THESIS

FOREST RECOVERY TRENDS FOLLOWING AN UNPRECEDENTED MOUNTAIN PINE BEETLE OUTBREAK IN THE SOUTHERN ROCKY MOUNTAINS

Submitted by

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ABSTRACT

FOREST RECOVERY TRENDS FOLLOWING AN UNPRECEDENTED MOUNTAIN PINE BEETLE OUTBREAK IN THE SOUTHERN ROCKY MOUNTAINS

Following the mountain pine beetle (MPB) outbreak in the early 2000s in the southern Rocky Mountains, questions remain about what the structure and composition of lodgepole pine forests will look like as they recover. I used Forest Inventory and Analysis data collected by the US Department of Agriculture Forest Service, together with hierarchical cluster analysis, to separate 626 subplots into unique forest type groups based on their post-outbreak overstory and understory stand structure and composition. The subplots had all been dominated by lodgepole pine in the overstory prior to the outbreak and had all experienced at least 10% basal area mortality. I verified the forest type groups through multi-response permutation procedures and characterized them through indicator species analysis. I used a random forest analysis to determine how a suite of abiotic and biotic variables were predictive of the forest type groups. Post-outbreak stands separated into five forest type groups. These groups all remained dominated by lodgepole pine in the overstory but had differing understory structures and compositions. Naming conventions for the groups were based on their “overstory/understory” dominance. The five forest type groups were lodgepole pine/lodgepole pine saplings (PICO/PICO.saps), lodgepole pine-subalpine fir/subalpine fir (PICO-ABLA/ABLA), lodgepole pine/sparse understory (PICO/Sparse), lodgepole pine/lodgepole pine seedlings (PICO/PICO.seeds), and lodgepole pine/quaking aspen (PICO/POTR). The six variables with the highest relative importance in predicting forest type were (in order) overstory basal area mortality, precipitation as snow, maximum July temperature, pre-outbreak basal area, pre-outbreak stand age, and precipitation as rain. Each of the five forest type groups varied in their probability of occurrence along gradients of the top six predictor variables. For example, the PICO/PICO.saps and PICO/Sparse groups were most likely to occur where basal area mortality was low, the PICO-ABLA/ABLA group was most likely to occur where basal area mortality was moderate to high, and the PICO/PICO.seeds and PICO/POTR groups were most likely to occur where basal area mortality was very high. Overall, my results suggest that as southern Rocky Mountain lodgepole pine forests affected by the MPB outbreak recover in the near-term, they will remain dominated by this species. However, they will have more structural and compositional diversity owing to a high degree of heterogeneity in abiotic and biotic factors, which will likely shape longer-term outcomes.

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1.1 Introduction

Following the mountain pine beetle (MPB) (*Dendroctonus ponderosae*) outbreak that occurred in the early 2000s across the Rocky Mountains, questions have arisen about how lodgepole pine (*Pinus contorta*) dominated forests will recover and what the structure and composition of these forests will look like. Furthermore, determining the drivers of these post-outbreak stand conditions has become ever more important as the frequency and severity of forest disturbances increase under the warming and drying conditions found under climate change (Allen et al., 2010; Raffa et al., 2008; van Mantgem et al., 2009).

The MPB, which is native to western North America, primarily affects lodgepole pine in addition to several other species of pine (*Pinus* spp.) (Amman, 1977; Evans and Speight, 2004). From 2000-2013, throughout the Rocky Mountains the MPB caused significant mortality of lodgepole pine across 7.4 million ha (Audley et al., 2020; Potter and Paschke, 2015; Raffa et al., 2008; van Mantgem et al., 2009). In Colorado, the MPB resulted in over 50% mortality for large diameter lodgepole pine trees (≥ 22.9 cm in diameter) from 2002-2012 (Thompson, 2017). The severity of this recent MPB outbreak in the southern Rocky Mountains was ultimately the result of an overly susceptible stand structure which consisted of higher stem densities and higher mean basal areas, which were particularly high within the southern Rocky Mountains (Hicke and Jenkins, 2008; Klutsch et al., 2009; Negron and Klutsch, 2017). Furthermore, these conditions were exacerbated by ongoing drought in the region inhibiting the ability of trees to defend themselves from the beetle (Creeden et al., 2014; Kolb et al., 2016; Udall and Overpeck, 2017). Lastly, warmer winter temperatures (Bentz and Mullins, 1999; Régnière and Bentz, 2007;

Thompson et al., 2020; Yuill, 1941), which can be attributed to climate change (Anderegg et al., 2013; van Mantgem et al., 2009), prevented any large scale MPB mortality allowing beetle populations to continue expanding during this outbreak.

Following this outbreak, the composition and structure of these lodgepole pine dominated forests have been found to be altered which has been driven by varying factors. Although lodgepole pine dominated forests often exist as pure stands, they can often be found as mixed stands with several co-occurring species such as subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and quaking aspen (*Populus tremuloides*). Previous studies have found these forests have experienced shifts in the residual overstory species composition and are projected to see gains in dominance in both basal area and density of these co-occurring species (Diskin et al., 2011; Pelz and Smith, 2012; Sibold et al., 2007). The largest gains of dominance were observed for subalpine fir and Engelmann spruce, particularly where mortality of lodgepole pine was higher, though lodgepole pine was still found to be the dominant overstory species in the majority of these stands (Collins et al., 2011; Diskin et al., 2011; Pelz et al., 2018; Perovich and Sibold, 2016). Previous studies have also found that understory regeneration and overstory recruitment in stands following the MPB outbreak was associated with pre-outbreak overstory composition, severity of overstory mortality, time since stand-replacing fire, moisture availability, and seed availability (Alfaro et al., 2015; Kayes and Tinker, 2012; Pelz and Smith, 2012; Perovich and Sibold, 2016; Sibold et al., 2007). Lodgepole pine regeneration and overstory recruitment was most likely to be favored on sites that were pure lodgepole pine (Diskin et al., 2011; Kayes and Tinker, 2012), had a higher severity of MPB caused mortality (Pelz et al., 2018; Pelz and Smith, 2012; Perovich and Sibold, 2016; Sibold et al., 2007), in stands that were generally younger (Perovich and Sibold, 2016; Sibold et al., 2007), as well as on drier sites (Kayes and Tinker, 2012; Perovich and Sibold, 2016; Sibold et al., 2007). Subalpine fir and to a lesser extent Engelmann spruce was likely to be favored for establishment and overstory recruitment where overstory mortality was moderate (Pelz et al., 2018; Perovich and Sibold, 2016; Sibold et al., 2007), in stands that were older since stand replacing disturbance (Perovich and Sibold, 2016; Sibold et al., 2007) and on sites with higher moisture availability (Andrus et al., 2018; Kayes and Tinker, 2012), but may be limited by potential seed source availability (Astrup et al., 2008; Perovich and Sibold, 2016). Quaking aspen was most likely to be favored for establishment and overstory recruitment where there was high light availability and more moisture availability, but was often limited by herbivory and lack of presence within the stand prior to the outbreak (Diskin et al., 2011; Kayes and Tinker, 2012; Pelz and Smith, 2012).

Further examination of additional potential predictors that are controlling or affecting post-outbreak composition and structure is warranted. Understanding how these different variables can influence post-outbreak composition and structure will allow land managers to identify situations which may lead to forest type conversion. Additionally, all studies previously investigating the controlling factors of forest composition and structure following MPB outbreaks have been focused on smaller study sites (6-1600 km^2) and it is important to determine if these findings will hold up on a broader landscape scale across the range of the MPB outbreak within the southern Rocky Mountains.

To address these questions, I used data collected by the Forest Inventory and Analysis (FIA) program of the United States Department of Agriculture Forest Service (USFS) to examine the recovery trends of lodgepole pine forests in the southern Rocky Mountains that were impacted by the MPB in the early 2000s. FIA subplots were classified into forest types based on their post-outbreak composition of live trees, saplings, and seedlings. The FIA data was then paired with soil, climate, and aerial insect and disease detection datasets to gain insights into how pre- and post-outbreak stand conditions, climate conditions, soil conditions, and the elapsed time since the outbreak have influenced these forest types. I hypothesized that the MPB outbreak created differing forest types according to the understory dominance of saplings and seedlings of various species. Additionally, I hypothesized that these forest type would be predicted by the variable effects of both abiotic and biotic factors.

1.2 Methods

1.2.1 Study area

The study area of interest was limited to lodgepole pine dominated forests in the Colorado and Wyoming portion of the Southern Rocky Mountains Ecoregion (US Environmental Protection Agency Level III, Ecoregion 21). The study area was further refined based on the spatial extent of the recent MPB outbreak as determined from aerial detection surveys (USDA, Forest Service, 2020) (Figure 1). Within the study area the MPB outbreak began around 2002, peaked in activity around 2009, and ended in approximately 2012 (Audley et al., 2020; Potter and Paschke, 2015; Thompson et al., 2017). In addition to lodgepole pine, forests found in the study area commonly contain Engelmann spruce, subalpine fir, and quaking aspen, along with minor components of Douglas-fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*), ponderosa pine (*Pinus ponderosa*), Rocky Mountain juniper (*Juniperus scopulorum*), and blue spruce (*Picea pungens*).

FIA subplots used across the study area (see subplot criteria below) range in elevation between 2300 and 3600 m. Total annual precipitation ranges from 367 mm at the driest sites to 1398 mm on the wettest sites, with 28 to 76% of precipitation falling as snow (PRISM, 2021).

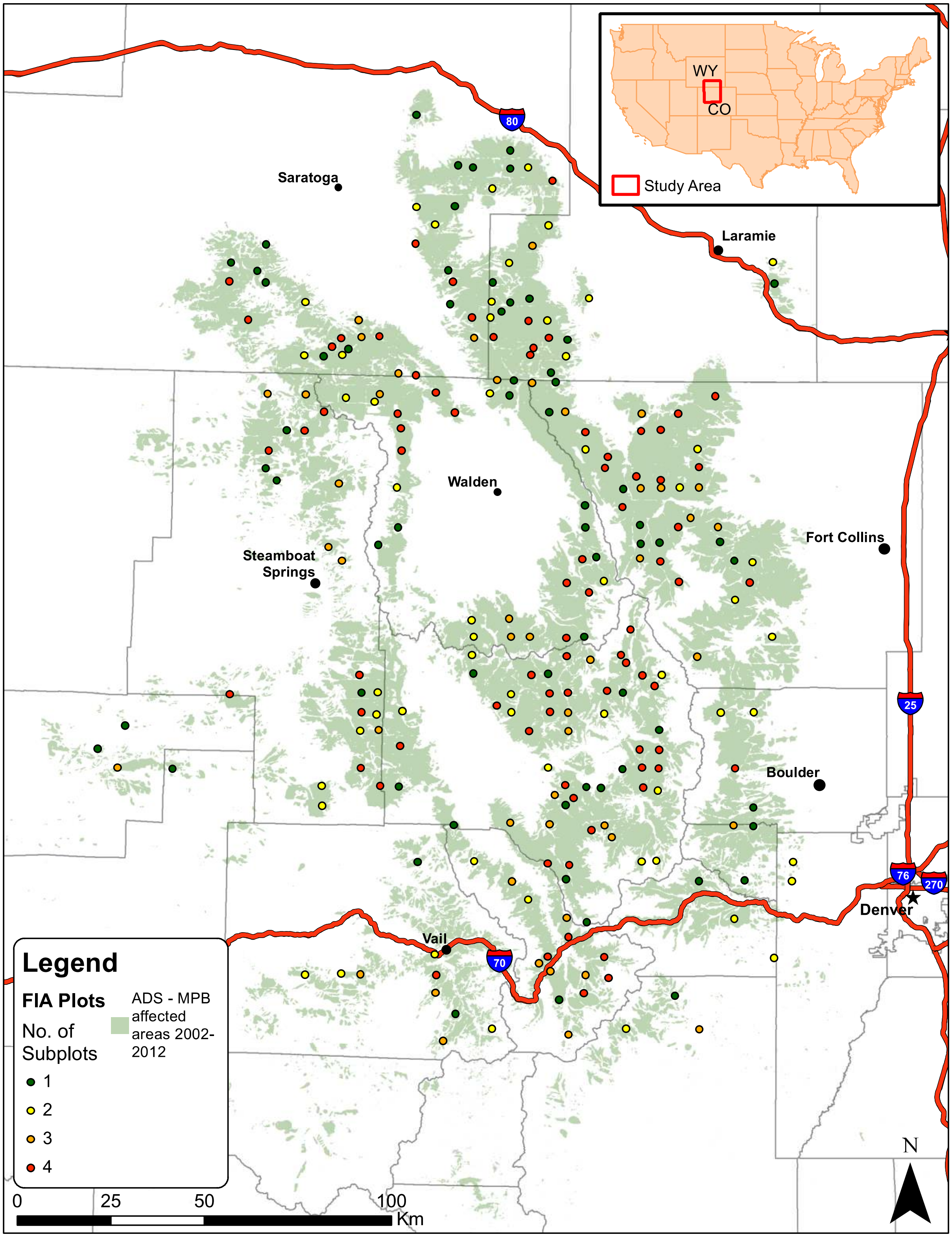

Figure 1. Map of the study area and the 244 FIA study plots. The number of subplots included from each plot is indicated by color. The area affected by the MPB from 2002-2012 as determined by the aerial detection survey is shown in green.

Mean annual temperatures range from about 1.3 to 6.2 °C, resulting in a range of 96 to 167 frost-free days (PRISM, 2021).

1.2.2 Forest inventory data

Forest inventory data for this study was obtained from the USFS's FIA program (USDA, Forest Service, 2021). The FIA program collects field data based on a systematic random sample of all forested land within the United States and its territories, regardless of ownership (Bechtold et al., 2005). FIA plots are randomly located within each cell of a 2402 ha hexagonal sampling frame placed over the landscape (Bechtold et al., 2005). Within the study area, in any given year, 10% of all accessible plots are sampled, such that all accessible plots are measured over a 10-year span.

Each FIA plot consists of four 168.1 m^2 (7.3 m radius) subplots located 36.6 m away from each other, and within each subplot is a 13.5 m^2 (2.1 m radius) microplot (Figure 2). For each plot, conditions regarding forest type, stand size, and ownership are delineated. For each subplot, variables related to topography (slope, aspect), characteristics of all trees (species, diameter at breast height, insect or disease issues, and live or dead status), understory vegetation (species and cover percent), and fuel loading (down woody debris transects) are recorded. For each microplot, variables related to saplings (species, diameter at breast height) and seedlings (species, count) are recorded. FIA defines a tree to be any live or standing dead tree greater than 12.7 cm in diameter at breast height (DBH) or diameter at root collar (DRC) depending on the species and growth form; a sapling is any live or standing dead tree between 2.5-12.6 cm DBH/DRC and a seedling is any live tree less than 2.5 cm DBH/DRC but greater than 15.2 cm tall for conifer species and 30.5 cm tall for hardwood species. Further details on all methods and variables collected on FIA plots can be found in the Rocky Mountain Research Station (RMRS) FIA Procedures Manual (RMRS - Forest Inventory & Analysis, 2020).

The analysis for this study was conducted at the scale of individual FIA subplots. FIA subplots were filtered within the study area based on a set of criteria. First, subplots measured outside the selected sampling period beginning in 2012, the approximate end of the MPB outbreak, through 2019, the most recent year FIA data were available, were excluded. Second, subplots were excluded if the pre-outbreak basal area of lodgepole pine trees was less than 50%. This metric was calculated as live lodgepole pine basal area plus recent mortality lodgepole pine basal area (trees that died within the previous 5-10 years) divided by total subplot basal area. Third, subplots were removed if they had any additional disturbances or silvicultural treatments recorded at the time of measurement, including fire, insects (excluding MPB), disease, or harvest. Fourth, subplots with limited MPB mortality (where lodgepole pine basal area mortality was <10% of total basal area) were removed from the analysis, as this small amount of mortality would be more similar to background mortality than to mortality from a large-scale disturbance. Last, subplots that straddled multiple conditions, such as forest and non-forest areas, were removed from the study. After implementing these criteria, the final study area included 626 subplots across 244 plots (Figure 1).

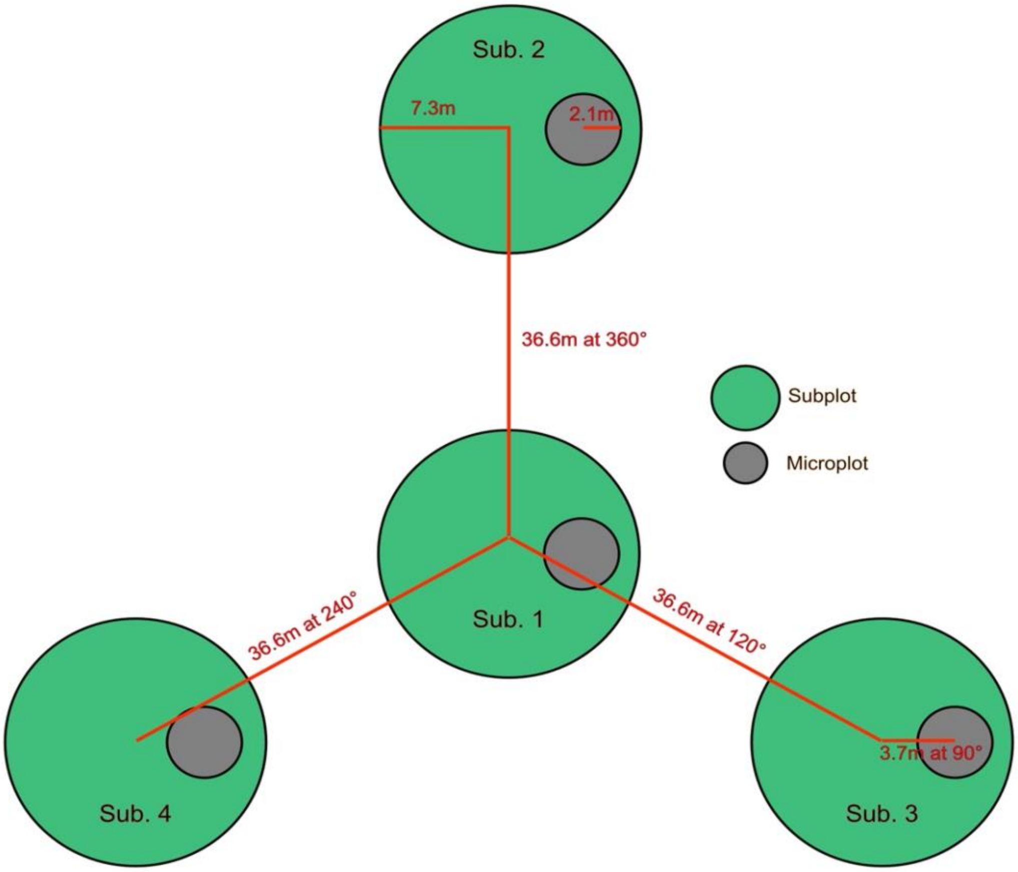

Figure 2. Diagram of the FIA plot layout

1.2.3 Abiotic and biotic predictor variables

Abiotic and biotic predictor variables were chosen based on their potential to affect post-MPB forest recovery. Initially, a set of 19 variables reflecting plot- or subplot-level climate, soils, pre- and post- outbreak stand structure, and years since the outbreak were considered. Strongly correlated variables that were shown to have little effect on preliminary model results were removed to improve model interpretability. Ultimately 14 variables were included in the final model. Climate variables included were actual evapotranspiration (AET), climatic water deficit (CWD), precipitation as snow (snow-water equivalent, SWE), precipitation as rain, maximum July temperature, and minimum January temperature. CWD was included as it reflects the amount of drought stress vegetation is under, and AET was included as it is a measure of water availability and energy for a given site (Redmond et al., 2018; Rodman et al., 2020; Stephenson, 1998). Precipitation and temperature variables were included because they have been shown to be tied to growth and establishment within subalpine forests (Andrus et al., 2018; Meromy et al., 2015; Peterson and Peterson, 1994). Edaphic variables included were soil available water capacity (AWC) and topographic wetness index (TWI). The inclusion of soil AWC and TWI is because soil moisture has been found to be associated with regeneration establishment and recruitment (Andrus et al., 2018; Foster et al., 2020; Redmond et al., 2018). Pre-outbreak stand condition variables included were pre-outbreak stand age and pre-outbreak stand basal area, as these variables have also been shown to have effects on regeneration establishment (Alfaro et al., 2015; Kayes and Tinker, 2012; Perovich and Sibold, 2016; Sibold et al., 2007). Post-outbreak stand condition variables included were basal mortality, shrub and herb cover, and forest floor depth. Basal area mortality has been shown to have drastic effects on species composition of regeneration following MPB outbreaks (Astrup et al., 2008; Pelz et al., 2018; Perovich and Sibold, 2016; Sibold et al., 2007), while shrub and herb cover and forest floor depth have been shown to create barriers to regeneration establishment and recruitment (Astrup et al., 2008; Stone and Wolfe, 1996; Vyse et al., 2009). Lastly, the outbreak variable of years since the outbreak was considered to ascertain if the elapsed time from the peak in the MPB outbreak to the time when the plot was measured influenced forest type development.

Abiotic and biotic predictor variables were acquired or calculated from the FIA database as well as from external data sources extracted by FIA analysts using precise (unfuzzed) FIA plot coordinates. Variables extracted included 800-m 30-year climate normals (PRISM, 2021), soil texture properties from the 30-m probabilistic remapping of soil survey geographic database (POLARIS; Chaney et al., 2016), and topographic indices calculated from digital elevation maps. Lastly, USDA Forest Service Aerial Detection Survey (ADS) data were acquired to help in determining the peak in MPB outbreak activity across the study area used in calculating years since outbreak (USDA, Forest Service, 2020). FIA vegetation structure, fuels, condition, and tree tables were used to determine pre- and post-outbreak stand condition variables (Table 1). Soil texture data from the top 200 cm of the soil profile, as determined by POLARIS (Chaney et al., 2016), were used to calculate the soil available water capacity (AWC) using equations from Saxton and Rawls (2006). Additionally, actual evapotranspiration (AET) and climatic water deficit (CWD) as well as total annual precipitation divided into snow and rain, were estimated using a Thornthwaite-type water balance model following the equations in Lutz et al. (2010; Dingman, 2015; Thornthwaite, 1948). These variables were based on monthly temperature and precipitation 30-year normals from PRISM (PRISM, 2021), soil AWC, and were calculated in R (R Core Team, 2020) with the CWD function created by Redmond (2019) using the RStudio interface (RStudio Team, 2021). PRISM data were also used to determine the 30-year normal July temperature maximums and January temperature minimums (PRISM, 2021). Topographic wetness index (TWI) was calculated using a 30-m digital elevation model. In addition, to determine years since the outbreak ADS data were used to determine the approximate peak in MPB activity based on the year the maximum hectares were affected in a 500-m radius around the plot. A detailed description of all predictor variables and their sources included in the analysis can be found in Table 1.

Table 1. Descriptions and sources of predictor variables included in the random forest analysis

Variable name	Description	Source
Climate Variables		
Actual Evapotranspiration (AET)	The availability of water and energy, based on 30-year climate normals (Rosenzweig, 1968; Lieth 1975, 1976).	AET was estimated using a Thornthwaite-type water balance model following the equations provided in Lutz et al. (2010; Dingman, 2015; Thornthwaite, 1948) and the CWD function created by Redmond (2019) in R (R Core Team, 2020). Based on monthly PRISM 800 m climate normals from 1981-2010 (PRISM, 2021) and soil AWC.
Climatic water deficit (CWD)	The amount of water by which potential evapotranspiration exceeds actual evapotranspiration based on 30-year climate normals.	CWD was estimated using a Thornthwaite-type water balance model following the equations provided in Lutz et al. (2010; Dingman, 2015; Thornthwaite, 1948) and the CWD function created by Redmond (2019) in R (R Core Team, 2020). Based on monthly PRISM 800 m climate normals from 1981-2010 (PRISM, 2021) and soil AWC.
Precipitation as snow	The 30-year normal amount of precipitation that fell as snow (snow water equivalent).	Calculated from PRISM 800 m climate normals from 1981-2010 using equations from the water balance model presented in Lutz et al. (2010; PRISM, 2021).
Precipitation as rain	The 30-year normal amount of precipitation that fell as rain.	Calculated from PRISM 800 m climate normals from 1981-2010 using equations from the water balance model presented in Lutz et al. (2010; PRISM, 2021).
Maximum July temperature	30-year normal average daily maximum July temperature.	Extracted from PRISM 800 m climate normals from 1981-2010 (PRISM, 2021).
Minimum January temperature	30-year normal average daily minimum January temperature.	Extracted from PRISM 800 m climate normals from 1981-2010 (PRISM, 2021).
Edaphic variables		
Soil available water capacity (AWC)	The amount of water holding capacity available for use by plants in the soil.	Calculated using equations from Saxton and Rawls (2006) based on soil texture profile obtained from the

		POLARIS dataset (Chaney et al., 2016)
Topographic wetness index (TWI)	A measure of relative site moisture.	Extracted from a 30-m digital elevation model.
Pre-outbreak condition variables		
Pre-outbreak stand age	Average age of trees cored for the condition the subplot occurs in	Calculated from FIA database condition tables.
Pre-outbreak stand basal area	Total basal area of all live trees ≥ 12.7 cm DBH pre-outbreak.	Calculated from FIA database tree tables.
Post-outbreak condition variables		
Basal area mortality	Basal area of dead lodgepole pine trees ≥ 12.7 cm DBH as percent of total live basal are pre-outbreak.	Calculated from FIA database tree tables.
Shrub and herb cover	Aerial canopy cover for all shrubs, forbs, and graminoids.	Calculated from FIA database vegetation structure tables.
Forest floor depth	Combined depth of duff and litter.	Calculated from FIA database down woody material duff, litter, fuel tables.
Outbreak variables		
Years since outbreak	The elapsed number of years following the end of the MPB outbreak to when the subplot was inventoried.	Inventory year is determined from the FIA plot tables and the MPB outbreak peak was determined using the USFS aerial detection survey by the maximum affected hectares within a 5 km radius of the plot.

1.2.4 Statistical analysis

1.2.4.1 Forest type identification and characterization

I used hierarchical cluster analysis (HCA) and multi-response permutation procedures (MRPP), together with FIA tree, sapling, and seedling subplot data to identify unique post-MPB forest types. Species that occurred on less than 5% of the subplots (limber pine (4.9% of subplots), ponderosa pine (1.1%), Rocky Mountain juniper (< 1.0%), and blue spruce (< 1.0%)) were considered rare and removed from the analysis. Removal of rare species is common in multivariate analysis because it reduces noise in the dataset, allowing for a clearer picture of compositional patterns (McCune and Grace, 2002). This resulted in 15 variables reflecting the abundance of five species (subalpine fir, lodgepole pine, Engelmann spruce, quaking aspen, and Douglas-fir) in each of three size classes (trees, saplings, seedlings). The data within each subplot were relativized by dividing each value by the total sum of all values within the species by size class combination. This reduced the emphasis on actual values, which were not necessarily comparable across variables (e.g., basal area values were used for trees and densities were used for seedlings and saplings) (Peck, 2016). After removing seven subplots that could not be included in the analysis because they contained all zero values, HCA was performed on the remaining 619 subplots using the vegan (Oksanen et al., 2020) and cluster (Maechler et al., 2019) packages in R. The analysis was completed using the Bray-Curtis distance measure, since Bray-Curtis works well with datasets containing a high proportion of zero values, and the Flexible Beta linkage method with a beta of -0.25, because it is does not distort the relationships among sample units and is also compatible with Bray-Curtis (Peck, 2016). HCA results produce a dendrogram linking each plot to other plots by hierarchical connections which can then be "cut" at various levels to create groups. I determined the optimal placement of the cut as the placement that resulted in the fewest number of groups while maintaining high homogeneity within the groups as determined by a series of MRPP analyses. MRPP compares differences between groups based on within-group similarities and produces a P value and measure of effect size (A) value. The A value denotes the within-group agreement; A equals 1 when all plots are identical within each group, and A equals 0 when all plots within a group equals the same expectation as one would see by chance (McCune and Grace, 2002; Peck, 2016). The optimal cut was determined when an increase in the number of groups no longer produced a large increase in

A. MRPP was completed using Bray-Curtis dissimilarities in the vegan package in R (McCune and Grace, 2002; Oksanen et al., 2020; Peck, 2016).

To provide insight into the makeup of the forest type groups identified through HCA, I conducted an Indicator Species Analysis (ISA) using the multipatt function from the indicspecies package (De Cáceres and Legendre, 2009) in R. ISA is useful in determining the relative abundance (B) and relative frequency (A) of species within each forest type group, where relative abundance measures the dominance of the species within a group it represents and relative frequency measures how often a species occurs only within the plots for the group it indicates. These two measures are then combined using the square root of A*B to get an overall indicator value. To determine the significance of the indicator values they were tested using a permutation test (n=999). For additional insight into the forest types, I analyzed the origin of the seedlings to determine if they had generally established pre- or post-outbreak. Seedling age is determined in the field for one seedling of each species per plot by whorl counts. Due to the limited number of seedlings with recorded ages in the FIA dataset, this analysis was done for all species within each forest type. Relative seedling ages were then calculated as the difference between the seedling establishment year (FIA inventory year minus field-recorded seedling age) and the ADS MPB peak year as previously determined for the plot. Thus, a relative age of 0 indicates that the seedling established during the year of the MPB peak, a negative age indicates that it established before the MPB peak, and a positive age indicates that it established after the MPB peak. A two-sided one sample sign test was then conducted for each forest type to determine if the median establishment year was different than zero. The sign test was completed in R using the BSDA package (Arnholt and Evans, 2021)

1.2.4.2 Abiotic and biotic drivers of forest types

I developed a Random Forest (RF) model to determine the importance of the abiotic and biotic variables in predicting the forest type groups. The RF model was developed in R using the ranger package (Wright and Ziegler, 2017). I completed five iterations of 10-fold cross-validation to fine tune the hyperparameters used in the final model. The final model considered two predictor variables for each split, a minimum size of the terminal nodes of 2, and used the "gini" split rule. Forest types were additionally weighted by the number of subplots per forest type group divided by the total number of subplots for each group to minimize the effect of varying sample sizes for each forest type group. Variable importance as determined by the RF model was then relativized for all variables and averaged for the final model over 1000 iterations using 5000 trees per iteration. Lastly, partial dependence plots (PDPs) were developed using the pdp package in R (Greenwell, 2017) with a 50 point grid resolution, from one iteration of the final RF model for all variables to determine the marginal effect on each forest type group predictor. Variable importance and PDPs were plotted using the ggplot2 package in R (Wickham, 2016).

1.3 Results

1.3.1 Forest type identification and characterization

HCA produced a dendrogram linking subplots by compositional similarity (Figure 3) and MRPP indicated that post-outbreak forests were best represented by five unique forest types ($p < 0.001$) with high homogeneity within them ($A = 0.233$). Based on ISA (Table 2), and boxplots of the tree, seedling, sapling abundances (Figure 4), the overstory/understory dominance of the forest types can be described as follows:

- **Lodgepole pine/lodgepole pine saplings (PICO/PICO.saps; n=157)** had high lodgepole pine (PICO) basal area in the overstory (median: 8.45 m^2 ha^{-1}) and high lodgepole pine sapling density in the understory (median: 1482 stems ha^{-1}). While Douglas-fir saplings were also indicative of this forest type, their density was low (median: 0 stems ha^{-1}).
- **Lodgepole pine-subalpine fir/subalpine fir (PICO-ABLA/ABLA; n=216)** had a mixed overstory with high basal areas of both lodgepole pine (median: 3.01 m^2 ha^{-1}) and subalpine fir (median: 1.74 m^2 ha^{-1}). The understory had high densities of subalpine fir seedlings (median: 2964 stems ha^{-1}). ISA indicated that subalpine fir saplings, as well as Engelmann spruce seedlings and saplings were also significant components of this forest type but their median densities were 0 stems ha^{-1}.
- **Lodgepole pine/sparse regeneration (PICO/Sparse; n=130)** had only overstory lodgepole pine trees as an indicator, which had a very high basal area (median: 10.98 m^2 ha^{-1}). This forest type did not contain high densities of any species in the understory sapling or seedling layers.
- **Lodgepole pine/lodgepole pine seedlings (PICO/PICO.seeds, n=57)** was characterized by high lodgepole pine basal area in the overstory (median: 4.38 m^2 ha^{-1}) and high lodgepole pine seedling densities in the understory (median: 5928 stems ha^{-1}).
- **Lodgepole pine/quaking aspen (PICO/POTR; n=59)** had high lodgepole pine basal area in the overstory (3.71 m^2 ha^{-1}) and high densities of quaking aspen (POTR) seedlings in the understory (4446 stems ha^{-1}). ISA suggested that both quaking aspen seedlings and saplings were indicative of this forest type, although the sapling layer had a median density of 0 stems ha^{-1}.

Representative photos showing these five forest types can be found in Figure 5. The spatial distribution of the forest types can be found in Figure 6.

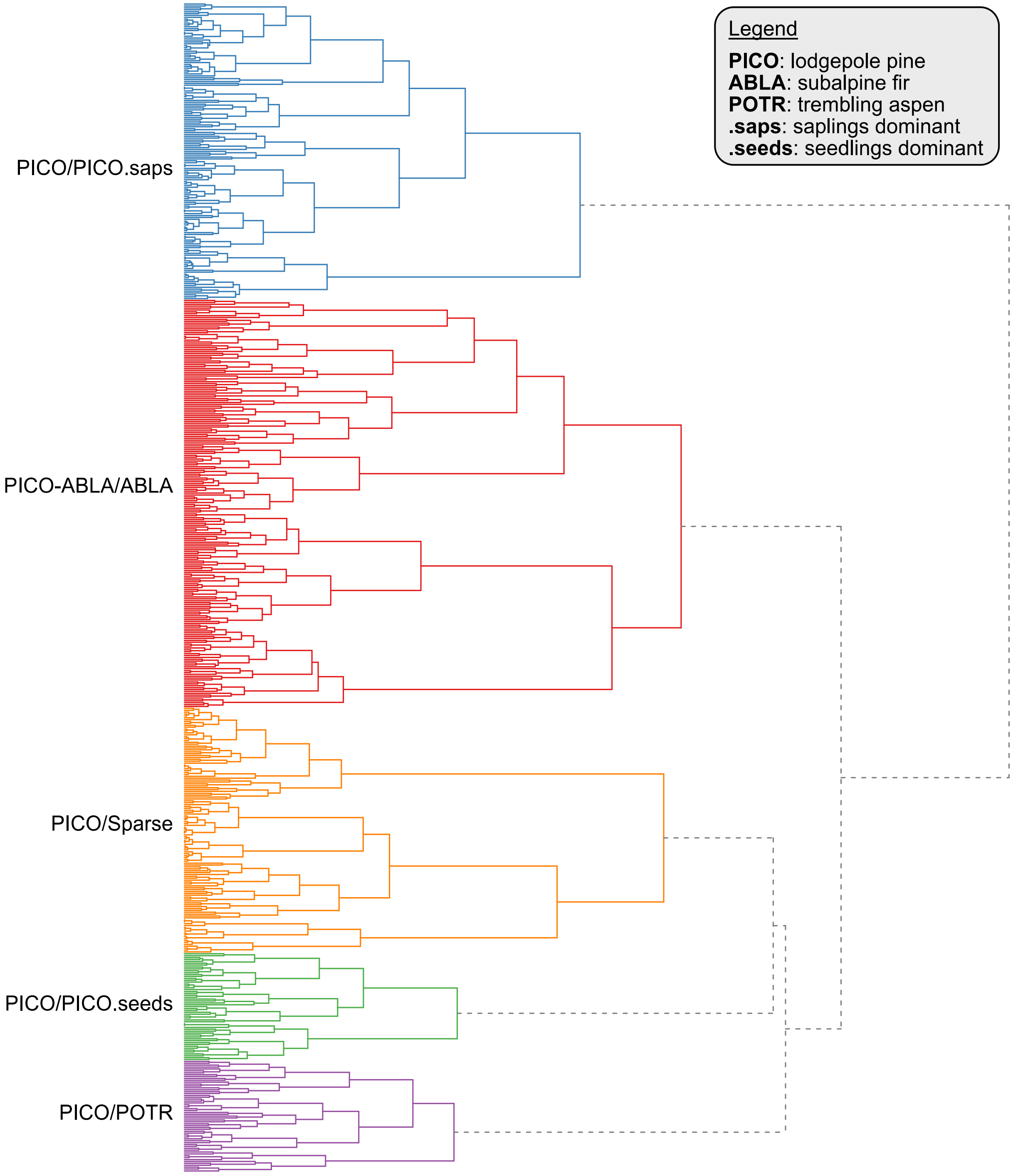

Figure 3. Dendrogram produced by hierarchical cluster analysis relating all subplots

Table 2. Indicator Species Analysis showing relative abundance and frequency of species in each forest type, only significant indicators shown ($p<0.05$).

Indicator Species by Forest Type	**Relative Frequency (A)**	**Relative Abundance (B)**	**Indicator Value (Sqrt(A*B))**	**P Value**
PICO/PICO.saps				
Lodgepole pine saplings	0.987	0.860	0.921	0.001
Douglas-fir saplings	0.038	0.938	0.189	0.024
PICO-ABLA/ABLA				
Subalpine fir trees	0.611	0.505	0.556	0.001
Subalpine fir saplings	0.389	0.696	0.520	0.001
Subalpine fir seedlings	0.824	0.657	0.736	0.001
Engelmann spruce trees	0.407	0.560	0.478	0.001
Engelmann spruce saplings	0.153	0.577	0.297	0.005
Engelmann spruce seedlings	0.232	0.574	0.364	0.002
PICO/sparse				
Lodgepole pine trees	1	0.356	0.597	0.001
PICO/PICO.seeds				
Lodgepole pine seedlings	1	0.803	0.896	0.001
PICO/POTR				
Quaking aspen trees	0.390	0.669	0.511	0.001
Quaking aspen saplings	0.254	0.964	0.495	0.001
Quaking aspen seedlings	0.949	0.945	0.947	0.001

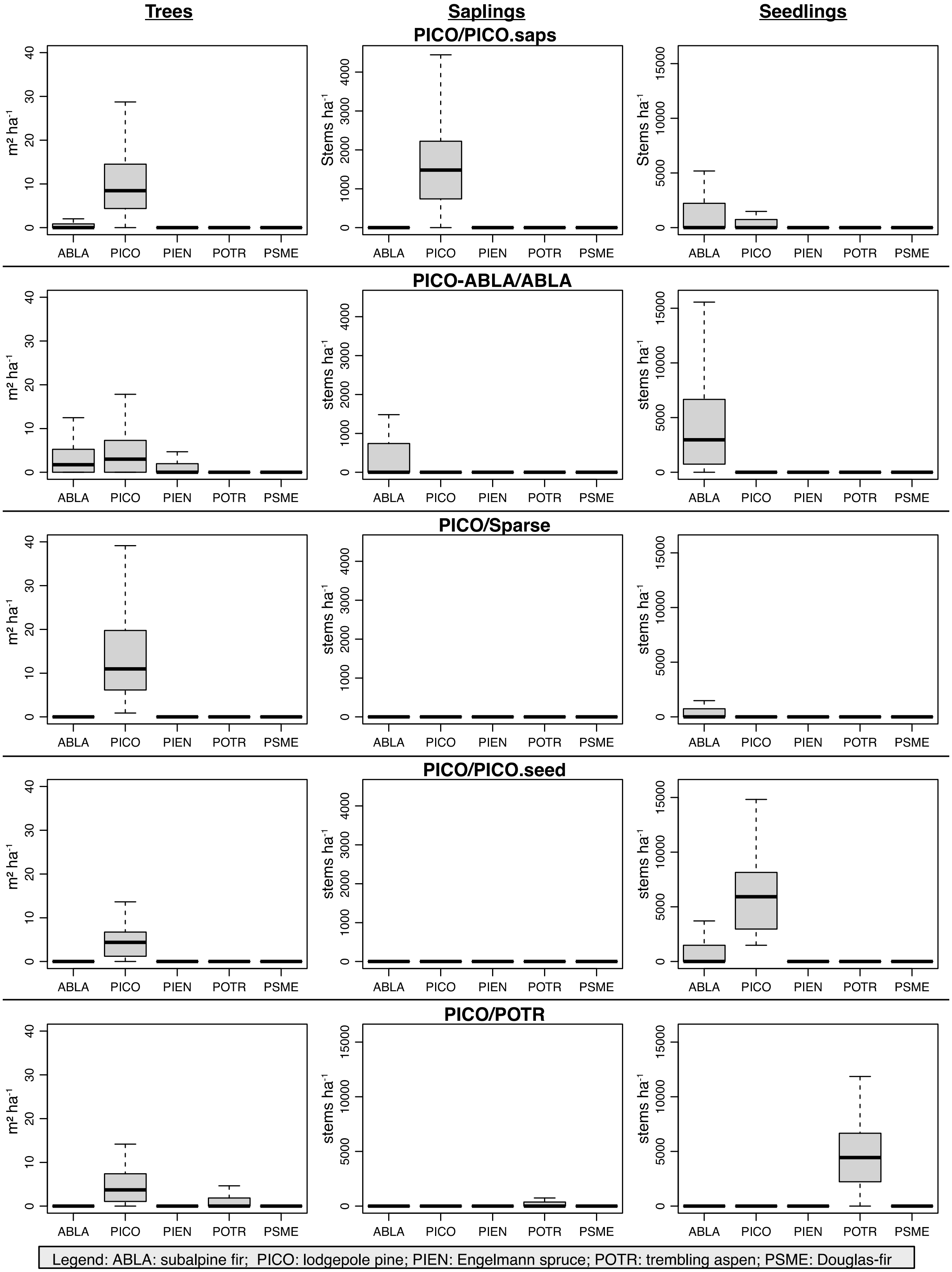

Figure 4. Boxplots of species basal area for trees and densities for saplings and seedlings for each size class and forest type. Boxplot whiskers represent 1.5 times the interquartile range.

Figure 5. Representative photos of each forest type; top left: PICO/PICO.saps, top right: PICO-ABLA/ABLA, middle left: PICO/Sparse, middle right: PICO/PICO.seeds, bottom left: PICO/POTR

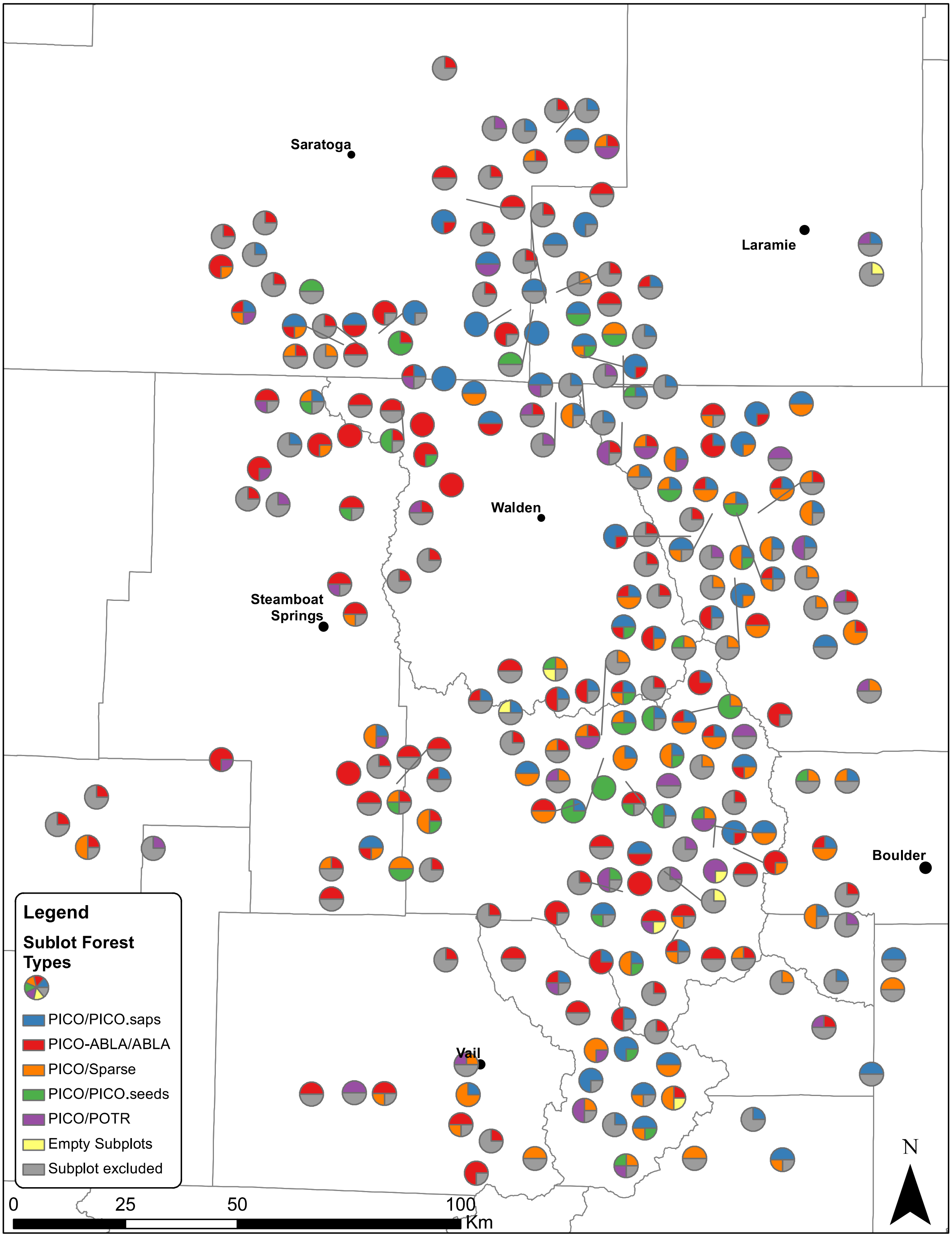

Figure 6. Map depicting forest types of all subplots, where each pie chart quarter represents 1 of 4 subplots in each plot.

Analyzing seedling age data relative to the outbreak year provided additional insight into the nature of the forest types (Table 3). I found that in the PICO/PICO.saps and PICO-ABLA/ABLA forest types, the majority of seedlings established prior to the outbreak, with the median relative age of establishment of -2 years and -1 years respectively ($p = 0.017$ and 0.043 respectively) before the outbreak year. I failed to reject the hypothesis that the median relative seedling age was not equal to zero for the PICO/Sparse and PICO/PICO.seeds forest types ($p = 0.883$, and 0.111, respectively). Meanwhile, in the PICO/POTR forest type, the majority of the seedlings established after the peak of the outbreak and had a median relative age of 2 years ($p = 0.003$) after the outbreak.

Table 3. Results of one sample sign test conducted for regeneration establishment pre- vs. post-outbreak. (H_0: median = 0; H_a: median <> 0; $p<0.05$)

	PICO/ PICO.saps	**PICO-ABLA/ABLA**	**PICO/ Sparse**	**PICO/ PICO.seeds**	**PICO/ POTR**
N	81	175	48	61	58
S-statistic	28	69	22	35	37
P-value	0.017	0.043	0.883	0.111	0.003
95% CI	(-4, -1)	(-3, 0)	(-4, 2)	(0, 3)	(1, 3)
Median	-2	-1	-0.5	2	2
Conclusion	Reject H_0	Reject H_0	Fail to reject H_0	Fail to reject H_0	Reject H_0

1.3.2 Abiotic and biotic drivers of forest types

The RF analysis indicated that the 14 abiotic and biotic predictor variables were mixed in their ability to predict forest types. Basal area mortality and precipitation as snow were the two most important variables (relative importance of 17.5% and 16.2%, respectively) (Figure 7). Also relatively important were maximum July temperature (10.8%), pre-outbreak basal area

(10.6%), pre-outbreak stand age (7.6%), and precipitation as rain (7.3%). All other variables had relative importance values of less than 7% and are not discussed further.

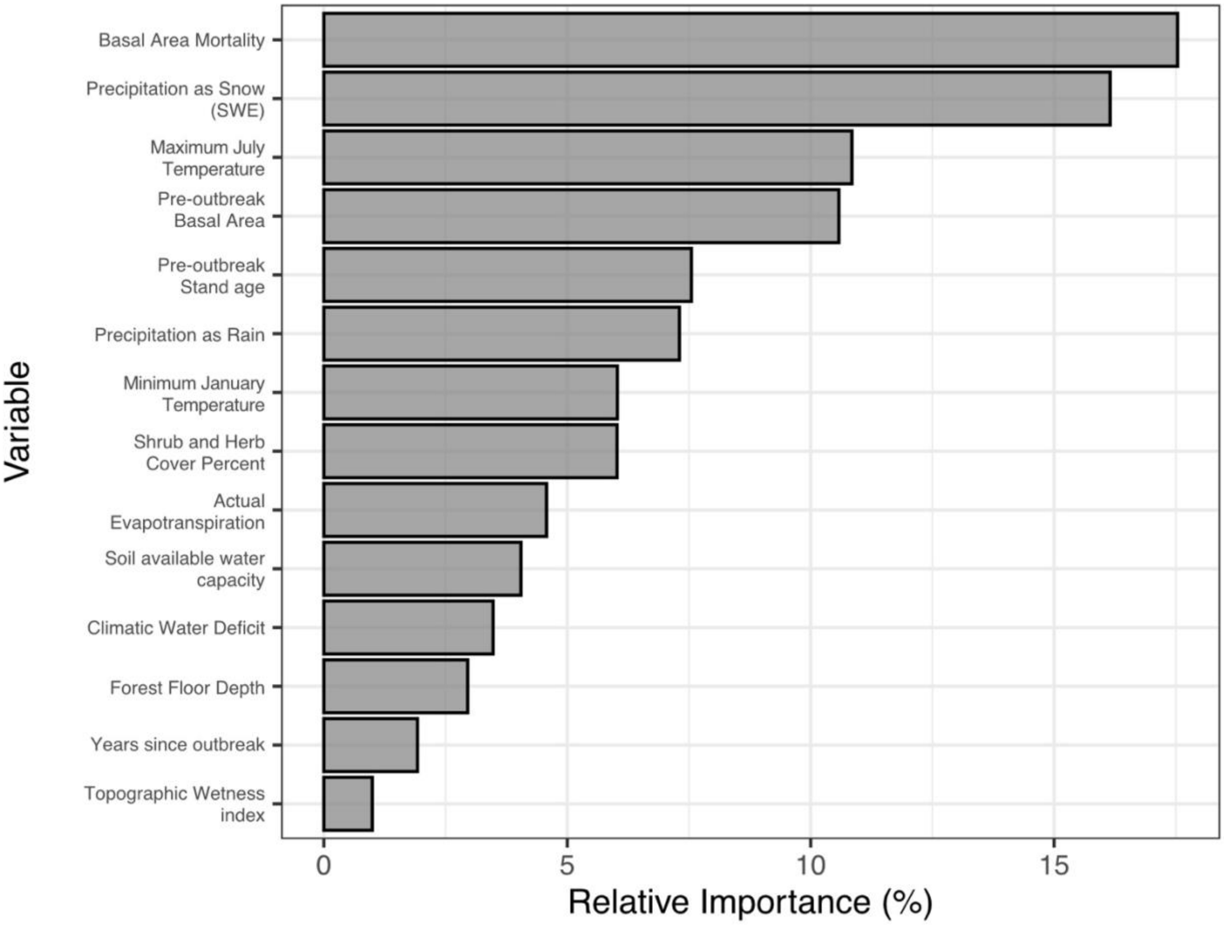

Figure 7. Relative variable importance for variables included in final random forest model.

Basal area mortality had drastic effects on almost all forest types (Figure 8A). PICO/PICO.saps and PICO/Sparse both decreased in probability of occurrence as basal area mortality increased, decreasing rather drastically when basal area mortality increased beyond 50%. PICO-ABLA/ABLA increased in probability as basal area mortality increased to 50%, plateaued in probability between 50 and 95% mortality, then decreased strongly in probability when mortality was greater than 95%. Lastly PICO/PICO.seeds and PICO/POTR both increased in probability as basal area mortality increased, with dramatic increases occuring when basal area mortality exceeded 95%..

Of the five forest types, I found that the PICO-ABLA/ABLA forest type was the one whose relative probability of occurrence was most strongly affected by the amount of precipitation falling as snow (Figure 8B). When precipitation as snow was around 250 mm, PICO-ABLA/ABLA, PICO/PICO.saps, and PICO/Sparse were more likely to occur than PICO/POTR and PICO/PICO.seeds. As precipitation as snow increased the probability of PICO-ABLA/ABLA increased signficantly, while PICO/PICO.saps, PICO/Sparse, and PICO/POTR decreased in probability, and PICO/PICO.seeds was unaffected.

Maximum July temperature had similar effects on the probability of group membership for all forest types except PICO/POTR, where they all saw a decrease in probability as temperatures increased greater than 23.5 °C (Figure 8C). PICO/POTR however saw a fairly drastic increase in relative probability of occurrence at maximum July temperatures greater than 23.5 °C.

Pre-outbreak basal area also had an influence on all five forest types, with the largest effect on the PICO-ABLA/ABLA forest type, which along with the PICO/Sparse forest type saw the relative probability of occurrence increase as pre-outbreak basal area increased (Figure 8D). PICO/PICO.saps also saw a large effect, and along with PICO/POTR, saw relative probability of occurrence decrease as pre-outbreak basal area increased. PICO/PICO.seeds only saw a decrease in relative probability of occurrence as pre-outbreak basal area increased greater than 20 m^2 ha^{-1}.

Pre-outbreak stand age had the strongest effect on the probability of PICO-ABLA/ABLA and PICO/PICO.saps (Figure 8E). PICO-ABLA/ABLA saw an increase in relative probability of occurrence as pre-outbreak stand age increased, with a dip in probability of occurrence that occurred between 100-175 years. PICO/PICO.saps meanwhile, saw a decrease in relative probability of occurrence betweeen 25-175 years. PICO/PICO.seeds and PICO/POTR saw minimal effects, but generally decreased in relative probability of occurrence as pre-outbreak stand age increased. PICO/Sparse also saw minimal effects from pre-outbreak stand age, but generally increased in relative probability of occurrence as pre-outbreak stand age increased up to about 175 years.

Precipitation as rain also had the largest effect on PICO-ABLA/ABLA with more minor effects on the other forest types. PICO-ABLA/ABLA increased in relative probability of occurrence as precipitation as rain increased, but tapered off in its likelihood of occurrence around 360 mm. PICO/POTR also slightly increased as precipitation as rain increased while both PICO/PICO.saps and PICO/PICO.seeds both saw slight decreases in probability as precipitation as rain increased. Precipitation as rain had little effect on the PICO/Sparse forest type.

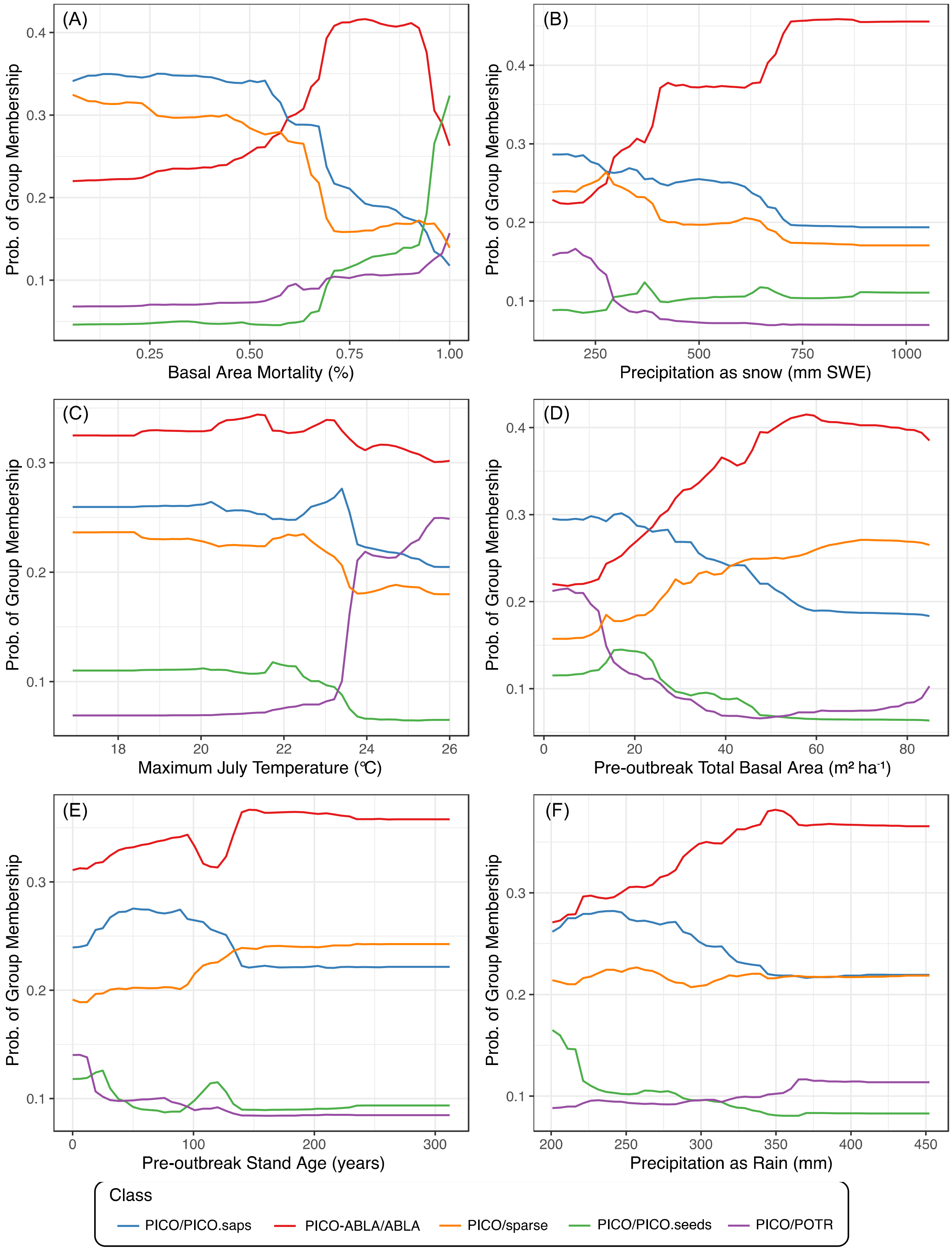

Figure 8. Partial dependance plots for all forest types and top six most important variables.

1.4 Discussion

Across the Southern Rocky Mountain Ecoregion, forests that were dominated by lodgepole pine are recovering from the recent mountain pine beetle outbreak and are experiencing varying forest trajectories. Across the study area, we see a high diversity of responses with five different primary forest type groups forming. All the forest types delineated here are still dominated by lodgepole pine in the overstory but contain compositionally distinct sapling and seedling understory layers. Out of the 626 subplots examined for this study, 55% (344 subplots in PICO/PICO.saps, PICO/Sparse, and PICO/PICO.seeds) will likely remain dominated by lodgepole pine for years to come, 35% (216 subplots in PICO-ABLA/ABLA) are on a trajectory transitioning towards subalpine fir dominance, which will likely include a smaller component of Engelmann spruce, and 9% (59 subplots in PICO/POTR) are on a trajectory transitioning towards quaking aspen dominance. Additionally, 1% (six of the seven subplots that were removed from analyses) of the subplots had no live trees at all and a conversion to non-forest land is possible.

The forest types found here are also comparable to the five types found by Diskin et al. (2011), but with two key differences: Diskin et al. (2011) did not find the PICO/PICO.saps forest type, and I did not find that Engelmann spruce was prevalent enough in the understory to constitute a separate forest type from the PICO-ABLA/ABLA type, as they did. These key differences could be explained by the discrepancies in study scale and timing, where the previous study occurred within the western portion of Rocky Mountain National Park and sampled their plots in 2008 while the outbreak was still underway. Based on the limited area of the earlier study it is possible they missed the PICO/PICO.saps forest type, also because the outbreak was still under way subalpine fir regeneration may not have yet gained dominance amongst existing Engelmann spruce regeneration.

Within this study, I found that the origination of the understory layer differed between forest type. In the PICO/PICO.saps and PICO-ABLA/ABLA forest types, the understory layer primarily originated pre-outbreak. This occurrence was apparent for different reasons, within the PICO/PICO.saps forest type, while there was a dense layer of lodgepole pine saplings the limited seedlings found here consisted primarily of subalpine fir, which is more likely to establish in low light conditions found in dense stands such as these. However, subalpine fir regeneration may have been limited in these stands due to moisture availability since these stands were more likely on sites that had lower rates of precipitation. Furthermore, because these stands were less likely to experience high levels of basal area mortality, additional establishment of lodgepole pine or quaking aspen regeneration was likely limited by light availability. Meanwhile, within the PICO-ABLA/ABLA forest type the majority of regeneration consisted of subalpine fir which had established pre-outbreak. This is most likely due to these stands having a high pre-outbreak basal area that included a component of subalpine fir trees and that these stands were generally older since a stand replacing disturbance, as well as being found on sites with higher precipitation. These conditions are quite favorable for the establishment of subalpine fir, which likely would have been ubiquitous in the understory in these stands leading up to the outbreak (Collins et al., 2011; Pelz and Smith, 2012). Within the PICO/Sparse, PICO/PICO.seeds, and PICO/POTR forest types, regeneration generally established either around the time of the peak in the MPB outbreak or soon thereafter. For both the PICO/PICO.seeds and PICO/POTR forest types this was most likely because these stands were common in places that had the highest levels of basal area mortality (> 95%), which allowed for early-seral, shade-intolerant species, such as lodgepole pine and quaking aspen to establish or sprout in nearly full sunlight (Pelz et al., 2018; Pelz and Smith, 2012; Sibold et al., 2007). Lastly, within the PICO/Sparse forest type, while there was little regeneration here, what did exist most likely occurred within small openings created through the limited basal area mortality the MPB created. While, these stands lacked abundant advanced regeneration, similar to the PICO/PICO.saps forest type, regeneration would have been limited in these sites since they were most likely to be found where pre-outbreak basal area was high and on sites with lower precipitation as snow (Kayes and Tinker, 2012; Pelz and Smith, 2012).

The PICO/PICO.saps forest type was most likely to be found where basal area mortality, pre-outbreak basal area, precipitation as snow, and maximum July temperature were all lower as well as where pre-outbreak stand age is younger. Although, these stands were more likely where pre-outbreak basal area is low, given the high sapling density present post-outbreak, they would have been expected to be densely stocked with lodgepole pine saplings prior to the outbreak. These stands were also common where overstory mortality was minimal, suggesting that these stands remain relatively unchanged following the outbreak. The description of these stands implies that they were densely stocked with saplings, which would have contributed minimally to the overall basal area, and would have been experiencing suppressed tree growth due to intense competition, potentially leading to stagnation in these stands (Lotan and Critchfield, 1990; Tait et al., 1988). The result of the MPB outbreak on these sites was a reduction in overall basal area, due to the largest trees in these stands experiencing most of the mortality but had a minimal effect on the overall stems ha^{-1}. These stands post-outbreak will tend to see existing advanced regeneration, consisting of pole-sized lodgepole pine saplings, gaining dominance with very little new seedling establishment occurring.

The PICO-ABLA/ABLA forest type was most likely to be found where precipitation (both as snow and rain), pre-outbreak basal area, and stand age are high, where basal area mortality was moderate to high, and where maximum July temperatures are low (Figure 8). These results correspond with the life history of subalpine fir which is less drought tolerant and more sensitive to heat than lodgepole pine and quaking aspen (Burns et al., 1990a, 1990b; Redmond and Kelsey, 2018). Subalpine fir regeneration has also been found to be dependent on high snow pack depths to establish, which can mitigate the effects of climatic conditions by increasing soil moisture and reducing the length of summer drought (Andrus et al., 2018; Hessl and Baker, 1997). The drop in probability of occurrence when basal area mortality is greater than 95% is most likely attributed to the lack of seed source availability for subalpine fir on these sites. Subalpine fir establishment has been found to be dependent on seed source availability in MPB affected forests (Perovich and Sibold, 2016), and seed dispersal for subalpine fir is likely limited to a maximum dispersal range of 150 m (Alexander, 1987; Noble and Ronco, 1978). Stands that experienced these extremely high levels of mortality, would have likely consisted predominantly of lodgepole pine within the overstory prior to the outbreak and subalpine fir would presumably have been rare in these stands, given that they would have been at a minimum 95% lodgepole pine.

The PICO/Sparse forest type, similar to PICO/PICO.saps was most likely to be found where basal area mortality, precipitation as snow, and maximum July temperatures were low. The major difference between this forest type and PICO/PICO.saps though, was that these forests were more likely to be found where pre-outbreak basal was high. This in combination with the overall lack of regeneration in these stands suggests that these forests consist of large diameter trees and will remain mostly unchanged following the MPB outbreak, as there was not enough overstory mortality to trigger a pulse in regeneration. Furthermore, since these forest types were likely found where precipitation as snow is lower, subalpine fir may be limited from establishment beneath the existing canopy. These forest types will potentially see only new recruitment of regeneration occurring in small canopy gaps created by the limited MPB mortality.

The PICO/PICO.seeds forest type was most likely to occur where basal area mortality was greater than 95% and was most common when pre-outbreak basal area was lower, between 15-40 m^2 ha^{-1}. This is also congruent with the life history for lodgepole pine, where seed germination and is best under full sunlight, moist seed beds, and temperatures that range between 21-28 °C (Bates, 1930; Haasis and Thrupp, 1931; Lotan and Critchfield, 1990; Lotan and Perry, 1983; Minore, 1972). Within these sites I found that most of the regeneration had established around the peak of the MPB outbreak, which likely occurred simultaneously with the overstory mortality which allowed full sunlight to reach the forest floor, accelerating germination of lodgepole pine. Alternatively, on sites where pre-outbreak basal area was higher and mortality lower, lodgepole pine regeneration establishment would have been limited by the lack of light availability. While lodgepole pine seedlings can often germinate under heavy shade, germination under full shade is still inhibited and survival after one year is even less likely (Lotan and Critchfield, 1990; Minore, 1972). These forests have likely experienced mortality akin to a stand replacing disturbance, which has reset the trajectory of these stands from lodgepole pine overstory dominance to lodgepole pine seedling dominance. This trajectory will eventually lead to similar lodgepole pine overstory dominance in the future.

The PICO/POTR forest type was most likely to be found on sites that saw high basal area mortality, are warmer, where precipitation as snow is lower, precipitation as rain is higher, and where pre-outbreak basal area was lower. It is likely that a high proportion of the aspen regeneration found on these sites established asexually (McDonough, 1979; Peraia, 1990), implying these sites had a component of aspen within the subplot or nearby that existed prior to the outbreak. This existing aspen component would have responded to the increase in soil temperature created by the increase in light caused by the overstory mortality, which would have triggered a hormonal response within the root system to induce root suckering (Maini and Horton, 1966; Zasada and Schier, 1973). The ability of aspen to establish asexually in response to changing conditions would have thus allowed aspen to establish and grow more rapidly following the outbreak giving aspen regeneration a competitive advantage when compared to other species that originated from seed. These forest types, similar to the PICO/PICO.seeds forest type, also likely experienced mortality that was analogous to a stand replacing disturbance, allowing for the establishment of quaking aspen across these sites. The trajectory of these forests will likely see aspen come to dominate the overstory replacing lodgepole pine as the dominant species.

1.5 Conclusions and Implications

This study provides insight into how lodgepole pine forests across the Southern Rocky Mountain Ecoregion of Wyoming and Colorado are recovering following an unprecedented MPB outbreak. At a broader scale of examination, I found that the overwhelming majority of stands will remain forested, and most will remain lodgepole pine dominated for the short-term. However, these stands will have a more diverse stand structure and composition then existed previously, which will likely shape future developmental trajectories. Stands that are likely to remain dominated by lodgepole pine are those that saw minimal basal area mortality following the MPB outbreak, which did not create enough opportunity for competing species to be recruited to the overstory. Also, stands that saw basal area mortality greater than 95% saw new lodgepole pine regeneration that will likely repopulate these stands. Similarly, aspen can be expected to gain dominance on these sites where mortality was greater than 95% but are more likely on warmer sites that see more precipitation as rain, and where overall pre-outbreak basal area was lower. Lastly, subalpine fir with a component of Engelmann spruce is expected to gain dominance on sites that saw moderate to high levels of basal area mortality, particularly on sites that had high amounts of pre-outbreak basal area, and on sites that have greater amounts of precipitation (both snow and rain). These results corroborate previous research that found forest composition following the 2000s MPB outbreak was primarily influenced by overstory mortality and moisture availability (Kayes and Tinker, 2012; Pelz et al., 2018; Perovich and Sibold, 2016).

Ultimately these trajectories are still not guaranteed, as they could be altered by additional disturbances. Wildfires, particularly stand-replacing wildfires, are the most likely disturbance that would have an outsized effect on how these stands continue to develop. For example, the 2010 Church Park fire in northern Colorado was one of the first wildfires to burn in MPB affected lodgepole pine stands. Rhoades et al. (2018) found four years after this fire that conifer seedlings had been mostly consumed by the fire, but quaking aspen regeneration was relatively unaffected. Since then, there have been a number of fires that have occurred in these forests, in 2020 alone the two largest wildfires in Colorado history (Cameron Peak and East Troublesome) and one of the largest wildfires in Wyoming history (Mullen), all burned within this study area (Rocky Mountain Area Coordination Center, 2020). Additional studies on the long-term effects that fires will have on these forests could help further our understanding of the compounding effects of multiple disturbances on an ecosystem. Forest management will also have an outsized influence on the trajectories of MPB affected stands. For example, Collins et al.

(2012, 2011) found that in MPB affected stands treated with salvage logging, lodgepole pine seedlings were most likely to be the dominant species as opposed to the variations in regeneration found in this study.

Furthermore, the effects of warmer and drier conditions projected under climate change will also have an impact on the ability of these forests to continue along these trajectories. For example, with the six subplots that had no live trees, while the trajectories of these subplots remain unknown, there is the possibility that these forests could no longer be suitable to support a forested cover type. Further research may be needed to determine the extent of previously forested sites that are no longer capable of supporting forested ecosystems.

A number of studies have previously addressed questions regarding the trajectories of lodgepole pine forests affected by the MPB outbreak of the early 2000s. This study confirmed that those findings hold up at a landscape scale, and further synthesized the controlling factors to regeneration establishment and dominance in these forests. I demonstrated here the utility of FIA data to answer ecological questions following an expansive disturbance. Future research in this topic should make use of FIA data to look more specifically at the effects of climate change and the propensity for wildfire to factor into the impending outcomes for the species found in these forests.

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