of bark and the general state of decay.

### Analyses

#### Effects of previous MPB attacks

Size and age class distributions were constructed for all live plus beetle-killed trees using 5 cm and 5 year intervals to discern past MPB disturbances and subsequent recruitment events. We analyzed the spatial distribution of trees in the plot using the univariate O-ring statistic  $O(r)$  (Wiegand and Moloney 2004), which is a neighborhood density function that uses rings of given widths to estimate patterns at a series of spatial scales. The O-ring statistic has an advantage over the univariate Ripley  $K(t)$  function (Diggle 1983; Illian et al. 2008) in that it can isolate specific distance classes rather than using a cumulative algorithm where large-scale spatial patterns may be biased by small-scale patterns (Wiegand and Moloney 2004). Spatial attraction (clustering) of trees at a

given scale produces positive values (significantly >0) of  $O(r)$  and spatial repulsion (regularity) results in negative values. Values of  $O(r)$  were calculated for distances 1–25 m at 1 m intervals. Monte Carlo simulations were used to approximate 99% confidence envelopes for values of  $O(r)$  by generating 1000 sets of random coordinates. O-ring analyses were completed using SpPack (Perry 2004).

#### Characteristics of attacked trees

We examined the frequency of MPB attack on given tree ages and sizes by constructing size and age class distributions of beetle-killed trees using 5 cm and 5 year intervals. The  $\chi^2$  goodness-of-fit test was used to compare the incidence of MPB attack on large trees (>23 cm DBH) and on small trees (<23 cm DBH) (Mitchell and Preisler 1991) with that expected under a random distribution for each year of the study.

We modeled the incidence of beetle attack on trees in the plot using logistic regression for each of the three years of the study, with tree diameter, tree age, tree vigor, and cone production as predictor variables. Tree vigor was determined as the average of the last 5 years of annual stemwood increment divided by leaf area (Waring et al. 1980). Foliar biomass was determined for stands >40 years old using measurements of diameter, crown height and depth, and sapwood and an allometric equation developed for lodgepole pine in the Greater Yellowstone Ecosystem to predict foliar biomass from tree diameter and height (Arcano 2005), such that vigor could be determined for trees that had already died. Total leaf area was calculated by multiplying foliar biomass by 9.518 m<sup>2</sup>/kg (Kaufman and Troendle 1981). Cone production was included in the logistic regression to test the hypothesis that resources allocated to reproduction may reduce those allocated to plant defense against beetle attack. Cone production was recorded in the field as a categorical variable and reclassified as an ordinal dummy variable, ordered to increase with hypothesized physiological cost: (0) no cone production, (1) predominately open (nonserotinous) cones, (2) predominately closed (serotinous) cones.

#### Spatial patterns of attacked trees over time

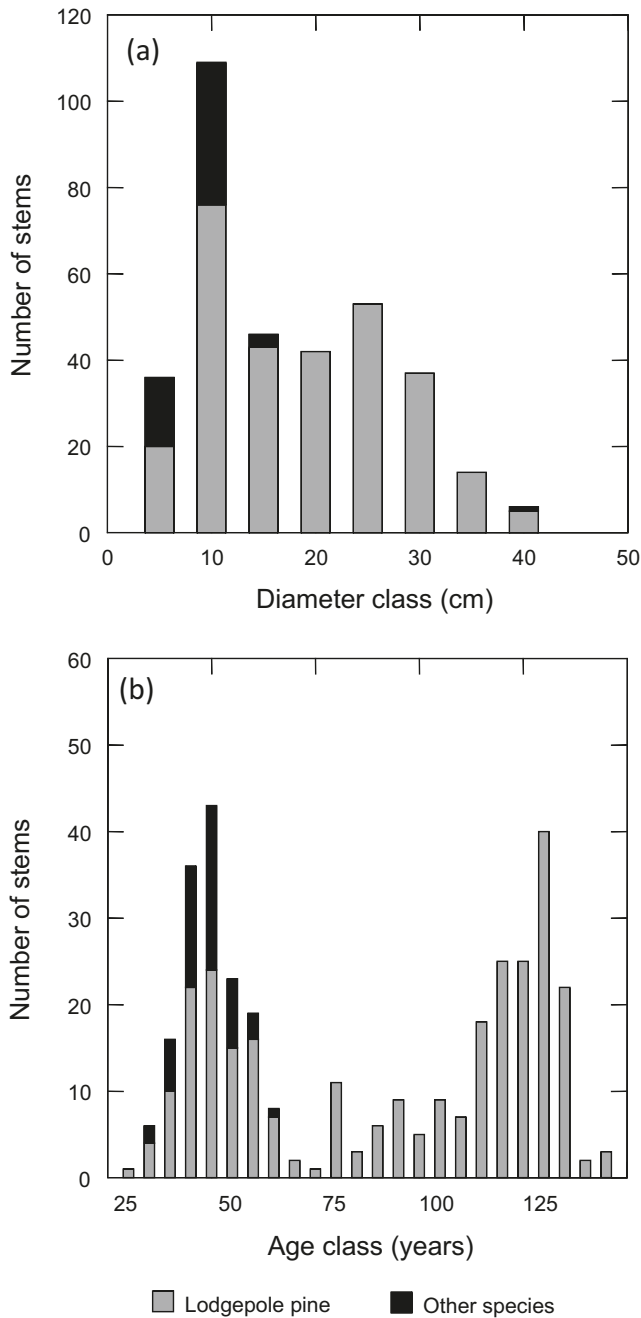
We analyzed the cumulative spatial distribution of beetle-killed trees in the plot using the O-ring statistic  $O(r)$  for each of the three years of the study to examine Burnell's (1977) hypothesis that the distribution of attacked trees follows a random model. We used a transformation of Ripley's bivariate  $K_{12}(t)$  function,  $L_{12}(t)$ , which calculates the spatial association of individuals of two populations (Illian et al. 2008), to test whether small beetle-killed trees are spatially attracted to or repulsed from large beetle-killed trees, as predicted by Mitchell and Preisler (1991) and Preisler and Mitchell (1993).

### Results

Despite a history of previous beetle attack, the diameter class distribution for all live and dead trees in the stand resembled a bell-shaped distribution characteristic of even-aged stands (Oliver and Larsen 1990) except for a higher proportion of trees in the <5, 5–10, and especially 10–15 cm classes (Fig. 1a). All but one individual of species other than lodgepole pine were in the three smallest size



**Fig. 1.** (a) Diameter class and (b) age class distributions for live and dead trees of all species in a lodgepole pine (*Pinus contorta* var. *latifolia*) forest at Grand Teton National Park in 2010.



classes, but their abundance did not solely explain the higher proportion of small trees in the stand. Other than the disproportionate number of small trees, the median size class for lodgepole pine was in the 20–25 cm size class (Fig. 1a). The corresponding age class distribution was bimodal, with one peak of successful establishment occurring between about 1875 and 1900 (110–130 years ago) and a second peak between about 1950 and 1970 (40–60 years ago) (Fig. 1b). Individuals of species other than lodgepole pine were restricted to the second peak of successful establishment, but again are

not solely responsible for it. The timing of the second peak of successful establishment (the younger and smaller trees within the stand) corresponds well to the timing of the previous MPB attack between 1950 and 1970, although low-level, relatively continuous successful seedling establishment of lodgepole pine occurred between 1900 and 1950.

Conservative analyses of current coarse woody debris revealed that former stand density was about 1950 stems/ha prior to the MPB outbreak in the 1960s, approximately 22% higher than the current density of the stand. Current basal area of lodgepole pine coarse woody debris killed by MPB was 5.24 m<sup>2</sup>/ha; by removing the basal area of young trees from the analysis, we estimate that stand basal area was approximately 34.5 m<sup>2</sup>/ha prior to the MPB outbreak in the 1960s, only slightly higher than current basal area (33.3 m<sup>2</sup>/ha). Spatial point pattern analysis of all trees prior to the current MPB attack shows spatial aggregation only for trees within 1 m, likely corresponding to clumping of smaller and more recently regenerated trees, and a regular distribution of trees at 17–19 m, but an otherwise random distribution of trees across the stand (Table 1).

The diameter class distribution of beetle-killed trees shows mortality of all sized stems but a higher proportion of trees >20 cm killed (74%) compared with those <20 cm (26%) by the final year of the study, with most killed trees having diameters of 20–35 cm (Fig. 2a). The corresponding age distribution of beetle-killed trees suggests that most attacked trees (70%) are older (>110 years) as well as larger, although trees <110 years are also killed at much lower proportions (30%) (Fig. 2b). Using the 23 cm diameter threshold of Mitchell and Preisler (1991), the  $\chi^2$  goodness-of-fit test shows that although both large and small trees were attacked in all three years, larger trees were attacked in a nonrandom manner at a high level of significance ( $p < 0.0001$  for all years), despite increasing cumulative mortality (Table 2). Similar to the meta-analysis conducted by Björklund and Lindgren (2009), we found that 100% of trees >30 cm DBH were killed or attacked by MPB, but mortality of trees <10 cm DBH was only 21%. About 96% of the stand basal area was found in lodgepole pine and 3% in lodgepole pine <10 cm DBH. By 2010, over 68% of the lodgepole pine basal area had been killed by MPB, and 2.5% of the killed basal area was for trees <10 cm DBH. Logistic regression identified tree diameter as the only significant variable in the model predicting MPB attack on a given tree, regardless of year, for the mortality level found at our study site (Table 3). Odds ratio analyses from the logistic regression suggested that odds of beetle attack increased by 4.8 times for every 5 cm increase in diameter in 2008, by 5.1 times in 2009, and by 5.2 times in 2010. All other independent variables included the value 1 within their 95% confidence interval for all years and thus are not associated with beetle attack in this stand (Table 3).

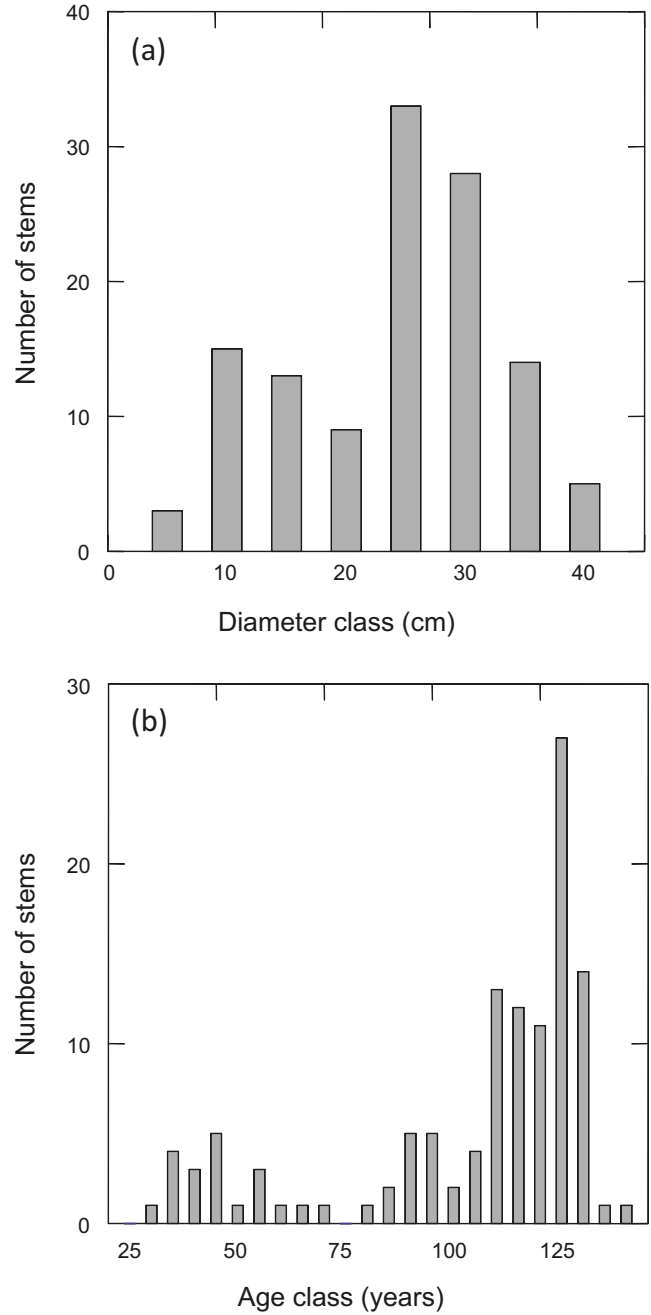
The spatial point pattern of only beetle-killed trees resembles that for all trees, but killed trees are spatially aggregated for slightly longer distances (up to 2 m) and exhibit regularity over slightly wider range of distances (15–19 m) (Table 1; Fig. 3). Beetle attack exhibited randomness at distances of 3–11 m. Clumping of killed trees at distances <2 m that occurs in all three years may approximate the dispersal distance of MPB between trees in a stand and suggests that trees tend to be killed only when very close together. The random pat-

**Table 1.** Univariate ( $O(r)$ ) analysis of spatial point patterns of live and mountain pine beetle (*Dendroctonus ponderosae*) killed trees and bivariate ( $L_{12}(t)$ ) analysis using the transformation of Ripley's  $K(t)$  function within a lodgepole pine (*Pinus contorta* var. *latifolia*) forest at Grand Teton National Park.

Distance (m)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<b><math>O(r)</math> analysis</b>																									
All trees	+																								
Killed by 2008	+	+																							
Killed by 2009		+	+																						
Killed by 2010			+																						
Killed by 2010																									
<b><math>L_{12}(t)</math> analysis</b>																									
All live large vs. small, 2010	+	+	+	+																					
Large vs. small, 2008	+	+	+	+																					
Large vs. small, 2009	+	+	+	+				+	+	+															
Large vs. small, 2010	+	+	+	+				+	+	+															

**Note:** For both analyses, + indicates spatial aggregation, - indicates spatial regularity, and a blank cell denotes spatial randomness. Spatial patterns were determined using a 99% confidence envelope based on 1000 Monte Carlo simulations.

**Fig. 2.** (a) Diameter class and (b) age class distributions for trees killed by the mountain pine beetle (*Dendroctonus ponderosae*) in a lodgepole pine (*Pinus contorta* var. *latifolia*) forest at Grand Teton National Park in 2010.



tern that exists for most spatial scales for all trees suggests that the pre-existing spatial pattern of trees prior to the current outbreak is not likely to have constrained the spatial pattern of the current MPB attack. Bivariate point pattern analysis ( $L_{12}(t)$ ) revealed that small beetle-killed trees are clustered near large killed trees only at very short distances (<3 m) in all years but are spatially repulsed at large scales (>19 m), suggesting that small trees are attacked mainly based on their proximity to larger, more targeted trees (Table 1).

**Table 2.**  $\chi^2$  goodness-of-fit results for mountain pine beetle (*Dendroctonus ponderosae*) killed trees with diameters larger and smaller than 23 cm for years 2008–2010 in a lodgepole pine (*Pinus contorta* var. *latifolia*) forest at Grand Teton National Park.

Year	Tree mortality (%)	Expected if random		Observed		$\chi^2$	<i>p</i>
		Large trees (>23 cm)	Small trees (<23 cm)	Large trees (>23 cm)	Small trees (<23 cm)		
2008	32	27	79	45	61	16.10	<0.0001
2009	39	29	85	49	65	18.50	<0.0001
2010	44	31	90	53	68	20.99	<0.0001

**Note:** The proportion of larger trees killed was significantly greater than expected for a random distribution for all years.

**Table 3.** Results of logistic regression analyses predicting mountain pine beetle (*Dendroctonus ponderosae*) attack on a given tree as a function of the independent variables for a lodgepole pine (*Pinus contorta* var. *latifolia*) forest at Grand Teton National Park between 2008 and 2010.

Variable	df	Parameter estimate	Wald $\chi^2$	Pr > $\chi^2$
<b>2008</b>				
Intercept	1	-1.976	8.323	0.004
Tree diameter	1	0.157	26.698	<0.001
Tree age	1	-0.006	1.028	0.310
Cone production	1	-0.135	0.331	0.565
Tree vigor	1	-0.007	1.006	0.316
<b>2009</b>				
Intercept	1	-2.207	10.472	0.001
Tree diameter	1	0.163	27.826	<0.001
Tree age	1	-0.005	0.633	0.426
Cone production	1	-0.234	0.984	0.321
Tree vigor	1	-0.004	0.301	0.583
<b>2010</b>				
Intercept	1	-1.497	5.144	0.023
Tree diameter	1	0.164	27.921	<0.001
Tree age	1	-0.006	0.857	0.354
Cone production	1	-0.233	0.970	0.324
Tree vigor	1	-0.010	2.214	0.137

**Note:** Tree diameter was the only significant variable in the model for all years.

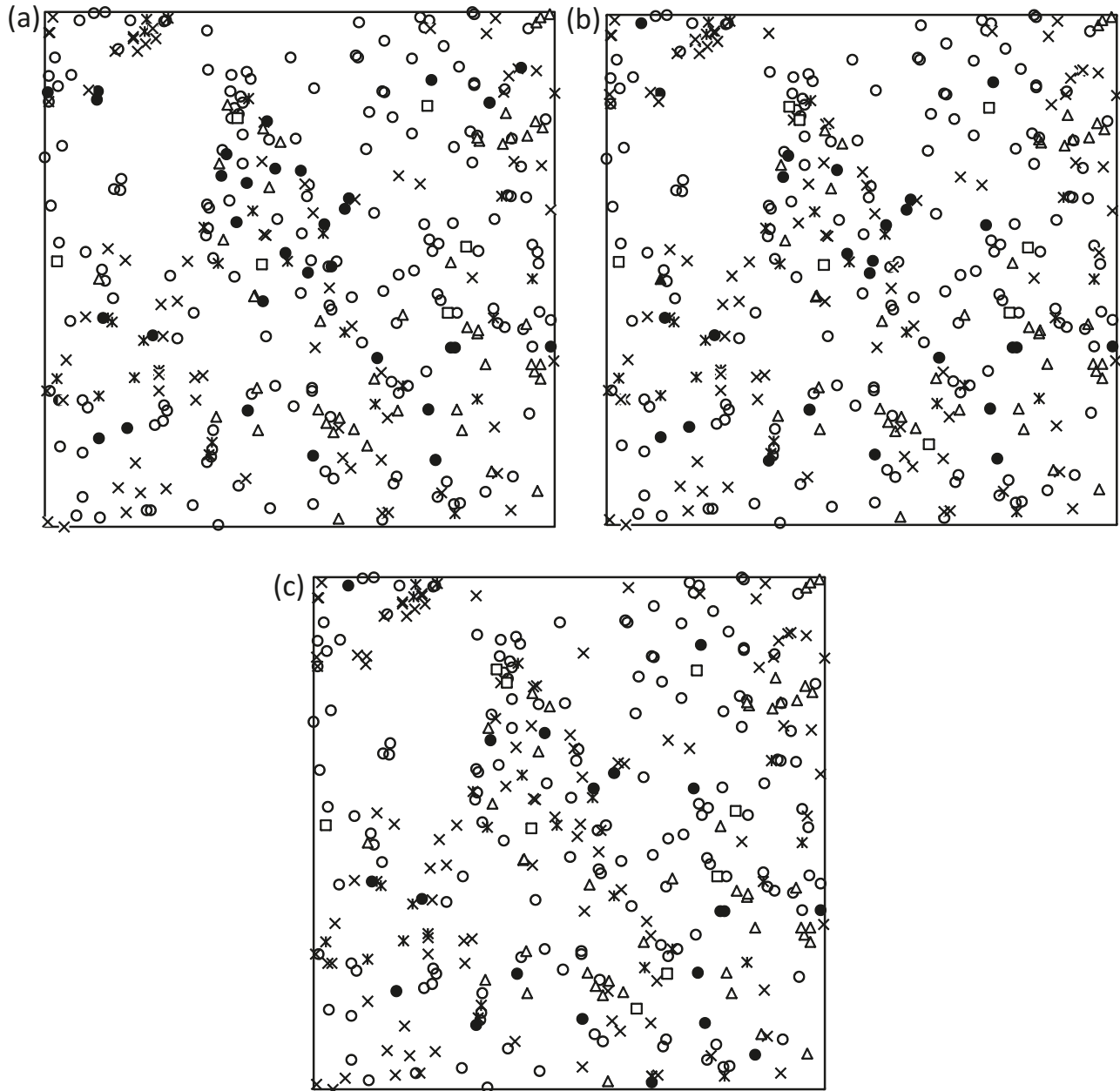
## Discussion

Our overall hypothesis was that MPB attack in lodgepole pine forests affected by (i) a low- or moderate-severity outbreak and (or) (ii) a previous insect outbreak may differ from that described in published studies that may have examined high-severity outbreaks and (or) stands never attacked. However, our study generally concurs with many studies describing spatial patterns of MPB attack in lodgepole pine forests, particularly with regard to the independent variables used to predict MPB attack and the spatial pattern of the attack itself. Tree size (diameter) was the primary predictor of beetle attack with tree mortality ranging only from 32% to 44% in our study (Table 3), similar to what has been shown with meta-analyses of the diameter – MPB attack relationship (Björklund and Lindgren 2009). Large trees (>20 cm DBH) were attacked preferentially rather than randomly even when smaller trees represented >60% of all lodgepole pine in the stand (Fig. 1), and this pattern of tree selection by MPB did not change with increasing mortality across the three years of this study (Table 2). The relationship between tree size and MPB attack in this study is not surprising given the high availability of preferred, larger host trees when outbreak severity is low to moderate, and it suggests that the relationship

between tree diameter and beetle attack is probably robust across outbreak severities. Large trees are therefore likely the main factor maintaining the outbreak even at lower severities (Mitchell and Preisler 1991).

Preference by MPB for large trees in this study reiterates the trends noted in many published studies, but we also note that stand structure at our study site was strongly altered by a previous MPB outbreak that occurred in the 1960s. Using current levels of coarse woody debris in the stand, we estimated that the current tree density is approximately 22% lower than prior to the 1960s outbreak, even with the successful establishment of small trees through the 1970s. Notably, basal area was estimated to be only about 3% higher prior to the 1960s, suggesting a previous stand structure characterized by moderate- or pole-sized-diameter trees at a higher density, typical of 70–80 year old lodgepole pine stands in the Greater Yellowstone Ecosystem (Kashian et al. 2005) and reported as preferable for MPB attack by Fettig et al. (2007). Our estimates of both density and basal area of the stand prior to MPB attack 50 years ago are based on the current condition of subsequent coarse woody debris in the stand, likely to be underestimates because of decay that could eliminate biomass and at least some indicative beetle gal-

**Fig. 3.** Stem maps of all trees >4 cm diameter at breast height in a 50 m × 50 m plot in a lodgepole pine (*Pinus contorta* var. *latifolia*) forest at Grand Teton National Park for (a) 2008, (b) 2009, and (c) 2010. Open circles indicate live lodgepole pine, crosses indicate beetle-killed lodgepole pine, solid circles indicate lodgepole pine attacked that year, triangles indicate live trees of other species, and squares indicate dead trees of other species (not beetle killed).



leries. The current stand has younger and smaller lodgepole pine overall than the stand did prior to the last outbreak, with only minimal and recent influx of other species (Fig. 1). Despite recent predictions of forest compositional changes resulting from high-severity MPB outbreaks in lodgepole pine (Astrup et al. 2008), the 1960s outbreak in our stand created mainly structural changes, probably because the historical outbreak was of lower severity and occurred in a relatively young stand at the time (Sibold et al. 2007). It is likely that the 1960s outbreak maintained the small-scale clustering of trees seen today because MPB consistently kills trees in groups (Cole and Amman 1980; Amman and Cole 1983), but it may also have created the random distribution

of trees at moderate to large scales that exists today, a pattern characteristic of lodgepole pine stands that have experienced either density-dependent mortality or a secondary disturbance following stand-replacing wildfire (He and Duncan 2000; Kashian et al. 2005). It is notable that the successful establishment of small trees following the historical attack occurred near the larger trees (Table 1), which is unusual compared with stands regenerated by fire (Kashian et al. 2005), and suggests that beetles alter spatial pattern of trees as well as stand structure. A stand characterized by lower density, an uneven-aged structure, and a more mixed species composition, all caused by a previous outbreak in our study, is likely to be less susceptible to a future high-severity MPB outbreak.



Larger trees were preferentially attacked by MPB in our stand and are likely the drivers of the outbreak, but a significant number of small trees were also killed by MPB during each year of the study (Table 2). We noted a higher percentage of beetle-killed small trees compared with a meta-analysis of 27 MPB studies (<4% mortality for trees <10 cm DBH versus 21% in our study) by Björklund and Lindgren (2009). About one third of the lodgepole pine in the stand was <10 cm DBH; nearly 16% of all trees killed by MPB by 2010 were <10 cm DBH, but this represented <3% of the killed basal area. Mitchell and Preisler (1991) and Björklund and Lindgren (2009) defined a diameter of 23 cm as the threshold differentiating large and small trees facing MPB attack, with the idea that trees <23 cm would not yield enough adult beetles to sustain an outbreak (Cole and Amman 1969). About 73% of all the lodgepole pine trees in the stand were <23 cm; 53% of all trees killed by MPB by 2010 were <23 cm, representing 29% of the killed basal area. Together with relatively low density, this high proportion of small trees in the stand probably limits the production of beetles and may partially explain why the outbreak remains relatively low to moderate in severity. A broad-scale examination of outbreak dynamics across the landscape would be necessary to adequately test and substantiate this claim.

Similar to Preisler and Mitchell (1993) and Mitchell and Preisler (1991), spatial point pattern analyses suggested that MPB attack of small trees in our study was based mainly on proximity to large trees, given that small beetle-killed trees were usually spatially aggregated with large beetle-killed trees (Table 1). Notably, small trees in general were spatially aggregated with large trees in the stand such that small trees were positioned in a manner that made them more vulnerable to attack by MPB. Astrup et al. (2008) documented low establishment of lodgepole pine after MPB outbreaks because of a dominant moss layer on the forest floor and thus poor seedbed substrate availability. At our study site, the forest floor was dominated by grasses and thus a sod layer that would probably also limit successful seedling establishment, except beneath the crowns of older lodgepole pine where forest floor vegetation was sharply reduced. The spatial location of the more favorable substrate may explain the successful establishment of new lodgepole pine seedlings nearest large trees in the stand as well as the proliferation and release of this regeneration once larger trees were killed by MPB in the 1960s. Spatially aggregated trees are unusual for lodgepole pine stands >125 years old that are regenerated by stand-replacing wildfire; Kashian et al. (2005) found fine-scale clustering in only three of 23 stands studied. An aggregated spatial pattern of regeneration would therefore represent a fundamental change in stand structure if it were attributable to previous MPB outbreaks. Specifically, mortality of smaller trees caused by stand structure altered by a previous outbreak would presumably affect the future persistence of lodgepole pine, particularly if stands suffer multiple MPB attacks before the next stand-replacing wildfire.

Our hypothesis that beetle attack and tree mortality would be affected by independent variables in addition to diameter was not supported by this study. Most notably, tree vigor was unimportant in explaining beetle attack, although this is consistent with a myriad of other studies that examined epidemic population levels of MPB (Amman et al. 1988; Bartos

and Amman 1989; Logan et al. 1998). We also hypothesized that the type of cone production (no cones, open cones, or serotinous cones) would be an important predictor of tree mortality because it would require resources that would reduce allocation toward tree defense and resistance to beetle attack, but cone production was unimportant in explaining beetle attack. Tree age was also found to be unimportant despite our expectation that it would be related to tree diameter; the binomial nature of the stand and the associated lack of size structure likely account for this result.

We acknowledge that a major limitation and caveat of this study is its lack of replication. Although sampled over multiple growing seasons, our study includes only one stand that cannot be considered to be representative of lodgepole pine stands across its distribution or even in the Greater Yellowstone Ecosystem. Strong inference would require the examination of multiple stands once attacked by beetles and (or) are currently attacked at low severity across multiple regions and locations (Björklund and Lindgren 2009). We emphasize, however, that our objective was not to represent all stands susceptible to MPB attack but instead to encourage initial exploration regarding whether a stand with a history of previous attack and attacked at lower severity was well represented in the extensive literature describing beetle mortality. Future research is certainly necessary to show that the spatial patterns of regeneration that we found are consistent across beetle-attacked stands in the region and western North America.

We conclude that spatial patterns of attack (attack mainly on large trees, with small trees attacked only due to their proximity) are consistent across outbreak severities. However, we suggest that MPB outbreaks alter a stand by reducing density, reinforcing spatial aggregation of small and large trees, and (to a lesser extent) increasing the presence of non-susceptible species, such that their disproportionate effect on younger trees may have implications for the stand at least until it is burned and regenerated by stand-replacing wildfire. The current unprecedented MPB outbreak in North America will immediately create extensive outbreak-affected stands, at least some of which will be affected by one or more additional outbreaks before stand structure is "reset" by stand-replacing wildfire. Thus, understanding or predicting stand dynamics under the scenario that small trees are increasingly attacked by MPB will become increasingly important as outbreaks increase in frequency and extent, as predicted with global climate change (Dale et al. 2001).

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