AN ABSTRACT OF THE THESIS OF

Andrew G. Merschel for the degree of Master of Science in Forest Science presented on December 14, 2012.

Title: Mixed-Conifer Forests of Central Oregon: Structure, Composition, History of Establishment, and Growth

Abstract approved:

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Thomas A. Spies

The structure and composition of mixed-conifer forest (MCF) in central Oregon has been altered by fire exclusion and logging. The resulting increased density, spatial contagion, and loss of fire resistant trees decrease the resiliency of this ecosystem to fire, drought, and insects. The historical and current composition and structure of MCF are characterized by steep environmental gradients and a complex mixed-severity fire regime. This inherent variation makes it difficult to determine the magnitude of anthropogenic effects and set objectives for restoration and management. As a result, there is a lack of consensus regarding how MCF should be managed and restored across the landscape. My primary research objectives were to: (1) Characterize the current structure and composition of MCF and how these vary with environmental setting; and (2) Characterize establishment and tree growth patterns in MCF in different environmental settings. To address these objectives, I collected field data on structure and composition and increment cores across a range of environmental conditions in MCF of the eastern Cascades and Ochoco Mountains.

I used cluster analysis to identify four stand types based on structure and composition in the eastern Cascades study area and four analogous types in the Ochoco Mountains study area. Variation in understory composition and the presence of large diameter shade tolerant species distinguish each type. Stand types occupied distinct environmental settings along a climatic gradient of increasing precipitation and elevation. At relatively dry PIPO sites understories were dominated by ponderosa pine. At wetter PIPO/PSME and PIPO ABGC sites understories were dominated by shade tolerant species, but ponderosa pine was dominant in the overstory. At the coolest and wettest PIPO/PSME/ABGC sites understories were dominated by grand fir and shade tolerant species were common in the overstory.

In the eastern Cascades current density of all live trees and snags was 432, 461, 570, 372 trees per hectare (TPH) for the four stand types identified. Stand types in the drier Ochoco Mountains were currently less dense at 279, 304, 212, and 307 TPH. Current MCF densities in both areas are 2-3 times higher than densities estimated for the late 19th and early 20th centuries from other studies in those two areas. Reconstruction of cuts in each stand type indicates that the density of large diameter ponderosa pine has been reduced by approximately 50% in all stand types in both study regions.

Age histograms demonstrate that current density and composition of MCF stand types is a product of abrupt increases in tree establishment following fire exclusion in the late 19th century. The number of trees established increased after 1900 in all stand types, but the timing and composition of changes in establishment varied with climate. At dry PIPO sites increases in establishment were delayed until the 1920s and 1930s and were

composed of ponderosa pine. At PIPO/PSME and PIPO/ABGC sites with intermediate precipitation, establishment was dominated by ponderosa pine prior to 1900, but after 1900 establishment was dominated by a large pulse of Douglas-fir and grand fir. At the wettest PIPO/PSME/ABGC there was less evidence of changes in structure and composition over time. My results indicate that compared to dry pine and dry-mixed conifer sites, relatively productive moist mixed-conifer sites were characterized by large changes in structure and composition. Such sites could be considered more ecologically altered by lack of fire than drier forest types that had high fire frequencies but slower rates of stand development and less plant community change.

Radial growth patterns of cored ponderosa pines differed between the eastern Cascades and Ochoco Mountains. In the eastern Cascades mean growth rates and variance decreased during favorable climatic periods after 1900. This is likely related to increased competition, and provides evidence that current stand density lacks a temporal analog in the 18th and 19th centuries. Sensitivity of growth to climate and harvest suggest competition for water in the denser forest of the eastern Cascades, and indicates thinning will increase the diameter growth rate of large old pines. In the Ochoco Mountains, ponderosa pine tree growth was less responsive to climate prior to fire exclusion in the late 1800s, and growth did not respond to fire events. This suggests competition among trees was historically low in this region. After fire exclusion growth became more responsive to wet and dry climatic cycles, which may indicate that increased density and competition made trees more responsive to climate variability. Patterns of slow and fast growth appeared to differ between study regions and likely differ at the sub-regional scale. Further analysis of the relationship between growth and climate in different environmental settings is needed to distinguish where stand development has been modified by disruption of fire regimes.

Mixed-Conifer Forests of Central Oregon: Structure, Composition, History of Establishment, and Growth

by
Andrew G. Merschel

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APPROVED:

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Major Professor, representing Forest Science

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Head of the Department of Forest Ecosystems & Society

____
Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes the release of my thesis to any reader upon request.

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Andrew G. Merschel, Author

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CHAPTER 1: INTRODUCTION

Mixed-conifer forest (MCF) in the eastern Cascades and Ochoco Mountains is found between relatively dry ponderosa pine (*Pinus ponderosa*) woodlands and relatively wet grand fir (*Abies grandis*) and mountain hemlock (*Tsuga mertensiana*) forest types (Franklin and Dyrness 1973). Prior to fire exclusion in the late 1800s mature dry ponderosa pine forest would have been best categorized as old forest with a single canopy stratum (O'Hara et al. 1996). In contrast, wet MCF stands dominated by grand fir and mountain hemlock are dense and multilayered and resemble old forest structure west of the Cascades (Spies et al. 2006). In the transition between theses forest types, steep climatic and topographic gradients result in a complex mosaic of stand structures and species composition (Simpson 2007). Landscape heterogeneity is further driven by a poorly understood mixed-severity fire regime with variable fire return intervals and burn intensities (Hessburg et al. 2005 and Halofsky et al. 2011).

Disruption of the historical fire regime and selective logging have modified structure and composition by increasing density, spatial contagion, and the proportion of fire sensitive species throughout western forests (Hessburg and Agee 2003). However, the extent and magnitude of this change in relation to landscape variation in climate and environment are unknown. These changes are a concern to managers because they increase the risk of high-severity wildfire, and may increase mortality in drought and insect outbreaks (Hessburg et al. 1994, Hemstrom 2001, Hessburg et al. 2005, Fitzgerald 2005, and Powell 2011). Furthermore, past logging and successional changes may have altered stand dynamics and recruitment of large ponderosa pine that are both resistant to low and mixed-severity fire and provide numerous ecological and social values. Our limited understanding of the complexity of MCF and its historic disturbance regime has contributed to a lack of consensus on how MCF has changed with fire exclusion and logging and how much restoration is needed. Many researchers argue that the majority of MCF was historically open, dominated by ponderosa pine, and was maintained by frequent low-severity fire (Hemstrom 2001, Heyerdahl et al. 2001, Fitzgerald 2005, Hessburg et al. 2005, and Spies et al. 2006). More recent studies suggest considerable variability in historical stand densities and composition and implicate stand replacing fire as a driver of forest dynamics structure in MCF (Hessburg et al. 2007, Baker 2012, and Williams and Baker 2012). If these forests were historically denser than originally assumed restoration actions may be less warranted.

Hemstrom (2001) indicated that the current range of density, vertical continuity, and species composition need to be quantified and related to their environmental drivers of climate and topography to understand changes related to fire exclusion. Spies et al. (2006) also reported that updated definitions of structure and composition were needed to describe the current state of MCF, and organize it into types based on forest fire regime (Spies et al. 2006).

In Chapter 2, I characterize the current state of MCF vegetation based on data I collected at 179 sample sites across the eastern Cascades and Ochoco Mountains. I also compare the current structure and composition of MCF to limited historical records. Specific questions addressed were: 1) Are there distinct structure and composition types of MCF; 2) How are climate and topography associated with variation in stand structure composition; and 3) How does current structure and composition compare to historical records and recent reconstructions of MCF?

In Chapter 3, I use my MCF stand typology and ~3,500 increment cores that were collected at the same sample sites to address the following questions: 1) For extant trees, is the composition and number of trees established different before and after fire exclusion; and 2) What are the patterns of growth (slow and fast) in old-growth ponderosa pine, and how are they related to climate and disturbance? Question one was addressed using age structure developed from increment cores grouped by MCF stand type, which allowed changes in establishment and composition unique to stand types and their environmental setting to be identified. Question two was addressed using 300-year growth chronologies developed from old-growth ponderosa pine. Annual growth for a particular tree species is dependent on both climate and competition with neighboring trees (Cook 1987). Growth chronologies were used to determine how growth varied among sites and to assess whether growth patterns have changed in the last century. I then explored how these growth patterns are related to climate and potentially increased competition which has resulted from fire exclusion. Chapter 3 concludes with a discussion of the management implications of variable response of MCF vegetation to fire exclusion, further research needs, and the limitations of this study.

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CHAPTER 2: VARIATION IN STRUCTURE AND COMPOSITION OF OLD-GROWTH MIXED-CONIFER FOREST IN THE EASTERN CASCADES AND OCHOCO MOUNTAINS

ABSTRACT

The restoration of mixed-conifer forests (MCF) presents one of the most significant management challenges in Pacific Northwest forests. This forest type has been altered by fire exclusion and logging and there is no consensus on how to restore it. The restoration challenge is partly a result of variation in its structure and composition and the complexity of the fire regime in MCF. While most studies conclude increased density and shifts in composition are the result of fire exclusion and management practices, a few suggest that current MCF is actually similar in density and composition to MCF in the late 19th century. Management and restoration of MCF requires an understanding of current structure and composition and its variation with broad climatic and topographic gradients.

This study addresses three questions: 1) Are there distinct structure and composition types of MCF; 2) How are climate and topography associated with variation in stand structure and composition; and 3) How does current structure and composition compare to historical conditions estimated from records? Data on structure and composition were collected in 2009 and 2010 at 179 MCF sample sites to address these questions in two study areas including the eastern Cascades and Ochoco Mountains.

Using cluster analysis I developed a total of eight MCF types with four analogous types belonging to each study area. Types were distinguished based on differences in species composition and structure. Non-metric multi-dimensional scaling (NMS) demonstrated that MCF types occupied distinct environments along climatic and topographic gradients. Current mean density in MCF Types ranged from 432-569 TPH in the eastern Cascades and 212-307 TPH in the Ochoco Mountains. These values are 2-3 time higher than historical records for dry-mixed conifer forest of 152 TPH in the eastern Cascades and 110 TPH in the Ochoco Mountains. Mean density in the eastern Cascades is also higher than the 3rd quartile of 318 TPH reported for a landscape reconstruction of stand density during the late 1800s. Selective logging of ponderosa pine in the 20th century reduced the density of all trees >50 cm in diameter at breast height by approximately half relative to historical density in both study areas. Recovery of fire tolerant early seral trees may be limited by competition with shade tolerant species. The current structure and composition of MCF supports the hypothesis that the current density of MCF is much higher than it was historically. Knowledge of variation in current structure and composition across environmental gradients can be used to develop restoration and management plans.

INTRODUCTION

Mixed-conifer forest (MCF) is found in the transition between dry ponderosa pine (*Pinus ponderosa)* woodlands and moist grand fir (*Abies grandis)* forest types (Franklin and Dyrness 1988). A combination of steep ecological gradients and a mixed-severity fire regime historically created a mosaic of structurally and compositionally diverse forest. Prior to European settlement, structure in low elevation dry MCF has often been described as park like with large widely-spaced fire resistant trees (Munger 1917). In contrast, upper elevation wet MCF was multilayered with structure similar to that found in the wet forest provinces west of the Cascades (Spies et al. 2006). Logging and fire exclusion during the late 1800s and 1900s have altered the historic structure, composition, and landscape pattern of MCF (Camp et al. 1997, Heyerdahl et al. 2001, Agee 2003, Hessburg and Agee 2003, Hessburg et al. 2005). The proportion of mid-seral multilayered forest has increased substantially since European settlement (Hessburg et al. 1994, Camp et al. 1997, Agee 1998, Hemstrom 2001 and Hessburg et al. 2005). As a result, remaining stands with intact old-growth trees face increased risk of mortality from high-severity wildfire, insects, and drought (Fitzgerald 2005, and Youngblood et al. 2004).

The magnitude of change in structure and composition in MCF is poorly understood. This is reflected in conflicting ideas regarding pre-settlement conditions in

MCF. Many researchers argue that the majority of dry MCF was historically open, dominated by ponderosa pine, and was maintained by frequent low-severity fire (Hessburg et al. 1999, Hemstrom 2001, Heyerdahl et al. 2001, Fitzgerald 2005, Hessburg et al. 2005, and Spies et al. 2006). Other researchers report considerable variability in historical stand densities and composition implicating stand-replacing fire as a major driver of forest structure in the MCF landscape (Hessburg et al. 2007, Baker 2012, and Williams and Baker 2012).

MCF can be considered a transitional forest type since structure and composition continuously changes along a gradient between ponderosa pine woodlands and multistoried forests dominated by grand fir. A lack of consensus on changes since European settlement is related to a poor understanding of variation in current structure and composition along this gradient. To analyze changes in MCF, the current range of density, vertical continuity, and species composition need to be quantified and related to their environmental drivers of climate and topography (Hemstrom 2001). Updated definitions of structure and composition should describe the current state of MCF and organize it into types based on forest maintained by frequent low-severity fire and forest maintained by infrequent high-severity fire (Spies et al. 2006). An understanding of different structure and composition types and their distribution across the environment may help us to differentiate types that are a product of natural versus anthropogenic drivers of change including fire exclusion and logging. Managers require this information to guide restoration and management for MCF.

My overall objective was to describe the current structure and composition of MCF and determine how these attributes are related to major climatic and topographic gradients across the eastern Cascade and Ochoco mountains of Oregon. To accomplish this objective, I used data on structure and composition collected from 179 sample sites in the Deschutes and the Ochoco National Forests in the summers of 2009 and 2010. These sites span the gradient in MCF from low elevation ponderosa pine woodlands to upper elevation forests dominated by grand fir. Specific questions addressed were:

1) Are there distinct structure and composition types of MCF?

2) How are climate and topography associated with variation in stand structure and composition?

3) How does current structure and composition compare to historical records and recent reconstructions of MCF?

Answering the first question will provide a basis for developing minimum structural criteria for MCF quantifying the loss of old overstory trees in the study area, and providing a benchmark to determine how MCF has changed since European settlement. Answering the second question will allow scientists and managers to distinguish environmental drivers of structure and composition from anthropogenic drivers. The third question will describe the magnitude of change in density and composition in MCF in relation to environmental setting.

METHODS

Study area

MCF occurs between relatively dry ponderosa pine woodlands and relatively moist grand fir and mountain hemlock (*Tsuga mertensiana*) forest types (Franklin and Dyrness 1973). Steep climatic and topographic gradients result in a complex mosaic of stand structures and species composition. Mixed-conifer forests are commonly subdivided into three groups along a gradient of increasing precipitation including dry mixed-conifer, moist mixed-conifer, and wet mixed-conifer (Simpson 2007). Relatively xeric dry mixed-conifer forests are dominated by ponderosa pine, have low levels of vertical continuity, and have a park like appearance due to wide spacing of medium to large old trees (Munger 1917). These old-growth forests would best be categorized as old forest with a single-stratum (O'hara et al 1996). In moist mixed-conifer forests, ponderosa pine remains an overstory dominant while Douglas-fir *(Pseudotsuga menziesii)* and grand fir are common understory components (Agee 1993), which results in increased density and vertical continuity. Moist mixed-conifer forest transitions to wet mixed-conifer forest where Douglas-fir and/or grand fir are present in all canopy strata (Simpson 2007). Structure at wet mixed-conifer sites resembles old-growth forest in the wet forest provinces west of the Cascades (Spies et al. 2006). In contrast to dry mixed-conifer old-growth, wet mixed conifer old-growth sites would be considered old forest with multiple strata (O'Hara et al. 1996). At a finer scale, physical site characteristics including aspect, slope, soil properties, and topographic position, create diversity in stand structure and composition.

Mixed-conifer forests are found in three potential vegetation types (PVT) based on climax forest cover. Each PVT is further subdivided by Plant Association Groups (PAG) based on understory herb and shrub composition. PVTs in mixed-conifer forest include grand fir/white fir, Douglas-fir, and ponderosa pine described by Simpson 2007 in the eastern Cascades, and by Johnson and Clausnitzer (1991) in the Ochoco mountains. Major species in both the eastern Cascades and the Ochoco Mountains include ponderosa pine, Douglas-fir, and grand fir (Franklin and Dyrness 1988, Simpson 2007). Ponderosa pine is a dominant overstory component in most stands in all PVTs. In the Douglas-fir and grand fir/white fir PVT, Douglas-fir is generally co-dominant in the overstory except where it is excluded by Mazama ash and pumice deposits (Simpson 2007). Grand fir is only an overstory dominant in the wet PAG types of the grand fir/white fir PVT. Minor species in the eastern Cascades study area include lodgepole pine (*Pinus contorta*), sugar pine (*Pinus lambertiana*), western white pine (*Pinus monticola)*, Shasta red fir (*Abies magnifica var. Shastensis*), incense-cedar (*Calocedrus decurrens*), and western larch

(*Larix occidentalis*). Minor species in the Ochoco Mountains include western larch and western juniper (*Juniperus, occidentalis*).

Common shrubs in all PVTs include greenleaf manzanita (*Arctostaphylos patula*), snowbrush ceanothus (*Ceanothus velutinus*), golden chinquapin (*Castanopsis chrysophylla*), oceanspray (*Holodiscus discolor*), snowberry (*Symphoricarpus albus*), and currant (*Ribes spp*). Recently disturbed areas are often occupied by dense cover of both greenleaf manzanita and snowbrush ceanothus (Franklin and Dyrness 1988). Wet mixed-conifer sites of the grand fir/white fire series are indicated by herb rich understory vegetation (Simpson 2007). Common species include queencup beadlily (*Clintonia uniflora*), twinflower (*Linnaea borealis*), and common prince's pine (*Chimaphila umbellata*). In contrast dry-mixed conifer sites are dominated by shrubs and graminoids which respond quickly to disturbance including snowberry, pinegrass (*Calamagrostis rubescens*), Idaho fescue, (*Festuca idahoensis*), and elk sedge, (*Carex geyeri*).

Environmental setting

In the eastern Cascades mixed-conifer forests are found between 1100-1500 meters in elevation, but occur at higher elevations in the Ochoco Mountains between 1500-2000 meters. Climate in both study areas is Mediterranean, with hot dry summers and relatively wet and cold winters. Mixed-conifer forests in the eastern Cascades have one of the steepest precipitation gradients in the world (Simpson 2007). Moving from the

Cascade crest east, annual precipitation decreases by 280 cm in a span of 15 miles. Dry mixed-conifer forest in the eastern Cascades in the driest PAG groups receives 55cm of precipitation annually while wet mixed-conifer PAG groups receive up to 110cm of precipitation. Compared to the eastern Cascades MCF in the Ochoco Mountains is drier receiving 35cm of precipitation in dry MCF and up to 75cm in wet MCF. In both regions only 10% of annual precipitation falls between June-August. Mean annual maximum temperature ranges from 10-15 ˚C.

Fire regime

Mixed-conifer forest has a mixed-severity fire regime that exhibits characteristics of both low-severity and high-severity fire regimes. At low elevations a low-severity fire regime creates stands dominated by fire resistant species such as ponderosa pine (Agee 1993). Fire historically burned these sites on average of every 7-20 years with stand mortality less than 25% (Agee 1994). Upper elevation mixed-conifer forest is classified as a high-severity fire regime, in which dense multistoried stands dominated by fire intolerant grand fir develop under a much longer fire interval that ranges from 33-100 years (Agee 2003). The disturbance regime of the majority of MCF is characterized by neither low nor high-severity fire, and is best described as mixed-severity.

The mixed-severity fire regime is poorly understood due to its broad range of fire effects (Hessburg et al. 2005). Mixed-severity fires give rise to unique patch dynamics and ecosystem responses, and are more than a simple intermediate between low- and high-severity fire regimes (Halofsky et al. 2011). Mixed-severity fire regimes exhibit intermediate fire return intervals, burn intensities that range from underburning to stand replacement, and create intermediately sized patches with significant edge (Hessburg, Agee, and Franklin 2003). Combinations of surface, torching, and crown fire behavior both within and between fires result in patches of live and dead understory and overstory vegetation (Lentiel et al. 2005, and Perry et al. 2011). Agee (1998) summarizes the spatial heterogeneity and difference in patch sizes observed among low, mixed, and high-severity fire regimes. The high degree of patch edge, variation in patch size, and burn complexity evident in the mixed-severity fire regime is a critical driver of stand structure and composition in mixed-conifer forest.

Logging, fire exclusion, and management history

The forest structure and composition of semi-arid western forests has been homogenized and structurally simplified by the combined effects of logging and fire exclusion (Hemstrom 2001, Hessburg et al. 2005, Brown et al. 2008, Scholl and Taylor 2010, and Naficy et al. 2010). Clearcutting or partial overstory removal of old-growth ponderosa pine followed by management of advanced regeneration of shade tolerant trees was the prominent silvicultural methods used in mixed conifer forest (Seidel 1981). Repeated selective harvest of old-growth ponderosa pine and other fire resistant trees advanced secondary succession by creating small canopy gaps, which favored the regeneration of Douglas-fir and grand fir (Fitzgerald 2005 and Naficy et al. 2010). Coupled with fire exclusion this history of logging has dramatically reduced the area and patch size of single stratum forest dominated by large early seral pines and Douglas-firs while increasing late-seral forest characterized by multilayer strata of the Douglas-fir and grand fir zones (Hessburg et al. 1999, Hemstrom 2003, Hessburg et al. 2005, Camp et al. 1997, and Camp 1999). Increased contagion in canopy cover and dense understories has eliminated spatial isolation of forest structures that historically supported high-severity (Camp et al. 1997 and Hessburg et al. 2005).

The combination of logging and fire exclusion effects has increased the probability of high-intensity stand-replacing wildfires (Camp 1999, Fitzgerald 2005, Perry et al. 2004, and Buchanan 2010). In recent decades large portions of remnant MCF have been lost in the Biscuit, B&B complex, Black Crater, Davis Lake, and Mill Creek fires. Fifty-one percent of all area burned in fires larger than 2,000 hectares during 1984-2007 was classified as high-severity fire in the central and southern portions of the eastern Cascades (Reilly 2012). Using the same criteria 33% of the area burnt in the Blue Mountains region, which encompasses the Ochoco Mountains, was classified as high-severity (Reilly 2012). In addition to high mortality in fires, MCF are threatened by drought and insect outbreaks because Douglas-fir and grand fir in contemporary forests are more susceptible to insects, disease, and drought than the ponderosa pine they have replaced (Hessburg et al. 1994, and Powell 2011), and mortality rates of remnant old-growth ponderosa pines are higher due to increased stand density (Fitzgerald 2005).

Site selection

My goal was to sample the full range of variation in structure and composition associated with the gradient from low elevation dry-mixed conifer forest to upper elevation wet-mixed conifer forest. We sampled mixed-conifer sites with intact old-growth structure and no recent high-severity fire. Potential sample sites were selected in Arc-Map using the plant association layer for the Deschutes and Ochoco National Forests and the Gradient Nearest Neighbor (GNN) vegetation map (Figure 2.1). The GNN vegetation map predicts forest vegetation and stand structure through imputation using Landsat imagery, geographic information system (GIS) layers, and field plots (Ohmann and Gregory 2002). GNN data were obtained from the Landscape Ecology, Modeling, Mapping, and Analysis (LEMMA) website at http://www.fsl.orst.edu/lemma/splash.php.

The PVT layer was used to limit the potential sample area within each national forest to areas classified as ponderosa pine, Douglas-fir, or grand fir/white fir. While climax ponderosa pine sites are not generally classified as mixed-conifer, we included moist ponderosa pine plant association groups because they are often transitional to both the grand fir/white fir series and the Douglas-fir series (Simpson 2007). The GNN

TPH_ge_50 variable predicts the density in trees per hectare (TPH) of trees>50 cm in diameter at breast height (DBH). This variable was used to select sites with large old overstory trees. Half of all potential sample sites were placed in areas with a minimum density of 5 TPH with a DBH of >50cm and half of all potential sites were placed in areas with a minimum density of 25 TPH with a DBH of >50cm. This range of large overstory trees was selected in order to capture sites that had lower overstory densities due to either site conditions or logging history. GNN canopy cover estimates were used to limit the sample area to areas with >20% canopy cover. Finally, all areas <60 m from a patch edge, or <55 m from a road, and all areas burnt in the B&B complex fire and the Davis fire were eliminated from the sample area. These areas were eliminated to ensure sample plots were placed in mature stands. Sample sites were randomly placed in the forest area that met these criteria.

Field data collection

Merschel's sample sites

A total of 53 sites were sampled in the Deschutes National Forest and 36 sites were sampled in the Ochoco National Forest during the summer of 2009 (Figure 2.1). Field measurements were collected using a design based on the PNW-FIA Annual Plot Design. Each site was sampled with 4 plots (Figure 2.2). Site centers were located at plot 1, which was located using a Garmin 60csx GPS, aerial photos, and ground surveying methods. Plots 2-4 were located 36.6 m from plot 1, with plot 2 to the north, plot 3 to the southeast, and plot 4 to the southwest. Each plot had a 17.84 m radius, a subplot with a radius of 7.28 m, and a microplot with a radius of 2.50 m. Sample plot layout is depicted in Figure 2.2. Sites collected specifically for this study are classified as Merschel's sample sites.

The species type, DBH, crown class, and the height to live branches were recorded for all trees > 50cm DBH within each plot. The species type, snag height to the nearest meter, and snag decay class were recorded for snags >50 cm. Snags less than 2.0 m in height were not recorded. Snag decay class was rated on a 1-5 scale with 1 being sound and 5 being rotten. The species type, diameter at cut height, cut height, and approximate cut age were recorded for all cut stumps > 50 cm at cut height. Cut age was recorded as R=recent cut<20 years old or 0=old cut>20 years old. Within each subplot the same information was recorded for all trees and snags >10cm diameter at breast height. Regeneration of trees <10cm was measured within each microplot. Counts of regenerating trees in three size classes based on tree height were recorded for each species present for trees <1.37 m tall. Size classes were (0.1-.0.5 m), (0.5-1.0 m), and (1.0-1.37 m). Counts of regenerating trees in 5 height classes based on DBH were recorded for each species with saplings >1.37 m tall. DBH classes were (0.1-2 cm), (2-4 cm), (4-6 cm), (6-8 cm), and (8-10 cm).

Heyerdahl's additional sample sites

Additional sample sites were added from Emily Heyerdahl's study of, "*Fire and Forest Histories of Mixed-conifer Forests in Central Oregon"* (Heyerdahl 2012). Hereafter these sample sites are referred to as Heyerdahl's sample sites. Heyerdahl's sample sites were added from the Green Ridge study area in the Deschutes National Forest and the McKay and Lytle Creek study areas in the Ochoco National Forest. Each study site was carefully placed in mature mixed-conifer forest in areas with minimal evidence and past history of logging. Sample sites were placed every 500 m on an eight by four grid creating a total of 32 sites per sample area (Figure 2.3). Six sample sites were not sampled due to terrain difficulty or because they lacked a sufficient number of sample trees. Therefore a total of 90 additional sample sites were included in to the data set.

A variable radius plot was used to measure structure and composition at each sample site. Starting from the center of each sample site the first 30 trees and snags greater than 20 cm at DBH were measured and used to determine stand structure and composition. The distance to the 30th tree from the sample site center was the radius for each sample site. Average sample site size was 0.17 hectares with a range of 0.06-0.36 hectares. Saplings and poles were trees 0-20 cm at DBH and greater than 1.4 meters in height. These trees were tallied by species, diameter class, and status in a 5.64 m radius of each sample site. DBH classes were: 2.5 (0 – 5 cm), 7.5 (5 – 10 cm), 15 (10 – 20 cm). Status classes were: Healthy, Unhealthy, Sick (dead in 5-10 yrs), and Dead.

Data preparation and old-growth reconstruction

Densities of large overstory trees were calculated by reconstructing the DBH of each tree based on its diameter at cut height for cuts ≥50 cm at cut height. This reconstruction was done using one of three species specific 'taper' equations for grand fir, ponderosa pine, and Douglas-fir (Table 2.1). Equations were empirically derived by measuring the DBH of 50 live trees of each species at 10 cm, 40 cm, and 137 cm (breast height). These measurements produced the average taper from 10cm to breast height and from 40cm to breast height. Separate equations were used to reconstruct trees from cuts that were less than 40cm high, and for cuts that were taller than 40cm. See Table 2.1 for species-specific taper equations.

The density in trees per hectare (TPH) for all trees, snags, and stumps was calculated for each species present at each plot. First the sum of all trees, snags, and reconstructed stumps was calculated for eight 10cm diameter classes ranging from 0.1-9.9cm 10-19.9cm, 20-29.9cm, 30-39.9cm, 40-49.9cm, 50-59.cm, 60-69.9cm, and 70cm. Density was calculated by multiplying the count in each class by a scaling factor appropriate to the plot it was measured in. For large trees, snags and reconstructed stumps found in the 17.84m radius plot the expansion factor was 10; for trees and snags in the subplot the expansion factor was 60.06; and for all regeneration in the microplot the expansion factor was 509.30. For additional sample sites obtained from Emily Heyerdahl's study of gridded fire history sites, I performed density calculations for identical species and diameter classes. Density was calculated by dividing the number of individuals within a species and size class by the area of the variable radius sample plot measured in hectares.

Multivariate analysis data preparation

Two species matrices were created for hierarchical agglomerative cluster analysis and non-metric multidimensional scaling (NMS). Separate species matrices were created for the eastern Cascades and Ochoco Mountains because of environmental and topographic differences in elevation, precipitation, and slope (Table 2.4). Prior to matrix creation the density of trees, snags, and cuts within each size class were aggregated to represent the total occurrence of each species at a site. Species matrices were intended to represent stand structure and composition for all sample stands within each study area by treating each size class of a species as a single species in the matrix. For example, all ponderosa pine 10.0-29.9 cm in DBH were treated as a single species. In this way each species matrix recorded both structure and composition.

For ponderosa pine, Douglas-fir, and grand fir/white fir four diameter classes were used in four species size classes in both the eastern Cascades and Ochoco National

Forests. Size classes were 10.0-29cm, 30.0-49.9cm, 50.0-69.9cm, and >70cm at DBH. I experimented with several size classes and eventually choose four size classes because they produced the most interpretable MCF stand types. Minor species including lodgepole pine, incense-cedar, western larch, and western juniper were grouped into two species size classes representing all trees and snags <50cm in DBH and all trees and snags >50cm in DBH. Rare species size classes occurring at less than three sites in each study area were eliminated from each species matrix. In each study area, performance at each sample stand was represented with absolute density in a total of 17 species-size class. Cluster analysis used these species-size classes to classify structure and composition types. Because the difference between the largest and smallest non-zero density values in each species size class was often greater than an order of magnitude, a logarithmic transformation was performed within the species matrix. To avoid the problem of log (0) being undefined, the value one was added to all zero values within the species matrix prior to log transformation following the procedure by McCune and Grace (2002). After transformation the coefficient of variation for sites was low for the eastern Cascades (23.67%) and the Ochoco Mountains (24.97%). I performed no further relativization or transformation as they would have a small effect on the qualitative outcome of the analysis (McCune and Grace 2002).

After the log plus one transformation, outlier analysis was conducted in PC ORD v.6 (McCune and Medford 2010) with Euclidean distance for each species size class and each site. All values over 2.0 standard deviations from the overall mean were flagged as potential outliers. Grand fir/white fir in the 10-29.9 cm size class and ponderosa pine in the 10-29.9 cm size were identified as potential outliers. Because higher than average values were expected at each site for these small diameter species size classes, there was no sound ecological reason to remove these species size classes from further analyses. Similarly, four sites in each species matrix were identified as potential outliers in each study area. After examination of the structure and composition of these sites I could see no ecological reason to exclude them from further analysis.

A separate environmental matrix was constructed for both the eastern Cascades and the Ochoco Mountains to investigate climatic and topographic drivers of structure and composition in MCF with the NMS ordination method (Table 2.2). Each environmental matrix had 13 quantitative variables describing the location, climate, and physiographic setting of each sample site. Physical location was described with UTM NAD 83 coordinates easting and northing. Climate was described with mean annual precipitation and mean annual maximum temperature. Climatic variables represent averages from 1971-2000 and were downloaded from the PRISM website (http://www.prism.oregonstate.edu/, Daly et al. 2002). Topographic setting was described by eight variables including elevation, slope gradient, transformed aspect, heatload, and topographic position index (TPI). TPI was calculated at fine (150 m), medium, (300 m), and coarse scales (450 m). All topographic variables were calculated and extracted from a 30 m DEM in ArcMap using the Extract Values to Points analysis tool (ESRI 2010).

Data analysis

Grouping of sample sites based on their species composition and structure was performed with PC-ORD v.6 (McCune and Mefford 2010) using hierarchical agglomerative cluster analysis with Sorensen distance and a flexible beta of 0.25. Dendrograms were scaled by Wishard's objective function (the sum of the error sum of squares from each group centroid to the group members), which was scaled to the percent of information remaining (McCune and Grace 2002). Dendrograms were cut by examining stem length and branching distribution to identify a pruning point that compromises between maximizing within-group homogeneity and between-group differences and minimizing the number of groups (McCune and Grace 2002). Groups identified in cluster analysis were classified as unique structure and composition types of MCF. Structure and composition within each MCF type was summarized by the mean, median, and standard deviation of density for live trees, reconstructed old-growth trees, and snags in four DBH classes ranging from 10-29.9 cm, 30-49.9 cm, 50-69.9cm, and 70.0 cm.

The categorical ‘group’ variable within the environmental matrix was used to graphically determine if MCF types were distinguished in ordination space and to compare locations of groups to ordination axes. Distinctiveness of the MCF groups in environmental space was statistically evaluated using the Multi-Response Permutation Procedure (MRPP) (Biondini et al. 1988). To equalize variance of environmental variables measured on different scales in different units, each environmental matrix was standardized prior to analysis by subtracting the mean and dividing by the SD of each variable. MRPP was conducted with Euclidean distance as it is compatible with negative numbers produced through standardization of environmental matrices. MRPP was used to test the hypothesis of no difference between groups within the environmental matrix.

Relationships between MCF structure and composition types and climatic and topographic setting were analyzed using the NMS ordination technique (Mather 1976) in PC-ORD v.6 (McCune and Mefford 2010). This analysis looks at the relationships between sample sites, MCF types, and the relationships between MCF types and climatic and topographic setting. NMS was conducted on the slow and thorough autopilot method with random starting configurations. Two hundred and fifty runs were conducted with a maximum of 500 iterations per run with a stability criterion of 0.00001. Significance of the ordination axes was evaluated with a Monte Carlo test with 250 iterations. Structure and composition of MCF was related to the environmental matrix with a bi-plot overlay where the lengths of the vectors represent the strength of correlations between climatic and topographic variables and ordinations axes.

RESULTS

Hierarchical clustering of sample stands

Distinct types of MCF were identified through hierarchical clustering in both the eastern Cascades and Ochoco Mountains (Figures 2.4 and 2.5). Both dendrograms for the eastern Cascades and Ochoco Mountains study areas were pruned with approximately 40% information remaining. Within each stand type identified branching was concentrated at short distances producing 5 and 4 homogenous MCF stand types in the eastern Cascades and Ochoco Mountains respectively. Two-way cluster dendrograms displayed clear differences in understory and overstory dominance of ponderosa pine, Douglas-fir, and grand fir. The composition of PIPO, PIPO/PSME, PIPO/ABGC, and PIPO/PSME/ABGC types was similar in each study area, but it was important to develop them separately because of differences in overall density.

In the eastern Cascades and Ochoco Mountains, MRPP demonstrated that MCF types identified in cluster analysis were distinct in environmental space (Table 2.3). The A statistic describes within group homogeneity (McCune and Grace 2002). An A statistic of 1.0 indicates all samples within groups are identical while an A statistic of 0.0 indicates homogeneity equals expectation by chance. In community ecology A values are commonly less than 0.1. Stand types in the eastern Cascades showed within group structure in environmental space with a chance corrected within group agreement, A of 0.063 (p-value=0.0001). Stand types in the Ochoco Mountains showed within group structure in environmental space with a chance corrected within group agreement, A of 0.057 (p-value=0001).

Stand types identified for the eastern Cascades and Ochoco Mountains were analogous in composition although stands in the Ochoco mountains had much lower average density of live trees and snags (Tables 2.7 and 2.8). To describe stand types I developed names based on the species that were dominant in the overstory and understory. For example, PIPO/PSME describes stands with an overstory dominated by ponderosa pine and an understory dominated by Douglas-fir. I excluded the stand type dominated exclusively by grand fir in the eastern Cascades because it represents a small sample of 5 sites on the transition from the grand fir forest vegetation zone to the relatively cool and wet montane mountain hemlock and subalpine fir (*Abies lasiocarpa*) zones (Franklin and Dyrness 1988). Ponderosa pine and Douglas-fir are absent or extremely rare at these cool wet sites while mountain hemlock and noble fir (*Abies amabilis*) are common. These sites were retained for NMS ordinations to represent the upper bound of the MCF type.

Structure and composition of MCF Types

Ponderosa pine is a dominant overstory species by density in all MCF types in the eastern Cascades and Ochoco Mountains (Figures 2.9 and 2.10). The PIPO type in the eastern Cascades and Ochoco mountains is unique in that it is dominated by ponderosa pine in all lower canopy strata (Tables 2.5 and 2.6). Douglas-fir and grand fir are extremely rare in the overstory, but may constitute a small proportion of the understory. In the Ochoco Mountains, western juniper is a prominent component of stand structure at more than half of the PIPO stands sampled (Figure 2.5). Lodgepole pine is an important component at approximately one-fourth of PIPO sites in the eastern Cascades (Figure 2.4).

PIPO/PSME stands in both study areas are distinguished by the presence of Douglas-fir in all canopy strata (Tables 2.5 and 2.6). In the eastern Cascades Douglas-fir occupies all canopy strata at most sites and shares dominance in the overstory with ponderosa pine in the 50-69.9 cm and >70 cm DBH classes (Figure 2.8). Ponderosa pine generally is half as abundant as Douglas-fir in the understory. In contrast, ponderosa pine is about twice as dominant in the overstory in the Ochoco Mountains and equally dominant in the understory (Figure 2.9). Grand fir is extremely rare or absent in the overstory in PIPO/PSME stands in both study areas but is a minor component in the understory in most stands in the eastern Cascades (Figure 2.8). Additionally, incense-cedar is an important understory component in PIPO/PSME stands in the eastern Cascades (Figure 2.4).

PIPO/ABGC stands are distinguished by dominance or co-dominance of grand fir or white fir in the understory (Table 2.5 and 2.6). Ponderosa pine is excluded in the understory by grand fir in the eastern Cascades (Figure 2.9), but it is co-dominant with grand fir in the understory at sites in the Ochoco Mountains (Figure 2.10). In the eastern Cascades, grand fir is co-dominant with ponderosa pine the 50-69.9 cm DBH class while ponderosa pine is clearly dominant in the >70 cm DBH class (Table 2.5). In the Ochoco Mountains ponderosa pine dominates the overstory in both size classes (Table 2.6). Grand fir is a minor overstory component at some sites, but is absent in the overstory at more than half of Type 3 sites (Table 2.6). Douglas-fir is rare or absent in all canopy strata in both study areas (Tables 2.5 and 2.6).

PIPO/PSME/ABGC stands are distinguished by the dominance of all three species in different portions of canopy strata (Figures 2.9 and 2.10). In general early seral ponderosa pine and intermediately shade tolerant Douglas-fir are absent in the understory and grand fir is the dominant species in both the 10-29.9 cm and 30-49.9 cm size classes Tables 2.5 and 2.6). Ponderosa pine, Douglas-fir and grand fir are co-dominant in the 50-69.9 cm size class. Ponderosa pine is the dominant tree in the >70 cm size class, but in contrast to Types 2 and 3 grand fir is a significant component of the largest size class. In both study areas western larch is an important overstory component at many Type 4 sites (Figures 2.4 and 2.5).

Eastern Cascades - Relationship of environmental gradients to structure and composition

A two dimensional solution was chosen for the NMS ordination of sample stands in environmental space for the eastern Cascades (Figure 2.6). Final stress was 13.99 after 72 iterations with a final instability of 0.0001 (p =0.0040 that a similar value could have been obtained by chance from a Monte Carlo simulation with 250 runs). The cumulative R^2 for both axes was 0.893. Axis 1 represents a strong climatic gradient of decreasing maximum temperature (r=-0.646) and increasing average annual precipitation (r=0.595), which is related to increasing elevation (r=.486) (Table 2.11). Axis 2 was most strongly correlated with northing (R^2=0.329), slope (R^2=0.075) and heatload (R^2=0.063). Axis 2 represents a geographic gradient of increasing latitude and a relatively weak topographic gradient related to slope and heatload (Table 2.11).

Prominent species are separated by a steep gradient of decreasing maximum temperature and increasing precipitation represented by Axis 1 (Figure 2.8). Ponderosa pine in the 10-29.9 cm and 30-49.9 cm DBH class is strongly and negatively associated with Axis 1 (r= -0.683, and r= -0.716 respectively). Douglas-fir in the same size classes is placed centrally located along Axis 1 (r = -0.246 and r= -0.211) while grand fir is strongly and positively associated with Axis 1 (r =0.679 and r= 0.688). As species dominance transitions along the climatic gradient in the eastern Cascades PIPO and PIPO/PSME stands transition into PIPO/ABGC and PIPO/PSME/ABGC stands respectively (Figure 2.6). The strong association of ponderosa pine with the driest and warmest environments suggests that a xeric climate enables it to maintain understory dominance in PIPO stands. Douglas-fir becomes dominant with increasing moisture and decreasing temperature and in turn is replaced by grand fir at the coldest and wettest MCF sites. Overall structure and composition transition from PIPO stands almost exclusively dominated by ponderosa pine to PIPO/PSME/ABGC stands where ponderosa pine is restricted to the overstory and grand fir and or Douglas-fir are prominent overstory components.

PIPO and PIPO/PSME stands are separated from PIPO/ABGC and PIPO/PSME/ABGC stands along Axis 2 by a geographic gradient of increasing latitude as values decrease along Axis 2. In environmental space all DBH classes of Douglas-fir are negatively associated with Axis 2 (Table 2.13). This indicates that composition in the southern half of the eastern Cascades was characterized by low dominance of Douglas-fir in the understory in PIPO stands and low overstory dominance in PIPO/ABGC stands. Conversely in the northern portion of the study area Douglas-fir becomes the dominant understory species in PIPO/PSME stands and a prominent overstory species at

PIPO/PSME/ABGC stands. Topographic and climatic variables investigated do not provide an explanation for the exclusion of Douglas-fir in PIPO and PIPO/ABGC stands. Simpson (2008) suggests that Mazama ash deposits are responsible for the absence of Douglas-fir in the southern portion of the Deschutes National Forest, but I did not have adequate soil data to evaluate the relationship between Douglas-fir and soil characteristics. As a result PIPO stands transition to PIPO/ABGC stands at sites where Douglas-fir is absent. In the northern half of the study area PIPO/PSME stands occupy the same portion of the temperature and precipitation gradient as PIPO stands and transition to PIPO/PSME/ABGC stands. This indicates that Douglas-fir is competitive with ponderosa pine at the most xeric MCF sites in the northern part of the study area.

Ochoco Mountains - Relationship of environmental gradients to structure and composition

A two dimensional solution was chosen for the NMS ordination of sample stands in environmental space for the Ochoco Mountains (Figure 2.9). Final stress was 16.94 after 45 iterations with a final instability of 0.0001 (p =0.0040 that a similar value could have been obtained by chance from a Monte Carlo simulation with 250 runs). The cumulative R^2 for both axes was 0.865.

Similar to the eastern Cascades Axis 1 was most strongly correlated with precipitation, (r=0.457), maximum temperature (r=-0.440), and elevation (r=0.345) and represents a climatic gradient (Table 2.12). In comparison to the eastern Cascades, correlations between climatic variables and Axis 1 are weaker in the Ochoco Mountains, which have a narrower range of precipitation than the eastern Cascades (Table 2.4). Despite the weaker climatic gradient ponderosa pine and grand fir were distinctly separated along Axis 1(Figure 2.9). A transition from PIPO and PIPO/PSME stands to PIPO/ABGC stands, and finally PIPO/PSME/ABGC stands occurs with increasing precipitation and decreasing temperature (Figure 2.8). This transition differs from the eastern Cascades where PIPO/ABGC stands transition to PIPO/PSME/ABGC stands along a geographic rather than climatic gradient.

Axis 2 represents a topographic gradient associated with solar radiation which is represented by a combination of slope and the similar variables of PRR and PDIR (Figure 2.8). Slope is positively correlated with Axis 2 (r=0.275) while PDIR (r=-0.325) and PRR (r=-0.349) are negatively associated with Axis 2. Increasing scores along Axis 2 are associated with relatively steep sites with low solar radiation at mesic aspects. PDIR is additionally negatively associated with increasing values of Axis 1 (r=-0.301). Within ordination space low scores along both Axis 1 and 2 represent environments with relatively gentle slopes and relatively high solar radiation.

While ponderosa pine and Douglas-fir share similar locations in environmental space along Axis 1, they are differentiated along a topographic gradient along Axis 2.

Understory Douglas-fir trees in the 10.0-29.9 cm and 30.0-49.9 cm DBH classes are positively associated with Axis 2 (r=0.683 and r=0.715). Increasing values along Axis 2 represent environments with steep slopes and low solar intensity as indicated by a negative association of PDIR and PRR with Axis 2. Therefore, Douglas-fir and PIPO/PSME stands are associated with warm and dry sites on steep slopes with low solar intensity. In contrast, PIPO stands that have a dominant understory of ponderosa pine and a component of western juniper are found at warm and dry areas on flat slopes or ridge tops with high solar intensity. Table 2.4 supports these relationships as PIPO/PSME sites have the highest mean and median slope and PIPO sites have the highest mean and median values for TPI 300 and PRR.

Reconstructed density of old-growth trees

Comparison of current with reconstructed densities of overstory trees shows that overstory ponderosa pine has been reduced by logging in all MCF types (Tables 2.5 and 2.6). The current median density of all overstory trees among all MCF types is less than half of reconstructed median values with PIPO stands experiencing the largest proportional reduction in overstory tree density. Ponderosa pine was the primary species removed in selective logging in all stand types with the exception of PIPO/PSME stands in the eastern Cascades where overstory Douglas-fir in the >70 cm DBH class increased from a mean value of 2.8 to 7.5 TPH after reconstruction (Table 2.5).

DISCUSSION

MCF stand types were organized by current structure and composition. All types had relatively high stand densities, and canopies with multiple strata. Prior to selective logging, large overstory ponderosa pine was common across a wide range of climatic and topographic gradients. Current densities of large overstory ponderosa pine are approximately half of pre logging densities based on stump reconstruction. Large shade tolerant trees were absent at PIPO stands, scattered and rare at PIPO/PSME and PIPO/ABGC stands, and were common in the overstory in PIPO/PSME/ABGC stands. NMS ordinations of stand types demonstrated that structure and composition is associated with site environmental conditions. Understory composition was distinct among stand types and transitioned from ponderosa pine and Douglas-fir to grand fir as sites became progressively wetter and cooler. Understory dominance of Douglas-fir at hot and dry sites was associated with northern latitudes in the eastern Cascades and steeply sloped sites with low solar insolation in the Ochoco Mountains.

Changes in Structure and Composition in MCF

Stand Density

Munger (1917) reported a density of 136 TPH for ponderosa pine forest, and 152 TPH in dry-mixed conifer forest in the eastern Cascades in the early 20th century. Munger described ponderosa pine and dry MCF stands as open with widely spaced trees, but noted that stand density was variable as open stands of mature trees were interrupted by treeless areas or denser patches of young trees. In contrast the majority of sites with similar composition visited in this study were dense with uniformly spaced trees and mean density for only understory trees 10-50 cm at DBH was 246 and 240 TPH for the PIPO and PIPO/PSME types respectively. A limitation of comparisons to Munger's historic estimates of stand density is that they are based on a limited number of sample sites that aren't spatially extensive. Additionally my sample was limited to areas with greater than 20% canopy cover.

The eastern Cascades study area partly overlaps with a spatially extensive reconstruction of structure and composition in central Oregon developed using GLO data from the late 19th and early 20th century (Baker 2012). This study encompassed a wide range of dry forest types including lodgepole pine types, and attempted to exclude what was considered "moist mixed conifer" types. Moist mixed-conifer sites were areas where Engelmann spruce (*Picea engelmanni*), Shasta red fir (*Abies magnifica var Shastensis*), or western white pine (*Pinus montcola*) were the second most abundant species in the stand, or areas where grand fir was the most abundant species. The reconstruction area spanned the ponderosa pine, dry Douglas-fir and grand fir / white fir, and lodgepole pine plant association groups (PAG) described by Simpson (2007). My inventory is also spatially extensive, but spans a broader moisture gradient including what Baker (2012) considered moist mixed conifer forests found in moist and wet Douglas fir and grand fir/white fir PAGs. Additionally structure and composition is reported for MCF organized by environmental zones.

Comparisons of early 20th century and present day density between Baker's reconstructed values and my inventory values should recognize that Baker's reconstruction was primarily focused on dry MCF and included a significant portion of lodgepole pine types. However, I rarely encountered Baker's indicator species of moist mixed-conifer forest at my sample sites, and sites with these species would have been classified in the wettest PIPO/PSME/ABGC type, which had a mean density of 310 TPH. For drier PIPO, PIPO/PSME, and PIPO/ABGC MCF types, which more closely coincide with Baker's reconstruction, present day mean values for density of live trees and snags in older MCF were 432, 461, and 569 TPH in the eastern Cascades. In comparison Baker's reconstruction suggests density in similar ponderosa pine and dry MCF was 219 and 275 TPH respectively in the eastern Cascades during the early 20th century. This spatially extensive comparison suggests that density in dry MCF has more than doubled during the 20th century. Furthermore median reconstructed values for ponderosa pine and dry MCF were 195 and 239 TPH (Baker 2012), while present day median values for the PIPO, PIPO/PSME, and PIPO/ABGC type were 425, 456, and 553 TPH. Both mean and median values for density of contemporary MCF are nearly equal to or considerably higher than third quartile of 318 TPH for reconstructed density of dry forests during the early 20th century (Baker 2012). The lease dense stands in the dry forest landscape today would have been characterized as relatively dense in comparison to the rest of the forest landscape in the early 20th century.

Current density is considerably lower in the Ochoco Mountains in comparison to the eastern Cascades. Lower density is likely related to climate in the Ochoco Mountains area which is significantly more arid than the eastern Cascades (Table 2.4). The Mill Creek track in the western Ochoco Mountains provides one reasonable estimate of dry-forest density prior to fire exclusion and logging. Density estimates from 1910 for the Mill Creek tract report a mean of 110 for all stems > 20cm DBH (Munger 1912). Contemporary mean densities in the Ochoco Mountains in each of the four types identified is 279, 304, 212 and 307 TPH for all stems >10 cm DBH. The Ochoco Mountains and eastern Cascades study areas have had similar management activities since the late 19th century including fire exclusion, selective logging, and heavy grazing (Powell 2011). In contrast to the eastern Cascades, the Ochoco study area had several sites that were relatively open as 21 of 94 sites had densities of less than 150 TPH. These sites were concentrated in two small geographic areas within Emily Heyerdahl's McKay and Lytle Creek fire history samples sites. These sites with relatively low density were well distributed across MCF Types and therefore were represented across a broad range of climatic and topographic settings.

Composition

Changes with density have been accompanied with changes in composition toward the less fire tolerant species of grand fir and Douglas-fir. Munger (1917) reported that only western larch grew with ponderosa pine in mixed-conifer forests while grand fir and Douglas-fir occurred to a large extent in single species groups. Currently small diameter fire intolerant trees are well distributed throughout MCF types. The corresponding absence of large overstory fire intolerant trees at xeric PIPO and PIPO/PSME sites and their scarcity at the majority of PIPO/ABGC sites provides evidence that fire exclusion has led to a shift in species composition.

In my inventory of MCF, I found limited evidence for the occurrence of topographic fire refugia. Fire refugia are topographic positions where longer fire return intervals allow the development of fire sensitive and shade tolerant species within fire prone landscapes (Camp 1997). Mature refugial stands are dense, multilayered, have an overstory dominated by late seral species, and are found within a matrix of relatively open forest vegetation dominated by early seral species. Stands with refugial-type-vegetation occurred at PIPO/ABGC and PIPO/PSME/ABGC sites. Ordination demonstrated that this refugial structure and composition was found at the highest elevations with correspondingly high precipitation, and was not associated with local topography. Therefore these sites do not qualify as refugia in a strict sense as they were not found within a larger matrix of fire prone forest. Longer fire return intervals, which enabled the development of late seral vegetation at these sites, were likely driven by climate rather than topographic setting. The rarity of true refugial stands at lower and middle elevations among my randomly selected sites suggests that they are not common in the eastern Cascades and Ochoco Mountains. However, the sampling procedure used to select sample sites may have missed isolated topographic fire refugia at lower elevations because I did not specifically target areas that would most likely to escape frequent fires. These areas include perched water tables, stream confluences, headwalls, and environments with low solar isolation, which represent a small portion of the MCF landscape (Camp 1997).

Although understory Douglas-fir was found at steep sites with low solar insolation, associations between topographic setting and species composition may have also been obscured by the method used to select sample sites. Collectively gradients of temperature, precipitation, and elevation showed strong associations with composition while topographic variables of aspect, TPI, and heatload showed weak associations. This result is surprising because other investigators report differences in composition between north and south slopes in dry eastside forests (Munger 1917 and Ohmann and Spies

1998). Based on my field experience in MCF I would agree that composition is strongly associated with topography, but this relationship is variable at different climatic settings. The association between topography and composition at the scale of a single landform was likely lost because sample sites were place over a broad geographic area with a wide range of elevation precipitation and temperature. For example, structure and composition at two of my sites that were both on north slopes may have been different because the sites were at contrasting elevations. This agrees with Ohmann and Spies (1998) finding that small geographic scales are necessary to detect variation in composition related to topographic setting. A better understanding of how topography influences structure and composition at finer scales would help guide management of MCF vegetation at relatively fine scales. To improve our understanding of the relationship between topographic setting and composition sample plots should be selected from a broad range of topographic settings that have a limited range of precipitation and temperature.

Loss of overstory ponderosa pine

The presence of large ponderosa pine in all MCF stand types and its central placement in NMS ordinations indicate that mature ponderosa pine was a pervasive component of stand structure and composition in MCF. Selective harvest of mature ponderosa pine was common during the 20th century, and reconstruction of cuts shows current densities of large diameter ponderosa pine are half of pre harvest densities.

Based on the Region 6 interim old-growth definitions, low productivity MCF sites must have at least 25 TPH >53 cm DBH and high productivity MCF sites must have at least 38 TPH >53 cm DBH to qualify as old-growth forest (Hopkins et al. 1992). Prior to reconstruction the majority of sample stands do not qualify as old-growth. After reconstruction mean and median densities of all trees > 50 cm at DBH exceed the minimum required densities for low and high productivity sites in each of the MCF structural types identified. Collectively, this suggests that large overstory ponderosa pine was historically ubiquitous and persistent prior to fire exclusion in MCF that ranges from dry to wet.

At PIPO/ABGC and PIPO/PSME/ABGC sites found at higher elevations, shade tolerant trees make up a significant proportion of the density of large overstory trees and dominate the understory. My record of large overstory ponderosa pine at these relatively wet sites suggests that fire historically allowed ponderosa pine to establish and mature in environments where Douglas-fir and grand fir are more competitive in the absence of disturbance. The current scarcity of understory ponderosa pine and predominance of understory grand fir and Douglas-fir indicates harvested overstory ponderosa pine will not be replaced in moist and wet MCF. Competition in dense stands sharply reduces the growth rate of understory ponderosa pine preventing new recruitment of large diameter fire resistant trees (Harrod et al. 1999). Furthermore high stand density reduces the vigor of extant large diameter ponderosa pine (Kolb et al. 2007) increasing insect and drought mortality (Fitzgerald 2005). Overall recovery of historic densities of large diameter ponderosa pine may be impeded by a lack of small diameter ponderosa pine, slow growth rates, and mortality of extant large diameter trees. Future patches of moderate and high-severity wildfire present an opportunity to recover ponderosa pine and other early seral plant species at moist and wet MCF sites (Perry et al. 2011).

It is important to note that the reconstructed density of overstory trees only provides a best available estimate of density of these trees had they not been logged. Using stumps to calculate what overstory density would have been today if logging had not occurred may slightly overestimate historic density, as some of the older trees harvested would have died even if they were not harvested. Additionally, individuals that were left in the stand may not have grown into the larger diameter classes without the removal of dominant trees at the site.

Utility of MCF Stand Types and Management Implications

PVT classifies MCF vegetation based on the potential climax vegetation at a site, which is dependent on environmental setting and not historic disturbance regime (Johnson and Clausnitzer 1991 and Simpson 2007). The resulting landscape pattern of PVTs is used to guide restoration of structure and composition at sites altered by fire exclusion and logging (Brown et al. 2004). This may be problematic in MCF where fires historically prevented establishment and development of late successional species. As a result of fire exclusion, the extent of both the Douglas-fir and grand PVT has expanded as MCF stand types now contain understory shade tolerant species where mature shade tolerants are rare or absent. MCF stand types observed in this investigation differ from PVTs because they are based on current structure and composition, which is related to historic disturbance regime and management, in addition to environmental setting. Knowledge of current stand types and their PVT can be used to set priorities in restoration planning. To increase their utility the stand types developed in this investigation would need to be mapped across the landscape.

Overall the results of this investigation highlight that MCF stands have reduced density of mature fire resistant trees, have high densities of small diameter trees, and are composed of a high proportion of shade tolerant trees. These conditions are undesirable because they increase mortality in wildfires and may increase mortality due to droughts insects, and disease (Hemstrom 2001, Fitzgerald 2005, Hessburg et al. 2005, and Powell 2011). Stand Types elucidate variation in MCF and can be used to tailor restoration treatments designed to restore structure and composition that is more resilient to mortality in future wildfires, droughts, and disease outbreaks. Brown et al (2004), Fitzgerald (2005), and Powell (2011) provide thorough descriptions of how thinning and fire may be used to accomplish these objectives in dry forests. Here I provide a brief summary of additional restoration considerations based on the current structure and composition of the stand types I developed.

Ponderosa pine is well represented by small diameter trees at PIPO and PIPO/PSME sites and may recruit into large diameter overstory trees in the absence of high-severity disturbance. However, the high density of small diameter trees at these sites threatens persistence of extant large old-growth trees in drought events and insect outbreaks (Kolb et al. 2007), and slows recruitment of future large diameter trees (Harrod et al 1999 and Cochran and Barrett 1999). Historically, structure in MCF dominated by ponderosa pine was characterized by widely spaced trees, interspersed with clumps of large trees, and patches of regenerating saplings (Munger 1917 and Youngblood et al. 2004). Diameter distribution was long tailed with overstory trees well distributed across large diameter classes (Munger 1912 and Cowlin 1942). The uniform density and diameter distribution of current understory trees established during fire exclusion at my sites contrasts with these descriptions of structure developed in forests with more frequent fire. Thinning of understory trees could be used to restore structure at these sites by accelerating growth of small diameter trees (Cochran and Barrett 1999 and Fitzgerald 2005), by mimicking their historic spatial pattern (Youngblood et al. 2004), and by increasing the vigor and resilience of extant old-growth trees to drought and insects (Latham and Tappeiner 2002, and Kolb et al. 2007).

At PIPO/ABGC sites small diameter ponderosa pines are extremely rare in comparison to grand fir. While there is limited data about the competitiveness of ponderosa pine in stands dominated by grand fir it will likely be excluded in the absence of disturbance because grand fir is shade tolerant and high stand density is related to poor height and diameter growth in ponderosa pine (Cochran and Barrett 1999). At PIPO/ABGC sites thinning could be used to increase the vigor of small diameter ponderosa pine so that they can replace extant and logged overstory ponderosa pine. Thinning at PIPO, PIPO/PSME, and PIPO/ABGC would additionally increase the likelihood that extant large diameter trees, which take centuries to develop, will persist during future disturbances by lowering fire severity and increasing their resistance to disease and drought (Fitzgerald 2005 and Powell 2011).

Precise boundaries based on environmental conditions of areas that should be treated or not treated to restore structure do not exist. However, PIPO/ABGC and PIPO/PSME/ABGC sites where large diameter grand fir or Douglas-fir are dominant in the overstory may represent areas that were not prone to frequent fire. If these stands are left untreated they can provide habitat for late seral plant and animal species associated with late successional MCF. Because these sites were found at high elevations, strategic placement of thinning treatments at PIPO, PIPO/PSME, and PIPO/ABGC sites at lower elevations can decrease the likelihood that these sites will experience high-severity fire wildfires (Buchanan 2010). A combination of thinning and burning treatments at these sites could increase the resilience of mature fire resistant trees to wildfire and insects and provide habitat for species associated with fire climax vegetation.

CONCLUSIONS

Inherent variability in structure and composition in MCF has limited our understanding of how fire exclusion and selective logging have reduced the density of large fire tolerant ponderosa pine and increased the density of fire sensitive late seral species. Determining the magnitude of changes in structure and composition in MCF is dependent on improving our understanding of the ecology of this forest type. My study was an important step in this process as current variation in structure in composition was described and related to environmental setting. Species composition in MCF of the eastern Cascades and Ochoco Mountains was variable and most strongly associated with increasing precipitation and decreasing temperature. However, stand density was best characterized as uniformly high when compared to historical records at MCF sites ranging from dry to wet due to dense understory canopies found at the majority of sample sites. High understory densities may have historically occurred in patches, but not uniformly across the landscape (Perry et al. 2011). Exclusion of fire has likely reduced patches of forest MCF in various successional stages as late seral vegetation has become prevalent. Prevalence of late seral vegetation in MCF may limit the recovery of large fire resistant ponderosa pine, reduces habitat available for species associated with early seral and fire climax vegetation, and may increase mortality in wildfires, drought, and insect outbreaks.

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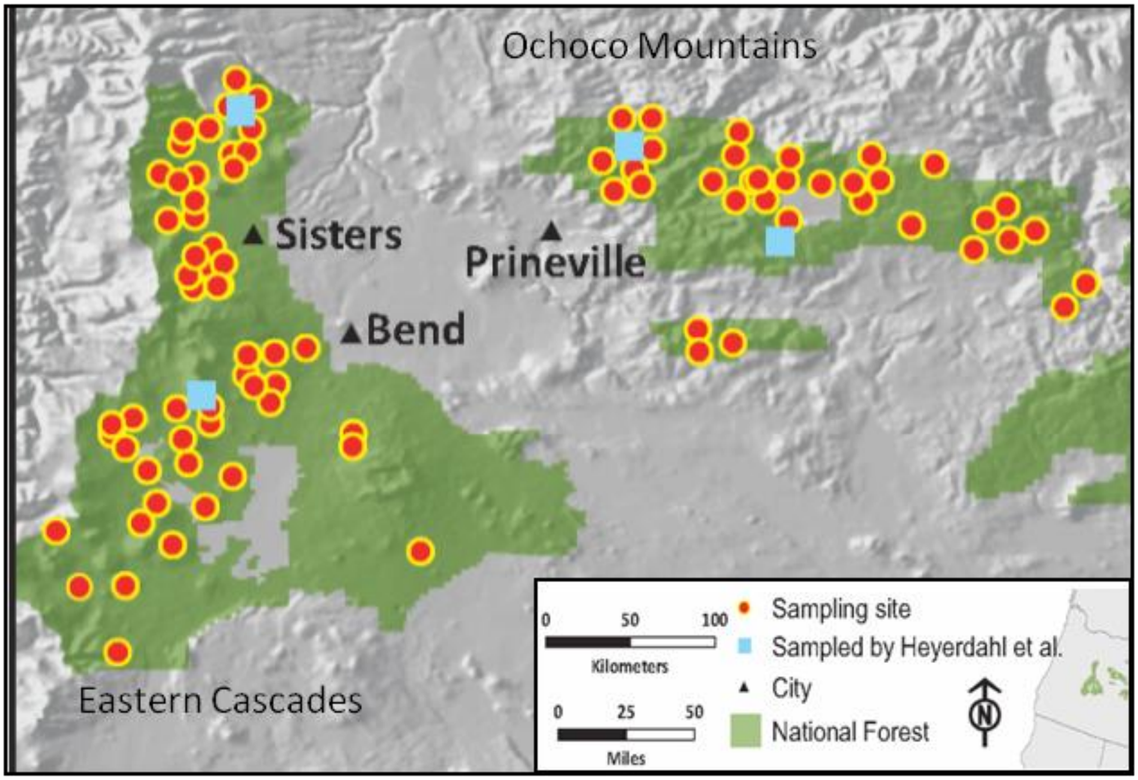

Figure 2.1: Eastern Cascades and Ochoco Mountains study areas and study site locations.

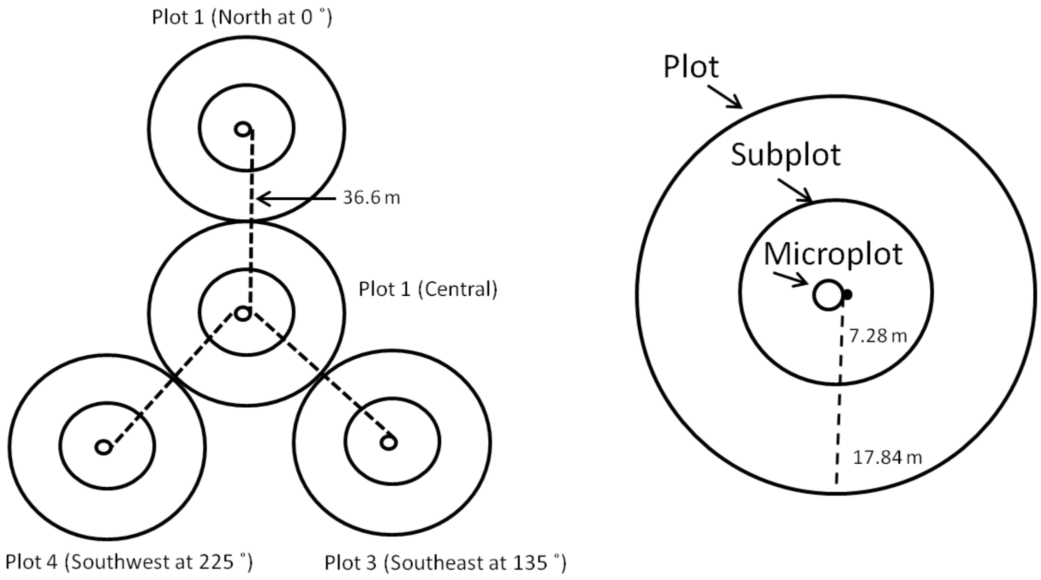

Figure 2.2: Sample plot layout at Merschel's sample sites: (left) arrangement of sample plots at a sample site, (right) detail of individual plot layout showing location of subplot and microplot. Plot radius was 17.84 m, subplot radius was 7.28 m, and microplot radius was 2.5 m.

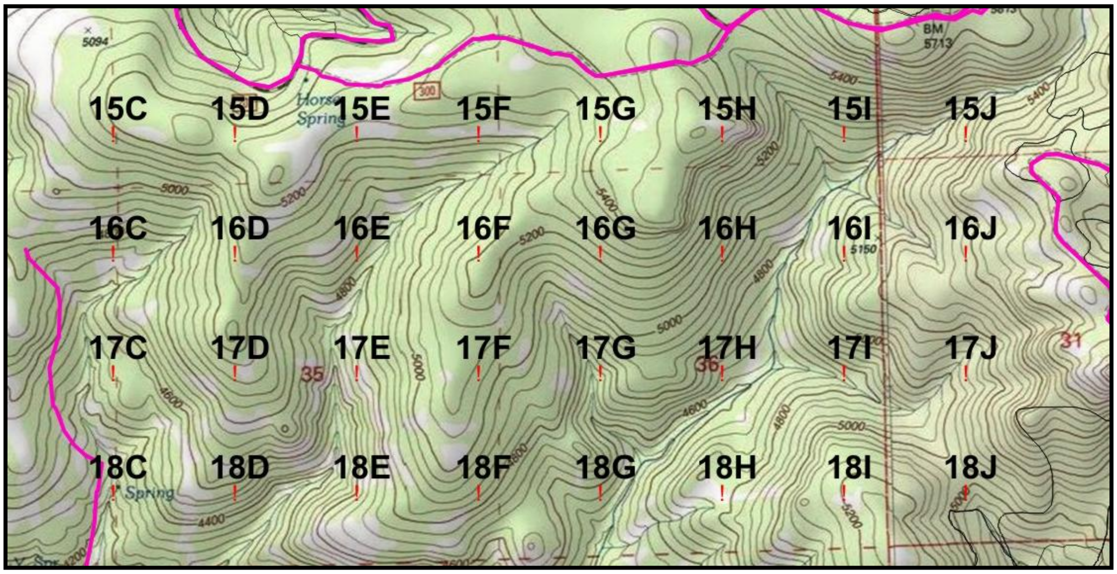

Figure 2.3: Sample plot layout at McKay study area for Heyerdahl's study of fire and forest histories of mixed-conifer forests in central Oregon. 32 samples plots were placed every 500 meters on an 8 by 4 grid at Green Ridge, McKay, and Lytle study areas.

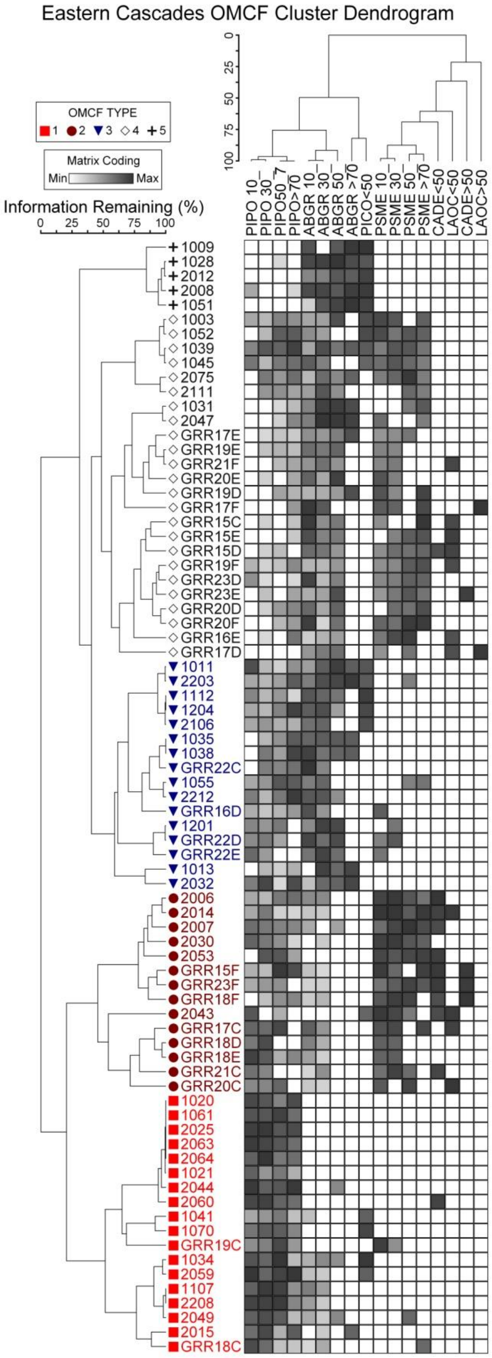

Figure 2.4: Eastern Cascades dendrogram produced in hierarchical cluster analysis. Rows represent sample stands and columns represent species grouped by DBH class. Darker shading indicates higher density of a species size class at a sample stand.

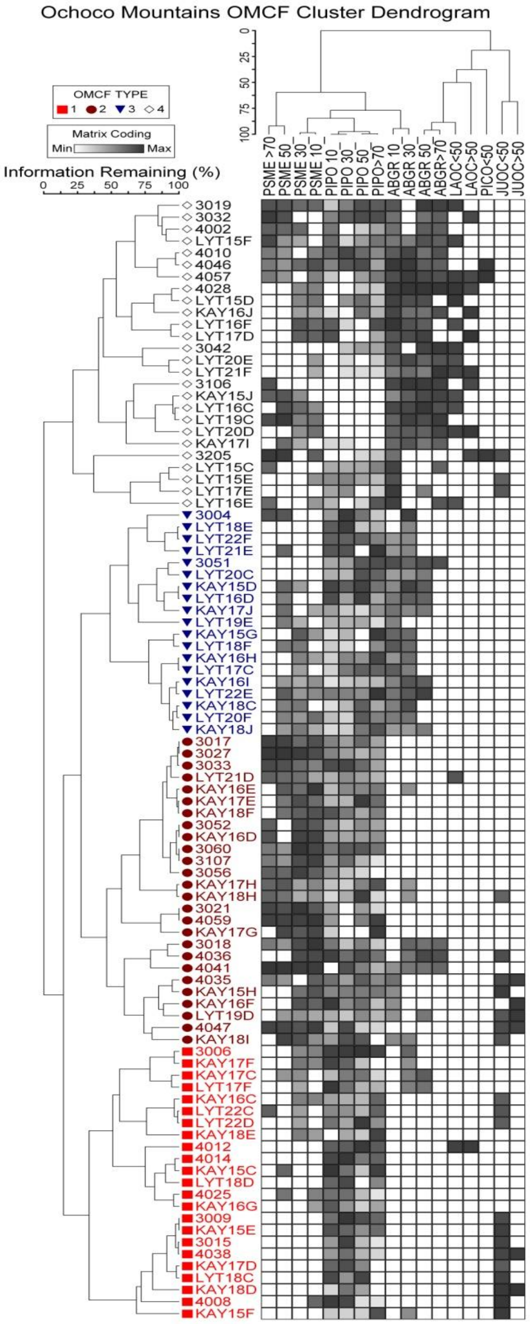

Figure 2.5: Ochoco Mountains dendrogram produced in hierarchical cluster analysis. Rows represent sample stands and columns represent species grouped by DBH class. Darker shading indicates higher density of a species size class at a sample stand.

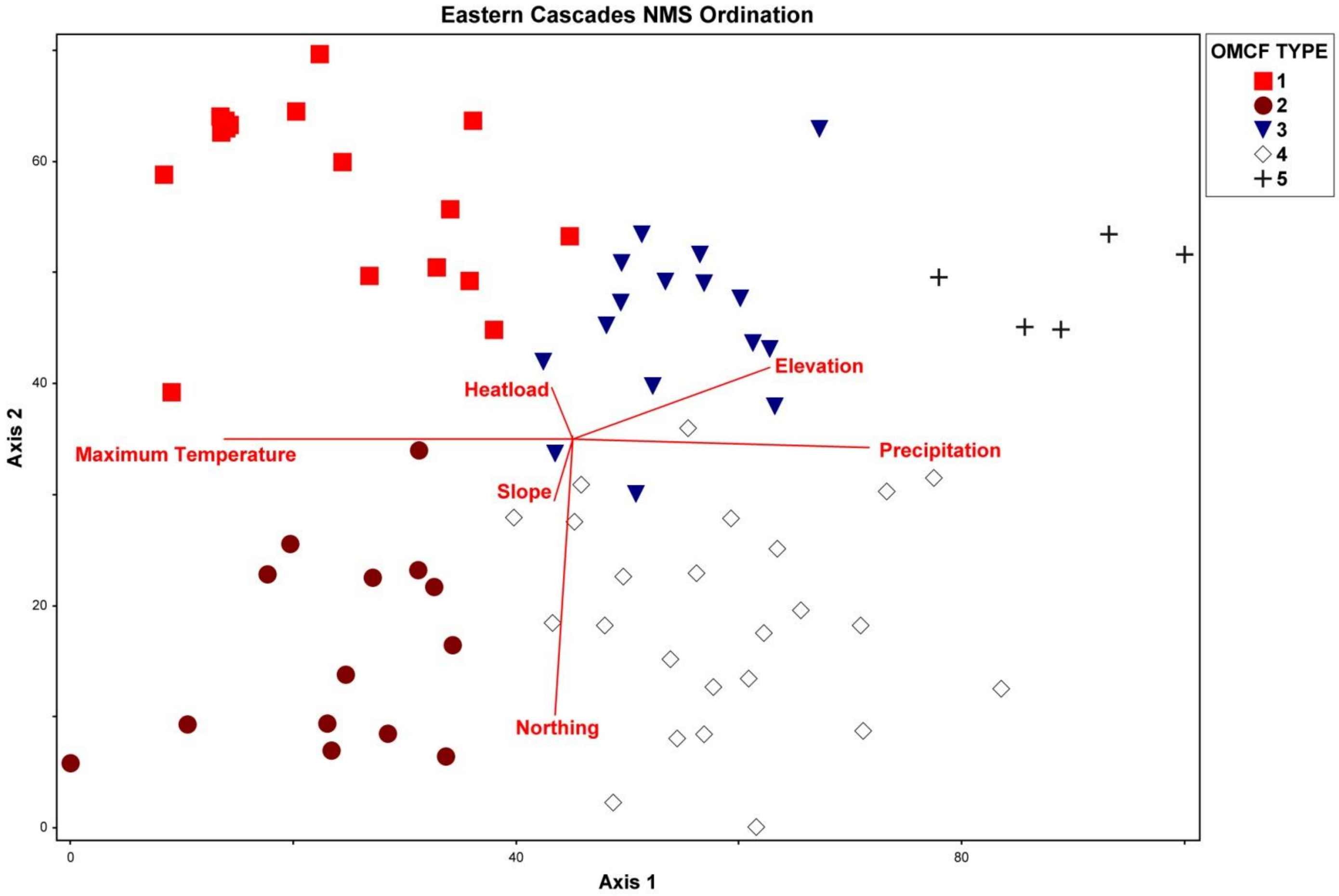

Figure 2.6: Eastern Cascades NMS ordination displaying MCF sites in environmental space

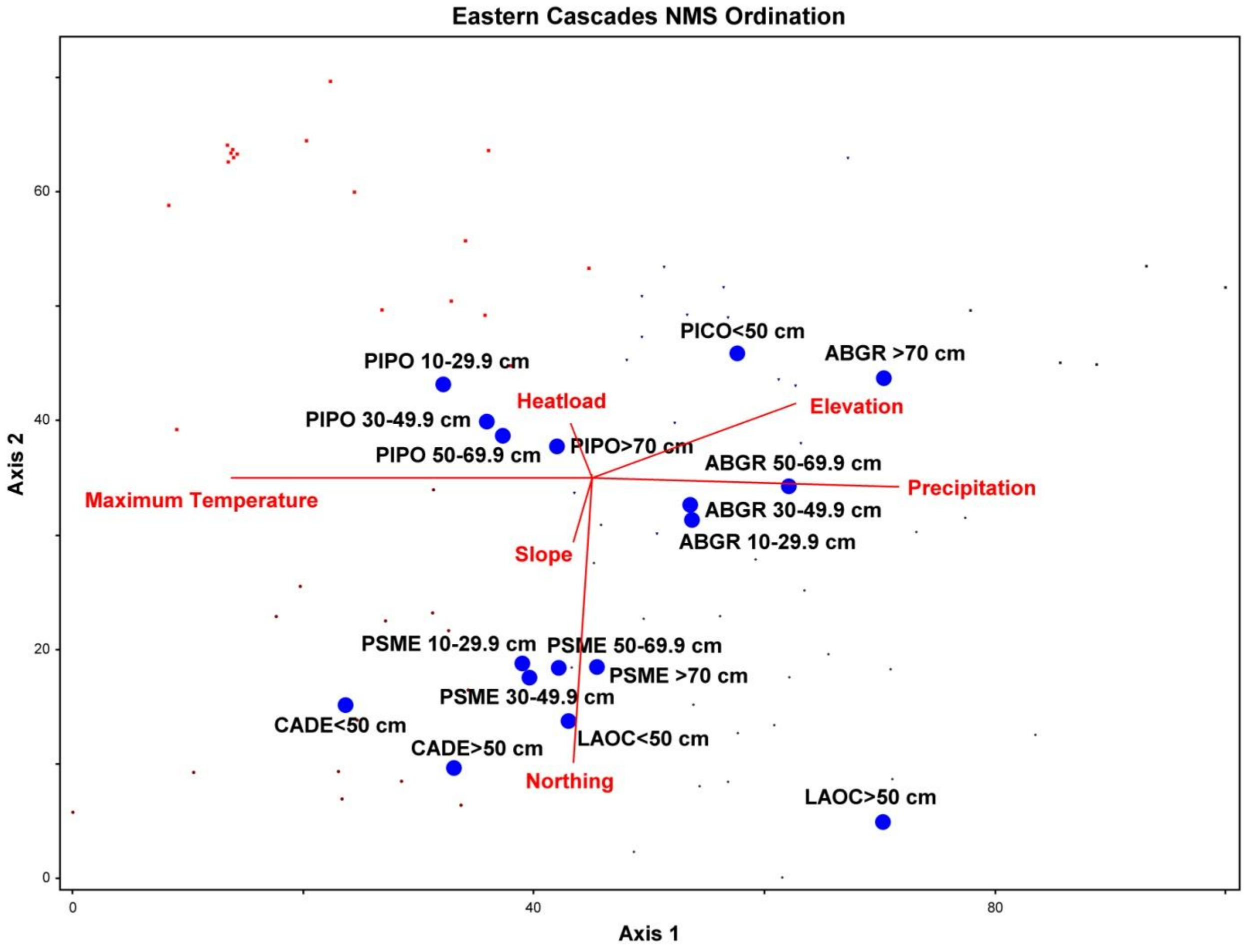

Figure 2.7: Eastern Cascades NMS ordination displaying species size classes in environmental space

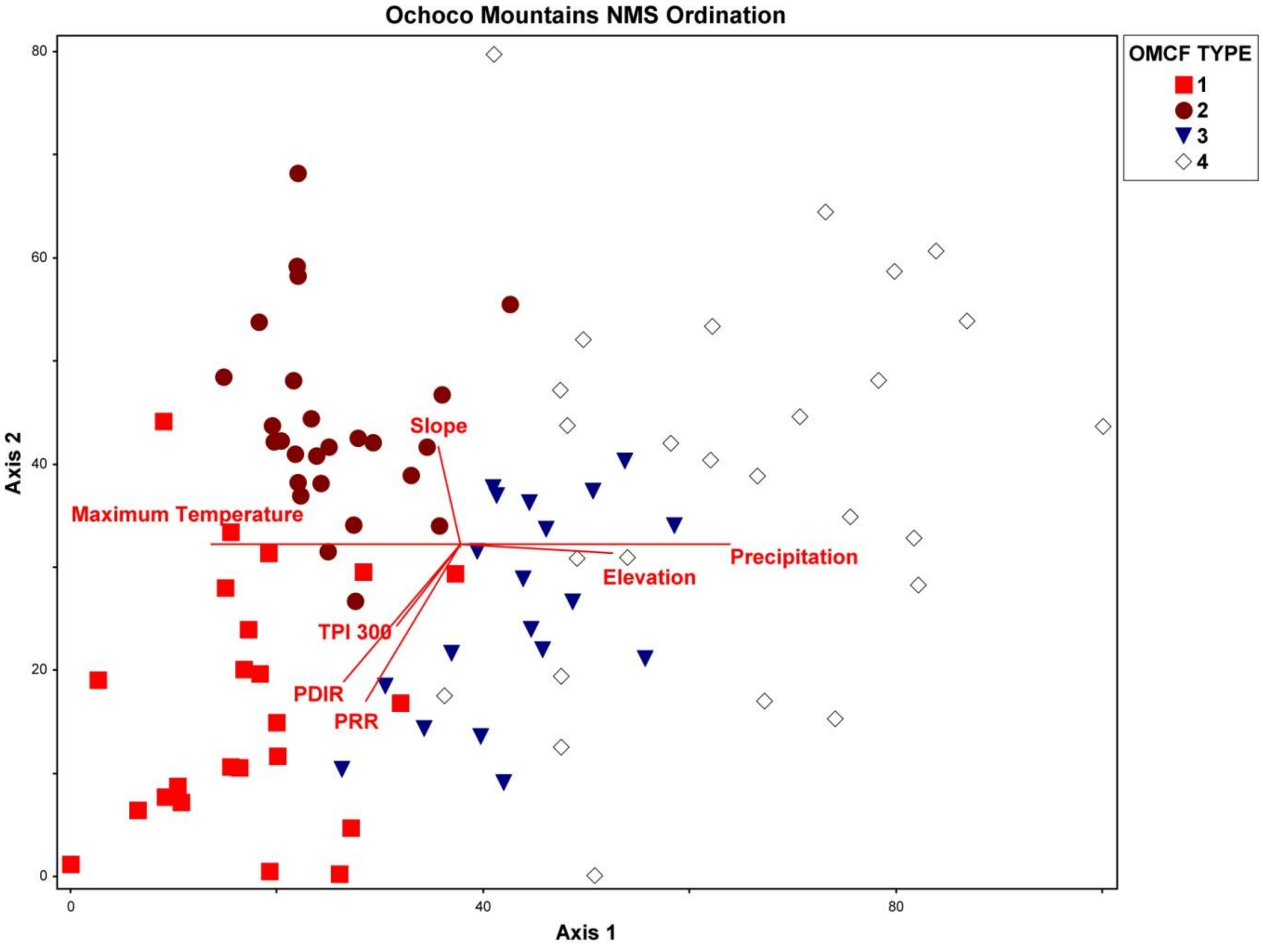

Figure 2.8: Ochoco Mountains NMS ordination displaying MCF sites in environmental space

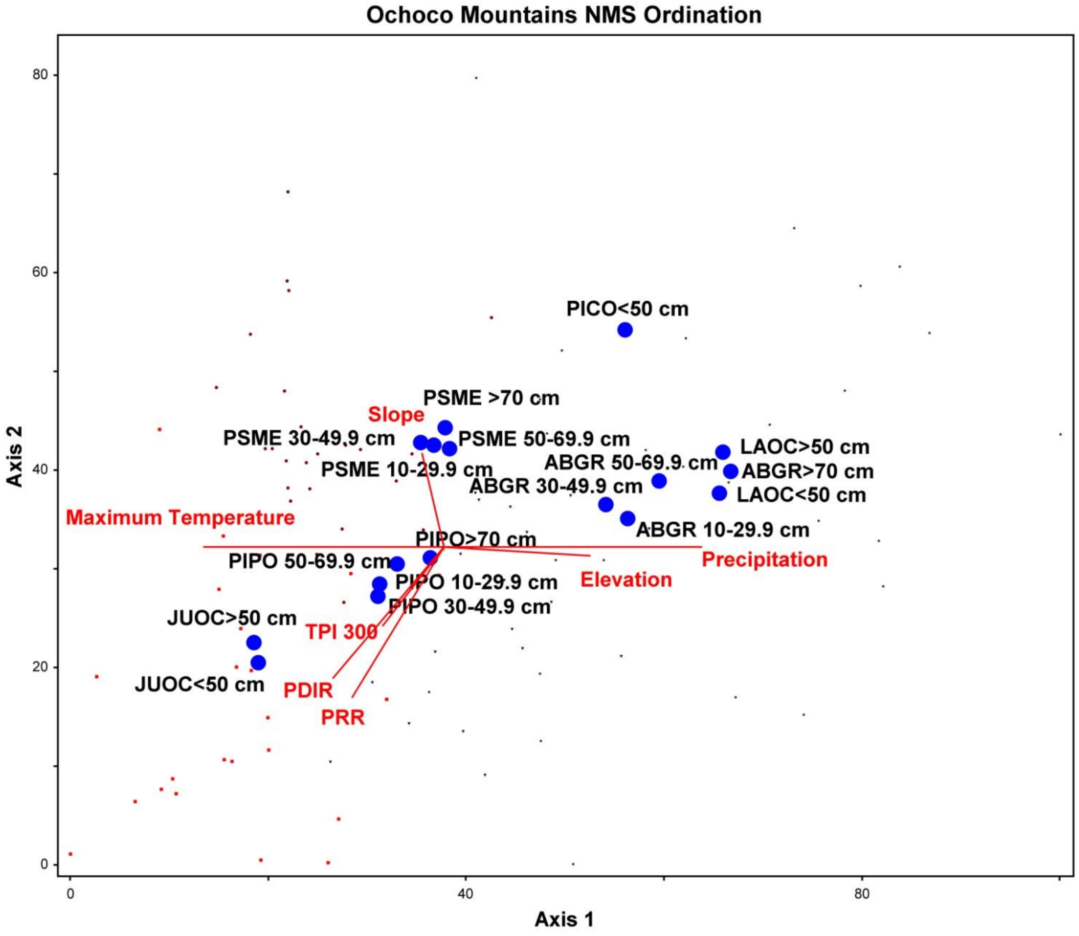

Figure 2.9: Ochoco Mountains NMS ordination displaying species size classes in environmental space

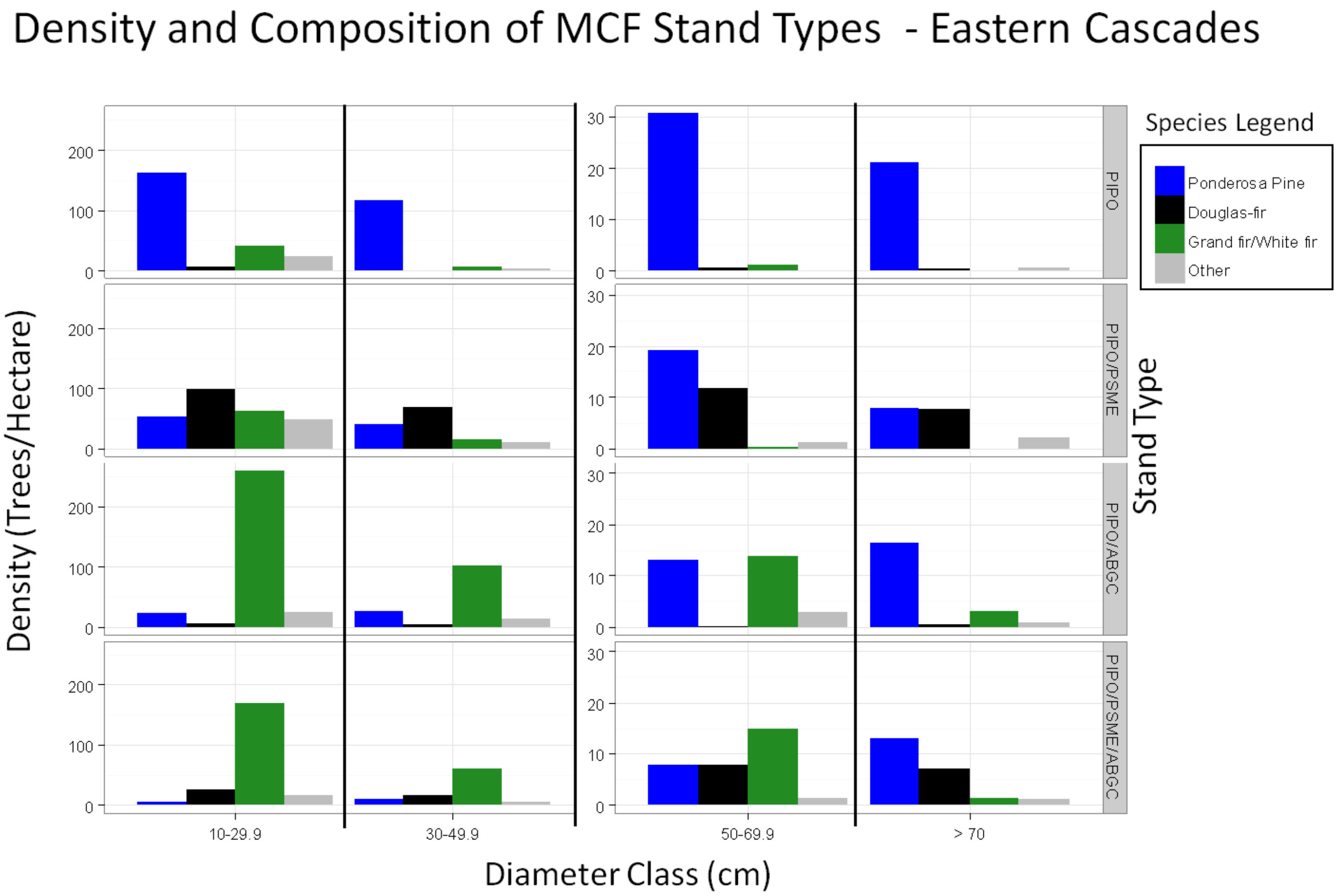

Figure 2.10: Density and composition of stand types organized by diameter classes for the eastern Cascades

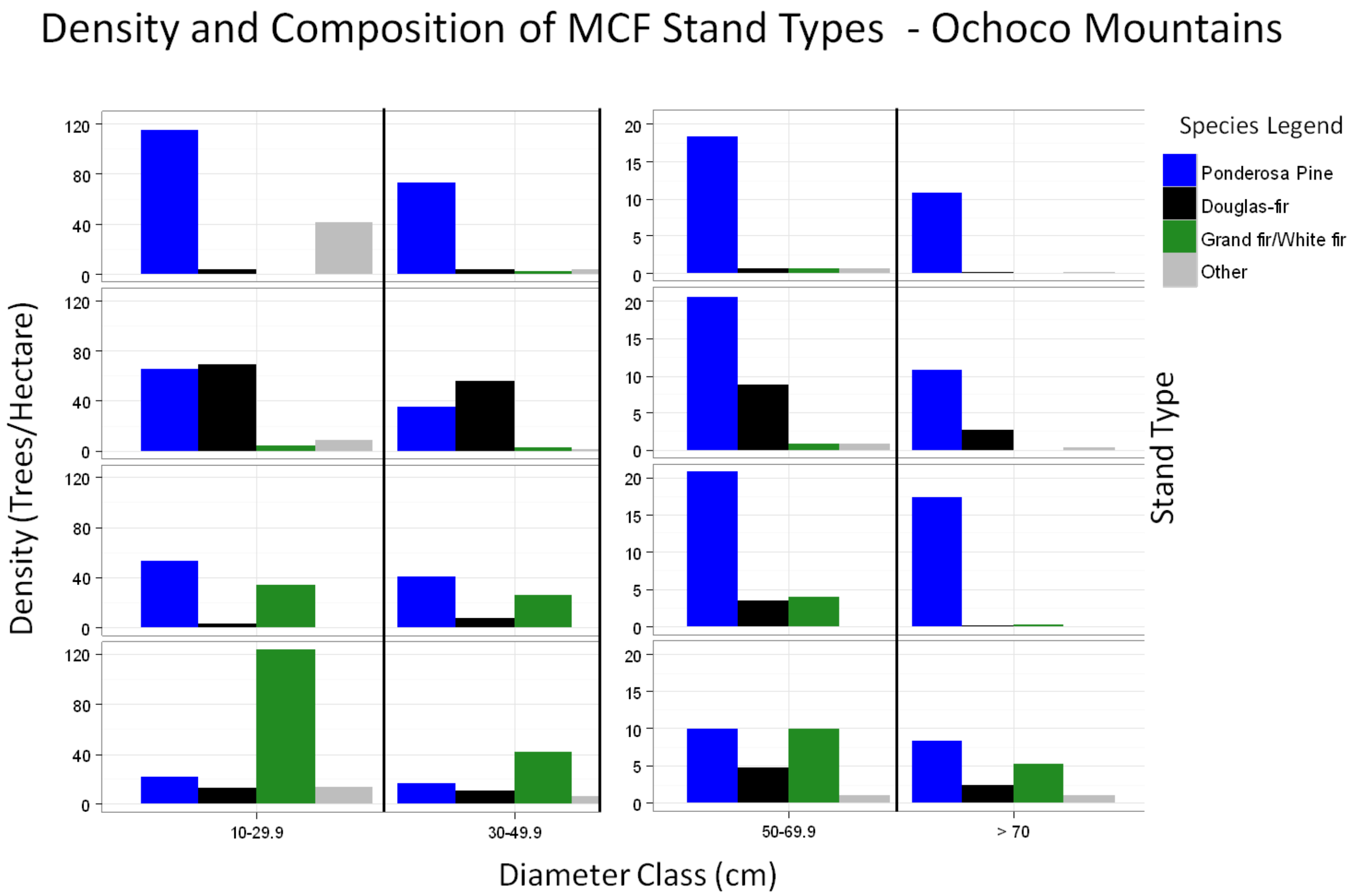

Figure 2.11: Density and composition of stand types organized by diameter classes for the Ochoco Mountains

Table 2.1: Taper equations for reconstructing the diameter at breast height of cut trees

Species	Cut Height	
	10 cm cut height	40 cm cut height
Ponderosa pine	y = 0.8356x - 2.1322	y = 0.9031x + 0.0151
Douglas-fir	y = 0.7103x + 5.3832	y = 0.8086x + 4.4907
Grand fir	y = 0.6937x + 5.2034	y = 0.842x + 2.5463

Table 2.2: Description of variables used in environmental matrices for the Eastern Cascades and Ochoco Mountains

Category		
Variable	Units	Description
Physical Location		
Easting	m	X coordinate of sample site using the UTM NAD 83 projection
Northing	m	Y coordinate of sample site using the UTM NAD 83 projection
Climate		
Maximum Temperature	©	Mean annual maximum temperature obtained from 1971-2000 Prism Climate Normals (PRISM, 2012).
Precipitation	cm	Mean annual precipitation obtained from 1971-2000 Prism Climate Normals (PRISM, 2012).
Topographic Position		
Elevation	m	Sample site height above sea level
Slope Gradient	%	Slope steepness measured as a percent
Transformed Aspect	none	Transformation of aspect to a continuous varaible ranging from 0 (southwest) to 2 (northeast) (Beers et al. 1966). *Asp = 1 + cos(*45^{o}*- aspect)*
Potential Direct Incident Radiation	MJ/cm/year	Maximum potential annual solar radiation (McCune and Dylan 2002).
Heatload	none	Index of potential direct incident radiation adjusted for aspect and slope (McCune and Dylan 2002).
Potential Relative Radiation	none	Relative annual solar insolation while accounting for shading by surrounding topographic features (Pierce et al. 2005).
Topographic Position Index	m	Focal pixel height above the minimum elevation in a neighborhood of radius 150 m (fine), 300 m (medium), and 450 m (coarse). Neighborhood diameter is 1/4 the median slope length (Weiss 2001).

Table 2.3: MRPP test of OMCF type agreement in environmental space. "A" is the chance-corrected within group agreement statistic, a measure of within group similarity ranging from 0 to 1 (McCune and Grace 2002).

	A	p-value
Eastern Cascades Types	0.063	0.0001
Ochoco Mountains Types	0.057	0.0001

Table 2.4: Summary of environmental values for sample sites grouped by type. Values are mean followed by median in italics.

		Elevation (m)		Maximum Temperature ©		Precipitation (cm)		Slope Gradient (%)		Transformed Aspect		PDIR MJ/cm/year		Heatload		Potential Relative Radiation		Topographic Position Index (300m)	
Eastern Cascades																			
Type	Sample Size																		
1	18	1379.1	*1409.5*	13.4	*13.3*	72.0	*73.5*	8.2	*5.4*	1.4	*1.6*	0.8	*0.8*	0.8	*0.8*	1663.3	*1654.5*	4.9	*2.0*
2	14	1258.9	*1308.0*	13.2	*12.7*	78.8	*86.7*	14.2	*13.8*	0.9	*0.8*	0.8	*0.8*	0.8	*0.8*	1662.6	*1720.5*	7.1	*4.0*
3	16	1485.0	*1457.5*	12.2	*12.3*	97.4	*100.0*	9.2	*9.0*	0.9	*1.1*	0.8	*0.8*	0.8	*0.8*	1708.3	*1693.0*	2.6	*2.0*
4	24	1404.3	*1405.0*	12.5	*12.4*	92.0	*90.7*	9.9	*8.6*	1.0	*0.9*	0.8	*0.8*	0.7	*0.7*	1655.4	*1637.0*	-1.0	*-2.5*
5	5	1671.6	*1668.0*	10.9	*10.7*	103.6	*107.6*	7.6	*5.8*	1.4	*1.6*	0.8	*0.8*	0.8	*0.8*	1687.0	*1658.0*	6.8	*1.0*
All Sites	77	1406.1	*1423.0*	12.7	*12.5*	86.8	*90.4*	10.0	*8.6*	1.1	*1.1*	0.8	*0.8*	0.8	*0.8*	1671.6	*1665.0*	3.1	*0.0*
Ochoco Mountains																			
Type	Sample Size																		
1	23	1547.5	*1571.0*	12.4	*12.3*	52.4	*47.2*	11.5	*12.0*	1.1	*0.9*	0.8	*0.8*	0.8	*0.8*	1772.8	*1799.0*	6.9	*8.0*
2	26	1465.2	*1473.5*	12.9	*12.6*	48.2	*46.4*	14.9	*15.8*	1.0	*1.1*	0.8	*0.8*	0.8	*0.8*	1609.0	*1652.0*	4.3	*3.0*
3	19	1574.4	*1588.0*	12.1	*11.9*	56.6	*59.8*	11.3	*9.8*	1.0	*0.9*	0.8	*0.8*	0.8	*0.8*	1716.9	*1758.0*	-1.9	*3.0*
4	26	1645.0	*1659.5*	11.6	*11.5*	66.1	*67.9*	10.0	*8.8*	1.0	*1.2*	0.7	*0.8*	0.7	*0.8*	1570.5	*1608.0*	1.1	*2.0*
All Sites	94	1557.1	*1584.5*	12.3	*12.1*	55.9	*56.7*	12.0	*11.9*	1.0	*1.0*	0.8	*0.9*	0.8	*0.8*	1660.2	*1679.5*	2.8	*3.5*

Table 2.5: Eastern Cascades density and composition of live and reconstructed trees by stand type

	OMCF TYPE											
Variable	PIPO (n = 18)			PIPO/PSME (n = 14)			PIPO/ABGC (n = 16)			PIPO/PSME/ABGC (n = 24)		
	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error
Reconstructed Overstory Density												
50-69.9 cm												
Ponderosa pine	30.58	30.00	3.18	19.20	20.00	3.08	13.08	11.81	2.13	7.87	9.20	1.88
Douglas-fir	0.56	0.00	0.56	11.95	12.50	2.71	0.16	0.00	0.16	7.88	7.42	1.52
Grand fir	1.11	0.00	0.68	0.18	0.00	0.18	13.75	15.00	3.20	14.86	14.95	3.05
Other	0	0.00	0.00	1.25	0.00	0.78	2.81	0.00	2.81	1.45	3.70	0.76
>70 cm												
Ponderosa pine	21.13	20.00	2.88	7.78	3.75	2.34	16.50	17.50	3.42	12.95	9.07	1.85
Douglas-fir	0.35	0.00	0.35	7.54	2.50	2.41	0.31	0.00	0.31	7.04	7.63	1.56
Grand fir	0	0.00	0.00	0.00	0.00	0.00	3.13	0.00	1.43	1.40	3.44	0.70
Other	0.42	0.00	0.30	2.09	0.00	1.21	0.94	0.00	0.45	1.04	2.85	0.58
Live Overstory Trees												
50-69.9 cm												
Ponderosa pine	14.33	12.50	2.57	12.18	10.00	3.26	10.05	7.50	2.13	4.27	0.00	1.44
Douglas-fir	0.56	0.00	0.56	8.91	8.30	2.02	0.16	0.00	0.16	6.89	6.11	1.39
Grand fir	1.11	0.00	0.68	0.18	0.00	0.18	12.81	10.00	3.19	13.61	10.17	3.04
Other	0.00	0.00	0.00	1.25	0.00	0.78	2.81	0.00	2.81	1.45	0.00	0.76
>70 cm												
Ponderosa pine	10.02	2.50	3.27	4.59	0.00	1.90	10.25	8.75	2.29	8.64	6.67	1.52
Douglas-fir	0.35	0.00	0.35	2.78	0.00	1.69	0.31	0.00	0.31	6.73	5.00	1.56
Grand fir	0.00	0.00	0.00	0.00	0.00	0.00	2.34	0.00	1.30	1.40	0.00	0.70
Other	0.00	0.00	0.00	1.73	0.00	1.20	0.31	0.00	0.31	0.63	0.00	0.46
Live Understory Trees												
10-29.9 cm												
Ponderosa pine	161.49	150.15	30.82	51.90	31.82	14.52	22.97	15.02	8.82	4.73	12.95	2.64
Douglas-fir	6.25	0.00	6.25	97.83	76.36	21.77	4.86	0.00	3.24	25.49	42.28	8.63
Grand fir	39.21	0.00	16.78	63.07	23.64	20.20	260.50	217.61	47.33	170.18	90.09	18.39
Other	24.19	0.00	10.87	48.05	16.60	20.59	23.46	0.00	9.69	16.20	53.12	10.84
30-49.9 cm												
Ponderosa pine	115.34	97.60	18.04	40.77	37.52	9.61	27.64	15.02	8.91	8.68	19.02	3.88
Douglas-fir	0.23	0.00	0.23	70.22	55.03	14.12	3.72	0.00	2.87	16.03	15.19	3.10
Grand fir	5.84	0.00	3.01	14.87	10.00	3.94	102.93	90.09	13.51	59.82	49.73	10.15
Other	1.67	0.00	1.67	10.22	0.00	4.16	13.14	0.00	8.21	4.08	7.41	1.51

Table 2.6: Ochoco Mountains density and composition of live and reconstructed trees by stand type

	OMCF TYPE											
Variable	PIPO (n = 18)			PIPO/PSME (n = 14)			PIPO/ABGC (n = 16)			PIPO/PSME/ABGC (n = 24)		
	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error
Reconstructed Overstory Density												
50-69.9 cm												
Ponderosa pine	18.44	14.29	2.94	20.46	18.61	2.50	20.84	21.05	3.39	10.04	5.67	2.20
Douglas-fir	0.76	0.00	0.53	8.73	8.33	1.76	3.53	4.00	0.88	4.83	0.00	1.65
Grand fir	0.65	0.00	0.48	0.75	0.00	0.43	3.99	0.00	1.80	9.98	6.90	2.01
Other	0.61	0.00	0.44	0.82	0.00	0.59	0.00	0.00	0.00	1.04	0.00	0.52
>70 cm												
Ponderosa pine	10.88	7.69	2.24	10.82	9.09	1.84	17.36	11.76	3.06	8.34	7.08	1.47
Douglas-fir	0.22	0.00	0.22	2.61	0.00	0.81	0.13	0.00	0.13	2.40	0.00	0.84
Grand fir	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.00	0.26	5.33	4.77	1.03
Other	0.22	0.00	0.15	0.38	0.00	0.18	0.00	0.00	0.00	1.10	0.00	0.48
Live Overstory Trees												
50-69.9 cm												
Ponderosa pine	11.38	6.25	2.65	16.00	14.84	2.42	14.71	10.00	3.00	6.59	1.25	1.89
Douglas-fir	0.76	0.00	0.53	7.61	4.58	1.73	3.22	0.00	0.89	4.73	0.00	1.65
Grand fir	0.65	0.00	0.48	0.37	0.00	0.21	3.73	0.00	1.81	9.50	6.90	2.00
Other	0.61	0.00	0.44	0.82	0.00	0.59	0.00	0.00	0.00	1.04	0.00	0.52
>70 cm												
Ponderosa pine	6.85	0.00	2.07	9.12	6.25	1.85	13.23	10.00	3.01	6.70	5.00	1.31
Douglas-fir	0.00	0.00	0.00	1.17	0.00	0.39	0.13	0.00	0.13	2.20	0.00	0.78
Grand fir	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.76	2.81	0.99
Other	0.22	0.00	0.15	0.10	0.00	0.10	0.00	0.00	0.00	0.81	0.00	0.47
Live Understory Trees												
10-29.9 cm												
Ponderosa pine	115.17	107.69	19.49	65.09	45.05	13.08	52.58	25.00	14.49	21.81	4.77	5.97
Douglas-fir	3.90	0.00	1.60	68.95	45.05	15.78	3.05	0.00	1.33	12.35	8.51	3.32
Grand fir	0.00	0.00	0.00	4.13	0.00	2.01	33.68	20.00	9.35	123.95	121.54	23.33
Other	40.89	4.76	14.35	8.98	0.00	4.60	0.00	0.00	0.00	13.47	0.00	8.10
30-49.9 cm												
Ponderosa pine	73.41	50.00	12.25	35.11	30.03	6.05	41.17	23.53	10.64	16.68	1.92	5.36
Douglas-fir	4.58	0.00	1.53	55.91	45.05	8.49	7.46	4.55	2.15	10.80	4.77	2.47
Grand fir	2.50	0.00	1.45	3.23	0.00	1.39	25.92	17.65	5.69	41.81	40.45	9.14
Other	4.59	0.00	2.75	0.74	0.00	0.59	0.00	0.00	0.00	6.03	0.00	2.32

Table 2.7: Easten Cascades density of all live trees and snags by stand type

	OMCF TYPE											
	PIPO			PIPO/PSME			PIPO/ABGC			PIPO/PSME/ABGC		
Variable	(n = 18)			(n = 14)			(n = 16)			(n = 24)		
	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error
All Live Trees and Snags												
Ponderosa pine	342.24	297.76	42.91	115.64	116.76	17.02	97.21	80.56	15.30	30.32	19.62	7.54
Douglas-fir	7.38	0.00	6.46	187.61	168.57	27.58	9.20	0.00	4.47	57.23	36.47	10.09
Grand fir	50.05	0.00	20.16	84.01	44.16	22.19	407.52	431.66	52.01	259.08	226.97	26.05
Other	32.67	0.00	15.56	73.88	59.80	23.19	55.83	0.00	26.04	25.47	2.50	12.43
All Species	432.35	425.41	47.24	461.14	456.11	44.81	569.76	553.03	44.90	372.11	310.59	34.59

Table 2.8: Ochoco Mountains density of all live trees and snags by stand type

	OMCF TYPE											
	PIPO			PIPO/PSME			PIPO/ABGC			PIPO/PSME/ABGC		
Variable	(n = 18)			(n = 14)			(n = 16)			(n = 24)		
	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error
All Live Trees and Snags												
Ponderosa pine	215.68	200.00	25.86	132.39	112.19	15.86	126.50	95.06	18.57	55.56	44.72	11.85
Douglas-fir	9.68	5.00	2.52	152.09	111.72	23.03	14.74	10.00	3.09	32.00	23.76	5.50
Grand fir	3.84	0.00	1.82	8.50	0.00	2.59	71.14	64.71	14.09	195.40	173.54	35.45
Other	49.96	4.76	17.07	10.73	0.00	4.78	0.00	0.00	0.00	24.73	9.29	9.48
All Species	279.16	230.77	33.48	303.72	285.13	26.72	212.39	200.00	21.24	307.69	245.09	42.78

Table 2.9: Eastern Cascades snag density and composition by stand type.

	OMCF TYPE											
Variable	PIPO (n = 18)			PIPO/PSME (n = 14)			PIPO/ABGC (n = 16)			PIPO/PSME/ABGC (n = 24)		
	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error
Overstory Snags												
50-69.9 cm												
Ponderosa pine	1.39	0.00	0.50	0.65	0.00	0.36	1.56	0.00	0.60	0.42	0.00	0.19
Douglas-fir	0.00	0.00	0.00	0.18	0.00	0.18	0.16	0.00	0.16	0.63	0.00	0.38
Grand fir	0.42	0.00	0.42	1.43	0.00	1.43	1.09	0.00	0.51	1.77	0.00	1.16
Other	0.00	0.00	0.00	0.18	0.00	0.18	0.16	0.00	0.16	0.00	0.00	0.00
>70 cm												
Ponderosa pine	1.23	0.00	0.57	0.36	0.00	0.24	1.77	0.00	0.67	1.18	0.00	0.53
Douglas-fir	0.00	0.00	0.00	0.18	0.00	0.18	0.00	0.00	0.00	0.21	0.00	0.14
Grand fir	0.14	0.00	0.14	0.18	0.00	0.18	0.63	0.00	0.48	0.42	0.00	0.33
Other	0.14	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Understory Snags												
10-29.9 cm												
Ponderosa pine	32.53	22.52	8.77	1.37	0.00	1.09	7.51	0.00	3.06	1.00	0.00	0.72
Douglas-fir	0.00	0.00	0.00	6.44	0.00	6.44	0.00	0.00	0.00	0.63	0.00	0.63
Grand fir	1.67	0.00	1.14	4.29	0.00	2.91	18.77	0.00	8.94	5.01	0.00	2.81
Other	5.01	0.00	5.01	9.65	0.00	5.13	11.26	0.00	5.22	3.13	0.00	1.56
30-49.9 cm												
Ponderosa pine	6.67	0.00	3.03	0.51	0.00	0.51	4.52	0.00	2.13	2.53	0.00	1.46
Douglas-fir	0.00	0.00	0.00	1.07	0.00	1.07	0.00	0.00	0.00	0.63	0.00	0.63
Grand fir	1.67	0.00	1.14	0.00	0.00	0.00	8.45	0.00	3.35	6.88	0.00	4.24
Other	0.83	0.00	0.83	2.15	0.00	2.15	5.26	0.00	2.25	0.00	0.00	0.00

Table 2.10: Ochoco Mountains snag density and composition by stand type.

	OMCF TYPE											
	PIPO			PIPO/PSME			PIPO/ABGC			PIPO/PSME/ABGC		
Variable	(n = 18)			(n = 14)			(n = 16)			(n = 24)		
	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error	Mean	Median	Std. Error
Overstory Snags												
50-69.9 cm												
Ponderosa pine	1.12	0.00	0.47	1.55	0.00	0.49	1.81	0.00	0.72	0.19	0.00	0.19
Douglas-fir	0.22	0.00	0.22	0.66	0.00	0.29	0.29	0.00	0.29	0.29	0.00	0.21
Grand fir	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.13	0.87	0.00	0.48
Other	0.50	0.00	0.41	0.10	0.00	0.10	0.00	0.00	0.00	0.19	0.00	0.13
>70 cm												
Ponderosa pine	1.30	0.00	0.54	1.07	0.00	0.45	1.67	0.00	1.11	0.20	0.00	0.14
Douglas-fir	0.00	0.00	0.00	0.19	0.00	0.13	0.00	0.00	0.00	0.67	0.00	0.43
Grand fir	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.22	0.00	0.49
Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Understory Snags												
10-29.9 cm												
Ponderosa pine	5.19	0.00	2.17	1.73	0.00	0.86	1.34	0.00	0.78	1.41	0.00	1.00
Douglas-fir	0.00	0.00	0.00	13.28	0.00	5.22	0.28	0.00	0.28	0.96	0.00	0.68
Grand fir	0.00	0.00	0.00	0.77	0.00	0.61	5.53	0.00	5.53	8.23	0.00	4.49
Other	2.35	0.00	1.98	0.00	0.00	0.00	0.00	0.00	0.00	1.73	0.00	1.27
30-49.9 cm												
Ponderosa pine	1.27	0.00	0.71	2.72	0.00	1.63	0.00	0.00	0.00	1.96	0.00	0.92
Douglas-fir	0.22	0.00	0.22	4.32	0.00	2.13	0.31	0.00	0.31	0.00	0.00	0.00
Grand fir	0.69	0.00	0.49	0.00	0.00	0.00	2.15	0.00	1.86	5.06	0.00	2.33
Other	0.79	0.00	0.79	0.00	0.00	0.00	0.00	0.00	0.00	1.45	0.00	1.18

Table 2.11: Environmental variable correlations with NMS ordination of species sizes classes for the Eastern Cascades. See Table 2.2 for explanation of environmental variables

Axis:	1			2		
	r	r-sq	tau	r	r-sq	tau
Easting	-0.253	0.064	-0.055	-0.014	0	-0.173
Northing	-0.145	0.021	-0.058	-0.574	0.329	-0.421
Elevation	0.486	0.236	0.258	0.294	0.086	0.247
Precipitation	0.595	0.354	0.387	-0.106	0.011	-0.04
Maximum Temperature	-0.646	0.417	-0.422	0	0	0.021
Slope Gradient	-0.149	0.022	-0.04	-0.273	0.075	-0.206
Transformed Aspect	-0.047	0.002	-0.062	0.147	0.022	0.098
Potential Direct Incident Radiation	-0.042	0.002	-0.052	0.176	0.031	0.08
Heatload	-0.159	0.025	-0.142	0.25	0.063	0.122
Potential Relative Radiation	0.065	0.004	0.002	0.1	0.01	0.033
Topographic Position Index (150)	-0.108	0.012	-0.081	0.124	0.015	0.065
Topographic Position Index (300)	-0.095	0.009	-0.119	0.103	0.011	0.106
Topographic Position Index (450)	-0.095	0.009	-0.119	0.103	0.011	0.106

Table 2.12: Environmental variable correlations with NMS ordination of species sizes classes for the Ochoco Mountains. See Table 2.2 for explanation of environmental variables

Axis:	1			2		
	r	r-sq	tau	r	r-sq	tau
Easting	0.174	0.03	0.268	-0.158	0.025	-0.105
Northing	-0.056	0.003	-0.073	0.09	0.008	0.053
Elevation	0.345	0.119	0.249	-0.084	0.007	-0.091
Precipitation	0.457	0.209	0.362	-0.026	0.001	-0.033
Maximum Temperature	-0.44	0.194	-0.329	0.018	0	0.026
Slope Gradient	-0.134	0.018	-0.098	0.274	0.075	0.187
Transformed Aspect	-0.128	0.016	-0.056	-0.083	0.007	-0.063
Potential Direct Incident Radiation	-0.301	0.091	-0.228	-0.325	0.106	-0.251
Heatload	-0.227	0.052	-0.18	-0.188	0.035	-0.119
Potential Relative Radiation	-0.272	0.074	-0.222	-0.349	0.122	-0.266
Topographic Position Index (150)	-0.2	0.04	-0.122	-0.196	0.038	-0.146
Topographic Position Index (300)	-0.222	0.049	-0.135	-0.253	0.064	-0.201
Topographic Position Index (450)	-0.222	0.049	-0.135	-0.253	0.064	-0.201

Table 2.13: Species size class correlation scores with Axis 1 and 2 for NMS ordiation of species size classes for the Eastern Cascades.

Axis:	1			2		
	r	r-sq	tau	r	r-sq	tau
ABGR 10-29.9 cm	0.697	0.486	0.508	-0.339	0.115	-0.162
ABGR 30-49.9 cm	0.688	0.474	0.567	-0.217	0.047	-0.022
ABGR 50-69.9 cm	0.79	0.624	0.616	-0.036	0.001	-0.001
ABGR >70 cm	0.596	0.355	0.446	0.236	0.056	0.184
PIPO 10-29.9 cm	-0.683	0.466	-0.525	0.497	0.247	0.38
PIPO 30-49.9 cm	-0.716	0.513	-0.553	0.445	0.198	0.355
PIPO 50-69.9 cm	-0.625	0.391	-0.494	0.341	0.116	0.242
PIPO>70 cm	-0.259	0.067	-0.206	0.27	0.073	0.223
PSME 10-29.9 cm	-0.246	0.061	-0.16	-0.748	0.559	-0.557
PSME 30-49.9 cm	-0.211	0.044	-0.177	-0.775	0.601	-0.582
PSME 50-69.9 cm	-0.1	0.01	-0.075	-0.644	0.415	-0.501
PSME >70 cm	0.012	0	0.024	-0.613	0.376	-0.481
PICO<50 cm	0.316	0.1	0.18	0.316	0.1	0.242
CADE<50 cm	-0.373	0.139	-0.303	-0.397	0.158	-0.335
CADE>50 cm	-0.125	0.016	-0.086	-0.303	0.092	-0.257
LAOC<50 cm	-0.037	0.001	0.029	-0.432	0.187	-0.357
LAOC>50 cm	0.182	0.033	0.167	-0.249	0.062	-0.197

Table 2.14: Species size class correlation scores with Axis 1 and 2 for NMS ordiation of species size classes for the Ochoco Mountains.

Axis:	1			2		
	r	r-sq	tau	r	r-sq	tau
ABGR 10-29.9 cm	0.822	0.675	0.682	0.165	0.027	0.105
ABGR 30-49.9 cm	0.699	0.489	0.559	0.238	0.057	0.18
ABGR 50-69.9 cm	0.741	0.549	0.577	0.296	0.088	0.229
ABGR >70 cm	0.751	0.564	0.541	0.258	0.066	0.212
PIPO 10-29.9 cm	-0.598	0.357	-0.348	-0.432	0.187	-0.269
PIPO 30-49.9 cm	-0.616	0.379	-0.38	-0.585	0.343	-0.354
PIPO 50-69.9 cm	-0.447	0.2	-0.11	-0.2	0.04	-0.107
PIPO>70 cm	-0.14	0.019	-0.014	-0.131	0.017	-0.1
PSME 10-29.9 cm	-0.117	0.014	-0.082	0.683	0.466	0.548
PSME 30-49.9 cm	-0.055	0.003	-0.053	0.715	0.511	0.593
PSME 50-69.9 cm	0.025	0.001	0.052	0.569	0.324	0.411
PSME >70 cm	0.003	0	0.006	0.481	0.231	0.385
JUOC<50 cm	-0.444	0.197	-0.371	-0.355	0.126	-0.269
JUOC>50 cm	-0.222	0.049	-0.186	-0.142	0.02	-0.079
LAOC<50 cm	0.542	0.293	0.386	0.137	0.019	0.126
LAOC>50 cm	0.423	0.179	0.306	0.187	0.035	0.146
PICO<50 cm	0.15	0.022	0.125	0.232	0.054	0.187

CHAPTER 3: CHANGES IN ESTABLISHMENT AND GROWTH PATTERNS IN MIXED-CONIFER FORESTS DURING THE 20TH CENTURY

ABSTRACT

Fire exclusion has increased density, canopy continuity, and the dominance of shade tolerant species in dry forests across the western U.S. These changes in structure and composition are a concern to managers because they can increase the probability of large high-severity wildfire, decrease resilience to drought and insects, and modify the proportion of habitat available for threatened and endangered species with contrasting habitat requirements. Current diversity in structure and composition found in mixed-conifer forest (MCF) of central Oregon is related to wide variation in climate and topography, and a complex historical mixed-severity fire regime. Restoration of MCF requires an understanding of the magnitude and landscape pattern of changes in structure and composition. Currently changes are poorly understood due to the complexity of this forest type and a lack of dendroecological studies.

In this study I used dendroecological methods to address two questions: 1) for extant trees, is the composition and number of trees established different before and after fire exclusion; and 2) what are the patterns of growth (slow and fast) in old-growth ponderosa pine, and how are they related to climate and disturbance? I used approximately 3,500 increment cores collected in two study areas to address these questions in MCF of the eastern Cascades and Ochoco Mountains. Question 1 was

examined separately in 8 types of MCF distinguished by their current stand structure, composition, and the environmental setting where they are found (See Chapter 2). Age histograms of MCF types demonstrate that establishment and survival of all species increased dramatically following fire exclusion in the PIPO, PIPO/PSME, and PIPO/ABGC types. Additionally, composition at PIPO/PSME and PIPO/ABGC types has shifted from dominance of ponderosa pine to dominance of shade tolerant species. The predominance of shade tolerant establishment at these wetter and more productive sites illustrates a change in forest type, which in turn indicates these sites may have high priority for restoration as they are comparably sensitive to fire exclusion.

To address my second Question I examined the patterns of growth reduction and growth release in ponderosa pine trees separately for the eastern Cascades and Ochoco Mountains, and developed growth chronologies for two study sites from a related study with detailed records of fire history. A decrease in the proportion of trees releasing in the eastern Cascades and anomalous growth patterns at both fire history sites during the 20th century suggests that current structure and composition of MCF may lack an historical analog for the period I investigated. However, further investigation of the relationship between climate and growth must be conducted in order to distinguish changes in growth related to climate from those related to disruption of fire and densification. Variation in changes in establishment and composition among MCF types and differential responses of growth to fire exclusion highlight the complex response that MCF has had to fire exclusion.

INTRODUCTION

Management of mixed-conifer forest (MCF) in the Pacific Northwest is challenged by heterogeneity in structure and composition and fire regime associated with steep environmental gradients. These forests represent the most complex forest type in the Pacific Northwest (Agee 1993), and the mixed-severity fire regime characteristic of MCF is the least understood (Halofsky et al. 2011 and Perry et al. 2011). Fire exclusion in mixed conifer forest throughout the 20th century is hypothesized to have increased density and spatial contagion while shifting species composition from fire tolerant to fire intolerant species (Arno 1995, Hessburg et al. 2005, and Fitzgerald 2005). A recent inventory and analysis of MCF described in Chapter 2 supports this hypothesis and provides the opportunity to investigate the magnitude of changes in density and composition in MCF types found in distinct environmental settings.

Plant communities where succession is constrained by disturbance regime are referred to as disclimax communities (Lincoln et al. 1998). Wildfires in MCF can truncate succession and maintain disclimax or fire climax vegetation (Lunan and Habeck 1973). Mature fire climax stands often have open canopies and are dominated by mature fire resistant species such as ponderosa pine (*Pinus ponderosa*) and western larch (*Larix* *occidentalis*). With longer fire return intervals, stands develop multi-storied canopies composed of shade tolerant species including grand fir (*Abies grandis*) and Douglas-fir (*Psedotsuga menziesii*) (Powell 2011). A mosaic of early seral, fire climax and late successional vegetation is created by mixed-severity fire (Perry et al. 2011), which is characterized by variable fire severities and return intervals (Agee 1998). Prior to fire exclusion this mosaic was probably made up of many small patches of similar vegetation and relatively few large patches. Disruption of mixed-severity fire regimes allow stands to develop understory canopies eliminating the patchy pattern of early seral, fire climax, and late successional vegetation in mixed-severity fire regimes (Perry et al. 2011). It may be possible to use historical patterns of establishment and growth to understand how anthropogenic influences on fire regimes have altered stand development in MCF.

Succession in the absence of fire in MCF has important management implications in MCF of central Oregon. Late successional MCF with multiple canopy layers, high levels of canopy closure and high densities of Douglas-fir or grand fir, provides habitat for the endangered northern spotted owl, (*Strix occidentalis caurina*) (Buchanan et al. 1995). Fire climax MCF with single layered canopies dominated by large mature trees is required for the flammulated owl (*Otus flammeolus*), white-headed woodpecker (*Picoides albolarvatus*), and pygmy nuthatch (*Sitta pygmaea*) (Wisdom et al. 1999). While fire exclusion provides additional habitat for species associated with climax forests it simultaneously decreases habitat critical to species associated with open or patchy forests. Although late successional MCF was present in the landscape in fire refugia (Camp 1997), conversion of fire climax forest may result in the loss of habitat for all species of concern as resilience to disturbance decreases across the landscape. Late successional and homogeneous MCF is thought to be more susceptible to mortality from high-severity wildfire, insect outbreaks, and drought (Hessburg et al. 1994, Sloan 1998, Camp 1999, Hemstrom 2001, Agee 2003, Fitzgerald 2005, Hessburg et al. 2005, and Powell 2011). Managers currently face a dilemma between maintaining habitat for the spotted owl and restoring the long term resiliency of MCF structure and composition to fire and other disturbances (Buchanan 2010).

Dendroecology is frequently used in studies of forest dynamics to investigate stand development and the response of tree populations to climate and disturbance (Fritts and Swetnam 1989, Abrams et al. 1995, and Speer 2010). Abrams et al. (1995) demonstrated that age structure coupled with radial growth chronologies can be used to increase our understanding of disturbance, successional dynamics, species life history attributes, and ecological history. Several studies have used dendroecological techniques to examine changes in MCF due to fire exclusion in the western U.S. (Sloan 1998, Camp 1999, Youngblood et al. 2004, Naficy et al 2010, Scholl and Taylor 2010), but studies focused on MCF in the central Oregon are absent (Baker 2012). These studies use a combination of establishment history and historical records are used to reconstruct forest structure and composition prior to European settlement. Effects of fire exclusion and logging are inferred from changes in establishment rate and composition and through direct comparison of reconstructed and contemporary forest structure and composition.

I used dendroecological techniques to examine establishment and growth history in MCF at 152 sample sites in the eastern Cascades and Ochoco Mountains. I was unable to reconstruct pre Euro-American forest structure and composition at my sample sites because they lacked data of the ages of dead trees and snags within plots, and trees that had been removed in thinning and logging operations. To mitigate this limitation I coupled the establishment history of MCF types with a multi-century record of annual growth in ponderosa pine. Recent studies of changes in disturbance, structure, and composition have employed similar methods in mixed-conifer forests in central Idaho (Arabas et al. 2008) and southwestern Oregon (Messier et al. 2012). Specific questions in this investigation were:

1) For extant trees, is the composition and number of trees established different before and after fire exclusion?

2) Do growth histories of old-growth ponderosa pine indicate changes in competitive interactions and succession in MCF?

Question 1 was investigated in four analogous MCF Types in the eastern Cascades and Ochoco Mountains. Based on the current understory density at each type I hypothesize that succession during fire exclusion increased density and dominance of shade tolerant species. Additionally shifts in composition are greatest at PIPO/ABGC sites where increased moisture enables grand fir to compete with ponderosa pine in the understory. One criticism of establishment records is that they may not account for all trees that may have established in the past as evidence of these individuals is lost to mechanical removal, wildfire, and decay (Moore et al. 2004, Baker 2012, and Lydersen and North 2012). Question 2 is designed to account for this by using a multicentury record of growth of ponderosa pine that is dependent on stand dynamics. I hypothesize succession in MCF has altered long term suppression and release patterns of ponderosa pine providing further evidence that dense late successional MCF was rare in my study area prior to fire exclusion.

METHODS

Study Area

MCF is found in three potential vegetation types (PVT) based on assumed forest composition. Each PVT is further subdivided by Plant Association Groups (PAG) based on understory herb and shrub composition. PVTs in MCF include grand fir/white fir, Douglas-fir, and ponderosa pine described by Simpson (2007) in the eastern Cascades and Johnson and Clausnitzer (1991) in the Ochoco mountains. Major species in both the eastern Cascades and the Ochoco Mountains include ponderosa pine, Douglas-fir, and grand fir (Franklin and Dyrness 1973 and Simpson 2007). Ponderosa pine is a dominant overstory component in most stands in all PVTs. In the Douglas-fir and grand fir/white fir PVT, Douglas-fir is generally co-dominant in the overstory expect where it is excluded by Mazama ash and pumice deposits (Simpson 2007). Grand fir is only an overstory dominant in the wet PAG types of the grand fir/white fir PVT. Minor species in the eastern Cascades study area include lodgepole pine (*Pinus contorta*), sugar pine (*Pinus lambertiana*), western white pine (*Pinus monticola*), Shasta red fir, (*Abies magnifica var. Shastensis*), incense-cedar (*Calocedrus decurrens*), and western larch (*Larix occidentalis*). Minor species in the Ochoco Mountains include western larch and western juniper (*Juniperus, occidentalis*).

Environmental Setting

MCF is found between 1100-1500 meters in elevation in the eastern Cascades, but occurs at higher elevations in the Ochoco Mountains between 1500-2000 meters in elevation. Climate in both study areas is Mediterranean with hot, dry summers and relatively wet, cold winters. MCF in the eastern cascades has one of the steepest precipitation gradients in the world (Simpson 2007). Moving from the Cascade crest east, annual precipitation decreases by 280 cm in a span of 15 miles. Dry MCF in the eastern Cascades in the driest PAG groups receives 55 cm of precipitation annually while wet MCF PAG groups receive up to 110 cm of precipitation. MCF in the Ochoco Mountains is drier receiving 35 cm of precipitation in dry MCF and up to 75 cm in wet MCF. In both regions only 10% of annual precipitation falls between June and August. Mean annual maximum temperature ranges from 10-15 ˚C.

Fire Regime

MCF has a mixed-severity fire regime that exhibits characteristics of both low-severity and high-severity fire regimes. At low elevations a low-severity fire regime creates stands dominated by fire resistant species such as ponderosa pine (Agee 1993). Fire historically burned these sites on average of 7-20 years and stand mortality was less than 25% (Agee 1994). Upper elevation MCF is classified as a high-severity fire regime. Dense multistoried stands dominated by fire intolerant grand fir develop under a much longer fire interval ranging from 33-100 years (Agee 2003). The disturbance regime of the majority of MCF cannot be described as part of the low or high-severity fire regime and is best described as mixed-severity.

The mixed-severity fire regime is poorly understood due to its broad range of fire effects (Hessburg et al. 2005). Mixed-severity fires give rise to unique patch dynamics, ecosystem responses, and are more than simple intermediate between low and high-severity fire regimes (Halofsky et al. 2011). Mixed-severity fire regimes exhibit intermediate fire return intervals, burn intensities that range from underburning to stand replacement, and create intermediate patches with significant edge (Hessburg et al. 2005). Combinations of surface, torching, and crown fire behavior both within and between fires result in patches of live and dead understory and overstory vegetation (Lentiel et al, 2005). Appendix 2.1 summarizes the spatial heterogeneity and difference in patch sizes observed among low, mixed, and high-severity fire regimes (Agee 1998). The high degree of patch edge, variation in patch size, and burn complexity evident in the mixed-severity fire regime is a critical driver of stand structure and composition in MCF (Perry et al. 2011).

Field Data Collection

To evaluate changes in establishment survival and growth of trees in MCF, I collected 1326 increment cores in the eastern Cascades and the Ochoco Mountains (Figure 3.1). An additional 2,126 cores were collected by Emily Heyerdahl in a related study describing fire and forest histories in mixed-conifer forests of central Oregon. See the methods section of Chapter 2, "*Variation in Structure and Composition of Old-growth mixed-conifer Forests in the eastern Cascades and Ochoco Mountains,"* for a description of sample site selection and physical layout. Collection procedure for increment cores was different for each study and is described below.

Of the 89 sites originally sampled for Chapter 2, 62 were revisited for increment core collection. The density of trees >50 cm was used to identify sample sites with intact overstory structure. Sites where logging had removed nearly all trees >50 cm in diameter at breast height (DBH) were not revisited. Core samples were collected within the boundaries of the four sample plots at each site (Figure 2.3). The number of cores collected at each site was variable and dependent on the existing structure and composition. Three increment cores were removed from each species present in four DBH classes ranging from 10.0-29.9 cm, 30.0-49.9 cm, 50.0-69.9 cm, and >70.0 cm. If a species was present in all four DBH classes 12 increment cores were collected for that species. At most sites this was not possible as shade tolerant species were commonly absent in the large diameter classes and intolerant species were absent in the small diameter classes. Extant trees of the same species and size class were used to replace removed cohorts if selective logging had removed trees >50 cm DBH in sample plots. All replacement trees were within 50 meters of the original sample site and were collected from areas of similar stand structure and composition. Overall the range of cores collected across all sites was 15-42 with a mean of 23. Cores were collected at 40cm from ground height and trees were cored perpendicular to slope direction on steeply sloped sites. If trees were rotten cores were obtained at DBH. Height of core collection was recorded for each sample collected.

Cores collected from Emily Heyerdahl's study of, "*Fire and Forest Histories of Mixed-conifer Forests in Central Oregon,"* were collected from three gridded study areas in the Deschutes and Ochoco National forests. Sample sites were placed every 500 meters on an eight by four grid creating a total of 32 plots per sample site. Sample sites were carefully placed in mature mixed-conifer forest in areas with minimal evidence of logging. At each of the 3 sample sites, 2 sample plots were not sampled due to terrain difficulty or because the site lacked a sufficient number of sample trees. Therefore a total of 90 sample plots distributed across three sample sites were sampled. The spatial layout of sample sites and the location of study areas are spatially depicted in Figure (3.1).

A variable radius plot was used to measure structure and composition and select trees, snags, and logs for increment core collection a each sample plot. Starting from the center of each sample plot the first 30 trees and snags greater than 20 cm at DBH were measured and recorded. The distance to the 30th tree from the sample plot center was equal to the radius for each sample plot. Average plot size was 0.17 hectares with a range of 0.06-0.36 hectares. Increment cores were extracted from all trees and snags greater than 20 cm at DBH within the plot radius at each sample site to determine age structure. Cores were extracted at 15 cm above ground height from all sound trees and snags. If a core could not be obtained at 15 cm cores were collected at DBH. Samples were obtained with a chainsaw for all stumps and logs with a large end diameter of greater than 20 cm.

Sample Preparation

All increment core samples were mounted and sanded until cell structure was clearly visible following standard techniques described by Stokes and Smiley (1996). The oldest and highest quality samples were visually crossdated using the list-year method (Yamaguchi 1991), and then measured using a VELMEX tree-ring measurement system with a precision of 0.001 mm. Crossdating accuracy was evaluated using the software program COFECHA (Holmes 1983, Grissino-Mayer 2001). Any measurement time series with potential errors identified by COFECHA were visually checked and if necessary re-dated and re-measured. Calendar years were then assigned to all tree rings in remaining samples using a combination of visual crossdating of ring widths and cross-correlation of measured ring-width series (Holmes 1983 and Swetnam et al. 1995). For cores that did not intersect the pith the number of rings to pith was estimated based on the curvature of the innermost rings sampled (Applequist 1958, and Duncan 1989).

Annual ring width increment (RWI) was measured for all ponderosa pine cores collected at sixty-two structure and composition sites. This excludes the majority of cores collected at Heyeredahl’s Green Ridge, McKay, and Lytle fire history sites. A total of 618 cores were measured from bark to the innermost ring using a VELMEX tree-ring measurement system with a precision of 0.001mm. Accuracy of crossdating was checked using COFECHA for each sample measured (Holmes 1983). These measurement time series were used to examine patterns in release and growth reduction across the study area and identify growth anomalies related to changes in establishment and density in MCF. An additional forty increment cores were collected from Heyerdahl's Sheridan and McKay fire history sites, which had a detailed reconstruction of fire occurrence. These additional cores were collected from mature overstory ponderosa pine. Using these cores I created multicentury growth chronologies to investigate the relationship between known fire events and growth.

Analysis Methods

Detection of changes in establishment in MCF

To investigate and compare the current and historic pattern of disturbance in mixed-conifer forest, I constructed establishment histograms for each MCF stand type identified in Chapter 2. All tree establishment dates were aggregated by MCF type they were extracted from. The age structure within each site type was graphically expressed as the amount of individuals that had established and survived at each site during each decade since the year 1600. Establishment was grouped by the most prominent species found at each type. In this analysis I used 3,452 increment cores collected at both the structure and composition sample sites described in Chapter 2 and Emily Heyerdahl's gridded fire history sample sites (Figure 3.1).

Investigation of growth histories of old-growth ponderosa pine

Annual ring width increment for a particular tree species is dependent on the age-size related trend, climatic conditions, local endogenous disturbance, and standwide exogenous disturbance (Cook 1987). The principle of aggregate growth relies on the axiom that each of these factors leaves a signal in annual ring width increment each year (Cook 1987 and Speer 2010). By controlling for unwanted signals or noise a researcher can isolate information relevant to the particular question of interest. I used a combination of boundary line release criteria (Black and Abrams 2003), suppression criteria, and growth chronologies to investigate relationships between growth and climate and growth and standwide disturbance.

In the absence of climatic effects, periods of release are related to mortality from periodic disturbance. Sudden increases in growth may be exhibited by surviving trees as they have increased access to water, sunlight, and nutrients (Black and Abrams 2003). I attempted to detect true ecological releases due to disturbance while controlling for climate and the variation in age and size of sample trees using boundary line release criteria developed by Black and Abrams (2003). The boundary line method utilizes a species specific negative exponential curve that represents the maximum release potential given the mean annual growth 10 years prior to a release event.

For each measurement time series a running mean was used to calculate percent growth change (Nowacki and Abrams 1997). The running mean is calculated using the equation $(M_2 - M_1)/M_1$, where M_1 is the mean of 10 years of prior growth and M_2 is the mean of 10 years of subsequent growth. In each period where percent growth change exceeded 25% the release was scaled to maximum possible release values as predicted by the boundary line equation for ponderosa pine which was $665.79 \times 10^{\wedge}-.9453M_1$ (Black and Abrams 2004, and Arabas et al. 2008). Releases which were 25% of the maximum potential release predicted by the boundary line equation were classified as release events. A threshold of 25% was used because it has been effective at excluding release events which are related to climate (Nowacki and Abrams 1997 and Arabas et al. 2008). Although many methods have been used to detect release events the boundary line method was preferred because prior growth and release response is largely independent of the age and size related growth trend of sample trees (Black and Abrams 2003).

The OUTBREAK program (Holmes and Swetnam 1996) was used to screen for patterns in growth reduction for each measurement time series. OUTBREAK has been commonly used to detect relatively dramatic suppression in growth that can be assigned to a temporally distinct event such as fire or insect disturbance (Swetnam 1985, Speer et al. 2001, and Arabas et al. 2008). If growth suppression in MCF has occurred because of increased stand density and competition for growth resources, growth reductions would be gradual as sample sites would have filled in over a period of decades. Therefore I used relatively conservative suppression criteria, which identify gradual reductions in growth.

Periods of long term growth reduction were identified with the following procedure. All tree ring measurement series were first detrended and standardized with a modified negative exponential (MNE) curve. Detrending produces a dimensionless ring width index (RWI) with a series mean equal to 1.0, and removes age related growth trends and differences in growth rates between sample trees (Cook and Kairiukstis 1990, Fritts 2001, and Speer 2010). The conservative MNE detrending method was used to preserve growth variability related to climate and stands dynamics (Speer 2010), and was performed in the dplR package in R software (Bunn 2008). Each detrended measurement time series was analyzed in OUTBREAK to detect periods of growth reduction. Growth reduction criteria specified that all reductions in growth had to remain more than one standard deviation below the series mean for a minimum of five years with the initial rate of decrease in annual growth reduction set to 0.250.

Release and growth reduction periods for the eastern Cascades and Ochoco Mountains study areas were summarized by calculating the proportion of all ponderosa pine that met respective criteria for the time period 1700-1999. This analysis period was used because I had a minimum sample depth of 30 tree ring measurement series after the year 1700. In this analysis I used measurement series developed from overstory trees which were established prior to 1850. Older trees were used because they had responded to stand competition and climate before and after the decrease in fire frequency in MCF. To summarize growth release and growth reduction I calculated the mean annual proportion (MPY) and coefficient of variation (CV) of trees exhibiting growth reduction or growth release between 1700 and 1900 and between 1900 and 1999. CV was used to evaluate variance because of unequal length of analysis periods.

I created composite chronologies of RWI for the eastern Cascades and the Ochoco Mountains to identify long term changes in growth related to succession and increased competition in MCF. Composite chronologies were created from several multi-century measurement times series collected from old-growth ponderosa pine at the Sheridan and McKay fire history sites. R software with the Dendrochronology Program Library (dplR) package (Bunn 2008) was used to create and graphically display chronologies.

Each tree ring measurement series was initially detrended for size related growth effects with a modified negative exponential curve (Fritts 2001). Detrended series were truncated to a minimum sample size of 14 and averaged into master chronologies using a biweight robust mean to reduce the effects of outliers. R’s boot library was used to calculate upper and lower 99% confidence intervals with 1000 bootstrap replicates for mean annual growth (Canty and Ripley 2007). CV was calculated for RWI to analyze variability in growth over in different time periods. To summarize trends in growth, a 20 year spline was fit to mean annual growth for the Sheridan and McKay fire history sites. A 20 year spline leaves 99% of the variance at a period of 6 years and 50% of the variance at 20 years (Speer 2010). This relatively aggressive spline was used to highlight tree growth response to discrete disturbance events and changes in climate. Using longer spline lengths obscured the timing of growth responses to discrete events at each site.

Comparison of growth anomalies to climate

Palmer Drought Severity Index (PDSI) is based on precipitation and temperature that indicates moisture available for growth (Palmer 1965). Negative PDSI values are associated with drought conditions while positive values are associated with cool and wet conditions. To evaluate the relationship between climate and growth I graphically compared a 20 year mean of annual PDSI values to patterns of release, growth reduction, and to annual growth at the Sheridan and Kay fire history sites. PDSI values for each month between 1700 and 1999 were obtained from the National Climate Data Center (NOAA 2012).

RESULTS

Age Histograms

Histograms of age structure for the eastern Cascades and Ochoco Mountains display clear changes in the amount of tree establishment and survival of all species beginning in the late 19th and early 20th century (Figures 3.2-3.9). Increases in establishment and survival are represented by abrupt peaks in all MCF types with the exception of the PIPO/PSME/ABGC type in the Ochoco Mountains (Figure 3.9). The most shade tolerant species within each MCF type is primarily responsible for peaks in establishment, but abundant ponderosa pine less than 110 years old accounts for the majority of increased establishment in the PIPO type. Similarly, relatively young Douglas-fir and grand fir account for peaks in establishment in PIPO/PSME and PIPO/ABGC types respectively. Grand fir composes the majority of the increase in the PIPO/PSME/ABGC type in the eastern Cascades.

The timing of increased establishment is variable among MCF types and between the eastern Cascades and Ochoco Mountains study areas. Establishment peaks in the eastern Cascades in the 1940s in the PIPO, and PIPO/PSME types, in the 1920s in the PIPO/ABGC type, and in the first decade of the 20th century in the PIPO/PSME/ABGC type. Establishment peaks occur earlier in the PIPO and PIPO/PSME types in the Ochoco Mountains during the first two decades of the 20th century. Establishment in the PIPO/ABGC Type clearly increases in the first decade of the 20th century, but does not peak until the 1930's. Increases in establishment are least dramatic in the

PIPO/PSME/ABGC type and are best characterized as a prolonged period of increased establishment lasting from the 1870's to the 1940's. Peak increases in establishment and survival are followed by abrupt decreases in establishment in all MCF types in both study areas. After the 1940's the number of establishment events of the prominent understory species declines to levels that are lower in comparison to the mid 19th century.

Changes in composition are the result of increased establishment and occurrence of Douglas-fir and grand fir in all MCF types. Ponderosa pine demonstrates relatively continuous recruitment during the 18th and 19th century and makes up the majority of all trees established during this time period in all stand types. Douglas-fir and grand fir compose the majority of all trees established in the PIPO/PSME and PIPO/ABGC types during the 20th century. Additionally, these species are present in MCF types where the occurrence of individuals of the same species established before 1900 is rare. Douglas-fir and grand fir less than 100 years old are present at nearly all PIPO sites while only 3 individuals older than 100 years were found among all PIPO sites in the eastern Cascades. Similarly, grand fir established after 1900 is common at eastern Cascade PIPO/PSME sites where no individuals older than 110 years were found. In the Ochoco Mountains Douglas-fir and grand fir older than 110 years were found at most PIPO/PSME and PIPO/ABGC sites, but these individuals were rare in comparison to ponderosa pine.

Patterns of release and growth reduction in the eastern Cascades and Ochoco Mountains

Distinct periods of growth release and reduction were visible between 1700 and 1999 (Figures 3.10 and 3.11). Periods where a relatively large proportion of trees exhibit growth reduction were typically followed by periods in which relatively large proportions of trees exhibit growth release. An overlay of a 20-year mean of annual PDSI values indicates that drought and recovery from drought were associated with a cyclical pattern of growth reduction and release in MCF of central Oregon. Negative values of PDSI are associated with peaks in growth reduction and increasingly positive values of PDSI are associated with peaks in growth release.

The proportion of trees exhibiting release in the eastern Cascades noticeably decreased during the 20th century (Figure 3.10). Peaks in the proportion of trees exhibiting release are flattened following growth reduction events in comparison to the 18th and 19th century. Prior to the 20th century the MPY of all trees exhibiting release was higher and more variable, but MPY of trees exhibiting reduced growth was similar before and after 1900.

In the Ochoco Mountains trees were less likely to release during cool and wet climatic periods in comparison to the eastern Cascades (Figure 3.11). Peaks in the proportion of trees exhibiting release are relatively similar before and after 1900 with the exception of the large peak in tree release in the 1940s (Figure 3.11). The CV increases after 1900 for growth release and reduction as a large proportion of trees responds to the dust bowl drought, which is indicated by extremely negative values of PDSI in the late 1920s. The proportion of trees with reduced growth was higher after 1900 because of the dust bowl drought, and also because the proportion remains high under moderate climate observed between the years 1950-1975.

Growth Chronologies at Sheridan and Kay Fire History Sites

At the Sheridan fire history site periods of increasing RWI are preceded by four fire events between 1750 and 1889 and also coincide with periods of increased PDSI (Figure 3.12). During the 20th century, fires are absent at the site and growth decreases during the extreme drought occurring during the1920s and early 1930s. Following this drought RWI is consistently below the series average and growth remains stable between 1900 and 1975 as evidenced by the smoothing spline and the CV for this period (0.13). Growth does not respond to relatively cool and wet period following the dust bowl drought as it did after other droughts prior to fire exclusion. In the 1970s RWI dramatically increases following a harvest event, which results in the high CV for the time period between 1900 and 1999.

At the McKay fire history site variability in long term growth trends increases after fire exclusion (Figure 3.13). Prior to 1900 annual RWI is highly variable from year to year but long term trends in RWI show relatively small deviation from the series mean of 1.0. Periods of increasing and decreasing RWI are short and have no apparent relationship with fire events or long term trends in PDSI. After 1900 variability in annual RWI is similar but long term variability increases, which is reflected by an increase in the CV for RWI during 1900-1999. In the 20th century the 20 year spline follows long term trends in PDSI and growth shows greater deviation above and below the series mean of RWI. Growth appears to be strongly associated with decadal trends in climate at the McKay fire history site during the 20th century, but not in the 18th and 19th centuries.

DISCUSSION

Implications of age structure of MCF types

The changes in establishment and composition over time that I found in central Oregon are similar to those found in MCF in southwest Oregon (Messier et al 2012), Idaho (Sloan 1998), Washington (Camp 1999), and California (Scholl and Taylor 2010). My study is unique because I characterized dynamics in different stand types and environmental settings. The current age structure of MCF types demonstrate that establishment of all species increased in the early 20th century and that PIPO/PSME and PIPO/ABGC types have shifted from dominance of ponderosa pine to dominance of shade tolerant species. These findings support the conclusion that MCF is currently much denser and composed of a higher proportion of shade tolerant species in comparison to the 18th and 19th centuries. Current structure and composition coupled with age structure can be used to differentiate environments that historically maintained fire climax vegetation versus environments where development of late successional vegetation was likely.

Prior to fire exclusion mixed-severity fire even in relatively moist PIPO/ABGC sites would have maintained vegetation composed primarily of ponderosa pine. Nearly all of the sample stands examined in the PIPO, PIPO/PSME, and PIPO/ABGC types would be classified as the grand fir/white fir PVT today, but would have been classified as the ponderosa pine PVT in the 19th century. Combined with the loss of overstory pine and the dominance of shade tolerant species at PIPO/PSME and PIPO/ABGC sites this raises doubt of the persistence of ponderosa pine in these environmental settings. Age structure shows establishment of ponderosa pine decreased following increased establishment of shade tolerant species. Extant large diameter ponderosa pines are likely to be replaced by relatively abundant and competitive shade tolerant species in the absence of disturbance. When fire returns to these sites, shade tolerants may still dominate regeneration due to presence of abundant shade tolerant seed sources at local and landscape scales (Perry et al. 2011).

Changes in establishment in my stand types indicate that environmental setting controls composition at dry PIPO sites, and that fire historically controlled composition at more mesic PIPO/PSME and PIPO/ABGC sites characterized by a mixed-severity fire regime. PVT is used to indicate historic fire regime which is used to prioritize restoration treatments in forests where fire has been excluded (Brown et al. 2004). Highest priority is given to restoring structure and composition in low-severity fire regimes found in ponderosa pine and dry mixed-conifer PVTs in forest composed of fire resistant ponderosa pine, western larch, and Douglas-fir. Intermediate restoration priority is given to grand fir and white fir PVTs similar to my PIPO/ABGC type, where cooler and moister conditions allow the establishment of less fire and drought tolerant species. These sites receive lower priority because they have theoretically experienced less ecological change as fire exclusion has prevented 1-4 fire cycles at mixed-severity sites in comparison to 10 or more fire cycles at low-severity sites (Brown et al. 2004). However, age histograms at PIPO/ABGC sites suggests that these sites have may have experienced even greater ecological change as increased establishment rate was accompanied by a shift in composition from fire and drought tolerant species to grand fir. Succession at moist mixed-conifer sites differs from dry mixed-conifer forests in that their climatic setting allows the establishment shade tolerant species in the absence of fire. Therefore the interaction between pathway of succession and interruption of disturbance regime is an important consideration when characterizing the ecological effects of fire exclusion in MCF and developing restoration plans.

Relationship of growth patterns to climate

In this investigation I attempted to detect disturbance related release events using the boundary line method (Black and Abrams 2003). The synchrony in the pattern of growth reduction and release across my extensive sample sites suggests that climate was associated with this pattern as it is the one pervasive influence across the study area. A comparison of the running mean of PDSI to the temporal pattern of growth supports this idea as droughts were associated with periods of reduced growth and cool wet periods were associated with growth release. For disturbance to drive the pattern of growth release and reduction, disturbance events would need to be temporally synchronized across my sample sites. This is unlikely due to the broad distribution of my sample sites (Figure 3.1), and because small fires historically occurred in central Oregon in any given year regardless of precipitation (Heyerdahl et al. 2001). Therefore, I assume that the major release events I detected are best characterized as growth recovery following climatically driven periods of reduced growth.

To detect growth releases related to disturbance the boundary line method relies on the assumption that releases due to climate are of lesser magnitude than releases caused by disturbance within stands (Black and Abrams 2003). The use of growth histories from mature ponderosa pine and growth release in response to cool wet climatic periods provide a plausible explanation of why the use of the boundary line method in this case may violate this assumption. Boundary line release criteria was originally used in forests of the eastern United States where trees are primarily competing for light and have large growth releases following disturbance due to increased light availability (Black and Abrams 2003). In comparison, ponderosa pine in MCF of central Oregon may have a small growth response to disturbance because stands were historically open (Munger 1917), and low-severity fires caused minimal mortality to large trees (Brown et al. 2004). The Pacific Decadal Oscillation (PDO) is a fluctuation of Pacific sea surface temperatures that produces warm and dry versus cool and wet climatic conditions in the Pacific Northwest that persist for decades (Gedalof et al. 2002). Fluctuations in smoothed PDSI in figures 3.10 and 3.11 are likely a result of this climatic cycle. Biondi et al. (1999) demonstrated that patterns in growth can be strongly driven by the PDO, and patterns of growth reduction and release in trees I sampled oscillate with droughts and cool wet periods indicated by PDSI (Figures 3.10 and 3.11). Because the PDO may produce growth releases of ponderosa pine that are greater or equal in magnitude to releases caused by disturbance the ability of the boundary line method to filter releases caused by disturbance appears limited. If the boundary line method is used to chronicle disturbance in my study area, growth histories should be filtered to remove climatically related release events (Arabas et al. 2008).

Implications of growth reduction and growth release

Patterns of growth reduction and growth release in the eastern Cascades support the hypothesis that densification of stands following fire exclusion has modified growth patterns in old-growth ponderosa pine. The height of peaks in the proportion of old-growth ponderosa pine releasing after a growth reduction period declines dramatically after the late 1800s in the eastern Cascades. This change in pattern suggests that the dense understory cohort established in the early 20th century has reduced the ability of ponderosa pine to respond to periods of wetter climate favorable to increased growth. Climatically driven release events may be muted by dense cohorts of understory trees that compete for additional moisture during cool and wet periods. McDowell et al. (2003) investigated growth response of individual >250 year old ponderosa pine to understory thinning in central Oregon and found that individuals in stands that had received understory thinning had higher water availability, photosynthetic capacity, and diameter growth in comparison to untreated stands. Their results support the explanation that understory trees inhibit growth in old-growth pine, and therefore may be related to the decrease in the proportion of trees exhibiting release during the 20th century.

In the Ochoco Mountains the pattern of release peaks did not change over the period of record with the exception of growth release following the dust bowl drought. Changes in the proportion of trees releasing during climatic periods favorable to growth would be more difficult to detect as peaks in the proportion of trees exhibiting release were low before and after 1900. This weaker response may occur because precipitation is too low to support rapid growth even during wet periods in the drier Ochoco Mountains. The large peak of growth reduction and growth release associated with the severe dust bowl drought in the late 1920s and early 1930s suggests that growth of ponderosa pine was more sensitive to drought events in the drier Ochoco Mountains than in the eastern Cascades in the 20th century. Higher sensitivity to drought could be related to the drier climate in the Ochoco Mountains and the intensity of the dust bowl drought. Alternatively, densification following fire exclusion in the early 20th century could also be a factor in the magnitude of this response. Ponderosa pine in denser stands in the 20th century may have exhibited greater sensitivity to drought as ponderosa pine in high density stands have minimal water availability in comparison to low density stands primarily during periods of extreme drought (Skov et al. 2004).

A decrease in the variability in growth reduction and release in the eastern Cascades after 1900 is consistent with the effects of increased competition for resources as a result of infilling of understory trees. Conversely, the increase in variation in growth reduction and release in the Ochoco Mountains appears to be related to higher sensitivity to the dust bowl drought during the early 20th century. Examining how tree populations respond to relatively wet periods before and after fire may be a viable way to investigate where fire exclusion has altered competition in the eastern Cascades at the site level. In contrast this method may have limited utility in the Ochoco Mountains where growth release was less sensitive to wet periods prior to fire exclusion.

Implications of growth histories at Sheridan and McKay sites

Changes in annual growth and its relationship to climate during the 20th century at the Sheridan and McKay sites suggest that disturbance alters competition among trees, and mediates the relationship between climate and growth at both sites. This presents an opportunity to use changes in the relationship between growth and climate as an indicator of changes in competition in MCF. A comparison of these two chronologies suggests that the change in disturbance regime at the two sites has had opposite effects on the growth--climate relationships. Analysis of the variation in growth before and after the disruption of fire at the eastern Cascades fire history site suggests that long term patterns in growth may be less sensitive to climate following fire exclusion. In contrast, at the Ochoco site, variation in growth is larger during the fire exclusion period, suggesting greater sensitivity to climate fluctuations at the drier environmental setting.

Trends in growth at Sheridan are reflective of the pattern of growth reduction and release in the eastern Cascades across a range of environments. Growth decreases during dry periods and increases during wet periods until this cycle is interrupted in the 20th century. Following the dust bowl drought RWI and variance in growth is comparatively low. This parallels the decrease in the proportion of trees releasing after 1900 in the eastern Cascades study area. The decrease in responsiveness of growth to oscillating wet and dry climatic periods suggests lack of fire and densification of stands may increase competition among trees, which buffers their growth response to changes in moisture. Studies by Latham and Tappeiner (2002) and McDowell (2003) have shown that mature ponderosa pine with declining vigor and growth rate can respond to the thinning of dense understory trees in stands that were presumably dense because of fire exclusion. These documented rebounds in steadily declining growth supports the explanation that densification modifies growth of mature ponderosa pine and therefore may modify growth response to wet and dry climatic cycles as I observed at the Sheridan fire history site. Furthermore, the dramatic release after the logging event in the 1970s provides evidence that competition among trees had a strong influence on tree growth at the Sheridan site. This growth release also indicates that thinning may increase vigor and therefore resilience of overstory old-growth pines to future fire, insect, and drought events as noted by Kolb et al. (2007).

Prior to fire exclusion at the McKay site there is some indication that growth decreases during droughts, but overall trends in growth and climate do not appear to be synchronous. In addition, growth at McKay shows relatively little amplitude and variance above and below the series mean prior to fire exclusion. Growth may be stable during this period because of a lack of competition among trees. If stand density was limited by frequent fires water would have been more available and adequate for growth during dry and wet periods. Skov et al. (2004) supports this interpretation; they found that water availability was much higher in ponderosa pine in thinned than in untreated stands primarily during extreme droughts. Collectively, this suggests that frequent fires limited inter-tree competition, which resulted in minimal growth sensitivity to drought. The lack of increased growth following fires provides additional evidence that competition was low at the McKay site, as fires did not rapidly increase the availability of growth resources to surviving trees.

Following fire exclusion variation in long term growth increased, and tended to follow the wet and dry climatic oscillations in the 20th century. A closer examination of individual tree chronologies reveals that growth of sample trees was more synchronous after 1900 than before suggesting that growth was more strongly associated with the pervasive influence of climate. Allen and Breshears (1998) documented in northern New Mexico that ponderosa pine were more adversely affected during drought and rapidly recovered following drought at ecotones where fire exclusion had increased stand density. A similar increase in growth sensitivity to climate due to densification may manifest at the McKay site where dry MCF vegetation transitions to juniper woodlands. Overall increased sensitivity to wet vs. dry climatic cycles following fire exclusion at the

McKay site suggests fire played an important role in maintaining drought resilience in dry MCF by regulating stand density. However, it is important to note that increased climatic sensitivity at the McKay site may additionally be related to the unusual intensity and duration of the dust bowl drought (Figure 3.13).

Limitations of Growth Histories

This investigation is unique because it highlights variability in changes in structure and composition, and uses the relationship of climate and growth to investigate whether current stand structure may have an analog in previous centuries. Changes in growth patterns in both study areas and at the fire history sites could be attributed to either climate or stand dynamics or climate and stand dynamics as both have been variable during the period of fire exclusion. A major limitation of this study is that the differential responses of growth to climate and disturbance at the Sheridan and McKay fire history sites represent a small sample of environmental variation in MCF. Growth response to climate, disturbance, and absence of disturbance is clearly different at these sites and the two broader study areas. I hypothesize that these differences are a result of variable influences of climate, disturbance, and competition in different environmental settings. Relationships between growth and climate and growth and disturbance must be understood at a finer scale before they can be used to determine how fire exclusion has altered stand dynamics across MCF. Using the precipitation gradient in MCF to investigate growth response to climate and fire exclusion in different environmental settings would be logical as precipitation is a primary driver of variation in structure and composition in MCF (Chapter 2).

Restoration Implications

This study provides the first characterization of age structure of MCF across environmental gradients in central Oregon. Overall the current age structure of MCF types supports the hypothesis that stand density and the dominance of shade tolerant species have increased in MCF during the 20th century. Several studies recommend understory thinning in MCF to increase resilience of MCF to wildfire, disease, and climate change, and to restore habitat for species associated with fire climax forest vegetation (Arno 1995, Brown et al. 2004, Stephen and Moghaddas 2005, Fitzgerald 2005, and Powell 2011). The current age structure of MCF types provides a record of changes during fire exclusion which can be used to estimate structure and composition in MCF prior to fire exclusion and guide restoration.

Age histograms for PIPO/PSME and PIPO/ABGC types in the eastern Cascades demonstrate how the frequency of old-growth Douglas-fir and grand fir has increased across the landscape over the last 125 years. Shade tolerants established before 1900 occurred at most PIPO/PSME and PIPO/ABGC sites, but generally less than two were found per site, which equates to approximately five TPH. During the 20th century these mature shade tolerants have reproduced prolifically and young shade tolerant trees are currently found at densities of 250-400 TPH at sites in the eastern Cascades (Table 2.6). Restoration of PIPO/PSME and PIPO/ABGC stands to approximate the structure of these forests prior to fire exclusion would require removal of nearly all individuals of shade tolerant species.

Age histograms from the Ochoco Mountains also demonstrate that the density of shade tolerants as well as ponderosa pine has increased at PIPO/PSME and PIPO/ABGC sites. Thus, thinning of understory ponderosa pine in addition to shade tolerant species would be necessary to restore pre-fire exclusion structure and composition. At PIPO sites in both the eastern Cascades and Ochoco Mountains ponderosa pine would be the target thinning species as other species are still rare at these sites. In all MCF stand types, reconstructed densities of large overstory trees (Tables 2.5 and 2.6) could be used to guide retention of small diameter trees at densities sufficient to replace individuals lost to logging and future mortality within the stand. Age structure in the wetter PIPO/PSME/ABGC type indicates understory and overstory shade tolerants were common at these sites prior to fire exclusion, and there is less evidence that the current structure and composition of these stands is different from their pre-Euroamerican condition.

CONCLUSIONS

Analysis of age distributions support the hypothesis that composition has shifted to shade tolerant species and density has increased following fire exclusion in the late 1800s and early 1900s in MCF. However, multiple successional pathways in MCF have resulted in variable changes in stand structure and composition. After 1900 establishment rates dramatically increased in the PIPO, PIPO/PSME, and PIPO/ABGC stand types. Environmental setting prevented shifts in composition from ponderosa pine to Douglas-fir or grand fir at PIPO sites during fire exclusion, but Douglas-fir and grand fir dominated establishment at PIPO/PSME and PIPO/ABGC sites respectively where establishment of ponderosa pine was predominant prior to 1900.

Growth histories of ponderosa pine suggest that annual growth patterns are different between the 19th and 20th centuries and different between the eastern Cascades and Ochoco study sites. In the eastern Cascades, growth is less variable and less responsive to climate in the 20th century. In contrast, growth is more variable and more responsive to climate in the Ochoco Mountains. It is difficult to attribute changes in growth patterns solely to fire exclusion because climate has also been variable over this period and additionally drives growth patterns. Variability in growth response to climate should be further evaluated before growth histories can be used identify changes in succession in MCF in different environmental settings.

Collectively age histograms and the growth histories of ponderosa pine in MCF highlight the range of responses of MCF to fire exclusion. Successful management of MCF rests on an understanding of variable response to fire exclusion and matching management plans to landscape variability. A one size fits all approach to research and restoration is inappropriate in MCF where response to fire exclusion has been diverse and dependent on environmental setting.

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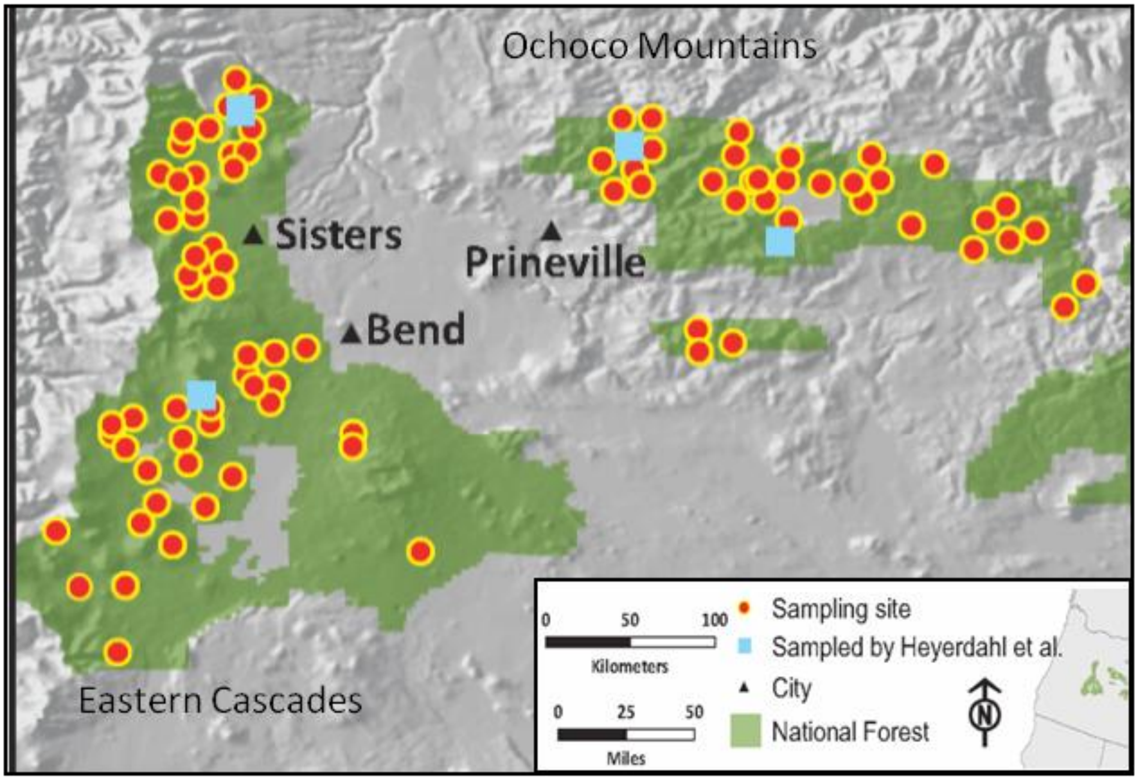

Figure 3.1: Eastern Cascades and Ochoco Mountains study areas and study site locations.

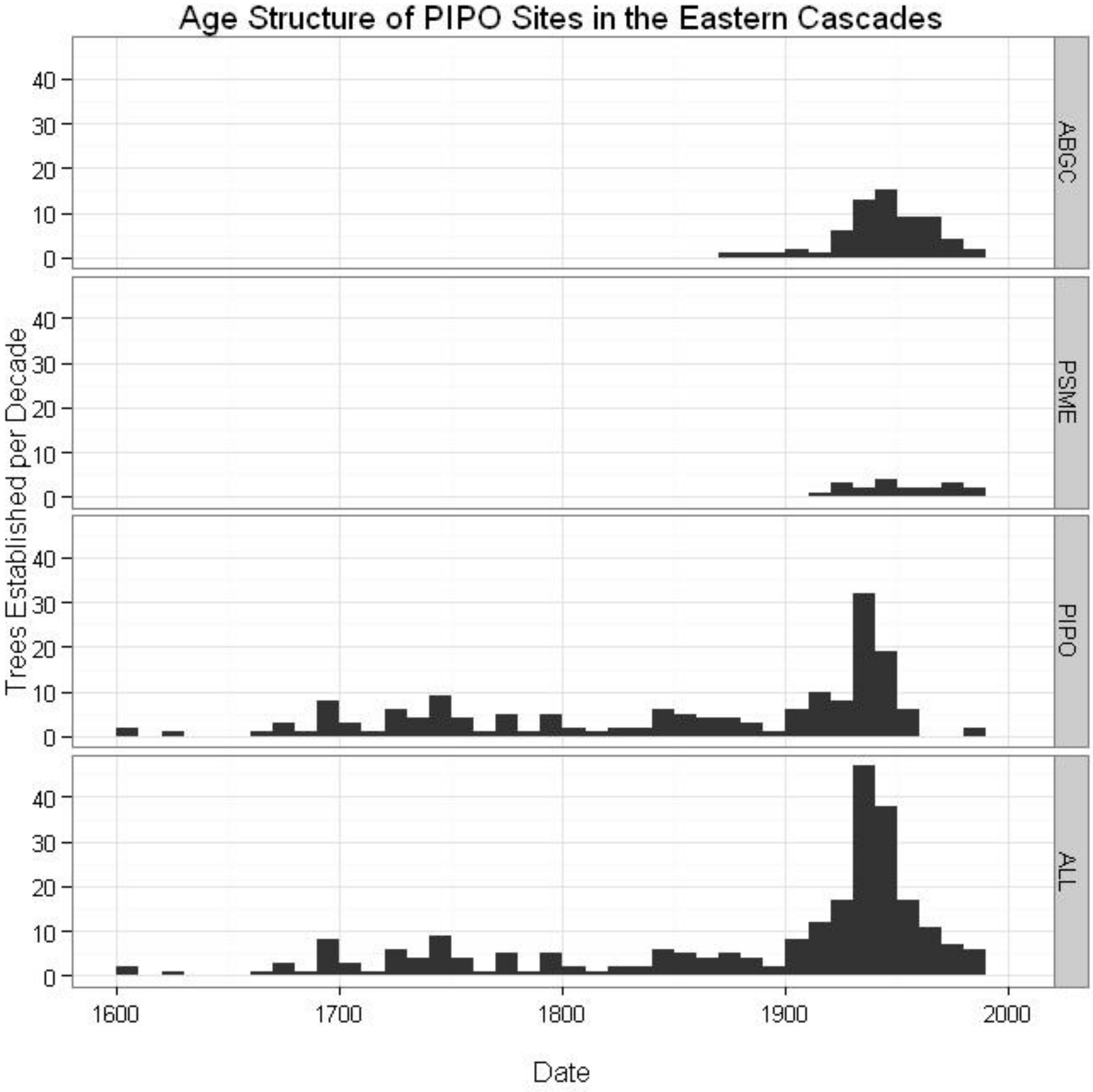

Figure 3.2: Age structure at PIPO sites in the Eastern Cascades

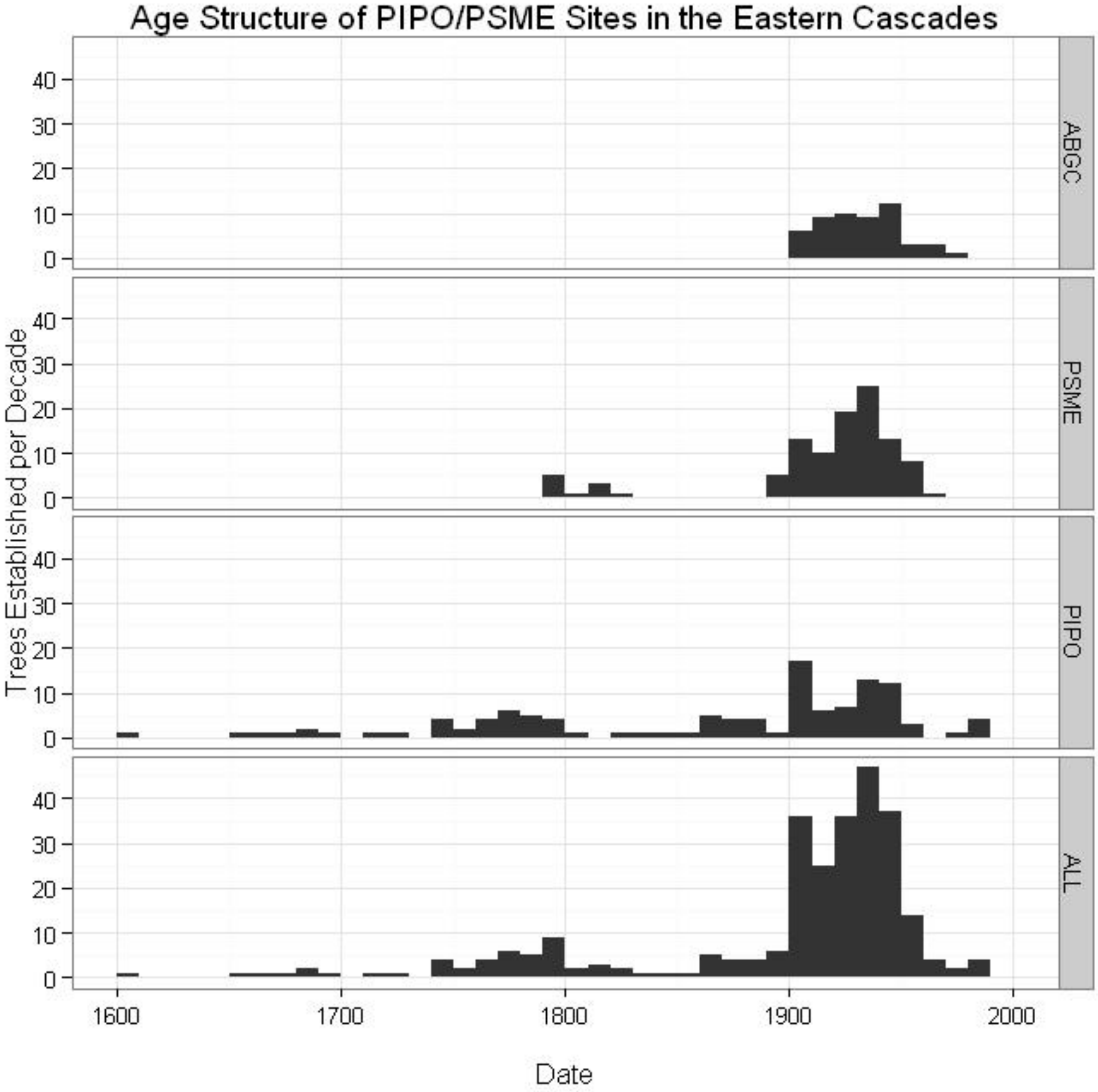

Figure 3.3: Age structure at PIPO/PSME sites in the Eastern Cascades

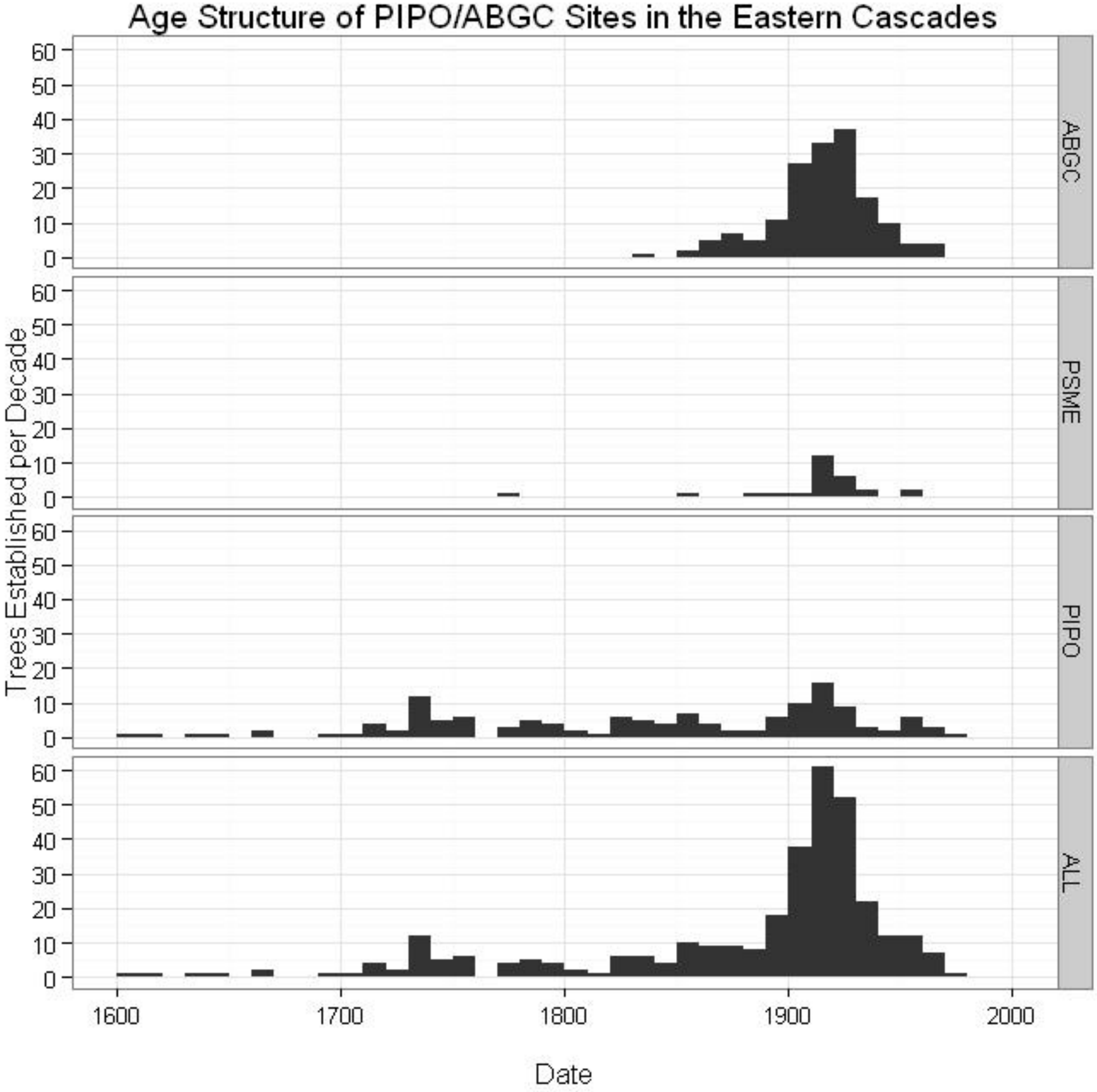

Figure 3.4: Age structure at PIPO/ABGC sites in the Eastern Cascades

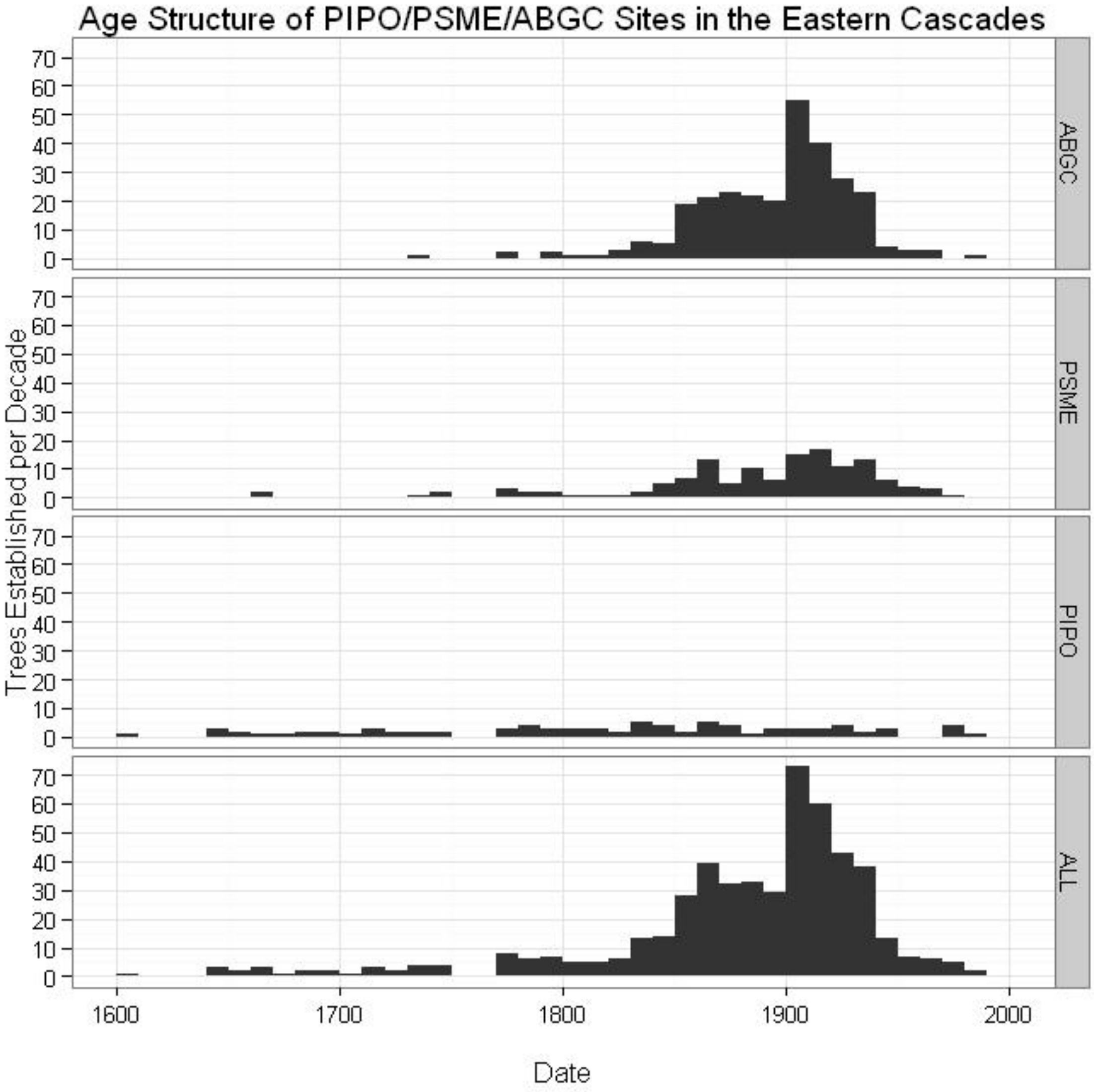

Figure 3.5: Age structure at PIPO/PSME/ABGC sites in the Eastern Cascades

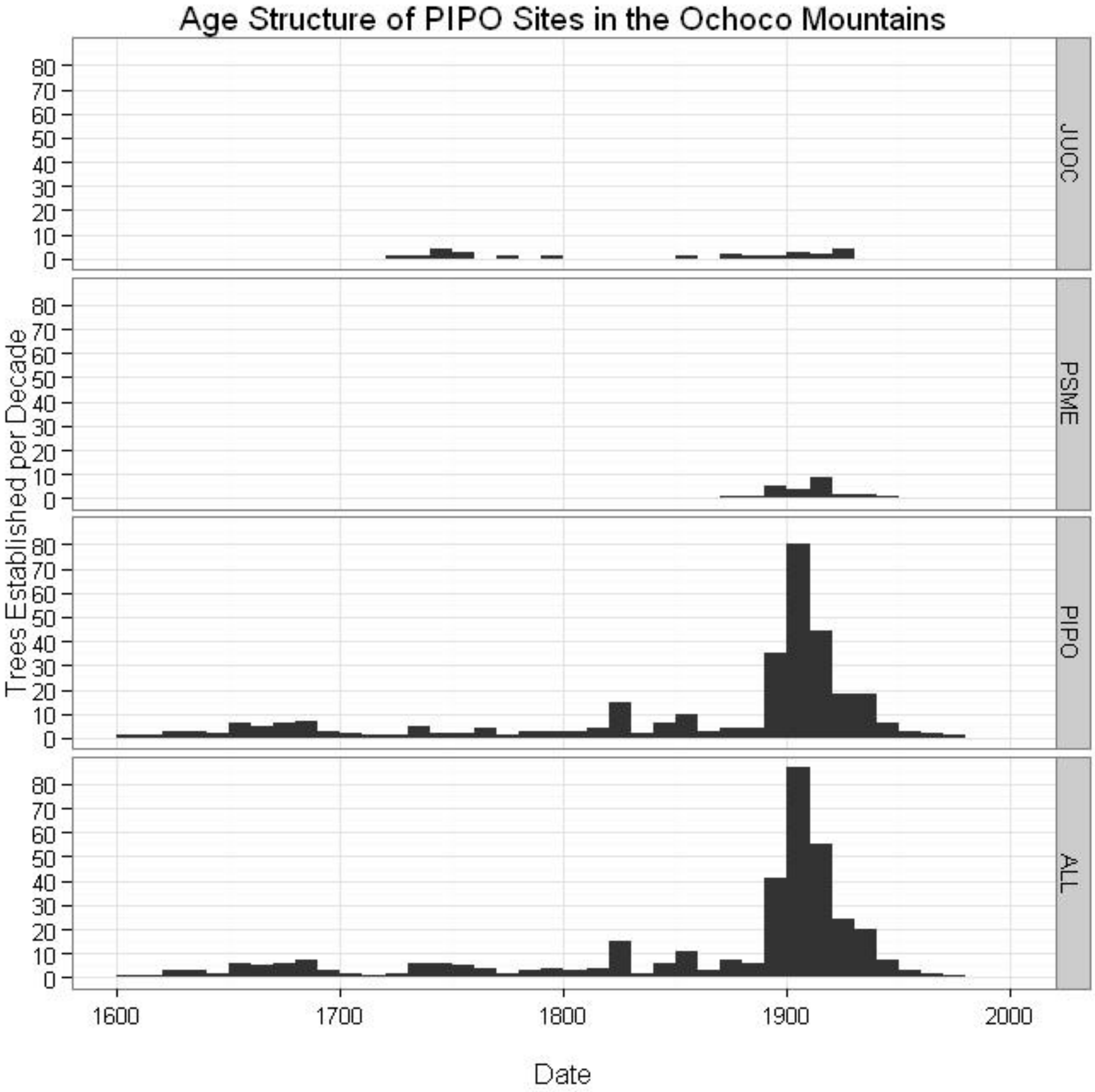

Figure 3.6: Age structure at PIPO sites in the Ochoco Mountains

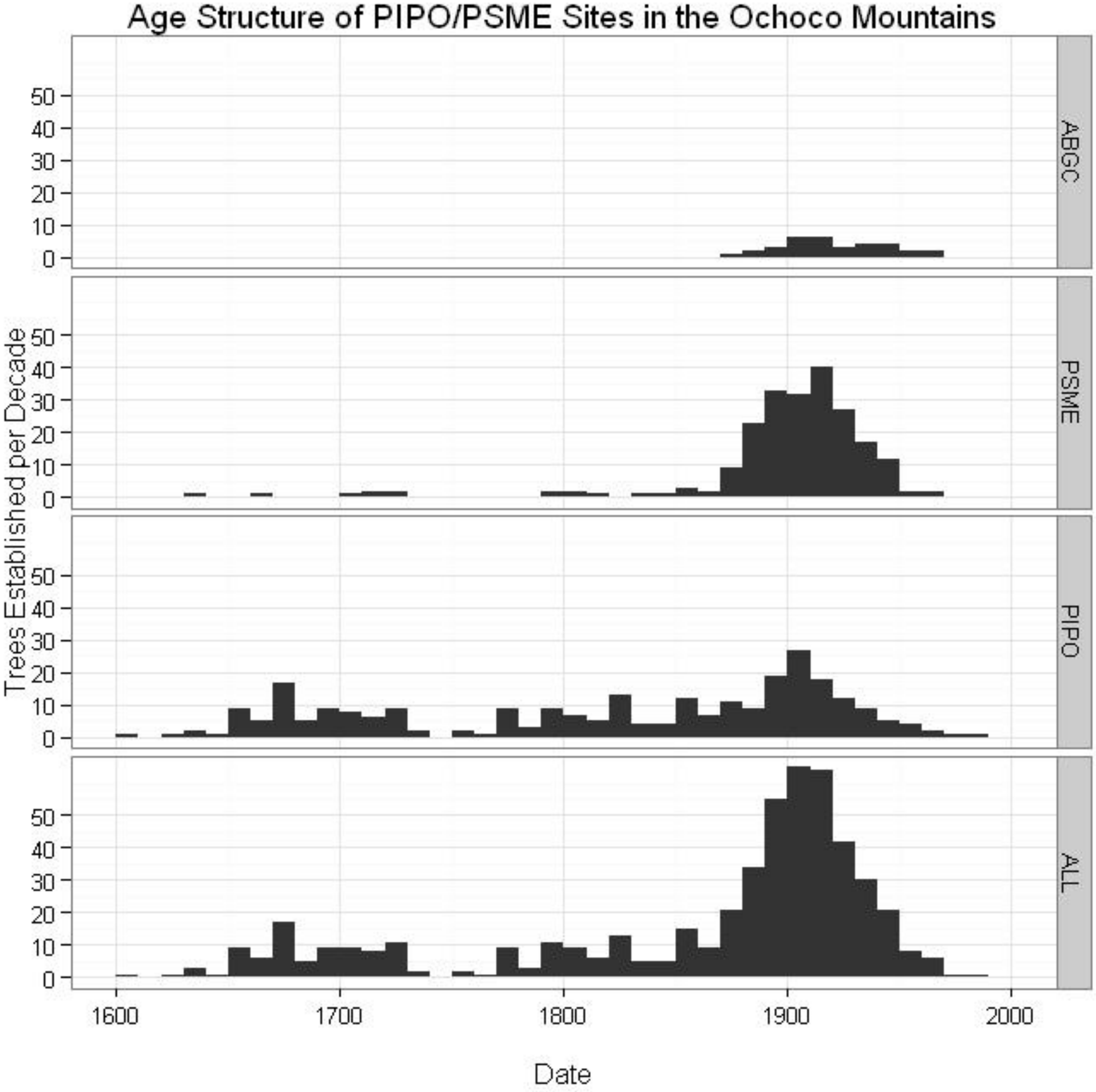

Figure 3.7: Age structure of PIPO/PSME sites in the Ochoco Mountains

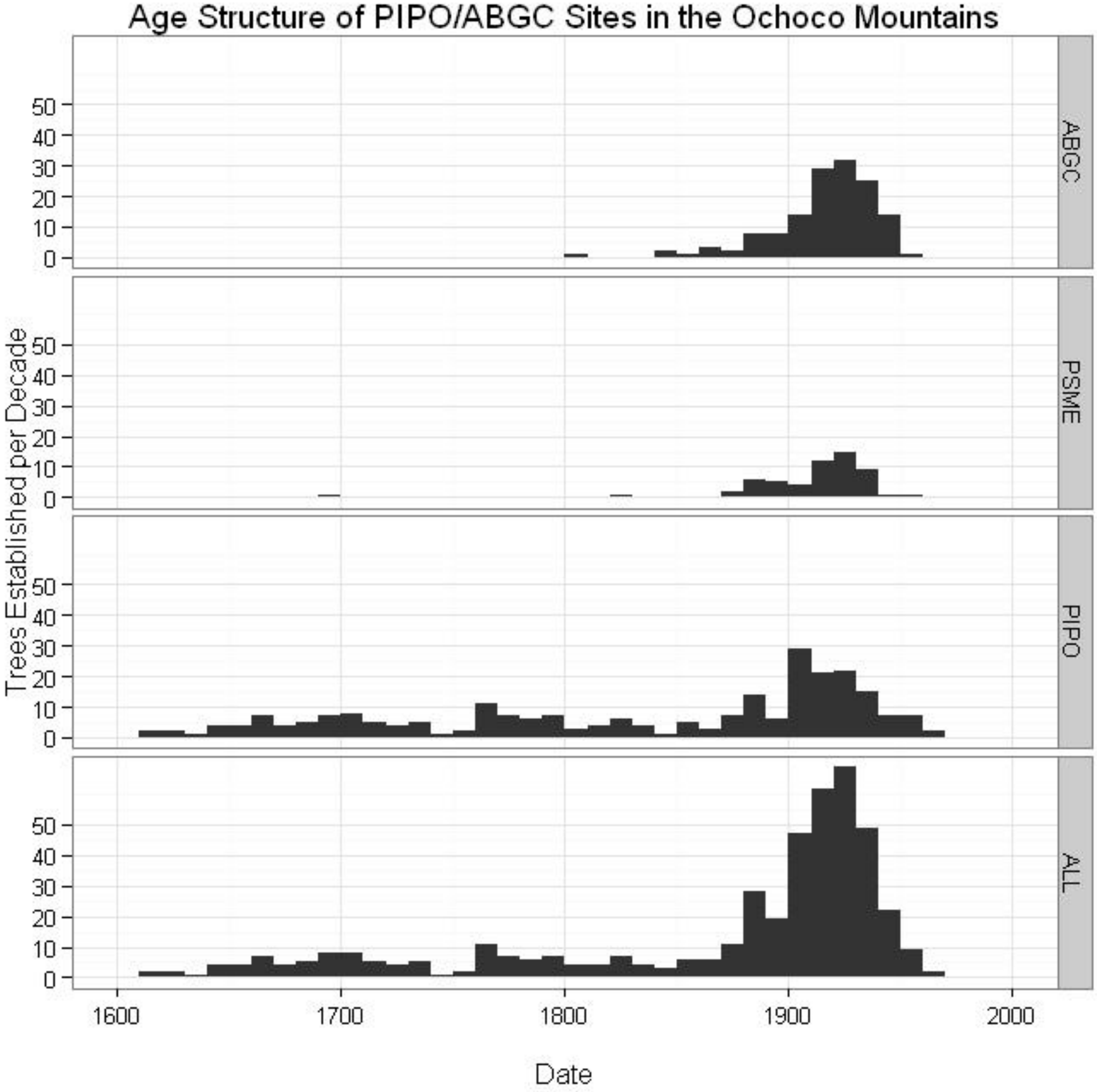

Figure 3.8: Age structure of PIPO/ABGC sites in the Ochoco Mountains

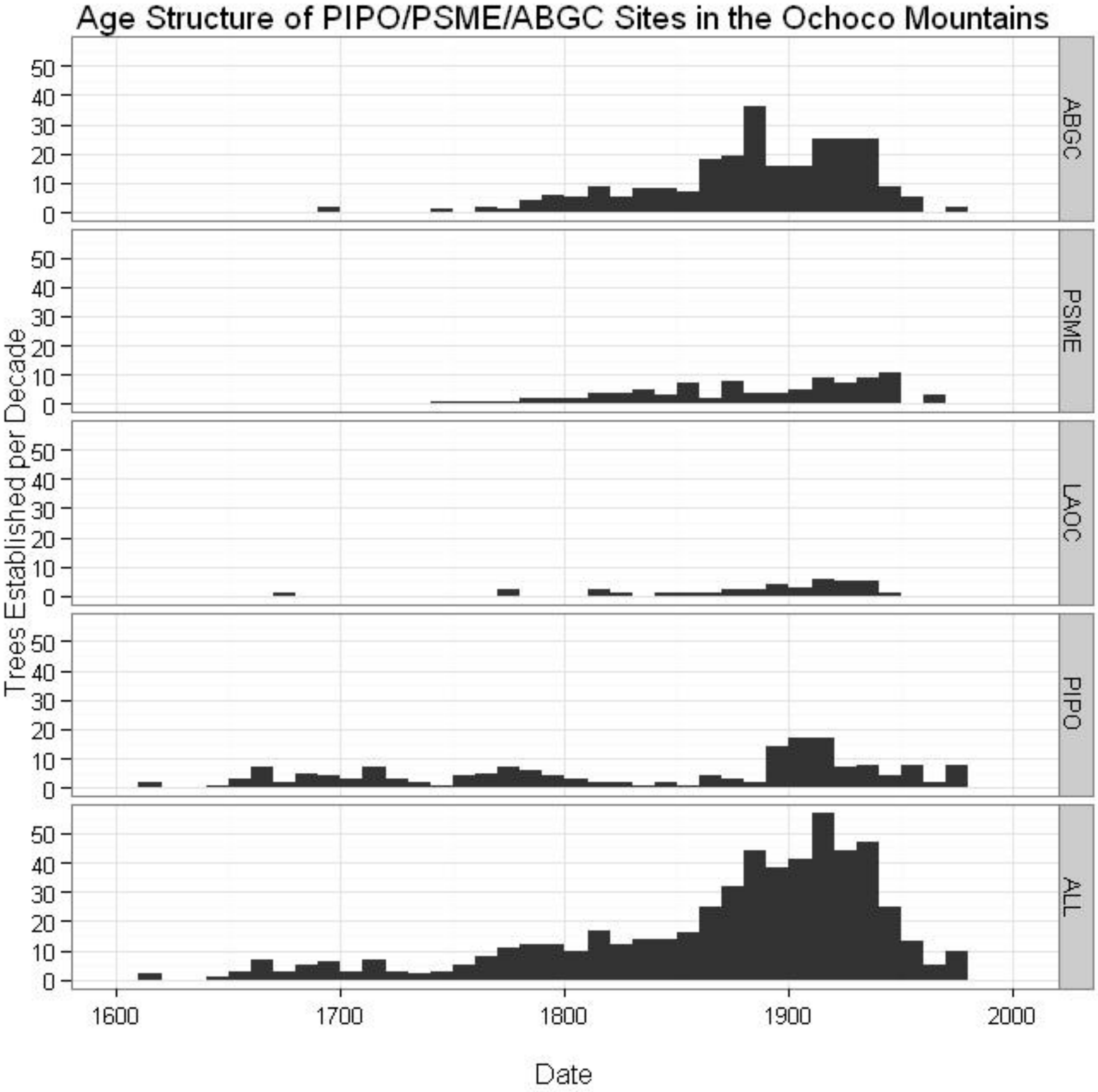

Figure 3.9: Age structure of PIPO/PSME/ABGC sites in the Ochoco Mountains

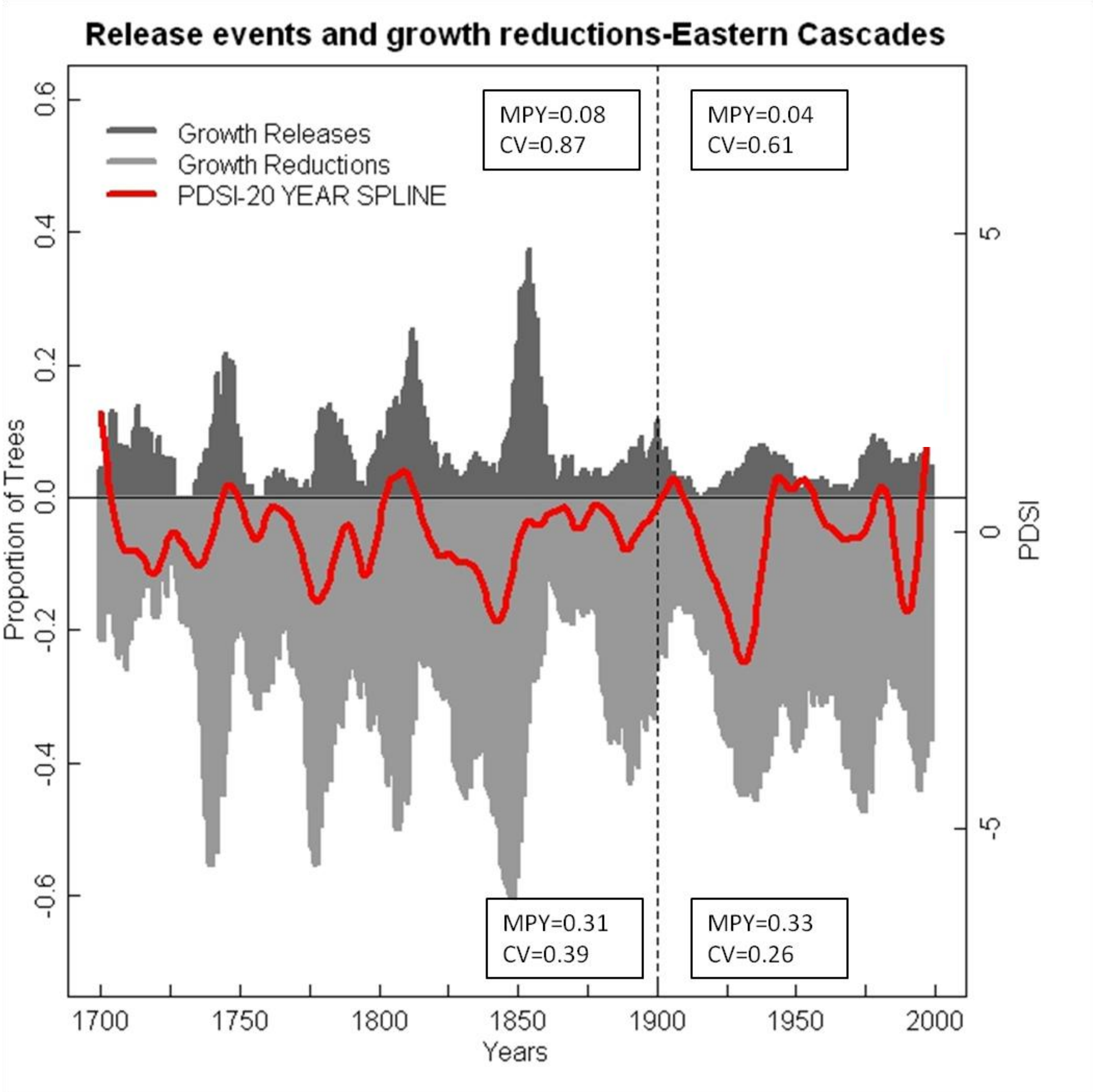

Figure 3.10: Pattern of suppression and release and relationship to PDSI in the Eastern Cascades. MPY is the mean proportion of trees exhibiting growth release or growth reduction in a year, and CV is the coefficient of variation of MPY.

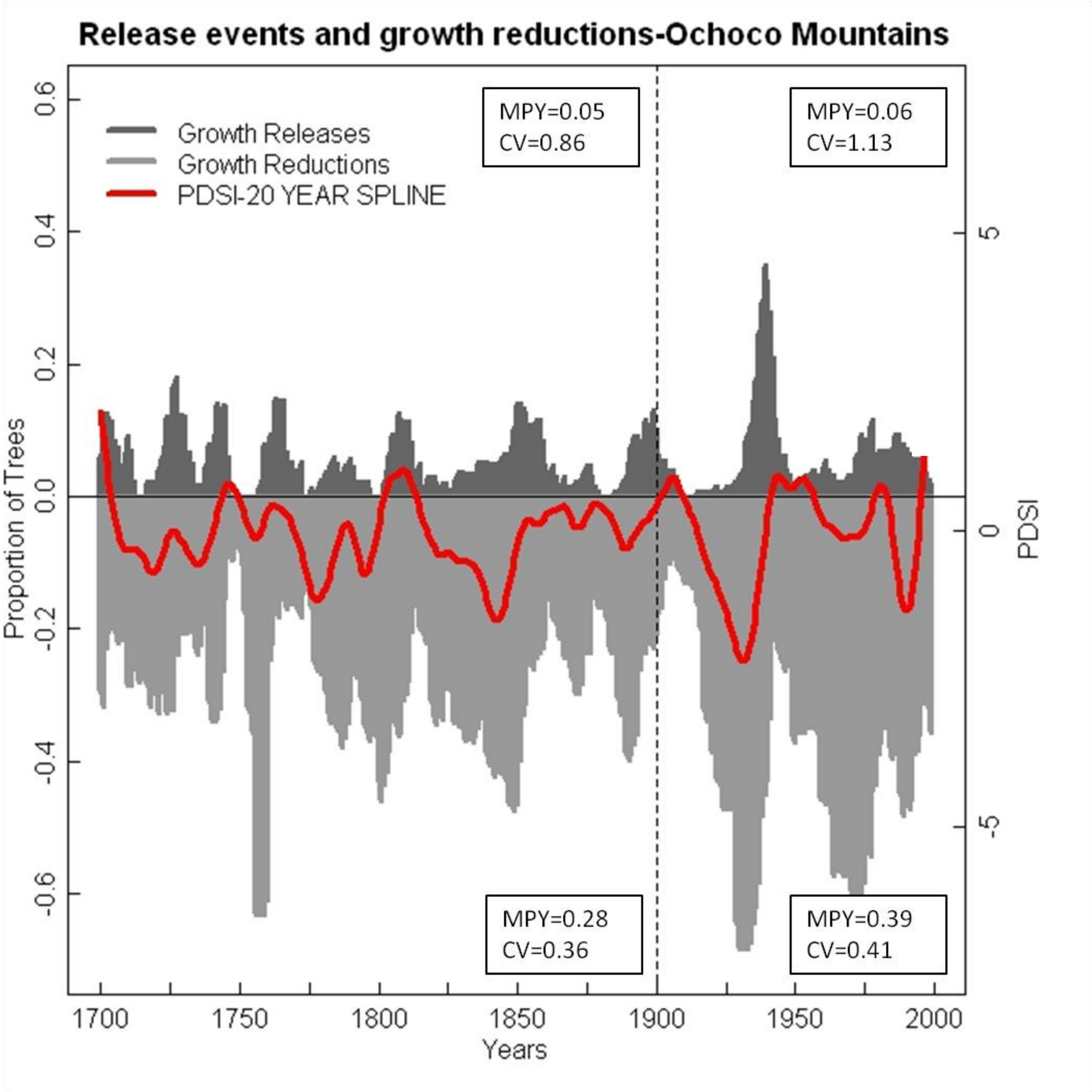

Figure 3.11: Pattern of suppression and release and relationship to PDSI in the Ochoco Mountains. MPY is the mean proportion of trees exhibiting growth release or growth reduction in a year, and CV is the coefficient of variation of MPY.

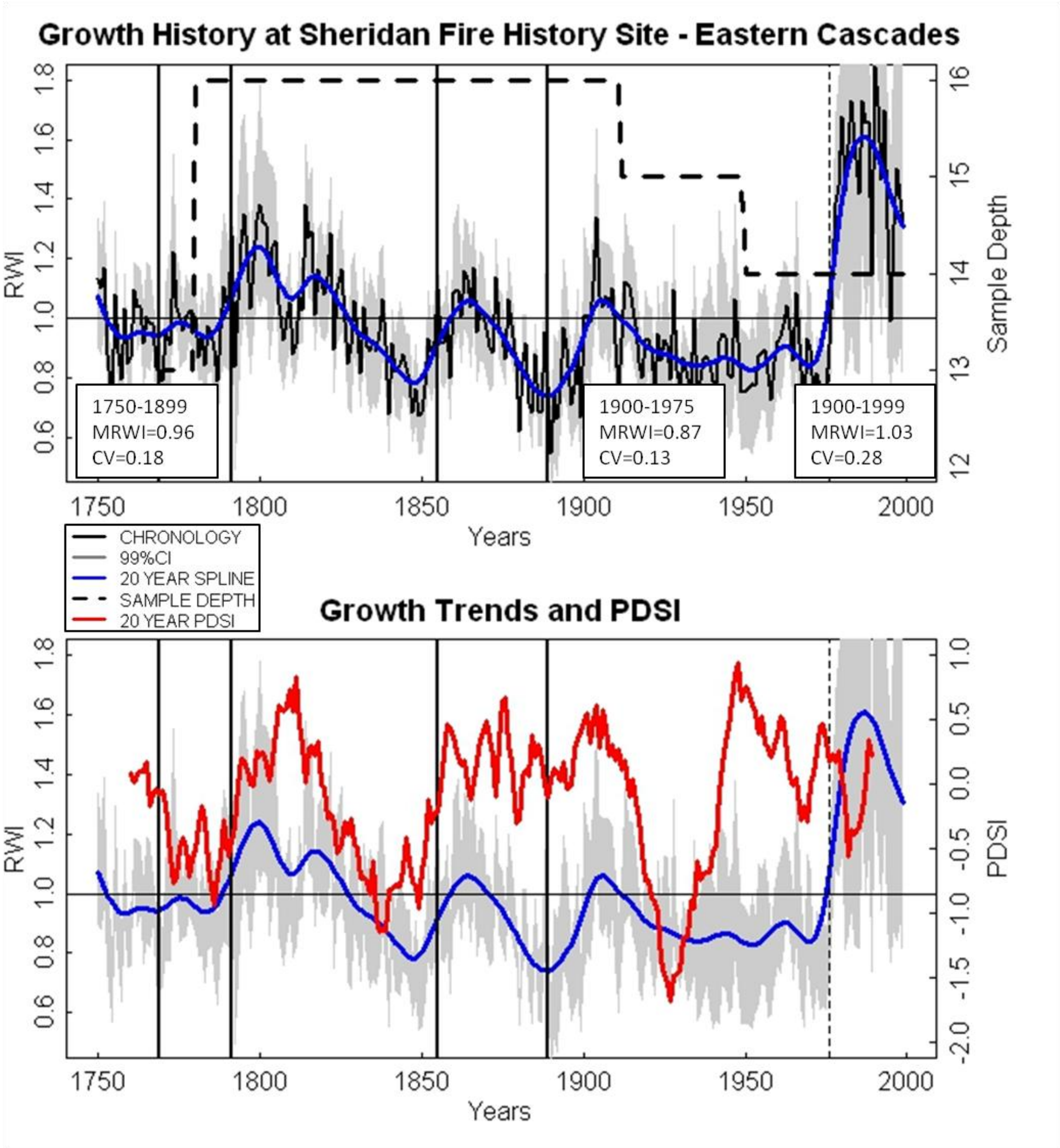

Figure 3.12: Growth history at Sheridan fire history site. The relationship between PDSI and RWI is indicated by a 20 year smoothing spline of RWI and 20 year moving average of PDSI. Solid vertical lines represent fire dates and the dashed vertical line represents a logging event. Mean ring width index (MWRI) and coefficient of variation (CV) are displayed for three analysis periods.

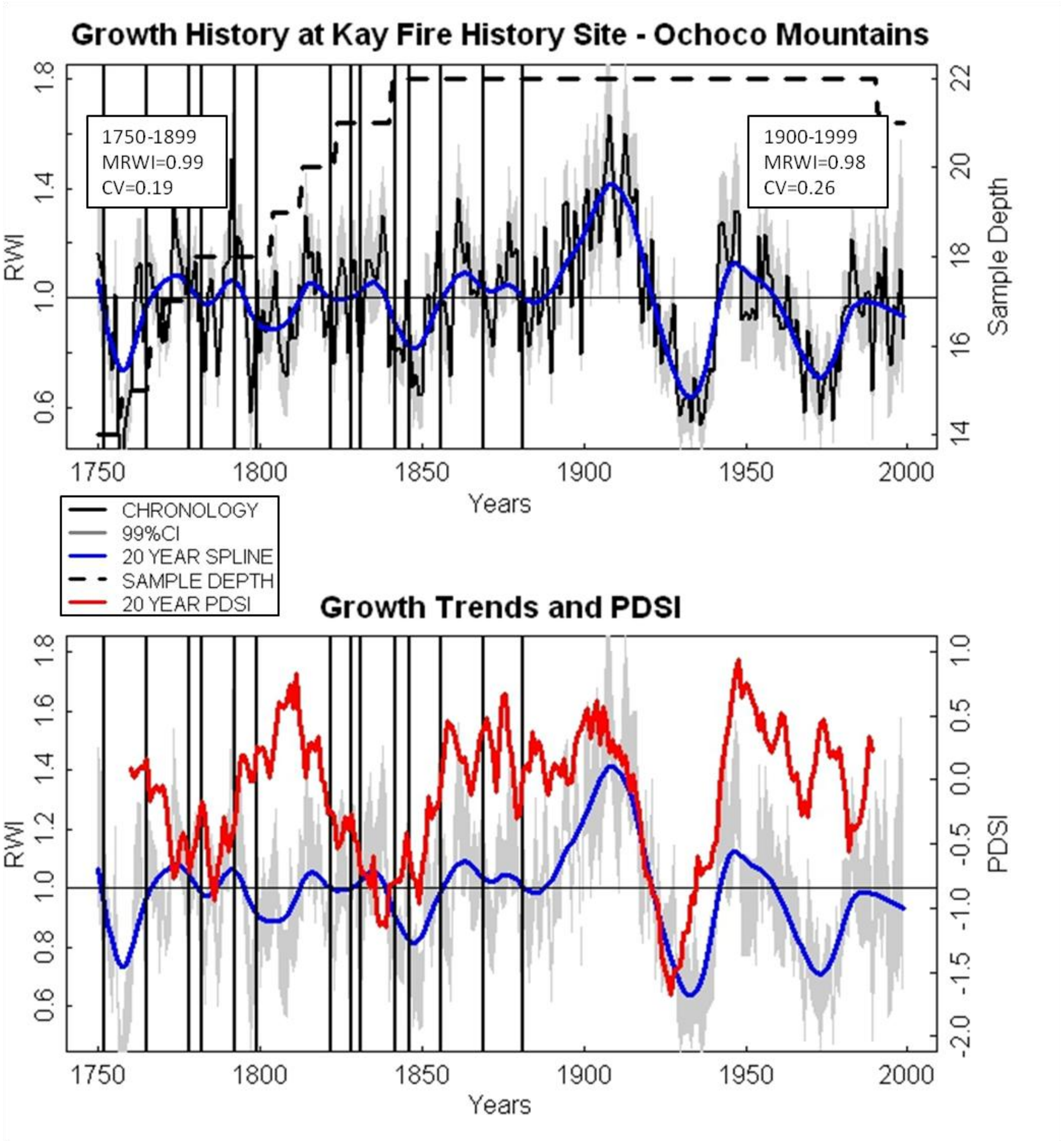

Figure 3.13: Growth history at the Kay fire history site. The relationship between PDSI and RWI is indicated by a 20 year smoothing spline of RWI and 20 year moving average of PDSI. Solid vertical lines represent fire dates. Mean ring width index (MWRI) and coefficient of variation (CV) are displayed for two analysis periods.

CHAPTER 4: CONCLUSION

This thesis describes the current structure and composition of MCF in the eastern Cascades and Ochoco Mountains and describes changes related to 20th century fire exclusion and logging. Chapter 2 demonstrates that variation in structure and composition is associated with environmental setting and that overall density in MCF has more than doubled in the 20th century in comparison to historical estimates. Additionally, density of large fire resistant ponderosa pine has been approximately halved throughout MCF. Recovery of this formerly pervasive component is likely limited by current density and shifts in composition. Understory ponderosa pine is scarce at PIPO/PSME, PIPO/ABGC, and PIPO/PSME/ABGC sites, and high density slows growth and therefore recruitment of large diameter ponderosa pine (Cochran and Barrett 1999 and Harrod et al. 1999). Stand types developed in Chapter 2 and analysis of age structure in Chapter 3 suggest that changes in composition have varied in different environmental settings. At dry PIPO sites shade tolerant trees are present but rare. In contrast, Douglas fir and grand fire are predominant in the understory at PIPO/PSME and PIPO/ABGC sites where there was minimal evidence of the establishment prior to fire exclusion.

In Chapter 2 MCF stand types were developed to illustrate the current state of MCF and relate structure and composition to environmental setting. Large diameter overstory ponderosa pine was historically common to all types, which were distinguished by the presence of Douglas-fir and grand fir in overstory and understory canopy layers. Transitions from dominance of ponderosa pine to Douglas-fir and finally grand between stand types were most strongly associated with increasing precipitation and decreasing temperature. However, PIPO/PSME stand types were found at the driest and hottest sites associated with northern latitudes in the eastern Cascades as well as at steeply sloped sites associated with low solar insolation in the Ochoco Mountains. Large overstory Douglas-fir and grand fir were rare at PIPO/PSME and PIPO/ABGC sites, but were common at PIPO/PSME/ABGC sites. Prior to 1900 under native fire regimes these sites would have been the primary location for habitat for late seral plant and animal species. I found little evidence of fire refugia in the eastern Cascades and Ochoco Mountains as late seral vegetation was strongly associated with high elevation and high precipitation, and not local topography. Current structure of MCF at the majority of PIPO, PIPO/PSME, and PIPO/ABGC sites visited is best described as dense and multilayered. Relatively open, old forest with single stratum maintained by low and mixed-severity fire was not found in my study although a low threshold of 20% was used to select sample sites.

In Chapter 3 I analyzed age structure to investigate changes in the number of trees established and composition of establishment in MCF stand types. Beginning in the early 20th century establishment of all species abruptly increased in all stand types except in the PIPO/PSME/ABGC type in the Ochoco Mountains. Shifts in composition were varied among stand types. Shade tolerant trees established at PIPO sites where there was no evidence of their establishment prior to 1900, but increases in total establishment were primarily due to increases in ponderosa pine establishment. At PIPO/PSME and PIPO/ABGC sites Douglas-fir and grand fir dominated establishment after 1900 although ponderosa pine previously dominated establishment at these sites. Analysis of age structure and current stand structure and composition of stand types indicates that current density and composition in MCF at PIPO, PIPO/PSME, and PIPO/ABGC sites lacks a temporal analog in the 18th and 19th centuries.

Conclusions from age structure analyses of live trees do not account for trees lost to mortality. Consequently, such analyses do not record stand density changes over time. To mitigate this limitation, I examined growth patterns of extant old-growth ponderosa pine, and used them as an indicator of competition effects and variation in stand density. In the eastern Cascades I found that the proportion of trees releasing after periods of growth reduction decreased in the 20th century. This suggests that fire exclusion and densification has increased competition in MCF of the eastern Cascades. This putative response to competition was not evident in the drier Ochoco Mountains. In that region the pattern of growth responses did not change after 1900 with the exception of the release following the extreme drought in the 1920s. My approach to validate changes in successional dynamics using growth of ponderosa pine requires further development, but it appears to hold promise.

Growth chronologies developed for the Sheridan and McKay fire history sites illustrated useful relationships between growth and climate and growth and competition. At the Sheridan site mean annual growth and variance in growth decreased in the 20th century and then rapidly increased following a logging event in 1975. This pattern suggests the relationship between climate and growth was modified by competition at the site because variability in growth increased with disturbance over the analysis period. The strong growth release following the logging event indicates that old-growth ponderosa pine can increase in vigor after thinning treatments. This suggests thinning and restoration treatments could be effective at increasing resilience of these trees to wildfire, insects, and drought.

At the McKay fire history site growth was relatively stable and does not show an obvious response to fire events or trends in climate prior to fire exclusion. Collectively this indicates that competition among trees was low. After fire exclusion growth patterns became more synchronized among trees and more closely followed long term trends in climate. This shift in growth patterns is potentially due to the interruption of the fire regime after 1900, but climate was also more variable after this time period. To improve the use of growth chronologies to detect changes in establishment and density in MCF, the relationship between growth and climate needs to be investigated across the broad range of environmental settings in which MCF is found. Patterns of growth reduction and growth chronologies at the Sheridan and McKay sites suggest that response to 20th century climate and altered disturbance regimes my manifest differently in different environments.

In this thesis I found that changes in density, composition, and growth during the 20th century varied with environment. Changes in MCF described here are based on sampled sites widely distributed across environmental gradients, and therefore represent broad scale patterns of change in MCF. Collectively, my studies indicate that efforts to restore the structure, composition, and dynamics of MCF should take into account environment at local and regional scales.

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