Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire

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Abstract

Recent large scale mountain pine beetle (*Dendroctonus ponderosae* Hopkins, MPB) outbreaks have created concern regarding increased fuel loadings and exacerbated fire behavior and have prompted a desire to understand the effects of sequential disturbances on the landscape. However, previous research has focused on quantifying fuel loadings and using operational fire behavior models, rather than direct field measurements, to understand changes in fire severity following MPB. The 2012 Pole Creek Fire in central Oregon partially occurred in gray stage (8-15 years post-MPB epidemic) lodgepole pine forests. We examined the combined effects of MPB and fire disturbances on stand structure, and investigated the influence of previous MPB severity and fire weather on subsequent fire severity and cumulative disturbance severity. We randomly selected and installed 52 plots over a gradient of MPB and fire severity combinations and measured stand structure and fire severity characteristics. Fire severity metrics representing both crown and surface fire decreased with increased MPB severity under extreme burning conditions, following expected trends for crown fire severity, but not surface fire severity. Cumulative basal area mortality increased with MPB severity under moderate burning conditions, while other cumulative disturbance severity metrics were unrelated or weakly related to MPB severity. High severity crown fire was common despite hypothesized low canopy fuel loadings during the gray stage, indicating the importance of understanding variable mortality density of MPB outbreaks. Although long-term studies are needed to understand ecosystem recovery trajectories over time, there was no indication that a loss of ecosystem resilience occurred as a result of two sequential disturbances in this landscape.

1. Introduction

Bark beetles are important drivers of tree mortality and forest structure in North American coniferous forests (Jenkins et al. 2008). Large scale bark beetle outbreaks of recent decades (Meddens et al. 2012; Raffa et al. 2008) have created concern regarding elevated fuel loadings and exacerbated fire behavior (Jenkins et al. 2012), prompting a desire to understand the effects of multiple sequential disturbances on the landscape. The influence of mountain pine beetle (*Dendroctonus ponderosae* Hopkins, MPB¹) on fuels succession and potential fire behavior in lodgepole pine (*Pinus contorta* Douglas ex Loudon) forests following an epidemic is of particular interest (Hicke et al. 2012; Jenkins et al. 2014). Large-scale assessments have not noted a consistent, region-wide relationship between MPB activity and wildfire occurrence (Hart et al. 2015; Kulakowski and Jarvis 2011; Meigs et al. 2015). However, when disturbances do overlap spatially and temporally, there is evidence that fire behaves differently than predicted by currently used models. Perrakis et al. (2014) found higher rates of crown fire spread and more frequent active crown fire in post-MPB red and gray stage lodgepole pine stands in British Columbia as compared with fire behavior model predictions. Fire severity also can vary with the magnitude of previous MPB epidemics in the Rocky Mountains (Harvey et al. 2014a, 2014b). Although the co-occurrence of these disturbances on the landscape is relatively rare in a given year (Meigs et al. 2015), it is important to understand their combined effects on fire behavior, which influences firefighter safety (Page et al. 2013), and fire severity, which may influence rates of ecosystem recovery (Harvey et al. 2014a). At localized scales, there is some evidence of a relationship between fire hazard and previous MPB activity, but this relationship varies with time since beetle attack (TSB²) and other factors like topography, drought, fire weather, and previous fire management (Harvey et al. 2014a, 2014b; Lynch et al. 2006).

¹ Mountain pine beetle

² Time since beetle

Mountain pine beetle has been a part of the disturbance regime in lodgepole pine forests for as long records exist (Roe and Amman 1970), and has the ability to cause mortality at a landscape scale in lodgepole pine forests when epidemics occur (Cole and Amman 1980, Hansen 2014). Mountain pine beetle outbreaks often occur in high density lodgepole pine stands, typically targets large diameter (> 23 cm) trees, and may last from several years to a decade (Cole and Amman 1980). Outbreaks collapse once most preferred host trees are killed, leaving smaller diameter lodgepole pine and non-host species (Hansen 2014). This is followed by the release of advance regeneration and suppressed lodgepole pine, or forest type conversion where lodgepole pine is seral (Diskin et al. 2011; Kayes and Tinker 2012; Pelz et al. 2015; Pelz and Smith 2012). Fuels characteristics following a MPB epidemic are highly dependent on TSB and have been well studied (e.g., Klutsch et al. 2011; Page and Jenkins 2007a; Schoennagel et al. 2012; Simard et al. 2011; Woolley et al. in review). The 2-4 years following epidemic initiation (i.e., the red stage) are characterized by substantial decreases in foliar moisture which is hypothesized to exacerbate crown fire behavior (Jolly et al. 2012; Page et al. 2012), although much uncertainty remains surrounding the importance of the proportion of green attacked trees in this relationship (Hoffman et al. 2012). Throughout this stage, canopy bulk density decreases as foliage senescence occurs, while litter and fine woody fuels may begin to increase (Page and Jenkins 2007a; Simard et al. 2011; Woolley et al. in review). The gray stage (4-15 years TSB) begins when dead foliage is absent from the canopy. During this time, active crown fire potential is hypothesized to decrease considerably due to low canopy bulk density (Hicke et al. 2012). Live woody fuels (i.e., seedlings, saplings, and shrubs), coarse woody fuel load, and fine woody fuel load increase, but there is disagreement among studies regarding the effect on surface fire potential (Klutsch et al. 2011; Page and Jenkins 2007b; Schoennagel et al. 2012;

Simard et al. 2011). During the old stage (15-30+ years TSB), seedling and sapling densities continue to increase (Pelz and Smith 2012; Simard et al. 2011), and continued snag fall adds to the coarse woody fuel load (Page and Jenkins 2007a; Schoennagel et al. 2012). Crown fire potential may increase with increased canopy bulk density driven by the release and ascension of advanced regeneration and suppressed trees to the overstory (Hicke et al. 2012).

Although the relationship between MPB and fire has been well-studied, the lodgepole pine forests of central Oregon are ecologically distinct from those of the Intermountain West, where much of the previous research was based. In central Oregon, lodgepole pine is typically a climax species, forming uneven-aged, single-species stands (Simpson 2007; Stuart et al. 1989), rather than a seral species as in Rocky Mountain lodgepole pine forests (Lotan et al. 1985). While the fire regime of seral lodgepole pine forests is typically considered to be high-severity and stand replacing, central Oregon lodgepole pine is characterized as having a mixed-severity fire regime (Agee 1993; Heyerdahl et al. 2014). This may have a strong influence on the relationship between MPB severity and fire severity. Furthermore, central Oregon lodgepole pine forests exhibit low levels of cone serotiny as compared with Rocky Mountain lodgepole pine forests (Lotan and Critchfield 1990; Mowat 1960), which could lead to a significantly different post-fire stand development trajectory.

Previous research has largely focused on quantifying fuel loadings and using operational fire behavior models to investigate changes to potential fire behavior following MPB outbreaks (Hicke et al. 2012). Although these studies provide useful information regarding changes in fuel structure over time, the accuracy of fire behavior models using fuel loadings from MPB-affected stands is unknown due to limitations of currently available operational fire behavior models (Affleck et al. 2012; Cruz and Alexander 2010). Additionally, effects on the ecosystem

following multiple disturbances cannot be obtained from fire behavior models, thus, direct pre- and post-fire field measurements and observations are needed. Incorporation of fire weather data is also informative as previous studies have found variability around the relationship between previous MPB and fire severity to be partially explained by burning conditions (Harvey et al. 2014a, 2014b; Prichard and Kennedy 2014). Some recent studies have aimed to address the issue of fire behavior and fire severity following MPB by investigating fires which burned through post-MPB stands in the Rocky Mountains (Harvey et al. 2014a, 2014b). However, the relationship between fire severity and MPB severity is not fully understood; the study of additional fires in other regions and in later TSB stages would benefit the understanding of this disturbance interaction (Harvey et al. 2014b).

Predicted increases in disturbance magnitude and frequency under changing climate conditions (Dale et al. 2001) necessitate the investigation of interactions between successive forest disturbances. Understanding the effect of one disturbance on the severity of the next disturbance (i.e., linked disturbance effects; Simard et al. 2011), is instructive for management objectives such as the allocation of fuels treatments in stands with increased fire hazard and the identification of areas which may pose additional difficulties during firefighting operations (Page et al 2013). In contrast, predictions of stand development trajectories and ecosystem reorganization are strongly influenced by compound disturbance effects, in which disturbance effects on the ecosystem combine in a non-additive manner (Paine et al. 1998; Turner 2010). Compound disturbance effects in various forested ecosystems can lead to alteration of forest successional patterns and may result in a state change if the ecosystem is not resilient to these effects (Buma 2015). Compound disturbance effects are unique because they cannot be predicted by observing each disturbance individually; they must be observed where they overlap

to be understood (Paine et al. 1998). Therefore, in addition to investigating the effect of previous MPB severity on fire severity (linked disturbance effect), it is imperative to address the relationship of combined disturbance severity on ecosystem response to determine the possibility of compound disturbance effects.

A large portion of the 2012 Pole Creek Fire in central Oregon's Eastern Cascade Mountains burned in lodgepole pine forests which had experienced a MPB epidemic 8-15 years prior to fire. The Pole Creek Fire burned with mixed-severity, providing an opportunity to examine the combined effects of a single MPB outbreak and fire event at various intensities in lodgepole pine forests of central Oregon. The objectives of this case study were: 1) to quantify changes in stand structure over time following both MPB and fire, 2) to determine the effect of prior MPB severity and fire weather on subsequent surface fire severity, crown fire severity, and cumulative disturbance severity. We expected that changes to stand structure would occur at similar magnitudes over both disturbances and that lodgepole pine would remain the dominant tree species. We hypothesized that surface fire severity would increase with MPB severity due to increased surface fuel loadings (Page and Jenkins 2007a; Schoennagel et al. 2012), while we anticipated that crown fire severity would decrease as a result of decreased canopy bulk density (Klutsch et al. 2011; Simard et al. 2011; Woolley et al. in review). We hypothesized that cumulative disturbance severity would not vary with MPB severity because of the expected inverse relationship between MPB severity and fire severity.

2. Methods

2.1 Study area

The Pole Creek Fire burned within the Deschutes National Forest in the central Oregon East Cascade Mountains during the summer of 2012 (Figure 1). The area burned approximately

40% as high severity, stand-replacement fire, 36% in moderate severity, and 24% in low severity (ODA OHA Report 2014). The fire burned mostly in lodgepole pine and mountain hemlock (*Tsuga mertensiana* Bong. Carrière) plant associations (Simpson 2007). Much of the lodgepole pine forest type experienced a mountain pine beetle epidemic 8-15 years prior to the fire (USDA Forest Service 2013). Our study was confined to lodgepole pine-dominated stands with prior evidence of MPB activity and no recent management activity. Estimates of historical fire return intervals range from 26-82 years near Newberry Crater (Heyerdahl et al. 2014), to 60 years in Crater Lake National Park (Agee 1981), to 60-350 years on the Fremont National Forest (Stuart 1983). These represent the fire histories of lodgepole pine nearest to the Pole Creek Fire area, although these sites are located south of the study area. Average annual temperature in the study area is 3.6 °C with an average minimum temperature of -7.1 °C in January and an average maximum temperature of 21.0 °C in July. On average, the study area receives 152 cm of precipitation annually (PRISM Climate Group 2015). Elevation ranges from 1500 to 2050 meters (m), with slopes ranging from 0 to 30%. Subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), whitebark pine (*Pinus albicaulis* Engelm.), ponderosa pine (*P. ponderosa* Lawson & C. Lawson), and mountain hemlock were present in low abundances. Pinemat manzanita (*Arctostaphylos nevadensis* A. Gray), yellow rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.), silvery lupine (*Lupinus argenteus* Pursh), long-stolon sedge (*Carex inops* L.H. Bailey), and Ross' sedge (*C. rossii* Boott) were commonly found in the understory.

2.2 Sampling design and field measurements

We located 52 plots in lodgepole pine-dominated stands that had been mapped by Aerial Detection Survey (ADS) (McConnell et al. 2000) as experiencing a MPB epidemic within the past 8-15 years. We designed the study using a factorial design, representing combinations of

MPB severity (low, moderate, high) and fire severity (unburned, low, moderate, high; Figure 2) to ensure that the full range of disturbance conditions was captured. MPB severity categories used for plot selection were obtained using ADS data with categories represented as follows: low = 12-37 trees/ha MPB mortality, moderate = 38-74 trees/ha MPB mortality, high > 74 trees/ha MPB mortality. We did not sample stands with MPB mortality under 12 trees/ha as we considered this level of mortality to be endemic for the purposes of this study, and were interested in epidemic levels only (Andris Eglitis, Forest Health Protection, USDA Forest Service, Bend, Oregon, USA, personal communication). Fire severity categories were determined using differenced Normalized Burn Ratio (dNBR) for the fire area (Key and Benson 2006; Crystal Kolden, University of Idaho, Moscow, Idaho, USA, personal communication). We randomly located five plot locations for each disturbance severity combination using ArcGIS 10.2, for a total of 60 plots (ESRI 2013). However, we established only 52 plots, as we were unable to find suitable replacements for 8 of the unburned plot replicates, due to inconsistencies with dNBR data and ground observations (e.g., evidence of fire management activities or burned areas within plots). Plot locations were selected using generalized random-tessellation stratified (GRTS) design to avoid issues with spatial autocorrelation by incorporating spatial balance within a random sampling design (Stevens and Olsen 2004).

We completed field sampling during the summer of 2013. We estimated Composite Burn Index (CBI; Key and Benson 2006) at each plot prior to accepting dNBR fire severity classification. If the CBI rating did not generally align with previously set fire severity categories, a replacement plot was located. We sampled all trees (diameter at breast height [DBH] ≥ 5.0 cm) within an 11.3 meter radius (0.04 ha) circular plot. We recorded DBH, tree height, bole char height, percent circumference bole char, and percent crown volume scorched

and consumed by fire. Live trees were also assessed for crown class and height to crown base. Cause of death was assigned for all snags. We assigned cause of death and measured approximate DBH of downed woody material $\text{DBH} \geq 7.7$ cm. We attributed cause of death to MPB if j-shaped galleries were present on the bole of the tree. However, in plots which experienced high severity fire, many snags and downed logs were highly consumed and galleries were occasionally not visible. We classified lodgepole pine snags and logs over 15 cm DBH as killed by MPB if other snags or logs of a similar size in the same plot had MPB galleries (see Appendix A for further cause of death classification criteria). We established four 25 m transects in the cardinal directions, along which we counted points with surface char (e.g., charred soil, wood, or litter) at 0.25 m intervals. We measured seedlings and saplings < 5 cm DBH for height and basal diameter in four 3.2 m radius (0.004 ha) subplots located 25 m from plot center in the ordinal directions. We measured soil char depth at four points within each subplot to obtain an average soil char depth.

2.3 Fire weather

We created a single variable to represent fire weather using daily fire progression maps and weather data from remote automated weather stations (RAWS) to separate daily progression into moderate or extreme burning conditions. Moderate burning conditions were characterized by maximum temperatures under 20 °C, minimum relative humidity over 20%, and maximum relative humidity of at least 60%. Extreme burning conditions were characterized by maximum temperatures over 20 °C, minimum relative humidity ranging from 0 to 20%, and maximum relative humidity below 60% (see Appendix B for burning condition classification criteria). Wind speed was poorly captured by the nearest RAWS (Jon Bonk, National Weather Service,

Portland, Oregon, USA, personal communication) and was not used to create the burning condition metric.

2.4 Statistical analysis

We used data measured in the field to represent mountain pine beetle and fire severity in statistical analyses, rather than the categories assigned using ADS data and dNBR values. Although the study was designed as a factorial, we analyzed the data as continuous variables, to capture a continuum of disturbance severity. Density and basal area mortality from MPB and fire were estimated using cause of death data for snags and downed logs. We reconstructed live and dead (snag) stem density, live and dead (snag) basal area, percentage of live basal area which was lodgepole pine, and quadratic mean diameter (QMD) values pre-MPB, post-MPB (pre-fire), and post-fire stages. We assumed that trees < 8 cm DBH that were killed by fire or live following fire established after the MPB outbreak and did not include them in our estimates of pre-MPB stand structure. We conducted one sample t-tests of differences in values of stand structure characteristics among stages (pre-MPB, post-MPB, post-fire) at the plot level to detect whether changes were statistically different from zero and used the Bonferroni correction for multiple comparisons ($\alpha = 0.017$). Due to very low estimates of pre-MPB snags, we chose not to make comparisons with pre-MPB snag density or basal area, as it is likely that these snags were consumed by fire.

Mountain pine beetle outbreak severity (hereafter, MPB severity) was estimated from total basal area killed by MPB. We assessed plot-level fire severity using six separate metrics representing various vertical strata and fire effects. We quantified surface fire severity using soil char depth (an average of the four subplot soil char depths) and proportion of ground charred (converted from total counts of charred points along the four transects). We estimated crown fire

severity using average bole char height and proportion of canopy consumed (trees live prior to fire which had 100% canopy consumption as a proportion of total trees live prior to fire). We assessed overall fire severity using total basal area killed by fire and average CBI. We quantified cumulative disturbance effects using four separate metrics representing combined effects from MPB and fire disturbances. We estimated cumulative basal area mortality (total basal area killed by MPB and fire disturbances) and post-fire live basal area. Many plots lacked live trees and regeneration following fire, so we also assessed two binary response variables, post-fire tree survival (presence or absence of at least one tree following fire) and post-fire regeneration presence (presence or absence of at least one seedling or sapling following fire), to understand seed source availability and the potential for ecosystem recovery.

We used linear models to determine the relationship between MPB severity and fire or cumulative disturbance severity metrics: average bole char height, average CBI, soil char depth, and post-fire basal area. We log-transformed basal area killed by fire and we log-log transformed cumulative basal area mortality to correct for heteroscedasticity prior to fitting linear models with MPB severity. When the assumption of a normal distribution was not met, we used generalized linear models assuming a binomial distribution (i.e., logistic regression) to determine the effect of MPB severity on proportion of ground charred, proportion of canopy consumed, post-fire tree survival, and post-fire regeneration presence. We corrected for overdispersion when necessary. We included burning condition as a covariate in all models, as well as an interaction term between MPB severity and burning condition, to assess interactive effects of predictors of fire severity. All statistical analyses were conducted using R statistical software (R Development Team 2014). Reported values are means and standard errors unless otherwise noted. For all severity analyses, we set $\alpha = 0.10$ and interpret $0.05 < P < 0.10$ as suggestive

evidence of a relationship to increase the chance of capturing ecological relationships and to reduce the probability of making a Type II error.

3. Results

3.1 Structural changes

Stand structure within the Pole Creek Fire area was significantly altered by MPB and fire disturbances (Figure 3). There was an estimated mean decrease in live density of 288 stems/ha ($t_{51} = 5.30$, $p < 0.001$) and 912 stems/ha ($t_{51} = 8.10$, $p < 0.001$) between the pre-MPB and post-MPB stage, and between the post-MPB and the post-fire stage, respectively. This resulted in over a five-fold decrease in live density between pre-MPB and post-fire stages ($t_{51} = 13.56$, $p < 0.001$; Figure 3). Similarly, mean live basal area declined significantly between pre-MPB and post-fire stages ($t_{51} = 19.52$, $p < 0.001$), decreasing by an estimated 19.1 m²/ha following MPB ($t_{51} = 12.28$, $p < 0.001$) and decreasing by an additional 16.4 m²/ha following fire ($t_{51} = 8.29$, $p < 0.001$; Figure 3). Conversely, mean snag density increased from post-MPB levels by an estimated 696 stems/ha following fire ($t_{51} = 6.72$, $p < 0.001$), while mean snag basal area increased by an estimated 10.6 m²/ha ($t_{51} = 5.23$, $p < 0.001$; Figure 3). Mean QMD decreased by an estimated 3.2 cm between pre-MPB and post-MPB stages ($t_{51} = 9.94$, $p < 0.001$), then increased by an estimated 3.5 cm between post-MPB and post-fire stages ($t_{26} = 4.14$, $p < 0.001$), and resulted in no difference between pre-MPB and post-fire mean QMD ($t_{26} = 0.018$, $p = 0.986$; Figure 3). There was evidence of an estimated 11% decrease in mean live basal area which was lodgepole pine between pre-MPB and post-MPB stages ($t_{51} = 7.46$, $p < 0.001$). However, there was no statistical evidence of a difference in percentage of live basal area which was lodgepole pine between post-MPB and post-fire stages ($t_{26} = 1.43$, $p = 0.164$) or pre-MPB and post-fire stages ($t_{26} = 1.06$, $p = 0.297$; Figure 3). Additionally, these trends indicate general structural

changes following disturbance in the study area, but we also note that there was a wide range of values represented for all pre-MPB, post-MPB, and post-fire stand structure metrics at the individual plot level (Appendix C).

3.2 Influence of MPB severity on fire and cumulative disturbance severity

Each of the six metrics representing crown, surface, and overall fire severity decreased with increased MPB severity in plots which burned under extreme burning conditions (Figure 4). Average bole char height, CBI, and soil char depth decreased by an estimated 1.25 m, 0.48 units, and 0.24 cm, respectively, with each 10 m²/ha increase in MPB-killed basal area, under extreme burning conditions (Table 1). There were decreasing proportional changes of 0.09 and 0.052 in canopy consumed and ground charred, respectively, for each 1 m²/ha increase in MPB-killed basal area, under extreme burning conditions (Table 1). Basal area killed by fire decreased by an estimated 8.2% under extreme burning conditions for each 1 m²/ha increase in MPB-killed basal area (Table 1). However, there was no evidence of a relationship between MPB severity and any of the metrics used to describe fire severity under moderate burning conditions (Table 1). The interaction between MPB severity and burning condition was only statistically significant in the relationship of basal area killed by fire to MPB severity ($P = 0.034$), indicating substantial variability around these relationships, particularly under moderate burning conditions (Table 1).

In general, cumulative disturbance severity was not as strongly related to MPB severity as was fire severity (Figure 5). Cumulative basal area mortality was the only cumulative disturbance severity metric of the four metrics tested that was strongly related to MPB severity, and there was strong evidence of an interaction between MPB severity and burning condition ($P = 0.005$). There was an estimated 7.1% increase in cumulative basal area mortality with each 10% increase in basal area killed by MPB under moderate burning conditions, while there was

no evidence of a relationship under extreme burning conditions (Table 2). Post-fire live basal area and probability of post-fire tree survival were not related to MPB severity under moderate or extreme burning conditions (Figure 5; Table 2). There was suggestive evidence that probability of post-fire regeneration presence increased with MPB severity, under moderate burning conditions, but this relationship was highly variable ($P = 0.091$; Table 2).

4. Discussion

Several landscape-scale assessments have indicated that MPB-affected lodgepole pine forest are not more likely to experience wildfire than their unattacked counterparts (Hart et al. 2015; Kulakowski and Jarvis 2011; Meigs et al. 2015), but it is important to understand the combined effects of these disturbances when they do overlap in space and time, as they did in the Pole Creek Fire. Although this is a case study of a single MPB outbreak and fire event, the findings of this study illuminate some of the uncertainties associated with previous fuels succession research by examining the relationship between fire severity and previous MPB outbreak severity using empirical data. There was evidence that the Pole Creek Fire and MPB outbreak it overlapped were linked disturbances, as fire severity decreased with increasing MPB severity in all vertical strata when burning conditions were extreme. This result generally supports the findings of previous post-MPB fuels and potential fire behavior research for gray stage stands (Harvey et al. 2014a; Hicke et al. 2012).

Given trends of lowered canopy bulk density during this stage in both Rocky Mountain (Klutsch et al. 2011; Simard et al. 2011) and central Oregon (Woolley et al. in review) lodgepole pine forests, we expected that crown fire severity would decrease with increased MPB severity, similar to previous findings in the Intermountain West (Harvey et al. 2014a, 2014b). This hypothesis was supported, as measures of crown fire severity (proportion of canopy consumed

by fire and average bole char height) as well as overall fire severity (basal area killed by fire and average CBI), decreased with increased MPB severity under extreme burning conditions (Figure 4). High severity crown fire was common in the Pole Creek fire, as indicated by the substantial number of plots with over 75% canopy consumption and with average bole char heights over two meters (Figure 4), the average canopy base height for gray stage lodgepole pine stands in central Oregon (Woolley et al. in review). This suggests that previous hypotheses that the potential for severe crown fire is low in gray stage lodgepole pine forests (Hicke et al. 2012) may not apply in central Oregon. Central Oregon lodgepole pine forests have an uneven-aged structure (Simpson 2007; Stuart et al. 1989), which may contribute to more variation in MPB severity across the landscape than is often observed in single-aged Rocky Mountain lodgepole pine forests. However, many studies of post-MPB stand structure in the Rocky Mountains indicate that lodgepole pine is nearly always present following an outbreak (Collins et al. 2011; Diskin et al. 2011; Klutsch et al. 2009; Pelz et al. 2015) and 100% overstory mortality is rare (Simard et al. 2012). This indicates that heterogeneity within post-MPB stands may also be important to consider when addressing questions regarding fire severity in Rocky Mountain lodgepole pine forests. Although the overall trend of fuels succession suggests lower crown fire potential during the gray stage due to lowered canopy bulk density (Hicke et al 2012), it is important to recognize that high levels of structural variability in post-MPB landscapes (Hansen 2014) can lead to diverse fire behavior and fire severity.

Surface fire severity was expected to increase with increased MPB severity due to high surface fuel loadings during this TSB (Page and Jenkins 2007a; Schoennagel et al. 2012), which were expected to be elevated at higher levels of MPB mortality. However, both measures of surface fire severity (proportion of ground charred and soil char depth) decreased with increased

MPB severity under extreme burning conditions (Figure 4). This unexpected trend may be related to the low levels of litter and duff in central Oregon lodgepole pine forests compared with Rocky Mountain lodgepole pine forests (Agee 1993). Additionally, the high level of variability surrounding these relationships indicates that there were likely many other factors driving surface fire severity; the use of a different surface fire severity metric may also have indicated a different relationship. It is possible that surface fire severity measured as consumption of downed woody fuels or mortality of understory species may have increased with MPB severity. However, without pre-fire measurements of live and downed woody surface fuels, we could not calculate these measures with any precision. Experimental burning should be conducted on MPB-affected plots for which there is an inventory of pre-fire fuels in all strata to further understand this relationship.

There was evidence of a relationship between MPB severity and fire severity only under extreme burning conditions, indicating a possible influence of fire weather on this relationship. We hypothesize that this shows that fire severity is driven by extreme fire weather at low levels of MPB severity, when more canopy fuels are available, but at higher levels of MPB severity, forest stands become canopy fuel-limited and high severity fire does not occur despite extreme weather conditions. However, the interactive effect between MPB severity and burning condition was only statistically detectable when fire severity was defined as basal area killed by fire (Table 1). This indicates a high level of variability around the relationship of fire severity to MPB severity under moderate burning conditions (Figure 4). We hypothesize that some of the variability of this relationship may be related to factors not incorporated in this study, such as topographical features or pre-fire surface fuel loading. Future research should attempt to include these omitted variables to increase understanding of this relationship. Previous findings

regarding the effects of burning conditions on the relationship between MPB outbreak severity and fire severity are not consistent. Some studies indicate that the relationship between fire severity and MPB severity is overridden by fire weather under extreme burning conditions (Harvey et al. 2014a). Other work indicates that a detectable effect of previous bark beetle outbreak severity on fire severity remains even under extreme burning conditions in both Engelmann spruce (Bigler et al. 2005) and lodgepole pine forests (Prichard and Kennedy 2014) and in some circumstances the effect is observed only under extreme burning conditions (Harvey et al. 2014b). These differences likely arise from disparities in definitions of extreme and moderate burning conditions, as this distinction is coarse and groups multiple aspects of fire weather into a single variable. Additionally, there are difficulties in obtaining accurate local fire weather data in real time for sites within a fire, as observations often come from few weather stations near or within the fire perimeter. Collection of fine-scale fire weather data at a plot scale is necessary to better understand the complex relationships between fire severity, MPB severity, and fire weather. The development of teams dedicated to real-time fire behavior observation should be prioritized to aid in the collection of detailed fire weather and fire behavior data for use in future studies of disturbance interaction.

Cumulative disturbance severity metrics did not demonstrate a consistent relationship with MPB severity in the Pole Creek Fire. Cumulative basal area mortality was positively related to MPB severity under moderate burning conditions, but this relationship was not apparent under extreme burning conditions (Table 2). This indicates that the effect of previous MPB severity on cumulative basal area mortality is overridden under extreme burning conditions (i.e., cumulative basal area mortality is driven primarily by fire severity), while this is not the case under moderate burning conditions. Post-fire live basal area and post-fire tree survival were

not related to MPB severity (Figure 5), suggesting that post-fire stand development trajectories may not be slowed at higher levels of MPB, as surviving trees represent available seed sources for natural regeneration of the stand. We suggest that the lack of a trend between MPB severity and post-fire tree survival and live basal area may be attributed to the 8 to 15 year lag between disturbances. During the time between the MPB outbreak and fire, advanced regeneration was likely released to the overstory (Collins et al. 2011; Hansen 2014), leading to some re-establishment of the stand prior to fire. There was also suggestive evidence that post-fire regeneration presence increased with MPB severity, but the high level of variability in this relationship necessitates further investigation to verify the existence of a biological relationship (Table 2). There is no evidence to suggest that compound disturbance effects are altering ecosystem recovery patterns or pushing the ecosystem into a novel state, as demonstrated in some other systems experiencing successive disturbances (Buma and Wessman 2011; Harvey et al. 2013; Kulakowski et al. 2013). However, long-term stand development studies are needed to understand these dynamics over time, as well as how they would be altered at various time lags between disturbances.

Stand structure changed significantly following both the MPB epidemic and the Pole Creek Fire. Live basal area and density decreased over both disturbances, while snag basal area and density increased, as expected (Figure 3). Quadratic mean diameter and percent basal area which was lodgepole pine decreased following MPB, but returned to pre-MPB levels following fire in plots with live trees following fire (Figure 3). However, there was considerable variation in each of these structural attributes at a plot level pre-MPB, post-MPB, and post-fire (Appendix C), indicating heterogeneity on the landscape prior to and following these disturbances. Central Oregon lodgepole pine forests differ from those of the Rocky Mountains, where lodgepole pine

is seral and establishes in even-aged stands following stand-replacement fire (Lotan et al. 1985, Romme 1980). Lodgepole pine in central Oregon often exists in climax, uneven-aged stands (Simpson 2007; Stuart et al. 1989), experiences a mixed-severity fire regime (Agee 1993; Heyerdahl et al. 2014), and exhibits low levels of cone serotiny (Lotan and Critchfield 1990; Mowat 1960). Our study area was at a higher elevation than many of the lodgepole pine forests in the region and included some stands which were not climax lodgepole pine. However, the study area generally reflects biological conditions more similar to central Oregon climax lodgepole pine forests than Rocky Mountain seral lodgepole pine forests. Previous work in this region has shown that mountain pine beetle, pine engraver (*Ips pini* Say), and various decay fungi interact to create structurally heterogeneous landscapes of lodgepole pine forest, which is perpetuated by a mixed-severity fire regime (Gara et al. 1985; Geiszler et al. 1980). Variable dwarf mistletoe (*Arceuthobium americanum* Nutt. Ex Engelm.) severity also contributes to heterogeneous stand structure following MPB epidemics in this region, which may influence the pattern of future MPB epidemics on the landscape (Agne et al. 2014). The structural heterogeneity in the study area following MPB and fire fits with the previous understanding that this region's mixed-severity disturbance regime leads to structural conditions which perpetuate a mixed-severity disturbance regime, indicating ecosystem resilience.

The wide range in percentage of live trees which were lodgepole pine observed indicates that some parts of the study area were likely transitioning to mixed conifer forests as a result of the MPB epidemic. It is unclear however, whether the several stands which continued to have low representation of lodgepole pine following fire will be converted to mixed-conifer stands as this data represents site conditions only one year post-fire. Given the overall trend of increased percentage lodgepole pine following fire as compared with the post-MPB stage (Figure 3), it is

unlikely that conversion to a different forest type will be common within the study area. However, long-term studies of ecosystem recovery following disturbances of various combinations and magnitudes are needed to understand how these processes occur over time. Previous work has shown variability of species composition following MPB with evidence of both species composition shifts and the persistence of lodgepole pine on the landscape, depending on pre-outbreak stand conditions (Diskin et al. 2011; Kayes and Tinker 2012; Pelz et al. 2015; Pelz and Smith 2012). However, these studies were conducted in Rocky Mountain lodgepole pine forests, where lodgepole pine is seral. The results from this study indicate that lodgepole pine remains the dominant species in this region following MPB, although several stands contained a large component of other overstory species, such as subalpine fir and mountain hemlock. These stands likely represent areas in transitional zones between climax lodgepole pine and mixed-conifer vegetation types. In addition, our results support previous findings from work in the Rocky Mountains that the occurrence of MPB followed closely in time by wildfire (Edwards et al. 2015; Harvey et al. 2014a) favors the persistence of lodgepole pine. Although these results are similar, the mechanism driving this relationship likely differs between ecological regions. The mechanism of lodgepole pine persistence following fire suggested by previous studies (i.e., serotiny), is uncommon in the lodgepole pine forests of central Oregon (Lotan and Critchfield 1990; Mowat 1960). However, there is evidence that the abundant soil moisture and moderate microclimate provided by snags and downed woody debris are beneficial to the regeneration of lodgepole pine in this region (Stuart et al. 1989).

The findings of this research have important implications for the management of forests previously disturbed by MPB, particularly in central Oregon lodgepole pine forests. These results suggest that it may be possible to use MPB severity data to target individual stands within

gray stage post-MPB lodgepole pine forests for fuels reduction treatments (Jenkins et al 2012), which would be particularly important in the wildland-urban interface or other areas where resource protection objectives are of high importance. If stands are selected for treatment, those with lower MPB mortality density should be targeted. High severity fire was more prevalent in stands with low MPB mortality due to the higher proportion of live trees (and therefore fine aerial fuels) remaining. However, the high level of variability associated with these disturbances presents challenges with interpreting their relationships to one another, as well as to future stand trajectory patterns. The results of this study represent findings from a single fire which overlapped a single MPB outbreak. Data from additional fires overlapping MPB events, ranging from outbreaks in the red stage to several decades since MPB outbreak, must be investigated to gain a greater understanding of the complex relationship between these disturbance agents.

Additional challenges in active fire management are posed in gray stage stands as increased snag density is associated with increased direct hazard to firefighters while higher coarse woody debris loadings are associated with increased difficulty of fire suppression activities like fireline construction (Page et al. 2013; Jenkins et al. 2014). These hazards are further increased in stands with heavy MPB mortality. However, it appears that the stands with the highest MPB mortality density effectively acted as fire breaks and generally experienced low severity surface fire or did not burn. It is important for managers to understand the increased hazards associated with firefighting operations in post-MPB stands, but stands with high MPB mortality may act as natural fuels treatments on the landscape by limiting severe crown fire. This information must also be put in the context of many other factors not included in this study which influence fire behavior and fire severity. Differences between cumulative basal area mortality and post-fire live basal area among MPB severities are small and perhaps completely

negligible. This indicates that there is no evidence that an MPB epidemic followed by a fire leads to a state change in this system and ecological management interventions are not necessary for ensuring forest resilience. However, monitoring programs should be initiated to follow stand development trajectories to understand these patterns over time.

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Tables

Table 1. Effects of mountain pine beetle (MPB) killed basal area (BA) under moderate and extreme burning conditions (BC) on fire severity metrics.

Response Variable	Estimate	Test	95% CI		P
Explanatory Variables		Statistic	Lower	Upper	
Average Bole Char Height (m) ^a					
MPB-killed BA : BC moderate	-0.093	$t_{48} = 0.341$	-0.244	0.058	0.223
MPB-killed BA : BC extreme	-0.125	$t_{48} = -2.208$	-0.239	-0.011	0.032
MPB-killed BA*BC ^b		$F_{1,48} = 0.116$			0.735
Average Composite Burn Index ^a					
MPB-killed BA : BC moderate	-0.020	$t_{48} = -1.054$	-0.059	0.018	0.297
MPB-killed BA : BC extreme	-0.048	$t_{48} = -3.380$	-0.076	-0.019	0.001
MPB-killed BA*BC ^b		$F_{1,48} = 1.416$			0.240
BA Killed by Fire (m ² /ha) ^c					
MPB-killed BA : BC moderate	0.997	$t_{48} = -0.117$	0.938	1.058	0.908
MPB-killed BA : BC extreme	0.918	$t_{48} = -3.781$	0.878	0.961	<0.001
MPB-killed BA*BC ^b		$F_{1,48} = 4.753$			0.034
Proportion of Canopy Consumed ^d					
MPB-killed BA : BC moderate	0.944	$z_{48} = -1.298$	0.858	1.025	0.194
MPB-killed BA : BC extreme	0.910	$z_{48} = -2.057$	0.817	0.984	0.040
MPB-killed BA*BC ^b		$\chi^2_1 = 0.349$			0.554
Proportion of Ground Charred ^d					
MPB-killed BA : BC moderate	0.994	$z_{48} = -0.247$	0.945	1.044	0.805
MPB-killed BA : BC extreme	0.948	$z_{48} = -2.677$	0.910	0.985	0.007
MPB-killed BA*BC ^b		$\chi^2_1 = 2.194$			0.139
Soil Char Depth (cm) ^a					
MPB-killed BA : BC moderate	0.001	$t_{48} = 0.050$	-0.030	0.032	0.960
MPB-killed BA : BC extreme	-0.024	$t_{48} = -2.058$	-0.047	-0.001	0.045
MPB-killed BA*BC ^b		$F_{1,48} = 1.631$			0.208

^a Response variable fit to a normal distribution. Estimates and confidence intervals are reported as means.

^b Significance test of the statistical interaction between MPB-killed BA and burning conditions.

^c Response variable log-transformed; estimates are reported as medians; medians and confidence intervals reported on the multiplicative scale; values over one represent a positive relationship and values below one represent a negative relationship.

^d Response variable fit to binomial distribution. Estimates and confidence intervals are reported as odds ratios; values over one represent a positive relationship and values below one represent a negative relationship.

Table 2. Effects of mountain pine beetle (MPB)-killed basal area (BA) under moderate and extreme burning conditions (BC) on cumulative disturbance severity metrics.

Response Variable	Estimate	Test	95% CI		P
Explanatory Variables		Statistic	Lower	Upper	
Post-fire Live BA (m ² /ha) ^a					
MPB-killed BA : BC moderate	0.219	t ₄₈ = 0.980	-0.230	0.668	0.332
MPB-killed BA : BC extreme	0.256	t ₄₈ = 1.522	-0.082	0.594	0.134
MPB-killed BA*BC ^b		F _{1,48} = 0.018			0.895
Cumulative BA Mortality (m ² /ha) ^c					
MPB-killed BA : BC moderate	1.071	t ₄₈ = 4.892	1.041	1.102	<0.001
MPB-killed BA : BC extreme	1.012	t ₄₈ = 0.956	0.987	1.039	0.344
MPB-killed BA*BC ^b		F _{1,48} = 8.835			0.005
Probability of Post-fire Tree Survival ^d					
MPB-killed BA : BC moderate	1.061	z ₄₈ = 1.216	0.969	1.182	0.224
MPB-killed BA : BC extreme	1.052	z ₄₈ = 1.400	0.983	1.137	0.162
MPB-killed BA*BC ^b		χ ₁ = 0.021			0.885
Probability of Post-fire Regeneration Presence ^c					
MPB-killed BA : BC moderate	1.101	z ₄₈ = 1.689	0.996	1.257	0.091
MPB-killed BA : BC extreme	1.035	z ₄₈ = 0.981	0.968	1.115	0.327
MPB-killed BA*BC ^b		χ ₁ = 0.906			0.341

^a Response variable fit to a normal distribution. Estimates and confidence intervals are reported as means.

^b Significance test of the statistical interaction between MPB-killed BA and burning conditions.

^c Explanatory and response variables log-transformed; estimates are reported as medians given a 10% change in the explanatory variable; medians and confidence intervals reported on the multiplicative scale; values over one represent a positive relationship and values below one represent a negative relationship.

^d Response variable fit to binomial distribution. Estimates and confidence intervals are reported as odds ratios; values over one represent a positive relationship and values below one represent a negative relationship.

532 **Figure captions**

533 Figure 1. Sampling map of plot network located within the Pole Creek Fire perimeter in the
534 Deschutes National Forest, Oregon.

535 Figure 2. Photos of field plots representing the four categories of fire severity used in plot
536 selection: A) unburned, B) low severity, C) moderate severity, and D) high severity.

537
538 Figure 3. Mean ($\pm 95\%$ CI) values for stand structure attributes prior to MPB epidemic, following
539 MPB epidemic, and following fire³.

540 Figure 4. Fire severity metrics vs. basal area (BA) killed by mountain pine beetle (MPB) by
541 burning condition.

542 Figure 5. Cumulative disturbance severity metrics vs. basal area (BA) killed by mountain pine
543 beetle (MPB) by burning condition.

³ Letters above each bar indicate results of comparisons among the three stages; different letters indicate differences in means are significantly different from zero (Bonferroni correction for multiple comparisons; $\alpha = 0.017$). *Data not shown due to probable underestimation of pre-MPB snag density and snag basal area.

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729 Appendices

730 Appendix A. Cause and timing of death classification criteria used for reconstruction of MPB
731 epidemic and fire severity. Adapted from Harvey et al. (2014).

Classification	Description	Trees sampled (%)
Pre-disturbance snag (dead prior to MPB epidemic and fire)	Highly consumed bole, highly weathered/decayed, no evidence of MPB activity, dead at time of sampling	0.86
Killed by MPB prior to fire -- Visible cambium	No needles remaining in crown, fully excavated MPB galleries in cambium, exit holes in bark (if remaining), dry cambial tissue, dead at time of sampling	23.73
Killed by MPB prior to fire -- No visible cambium	No needles remaining in crown, deeply charred bole, no remaining cambial tissue in which to find MPB galleries, > 15 cm DBH, dead at time of sampling	2.04
Killed by fire	Charred bark, branches, outer sapwood, no evidence of MPB (galleries or exit holes), not highly decayed/weathered, dead at time of sampling	50.83
Killed by fire -- MPB present at time of fire	Charred bark, branches, outer sapwood, partial MPB galleries, adult beetles present under bark, no exit holes, not highly decayed/weathered, dead at time of sampling	0.24
Live tree	Green foliage, no sign of MPB activity	16.50
Unknown cause and timing of death	No needles remaining in crown, deeply charred bole, no remaining cambial tissue, < 15 cm DBH, dead at time of sampling	5.81

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734 Appendix B. Fire weather attributes of plots burned under extreme and moderate burning
735 conditions.

736				
Burning Condition	Minimum Relative Humidity (%)	Maximum Relative Humidity (%)	Average Temperature (°C)	Maximum Temperature (°C)
Extreme	0 - 20	26 - 57	12.1 - 19.9	22.2 - 27.8
Moderate	20 - 44	62 - 97	7.2 - 12.5	13.3 - 20.3

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740 Appendix C. Stand structure metrics representing conditions prior to mountain pine beetle epidemic (Pre-MPB), following mountain
741 pine beetle epidemic and prior to fire (Post-MPB), and following fire (Post-Fire) for each of 52 plots.
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Plot	Pre-MPB				Post-MPB						Post-Fire					
				LP				Snag	LP				Snag	QMD	LP	
	BA (m ² /ha)	Density (stems/ha)	QMD (cm)	BA (%)	BA (m ² /ha)	BA (m ² /ha)	Density (stems/ha)	Density (stems/ha)	QMD (cm)	BA (%)	BA (m ² /ha)	BA (m ² /ha)	Density (stems/ha)	Density (stems/ha)	QMD (cm)	BA (%)
HH1	41.8	1825	17.1	93.8	27.7	14.6	1375	625	16.0	89.3	0.0	36.7	0	1700	1700	-
HH2	40.4	1375	19.4	45.1	20.5	20.6	975	575	16.3	13.2	0.0	34.6	0	1375	1375	-
HH3	29.3	1700	14.8	77.2	19.4	10.9	1375	600	13.4	62.8	0.0	28.4	0	1900	-	-
HH4	33.2	2600	12.8	80.2	26.4	8.4	2400	650	11.9	70.9	0.0	29.9	0	2600	-	-
HH6	55.2	1325	23.0	27.6	29.9	25.9	1000	500	19.5	6.9	0.0	50.4	0	1325	-	-
HL3	46.4	1125	22.9	91.3	9.2	37.8	575	725	14.3	88.6	7.6	35.8	350	825	16.62	86.1
HL4	58.5	1900	19.8	93.8	22.1	37.6	1125	1125	15.8	100.0	17.2	38.8	575	1500	19.49	100.0
HL1B	52.5	850	28.0	67.3	5.8	46.8	275	625	16.4	72.9	0.0	36.7	0	575	-	-
HL4B	43.2	1475	19.3	97.4	14.7	29.8	975	900	13.9	89.1	11.5	26.3	600	1050	15.63	93.3
HL5B	36.0	1225	19.3	87.4	14.5	21.9	725	650	16.0	66.9	9.4	19.1	325	800	19.14	87.7
HM1	42.3	950	23.8	88.7	15.8	26.8	575	475	18.7	69.2	5.6	32.4	75	875	30.83	14.7
HM2	35.7	1650	16.6	45.1	25.1	11.4	1200	625	16.3	36.4	0.0	31.6	0	1700	-	-
HM3	28.6	1050	18.7	73.7	22.3	7.2	1000	300	16.9	66.3	0.0	24.3	0	1100	-	-
HM6	41.5	1500	18.8	48.8	26.7	15.5	1200	500	16.8	29.9	1.2	33.5	25	1400	24.6	100.0
HM5B	35.5	1025	21.0	88.6	18.6	17.3	725	400	18.1	85.8	0.0	32.9	0	1050	.	.
HU2	38.2	1450	18.3	85.9	17.1	22.6	1275	600	13.0	66.6	17.1	22.6	1275	600	13.03	66.6
HU5	45.2	825	26.4	93.2	9.6	35.7	325	525	19.4	100.0	9.6	35.6	325	500	19.41	100.0
LH1	39.8	2175	15.3	81.8	29.4	12.3	1975	675	13.8	72.5	0.0	40.7	0	2575	-	-
LH2	40.9	2700	13.9	75.2	32.2	12.0	2925	700	11.8	64.5	0.0	39.8	0	3400	-	-
LH4	49.1	1675	19.3	43.1	40.7	10.3	1800	400	17.0	29.7	0.0	48.0	0	2025	-	-
LH6	74.8	1525	25.0	25.1	68.8	8.0	1900	225	21.5	16.5	0.0	72.9	0	2025	-	-
LH6B	39.0	1725	17.0	69.6	19.3	20.8	1350	700	13.5	55.5	0.0	29.6	0	1700	-	-
LL1	21.2	750	19.0	66.3	12.2	9.3	475	350	18.1	69.6	12.2	6.4	475	225	18.09	69.6
LL2	33.6	900	21.8	100.0	10.7	23.2	475	525	17.0	98.1	7.8	20.3	375	450	16.27	97.4
LL1B	35.9	575	28.2	31.8	27.7	8.7	525	200	25.9	11.4	25.4	6.7	275	350	34.27	9.5
LL1BB	29.1	775	21.9	87.1	14.5	14.7	425	375	20.8	74.1	7.1	12.1	175	350	22.76	100.0
LL2B	58.7	1875	20.0	90.2	23.5	36.7	1500	850	14.1	73.1	15.8	38.1	750	1400	16.38	87.5
LM1	55.8	4325	12.8	61.4	50.8	15.0	6175	1025	10.2	43.5	23.1	34.8	2250	4325	11.44	43.8
LM3	40.2	2150	15.4	87.4	21.0	19.9	1450	875	13.6	74.5	0.0	32.3	0	1875	-	-
LM4	45.1	2050	16.7	94.5	31.0	14.5	1650	500	15.5	91.6	0.0	42.1	0	1875	-	-
LM3B	46.5	2200	16.4	100.0	32.8	14.1	1775	525	15.3	99.5	1.7	35.8	25	1725	28.9	100.0
LM5B	47.4	1650	19.1	67.9	33.8	15.5	1575	550	16.5	70.7	1.9	44.0	25	1775	30.7	100.0

LU2	57.5	1150	25.2	69.3	26.3	32.3	800	650	20.4	51.8	26.3	26.8	800	500	20.43	51.8
LU4	54.8	2000	18.7	99.5	24.7	31.2	1275	1075	15.7	98.5	24.7	27.0	1275	925	15.7	98.5
LU6B	54.7	1675	20.4	89.5	17.5	38.7	925	1175	15.5	66.0	17.0	38.7	900	1175	15.49	65.1
MH1	32.5	1550	16.3	64.8	26.2	7.4	1550	350	14.7	56.1	0.0	27.0	0	1625	-	-
MH3	28.1	1500	15.5	41.8	22.0	7.2	1275	525	14.8	26.4	0.0	27.9	0	1700	-	-
MH4	34.3	1525	16.9	76.2	12.7	22.6	1075	800	12.3	27.3	0.0	24.0	0	1475	-	-
MH5	36.2	1050	21.0	67.4	20.5	16.0	825	325	17.8	60.4	0.0	26.7	0	975	-	-
MH6B	57.9	1650	21.1	35.9	42.9	15.9	1375	525	19.9	13.0	0.0	51.8	0	1725	-	-
ML4	50.5	1625	19.9	94.7	16.3	34.7	1000	775	14.4	90.0	12.5	30.0	475	1075	18.26	95.6
ML6	64.4	1650	22.3	32.4	51.4	14.3	1325	675	22.2	14.9	33.1	29.4	600	1150	26.52	13.1
ML1B	24.0	700	20.9	59.7	19.1	5.3	625	150	19.7	48.8	9.0	9.6	250	375	21.39	52.9
ML3B	19.2	675	19.0	94.9	7.1	12.4	400	375	15.0	84.9	6.0	13.0	250	475	17.39	89.5
ML6B	45.1	775	27.3	43.6	32.7	12.6	575	225	26.9	22.1	31.8	11.9	500	200	28.49	22.7
MM1	36.1	925	22.3	94.7	27.9	8.6	825	200	20.7	94.8	0.0	27.7	0	825	-	-
MM3	50.0	1325	21.9	53.2	18.7	31.7	975	475	15.7	14.3	0.0	42.9	0	1300	-	-
MM4	48.6	1850	18.3	99.5	22.2	26.7	1075	900	16.2	99.0	0.0	39.6	0	1450	-	-
MM5	53.3	1050	25.4	81.8	12.7	41.0	500	650	18.0	66.2	0.0	36.8	0	775	-	-
MM6	40.7	1150	21.2	87.2	18.9	23.0	1025	500	15.3	70.5	5.0	21.4	100	1075	25.26	100.0
MU5	67.0	2500	18.5	95.5	34.4	33.7	1700	1150	16.1	93.0	34.4	28.2	1700	900	16.06	93.0
MU6	18.0	650	18.8	100.0	14.7	3.6	650	125	17.0	100.0	14.7	0.7	650	75	16.98	100.0

744 BA = basal area, QMD = quadratic mean diameter, LP BA = live lodgepole pine basal area as a percentage of total live basal area. “ –

745 ” = no value due to lack of live trees on plot.

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