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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 ⩾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 (⩽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 ⩾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,