



# Mountain pine beetle-caused mortality over eight years in two pine hosts in mixed-conifer stands of the southern Rocky Mountains



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## ABSTRACT

Eruptive mountain pine beetle (*Dendroctonus ponderosae*, MPB) populations have caused widespread mortality of pines throughout western North America since the late 1990s. Early work by A.D. Hopkins suggested that when alternate host species are available, MPB will prefer to breed in the host to which it has become adapted. In Colorado, epidemic MPB populations that originated in lodgepole pine expanded into mixed-conifer stands containing ponderosa pine, a related host. We evaluated the susceptibility of both hosts to successful MPB colonization in a survey of 19 sites in pine-dominated mixed-conifer stands spanning 140 km of the Front Range, CO, USA. In each of three 0.2-ha plots at each site, we (1) assessed trees in the annual flights of 2008–2011 to compare MPB-caused mortality between lodgepole and ponderosa pine; (2) recorded previous MPB-caused tree mortality from 2004–2007 to establish baseline mortality levels; and (3) measured characteristics of the stands (e.g. tree basal area) and sites (e.g. elevation, aspect) that might be correlated with MPB colonization. Uninfested average live basal area of lodgepole and ponderosa pine was 74% of total basal area before 2004. We found that for both species, annual percent basal area of attacked trees was greatest in one year (2009), and was lower in all other years (2004–2007, 2008, 2010, and 2011). Both pine species had similar average total mortality of 38–39% by 2011. Significant predictors of ponderosa pine mortality in a given year were basal area of uninfested ponderosa pine and the previous year's mortality levels in both ponderosa and lodgepole pine. Lodgepole pine mortality was predicted by uninfested basal areas of both lodgepole and ponderosa pine, and the previous year's lodgepole pine mortality. These results indicate host selection by MPB from lodgepole pine natal hosts into ponderosa pine the following year, but not the reverse. In both species, diameters of attacked trees within each year were similar, and were progressively smaller the last four years of the study period. Our results suggest that, in contrast to previous reports, ponderosa and lodgepole pine were equally susceptible to MPB infestation in the CO Front Range during our study period. This suggests that forest managers may anticipate similar impacts in both hosts during similar environmental conditions when epidemic-level MPB populations are active in mixed-pine stands.

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## 1. Introduction

The mountain pine beetle (*Dendroctonus ponderosae*, MPB) is considered the most destructive of all native western North American forest insects (Furniss and Carolin, 1977). It attacks all native and exotic pines in western North America (Safranyik and Carroll, 2006). Beetle populations persist at low, endemic levels in numerous forest types, but can expand rapidly into epidemic levels if conditions occur that either decrease the resistance of the host trees, increase the annual survival of the beetles, or both (Raffa et al.,

2008; Bentz et al., 2010). Eruptive MPB populations that developed over the past two decades in western North America have caused pine mortality throughout millions of hectares since the late 1990s (Meddens et al., 2012). The scale and intensity of recent epidemics have been attributed to several factors acting in concert: an increase in both winter and summer temperatures, promoting MPB survival and reproduction; an increase in contiguous area of pine-dominated stands whose age and density were optimally susceptible to MPB attack; and a decrease in resistance of individual trees due to drought stress (Bentz et al., 2010; Raffa et al., 2008; Taylor et al., 2006).

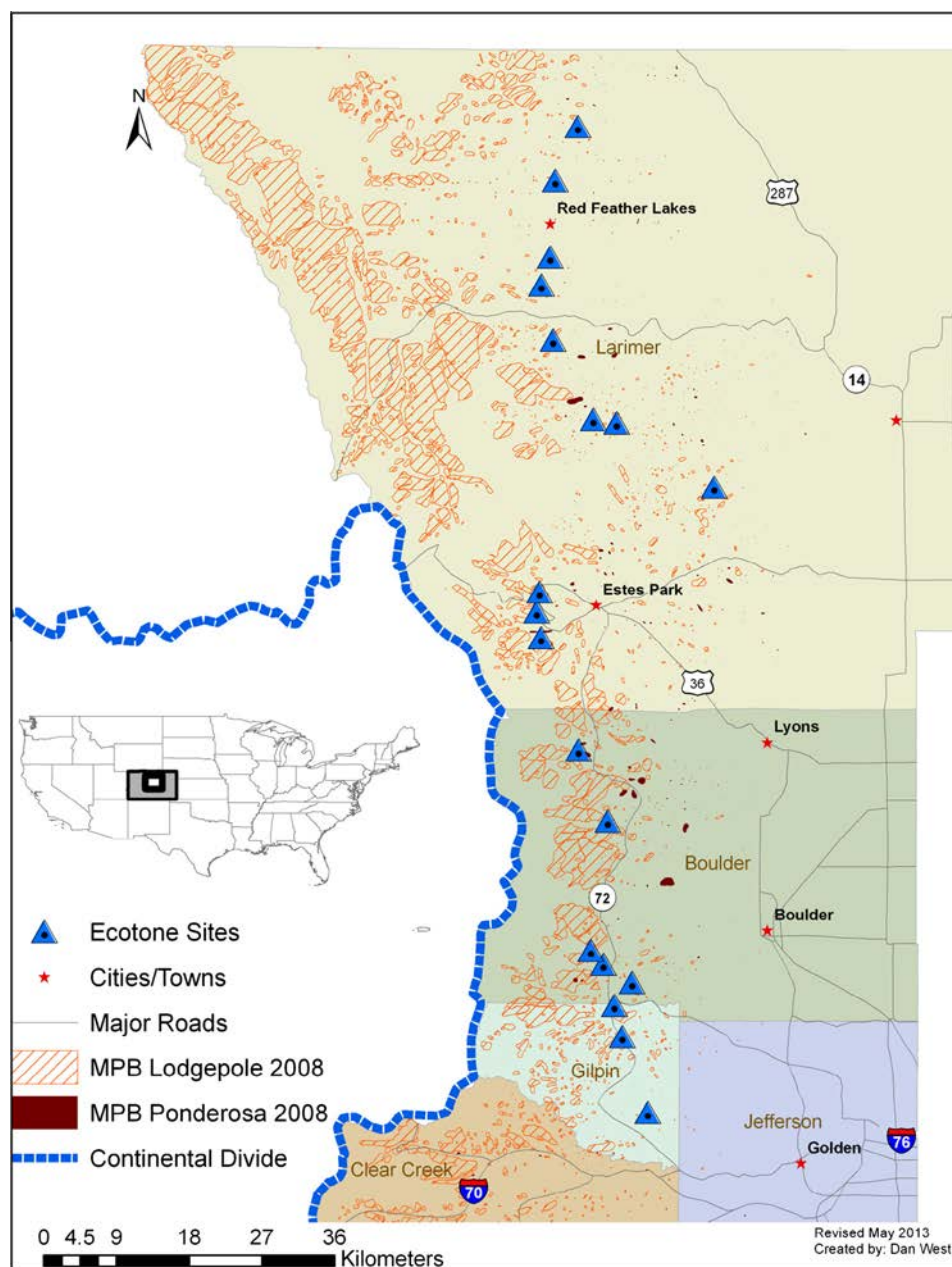
In the forests of Colorado and southern Wyoming, epidemic populations of MPBs killed trees across more than 1.6 million

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hectares between 1996 and 2011 (USFS, 2011). Primarily lodgepole (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson) and ponderosa pines (*Pinus ponderosa* Lawson var. *scopulorum* Engelm.) were killed along with some mortality in limber pine (*Pinus flexilis* James) and bristlecone pine (*Pinus aristata* Engelm.; USFS, 2011). Colorado has approximately 800,000 hectares of ponderosa pine, commonly found from 1800 to 2750 m of elevation, while lodgepole pine occupies about 600,000 hectares between 2450 and 3050 m (CSFS, 2012). East of the Continental Divide in Colorado, the two species overlap in a mixed-conifer 'ecotone' zone on the eastern slopes of the Front Range mountains. These mixed-conifer stands grow at intermediate elevations (between 2450 and 2750 m) and include other conifer species such as Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), limber pine (*P. flexilis* James), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.).

Before 2007, the MPB outbreak in Colorado predominantly affected lodgepole pine forests on the west side of the Continental Divide (Witcosky, 2009). In 2007–2008, Aerial Detection Surveys (ADS) conducted by the U.S. Forest Service and its partners in Colorado documented increasing mortality from MPB in lodgepole-dominated pine forests east of the Continental Divide along the Colorado Front Range (Fig. 1; Witcosky 2008, 2009), raising concerns about the potential spread of MPB populations to ponderosa pine-dominated forests. The Front Range urban corridor contains most of Colorado's major population centers with a rapidly expanding wildland-urban interface; thus, there are significant values at risk from beetle-induced forest mortality (e.g. potential changes in wildfire hazard, hydrologic function, recreational opportunities, and aesthetic values; Binkley and Duncan, 2009; Witcosky, 2009). In 2008, the susceptibility of large tracts of ponderosa pine forest adjacent to infested



**Fig. 1.** Study sites (2009–2011) in the lodgepole–ponderosa pine ecotone along the Front Range, CO. USDA Forest Service and its partners, 2008 Aerial Detection Survey data depicting mountain pine beetle-caused mortality in lodgepole pines and ponderosa pines in 2007.

lodgepole pine- or mixed-conifer stands in the Front Range was largely unknown.

Several major sources of uncertainty were identified regarding the likelihood MPB populations would reach epidemic levels in ponderosa pine as beetle populations progressed eastward from higher elevation lodgepole pine. First, there has been no documentation that previous MPB outbreaks in Colorado moved from one host species to cause epidemic-level mortality in another host. The ADS data for Colorado forests affected by insects and disease between 1956 and 2008 noted numerous MPB outbreaks in either ponderosa or lodgepole pine (USDA Forest Service, Region 2, Forest Health Protection). However, the maps did not identify areas with high levels of mortality resulting from epidemic-level MPB populations in ponderosa pine adjacent to areas of high lodgepole pine mortality in the same or successive years. Biological evaluations by entomologists and annual reports prepared by the same agencies between 1975 and 2005 also did not document infestations that started in either lodgepole or ponderosa pine and then spread into the other host (Cain and Howell, 2005; Lessard et al., 1987; USDA Forest Service, Region 2, Forest Health Management). However, no prior outbreaks on record have attained the magnitude of the recent outbreak that developed in the late 1990s. Recently, evidence of range expansion and potential host transition by the MPB from lodgepole pine to jack pine has been reported from Canada (Cullingham et al., 2011; de la Giroday et al., 2012; Safranyik et al., 2010).

A second major source of uncertainty involved the differences in stand characteristics, such as tree diameters, tree densities, and stand ages between the two pine species in the Colorado Front Range. Previous studies suggest that tree diameter and the density of stands may be associated with different amounts of beetle-caused mortality (Fettig et al., 2007; Safranyik and Carroll, 2006). Greater proportions of MPB attacks during outbreaks have consistently been recorded on trees with >18 cm diameter at breast height (dbh) in many pine species (e.g. Fettig et al., 2007; McCambridge et al., 1982; Negron and Popp, 2004; Preisler and Mitchell, 1993), suggesting the thicker phloem of larger trees represents a better source of food (Safranyik and Carroll, 2006). In the Front Range, lodgepole pine tends to grow in relatively dense, even-aged, small-diameter stands as a result of past stand-replacing fires that trigger uniform regeneration (Knowles and Grant, 1983; Lotan and Perry, 1983). In contrast, ponderosa forests often have a more open, multi-cohort, patchy stand structure which includes trees of diverse diameters and ages (Peet, 1981; Knowles and Grant, 1983; Negron and Popp, 2004). Greater mortality has often been recorded in stands with mean tree ages between 60 and 125 years old (e.g. Bollenbacher and Gibson, 1986; reviewed in Fettig et al., 2007). In Colorado during the 1980's, a survey indicated substantial differences in the size and age distributions of lodgepole and ponderosa pine forests (Knowles and Grant, 1983). Despite a lack of information specific to mixed-conifer stands in the Front Range, these findings suggested the different characteristics of trees and stands of the two pine species in the area might result in differential preferences and host selection behavior by MPB in both mixed-conifer forests (where individuals of both species are present) and adjacent, lower-elevation forests dominated by ponderosa pine.

The third major source of uncertainty regarding potential MPB effects on ponderosa pine was the unknown probability of successful infestation and reproduction by the insects in this host, compared to lodgepole pine. Early observations by A.D. Hopkins suggested that when alternate hosts are available in mixed-conifer pine stands, the MPB will prefer to breed in the host to which it has become adapted (Hopkins, 1916, 1917). According to this hypothesis, MPBs would be unlikely to infest ponderosa pine if they developed in lodgepole pine as their natal host. The

hypothesis is commonly known as Hopkins' Host Selection Principle, and its predictions have generally been supported during previous outbreaks in Colorado in which, as described above, infestations largely remained in their original host species. However, several studies testing or addressing the hypothesis have generated mixed evidence, leaving the principle subject to controversy in recent decades (reviewed in Barron, 2001). Three observational studies in mixed-conifer stands of the Rocky Mountains found higher levels of mortality in the beetles' initial host species than in alternate host species nearby, indicating support for Hopkins' Host Selection Principle (Baker et al., 1971; Dean, 2007; Raffa et al., 2013). However, manipulative experiments in which samples of different pine species were offered to successive generations of the MPB did not find support for the hypothesis (Raffa et al., 2013; Richmond, 1933). In spite of its relevance to forest management decisions when bark beetle outbreaks reach epidemic-population levels where multiple potential host species are present, few empirical tests of Hopkins' Host Selection Principle have been conducted.

In 2009, we initiated an annual field survey in the Colorado Front Range to evaluate whether the MPB would transition from lodgepole pine in high-elevation forests into ponderosa pine in the mixed-conifer ecotone, and threaten adjacent lower elevation ponderosa pine-dominated stands. We addressed four primary questions. First, we asked "Is the amount of MPB-caused mortality in ponderosa pine similar to that in lodgepole pine in the mixed-conifer ecotone?" Second, we compared annual mortality caused by MPB from 2004–2011 in both species to ask "Over time, is one pine host preferred over the other?" Third, to further our understanding of which size classes of trees had sustained mortality in each host, and whether the largest diameter classes were exhausted over time, we asked "What size trees are attacked in each species in each year?" Finally, we asked "Do site factors or stand characteristics affect the amount of MPB-caused mortality in either species?"

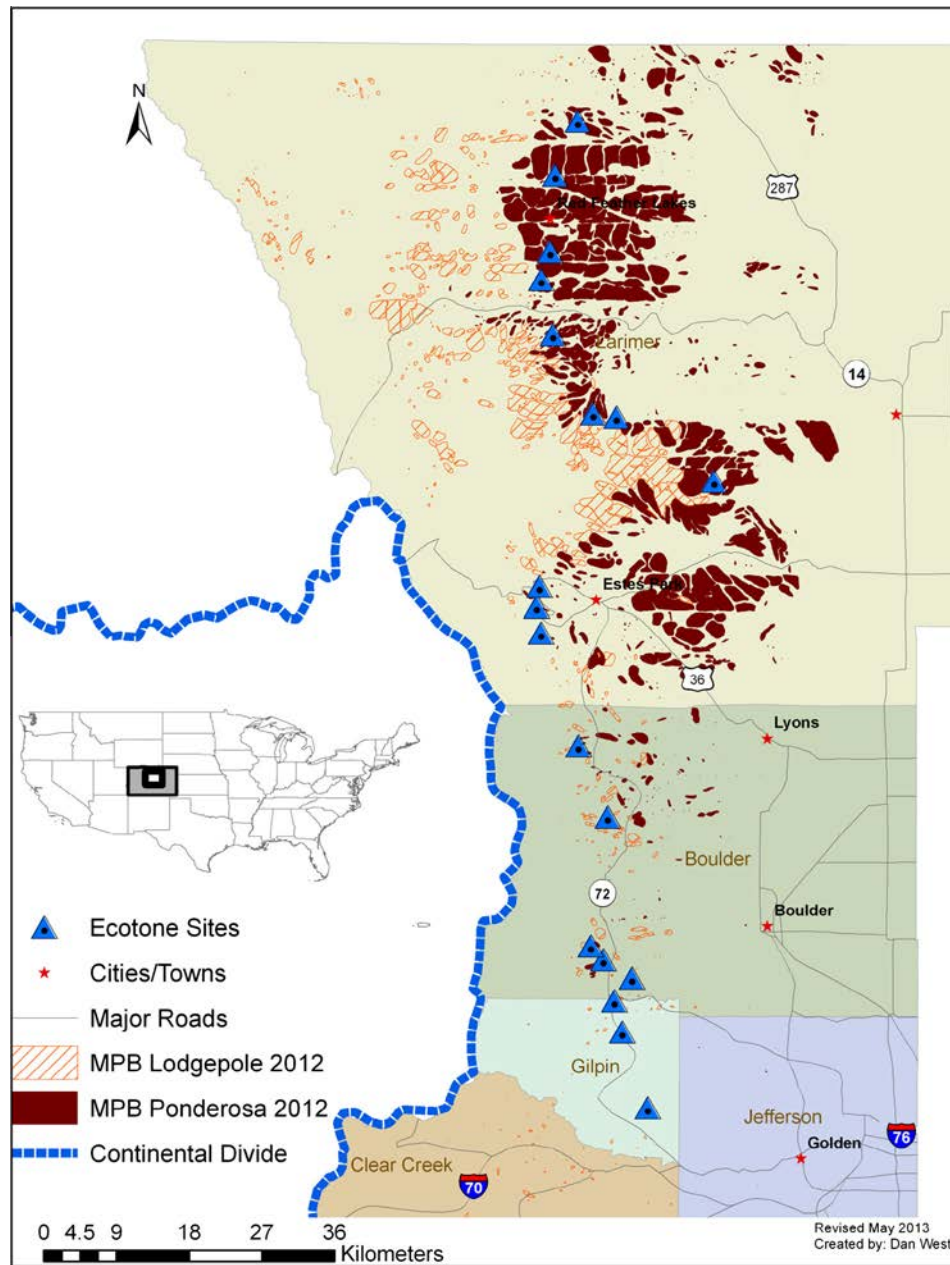
## 2. Methods

We sampled 19 sites in the mixed-conifer lodgepole–ponderosa ecotone spanning approximately 140 km of the northern Front Range, CO (2440–2740 m; Figs. 1 and 2). Sites were established near epidemic-level MPB populations that had migrated eastward from lodgepole-dominated stands. Sites were located on lands managed by the USDA Forest Service, National Park Service, Colorado State Parks, Colorado State Forest Service, and Boulder County Parks and Open Space. We established three 0.2 ha plots (20 m × 100 m) spaced at least 0.8 km apart at each site. At each site, MPBs were active and had attacked several lodgepole pine trees within 5 m of each plot in the previous year.

In each plot, we inspected all trees with dbh > 2.5 cm during four separate surveys. The first survey was conducted in June 2009, prior to the annual MPB flight in 2009, allowing us to record beetle infestations from summer/fall 2008 as well as evidence of any attacks in previous years. Beetle emergence predominantly occurred in mid-July through mid-August throughout our sites and attacks were predominantly completed by mid-September (West, 2013). The second, third, and fourth surveys were conducted after the beetle flight, in September to November of 2009, 2010, and 2011, allowing us to document beetle attacks in those years.

We recorded in each 0.2 ha plot the characteristics of all trees affected by MPB (species, diameter at breast height (1.4 m above forest floor), and other detectable disease presence or insect activity. MPB activity was classified as a mass attack if 360 degrees of the tree's circumference had the presence of pitch tubes and boring





**Fig. 2.** Study sites (2009–2011) in the lodgepole-ponderosa pine ecotone along the Front Range, CO. USDA Forest Service and its partners, 2012 Aerial Detection Survey data depicting mountain pine beetle-caused mortality in lodgepole pines and ponderosa pines in 2011.

dust (frass) at the root collar. If less than 180 degrees of the circumference had the presence of pitch tubes and boring dust at the root collar, and the tree had survived, we recorded a partial (strip) attack. If a tree had been killed by MPBs between 2004 and 2007 (i.e. prior to our initial survey), we estimated the year of death based on the degradation status of needles and fine twigs, as described in Klutsch et al., 2009. If a tree had been attacked in multiple years, the level of attack was recorded for each year as separate beetle populations had infested the tree each year. To characterize the stands at each site, we established three 0.02 ha subplots (radius 8.0 m) within each of the three 0.2 ha survey plots at 0 m, 50 m, and 100 m arranged on a center transect. In these subplots, we recorded dbh and health status (live: uninfested, dead: no MPB evidence, mass attacked or partially attacked by MPBs and/or other agents of disease/mortality) of all trees >2.5 cm dbh. We used these subplot data to calculate stand

attributes (basal area (BA;  $m^2/ha$ ) and trees per hectare (TPH)) and to quantify site characteristics (elevation (m), slope (%), aspect quadrants partitioned by cardinal directions) that could affect MPB activity.

In 2009, the first year of this study, 15 sites (45 plots) were established and surveyed in June–July (pre-MPB flight) and post-MPB flight in 2009–2011 (September–November). Prior to our 2010 fall surveys, forest management activities removed some trees recently infested by MPBs, and (or) healthy trees during stand-level thinning. Because these activities had the potential to alter the MPB populations in or near our monitoring plots, we excluded the affected plots from the study (4 plots on Boulder County Parks and Open Space lands and 1 plot on National Park Service lands). In 2010, we established four additional sites (12 plots) throughout the study area and collected the same data on MPB activity and stand characteristics at these sites, spanning

the same time period (2004–2011). By 2012, we had measured MPB activity from 2004–2011 at a total of 19 sites.

### 3. Data analyses

For each year and site, we calculated the average basal area and trees per hectare from the data collected at the 9 subplots per site in the initial survey year. These data were used to determine how much host type (BA and TPH) of lodgepole and ponderosa pine was available for infestation to the MPB – as well as overall stocking levels for all species. For all data analyses, we quantified MPB activity at each site as the mean TPH or BA per hectare killed by MPB per year, per host species, across the 3 plots. Mortality was quantified at the 0.2 ha plot level, and uninfested stand characteristics were quantified at the subplot level (0.02 ha), to account for the patchy nature of MPB-caused tree mortality within the plots.

To test for differences in MPB impacts among years between lodgepole and ponderosa pine, we used a mixed model approach (Proc Glimmix, SAS) comparing annual mean MPB-caused mortality in the two species (percentage of BA killed). We treated species, year, and the species\*year interaction as fixed effects and site as a random effect. We averaged the annual mortality from 2004–2007 across all sites to represent the pre-outbreak mortality caused by MPB before populations reached epidemic levels in the Front Range (Witcosky, 2008). We compared the mortality we measured in each year from 2008 through 2011 to the pre-outbreak incipient-epidemic populations and mortality levels recorded in 2004–2007 and each subsequent year's mortality. Thus, our analyses focused on 5 time periods: average annual mortality from 2004–2007; and mortality recorded in 2008, 2009, 2010, and 2011. Due to skewness in the distributions of MPB-caused tree mortality over time, square root transformations were performed prior to analyses. Means were back-transformed for presentation. Upper and lower confidence bounds (half Least Significant Differences (LSDs;  $1.4 \times \text{Standard Error (SE) of the mean}$ ) were calculated from square root back-transformed ( $\text{mean} \pm 1/2 \text{ LSD}$ ) values to compare mortality between years in both species.

To assess the diameter of trees MPB preferentially selected over time, we compared the diameter of MPB-killed trees at each plot (3 per site), in each year, using a mixed model, treating host species and year as fixed effects (Proc Glimmix, SAS). We performed a linear contrast of diameter distributions over the last four years (2008–2011) to test whether sizes of killed trees decreased over time, compared to the size of trees killed when MPB populations were at background levels prior to 2008 (2004–2007). Tree diameters were  $\log_{10}$ -transformed prior to analysis and back-transformed for presentation of results, as previously described.

To determine which factors were associated with MPB-caused mortality levels (basal area;  $\text{m}^2/\text{ha}$ ) at each plot in either respective response variable of ponderosa or lodgepole pine in a given year

( $t$ ), and if site factors impacted MPB-caused mortality in either tree species, we used a mixed model (Proc Glimmix, SAS) with the following fixed effects: basal area of uninfested ponderosa and lodgepole pine at the start of our survey, total basal area of all species in plots (live and standing dead), basal area of all species in the plots other than pines, previous year's MPB-caused mortality levels (basal area) in both lodgepole and ponderosa pine species ( $t - 1$ ), year of infestation, plot slope, aspect, and elevation. To reduce the influence of high leverage points due to skewed values within the distribution of available basal area and MPB-caused mortality in ponderosa and lodgepole pines prior to attack, we performed  $\log_{10}$ -transformations on these variables. Upper and lower confidence bounds were calculated from  $\log_{10}$  back-transformed values ( $\text{mean} \pm 1/2 \text{ LSD}$ ). Mortality estimates were back-transformed from the  $\log_{10}$  values for presentation of the results. This descriptive model was not validated with an additional dataset, which limits its predictive capability to estimate exactly how much mortality could be expected in a given location outside of the parameters of the study.

### 4. Results

Live tree basal area in our plots at the start of the study was dominated by lodgepole pine (41%) and ponderosa pine (33%; Table 1). All sites exhibited MPB-caused mortality in at least one of the three plots per site in both lodgepole and ponderosa pine over the surveyed periods (Table 2). Our comparison of MPB-caused mortality in lodgepole pine to ponderosa pine over the course of five time periods (2004–2007, 2008, 2009, 2010, 2011) indicated differences in percent basal area killed between time periods ( $P = 0.0014$ ,  $F_{1, 4} = 3.32$ ; Fig. 3), but not between species ( $P = 0.07$ ,  $F_{1, 4} = 4.65$ ). There were no species\*time interactions ( $P = 0.41$ ,  $F_{1, 4} = 0.99$ ). The mean of the cumulative percent mortality across all sites and measurement periods in both lodgepole and ponderosa pine was 38% of the original pine basal area. The mean of the cumulative mortality (2004–2011) of ponderosa pine across the different sites was 37.9% and ranged from 1% to 100%, while lodgepole pine was 39.0% across the different sites with a similar range from 8% to 94%. Annual percent mortality for combined lodgepole and ponderosa pine in 2004–2007 (2.4%) was not different from that in 2008 (6.5%), 2010 (5.2%), and 2011 (5.2%), though mortality was significantly greater in 2009 (11.4%) than all other time periods observed (Fig. 3).

The MPB attacked smaller diameter lodgepole pine (24.8 cm) trees compared to ponderosa pine (27.5 cm) ( $P = 0.0002$ ,  $F_{1, 275} = 13.8$ ; Table 3). The attacked tree sizes ranged from 15.2 cm to 51.3 cm for lodgepole and 14.5 cm to 57.4 cm for ponderosa pine. At the onset of our surveys, the average uninfested lodgepole pine diameter was 19.7 cm, while the average uninfested ponderosa pine diameter was 23.5 cm. We found overall

**Table 1**

Live trees per hectare and basal areas ( $\text{m}^2/\text{ha}$  greater than 2.5 cm diameter at 1.4 m) in 2008 across 19 Front Range, CO. sites.

Species	TPH <sup>a</sup>	Std Error	BA $\text{m}^2/\text{ha}$ <sup>b</sup>	Std Error	DBH <sup>c</sup>	Std Error
<i>Pinus contorta</i>	396	35.8	12.1	0.8	19.7	0.6
<i>Pinus ponderosa</i>	212	23.9	9.7	0.8	23.5	1.1
<i>Pinus flexilis</i>	80	18.8	1.2	0.3	13.4	1.5
<i>Pseudotsuga menziesii</i>	124	31.2	2.9	0.5	16.7	1.4
<i>Picea engelmannii</i>	54	21.7	2.2	1.2	20.1	1.9
<i>Abies lasiocarpa</i>	49	16.5	0.3	0.1	8.1	2.3
<i>Populus tremuloides</i>	128	25.8	1.1	0.3	11.4	1.1
<i>Juniperus scopulorum</i>	17	0.0	0.1	0.1	9.1	2.8

<sup>a</sup> Mean trees per hectare calculated from 3 plots per site ( $n = 57$ ).

<sup>b</sup> Basal area; square meters per hectare calculated from 3 plots per site ( $n = 57$ ).

<sup>c</sup> Diameter at 1.4 m (centimeters).

**Table 2**

Average live uninfested and average site cumulative mountain pine beetle (*Dendroctonus ponderosae*)-caused mortality (2004–2011) in *Pinus contorta* (lodgepole pine) and *Pinus ponderosa* (ponderosa pine) within Front Range, CO. Sites ( $n = 19$ ) are ordered north to south (see Figs. 1 and 2). Sites comprised 3–0.20 ha plots in the lodgepole-ponderosa pine ecotone.

Site	Lodgepole pine – <i>P. contorta</i>								Ponderosa pine – <i>P. ponderosa</i>							
	Live Stand Ba <sup>a</sup>	SE	BA Prop. killed	Live Stand TPH <sup>b</sup>	Live Stand Dbh <sup>c</sup>	SE	Infested Dbh <sup>d</sup>	SE	Live Stand Ba <sup>a</sup>	SE	BA Prop. killed	Live Stand TPH <sup>b</sup>	Live Stand Dbh <sup>c</sup>	SE	Infested Dbh <sup>d</sup>	SE
Sheep Creek	9.5	4.6	0.81	472	13.3	0.2	25.4	1.6	14.4	8.7	0.56	329	21.0	0.6	27.1	1.0
Creedmore Lake	10.5	3.8	0.94	362	16.7	3.5	25.0	1.5	12.8	2.0	0.77	390	20.2	3.6	25.6	2.2
Molly Lake	12.5	0.4	0.31	494	16.6	0.6	22.4	1.5	10.3	1.0	0.49	313	21.7	6.8	26.1	3.5
Manhattan Rd	9.2	3.9	0.32	280	17.9	3.3	30.5	3.9	9.6	0.9	0.59	209	20.4	0.2	29.8	2.7
Bennett Creek	12.1	2.2	0.68	264	22.5	1.1	25.6	1.4	9.4	2.3	0.68	165	25.0	1.8	31.1	1.2
Pennock Pass N	18.2	5.2	0.50	587	21.7	3.2	23.3	3.0	6.3	2.3	0.48	121	22.1	3.3	30.0	2.6
Pennock Pass S	17.7	6.2	0.41	642	17.3	1.1	23.4	0.7	5.7	1.0	0.66	165	19.2	2.1	19.7	9.9
Stringtown	8.8	0.7	0.40	247	19.5	2.1	24.7	0.9	4.1	0.7	0.07	104	20.6	7.7	9.0	9.0
Horseshoe Park	10.7	0.8	0.77	225	23.7	1.8	27.2	2.4	7.4	2.1	1.09	170	29.8	10.3	28.7	1.8
Upper Beaver Meadows	10.6	2.0	0.36	313	20.5	1.0	23.6	1.5	17.7	0.9	0.58	362	22.9	1.4	27.0	2.5
Hollowell Park	13.6	1.3	0.36	373	20.0	1.2	26.9	1.4	9.3	1.6	0.69	82	39.2	4.6	37.2	1.7
Wildbasin	5.0	1.5	0.52	104	24.4	3.4	25.0	1.9	16.8	4.0	0.04	412	22.9	2.9	24.3	2.2
Prescott	12.1	5.9	0.16	351	21.6	3.2	32.9	3.4	5.1	3.7	0.08	77	17.3	9.3	18.2	9.3
Reynolds Ranch <sup>‡</sup>	10.2	4.1	0.08	274	22.5	3.4	26.0	1.7	9.3	5.7	0.04	132	24.2	1.7	20.2	11.8
Delonde Meadows	11.7	5.0	0.16	357	23.8	5.0	25.5	4.2	14.4	2.4	0.01	357	23.9	4.5	6.4	6.4
Mud Lake	17.2	1.9	0.13	747	16.0	0.6	21.4	2.0	9.1	4.3	0.10	187	22.2	1.3	16.8	8.5
Lump Gulch	15.8	6.2	0.10	681	16.5	1.2	25.5	0.5	11.9	4.8	0.10	274	23.6	3.3	7.3	7.3
Kelly Dahl	12.4	2.7	0.25	406	17.7	2.1	26.8	2.2	8.6	2.2	0.05	137	26.0	2.0	13.4	13.4
Green Ranch	12.1	0.8	0.14	351	21.9	4.8	27.5	3.9	2.5	0.4	0.13	49	24.0	3.4	9.4	9.4
Average	12.1		0.39	396	19.7		25.7		9.7		0.38	212	23.5		21.4	

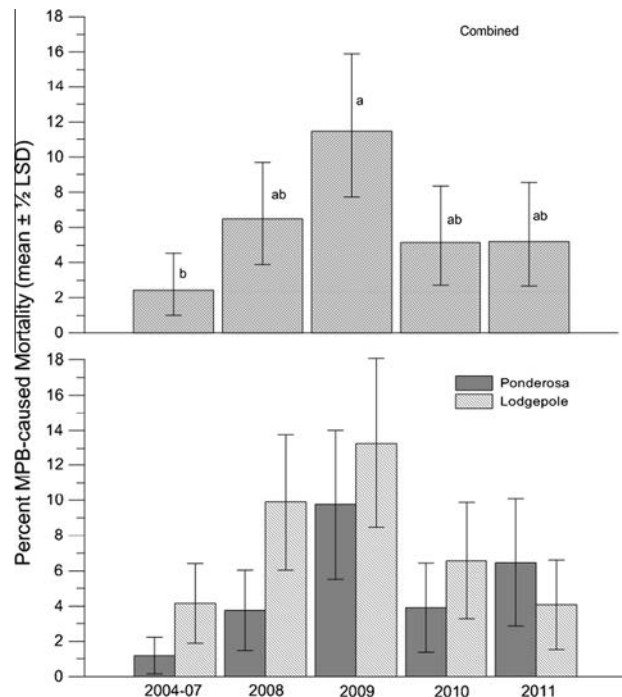
<sup>‡</sup> Site excluded beginning in 2010 due to management activities.

<sup>a</sup> Mean basal area, square meters per hectare of trees >2.5 cm from 3 plots per site in 2004.

<sup>b</sup> Mean trees per hectare >2.5 cm diameter breast height from 3 plots per site in 2004.

<sup>c</sup> Average diameter at breast height (1.4 m) in centimeters of uninfested trees >2.5 cm from 3 plots per site in 2004.

<sup>d</sup> Average diameter at breast height (1.4 m) in centimeters of MPB infested trees from 3 plots per site (2004–2011).



**Fig. 3.** Annual percent basal area ( $\text{m}^2/\text{ha}$ ; mean  $\pm \frac{1}{2}$  LSD) of mountain pine beetle-caused mortality of that year's available uninfested lodgepole and ponderosa pine basal area in 2004–2011 along the Front Range, CO. Differing letters indicate significant differences between years for the combined pine species ( $\alpha = 0.05$ ). No differences were detected within a given year between pine species.  $n = 19$  sites with 57 plots; 3 plots per site.

differences between infested tree diameters across years ( $P = 0.01$ ,  $F_{4, 275} = 3.3$ ), but no interactions between species and year ( $P = 0.68$ ,  $F_{4, 275} = 0.6$ ). From 2008 to 2011, the diameters of

infested trees of both species decreased significantly (linear contrast  $P = 0.0005$ ,  $F_{1, 275} = 13.8$ ).

Our analysis of which factors influenced the current year's ( $t$ ) mortality in ponderosa pine revealed that the basal area infested in the previous year ( $t - 1$ ) in both ponderosa pine ( $P = 0.007$ ,  $F_{1, 221} = 7.47$ ) and lodgepole pine ( $P = 0.009$ ,  $F_{1, 221} = 6.96$ ) were significant factors. In addition, the available uninfested basal area in ponderosa pine ( $P = 0.017$ ,  $F_{1, 221} = 5.8$ ) and the year ( $P = 0.0007$ ,  $F_{3, 221} = 5.9$ ) were also significant overall predictors of MPB-caused mortality in a given year in ponderosa pine (Table 4; Fig. 4). No other site or stand variables were significant predictors of the current year's ponderosa pine mortality. In comparison, the basal area of the current year's MPB-caused mortality in lodgepole pine ( $t$ ) was influenced by the previous year's ( $t - 1$ ) infested basal area of only lodgepole pine ( $P < 0.0001$ ,  $F_{1, 221} = 29.5$ ); the covariates of year ( $P < 0.0001$ ,  $F_{3, 221} = 18.6$ ) and the available lodgepole pine and ponderosa pine basal areas ( $P = 0.007$ ,  $F_{1, 221} = 7.5$ ;  $P = 0.03$ ,  $F_{1, 221} = 4.5$ , respectively) were also significant. No other site or stand factors were significant predictors of the current year's lodgepole pine mortality.

## 5. Discussion

In answer to our first question, we found similar annual levels of MPB-caused mortality (infested basal area/uninfested basal area) in ponderosa and lodgepole pine in each survey period (2004–2007, 2008, 2009, 2010, and 2011) which differ from findings of previous observational studies. These studies reported higher levels of mortality in the host species in which an outbreak began, compared to the mortality experienced by alternate hosts in the same stands (Baker et al., 1971; Dean, 2007; Raffa et al., 2013). Our results also diverge from reports and observations made over many previous decades by aerial surveyors and professional

**Table 3**

Average diameter (cm) of mountain pine beetle-caused lodgepole and ponderosa pine mortality by year along the Front Range, CO. Differing letters (a,b) indicate significance at  $\alpha = .05$  of the combined yearly means derived from a linear contrast between years and species. Differing letters (c,d) between the overall mean of mountain pine beetle-caused mortality indicate significance at  $\alpha = .05$  from a mixed model. No significant differences were detected between species within a given year.  $n = 57$  plots. Mean (lower LSD, Upper LSD).

	2004–2007	2008	2009	2010	2011	Overall mean
Lodgepole pine	25.8 (24.5, 27.1)	26.5 (25.3, 27.7)	25.5 (24.4, 26.6)	24.8 (23.4, 26.3)	21.8 (20.4, 23.3)	24.8 (24.2, 25.4) <sup>c</sup>
Ponderosa pine	26.5 (24.6, 28.5)	29.4 (27.7, 31.2)	28.0 (26.5, 29.6)	28.0 (26.1, 30.0)	25.8 (23.9, 27.9)	27.5 (26.7, 28.3) <sup>d</sup>
Combined Yearly Mean	26.1 (25.0, 27.3) <sup>a</sup>	27.9 (26.9, 29.0) <sup>a</sup>	27.0 (25.8, 27.7) <sup>a</sup>	26.3 (25.1, 27.6) <sup>a</sup>	23.7 (22.5, 25.0) <sup>b</sup>	

**Table 4**

Mixed model regression effects for estimating the current year's mountain pine beetle-caused pine mortality (lodgepole and ponderosa pine basal areas (BA);  $m^2/ha$ ) in response to the previous year's mountain pine beetle-caused mortality in ponderosa pine and/or lodgepole pine, with the available pine basal area by year (2008–2011).

Effect	Coeff	Num DF	Den DF	P value
<i>Response = Ponderosa pine</i>				
Intercept	−0.9598			
$\log_{10}$ Previous year ponderosa BA	0.2191	1	221	0.007
$\log_{10}$ Previous year lodgepole BA	0.2020	1	221	0.009
$\log_{10}$ Ponderosa uninfested BA	0.2737	1	221	0.017
Year		3	221	0.0007
	Coeff	LS Means		
2008	0.1486	−1.3776		
2009	0.3358	−1.1904		
2010	−0.2055	−1.7318		
2011	0	−1.5263		
Pearson $X^2/DF$ fit statistic = 0.54				
The average lagged $\log_{10}$ lodgepole and median available $\log_{10}$ ponderosa used in graphing were −1.2302 and 0.1955, respectively.				
Effect	Coeff	Num DF	Den DF	P value
<i>Response = Lodgepole pine</i>				
Intercept	−1.1641			
$\log_{10}$ Previous year lodgepole BA	0.3300	1	221	<0.0001
$\log_{10}$ Ponderosa uninfested BA	0.2775	1	221	0.007
$\log_{10}$ Lodgepole uninfested BA	0.3494	1	221	0.034
Year		3	221	<0.0001
	Coeff	LS Means		
2008	0.5157	−0.9483		
2009	0.5157	−0.9483		
2010	−0.0846	−1.5486		
2011	0	−1.4640		
Pearson $X^2/DF$ fit statistic = 0.32				

entomologists in Colorado who have not documented significant movement of MPB among hosts in previous outbreaks (Cain and Howell, 2005; Lessard et al., 1987; Witcosky, 2008, 2009). Although the future trajectory of MPB populations in our study area is uncertain, ADS data show a considerable decrease in the number of acres of forest annually infested by MPB in Colorado in the 2 years following our surveys, suggesting that our study captured years of peak mortality in the current outbreak and can be legitimately compared to studies conducted during past outbreaks. One other recent field study found similar results in British Columbia, where high levels of MPB-induced mortality were found in ponderosa pine (72% average mortality) and suggested beetles from nearby lodgepole stands had initiated the infestation (Klenner and Arsenaault, 2009). Our results also align with those of an early laboratory study of host selection in the MPB (Richmond, 1933) and a more recent field experiment (Cerezke, 1995) in which insects infested cut sections of trees of different species in relatively equal proportions.

Our second research question addressed whether one host species was preferred throughout the course of the outbreak or

whether species preference changed through time. Based on the similar levels of annual mortality and total mortality (38–39% of the initial uninfested basal area) between lodgepole vs. ponderosa pine, we concluded that MPB did not demonstrate a clear host preference in the context of this field study. Although we could not track the natal host species of beetles infesting each new host tree, annual mortality data (ADS, USDA Forest Service) indicate that much greater proportions of lodgepole pine than ponderosa pine were progressively killed in areas adjacent to our study sites prior to our surveys. Contrary to the predictions of Hopkins' Host Selection Principle, beetles did not continue to infest lodgepole pine in consistently greater proportions than ponderosa pine over time. They also did not cause significantly greater mortality in ponderosa than lodgepole pine. To address host selection dynamics fully, additional field-based studies (e.g. a mark/recapture experiment with parental beetle identification in selected trees), and/or a population-level genetic analysis beyond the scope of our study would be needed to confirm natal host species of beetles infesting ponderosa vs. lodgepole pine over time. However, recent MPB host selection behavior experiments found beetles infested ponderosa



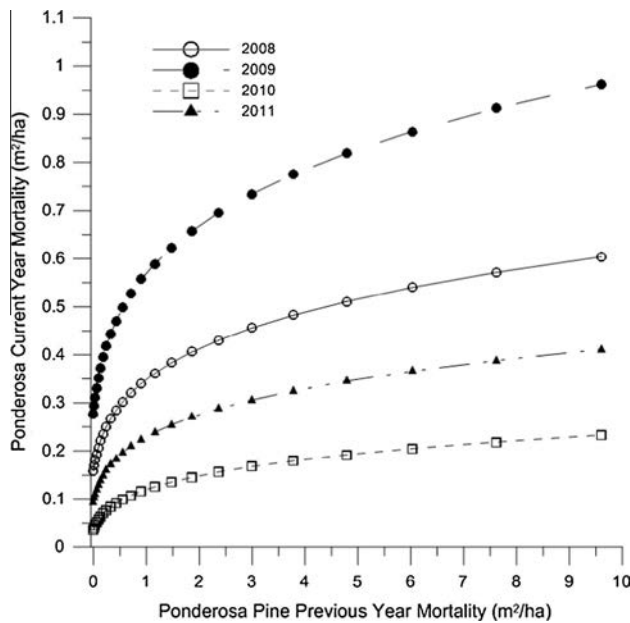


Fig. 4. Response curve for the current year's basal area of ponderosa pine mountain pine beetle-caused mortality in response to the lagged (previous year) basal area of mountain pine beetle infested ponderosa pine, with the average previous years' mountain pine beetle infested lodgepole pine basal area, and available uninfested median ponderosa pine by year (2008–2011; see Table 4).

pine cut logs at a rate of 2:1 (over lodgepole pine) after completing their natal development in lodgepole (West, 2013).

Some aspects of our results indicated differences in mountain pine beetles' selection patterns between the two host species over time. Our modeling found that significant predictors of mortality of each year's infested basal area for each species included the previous year's infested basal area of lodgepole pine (for both species) and the previous year's infested basal area of ponderosa pine (for ponderosa pine only.) This may reflect MPB movement from lodgepole pine natal hosts into ponderosa pine, but not movement from ponderosa pine natal hosts into lodgepole pine. However, we emphasize that neither our field study nor those of other researchers (Baker et al., 1971; Dean, 2007; Klenner and Arsenault, 2009; Raffa et al., 2013) were able to directly examine MPB host selection behavior and outcomes under natural conditions. We initiated controlled experiments in both the field and laboratory to investigate these processes in more detail (West, 2013).

Our third question asked what size trees were attacked in each species in each year. We found the diameter of trees attacked in both species across years was between 21 and 29 cm. There were no significant differences between species in dbh of attacked trees per year (Table 3). The mean dbh of all attacked trees was slightly, although significantly, greater for ponderosa pine than for lodgepole. However, the uninfested stand diameter was also slightly greater for ponderosa pine than for lodgepole (23.5 cm  $\pm$  0.4 vs. 19.7 cm  $\pm$  0.2 (mean  $\pm$  SE), respectively), which could account for the slight differences we detected in infested diameters between the two species. Relatively large diameter trees are the preferred size class for the MPB during outbreaks in many pine hosts (Fettig et al., 2007; Raffa et al., 2008; Safranyik and Carroll, 2006). The diameters of infested trees in our study area prior to 2008 (lodgepole: 25.8 cm; ponderosa: 26.5 cm) were larger than the uninfested tree diameters (lodgepole: 19.7 cm; ponderosa: 23.5 cm). By 2011, the average of the cumulative infested dbh across sites was greater than the stand average dbh for lodgepole pine at all sites (Table 2). For ponderosa pine, the average of the cumulative infested dbh across sites was greater than the stand

average at 10 of the 19 sites, with the greatest variability occurring at locations with low infested basal area. Overall, the results showed fairly similar use of dbh size classes on average in both species over time (Table 3), despite somewhat variable infestation patterns among sites for ponderosa pine. In contrast, Dean (2007) found that MPB consistently attacked significantly larger size classes of limber pine than lodgepole pine for 3 years at her study sites, and speculated that this represented a strong host preference over time. However, a greater proportion of larger limber pines than lodgepole pines were available for attack at her sites. In our study, the availability of slightly larger ponderosa pines could have influenced the host selection behavior of the MPBs; this factor would merit further investigation. Possibly the role of tree diameter in MPB host selection behavior could account for conflicting results between previous lab- and field-based studies (e.g. the lab results of Richmond (1933), vs. the field results of Baker et al. (1971) and Dean (2007)).

In answer to our final question about the role of stand characteristics in predicting pine mortality, we identified several significant relationships. For lodgepole pine, infestation levels increased with both the amount of basal area of lodgepole pine available for infestation, and the amount of uninfested ponderosa pine basal area. For ponderosa pine, infestation increased with the amount of uninfested basal area of only ponderosa pine. The total basal area of all conifer species present in the stands was not a significant predictor of mortality for either host species. In general, these findings support those of previous studies that found a positive relationship between the density or basal area of host trees and the amount of mortality (Fettig et al., 2007 and references therein; Safranyik and Carroll, 2006). However, no information exists on the relationship between stand conditions and MPB impacts in forest types with more than one host, leaving susceptibility in the mixed-conifer zone difficult to predict. Our results suggest both lodgepole and ponderosa pines are susceptible when growing in sympatry during a single MPB outbreak. In ponderosa pine-dominated stands, Negron and Popp (2004) identified a 50% greater probability of infestation when basal area exceeded 17 m²/ha, while Bollenbacher and Gibson (1986) suggested lodgepole pine-dominated stands with 29.8 m²/ha were susceptible for increased mortality. Our sites had an average combined basal area for lodgepole and ponderosa pine of 21.8 m²/ha, with 12.1 m²/ha in lodgepole pine and 9.7 m²/ha in ponderosa pine (Table 2). Considering each species individually, stocking levels were not high enough to appear susceptible to high mortality based on previous single-species studies, but the combined basal area for both pines fell into the susceptible range at most sites. Our results indicate that under the conditions of our study, total pine basal area (both lodgepole and ponderosa pines) predicted mortality for lodgepole pine, and uninfested ponderosa pine basal area predicted mortality for ponderosa pine.

Several factors acting individually or in concert may have influenced the patterns of mortality we found, but our analyses indicated that the site characteristics we measured (slope, aspect, and elevation) did not play a significant role. Other abiotic factors, such as seasonal temperatures, patterns and amount of precipitation, and soil moisture, may have been instrumental in enhancing MPB survival and population expansion, altering tree physiology such that tree defenses were weakened, or both (Raffa et al., 2008; Chapman et al., 2012; Simard et al., 2012). Direct measurement of these abiotic variables was beyond the scope of our field study, but a recent analysis in Colorado identified strong synchronization of MPB-induced mortality in lodgepole pine with patterns of drought over the past 2 decades (Chapman et al., 2012). The amount and chemical composition of the oleoresin that trees produce to resist attack by beetles is affected by physiological stress (Raffa et al., 2008; Lusebrink et al., 2011). Thus, the defense



systems of several species of pine can be compromised after certain thresholds of temperature- or moisture-related stress are exceeded (Raffa et al., 2008; Millar et al., 2012; Six et al., 2014). Lack of effective tree defenses in both species in our field study at sites recently stressed by drought and with high populations of beetles may explain the similarity between our findings and those of Klenner and Arsenault (2009) in the recent outbreaks, as well as the similarity between our findings and those of previous experimental studies (Cerezke, 1995; Richmond, 1933; Wood, 1963) in which no tree defenses were present in the cut sections of alternate host tree species that insects infested.

The results from this study have several potential implications for management of pine forests in the Front Range, as well as in other forests containing several host species that are threatened by epidemic levels of MPB. On average, we found similar infestation of both lodgepole and ponderosa pine hosts, suggesting that under the conditions of our study, including substantial drought, beetles did not differentiate between the two species and were able to overcome the defenses of large-diameter trees in both hosts. In both species, we found that on average, the amount of mortality increased when the previous year's infestation levels were low (Fig. 4). For example, when average basal areas from the previous year's ponderosa pine beetle-caused mortality were 0–0.9 m<sup>2</sup>/ha, the next years predicted ponderosa pine mortality basal areas ranged from 0.08 to near 0.28 m<sup>2</sup>/ha. When the previous year's beetle-caused mortality levels were much greater (e.g. 7.6–9.6 m<sup>2</sup>/ha), the next year's mortality basal areas were predicted between 0.01 to near 0.05 m<sup>2</sup>/ha, representing a “tapering off” effect in highly impacted areas over time. It may also be of particular interest to land managers that MPB-caused mortality only significantly increased more than background levels (2004–2007) in both hosts for a single year rather than lasting multiple years (Fig. 3). Given that lodgepole and ponderosa pines were attacked and subsequently killed in similar proportions suggests that within the parameters of the study (consecutive years of drought with subsequent epidemic-level MPB populations in the mixed-pine transition forests of variable age/densities of the Front Range), there is no evidence that favoring or promoting either pine species over the other in terms of retention, planting, etc. within the mixed-pine zones will provide for enhanced resilience to future MPB attack. Awareness of these dynamics may help forest managers and landowners prepare for probable impacts of outbreaks that begin in either host.

However, we note two caveats relevant to future management considerations. First, although we found larger-diameter trees were attacked in both species over time, there was not a complete loss of trees in any size class across the different sites. Considerable basal area and numbers of large trees remain, even at the sites which experienced greatest mortality (Table 2). Second, among the sites there was considerable variation in beetle-induced mortality in both host species throughout the study (Table 2). Chapman et al. (2012) also identified variable patterns of infestation of ponderosa pine compared to lodgepole pine in Colorado in recent decades, although the time series of ADS data they analyzed ended soon after our field study began. ADS maps for 2007 and 2011 (Figs. 1 and 2) show that expansion of MPB-affected areas in ponderosa pine forest varied across the study area. It is not clear which factors were responsible for this variation and what the future trends may be in this region as environmental conditions and host availability change over time. As other studies have found, assessments of beetle “pressure” at the landscape scale (defined in terms of a site's proximity to recently infested areas; Chojnacky et al., 2000; Simard et al., 2012) will help refine predictions of the probable effects of MPB at the site- and stand scales we examined (Chapman et al., 2012; Simard et al., 2012). To be most effective, management plans would ideally incorporate metrics of

beetle pressure across the landscape, among sites, and within stands (Simard et al., 2012). A primary contribution of our study was to demonstrate that at all of these scales, the MPB can, and in future may continue to, cause similar impacts in two host species during a given epidemic.

The findings within this study reinforce the emphasis of several recent studies and reviews (Chapman et al., 2012; Raffa et al., 2008; Simard et al., 2012; Six et al., 2014) that drivers of MPB dynamics act at numerous spatial and temporal scales. Environmental conditions, host availability, and host condition all need to align before MPB populations are able to increase, erupt into epidemic levels, and expand across a landscape (Raffa et al., 2008). The hypothesized links between warming climate trends, annual MPB survival, and decrease in tree defenses may increase the vulnerability of all host species to the MPB (Bentz et al., 2010; Safranyik et al., 2010).

Although we report the first clear evidence of similar mortality caused by MPB in two pine host species over several years of natural growing conditions in the field, in this setting we could not track important consequences such as the insects' relative reproductive success in the two hosts, the future host selection by brood emerging from ponderosa pine, the fitness of offspring that developed in both species, and other factors reflecting the two hosts' respective short- and long-term “quality”. To evaluate these processes, we initiated more detailed studies examining host selection behavior, tree defenses, and reproductive success of MPB under controlled experimental conditions (West, 2013). As other studies document dispersal of MPB into areas with “naïve” hosts beyond their known or typical range (Safranyik et al., 2010; Cudmore et al., 2010; de la Giroday et al., 2012; Raffa et al., 2013) and report longer-term, broader-scale trends toward a warmer and drier climate in many parts of the insect's current range (Bentz et al., 2010; Evangelista et al., 2011), our findings add to a growing body of evidence that interactions between the MPB and its hosts may involve dynamics and effects that have not been documented in the past.

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