AN ABSTRACT OF THE THESIS OF

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Title: Silvicultural Treatment Impacts on Understory Trees and 20-Year Understory Vegetation Dynamics in Mature Douglas-Fir Forests

Abstract approved:

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Policy regarding the management of public forests has undergone a drastic shift over the past couple of decades due to the loss old-growth forests in the Pacific Northwest (PNW) of the United States. For much of the 20th century, forest management on public lands emphasized timber production through the use of even-aged management practices. There has been increasing recognition, however, that traditional even-aged management approaches are unable to support species that rely on the complex, heterogeneous structures provided by old-growth forests. In response, public forest managers have redirected their focus to developing more ecologically sustainable forests capable of meeting a broad array of objectives including an increasing emphasis on the development of late-seral and old-growth characteristics.

Thinning has been identified as a promising method for promoting late-seral characteristics in managed stands. Recent long-term studies have shown that thinning stands does indeed accelerate the development of at least some late-seral structure characteristics, particularly when varying levels of thinning intensity and non-uniform retention patterns are incorporated into silvicultural prescriptions. Likewise, thinning

has also shown some ability to increase the abundance of late-seral associated plant species in the understory.

The impacts of thinning on vegetation dynamics are complicated by external factors such as natural disturbance events and the influence of pre-treatment vegetation on post-treatment communities. Within the context of managing for late-seral attributes, thinning is used to imitate natural disturbance processes. However, this does not preclude the occurrence of natural disturbances, which may either disrupt or compound treatment effects. Initial site conditions create another potential complication for the development of late-seral attributes by limiting the potential for change in understory communities. While some studies have shown that thinning improves late-seral plant abundance, others have found that the legacy of pre-treatment vegetation has a stronger impact on post-treatment communities. This study focused on the impacts of ice storm disturbance and pre-treatment vegetation on the understory of mature Douglas-fir forests using the ongoing Mature Forest Study (MFS), a long-term silvicultural experiment evaluating the effects of thinning and understory vegetation management treatments, as a framework.

The first study examined the impact of an ice storm (glaze disturbance) on planted understory trees. Specifically, I looked at the effect of understory tree species, tree size, and overstory neighborhood environment on the type (bending, crown loss), source (ice loading, falling debris), and severity of damage experienced by planted understory trees at one of the MFS sites. Tree species, size, and overstory environment all affected the amount of understory glaze damage. Frequency and severity of damage both varied among underplanted tree species. In general, smaller trees were more prone to being bent, while larger trees were more susceptible to crown loss. The Douglas-fir component of the overstory provided enough additional sheltering that the increased risk to understory trees from falling debris was balanced by a corresponding decrease in the odds of damage by ice loading. This was not the case for the hardwood component; increasing risk of damage to understory trees from falling debris with increasing hardwood basal area drove an overall increase in the

risk of understory damage as hardwood basal area increased. This study suggests that species, tree size, and overstory environment all need to be considered by managers hoping to reduce glaze damage risk to younger cohorts in multi-aged stands.

The second study investigated the impacts of thinning intensity and herbicide application on the long-term (20-year post-treatment) development of understory vegetation communities on both of the MFS sites. Trends were examined with a focus on the ability of herbicide application, in concert with thinning treatments, to reduce the legacy of common pre-treatment species and promote the abundance of late-seral associates. Results indicated that both thinning intensity and herbicide application affected 20-year changes in understory plant community composition. Herbicide application was associated with a decrease in the abundance of common pre-treatment species, suggesting that it did reduce the legacy effect. However, this was not associated with any change in the abundance of late-seral species. While light thinning showed some ability to mitigate decline in late-seral species relative to higher intensity thinnings, there was no evidence of treatment interaction with herbicide application. These results suggest that while managers may be able to reduce the influence of initial site conditions on post-treatment vegetation communities, the use of herbicides offers little control over the successional trajectory of the understory. Light thinning appears to be the most effective means of increasing late-seral species abundance, although the use of herbicides to meet other management objectives is not contraindicated by the results of this study. Overall, these results suggest that the best options available to managers to both reduce glaze disturbance impacts to understory trees and hasten the development of late-seral plant communities are heavy thinning with unmanaged leave patches to provide late-seral refugia, or light thinning with gaps to provide growing space for better tree regeneration.

Silvicultural Treatment Impacts on Understory Trees and 20-Year Understory
Vegetation Dynamics in Mature Douglas-Fir Forests

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

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Jim E. Priebe, Author

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CONTRIBUTION OF AUTHORS

Dr. Matt Powers was involved in the development of all research questions and results interpretations, as well as editing the contents of this thesis. Liz Cole assisted with the data collection for ice storm damage, and has been the project coordinator and primary data collector for all research in the Mature Forest Study since its inception.

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1. GENERAL INTRODUCTION

In the past, management of public lands in the Pacific Northwest of the United States (PNW) was focused on even-aged management with an emphasis on timber production. Over the past couple of decades, however, societal values regarding the use of public forest lands have shifted (Franklin and Johnson, 2014; Steel et al., 1994). In the early 1990s, several species, including the northern spotted owl (*Strix occidentalis caurina*) and marbled murrelet (*Brachyramphus marmoratus*) were listed as threatened by the federal government. The loss of old-growth habitat, which these species rely on for nesting, was identified as the primary threat to these endangered species (Doak, 1989; Hamer and Nelson, 1995; Hershey et al., 1998). Concerned with the decline in these and other species, both government and the public have begun to favor a more ecologically sustainable, ecosystem-based approach to public forest management that retains the types of structures that these and other species require for their survival. This has influenced policy and public land use at both the federal (USDA and USDI, 1994) and state (Oregon Department of Forestry, 2010) levels. The Oregon Department of Forestry, for instance, now manages state forests to maintain "healthy, productive, and sustainable forest ecosystems… that provide a full range of social, economic, and environmental benefits." This includes not only timber production, but other objectives such as recreation, protection of water supplies, and provision of a range of structures for habitat and the preservation of biodiversity.

The even-aged management that was primarily used on public forestland in the 20th century has been unable to meet such a broad array of objectives. By limiting the overstory to a single age/size class of trees, even-aged management simplifies stand structure (Hansen et al., 1991; Swanson and Franklin, 1992). The simplification of stand structure, in turn, homogenizes stand environment, reducing the variety of available habitat types. Ultimately, this leads to a decrease in biodiversity as species that rely on absent environments (such as the spotted owl) are extirpated.

Because of their ability to support a diverse array of species (D'Amato et al., 2009; Hansen et al., 1991), silviculturists have begun looking to old-growth forests as exemplars of healthy ecosystems. Old-growth provides many ecosystem functions beyond fostering biodiversity as well, such as sequestering carbon (Luyssaert et al., 2008) and providing structural complexity (Franklin and Van Pelt, 2004). Far from being even-aged, old-growth forests have a high degree of vertical and horizontal heterogeneity, with an overstory composed of trees in a range of age/size classes (Franklin and Van Pelt, 2004). Centuries of natural processes create a patchy mosaic of communities and structural features (Hansen et al., 1991); this includes snags and fallen deadwood for wildlife habitat (Thomas et al., 1979), canopy gaps that favor early colonizers and light-responsive shade tolerant species (Goldblum, 1997; Spies and Franklin, 1991), and areas of closed canopy that favor shade tolerant species (Spies and Franklin, 1991). Late-seral associated species in particular rely on the diverse structural conditions provided by old-growth forests (Halpern and Spies, 1995; Lindh and Muir, 2004).

The combination of these factors creates the high level of biodiversity for which late-seral, old-growth forests are known. This holds true for both plant (Halpern and Spies, 1995) and animal (Tews et al., 2004) species. In addition to the ethical concerns regarding the preservation of species, high biodiversity increases ecosystem resilience to degradation in the face external forces such as human-caused disturbance and climate change (Drever et al., 2006; Thompson et al., 2009). For example, high diversity provides functional group redundancy, ensuring that important ecosystem functions are not lost if environmental conditions change (Fischer et al., 2006).

In natural forests, structural heterogeneity develops as a result of disturbance history (Franklin and Van Pelt, 2004; Franklin et al., 2002; Hanson and Lorimer, 2007; Spies et al., 1990). Repeated disturbance at a range of spatial and temporal scales produce the mosaic of structures for which old-growth forests are known (Drever et al., 2006; Scheller and Mladenoff, 2002). In the PNW, the main sources of disturbance are windthrow, wildfire, and disease (Spies and Cline, 1988). Windthrow produces canopy gaps of varying sizes, depending on the severity of the event. These canopy gaps release suppressed trees, improve growth, and alter the vegetation community in the understory (Palmer et al., 2000; Rumbaitis del Rio, 2006; Van Pelt

and Franklin, 1999). Wildfire often acts on a larger scale than windthrow, creating a landscape-level mosaic of different age classes (Heinselman, 1973). Fire also recycles nutrients, boosting productivity in the aftermath of the disturbance (Boerner, 1982). Ice storms are a far less common source of disturbance in the PNW, particularly compared to the eastern half of the US (Changnon, 2003), but still have the potential to produce long-lasting impacts on a forest system.

The discrepancies between unmanaged and traditionally managed stands have led to an increased focus on developing old-growth characteristics in managed forests (Puettmann and Ammer, 2007). There is widespread recognition that silviculturists will need new tools and management strategies in order to face current and future challenges to the region's forests (Bauhus et al., 2009; Puettmann and Ammer, 2007). Part of this strategy is the retention of unmanaged reserves that can act as refugia for late-seral species (Bengtsson et al., 2003). However, the retention of unmanaged forests in reserves alone is insufficient to maintain the health and sustainability of a forest (Fischer et al., 2006); current research recognizes the need to develop greater structural complexity in managed stands as well. This has resulted in a focus on mimicking disturbance (Drever et al., 2006), longer stand rotations (Puettmann and Ammer, 2007), and accelerating the development of old-growth structural features (Bailey and Tappeiner, 1998).

Thinning is one tool that silviculturists can use to promote structural development. There is a substantial body of literature showing that thinning can accelerate the development of at least some late-seral structural features in a stand (Bailey and Tappeiner, 1998; Dodson et al., 2012; Schütz, 2002). As a result of this acceleration, thinning also has the potential to increase the abundance of late-seral vegetation in managed stands, bringing them closer to old-growth conditions (Bailey et al., 1998; Lindh and Muir, 2004). Variable density thinning (VDT) has the potential to be particularly effective, compared to standard uniform thinning. VDT involves varying the level of overstory retention across a stand, as well as varying the pattern of retention by including unharvested leave areas (skips) and multi-tree openings (gaps) (Harrington, 2009). This non-uniform method of thinning places an emphasis on creating structural and community heterogeneity within a stand, more closely imitating the effects of disturbance on natural forests (Ares et al., 2009; Harrington et al., 2005; Maguire et al., 2007).

Given that thinning performs many of the same functions as natural disturbance, there exists the potential for silvicultural and natural disturbances to interact, either disrupting or compounding the effects of management. There is already a substantial body of literature on the impacts of fire and windthrow in forests in the PNW, but the impacts of ice storms have not been heavily researched in this area.

An ice storm, also known as a "glaze event," is defined by the National Weather Service (2009) as any storm where ice accumulation is at least 6.35 mm. Severe glaze events create a partial canopy disturbance, potentially modifying forest structure and communities by damaging trees and shrubs in both the overstory and the understory. This damage can occur as a result of either ice loading or mechanical damage from falling trees and branches (Boerner et al., 1988). The damage caused by glaze events can vary widely in both type and severity, ranging from slight bending and mild crown loss to severe bending, uprooting, or complete crown loss (Bragg et al., 2003; Nykänen et al., 1997). In general, milder forms of damage are unlikely to significantly impact tree growth and survival (Bragg and Shelton, 2010; Bragg et al., 2003). Conversely, trees that are severely damaged have a high chance of mortality, and full recovery is unlikely even for those that survive.

The impacts of glaze events are complicated by a large number of influencing variables at scales of both individual trees and stands. One of the primary factors influencing damage susceptibility at the individual tree scale is species (Boerner et al., 1988; Lafon, 2006). This is because species is a major determinant of physical properties such as wood strength, branch angle, and crown form (Bragg et al., 2003; Bruederle and Stearns, 1985; Van Dyke, 1999). These properties influence things such as resistance to breakage (Wilson et al., 2013), crown area available for interception (Lemon, 1961), and the ability of branches to shed ice/snow (Sampson and Wurtz, 1994). Another factor that influences a tree's susceptibility to glaze damage is size, regardless of its species. As with species, tree size can affect both the type (Lafon, 2006; Shepard, 1975) and severity (Hopkin et al., 2003; Nielsen et al., 2003) of damage. In general, larger trees are more likely to experience crown breakage, while smaller, more flexible trees are likely to bend instead. Overall, glaze damage severity tends to peak in trees that fall into intermediate size classes.

Damage to trees is also affected by the surrounding stand environment. Due to their greater exposure, dominant/codominant trees are more likely to be damaged than suppressed individuals, which receive some degree of shelter (Rebertus et al., 1997). There is some evidence of variation within the dominant layer as well, as dominant trees appear to show less susceptibility than codominant ones (Warrillow and Mou, 1999). At an even coarser scale, the amount of damage to a stand is also strongly connected to elevation and slope aspect and inclination (Rhoades, 1999; Seischab et al., 1993). All of these variables come into play in determining overstory susceptibility to damage, which in turn impacts the amount of damage to understory cohorts (Boerner et al., 1988; Bragg et al., 2003). In multi-species stands, this can lead to a shift in overstory species composition and alter successional trajectories (Lemon, 1961; Smith, 2000; Whitney and Johnson, 1984).

While glaze events are relatively uncommon in the Oregon Coast Range (only five major events from 1949-2000; Changnon, 2013), they still have the potential to alter long-term stand development. With all of the different variables that influence damage susceptibility, these alterations can be extremely difficult to predict. For instance, there is conflicting information on whether conifers are more (Boerner et al., 1988; Lemon, 1961) or less (Bruederle and Stearns, 1985; Irland, 2000; Nielsen et al., 2003) susceptible to damage than hardwoods. These difficulties extend to understanding how glaze disturbances interact with common management practices. As an example, some researchers have found that thinning increases short-term susceptibility to damage (McCulloch, 1943; Shepard, 1975), while others have found no such effect (Nielsen et al., 2003).

In the past, there was relatively little need to understand the impacts of glaze disturbances within the context of westside forestry in Oregon. Since traditional management uses short rotation cycles, the risk of a stand experiencing a severe glaze event within a particular rotation is relatively low. With the longer rotation cycles suggested by researchers such as Puettmann and Ammer (2007) for developing late-seral stand characteristics, however, the odds of a glaze event occurring during a given stand's lifetime become higher. At present, there is particularly little information on how these interactions impact damage to understory cohorts. Since the health and survival of understory trees is critical to the future development of complex, multi-aged stands,

this should be of particular concern to managers seeking to promote late-seral stand characteristics. The ice storm that struck the central Oregon Coast Range in November 2014 (Norlander and Kanaskie, 2014; Withrow-Robinson, 2014) provided an excellent opportunity to expand knowledge of this subject.

Potential complications regarding the use of thinning to accelerate the development of late-seral characteristics extend beyond those that arise from additional disturbances, however. The impacts of thinning on understory vegetation communities can be unclear as well. Variable density thinning is generally understood to improve the diversity and cover of understory communities, but can also have either minimal (Ares et al., 2009; Davis and Puettmann, 2009) or even detrimental (Alaback and Herman, 1988) impacts on these metrics as well. The effects of thinning on understory vegetation dynamics are further complicated by the influence of thinning intensity (Battles et al., 2001; Griffis et al., 2001). For instance, the late-seral species (such as *Mahonia nervosa* and *Adenocaulon bicolor* in this study) that silviculturists often wish to promote generally perform better under lighter thinnings, and can respond negatively to more intense disturbance.

The legacy of pre-treatment vegetation can also impede the development of desired community assemblages. The dominant species within the understory usually persist even after treatment (Halpern and Lutz, 2013; Hughes and Fahey, 1991). With higher initial abundances and a greater concentration of propagules, dominant species can easily recolonize disturbed areas and out-compete other vegetation (Tappeiner et al., 2001). Favorable site conditions may render them even more resistant to competition (McGlone et al., 2011). Unfortunately, this "legacy effect" can depress diversity (Ristau et al., 2011), and could potentially limit the abundance of desirable late-seral species.

The effects of thinning intensity and legacy effects from pre-treatment vegetation can make it difficult for silviculturists to promote a desired suite of species through overstory density reductions alone. One possibility for dealing with this is the use of vegetation management tools, such as herbicide application. Past research has shown that herbicides are effective at reducing the legacy effect on controlling the abundance of dominant species (Iglay et al., 2010; Ristau et

al., 2011). This opens space in the understory for less common plant species, increasing their abundance and overall community diversity (DiTomaso et al., 1997; Getsinger et al., 1997).

In today's society, the use of herbicides is often met with concern from the public. However, proper application of appropriate herbicides poses little risk to human or ecosystem health (Newton et al., 2008; Wagner et al., 2004). While risks have not been evaluated in forest systems managed for late-seral characteristics specifically, reductions in species diversity following herbicide application in other systems are typically transient (DiTomaso et al., 1997; Rice et al., 1997). Considering the potential risks and benefits, investigation into the use of herbicides to promote late-seral vegetation is a worthwhile endeavor. In particular, the interaction of herbicide treatment and thinning treatment in the development of late-seral understory communities is currently undocumented.

The Mature Forest Study (MFS) in the Oregon Coast Range provides an excellent opportunity to examine how overstory density reductions and understory vegetation management treatments interact with each other and with natural disturbance events including an ice storm in November of 2014 to influence the development of the understory. The MFS was established to study the effects of a combination of VDT, planting, and understory vegetation management on overstory tree growth and the development of late-seral characteristics such as structural and plant community diversity in mature Douglas-fir forests (Brandeis et al., 2001; Newton and Cole, 2015). Treatment plots were established at two sites: a 50-year-old Douglas-fir stand in McDonald Forest in the foothills of the central Oregon Coast Range, and another 50-year-old Douglas-fir/western hemlock stand in Blodgett Forest in the northern Coast Range. Study plots received either uniform or gap thinning, ranging from high to low retention, as well as either herbicide spray or no herbicide spray. In addition, all study plots were underplanted with Douglas-fir, grand fir (McDonald only), western hemlock, and western redcedar. The MFS is an ongoing study already past its twentieth year. At the time of the 2014 ice storm (affected McDonald only) and the most recent measurement period, the overstory cohorts at McDonald and Blodgett were approximately 70 years old.

Broadly, this study aims to elucidate the impacts of silvicultural treatment and natural disturbance on the understory of mature Douglas-fir forests. My investigation focused on two

aspects of the understory: the younger cohort of planted understory trees and the longer-term development of understory vegetation communities, both of which are of concern to public forest managers seeking to develop late-seral characteristics in managed stands. I focused on two broad research questions:

Research Question 1: How do neighborhood-scale overstory environment and individual tree characteristics affect the damage done to understory trees by a glaze disturbance? More specifically, this study sought to determine: (1) how frequency of damage presence, type, and severity differed among planted understory tree species; (2) how likelihood of total damage and damage from direct (ice loading) and indirect (falling debris) damage varied with the density of conifers and hardwoods in the overstory; and (3) how severity of crown and bending damage varied with planted understory tree size. By answering these questions, I hope to provide a clearer picture of how glaze disturbance impacts the understory in managed stands, and how managers can mitigate potential risks.

Research Question 2: How do vegetation management and retention level (i.e. thinning intensity) affect the strength of the legacy effect of pre-treatment vegetation and influence the development of the understory community? More specifically, this study sought to determine: (1) how retention level and herbicide application affect changes in community composition from pre-treatment conditions; (2) how these treatments affect the richness and abundance of common understory species; (3) how these treatments affect the richness and abundance of early- and late-seral-associated understory species; and (4) whether understory vegetation responses to herbicide application vary with retention level. By answering these questions, I hope to whether herbicide application reduces legacy effects of pre-treatment vegetation, and if so, whether late-seral-associated species benefit from this potential reduction across a range of thinning intensities.

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2. MANUSCRIPT 1: EFFECT OF SPECIES, TREE SIZE, AND OVERSTORY ENVIRONMENT ON ICE STORM DAMAGE TO UNDERSTORY TREES IN A MATURE DOUGLAS-FIR FOREST

2.1. Abstract

When managing forests on extended rotations for development of late-seral stand characteristics, silviculturists need to account for numerous factors, including the possibility of canopy disturbance from natural agents. Glaze events (i.e. ice storms) are a potential source of disturbance whose effects have not been researched in forests in the PNW. This study examines the effects of overstory environment, species, and size on presence, source, and severity of damage sustained by understory trees in a mature Douglas-fir forest as a result of the November 2014 glaze event in the central Oregon Coast Range. Trees were measured for total height, DBH, and basal diameter, and visually rated for damage type (bending, crown loss), source (direct damage from ice loading or indirect damage from falling debris), and severity. Effect of species on damage presence and severity was tested using contingency table analysis; the relationships between damage source and conifer and hardwood basal area were tested using binary logistic mixed models; the relationships between damage severity and understory tree DBH and height:diameter ratio were tested using ordinal logistic mixed models. Frequency of damage and damage severity were found to differ between some species. Western redcedar was less prone to crown damage and more prone to bending damage than the other three species, while western hemlock showed the opposite trend. Overall, redcedar was damaged least frequently, and hemlock was damaged most frequently. Increasing overstory conifer and hardwood basal area were found to reduce the odds of direct damage and increase the odds of indirect damage on understory trees. DBH was negatively associated with bending damage severity and positively associated with crown damage severity; height:diameter ratio was positively associated with severity of both damage types. These results suggest that managers may want to consider overstory environment, species, and understory tree size when assessing and controlling for risk from future glaze events.

2.2. Introduction

Historically, forest management in the Pacific Northwest (USA) has focused on maximizing timber production. In recent years however, cultural values have expanded to

include a broader array of uses for forest land, including protecting water supplies and fish populations, fostering biodiversity, recreation, aesthetic value, and carbon sequestration, among others. Traditional intensive management has been unable to meet the full range of objectives that contemporary society demands. The focus on maximized production and even-aged management simplifies forest structure, homogenizing habitat types and limiting the diversity of both vegetation and wildlife (Hansen et al., 1991; Swanson and Franklin, 1992).

Because of this, researchers and forest managers have been changing their focus to multi-objective management strategies capable of satisfying a range of human and ecological needs (Puettmann and Ammer, 2007). This has been especially true for the publicly-owned forestlands in the PNW since the introduction of the Northwest Forest Plan in 1994 (USDA and USDI, 1994). This shift in federal policy has, in turn, guided public land management at lower levels of government toward similar ecologically sustainable, multi-use approaches. For instance, current management on Oregon's state forestlands is guided by the principle of providing a sustainable source of timber for human use, while simultaneously maintaining "healthy, productive, and sustainable forest ecosystems… that provide a full range of social, economic, and environmental benefits" (Oregon Department of Forestry, 2010).

Maintaining "healthy, productive, and sustainable" forests is a complex challenge, however. To remain healthy in perpetuity, forest ecosystems must have the capacity to cope with human use, natural disturbance, and changing climatic and environmental conditions (Drever et al., 2006; Thompson et al., 2009). One of the main contributing factors to this resilience is structural complexity, both at a patch and landscape scale. Structural complexity promotes biodiversity and increases the capacity of a forest to absorb external impacts without losing important ecosystem functions (Fischer et al., 2006; Thompson et al., 2009); it is also a key component of late-seral (i.e. old-growth) forests (Franklin et al., 2002; Seidl et al., 2014; Spies, 1998).

Managers have developed a variety of methods to artificially hasten the development of late-seral structure in managed forests. One such tool is variable density thinning (VDT), which mimics the effects of self-thinning and disturbance (Bailey and Tappeiner, 1998; Dodson et al., 2012; Schütz, 2002). The "variable" nature of VDT creates stands with both spatial and temporal

variation in tree age, density, and canopy structure, more similar to old-growth forests (Bailey and Tappeiner, 1998).

In unmanaged forests, structural complexity is developed through natural processes such as self-thinning, understory suppression and release, and disturbances (Brokaw, 1985; Franklin and Van Pelt, 2004; Franklin et al., 2002; Hanson and Lorimer, 2007). Disturbance regimes in particular are critical to the development of complex forest structures. Repeated disturbance across multiple spatial and temporal scales creates a mosaic of structural features that promotes biodiversity and ecosystem resilience (Drever et al., 2006; Franklin et al., 2002; Seidl et al., 2014; Spies, 1998). Because of these processes, biodiversity tends to be relatively high in late-seral forests, a factor that contributes to their stability and resilience (D'Amato et al., 2009; Halpern and Spies, 1995; Thompson et al., 2009).

In the Oregon Coast Range, wildfire and windthrow are the two primary sources of natural disturbance (Spies and Cline, 1988). In general, windthrow produces canopy gaps of varying sizes, releasing suppressed understory trees and altering local vegetation communities (Palmer et al., 2000; Rumbaitis del Rio, 2006; Van Pelt and Franklin, 1999). On a coarser scale, fire regimes cycle nutrients and create a landscape-level patchwork of different age classes (Boerner, 1982; Heinselman, 1973). Because of their frequency and influence on the landscape, a large body of research exists on these processes and their effects on forest ecosystems in the region, as well their implications for management. Major ice storms are not a prominent form of disturbance in the Coast Range, but still occur periodically (Changnon, 2003). From 1949-2000, there were five severe ice storms across the PNW. By contrast, the return interval of severe, stand-replacing fire in Douglas-fir forests in the PNW is in the range of 150-250 years, with more frequent light-moderate fires (Agee, 1993).

According to the National Weather Service (NWS), an ice storm, or "glaze event," is defined as an event where ice accumulations reach at least 6.35 mm (National Weather Service, 2009). Glaze events create partial canopy disturbances that modify forest structure by altering the overstory environment, as well as damaging understory trees and shrubs. Ice storms can damage trees in several ways, with varying degrees of severity (Bragg et al., 2003; Nykänen et al., 1997). At the mild end of the spectrum, trees may bend slightly or experience minor crown loss. In

general, trees will not suffer long-term negative effects from such minor damage (Bragg and Shelton, 2010). At the other end, trees may be bent prone, uprooted, or suffer major or complete crown loss. Trees that receive severe damage are at high risk of mortality, and those that survive are unlikely to recover fully (Bragg and Shelton, 2010; Bragg et al., 2003). Numerous factors affect a tree's resistance to glaze damage, including green wood strength, crown form, species, size, and stand environment (Bruederle and Stearns, 1985; Hopkin et al., 2003; Lemon, 1961; Nielsen et al., 2003). Additionally, damage may result from either direct (i.e. ice loading) or indirect (i.e. falling debris) sources (Boerner et al., 1988).

As with any disturbance, glaze events can interact with previous management, such as VDT, disrupting or compounding the impacts of silvicultural treatments. The effects of these interactions can be difficult to predict, due to the sheer number of variables that contribute glaze damage (Bragg et al., 2003). For instance, looking at stands in eastern Ontario, Nielsen et al. (2003) found some variation in overstory damage with stand type, but no significant difference between managed and unmanaged stands; others, however, have found that recent thinning can make stands much more susceptible to glaze damage (McCulloch, 1943; Shepard, 1975).

Disturbance/management interactions are further complicated by the large number of factors that impact both individual tree and stand-level responses to glaze events. At the individual tree scale, the type and severity of glaze damage sustained can be influenced by species (Boerner et al., 1988; Lafon, 2006). These variations derive from the physical properties of different tree species, such as crown form, branch angle, and wood strength (Bragg et al., 2003; Bruederle and Stearns, 1985; Van Dyke, 1999). For instance, since ice interception is a function of crown surface area (Lemon, 1961), species with wider crowns are at increased risk of glaze damage. Partly as a consequence of greater surface area, conifers are generally considered more susceptible to glaze damage than deciduous hardwoods (Boerner et al., 1988; Lemon, 1961), although there is disagreement over the strength of this trend (Bruederle and Stearns, 1985; Irland, 2000; Nielsen et al., 2003). Differences in species susceptibility can have far-reaching consequences, altering species composition and the rate of successional change in forest stands (Lemon, 1961; Smith, 2000; Whitney and Johnson, 1984).

Tree size also plays a role in glaze damage susceptibility, independent of species. Past research has shown that tree size is related to both damage type (Lafon, 2006; Shepard, 1975) and damage severity (Hopkin et al., 2003; Nielsen et al., 2003). In general, smaller trees tend to be more prone to bending, while larger individuals are more likely to lose canopy. Damage severity tends to show a non-linear trend, where small trees tend to receive the least severe damage, intermediate-sized trees receive the most, and large trees receive an intermediate amount. Relatedly, canopy position also contributes to individual tree damage. Trees occupying dominant/codominant positions in the canopy generally receive more damage than suppressed trees (Rebertus et al., 1997), as they are more exposed. Some variation can occur within the dominant positions as well, as dominant individuals may display lighter damage than codominant or intermediate trees (Warrillow and Mou, 1999). All of these factors, along with environment, topography, and storm severity, influence the amount of glaze damage received by the forest canopy; in turn, the canopy environment and severity of canopy damage affect the damage to understory trees (Bragg et al., 2003).

This information, however, comes from regions where glaze events are more common, such as Canada and the northeastern US. To the author's knowledge, almost no literature on the impacts of glaze disturbances in westside forests in the PNW currently exists. Infrequent disturbance events may pose limited concerns for managers focused on intensively-managed, short rotation plantations. However, now that managing for multi-aged stands with longer rotations is more common in the PNW and elsewhere, understanding how glaze events affect these systems has become more important. While significant glaze events are rare, they have the potential to have long-term impacts on these multi-aged stands (Abrams and Scott, 1989; Lemon, 1961; Whitney and Johnson, 1984). In particular, little information exists on how glaze disturbance impacts understory cohorts, a critical component of multi-aged systems.

In November 2014, a major ice storm struck the central Oregon Coast Range, causing significant overstory damage. The ice ranged from 13-19 mm in thickness, and caused branch loss, top break-out, and uprooting across 6,600 acres of forestland centered around Blodgett, OR (Norlander and Kanaskie, 2014; Withrow-Robinson, 2014). This storm provided an excellent opportunity to study the interactions between disturbance and management on the understory

cohort of a Douglas-fir stand managed using a multi-aged system. The Mature Forest Study (MFS) is an ongoing silvicultural study just past its twentieth year. The primary goal of the MFS is promote the growth of dominant overstory trees while increasing stand structural diversity, using a combination of VDT, planting, and understory vegetation management (Brandeis et al., 2001; Newton and Cole, 2015). One of the sites for this study is located in the foothills of the Coast Range, an area that received significant storm damage. Using the MFS as a framework, the objectives of this study were to determine how: (1) frequency of damage presence, type, and severity differed among planted understory tree species; (2) likelihood of total, direct, and indirect damage varied with overstory density; (3) severity of crown and bending damage varied with planted understory tree size.

2.3. Methods

2.3.1. Study site

All data for this study were collected at the McDonald Forest site within the Mature Forest Study (MFS). The MFS is a long-term silviculture experiment with study sites on two Oregon State University-owned Douglas-fir forests in the Coast Range of northwestern Oregon: McDonald and Blodgett (detailed site descriptions are available in Nabel et al. 2013).

McDonald Forest is located in the eastern Oregon Coast Range, 8 km north of Corvallis, OR. The area has a warm climate with a long summer dry season and low relative humidity. When the MFS began, the overstory at McDonald was composed mostly of 50-year-old planted Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), mixed with some naturally regenerated bigleaf maple (*Acer macrophyllum* Pursh) and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) scattered throughout. The understory was mainly dominated by fern and shrub species. The most abundant of these were western sword fern (*Polystichum munitum* (Kaulf.) C. Presl.), western bracken fern (*Pteridium aquilinum* (L.) Kuhn), trailing blackberry (*Rubus ursinus* Cham. & Schltdl.), Himalaya blackberry (*Rubus armeniacus* Focke), Pacific poison oak (*Toxicodendron diversilobum* (Torr. & A. Gray) Greene), hazel (*Corylus cornuta* Marshall), and ocean spray (*Holodiscus discolor* (Pursh) Maxim.). Prior to the MFS, the site was thinned in 1964 and again in 1980. The glaze event occurred in November 2014, 21 years after the original MFS treatments

were conducted; thus, at the time of this study, the overstory was approximately 70 years old, and the understory was 21 years old.

2.3.2. Experimental design

The Mature Forest Study was designed as a randomized complete block experiment with a split-split plot arrangement of treatments (Fig. 2.1). Three 20-ha blocks were established by relative site quality in McDonald Forest, using elevation as a proxy. Lower slope positions were equated to higher site quality.

Each of the three blocks contained two 10-ha units. Within blocks, each unit was randomly assigned to receive either uniform thinning or gap thinning treatments. In uniform treatments, residual trees were left evenly-spaced throughout the whole plot. In the gap treatments, twelve 0.10-ha gaps and an equal number of 0.06-ha gaps were cleared within a matrix of evenly spaced trees.

Each unit was divided into four 2.5-ha plots. Within units, each plot was randomly assigned to receive light thinning, moderate thinning, moderate-heavy thinning, or heavy thinning (Table 2.1). All plots were thinned from below during fall 1993. The medium and medium-high treatments were all rethinned to initial post-thinning density after 8 years. Overall, basal area was equivalent at each level of thinning for uniform and gap plots.

Each of these plots was further divided into three 0.5-ha subplots, surrounded by an 18-m buffer. Within plots, each subplot was randomly assigned to receive no vegetation management treatment, spray treatment, or release treatment. Buffers were left untreated. Spraying was done in late summer, at least one month before thinning. The main herbicide used was a mixture of glyphosate and imazapyr. Herbicide was applied as a broadcast spray across subplots using the "waving wand" method.

Understory tree sampling occurred at the level of grids of planted trees within each of the subplots nested within plots (Fig. 2.2). Each plot was underplanted in a matrix consisting of 32 columns. Western redcedar, Douglas-fir, grand fir, and western hemlock seedlings were planted in pairs of columns by species, with a repeating order for the pairs (e.g. DDGGHHCC, repeated four times) randomly generated for each plot. Each of the subplots contained a 15 row subset of this plot-level matrix. Western redcedar seedlings were Plug+2 transplants, while all other

seedlings were Plug+1 transplants. Within each of these subplot-level matrices, four 8-column by 3-row grids of planted trees were selected for sampling. Each grid contained one 8-column sequence of column-pairs of seedlings (e.g. columns 1-8, 9-16). The 3-row range of planted trees (e.g. rows 9-11) was selected randomly for each grid.

In total, the study sample initially consisted of three blocks, six units, 24 plots, 72 subplots, 288 grids, and 6,912 trees (1,728 of each species). Based on an inventory conducted in summer 2015, 2435 sampled trees and 279 grids remained when the storm occurred. The remaining sampled understory trees and grids were lost to mortality over the 21 years since planting. Survival was uneven across both species and plots. At the time of this study, 1185 redcedar, 259 Douglas-fir, 701 grand fir, and 290 hemlock remained. All of these trees were resampled for this study.

2.3.3. Measurements

Each sampled understory tree was measured for total height, diameter at breast height (DBH), and basal diameter (BD; measured at 15 cm above the root collar). Sampled trees ranged widely in size: DBH ranged from 0-22.7 cm (mean: 6.0 cm) in western redcedar, 0-19.9 cm (mean: 4.8 cm) in Douglas-fir, 0-23.1 cm (mean: 4.1 cm) in grand fir, and 0-22.1 cm (mean: 7.5 cm) in western hemlock. Height was measured using either a 7.5-m extendable PVC height pole or a Haglöf Vertex III hypsometer. DBH and basal diameter were both measured using either 150 mm calipers or a diameter tape. In addition, each understory tree was visually rated for bending damage (Table 2.2) and crown damage (Table 2.3), and the source of damage was identified. Damage source was either direct (ice-loading) or indirect (falling debris). Damage was judged indirect if fallen debris of sufficient size to cause the damage was found within close proximity to a damaged tree and was in a position where it could reasonably be assumed to have been responsible for the damage, to the best of the author's judgment; any recent damage that did not meet these criteria was assumed to be a result of ice loading. For each column-pair of a particular species in each grid, overstory hardwood and conifer basal areas (BA) were estimated at a central point among the surviving planted trees using variable-radius plots (Fig. 2.2). Overstory hardwood BA was estimated using a basal area factor (BAF) 10 prism; overstory conifer BA was estimated using a BAF 20 prism. This was done rather than simply using the

overstory treatment category as a predictor to give a better estimate of the underplanted trees'
immediate overstory environment, and to account for variation in overstory density within each
retention treatment level. The MFS 20-year planted seedling size measurements were used for
this study, which were collected 16 months prior to the glaze event. All other data were collected
during the first growing season after the glaze event in summer 2015.

2.3.4. Analysis

2.3.4.1. Damage and species

Contingency table analyses with chi-squared tests for independence were used to
examine whether there was an effect of sapling species on degree of crown damage, degree of
bending damage, and presence/absence of damage. Trees that were uprooted (Damage Class 5)
were excluded from the contingency table analysis for crown damage due to low sample size (n
= 17 across all four species) and a lack of comparability to the other classes. Independence of
observations was assumed based on study design. Contingency tables of expected cell
frequencies were calculated to evaluate whether all cells had expected counts greater than five,
another requirement for the chi-squared distribution to be a valid approximation. Pearson
residuals were used to evaluate which categories differed from expected count values (Agresti,
2013).

2.3.4.2. Damage source and overstory environment

Logistic mixed effects regression models were used to examine the effects of planted
understory tree species, overstory hardwood BA, and overstory conifer BA on presence/absence
of damage to understory trees, as well as damage source (direct or indirect). The models used
were defined by the mathematical formula

$$log\left(\frac{p}{1-p}\right)_{ijk} \sim \beta_0 I_{0i} + \beta_1 I_{1i} + \beta_2 I_{2i} + \beta_3 I_{3i} + \beta_4 X_{4i} + \beta_5 X_{5i} + s_k + g_j$$

where

$log\left(\frac{p}{1-p}\right)_{ijk}$ is the log odds of response (damage, direct damage, or indirect damage) of the ith

understory tree, Y_i, being a 1, where $Y_i \sim$ Bernoulli (p), i = 1-2435 understory
trees, j = 1-279 subplots, k = 1-72 grids,

$\boldsymbol{\beta_0}$ is the estimated log odds of damage for western redcedar accounting for hardwood and conifer basal area,

$\boldsymbol{\beta_1}$ is the estimated log odds of damage for Douglas-fir accounting for hardwood and conifer basal area,

$\boldsymbol{\beta_2}$ is the estimated log odds of damage for grand fir accounting for hardwood and conifer basal area,

$\boldsymbol{\beta_3}$ is the estimated log odds of damage for western hemlock accounting for hardwood and conifer basal area,

$\boldsymbol{\beta_4}$ is the estimated increment in log odds of damage for an increase in hardwood basal area of 1 m^2 ha^{-1},

$\boldsymbol{\beta_5}$ is the estimated increment in log odds of damage for an increase in conifer basal area of 1 m^2 ha^{-1},

$\boldsymbol{I_{0i}}$ is 1 if the species of the ith tree is western redcedar, and 0 otherwise,

$\boldsymbol{I_{1i}}$ is 1 if the species of the ith tree is Douglas-fir, and 0 otherwise,

$\boldsymbol{I_{2i}}$ is 1 if the species of the ith tree is grand fir, and 0 otherwise,

$\boldsymbol{I_{3i}}$ is 1 if the species of the ith tree is western hemlock, and 0 otherwise,

$\boldsymbol{X_{4i}}$ is the overstory hardwood basal area around the ith tree in m^2 ha^{-1},

$\boldsymbol{X_{5i}}$ is the overstory conifer basal area around the ith tree in m^2 ha^{-1},

s_k is the random effect of the kth subplot on the log odds of damage, $s_k \sim N(0, \sigma_s^2)$ and $Cov(s_k, s_{k'}) = 0$, and

$\boldsymbol{g_j}$ is the random effect of jth grid nested within subplots on the log odds of damage, $g_j \sim N(0, \sigma_g^2)$ and $Cov(g_j, g_{j'}) = 0$.

2.3.4.3. Damage severity and understory tree size

Ordinal mixed effects regression models were used to examine the effects of understory tree species and size on the severity of bending damage and crown damage. As with the contingency table analysis, uprooted trees were excluded from the model for crown damage severity. The models used were defined by the mathematical formula

$$log\left(\frac{P(Y_i \leq m)}{P(Y_i > m)}\right) \sim \alpha_m - \beta_0 I_{0i} - \beta_1 I_{1i} - \beta_2 I_{2i} - \beta_3 X_{3i} - \beta_4 X_{4i} - \beta_5 X_{5i} - \beta_6 X_{6i} - s_k$$
$$- g_j$$

where

$log\left(\frac{P(Y_i \leq m)}{P(Y_i > m)}\right)$ is the proportional log odds of the ith understory tree, Y_i, falling into damage class m or below, where $Y_i \sim$ Multinomial $(p_0,\ldots p_{m-1})$, i = 1-2416, j = 1-279, k = 1-72, m (bending) = 0-2, m (crown) = 0-4,

α_m is the log odds for falling into the mth damage class or lower, where the β's are proportional for all levels of α,

β_0 is the incremental effect of being a Douglas-fir on the log odds of falling within a higher damage class,

β_1 is the incremental effect of being a grand fir on the log odds of falling within a higher damage class,

β_2 is the incremental effect of being a western hemlock on the log odds of falling into a higher damage class,

β_3 is the effect of an increase of 1 in height:diameter ratio on the log odds of a tree falling into a higher damage class; height:diameter ratio was calculated using basal diameter rather than DBH, as many trees had height below DBH,

β_4 is the effect of a 1-cm increase in DBH on the log odds of a tree falling into a higher damage class,

β_5 is the effect of a 1-m^2 ha^{-1} increase in hardwood basal area on the log odds of a tree falling into a higher damage class,

β_6 is the effect of a 1-m^2 ha^{-1} increase in conifer basal area on the log odds of a tree falling into a higher damage class,

I_{0i} is 1 when the species is Douglas-fir, and 0 otherwise,

I_{1i} is 1 when the species is grand fir, and 0 otherwise,

I_{2i} is 1 when the species is western hemlock, and 0 otherwise,

X_{3i} is the height:diameter ratio of the ith tree,

X_{4i} is the DBH of the ith tree in cm,

X_{5i}	is the overstory hardwood basal area around the ith tree in m^2 ha^{-1},
X_{6i}	is the overstory conifer basal area around the ith tree in m^2 ha^{-1},
s_k	is the random effect of the kth subplot on the log odds of a tree falling into a higher damage class, $s_k \sim N(0, \sigma_s^2)$ and $Cov(s_k,s_{k'}) = 0$, and
g_j	is the random effect of the jth grid on the log odds of a tree falling into a higher damage class, $g_j \sim N(0, \sigma_g^2)$ and $Cov(g_j,g_{j'}) = 0$.

Species was included in both the logistic and ordinal models to account for potential differences in damage response as a result of physiological differences in the planted species. Overstory hardwood and conifer BA were included in the ordinal models as covariates. Parameters were estimated using Laplace approximation of maximum likelihood, and significance of the overall models and variables were obtained from chi-squared likelihood ratio tests (LRT). For the logistic models for presence/source of damage, if species had a statistically significant influence, Bonferroni-adjusted pairwise comparisons were performed between all understory tree species to identify between which species these differences occurred. All results are presented in terms of odds and odds ratios. Odds is defined as the probability of an event occurring divided by the probability of it not occurring. An odds ratio is a multiplicative change in odds; thus, an odds ratio of 1.5 would indicate a 50% increase in odds associated with the specified change in an independent variable.

Assumptions were checked for the logistic and ordinal regression models to ensure the validity of the analyses. Random effects were used to compensate for a lack of spatial independence among observations due to the clustering of individual understory trees within grids and subplots. Variance inflation factors were calculated for the model parameters to assess multicollinearity. Overdispersion was checked using a comparison between Pearson residuals and residual degrees of freedom. Linearity of continuous predictors with the logit of the models was checked graphically for each species using the residuals from binomial response models at the grid level.

Finally, the proportional odds assumption for the ordinal models was checked by comparing parameter confidence intervals across separate binomial models for each threshold

level (e.g. $\frac{P(Y_i \leq 0)}{P(Y_i > 0)}$ vs. $\frac{P(Y_i \leq 1)}{P(Y_i > 1)}$). This assumption was not met for initial models of bending or crown damage severity. In the bending severity model, there was quasi-complete separation in DBH caused by limited data in the "prone" damage class (DC 3), particularly at higher values of DBH. This was resolved by combining DC 3 with DC 2. For the crown damage severity model, the same occurred for DBH at DC's 3 and 4. Since the lack of data occurred at larger values of DBH, rather than combine the top three damage classes, the data set for the crown damage severity model was limited to understory trees with DBH ≤ 10 cm.

2.4. Results

2.4.1. Damage and understory tree species

2.4.1.1. Total damage

A chi-squared test for independence on the contingency table of understory tree species and presence/absence of damage provides evidence that species has a statistically significant association with presence of damage (Table 2.4; $\chi^2_3 = 28.2$, P < 0.001). A plot of the Pearson residuals shows that the significance of this result comes primarily from the frequencies of damage in western redcedar and western hemlock (Fig. 2.3). Accounting for all types of damage, redcedar was damaged less often than expected, while hemlock was damaged more frequently than expected. Additionally, hemlock showed no damage less frequently than expected.

2.3.1.2. Bending damage

A chi-squared test for independence on the contingency table of understory tree species and bending damage class provides evidence that species has a statistically significant association with the degree of bending damage (Table 2.5; $\chi^2_9 = 54.4$, P < 0.001). A plot of the Pearson residuals shows that the significance of this result comes primarily from contrasts in prone and mostly prone frequencies (Fig. 2.4). Unlike the results for crown damage, western redcedar was made prone by ice damage significantly more frequently than expected. Douglas-fir was made mostly prone at a similar amount more than expectation. Both hemlock and grand fir, contrarily, were found prone less than expected.

2.4.1.3. Crown damage

A chi-squared test for independence on the contingency table of understory tree species and crown damage class (excluding uprooting) provides evidence that species has a statistically

significant association with the degree of crown damage (Table 2.6; $\chi^2_{12} = 79.9$, P < 0.001). A plot of the Pearson residuals shows that the significance of this result comes primarily from redcedar and hemlock (Fig. 2.5). Both Douglas-fir and grand fir saplings displayed damage frequencies within the expected range, with the exception that grand fir received severe crown damage more often than expected. Redcedar received no damage more frequently than expected, and received anything more than minor damage less often than expected, particularly in the moderate-severe crown loss range. Hemlock received more damage than expected; it took no damage less than expected, had moderate crown loss more frequently than expected, and moderate-severe crown loss much more frequently than expected.

2.4.2. Damage source and overstory environment

2.4.2.1. Total damage

The logistic mixed model for presence of damage showed overall significance against the null model consisting only of the intercept with nested random effects (LR $\chi^2_{11} = 38.0$, P < 0.001). The odds of damage differed among species when accounting for overstory basal area (Table 2.7; LR $\chi^2_3 = 26.4$, P < 0.001). This is consistent with the results found for presence of damage in the contingency table analysis when overstory was ignored. Pairwise comparisons of the four species showed that redcedar had significantly lower odds of damage than Douglas-fir (Wald Z = -2.95, P = 0.003) and hemlock (Wald Z = -4.70, P < 0.001). Redcedar also showed lower odds of damage than grand fir, although this difference only approached significance (Wald Z = -2.72, P = 0.007). None of the other species differed significantly from each other (Table 2.8). The lower odds for redcedar taking damage when accounting for basal area are consistent with the results of the contingency table analysis, when overstory was ignored. That western hemlock had the highest odds of taking damage is also consistent with the results contingency table analysis.

The association of hardwood basal area with odds of damage was statistically significant (Table 2.7; LR $\chi^2_3 = 11.6$, P < 0.001). The estimated odds of an understory tree being damaged increased by 1.30 times for every 5-m^{2}ha^{-1} increase in hardwood basal area (99.$\overline{4}$% CI 1.06-1.59). The association of conifer basal area with odds of damage, however, was not significant (Table 2.7; LR $\chi^2_3 = 0.37$, P = 0.544).

2.4.2.2. Direct damage

The logistic mixed model for presence of direct damage showed overall significance against the null model consisting only of the intercept with nested random effects (LR χ^2_{11} = 78.3, P < 0.001). The odds of direct damage differed among species when accounting for overstory basal area (Table 2.9; LR χ^2_3 = 47.6, P < 0.001). As with total damage, western redcedar displayed significantly lower odds of direct damage than Douglas-fir (Wald Z = -3.47, P < 0.001), grand fir (Wald Z = -4.89, P < 0.001), and hemlock (Wald Z = -6.20, P < 0.001). None of the other species differed significantly from each other (see Table 2.10).

The association of hardwood basal area with odds of direct damage was statistically significant (Table 2.9; LR χ^2_3 = 13.2, P < 0.001). The estimated odds of an understory tree receiving direct damage decreased by 0.68 times for every 5-m^{2}ha^{-1} increase in hardwood basal area (99.$\overline{4}$% CI 0.50-0.92). The association of conifer basal area with odds of direct damage was also statistically significant (Table 2.9; LR χ^2_3 = 17.3, P < 0.001). The estimated odds of an understory tree receiving direct damage decreased by 0.85 times for every 5-m^{2}ha^{-1} increase in conifer basal area (99.$\overline{4}$% CI 0.77-0.95).

2.4.2.3. Indirect damage

The logistic mixed model for presence of indirect damage showed overall significance against the null model consisting only of the intercept with nested random effects (LR χ^2_{11} = 43.4, P < 0.001). Unlike with total and direct damage, the odds of indirect damage did not differ among species when accounting for overstory basal area (Table 2.11; LR χ^2_3 = 2.48, P = 0.480). The association of hardwood basal area with odds of indirect damage was statistically significant (Table 2.11; LR χ^2_3 = 38.7, P < 0.001). The estimated odds of an understory tree receiving indirect damage increased by 1.98 times for every 5-m^{2}ha^{-1} increase in hardwood basal area (98.$\overline{3}$% CI 1.53-2.55). The association of conifer basal area with odds of direct damage was also statistically significant (Table 2.11; LR χ^2_3 = 7.63, P = 0.006). The estimated odds of an understory tree receiving direct damage increased by 1.12 times for every 5-m^{2}ha^{-1} increase in conifer basal area (98.$\overline{3}$% CI 1.02-1.24).

2.4.3. Damage severity and understory tree size

2.4.3.1. Bending damage

The ordinal mixed model for severity of bending damage showed overall significance against the null model consisting only of the intercept with nested random effects (LR $\chi_7^2 = 81.5$, P < 0.001). The odds of an understory tree falling in a higher response category (higher severity of bending damage) differed between species (Table 2.12; LR $\chi_3^2 = 16.6$, < 0.001). The association of height:diameter ratio with bending damage severity was also statistically significant (Table 2.12; LR $\chi_1^2 = 17.8$, P < 0.001). For every 10 increase in height:diameter ratio, the odds of an understory tree receiving a higher severity of bending damage increased by 1.19 times (98.$\overline{3}$% CI 1.08-1.31). The association of DBH with bending damage severity showed the opposite trend (Table 2.12; LR $\chi_1^2 = 6.79$, P = 0.009). For every 2 cm increase in DBH, the odds of an understory tree receiving a higher severity of bending damage decreased by 0.89 times (98.$\overline{3}$% CI 0.80-0.99).

2.4.3.2. Crown damage

The ordinal mixed model for severity of crown damage showed overall significance against the null model consisting only of the intercept with nested random effects (LR $\chi_7^2 =$ 114.2, P < 0.001). The odds of an understory tree falling in a higher response category (higher severity of crown damage) differed between species (Table 2.13; LR $\chi_3^2 = 55.6$, < 0.001). The association of height:diameter ratio with crown damage severity was somewhat statistically significant (Table 2.13; LR $\chi_1^2 = 6.79$, P = 0.009). For every 10 increase in height:diameter ratio, the odds of an understory tree receiving a higher severity of crown damage increased by 1.12 times (98.$\overline{3}$% CI 1.01-1.25). The association of DBH with crown damage severity was stronger (Table 2.13; LR $\chi_1^2 = 60.5$, P < 0.001). For every 2 cm increase in DBH, the odds of an understory tree receiving a higher severity of crown damage increased by 1.49 times (98.$\overline{3}$% CI 1.31-1.69).

2.5. Discussion

Like any form of natural disturbance, the impacts of glaze events are influenced by a wide array of factors, many of which cannot easily be predicted or managed for (Bragg et al., 2003; Nykänen et al., 1997). Few studies, however, have evaluated sources of variability in glaze

damage among trees in the understory cohorts of multi-aged stands, or in the moist conifer forests of the Pacific Northwest in general. The results presented here provide implications for managing risk to understory trees associated with glaze damage in multi-aged, Douglas-fir-dominated systems. Understory tree species and size, as well as overstory environment, affected the likelihood and severity of damage received by understory trees. This study found evidence of large differences in damage susceptibility among conifer species in the understory cohort, although these interspecific differences were more pronounced when associated with direct damage from ice loading than in response to indirect damage from falling debris. There was also evidence that greater amounts of bigleaf maple in the overstory increased the likelihood of damage to trees in the understory, driven by a large increase in the likelihood of indirect damage. Finally, there was evidence that, in general, understory trees became more likely to lose crown than bend as they increased in size.

2.5.1. Species

The understory species in this study exhibited a range of responses to glaze damage, both in terms of overall resistance, and resistance towards a particular type of damage. Overall, western redcedar was the most resistant to glaze damage, and was more likely to bend than lose crown; Douglas-fir and grand fir were moderately resistant, and showed no strong tendency toward either type of damage; western hemlock was the least resistant to damage, and more likely to lose crown than bend. Western hemlock trees lost from 50-90% of their crown with particularly high frequency; crown loss of this severity will significantly reduce the likelihood of long-term survival and viability for damaged individuals (Bragg and Shelton, 2010).

These results are consistent with the literature on the effect of species on susceptibility/resistance to glaze damage in overstory-sized trees. Previous studies have shown that in the overstory, species have different resistances to glaze damage (Boerner et al., 1988; Lafon, 2006). Variation in resistance stems from several species-specific characteristics, including growth form and the wood's mechanical properties (Bruederle and Stearns, 1985). The exact suite of characteristics responsible is difficult to isolate, although wood strength alone is unlikely to be the explanation. Western redcedar has lower specific gravity and fracture toughness than western hemlock (Miles and Smith, 2009; Wilson et al., 2013), which intuitively would make it more

susceptible to crown breakage from ice loading. Warillow and Mou (1999), however, found that wood strength does not always correlate with ice damage severity. Most likely, the variation in resistances among the species in this study were due to other factors, such as crown form, leaf and branch morphology, or tree health.

Since the contingency table analyses did not account for any other variables, there is some possibility that the differences in damage seen in this study could have resulted from uneven survival and growth among species prior to the ice storm. For instance, more redcedar was able to survive in suppressed conditions where they remained smaller, and thus more susceptible to being bent than broken. However, the relationships among the four planted species generally held true even after accounting for overstory environment and understory tree size in logistic regression models. The one exception to these interspecific differences in damage was indirect damage, where there was no difference in damage likelihood among species. Most likely, the interspecific variations in damage resistance were trivial relative to the force applied by debris falling from a canopy ranging from 41-46 m in height. Taken together with previous studies' findings, the results of this study suggest that interspecific variation in glaze damage resistance occurs regardless of canopy stratum and size.

Lastly, the contingency table analyses indicated that the trends in total damage were primarily driven by trends in crown damage rather than bending. As previously stated, western redcedar was damaged less frequently than the other species overall, while western hemlock was damaged more frequently; this mirrors trends seen in crown damage, while bending damage exhibited different patterns (Figs. 2.3-2.5). Crown damage also occurred in approximately twice as many sampled understory trees as bending damage (n = 547 vs. n = 267). Because total damage was driven by crown damage, species susceptible to crown damage, such as western hemlock in this study, are at more risk overall. This has particularly severe long-term consequences on tree survival. Crown damage resulting from top-breakout or bole snapping, as most of the crown damage observed in this study did, is more likely to induce mortality than bending (Lafon, 2006). This could differ between stands, however, depending on species composition and other factors.

2.5.2. Overstory environment

When assessing the risk of glaze damage to understory trees, the relationship between the overstory and understory can be thought of as a balance between the risks of direct and indirect damage. Additional canopy basal area increases the amount of shelter provided to understory trees from direct ice loading, but also increases the quantity of potential debris that could damage them. Whether damage risk increases or decreases with increasing overstory density depends on how much shelter overstory trees provide in comparison to their damage susceptibility. Both of these factors can vary with species and type of tree (hardwood vs. conifer), based on their associated physical and mechanical properties (Boerner et al., 1988; Bruederle and Stearns, 1985; Lafon, 2006).

Intuitively, it seems that the additional shelter provided by a higher density of overstory conifer (primarily Douglas-fir) would have more than compensated for the increased risk of falling debris, thus reducing likelihood of damage to the understory cohort. However, the results showed no evidence of this trend. While direct and indirect damage did indeed show opposing trends with changing conifer basal area, the magnitudes of the effects were roughly equivalent (Fig. 2.6A). Because of this, there was no change in overall likelihood of damage as conifer basal area changed. This suggests that any risk reduction due to the greater sheltering associated with higher overstory conifer densities is offset by the increased risk of damage from falling debris.

In addition, the changes in damage likelihoods with changing basal area were relatively small. This came as a surprise, as ice interception is in large part a function of the surface area of the tree at the time of the glaze event (Lemon, 1961). Since conifers retain their needles in winter, it would follow that the amount of ice intercepted should increase more dramatically with basal area, creating an equivalent decline in the risk of direct damage. One possible explanation is that Douglas-fir was able to able to shed ice from its branches, thus reducing total interception. However, there is no current research on snow/ice shedding efficiency in Douglas-fir that the author is aware of to support this possibility. Indeed, the more horizontal branching angles of Douglas-fir are associated with lower snow/ice shedding efficiency (Nykänen et al., 1997; Roeh and Maguire, 1997). The low rate of change in the risk of indirect damage is easier to explain.

Douglas-fir has a relatively low susceptibility to ice damage (Nykänen et al., 1997), so the added risk of indirect damage in areas with denser canopies should be relatively low.

The hardwood component of the overstory, which was primarily composed of bigleaf maple, displayed similar opposing trends of direct and indirect damage. Unlike the conifer component of the canopy, however, the increase in indirect damage risk with overstory hardwood basal area was larger than the corresponding decrease in risk of direct damage from ice loading (Fig. 2.6A). As a result, there was an overall increase in the risk of damage to the understory with increasing hardwood basal area. This implies that higher hardwood densities in the overstory did not provide sufficient shelter to compensate for the higher risk of falling debris.

Comparing the relationships between damage presence and overstory conifer and hardwood shows that the density of bigleaf maple in the overstory was more influential than the density of overstory Douglas-fir on the likelihood of damage to understory trees. For every 5 m^2 ha^{-1} increase in conifer basal area, there was just a 2% decrease in the odds of an understory tree being damaged; a 5 m^2 ha^{-1} increase in hardwood basal area, however, was associated with a 30% increase in the odds of damage. These results run counter to the generally accepted trends in glaze damage to conifers and hardwoods. There is general agreement among researchers that due to crown structure and retention of leaves, conifers are more susceptible to damage than hardwoods (Boerner et al., 1988; Lemon, 1961; Whitney and Johnson, 1984). Anecdotally, however, this was not the case at the McDonald Forest site: judging by the relative amounts of fallen debris, bigleaf maple seemed to be especially susceptible to damage, despite its low surface area. The finding of this study that understory damage risk increased with hardwood density, but not conifer density, further supports this observation.

Assuming that some unobserved factor was not responsible for the difference, this was most likely due to species variation. Although conifers receive more damage than hardwoods in general, there is broad variation and overlap within each of these categories (Bruederle and Stearns, 1985; Nykänen et al., 1997). There is currently no research on glaze damage susceptibility in bigleaf maple, but it is possible that it is more prone to damage than the relatively resistant Douglas-fir. As with western hemlock and western redcedar, however, wood strength alone is insufficient to explain this difference, as Douglas-fir and bigleaf maple exhibit

nearly identical specific gravities (Miles and Smith, 2009). This susceptibility to damage, combined with bigleaf maple's deciduous nature, which would reduce interception during winter storm events, could make it a risk to any understory trees growing nearby.

The finding that increasing overstory cover either did not reduce or increase damage risk to understory trees contradicts several previous studies. Other researchers have found that the understory layers suffer less damage during glaze events than the overstory (Rebertus et al., 1997; Rhoades, 1999; Whitney and Johnson, 1984). This would suggest that in many systems, the overstory does provide a large sheltering effect, limiting understory damage.

However, it is possible that the reduced understory damage seen in these studies was the result of other factors, such as tree size. Conclusions for these other stories were drawn from comparisons between quantities of overstory and understory damage, rather than comparisons between understory damage and immediate overstory environment. Further, there is some corroborating evidence that indirect damage may be a greater threat to understory trees than ice loading. Although they did find less damage in the understory than the overstory, Whitney and Johnson (1984) observed that most of this damage came from falling branches. Similarly, Duguay et al. (2001) found high rates of damage among saplings, most of which was caused by falling debris. This is consistent with this study's findings that falling debris had a stronger influence on damage severity than ice loading.

2.5.3. Size

Both relative width (height:diameter ratio) and absolute stem diameter of understory trees influenced bending and crown damage severity. Counter to prior expectations that an increase in height:diameter ratio would cause a shift from crown loss to bending, it actually resulted in an increase in severity of both damage types (Fig. 2.6B): a 10 unit increase in height:diameter ratio was associated with a 8-31% increase (Table 2.12; 98.3% CI) in the odds of more severe bending damage to understory trees, and a 1-25% increase (Table 2.13; 98.3% CI) in the odds of more severe crown damage. This suggests that trees that were taller relative to their width were more susceptible to damage in general. This is somewhat of a concern, as understory trees in a multi-aged stand often do not have access to sufficient resources, thus reducing growth and increasing height:diameter ratio (Acker et al., 1998; Lam and Maguire, 2011). Further, height:diameter

ratios of understory trees increase with increasing residual overstory densities (Lam and Maguire, 2011). This suggests that trees grown in more open understory environments, such as canopy gaps, may be slightly more resistant to glaze damage, due to the increased likelihood of a lower height:diameter ratio. Since the results of this study also suggest that residual overstory trees do not provide a strong sheltering effect during glaze events, trees grown in more open environments may be at lower risk of damage overall.

Absolute stem diameter had a much stronger influence on damage severity than height:diameter ratio. Change in DBH had opposing effects on bending and crown damage severity: an increase in DBH moderately reduced bending severity, while greatly increasing likelihood of higher-severity crown loss (Fig. 2.6B). This is consistent with trends in overstory trees, where increasing diameter tends to shift damage from bending to crown loss as well (Lafon, 2006; Proulx and Greene, 2001). These results, however, only appear to be true for trees less than or equal to 10 cm DBH.

The results for crown damage presented here had to be limited in scope to sampled trees with a DBH of 10 cm or less (n = 2020). This was done solely for statistical reasons, as almost no trees larger than that size (n = 413) fell into the higher damage classes (>50% crown loss), causing the models to violate the proportional odds assumption when these data were included. This in itself tells an interesting story, however. The absence of severe crown damage in understory trees greater than 10 cm DBH may suggest that beyond a certain diameter, the likelihood of a stem breaking low enough to cause severe crown loss declines precipitously, regardless of species. Consequently, beyond a certain size, the risk of an understory tree receiving enough damage to severely impact its future growth and survival should also decline. The strength of this trend, of course, would likely depend on the severity of the glaze disturbance, with more severe events damaging trees regardless of size.

This conclusion is further supported both by overstory data collected within the MFS after the 2014 glaze event, as well as research conducted in other forests. Data collected on the overstory conifers during winter 2014 show that the majority of top breakouts occurred at diameters of 10 cm or less, and most of the remainder occurred at diameters of 10-15 cm (Table A.1; Liz Cole, unpublished data). Likewise, in a study on the impact of a glaze event on a

hardwood forest, Hooper et al. (2001) found that only 4.2% of downed branches had a diameter >10 cm.

This suggests that there are some guidelines that managers could follow when assessing and managing for risk of ice damage to understory cohorts. Small trees are at increased risk of bending, but because they can easily recover from less severe bending damage, much of the damage will be temporary (Bragg and Shelton, 2010). Damage source is relevant here, however, as understory trees pinned by debris will be unable to recover (Bragg et al., 2003) Intermediate-sized trees require the most concern, as they become more rigid and prone to debilitating crown loss. Risk decreases again as trees approach the midstory, since at this stage crown loss is more likely to be small enough that the trees can recover and remain healthy. Previous studies have also found this pattern of damage risk, suggesting that it holds across different forest types (Lafon, 2006; Proulx and Greene, 2001; Shepard, 1975). Therefore, while this pattern will still vary some by species, size is a strong enough predictor of potential damage type and severity that these guidelines should be broadly applicable.

2.6. Management Implications

Irregular disturbances such as glaze events in the PNW are challenging to plan for when managing a forest; the sheer number of contributing factors makes stand response impossible to fully predict. This may not matter if a manager's primary goal is the development of heterogeneous late-seral structure, as gap-generating disturbances like glaze events contribute to structural development (Franklin et al., 2002). If a manager has additional objectives such as wood production, however, intervention may be required to limit potential damage. There are some aspects of a silvicultural system that managers can focus on when assessing risk of glaze damage to the understory in multi-aged stands, as well as potential avenues for risk mitigation. This study suggests that understory tree species and size, as well as overstory environment, all contribute to the risk of glaze damage to understory trees. When incorporating this information into a silvicultural prescription, this study suggests managers use a simple three step process for assessing and mitigating risk:

1) **Assess species risk.** Managers have numerous considerations that impact their decisions regarding which species to plant in a stand, many of which are of much greater concern

than infrequent disturbance events. Because of this, many managers may decide that understory species composition does not offer a good opportunity for risk management. However, it is still helpful to understand relative species risks when considering potential compensatory measures for reducing glaze damage risk. For instance, a more resistant species such as western redcedar would require less risk mitigation than a more susceptible species such as western hemlock. Due to variation in glaze resistance between species, this must be assessed on a by-species basis based on physical characteristics such as crown form, wood strength, etc.

2) **Consider tree size.** Results suggest that there may be a cutoff for branch/stem diameter beyond which both severe bending and breaking becomes much less likely. While this cutoff likely varies between species, a general approach can still be extrapolated. When understory trees are small, compensatory measures should be taken to reduce risk of severe damage; conversely, once understory trees have reached sufficient size (10-20 cm DBH), there is likely little advantage to management action because most damage will not be severe enough to significantly impede future growth and survival. If a glaze event is severe enough to cause widespread major damage to trees of this size, then management action would likely be insufficient to protect them regardless.

3) **Manage overstory environment.** Out of the three aspects of glaze damage risk examined in this study, overstory environment is the only one that has the potential to be directly manipulated after understory cohort establishment. As with understory tree species, managers should first consider the species present in the overstory around their understory cohort in order to determine the amount of risk presented. This information can then be used in combination with the understory risk assessment to create a management plan. For instance, if the understory is composed of high-risk species (e.g., western hemlock in this study), then the manager may wish to reduce the density of any glaze-susceptible species in the surrounding overstory (e.g., bigleaf maple in this study), while retaining glaze-resistant species. Although no overall reduction in damage with higher overstory density was found, other studies have found a significant sheltering effect from the overstory (Rhoades, 1999; Whitney and Johnson, 1984). Lacking any

specific information on this subject in the systems they are managing, managers should use their knowledge of individual species resistances to loading and mechanical damage to estimate the degree of this sheltering effect as best they can. This should of course be balanced with the resource needs of the understory, as a dense, sheltering overstory will suppress growth, extending the high-risk period for understory trees.

2.7. Tables

Table 2.1: Post-thinning overstory basal areas (BA), relative densities, and relative density indices (RDI) at McDonald Forest site of Mature Forest Study. See Nabel et al. (2013).

Overstory Retention Level	BA (m^2 ha^{-1})	Relative Density	RDI
Low	16.7–18.8	2.6	0.18
Medium	19.3–25.1	3.3	0.23
Med-High	26.9–29.6	4.0	0.27
High	27.7–32.9	4.6	0.31

Table 2.2: Damage class scale for bending damage.

Bending Damage Class	Amount of Bending
0	No damage
1	Light ($<45^{o}$)
2	Heavy ($>45^{o}$)
3	Prone

Table 2.3: Damage class scale for crown loss.

Crown Damage Class	Amount of Crown Loss
0	No damage
1	Minor (<10%)
2	Moderate (10-50%)
3	Moderate-Severe (50-90%)
4	Severe (>90%)
5	Uprooted

Table 2.4: Frequency of damage occurrence by species. Proportions of sampled trees are in parentheses.

	Damaged		
	No	Yes	Total
Western redcedar	893 (36.7%)	292 (12.0%)	1185 (48.7%)
Douglas-fir	171 (7.0%)	88 (3.6%)	259 (10.6%)
Grand fir	494 (20.3%)	207 (8.5%)	701 (28.8%)
Western hemlock	177 (7.3%)	113 (4.6%)	290 (11.9%)
Total	1735 (71.3%)	700 (28.7%)	2435 (100%)

Table 2.5: Frequency of bending damage occurrence by species and degree of damage. 0 = no bending, 1 = < 45° bend from vertical, 2 = > 45° bend from vertical to nearly prone, 3 = nearly prone to prone. Proportions of sampled trees are in parentheses.

| | Bending Damage Class | | | | |
	0	1	2	3	Total
Western redcedar	1038 (42.6%)	43 (1.8%)	35 (1.4%)	69 (2.8%)	1185 (48.7%)
Douglas-fir	219 (9.0%)	17 (0.7%)	17 (0.7%)	6 (0.2%)	259 (10.6%)
Grand fir	647 (26.6%)	21 (0.9%)	23 (0.9%)	10 (0.4%)	701 (28.8%)
Western hemlock	264 (10.8%)	18 (0.7%)	5 (0.2%)	3 (0.1%)	290 (11.9%)
Total	2168 (89.0%)	99 (4.1%)	80 (3.2%)	88 (3.5%)	2435 (100%)

Table 2.6: Frequency of crown damage occurrence by species and degree of damage. 0 = no crown loss, 1 = <10% crown loss, 2 = 10-50% crown loss, 3 = 50-90% crown loss, 4 = >90% crown loss. Proportions of sampled trees are in parentheses.

	Crown Damage Class					
	0	1	2	3	4	Total
Western redcedar	980	80	66	25	24	1175
	(40.5%)	(3.3%)	(2.7%)	(1.0%)	(1.0%)	(48.5%)
Douglas-fir	194	14	29	13	6	256
	(8.0%)	(0.6%)	(1.2%)	(0.5%)	(0.2%)	(10.5%)
Grand fir	521	48	61	37	33	700
	(21.5%)	(2.0%)	(2.5%)	(1.5%)	(1.4%)	(28.8%)
Western hemlock	193	16	38	28	12	287
	(8.0%)	(0.7%)	(1.6%)	(1.2%)	(0.5%)	(11.9%)
Total	1888	158	194	103	75	2418
	(78.0%)	(6.6%)	(8.0%)	(4.2%)	(3.1%)	(100%)

Table 2.7: Summary of results for logistic mixed model examining relationship of species, hardwood basal area (BA), and conifer BA with presence of damage from any source (n = 2435), including log odds (linear parameter estimates), odds ratios with $99.\overline{4}\%$ Wald confidence intervals (CI), and likelihood ratio test P-values for independent variables. The odds ratios for change in basal area (BA) were calculated using a slope interval of 5 m^2 ha^{-1}.

	Log Odds	Odds Ratio Increments	Odds Ratios	Odds $99.\overline{4}\%$ Wald CI		P-values
				Lower	Upper	
Species						<0.001**
Western redcedar	-1.32		0.27	0.14	0.52	
Douglas-fir	-0.84		0.43	0.21	0.88	
Grand fir	-1.01		0.36	0.18	0.72	
Western hemlock	-0.62		0.54	0.26	1.11	
Hardwood BA	0.05	5 m^2 ha^{-1}	1.30	1.06	1.59	<0.001**
Conifer BA	-0.003	5 m^2 ha^{-1}	0.98	0.91	1.06	.544

** indicates significance at familywise $\alpha = 0.05$ level (individual $\alpha^* = 0.05/9$)

Table 2.8: Odds ratios for pairwise comparisons of odds of damage between species (row – column), accounting for hardwood and conifer basal area. P-values are in parentheses.

	Douglas-fir	Grand fir	Western hemlock
Western redcedar	0.62 (0.003)**	0.73 (0.007)*	0.50 (<0.001)**
Douglas-fir		1.18 (0.328)	0.80 (0.237)
Grand Fir			0.68 (0.013)

** indicates significance at familywise $\alpha = 0.05$ level (individual $\alpha^* = 0.05/9$)

* indicates that value approaches significance

Table 2.9: Summary of results for logistic mixed model examining relationship of species, hardwood basal area (BA), and conifer BA with presence of direct damage (n = 2435), including log odds (linear parameter estimates), odds ratios with 99.$\overline{4}$% Wald confidence intervals (CI), and likelihood ratio test P-values for independent variables. The odds ratios for change in basal area (BA) were calculated using a slope interval of 5 m^2 ha^{-1}.

	Log Odds	Odds Ratio Increments	Odds Ratios	Odds 99.$\overline{4}$% Wald CI		P-values
				Lower	Upper	
Species						<0.001**
Western redcedar	-1.12		0.33	0.13	0.80	
Douglas-fir	-0.42		0.66	0.26	1.67	
Grand fir	-0.39		0.68	0.28	1.67	
Western hemlock	0.01		1.01	0.40	2.54	
Hardwood BA	-0.08	5 m^2 ha^{-1}	0.68	0.50	0.92	<0.001**
Conifer BA	-0.03	5 m^2 ha^{-1}	0.85	0.77	0.95	<0.001**

** indicates significance at familywise $\alpha = 0.05$ level (individual $\alpha^* = 0.05/9$)

Table 2.10: Odds ratios for pairwise comparisons of odds of direct damage between species (row – column), accounting for hardwood and conifer basal area. P-values are in parentheses.

	Douglas-fir	Grand Fir	Western hemlock
Western redcedar	0.50 (<0.001)**	0.48 (<0.001)**	0.33 (<0.001)**
Douglas-fir		0.97 (0.870)	0.65 (0.061)
Grand fir			0.68 (0.032)

** indicates significance at familywise $\alpha = 0.05$ level (individual $\alpha^* = 0.05/9$)

Table 2.11: Summary of results for logistic mixed model examining relationship of species, hardwood basal area (BA), and conifer BA with presence of indirect damage (n = 2435), including log odds (linear parameter estimates), odds ratios with 98.$\overline{3}$% Wald confidence intervals (CI), and likelihood ratio test P-values for independent variables.

	Log Odds	Odds Ratio Increments	Odds Ratios	Odds 98.$\overline{3}$% Wald CI		P-values
				Lower	Upper	
Species						0.480
Western redcedar	-3.57		0.03	0.01	0.07	
Douglas-fir	-3.41		0.03	0.01	0.09	
Grand fir	-3.76		0.02	0.01	0.06	
Western hemlock	-3.57		0.03	0.01	0.08	
Hardwood BA	0.14	5 m^2 ha^{-1}	1.98	1.53	2.55	<0.001**
Conifer BA	0.02	5 m^2 ha^{-1}	1.12	1.02	1.24	0.006**

** indicates significance at familywise α = 0.05 level (individual α^* = 0.05/3)

Table 2.12: Summary of results for ordinal mixed model examining relationship of species, height:diameter (HD) ratio, diameter at breast height (DBH), hardwood basal area (BA), and conifer BA with severity of bending damage (n = 2433), including log odds (linear parameter estimates), odds ratios with $98.\overline{3}\%$ Wald confidence intervals (CI), and likelihood ratio test P-values for independent variables. The thresholds indicate the log odds of an understory tree falling below a particular damage class (0 = no bending, 1 = <45° lean from vertical, 2 = >45° lean from vertical).

	Log Odds	Odds Ratio Increments	Odds Ratios	Odds $98.\overline{3}\%$ Wald CI		P-values
				Lower	Upper	
Threshold						
P < 1	3.55					
P < 2	4.12					
Species						<0.001**
Western redcedar (ref)						
Douglas-fir	0.26		1.29	0.77	2.17	
Grand fir	-0.58		0.56	0.36	0.86	
Western hemlock	-0.28		0.75	0.42	1.34	
HD Ratio	0.02	10	1.19	1.08	1.31	<0.001**
DBH	-0.06	2 cm	0.89	0.80	0.99	0.009**
Hardwood BA	0.08	5 m^2 ha^{-1}	1.52	1.22	1.90	<0.001**
Conifer BA	0.004	5 m^2 ha^{-1}	1.02	0.93	1.12	0.559

** indicates significance at familywise α = 0.05 level (individual α^* = 0.05/3)

Table 2.13: Summary of results for ordinal mixed model examining relationship of species, height:diameter (HD) ratio, diameter at breast height (DBH), hardwood basal area (BA), and conifer BA with severity of crown damage (n = 2416), including log odds (linear parameter estimates), odds ratios with 98.$\overline{3}$% Wald confidence intervals (CI), and likelihood ratio test P-values for independent variables. The thresholds indicate the log odds of an understory tree falling below a particular damage class (0 = no damage, 1 = <10% crown loss, 2 = 10-50% crown loss, 3 = 50-90% crown loss, 4 = >90% crown loss).

	Log Odds	Odds Ratio Increments	Odds Ratios	Odds 98.$\overline{3}$% Wald CI		P-values
				Lower	Upper	
Threshold						
P < 1	4.63					
P < 2	5.25					
P < 3	5.86					
P < 4	6.68					
Species						<0.001**
Western redcedar (ref)						
Douglas-fir	0.80		2.22	1.32	3.72	
Grand fir	1.08		2.96	2.04	4.28	
Western hemlock	0.83		2.29	1.38	3.81	
HD Ratio	0.01	10	1.12	1.01	1.25	0.010**
DBH	0.20	2 cm	1.49	1.31	1.69	<0.001**
Hardwood BA	0.07	5 m^2 ha^{-1}	1.52	1.13	1.81	<0.001**
Conifer BA	0.01	5 m^2 ha^{-1}	1.02	0.96	1.16	0.175

** indicates significance at familywise α = 0.05 level (individual α^* = 0.05/3)

2.8. Figures
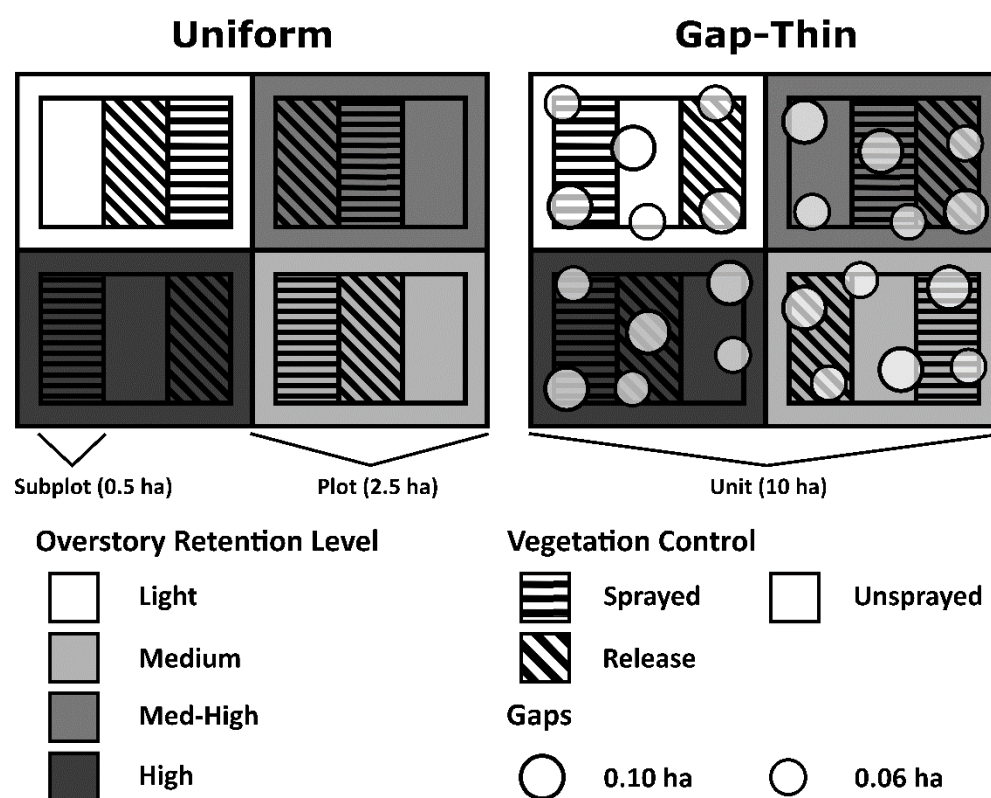
Figure 2.1: Example block design at McDonald Forest site of Mature Forest Study. Adapted from Nabel et al. (2013).
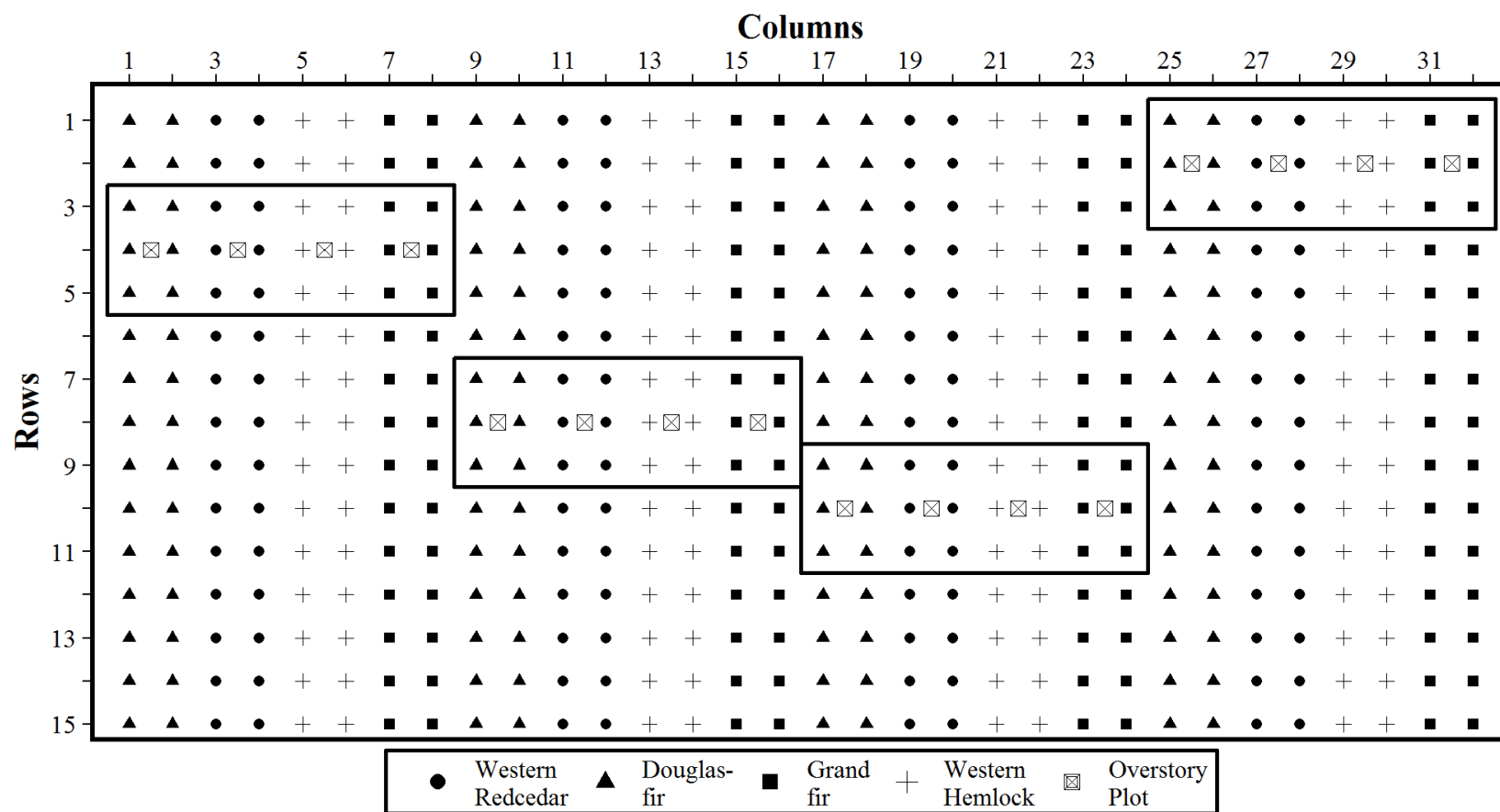
Figure 2.2: Tree planting matrix in example subplot at McDonald. Eight by three rectangles delineate sampling grids.
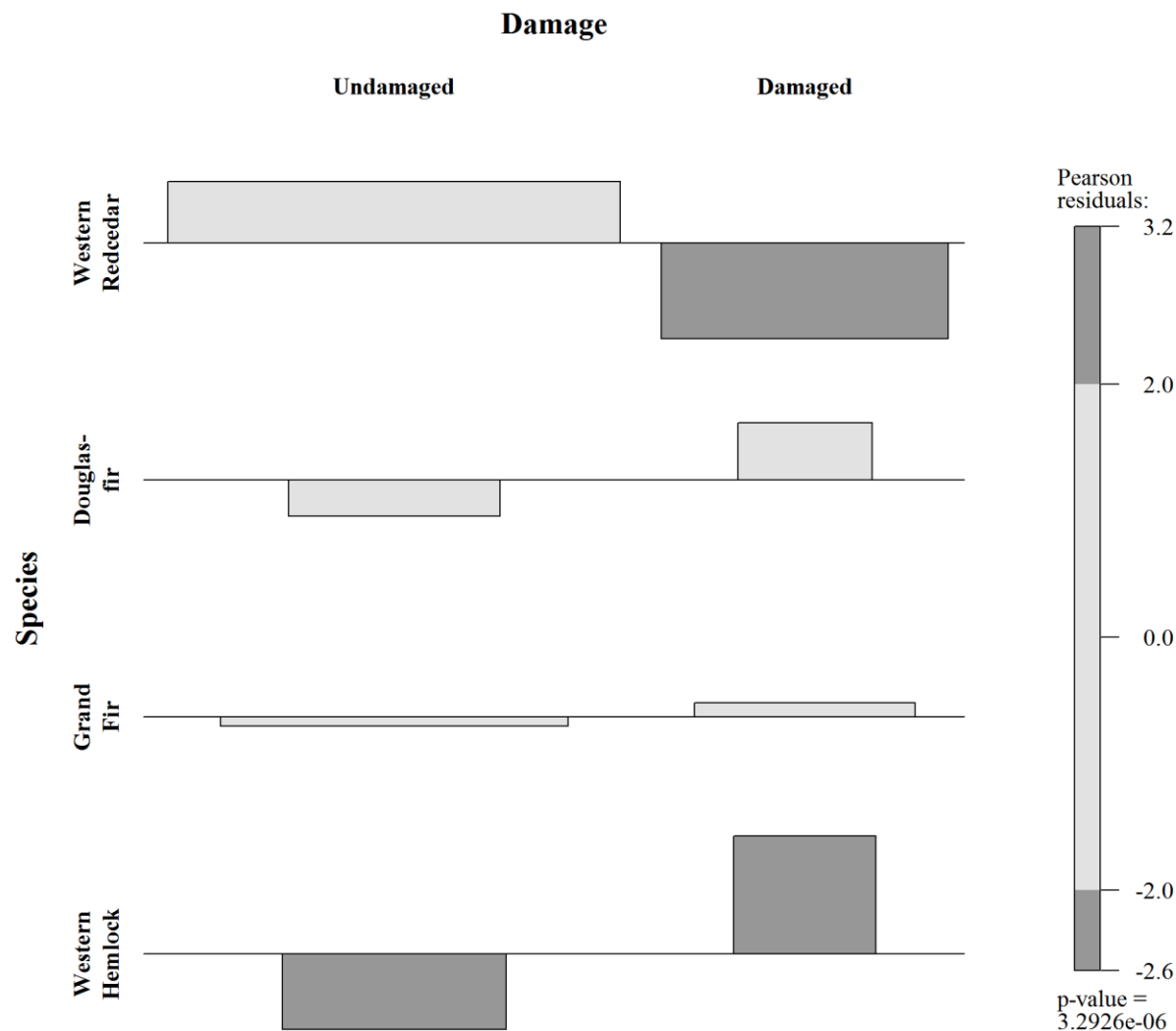
Figure 2.3: Association plot of Pearson residuals of understory tree species/presence of damage contingency table. Includes damage of any type from all sources. Bars above axes indicate more frequent damage than expected, bars below axes indicate less frequent damage than expected, light gray indicates residuals <|±2.0|, medium gray indicates residuals >|±2.0|.
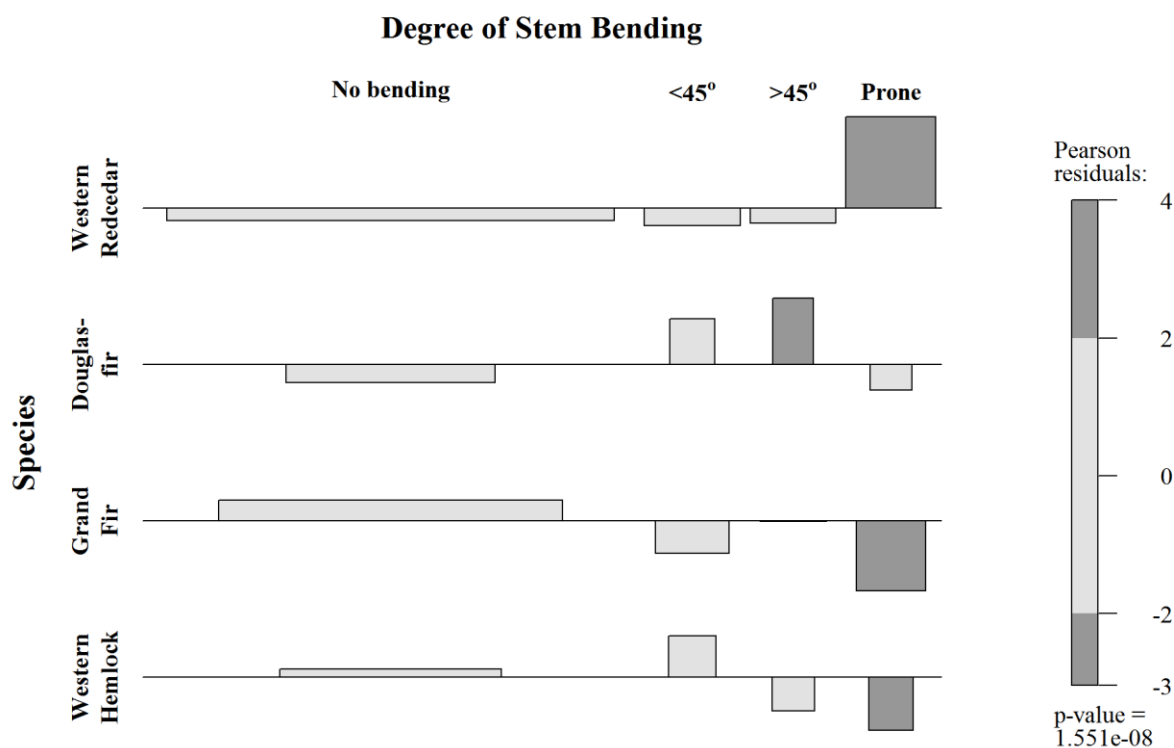
Figure 2.4: Association plot of Pearson residuals of understory tree species/bending damage class contingency table. Bending was estimated as degree bent from vertical. Bars above axes indicate more frequent damage than expected, bars below axes indicate less frequent damage than expected, light gray indicates residuals <|±2.0|, medium gray indicates residuals >|±2.0|.
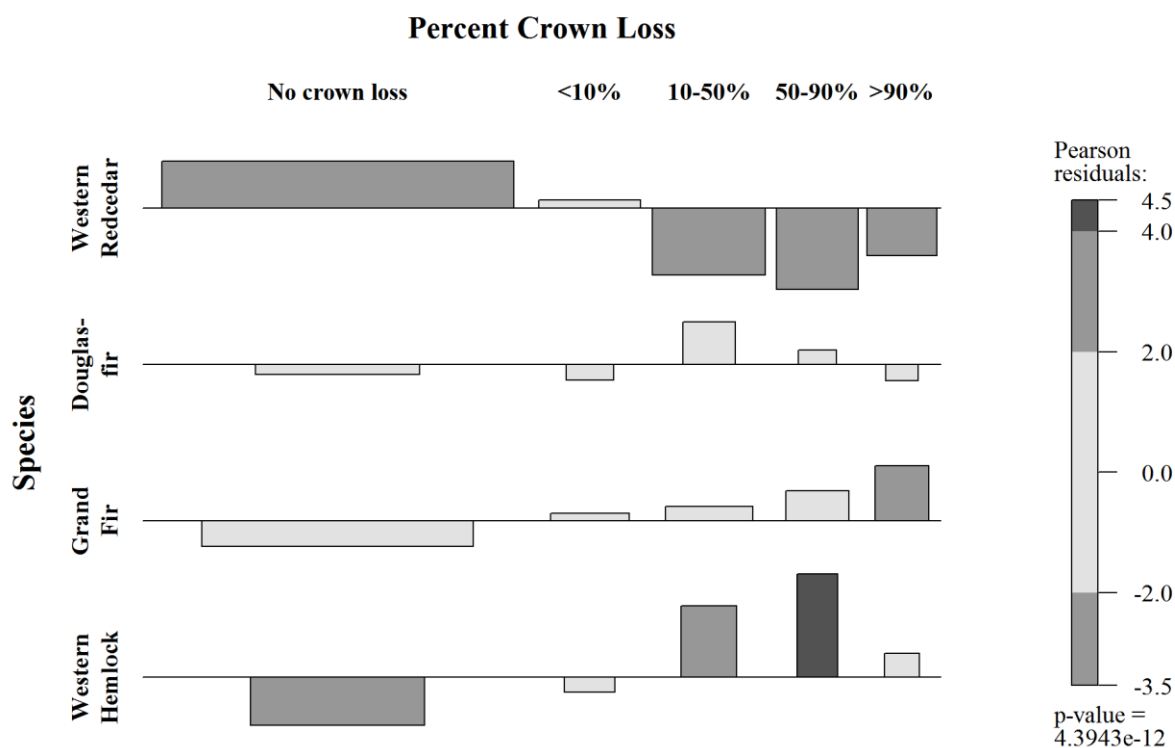
Figure 2.5: Association plot of Pearson residuals of understory tree species/crown damage class contingency table. Bars above axes indicate more frequent damage than expected, bars below axes indicate less frequent damage than expected, light gray indicates residuals <|±2.0|, medium gray indicates residuals >|±2.0|, dark gray indicates residuals >|±4.0|.

A	Direct	Indirect	Total
Conifer BA	↓ ＋ ↑	＝	⟷
Hardwood BA	↓ ＋ ⬆	＝	⬆

B	Bending	Crown loss
H:D Ratio	⬆	↑
DBH	↓	⬆

Figure 2.6: Trends in (A) direct, indirect, and total damage with changes in conifer and hardwood basal area (BA) and (B) bending damage and crown loss with changes in height:diameter (H:D) ratio and diameter at breast height (DBH). Arrow direction indicates whether association was positive or negative; arrow width indicates relative magnitude of association, based on changes in log odds of damage response in logistic mixed models. Relative magnitudes of association are based on increments of 5 m^2 ha^{-1} BA, 10 units H:D ratio, and 2 cm DBH.

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3. MANUSCRIPT 2: THINNING INTENSITY AND HERBICIDE TREATMENT IMPACTS ON 20-YEAR UNDERSTORY VEGETATION DYNAMICS IN A MATURE DOUGLAS-FIR FOREST

3.1. Abstract

Accelerating the development of late-seral understory communities has become a large concern for public forest managers. Promoting the development of late-seral species can be challenging, however, complicated by initial site conditions. In particular, the legacy effects of dominant pre-treatment species may continue to limit available growing space following thinning treatment, hindering the development of desired late-seral communities. Herbicide application is one possible method for reducing this legacy effect. This study examined the longer-term (20-year post-treatment) effects of retention level (i.e. thinning intensity) and herbicide application on understory plant communities at two sites in the Oregon Coast Range, focusing on these treatments' ability to reduce the legacy effects of pre-treatment species and increase the abundance of late-seral species. Changes in community composition across thinning intensities, herbicide spray treatment, and measurement periods (pre-treatment and post-treatment years 1, 5, 10, and 20) were assessed using nonmetric multidimensional scaling. Overall compositional change was quantified using percent dissimilarity between pre-treatment and post-treatment communities. Changes in abundances of common species and species groups were calculated using change in species richness, total frequency, and relative frequency over time. Common species were defined as species that were present in >25% or >50% of pre-treatment sample points within a stand. Species groups were defined by growth form (forbs/shrubs) and seral group (early/late). Changes in percent dissimilarity and common species and seral group abundance from pre-treatment to post-treatment (years 5 and 20 only) were compared among thinning and herbicide treatments using mixed-effects ANOVA models. Results indicated that, in general, both retention level and herbicide treatment impacted 20-year changes in community composition. Herbicide application was also effective in reducing the abundance of common species. However, this did not result in an increased abundance of late-seral species. Low overstory retention was more detrimental to late-seral species than high overstory retention. These results suggest that while herbicide application can reduce the

abundance of pre-treatment vegetation, combining it with thinning neither helps nor harms the development of late-seral communities.

3.2. Introduction

In recent years, the scarcity of natural, old-growth forests in the Pacific Northwest of the United States (PNW) has become an issue of great concern for ecologists, land managers, and the public. Years of human use and a focus on timber production have caused a decline in land occupied by old-growth forests, resulting in a loss of the ecological functions that they provide (Davis et al., 2015; Hansen et al., 1991; Lindenmayer and McCarthy, 2002). Old-growth forests are known to sequester carbon (Luyssaert et al., 2008) and foster high and unique levels of biodiversity, including late-seral species that rely on the structural elements that such stands provide (D'Amato et al., 2009; Halpern and Spies, 1995; Stewart, 1988). These are generally species with greater shade tolerance, limited dispersal range, and the ability to rapidly expand into canopy gaps (Spies and Franklin, 1991). As such, late-seral species rely on structurally complex stands with a high degree of horizontal and vertical heterogeneity (Halpern and Spies, 1995; Spies and Franklin, 1991).

In natural old-growth forests, these complex structural characteristics develop over decades or centuries, shaped by processes such as self-thinning, understory regeneration, and repeated, multi-scale disturbances (Franklin and Van Pelt, 2004; Franklin et al., 2002; Hanson and Lorimer, 2007; Spies et al., 1990). Disturbance history, in particular, is a crucial driver of stand development. Periodic disturbance at both small and large scales produces a patchy mosaic of structural features, microclimates, and plant communities (Drever et al., 2006; Franklin et al., 2002; Scheller and Mladenoff, 2002). In turn, this structural complexity and the biodiversity it promotes increase ecosystem resilience, improving a forest's ability to remain healthy in the face of stressors such as future natural disturbance, human use, and climate change (Drever et al., 2006; Seidl et al., 2014; Thompson et al., 2009).

Traditional even-aged management approaches focused on timber production, however, are not conducive to the generation of old, structurally complex forest stands. Even-aged management homogenizes the canopy and reduces variation in habitat types, consequently limiting plant diversity (Hansen et al., 1991). Since the late-seral features of old-growth forests

take so long to develop naturally, managers often wish to artificially accelerate the process. Thinning, particularly variable density thinning (VDT), provides a powerful option for mimicking the effects of disturbance in an accelerated timeframe (Bailey and Tappeiner, 1998; Dodson et al., 2012; Schütz, 2002). In a variable density thinning, a stand is thinned to include multiple levels of retention, as well as varying retention pattern through the use of multi-tree openings (gaps) and unharvested leave areas (skips) (Harrington, 2009). Because of its focus on variability, VDT can help create a heterogeneous stand structure more similar to that of old-growth forests than stands managed using traditional even-aged approaches (Bailey and Tappeiner, 1998). As in old-growth forests, the spatial variability generated by VDT can promote both species diversity and the growth of late-seral vegetation (Aukema and Carey, 2008; Lindh and Muir, 2004; Spies and Franklin, 1991).

Incorporating thinning into a silvicultural system does not guarantee that development of a late-seral understory community will be accelerated, though. Thinning treatments may have a minimal (Ares et al., 2009; Davis and Puettmann, 2009) or even detrimental (Alaback and Herman, 1988) influence on late-seral vegetation. Understory responses to thinning are further complicated by thinning intensity. In general, species diversity increases with increasing thinning intensity (Griffis et al., 2001). However, this is usually a result of a greater abundance of early seral species (Ares et al., 2010); late-seral species abundance typically decreases in higher intensity thinning treatments (Halpern et al., 2012). As a result, lighter thinnings are generally considered preferable for promoting late-seral plant communities (Battles et al., 2001).

Thinning impacts on understory vegetation are also modified by the composition of the pre-treatment community. Due to their initial abundance, dominant species have a greater chance of maintaining a strong presence in the understory following initial disturbance (Halpern and Lutz, 2013; Hughes and Fahey, 1991). They are also likely to have a greater concentration of propagules, allowing for rapid reestablishment following damage by harvesting (Tappeiner et al., 2001). Even in the face of colonization by aggressive invasive species, site conditions may favor pre-treatment dominants (McGlone et al., 2011).

The persistence of dominant species in high abundances creates a "legacy effect" in the understory, which can make it difficult for managers to promote a particular suite of desired late-

seral species. Vegetation management through herbicide use may offer one solution to this problem. Previous studies have shown that herbicide use can be effective at reducing dominant species abundance (Iglay et al., 2010; Ristau et al., 2011). In doing so, growing space can be opened up for less common species, improving community abundance and diversity (DiTomaso et al., 1997; Getsinger et al., 1997). Whether this can benefit late-seral species in particular has not yet been investigated. Despite public skepticism regarding the use of herbicides, when used properly for management there is little significant risk to forest ecosystem health (Newton et al., 2008; Wagner et al., 2004). Further, any reductions to plant community diversity are typically transient (DiTomaso et al., 1997; Rice et al., 1997).

Using the ongoing Mature Forest Study (MFS), this study aimed to quantify how the combination of thinning and vegetation management influence the development of understory plant communities in mature Douglas-fir forests. The overarching goal of the MFS is to increase overstory tree growth while promoting the development of late-seral structural features and understory community composition through the use of VDT and understory vegetation management treatments (Brandeis et al., 2001; Newton and Cole, 2015). With twenty years of post-treatment vegetation data to draw from, this study offers an excellent opportunity to investigate impacts of these treatments on the understory community over a longer time period than other studies allow. To the author's knowledge, there is no information available on the interaction between thinning and herbicide use, and none on the impact of herbicide use on the abundance of specific seral groups in Douglas-fir forests. Several aspects of treatment impacts on the understory were investigated in this study: (1) how retention level and herbicide application affect change in community composition from pre-treatment conditions; (2) how these treatments affect the richness and abundance of common understory species; (3) how these treatments affect the richness and abundance of early- and late-seral associated understory species; and (4) whether understory vegetation responses to herbicide application vary with retention level. Specifically, I was interested in determining whether herbicide application resulted in a reduction in the legacy effect of common pre-treatment species beyond the initial few years following treatment, and if so, whether these potential reductions in common species abundance benefit late-seral-associated species across a range of thinning intensities.

3.3. Methods

3.3.1. Study sites

      All data for this study were collected from the Mature Forest Study (MFS), an ongoing silvicultural experiment looking at the long-term impacts of thinning and vegetation control on the development of multi-aged stands with late-seral characteristics. The MFS consists of study sites on two Oregon State University-owned Douglas-fir forests (Blodgett and McDonald) in the Coast Range of northwestern Oregon.

      McDonald Forest is located 8 km north of Corvallis, OR, in the eastern Coast Range. The climate is warm with a summer dry season and low relative humidity. Annual precipitation ranges from 102-152 cm per year, with 80-85% falling during October-April. At the time of the initial experimental thinning (1993), the overstory was composed primarily of 50-year-old planted Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco; 70 years old at time of most recent measuring period), with scattered naturally-regenerated grand fir (*Abies grandis* [Douglas ex D. Don] Lindl.) and bigleaf maple (*Acer macrophyllum* Pursh). The site had previously been thinned in 1964 and 1980. The understory is mainly dominated by fern and shrub species, the most abundant being: western sword fern (*Polystichum munitum* [Kaulf.] C. Presl.), western bracken fern (*Pteridium aquilinum* [L.] Kuhn), trailing blackberry (*Rubus ursinus* Cham. & Schltdl.), Himalaya blackberry (*Rubus armeniacus* Focke), Pacific poison oak (*Toxicodendron diversilobum* [Torr. & A. Gray] Greene), hazel (*Corylus cornuta* Marshall), and ocean spray (*Holodiscus discolor* [Pursh] Maxim.). Advance regeneration of both Douglas-fir and grand fir are also present throughout the site.

      Blodgett Forest is located approximately 10 km west of Clatskanie, OR and 3 km south of the Columbia River, in the northern Oregon Coast Range. Compared with McDonald Forest, the climate is moister, with a shorter summer dry season, higher relative humidity, and higher annual rainfall (152-200 cm per year; 80-85% October-April) . At the time of initial experimental thinning (1995), the overstory at Blodgett was composed of a mixture of 50-55-year-old Douglas-fir and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.; 70-75 years old at time of most recent measurement period), with some sparsely scattered western redcedar (*Thuja plicata* [D.] Don) and red alder (*Alnus rubra* Bong.). Overstory composition varied across the

site, ranging from mostly Douglas-fir to primarily hemlock. Blodgett developed from naturally regenerated clearcuts in the 1930s, and was thinned once prior to the MFS, in 1987. Like McDonald, Blodgett has a well-developed understory community, dominated by ferns and shrubs. The most abundant species are western sword fern, western bracken fern, deer fern (*Blechnum spicant* [L.] Roth), salal (*Gaultheria shallon* Pursh), Oregon grape (*Mahonia nervosa* [Pursh] Nutt.), salmonberry (*Rubus spectabilis* Pursh), red huckleberry (*Vaccinium parvifolium* Sm.), and abundant western hemlock advance regeneration.

3.3.2. Experimental design

The MFS used a randomized complete block, split-split plot design (Fig. 3.1). The McDonald site was blocked according to slope position, with lower slope position corresponding to greater soil depth and site quality. Blodgett was blocked according to the amount of western hemlock present in the overstory at the time of thinning.

Each site consisted of three 20-ha blocks, each of which was divided into two 10-ha units. Within blocks, these units were randomly assigned to either a uniform or gap-thinning treatment. All units were divided into four (McDonald) or three (Blodgett) 2.5-ha plots, which were randomly assigned to receive either low, medium, medium-high (McDonald only), or high retention thinning (Table 3.1). Each plot consisted of an interior 1.5-ha measurement plot surrounded by an 18-m buffer. Residual densities were approximately the same in uniform and gap-thinned plots of equivalent thinning treatments. In the uniform thinning plots, the residual trees were evenly distributed throughout, while in each gap-thinned plot, three 0.10-ha gaps and three 0.06-ha gaps were cleared. The matrix between gaps was thinned uniformly if necessary to achieve the desired plot-wide basal area. All plots were thinned from below, with harvesting operations conducted in summer 1993 at McDonald and fall/winter 1995-1996 at Blodgett. The medium and medium-high retention plots at McDonald were re-thinned back to original thinning basal areas during year 8 to release suppressed underplanted seedlings.

Each 1.5-ha overstory treatment plot was further divided into three 0.5-ha (McDonald) or two 0.75-ha (Blodgett) subplots, which were randomly assigned an understory vegetation treatment: no spray, spray, or release spray (McDonald only). The no spray treatment received no understory treatment beyond logging impacts and planting of understory seedlings.

In the spray treatments, herbicide was applied as a broadcast spray using the "waving wand" method. At McDonald, the herbicide treatment was applied in summer 1993, and consisted of 1.6 kg ha^{-1} glyphosate and 0.14 kg ha^{-1} imazapyr in 47 L ha^{-1} water. At Blodgett, the treatment was applied in late summer 1995, and consisted of 1.6 kg ha^{-1} glyphosate, 0.2 kg ha^{-1} imazapyr, and 0.16 kg ha^{-1} sulfometuron in 28 L ha^{-1} water. Subplots at Blodgett with an evergreen shrub presence were treated with an additional 3.3 kg ha^{-1} triclopyr ester. Due to a delay in log removal at Blodgett, the spray treatment had to be reapplied in fall 1996. This reapplication consisted of 0.16 kg ha^{-1} sulfometuron plus 2,4-dichlorophenoxyacetic acid or 2,4-dichlorophenoxyacetic acid and diclorprop at a 1.1 kg ha^{-1} phenoxy acid equivalent in 28 L ha^{-1} water. An additional 2.2 kg ha^{-1} triclopyr ester was used in subplots with a strong evergreen shrub presence. Release spray treatment subplots in McDonald received direct foliage application of Garlon 4 (3% triclopyr) in oil or Accord (3% glyphosate) in water. This was applied to vegetation around individual planted seedlings to release them from competition. Since it was not conducted at the Blodgett site, vegetation data from the release spray treatment were not included in this study.

The interior 1.5-ha measurement plots were underplanted in January 1994 at McDonald and February 1997 at Blodgett, with 3-m x 3-m and 3-m x 4-m spacing, respectively. Douglas-fir, grand fir, western hemlock, and western redcedar were planted in randomized double rows at McDonald; all species except grand fir were planted at Blodgett. With the exception of western redcedar seedlings at McDonald, which were Plug+2 transplants, all planted seedlings were Plug+1 transplants.

3.3.3. Sampling and data collection

Understory vegetation was assessed on 10 (McDonald) or 15 (Blodgett) permanent sample points established within each subplot. Sample points were established and measured during the growing season prior to thinning, and re-measured 1, 3, 5, 7, 10, 15, and 20 years after thinning.

Community composition was estimated within 1-m and 5-m radius nested sample plots at each point. All forb species within the 1-m sample plots were recorded. The presences of grass species and sedge and rush were recorded as well, although individual species were not recorded.

In the 5-m sample plots, all shrub and fern species were recorded. Shrubs and ferns were divided into three layers: low (1-1.49 m), mid (1.5-5 m), and tall (5-15 m), with anything above 15 m counted as overstory.

3.3.4. Responses and data aggregation

The impact of thinning and spray treatments on the pre-treatment vegetation legacy effect was examined through overall change in understory community composition, as well as changes in the abundances of seral groups and common species between pre-treatment and post-treatment. All responses were calculated for two separate time intervals (pre-treatment to five years post-treatment and pre-treatment to 20 years post-treatment).

Overall compositional change was quantified as Bray-Curtis percent dissimilarity (PD) between pre-treatment and post-treatment communities. Bray-Curtis dissimilarity between two samples *i* and *i'* was calculated using the formula:

$$PD_{ii'} = \frac{\sum_{j=1}^{p}|n_{ij} - n_{i'j}|}{\sum_{j=1}^{p}n_{ij} + \sum_{j=1}^{p}n_{i'j}}$$

All individual species were included, although grasses and sedges/rushes were not differentiated by species. However, grass cover was common on McDonald only, and mainly consisted of false brome; sedges and rushes were uncommon on both sites. For this study, shrub and fern species were not separated by height, so species that occurred in multiple height layers were only counted once per sampling point. Additionally, understory was defined as vegetation ≤5 m tall (low and mid layers only). Abundance for all species was calculated as the frequency of sampling points in which a species was present within each retention treatment x vegetation treatment subplot.

Changes in the abundance of species that were common prior to treatment were analyzed to evaluate potential treatment impacts on legacy effects associated with the persistence of pre-treatment vegetation communities. Common species were defined using two thresholds: species that occurred in >25% and >50% of sample points at a site (Table 3.2). At each threshold, all common species were aggregated into a single group within treatment subplots. For each common species group, pre-treatment to five- and twenty-year post-treatment change was examined using the changes in several measures of abundance: species richness, total (summed)

frequency, and relative (proportional) frequency. To calculate total frequency for common species groups, frequency for each individual species within that category was first calculated as the percentage of sample points in a treatment subplot where that species was present. Frequency estimates for all species in a common species group were then summed within each treatment subplot to get total frequency. Relative frequency was calculated as the ratio of the total frequency of the category being analyzed to the total frequency of all species in the subplot. Changes in abundance metrics were calculated as the difference between post-treatment and pre-treatment subplots for each time interval (i.e., five and twenty years post-treatment).

For seral group response, species were aggregated by growth form and seral group into the following groupings (Table 3.3): early seral forbs (n = 35), late seral forbs (n = 15), early seral shrubs (n = 12) and late seral shrubs (n = 9). Seral classifications were made based on previous studies in the region (Dyrness, 1973; Halpern and Lutz, 2013; Halpern and Spies, 1995; Halpern, 1989; Halpern et al., 2012). Ferns and naturally regenerated trees were included as shrubs, with seral classification based additionally on site history. Seral group richness, total frequency, and relative frequency were calculated in the same manner as for common species groups.

3.3.5. Analysis

Community composition was analyzed using non-metric multidimensional scaling (NMDS; Kruskal, 1964) to show compositional differences between treatments, as well as changes over time. Individual species abundances were aggregated by subplot as described above, then averaged across all six units for each density x vegetation treatment (McDonald, n = 8 samples/year; Blodgett, n = 6 samples/year). For the NMDS analysis, five sampling times were included: pre-treatment and post-treatment years 1, 5, 10, and 20. Bray-Curtis was used as the distance measure for analysis. Following McCune and Grace (2002), all ordinations were run using a random starting configuration and a maximum of 500 iterations. Models were rerun a maximum of 50 times, or until an instability criterion of 0.00001 was reached. Monte Carlo tests were performed to establish that the final axes were stronger than chance. The final solutions for both sites were two-dimensional, with stresses of 0.14 (Blodgett) and 0.16 (McDonald). The amount of variation explained by the first axis was maximized by rotating the final solutions.

PD, common species responses, and seral group responses were analyzed using mixed-effects ANOVA models with density treatment, understory spray treatment, and their interaction as fixed effects, and block, unit, and plot as random effects. Separate models were used for each site, time interval (5 and 20 years post-treatment only), and response variable (PD, species richness, total frequency, and relative frequency). Model residuals were assessed for homoscedasticity and normality using diagnostic plots; responses were square root transformed when necessary. Effects were considered significant at $\alpha = 0.05$, and Tukey's HSD was used to adjust for multiple comparisons. All analyses were performed separately for McDonald and Blodgett to prevent results from being confounded by the differences in understory communities and abiotic conditions between these sites.

Although the MFS incorporated two different patterns of retention (uniform thin and gap thin), evaluating the community differences between uniform thinned and gap thinned stands was not of concern in this study. Thus retention pattern was only included as the "unit" random effect in the models. The exclusion of this variable should not significantly impact the findings of this study. While others have found that there are within-treatment differences in understory response between gaps and matrix, this did not equate to significant differences in treatment-level response between different patterns of retention (Halpern et al., 2005). In addition, adding retention pattern and its interactions with retention level and spray treatment as additional fixed effects would risk over-parameterizing the models, reducing the ability to detect treatment-level differences.

3.4. Results

3.4.1. Compositional change

Both the Blodgett and McDonald sites displayed compositional change over time in NMDS space (Fig. 3.2). The magnitude of change in NMDS space from pre-treatment composition appeared greater for the spray treatment than the no spray treatment across sites and retention levels. The spray treatments seemed to remain distinct through post-treatment year 10, but began to converge and overlap by year 20, particularly at Blodgett. Both sites displayed a possible retention level effect, as well, although only within vegetation management treatment groupings. In the spray treatment at Blodgett, the low retention treatment was separated in

NMDS space from the other two retention treatments along axis 1 in years one and five, although there appeared to be little difference in the magnitude of change from pre-treatment conditions. This separation disappeared in subsequent measurement periods. In the no spray treatments at McDonald, the magnitude of compositional change appeared greater in the low retention treatment than the high retention one; no such pattern was observable within the spray treatments. The pattern of compositional change among retention levels at McDonald seemed to remain largely stable through year 20.

Results from PD analyses largely agreed with NMDS results. PD at both sites differed between spray treatments for both time intervals (i.e. 5 and 20 years post-treatment), while retention treatments differed only at McDonald at year 5 (Table 3.4); the spray x retention interaction was not significant in any of the models (Table 3.4).

In all comparisons, the spray treatment resulted in greater compositional dissimilarity from pre-treatment conditions relative to the no spray treatment (Fig. 3.3A). At Blodgett, the difference in PD between spray and no spray treatments was 10.6% at year 5 ($t_{15} = 4.9$, $P < 0.001$) and 3.4% at year 20 ($t_{15} = 2.6$, $P = .020$). At McDonald, the difference in PD was 11.2% at year 5 ($t_{20} = 7.9$, $P < 0.001$) and 7.0% at year 20 ($t_{20} = 5.0$, $P < 0.001$).

Retention treatment effects on PD were similar to the NMDS results as well (Fig. 3.3B). Retention level had no impact on community dissimilarity at Blodgett. At McDonald, dissimilarity was higher in the low retention treatment than the high retention treatment. The difference in PD between low and high retention was 8.3% at year 5 ($t_{15} = 4.2$, $P = 0.004$) and 6.0% at year 20 ($t_{15} = 3.0$, $P = 0.038$). Although the retention level effect only approached significance at year 20 (Table 3.4), the high/low retention contrast remained significant.

3.4.2. Common species response

3.4.2.1. Herbicide treatment

Common species response to vegetation treatment was generally consistent and significant across richness and abundance metrics, cutoff threshold, and post-treatment year (Table 3.5). At Blodgett, richness and total frequency in the no spray treatment generally increased from pre-treatment levels, while richness and total frequency in the spray treatment and relative frequency in both treatments decreased (Fig. 3.4). Using the 25% cutoff threshold,

five-year changes in richness (-0.5, t_{15} = 4.4, P < 0.001), total frequency (-264.4%, t_{15} = 10.2, P < 0.001), and relative frequency (-11.9%, t_{15} = 5.2, P < 0.001) were more negative in the spray treatment than the no spray treatment. Using the 50% cutoff threshold, five-year changes in richness (-0.4, t_{15} = 3.2, P = 0.006), total frequency (-148.3%, t_{15} = 10.1, P < 0.001), and relative frequency (-5.5%, t_{15} = 2.9, P = 0.012) were similarly more negative in the spray treatment.

All spray treatment effects on common species at Blodgett persisted until 20 years post-treatment (Fig. 3.4). Using the 25% cutoff threshold, twenty-year changes in richness (-0.6, t_{15} = 2.5, P = 0.025), total frequency (-142.8%, t_{15} = 5.4, P < 0.001), and relative frequency (-6.0%, t_{15} = 4.0, P = 0.001) were more negative in the spray treatment than the no spray treatment. Using the 50% cutoff threshold, twenty-year changes in richness (-0.4, t_{15} = 3.2, P = 0.010), total frequency (-100.0%, t_{15} = 5.1, P < 0.001), and relative frequency (-4.1%, t_{15} = 2.8, P = 0.015) were again more negative in the spray treatment.

Spray treatments had similar impacts on five-year changes in richness and abundance of common species at McDonald to those found at Blodgett, except that the increase in total frequency from pre-treatment levels in the no spray treatment was minimal (Table 3.5; Fig. 3.4). Using the 25% cutoff threshold, five-year changes in richness (-1.1, t_{15} = 3.0, P = 0.006), total frequency (-132.1%, t_{20} = 3.5, P = 0.002), and relative frequency (-8.4%, t_{20} = 4.7, P < 0.001) were more negative in the spray treatment than the no spray treatment. Using the 50% cutoff threshold, five-year changes in richness (-0.5, t_{20} = 2.6, P = 0.017), total frequency (-43.9%, t_{20} = 2.6, P = 0.018), and relative frequency (-5.4%, t_{20} = 3.2, P = 0.004) were similarly more negative in the spray treatment. Only differences in relative frequency remained significant until twenty years post-treatment (Table 3.5). Relative frequency in the spray treatment changed from pre-treatment levels by -6.1% (25% cutoff; t_{20} = 3.4, P = 0.003) and -4.8% (50% cutoff; t_{20} = 3.0, P = 0.007) relative to the no spray treatment.

3.4.2.2. Retention level and treatment interactions

Retention level had a much smaller impact on post-treatment changes in common species abundance than vegetation spray treatment. At Blodgett, the only significant retention treatment effect was for total frequency of common species at the 50% cutoff at year 20 (Table 3.5). Total frequency in the low retention treatment decreased slightly from pre-treatment levels,

while it increased slightly in the medium and high retention (Fig. 3.5). This resulted in the total frequency change in low retention being 58.3% (t_{10} = 3.2, P = 0.022) more negative compared to high retention. At McDonald, there was some effect of retention treatment on relative frequency of common species five years post-treatment (Table 3.5). Relative frequency decreased from pre-treatment in all treatments, with changes in the higher retention treatments being less negative (Fig. 3.5). Compared to high retention, the change in relative frequency in medium retention was 8.0% (25% cutoff; t_{15} = 3.2, P = 0.028) and 7.2% (50% cutoff; t_{15} = 3.0, P = 0.041) more negative, and frequency in low retention was 9.3% (50% cutoff; t_{15} = 3.9, P = 0.007) more negative. Retention level effects at McDonald were not significant at year 20 for either cutoff threshold (Fig. 3.5).

There was evidence of some interaction between vegetation and retention level at Blodgett, but not at McDonald (Table 3.5). There were significant interactions at Blodgett for changes in total frequency five-years post-treatment and relative frequency 20 years post-treatment for both cutoff thresholds. Five years post-treatment, contrasts at the 25% cutoff reflected the vegetation treatment main effect, with retention level only affecting the magnitude of the difference between the spray and no spray treatments (Table 3.6). The interaction was slightly more complicated at the 50% cutoff threshold, but in general showed a similar trend (Table 3.6). Interactions for relative frequency 20 years post-treatment only showed a difference between medium retention x spray and medium retention x no spray at the 50% cutoff (Table 3.6). For both cutoff thresholds, the change in relative frequency in the medium retention x spray treatment was more negative than in the medium retention x no spray treatment.

3.4.3. Seral group response

3.4.3.1. Herbicide treatment

Trends in seral group responses across treatment were less consistent than those seen in community composition (PD) and common species for both vegetation and retention treatments. At Blodgett, vegetation treatment had significant effects on five-year changes in richness, total frequency, and relative frequency of early shrubs (Table 3.7). Five years post-treatment, early-seral shrubs in the no spray treatment had increased in richness, total frequency, and relative frequency, but decreased in each of these metrics in the spray treatment (Fig. 3.6). As a result,

the changes in early-seral shrub richness (0.8, $t_{15} = 2.8$, P = 0.013), total frequency (44.4%, $t_{15} =$ 3.7, P = .002), and relative frequency (4.0%, $t_{15} = 2.4$, P = 0.032) were more positive in the no spray treatment than the spray treatment. Spray treatment did not significantly impact changes in abundance metrics from pre-treatment levels in early-seral forbs at either time interval, or twenty-year changes in early-seral shrubs.

Early-seral vegetation at McDonald often displayed minimal to slightly positive changes from pre-treatment conditions in the no spray treatments, but increased greatly in richness and abundance in the spray treatment, particularly for early-seral forbs (Fig. 3.6). As a result, the five-year changes in early-seral forb richness (2.8, $t_{20} = 3.3$, P = 0.003), total frequency (72.9%, $t_{20} = 3.7$, P = 0.001), and relative frequency (4.9%, $t_{20} = 2.1$, P = 0.49) were more positive in the spray treatment compared to the no spray treatment. Early-seral shrubs showed a more positive change in relative frequency in the spray treatment, as well (6.1%, $t_{20} = 2.8$, P = 0.011). Like Blodgett, spray treatment effects on early-seral vegetation at McDonald generally did not persist until the 20-year measurements.

Late-seral vegetation displayed a less consistent short-term effect than early-seral vegetation. At Blodgett, vegetation treatment had significant but opposing effects on post-treatment changes in total frequency and relative frequency of late-seral shrubs (Table 3.7; Fig. 3.6). Five years post-treatment, total late-seral shrub frequency had increased slightly in the no spray treatment, but decreased slightly in the spray treatment. Relative frequency decreased in both treatments, but less so in the spray treatment. As a result, the change in total late-seral shrub frequency was 62.6% more positive ($t_{15} = 5.4$, P < 0.001) in the no spray treatment, but the change in relative frequency was 7.2% more negative ($t_{15} = 3.9$, P = 0.001). Only the change in total frequency persisted until 20 years post-treatment.

Late-seral vegetation at McDonald generally showed little vegetation treatment effect. Five years post-treatment, relative frequency of late-seral forbs had decreased in both treatments, but slightly less so in the no-spray treatment (Table 3.7; Fig. 3.6). Total frequency of late-seral shrubs showed a similar relationship, although frequency increased slightly in the no spray treatment (Table 3.7; Fig. 3.6). The change in relative late-seral forb frequency was 3.5% more positive ($t_{20} = 2.5$, P = 0.020) in the no spray treatment, and the change in total late-seral shrub

frequency was 60.4% higher (t_{20} = 3.8, P = 0.001). Only the change in relative late-seral forb frequency persisted until 20 years post-treatment.

3.4.3.2. Retention level and treatment interactions

Retention level had no impact on post-treatment changes in either early or late-seral vegetation richness or abundance at Blodgett for either time interval (Table 3.7). At McDonald, retention level generally had significant impacts on changes in total and relative frequency for all seral groups and time intervals (Table 3.7). Five-years post-treatment, early-seral vegetation abundance consistently ranged from increasing in low retention to slightly decreasing in high retention at McDonald (Fig. 3.7). As a result, the changes in early-seral forb richness (4.2, t_{15} = 3.2, P = 0.027), total frequency (125%, t_{15} = 4.5, P = 0.002), and relative frequency (16.8%, t_{15} = 5.1, P < 0.001) in low retention were more positive than in high retention; the change in early-seral shrub total frequency (101.7%, t_{15} = 5.0, P < 0.001) and relative frequency (12.0%, t_{15} = 3.8, P = 0.008) was also more positive in low retention than in high retention. This retention treatment effect persisted until year 20 for shrubs, but not forbs.

In general, retention level had little short-term impact on late-seral vegetation at McDonald, only affecting five-year changes in relative frequency of late-seral shrubs (Table 3.7). Relative frequency decreased from pre-treatment at all retention levels, although the change was minimal in high retention (Fig. 3.7). Relative frequency dropped by 10.8% less in the high retention than in low retention (t_{15} = 3.2, P = 0.024). This effect persisted until year 20. Additionally, late-seral forbs showed some longer-term response to retention level (Table 3.7). Twenty years post-treatment, total and relative frequency of late-seral forbs had increased slightly in high retention and decreased slightly at all other retention levels (Fig. 3.7). As a result, the change in total frequency in high retention was 44.2% more positive than in low retention (t_{15} = 3.1, P = 0.032), 46.7% more positive than in medium retention (t_{15} = 3.1, P = 0.034), and 52.5% more positive than in medium-high retention (t_{15} = 3.1, P = 0.035). The change in relative frequency in high retention was 8.7% more positive than in medium retention (t_{15} = 3.1, P = 0.033), 7.7% more positive than in low retention, and 7.5% more positive than in medium-high retention, although the latter two only approached significance (P = 0.065 and P = 0.078, respectively).

There was little interaction between vegetation and retention level at either site; the only statistically significant interactions occurred for changes in early-seral shrub richness at Blodgett (Tables 3.7 and 3.8). Five years post-treatment, change in species richness in the low retention x no spray treatment was more positive than in the low retention x spray (1.8, $t_{10} = 3.9$, $P = 0.016$) and high retention x spray treatments (2.0, $t_{10} = 3.5$, $P = 0.046$). Although the interaction was also significant for changes in early-seral shrub richness at year 20, none of the contrasts were significant (Tables 3.7 and 3.8).

3.5. Discussion

3.5.1. General community changes

This study shows that herbicide treatment has had a strong impact on the overall development of understory plant communities within the MFS. There was limited evidence that thinning impacted community development as well, but this was not consistent across sites. As evidenced by the NMDS results, all treatments altered community composition at both the Blodgett and McDonald sites. This agrees with previous studies that have shown that thinning (Bailey et al., 1998; Lindh and Muir, 2004; Palmer et al., 2000) and herbicide application or other forms of vegetation control (Iglay et al., 2010; Rice et al., 1997; Ristau et al., 2011) have the potential to alter the overall composition of plant communities. Further, there is no evidence that either site has returned to pre-treatment conditions after 20 years of development. This study suggests that this trend could be due in part to 20-year changes in the abundances of common and late-seral species at the two sites. This longer-term response to disturbance is similar to what has been observed in other studies and systems (Halpern et al., 2012; Palmer et al., 2000) and adds to the vast literature describing the importance of disturbance history to forest communities (Attiwill, 1994).

The effect of herbicide treatment was consistent across sites. At both Blodgett and McDonald, plant communities in the spray treatment changed more from initial conditions than those in the no spray treatment. Contrary to other studies that have found this effect to be transient (Hawkins et al., 2013; Miller et al., 1999), the influence of herbicide application at the MFS sites has persisted for 20 years. This appears to be due in part to the greater reductions in abundance of common pre-treatment species in the spray treatment compared to the no spray

treatment. The influence of retention level was less clear. While all levels of treatment altered community composition, the relative impacts of different thinning intensities were not consistent between sites (Fig. 3.3B). At McDonald, there was a clear trend of increasing dissimilarity with decreasing overstory retention; retention level had no such effect at Blodgett. Although retention level appeared to impact understory communities five years after treatment at Blodgett, this effect was not significant and had disappeared completely by year 20, likely due to the high abundance of western hemlock regeneration in the understory there.

That the two sites in this study did not display similar results is consistent with the literature. While some studies have found that understory changes depend on thinning intensity (Ares et al., 2010; Halpern et al., 2005), others have found no such effect, particularly after longer time periods (Davis and Puettmann, 2009; He and Barclay, 2000; Wilson and Puettmann, 2007). Although it is clear that even less-severe disturbances can drive changes in community composition, the influence of intensity is likely complicated by other factors such as site-specific variation in environmental and initial stand conditions.

3.5.2. Common species response

3.5.2.1. Herbicide treatment

The differences in compositional change between the spray and no spray treatments was partially driven by how the most common species at each site responded. In general, the abundance of common pre-treatment species declined in the spray treatment, while exhibiting more limited change in the no spray treatment. Not only did herbicide application reduce total frequency of common species, it reduced their relative importance in the understory as well (Fig. 3.4). This is consistent with previous research on herbicide use in a variety of ecosystems. In their study of understory response to herbicide treatment in a northern hardwood forest, Ristau et al. (2011) found that herbicide application reduced the dominant fern component, shifting relative abundance toward other species. This was due in part to the resilience of herb species to treatment, a trend that also mostly held true for early and late-seral herbs in the MFS as well.

By this measure, herbicide application was potentially successful in reducing the legacy effect of pre-treatment communities. Herbicides are often used to open growing space and allow less prominent species to move in (Getsinger et al., 1997; Iglay et al., 2010), and the more

negative change in relative frequency in the spray treatment (4.1-6.1% twenty years post-treatment) suggests that herbicide application reduced growing space allocation to common pre-treatment species at the MFS sites as well. As with overall compositional change, the effects of herbicide spray on common species has persisted until 20 years post-treatment. There appeared to be some decline in the size of the effect relative to that five years post-treatment, suggesting that common species may eventually recover to their pre-treatment importance. This is merely speculation however, as it was not tested statistically.

3.5.2.2. Retention level

Unlike herbicide treatment, overstory density management treatments appeared to have little impact on the abundance of common understory species. Although there was a slight decline in the relative abundance of common species with decreasing retention level at McDonald by post-treatment year five, this trend had disappeared by year 20. On its own, thinning seemed to have limited influence on the importance of dominant species. Dyrness (1973), for instance, found that logging did not remove characteristic species. Most likely, the strength of the canopy's influence is relatively weak and overridden by other factors, such as site condition and topography (Gracia et al., 2007), and pre-treatment species composition (Halpern and Lutz, 2013; Hughes and Fahey, 1991). The latter is particularly important. Established dominant species often have an advantage over post-disturbance invaders, and can easily weather the transient short-term shifts in community composition (McGlone et al., 2011). In addition, dominant species have a greater concentration of propagules with which to reestablish themselves after disturbance (Tappeiner et al., 2001). This can vary depending on how sensitive the dominant species in a particular stand are to disturbance, however (He and Barclay, 2000).

3.5.3. Seral group response

3.5.3.1. Herbicide treatment

The impacts of herbicide treatment on early and late-seral species were somewhat inconsistent, although they did tend to be restricted to the short term, mostly. Five-years post-treatment, spray treatment tended to be detrimental to early-seral shrubs at Blodgett, but did not significantly impact early-seral forbs. At McDonald, however, spray treatment increased the richness and abundance of early-seral forbs, as well as increasing the relative importance of

early-seral forbs and shrubs. These effects had largely disappeared by year 20, however, displaying the transient impact of disturbance on early-seral vegetation communities (Ares et al., 2009; Halpern et al., 2012). The only exception was a slight benefit of spray treatment to early-seral shrubs at McDonald at year 20, although the evidence for this is limited.

Late-seral species seemed to be less influenced by herbicide treatment than early-seral species. The only impact of the spray treatment on late-seral forbs at either site was a slight detrimental effect on the relative importance of late-seral forbs at McDonald, although this did persist until post-treatment year 20. Late-seral shrubs showed a similar short-term detrimental impact of spray treatment on total frequency at both sites, although this effect only persisted to year 20 at Blodgett. Despite the negative effect on total late-seral shrub frequency at Blodgett, herbicide application actually mitigated the short-term decline in late-seral shrub importance at Blodgett. This is difficult to explain; speculatively, it may be that spray treatment was not quite as harmful to late-seral shrubs at Blodgett as it was to other species.

Unfortunately, while there is extensive literature on the impacts of thinning on different seral groups, there is a dearth of similar information for herbicide or other vegetation control methods. Studies on the effects of vegetation control treatments on plant communities tend to focus on either overall composition or particular species of interest, such as invasives (Getsinger et al., 1997; Hawkins et al., 2013; Rice et al., 1997). To the author's knowledge, there is no literature on the effects of herbicide treatment on early and late-seral forest species to act as a point of comparison for findings in this study.

On the MFS, herbicide use appears to have had no 20-year impact on the richness, abundance, and importance of early -seral understory species, and only limited impact on late-seral species. Herbicide use had some negative impact on the total frequency of late-seral shrubs at Blodgett, but not on their relative importance in the community. A small negative herbicide impact was observed on the relative importance of late-seral forbs at McDonald as well, although total frequency did not differ between vegetation management treatments. While the spray treatment was successful in reducing the importance of the dominant pre-treatment species, there is no evidence that this resulted in the promotion of desired late-seral associates. Most likely, the species that benefited most from the increased growing space were either forest generalists, or

simply proximate species positioned to quickly take advantage of competitive release. Regardless, more research is needed to corroborate these findings across a broader range of site conditions and stand structures.

3.5.3.2. Retention level

While retention level had little effect on the 20-year change in common species abundance, it did show some potential to impact the abundance of late-seral species. However, this appeared be heavily dependent on site conditions. Retention level had no discernable effect on either early or late-seral forbs and shrubs at Blodgett. Response to thinning at Blodgett generally seemed to be fairly limited, and was similar across retention levels. This may have been due to the vigorous growth of both naturally and artificially regenerated western hemlock in the understory at this site. The widespread presence of western hemlock regeneration in both the pre- and post-treatment communities severely limits available resources in the understory, including light, restricting the growth and survival of other species. As a result, there was likely little room for change in the understory communities there. Alaback and Herman (1988) observed a similar situation in a western hemlock-Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest in the Oregon Coast Range. High density of western hemlock saplings on their study sites reduced both shrub and herb frequency, resulting in a two-layered canopy with limited understory diversity.

In contrast, retention level had pronounced impacts on seral groups at McDonald, where the presence of tree regeneration in the understory was far more limited. Retention level had a particularly strong influence on the abundance of early-seral vegetation at McDonald. As with many previous studies (Ares et al., 2010; Griffis et al., 2001), the results of this study showed that lower overstory densities benefited both early-seral forbs and shrubs, increasing their richness, total frequency, and relative abundance. Conversely, the highest retention treatment appeared to result in a slight decline in early-seral species abundance. The effect of retention level persisted through year 20 for early seral shrubs, although early-seral abundance became more negative over time in all retention levels, returning to pre-thinning levels in the lower retention units. This is to be expected, as shrubs respond more gradually to disturbance than forbs, and changes persist longer (Halpern, 1989; Harrington et al., 2005).

Similar to other studies (Ares et al., 2010; Halpern et al., 2005), thinning appeared to have a slightly detrimental short-term impact on late-seral vegetation at McDonald. As Halpern et al. (2005) reported, this short-term decline in the relative importance of late-seral vegetation following thinning was exacerbated by heavier disturbance (i.e., lower retention levels) for late-seral shrubs. Late-seral forbs, however, displayed no variation in short-term response to different thinning intensities.

Retention level continued to influence abundance of late-seral vegetation at McDonald after 20 years. Unlike early-seral species, late-seral species often show longer-term response to thinning. Previous studies have shown that late-seral vegetation responds positively in the longer term to thinning in mature forests, as compared to unthinned controls (Bailey et al., 1998; Lindh and Muir, 2004). By 20 years post-treatment, late-seral forbs had begun displaying some of this positive response at McDonald. While abundance remained somewhat depressed in more heavily thinned plots, late-seral forbs increased in abundance and importance in high retention, likely due to higher shade tolerance.

Unlike late-seral forbs, late-seral shrub frequency still trended below pre-treatment levels after 20 years, and the relative abundance of late seral shrubs remained particularly depressed in lower retention plots. This can be explained by the slower response of shrubs to disturbance, as well as persistence of the negative impacts of heavier thinning (Battles et al., 2001; Halpern et al., 2012). The decline of late-seral shrubs does not necessarily indicate a lasting pattern, however; changes in the understory often lag behind changes in the overstory (Thomas et al., 1999). At a stand scale, late-seral species are generally resilient to disturbance, but can take a long time to recover (Halpern and Spies, 1995; Halpern et al., 2012). This is particularly true in heavily disturbed areas. Given sufficient time, it is possible that late-seral shrubs will make a full recovery.

3.6. Management Implications

This study suggests that herbicide application and thinning impact different aspects of 20-year understory plant community development. Herbicide treatment reduced common species abundance, and temporarily reduced early seral shrub abundance at one study site, but generally had few consistent impacts on late-seral vegetation. Thinning affected both early and late-seral

species abundance at the drier site (McDonald), but had no 20-year impacts on common species at either site.

As has been suggested by other authors (Battles et al., 2001; Halpern et al., 2005; Lindh and Muir, 2004), this study indicates that the best way to increase the abundance of late-seral species may be light thinning. Light thinning minimizes disturbance while maintaining higher shade conditions favorable to late-seral species. While herbicide application did not seem to provide any additional benefit to late seral species, there was little evidence that it was consistently harmful either. This gives managers more flexibility in achieving multiple objectives within a stand, such as promoting seedling establishment or reducing water stress. If the only objective for a stand is to promote late-seral communities, then evidence from this study suggests there is no need to take on the expense of applying herbicides. If, however, herbicide application is desired to meet other objectives, evidence suggests it will have limited impacts on the development of late-seral understory plant communities in the long term, if used properly.

Care should still be taken to understand the understory dynamics of a stand before opting for vegetation control, however. While the spray treatment was successful in reducing legacy effects of dominant pre-treatment vegetation, it did not discriminate based on seral group. Although it was not consistently detrimental to late-seral vegetation overall in this study, there was some overlap between common species and late-seral shrubs. Five out of nine late-seral shrub species at Blodgett and three out of nine at McDonald were also classified as common species. Since common species as a group were negatively impacted by spray treatment, it is possible that herbicide use could be detrimental in a stand whose understory is already dominated by late-seral species. Therefore, managers should first assess which species are common in their stand, and decide whether they wish to reduce the abundance of those species. From there, herbicide application can be tailored to the target species.

3.7. Tables

Table 3.1: Post-thinning overstory basal areas (BA), relative densities, and relative density indices (RDI) of overstory retention levels at Blodgett and McDonald.

Overstory retention level	Blodgett		
	BA (m^2 ha^{-1})	Relative density	RDI
Low	18.6-21.1	3.0	0.17
Medium	24.5-28.2	3.9	0.23
High	30.8-33.5	4.9	0.27
	McDonald		
	BA (m^2 ha^{-1})	Relative density	RDI
Low	16.7-18.8	2.6	0.18
Medium	19.3-25.1	3.3	0.23
Medium-High	26.9-29.6	4.0	0.27
High	27.7-32.9	4.6	0.31

Table 3.2: List of most common pre-treatment species by site and cutoff threshold.

Blodgett (50% cutoff)	McDonald (50% cutoff)
Acer circinatum	*Acer macrophyllum*
Mahonia nervosa	*Corylus cornuta*
Oxalis oregana	*Galium* sp.
Polystichum munitum	*Nemophila parviflora*
Tsuga heterophylla	*Osmorhiza berteroi*
Vaccinium parvifolium	*Polystichum munitum*
Additional sp. (25% cutoff)	*Pteridium aquilinum*
Gaultheria shallon	*Symphoricarpus albus*
Pteridium aquilinum	**Additional sp. (25% cutoff)**
Rubus parviflorus	*Adenocaulon bicolor*
Rubus spectabilis	*Claytonia sibirica*
	Rosa gymnocarpa
	Rubus leucodermis
	Rubus parviflorus
	Toxicodendron diversilobum
	Trientalis latifolia

Table 3.3: List of species list by seral group and growth form.

Early seral forbs	Asarum caudatum
Agoseris sp.	*Clintonia uniflora*
Anaphalis margaritacea	*Goodyera oblongifolia*
Cardamime oligosperma	*Maianthemum racemosum*
Chamerion angustifolium	*Maianthemum stellatum*
Chrysanthemum leucanthemum	*Prosartes hookeri*
Cirsium arvense	*Prosartes smithii*
Cirsium vulgare	*Streptopus lanceolatus*
Claytonia perfoliata	*Synthyris reniformis*
Claytonia sibirica	*Tiarella trifoliata*
Collomia heterophylla	*Trilium ovatum*
Epilobium ciliatum	*Vancouveria hexandra*
Epilobium minutum	**Early seral shrubs**
Equisetum arvense	*Amelanchier alnifolia*
Fragaria vesca	*Ceanothus sanguineus*
Hypericum perforatum	*Lonicera ciliosa*
Hypochaeris radicata	*Ribes divaricatum*
Iris tenax	*Ribes sanguineum*
Lactuca serriola	*Rubus armeniacus*
Lotus crassifolius	*Rubus laciniatus*
Lotus micranthus	*Rubus leucodermis*
Lotus unifoliolatus	*Rubus parviflorus*
Nemophila parviflora	*Rubus spectabilis*
Phacelia heterophylla	*Sambucus nigra*
Prunella vulgaris	*Sambucus racemosa*
Ranunculus uncinatus	**Late seral shrubs**
Rumex acetosella	*Abies grandis* (McDonald only)
Senecio jacobaea	*Acer circinatum*
Senecio sylvaticus	*Cornus nuttallii*
Silene sp.	*Corylus cornuta*
Stachys sp.	*Gaultheria shallon*
Stellaria calycantha	*Mahonia nervosa*
Stellaria crispa	*Polystichum munitum*
Tellima grandiflora	*Prunus emarginata*
Trifolium repens	*Pteridium aquilinum*
Late seral forbs	*Taxus brevifolia*
Achlys triphylla	*Thuja plicata* (Blodgett only)
Adenocaulon bicolor	*Tsuga heterophylla* (Blodgett only)

Table 3.4: ANOVA results table for percent dissimilarity analysis. Model effects are retention treatment (D), vegetation control treatment (V), and their interaction (D:V).

Site	Effect	DF	Year 5		Year 20	
			F value	P value	F value	P value
	D	2, 10	3.2	0.083	0.9	0.430
Blodgett	V	1, 15	24.3	<0.001*	6.7	0.020*
	D:V	2, 15	0.3	0.769	2.0	0.172
	D	3, 15	6.2	0.006*	3.2	0.055
McDonald	V	1, 20	98.2	<0.001*	24.7	<0.001*
	D:V	3, 20	1.5	0.242	0.6	0.621

* indicates significant P value (α = 0.05)

Table 3.5: ANOVA results table for common species analysis. Sites are Blodgett (B) and McDonald (M); responses are change in richness (R), total frequency (TF) and relative frequency (RF) relative to pre-treatment values; cutoff thresholds for the definition of common species are species present in >25% or >50% of retention level x vegetation treatment subplots; model effects are retention treatment (D), vegetation control treatment (V), and their interaction (D:V).

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Table 3.5

Site	Response	Cutoff	Effect	DF	Year 5		Year 20	
					F value	P value	F value	P value
B	R	25%	D	2, 10	0.1	0.890	0.7	0.503
B	R	25%	V	1, 15	20.3	<0.001*	6.2	0.025*
B	R	25%	D:V	2, 15	2.2	0.143	1.0	0.398
B	R	50%	D	2, 10	1.1	0.372	1.6	0.259
B	R	50%	V	1, 15	10	0.006*	8.4	0.011*
B	R	50%	D:V	2, 15	1.1	0.360	0.2	0.843
B	TF	25%	D	2, 10	1.3	0.307	0.9	0.436
B	TF	25%	V	1, 15	104.2	<0.001*	29.6	<0.001*
B	TF	25%	D:V	2, 15	6.4	0.010*	2.7	0.097
B	TF	50%	D	2, 10	2.3	0.148	6.3	0.017*
B	TF	50%	V	1, 15	101.9	<0.001*	45.7	<0.001*
B	TF	50%	D:V	2, 15	7.4	0.006*	1.5	0.250
B	RF	25%	D	2, 10	1.9	0.193	0.3	0.782
B	RF	25%	V	1, 15	35.4	<0.001*	15.9	0.001*
B	RF	25%	D:V	2, 15	1.4	0.280	5.3	0.018*
B	RF	50%	D	2, 10	1.9	0.198	0.7	0.503
B	RF	50%	V	1, 15	8.2	0.012*	7.6	0.015*
B	RF	50%	D:V	2, 15	1.3	0.298	4.5	0.030*
M	R	25%	D	3, 15	1.5	0.254	0.6	0.63
M	R	25%	V	1, 20	9.3	0.006*	0.0	1.000
M	R	25%	D:V	3, 20	1.5	0.252	1.7	0.206
M	R	50%	D	3, 15	2.1	0.139	1.4	0.277
M	R	50%	V	1, 20	6.8	0.017*	4.3	0.051
M	R	50%	D:V	3, 20	1.6	0.214	4.3	0.017*
M	TF	25%	D	3, 15	1.0	0.421	0.2	0.868
M	TF	25%	V	1, 20	12.1	0.002*	2.0	0.171
M	TF	25%	D:V	3, 20	0.7	0.578	0.3	0.799
M	TF	50%	D	3, 15	0.7	0.578	0.0	0.987
M	TF	50%	V	1, 20	6.7	0.018*	3.8	0.066
M	TF	50%	D:V	3, 20	0.1	0.962	0.3	0.848
M	RF	25%	D	3, 15	3.9	0.031*	2.8	0.076
M	RF	25%	V	1, 20	22.4	<0.001*	11.2	0.003*
M	RF	25%	D:V	3, 20	1.9	0.160	1.0	0.426
M	RF	50%	D	3, 15	5.6	0.009*	1.4	0.280
M	RF	50%	V	1, 20	10.3	0.004*	8.9	0.007*
M	RF	50%	D:V	3, 20	1.6	0.225	1.1	0.387

* indicates significant P value ($\alpha = 0.05$)

Table 3.6: Retention level x vegetation treatment interaction contrasts at Blodgett for pre-treatment to post-treatment changes in common species total frequency (TF) five years post-treatment and relative frequency (RF) 20 years post-treatment. Contrasts were performed using Tukey's HSD to adjust for multiple comparisons.

Year	Response	Contrast		DF	25% cutoff threshold			50% cutoff threshold		
					Estimate	t value	P value	Estimate	t ratio	P value
5	TF	HI, no spray	LO, no spray	10	-78.3	-1.7	0.535	5.0	0.2	1.000
5	TF	HI, no spray	MD, no spray	10	11.7	0.3	1.000	30.0	1.2	0.837
5	TF	HI, no spray	HI, spray	15	273.3	6.1	<0.001*	183.3	7.2	<0.001*
5	TF	HI, no spray	LO, spray	10	295.0	6.6	0.001*	198.3	7.8	<0.001*
5	TF	HI, no spray	MD, spray	10	158.3	3.5	0.046*	98.3	3.9	0.028*
5	TF	LO, no spray	MD, no spray	10	90.0	2.0	0.401	25.0	1.0	0.914
5	TF	LO, no spray	HI, spray	10	351.7	7.8	<0.001*	178.3	7.0	<0.001*
5	TF	LO, no spray	LO, spray	15	373.3	8.3	<0.001*	193.3	7.6	<0.001*
5	TF	LO, no spray	MD, spray	10	236.7	5.3	0.004*	93.3	3.7	0.037*
5	TF	MD, no spray	HI, spray	10	261.7	5.8	0.002*	153.3	6.0	0.001*
5	TF	MD, no spray	LO, spray	10	283.3	6.3	0.001*	168.3	6.6	0.001*
5	TF	MD, no spray	MD, spray	15	146.7	3.3	0.048*	68.3	2.7	0.136
5	TF	HI, spray	LO, spray	10	21.7	0.5	0.996	15.0	0.6	0.989
5	TF	HI, spray	MD, spray	10	-115.0	-2.6	0.193	-85.0	-3.3	0.061
5	TF	LO, spray	MD, spray	10	-136.7	-3.0	0.095	-100.0	-3.9	0.025*
20	RF	HI, no spray	LO, no spray	10	4.3	1.0	0.895	6.6	1.5	0.667
20	RF	HI, no spray	MD, no spray	10	-0.6	-0.1	1.000	1.1	0.3	1.000
20	RF	HI, no spray	HI, spray	15	5.7	2.2	0.294	3.6	1.4	0.716
20	RF	HI, no spray	LO, spray	10	4.4	1.1	0.885	5.5	1.3	0.800
20	RF	HI, no spray	MD, spray	10	11.6	2.8	0.136	10.8	2.5	0.220
20	RF	LO, no spray	MD, no spray	10	-4.9	-1.2	0.835	-5.5	-1.3	0.801

* indicates significant P value ($\alpha = 0.05$)

Table 3.6 (Continued)

Year	Response	Contrast		DF	25% cutoff threshold			50% cutoff threshold		
					Estimate	t value	P value	Estimate	t ratio	P value
20	RF	LO, no spray	HI, spray	10	1.5	0.4	0.999	-2.9	-0.7	0.981
20	RF	LO, no spray	LO, spray	15	0.1	0.0	1.000	-1.1	-0.4	0.998
20	RF	LO, no spray	MD, spray	10	7.3	1.8	0.521	4.2	1.0	0.920
20	RF	MD, no spray	HI, spray	10	6.3	1.5	0.649	2.5	0.6	0.990
20	RF	MD, no spray	LO, spray	10	5.0	1.2	0.823	4.4	1.0	0.906
20	RF	MD, no spray	MD, spray	15	12.2	4.7	0.003*	9.6	3.8	0.018*
20	RF	HI, spray	LO, spray	10	-1.4	-0.3	0.999	1.9	0.4	0.998
20	RF	HI, spray	MD, spray	10	5.8	1.4	0.720	7.1	1.6	0.594
20	RF	LO, spray	MD, spray	10	7.2	1.7	0.536	5.3	1.2	0.822

* indicates significant P value ($\alpha = 0.05$)

Table 3.7: ANOVA results table for seral group analysis. Sites are Blodgett (B) and McDonald (M); responses are changes in richness (R), total frequency (TF), and relative frequency (RF) relative to pre-treatment values; seral groups are early (E) and late (L); growth forms are forbs (F) and shrubs (S); model effects are retention treatment (D), vegetation control treatment (V), and their interaction (D:V).

Table 3.7

Site	Response	Seral Group	Growth Form	Effect	DF	Year 5		Year 20	
						F value	P value	F value	P value
B	R	E	F	D	2, 10	2.9	0.100	0.6	0.568
B	R	E	F	V	1, 15	1.2	0.285	0.4	0.526
B	R	E	F	D:V	2, 15	1.3	0.314	3.3	0.064
B	R	E	S	D	2, 10	1.5	0.272	0.1	0.913
B	R	E	S	V	1, 15	8.0	0.013*	1.5	0.236
B	R	E	S	D:V	2, 15	6.2	0.011*	4.7	0.026*
B	R	L	F	D	2, 10	0.7	0.503	0.2	0.854
B	R	L	F	V	1, 15	0.6	0.450	0.0	0.883
B	R	L	F	D:V	2, 15	1.4	0.274	3.5	0.057
B	R	L	S	D	2, 10	1.2	0.344	2.6	0.124
B	R	L	S	V	1, 15	0.0	1.000	0.0	0.953
B	R	L	S	D:V	2, 15	1.6	0.237	0.6	0.554
B	TF	E	F	D	2, 10	2.5	0.135	0.7	0.511
B	TF	E	F	V	1, 15	2.3	0.150	1.1	0.316
B	TF	E	F	D:V	2, 15	1.5	0.249	2.1	0.151
B	TF	E	S	D	2, 10	2.0	0.191	0.1	0.930
B	TF	E	S	V	1, 15	13.7	0.002*	2.5	0.137
B	TF	E	S	D:V	2, 15	3.4	0.061	1.7	0.209
B	TF	L	F	D	2, 10	0.7	0.501	0.6	0.579
B	TF	L	F	V	1, 15	0.1	0.802	0.0	0.958
B	TF	L	F	D:V	2, 15	0.4	0.666	2.0	0.168
B	TF	L	S	D	2, 10	0.6	0.548	1.3	0.316
B	TF	L	S	V	1, 15	21.5	<0.001*	7.0	0.018*
B	TF	L	S	D:V	2, 15	0.8	0.454	2.9	0.088
B	RF	E	F	D	2, 10	2.0	0.186	1.9	0.205
B	RF	E	F	V	1, 15	0.1	0.753	0.0	0.865
B	RF	E	F	D:V	2, 15	1.3	0.308	0.9	0.433
B	RF	E	S	D	2, 10	1.6	0.240	0.1	0.951
B	RF	E	S	V	1, 15	5.6	0.032*	1.1	0.321
B	RF	E	S	D:V	2, 15	1.7	0.216	0.6	0.547
B	RF	L	F	D	2, 10	1.1	0.384	0.1	0.879
B	RF	L	F	V	1, 15	0.6	0.447	0.0	0.977
B	RF	L	F	D:V	2, 15	0.1	0.903	0.1	0.918
B	RF	L	S	D	2, 10	2.6	0.124	1.0	0.417
B	RF	L	S	V	1, 15	15.4	0.001*	0.4	0.516
B	RF	L	S	D:V	2, 15	1.5	0.258	2.6	0.111

* indicates significant P value ($\alpha = 0.05$)

Table 3.7 (Continued)

Site	Response	Seral Group	Growth Form	Effect	DF	Year 5 F value	Year 5 P value	Year 20 F value	Year 20 P value
M	R	E	F	D	3, 15	4.2	0.024*	1.7	0.218
M	R	E	F	V	1, 20	11.0	0.003*	0.7	0.400
M	R	E	F	D:V	3, 20	1.1	0.367	1.2	0.345
M	R	E	S	D	3, 15	2.5	0.096	2.4	0.111
M	R	E	S	V	1, 20	1.4	0.254	0.9	0.364
M	R	E	S	D:V	3, 20	0.7	0.590	1.0	0.423
M	R	L	F	D	3, 15	0.9	0.447	2.0	0.151
M	R	L	F	V	1, 20	0.3	0.602	0.0	0.920
M	R	L	F	D:V	3, 20	0.8	0.486	0.7	0.563
M	R	L	S	D	3, 15	2.3	0.121	1.5	0.254
M	R	L	S	V	1, 20	0.4	0.548	0.2	0.692
M	R	L	S	D:V	3, 20	2.2	0.122	1.7	0.200
M	TF	E	F	D	3, 15	7.2	0.003*	1.3	0.307
M	TF	E	F	V	1, 20	13.5	0.001*	0.0	0.981
M	TF	E	F	D:V	3, 20	1.3	0.292	2.1	0.136
M	TF	E	S	D	3, 15	9.5	0.001*	5.3	0.011*
M	TF	E	S	V	1, 20	1.6	0.220	8.0	0.010*
M	TF	E	S	D:V	3, 20	0.5	0.679	1.1	0.372
M	TF	L	F	D	3, 15	1.8	0.189	5.0	0.014*
M	TF	L	F	V	1, 20	2.1	0.165	1.4	0.243
M	TF	L	F	D:V	3, 20	0.4	0.760	1.9	0.164
M	TF	L	S	D	3, 15	1.4	0.268	0.6	0.616
M	TF	L	S	V	1, 20	14.6	0.001*	2.0	0.173
M	TF	L	S	D:V	3, 20	0.6	0.617	0.2	0.896
M	RF	E	F	D	3, 15	9.5	0.001*	1.4	0.292
M	RF	E	F	V	1, 20	4.4	0.049*	0.1	0.770
M	RF	E	F	D:V	3, 20	0.5	0.676	1.7	0.204
M	RF	E	S	D	3, 15	5.0	0.014*	3.6	0.039*
M	RF	E	S	V	1, 20	7.8	0.011*	4.2	0.054
M	RF	E	S	D:V	3, 20	0.7	0.545	0.3	0.839
M	RF	L	F	D	3, 15	2.5	0.097	4.1	0.027*
M	RF	L	F	V	1, 20	6.3	0.021*	6.2	0.022*
M	RF	L	F	D:V	3, 20	0.2	0.887	2.1	0.134
M	RF	L	S	D	3, 15	3.7	0.036*	2.9	0.071
M	RF	L	S	V	1, 20	0.0	0.908	0.4	0.522
M	RF	L	S	D:V	3, 20	0.7	0.552	0.6	0.645

* indicates significant P value ($\alpha = 0.05$)

Table 3.8: Retention level x vegetation treatment interaction contrasts for pre-treatment to post-treatment changes in richness of early-seral shrubs at Blodgett. Contrasts were performed using Tukey's HSD to adjust for multiple comparisons.

Contrast		DF	Year 5			Year 20		
			Estimate	t value	P value	Estimate	t value	P value
HI, no spray	LO, no spray	10	-1.0	-1.8	0.526	-0.2	-0.5	0.997
HI, no spray	MD, no spray	10	0.0	0.0	1.000	0.3	0.9	0.938
HI, no spray	HI, spray	15	1.0	2.1	0.336	0.8	1.8	0.504
HI, no spray	LO, spray	10	0.8	1.5	0.689	0.8	1.7	0.554
HI, no spray	MD, spray	10	-0.5	-0.9	0.943	-0.5	-1.0	0.898
LO, no spray	MD, no spray	10	1.0	1.8	0.526	0.5	1.4	0.753
LO, no spray	HI, spray	10	2.0	3.5	0.046*	1.0	2.1	0.379
LO, no spray	LO, spray	15	1.8	3.9	0.016*	1.0	2.1	0.320
LO, no spray	MD, spray	10	0.5	0.9	0.943	-0.3	-0.7	0.980
MD, no spray	HI, spray	10	1.0	1.8	0.526	0.5	1.0	0.898
MD, no spray	LO, spray	10	0.8	1.5	0.689	0.5	1.0	0.898
MD, no spray	MD, spray	15	-0.5	-1.1	0.893	-0.8	-1.8	0.504
HI, spray	LO, spray	10	-0.2	-0.3	1.000	0.0	0.0	1.000
HI, spray	MD, spray	10	-1.5	-2.6	0.172	-1.3	-2.3	0.278
LO, spray	MD, spray	10	-1.3	-2.4	0.259	-1.3	-2.3	0.278

* indicates significant P value ($\alpha = 0.05$)

3.8. Figures
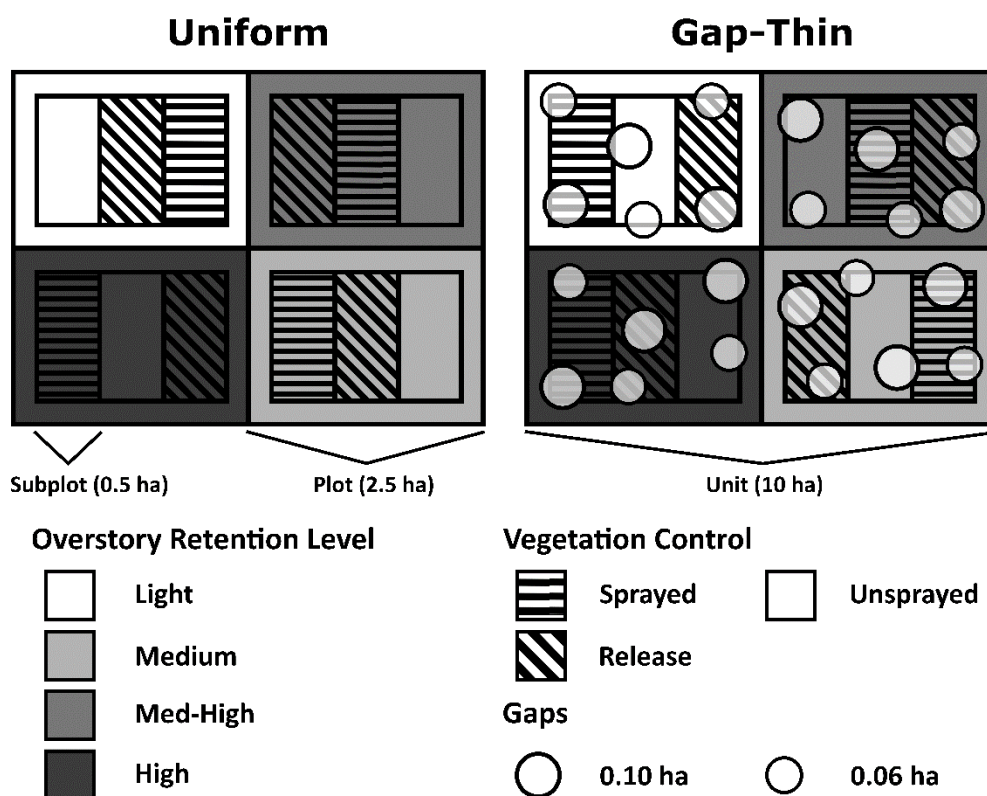
Figure 3.1: Study layout of the Mature Forest Study. Example is the study design at McDonald; Blodgett was laid out similarly, except the medium-high retention and release spray treatments were excluded.
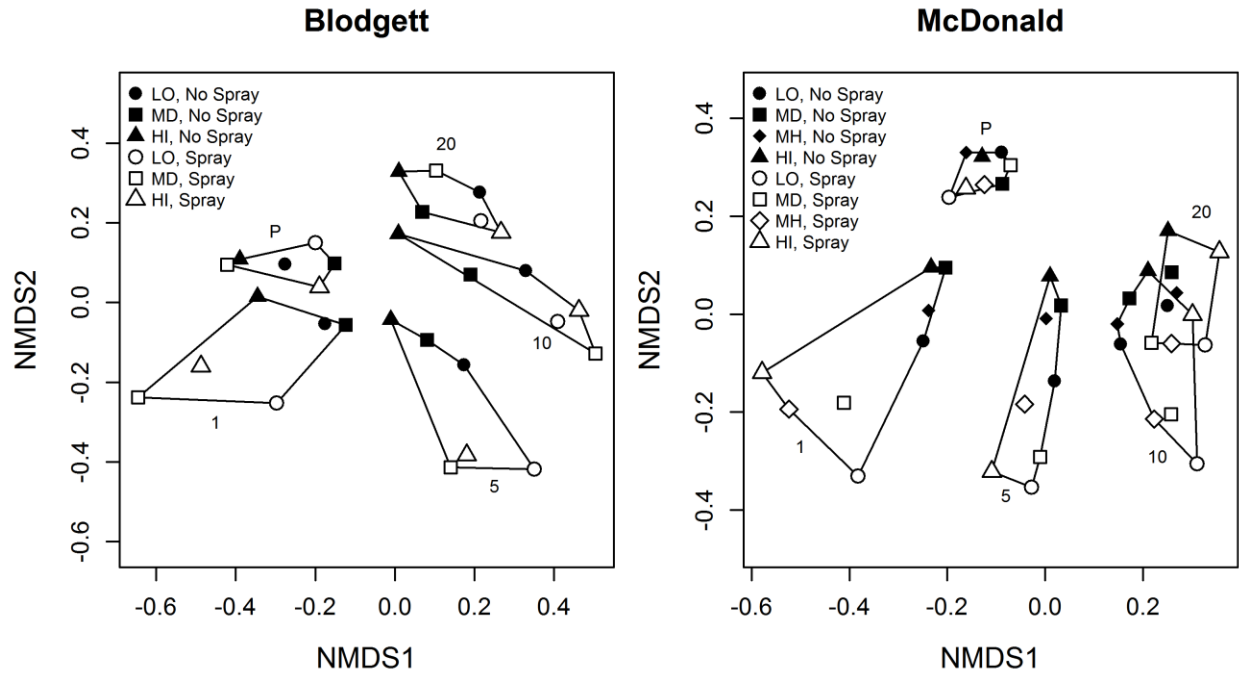
Figure 3.2: Non-metric multidimensional scaling (NMDS) ordinations of understory community composition at Blodgett and McDonald. Points represent average species composition for each retention level x vegetation treatment (Blodgett, n = 6 samples/year; McDonald, n = 8 samples/year). Point shapes represent different retention treatments. Solid fill represents the no spray treatment, empty fill represents the spray treatment. Polygons encapsulate each measurement period (pre-treatment (P), and post-treatment years 1, 5, 10, and 20).
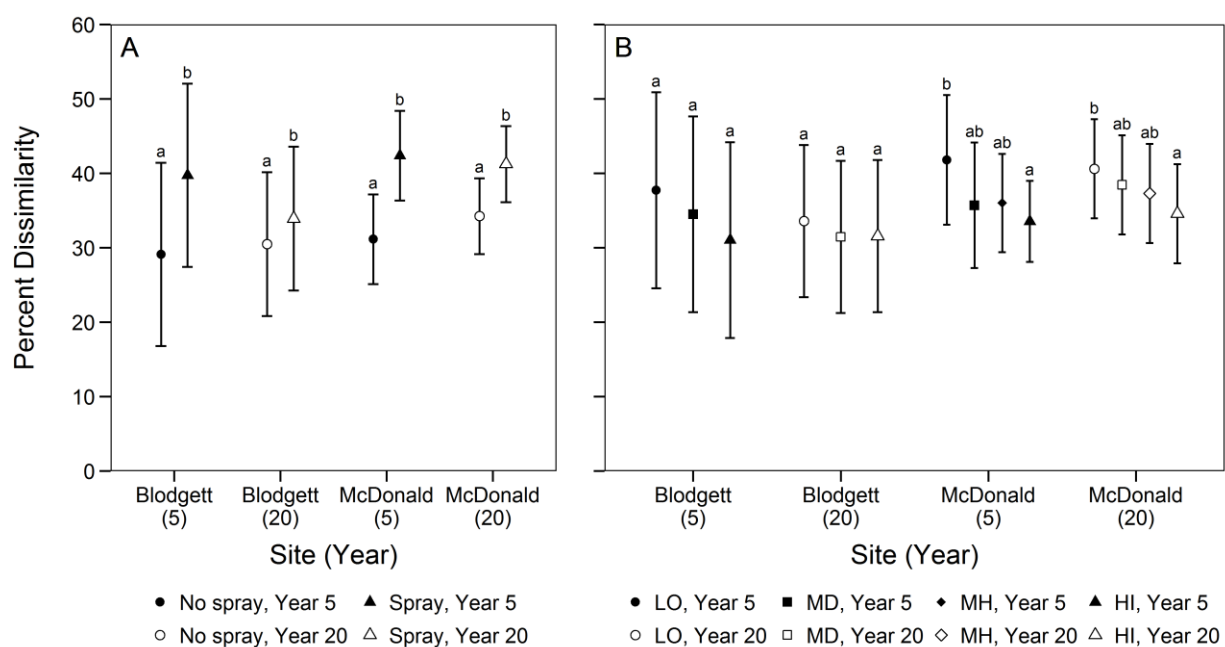
Figure 3.3: Understory community composition response (percent dissimilarity; mean ± 95% CI) to vegetation management treatment (A) and retention treatment (B) at Blodgett and McDonald. Comparisons were made between pre-treatment and post-treatment years 5 and 20. Solid fill represents five-year post-treatment changes; empty fill represents twenty-year post-treatment changes; shapes represent vegetation treatment (A) and retention treatment (B). Lettering above the error bars indicates whether means for a given site and year differed significantly from one another at α = 0.05.
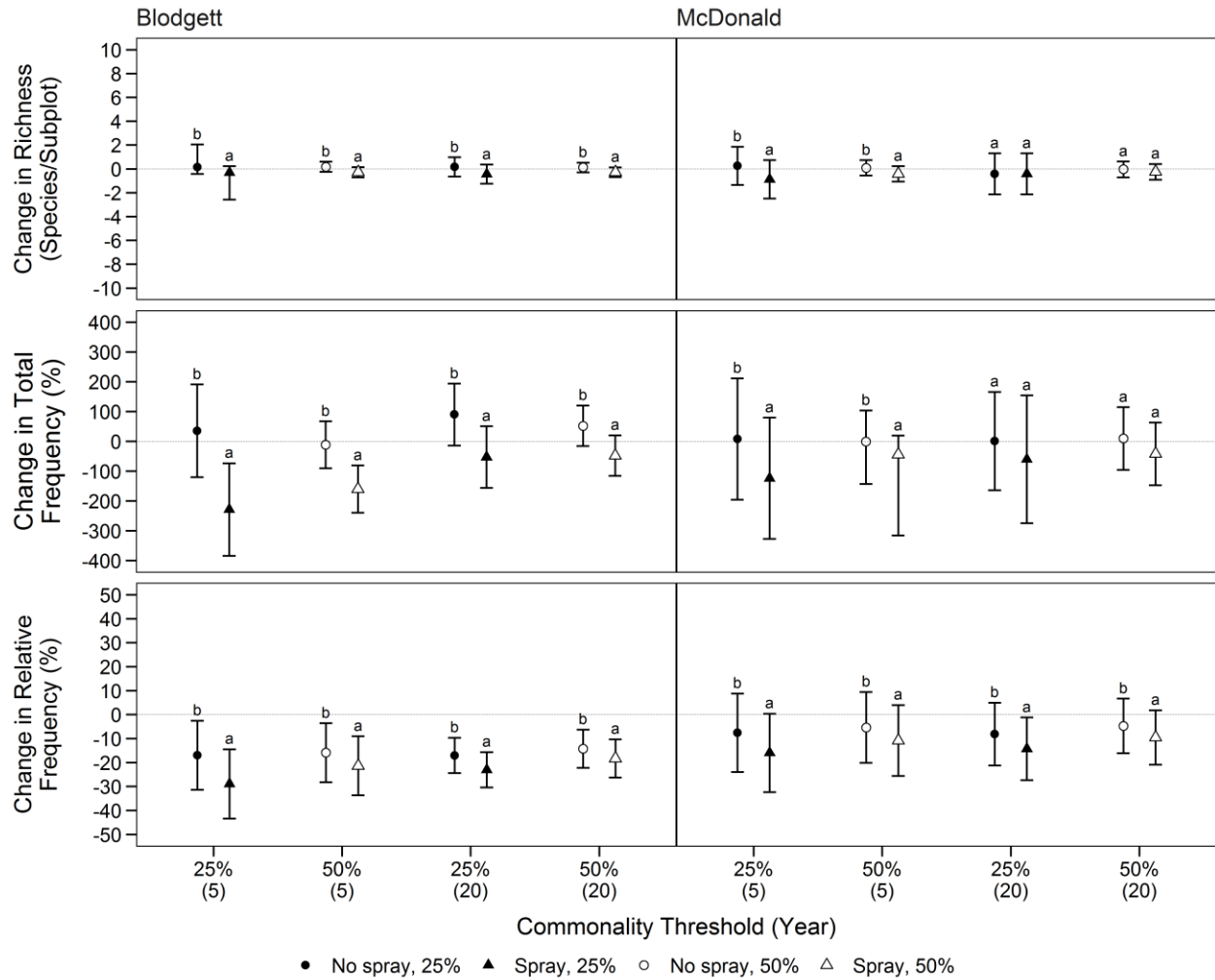
Figure 3.4: Common species responses (mean ± 95% CI) to vegetation management treatment at Blodgett and McDonald. Responses include five- and twenty-year post-treatment changes in species richness, total frequency, and relative frequency of common species. Common species were defined using two different cutoff thresholds (species that occurred in >25% or >50% of sample points at a site). Solid fill represents common species response for the 25% cutoff; empty fill represents common species response at the 50% cutoff; shapes represent vegetation treatment. Lettering above the error bars indicates whether means for a given cutoff and year differed significantly from one another at α = 0.05.

Figure 3.5: Common species responses (mean ± 95% CI) to retention treatment at Blodgett and McDonald. Responses include five- and twenty-year post-treatment changes in species richness, total frequency, and relative frequency of common species. Common species were defined using two different cutoff thresholds (species that occurred in >25% or >50% of sample points at a site). Solid fill represents common species response for the 25% cutoff; empty fill represents common species response at the 50% cutoff; shapes represent retention levels. Lettering above the error bars indicates whether means for a given cutoff and year differed significantly from one another at α = 0.05.

Figure 3.6: Seral group responses (mean ± 95% CI) to vegetation management treatment at Blodgett and McDonald. Responses include five- and twenty-year post-treatment changes in species richness, total frequency, and relative frequency of early- and late-seral forbs and shrubs. Solid fill represents forb response; empty fill represents shrub response; shapes represent vegetation treatment. Lettering above the error bars indicates whether means for a given growth form and year differed significantly from one another at α = 0.05.

Figure 3.7: Seral group responses (mean ± 95% CI) to retention treatment at Blodgett and McDonald. Responses include five- and twenty-year post-treatment changes in species richness, total frequency, and relative frequency of early- and late- seral forbs and shrubs. Solid fill represents forb response; empty fill represents shrub response; shapes represent retention levels. Lettering above the error bars indicates whether means for a given growth form and year differed significantly from one another at $\alpha = 0.05$.
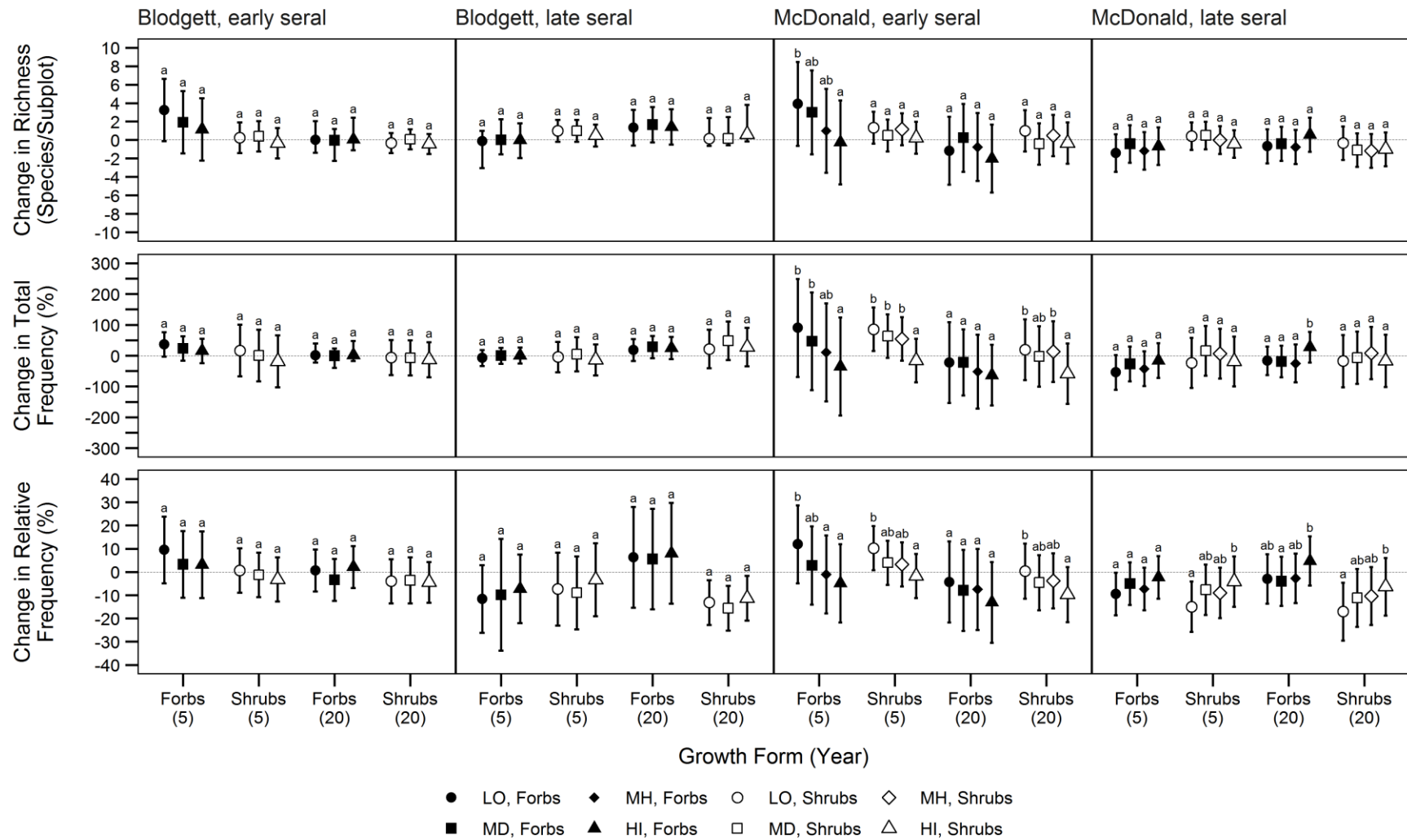
Figure 3.7

3.9. References

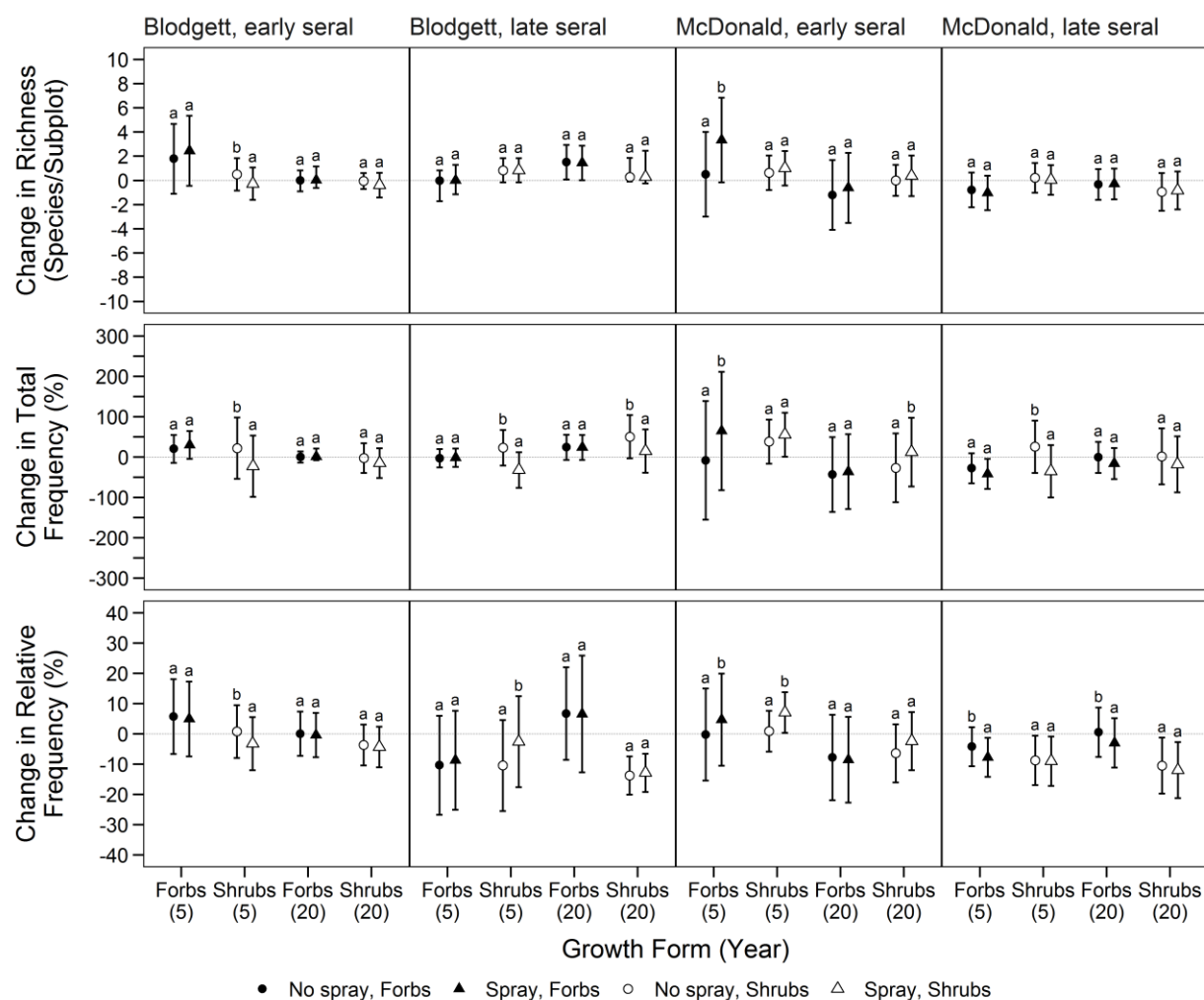Alaback, P.B., Herman, F.R., 1988. Long-term response of understory vegetation to stand density in *Picea-Tsuga* forests. Can. J. For. Res. 18, 1522–1530.

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4. CONCLUSIONS AND MANAGEMENT IMPLICATIONS

4.1. Conclusions

This study examined the impacts of silvicultural treatments and glaze disturbance on the understory of mature (50-70 years old) Douglas-fir forests. Investigation was focused on two aspects of understory dynamics: the individual tree and overstory neighborhood factors influencing damage caused by a glaze disturbance to underplanted trees, and the long-term (20-year post-treatment) impacts of retention level and herbicide application on understory vegetation communities, particularly the abundance of common pre-treatment species and late-seral species. Both disturbance risk and the development of late-seral plant communities are key considerations for silviculturists managing public forests for the creation of complex, multi-aged late-seral stands. The Mature Forest Study (MFS), a long-term study on the acceleration of late-seral characteristics in mature Douglas-fir forests, provided a framework for addressing these issues. Working within the framework of the MFS system, I had the opportunity to extend knowledge of how thinning and vegetation management impact these aspects of understory development in forests managed for late-seral characteristics.

The results of the first part of this study suggest that tree species, tree size, and neighborhood overstory environment all had an effect on the damage understory trees received from a glaze disturbance that struck the central Oregon Coast Range in November 2014. This is consistent with the literature regarding glaze damage to overstory trees (Bragg et al., 2003). Understory tree species affected both damage type and severity, with western hemlock being the most susceptible to damage, and western redcedar the least susceptible.

Understory tree size was related to both damage type and severity. Despite being substantially smaller in size, the trees in this study showed similar patterns in damage type and severity to overstory trees in other studies (Hopkin et al., 2003; Lafon, 2004; Nielsen et al., 2003; Shepard, 1975). In general, smaller trees were more susceptible to being bent, while larger trees were more susceptible to crown loss. However, the number of understory trees that were severely damaged dropped precipitously once DBH exceeded approximately 10 cm. Data on overstory top breakout caused by the same glaze event (Liz Cole, unpublished data), as well as past research on downed branches following glaze disturbance (Hooper et al., 2001) support the idea

that most breakage occurs in stems and branches with diameters less than 10 cm. This suggests that once understory trees reach a certain size (~10-20 cm DBH), the risk of severe glaze damage becomes much lower.

Conifer overstory density, and thus thinning intensity, had no significant effect on the likelihood of damage to understory trees. Although the odds of damage by falling debris increased with Douglas-fir basal area, the additional shelter provided a comparable reduction in the odds of damage by ice loading, resulting in a net neutral effect on the overall odds of damage. Hardwood (primarily bigleaf maple) density was important, however, driven by large increases in damage from falling debris at higher densities. This suggests that overstory tree species is not only relevant to overstory damage, but understory damage as well. Although the results of this study are consistent with the idea that hardwoods are less resistant to glaze damage than conifers, as suggested by some authors (Bruederle and Stearns, 1985; Nielsen et al., 2003), the differences in damage susceptibility between species are likely more complex than a hardwood/conifer divide (Nykänen et al., 1997).

The results of the second part of this study suggest that the magnitude of 20-year change in understory plant communities is altered by both herbicide application and retention level. Magnitude of compositional change was greater in spray-treated plots, and under lower overstory retentions, although other site-specific variables may mitigate the latter. This study found that herbicide application did indeed reduce the legacy effect of common species, consistent with previous studies (Iglay et al., 2010; Ristau et al., 2011). Contrary to some studies (Hawkins et al., 2013; Miller et al., 1999), this reduction lasted well beyond the initial few years following treatment. These changes did not translate into an increase in late-seral species abundance in spray treatments, however. Indeed, there was no suggestion that herbicide application improved late-seral species abundance at all.

Retention level did have an effect on late-seral species abundance, which is consistent with other studies (Battles et al., 2001; Griffis et al., 2001). The results of this study provided some evidence that late-seral species performed better under lighter thinnings, barring additional complicating factors on the site (e.g. the dominance of western hemlock in the understory at Blodgett). Retention level had no effect on the abundance of common species, however, unlike

herbicide application. Despite the seemingly complimentary effects of herbicide application and thinning, though, there was little evidence to suggest that the treatments compounded to further improve late-seral abundance in lightly thinned, spray-treated plots.

4.2. Management Implications

Public forestland managers should consider understory tree species when planning how to mitigate glaze disturbance risk in multi-aged stands. As shown by this and other studies (e.g., Boerner et al. 1988; Lafon 2006), tree species does affect glaze damage susceptibility. If managers are concerned with the risk of glaze damage to their understory cohort, it may be worth planting trees that are more resistant to glaze damage. Considering the low frequency of occurrence of severe ice storms in westside forests in the PNW, however, other factors are likely more important in determining desired species composition. In this case, mitigation for other types of risk (e.g. fire or disease) may be preferable.

Another way to manage glaze damage risk is to modify the overstory. If the overstory is composed of lower-risk species, such as Douglas-fir in this study, findings presented here suggest overstory density is not a concern; the additional shelter provided by the overstory balances the increased risk of falling debris. In other stands with similarly resistant overstories, therefore, density management should have little effect on glaze damage risk to the understory. However, in situations where the overstory is composed of higher-risk species, such as bigleaf maple in this study, managers may wish to reduce the density of these species if their understory trees are also at higher risk of glaze damage. This would include less damage-resistant understory tree species (e.g., western hemlock in this study) as well as smaller trees, which are unlikely to survive if pinned by debris (Bragg et al., 2003). Managers need to factor in their other objectives when addressing disturbance risk, however, as multiple overstory species may be considered desirable in a forest managed for habitat diversity and including late-seral characteristics.

Growth of the understory cohort also needs to be taken into account when managing the overstory to reduce understory glaze damage risk. While the density of overstory Douglas-fir at McDonald did not directly affect the likelihood of understory tree damage, higher overstory densities still limit tree growth and increase height:diameter ratio (Acker et al., 1998; Lam and

Maguire, 2011). Thus, higher overstory densities can result in more fragile understory trees, and extend the time before they reach the 10-20 cm DBH threshold that appears to limit risk of severe damage. This suggests that it may be best to thin to lower densities and reduce the time it takes the younger cohort to reach the midstory and overstory. On public forestland, this approach would be consistent with the objective of accelerating the development of heterogeneous late-seral structure, as it would reduce the time until the formation of a new overstory cohort. Additionally, heavier thinnings are better at increasing within-stand variability (Bailey and Tappeiner, 1998).

However, heavy thinning is contrary to the suggestions of this and other studies (Battles et al., 2001; Halpern et al., 2005; Lindh and Muir, 2004) on promoting the development of late-seral plant communities. Late-seral species generally do better under higher retentions, meaning frequent light thinnings are the best way to increase their abundance. This creates a potential conundrum for managers hoping to both mitigate glaze disturbance risk and promote late-seral vegetation.

Heavy thinning with unharvested leave patches and light thinning with gaps provide two potential avenues for resolving this conflict. Performing a heavy thin will accelerate both overstory and understory tree growth in the harvested areas and increase stand heterogeneity. Meanwhile, leave patches will further increase stand heterogeneity, while also acting as refugia for late-seral species (Bengtsson et al., 2003; Halpern et al., 2012). Late-seral species will take longer to recover in the thinned areas (Halpern et al., 2012), but the leave patches should ensure their continued persistence in a stand until recovery occurs. Conversely, performing a light thin will limit tree growth (Lam and Maguire, 2011), but improve the abundance of late-seral understory species (Battles et al., 2001). The inclusion of gaps will compensate for this, providing growing space for tree regeneration (Brokaw, 1985; Van Pelt and Franklin, 1999), allowing for the creation of a second overstory age class.

This and other studies (e.g., Iglay et al. 2010; Ristau et al. 2011) suggest that the application of herbicides can reduce the pre-treatment legacy of dominant pre-treatment vegetation. However, this does not seem to correspond to an increase in late-seral vegetation. For managers hoping to increase the abundance of these species, herbicide application may not be a

worthwhile investment. However, there was no consistent evidence of a detrimental long-term impact of herbicides on late-seral vegetation either. Thus, the use of herbicides does not appear to be contraindicated if managers wish to use them to achieve other objectives. For instance, if a particular site has a dominant species or invasive that managers wish to reduce in abundance, herbicide application would be a beneficial addition to their silvicultural prescription. In addition, site preparation with herbicides, as was done at the MFS sites, is known to improve seedling establishment and understory tree growth (Cole and Newton, 2009; Nilsson and Allen, 2003). This would both assist in the regeneration of a second canopy layer and potentially help trees reach glaze-resistant sizes more quickly.

4.3. Limitations and Further Research

The main limitation of these studies is that they could only be carried out on one (glaze damage) or two (understory community) sites, across a small range of stand types and environmental conditions. This makes broader inference to other forest systems difficult. Since there is little available literature on either the impacts of ice storms on forests in the PNW or the effects of herbicide application on reducing legacy effects and promoting late-seral vegetation, further research under a wider range of conditions would be valuable. While studying the long-term effects of herbicide application and thinning treatments is feasible, studying glaze disturbances presents a significant challenge to researchers. With no way to predict their occurrence, future research relies entirely on using pre-established study systems to take advantage of opportunities whenever a severe glaze disturbance occurs.

The MFS provides a continuing opportunity to study the long-term effects of glaze disturbance in a Douglas-fir forest. Damage and morphometric measurements were recorded for planted understory trees at McDonald following the November 2014 glaze disturbance. Following up on these measurements could provide information on the future growth and survival of damaged understory trees, as compared to undamaged trees. This would contribute information that does not currently exist for several tree species common to the Coast Range of the PNW.

Lastly, while there are currently several long-term studies looking at the effects of thinning treatments on understory plant communities in the PNW, such as the Demonstration of

Ecosystem Management Options (DEMO) study (see Halpern et al. 2012), Density Management Study (DMS; see Ares et al. 2009), and Olympic Habitat Development Study (OHDS; see Harrington et al. 2005), this is the first study to include herbicide spray treatments. Continuing to observe changes to the understory community in the MFS will be invaluable in providing information on late-seral community development not available in other study systems.

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APPENDIX

Table A.1: Count table of top breakout in overstory conifer trees at McDonald as a result of the November 2014 ice storm. Diameter classes indicate the diameters at which breakage occurred.

Table A.1

Unit	Plot	Subplot	No break	<1"	1-2"	2-4"	4-6"	6-8"	8-10"	10-12"	12-14"	14-16"	16-18"	18-20"	>20"	Total
									Diameter at break							
A	1	1	13	0	2	13	7	4	1	0	0	0	0	0	0	40
A	1	2	11	0	1	10	8	2	1	0	0	0	0	0	0	33
A	1	3	19	0	0	19	3	0	1	0	0	0	0	0	0	42
A	2	1	21	0	1	9	2	1	0	1	0	0	0	0	0	35
A	2	2	13	0	0	8	5	0	0	0	0	0	0	0	0	26
A	2	3	21	0	3	4	2	0	0	0	0	0	0	0	0	30
A	3	1	12	2	3	57	14	8	1	0	0	0	0	0	0	97
A	3	2	22	1	10	31	12	1	0	0	0	0	0	0	0	77
A	3	3	18	0	3	30	29	10	0	0	0	0	0	0	0	90
A	4	1	27	1	5	17	4	1	0	0	0	0	0	0	0	55
A	4	2	23	2	4	12	5	1	0	0	0	0	0	0	0	47
A	4	3	23	3	9	15	4	0	1	1	0	0	0	0	0	56
B	1	1	20	3	2	14	14	5	0	0	0	0	0	0	0	58
B	1	2	13	4	10	11	11	0	0	0	0	0	0	0	0	49
B	1	3	17	5	2	17	10	5	0	0	0	1	0	1	0	58
B	2	1	2	0	10	19	2	1	0	1	1	0	1	0	0	37
B	2	2	6	1	8	20	4	2	1	0	0	0	1	0	0	43
B	2	3	1	0	3	28	7	2	1	0	0	0	0	0	0	42
B	3	1	9	1	5	18	11	7	0	1	1	0	1	0	1	55
B	3	2	4	0	11	24	8	4	7	4	1	3	0	0	0	66
B	3	3	7	2	2	17	18	8	3	2	1	1	1	0	0	62
B	4	1	21	2	9	34	18	3	0	0	0	0	1	0	0	88
B	4	2	12	5	13	23	6	1	1	0	0	0	0	0	0	61
B	4	3	18	2	1	16	8	3	0	0	0	0	0	0	0	48

Table A.1 (Continued)

Unit	Plot	Subplot	No break	Diameter at break												Total
				<1"	1-2"	2-4"	4-6"	6-8"	8-10"	10-12"	12-14"	14-16"	16-18"	18-20"	>20"	
C	1	1	3	0	2	13	11	4	0	0	0	0	0	0	0	33
C	1	2	7	1	4	8	19	2	0	0	0	0	0	0	0	41
C	1	3	17	2	10	15	11	1	0	0	0	0	0	0	0	56
C	2	1	5	0	4	13	18	4	0	0	0	0	0	0	0	44
C	2	2	14	1	2	21	19	6	0	0	0	0	0	0	0	63
C	2	3	11	1	3	14	14	3	0	0	0	0	0	0	0	46
C	3	1	4	10	15	13	3	0	0	0	0	0	0	0	0	45
C	3	2	6	6	10	13	1	0	0	0	0	0	0	0	0	36
C	3	3	11	6	10	16	0	0	0	0	0	0	0	0	0	43
C	4	1	35	4	20	41	9	1	1	1	0	0	0	0	0	112
C	4	2	35	9	15	35	11	0	0	0	0	0	1	0	0	106
C	4	3	22	11	29	40	5	2	1	0	0	0	0	0	0	110
D	1	1	10	3	10	15	2	0	0	0	0	0	0	0	0	40
D	1	2	9	5	10	19	4	0	2	0	0	0	0	0	0	49
D	1	3	15	2	15	16	4	1	0	0	0	0	0	1	0	54
D	2	1	9	7	3	15	3	0	0	0	0	0	0	0	0	37
D	2	2	8	1	8	16	2	1	0	0	0	0	0	0	0	36
D	2	3	12	1	10	16	4	0	0	0	0	0	0	0	0	43
D	3	1	18	2	3	21	27	12	1	3	0	0	0	0	0	87
D	3	2	18	2	3	16	21	14	6	2	0	0	0	0	0	82
D	3	3	42	1	5	25	20	7	3	2	0	0	0	0	0	105
D	4	1	14	8	16	17	2	0	0	0	0	0	0	0	0	57
D	4	2	20	7	17	10	2	1	0	0	0	0	0	0	0	57
D	4	3	21	4	13	16	0	0	0	0	0	0	0	0	0	54

Table A.1 (Continued)

Unit	Plot	Subplot	No break	<1"	1-2"	2-4"	4-6"	6-8"	8-10"	10-12"	12-14"	14-16"	16-18"	18-20"	>20"	Total
									Diameter at break							
E	1	2	4	2	5	21	4	0	0	0	0	0	0	0	0	36
E	1	3	9	2	6	15	3	1	0	0	0	0	0	0	0	36
E	2	1	13	9	20	17	0	2	0	0	0	0	0	0	0	61
E	2	2	11	8	14	17	1	1	1	0	0	0	1	0	0	54
E	2	3	14	9	19	8	0	0	0	0	0	0	0	0	0	50
E	3	1	45	12	11	18	6	1	2	0	0	0	0	0	0	95
E	3	2	37	12	9	12	7	5	2	0	0	0	0	0	0	84
E	3	3	46	8	11	22	9	7	0	0	0	0	0	0	0	103
E	4	1	37	10	13	8	2	0	0	0	0	0	0	0	0	70
E	4	2	24	8	8	6	2	0	0	0	0	0	0	0	0	48
E	4	3	23	6	10	4	2	3	0	0	0	0	0	0	0	48
F	1	1	4	3	9	35	7	2	3	2	0	0	0	0	0	65
F	1	2	7	4	7	30	7	2	2	1	2	2	0	0	1	65
F	1	3	13	2	8	31	10	2	2	1	0	0	0	0	0	69
F	2	1	18	3	9	15	1	1	0	0	0	0	0	0	0	47
F	2	2	22	2	3	13	3	0	0	0	0	0	0	0	0	43
F	2	3	8	1	19	10	1	0	0	0	0	0	0	0	0	39
F	3	1	10	1	3	24	4	0	0	0	0	0	0	0	0	42
F	3	2	9	5	5	13	5	0	0	0	0	0	0	0	0	37
F	3	3	8	6	11	18	3	0	0	0	0	0	0	0	0	46
F	4	1	11	3	4	42	22	3	6	0	0	0	0	0	0	91
F	4	2	15	7	16	21	9	9	1	1	0	0	0	0	0	79
F	4	3	24	9	9	45	13	11	0	0	0	0	1	0	0	112
Total			1134	260	585	1376	552	179	51	23	6	7	8	2	2	4185