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Thirty year change in lodgepole and lodgepole/mixed conifer forest structure following 1980s mountain pine beetle outbreak in western Colorado, USA

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ABSTRACT

Current mortality in lodgepole pine caused by mountain pine beetle (MPB) throughout much of western North America has resulted in concern about future forest structure. To better understand the long-term effects of the current mortality, and how it might differ depending on forest species composition, we measured forest vegetation and woody fuel accumulations in forest affected by a MPB outbreak in the late 1970s and early 1980s and compared conditions to 1980s USDA Forest Service data to quantify changes in the approximately 30 years following tree mortality. Stands were classified into two forest type groups based on species composition prior to 1970s/1980s MPB mortality: lodgepole pine and mixed conifer. In the 30 years after MPB mortality, lodgepole pine stands' overstory recovered to 91% of pre-mortality total basal area and 93% of overstory trees ha^{-1}. Mixed conifer stands' basal area and overstory trees ha^{-1} remained significantly reduced. In both forest types relative basal area and trees ha^{-1} of non-pine species increased, and understory trees ha^{-1} increased roughly fivefold. In lodgepole pine stands, the most abundant species in the 1980s understory was subalpine fir, followed by lodgepole pine. By the 2010s, subalpine fir and aspen were the most abundant understory tree species. In mixed conifer stands, subalpine fir and Engelmann spruce dominated all understory size classes in the 1980s and the 2010s. Total down woody fuels were greater in mixed conifer (103 Mg ha^{-1}) than lodgepole pine stands (60 Mg ha^{-1}) due to higher rotten fuel accumulation in mixed conifer than lodgepole pine stands. Overall, our results suggest that long-term forest recovery trajectories are dependent on pre-outbreak species composition, though understory densities are likely to increase regardless of non-pine species abundances. These shifts in species and size composition by 30 years after outbreak likely have substantial impacts on forest health, potential fire behavior and ecosystem processes. We speculate that forest recovery following the current MPB outbreak in these areas will be similar to observed changes following the 1970s/1980s outbreak.

1. Introduction

The current mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) outbreak has killed lodgepole pine (*Pinus contorta* var. *latifolia*) overstory trees on many million hectares of lodgepole pine and lodgepole pine/mixed conifer forest in western North America (Raffa et al., 2008). The disturbance will have a large impact on forest structure across an entire region and there is serious concern over future forest conditions and wildfire hazard. Mountain pine beetle usually kills larger lodgepole pine trees (Cole and Amman, 1969; Amman and Baker, 1972) but leaves the remaining trees and vegetation alive and the forest floor undisturbed. This is a much different disturbance from stand-replacing wildfires of the mid-1800s that were responsible for establishment of much of the current lodgepole pine forest of western North America (e.g. Bigler et al., 2005). Long-term forest recovery following forest disturbance due to MPB is less well understood than forest recovery following fire, but it is likely to differ depending on depend on pre-outbreak species composition (Collins et al., 2011; Kayes and Tinker, 2012).

The forest species composition and density following a MPB epidemic is determined by initial forest species composition, forest density, and host selection by beetles. Mountain pine beetles attack all *Pinus* spp., typically killing larger trees (<5% of trees <15 cm dbh are killed during epidemics [Cole and Amman, 1969; Amman and Baker, 1972]), though they will infest smaller diameter trees when larger trees are scarce (Cole and Amman, 1969; Leatherman et al., 2010). Forest composition immediately following MPB mortality will therefore be dominated by surviving predominantly small lodgepole pine and non-host species present, such as shade-intolerant aspen (*Populus tremuloides*) and shade-tolerant Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Long-term species dominance will be a

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combined result of post-MPB forest composition and species' ability to grow given the post-MPB forest environment (Diskin et al., 2011). It is therefore likely forest species composition before outbreak will play a large role in time to recovery following outbreak. Forest growth projections suggest that the majority of nearly pure lodgepole pine forest will recover to pre-outbreak overstory density within 50–100 years (Diskin, 2010; Collins et al., 2011), while forest of mixed lodgepole pine and aspen and mixed lodgepole pine, Engelmann spruce and subalpine fir may recover within 20–50 years (Diskin, 2010).

Forest trajectories will also depend on the composition of advance regeneration present before MPB outbreak. Advance regeneration is more important than post-disturbance establishment in the recovery of MPB-affected forests (Astrup et al., 2008; Collins et al., 2011; Kayes and Tinker, 2012) because tree establishment following MPB is usually patchy and slow due to heterogeneous spatial distribution of mortality and consequent light and substrate limitations (Vyse et al., 2009; Collins et al., 2011). In contrast, advance regeneration can respond immediately to increased light availability with rapid growth. In lodgepole pine-dominated forests advance regeneration often has a large component of shade-tolerant species that have successfully established beneath an existing canopy, though shade-intolerant lodgepole and aspen may also be present (Axelson et al., 2009; Collins et al., 2011). In mixed lodgepole pine, Engelmann spruce and subalpine fir forest, advance regeneration will be even more dominated by the shade-tolerant species present (e.g. Kayes and Tinker, 2012).

The belief that MPB changes forest fire hazard is driving much of the concern about future forest structure (*sensu* Jenkins et al., 2008, 2012). Once all needles have fallen from dead trees, usually within four years of tree mortality (Klutsch et al., 2009), probability of crown fire ignition is likely lower because there are too few fine fuels (needles) to cause crown fire spread (Page and Jenkins, 2007b; Simard et al., 2011), though the effects of MPB mortality on potential fire behavior are controversial (e.g. Moran and Cochrane, 2012; Jolly et al., 2012; Simard et al., 2012). Dead woody fuels on the forest floor surface increase following MPB, the amount and accumulation rate of which depends on MPB mortality and tree fall rates (*sensu* Jenkins et al., 2012). Post-disturbance releases of advance regeneration and tree establishment increase the live fuel load near the surface, which is likely to increase fire spread. High understory tree desities may provide enough fuel to ignite coarse woody debris (woody fuels $\geqslant$7.62 cm diameter) that would substantially contribute to fire severity if fire were to occur (Bigler et al., 2005; Jenkins et al., 2008; Collins et al., submitted for publication).

Few studies have measured the long-term consequences of MPB on forest species composition and structure. We have a good understanding of the effects of MPB over the short term ($\leqslant$10 years) (e.g. Amman and Baker, 1972; Axelson et al., 2010; Collins et al., 2010, 2011; Diskin et al., 2011; Muir, 1993; Sibold et al., 2007; Vyse et al., 2009). Our understanding of the long-term effects of this disturbance on forests is largely based on research that has quantified short-term effects and used these to model long-term (>20 years) implications for stand structure and fuel loads (Klutsch et al., 2009; Diskin, 2010; Collins et al., 2011). There have been quantifications of forest vegetation and fuel complex 20 + years following MPB, but they are of limited applicability. Forest vegetation and surface fuels were quantified from 25-year post-outbreak stands in Utah, but only at one site (Page and Jenkins, 2007a). Simard et al. (2011) present a chronosequence of forest vegetation, surface fuels and predicted fire behavior from 0 to 36 years post-MPB. However, only 10 locations were 20+ years post-MPB, and all data were collected from stands with lodgepole pine was $\geqslant$94% basal area. There have been no long-term longitudinal studies that compare the vegetation change following MPB at the same site through time. Furthermore, the majority of this research has been done in nearly-pure lodgepole pine stands (e.g. Collins et al., 2011; Diskin et al., 2011; Klutsch et al., 2009; Romme et al., 1986; Simard et al., 2011). Because the post-MPB trajectory stands is likely to be substantially different depending on species composition (Diskin, 2010; Kayes and Tinker, 2012), increasing our understanding of the long-term impacts of MPB on forests with different species compositions is essential for management to be effective and avoid unintended ecological and social consequences.

A MPB outbreak in the late 1970s and early 1980s caused lodgepole pine mortality on several hundred thousand hectares throughout the Rocky Mountains (Romme et al., 1986), affecting approximately 77,000 hectares in Colorado (West, 2010). Mortality rates were similar to the current MPB outbreak (see Rust, 1987; Romme et al., 1986; Simard et al., 2011, USDA Forest Service *unpublished data*). Mortality occurred in forests of pure lodgepole pine, lodgepole pine mixed with aspen and mixed conifer stands of lodgepole, subalpine fir and Engelmann spruce (Amman and McGregor, 1985). We visited areas severely affected by this outbreak and assessed vegetation recovery and fuel load accumulated in lodgepole pine and mixed conifer (lodgepole pine mixed with subalpine fir and Engelmann spruce) stands during the 30 years following this mortality event. This allows us to quantify the long-term effect of MPB on forest composition and fuel complex in different pre-outbreak forest types, which can be used to better guide management reactions to the current outbreak. We also quantified the effects of the 2000s MPB mortality in these areas. Using 1980s and 2010s forest inventory data, we address the following questions:

1. Do stands recover to pre-outbreak overstory density and species composition in 25–30 years following MPB outbreak? How does current understory tree density and species composition compare to the 1980s understory in these stands?
2. How does initial stand composition impact the forest vegetation recovery in 25–30 years following MPB?
3. What is the fuels complex in stands 25–30 years after MPB infestation, and does it differ depending on pre-outbreak species composition?

2. Methods

2.1. Study area

This study was conducted in the Eagle/Holy Cross Ranger District of the White River National Forest roughly 130 km west of Denver, Colorado, USA (Fig. 1). The area is dominated by mountainous terrain, with a temperate continental climate. Elevations ranged from 2590 to 3100 m, with annual precipitation averaging 520 to 680 mm. The majority of precipitation falls as snow between October and May. Annually, average maximum temperature is between 8.6 and 11.9 degrees Celsius (°C) and average minimum temperature is between −5.0 and −2.9 °C for the whole study area (PRISM Climate Group, 2006). Forest vegetation is generally dominated by lodgepole pine or aspen at lower elevations and/or southern aspects, with an occasional component of Douglas-fir. At higher elevations and/or more northerly aspects, subalpine fir and Engelmann spruce frequently dominate, though lodgepole and aspen are often also present.

2.2. Site selection

We identified potential study sites that had high rates of MPB-caused mortality during the late 1970s/early 1980s using two sources of information: 1980s USDA Forest Service inventory and maps from annual forest health aerial detection surveys (West,

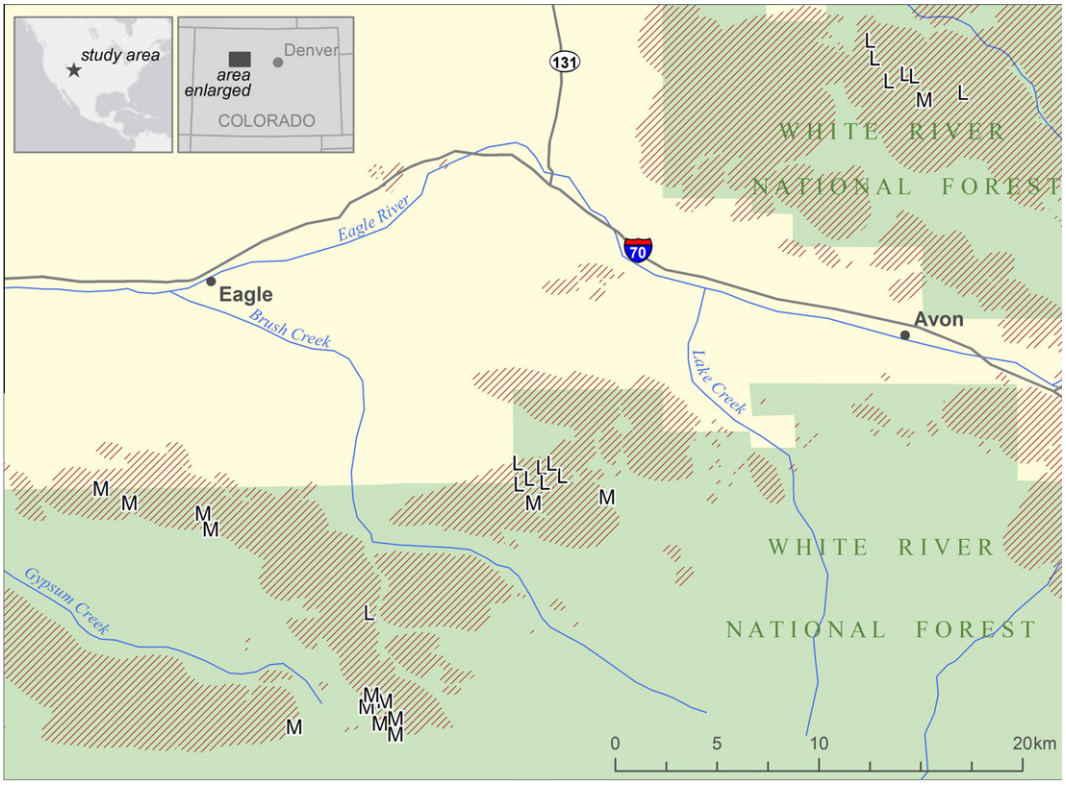

Fig. 1. Study area location in Colorado, USA. Sampled stands are marked by 1980s forest type: "M" marks mixed conifer stands, "L" marks lodgepole pine stands (as defined in Methods). Hatch-marking indicates areas of mountain pine beetle mortality according to 1980s aerial forest health survey maps.

2010). Forest health survey flights recorded location and intensity of tree mortality on hand-marked maps. The mortality areas recorded by surveys during and after the 1970s/1980s MPB outbreak (1980 to 1988) were digitized using ArcGIS 9.3 (ESRI, 2007; West, 2010). These maps provide locations and annual timing of tree mortality, though spatial accuracy is limited due to the imprecision of hand-drawn polygons. Spatially-explicit USDA Forest Service forest inventory data recorded from 1980 to 1988 provided more exact mortality information. We found 230 stands where standing dead lodgepole pine made up $\geqslant$30% of total lodgepole pine basal area. We intersected these data sources using ArcGIS 9.3 (ESRI, 2007) to identify 132 stands where: (1) 1980s MPB activity was observed in aerial surveys no more than 1000 m from a stand center, and (2) 1980s forest inventory data showed $\geqslant$30% basal area mortality of lodgepole pine.

We randomly selected 50 sites for field inspection from the 132 potential sites where aerial survey and forest inventory data indicated high 1970s/1980s MPB. We screened each potential site for evidence that recorded mortality was caused by MPB by examining older dead trees for MPB beetle galleries and dead wood to check for blue stain. We rejected the stand if evidence of MPB as the mortality agent was not found. We also verified that no substantial biomass removal (such as timber harvest or firewood cutting) had occurred in the half century before 1970s/1980s MPB infestation. Twenty-eight stands were selected for sampling. These areas were also affected by the 2000s MPB epidemic, with the majority of mortality occurring from 2002 to 2009 (USDA Forest Service, 2011).

We repeated forest inventory according to common stand exam data collection protocol in 2010 and 2011 (USDA Forest Service, 2007). The repeated forest inventory allowed us to compare current species and age structure to the 1980s stand structure (e.g., Smith and Smith, 2005). We also measured down woody debris (surface fuel) accumulations in each stand in the 2010s.

2.3. Data collection

Stand inventory data were collected by the USDA Forest Service between 1980 and 1988 according to contemporaneous common stand exam protocol. Five to 18 plot centers were placed systematically on a grid in each stand. At each plot center, a variable radius plot (BAF 6.9, 9.2 or 13.8 m^2 ha^{-1}) and a fixed radius plot (13.5 or 8.1 m^2) were installed. In variable radii plots, used to quantify overstory (trees $\geqslant$12.7 cm dbh) composition, attributes of "in" trees were recorded. Trees are "in" or "out" based on their distance from plot center and their dbh. For each "in" tree, species, status (live or dead) and dbh were recorded. Understory trees ($\geqslant$0.3 m tall and <12.7 cm dbh) were measured in 13.5 m^2 fixed-area plots. Tree species, status (live or dead), dbh and height were recorded for trees $\geqslant$2.5 cm and <12.7 cm dbh. Species-specific counts of live trees $\geqslant$0.3 m tall and <2.5 cm dbh were recorded by 0.3 m height classes. The exact locations of each plot center had been lost, but the geographic boundaries of each stand (within which plots were measured in the 1980s) were available in the 2010s. Therefore, though we could not directly repeat plot measurements in the 2010s, we could sample the same populations (stands) and compare the sample of plots from each time period to assess stand change through time.

In 2010–2011, we repeated forest inventory. We systematically located ten plot centers on a grid in each stand, where a 4.6 m^2 ha^{-1} BAF variable radius plot, a 40.5 m^2 fixed-radius plot, and 21.3 m-long Brown's transect were measured (Brown, 1974). For each "in" tree we recorded species, status (live or dead), dbh and crown base height (cbh). For lodgepole pine trees, we also recorded current MPB infestation and MPB-caused mortality within the last 10 years. We measured understory trees in 10, 40.5 m^2 and 10, 1.2 m^2 fixed-area plots per stand. In each 40.5 m^2 fixed-area plot, live and dead tree species, dbh and cbh were recorded

for subcanopy trees (⩾3.8 and <12.7 cm dbh). Species-specific counts of seedlings/saplings (trees ⩾0.6 m tall and <3.8 cm dbh) were recorded by height classes: 0.61–1.37 m tall and ⩾1.37 m tall to <3.8 cm dbh. To assess small seedling (trees 0.01–0.6 m tall) density, we recorded counts (by species) of trees less than 0.6 m tall in a 1.2 m^2 fixed-radius plot. We measured heights and destructively sampled a cross-section at root collar of up to 10 randomly selected *P. contorta*, *P. tremuloides*, *A. lasiocarpa* and *P. engelmannii* seedlings/saplings in each stand to age trees 0.6 m tall to <3.8 cm dbh. In lodgepole pine stands, we aged 76 trees: 13 *P. contorta*, 18 *P. tremuloides*, 40 *A. lasiocarpa* and 5 *P. engelmannii*. In mixed conifer stands, we aged 84 trees: 14 *P. contorta*, 4 *P. tremuloides*, 48 *A. lasiocarpa* and 18 *P. engelmannii*. We counted tree rings under a microscope to determine tree age.

We measured woody surface fuels along transects using Brown's planar intercept method to quantify down woody debris accumulations (Brown, 1974). Each transect began at plot center and ran along a random azimuth 21.3 m. We tallied fine woody debris (dead woody fuels ⩽7.62 cm diameter [FWD]) that intersected varying lengths of transect plane in the following diameter size classes: 0–.64 cm (1-h) and .64–3.8 cm (10-h) fuels along the first 1.8 m and 3.8 cm–7.62 cm (100-h) fuels along the first 4.6 m. For coarse woody debris (fuels with diameter at transect intersection ⩾7.62 cm [CWD]), we recorded diameter and species (when possible) for all intersections along the 21.3 m transect plane. Fuels leaning through the transect plane creating an angle <45° with the ground were included. We recorded litter, duff and total fuel bed depth at two points on each transect.

2.4. Data analysis

Plot tree and fuels transect data were averaged to the stand level for the 2010s and 1980s data sets. Basal area was calculated to include overstory trees (⩾12.7 cm dbh). Overstory average stand diameter (ASD), the diameter of the tree with mean basal area (equivalent to quadratic mean diameter [QMD]), was also calculated at the stand level. Dead lodgepole pine tree number and basal area was added to live lodgepole pine tree numbers and basal area to estimate pre-outbreak stand conditions in the 1980s and 2010s. Trees killed in the 1980s were not included in the 2010s pre-outbreak estimation.

Stands were divided into initial forest composition types, either lodgepole pine or mixed conifer, based on species percentages of total stand basal area in the 1980s. These forest types were located on sites with different climatic and topographic characteristics. Lodgepole pine forest type stands (n = 14) were 86–100% *P. contorta* and *P. tremuloides* and 0–14% shade-tolerant species (*A. lasiocarpa* and *P. engelmannii*). Lodgepole pine stands' elevation ranged from 2590 to 2920 m, with average precipitation of 520 to 610 mm annually, and average annual minimum temperatures between −5.0 and −3.1 °C and maximum temperatures of 9.3 to 11.9 °C. Mixed conifer forest type stands (n = 14) were 39–79% *P. contorta* and *P. tremuloides* and 21–56% *P. engelmannii*/*A. lasiocarpa*. Mixed conifer stands were cooler, higher and wetter than lodgepole pine stands, with stand elevations ranging from 2860 to 3100 m, average precipitation of 590 to 680 mm annually, average annual minimum temperatures between −4.7 and −2.9 °C and maximum temperatures of 8.6 to 9.9 °C. "Lodgepole pine" will refer to lodgepole pine stands and "mixed conifer" will refer to mixed conifer stands as defined here for the remainder of this paper. "*P. contorta*" will be used when referring to trees of the species commonly known as lodgepole pine.

We used a Wilcoxon rank sum test to compare 1980s and 2010s forest structure between forest types (lodgepole pine vs. mixed conifer) (SAS Institute, 2002–2010). We used the Wilcoxon signed rank test to analyze overstory and understory tree composition changes in lodgepole pine and mixed conifer stands through time (SAS Institute, 2002–2010). We square root-transformed understory density before analysis because there were many null observations. We used Wilcoxon rank sum tests to compare 2010s seedling/sapling tree ages and surface fuel load categories between forest types (SAS Institute, 2002–2010).

We did a regression analysis using all stands (n = 28) to determine the relationship between the proportion of pre-1980s outbreak stand basal area in *A. lasiocarpa* and *P. engelmannii* and net basal area change from the 1980s to the 2010s. Net basal area change was calculated by subtracting 1980s live basal area from 2010s live basal area plus 2000s MPB-mortality. Proportion data were normalized for analysis by taking the arcsine of the square-root of the proportion. The analysis was done using PROC REG in SAS (SAS Institute, 2002–2010).

3. Results

3.1. Overstory

Roughly half of *P. contorta* overstory trees were killed in the 1980s MPB outbreak in both lodgepole and mixed conifer stands (Table 1, Fig. 2a and b). Post-outbreak live basal was significantly higher in mixed conifer, at 27.7 m^2 ha^{-1}, than in lodgepole pine, at 20.1 m^2 ha^{-1} (Table 1). Pre-outbreak differences in species composition were exaggerated by the 1980s MPB mortality; *P. contorta* was 81% of live basal area in lodgepole pine but only 53% in mixed conifer stands after the outbreak. Average stand diameter (ASD) in lodgepole stands was significantly lower following the outbreak while in mixed conifer stands ASD was unchanged (Fig. 3).

Lodgepole pine and mixed conifer stands did not differ significantly in overstory basal area, trees ha^{-1}, or ASD before the 1970s/1980s MPB outbreak (Table 1). In lodgepole pine stands, there were on average 754 overstory trees ha^{-1} and basal area of 36.9 m^2 ha^{-1}. In mixed conifer stands, there were on average 859 overstory trees ha^{-1} and basal area of 40.1 m^2 ha^{-1} (Table 1, Fig. 4). Overstory species composition varied between forest types. In lodgepole pine stands, pre-outbreak basal area was 89% *P. contorta* and 6% *P. tremuloides*, and the majority of trees >15 cm dbh were *P. contorta*. Average basal area in mixed conifer stands was 66% *P. contorta*, 24% *A. lasiocarpa*, and 8% *P. engelmannii*. Mixed conifer stands had significantly less *P. contorta* and *P. tremuloides* but significantly more *A. lasiocarpa* and *P. engelmannii* than lodgepole pine stands. In mixed conifer stands *A. lasiocarpa* and *P. engelmannii* trees were more abundant and larger than in lodgepole pine stands (Fig. 2a and b).

Overstory change following the 1980s MPB outbreak differed between lodgepole pine and mixed conifer forest types. When all stands were analyzed together, there was a weak relationship between proportion 1980s basal area in *A. lasiocarpa*/*P. engelmannii* and net basal area change from after the 1980s MPB outbreak to before the 2000s MPB outbreak (P = 0.0018, R^2 = 0.3204) (Fig. 5). When separated into forest type groups, lodgepole pine stands had significant overstory basal area and tree ha^{-1} gain while mixed conifer stands did not in the 25–30 years following 1980s MPB mortality (Table 1, Fig. 4). Lodgepole pine stands recovered an average of 9.9 of the 16.8 m^2 ha^{-1} *P. contorta* basal area killed during the 1980s, and 145 of the 265 *P. contorta* overstory trees killed (Table 1; Fig. 4a and b). *P. contorta* ASD increased from 24.2 cm immediately after the 1980s outbreak to 26.4 cm before the current outbreak. 2010s ASD was not different from ASD before the 1980s MPB outbreak (26.3 cm) in lodgepole pine stands (Fig. 3a). Other species' basal areas also increased from the 1980s to 2010s in lodgepole pine stands, though overstory trees ha^{-1} did not increase (Fig. 4a and b). In lodgepole pine stands, *P. contorta*

Table 1
Lodgepole pine and mixed conifer stands' overstory ($\geqslant$12.7 cm dbh) mean basal area (m^2 ha^{-1}), tree density (ha^{-1}) and average diameter in the 1980s and 2010s. Pre-1980s and current MPB totals include basal area and trees ha^{-1} killed in the indicated outbreak. *P*-values are two-sided results of Wilcoxon rank sum tests. Bold italics indicate significant changes ($\alpha = 0.05$).

	Overstory basal area (m^2 ha^{-1})					Overstory tree density (trees ha^{-1})					Overstory average stand diameter (cm)				
	Lodgepole pine		**Mixed conifer**		*P*	**Lodgepole pine**		**Mixed conifer**		*P*	**Lodgepole pine**		**Mixed conifer**		*P*
	Mean	*Std. Err.*	*Mean*	*Std. Err.*		*Mean*	*Std. Err.*	*Mean*	*Std. Err.*		*Mean*	*Std. Err.*	*Mean*	*Std. Err.*	
Pro 1980s MPB total	36.9	2.1	40.1	2.7	0.7599	754	56	859	44	0.1636	25.4	1.0	24.4	0.8	0.9459
Total 1980s live	20.1	1.8	27.7	1.9	***0.0202***	489	44	636	39	***0.0350***	23.1	0.9	23.7	0.8	0.6347
1980 live PICO	15.9	1.3	13.9	1.7	0.2675	352	28	279	44	0.0939	24.2	1.0	26.4	1.4	0.2852
1980 dead PICO	16.8	1.8	12.4	1.5	0.1154	265	34	223	25	0.3761	29.0	1.2	26.8	1.2	0.4028
1980 total non-PICO	4.2	0.9	13.8	1.5	***<.0001***	137	36	357	29	***0.0002***	23.3	2.4	22.2	1.2	0.8674
1980 ABLA	0.5	0.3	9.7	1.8	***<.0001***	8	5	246	34	***<.0001***	31.4	4.2	21.9	1.1	0.0676
1980 PIEN	1.0	0.5	3.4	0.6	***0.0046***	18	10	99	18	***0.0004***	30.0	5.4	22.0	1.9	0.2615
1980 POTR	2.1	0.6	0.4	0.4	***0.0036***	106	37	10	10	***0.0019***	18.8	2.5	22.7	-	0.4000
1980 PSME	0.5	0.3	0.3	0.2	0.8593	5	3	3	2	0.7890	38.2	1.4	36.8	2.4	1.0000
Pre-2000s MPB total	33.6	2.7	29.9	1.6	0.2903	702	67	701	47	0.9100	25.2	0.9	23.6	0.7	0.1936
Total 2010s live	17.4	2.1	25.0	2.1	***0.0265***	449	61	619	55	***0.0497***	22.7	0.8	22.8	0.6	0.9459
2010s live PICO	9.6	2.0	9.6	1.4	0.7087	244	56	216	29	0.8388	23.3	0.9	23.8	1.1	0.9459
2010s dead PICO	16.2	1.9	5.0	1.4	***<.0001***	253	32	83	23	***0.0003***	29.3	1.1	28.7	1.2	0.5112
2010s total non-PICO	7.7	2.0	15.3	1.9	***0.0204***	205	44	402	48	***0.0350***	21.5	1.2	22.0	0.6	0.2852
2010s ABLA	2.0	0.6	8.6	1.2	***0.0003***	57	19	263	39	***0.0003***	22.5	1.9	21.2	0.7	1.0000
2010s PIEN	0.9	0.5	6.0	1.3	***<.0001***	19	9	114	28	***0.0004***	28.4	4.0	28.5	2.0	0.8154
2010s POTR	4.6	1.7	0.6	0.3	***0.0101***	128	39	24	11	***0.0072***	22.0	2.1	20.0	2.9	0.6461
2010s PSME	0.2	0.1	0.1	0.1	0.7304	1	1	1	0	0.7304	50.9	9.0	42.6	2.9	0.6667

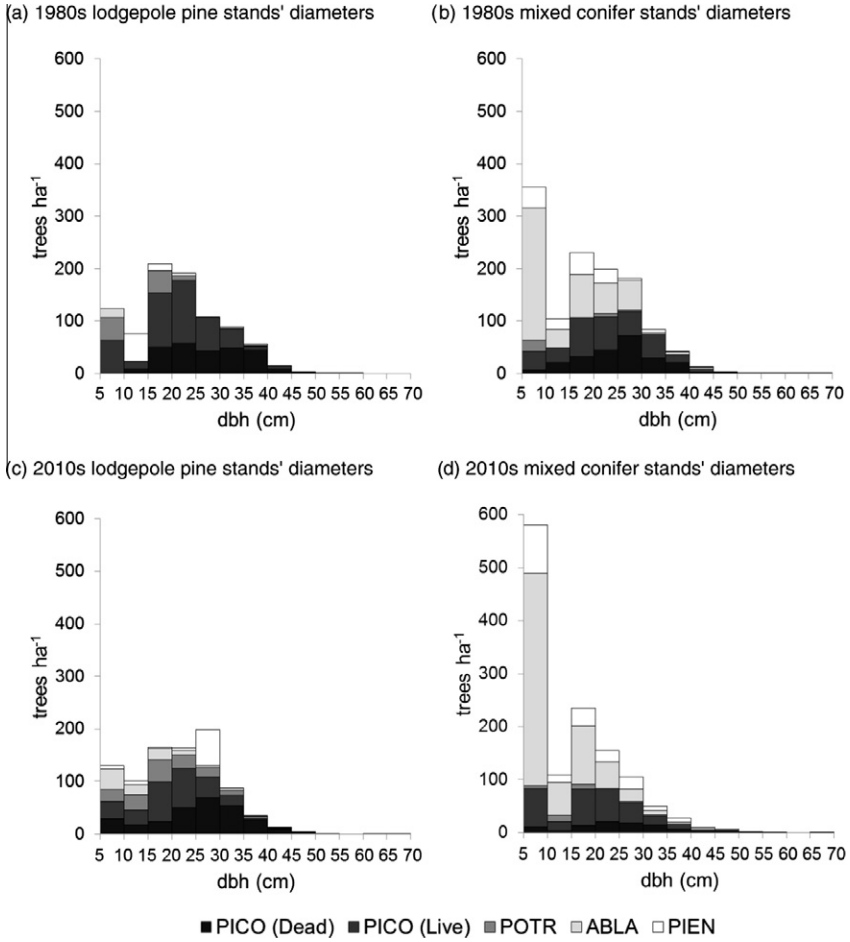

Fig. 2. Average diameter distributions of lodgepole pine (a, c) and mixed conifer (b, d) stands in the 1980s (a, b) and 2010s (c, d). Both forests types have more non-lodgepole pine trees in the smaller size classes in the 2010s than they did in the 1980s. Over all species, mixed conifer stand composition shifted towards smaller trees from the 1980s (b) to 2010s (d). Figure includes trees 5–70 cm dbh; there were <0.1 trees ha^{-1} >70 cm dbh. PICO = *Pinus contorta*, POTR = *Populus tremuloides*, ABLA = *Abies lasiocarpa*, PIEN = *Picea engelmannii*.

continued to dominate the overstory 25–30 years after MPB outbreak; before the 2000s MPB mortality, *P. contorta* made up an average of 77% of overstory basal area and 71% of trees, compared to 88% and 81% before 1980s MPB. Although non-pine ASD did not

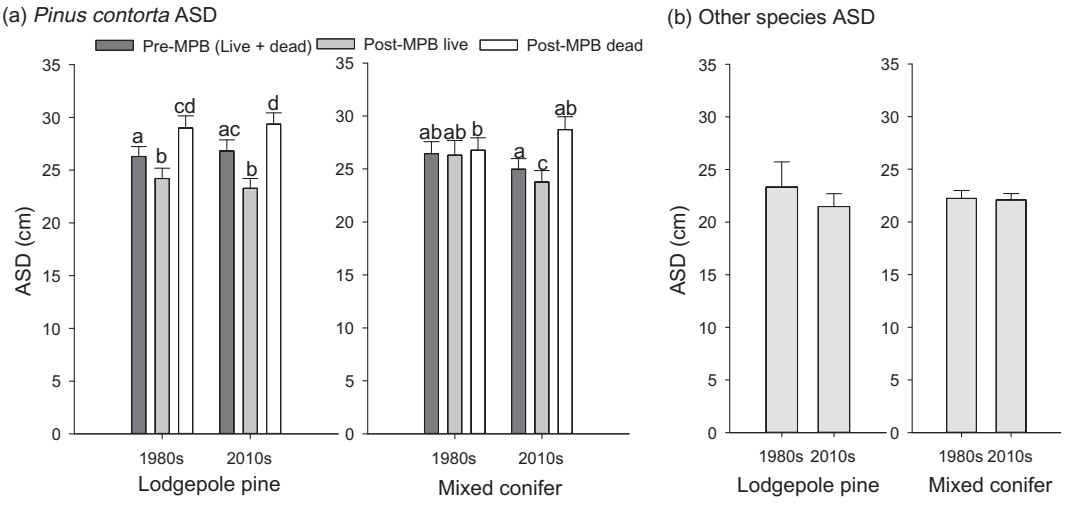

Fig. 3. Average stand diameter (ASD) for *Pinus contorta* (a) and other species (b) in lodgepole pine and mixed conifer stands in the 1980s and 2010s. Letters indicate significant differences among *P. contorta* ASDs through time in each forest type. *P. contorta* live ASD decreased due to the 1980s and 2010s MPB outbreaks in lodgepole pine stands, but only due to the 2010s outbreak in mixed conifer stands. Non-host species' ASD (b) did not significantly differ from the 1980s to 2010s in either forest type.

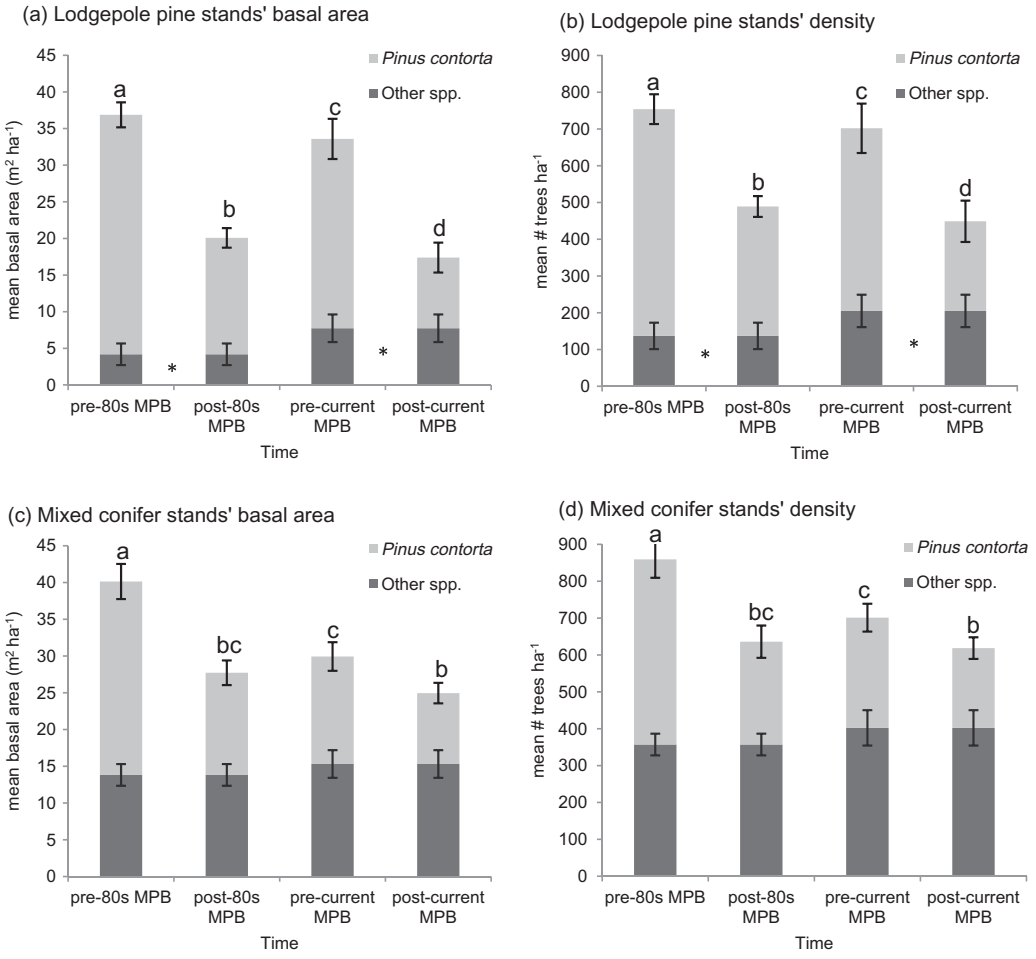

Fig. 4. Changes in overstory ($\geqslant$12.7 cm dbh) basal area and density through time. Mean overstory basal area (a, b) and trees ha^{-1} (c, d) of *P. contorta* and all other species in lodgepole pine (a, c) and mixed conifer (b, d) stands through time. Differences in letters above bars indicate significant differences in total and *P. contorta* basal area or trees ha^{-1} in stands through time. Asterisks (*) indicate significant differences between 1980s and 2010s non-pine species basal area and density. There was a significant increase of non-pine species in lodgepole pine stands (a, b) but not mixed conifer stands.

change from the 1980s to 2010s in lodgepole pine stands (Fig. 3b), *A. lasiocarpa*, *P. engelmannii* and *P. tremuloides* were more prevalent among trees >20 cm by the 2010s (Fig. 2a and c). In contrast to lodgepole pine stands, mixed conifer stands' overstory basal area

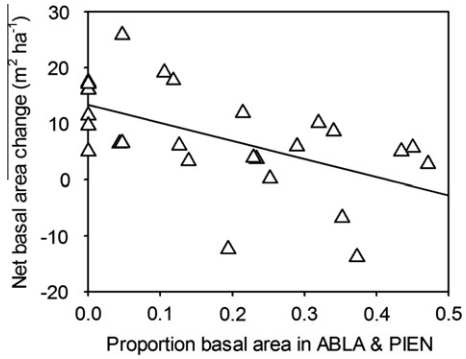

Fig. 5. Regression of proportion of pre-1980s MPB outbreak basal area in *Abies lasiocarpa* (ABLA) and *Picea engelmannii* (PIEN) and net basal area change from the 1980s to 2010s for all stands ($n = 28$). There was a moderately-strong relationship between proportion *Abies lasiocarpa*/*Picea engelmannii* and net basal area change in all stands ($n = 28$, $P = 0.0018$, $R^2 = 0.3204$). Net basal area change was calculated by subtracting 1980s live basal area from 2010s live basal area plus 2000s MPB-mortality. Proportion data were normalized for analysis by taking the arcsine of the square-root of the proportion. This graph shows non-transformed data to aid interpretability. Statistics are from analysis of transformed data.

and trees ha^{-1} did not increase and species composition shifted more towards non-pine species during the decades following 1980s MPB mortality. The overstory change was driven by the loss of the *P. contorta* component; there was no significant difference in non-pine tree species' basal area, trees ha^{-1} (Fig. 3c and d) or ASD (Fig. 3b) from the 1980s to 2010s. However, the ASD of *A. lasiocarpa* was lower ($P = 0.0676$) in the 2010s (21.9 cm) than 1980s (31.4 cm) due to higher numbers of small *A. lasiocarpa* in the overstory (Fig. 2b and c). *P. contorta* dominance of mixed conifer stand overstory decreased during this time; *P. contorta* was 66% and 58% of the basal area and trees ha^{-1} before the 1980s outbreak but was only 49% and 43% of total basal area and overstory trees ha^{-1} 25–30 years later.

The 2000s MPB outbreak resulted in greater overstory mortality (basal area and trees ha^{-1}) in lodgepole pine stands than mixed conifer stands though there was significant mortality in both forest types (Table 1, Fig. 4). In lodgepole pine stands, MPB killed 51% of *P. contorta* overstory trees and 63% of *P. contorta* basal area, reducing total basal area 48%. In mixed conifer stands, 2000s MPB killed 28% of *P. contorta* trees and 34% of *P. contorta* basal area, reducing total

Table 2
Understory trees density (ha^{-1}) in 1980s and 2010s. Mean trees per hectare (standard error) are shown. Bold italics indicate significant changes ($\alpha = 0.05$). *P*-values are one-sided results of Wilcoxon signed rank tests on square-root transformed numbers, where the null hypothesis is that 1980s tree densities are ⩾2010s tree densities.

Tree size:	<.61 m tall		⩾.61 m tall – 3.8 cm dbh			3.8–12.7 cm dbh		
	1980s	2010s	1980s	2010s	*P*	1980s	2010s	*P*
Pure lodgepole								
All spp.	–	3660 (859)	193 (77)	1349 (219)	***0.0001***	409 (156)	202 (37)	0.2362
PICO	–	437 (53)	32 (32)	85 (36)	***0.0127***	134 (50)	70 (12)	0.2760
POTR	–	906 (189)	11 (11)	916 (165)	***0.0001***	191 (126)	44 (17)	0.1250
ABLA	–	2177 (721)	138 (67)	309 (94)	***0.0083***	85 (55)	79 (27)	0.3184
PIEN	–	124 (53)	13 (13)	36 (15)	***0.0039***	0 (0)	9 (12)	***0.0313***
Mixed conifer								
All spp.		5417 (540)	840 (171)	6508 (2432)	***0.0009***	694 (96)	952 (142)	0.1304
PICO	–	484 (89)	32 (23)	116 (53)	***0.0098***	57 (24)	135 (39)	***0.0127***
POTR	–	190 (106)	11 (11)	123 (55)	***0.0391***	42 (33)	13 (7)	0.4063
ABLA	–	4025 (499)	708 (180)	5856 (2407)	***0.0083***	492 (95)	646 (141)	0.2708
PIEN	–	717 (125)	90 (33)	395 (129)	***0.0017***	103 (26)	158 (37)	0.0916

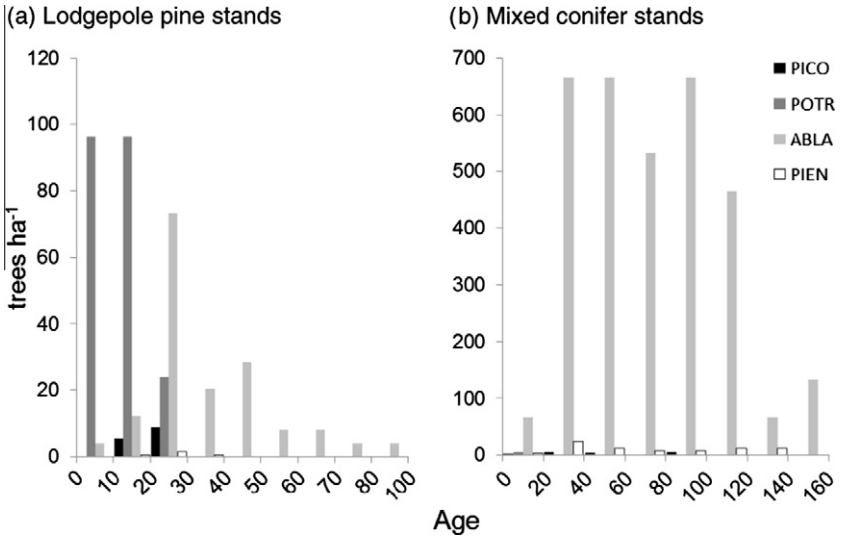

Fig. 6. Ages and numbers of seedlings/saplings (>0.6 m tall and >3.8 cm dbh) ha^{-1} in lodgepole pine (a) and mixed conifer (b) stands in the 2010s. Median ages of seedlings/saplings were significantly younger ($P < 0.0001$) in lodgepole pine (21 years) than in mixed conifer stands (58 years). In lodgepole pine stands, we aged 76 trees: 13 *Pinus contorta* (PICO), 18 *Populus tremuloides* (POTR), 40 *Abies lasiocarpa* (ABLA) and 5 *Picea engelmannii* (PIEN). In mixed conifer stands, we aged 84 trees: 14 *Pinus contorta*, 4 *Populus tremuloides*, 48 *Abies lasiocarpa* and 18 *Picea engelmannii*. These graphs represent the ages of these 160 trees scaled up by species to the 2010s average trees ha^{-1} of each forest type (see Fig. 2). Note differences in *x*- and *y*-axes between graphs.

basal area by only 16%. Mortality from the 2000s outbreak significantly reduced *P. contorta* ASD in both forest types (Fig. 3a).

3.2. Understory

Understory tree density and species composition changed from the 1980s to 2010s. Average density of seedlings/saplings (⩾0.6 m tall and <3.8 cm dbh) increased sevenfold in both forest types in the 25–30 years following MPB mortality, from 193 to 1349 trees ha^{-1} in lodgepole pine and from 840 to 6508 trees ha^{-1} in mixed conifer (Table 2). Subcanopy tree (3.8–12.7 cm dbh) numbers decreased from 409 to 202 in lodgepole pine stands and increased from 694 to 952 in mixed conifer stands, though these changes were not statistically significant ($P = 0.2362$ and $P = 0.1304$, respectively) (Table 2). In lodgepole pine stands in the 1980s, shade-tolerant *A. lasiocaripa* dominated the seedling/sapling size class, while the subcanopy was mostly shade-intolerant *P. contorta* and *P. tremuloides*. By the 2010s, *P. contorta* and *P. tremuloides* were dominant in lodgepole pine stands' seedling/sapling and subcanopy size classes. However, *A. lasiocarpa* was 59% of small seedlings (trees .01–.6 m tall) in the 2010s in lodgepole pine stands. In mixed conifer stands, shade tolerant *P. engelmannii* and *A. lasiocarpa* made up the majority of all understory size classes in the 1980s and 2010s. Shade tolerant species were most dominant in the smaller understory size classes in both forest types.

Median ages of seedlings/saplings were significantly younger ($P < .0001$) in lodgepole pine (21 years, $n = 76$) than in mixed conifer stands (58 years, $n = 84$) (Fig. 6). *P. contorta*, *A. lasiocarpa* and *P. engelmannii* seedling/saplings were younger in lodgepole pine stands than mixed conifer stands (all $P < 0.01$). Median ages for *P. tremuloides* were older in lodgepole pine stands (12 years, $n = 18$) than mixed conifer stands (5 years, $n = 4$) ($P = 0.0393$), though this may be an artifact of small sample size.

3.3. Surface fuels

Total dead surface fuel loads averaged 60.1 Mg ha^{-1} in lodgepole pine stands, significantly less than the 102.6 Mg ha^{-1} in mixed conifer stands (Table 3). There was significantly more rotten coarse woody debris (⩾7.62 cm diameter [CWD]) in mixed conifer than lodgepole pine stands (Table 3). Fine woody debris (<7.62 cm diameter [FWD]) load, litter depth and duff depth were not different between forest types.

Table 3
Mean down surface fuel loads and depths (standard error) comparison between lodgepole pine ($n = 14$) and mixed conifer ($n = 14$) stands affected by the 1980s MPB outbreak. There were significantly more total fuels, coarse woody debris fuels, and rotten coarse woody debris fuels in mixed conifer than lodgepole pine stands. *P*-values are two-sided results of Wilcoxon rank sum tests. Bold italics indicate significant changes ($\alpha = 0.05$).

	Lodgepole pine	Mixed conifer	*P*
	Mg ha^{-1} (Standard error)		
Total fuel load	60.1 (4.3)	102.6 (10.0)	***0.0007***
Coarse woody debris (CWD) total	51.1 (4.5)	92.9 (10.0)	***0.0007***
Sound CWD	40.3 (4.7)	40.7 (4.3)	0.9820
Sound PICO CWD	34.4 (4.9)	30.5 (3.9)	0.7688
Sound Non-PICO CWD	5.9 (1.2)	10.2 (2.2)	0.1898
Rotten CWD	10.8 (1.7)	52.2 (8.1)	***0.0002***
Rotten PICO CWD	7.6 (1.3)	27.8 (3.8)	***0.0002***
Rotten Non-PICO CWD	3.2 (0.9)	24.3 (4.4)	***0.0005***
Fine woody debris (FWD) total	8.9 (0.9)	9.8 (1.0)	0.7345
100-h fuels	5.2 (0.6)	6.0 (0.7)	0.3519
10-h fuels	3.2 (0.4)	3.2 (0.5)	0.4013
1-h fuels	0.6 (0.1)	0.5 (0.1)	0.8388
	cm (Standard error)		
Fuel bed depth	2.5 (0.7)	7.0 (2.0)	***0.0462***
Litter depth	2.7 (0.2)	2.2 (0.5)	0.4544
Duff depth	6.5 (0.5)	5.6 (0.5)	0.4347

4. Discussion

The 1970s/1980s MPB outbreak had a greater long-term effect on the overstory in mixed conifer stands than lodgepole pine stands. Lodgepole pine stands' overstory recovered about 60% of the basal area killed in the 1980s (10 of the 16 m^2 ha^{-1}) in the 25–30 years following MPB outbreak. Overstory trees ha^{-1} and basal area increased during this time, suggesting that basal area recovery in lodgepole pine stands was largely due to growth of established understory into newly-opened overstory. Overstory *P. contorta* and non-pine tree species' basal area and trees ha^{-1} increased significantly, though *P. contorta* was still dominant by 25–30 years after MPB outbreak. In mixed conifer stands, total and *P. contorta* overstory trees ha^{-1} or basal area did not increase following 1980s mortality. The result was a major shift towards *A. lasiocarpa* and *P. engelmannii* dominance in these stands. There was also significantly lower total basal area before the 2010s outbreak than before the 1980s outbreak in mixed conifer stands, even though they had higher 1980s surviving overstory than lodgepole pine stands.

The observed basal area reduction in mixed conifer stands contradicts predictions that *P. contorta* mixed with subalpine fir and spruce will recover quickly due to high surviving trees ha^{-1}and basal area (e.g., Diskin et al., 2011). High surviving basal area following the 1980s MPB mortality likely resulted in stands with lower light availability, reducing growth of overstory trees as compared to those in lodgepole pine stands. Total basal area in these stands was also likely reduced by root disease-caused *A. lasiocarpa* mortality that occurred in the study area during the 1990s (Tom Eager, *personal communication*). It is also possible that basal area stagnation in mixed conifer stands may have occurred due to a shift from a developed "mature" forest to one which is essentially in an early developmental stage due to lack of large trees (Schmid and Amman, 1992), resulting in lower stand basal area growth rates. Analysis of individual tree increment cores would allow for a more complete understanding of post-MPB tree growth in these stands, but was outside the scope of this study.

The fivefold increase in understory tree density from the 1980s to 2010s represents a substantial change in tree size distribution in both forest types. The majority of understory trees in the 2010s were species other than *P. contorta* in both forest types. *P. tremuloides* and *A. lasiocarpa* now dominate understory in lodgepole pine stands; in mixed conifer stands the understory is roughly 90% *A. lasiocarpa.* These established trees will likely become the future forest (Astrup et al., 2008; Collins et al., 2011; Kayes and Tinker, 2012), shifting the compositions of both stand types away from *P. contorta*. *A. lasiocarpa* and *P. engelmannii* will likely persist and grow into the overstory of both forest types. *P. tremuloides* sprouts are abundant in the understory of lodgepole pine stands and may grow into the overstory given favorable conditions. However, *P. tremuloides* growth into overstory may be limited by low light or drought and sprouts that fail to reach the canopy will likely die within a few years of canopy closure (Perala, 1990).

Differences between lodgepole pine and mixed conifer stands immediately following the 1980s MPB outbreak had implications for post-disturbance tree growth and establishment. Lower surviving tree basal area following the outbreak in lodgepole pine stands likely resulted in more light availability, allowing shade-intolerant *P. contorta* and *P. tremuloides* establishment and growth into the overstory (Lotan and Critchfield, 1990; Perala, 1990). Shade-tolerant *A. lasiocarpa* and *P. engelmannii* are more prevalent in the smallest understory size classes, presumably because they can take

advantage of the lower-light environments nearest the forest floor (e.g. Collins et al., 2011). In contrast to mixed conifer stands, the majority of understory seedlings/saplings in lodgepole pine stands were less than 30 years old, indicating they established during or after the 1980s outbreak. In mixed conifer stands, higher surviving basal area following the 1980s MPB mortality likely resulted in stands with lower light availability, favoring shade-tolerant over shade-intolerant species in the understory.

Overall, the post-MPB trajectories we observed are consistent with the long-held view that MPB speeds shifts in species dominance away from *P. contorta* to other non-pine species present (Roe and Amman, 1970; Amman, 1977; Schmid and Amman, 1992). In lodgepole pine stands by before the 2000s MPB outbreak, *P. contorta* declined slightly from 88% to 77% of basal area, while *P. tremuloides* had increased from 6% to 14% of basal area, and *A. lasiocarpa* increased from 1% to 6% when compared to conditions before the 1970s/1980s outbreak. However, by the 2010s lodgepole pine stands had high understory densities though there was little advance regeneration in the 1980s. The 2000s outbreak has killed a similar proportion of *P. contorta* as was killed in the 1980s. Therefore, barring dramatic climatic changes, we speculate that forest recovery following the current MPB outbreak will be similar to observed changes following the 1980s outbreak in these stands. The advance regeneration in lodgepole pine stands, dominated by *A. lasiocarpa* and *P. tremuloides,* not *P. contorta*, will experience a growth release and is likely to be the most important growing stock for the future forest following the current outbreak (e.g., Astrup et al., 2008). However, *P. tremuloides* understory may only grow to the overstory successfully in certain locations with favorable growing environments (high light and moisture) and under favorable climate conditions. *A. lasiocarpa* will continue to regenerate as the forest recovers from the current outbreak and understory light availability is reduced. The compound effect of multiple outbreaks in these lodgepole pine stands may result in a shift in dominance away from *P. contorta* towards *P. tremuloides,* and *A. lasiocarpa* in the long-term without fire occurrence. In mixed conifer stands, where 66% of basal area was *P. contorta* prior to 1980s MPB mortality, *P. contorta* was only 48% of overstory basal area 25–30 years later. With current MPB mortality, mixed conifer stands' average basal area was only 16% *P. contorta*. There is little *P. contorta* advance regeneration and likely to be little post-outbreak establishment. Mixed conifer stands will be heavily dominated by *A. lasiocarpa* and *P. engelmannii*, even though stand basal area averaged 66% *P. contorta* in the 1980s.

Surface fuel loads were significantly higher in mixed conifer than lodgepole pine stands, with likely has implications for potential fire behavior. Observed fuel loads in the 1, 10 and 100 h classes did not differ between forest types and were similar (within ~2 Mg/ha) to those reported by Page and Jenkins (2007a), Simard et al. (2011) and projections by Klutsch et al. (2009). However, total CWD in mixed conifer stands was nearly double that in lodgepole pine stands. Lodgepole pine average fuel loads (51 Mg ha^{-1} CWD, 78% sound) were consistent with those measured 35 years post epidemic by Simard et al. (2011) and projected by Klutsch et al. (2009) with an 80% tree fall rate. Mixed conifer stands had sound CWD equal to lodgepole pine stands (41 Mg ha^{-1}), but rotten CWD load was five times greater (52 Mg ha^{-1}), similar to surface fuel loads in mixed conifer with lodgepole pine stands 20 years post MPB epidemic in Utah, USA (Page and Jenkins, 2007a). These results make clear the importance of pre-outbreak stand structure to projecting post MPB mortality surface fuel loads. Stands largely comprised of lodgepole pine, such as our lodgepole pine stands and those measured by Simard et al. (2011) and Klutsch et al. (2009), will likely have lower surface fuel loads than stands with substantial components of shade-tolerant species. Forests with larger components of shade-tolerant species are likely to be wetter, more productive, and/or have longer times since last fire (e.g. Bigler et al., 2005). In several of our mixed conifer stands, growth releases suggest previous mountain pine beetle outbreaks in the mid-twentieth century and earlier (unpublished data). Tree mortality due to previous insect and disease outbreaks in mixed conifer stands likely increased surface fuel loads, resulting in high rotten woody debris loads. Rotten fuels combust more readily than sound fuels (*sensu* Hyde et al., 2011), which, combined with very high understory tree density, could substantially increase fire hazard in mixed conifer stands (e.g. Kulakowski and Veblen, 2007).

The long-term effects of the 1970s/1980s MPB outbreak on these stands differed depending on pre-outbreak species composition. Lodgepole pine stands remain dominated by *P. contorta*, though basal area and trees ha^{-1} of non-pine species had increased by 25–30 years later. Higher densities of shade-tolerant trees in the understory foreshadow possible future increases in overstory *A. lasiocarpa* and *P. engelmannii*. Mountain pine beetle-caused mortality has set mixed conifer stands on a speedy trajectory of reduced *P. contorta* dominance that is compounded by the current outbreak. All stands had high surface fuel loads, though mixed conifer stands had far more rotten fuels and denser understory tree vegetation than which could lead to more severe fire behavior than in lodgepole pine stands. Though this study was conducted only on specific stands in western Colorado, the differences between forest types' post-MPB recovery based on their initial conditions is relevant elsewhere. However, forest recovery from the current outbreak is likely to be affected by increasing climate changes, which could increase temperatures and change precipitation regimes, changing tree establishment patterns and growth.

The different trajectories observed highlight the importance of considering pre-MPB forest composition when considering management of the current outbreak. In lodgepole pine stands, forest management may not be necessary for *P. contorta* to remain dominant 25–30 years in the future. The likely increase of aspen in lodgepole pine stands' overstory may be socially desirable as aspen is valued for its aesthetics and can act as an effective forest fire fuel break (Van Wagner, 1977; Bigler et al., 2005). With the decline of aspen stands elsewhere in Colorado (Worrall et al., 2010), the increased aspen component following MPB could make up for declines of other stands. However, in the long term, with multiple MPB outbreaks and continued fire absence, these lodgepole pine stands may become increasingly dominated by shade-tolerant species. In mixed conifer stands, shade-tolerant species make up the majority of the stand immediately following MPB mortality, and continue to dominate decades later as total stand basal area growth has stagnated. Very high understory tree densities in mixed conifer stands increase fuel continuity resulting in a fuel complex that is likely more hazardous than in lodgepole pine stands. Therefore, if maintaining a *P. contorta* component in forests and reducing fire hazard is the desired outcome, focusing management efforts on areas with higher components of *P. engelmannii* and *A. lasiocarpa* will likely render the greatest benefit.

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