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Structural and Compositional Patterns in Forest Communities in the Intermountain West Across Multiple Scales

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STRUCTURAL AND COMPOSITIONAL PATTERNS IN FOREST COMMUNITIES IN THE INTERMOUNTAIN WEST ACROSS MULTIPLE SCALES

by

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ABSTRACT

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by

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Utah State University, 2015

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Across the Intermountain West, forest communities are being impacted by changing disturbance regimes, invasive species, and climate change. Tackling these complex issues will require researchers and managers to focus on building or maintaining resistance, resilience, and/or adaptation in forest systems. To explore how both basic and applied forest dynamics research can increase resistance and resilience, three studies were designed and implemented. The first study explored how different silvicultural treatments influenced metrics of resistance and resilience to the spruce beetle (*Dendroctonus rufipennis* (Kirby)) in spruce-fir forest. None of the applied treatments (single tree selection, group selection, or shelterwood with reserves) met all the desired objectives; managers will have to assess trade-offs between the traditional group selection treatment and a silvicultural alternative like shelterwood with reserves. The shelterwood with reserves with supplemental planting is recommended since it will result in short-term resistance and long-term resilience to the spruce beetle. The second study

explored patterns in forest structural attributes across the Intermountain West and developed a conceptual model for forest classification. By utilizing five structural attributes, forest communities were classified into three types: short single-layer forest, tall single-layer forest, and tall multi-layer forest. The classification system was independent of species and can facilitate the understanding of broad-scale forest dynamics. As individual species ranges shift with climate change, this model will offer managers a flexible tool as they focus on maintaining or building structural characteristics, which will increase resistance and resilience. The final study explored the basic forest dynamics of limber pine *(Pinus flexilis* James) across the Intermountain West. Limber pine is often described as a poor competitor and a specialist, dominant in harsh environmental conditions at both upper and lower elevations. However, across the Intermountain West, limber pine was a consistent component of forest communities and could be more accurately described as a generalist. As climate change continues to impact Western forests, a generalist like limber pine may be extremely important in maintaining resilient forest ecosystems. Climate change will impact how forests are managed now and in the future. These studies will assist managers and researchers in developing long-term forest management plans.

(147 pages)

PUBLIC ABSTRACT

Structural and Compositional Patterns in Forest Communities in the Intermountain West across Multiple Scales

Marcella A. Windmuller-Campione

The United States Department of Agriculture (USDA) strives to use science-based research to both protect and enhance the management of natural resources. From this overarching goal, the USDA has a specific objective to protect the health and sustainability of forest and rangeland ecosystems. Based on this specific objective, an Advisory Board of natural resource scientists within the Quinney College of Natural Resources (QCNR) was awarded a National Institute of Food and Agricultural (NIFA) grant to train two PhD and two MS students. Their research would focus on managing for resilient forest ecosystem in the Intermountain West.

With input from the advisory board and my PhD committee, my research focused on how to increase forest resilience at multiple scales. Locally, on the T.W. Daniel (TWD) Experimental Forest on the Logan Ranger District, three silvicultural trials were evaluated for resistance and resilience to the spruce beetle (partially funded by the TWD Forestry Fellowship). At the regional scale, a conceptual model was developed to classify forest communities based on structural features. The model was tested with data collected from 15 mountain ranges across the Intermountain West. Additionally, basic forest dynamics of limber pine (*Pinus flexilis* James.) were summarized across the Intermountain West. All three of these studies will aid in developing and implementing sound forest management practices to increase forest resilience.

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CHAPTER 1

INTRODUCTION

The concept of building resistance and resilience into forested systems has long been at the heart of sound forestry practices. Early European explorers and settlers in North America found a vast and what they thought was an endless supply of timber (William, 2005). This "endless" supply of timber helped to build and heat homes, created transportation networks, and was shipped back to Europe (MacCleery, 1992). As the population increased so did the demand for timber. Timber barrens exploited this "endless" supply of timber. Dr. Franklin B. Hough and others feared that these exploitive practices would exhaust forest resources (Williams, 2005). Dr. Hough became the first congressionally appointed forestry agent in 1876 and wrote many reports detailing the status of the Nation's Forests. In these reports, he called for sustainable forest management (Houghton, 1882). The practice of sustainable forest management continued to grow with the adoption of the Forest Reserve Act of 1891 and the establishment of the Forest Service in 1905. In 1918, Samuel Dana the Assistance Chief of Forest Investigation wrote a Bulletin to the United States Government calling for the implementation of sound silvicultural practices to reduce future devastation and restore productivity to already devastated areas (Dana, 1918). Almost 100 years later Dana's words would not be out of place when describing the current goals of the Forest Service; one of their main objectives is to ensure resistance, resilience, and adaptation in our forested systems. The threat is no longer the over exploitation of timber resources but how these timber and non-timber resources will be influenced by a range of environmental challenges.

Based on the differing management objectives, forests can be classified into one of three different forested systems: ‘production forests’, ‘preservation lands’, or ‘multiple benefit lands’ (Salwasser, 1990; Seymour and Hunter, 1992). Production forests and preservation lands can be thought of as the book ends when exploring the range of management. Production forests focus on the sustainable, consistent production of wood products (Salwasser, 1990; Seymour and Hunter, 1992). The overall objective on preservation lands is the maintenance of ecological function or historical conditions using active or passive management (Salwasser, 1990; Seymour and Hunter, 1992). Forests managed for multiple benefits span a large range of potential objectives but focus on the balance of both ecosystem system services and production (Salwasser, 1990; Seymour and Hunter, 1992). Many scientists (Beese et al., 2003; Franklin et al., 2002; Geldenhuys, 2010; Long, 2009; O’Hara and Ramage, 2013; Seymour et al., 2002; and citations within) have explored how management can emulate or incorporate natural disturbances and the subsequent influence these natural disturbances can have on both ecosystem services and productivity.

All three of the forest systems increase our understanding of how forests function. Future uncertainty due to climate change will influence overall forest management and the practice of these three different forest systems. Millar and colleagues (2007) developed a conceptual framework on how to build resistance, resilience, and adaptation into management strategies. For these management strategies to be successful, DeRose and Long (2014) suggest the use of measurable metrics of structure and composition which can be incorporated into silvicultural prescriptions.

Future management strategies will have to explicitly incorporate metrics of

resistance, resilience, and adaptation. In the Intermountain West, natural resource managers must consider many complex, often interacting issues. These issues include but are not limited to a growing population with broader values (Krannich et al., 2011), native and invasive insects, diseases, and plants (Bentz et al., 2010; Evangelistia et al., 2011; Funk et al., 2014; Régnière and Bentz, 2007), climate change (IPCC, 2013), and the legacy of past management decisions (e.g. fire policy (Marlon et al., 2012)). The geology, climate, and vast areas of public land make the Intermountain West a perfect area to explore these complex issues of resistance and resilience and how to actually incorporate them into effective forest management.

The Intermountain West roughly encompasses an eight state region which includes Montana, Idaho, Nevada, Utah, Wyoming, Colorado, New Mexico, and Arizona. This region is characterized by numerous mountain ranges, creating high mountain peaks but also many low intermountain basins (Long, 1995). These broad patterns of peaks and basins create steep environmental gradients which greatly influence the composition and structure of vegetative communities (Peet, 2000). These environmental gradients are consistent throughout the Intermountain West and have allowed scientists like Ramaley (1907), Daubenmire (1943), and Peet (2000) to describe vegetation zones. Daubenmire (1943) classified five vegetation zone based on the dominant overstory species: the oak-mountain mahogany zone, the juniper-pinyon zone, the ponderosa pine zone, the Douglas-fir zone, and the spruce-fir zone. These zones of vegetation generally can be observed from lower elevation (oak-mountain mahogany) to higher elevation (spruce-fir) in the above order.

Many of these forests types are experiencing novel interactions of both climate (e.g. IPCC, 2013) and disturbance dynamics (e.g. Bentz et al., 2010; Jenkins et al., 2014). Predicted changes in climate may shift the average range of individual species by 700 km north but decrease the average range by 12% (McKenney et al., 2008). There are also predictions about novel climate profiles; Rehfeldt (2006) predicts that by the end of the century, almost half of the current coniferous vegetation within Western U.S. will have a novel climate profile. The combination of climate change and species range shifts makes it imperative to understand current dynamics, functions, and processes of the forests of the Intermountain West.

My research in the Intermountain West focused on understanding how both local and regional species interactions influence forest resistance and resilience to future uncertainty. These studies spanned the range from basic to applied forest dynamics. At the local scale, a study using three silvilcultural treatments was implemented to quantify and test metrics of resistance and resilience in spruce-fir forests to the spruce beetle. Metrics of resistance and resilience were explicitly defined. At the regional scale, broad forest dynamics patterns were characterized. This characterization was done through the development of a conceptual model which classified forest communities based on structural attributes independent of the species composition. Many overstory trees within the Intermountain West have broad distributions. Limber pine (*Pinus flexilis* James), a five-needle white pine, has one of the broadest distributions in terms of both geography and elevation. However, very limited information is known about the ecology, forest dynamics, and eco-physiology of this species at the regional scale. The basic forest dynamics of limber pine were summarized and described across the Intermountain West.

By increasing our understanding of both basic and applied forest dynamics, managers within the Intermountain West will be better equipped to implement sound forest management practices which, aims to increase resistance and resilience to future climate uncertainty.

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CHAPTER 2[1]

IF LONG-TERM RESISTANCE TO A SPRUCE BEETLE EPIDEMIC IS FUTILE, CAN SILVICULTURAL TREATMENTS INCREASE RESILIENCE IN SPRUCE-FIR FORESTS IN THE CENTRALROCKY MOUNTAINS?

Abstract

Within the Central Rocky Mountains, spruce beetle populations have the potential to rapidly transition from endemic to epidemic levels in the spruce-fir (Engelmann spruce and subalpine fir) forest type. Conventional management has focused on creating resistance to spruce beetle outbreaks by manipulating the overstory density and composition. Three silvicultural treatments, single tree selection, group selection, and shelterwood with reserves, were established in a spruce-fir forest in northern Utah with the goals of increasing both resistance and resilience to outbreaks. Resistance and resilience metrics were explicitly defined. Pre-harvest and two post-harvest measurements were used to assess how the different silvicultural treatments influenced the metrics. The shelterwood with reserves was the only treatment to meet both the resistance and resilience criteria. This treatment, while not traditionally used, created a stand structure and composition that will be most resilient to climate induced increases in spruce beetle caused tree mortality. However, there will be a trade-off in composition and structure, especially Engelmann spruce, after a spruce beetle epidemic because the created structure is more uniform with fewer groups and gaps than commonly observed in spruce-fir forests. With changing climatic conditions, proactive forest management,

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such as the shelterwood with reserves in the spruce-fir forest type, is the best method for increasing short-term resistance and long-term resilience to spruce beetle outbreaks.

1. Introduction

Increasing global temperatures, expected changes in the hydrological system, increasing probability of extreme events, and changing land use patterns will influence the management of forest systems [1–4]. The genus *Picea* is an important component of managed forest systems and is widely distributed throughout the northern hemisphere [5]. Recent destructive insect outbreaks have occurred across Europe (spruce bark beetle (*Ips typographus*) in Norway spruce (*Picea abies* (L.) Karsten.) [6] and western North America (spruce beetle (*Dendroctonus rufipennis)* in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)) [7–9]. In western North America, the time for a spruce beetle to complete its life cycle is expected to decrease with warming temperatures, having potentially devastating effects on western spruce forests [10].

The spruce beetle is a native insect endemic to spruce forests across North America [7]. The spruce beetle can have a 1 to 3 year life cycle with adult spruce beetles boring into the main stem of the tree, feeding, and breeding in the live phloem; tree death occurs from girdling [11]. Under endemic population levels, spruce beetles live and breed in recently windthrown trees. Destructive storms can greatly increase the amount of recently windthrown trees. Alexander [12] recommended the removal of any large diameter Engelmann spruce trees that have fallen due to their increased susceptibility to a spruce beetle attack. Windthrow events in Europe also influence spruce bark beetle dynamics in Norway spruce forests [13]. Effective removal of down trees can lessen future beetle impacts in many different spruce forest types [12–14].

When population levels increase, spruce beetles will attack standing live trees, potentially transitioning to epidemic levels [7]. Historical spruce beetle epidemics have been reported throughout the Central Rocky Mountains including the White River Mountains in Colorado [15] and the Aquarius Plateau in Utah [16]. Within the last 20 years, epidemic spruce beetle populations have been extremely destructive across the Central Rocky Mountains [17] and outbreaks are expected to continue [18]. Of the 3.8 million hectares in Colorado, Utah, and Wyoming in the spruce and fir forest types, FIA (Forest Inventory and Analysis) data suggest nearly half of the area has experienced some level of mortality due to insects [19]. Recent spruce beetle epidemics have probably been driven by a combination of factors including susceptible stand structure and composition coupled with widespread drought [20]. Spruce beetles favor large diameter (>25 cm diameter at breast height (dbh)) Engelmann spruce for both protection and nutrition [21,22]. Recent dry conditions in high-density stands increase stresses on individual trees, decrease growth rates, and decrease defenses against the beetle, allowing spruce beetle populations to rapidly increase [8,18]. Changing climatic factors, especially increased summer temperatures are associated with an increased shift from semivoltine to univoltine life-cycles [10,23].

Management for the spruce beetle has focused on increasing resistance [24–26]. Resistance (risk *sensu* [27]), in this situation, is the decreased susceptibility to a spruce beetle outbreak through changes in structure and composition [2,28]. DeRose and Long [28] define this change in structure and composition at both the stand and the landscape level. A spruce beetle resistant stand has attributes, that decrease spruce beetle population growth and spruce beetle caused mortality within the stand. Landscape resistance is

defined as the overall spatial heterogeneity and structure, which decreases the likelihood of a spruce beetle epidemic [28]. When spruce beetles are at endemic levels, localized direct suppression techniques such as pheromone traps and trap trees can be used to reduce beetle populations [29,30]. Schmidt and Frye [25] developed a spruce beetle risk rating system that focuses on manipulating the stand structure and composition (*i.e.*, reduction of overstory density and the amount of large diameter spruce) to reduce the risk of spruce beetle outbreaks and increase resistance [25]. Manipulation of overstory structural characteristics has been shown to offer some short-term resistance to endemic spruce beetle populations [18,26,31]. However, once spruce beetle populations transition from endemic to epidemic levels, all mature spruce-fir stands, even ones managed for density reduction are not resistant. For example, on the Markagunt Plateau in southern Utah, spruce beetle populations transitioned from endemic to epidemic levels, killing over 90% of the Engelmann spruce trees greater than 5 cm in dbh over an area of at least 250 km^2 [18]. At the beginning of the epidemic, the spruce beetle attacked dense stands with large diameter Engelmann spruce [29], as predicted by the Schmid and Frye [25] risk rating system. Under this system, stands with low densities and small diameter spruce trees would be classified as potentially resistant; however, as the epidemic progressed the spruce beetle moved into these initially resistant stands [32]. As a result of this extensive epidemic, forest composition has shifted towards subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and aspen (*Populus tremuloides* Michx.) due to the limited number of mature live Engelmann spruce to serve as a seed source and the limited amount of spruce advance regeneration [18,32]. Realistically, modification of stand

composition and structure might only provide short-term resistance in the face of a spruce beetle epidemic [28,32].

Managing for resistance is only a part of a comprehensive spruce beetle strategy, which should also include a provision for increasing resilience. Resilience at the stand level is associated with desired (or at least acceptable) structure and composition after a spruce beetle epidemic. At the landscape level, resilience reflects desired levels of heterogeneity in composition, structure, and age diversity [28]. We define resilience at the stand level as the adequate stocking of Engelmann spruce in the regeneration layer post spruce beetle epidemic. Successful Engelmann spruce regeneration can be a rare event with good cone crops occurring every two to five years [12,33]. This sporadic cone production coupled with climatic variability creates long regeneration windows of 10 to 20 years [33,34]. Since Engelmann spruce regeneration is not guaranteed, it is the most limiting factor in ensuring a resilient forest with a future spruce component. By ensuring a minimum amount of Engelmann spruce regeneration, if and when a spruce beetle epidemic occurs, Engelmann spruce would not be lost from the stand. This would reduce the likelihood of the forest type shift that was observed in southern Utah [18,32]. Timely proactive forest management in spruce-fir stands can ensure a minimum level of stocking of Engelmann spruce, creating spruce beetle resilient stands.

In the Central Rocky Mountains, spruce beetle populations appear to be increasingly likely to transition from endemic to epidemic levels, and in some locations this has already occurred (e.g., southern Utah, [32]). In northern Utah, an experimental silvicultural trial was established to compare three silvicultural treatments: single tree selection, group selection, and shelterwood with reserves. In this paper, we present results

showing the short-term effect of these treatments on metrics of stand level resistance and resilience.

2. Methods

2.1. Study Species

Across the Central Rocky Mountains, the subalpine forest zone (2400–3200 m above sea level (asl)) is often typified by Engelmann spruce and subalpine fir coexisting in late successional communities [12]. This broad forest type can occur as low 1830 meters and as high as 3650 meters in elevation [35]. The FIA database from 2003 to 2012, estimates 3.8 million hectares of forested land in the fir and spruce forest types in Colorado, Wyoming, and Utah [19].

Engelmann spruce and subalpine fir have complementary life history strategies which allow for coexistence ([12,33,35–40], and references therein). Across the Rocky Mountains, the individual life histories of spruce and fir influence the stand structure. Engelmann spruce can be long-lived, (300+ years) but has inconsistent regeneration. Subalpine fir has more consistent and prolific regeneration but a shorter lifespan, e.g., 150 years [41]. Engelmann spruce is commonly dominant in number and basal area of large diameter trees with subalpine fir dominating in number and basal area of the small diameter trees and regenerating individuals [35,42].

The structure and composition of spruce-fir forests are influenced by disturbance history. Stand replacing disturbances are infrequent (+300 years) and typically reset succession with early dominance by lodgepole pine (*Pinus contorta* Dougl.) and/or aspen and the eventual succession to Engelmann spruce and subalpine fir [43]. In northern Utah, fires in spruce-fir forests increased in frequency during the Settlement Period

(1856–1909) due to increased human activity but then sharply decreased after 1910 due to fire suppression [44]. Intermediate disturbances, creating small or medium sized gaps, are common and create the characteristic variable structure and composition in spruce-fir forests of this region [45]. A number of interacting disturbance agents influences the creation of these small and medium gaps: windthrow, bark beetles, and root rot [45]. These disturbances collectively create both stand and landscape heterogeneity.

Spruce-fir forests in the Central Rocky Mountains have been managed using a variety of silvicultural systems [12,33,46]. A common management objective is to maintain stand heterogeneity and vertical structure by utilizing uneven-aged silvicultural methods [9,12,35,45,47]. Much of the focus is on the successful regeneration of Engelmann spruce [45–47]. Group selection historically has been the most commonly used treatment since windthrow, endemic spruce beetles, and root rot create stands dominated by groups and openings [45,46]. Group openings are generally less than twice the height of mature trees, resulting in favorable microsites for Engelmann spruce regeneration [45]. Single tree selection is generally not used in this forest type because openings are presumed to be too small for successful spruce regeneration [45].

2.2. Site Description

Utah State University's T.W. Daniel Experimental Forest (TWDEF) (41.86° N, 111.50°W) is located in the Bear River Range of northeastern Utah at an elevation of 2600 m (Figure 2.1). The TWDEF contains approximately 405 hectares in the spruce-fir type with an additional 6880 hectares in the surrounding Logan Ranger District of the Uinta-Wasatch-Cache National Forest. The TWDEF experiences a semi-arid climate, characteristic of the Intermountain West with 1044 mm of precipitation [48]. On average

80% of the precipitation falls as snow, melting between mid-May and mid-June. There is a pronounced summer drought with warm temperatures; highest average monthly temperatures occur in July (14.5 °C) [49]. Winter months are cold with January having the lowest average monthly temperature (–10 °C) [49]. Winter storms with high wind speeds occur frequently on the TWDEF. Due to these storms and extensive areas of root rot, there is the potential for high rates of windthrow especially adjacent to gaps. The soils on the TWDEF are generally classified within two soil orders, Mollisols or Alfisols [50,51]. These soils are considered to be carbonate-free and well drained with the majority of soil organic carbon observed in the O horizon [50]. Spodosols rarely occur on the TWDEF due to limited soil moisture [50]. Additional information on climatic variables, past, and current research can be found at the T.W. Daniel Experimental Forest website (http://danielforest.usu.edu/).

2.3. Silvicultural Treatments

In 1996, increasing spruce beetle populations were observed on the TWDEF, ands successful suppression efforts were initiated at that time [29]. A timeline of specific events is presented in Table 2.1.

In collaboration with the Logan Ranger District in 1999, three silvicultural treatments were established with the goals of increasing resistance and resilience to spruce beetle population outbreaks. The three treatments were single tree selection, group selection, and shelterwood with reserves. An uncut control was established to explore future spruce beetle spread; those data are not presented here. Individual harvest units are about 8 hectares; silvicultural treatments were assigned randomly to the harvest units and replicated twice.

Stand density index (SDI; ([52–54]) was used to determine the residual density for each treatment. SDI was calculated based on the trees per hectare and the quadratic mean diameter (QMD) [54]. The maximum SDI will vary by individual species but at 35% of maximum SDI, trees will fully occupy the stand [55]. As SDI increases, competition can increase individual tree stress and limit growth. The maximum SDI for Engelmann spruce is 1500 [56]. The maximum SDI for Engelmann spruce was used since all treatments favored the removal of subalpine fir. The single tree selection treatment left a residual SDI of 520 (37% of maximum SDI) favoring the removal of subalpine fir and the retention of aspen. Within the group selection treatment, 0.1 hectare patches were created, collectively treating 1/6th of the harvest units; the forest matrix was thinned to a residual SDI of 520 (37% of the maximum SDI) favoring the removal of subalpine fir and the retention of aspen. The uniform shelterwood with reserves treatment involved thinning from below to a residual SDI of 415 (28% of the maximum SDI), favoring the retention of Engelmann spruce.

In 1999, using a stratified random design, six variable radius plots with a basal area factor of 4.6 $m^2 \cdot ha^{-1}$ were placed within each of the treatments for a total of 18 plots across the 50 ha study area. On each plot, species, diameter at breast height (cm) (1.37 m), total height, and height to the base of the live crown were measured for each tree. In 2008, using a stratified random design, eight permanent plots were established within each treatment for a total of 24 plots across the study area (Figure 2.2). The radius of the nested subplots increased in size from the center point: (A) 0.01 hectare plot measuring trees between 4.1 and 10 cm dbh; (B) 0.05 hectare plot measuring trees between 10.1 and 25 cm dbh; (C) 0.10 hectare plot measuring trees greater than 25 cm dbh [57]. All

standing trees within the designated size class were tagged. Species, diameter at breast height, and total height were measured for all live and dead trees; height to live crown was recorded for live trees. Four permanent subplots were established in the cardinal directions to measure tree regeneration. All regenerating trees with heights greater than 20 cm and diameters less than 4 cm dbh within the 0.001 hectare subplots were tallied. Plots were remeasured following the same methods during the fall of 2013; ingrowth was tagged and measured.

Prior to harvesting, Engelmann spruce seeds were collected from the site. Subsequently, one-year-old seedlings were grown at the USDA Forest Service Lucky Peak Nursery in Idaho. In 2008, Engelmann spruce seedlings were planted at an effective density of 60 trees per hectare in the openings of the group selection and throughout the shelterwood with reserves units.

2.4. Defining Resistance and Resilience Metrics

2.4.1. Resistance

Resistance was defined as a function of overstory density, composition, and site index [25]. The Schmid and Frye [25] spruce beetle risk rating uses four different metrics: physiographic location, QMD of spruce tree greater than 25.4 cm in dbh, stand basal area ($m^2 \cdot ha^{-1}$), and proportion of the stand basal area ($m^2 \cdot ha^{-1}$) that is spruce [40] (Table 2.2). Values for each metric are rated as high (3), medium (2), or low (1) and the sum of the values is the stand risk rating. A stand risk overall score of 11–12 is defined as high, 10 as medium/high, 7–9 as medium, 6 as medium/low, and 4–5 as low (Table 2.2). Each metric was calculated by year and by treatment to assess overall risk to a spruce beetle outbreak.

2.4.2. Resilience

Resilience was defined at the stand level as being the minimum amount of Engelmann spruce regeneration necessary to maintain a spruce component post spruce beetle epidemic. Regenerating Engelmann spruce was defined as trees less than 4 cm in dbh but greater than 20 cm in height because the spruce beetle generally attacks trees greater than 5 cm in dbh [18]. If the primary management objective is spruce timber production, Alexander and Edminster [58] recommend approximately 1975 trees per hectare when using natural regeneration. However, their suggestion "is more than required for adequate stocking, but necessary to achieve uniform spacing, allow for possible future mortality, and provide options in selecting crop trees in subsequent thinnings" [59]. Since our primary goal is not spruce timber production and artificial regeneration was used to supplement natural regeneration, we used a minimum of 245 trees per hectare of regenerating Engelmann spruce.

2.5. Analysis

Stand data for 1999, 2008, and 2013 were expanded to trees per hectare, basal area per hectare, and SDI using the summation method [52,53]. Welch's one sided *t*-tests were used to compare differences between pre- and post-treatment total trees per hectare and total basal area per hectare. A *t*-test was performed on the pre-treatment data *versus* each of the post treatments (pre *vs.* single tree selection, pre *vs.* group selection, pre *vs.* shelterwood). Since sampling techniques varied from pre-harvest (variable radius) and post-harvest (fixed area), all trees less than 4 cm in dbh were excluded from this analysis, since trees less than 4 cm in dbh in 2008 and 2013 were classified as regeneration. Ducey [60] and Curtis [61] detail how inconsistent truncation can influence SDI. Repeated

measures ANOVA was used to test differences between years and treatments for density measures in the overstory. To assess resistance, the pre-harvest stand and the structures following the three treatments were rated using the spruce beetle risk rating system [25]. To assess resilience, one-way ANOVA was used to test differences between densities of total and Engelmann spruce regeneration in 2013.

3. Results

3.1. Overstory Composition, Structure, and Density

The three silvicultural treatments influenced the stand structure and composition on the TWDEF although in different ways. The pre-treatment diameter distribution was characteristic of spruce-fir forests with large diameter live Engelmann spruce and smaller diameter subalpine fir (Figure 2.3A). Dead Engelmann spruce and subalpine fir occurred across the range of diameter classes. All treatments shifted the diameter distributions to being more left skewed and decreased the amount of basal area in small diameter subalpine fir (Figure 2.3B–D). The shelterwood with reserves was thinned from below leaving primarily large diameter Engelmann spruce (Figure 2.3B). However, there was a wider range of diameters of Engelmann spruce among the single tree selection and the group selection (Figure 2.3C,D). The single tree selection had the highest residual basal area across all the size classes, including the smallest size class (4–9.9 cm). These small diameter trees do not greatly influence the overall basal area per hectare but do greatly influence the number of trees per hectare.

Prior to harvest, total overstory basal area and live basal area was 36.3 $m^2 \cdot ha^{-1}$ and 33.0 $m^2 \cdot ha^{-1}$, respectively. Total trees per hectare (tph) and live trees per hectare were 264 and 232, respectively. There was a significant decrease in total basal area per hectare and

trees per hectare in the shelterwood with reserves ($p = 0.002$; $p = 0.01$) by 2008. The group selection treatment also had a significant decrease in basal area per hectare ($p = 0.01$) but not in trees per hectare by 2008. There was little change in the basal area between pre- and post-treatment in the single tree selection units. However, there was an increase in the number of trees per hectare pre- and post-treatment, which was probably due to the large number of small diameter subalpine fir trees (Figure 2.3).

Live SDI and live basal area did significantly differ between treatments but not years (Figure 2.4). The single tree selection treatment had significantly greater live basal area per hectare and live SDI than either the shelterwood with reserves or the group selection treatments (Figure 2.4). Prior to harvest, the stand had an SDI of 516 or 34% of the maximum. By 2013, the group selection and the shelterwood with reserves both had SDIs of approximately 20% of the maximum. Single tree selection had a SDI of 34% of the maximum SDI in 2013.

3.2. Spruce Beetle Risk Rating System

The scores of the different treatments using the spruce beetle risk rating system [25] showed little change after they were implemented on the TWDEF (Table 2.3). The pre-harvest stand was rated as having a medium risk, with a total score of 8. This rating was due to the large diameter spruce, high stand basal area, and the high proportion of spruce. The shelterwood with reserves did lower the risk slightly to a 7.

Exploring how the individual components influenced the overall risk rating, the site index (base age 50 years) for Engelmann spruce was rated as a low risk for all years since it is slightly less than 24.4 m [61]. The QMD of Engelmann spruce greater than 25.4 cm in diameter metric was rated as high across all years and all treatments (Table 2.3). The

stand basal area metric was rated as having a medium risk to the spruce beetle pre-harvest. Post-harvest, by 2008 there were significant decreases in the basal area in the group selection and shelterwood with reserves, but there were only modest changes in the risk rating (Table 2.3). Small amounts of mortality between 2008 and 2013 caused a further small decrease in basal area (<3.0 $m^2 \cdot ha^{-1}$) which resulted in a lowered risk rating for the stand basal area metric for the group selection and the shelterwood with reserves treatments (Table 2.3). There were no significant decreases in density in the single tree selection or changes in the risk rating. The proportion of the stand that is spruce did not change between the pre-treatment and the shelterwood with reserves treatment. However, both the group selection and the single tree selection increased spruce composition to over 80% of the basal area in 2013, giving this metric a high risk.

3.3. Regeneration

Total regeneration was greater than 1500 tph for all treatments in 2013 (Table 2.4 and Figure 2.5). There was no significant difference between treatments for total regeneration in 2013. However, there was significantly more Engelmann spruce regeneration in the shelterwood with reserves compared to the single tree selection treatment by 2013 (Figure 2.5). The group selection was not significantly different from the other two treatments. The shelterwood with reserves and the group selection received supplemental planting of Engelmann spruce seedlings in 2008. This planting design created high variability in stocking within the group selection. The shelterwood with reserves was the only treatment that met the minimum stocking requirement of at least 245 tph of well distributed Engelmann spruce (Figure 2.5).

4. Discussion

This study was initiated in 1998 to explore silvicultural treatments that could increase short-term resistance and long-term resilience to spruce beetle caused mortality at the stand level. Since the development of this study, there has been increased research, mostly retrospectively, on spruce beetle dynamics [18,31, 32,40,63]. However, our study is unique for two reasons: (1) it tests a pro-active management strategy and (2) utilizes explicitly defined metrics of resistance and resilience to spruce beetle outbreaks. Management focused on stand density reduction techniques intended to create "resistant" (*sensu* [25]) stands is likely to be unsuccessful [26].

On the TWDEF, there was little change between the pre-treatment risk rating and any of the post-treatment risk ratings. The prescriptions for the three treatments favored the retention of Engelmann spruce. Furthermore, across, all three treatments, the majority of Engelmann spruce basal area was in trees greater than 25 cm dbh which is characteristic of spruce-fir forests of the Central Rocky Mountains [35]. Increasing resistance would require drastic changes in the structure and composition of these forests. Large diameter Engelmann spruce would need to be removed in order to decrease the QMD and proportion of live spruce [36]. It is important to note, however, that during an epidemic, even in low risk stands, Engelmann spruce greater than 4 cm in dbh can be attacked by spruce beetles [18,20]. Once at epidemic levels, it is no longer just the high-risk stands that are impacted but the entire landscape.

The shelterwood with reserves and group selection treatments implemented at the TWDEF resulted in substantial decreases in overstory basal area by 2008 from pre-harvest conditions. However, even with these significant decreases in basal area there

were only modest changes in the risk rating. Between 2008 and 2013, there was a slight decrease in basal area due to mortality and this small decrease changed that specific metric from a two to a one. Within the spruce beetle risk rating system, small changes can influence the risk rating. While, the spruce beetle risk rating system can be sensitive to small changes, it does give managers a starting point when implementing forest management practices. Our study is one of the first to demonstrate that these three different silvicultural treatments resulted in relatively similar spruce beetle risk ratings. However, these results are in line with retrospective studies that found limited "resistance" of stands treated for density reduction [26].

We propose that management of spruce-fir forests in the Central Rocky Mountains should focus on creating short-term resistance and long-term resilience. Short-term resistance is crucial to allow for the establishment of Engelmann spruce regeneration and is key to maintaining long-term resilience. Our study was conducted at the stand level, and we explicitly characterized a resilient stand as one with a minimum of 245 tph of Engelmann spruce regeneration. This metric was chosen because it will likely produce characteristic spruce-fir stand composition. As these trees mature and reach a QMD of 25 cm, the SDI of just Engelmann spruce will be 245 or approximately 16% of the maximum SDI. If we assume a stand basal area of 20 $m^2 \cdot ha^{-1}$ which is slightly lower than the stand basal area measurements for the group selection and shelterwood with reserves in 2013, Engelmann spruce basal area will be 12 $m^2 \cdot ha^{-1}$ or represent 60% of the total stand basal area. This stand composition would also produce a low (5) overall spruce beetle risk rating. The group selection had the second highest amount of Engelmann spruce regeneration with an average of 125 tph in 2013. Without any

subsequent regeneration, Engelmann spruce would only compose about 30% of the basal area and 8% of the maximum SDI. As the study continues to be monitored in the future, this metric can be adjusted based on future recruitment and mortality of the regenerating Engelmann spruce. This is one of the first studies to put a lower limit on Engelmann spruce regeneration when timber management is not the primary goal.

The long regeneration windows of Engelmann spruce are a major barrier in building resilient spruce-fir forests in the Central Rocky Mountains [12,64]. Resilience pre-harvest was very low due to the limited natural regeneration of Engelmann spruce. Natural regeneration of Engelmann spruce can be limited by irregular cone production, drought and extreme high and low temperatures, as well as, unfavorable microsite conditions [39,64]. Planting of Engelmann spruce is the only way to ensure adequate stocking in the short-term. Because seeds in our study were collected from numerous overstory spruces at the TWDEF, these seedlings are presumed to be locally adapted and to represent a range of genetic variability. An additional benefit of supplemental planting of Engelmann spruce is that these small diameter trees (<4 cm dbh) are generally not attacked by spruce beetles, decreasing the likelihood of a potential vegetation shift to aspen and/or subalpine fir. The lack of resistance and the resulting vegetation shift to aspen and subalpine fir on the Markagunt Plateau highlights how important resilience (adequate Engelmann spruce regeneration) is in maintaining the composition of spruce-fir forests in the Central Rocky Mountains. Resilience on the Markagunt Plateau will be low in the future due to the elimination of mature Engelmann spruce and limited spruce advanced regeneration [18,28]. Proactive density reduction methods that increase short-term resistance coupled with supplemental spruce planting to increase long-term

resilience can reduce the likelihood of a complete vegetation type shift after a spruce beetle epidemic.

Management for spruce beetle outbreaks currently and in the future at both the stand and landscape levels will need to be assessed in light of trade-offs between traditional management by group selection and silvicultural alternatives such as shelterwood with reserves (Table 2.5). This study was conducted at the stand level. At the TWDEF, the shelterwood with reserves coupled with supplemental planting met many of the objectives. However, by thinning from below, the structure shifted from a wide diameter distribution, containing small to large diameter trees in various gaps and densities, to more uniformly spaced large diameter spruce trees. Although, these large diameter spruces are attractive to the spruce beetle [18,40] they will produce large amounts of seeds and potentially supplement planted seedlings [28].

Forest management activities in the Central Rocky Mountains can be delayed by appeals and ligation (5 years for our study). This potential delay must be taken into consideration when planning forest management activities. The shelterwood with reserves, once implemented could be used to treat the entire stand, potentially influencing landscape level resistance and resilience. By contrast, the small area treated at each entry is a limitation of the group selection. A larger group opening could be used but is not recommended due to limitation in natural regeneration and increased mortality due to extreme temperatures and sunscald [12]. An additional issue with the group selection is time. Even with supplemental planting, the group selection treatment did not meet the minimum metric of resilience. In the absence of a spruce beetle epidemic, in future harvests, overstory density will be reduced and planting of Engelmann spruce will

continue; entries every 20 years will create age class and structural diversity, characteristic of spruce-fir stands [12]. Under this treatment, it will take another two cutting cycles to treat just half the stand. The cutting cycle could be reduced but due to the low productivity of the site would not be recommended because a 20-year cutting cycle is likely a minimum to ensure an economically viable harvest.

The traditional structure of spruce-fir forests would be retained in the group selection treatment. However, composition may shift with a spruce beetle outbreak because resilience (*i.e.*, adequate regeneration) would be limited in the short term. Given the increasing likelihood of stressed spruce trees due to increasing summer drought, the group selection method would not treat a large enough area of the stand quickly enough to provide adequate short-term resistance and long-term resilience at either the stand or landscape scale [20,30,65].

An additional concern, in any treatment, but especially the shelterwood with reserves and the group selection is the potential for windthrow [66]. Between 2008 and 2013, there were only minor differences in live basal area measurements and no discernible differences in incidence of windthrow between treatments (data not shown). While catastrophic windthrow did not happen in any of the silvicultural treatments on the TWDEF, any reduction in density has the potential for significant windthrow [12,66]. Collection of pre-harvest data, including crown ratio, may aid in selecting and removing less vigorous trees which may be more vulnerable to windthrow.

5. Conclusions

Forest managers across the world are confronted with uncertainty about how changing climatic conditions and subsequent interactions with disturbances will influence

forest composition and structure [67,68]. Changing conditions in spruce-fir forests throughout the Rocky Mountains and the boreal forest are greatly influencing disturbance regimes [69,70]. Managers will have to weigh trade-offs between traditional and novel management approaches [71]. Long-term studies on experimental forests allow researchers and scientists to explore how different management approaches can influence both short and long-term forest dynamics.

Future climate change is expected to greatly influence spruce beetle dynamics across western North America and changing disturbance dynamics will greatly influence how spruce-fir forests are managed [13,65,68,72,73]. Our study on the TWDEF is one of the first studies to test how different silvicultural treatments influence explicitly defined and quantified metrics of resistance and resilience to the spruce beetle. By using a long-term study design with permanent plots, both short (results presented here) and long-term forest dynamics can be explored. Additionally, when spruce beetle activity increases again on the TWDEF, our study will provide insight into potential differences in how spruce beetle populations build and spread in each of the different treatments. By using this long-term study design, these metrics of resistance and resilience can be tested and potentially adapted.

Managers will have to make difficult decisions as they plan for spruce beetle outbreaks. Traditional group selection harvests will maintain openings and groups, but potentially result in a loss of Engelmann spruce. Alternatively, the shelterwood with reserves will maintain a spruce component but with a novel structure. The shelterwood with reserves with supplemental planting was the only treatment to meet the resilience criteria on the TWDEF. If desired, increased structural variability could be built into this

treatment by varying the type of reserve trees in the shelterwood (*i.e.*, strip, uniform or clumped). To increase size diversity and decrease overall average diameter of Engelmann spruce, stands could be thinned from below to remove smaller diameter subalpine fir and thinned from above to remove some of the larger Engelmann spruce. However, as the planted Engelmann spruce mature, they will become susceptible to the spruce beetle with any of the treatments. The shelterwood with reserves and supplemental planting allows for the retention of Engelmann spruce in the future forest and time to plan future management activities which may include group selection. Our results suggest that in spruce-fir stands in northern Utah, shelterwood with reserves best meets the goals of short-term resistance and long-term resilience to the spruce beetle.

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Table 2.1. T.W. Daniel Experimental Forest in northern Utah spruce beetle management timeline. Additional information on suppression efforts and results can be found in [29].

T.W. Daniel Experimental Forest Spruce Beetle Management Timeline	
Year	Event
1996	- Increasing populations of spruce beetle - Survey to identify infested host trees - Removal of infested trees, trap trees established, and brush pile burning
1997	- Ground Surveys - Additional trap trees and pheromone baited traps
1998	- Ground Surveys - Additional trap trees and pheromone baited traps
1999	- Establishment of the current study to explore resistance and resilience to the spruce beetle - 18 variable radius plots were sampled to collect pre-treatment stand conditions
2000–2005	- Litigation - Collection of Engelmann spruce seeds
2006	- Harvesting of the single tree selection, group selection, and shelterwood with reserves - Seedlings grown in USDA Forest Service Lucky Peak Nursery
2008	- Planting of Engelmann spruce seedlings in the openings of the group selection and throughout the shelterwood with reserves - Establishment of 8 permanent plots per treatment
2013	- Remeasurement of permanent plots

Table 2.2. Risk rating system developed by Schmid and Frye [25].

	Physiographic Location/ Site Index	**QMD of Spruce >25.4 cm dbh**	**Stand Basal Area ($m^2 \cdot ha^{-1}$)**	**Proportion of Stand That Is Spruce (%)**
High (3)	Spruce on well-drained sites in creek bottoms	>40.6 cm	>34. 44	>65
Medium (2)	Spruce on sites with site index of 24.4 to 36.6 m	30.5–40.6 cm	22.96–34.44	50–65
Low (1)	Spruce on sites with site index of 12.2 to 24.4 m	<30.5 cm	<22.96	<50

Proportion of spruce in a stand was defined as the percent of basal area in spruce *versus* total overstory basal area.

Table 2.3. T.W. Daniel Experimental Forest Spruce Beetle Risk Rating by treatment adapted from Schmidt and Frye [25]—see Table 2.2. Numbers in parenthesis represent the rating from the spruce beetle risk rating system. The risk rating ranges between 1 and 3 with the lowest total score possible of 4 and highest total score possible of 12. Site index equations were from Clendenen [62]. Stand basal area is live standing trees greater than 4 cm in diameter. The proportion of stand that is spruce was calculated based on the proportion of live Engelmann spruce to total live basal area [40].

	Physiographic Location/ Site Index		**QMD of Spruce > 25.4 cm DBH**		**Stand Basal Area ($m^2 \cdot ha^{-1}$)**		**Proportion of Stand That is Spruce (%)**		**Total Risk Rating**
Pre	<24.4 m	(1)	55.1	(3)	33.0	(2)	65	(2)	8
2008									
Shelterwood with reserves	<24.4 m	(1)	67.0	(3)	23.2	(2)	64	(2)	8
Group selection	<24.4 m	(1)	64.4	(3)	24.1	(2)	76	(3)	9
Single tree selection	<24.4 m	(1)	62.1	(3)	33.8	(2)	84	(3)	9
2013									
Shelterwood with reserves	<24.4 m	(1)	69.6	(3)	21.7	(1)	65	(2)	7
Group selection	<24.4 m	(1)	66.3	(3)	21.1	(1)	81	(3)	8
Single tree selection	<24.4 m	(1)	62.9	(3)	33.8	(2)	84	(3)	9

Table 2.4. Regeneration density (trees per hectare) by treatment for 2008 and 2013 for the T.W. Daniel Experimental Forest. The associated standard errors are in parenthesis.

Treatment	Subalpine Fir		Lodgepole Pine		Engelmann Spruce		Aspen		Grand Total	
2008										
Shelterwood with reserves	812.5	(187.5)	0.0	(0)	0.0	(0)	750.0	(566.9)	1562.5	(640.4)
Group selection	437.5	(147.5)	0.0	(0)	0.0	(0)	250.0	(182.9)	687.5	(181.5)
Single tree selection	812.5	(244.4)	0.0	(0)	125.0	(47.5)	281.3	(185.6)	1218.8	(264.9)
2013										
Shelterwood with reserves	812.5	(220.3)	218.8	(218.8)	406.3	(124.4)	750.0	(592.0)	2187.5	(711.4)
Group selection	1031.3	(524.9)	0.0	(0)	125.0	(66.8)	937.5	(633.4)	2093.8	(710.2)
Single tree selection	781.3	(269.1)	0.0	(0)	62.5	(62.5)	750.0	(491.0)	1593.8	(528.1)

Table 2.5. Trade-offs between the different treatments assessed at the stand and landscape level.

	Shelterwood with Reserves	**Group Selection**	**Single Tree Selection**
Stand Level			
Reduced Basal Area	X	X	
Retention of Groups & Gaps		X	X
Diversity of Overstory Species	X	X	
Minimum Levels of Spruce Regeneration	X		
Landscape Level			
Ability to Treat Large Areas	X		

An X represents a treatment meeting the desired objective.

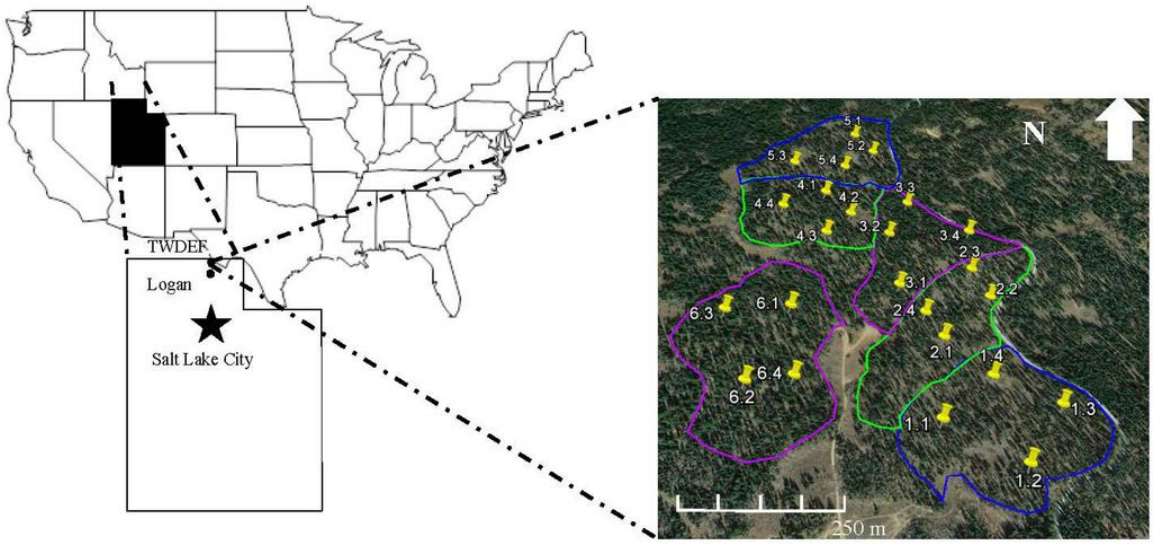

Figure 2.1. Location and study design layout for the spruce-fir silvicultural treatments at the Utah State University's T.W. Daniel Experimental Forest (TWDEF). Each treatment is outlined in a different color: shelterwood with reserves (blue); group selection (green); single tree selection (purple). Plot locations are highlighted in yellow. A stratified random sampling design was used within each treatment. Additional information on data collected at each sampling point can be found in following paragraphs and Figure 2.2. The map with the plot locations was made in Google Earth.

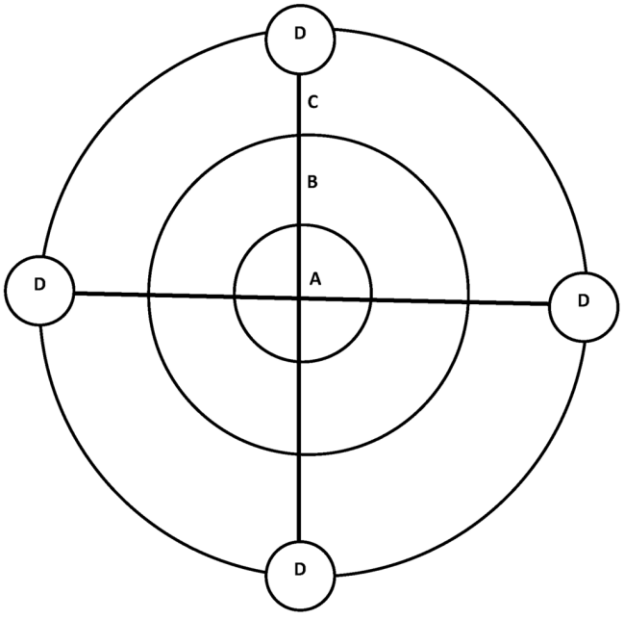

Figure 2.2. Permanent plot design established in 2008 and remeasured in 2013. The radius of the nested subplots increased in size from the center point; (A) 0.01 hectare plot measuring trees between 4.1 and 10 cm dbh; (B) 0.05 hectare plot measuring trees between 10.1 and 25 cm dbh; (C) 0.10 hectare plot measuring trees greater than 25 cm dbh. Regeneration plots were established at the four cardinal directions; (D) 0.001 hectare measuring tree regeneration with heights greater than 20 cm and diameters less than 4 cm dbh.

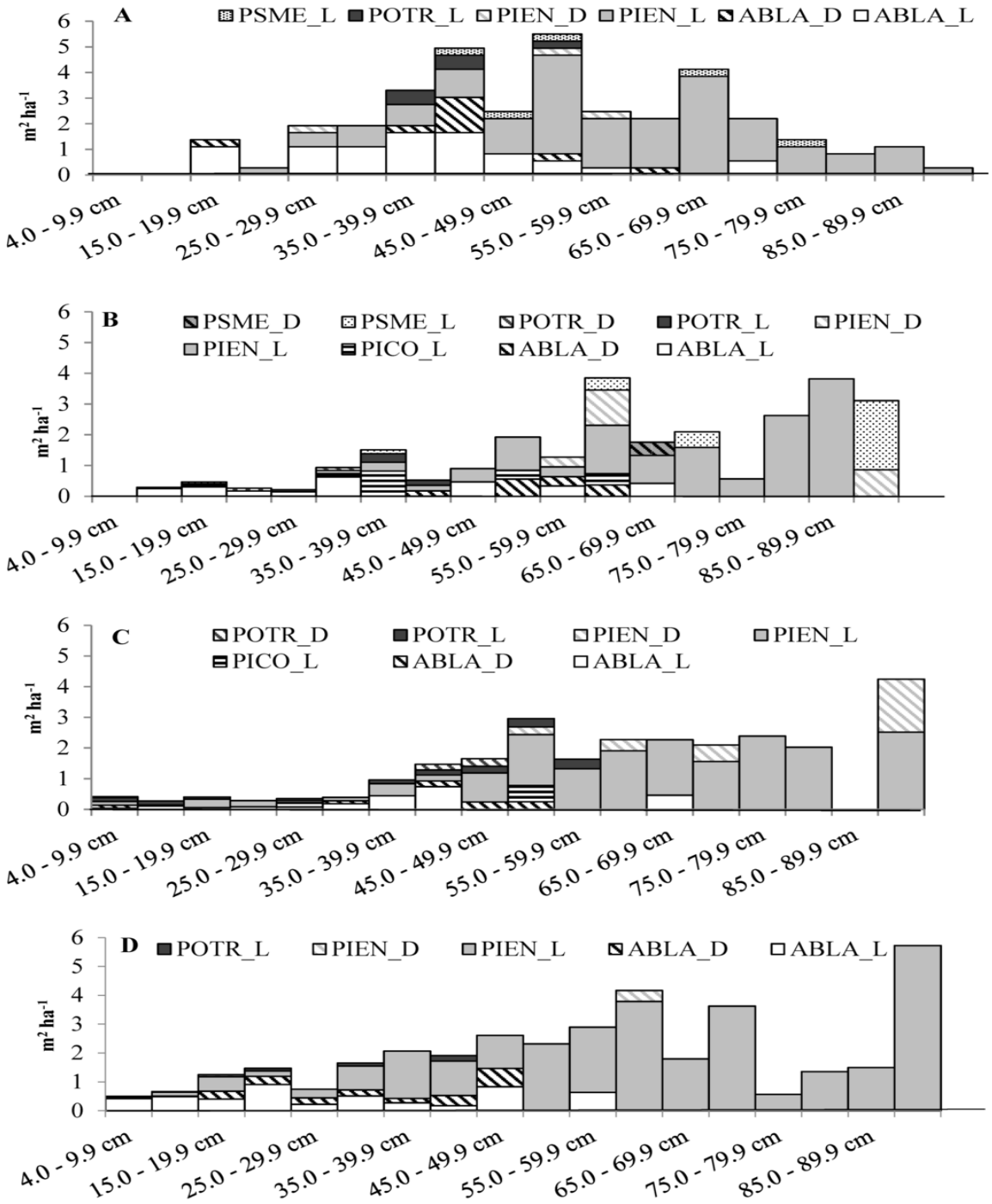

Figure 2.3. Diameter distribution (**A**) pre-treatment; (**B**) shelterwood with reserves 2013; (**C**) group selection 2013; (**D**) single tree selection 2013. Species codes are: PSME = *Pseudotsuga menziesii*; POTR = *Populus tremuloides*; PIEN = *Picea engelmannii*; PICO = *Pinus contorta*; ABLA = *Abies lasiocarpa*. The suffix L represents 'live' trees, while D is for "dead" trees.

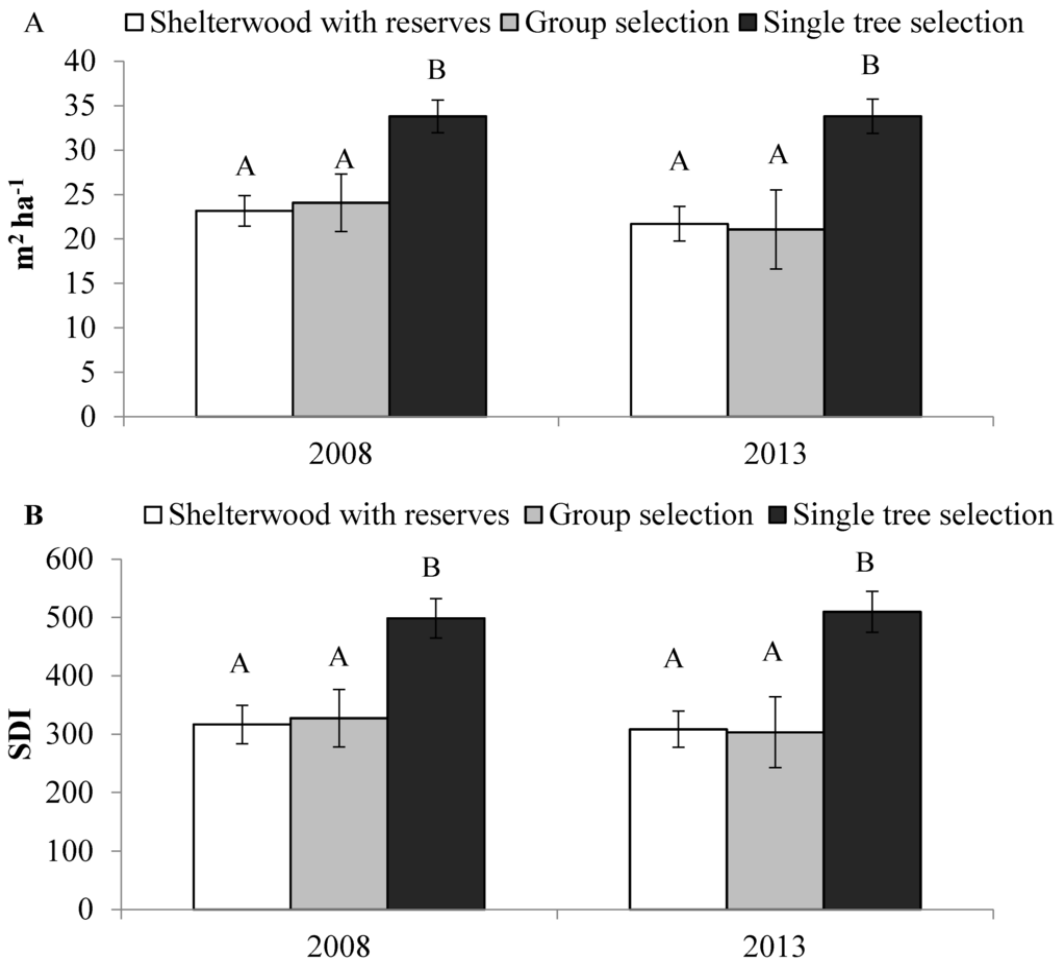

Figure 2.4. Repeated measures ANOVA for (**A**) live basal area per hectare and (**B**) live stand density index (SDI). The error bars represent the standard errors. Letters represent significant differences between treatments. No significant differences were observed between years.

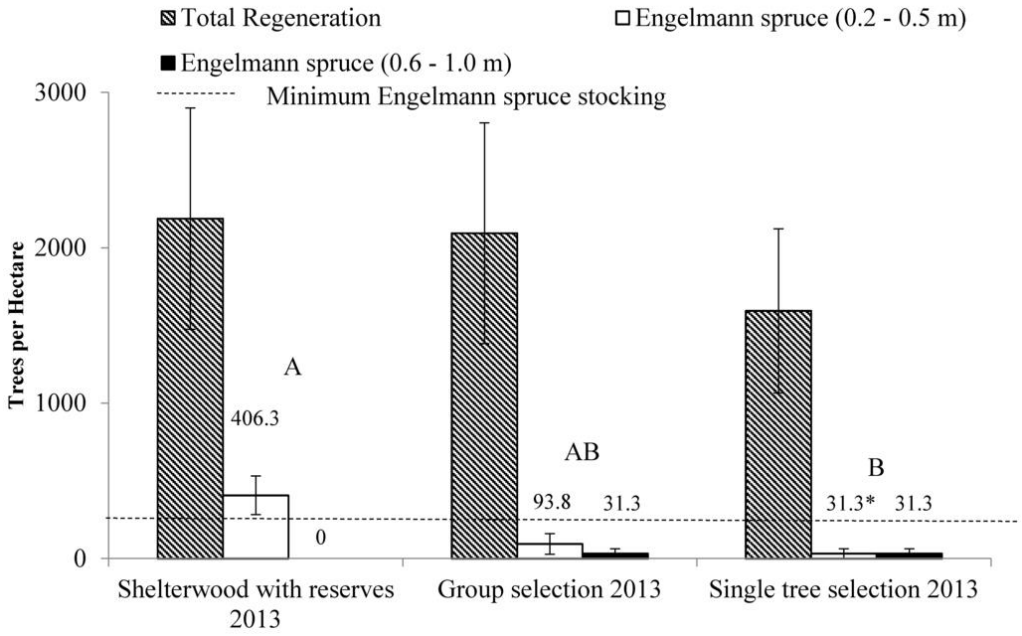

Figure 2.5. One-factor ANOVA for total tree regeneration and Engelmann spruce regeneration. The bars represent the standard errors. There were no significant differences between treatments for total density. Letters represent significant differences between treatments for total density of all size classes of Engelmann spruce trees per hectare (see Table 2.4 for total). * Engelmann spruce height was not recorded in 2013. Prior height measurement in 2008 was less than 0.5 m.

CHAPTER 3

A CONCEPTUAL MODEL FOR FOREST CLASSIFCATION BASED ON STRUCTURAL ATTRIBUTES IN THE INTERMOUNTAIN WEST, USA.

Abstract

Abiotic, biotic, and stochastic variables influence species distributions, resulting in the assembly of communities. Forest communities can be classified based on numerous metrics; one of the most common metrics is species composition. Broad classifications like "pinyon-juniper woodland" explicitly characterize the species composition; however, implicit to this classification is structure (e.g. short stature, low density, widely spaced). Building on the relationship between structure and environmental gradients, we developed a conceptual model which classifies forest communities based on five structural attributes: tree top height, tree diversity, space/relative density, and size diversity. Three structural types were described in the model: short single-layer forest, tall single-layer forest, and tall multi-layer forest. The model was tested with data collected from elevation gradients across the Intermountain West. Strong differences were observed between the three structural types and variables of top height, basal area, stand density index, and the diversity of size classes. There were also strong relationships between the structural types and stand age, canopy cover, and elevation. By utilizing structural attributes, this model may facilitate understanding of broad scale forest dynamics and potential management alternatives. This model also offer managers a versatile tool as they focus on building resistance, resilience or adaptation.

Introduction

Increasingly managers are developing silvicultural prescriptions which focus on maintaining or developing structural complexity (O'Hara 2014 and citations within). The structural development of a forest stand has been described through multiple conceptual models (Long and Smith 1984; Oliver and Larson 1996; O'Hara et al. 1996). These models capture how changes in structure influence important components of forest dynamics such as growth-growing space dynamics, site occupancy, and competition. Similarly, management tools, like density management diagrams (DMDs) have been developed to explore how management, or the lack of management, can influence future stand structure and potential disturbance agents like bark beetles (Anhold et al. 1996). Additionally, certain structural attributes have been found to be associated with quality wildlife habitat. For example, Northern Goshawk (*Accipiter gentilis*), a US Forest Service sensitive species in Regions 2-4, prefers hunting in moderately dense, mature forests even when prey abundance is higher under other forest conditions (Beier and Drennan 1997). Structure along with composition are key elements in determining stand resistance and resilience to a variety of disturbances (DeRose and Long 2014). Management which focuses on key structural attributes can increase wildlife habitat, improve forest health, improve financial returns, and increase resistance and resilience to disturbance (O'Hara 2014).

Forest structure and composition are expected to shift due to changing interactions between climate and disturbance agents, potentially creating novel ecosystems (Williams and Jackson 2007). By the end of this century, Rehfeldt and colleagues (2006) predict that almost half of the current coniferous vegetation within the

Western U.S. will have novel climate profiles. While, these predictions and the models on which the predictions are based, can and do aid in management decisions, they are often criticized since many only use biotic tolerances (reviewed by Guisan and Thuiller 2005). Newer models like the Forest Service Climate Change Tree Atlas are incorporating important abiotic variables like dispersal limitations in forecasts of future forest communities (Prasad et al. 2013).

While, structure and composition are both expected to change in the future, research has primarily focused on species distributions. The interactions among abiotic, biotic, and stochastic variables influence both the presence and the absence of species, resulting in the assembly of communities (Tokeshi 1999). These recognized plant communities have allowed the development of forest classification systems (Dufrêne and Legendre 1997) which range from simple to complex. The majority of these systems have a similar basis, classification of forest communities based on composition (actual, potential natural, climax, etc.). At the broadest scale, forests communities are classified by the dominant overstory vegetation (e.g. subalpine forest, pinyon-juniper woodland, subalpine white pine forest). Explicit to this classification is the species composition. For example, pinyon-juniper woodlands cover 40 million hectares of moisture-limited ecosystems across Western North American (Romme et al. 2009). Species composition will vary based on the distribution of individual pinyon and juniper species but implicit in this classification is that even as composition varies structural attributes will be similar.

Similar structural redundancies are observed when absences occur in the distribution of individual tree species. These absences often cannot easily be explained by environmental conditions or biotic interactions. For example, in the Intermountain

West ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm) is observed from northern Montana to southern Arizona and New Mexico. However, it is noticeably absent from a large region in the Intermountain West which includes northern Utah, western Wyoming, southern Idaho, and eastern Nevada; this absence has been referred to as the "donut hole" (Oliver and Ryker 1990). There are several hypothesizes on why this species may not be present in this area including past hydrological features such as Lake Bonneville (Thompson et al. 1993), limited summer moisture for seedling establishment (Steele et al. 1981; Anderson 1989), and the impact of glacial refugia on migration (Johansen and Latta 2003). Ponderosa pine trees have been successfully introduced and are regenerating in old USDA Forest Service planting locations within the "donut hole" (personal observation).

Not all absences occur across a wide regional scale, some absences occur at the local scale. For example, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) has an extremely broad distribution across much of the Rocky Mountains and is a common dominant species in the spruce-fir forest zone (Peet 2000). However, subalpine fir is noticeably absent in conditions that would elsewhere be associated with the spruce-fir zone in Great Basin National Park (GBNP) in southeastern Nevada.

In both examples, the absence of a particular species obviously influences the composition; however, within many forest systems there are often ecological redundancies due to the broad ecological tolerances of many overstory species. In the GBNP, the "spruce-fir" forest zone is composed of Engelmann spruce (*Picea engelmannii* Parry. ex Engelm.) and limber pine (*Pinus flexilis* James). While the composition differs, forests are structurally (high-density, multiple vegetative layers, a

diversity of diameter classes) similar to other "spruce-fir" forest communities (Peet 2000). This redundancy of similar structural elements observed across multiple species may be an important feature in forest classification now and in the future.

As scientists and managers continue to observe the impacts of climate change on the forested landscape and begin to plan for the future, forest classification systems will be needed to aid in management decisions. However, with species distribution models (SDMs) predicting changes in species ranges, many current forest classification systems which rely only on species composition may be of limited use when developing long-term (>100 years) silvicultural prescriptions and planning documents. For example in the Western United States, areas of suitable climate for subalpine species are expected to decline. The impacted for whitebark pine (*Pinus albicaulis* Engel.) is predicted to be especially severe; suitable climate areas dropped from approximately 20% to 0.5-7.0% by 2070-2100 (Hansen and Phillips 2015). Additionally, climate induced shifts in mountain pine beetle and the spread of the invasive blister rust pathogen may extirpate some whitebark pine populations, thus complicating model predictions (Keane et al. 2012). Models are also predicting future niche differences in overstory and regenerating individuals in the Western U.S.; lodgepole pine (*Pinus contorta* Dougl. Ex. Loud.) and ponderosa pine are expected to have large niche differences between adults and regenerating individuals (Bell et al. 2014). Less of a niche difference is expected in subalpine fir and Engelmann spruce. However, these models predictions are likely to be complicated by current and future changes in disturbances regimes like epidemic spruce beetle outbreaks and the balsam woolly adelgid (Livingston et al. 2000; Bentz et al. 2010). Changes in the distribution of species now and in the future will certainly

influence composition but may or may not influence overall structure.

The redundancies in structural attributes across broad forest community types are influenced by environmental gradients, such as elevation (Table 3.1). While plants do not respond directly to elevation, elevation is a single variable which captures broad changes in temperature and moisture (Peet 2000). Studies listed in Table 3.1 highlight important overarching trends in forest structural attributes across elevational gradients. For example, resource limitations like moisture influence structural attributes in a predictable way. When moisture is limiting, a stand may have low overstory density and an open canopy but still have full site occupancy (*sensu* open crown closure O'Hara et al. 1996). This moisture limitation, in combination with disturbance regimes, may influence lower treeline. Similarly, tree top height is sensitive to resource availability. Bud elongation is limited in umbrella pine (*Pinus pinea* L.) under drier conditions (Lanner 1989). Juniper height is also hypothesized to be related to moisture although the exact mechanisms which limit height growth is not known since species in the family Cupressaceae do not form terminal buds (personal communication Lanner 2015). It appears likely multiple variables influence forest structural attributes in ways which create repeatable patterns across the landscape.

From several broad repeatable patterns in structure, we developed a conceptual model which explicitly classifies forest communities based on structural attributes: tree top height, tree diversity, space/relative density, and size diversity (Table 3.2; Figure 3.1). The size diversity of a stand can be strongly influenced by the relationship between disturbance frequency and intensity and can be classified based on many metrics (Oliver and Larson 1996). We choose to use a count of the number of height and diameter

classes, quadratic mean diameter (QMD), and the shape of the diameter distributions. The conceptual model has three main structural types: short single-layer forests; tall single-layer forests; tall multi-layer forests (Table 3.2; Figure 3.1). The model was evaluated with data collected across elevational gradients in the Intermountain West. Based on this model, two hypothesizes were tested. First, we hypothesized that there would be strong relationships between each of the structural types and certain abiotic and biotic variables. For example, the short single-layer forest would be associated with resource limited sites (i.e. low elevation – moisture limitation or high-elevation – temperature limitation). The second hypothesis explored the relationship between the structural type and overstory species traits. While this model was developed independent of species, we expected certain traits to be more common in certain structural types. For example, the tall single-layer forest would be associated with species that are disturbance dependent like lodgepole pine in the Intermountain West.

Material and Methods

Site description

The Intermountain West roughly encompasses an eight state region which includes Montana, Idaho, Nevada, Utah, Wyoming, Colorado, New Mexico, and Arizona. Characteristic of this region is numerous high mountain peaks and low intermountain valleys with both a lower and upper treeline (Long 1994). These broad patterns of peaks and basins create steep environmental gradients, which greatly influence the composition and structure of vegetative communities (Peet 2000). Fenneman (1928) broadly describes eight physiographic provinces within the Intermountain West: the basin and

range, the Colorado Plateau, the Columbia Plateau, the Great Plains, the Wyoming Basin, the Northern Rocky Mountains, the Middle Rocky Mountains, and the Southern Rocky Mountains. Forest structure, composition, and successional processes including disturbance regimes within the Northern, Middle, and Southern Rocky Mountain have been described by Long (1994), Peet (2000), and Baker(2009) and citations within. Climate and disturbance regimes have been shown to be important drivers of treeline dynamics; moisture and disturbances limit lower treeline advancement and temperature, wind, and solar radiation limit upper treeline advancement (Miller and Wigand 1994; Holtmeier and Broll 2005).

Within the Intermountain West, many overstory tree species have broad latitudinal ranges but generally occur under similar ecological conditions (Burns and Honkala 1990; Peet 2000). These broad latitudinal ranges and the repeated landscape of mountains and valleys have allowed many scientists to observe and develop classifications based on patterns in forest vegetation (Daubenmire 1952; Peet 2000). These forest communities are often described by the dominant overstory species (Daubemire 1952; Peet 2000). For example, Peet (2000) used elevation and a temperature/moisture gradient to describe the distribution of the major vegetation zones of the Central Rockies Mountains. With increasing elevation, forest community zones transition from grassland, to Pinyon-Juniper, to Ponderosa pine, to Douglas-fir, to lodgepole pine, to spruce-fir, and finally to alpine meadows (Peet 2000). While, the exact species composition may vary between an individual mountain range, this repeatable pattern of how species change in dominance with increasing elevation serves as a foundation for how forests are currently classified in the Intermountain West. When

describing the different forest zones Peet (2000) stresses both the common species and the structure of these forest communities.

Data collection

Data were collected in 2013 and 2014 across fifteen mountain ranges in the Intermountain West (Figure 3.2). Mountain ranges needed to have an existing road network and were selected by using a combination of local knowledge and Google Earth. Additional information on each of the fifteen mountain ranges can be found in Table 3.3.

At each mountain range, ten relatively equidistant sampling points were selected in Google Earth (N=150). The exact distance between plots varied but was generally a few miles. The equidistance placement of plots was intended to capture the variation in vegetation along the elevation gradients. Plots were located within two miles of the existing road or trail network. When crews located the plots, a 30.5 m offset with a randomized azimuth was used to ensure an unbiased sampling location. Plots were not located in areas recently recovering from stand replacing disturbances.

At each sampling point, a modified Forest Inventory and Analysis (FIA) Phase 2 CORE sampling plot was used (O'Connell et al. 2014). Modification to the sampling design included the establishment and measurement of only two of the four subplots. No down woody material was sampled.

Conceptual model testing

Five important structural attributes were identified: tree height, tree species richness, spacing/relative density, a count of height and diameter classes, and diameter distributions (Table 3.2). Measures of tree diversity were included as an important

structural attribute because with increased species diversity there will most likely be differences in tree architecture, potentially increasing structural diversity (Poorter et al. 2006). Tree architecture differences are not necessarily captured in height, density, or diameter distribution measurements.

For each subplot, the five structural metrics were calculated and then averaged at the plot level (N=150). The specific calculations for each structural metric are outlined in Table 3.4. Calculations included all standing live and dead trees. A tree was defined as a woody species with a dbh (diameter at breast height) or drc (diameter at root collar) greater than 1 cm in diameter. A list of species classified as trees can be found in Interior West Forest Inventory & Analysis Phase 2 Field Procedures (O'Connell et al. 2014).

Based on the above metrics, each of the 150 plots was classified into one of the three structural types, regardless of the species present (see Appendix 3.A). Dominant characteristics of each structural type assisted in the classification. For the short single-layer forest, plots needed to have trees with a short stature, low basal area, and low diversity of height and diameter classes. For the tall single-layer forest, plots needed to have trees with a tall average height, medium to high density, and low diversity of height and diameter classes. For the tall multi-layer forest, plots needed to have trees with a tall average height, medium to high density, and high diversity of height and diameter classes

The classification method resulted in approximately half of the plots (73) classified as tall single-layer forests (Table 3.5). Short single-layer forests and tall multi-layer forests had approximately equal representation with 36 and 41 plots, respectively. One-way Anova with Tukey's Post Hoc Comparison test was used to assess differences among the structural types. Quartile-quantile regression plots were used to assess

normality of the residuals. TPH and Shannon's evenness were transformed using a square root transformation; prior to the square root transformation for Shannon's evenness a value of 1 was added since there were 0 values present. Anova analyses were performed on the transformed data but the untransformed values are presented in Table 3.5.

Signficant differences occurred among the three structural types for multiple metrics including top height, basal area, SDI, count of diameter classes, and the count of height classes (Table 3.5). However, there was less senstitivity for all metrics of tree diversity, trees per hectare, and the QMD. Shannon's diversity index and the number of trees per hectare were the least sensitive to differences among the three structural types. Measures of species richness and evennesses were significantly different between the short single-layer forest and the tall multi-layer forest ($p < 0.001$; $p < 0.01$); the tall single-layer forest was not significantly different from the other two structural types. For the QMD metric, there appears to be a threshold effect where trees reach a signficantly greater diameter in the tall single-layer forest and the tall multi-layer forest than the short single-layer forest ($p < 0.0001$; $p < 0.01$)

Analysis of the relationship between environmental variables & species to the conceptual model

The relationship among the three structural types, environmental variables, and species were explored using a non-metric multidimensional scaling ordination (NMS) in PC-Ord Version 6.08 (McCune and Mefford 2011). The primary matrix was composed of individual species basal area. Basal area was square root transformed to reduce the influence of plots with high basal area (Field et al. 1982). The environmental matrix (or secondary matrix) contained seven physiographic variables: slope, aspect, elevation,

percent basal area vegetation, canopy cover, presence of water, and stand age. Stand age was determined based on counting tree rings from tree cores in the field. Aspect was transformed using the Beers et al. (1966) formula where smaller numbers represent a southwest aspect and larger numbers represent a northeastern aspect. Also, included in the matrix was a structural type code which was associated with each plot; this was used to explore grouping based on structural type in the ordination. Auto-pilot mode (slow and thorough) was selected using Sørensen (Bray-Curtis) distance measurement (McCune and Grace 2002). An indicator analysis was also run using the three structural types as groups and a quantitative or binary response selected (Dufrêne & Legendre 1997, IASA Eq. 1.).

A random forest model in program R was used to further explore the potential relationship between the structural types and the environmental variables (Culter et al. 2007). The structural types were predicted based on the same physiographic variables from the NMS ordination. Partial dependence plots from the random forest models were used graphically explore the marginal effect of an individual variable on the model (Friedman 2001).

Results

Relationship between structural type and species

Thirty-one unique overstory species were observed across the 150 plots. No structural type had all 31 species. Within the tall single-layer forest type, 28 species were observed; 18 and 21 species were observed in the short single-layered forest type and tall multi-layered forest type, respectively (Table 3.6). The majority of species had higher

composition under one of the three structural types. A few species such as lodgepole pine, limber pine, and aspen (*Populus tremuloides* Michx.) had relatively similar composition across all three structural types (Table 3.6).

Non-metric multidimensional scaling (NMS) ordination

A non-metric multidimensional scaling (NMS) ordination was used to explore the potential relationships between overstory species, environmental variables, and the three structural types (Figure 3.3). A 3-dimensional solution with a final stress of 19.6 and 0.00 stability explained 46% of the variation. The final stress of this ordination is on the higher end; it likely would be reduced if rare species were removed (McCune and Grace 2002). However, we chose not to remove these rare species since they may be important structurally. Axis 1 explained 18% of the variation with axis 2 and 3 explaining 15% and 14%, respectively. Elevation was the only physiographic variable that was strongly correlated with Axis 1; no other physiographic variables were strongly correlated with axis 2 or 3.

There was strong clustering of plots within the tall multi-layer forest type and this cluster was associated with species that commonly occur under moister conditions at higher elevations (Figure 3.3). Engelmann spruce (0.0002), subalpine fir (0.0062), aspen (0.0018), Douglas-fir (0.0018) and corkbark fir (0.0002) were all significant indicators of the tall multi-layer forest type. There was more overlap in ordination space between the short single-layer and tall single-layer forest types (Figure 3.3). Pinyon pine was the only significant indicator of the short single-layer forest type ($p=0.0054$). No species was an indicator of the tall single-layer forest type.

Relationship between Structural Types and Environmental Variables

Random forest was used to further explore the relationship between the environmental variables and the three structural types. Stand age, elevation, and canopy cover were the most important predictor variables in the random forest model. Partial dependence plots were used to explore the marginal response of individual predictor variable within the random forest model (Culter et al. 2007). The y-axis represents a relative score with the focus being on the general trends for each individual predictor variable (Figure 3.4). The short single-layer forest was associated with low canopy cover. For the short single-layer forest, a similar trend was observed for stand age and elevation with an initial negative trend but at about 75 years old and 2700 m the trend turns positive. The tall multi-layer forest type was associated with greater stand age, elevation, and canopy cover. The tall single-layer forest type generally had greater variability in partial dependence plots. The tall single-layer forest was associated with lower to mid-elevation plots. There was more variability in the trends for stand age and canopy cover.

Discussion

The use of structural attributes to develop a broad forest classification was successful in grouping forests communities with different species but similar structural attributes. The model utilized average height, QMD, basal area, SDI, and the count of diameter and height classes to classify forest communities. However, tph, species diversity and diameter distributions were less sensitive to differences among the three structural types. This lack of sensitivity may be due to the sampling design and the region where the model was tested. For example, average tph was not significantly

different among the three structural types (Table 3.5) which may be due to the fact that all trees greater than 2.54 cm were included in all calculations. These smaller diameter trees have less of an impact on values of SDI and basal area but can result in large tph values. Within the short single-layer forest, this high tph may be influenced by clonal species like maple or oak which are generally small diameter, short trees which can form very dense clumps. Gamble oak, a common species in low elevation woodlands in the Intermountain West, can have up to 1,000 ramets per clone (Brown 1958; Simonin 2000). While tph is high, other metrics like basal area, SDI, average height, and QMD fit the short single-layer structural type.

Limited statistical and biological differences were observed between metrics of structural diversity in the Intermountain West. The Intermountain West contains a diversity of shrubs, forbs, and graminoid species but very limited tree diversity (Peet 1978; Van Buren et al. 2011). The inclusion of shrubs, forbs, and graminoids into the model may have allowed for species diversity metrics to vary between structural types. However, while a very important part of Intermountain ecosystems, the increased sampling time would probably not result in a change to the classification process (Appendix 3.A). Additionally, in regions with greater overstory species richness (i.e. Great Lakes/North East or the South East) the inclusion of tree diversity metrics may be an important part of classification between the less diverse tall single-layer forests and the more diverse tall multi-layer forests. Finally, it may have been naïve to have hypothesized differences in diameter distributions among the three structural types (Appendix 3.B). Numerous studies across the globe have documented how multiple diameter distributions may be observed within the same forest type based on management

history and the size of the plot (i.e. Essen et al. 1997; Rubin et al. 2006; Janowiak et al. 2008).

While certain structural metrics were more sensitive to differences between the three structural types, important relationships between environmental variables and species composition were observed within the conceptual model, supporting our two hypotheses. The hypothesized environmental differences were most apparent when comparing the short single-layer forest and the tall multi-layer forest type. The partial dependence plots for these two structural types highlight very different trends in the data for elevation, canopy cover, and stand age. These trends are consistent with other studies observing how structural attributes vary across environmental gradients (see citations in Table 3.1).

However, within each structural type, there was a range of variation, as shown in the NMS ordination (Figure 3.3). Classification can be developed to emphasize the "modal" or ideal conditions or the differences between boundaries (Whittaker 1963; Pfister and Arno 1980). Our conceptual model highlights the ideal conditions for each forest type with the understanding that there will be gradation between the three structural types. This gradation or range of variation is common in classification systems and highlights that species respond individualistically to environmental gradients (Whittaker 1962). Overall, the short single-layer and the tall multi-layer forest type were more strongly related to certain environmental variables and overstory species. For example, the tall multi-layer forest type generally was associated with species commonly observed in the subalpine forest zone; while, the short-single layer forest type was associated with species observed in the woodland zone.

However, there was greater variability in the tall single-layer forest type. This higher level of variability could be due to multiple reasons, one of which is the presence of transition zones. Transition zones are often considered important in forest ecosystems because of the potentially high levels of diversity (e.g. species) and are hypothesized to be sensitive to future climate change (Gosz 1992). However, habitat typing, the dominant forest classification system in the Intermountain West, purposely avoids transition zones (Pfister et al. 1977). Our sampling method did not avoid transition zones. The sampling of these transition zones both in space and time highlight important variability that is observed in forest ecosystems. The argument could be made that the higher variability in tall single-layer forest types may warrant the development of another structural type or a sub-type. The tall single-layer forest type would still be described as having tall trees, few vegetative layers, a medium to high QMD but would be split based on tree density. Subtype A would capture the low to medium density sites and Subtype B would capture the medium to high density sites.

The development of two subtypes is a valid option. However, the subtypes may be just highlighting successional or disturbance dynamics. For examples, this structural type could contain forests dominated by lodgepole pine, ponderosa pine, Douglas-fir, and aspen in multiple combinations. These forest types are generally considered productive and greatly shaped by disturbance or lack of it (Long 1994). Changing disturbance dynamics especially changes in fire regimes and insect populations are influencing these forest types across the Intermountain West (Jenkins et al. 2008). The use of one structural type, tall single-layer forest type, may increase the ability to compare silvicultural prescriptions across a wide range of overstory species which could lead to

novel management solutions.

The ability to compare forest conditions across multiple species and at multiple scales (regional, landscape, and locally) are two of the greatest strengths of this conceptual model. This comparability could allow for greater comparison of ecosystem processes across multiple regions. For example, the boreal forest land cover class stretches across multiple continents in the northern hemisphere and is considered extremely important in carbon storage (Bonan and Shugart 1989; Pan et al. 2011). Even though the species composition of the boreal forests land cover class differs between southern Canada (*Picea mariana, Picea glauca, Populus tremuloides, Abies balsamea* (Hély et al. 2000) and the Fennoscandian part of Russia (*Pinus sylvestris, Picea abies, Betual pendula, Populus treemula* (Gromtsev 2002)), these forests are structurally similar and are influenced by similar processes (de Groot et al. 2013). The comparison of forest systems with similar structure and processes may increase our basic understanding of how forest functions by identifying important mechanisms.

Forest structural attributes are not static in time; models develop by Long and Smith (1984), Oliver and Larson (1996), or Franklin and colleagues (2002) address many important components of stand development and forest succession. Our model accounts for potential changes in structural attributes due to succession, climate change, and/or disturbance. For example, a tall single-layer forest type, in the absence of disturbance, may in the future have structural attributes which would shift its classification to tall multi-layer forest type or under certain conditions (drought, insect epidemic) may shift the structural attributes and classification to short single-layer forest type. By accounting for potential shifts in structural attributes, this model allows managers to explore how

structural attributes may shift with changing conditions.

The interaction between climate change (Stocker et al. 2013), native and invasive pests and pathogens (e.g. Raffa et al. 2008), and fire regimes (e.g. Marlon et al. 2012) are expected to influence the composition and structure of forest communities in potentially unknown ways (Elith and Leathwick 2009; Williams and Jackson 2007). This lack of certainty increases the need for our management to be flexible. This conceptual model would allow for flexibility by allowing managers to focus on structure instead of species. Species will respond to climate change individually. However, within the Intermountain West there is redundancy in ecological tolerances of multiple species. The redundancy in tolerances and the broad environmental gradients result in repeatable patterns of structural, features which allows for classification of forest communities.

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Table 3.1: Relationship between structural attributes across and an environmental gradient represented by elevation.

	Height	**Tree Species Diversity**	**Spacing/ Relatively Density**	**Size Diversity**
Overarching Hypothesis	Hydraulic limitation & allocational allometry hypothesis (Yoder et al. 1994; Ryan & Yoder 1997; Koch 2004; Givnish et al. 2014).	Peaks at intermediate elevations (Peet 1978; Lomolino 2001; Colwell et al. 2004; Sang 2009)	"Full site" occupancy (Long & Smith 1984; Oliver & Larson 1996; O'Hara et al. 1996; Long et al. 2004).	Height and diameter classes and diameter distributions are strongly influenced by successional dynamics and disturbance intensity and frequency (Oliver & Larson 1996).
lower elevation	Limitations in timing and amount of moisture limit overall maximum height growth (Ryan & Yoder 1997)	Precipitation limits species richness (Grytnes 2003; Bhattarai et al. 2004; Sang 2009)	Resource limitation (moisture & temperature) allow full site occupancy before crown closture (*sensu* open stem exclusion (O'Hara et al. 1996))	Resource limitations (mostly moisture) limit the size diversity (O'Hara et al. 1996). Disturbances are generally high frequency and vary from low to high intensity (Kilgore 1981; Romme et al. 2009).
mid-elevation	Tree height is related to the ratio of precipitation and pan evaporation (Givnish et al. 2014)	Mid-elevation sites serve as transition zones increasing species richness (Lomolino 2001)	Full site occupancy occurs at crown closure. Mortality may be due to autogenic and allogenic causes (Oliver & Larson 1996)	Disturbances occur during stem exclusion or understory reinitiation, limiting the size diversity (Oliver & Larson 1990). Disturbances are mixed frequency and often high intensity (Kilgore 1981; Turner & Romme 1994)
high elevation	Tree height is related to the ratio of precipitation and pan evaporation (Givnish et al. 2014)	Temperature limits species richness (Grytnes 2003; Bhattarai et al. 2004; Sang 2009).	Short growing seasons limit growth and decomposition but full site occupancy occurs at crown closture. Mortality may be due to autogenic and allogenic causes (Oliver & Larson 1996)	High severity disturbances are rare (low frequency but high intensity) allowing for the high size diversity (Oliver & Larson 1990; Veblen et al. 1994).

Table 3.2: Hypothesized conceptual model using structural metrics to define forest communities in the Intermountain West.

	Short Single-Layer Forest	**Tall Single-Layer Forest**	**Tall Multi-Layer Forest**
Top Height	Short	Tall	Tall
Tree Species Diversity	Low 1 - 3	Potentially high 5 or more	Low 2 to 4
Spacing/ Relative Density	Widely spaced trees at low relative density	Densely packed trees at high relative density	Densely packed trees at high relative density
Diversity of Height & Diameter Classes	1	1-2	Many
Diameter distribution	Unimodal distribution with the mean centered at small diameter trees and an right skew	Unimodal centered at medium to large diameters	Reversed-J

Table 3.3: Additional information for each of the elevation transects. Precipitation and temperature data are from the PRISM database and are the average normals from 1981-2010 for the lowest and highest sampled point for each elevation transect.

State	County	Ownership	Lower & Upper Elevation (m)		Lower & Upper Total Precipitaiton (mm)		Lower & Upper Average Max July Temperature (C°)		Lower & Upper Average Min January Temperature (C°)	
Arizona	Apache	Navajo Indian Reservation	2397	2670	516.2	589.7	25.51	27.89	-7.27	-9.07
Arizona	Coconino	Coronado National Forest	2551	3459	689.5	1023.9	18.73	24.79	-7.67	-12.16
Arizona	Coconino	Kaibab National Forest	2096	2363	439.88	532.8	27.95	29.06	-5.52	-7.76
Arizona	Pima	Coronado National Forest	1748	2416	755.4	854	26.25	29.83	-0.79	-1.16
Arizona	Santa Cruz	Coronado National Forest	1713	2114	711.13	736.2	29.12	29.64	1.46	1.77
Idaho	Bear Lake	Uinta-Wasatch-Cache National Forest	2063	2460	672.7	940.8	23.37	26. 14	-10.59	-10.59
Idaho	Boise	Boise National Forest	1474	2073	522.2	773	22.14	28.84	-7.82	-6.09
Idaho	Cassia	Sawtoot National Forest	1901	2739	506.3	1004	20.80	27.19	-5.93	-10.5
Montana	Gallatin	Gallatin National Forest	1720	2470	605.4	974.6	20.64	24.6	-11.58	-12.19
Nevada	White Pine	Great Basin Nationa Park	2038	3184	310.2	780.1	20.77	29.85	-6.54	-11.72
Utah	Cache	Uinta-Wasatch-Cache National Forest	1534	2480	653.8	1074.8	23.59	29.07	-10.34	-10.97
Utah	San Juan	Manti - La Sal National Forest	1820	3089	738.3	1007	21.39	21.9	-8.94	-11.41
Utah	Summit	Uinta-Wasatch-Cache National Forest	2225	3317	371.1	652.43	17.67	27.22	-5.67	-11.78
Utah	Weber	Uinta-Wasatch-Cache National Forest	1661	2127	743.2	1100.9	25.69	29.25	-8.24	-8.64
Wyoming	Lincoln	Bridger- Teton National Forest & Bureau of Land Management Kemmerer Field Office	2260	2439	508.4	536.77	23.55	24.95	-12.49	-15.37

Table 3.4: Calculations for the five structural metrics in the conceptual model.

Structural Metric	Calculation
Tree Height	
Top Height	average height of all trees
Tree Diversity	
Shannon's diversity index	$H = \sum p_i \ln p_i$ p = the proportion of basal area of individual I H = Shannon's diversity index
Shannon's Evenness	$E_H = H/\ln S$ E_H = Shannon's evenness S = Species richness
Species Richness	Count of unique tree species
Spacing/Relative Density	
Basal area per hectare	= (0.00007854 * DBH^2) * Expansion Factor
Trees per hectare	= Count of trees * Expansion Factor
Stand Density Index	calculated using the summation method (Long and Daniel 1990; Shaw 2006) included live and dead trees
Diversity of Height and Diameter Classes	
Count of Diameter Classes	5 cm diameter classes were created and a richness value was calculated based on the occupancy of trees in each diameter class
Count of Height Classes	2 m height classes were created and a richness value was calculated based on the occupancy of trees in each height class
Diameter distribution	
Quadratic Mean Diameter (QMD)	=square root ((BA/ha/tph)/0.00007854)
Diameter distribution	using 5 cm diameter classes basal area was plotted and diameter distributions described. Average diameter distributions for each structural type are displayed in Appendix 3.B.

Table 3.5: Average structural attributes by structural type for the 150 plots across the Intermountain West. Standard errors are shown in parathesis.

		Short Single-Layer Forest		**Tall Single-Layer Forest**		**Tall Multi-Layer Forest**	
Height							
	Average Top Height (m)	5.38	(0.46)[a]	11.73	(0.59)[b]	15.60	(0.54)[c]
Tree Diversity							
	Richness	2.21	(0.17)[a]	2.87	(0.14)[ab]	3.28	(0.16)[b]
	Shannon's Diversity Index	0.57	(0.06)[a]	0.71	(0.05)[a]	0.85	(0.05)[a]
	Evenness*	0.60	(0.05)[a]	0.62	(0.03)[ab]	0.71	(0.03)[b]
Spacing/Relative Density							
	Basal Area (m^2ha^{-1})	10.93	(1.44)[a]	31.35	(1.88)[b]	56.14	(3.53)[c]
	TPH*	1123	(222)[a]	944	(125)[a]	1284	(115)[a]
	SDI	253	(33)[a]	575	(35)[b]	1015	(57)[c]
Diversity of Height and Diameter Classes							
	Count of Diameter Classes	2.39	(0.25)[a]	3.58	(0.18)[b]	5.94	(0.19)[c]
	Count of Height Classes	2.49	(0.22)[a]	3.81	(0.21)[b]	7.02	(0.31)[c]
Diameter Distribution							
	QMD (cm)	16.09[a]	(1.95)	28.59[b]	(1.76)	26.18[b]	(1.27)
	Diameter distribution	Flat		flat		polynomial	
N		36		73		41	

*Variables were transformed for analysis but the untransformed means and standards errors are displayed
Different lower cases letters represent significant differences.
An adjusted p-value of 0.005 was used due to multiple comparisons
Average diameter distribution are displayed in Figure 3.3

Table 3.6: Average percent of basal area per hectare by species for each of the three structural types

Species Code	Scientific Name	Short Single-Layer Forest	Tall Single-Layer Forest	Tall Multi-Layer Forest
ABCO	*Abies concolor*	-	3.65	0.07
ABLA	*Abies lasiocarpa*	4.35	7.34	11.22
ABLAAZ	*Abies lasiocarpa* var. *arizonica*	-	-	5.55
ACGL	*Acer glabrum*	-	0.06	-
ACGR	*Acer grandidentatum*	0.05	3.03	0.12
CELE	*Cercocarpus ledifolius*	0.57	0.16	-
JUDE	*Juniperus deppeana*	3.64	5.53	-
JUOS	*Juniperus osteosperma*	13.78	0.13	-
JUSC	*Juniperus scopulorum*	1.54	1.65	0.97
PIAR	*Pinus aristata*	-	-	4.58
PIAZ	*Pinus arizonica*	0.37	1.28	2.92
PICE	*Pinus cembroides*	-	0.19	-
PICO	*Pinus contorta*	6.71	4.11	9.09
PIDI	*Pinus discolor*	2.41	3.15	-
PIED	*Pinus edulis*	6.09	1.72	-
PIEN	*Picea engelmannii*	3.15	2.58	24.13
PIFL	*Pinus flexilis*	5.54	5.18	2.71
PILO	*Pinus longaeva*	-	1.44	-
PIMO	*Pinus monophylla*	-	0.11	-
PIPO	*Pinus ponderoa*	11.17	19.83	6.92
PIPU	*Picea pungens*	-	1.19	-
PIST	*Pinus strobiformis*	-	0.00	0.33
POTR	*Populus tremuloides*	13.24	13.85	16.83
PSME	*Pseudotsuga menziesii*	1.70	11.10	12.79
QUAR	*Quercus arizonica*	16.40	6.85	0.19
QUEM	*Quercus emoryi*	0.28	0.10	-
QUGA	*Quercus gambelii*	7.13	3.05	-
QUGR	*Quercus graciliformis*	-	0.05	-
QUHY	*Quercus hypoleucoides*	1.74	1.94	1.60
QURU	*Quercus rugosa*	0.15	0.00	-
SALIX	*Salix* spp.	-	0.76	-

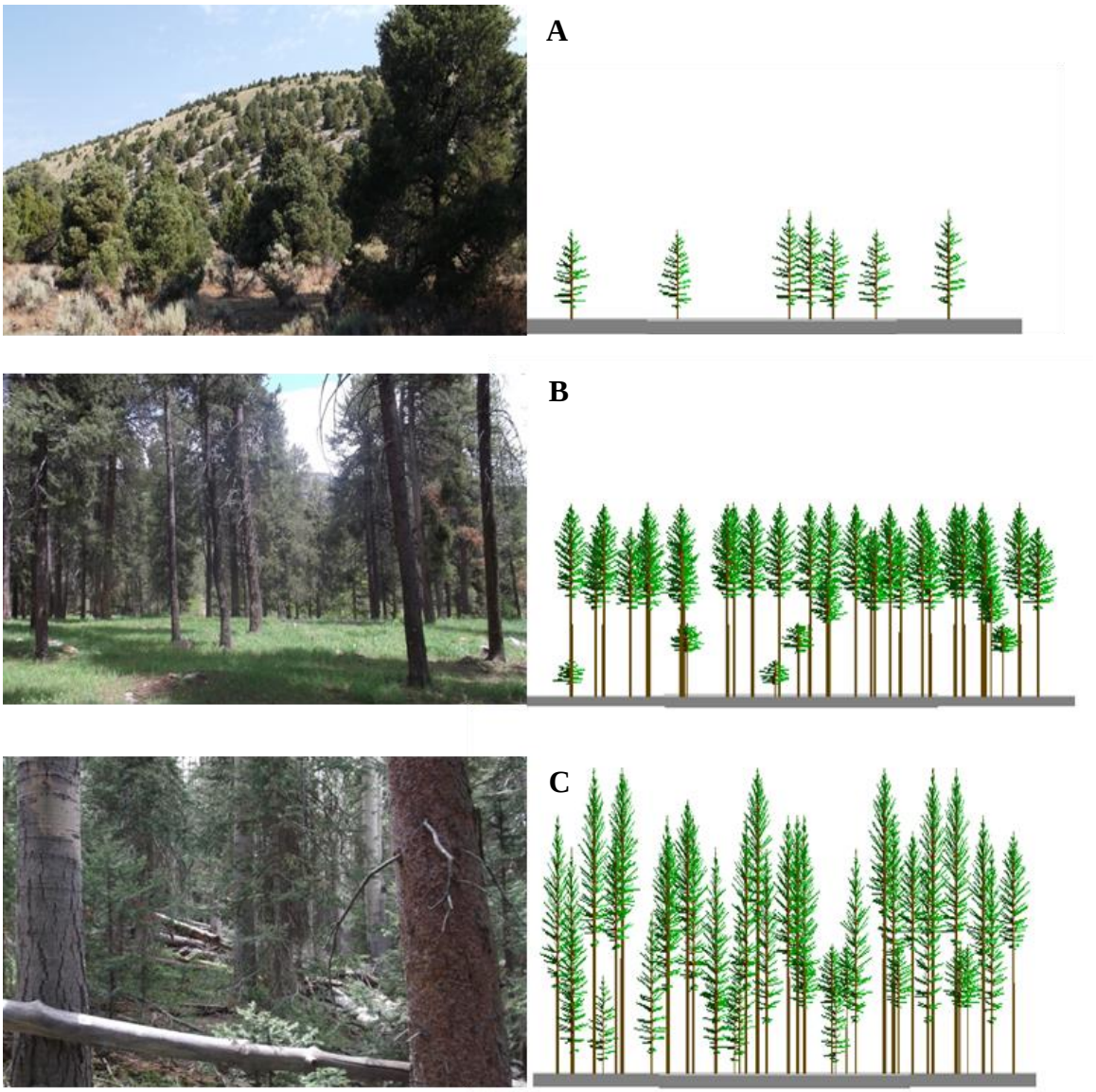


Figure 3.1: Photographic and stand visualization images of the three different structural types: A) Short Single-Layer Forest, B) Tall Single-Layer Forest and C) Tall Multi-Layer Forest. Stand visualization images were produced in the Stand Visualization System (SVS) (McGaughey 2004).

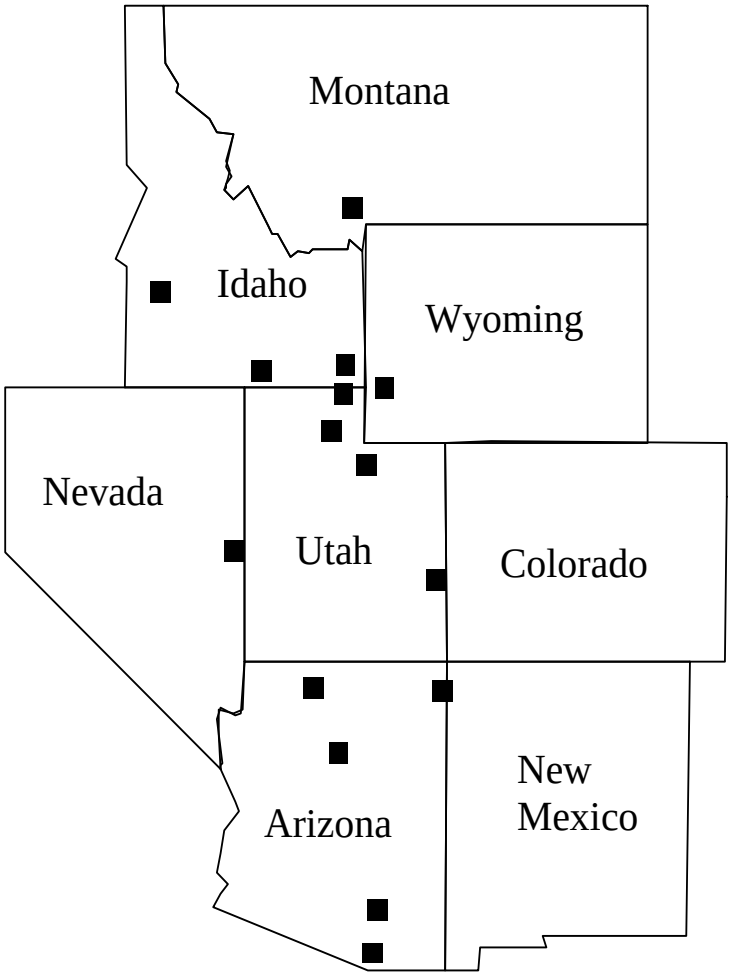


Figure 3.2: Location of each of the 15 elevation transect. At each elevation transect, 10 sampling points were established to capture the different forest types. Additional information regarding environmental variables is located in Table 3.3.

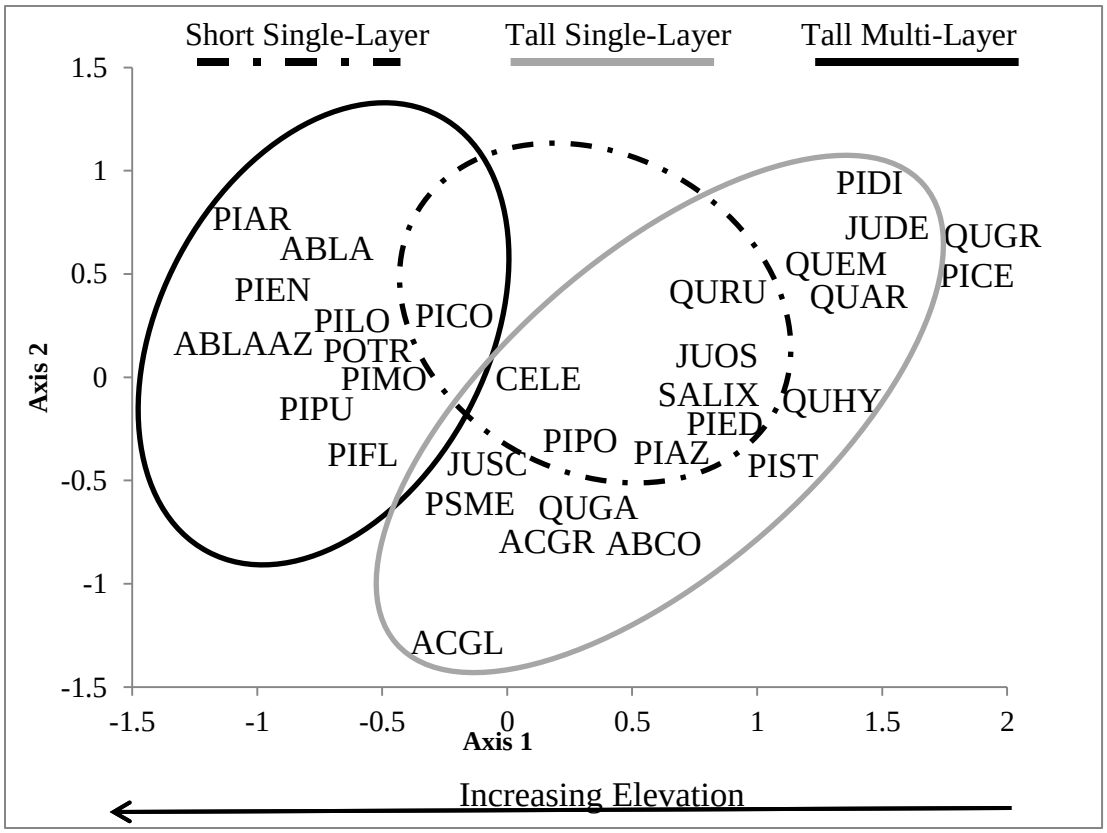


Figure 3.3: NMS ordination of the relationship between overstory basal area per hectare and physiographic variables of the three different structural types. The general locations of plots associated with the three structural types are outlined in different colors. Species codes and scientific names can be found in Table 3.6.

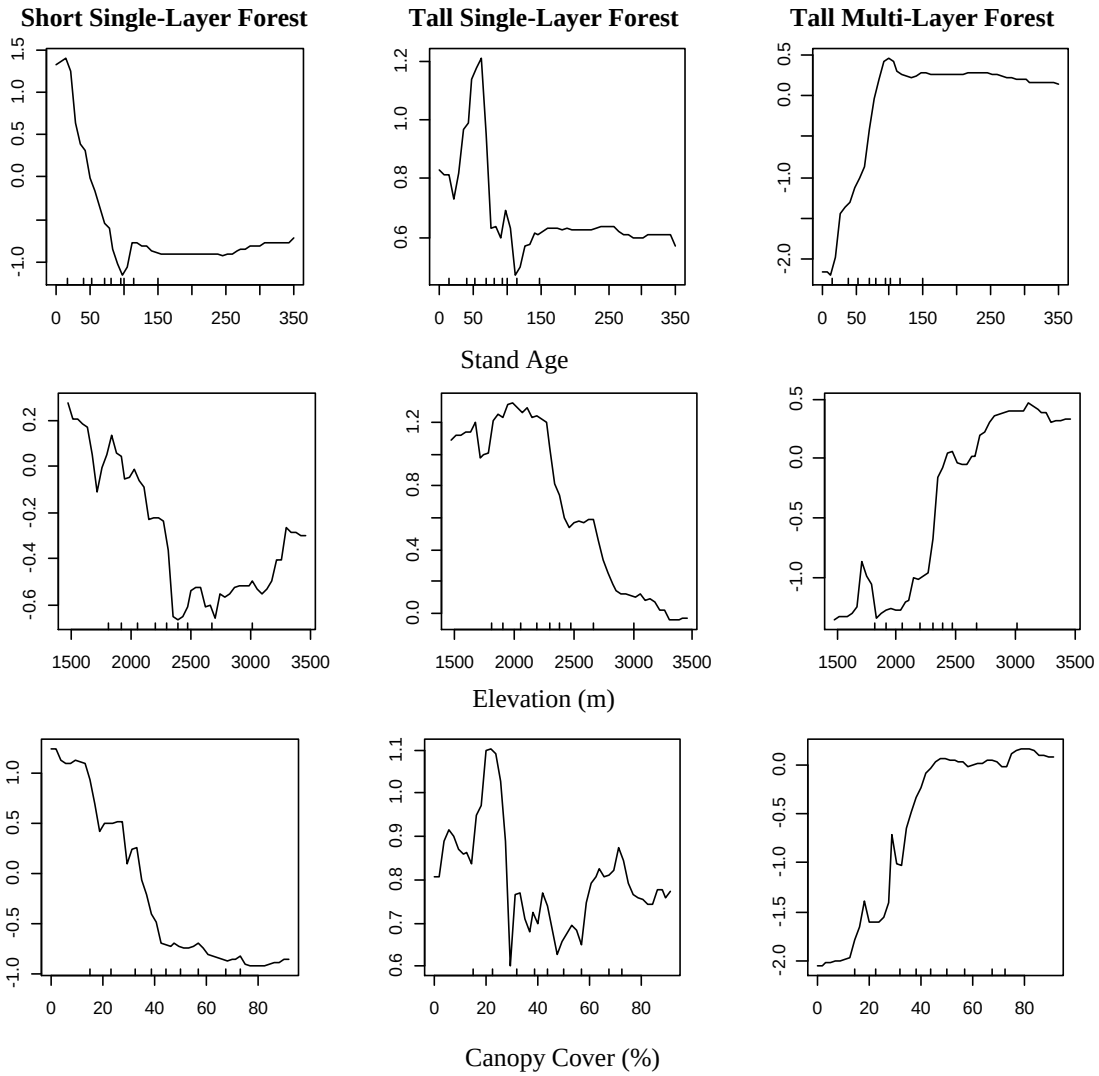
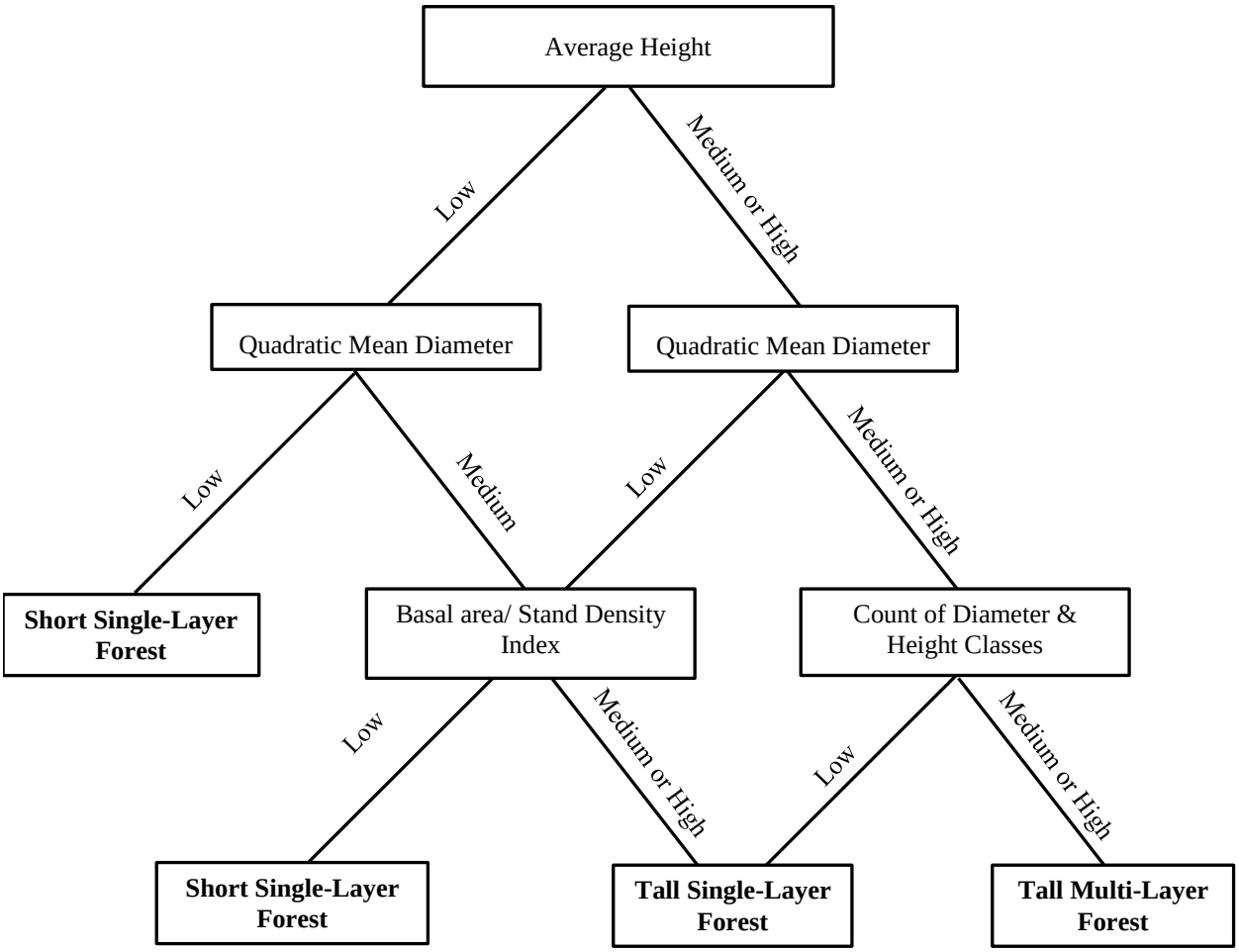


Figure 3.4: Partial dependence plots for the top three predictor variables (stand age, elevation, and canopy cover) from the random forest model. Partial dependency plots explore the marginal relationship between an individual predictor variable and the random forest model The y-axis represents a relative score with the focus being on the overall trend in the data.

Appendices

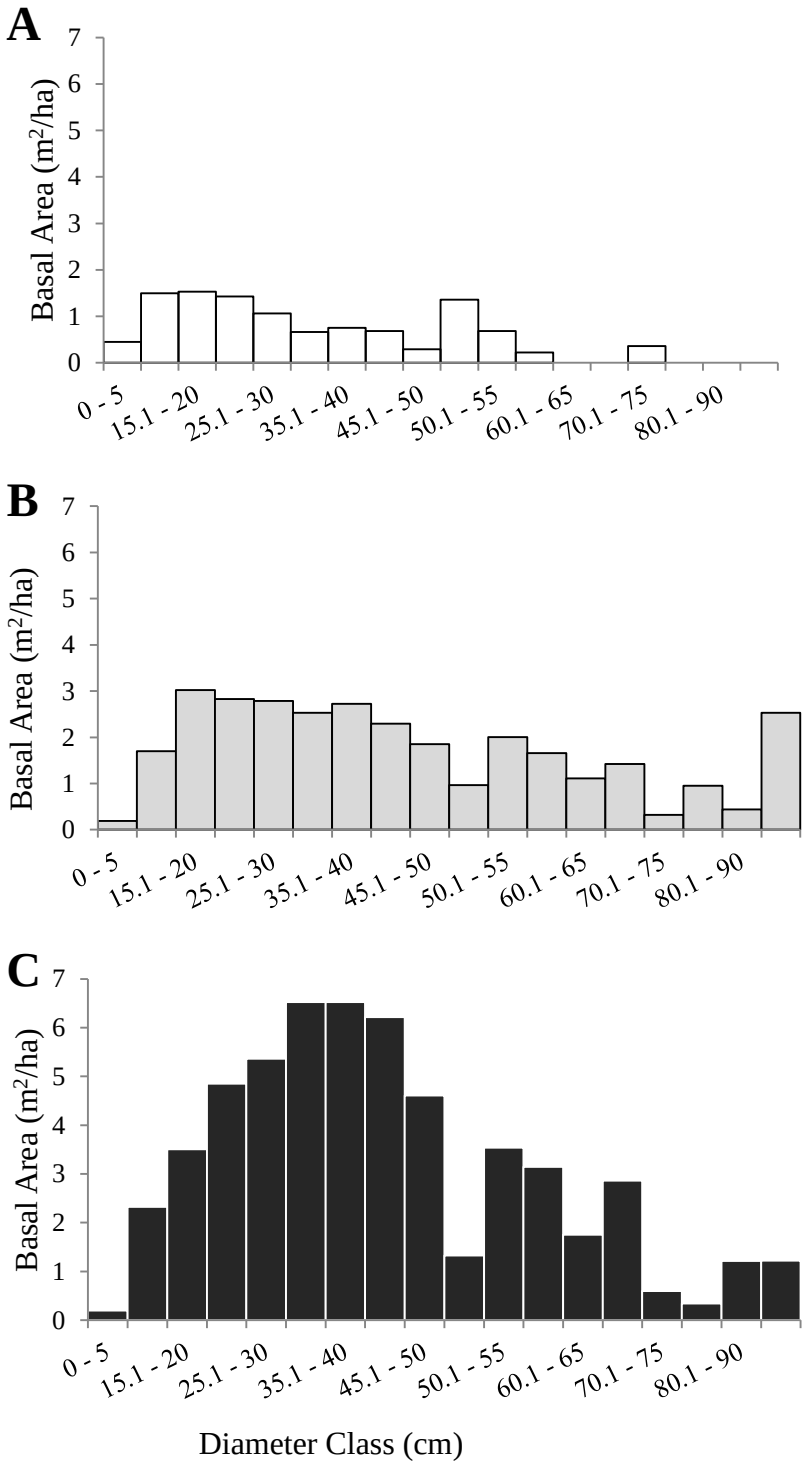
Appendix 3.A

Method for classify forest plots into one of the three structural types. The five structural metrics were calculated for each plot. Values of average height, quadratic mean diameter, basal area/stand density index, and count of diameter and height classes were assess and broadly described as low, medium, or high. Based on this assessment plots were placed into one of the three structural types.



Appendix 3.B

Average diameter distribution by structural type: (A) short single-layer forest type; (B) tall single-layer forest type; and (C) tall multi-layer forest type.



CHAPTER 4

LIMBER PINE (*PINUS FLEXILIS* JAMES) STRUCTURAL AND COMPOSITIONAL DYNAMICS ACROSS THE INTERMOUNTAIN WEST

Abstract

Within Western North America, limber pine (*Pinus flexilis* James) is observed across a broad elevation and geographic range. However, it is commonly described as a specialist, occurring under harsh environmental conditions at low or high elevations. Limber pine is a five-needle white pine which is currently threatened by interactions of climate change, mountain pine beetle, and white pine blister rust. Our goal was to explore the basic forest dynamics of limber pine across a broad geographic and elevation sampling design by utilizing the Forest Inventory and Analysis Database (FIAD). We hypothesized that limber pine would have a bi-modal species distribution and would be associated with harsh environmental conditions (i.e. moisture stress). The FIAD yielded 683 plots across the Intermountain West. Limber pine was observed to be a consistent component of forest communities regardless of elevation; it did not follow a uni-modal or bi-modal distribution. Additionally, limber pine was associated with more mesic conditions, ranging from a minor to dominant component. Limber pine may play different roles in forest communities depending on the structure and composition. This species would benefit from a better ecological understanding which will aid in a more complete understanding of potential functional types.

Introduction

The interactions between climate change and disturbance agents are influencing species composition and structure across a multitude of ecosystems (Fisichelli et al. 2013, Fettig et al. 2013, Linder et al. 2014). This is true for a group of Western North American tree species commonly referred to as the high five (Keane et al. 2011). The high five is composed of six five-needle white pines, which belong to the Family Pinaceae, Genus *Pinus* and the subgenus *Strobus.* The six species include whitebark (*Pinus albicaulis* Engelm.), limber (*P. flexilis* James), southwestern white (*P. strobiformis* Engelm.), foxtail (*P. balfouriana* Balf.), Rocky Mountain bristlecone (*P. aristata* Engelm.), and Great Basin bristlecone (*P. longaeva* D.K. Bailey). Unlike two other western five-needle pines, sugar pine (*P. lamertiana* Douglas) and Western white pine (*P. monticola* Dougl. ex D. Don), the high five pines are not commercially important for timber.

The high five have been grouped together because of morphological and ecological similarities (Peet 2000). They are generally characterized as fairly shade intolerant, poor competitors, and disturbance dependent (Knowles and Grant 1983, Schoettle 2004, Tomback et al. 2011). Within the subalpine forest zone, the high five are, individually, common components of the system but are rarely dominant except after stand replacing disturbances (i.e. fires) or under harsh environmental conditions which cannot support closed-canopy forests (Sherriff et al. 2001). These sites often have poor soil development and limited understory cover (Peet 2000). Overstory trees generally have short stature with semi-rounded crowns; trees are widely spaced as individuals or small groups (Peet 2000). Under these harsh conditions, individual trees can reach great

ages (>1,000 years), creating beautiful scenes that are sought after by recreationists (Keane et al. 2012).

In these harsh environments, the high five play important roles and have been characterized as keystone species (Keane et al. 2011). They provide valuable wildlife habitat (Tomback and Kendall 2001), serve as a wildlife food source (Kendall 1983, McCutchen 1996), influence snow dynamics and the timing of run-off (Logan and Powell 2001), and provide many benefits to humans (Keane et al. 2012). However, these species are currently threatened by multiple interacting disturbance agents including climate change, white pine blister rust (WPBR) (*Cronartium ribicola* J. C. Fisch), and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Johnson and Jacobi 2000, Kearns and Jacobi 2007, Bockino and Tinker 2012). WPBR is a non-native pathogen that kills trees by girdling (see Schoettle 2004 for additional life history information). Young trees are often more susceptible and killed quickly; trees can develop ontogenetic resistance with age (Schoettle 2004). Mountain pine beetle (MPB) occurs across much of the range of the high five (Raffa et al. 2008). It has been hypothesized that climate has historically constrained MPB due to the presence of suitable hosts occurring farther north and south of its historic range (Bentz et al. 2011). However, during an abnormally warm year, there was an extensive MPB outbreak in high elevation whitebark pine forests in the Greater Yellowstone Ecosystem (Gibbson et al. 2008). These abnormal warm years are becoming more common and mountain pine beetle activity has increased; it is predicted to continue to increase in these ecosystems (Logan and Bentz 1999, Gibson et al. 2008, Logan et al. 2010). The loss of these keystone species is hypothesized to influence important ecosystem dynamics (McKinney et al. 2009, McKinney et al. 2011). Range wide and

localized restoration strategies have been developed for some of the high five species (see The Alberta Whitebark and Limber Pine Recovery Team 2014, Keane et al. 2012).

The individual distributions of the high five vary from relatively small geographic areas (i.e. Rocky Mountain and Great Basin bristlecone pines) to broader geographic areas (i.e. whitebark and limber pines) (Burns and Honkala 1990). Limber pine not only has a large geographic range but also the broadest elevation range of any of the high five, occurring from 870 to 3800 m in elevation. It occurs across most of Western North America (southwestern Alberta and British Columbia in Canada to northern New Mexico and Arizona in the United States) in the Rocky Mountains, Basin and Range, White and Sierra Nevada mountain ranges, the Black Hills, and isolated populations in the Great Plains (Steele 1990).

While limber pine is grouped with the high five, it also occurs at lower elevations. Across its broad elevation range, limber pine is describe as an extremely poor competitor in closed-canopy forests, generally dominating under rocky, harsh environmental conditions at lower or upper elevations where it can reach great ages (Steele 1990, Schoettle 2004, Tomback and Achuff 2010). Under more mesic conditions in the montane and subalpine forest zone, limber pine is often the first species to establish after stand-replacing disturbances due to seed caches by corvid species like the Clark's nutcracker (Romme and Knight 1981, Veblen et al. 1994, Tomback et al. 2005, Brown and Schoettle 2008). These birds heavily influence the distribution of limber pine. Clark's Nutcracker can cache seeds up to 22 km away from a seed source; windswept ridges and areas with early spring ground exposure are preferred cache sites (Tomback and Linhart 1990, Steele 1990).

Following establishment, limber pine can serve as a "nurse tree" allowing the establishment and eventual succession of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) under favorable environmental conditions (Veblen 1986, Rebertus et al. 1991, Donnegan and Rebertus 1999). It is only on extremely xeric sites (centrifugal theory of community organization *sensu* Keddy and MacLellan 1990) where limber pine can form climax communities. Similar patterns of establishment and facilitation have been observed between limber pine and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) at lower elevations (Baumeister and Callaway 2006, Means 2011). Using Grime's life history strategy, limber pine could be described as a stress tolerator with few ruderal qualities (Grime 1988) or in more general terms as a habitat specialist, dominant under the harshest environmental conditions. However, others have suggested that limber pine's wide ecological tolerance better fits the description as a habitat generalist (Schoettle and Rochelle 2000, Letts et al. 2009).

An interpretation of these studies is that limber pine has a bi-modal species distribution and is competitively excluded from mid-elevation forest communities. This competitive exclusion hypothesis is based on local forest dynamics studies at both lower and upper elevations. There have been few studies of limber pine ecology across broad environmental and/or geographic gradients (but see Schuster and Mitton 1989, Schoettle and Rochelle 2000, Schuster and Mitton 2000, Jørgensen et al. 2002). Our study is one of first studies to explore general forest dynamics of limber pine across the extent of its ecological amplitude and to explore the competitive exclusion hypothesis across a broad elevation and geographic range. We hypothesized that limber pine would follow a bi-

modal distribution with greater basal area in low and high elevation sites; at mid-elevation sites, it would be competitively excluded as stands increased in age. Additionally, we hypothesized that there would be a positive relationship between limber pine basal area and environmental extreme conditions (i.e. lower total precipitation and/or higher or lower temperatures).

Methods

Study Area

The Intermountain West encompasses eight states including Montana, Idaho, Nevada, Utah, Wyoming, Colorado, New Mexico, and Arizona. Across these eight states, there are many diverse ecosystems including numerous mountain ranges, shrub steppes, and deserts. The major ecoregions that were the focus of this study were the Southern Rocky Mountain Steppe, Middle Rocky Mountain Steppe, Northern Rocky Mountain Forest- Steppe, and the Nevada –Utah Mountain Semidesert (Bailey 1998).

The climate of the Intermountain West is arid (< 250 mm/yr precipitation) to semi-arid (250 – 500 mm/yr precipitation) with higher elevations receiving additional precipitation due to orographic uplift (Knapp 1997). The majority of the precipitation falls through winter snowfall but in the southern portions (New Mexico, Arizona, southern Utah, and southern Colorado) the North American Monsoon provides important summer precipitation (Wise 2012). Yearly precipitation can be highly variable, resulting in both high and low precipitation years (Wang et al. 2009). Additionally, local, small-scale physiographic features (i.e. aspect, elevation, and slope) create high variability in moisture patterns (Mock 1996, Wang et al. 2009).

Study Design

A query of the Forest Inventory and Analysis Database (FIADB) in 2013 located all FIA plots containing limber pine in the overstory or regeneration layer within the Intermountain West. The current FIA sampling design includes the use of four, 0.017 hectare circular plots to measure site and tree variables. Additional information on the sample design can be found in Woudenberg et al. (2010). Some states were in the process of beginning their second round of annual inventories resulting in two years of data. The most recent sampling year was used so there were no repeated measurements within the dataset.

The data were separated by overstory and regenerating trees. Overstory trees were defined as limber pine with a diameter at breast height (dbh) greater than 2.54 cm. Overstory limber pine could be dead or alive. Regenerating limber pine were any individuals less than 2.54 cm in dbh but greater than 15.24 cm in height and only recorded if alive.

For a plot to be included in the final data sets, plots could only have one condition class; "conditions are defined by changes in land use or changes in vegetation that occur along more-or-less distinct boundaries" (Woudenberg et al. 2010). Additionally, plots needed to be associated with long-term climate data from the PRISM climate database (PRISM Climate Group 2004). This left a total of 849 plots with limber pine present in either the overstory or regeneration layer. The majority of plots, 681 plots, had limber pine present in the overstory. Of these 681 plots, 191 plots also had limber pine present in the regeneration layer. There were 168 plots that contained regenerating limber pine but did not have limber pine present in the overstory.

Statistics

Descriptive statistics of stand, site, and environmental variables were calculated using both the PRISM and FIADB databases. Overstory stand density metrics were expanded to trees per hectare (tph) and basal area per hectare; the regeneration layer was also expanded to tph. The percent composition of basal area of individual species was used to standardize the data due to the wide range of total stand basal area. Percent limber pine basal area was grouped into three categories: low (<25% limber pine), medium (25-75% limber pine), and high (>75% limber pine). Average yearly precipitation was grouped into three categories as well: < 400 mm, which is characteristic of the average yearly precipitation for pinyon-juniper woodlands (Romme et al. 2009); 400 – 900 mm, which is characteristic of the average yearly precipitation for mid-elevation forests (Hadley and Veblen 1993); and > 900 mm, which is characteristic of average yearly precipitation for spruce-fir forests (Hart and Lomas 1979). Additionally, stand age and elevation were categorized. Diameter distributions using average basal area per hectare with 5 cm diameter classes were used to explore species composition and forest dynamics. Finally, linear regression and conditional interference trees with program ctree (Horthorn et al. 2006) in the statistical program R were used to explore the relationship between environmental variables (average yearly precipitation, average yearly temperature), stand variables (total overstory basal area, live limber pine basal area, percent live limber pine), and limber pine regeneration.

Results

Limber pine was observed across a wide range of environmental conditions in many different forest types (Table 4.1). Across this broad environmental gradient, limber

pine was observed to be a consistent component of forest communities in the Intermountain West (Figure 4.1; Appendix 4.A). Many tree species, especially lower and upper elevation specialists (i.e. Utah juniper (*Juniperus osteosperama* (Torr.) Little*)*, Engelmann spruce), did not occur across the entire elevation gradient. For these species the percent basal area peaked at lower or upper elevation classes (Figure 4.1). A few species, including limber pine occurred across the elevation gradient. Of those species, Douglas-fir and lodgepole pine (*Pinus contora* Dougl. Ex. Loud.) followed a uni-modal distribution peaking at elevations between 1524-2133 m and 2134 – 2743 m, respectively. However, for the 681 plots where overstory limber pine was present, it was observed to be a consistent component of forest communities ranging on average between 13-25% of the basal area.

The majority of the 681 plots had limber pine as a minor component (<25% of the basal) of the stands. Stands dominated by limber pine (>75% of the basal area) were relatively rare and represent approximately 7% of the dataset. Additionally, while limber pine is commonly described as dominating under harsh climatic conditions, it was most commonly observed under relatively mesic conditions with average yearly precipitation between 400 – 900 mm. Stands were commonly between 101-250 years in age.

Exploring the subset of data with average yearly precipitation between 400- 900 mm, the average diameter distributions were relatively similar between plots with low, medium, and high percent limber pine basal area (Table 4.2; Figure 4.2). On average, these plots had approximately 25 m^2ha^{-1} of total basal area; plots with higher percent limber pine basal area were slightly lower with an average of 23 m^2ha^{-1}. Limber pine was

observed across a wide range of diameters; there was good representation of limber pine in the smaller diameter classes (<12.5 cm in dbh).

Limber pine regeneration was observed under similar environmental conditions as overstory limber pines. There was a weak but significant positive relationships between limber pine regeneration density and total yearly precipitation ($p<0.001$) and live limber pine basal area ($p=0.02$). In both regressions, the r-square values were less than 5% and it is unlikely these results are biologically significant. There was no relationship between average July precipitation, average July temperature, or yearly average temperature with limber pine regeneration. However, a more meaningful relationship was observed utilizing conditional inference trees (Figure 4.3). Live overstory basal area of limber pine and yearly precipitation were important predictors of limber pine regeneration. On average, there was lower limber pine regeneration in plots with yearly precipitation under 632 mm ($p<0.001$). Plots with less precipitation on average had 513 tph of limber pine compared to 792 tph on higher precipitation sites (Figure 4.3 A). On sites with higher precipitation (> 632 mm), limber pine regeneration was greater when live limber pine basal area was greater than 10.6 m^2ha^{-1} ($p = 0.021$). When live limber pine basal area was lower, limber pine regeneration averaged 707 tph compared to 1336 tph under higher limber pine basal (Figure 4.3 B).

Discussion

Limber pine is commonly grouped as a member of the high five. While, limber pine is morphologically similar to other species in the high-five, limber pine did not follow the hypothesized bi-modal distribution. Additionally, there was no association between greater limber pine composition and harsh environmental conditions (high or

low temperatures and precipitation). Because of this, limber pine should not be considered a specialist, competitive only in harsh environments, but rather a generalist occurring in many different forest ecosystems across the Intermountain West (Schoettle and Rochelle 2000).

Limber pine is often described as dominating under harsh environmental conditions (Veblen 1986, Peet 2000). When annual average precipitation is low (< 400 mm), limber pine can range from the dominant species to just a minor component. A similar proportion (~ 10%) of plots were observed to have low, medium, and high limber pine composition. Whether limber pine was a minor or major component of these forest stands, these plots had lower overall tree species richness compared to more mesic sites.

The majority of the plots containing limber pine were observed under more mesic conditions and were not dominated by limber pine. The diameter distributions of plots with a stand age between 101 -250 and average yearly precipitation between 400 – 900 mm could generally be described as having a fairly uni-modal distribution with many small trees and few large diameter trees. For all composition categories, limber pine was observed across almost all diameter classes, including the smaller diameter classes. These smaller diameter trees represent the future forests (Oliver and Larson 1996). This suggests that limber pine is not strictly an early seral species and is competitive across a range of stand and site variables.

The conventional (and our hypothesized) description of limber pine forest community structure and composition is quite limiting and does not capture the diversity of forest conditions where this species can occur. We suggest that limber pine management and research may benefit from the development of multiple functional types

similar to the system of functional types recently developed for another western generalist, trembling aspen (*Populus tremuloides* Michx.) (Rogers et al. 2014). Three main functional types may capture many of the limber pine communities: dominant self-replacing; invading; and mixed-species. Limber pine dominant communities generally have low diversity and lower density but can occur over a wide range of stand and site conditions. The invading limber communities highlight the dispersal ability of limber pine; many plots with limber pine regeneration did not have live limber trees present in the overstory. Finally, in mixed-species communities, limber pine adds species and structural diversity to a variety of forest communities across a wide range of stand conditions. This added diversity may increase forest resilience. Very little information is known about the role limber pine plays when it is a minor component. This lack of information is a large limitation in developing this type of model. Localized studies exploring all aspects of limber pine communities across its ecological amplitude are required to have a better understanding the variability of these forest communities.

There was high variability in environmental and stand conditions of the 359 plots where limber pine regeneration was observed. These variable site conditions may highlight additional differences between potential functional types. Greater limber pine regeneration was associated with higher average yearly precipitation and greater live limber pine basal. However, the presence of live limber pine on the plot does not guarantee the presence of regeneration; almost half of the plots where limber pine regeneration was present had no live limber trees present in the overstory, highlighting the proposed invading functional type. Of the 681 plots that had limber pine in the overstory, only 28% had regenerating limber pine. The low regeneration rate may be due

to differences in plot sizes between the overstory and the understory, ~1/10th of a hectare compared to ~1/120th of hectare, respectively. Limber pine regeneration may have been present on more of the sites but due to the smaller plot size was not quantified. Another possible reason could be differences in the niches of limber pine adults, seedlings, and saplings (Poorter 2007). Very little information is known about limber pine establishment requirements (Smith et al. 2011). Moyes and colleagues (2013) observed a negative relationship between seasonal moisture stress and limber pine seedling survival in the Front Range of Colorado. Moisture was also observed to be a limited factor for limber pine regeneration in parts of the Great Basin mountains (Millar et al. 2015). However, a more complex relationship was observed for high elevation five needle pines in the White Mountains (Barber 2013). Our results also highlight that precipitation may be a factor influencing limber pine regeneration success. Additional research is needed on how regeneration success is influenced by environmental and stand variables.

The consistent presence of overstory limber pine and regenerating individuals across broad environmental conditions may be important as forest managers focus on increasing resistance and resilience to climate change (DeRose and Long 2014, Seidl 2014). Species diversity has been hypothesized as a key component to maintaining resilient forest ecosystems (Folke et al. 2004, Haussler et al. 2013). Overstory tree species diversity in the Intermountain West is limited (Peet 1978, Peet 2000). In the vast majority of these communities, limber pine is not the dominant species. However, the presence of a generalist like limber pine or aspen may be extremely important in terms of species richness and resilience to a broad range of disturbance types.

Disturbances like stand replacing fires are predicted to increase in number due to interactions between land use history, climate change, and insect outbreaks (Jenkins et al. 2014 and citations within). Lodgepole pine, Engelmann spruce, and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) all have very limited long distance seed dispersal; over 80% the seeds fell within 75 m of the parent tree (McCaughy et al. 1986). However, limber pine can be distributed a long distance due to its mutualistic relationship with corvid bird species like the Clark's nutcracker and is often one of the first tree species to be observed regenerating after a severe stand-replacing disturbance (Rebertus et al. 1991, Donnegan and Rebertus 1999, Tomback et al. 2011). This long distance dispersal mechanism may be one of the reasons there were numerous plots that only had limber pine present in the regeneration layer. Limber pine's long distance dispersal ability may increase resilience in forest communities after large-scale severe stand replacing disturbances such as fire.

Higher species diversity has also been observed to decrease insect damage due to the associational resistance (Jactel and Brockerhoff 2007, Castagneyrol et al. 2013, Rigot et al. 2014). A meta-analysis of 47 different insect-tree interactions observed that there was less herbivory damage in mixed species stands than in pure stands (Jactel and Brockerhoff 2007). Many different western forests types are experiencing large insect outbreaks including spruce beetle (*Dendroctonus rufipennis*) in spruce-fir forests, pinyon pine beetle (*Ips confuses*) in pinyon-juniper woodlands, Douglas-fir beetle (*Dendroctonus pseudotsugae*) in Douglas-fir forests, and mountain pine beetle (*Dendroctonus ponderosae*) in pine forests. In many of these systems, limber pine is not a host species. However, it is a host for mountain pine beetle. Early observations by Hopkins (Hopkin's

Host Selection Principle (Hopkins 1916)) suggest that when multiple host species are present, mountain pine beetle will choose to breed in the same species as where it developed. The Hopkin's Host Selection Principle for mountain pine beetle has studies indicating support (Dean 2007, Raffa et al. 2013) and those where the hypothesis has not been supported (Raffa et al. 2013, West et al. 2014). When limber pine is present in low numbers in lodgepole or ponderosa pine forests and if mountain pine beetles do have a preference based on development, limber pine may play an important role in future forest dynamics. However, if mountain pine beetles do not display host preference, these low-density limber pine populations may be lost due to these large-scale outbreaks, decreasing stand diversity and resilience.

Some limber pine trees may be more resistant to mountain pine beetles. Limber pine trees with greater densities of resin ducts were more likely to survive a mountain pine beetle outbreak. These resistant trees were generally slower growing with less radial growth over both 5- and 10-year growth intervals (Ferrenberg et al. 2014). Additionally, previous climatic events and stand structure may influence stand resilience in limber pine communities (Millar et al. 2007). Dense limber pine stands in the Sierra Nevada mountain ranges of California experience significantly drought related mortality from 1985 to 1995. The drought acted as a natural thinning agent; limber pine that were killed during the drought established during the Little Ice Age and were adapted to the cooler, moister conditions. The reduction in density resulted in a more resilient stand since no additional mortality was observed during a subsequent drought from 1999-2004 (Millar et al. 2007).

An additional threat for all five-needle white pine communities is the invasive blister rust pathogen. However, recent work has identified the presence of a Cr4 allele in limber pine which is associated with blister rust resistance. Within the Southern Rocky Mountain populations, the allele occurs between 0 and 13.9%; due to this relatively high percent, it is hypothesized to be an inherited gene (Schoettle et al. 2014). This range of frequency of the resistance allele is higher than what was observed in western white pine and sugar pine (Kinloch 1980, Kinloch et al. 2003).

Limber pine is a component of many forest ecosystems across the Intermountain West. Our study is one of the firsts to document basic forest dynamic information on this species across both a geographic and elevation gradient. The data did not support either of our two hypothesizes: 1) limber pine does not, in fact, have a bi-modal distribution and 2) limber pine is not preferentially associated with harsher environmental conditions (i.e. moisture limitations). Additional information is needed on the genetics, ecophysiology, and forest dynamics of this broadly distributed species. Furthermore, management and research should aim to expand efforts to develop characterization of limber pine "functional types." By increasing the understanding of limber pine's range of roles (i.e. pioneer, invader, seral dominant, or seral minor) in forest communities in the Intermountain West, forest management plans and silvicultural prescriptions can be developed which focus on maintaining healthy limber pine communities in the face of numerous interacting threats. The maintenance of limber pine communities will be important for multiple objectives including snow hydrology, wildlife habitat and food source, and forest resilience. Limber pine's broad dispersal ability combined with its

ecological range may increase forest resilience with future climate change by facilitating the establishment of less tolerant individuals across the Intermountain West.

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Table 4.1: Summary stand conditions for limber pine plots across the Intermountain West.

	Total basal area (m^2ha^{-1})	Total limber pine basal area (m^2ha^{-1})	Live limber pine basal area (m^2ha^{-1})	Dead limber pine basal area (m^2ha^{-1})	Percent limber pine
Average	28.3	4.8	3.4	1.4	21.5
Standard error	0.6	0.3	0.2	0.1	1.1
Minimum	0.2	0.1	0.0	0.0	0.3
Maximum	117.7	43.9	39.2	31.9	100.0

	Elevation (m)	Yearly precipitation (mm)	Yearly temperature (C°)	Slope
Average	2499.7	625.2	4.1	39.4
Standard error	19.4	8.0	0.1	0.8
Minimum	1177.4	264.0	-3.0	0.0
Maximum	3547.0	1767.0	10.0	112.0

Table 4.2: The distribution of plots based on the percent of overstory limber pine, total yearly precipitation, and stand age.

	<25% PIFL	**26-75% PIFL**	**> 75% PIFL**	**Grand Total**
< 400 mm total precipitation				
< 25 years	4	0	1	5
26 – 100	13	2	0	15
101- 250	22	7	0	29
250 +	0	0	0	0
Unknown	0	0	4	4
400 - 900 mm total precipitation				
< 25 years	29	15	4	48
26 – 100	140	28	9	177
101- 250	222	57	10	289
250 +	15	5	2	22
Unknown	7	9	16	32
> 900 mm total precipitation				
< 25 years	7	1	0	8
26 – 100	7	7	0	14
101- 250	21	9	3	33
250 +	0	2	0	2
Unknown	2	0	1	3
Total	489	142	50	681

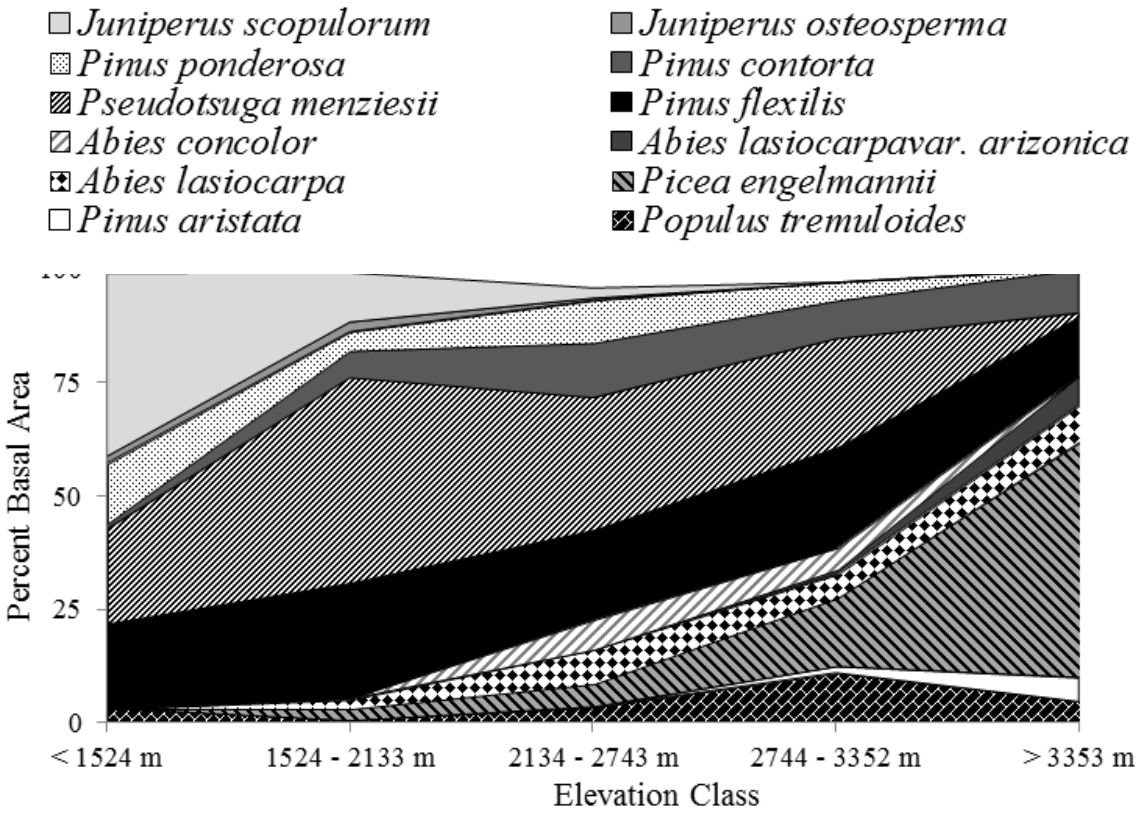


Figure 4.1: Percent basal area of the most abundant species by elevation class. A total of 23 unique overstory species were observed. Species not present represent less than 1% of the basal area by elevation class. Basal area measures includes stand live and dead trees. Numerical values for each species and elevation class can be found in Appendix A.

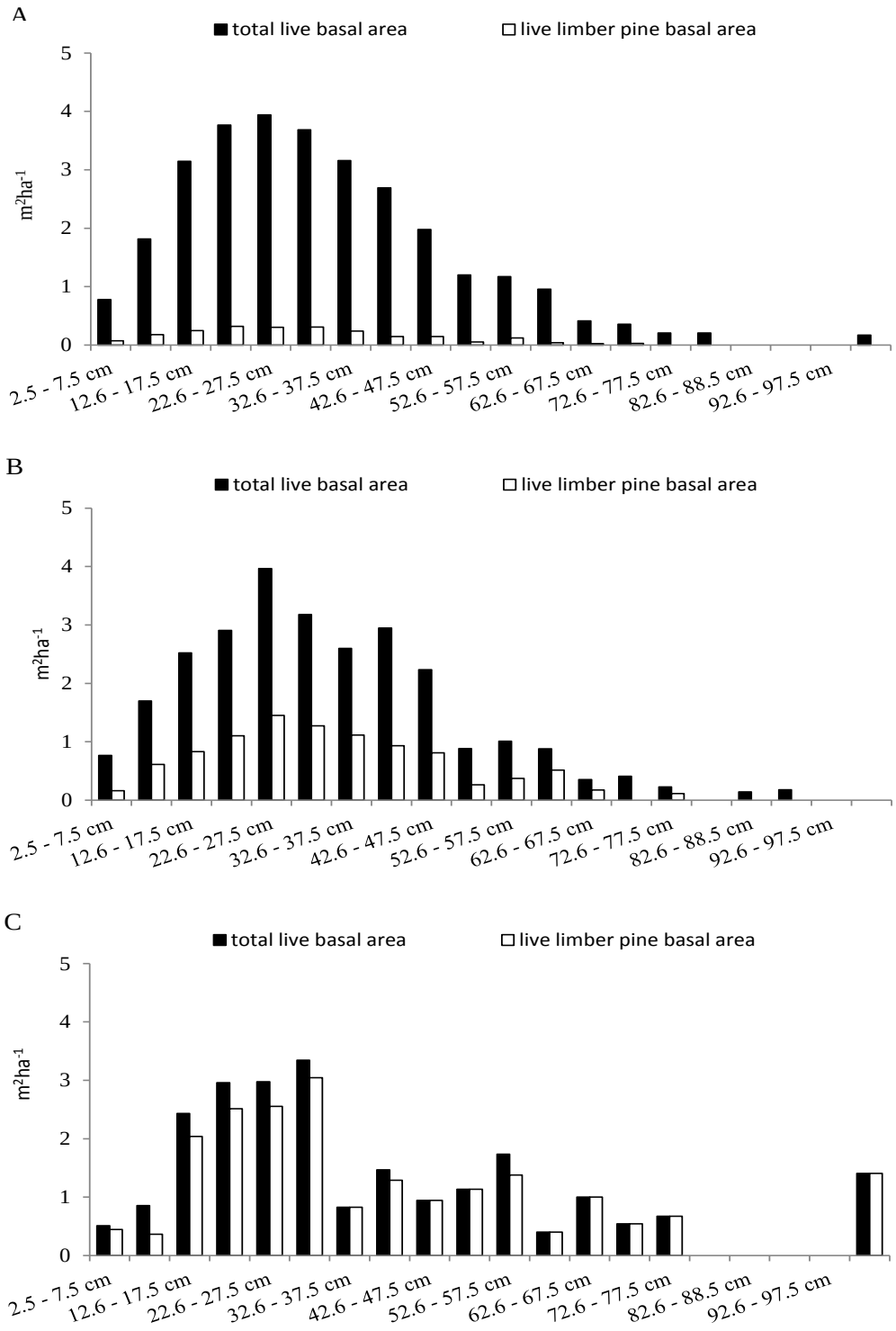


Figure 4.2: Diameter distributions for limber pine plots with average yearly precipitation between 400 – 900 mm broken up by average percent limber pine. A) Low percent limber

pine (<25% of the basal area); B) Medium percent limber pine (25 – 75% of the basal area); and C) High percent limber pine (>75% of the basal area).

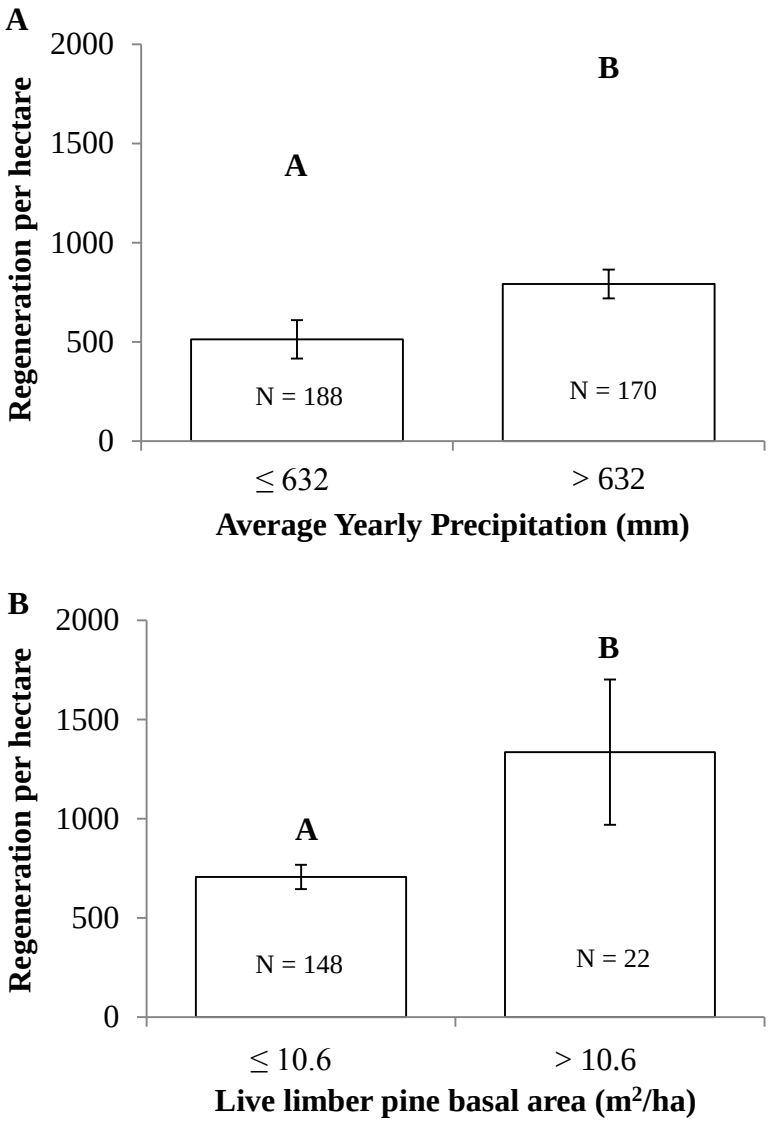


Figure 4.3: Average density of limber pine less than 2.54 cm in dbh across the Intermountain West. Using a conditional inference trees significant splits occurred based on average yearly precipitation and live limber pine basal area per hectare. A) The first significant split ($p<0.001$) was on plots with greater than 632 mm and those less than or equal to 632 mm of average yearly precipitation. B) Of the 170 plots with greater than 632 mm of average yearly precipitation, a second significant split ($p = 0.021$) occurred based on live limber pine basal area. Letters represent significant differences. Errors bars

represent stand errors. N is the total number of plots in each of the bars. One plot with greater than 10,000 regenerating limber pine per hectare was excluded from this analysis.

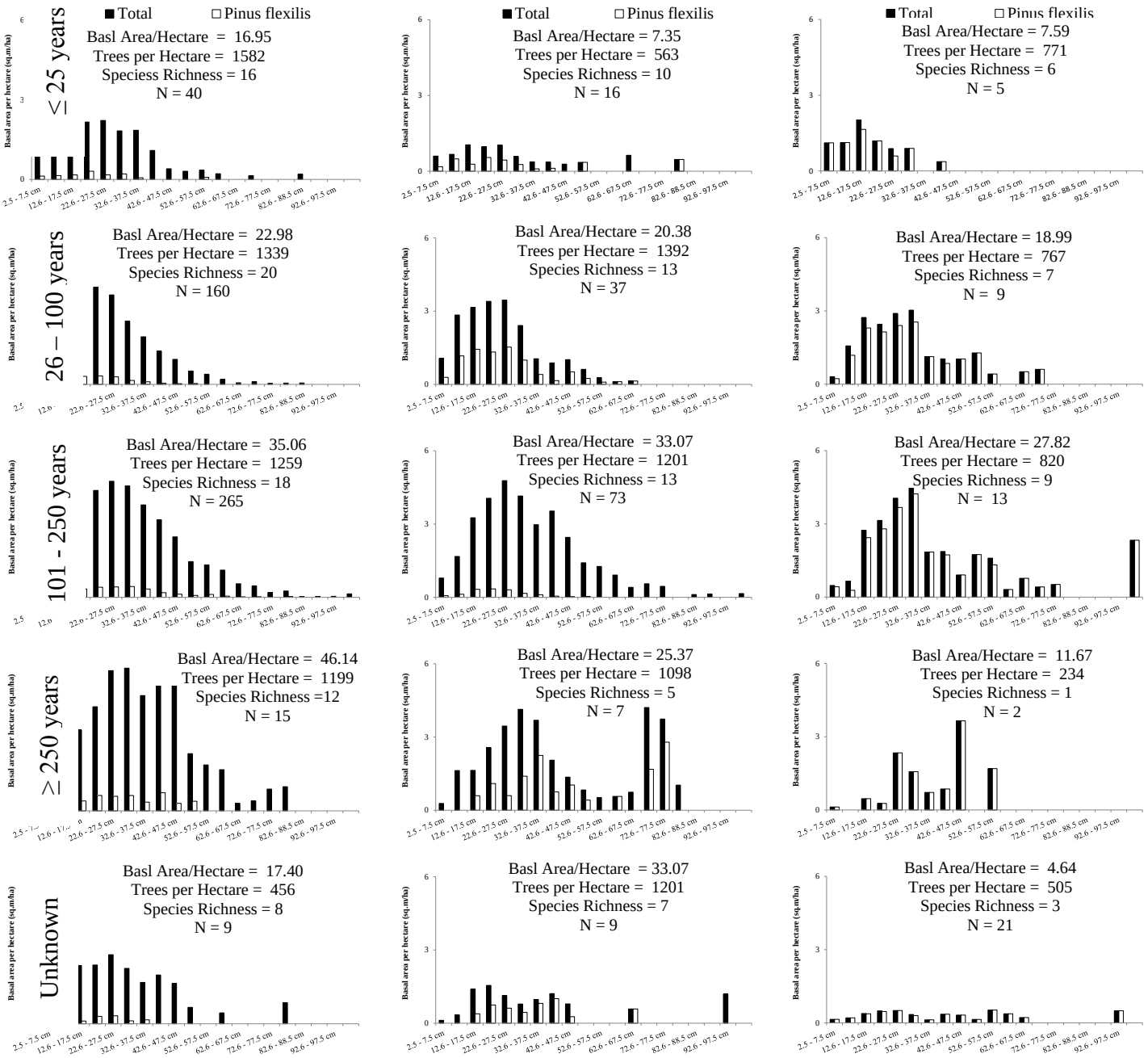
Appendices

Appendix 4.A: Percent basal area of the most abundant species by elevation with the associated standard errors in parenthesis. Basal area measures included both live and dead trees. Species are arranged from species associated with higher to lower elevation.

	<1524 m n = 25		**1524 - 2133 m** n = 139		**2134 - 2743 m** n = 285		**2744 - 3352 m** n=506		**>3353 m** n = 13	
Pinus aristata							1.33	(0.45)	5.21	(2.66)
Picea engelmannii			2.63	(0.71)	5.34	(0.77)	15.21	(1.59)	52.15	(7.61)
Abies lasiocarpa			2.00	(0.76)	7.49	(0.97)	5.12	(0.90)	8.00	(5.64)
*Abies lasiocarpa*var. *arizonica*							1.03	(0.32)	6.48	(4.12)
Abies concolor					6.56	(1.00)	4.71	(0.77)		
Populus tremuloides	3.19	(3.19)	0.66	(0.28)	3.33	(0.67)	11.02	(1.31)	4.64	(3.22)
Pinus flexilis	18.87	(3.74)	25.48	(2.55)	19.72	(1.48)	22.15	(1.79)	13.08	(3.12)
Pseudotsuga menziesii	20.68	(5.93)	45.21	(3.15)	29.19	(1.81)	23.99	(1.86)	0.74	(0.54)
Pinus contorta	1.37	(1.31)	5.87	(1.65)	12.06	(1.52)	8.40	(1.43)	9.70	(5.60)
Pinus ponderosa	13.09	(5.22)	4.30	(1.19)	9.40	(1.21)	3.96	(0.87)		
Juniperus osteosperma	1.47	(1.47)	2.12	(1.19)	0.45	(0.25)				
Juniperus scopulorum	40.42	(7.09)	10.89	(2.01)	2.25	(0.52)	0.13	(0.06)		

Appendix 4.B: Average basal area by age class and percent composition of limber pine. Black bars represent average basal area of all species except limber pine. Limber pine average basal area is in the associated white bars. Additional information on average density and trees per hectare is above each diameter distribution. Species richness is the total number of overstory species observed.

Percent *Pinus flexilis*



CHAPTER 5

CONCLUSION

As complex interactions between climate and disturbance regimes influence current and future forest communities, forest managers and researchers are challenged to develop management strategies which build or maintain resistance and/or resilience in forest communities (Messier et al., 2013 and citations within). Commonly when describing a resistance or resilience ecosystem a ball and cup conceptual model is used (Fiskley, 2003). The conceptual model highlights broad characteristics of an ecosystem and how a perturbation or disturbance may move the ball. A resistant ecosystem would have very little movement since resistance is defined as the capacity of ecological entities to withstand disturbances (Westman, 1978). Whereas, the ball may more move in a resilient ecosystem but will return to a similar location after the perturbation is over; Holling (1973) defines resilience as "… a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables" (Holling, 1973). However, translating these definitions into concrete measurable metrics which aid in forest management can be difficult. DeRose and Long (2014) developed a conceptual frameworks which suggest that managers focus on metrics of stand structure and species composition and how those metrics influence resistance and resilience at the stand and landscape scale.

Building on DeRose and Long's (2014) conceptual framework, my dissertation research explored how both basic and applied forest dynamics research could be used to build resistance and resilience in forest communities. My first data chapter, Chapter 2 "If Long-Term Resistance to a Spruce Beetle Epidemic is Futile, Can Silvicultural

Treatments Increase Resilience in Spruce-Fir Forests in the Central Rocky Mountains?" explored how explicitly characterized metrics of resistance and resilience to the spruce beetle (*Dendroctonus rufipennis* (Kirby)) differed between three different silvicultural treatments. Resistance was defined through metrics of overstory structure and composition (Schmidt and Frye, 1976); resilience was defined as a minimum amount of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) regeneration. None of the three treatments, single tree selection, group selection, ot shelterwood with reserves, met all of the management goals. When developing long-term forest management plans, forest managers will have to assess trade-offs. The single tree selection resulted in high density stands with very limited Engelmann spruce regeneration. The group selection, while traditionally used, maintained characteristic spruce-fir structure and composition but did not have adequate spruce regeneration even with supplemental planting. The shelterwood with reserves with the supplemental planting was the only treatment to have adequate spruce regeneration but it did significantly shift overstory density, resulting in a more uniform overstory. While, the shelterwood with reserve did shift the overstory structure, this treatment created a stand structure and composition that will likely have short-term resistance and long-term resilience. This study provides an example of how metrics of resistance and resilience could be quantified and used to assess the success of a forest management plan or silvicultural prescription.

Metrics of resistance and resilience can span the range from applied (Chapter 2) to conceptual (Chapter 3). My third chapter, "A Conceptual Model for Forest Classification Based on Structural Attributes in the Intermountain West, USA," explored the relationship between structural attributes and environmental gradients. Forest

communities were classified independent of species based on five structural attributes: tree top height, tree diversity, space/relative density, and size diversity. Three structural types were described in the model: short single-layer forest, tall single-layer forest, and tall multi-layer forest. The model was tested with data collected from elevation gradients across the Intermountain West. The three structural types were strongly related to stand variables. The conceptual model is an additional tool that forest managers and researchers can utilize when they are developing forest management plans. The model can highlight similarities and differences between forests with similar structural attributes but different species composition. This comparability is predicted to lead to an increased ability to share information and research, potentially leading to novel silvicultural alternatives. Additionally, as climate change shifts the range and distribution of individual species (Elith and Leathwick, 2009), traditional forest classification systems which utilize species composition as the main metric will be less useful in long-term forest planning. Forest managers will likely have to assess trade-offs in maintaining composition versus structure (D'Amato and Bradford, 2012; see also Chapter 2). The development of this conceptual model will likely assist managers as they assess trade-offs in terms of maintaining or building resistance and resilience.

For trade-offs to be assessed at both the stand and regional scale, information about the basic ecology of the forest system should be known. For many commercially important tree species in the Intermountain West, decades of forestry research inform management decisions and aid the direction of future research (Burns and Honkala, 1990). However, for non-commercially important species, like the high five, much less information is known (Keane et al., 2011). The high five is composed of five-needle

white pines that generally occur at upper elevations. These species are currently threatened by interactions between white pine blister rust (*Cronartium ribicola* J. C. Fisch), mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and climate change, creating a management concern (Bockino and Tinker, 2012; Kearns and Jacobi, 2007). To address part of this gap in knowledge, my fourth chapter "Limber pine (*Pinus flexilis* James) structural and compositional dynamics across the Intermountain West" explored basic forest dynamics of limber pine across a broad geographic and elevation range. Local studies on limber pine document its dominance under harsh environmental conditions at both lower and upper elevation (Donnegan and Rebertus, 1999). Based on these local studies, I hypothesized that limber pine would have a bi-modal species distribution, peaking at lower or upper elevations. However, across the Intermountain West, limber pine was observed to be a consistent part of forest communities where it occurred. It was observed across a broad range of environmental (temperature, precipitation) and site (slope, aspect, stand age) variables. However, there are potential differences in the functional role of limber pine in forest communities. To explore these differences further, it is recommend that forest functional types should be developed for limber pine. Additional local studies across the range of limber pine are needed to further explore the role of limber pine when it is a minor component of forest systems compared to the dominant overstory species. When limber pine is a minor species, it likely increases stand level diversity and maintains forest functions after severe disturbances because of its ability to regenerate. This combination may be important because these forest systems may be more resilient against future disturbances and climate change.

Complex interactions between disturbance regimes and climate change, has and will continue to influence management decisions, which should be based on the best available science (Keenan, 2015; Littell et al., 2012). Federal, tribal, state, and private employees and members of the Society of American Foresters (SAF) strive to practice sustainable manage across private and public forests in the United States. These goals rely on partnerships between researchers and managers. These partnerships can increase our basic understanding of both applied and basic forest function. My dissertation research spanned the range of basic and applied forest research with the goal of exploring metrics of resistance and resilience in forest ecosystems of the Intermountain West. This research should be applicable to many natural resource managers throughout the Intermountain West as they strive to build and maintain resistant and resilient forests in an uncertain future.

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Windmuller-Campione, M.A. & Long, J. The high-five: A Comparison of Forest Dynamics of Five Needle Pines in the Intermountain West.

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Windmuller-Campione, M.A & Long, J. (2014). Structural and Compositional Patterns in Forest Communities in the Intermountain West. *International Union of Forest Research Organization.* Salt Lake City, UT.

Windmuller-Campione, M.A & Long, J. (2013). Limber Pine Forest Dynamics across the Intermountain West. *Society of American Foresters National Convention.* Charleston, NC

Campione, M.A., Previant, W., Nagel, L. (2011). Herbaceous Community Compositional Changes in a Northern Hardwood Forest. *Michigan Technological University* ESC/BRC Student Research Forum. Houghton, MI
Honorable Mention

Campione, M.A., Previant, W., Nagel, L. (2010). The Response of the Herbaceous Layer after 50 Years of Management in a Northern Hardwoods Forest. *Society of American Foresters National Convention.* Albuquerque, NM

CONFERENCE ORGANIZATION

Organizing Committee Chairperson
"Restoring the West: Change Agents and Managing Forest Resilience". Sponsored by Utah State University, Logan, Utah. Attended by 150 participants representing universities, state/federal agencies, non-governmental organizations and private landowners. The Organizing Committee developed the conference theme, made speaker arrangements, developed the schedule of events, worked with USU Extension to advertise the conference, and coordinated logistics (timing of food, speaker microphones) during the conference.

CONFERENCES ATTENDANCE

Session Moderator: October 2011 --- Logan, Utah
Restoring the West

September 2011 --- Cody, Wyoming
Whitebark Pine Annual Conference

Panel discussion member: The Future of Forestry: October 2008 --- Lansing, Michigan
Michigan Chapter of the Society of American Foresters
April 2008 --- Marquette, Michigan

Upper Peninsula, Michigan Chapter of the Society of American Foresters
Quiz Bowl Team Leader – 4th place finish: October 2007 --- Portland, Oregon
National Society of American Foresters Convention

TEACHING EXPERIENCE

Instructor of Record – Utah State University

2014	WILD 4750 - Monitoring and Assessment in Natural Resource and Environmental Management (2 Sections)	
	Credit hours: 4	Students: 5

Invited Lectures – Utah State University

2015	WILD 3850 – Vegetation and Habitat Management
2013	WILD 3850 – Vegetation and Habitat Management
2013	WILD 5700 – Forest Assessment and Management

Teaching Assistant – Michigan Technological University

2009/10	FW 3010 – Silviculture	
	Credit hours: 4	Students: ~ 20
2009/10	FW 3150 – Timber Harvesting	
	Credit hours: 2	Students: ~ 20
2009/10	FW 3170 – Land Measurement and GPS	
	Credit hours: 1	Students: ~ 45
2009/10	FW 3190 – Multi-resource Assessment	
	Credit hours: 3	Students: ~ 45
2009/10	FW 3600 – Wildlife Habitat	
	Credit hours: 3	Students: ~ 45
2009/10	FW 3840 – Forest Health	
	Credit hours: 3	Students: ~ 45
2008/09	Creating your Success	
	Credit hours: 1	Students: ~ 15
2008	FW 2051 – Field Techniques	
	Credit hours: 2	Students: ~ 25
2007	BL 2160 – Botany	
	Credit hours: 4	Students: ~ 15

Other Experiences

2009/11 Assistant for National Advanced Silviculture Program

GRANTS & FELLOWSHIPS

August, 2014 --- T.W. Daniel PhD Fellowship (August 2014 – August 2015)
Amount: $68,000

May, 2013 --- Utah Agricultural Experiment Station. Structural and Compositional Patterns in Forest Communities in the Intermountain West across Multiple Scales
Authors: **Marcella A. Windmuller-Campione** & James N. Long
Amount: $16,232

October, 2013 --- Composition and structure of limber and whitebark pine stands in the Interior West and the silvicultural implications
Authors: James Long, John Shaw, **Marcella Windmuller-Campione**
Amount: $15,000

August, 2011 --- USDA National Needs Graduate Fellowship Competitive Grant (NIFA) (NO. 2011-38420-20087) (September 2011 – July 2014)
Amount: $102,000

March, 2013 --- Ecology Center Graduate Award. Forest Structure and Composition across the Intermountain West.
Authors: **Marcella Windmuller-Campione**
Amount: $3,5000

October, 2013 --- Ecology Center Student Travel award, Wildland Resources Student Travel award, RGS Graduate Student Travel Grant for National SAF Convention
Amount: $940

October, 2010 --- Ecosystem Science Center, Travel Grant for National SAF Convention

Amount: $500

July, 2010 --- Horner Fellowship for Northern Hardwood Management
Amount: $2,000

May, 2010 --- Ecosystem Science Center, Herbaceous community shifts: What affect will it have on habitat classification systems? Focusing on sampling of earthworm populations
Amount: $750

ADDITIONAL EXPERIENCE

Fall Semester 2009 & 2010, Teaching Assistant for Integrated Field Practicum.

- TA for six different classes including silviculture, forest health, wildlife habitat, and a multi-resource assessment course
- Organized help session for students in areas of data management and statistics
- Assisted instructors in coursework implementation
- Assisted students with class assignments including stand and stock tables, HSI models, and the q-factor
- Scouted field locations for various classes, graded various assignments, and dealt with all equipment needs

April --- June 2009 & April –-- June 2011, Assistant for NASP (National Advanced Silviculture Program) Module 3 & 5

- Coordinated logistics for 40+ Forest Service Employees

July 2008 --- August 2008, Kumasi, Ghana, Africa

- Piloted the international summer experience for the Pavlis Leadership Institute which consisted of 6 weeks abroad with little to no faculty oversight
- Focused on implementing laptops in rural villages

August 2008 & 2006, Orientation Team Leader for Michigan Technological University

- Familiarized new students with the University
- Presented useful information to students to excel throughout their college experience

May 2007----August 2008, Researcher, REU (Research Exchange for Undergraduates)
Advisor: Andrew Burton

- Studied the effects of nitrogen deposition on first year sugar maple seedlings
- Assisted in the design development and sampled sugar maple seedlings across the Michigan gradient study to quantify the effects of increased nitrogen
- Collected and examined mycorrhizal samples from first year sugar maple seedlings to determine what effect they had on growth and survival

May 2007----June 2007, GIS technician for Michigan Technological University
Robert Froese, Undergraduate research assistant

- Digitized Plat books

AWARDS

2014 T.W. Daniel Fellowship

2011 Nominated for Department TA of the year
2008-2009 Outstanding Forestry Student Award
Dean's list for 8 semesters (4 semesters with a 4.0 GPA)
2007-2008 Provost Award for Scholarship
2007-2009 Century II Campaign Undergrad scholarship
2007-2008 Class of 1965 scholarship
2007-2009 John and Mae Hakala Endowment
2006-2009 Pavlis Institute Scholarship

TECHNICAL TRAINING

Wilderness First Aid (WFA) – 16 hour course
FISTA Chainsaw Certified
Basic Wildland Firefighter class: S-130, S-190, I-100, L-180, FI-110
Basic Arc GIS certification

ADDITIONAL EXPERIENCE

FIA Sampling Protocol
Basic Forestry Stand Exam Measurements
Distance Delivered Education
FVS (Forest Vegetation Simulator)
Large Data Sets
I.D. of plants in the Lakes States & Intermountain West
Statistics in R
Earthworm sampling & identification
Python
Dendrochronology methods climatic reconstruction
PC-Ord
SAS
Arc GIS

EXTRACURRICULAR INVOLVEMENT

Utah State University

Graduate Student Representative on the Forest Ecologist Faculty Search
Graduate Student Council:
- President 2013 – 2014 & 2014 - 2015
- Ecolunch Coordinator Spring 2013
- Graduate Representative to Wildland Resources Department 2012 - 2013

Graduate Student Committee for Ecology Center Seminar Series

Michigan Technological University

Forestry Club/ Society of American Foresters (MTU chapter) Past: President, Secretary
Welcome speech for Open House at Michigan Technological University: Fall 2008
Welcome speech for Prospective Students at Michigan Technological University: Spring 2007
Xi Sigma Pi Forestry Honor's Society: 2007- 2008: Vice President
Leadershape Graduate Winter 2006
Pavlis Institute for Global Technology: 2006-2011
School of Forestry Student Advisory Committee: 2005-2011

PROFESSIOINAL ORGANIZATION MEMBERSHIPS

Society of American Foresters (SAF)
The American Association for the Advancement of Science (AAAS)
Ecological Society of American (ESA)

APPENDIX

Dear Marcella,

thank you very much for your email. My name is Echo Zhang. I am writing this email on behalf of Forests Editorial Office.

As the manuscript was published in Open Access format, you do NOT need any permission to reprint it in your dissertation. A statement has be published with the paper as below.

Should you need any further information, please do not hesitate to contact us. We look forward to collaborating with you in the near future again.

Kind regards,
Echo Zhang

Dr. Echo Zhang
Managing Editor
Forests (http://www.mdpi.com/journal/forests)

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On 2015/5/13 0:15, Marcella Windmuller-Campione wrote:

Ms. Fengjie Zhao,

As previously discussed, an article which I am first author of is a key part of my dissertation. Attached is a letter which has information regarding the publication of this article in my dissertation at Utah State University on proquest. The letter must be signed and returned.

Please, let me know if you have any questions,

Marcella Windmuller-Campione

PhD Candidate
Utah State University

On Sun, Dec 14, 2014 at 6:53 PM, fengjie.zhao@mdpi.com <mailto:fengjie.zhao@mdpi.com> <fengjie.zhao@mdpi.com <mailto:fengjie.zhao@mdpi.com>> wrote:

> Dear Dr. Windmuller-Campione,
>
> Thank you very much for your confirmation. We did some editorial work for your manuscript and the modified version is attached herewith. We will now process your submission further by the modified version and will keep you informed about the status of your submission.
>
> As the matter of "This article will be part of my dissertation at Utah State University in the USA." There is no problem with that.
>
> Please keep the modified version for your further revision. Thank you very much for your cooperation.
>
> Should you need any further information, please do not hesitate to contact us.
>
> Kind regards,
>
> Ms. Fengjie Zhao
> Assistant Editor
> E-Mail: fengjie.zhao@mdpi.com <mailto:fengjie.zhao@mdpi.com>