Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado

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A B S T R A C T

Lodgepole pine (*Pinus contorta* Dougl. ex Loud.)-dominated ecosystems in north-central Colorado are undergoing rapid and drastic changes associated with overstory tree mortality from a current mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak. To characterize stand characteristics and downed woody debris loads during the first 7 years of the outbreak, 221 plots (0.02 ha) were randomly established in infested and uninfested stands distributed across the Arapaho National Forest, Colorado. Mountain pine beetle initially attacked stands with higher lodgepole pine basal area, and lower density and basal area of Engelmann spruce (*Picea engelmannii* [Parry]), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt. var. *lasiocarpa*) compared to uninfested plots. Mountain pine beetle-affected stands had reduced total and lodgepole pine stocking and quadratic mean diameter. The density and basal area of live overstory lodgepole declined by 62% and 71% in infested plots, respectively. The mean diameter of live lodgepole pine was 53% lower than pre-outbreak in infested plots. Downed woody debris loads did not differ between uninfested plots and plots currently infested at the time of sampling to 3 or 4–7 years after initial infestation, but the projected downed coarse wood accumulations when 80% of the mountain pine beetle-killed trees fall indicated a fourfold increase. Depth of the litter layer and maximum height of grass and herbaceous vegetation were greater 4–7 years after initial infestation compared to uninfested plots, though understory plant percent cover was not different. Seedling and sapling density of all species combined was higher in uninfested plots but there was no difference between infested and uninfested plots for lodgepole pine alone. For trees ≥2.5 cm in diameter at breast height, the density of live lodgepole pine trees in mountain pine beetle-affected stands was higher than Engelmann spruce, subalpine fir, and aspen, (*Populus tremuloides* Michx.), in diameter classes comprised of trees from 2.5 cm to 30 cm in diameter, suggesting that lodgepole pine will remain as a dominant overstory tree after the bark beetle outbreak.

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1. Introduction

Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) is among the most widely distributed conifers in the western USA, comprising about 6 million hectares (Lotan and Critchfield, 1990). From Alaska to south Baja California and from the Pacific coast east to the Black Hills of South Dakota, lodgepole pine exhibits great ecological variability (Lotan and Critchfield, 1990). Various disturbance agents shape the structure and composition of lodgepole pine forests including fire (Clements, 1910; Romme, 1982; Lotan and Perry, 1983), blowdown (Mason, 1915; Alexander, 1964, 1967; Veblen et al., 1989), mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks (Roe and Amman, 1970; Amman, 1977), and dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) infestations (Hawksworth and Graham, 1963; Hawksworth and Hinds, 1964).

Mountain pine beetle at endemic population levels utilize diseased, lightning-struck, and senescing trees, among others, as refugia. Under favorable climatic and stand conditions, population densities of this bark beetle can increase rapidly and cause extensive tree mortality in mature lodgepole pine forests (Fettig

et al., 2007). The occurrence of favorable conditions for insect population growth or unfavorable conditions for trees, such as drought stress, or both, can cause eruptive bark beetle populations. It is well documented that lodgepole pine stand susceptibility to mountain pine beetle is related to factors such as stand density, basal area, and tree diameter (Amman, 1977; Amman and Logan, 1998). Larger diameter trees have thick phloem, which offers the insect a more suitable environment for population growth (Amman, 1972). In the late 1990s, increasing densities of mountain pine beetle-caused tree mortality were detected by Forest Health Management (USDA Forest Service) staff during aerials surveys in lodgepole pine forests of north-central Colorado (USDA Forest Service, 2005). From 2000 to 2008, mountain pine beetle killed large numbers of lodgepole pine trees in 770,000 ha of coniferous forests in Colorado (USDA Forest Service, http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/download/).

Three major factors appear to have coincided to foster this outbreak in lodgepole pine of north-central Colorado of unprecedented severity and extent since written records have been available. First, a period of drought stress, which makes trees more susceptible to insect attack (Mattson and Haack, 1987), in north-central Colorado began around 1998 and became particularly intense from about 2000 to 2002, as characterized by the Palmer Drought Severity Index (National Climatic Data Center, http://www.ncdc.noaa.gov/oa/ncdc.html). Second, a major mortality agent for mountain pine beetle is cold winter temperatures (Safranyik, 1978; Cole, 1981). Temperature data from Fraser Experimental Forest (USDA Forest Service, unpublished data) in north-central Colorado indicates that since at least 1992, minimum winter temperatures have scarcely reached −30 °C, which is about the temperature where supercooling may begin in mid-winter causing insect mortality (Bentz and Mullings, 1999). These warmer temperatures may be fostering increased winter mountain pine beetle survival (Nordhaus, 2009). Third, a large landscape of continuous lodgepole pine forest is susceptible to mountain pine beetle due to the availability of large diameter trees in dense stands. About 100,000 ha of lodgepole pine in the Arapaho National Forest are over 80 years old (USDA Forest Service, unpublished data), the age at which lodgepole pine becomes most susceptible to mountain pine beetle (Amman, 1977). An abundance of suitable host type is an important factor in stand susceptibility to outbreak levels of bark beetles (Schmid and Frye, 1976; Furniss et al., 1981; Negrón, 1998; Fettig et al., 2007).

When mountain pine beetle population levels become extremely high, bark beetle-caused tree mortality can create forest management challenges for land managers. For example, the occurrence of mortality in high-value settings such as recreation areas, ski resorts, campgrounds, visual corridors, watersheds, and forest land designated for timber production can be disruptive and negate certain investments. Real estate values can decrease and private land owners are faced with the high cost of protecting high-value trees or the removal of killed trees, or both. Furthermore, dead trees are eventually transformed from live standing biomass and crown fuels to downed fine and coarse woody debris, which has the potential to change wildfire hazard (Jenkins et al., 2008).

Mountain pine beetle, however, is an integral part of the ecology of these forests and influences ecosystem dynamics and resources. The insects contribute to shaping forest structure and composition (Amman, 1977). While the trees are dying, insects and other organisms inside the tree become an important source of food for many animals, particularly woodpeckers (McCambridge and Knight, 1972; Bull et al., 1997). Beetle-killed trees become perching and nesting habitat for many avian species and when dead trees fall they provide habitat for many small mammals and invertebrates (Bull et al., 1997). Habitats are created for other insects and fungi which are responsible for decomposition of

downed logs and returning nutrients to the soil (Edmonds and Eglitis, 1989; Apigian et al., 2006). Canopy structure, and water and nutrient demand by forest vegetation determine the amount, timing, and quality of water released from high-elevation watersheds (Troendle and King, 1985), and similar to forest harvesting or wildfire, extensive pine mortality will likely alter the delivery of clean water from areas affected by mountain pine beetle (Uunila et al., 2006). Previous research has documented increased streamflow following bark beetle outbreaks in western forests (Love, 1955; Bethlahmy, 1974; Potts, 1984; Troendle and Nanverkis, 2000).

Most research on the influence of mountain pine beetle on lodgepole pine ecosystems has been conducted in the Intermountain region of the western USA and western provinces in Canada. To address the lack of information about the influence of the current mountain pine beetle infestation on the structure of lodgepole pine forests in Colorado we conduced a study to: (1) identify structural and species composition similarities and differences between infested and uninfested stands; (2) characterize changes in stand characteristics caused by mountain pine beetle infestation; and (3) compare litter, duff, and fuel bed depths, downed woody debris loads, and understory vegetation characteristics in infested and uninfested stands.

2. Methods

2.1. Study site and plot selection

The study was conducted in the Sulphur Ranger District, Arapaho National Forest, Colorado (40°4′N, 106°0′W). Lodgepole pine covers about 45% of the 178,900 ha within the District, with an approximate elevational range of 2500–3500 m. Engelmann spruce (Picea engelmannii [Parry]), and subalpine fir (Abies lasiocarpa [Hook.] Nutt. var. lasiocarpa) make up 25% of the tree cover and are the predominant trees at higher elevations, north slopes, and along streams; 30% of the area consists of valley bottom, alpine vegetation, or exposed rock.

During 2006 and 2007, a geographic information system was used to randomly select potential plot locations within the lodgepole pine forest type from USDA Forest Service vegetation cover maps. Plots were distributed throughout the study area at least 0.4 km from roads and at a minimum distance of 0.4 km from each other. Plots were 0.02 ha (8.0 m radius) which adequately represent the small scale at which bark beetles influence forest stands (Olsen et al., 1996; Negrón et al., 2001). We established a total of 221 plots that were in uninfested areas (51 plots) and in areas with lodgepole pine either initially infested between 2000 and 2003 (68 plots), hereafter referred to as plots 4–7 years after infestation, or between 2004 and 2007 (102 plots), hereafter referred to as plots 0–3 years after infestation (0 represents current infestation in 2007). In a plot, the tree with the earliest year of infestation by mountain pine beetle determined the time since infestation category for the plot. The year a tree was infested by mountain pine beetle was estimated by degradation status of the crown. For plots 4–7 years after infestation, all needles had been shed from the earliest infested lodgepole pine, whereas for the plots 0–3 years after infestation, most needles remained on the infested lodgepole pines.

2.2. Stand structure and downed woody debris sampling

Site, forest structure, understory, and downed woody debris characteristics were measured in each plot. Elevation, aspect, and percent slope were measured at plot center. For each tree ≥2.5 cm in diameter at breast height (DBH, 1.37 m above ground), species, DBH, and condition were recorded. Tree condition included: live,

dead not from mountain pine beetle, currently attacked by mountain pine beetle, or previously killed by mountain pine beetle. Year of mountain pine beetle attack was estimated for previously killed trees by evaluating degradation classes of needles and branches as follows: 1 year previous = full crown of fading needles; 2 years previous ≥ 50% orange needles remaining; 3 years previous < 50% needles remaining; 4 years previous = no needles remaining but small and large twigs present; 5 years previous = only large twigs remaining; and 6 years previous and older = both small and large twigs not present (Keen, 1955). Some variation of tree degradation stage at each year after infestation likely occurred based on topographical features and moisture availability, among other conditions. Assessments, however, unlikely varied by more than 1 year. Currently infested trees were identified by the presence of boring debris at the base of the tree, pitch tubes, and life stages inside the tree. Seedlings/saplings, defined as live trees >0 cm in height to <2.5 cm in DBH, were recorded for species but were only counted in the 2007 sampling.

From the tree data collected, basal area, density, and quadratic mean diameter were calculated for infested and uninfested lodgepole pine and for non-host trees for mountain pine beetle, such as Engelmann spruce, subalpine fir, quaking aspen (*Populus tremuloides* Michx.), and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), which was only present in two plots. Total stand density index was calculated using the summation procedure, which represents individual tree utilization of the site (Stage, 1968; Long and Daniel, 1990).

Downed woody debris was recorded along three 7.32 m long modified Brown's planar transects that radiated from the center of each plot, systematically oriented at 30°, 150°, and 270° (Brown, 1974). Downed woody debris was counted using the following size classes: ≤0.6 cm, >0.6–2.5 cm, and >2.5–7.6 cm that correspond to 1-, 10-, and 100-h time lag fuel classes used by land managers, respectively. For downed wood >7.6 cm in diameter (1000-h time lag fuel class), the decay status (sound or rotten) and diameter where the downed wood intercepted the transect were recorded. Downed woody debris ≤2.5 cm in diameter was counted along a 1.83 m segment, the downed woody debris >2.5–7.6 cm in diameter was counted along a 3.05 m segment, and downed woody debris that exceeded 7.6 cm in diameter was measured along the entire length of each transect. Litter, duff, and fuel bed depth were measured at the end of each fuel transect. Within a 0.001 ha sub-plot (2 m radius) located 3.65 m from plot center, percent cover of vegetation, categorized as grass, forbs, or shrubs, was visually estimated and the maximum vegetation height measured.

We modeled future downed woody debris accumulations using published information on tree fall rates. Mitchell and Preisler (1998) indicated that about 10% of mountain pine beetle-killed lodgepole pine in Oregon had fallen 6 years after infestation and 80% after 12 years. In order to model future downed woody debris, we randomly chose mountain pine beetle-infested trees from infested plots, using 10% to represent what would fall within 6 years after infestation and 80% to represent what would fall within 12 years, to be converted to downed woody debris loads. Allometric equations, by fuel size class, were used to convert infested trees to downed woody debris loads (Brown, 1978; Pearson et al., 1984).

2.3. Data analyses

As our plots were distributed across a landscape it was important to check for spatial auto-correlation of stand characteristics and downed woody debris loads between plots. A lack of spatial auto-correlation was confirmed by incorporating spatial covariance into analyses and comparing the likelihood ratio test of the standard model to the spatial model. The performance of models with spatial covariance was not different and therefore it was not necessary to include spatial auto-correlation in analyses (SAS Institute, 1999).

We used logistic regression to identify stand attributes or physiographic characteristics that could be used to estimate the likelihood of infestation and modeled the response across the range of the predictor variable observed in the study. Using the logistic approach, models take the form:

$$P(\text{infestation}) = \frac{1}{1 + e^{-b'X}},$$

where $b'X$ represents a linear combination of explanatory variables X with their estimated parameters b, and e is the base of natural logarithms.

We examined the differences in stand characteristics between infested and uninfested plots and between pre-outbreak and 7 years after outbreak initiation in infested plots with a Wilcoxon rank sum and signed rank test, respectively. Pre-outbreak stand characteristics included live trees and trees killed by mountain pine beetle that were alive prior to the outbreak; outbreak stand characteristics included only trees that were alive at the time of sampling. We acknowledge that the outbreak had not collapsed at the time of our sampling and that tree mortality likely occurred in the infested plots after our sampling and may now be present in plots that were uninfested at the time of measurement. However, our infested plots represent the conditions initially selected by the mountain pine beetle. We compared the distribution of mountain pine beetle-killed trees to live trees across diameter classes within infested plots using a chi-square test. Seedlings/sapling density was fit to a negative binomial distribution and tested for differences between infested and uninfested plots with a *t*-test using elevation, aspect, and plot basal area as covariates (SAS Institute, 1999).

We tested for differences in the downed woody debris loads, as well as duff, litter, and fuel bed depths between infested plots and uninfested plots. The distributions of current and projected downed woody debris loads and the current depth of duff, litter, and fuel bed were moderately skewed and outliers were present in the data set. To limit the influence of skewness and outliers in the variables, a robust multiple regression was performed using a Bonferroni adjustment for multiple comparisons (SAS Institute, 1999) and median, median average deviation (MAD), and range for each downed woody debris size class are presented. Differences in mean vegetation percent cover among plots 0–3 years after infestation, 4–7 years after infestation and uninfested plots, were also fit to a negative binomial distribution with a *t*-test using elevation, aspect, and lodgepole pine density as covariates.

3. Results

3.1. Characteristics of infested stands

Mountain pine beetle-infested plots had significantly higher lodgepole pine basal area compared to uninfested plots (Table 1). In uninfested plots, the non-host tree species, subalpine fir and Engelmann spruce, had greater tree density and basal area than infested plots. Total non-host tree density and basal area were also higher in uninfested plots. Quadratic mean diameters for lodgepole pine and non-host tree species were not different between infested and uninfested plots.

Logistic regression modeling identified lodgepole pine basal area as a predictor of the probability of attack. The positive coefficient of lodgepole pine basal area indicates an increase in the predicted likelihood of attack as lodgepole pine basal area increases (Fig. 1). The estimated probability of infestation was 0.64 with a lodgepole pine basal area of 2 m²/ha, the lowest observed in our study.

Table 1
Means (standard error) for stand characteristics for trees with diameter at breast height ≥2.5 cm in plots infested by *Dendroctonus ponderosae* and uninfested plots, Arapaho National Forest, CO, 2006–2007. Non-host species include *Abies lasiocarpa*, *Picea engelmannii*, *Populus tremuloides*, and *Pseudotsuga menziesii*.

|	Infested plots (N = 170)	Uninfested plots (N = 51)	*p*-Value[^]
Trees/ha *Pinus contorta*	1028.4 (57.0)	956.1 (108.4)	0.269
Trees/ha *Abies lasiocarpa*	305.8 (45.5)	393.5 (74.8)	0.013
Trees/ha *Picea engelmannii*	157.1 (21.8)	300.2 (51.9)	<0.001
Trees/ha *Populus tremuloides*	42.0 (12.1)	42.0 (27.5)	0.350
Total non-host trees/ha	505.5 (54.7)	735.5 (102.1)	0.010
Total trees/ha	1533.8 (62.2)	1691.6 (109.8)	0.135
Basal area *P. contorta* (m^2/ha)	27.8 (0.9)	23.7 (2.7)	0.003
Basal area *A. lasiocarpa* (m^2/ha)	3.4 (0.5)	4.5 (0.9)	0.034
Basal area *P. engelmannii* (m^2/ha)	4.4 (0.7)	6.2 (1.1)	0.001
Basal area *P. tremuloides* (m^2/ha)	0.4 (0.2)	0.1 (0.1)	0.324
Total non-host basal area (m^2/ha)	8.2 (0.9)	10.8 (1.6)	0.032
Total basal area (m^2/ha)	36.0 (1.0)	34.5 (2.7)	0.264
Total stand density index	765.8 (20.5)	750.1 (49.8)	0.545
Quadratic mean diameter *P. contorta* (cm)	21.2 (0.5)	19.6 (0.9)	0.092
Quadratic mean diameter non-host species (cm)	14.0 (0.6)	12.8 (0.7)	0.396

[^] *p*-Value from Wilcoxon rank sum test.

We observed no patterns in infestation associated with physiographic characteristics. Elevation of infested (2898.0 ± 16.2 m [SEM]) and uninfested (2918.6 ± 24.6 m [SEM]) plots was not different (Wilcoxon rank sum test, *p* = 0.345). Furthermore, infested and uninfested plots did not differ in percent slope (25.5 ± 1.1% [SEM] and 24.1 ± 1.8% [SEM], respectively, *p* = 0.719). Infested and uninfested plots were distributed equally among north, east, south, and west facing slopes (chi-square = 3.40, df = 3, *p* = 0.334).

Seedling/sapling densities for all species, subalpine fir and Engelmann spruce were greater in uninfested plots but no differences were observed in the densities of lodgepole pine or aspen between infested and uninfested plots (Table 2). Lodgepole pine made up 20% of the seedlings/saplings in infested plots and 15% in uninfested plots. Aspen seedlings/saplings were present in 15% of infested plots and 10% of uninfested plots.

3.2. Effects of MPB on stand characteristics

Mountain pine beetle infestation killed 349.5 trees/ha (SEM = 18.5) and reduced stand basal area by 18.0 m^2/ha (SEM = 0.7) on average during 2000–2007 in areas affected by mountain pine beetle. Within infested plots, mountain pine beetle killed 62% (SEM = 2) of lodgepole pine ≥12.7 cm at breast height
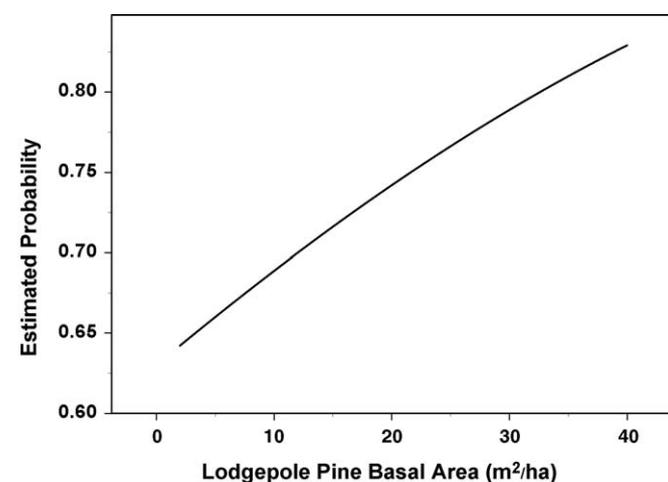
and reduced 71% (SEM = 2) of the lodgepole pine basal area. The percent of infested lodgepole pine per infested plot ranged from 5.5% to 100%.

A comparison of stand characteristics, including all trees with DBH ≥ 2.5 cm, in infested plots prior to the mountain pine beetle outbreak and 7 years after outbreak initiation, showed that mountain pine beetle-caused mortality greatly modified stand conditions (Table 3). There was a significant reduction in live tree density, basal area, stand density index, and quadratic mean diameter for both lodgepole pine and all tree species combined in infested plots (Table 3). For lodgepole pine, this represents reductions of 42%, 69%, and 34% in live tree density, basal area, and quadratic mean diameter, respectively.

Within the infested plots, including all trees with diameter at breast height ≥2.5 cm, the distribution of trees per diameter class killed by mountain pine beetle was significantly different than the distribution of live trees (chi-square = 291.5, *p* < 0.0001) (Fig. 2— live and infested *P. contorta* bars). The average DBH of lodgepole pine killed by mountain pine beetle (27.0 ± 0.6 cm [SEM]) was significantly greater compared to live lodgepole pine remaining in infested plots (12.8 ± 0.4 cm [SEM]) (*p* < 0.001). This resulted in a significantly smaller quadratic mean diameter of live lodgepole pine (13.9 ± 0.4 cm [SEM]) in infested plots than uninfested plots (19.6 ± 0.9 cm [SEM]) (*p* < 0.001). Lodgepole pine was the most abundant live tree species in the 2.5–30 cm diameter classes in infested plots when compared to Engelmann spruce, subalpine fir, and aspen (chi-square = 260.7, *p* < 0.001) (Fig. 2).

3.3. Effects of mountain pine beetle on downed woody debris

Downed fine and coarse woody debris loads were not different among categories of infested plots and uninfested plots (Table 4). The median litter depth was significantly greater in plots 4–7 years

Fig. 1. Logistic regression model estimating the probability of attack by *Dendroctonus ponderosae* using *Pinus contorta* basal area (intercept = 0.53, SE = 0.37, chi-square = 2.06, *p* = 0.15; estimate [lodgepole pine basal area] = 0.03, SE = 0.01, chi-square = 3.70, *p* = 0.05), Arapaho National Forest, CO, 2006–2007.

Table 2
Mean (standard error) density (trees/ha) of seedlings/saplings (defined as trees < 2.5 cm in diameter) in plots infested with *Dendroctonus ponderosae* and uninfested plots, Arapaho National Forest, CO, 2007.

	Infested plots (N = 89)	Uninfested plots (N = 27)	*p*-Value[^]
Pinus contorta	486.0 (85.1)	580.8 (183.9)	0.628
Abies lasiocarpa	578.1 (108.5)	3885.9 (1456.8)	<0.001
Picea engelmannii	145.0 (29.6)	642.3 (198.5)	0.001
Populus tremuloides	70.2 (15.4)	11.4 (13.6)	0.194
Total	2428.5 (288.4)	3877.4 (832.2)	0.059

[^] Significant differences in density tested with a *t*-test accounting for a negative binomial distribution.

Table 3
Mean (standard error) pre-outbreak and 7 years after outbreak initiation stand characteristics for trees with diameter at breast height ≥2.5 cm in plots infested by *Dendroctonus ponderosae* (N = 170), Arapaho National Forest, CO, 2006–2007.

|	Pre-outbreak	7 years after outbreak initiation	*p*-Value^
Trees/ha *Pinus contorta*	1028.4 (57.0)	592.9 (45.3)	<0.001
Trees/ha all species	1533.8 (62.2)	1063.4 (54.6)	<0.001
Basal area *P. contorta* (m²/ha)	27.8 (0.9)	8.5 (0.6)	<0.001
Basal area all species (m²/ha)	36.0 (1.0)	15.8 (0.9)	<0.001
Stand density index all species	765.8 (20.5)	365.4 (18.3)	<0.001
Quadratic mean diameter *P. contorta* (cm)	21.2 (0.5)	13.9 (0.4)	<0.001
Quadratic mean diameter all species (cm)	18.5 (0.3)	13.9 (0.3)	<0.001

^ *p*-Value from a Wilcoxon signed rank test.

Table 4
Median (median average deviation) downed woody debris (DWD) (Mg/ha) by size class, and duff, litter and fuel bed depth for infestation categories with *Dendroctonus ponderosae* and uninfested in *Pinus contorta* stands, Arapaho National Forest, CO, 2006–2007.

	Uninfested	0–3 years after infestation	4–7 years after infestation	R_n^2 test statistic	*p*-Value	Total range
	N = 51	N = 102	N = 68			N = 221
DWD ≤ 0.6 cm	0.5 (0.2)	0.4 (0.2)	0.5 (0.2)	4.77	0.092	0.1–2.4
DWD > 0.6–2.5 cm	1.1 (0.6)	1.1 (0.7)	1.4 (0.8)	2.46	0.289	0.0–14.4
DWD > 2.5–7.6 cm	2.3 (1.1)	2.3 (2.3)	2.3 (2.3)	1.71	0.436	0.0–27.8
DWD > 7.6 cm	14.4 (14.4)	12.7 (12.7)	19.2 (19.2)	1.93	0.380	0.0–252.8
Duff depth (cm)	1.7 (0.9)	2.0 (1.3)	1.8 (0.9)	1.21	0.545	0.0–8.0
Litter depth (cm)	1.3 (0.7)a	1.3 (0.6)a	1.8 (0.9)b	6.63	0.036	0.0–9.7
Fuel bed depth (cm)	4.0 (2.5)	4.6 (2.6)	4.7 (3.1)	0.75	0.686	0.0–15.2

Different letters between infestation categories and uninfested plots denote significance at *p*-Value < 0.05 tested with a robust linear regression with Bonferroni adjustment.
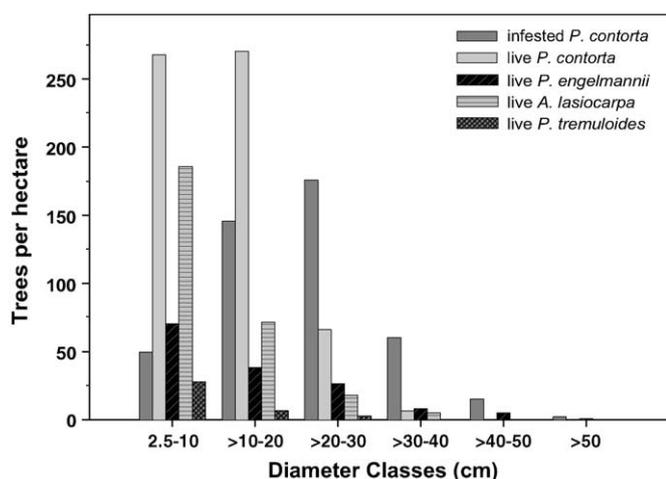
Fig. 2. Diameter distribution of *Dendroctonus ponderosae*-killed *Pinus contorta*, live *P. contorta*, live *Picea engelmannii, Abies lasiocarpa*, and *Populus tremuloides* in stands with *D. ponderosae* caused mortality, Arapaho National Forest, CO 2006–2007.

after initial infestation compared to plots in 0–3 years after initial infestation and uninfested plots. Modeling of future downed woody debris accumulations indicated no differences for any of the downed woody debris loads at 10% of tree fall (Table 5). However

significant increases in downed woody debris classes of ≤0.6 cm, >0.6–2.5 cm, and >7.6 cm are anticipated when 80% of the trees are down.

We observed no differences in percent ground cover for any of the understory vegetation classes evaluated or for all classes combined between the categories of tree mortality years or the uninfested plots (Table 6). Maximum height of grasses was significantly higher in plots 4–7 years after infestation compared to the uninfested plots, but not different from plots 0–3 years after infestation. Maximum height of herbs was significantly higher in plots 4–7 years after initial infestation compared to uninfested plots and plots 0–3 years after infestation.

4. Discussion

Mountain pine beetle populations in our study sites have initially shown a preference for densely stocked lodgepole pine stands. Mountain pine beetle has been more active in stands with higher lodgepole pine basal area, and lower tree density and basal area of non-host species. This is consistent with literature that indicates that various species of *Dendroctonus* bark beetles, including the mountain pine beetle, prefer densely stocked stands dominated by suitable host tree species (Fettig et al., 2007). Unexpectedly, we observed no differences in pre-outbreak quadratic mean diameter between infested and uninfested stands.

Table 5
Median (median average deviation) downed woody debris (DWD) (Mg/ha) amounts for uninfested plots, *Dendroctonus ponderosae* infested plots, and projected in infested plots with 10% and 80% of *Pinus contorta* tree fall, Arapaho National Forest, CO, 2006–2007.

	Plot infestation classes				R_n^2 test statistic
	Uninfested plots	Infested plots[a]	Projected 10% tree fall	Projected 80% tree fall	(*p*-Value)
	N = 51	N = 170	N = 170	N = 170	
DWD ≤ 0.6 cm	0.5 (0.2)a	0.4 (0.2)a	0.6 (0.3)a	2.0 (0.6)b	844.2 (<0.001)
DWD > 0.6–2.5 cm	1.1 (0.6)a	1.4 (0.8)a	1.4 (0.7)a	2.8 (0.8)b	211.2 (<0.001)
DWD > 2.5–7.6 cm	2.3 (1.1)a	2.3 (2.3)a	2.3 (2.1)a	2.7 (1.7)a	8.7 (0.034)
DWD > 7.6 cm	14.4 (14.4)a	15.4 (15.4)a	21.1 (16.0)a	64.2 (28.5)b	172.9 (<0.001)

Different letters within fuel size class denote significance at *p*-Value < 0.05 tested with a robust linear test. Bonferroni adjustment was made for multiple comparisons.
[a] Infested plots do not have fallen *D. ponderosae*-killed trees from the current bark beetle outbreak.

Table 6
Mean (standard error) percent cover and maximum vegetation height for understory vegetation by *Dendroctonus ponderosae* infestation category in *Pinus contorta* stands, Arapaho National Forest, CO, 2006–2007.

	Uninfested	0–3 years after infestation	4–7 years after infestation	F-value[^]	p-Value[^]
	$N = 51$	$N = 102$	$N = 68$		
Percent cover					
All vegetation	62.3 (4.6)	59.6 (3.2)	57.6 (3.6)	0.35	0.709
Shrubs	46.9 (4.5)	41.2 (2.8)	35.7 (3.0)	2.39	0.094
Grass	5.6 (1.5)	8.5 (1.7)	11.1 (2.6)	1.83	0.164
Herb	8.1 (1.7)	8.0 (1.2)	9.9 (1.8)	0.43	0.654
Average maximum height (cm)[a]					
All vegetation	36.3 (3.5)	33.9 (2.3)	40.8 (3.3)	1.53	0.218
Shrubs	32.2 (3.7)	30.5 (2.5)	31.8 (3.2)	0.10	0.906
Grass	21.6 (2.9)b	23.8 (2.1)ab	34.8 (3.2)a	5.99	0.003
Herb	13.9 (1.6)b	18.9 (1.4)b	22.0 (2.0)a	5.01	0.008

Different letters denote significant difference at $p < 0.05$.

[a] Number of observations within the groups of years of initial infestation by *D. ponderosae* (2000–2003, 2004–2007, and uninfested) were: 68, 99, and 51 for total vegetation; 63, 97, and 47 for shrubs; 58, 86, and 39 for herbs; and 43, 48, and 21 for grass, respectively.

[^] Data fit to a negative bionomical distribution.

However, within infested stands, mountain pine beetle exhibited preference for larger diameter trees as killed trees were significantly larger than the residual live trees. In addition, the distribution of live lodgepole pine and mountain pine beetle-killed trees by diameter classes in infested plots indicates preference for large diameter trees, which is also consistent with the literature (Cole and Amman, 1969; Amman et al., 1977).

The lack of differences in quadratic mean diameters between infested and uninfested stands suggests an abundance of forest land where suitable diameter classes occur. The logistic regression modeling indicated a high likelihood of infestation with a lodgepole pine basal area as low as $2 \, m^2/ha$. Studies have suggested that stands thinned to a basal area of $27.5 \, m^2/ha$ in pure lodgepole pine forests exhibit reduced susceptibility to mountain pine beetle (Mata et al., 2003). The resulting logistic model is indicative of the magnitude of the outbreak, where essentially all stands with suitable diameter classes are exhibiting high levels of tree mortality. Our logistic model cannot be used for identifying susceptible stands but illustrates the severity of the outbreak.

Lodgepole pine stands attacked by mountain pine beetle had a pre-outbreak total stand density index of 766, whereas uninfested stands had a pre-outbreak total stand density index of 750. Using the maximum stand density index of 1420 for mixed stands of lodgepole pine, Engelmann spruce, and subalpine fir (J.D. Shaw, personal communication), infested and uninfested stands were growing at 54% and 53% of the maximum stand density index, respectively. At these levels tree growth is reduced substantially by competition (Langsaeter, 1941 as cited by Long, 1985), a further indication of the high susceptibility of these forests to insect attack. No differences where observed prior to the outbreak in total basal area or quadratic mean diameter of lodgepole pine in infested and uninfested plots. Infested plots, however, had significantly higher lodgepole pine basal area. High proportions of host type in susceptible stages foster elevated mortality during outbreaks. Managing species composition in forest stands where these mixed forests naturally occur may help mitigate mortality levels in the future.

Quantification of downed woody debris showed no change in mountain pine beetle-affected stands within 7 years after outbreak initiation, which was unexpected as we anticipated the initiation of tree fall. Lodgepole pine killed by mountain pine beetle in Oregon began falling in about 3–5 years after infestation and 80–90% of killed trees fell within 10–12 years (Mitchell and Preisler, 1998). Rate of fall will be affected by stand density, wind patterns, aspects, and soil moisture (Keen, 1955). A combination of these factors may be contributing to a slower fall rate of mountain pine beetle-killed trees. It follows that downed woody debris accumulations may take longer in our study sites.

The depth of fine litter increased by about 40% in plots 4–7 years after infestation compared to plots 0–3 years after infestation and uninfested plots, as enough time had elapsed for most of the needles and some of the twigs to drop from these trees. Mortality that had occurred between 0 and 3 years after infestation includes trees that still had a large component of needles attached at the time of measurement. This is consistent with studies on mountain pine beetle epidemics in lodgepole pine forests in Utah and Idaho, where Page and Jenkins (2007a) showed a greater amount of litter in current epidemic stands compared to stands with endemic levels of mountain pine beetle.

We did not observe differences in understory vegetation percent cover 7 years after mountain pine beetle-induced tree mortality. Various studies have reported increases in understory vegetation after bark beetle outbreaks (Amman, 1977; McCambridge et al., 1982; Stone and Wolfe, 1996; McMillin and Allen, 2000; McMillin et al., 2003; Lynch et al., 2006; Page and Jenkins, 2007a). It is likely that our study area will exhibit an increase in understory vegetation biomass in years to come. We did observe greater average maximum height of vegetation in plots 4–7 years after infestation for grasses and herbs, a likely result of mountain pine beetle-caused opening of the canopy.

The lack of tree fall in our plots suggests that tree fall rates will be slower in north-central Colorado than those reported by Mitchell and Preisler (1998) for Oregon. Nevertheless, when 10% of killed trees fall, the amount of downed woody debris in infested plots would not be different from that of uninfested plots. With 80% of the trees down, we anticipate significant increases in all downed woody debris classes except the 2.5–7.6 cm class when compared to uninfested plots. The median amount of coarse woody debris >7.6 cm that is expected to be on the ground is 64.2 Mg/ha (MAD = 28.5). The historical range of coarse downed woody debris loads found in Montana lodgepole pine forests is suggested to be 27–58 Mg/ha (Brown and See, 1981). However, Tinker and Knight (2000) reported higher amounts of coarse woody debris, including snags, in lodgepole pine forests; a range of 41–284 Mg/ha for burned lodgepole pine stands in Yellowstone National Park, Wyoming and 52–123 Mg/ha for previously clearcut stands in the Medicine Bow National Forest, WY. Coarse woody debris amounts are highly variable (Brown et al., 2003), therefore, the amount of downed woody debris projected to accumulate after tree fall in our study sites is not likely to be different from that reported for historical and disturbed stands. Coarse woody debris

accumulation from the mountain pine beetle outbreak will persist for many decades due to slow degradation rates. Brown et al. (1998) found that windthrown lodgepole pine logs in north-central Colorado took more than 150 years to completely decompose, though degradation rates may be more rapid due to bark beetle infestation (Busse, 1994).

Coarse woody debris plays a crucial role in the ecology of forest ecosystems by providing habitat for many organisms including invertebrates, reptiles, amphibians, fish, and small mammals (Harmon et al., 1986; Tallmon and Mills, 1994; Bunnell, 1995; Carey and Johnson, 1995; Torgersen and Bull, 1995; James and M'Closkey, 2003; McCay and Komoroski, 2004; Apigian et al., 2006; Patrick et al., 2006); fostering retention of sediments and stream characteristics (Harmon et al., 1986; Naiman et al., 2002); and contributing to nutrient cycling (Spies et al., 1988); and nitrogen fixation (Harmon et al., 1986). However, the amount of downed coarse woody debris that will accumulate over time as a result of bark beetle-caused mortality in north-central Colorado was unknown. Our data and modeling provides a quantification of what may be expected. If downed woody debris management is considered for stands affected by the mountain pine beetle outbreak, managers need to balance management objectives with the ecological benefits of coarse woody debris.

The density and species composition of established understory trees combined with recruitment of new seedlings will characterize how stands respond after the current mountain pine beetle infestation. For example, mountain pine beetle infestations that killed 40–70% of the overstory lodgepole pine in Wyoming forests during the 1960s and 1970s stimulated a two to threefold increase in growth of the surviving trees for two decades (Romme et al., 1986). Veblen et al. (1989) demonstrated that canopy mortality and structural changes from windthrow in lodgepole pine-dominated stands enhanced the growth of midstory Engelmann spruce and subalpine fir. By removing canopy trees, both blowdowns and mountain pine beetle outbreaks have also been shown to promote lodgepole pine and subalpine fir seedling establishment in forests of Colorado (Sibold et al., 2007).

Mountain pine beetle-caused mortality will likely result in an uneven aged stand structure comprised of surviving lodgepole pine and canopy Engelmann spruce and subalpine fir and released understory trees. New seedlings may establish under canopy gaps depending on factors such as site moisture and available seedbed. However, as lodgepole pine remains the most abundant tree species in the 2.5–30 cm diameter classes it will likely continue to dominate the stands in the future. Aspen has the capacity to take advantage of openings in the canopy by sprouting from root stock, but was only a component in the overstory in 14% of the plots.

Future disturbances, their intensity, frequency, and interactions will also determine future forest structure and composition. Although mixed severity fires occur in lower elevation lodgepole pine forests in the Rocky Mountains, historically, these forests are characterized by infrequent, high intensity, stand replacing fires and a return interval between 20 and 300 years (Houston, 1973; Arno, 1980; Romme, 1982). These stand replacing fires are driven by extreme dry conditions and less by surface fuels, however, after extensive bark beetle-caused tree mortality, fire hazard or behavior could be altered due to changes in surface fuel loads (Page and Jenkins, 2007a), the development of fuel ladders (Lynch et al., 2006), and lowering of relative humidity with increased surface wind speed in mountain pine beetle-killed stands (Pollet and Omi, 2002; Page and Jenkins, 2007b). Litter depth was greater in infested stands compared to uninfested stands and could result in increases in flame height and rate of spread (Burgan, 1987; Savadogo et al., 2007) which may kill new regeneration.

Lodgepole pine forests are susceptible to windthrow (Oliver and Larson, 1996), particularly after partial cutting as the stands become more open (Alexander, 1986). From the standpoint of tree fall, the mountain pine beetle outbreak mimics a large-scale partial cutting without logging activities. If windthrow events occur in areas where Engelmann spruce or subalpine fir, or both, are abundant it can set the stage for the development of epidemic population densities of spruce beetle, (*Dendroctonus ruffipennis* Kirby) which utilizes spruce as its host, or the western balsam bark beetles (*Dryocoetes confusus* Swaine) which uses subalpine fir as its primary host (Bright, 1963). Population levels of these insects can increase in downed trees and later invade live surrounding stands (Massey and Wygant, 1954; McMillin et al., 2003).

Fragmentation of the overstory as a result of mountain pine beetle-caused mortality and the response of understory vegetation will determine the rate, magnitude and duration of watershed change. Water uptake has been shown to decline substantially within weeks after mountain pine beetles infest lodgepole pine (R.M. Hubbard, unpublished data), yet canopy interception of precipitation will change little until dead pines shed foliage and branches. As overstory trees die and fall, understory conifer crowns will regulate both snowfall interception and surface roughness. Increased light, water, and nutrients will stimulate the residual vegetation (Romme et al., 1986), and where the understory is abundant, its rapid growth and higher water use per unit leaf area may diminish the amount of water and nutrients available for export (Hubbard et al., 1999).

Effects of the current mountain pine beetle outbreak on ecological processes such as downed wood accumulation and decomposition, hydrology, windthrow events, and others in lodgepole pine forests of north-central Colorado will be long lasting. Native bark beetles are important disturbance agents in forest ecosystems and have co-evolved with their hosts for millennia. Under a climate change scenario it is foreseen that disturbance processes may change in frequency and become more intense (Dale et al., 2001) with eruptive forest insects having the potential to create large-scale ecological changes (Logan et al., 2003). The distribution, range, and abundance of different conifer species will depend on their response to increasing temperatures (Nielson et al., 2005). It will be imperative to continue long term monitoring of ecological processes after these extensive bark beetle outbreaks as lessons may be of benefit to understand these novel interactions and to mitigate, as appropriate, future bark beetle outbreaks if they continue to be exacerbated under a changing climate scenario.

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