

AN ABSTRACT OF THE DISSERTATION OF

Christopher J. Dunn for the degree of Doctor of Philosophy in Forest Resources
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Title: Mixed-Severity Fire Effects on Biological Legacies and Vegetation Response in
Pseudotsuga Forests of Western Oregon's Central Cascades, USA

Abstract approved:

John Duff Bailey

Mixed-severity fire occurrence is increasingly recognized in *Pseudotsuga* forests of the Pacific Northwest, but questions remain about how tree mortality varies, and forest structure is altered, across the disturbance gradient observed in these fires. Therefore, we sampled live and dead biological legacies at 45 one ha plots, with four 0.10 ha nested plots, stratified across an unburned, low, moderate and high-severity fire gradient. We used severity estimates based on differenced Normalized Burn Ratio (dNBR), and captured a disturbance gradient, but plots in our low-severity class underestimated fire effects because of misclassification or delayed mortality. We estimated probability of mortality for shade-intolerant (Douglas-fir, incense-cedar, sugar pine) and shade-tolerant (western hemlock, western redcedar, true fir) trees from 5,079 sampled trees and snags. The probability of mortality was higher for shade-tolerant species across all fire-severity classes, and decreased with increasing DBH except for western hemlock. Only large, shade-intolerant trees survived high-severity fire. Post-fire snag fall and fragmentation were estimated from 2,746 sampled snags and logs. The probability of snag fall decreased with increasing DBH for all species, and was positively correlated with fire severity, except for Douglas-fir that had a higher probability following low-severity fire. Snag fragmentation was positively correlated with DBH and fire severity for all species. We also estimated the coefficient of variation within- and among-plots by fire severity class, as well as across all sampled conditions. Structural attributes varied more within- than among-plots, likely a result of increasing sub-hectare

patchy mortality as fire intensity increased. Although vertical and horizontal structural diversity increased at sub-hectare scales, the coefficient of variation was highest for all structural attributes when compared across all fire severity classes. Therefore, the range of fire effects observed in mixed-severity fires may be functionally important in creating structural complexity across landscapes, which is an important attribute of old-growth forests in the Pacific Northwest.

Understory vegetation response to mixed-severity fires has not been characterized for these forests even though the majority of vegetation diversity is found in these vegetation layers. Therefore, we sampled forest structure (1000 m² circular plots) and understory vegetation (100 m² plots) at 168 collocated plots stratified across unburned, low, moderate and high-severity conditions 10 years (Tiller Complex) and 22 years (Warner Fire) post-fire. We focused on shrub species, but sampled forbs, graminoids, ferns and moss as functional groups. Offsite colonization and fire stimulated soil seedbanks increased the total species richness from 23 to 46. The life-history strategies of residual and colonizing species resulted in three dominant species response-curves to the magnitude of disturbance: 1) 'disturbance-sensitive', when relative abundance was highest in unburned plots and continued to decline with increasing fire severity, 2) 'disturbance-stimulated', when relative abundance was highest following low or moderate-severity fire and 3) 'disturbance-amplified', when relative abundance increased with increasing fire severity. Residual and colonizing species assemblages promoted five or six distinct understory communities, dominantly driven by legacy tree basal area rather than the proportion of basal area killed. Understory communities were rarely associated with one disturbance severity class as fire refugia, variation in overstory and understory fire severity, and compensatory conditions offset fire effects. Early-seral habitats were the most different from unburned forests, but were not the only post-fire conditions important across these burned landscapes. Interactions among live and dead forest structures following low or moderate-severity fire, and the vegetation response to these conditions, are also unique to the post-fire landscape and likely important for various wildlife species. Therefore, if ecological forestry paradigms focus dominantly on creating old-growth structure or early-seral habitats, they might exclude important conditions that contribute to the landscape structural complexity created by mixed-severity fires.

Additionally, tree regeneration response to mixed-severity fires has not been characterized for these forests even though they offer insight into one aspect of the resilience of these ecosystems to disturbance. Therefore, we sampled forest structure (1000 m² circular plots) and regeneration dynamics (100 m² plots) at 168 collocated plots stratified across unburned, low, moderate and high-severity conditions 10 years (Tiller Complex) and 22 years (Warner Fire) post-fire. The largest marginal increase in tree mortality (stems ha⁻¹) occurred between unburned and low-severity fires, given preferential mortality of small trees and shade-tolerant species, but basal area mortality had the largest marginal increase moving from moderate to high-severity. Pairwise comparisons of legacy tree basal area between low and moderate-severity weren't as significant as other comparisons, but did capture a gradient of increasing fire effects. Quadratic mean diameter and canopy base height were positively correlated with fire severity as incrementally larger trees were killed and canopy ascension followed. Regeneration density increased regardless of severity, relative to unburned forests (median density of 1,384 trees ha⁻¹), but the highest median density (16,220 trees ha⁻¹) followed low-severity fire at the Tiller Complex and moderate-severity fire (14,472 trees ha⁻¹) at Warner Fire. Plot-level average species richness was highest following these same fire severity classes, supporting the Intermediate Disturbance Hypothesis. Statistically distinct regeneration communities occurred across the fire severity gradient at both fire sites. The relative abundance of shade-tolerant tree species decreased as fire severity increased, except for a divergent response following stand-initiation at the Warner Fire. While divergent successional pathways were evident within a couple decades following stand-initiation, low or moderate-severity fires also modified successional trajectories and may be the most functionally important disturbance magnitude because it has the greatest potential to increase compositional and structural diversity. Incorporating mixed-severity fire effects into landscape management of *Pseudotsuga* forests could increase structural complexity at stand and landscape-scales.

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Mixed-Severity Fire Effects on Biological Legacies and Vegetation
Response in *Pseudotsuga* Forests of Western Oregon's Central Cascades,
USA

by
Christopher J. Dunn

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APPROVED:

Major Professor, representing Forest Resources

Head of the Department of Forest Engineering, Resources and Management

Dean of the Graduate School

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

Christopher J. Dunn, Author

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MIXED-SEVERITY FIRE EFFECTS ON BIOLOGICAL LEGACIES AND VEGETATION RESPONSE IN *PSEUDOTSUGA* FORESTS OF WESTERN OREGON'S CENTRAL CASCADES, USA

CHAPTER 1: INTRODUCTION

Natural disturbances have important functional roles depending on the disturbance type, magnitude and spatial and temporal attributes. In their seminal book on the ecology of natural disturbances, Pickett and White (1985) defined a disturbance as "... any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment". This type of disturbance is classified as an episodic-disturbance and includes wildfires, floods, hurricanes and other events with a relatively short and observable temporal scale. However, another type of disturbance is a chronic-disturbance that occurs more slowly and often influences broader spatial scales simultaneously. Climate change, glaciation and pollution are all examples of chronic-disturbances with unknown endpoints or trajectories. When classifying disturbances into one of these conceptual models, it is best to consider the characteristics of the disturbance (e.g., return interval, severity) within the context of the life history of the individual, forest or landscape being impacted.

Fire directly impacts vegetative communities by altering successional trajectories, often favoring one flora and fauna community at the expense of another. This paradox underlies the importance of maintaining natural disturbance processes since the lack of fire (chronic), or conversely uncharacteristic fires (episodic) , may be detrimental to the resilience of these ecosystems. The two dominant fire-vegetation interactions that influence community composition and structure are consistent with the two-class system for categorizing disturbances: chronic-disturbance and episodic-disturbance.

In frequent-fire forests, wildland fires can regulate the understory and overstory structure by inhibiting the establishment of species not adapted to persistent fire disturbance. Although a fire event is discrete in space and time, the cumulative effect of frequent fires maintains the biological community in a "steady-state" or successional stage by mediating forest density and promoting dominance by fire-tolerant species. These effects

are more aligned with chronic-disturbances and therefore without recurring fire, understory and overstory species gradually transition to dominance by fire-intolerant species. This fire-vegetation interaction is most evident in highly-productive longleaf pine/wiregrass forests of the southeastern U.S., which quickly transition to dominance by other species in the absence of fire. Many of the ponderosa pine and mixed-conifer forests of the intermountain west and Sierra Nevada Range in California are similar to this type.

Fire's functional role is different in forests with longer fire return intervals and which are subject to stand-replacement events; however, they are no less important to their resilience. Episodic-disturbances also control the distribution of biological legacies (live and dead structures present following a disturbance) across space and time. Live biological legacies provide refuge for species reliant on crowns for nesting and roosting, retain a seed bank for propagating the next generation forest, and support belowground mycorrhizal symbionts that increase water and nutrient acquisition by legacy and regenerating vegetation (Bond et al., 2009, Louma et al., 2006, Seidl et al., 2014). Dead biological legacies provide structural habitat valuable to multiple vertebrate and invertebrate species as both snags and logs, such as cavity nesting woodpeckers. The importance of the changes wrought by intense but infrequent wildfires is evident when high severity fire creates early-seral conditions that support distinct biological communities that are inhibited by dominance of long-lived species like Douglas-fir/western hemlock trees in the western Cascade Range.

Wildfires are, by nature, landscape-scale events. Fires control the distribution of forest structure and composition across landscapes where they are the dominant disturbance agent. The cumulative effects of individual tree and/or stand-level mortality create landscape patterns important for maintaining structural and compositional diversity. These patterns are dependent on the fires mortality patch-size distribution, the distance between patches, and their clustered or even distribution within the fire boundary. As fire frequency decreases, mortality patch-size typically increases. Wildfire's influence on forest development is often dominated by one of the severity classes (Perry et al., 2011), but, as with all large disturbances, large wildfires are characterized by substantial heterogeneity in the intensity of the fire.

The distribution and size of mortality patches significantly influence the connectivity of forest habitats. The viability of floral and faunal species is partially dependent on their ability to emigrate or immigrate from various patches to share genetic resources, or provide individuals an opportunity to colonize areas where resources are abundant. For example, seed dispersal from live biological legacies and the successful establishment of the next generation forest is partially controlled by the distance from seed source. Therefore, patch-sizes that exceed the dispersal distance may have protracted regeneration and a longer transition to old-growth conditions. Maintaining the distribution, size and type of mortality patch-sizes (often referred to as spatial complexity) across landscapes may improve species resilience by maintaining widely distributed diverse conditions that will prevent loss from the next wildland fire.

Understanding fire's historical role in developing North America's forested communities, particularly in complex forest types, is critical for creating management practices that improve forest resilience to an uncertain future. Fire ecologists typically refer to conditions that existed prior to Euro-American settlement of North America to quantify historical characteristics of wildfires summarized as fire regimes. Fire regimes are a suite of characteristics that describe the spatial and temporal characteristics and magnitude of wildland fires over relatively long time periods. Fire regimes are most commonly described by their relative frequency and severity for a particular forest type (Agee, 1993; Hessburg). These characteristics are linked to forest age-structure to understand fire's ecological role in developing the forests supportive of flora and fauna communities present upon Euro-American arrival.

Low-severity: Forests with low-severity fire regimes burned at high-frequencies (<20 year mean fire return intervals) during periods when fine fuels dried and annual grasses completed their growth cycles. These fires burned across broad areas because of relatively contiguous dry fuel conditions, but would be impeded by recent fires that consumed fuels. The spatial complexity - or distribution, size and severity of mortality patch sizes - of individual fires was low because of their low intensities, primarily killing young, regenerating trees. This resulted in relatively low recruitment of single or small groups of overstory trees across time, creating forests with high spatial complexity at small scales especially responsive

to small scale variation in productivity. Most frequent-fire forests across the North American landscape, including ponderosa pine forests of Arizona, Idaho, New Mexico, Oregon and Montana, historically had a low-severity fire regime over large areas. Longleaf pine forests of the southeastern U.S. had the highest frequency, low-severity fire regime in the United States and typically burned at intervals <3 years. Single or small group tree mortality from wildfire was commonplace in these forests as the dominant disturbance regime historically influencing the composition and structure of these forests was high-frequency, low-severity fire. Generally, these forests have not experienced a fire over a period many times their historical mean fire interval.

Mixed-severity: Forests with a mixed-severity fire regime burned at intervals that could vary significantly, but typically averaged from 20-100 years between fires. The extent of these fires spanned a range of relatively small (<100 acres) to very large (>10,000 acres) depending on the timing of ignition. The longer fire return intervals resulted in greater burn severity spatial complexity because of significant variability in the magnitude of fire effects. Landscape level structural and compositional diversity would be greatest within mixed-severity fire boundaries relative to other fire regimes. Forests with a mixed-severity fire regime included mixed evergreen-conifer forests of the Klamath Mountains of southwest Oregon, mixed conifer forests of the northern Rockies and the Sierra Nevada, and much of the Douglas-fir/western hemlock forests of the Cascade Range. Typically, >70% of fire extent burned at low or moderate severity. Landscape scale structural and compositional diversity was likely highest in these forests because of highly variable return intervals and fire effects, as well as their higher productivity and therefore response to fire-free periods.

High-severity: Forests with a high-severity fire regime had mean fire return intervals ranging from 100 to >300 years. Fires can be very large in forests with this fire regime, often exceeding 100,000 acres when ignited during extreme fire weather conditions (e.g., 2006 Tripod Fire in Washington, 1988 Yellowstone Fires in Wyoming, or the 1996 Charlton Fire in Oregon). The longer fire return intervals result in greater burn severity, and relatively low spatial complexity, because a larger proportion of the fire burned at high-severity than other severity types. Mortality patch-sizes are relatively large resetting successional processes and developing with relatively homogenous structural conditions. Forest structure diversifies

over time as succession proceeds towards old-growth conditions, especially in productive forests like Pacific silver fir or mountain hemlock forests of the Washington's western Cascades. It is important to recognize that these fires do include other severity types, and therefore the stand-replacing conditions are embedded within a larger complex of fire severities and unburned forest conditions. Lodgepole pine forests of the greater Rocky Mountain Region historically had a high-severity fire regime and, over time, have developed regeneration strategies (fire-mediated serotiny) to cope with this type of disturbance. Most of these forests have not missed a fire cycle and therefore often burn with similar characteristics.

Western Cascades

Douglas-fir/western hemlock forests (*Pseudotsuga menziesii*/*Tsuga heterophylla*) of the Pacific Northwest (PNW) are typically characterized as having an episodic-disturbance regime of low-frequency, high-severity fire (Agee, 1993). This disturbance regime has been challenged by recent fire-history and age-structure studies in western Oregon's central Cascades that showed mean fire return intervals of 95-150 years and effects spanning a disturbance gradient from low to high-severity (Means, 1982, Morrison and Swanson, 1990, Weisberg, 2004; Tepley et al., 2013). Non-stand replacing portions of these fires accounted for >70% of the burned area in at least two watersheds in Oregon's western Cascades during the 19th century (Morrison and Swanson, 1990), with similar results occurring in the more recent 1991 Warner Fire (Kushla and Ripple, 1997). Mixed-severity fires may be more common and ecologically important in these forests than previously suggested, contributing to the development of structural complexity indicative of old-growth forests in the PNW (Tepley et al., 2013).

Research into mixed-severity fires, particularly in wet forests like *Pseudotsuga* forests of the PNW, haven't received as much attention as other forest types and fire regimes. In the western US, much of this is a result of the dramatic changes that have occurred in dry-forest environments following fire exclusion. During the past 100 -150 years, frequent-fire forests have missed several fire cycles, increased in fuel loadings, and now burn with greater severity than historical fires. This has been further exacerbated by the

expansion of the wildland urban interface which primarily occurs adjacent to these frequent-fire forests. The perception that these forests had a high-severity fire regime also inhibited research into mixed-severity fires in these forests, even though mixed-severity fire occurrence was first proposed in the 1980's. Additionally, fire suppression during the second half of the 20th century remained very effective, aided by generally cooler and wetter conditions in the PNW, preventing the occurrence of large wildland fires in these forest types. After the 1991 Warner Fire burned, and salvage logging was prevented, a long-term naturally recovering fire research site became available. Many fires have burned in *Pseudotsuga* forests since, primarily at more southerly latitudes in the western Cascades. These fires now offer the opportunity to better understand mixed-severity fire as an important ecosystem process in these forests.

Fire effects span all scales of biological organization and are both a limiting and regulating force in terrestrial ecosystems. Mixed-severity fires span a gradient in fire effects, and therefore may, within a single fire event or over successive fire cycles, simultaneously limit and promote similar ecological processes depending on the magnitude of the disturbance. Investigating the ecological role of mixed-severity fire in *Pseudotsuga* forests could focus on a multitude of ecosystem components. For this study, we elected to investigate three prominent attributes of fire effects and ecosystem responses to a mixed-severity fire gradient: 1) mixed-severity fire effects on forest structure, 2) understory vegetation response to the disturbance gradient, and 3) tree regeneration response and successional trajectories across the disturbance gradient. This document has been organized into three manuscripts covering these subjects and provides an initial assessment as to whether or not mixed-severity fire is an important ecological process in these forests.

CHAPTER 2: MIXED-SEVERITY FIRE INCREASES STRUCTURAL DIVERSITY OF *PSEUDOTSUGA* FORESTS IN OREGON'S WESTERN CASCADES, USA

Abstract

Mixed-severity fires are increasingly recognized in *Pseudotsuga* forests of the Pacific Northwest, but questions remain about how tree mortality varies, and forest structure is altered, across the disturbance gradient observed in these fires. Therefore, we sampled live and dead biological legacies at 57 large plots stratified across an unburned, low, moderate and high-severity fire gradient. We used severity estimates based on differenced Normalized Burn Ratio (dNBR), and captured a disturbance gradient, but plots in our low-severity class underestimated fire effects because of misclassification or delayed mortality. We estimated probability of mortality for shade-intolerant (Douglas-fir, incense-cedar, sugar pine) and shade-tolerant (western hemlock, western redcedar, true fir) trees from 5,079 sampled trees and snags. The probability of mortality was higher for shade-tolerant species across all fire-severity classes, and decreased with increasing DBH except for western hemlock. Only large, shade-intolerant trees survived high-severity fire. Post-fire snag fall and fragmentation were estimated from 2,746 sampled snags and logs. The probability of snag fall decreased with increasing DBH for all species, and was positively correlated with fire severity, except for Douglas-fir that had a higher probability following low-severity fire. Snag fragmentation was positively correlated with DBH and fire severity for all species. We also estimated the coefficient of variation within- and among-plots by fire severity class, as well as across all sampled conditions. Structural attributes varied more within- than among-plots, likely a result of increasing sub-hectare patchy mortality as fire intensity increased. Although vertical and horizontal structural diversity increased at sub-hectare scales, the coefficient of variation was highest for all structural attributes when compared across all fire severity classes. Therefore, the range of fire effects observed in mixed-severity fires may be functionally important in creating structural complexity across landscapes, which is an important attribute of old-growth forests in the Pacific Northwest.

Introduction

Fire is an important disturbance process in many terrestrial ecosystems where it influences the distribution of living and dead biological legacies (Bond and Keeley, 2005, Harmon et al., 1986). Legacy trees, snags and logs are variously distributed through space and time and interact with regenerating vegetation, supporting a diverse array of flora and fauna, as well as ecosystem processes controlled by the availability and abundance of these resources (Franklin and MacMahan, 2000, Odum, 1969, Turner et al., 2003). For example, live biological legacies provide refuge for species reliant on crowns for nesting (Bond et al., 2009), retain a seed bank for propagating the next generation forest (Seidl et al., 2014), and support belowground mycorrhizal symbionts that increase water and nutrient acquisition by legacy and regenerating vegetation (Louma et al., 2006, Simard, 2009). Dead biological legacies provide structural habitat valuable to multiple vertebrate and invertebrate species as both snags and logs (Bull et al., 1997); they function as long-term nutrient and carbon stores, are the primary energy source for saprophyte communities, and contribute to soil development (Harmon et al., 1986, Triska and Cromack, 1980, Tinker and Knight, 2000). In general, biological legacies continue to provide ecological functions for several hundred years post-fire depending on mortality, snag fall and fragmentation, and decay of this coarse woody detritus.

The ecosystem function of fire depends on the biological community's short and long-term response to the magnitude and frequency of the disturbance (Wright and Heinzelman, 1973, Turner, 2010). For much of the 20th century, fire was viewed as a disruption to the equilibrium steady state of successional processes, a paradigm founded in the 'Clementsian' view of forest dynamics (Clements, 1936, Oliver and Larson, 1996). As the field of disturbance ecology advanced, especially since the 1980s, ecologists and managers developed a greater understanding of the importance of disturbance processes in maintaining the resilience of biological communities (Holling, 1973, Pickett and White, 1985). In the western U.S., this has been most exemplified by the loss of fire's functional role in mediating the structure and composition of dry-forests with mean fire return intervals <20 years (Heyerdahl et al., 2001). Today, disturbance processes are typically viewed from the

perspective of pattern and process at landscape scales. Patch size and spatial complexity are primary attributes of fire regimes that influence ecosystem response, and the diversity in its response, which are important for maintaining resilience across space in time (Perry et al., 2011, Turner et al., 2010).

Wildfires have played an important role in the structure and function of Douglas-fir/western hemlock (*Pseudotsuga menziesii*/*Tsuga heterophylla*, hereto referred to as *Pseudotsuga* forests) forests found extensively throughout the western Cascade Range of the Pacific Northwest (PNW). Episodic, stand-replacing fires occurring at intervals from 200 – 300 years have dominated perceptions of fire regimes in this forest type (Agee, 1993). Under this disturbance regime, stand initiation is followed by a gradual transition to structurally complex, old-growth forests that have been the focus of conservation efforts for decades (Franklin et al., 2002, Swanson and Franklin, 1992). Several fire-history and age-structure studies in western Oregon's central Cascades have described mixed-severity fire in *Pseudotsuga* forests, with mean fire return intervals ranging from 95-150 years (Means, 1982, Morrison and Swanson, 1990, Tepley et al., 2013, Weisberg, 2004). Low or moderate-severity fire accounted for >70% of the burned area in at least two watersheds in Oregon's western Cascades during the 19th century (Morrison and Swanson, 1990), with similar results occurring in the more recent 1991 Warner Fire (Kushla and Ripple, 1997). Therefore, mixed-severity fires may be more common and ecologically important than previously suggested by commonly used successional models (Franklin et al., 2002).

Fire history studies using dendrochronology are highly beneficial because they capture long-term forest development, but they typically infer disturbance processes from existing forest structure (Tepley et al., 2014). Therefore, these studies are confounded by the cumulative effects and loss of information to subsequent disturbances, leaving unanswered questions about how variability in fire intensity restructures these forests. Fortunately, new methodologies have been developed to quantify fire severity (Key and Benson, 2005, Miller and Thode, 2007) and several fires have burned with mixed-severity (pyrodiversity) in western Oregon's Douglas-fir/western hemlock forests in recent decades (Kushla and Ripple, 1997, MTBS, 2014). These fires offer the opportunity to assess the distribution of live and dead biological legacies, as well as the horizontal and vertical restructuring of these forests in

response to a fire severity gradient. Specifically, we sought answers to the following questions: 1) How does the probability of mortality vary by tree species across a fire-severity gradient? 2) Do snag fall and fragmentation rates vary by species, size and fire-severity? and 3) Does mixed-severity increase structural diversity important to the development of Douglas-fir/western hemlock forests in Oregon?

Methods

Study Area

Pseudotsuga forests of western Oregon's central Cascades are dominant from 500 – 1300 meters elevation, extending from the State of Washington to the South Umpqua River Watershed (Franklin and Dyrness, 1988). We sampled fires in this forest type between the Middle Fork of the Willamette River Watershed near Oakridge, OR (43° 4' 1.6032" N), and south to the North/South Umpqua River Watershed divide (43° 43' 36.8688" N) to capture a productivity gradient in this forest type. The climate is typical of maritime conditions with cool, wet winters and warm, dry summers. Average annual precipitation ranges from 1339 – 1761 mm per annum, with ~75% falling from November through April. Average maximum temperatures range from 27.5 °C in August, to 4.3 °C in December, and average minimum temperatures range from 9.1 °C in August to -2.8 °C in December (Daly et al., 2002, www.prismclimate.org). There is a north-south climatic gradient such that temperatures increase and moisture decreases from north to south. Douglas-fir, sugar pine (*Pinus lambertiana*) and incense-cedar (*Calocedrus decurrens*) were common fire-tolerant tree species encountered in our study area. Western hemlock, western redcedar (*Thuja plicata*), white fir (*Abies concolor*), grand fir (*Abies grandis*), and Pacific yew (*Taxus brevifolia*) were common fire-intolerant tree species. Giant chinkapin (*Castanopsis chrysolepsis*), bigleaf maple (*Acer macrophyllum*), Pacific madrone (*Arbutus menziesii*) and Pacific dogwood (*Cornus nuttallii*) are common hardwood trees. The potential vegetation type transitions to silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) at higher elevations, with dry Douglas-fir, Oregon white oak (*Quercus garryana*) and ponderosa pine (*Pinus ponderosa*) forests occurring at lower elevations. Douglas-fir and white fir forests are common at more southerly latitudes within and beyond our study area.

Sampling Design

Several large fires occurred within our study area during the past several decades, accounting for a total of 76,746 ha burned between 1987 and 2014 (Figure 2.1). Approximately 8,782 ha burned in 1987 and 1988, followed by 9,037 ha in 1996, 36,437 ha in 2002, and 20,049 ha burned in 2008 - 2009. The most recent fire, Deception Creek Complex, burned an additional 2,441 ha near Oakridge, OR in 2014. We concentrated our sampling within the 2002 Tiller Complex (10 years post-fire) and the 1991 Warner Fire (22 years post-fire), which burned 36,347 ha and 3,723 ha, respectively.

Sampling was constrained to mature/old-growth (M/OG) *Pseudotsuga* forests without evidence of direct anthropogenic disturbance or fire occurrence during the past 100 years of recorded fire history. We randomly located 6 intensive plots within three fire-severity classes (i.e. low, moderate, high), at 10 and 22 years post-fire, and 1 intensive plot across the fire-severity gradient 4 years post-fire (due to time/financial limitations and information value). An additional 6 intensive sampling plots were placed in unburned stands as a reference group (Figure 2.1). Only the south slope of the Warner Fire was sampled because climatic conditions, combined with the north aspect, developed much wetter forests (e.g., Pacific silver fir was often dominant) we considered different from our intended study area. Plots were randomly selected using equal probability point sampling in ArcMap 10.0 (ESRI, 2011), and were constrained to a minimum of 400 m apart within a severity class to disperse sample plots across a broader area. Fire severity was determined from maps derived by the Monitoring Trends in Burn Severity program (MTBS, 2011). The severity classes were intended to represent low-severity as <25% basal area mortality, moderate-severity as 25 – 75% basal area mortality, and high-severity as >75% basal area mortality.

Biological Legacies

We sampled live and dead biological legacies (trees and snags) within a 1-ha circular plot at four nested subplots (Figure 2.2). A random azimuth determined the direction between subplots one and two that were placed 36.6 m apart. Subplots three and four were placed systematically at 120 and 240 degrees from plot one. Standing and fallen live and dead biological legacies 2.54 – 10.0 cm diameter at breast height (DBH) were sampled in a

5.64 m (1/100th ha) radius subplot, >10.0 – 40.0 cm DBH within an 8.92 m radius subplot (1/40th ha), and > 40 cm DBH at 17.84 m radius subplot (1/10th ha). All biological legacies >70 cm DBH were sampled within the 1-ha plot to capture large, spatially disperse individuals. We recorded species, DBH (cm), total height (m), canopy base height (m) and percent bole scorch for all trees. We recorded species, DBH, condition (i.e. standing whole, standing broken, fallen), height, percent bark, percent bole scorch and decay class for all dead biological legacies. Decay classes were based on the five-class system developed for Douglas-fir, but adapted for species differences (Maser et al., 1979, Cline et al., 1980). Snags < 2m in height were considered fallen. Pre-fire snags were separated from fire created snags if >5% of the bole sapwood was consumed or turned to charcoal. We considered Douglas-fir, incense-cedar and sugar pine fire-tolerant and western hemlock, western redcedar and true fir (*Abies sp.*) fire-intolerant tree species (Brown and Smith, 2000).

Surface coarse woody detritus (logs) was sampled using a planar intercept method (DeVries, 1973). We recorded species, decay class and diameter at point of intersection for all logs >7.62 cm diameter along five transects. Four 79.8 m transects formed a square that touched the outer plot boundary at 4 points. One 40 m transect, perpendicular to the azimuth of plot orientation, was sampled through plot center. Average volume, cover and diameter were estimated at the plot level for statistical analysis.

Probability of mortality by species, fire severity class and DBH was estimated using a generalized linear-mixed model with a binomial distribution (Bates et al., 2014, R Development Core Team, 2008). We attempted to model interactions among species, fire severity class and DBH but the models would not converge even after trying several optimization methods and increasing the maximum number of optimization iterations, therefore interactions were excluded as predictor variables. Plot was included as a random effect to account for positive correlations among residuals given spatial autocorrelation within a plot. Fire-tolerant and fire-intolerant species were analyzed separately because 100% of fire-intolerant species died in high-severity fire, causing quasi-perfect separation in our model when high-severity conditions were included for these species. Sample size and descriptive statistics for this analysis are provided in Table 2.1.

The probability of snag fall and fragmentation (snag dynamics) by species, fire severity class, DBH and time-since-fire were estimated using generalized linear-mixed models with a binomial distribution. We attempted to model interactions among species, fire severity, DBH and time-since-fire, but the models similarly would not converge. We also estimated snag height following fragmentation using a linear mixed model. Again, plot was included as a random effect to account for positive correlations among residuals resulting from spatial autocorrelation of individual snags within a plot.

Forest Structural Attributes

We reconstructed pre-fire live basal area and stems per hectare for all plots to test if pre-fire differences might confound the results from our analyses. We also used plot-level and subplot-level estimates of tree and snag basal area and density to quantify fire severity. We used linear regression to test differences among groups because of our unbalanced study design (i.e. 6 unburned plots vs. 13 plots in fire severity classes). All comparisons were adjusted for multiple-comparisons using Tukey corrections in the multcomp package of R (Torsten et al., 2008).

Biological legacies were pooled to the subplot and plot level to compare structural attributes within and among fire severity classes. We were interested in live basal area ($\text{m}^2 \text{ha}^{-1}$), tree density (ha^{-1}), quadratic mean diameter (QMD) in centimeters, canopy base height (CBH) in meters, snag basal area ($\text{m}^2 \text{ha}^{-1}$) and snag density ($\# \text{ha}^{-1}$) as important vertical attributes of forest structure. Log volume, cover and diameter were estimated using equations developed by DeVries (1973). We pooled species into fire-tolerant and fire-intolerant groups to compare composition by fire severity class. Structural differences among fire severity classes were analyzed using linear regression to account for our unbalanced study design. Pair-wise comparisons were adjusted for multiple comparisons using Tukey corrections in multcomp package of R (Torsten et al., 2008).

We ultimately used the coefficient of variation to test within- and among-plot variability by fire severity class for several structural attributes and severity metrics. We compared the coefficient of variation at multiple scales to discern at what scale variability dominantly occurs, and tested for statistical differences in CV using linear regression as

described above. The high-severity fire class was not included in this analysis because most structural attributes were zero or zero inflated, making results from this test statistic spurious.

Results

Pre-fire Forest Structure and Fire Severity

Pre-fire basal area and forest density did not vary statistically across our fire severity classes at an $\alpha < 0.05$ (Figure 2.3). Reconstructed basal area averaged $66.5 \text{ m}^2 \text{ ha}^{-1}$ (SD = 16.4) across all plots (Table 2.1); reconstructed mean forest density had higher variability and averaged $591.4 \text{ trees ha}^{-1}$ (SD = 484.9). We observed moderately suggestive evidence of lower basal area and density within our high-severity class, which was partially driven by two moderate-severity plots having >2000 pre-fire small diameter ($<10\text{cm}$) hardwood and conifer trees, as well as lower estimates in high-severity plots. Despite efforts to the contrary, small diameter snags that had fallen and decayed or were buried in the high-severity class may have been missed during sampling, underestimating reconstructed estimates in this class. These observed differences weren't large enough to bias our results, especially since they were driven by missed small diameter snags in the high-severity plots that typically had 100% mortality.

Our stratified sampling captured a gradient in fire effects, but did exceed estimated mortality in our low-severity class (Figure 2.4). Low-severity fire averaged 30.7% (SD = 9.3) basal area mortality, which equated to 61.2% (SD = 14.6) of live trees ha^{-1} (Table 2.2). Moderate-severity plots averaged 46.9% (SD = 12.2) basal area mortality, 16.2% (SE = 3.8) higher than low-severity plots, with only 17.3% (SE = 4.3) more tree ha^{-1} mortality. In contrast, basal area mortality increased by a larger margin between moderate and high-severity plots, averaging an additional 49.7% (SE = 3.8) basal area mortality (mean = 96.6%, SD = 7.0), although this only represented a 20.9% (SE = 4.3) increase in tree ha^{-1} mortality as incrementally larger trees were killed with increasing fire severity. Only 31% of our high-severity plots had live biological legacies, ranging from 76.6% - 97.4% basal area mortality but still within anticipated mortality ranges.

Live Biological Legacies

We estimated probability of mortality for six conifer species from 5,079 samples and found that DBH, fire severity and species were the dominant factors influencing mortality (Table 2.3). We tested plot-level environmental variables and number of years post-fire for statistical significance, but none were significant at an $\alpha < 0.05$. DBH ranged from <4.0 to >100 cm for all tree species, though fire-tolerant trees (dominated by Douglas-fir) had a broader distribution and higher average DBH than fire-intolerant trees. The probability of mortality for fire-tolerant trees responded similarly to increasing DBH, but there was an interaction between species and DBH for fire-intolerant trees (Figure 2.5). Each centimeter increase in DBH resulted in a decrease in the probability of mortality by 1.03 times (95% confidence interval (CI) of 1.026 – 1.032) for fire-tolerant trees. True fir trees responded similarly to increasing DBH, (estimate = 1.03, 95% CI of 1.017 - 1.048, p-value < 0.0001), but mortality in fire-intolerant trees were consistently higher than fire-tolerant trees. DBH wasn't as influential of a factor in reducing the probability of mortality for western redcedar as it was for true fir (mean = 1.020, 95% CI of 1.008 to 1.032, p-value < 0.0001), although these species weren't statistically different. In contrast, western hemlock's probability of mortality did not decrease significantly with increasing DBH (mean = 1.002, 95% CI of 0.987 to 1.017, p-value = 0.84250), and therefore exhibited no resistance to mortality with increasing DBH.

The mortality response-curves of the six dominant conifer species varied across their diameter distribution and severity class (Figure 2.5). Fire-tolerant species exhibited little difference in their probability of mortality in unburned and low-severity plots. On average, the odds of mortality were only 1.41 times (95% CI of 0.50 – 4.02, p-value = 0.9128) greater between unburned and low-severity fire, although their variance suggests no significant difference (Table 2.3). As fire severity increased so did the odds of fire-tolerant tree mortality, increasing 2.46 times (95% CI of 1.08 to 5.61, p-value = 0.1397) from low- to moderate-severity and 154.50 times (95% CI of 57.91 to 412.22, p-value < 0.0001) from moderate- to high-severity fire. In contrast, the odds of fire-intolerant species mortality increased by 14.65 times (95% CI of 9.1 – 23.6, p-value < 0.0001) between unburned and low-severity fire. As fire severity increased so did the odds of mortality, increasing by 3.08 times

(95% CI of 1.75 to 5.44, p-value = 0.0003) from low- to moderate-severity fire, and increasing infinitely from moderate- to high-severity fire because no fire-intolerant trees survived in high-severity plots.

The probability of mortality varied by species within tolerance groups, but there was an interaction between species and DBH for fire-intolerant trees as previously described (Figure 5). Incense-cedar had the lowest probability of mortality in the fire-tolerant group, followed by Douglas-fir and sugar pine. The odds of mortality were 1.87 (95% CI of 1.29 - 2.72, p-value = 0.00265) and 4.24 (95% CI of 2.48 - 7.24, p-value <0.0001) times higher than incense-cedar for Douglas-fir and sugar pine, respectively. There was an interaction between species and DBH for fire-intolerant trees so species differences were dependent on DBH. Western hemlock had the lowest probability of mortality for trees <30 cm DBH, but true fir trees transitioned to having the lowest probability of mortality thereafter (Figure 2.5). Western redcedar had the highest probability of mortality among all fire-intolerant species except for individuals with >52 cm DBH, at which point it exhibited a lower probability of mortality than western hemlock.

Dead Biological Legacies

Snag fall was influenced by fire severity, species, and DBH and included interactions among these factors (Table 2.4). We tested plot level environmental variables for statistical significance in all analyses, but none were significant at an alpha <0.05. Estimates 10 and 22 years post-fire included snag fall from four years post-fire, so we removed samples collected from four years post-fire to simplify figures analysis. Our observed statistical interactions were dominantly driven by individual species variation within a severity class, but error bars typically overlapped suggesting these differences weren't large (Figure 2.6). The probability of snag fall consistently decreased with increasing DBH across species and fire severity classes, and generally increased with increasing fire severity except for Douglas-fir, which had a higher probability following low-severity fire. Sugar pine snags had the highest likelihood of falling across all fire severity classes, and western redcedar and incense-cedar were the least likely to fall, as evidenced by the maximum snag DBH that reached its half-life (i.e. ≥ 0.50 probability of falling) by 10-22 years post-fire (Table 2.5). Overall, the size and

species of snags influenced their transition from snags to logs, and the probability of this occurring by 10-22 years post-fire depended on fire severity.

Snag fragmentation rates were influenced by species, DBH, fire severity class and time-since-fire, with a statistical interaction occurring between fire severity and species (Table 2.6). Not all species of snags were sampled in each time-since-fire period and severity class, and the diameter distribution varied with species and severity class (Figure 2.7). Snag fragmentation was positively correlated with DBH and fire severity for all species, although there wasn't a statistically significant difference between low and moderate-severity plots. The proportion of fragmented snags exceeded 0.75 for all species and severity classes by 22 years post-fire, except western redcedar. Snag height was highly variable following fragmentation, but was positively correlated with DBH and negatively correlated with time-since-fire. Mean fragmented snag height could be estimated by the equation: Height (m) = $4.183237 (1.069606) + 0.171947 (0.009519) * \text{DBH} - 3.701433 (1.206324) * \text{22Yrs Post-fire}$. This regression equation only accounted for a small proportion of observed variation (marginal $R^2 = 0.27$ and conditional $R^2 = 0.35$). If snag height is biologically important for species habitat requirements, this equation may not be an effective estimate of habitat resource availability.

There was little difference in log characteristics by severity class, except for unburned conditions and 22 years following high-severity fire (Figure 2.8). Increased snag fragmentation between 10 and 22 years post-fire, especially following high-severity fire, contributed to this increase as snags naturally transitioned to logs. As snags continue to fragment and fall, we expect differences by severity class to increase because a greater abundance of larger diameter snags were present in higher severity classes and will continue to fall and fragment after 22 years post-fire.

Forest Structural Attributes

Plot-level live structural attributes varied significantly across our fire severity gradient (Figure 2.9). Pairwise comparisons of live basal area among all fire severity classes were significantly different at an $\alpha < 0.05$. Unburned plots averaged $69.2 \text{ m}^2 \text{ ha}^{-1}$ of live basal area and $722 \text{ trees ha}^{-1}$. Low-severity fire decreased live basal area by an average of $18.9 \text{ m}^2 \text{ ha}^{-1}$ (standard error (SE) = 6.53, p-value = 0.0295) and tree density by an average of

528 trees ha^{-1} (SE = 49.21, p-value <0.001). Moderate-severity fire decreased live basal area by $33.16 \text{ m}^2 \text{ ha}^{-1}$ (SE = 6.53, p-value <0.001) and tree density by an average of 595.8 trees ha^{-1} (SE = 49.21, p-value <0.001). This was equivalent to an additional $14.3 \text{ m}^2 \text{ ha}^{-1}$ (SE = 5.19, p-value = 0.0407) of live basal area and 67 trees ha^{-1} (SE=39.11, p-value = 0.3232) loss than occurred in low-severity fire. High-severity fire decreased live basal area by an average of $67.5 \text{ m}^2 \text{ ha}^{-1}$ (SE = 6.53, p-value <0.001) and tree density by an average of 718.9 trees ha^{-1} (SE = 49.21, p-value <0.001), or $34.4 \text{ m}^2 \text{ ha}^{-1}$ (SE = 5.19, p-value <0.001) of live basal area and 123.1 trees ha^{-1} (SE = 39.11, p-value = 0.0154) more than occurred in moderate-severity fire).

Quadratic mean diameter and canopy base height were positively correlated with fire severity (Table 2.2). Unburned plot QMD and CBH averaged 35.9 cm and 8.0 m, which increased by an average of 25.5 cm (SE = 9.61, p-value = 0.05421) and 9.5 m (SE = 3.77, p-value = 0.07211) following low-severity fire, respectively. Moderate severity fire increased QMD and CBH by 5.5 cm (SE = 7.64, p-value = 0.88424) and 1.3 m (SE = 3.00, p-value = 0.97411) more than low-severity fire, respectively. High-severity fire increased QMD and CBH by 33.5 cm (SE = 11.13, p-value = 0.02423) and 9.3 m (SE = 4.37, p-value = 0.16458) more than observed following moderate-severity fire, respectively. These high-severity plot estimates only included live biological legacies.

Structural attributes of dead biological legacies were inversely correlated with those for live biological legacies, but differences among fire severity classes weren't as statistically significant. Unburned plots averaged $9.0 \text{ m}^2 \text{ ha}^{-1}$ of snag basal area, which increased by $12.6 \text{ m}^2 \text{ ha}^{-1}$ (SE=5.08, p-value = 0.0779) to an average of $21.6 \text{ m}^2 \text{ ha}^{-1}$ following low-severity fire. Moderate severity fire created $31.3 \text{ m}^2 \text{ ha}^{-1}$ of snag basal area, or $9.8 \text{ m}^2 \text{ ha}^{-1}$ (SE = 4.03, p-value = 0.0880) more than low-severity fire. High-severity fire created $57.1 \text{ m}^2 \text{ ha}^{-1}$ of snag basal area, or $25.8 \text{ m}^2 \text{ ha}^{-1}$ (SE = 4.03, p-value <0.001) more than moderate-severity fire. Snag density was highly variable in all fire-severity classes and didn't exhibit a statistically significant difference, although some of this might be a result of missed small diameter snags during sampling.

Live and dead structural attributes varied greater within than among plots, and were greatest across all plots (Table 2.7). Average within-plot CV for tree basal area and density was positively correlated with fire severity and increased more between low and moderate-

severity than unburned and low-severity classes. In contrast, average within plot CV for snag basal area and density decreased with increasing fire severity. Higher within plot CV values in unburned forests resulted from a low abundance of snags because estimates were sensitive to large individuals. The coefficient of variation among plots was similar within each fire-severity class, suggesting plots were equally variable across a severity class. The greatest CV occurred across all plots (i.e. landscape scale) for all structural attributes except snag basal area, which was more variable in unburned forests. Structural attributes were more homogeneous following high-severity fire because a large proportion of these plots had 100% mortality, and therefore was not included in this analysis.

Discussion

Pseudotsuga forests of western Oregon's central Cascade Range burn with mixed-severity, including those summarized here and in fire history and stand development studies (Kushla and Ripple, 1997, Morrison and Swanson, 1990, Tepley et al., 2013). Fire severity is typically defined as the amount live biomass killed or combusted as a direct result of the fire disturbance (Keeley, 2009), and mixed severity therefore suggests a diverse spatial pattern to mortality. Tree mortality is a function of fire intensity against the trees autecological traits that promote resistance to fire mortality (Brown and Smith, 2000, Woolley et al., 2013). Autecological traits promoting fire-resistance and shade-tolerance appear inversely related (Figure 2.10), so the distribution of tree species with varying fire-resistance is determined by the available species pool and seral state of a forest. Fire intensity varies across space and time dependent on top-down climate forcing and bottom-up fuels and topographic controls (Perry et al., 2011). Therefore, mixed-severity fires should be expected in *Pseudotsuga* forests because fire intensity will vary considerably in mountainous terrain and forest composition changes across successional development over time and space (Franklin et al., 2002).

Basal area mortality exceeded estimates from fire severity maps in >85% of our low-severity plots, which may be a result of delayed mortality or inaccurate mapping. Mortality may be delayed 3-5 years after a fire (Ryan and Reinhardt, 1988, van Mantgem et al., 2011), and therefore was captured in our sampling. As much as 40% additional mortality has been

observed within 6-7 years after low or moderate-severity fire in *Pseudotsuga* forests; a percentage that increased with increasing fire severity (Brown et al., 2013). Satellite images obtained within months or a year post-fire are typically used to estimate fire severity, systematically underestimating fire effects by not capturing delayed mortality. This could explain why our low-severity class exhibited greater mortality than predicted, although fire severity maps also have considerable classification error (Miller and Thode, 2007). Nonetheless, our sampling captured a statistically significant trend in fire severity and structural conditions, providing a gradient to investigate mixed-severity fire's function in structuring these ecosystems.

The spatial variability of living biological legacies was greatest at sub-hectare and landscape scales. Sub-hectare variation in fire effects developed from small-scale patchy mortality (Boyden et al., 2005, Knapp and Keeley, 2006) that increased with increasing fire severity. Within a 1-ha plot we observed low-severity fire conditions occurring with sub-hectare patches of moderate-severity, and moderate-severity fire that included sub-hectare patches of high-severity fire (Figure 2.11), in what is best considered a continuous gradient of fire effects at multiple scales. A low abundance of live biological legacies occurred in only a small proportion of our high-severity plots, so high-severity fire sites are be more structurally homogeneous than other conditions. Low, moderate and high-severity patches are distributed across burned landscapes and cumulatively result in more structural variation than individual severity classes, suggesting mixed-severity fire effects are an important attribute of landscapes that should be promoted (Smucker et al., 2005). The existing unburned landscape is also important because it retains valuable biological resources and refuge for species negatively affected by fire, facilitating the regeneration of the burned area (Eberhart and Woodard, 1987, Seidl et al., 2014).

Ecological Importance of Mixed-Severity Fire

Wildfires are typically defined as discrete disturbance events that restructure forested landscapes by altering the abundance and distribution of live and dead biological legacies (Pickett and White, 1985). Near-term fire effects have an important function in providing structural resources beneficial to floral and faunal communities. The size-

distribution, species composition, and post-fire dynamics of live or dead biological legacies, and interactions among them, are significant determinants of habitat quality for many species (Fontaine et al., 2009, Hutto, 1995, Saab et al., 2005). Pyrodiversity diversifies structural attributes, thereby providing an opportunity for a diverse ecosystem response to a gradient in post-fire conditions. For example, the abundance of live biological legacies strongly influences understory vegetation communities (Franklin and MacMahon, 2000), which are important habitat components for many avian species (Cahall and Hayes, 2009). The ecological function of a tree is only partially fulfilled as a living organism because dead biological legacies provide important for nesting, roosting and foraging by many avian species, but also support saprophytic communities and their ecosystem function (Franklin et al., 1987, Spies et al., 1988, Harmon et al., 1986). Since the size-distribution and species composition of both live and dead biological legacies is controlled by the severity of the disturbance, mixed-severity fire may support more biodiversity such that “pyrodiversity begets biodiversity” (Martin and Sapsis, 1992).

The legacy of a fire persists for decades to centuries as ecosystems reorganize to newly available resources, altering both the composition and structure of the ecosystem (Holling, 1973). Tree species common in *Pseudotsuga* forests appear to have adapted to two dominant environmental pressures, seemingly promoting adaptive traits conducive to either fire-tolerance or shade-tolerance (Givnish, 1988, Harmon, 1984). In the absence of exogenous disturbance, successional processes gradually transition overstory dominance to fire-intolerant species capable of persisting as sub-dominant individuals that utilize environmental resources available following individual or group tree mortality (Comfort et al., 2010). Fire intercedes in succession by preferentially killing fire-intolerant trees and, depending on the magnitude of the disturbance, creates alternative successional trajectories (Tepley et al., 2013). For example, low-severity fire retains a relatively high abundance of fire-intolerant trees, maintaining their competitive advantage to fill overstory gaps and enhancing their probability of regenerating (Tepley et al., 2014). Moderate-severity fire significantly reduces the abundance of live biological legacies while retaining fire-tolerant and intolerant trees, releasing ecological resources and promoting the establishment of a mixed cohort of species (Larson and Franklin, 2005). High-severity fire killed all fire-intolerant

trees and the majority of fire-tolerant trees, thereby creating environmental conditions conducive to the establishment of a pioneering cohort of Douglas-fir that may dominate stand dynamics for centuries (Freund et al., 2014).

Complex vertical and horizontal structure is an important attribute of old-growth Douglas-fir/western hemlock forests in the western Cascades (Franklin et al., 1981). Vertical diversification has been purported to develop as small-scale disturbances, such as windthrow and root rot, create canopy gaps that are rapidly occupied by advanced regeneration or a new cohort of regenerating trees. The accumulation of these small gaps across landscapes facilitates horizontal diversification within this forest type (Franklin et al., 2002). Low or moderate-severity fire is an alternative pathway to developing both vertical and horizontal diversification, and may be the dominant facilitator of these conditions in portions of the Douglas-fir/western hemlock forest type (Weisberg, 2004). This effect may be most exemplified by moderate-severity fire where sub-hectare patches of high-severity fire occur within broader moderate-severity conditions (Figure 2.10). Post-fire conditions are fundamentally different than those created by individual or group tree mortality because mortality impacts a broader area. Post-fire light dynamics are thus greater than observed in small patches created by individual or small group mortality, and may be important to the establishment of diverse understory conditions (Van Pelt and Franklin, 2000). Mixed-severity fire further increases horizontal structural diversity across landscapes as the forest transitions among various levels of fire-severity and patch sizes, creating a complex mosaic of forest conditions with near and long-term structural and compositional variation important to the resilience of these ecosystems.

Conclusions

Fire is an important ecosystem process in Douglas-fir/western hemlock forests, and recent interests in early seral habitats suggest managers are realizing the importance of fire's functional role in restructuring these forests (Franklin and Johnson, 2012). Conservation efforts that focus only on old-growth and early-seral forest conditions ignore the importance of mixed-severity fire, especially since low or moderate-severity fire accounts for >70% of the burned area (Kushla and Ripple, 1997, Morrison and Swanson, 1990). Additionally, the time

period between the early-seral and old-growth conditions constitutes a large portion of a pioneering cohort's lifetime, exceeding estimated mean fire return intervals in nearby forests 2 or three fold (Morrison and Swanson, 1990). The distribution of live and dead biological legacies is dependent on fire intensity, species autecological traits that promote resistance to mortality and the forest's seral state at the time of disturbance (Figure 2.5). Variation in fire effects initiates structural change as diverse as the first order fire effects, with a legacy that will persist for decades or centuries (Seidl et al., 2014). Since fire return intervals can be as short as 95 years in western Oregon's central Cascades (Morrison and Swanson, 1990), and fire's functional role corresponds with the severity of the disturbance, existing old-growth forests may have missed a fire cycle that could have short and long-term negative effects on ecosystem resilience. This is particularly important in mature forests without existing vertical and horizontal structural diversity; conditions that could be accelerated by low and moderate-severity fire. The function of low or moderate-severity fire in developing structural complexity may be valuable to the resilience of these forests across the landscape and promoted in management regimes (Cissel et al., 1999).

Figures

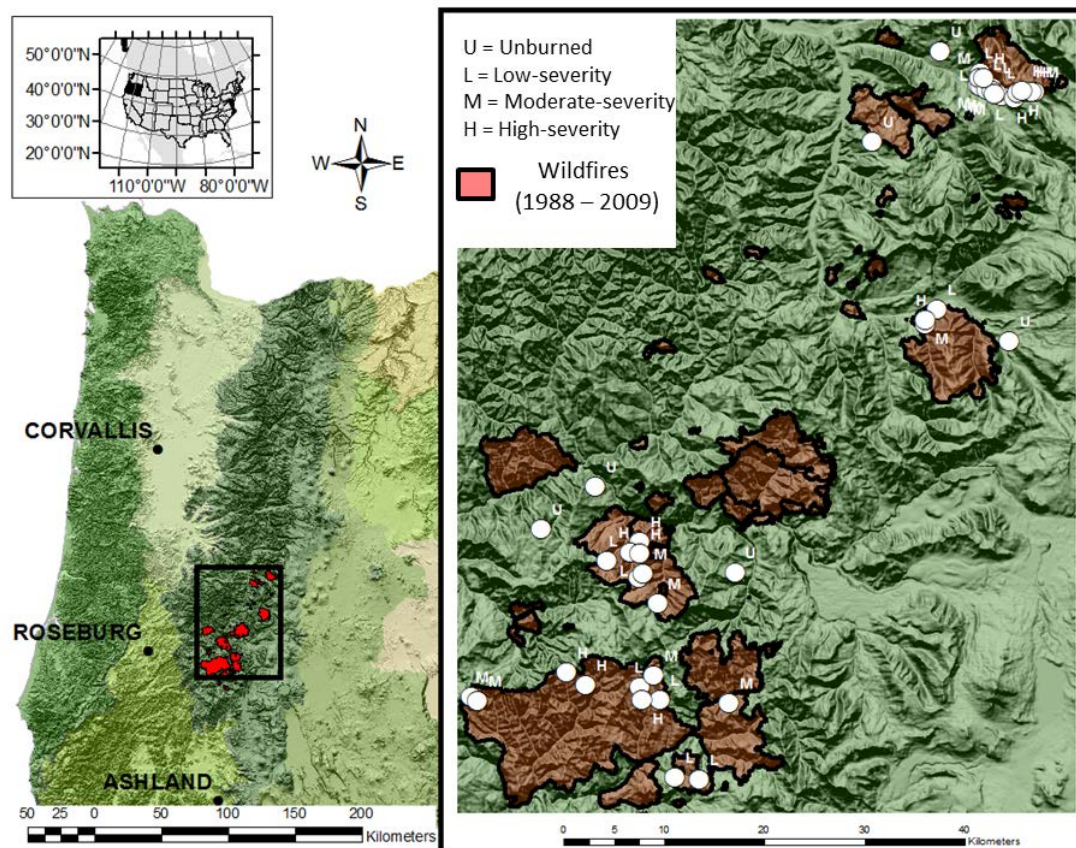


Figure 2.1: A map depicting fire extents and plot locations across our study area in Western Oregon's central Cascade Range.

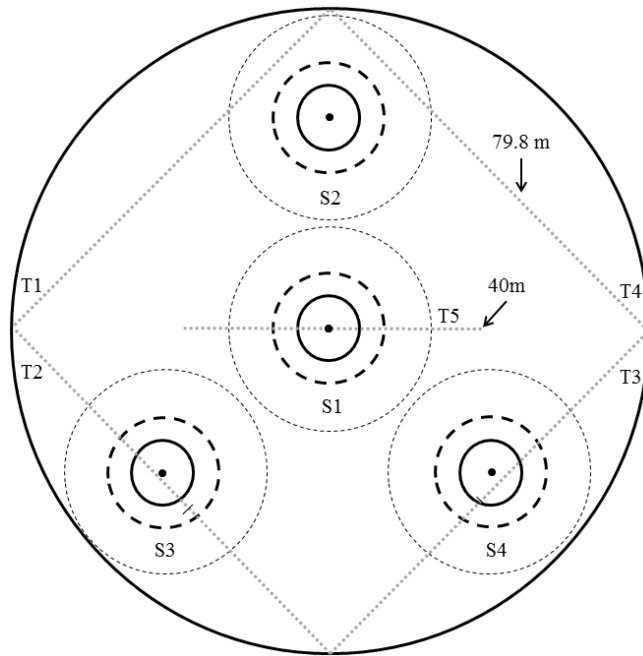


Figure 2.2: Sampling plot design for quantifying live and dead biological legacies following mixed-severity fire in Douglas-fir/western hemlock forests. Four variable-radius subplots were used to capture within-plot heterogeneity. Standing and fallen live and dead biological legacies 2.54 – 10.0 cm DBH were sampled in a 5.64 m (1/100th ha) radius subplot, >10.0 – 40.0 cm DBH within an 8.92 m radius subplot (1/40th ha), and > 40 cm DBH at 17.84 m radius subplot (1/10th ha). All biological legacies >70 cm DBH were sampled within the 1-ha plot to capture large, spatially disperse individuals. Four 79.8 m surface coarse woody detritus transects formed a square that touched the outer plot boundary at 4 points. One 40 m coarse woody detritus transect, perpendicular to the azimuth of plot orientation, was sampled through plot center.

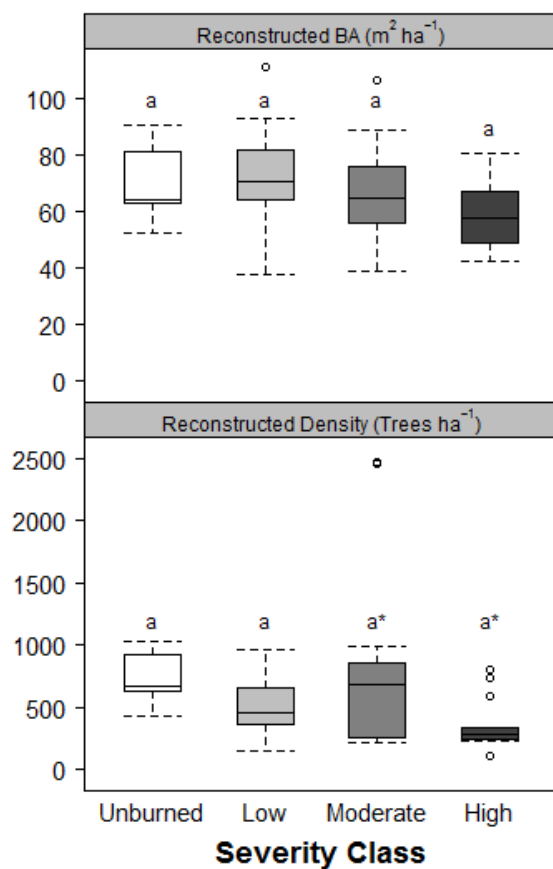


Figure 2.3: Reconstructed pre-fire tree basal area and forest density. Lower case letters indicate statistically different groups at $\alpha < 0.05$. * Represents statistically different groups at an $\alpha < 0.1$. Only high-severity fire conditions had moderately suggestive evidence of a difference, probably because some small diameter snags weren't evident during sampling because of burial or decay.

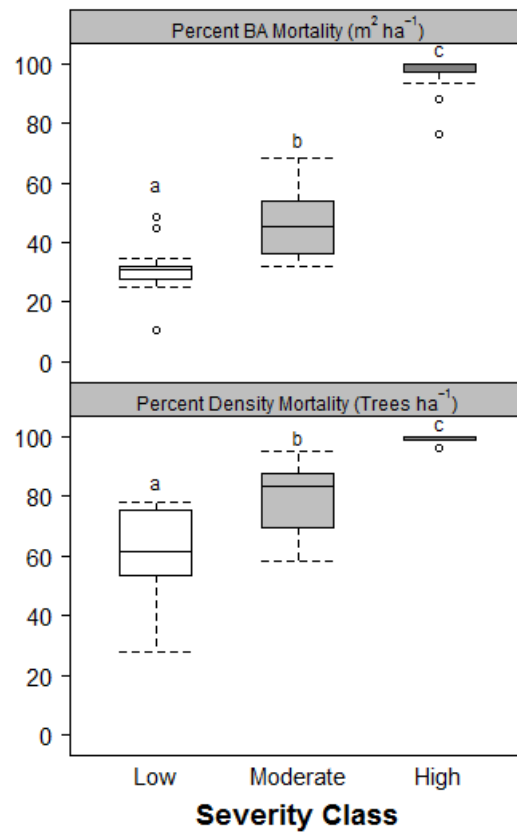


Figure 2.4: Fire severity was estimated from tree mortality and varies significantly across a priori severity classes. There is a statistically significant difference between all severity classes, but the difference between low and moderate is less than pairwise comparisons with high-severity. Lower case letters indicate statistically different groups at and alpha < 0.05.

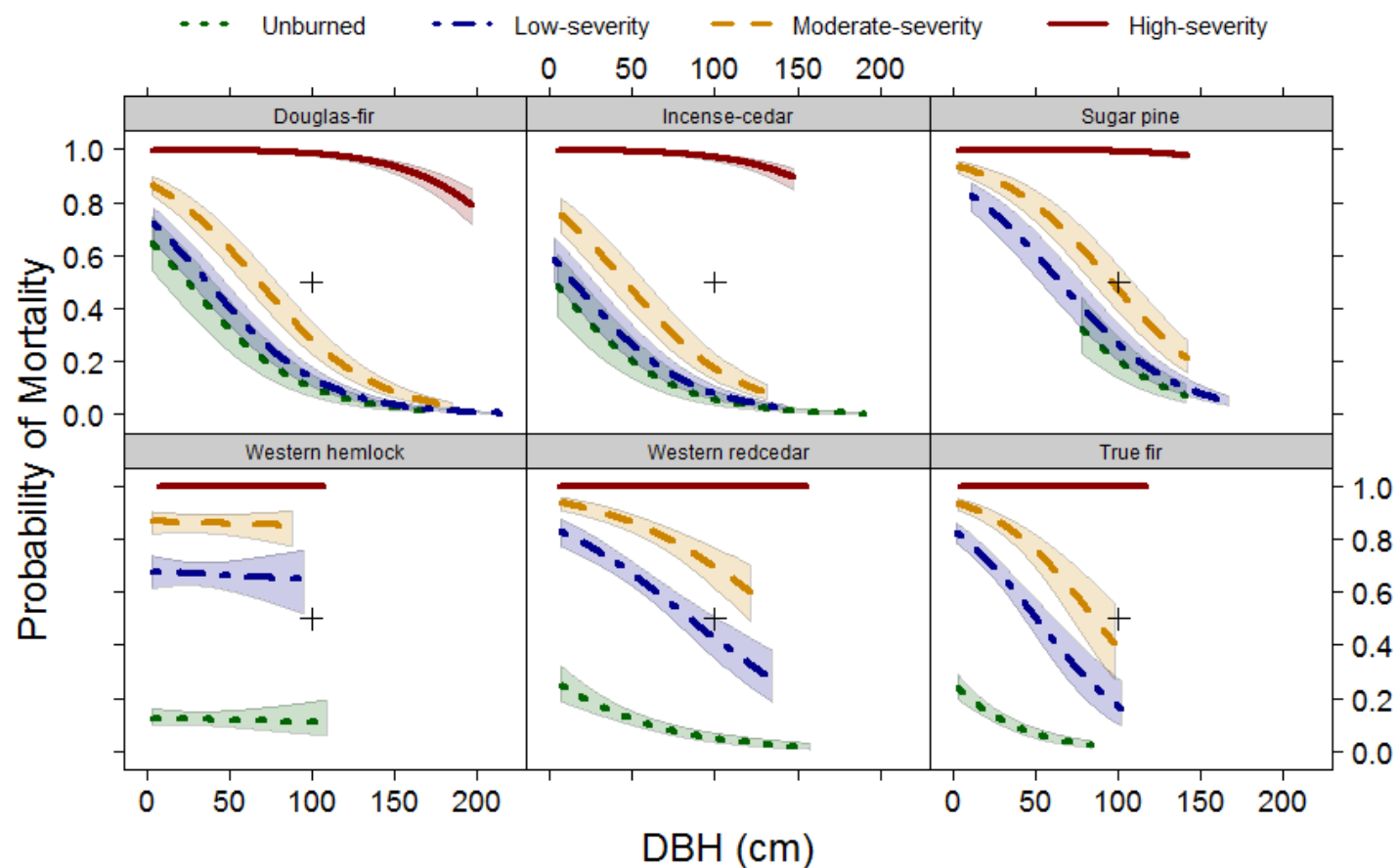


Figure 2.5: Conditional probabilities and standard deviations for estimating mortality across a burn severity gradient. Fire-tolerant trees are depicted in the top row and fire-intolerant trees in the bottom. Burn severity has the greatest effect within tolerance groups, but variability among species was also observed. + was included for visual comparison and indicates a 100 cm DBH tree with a 0.50 probability of mortality.

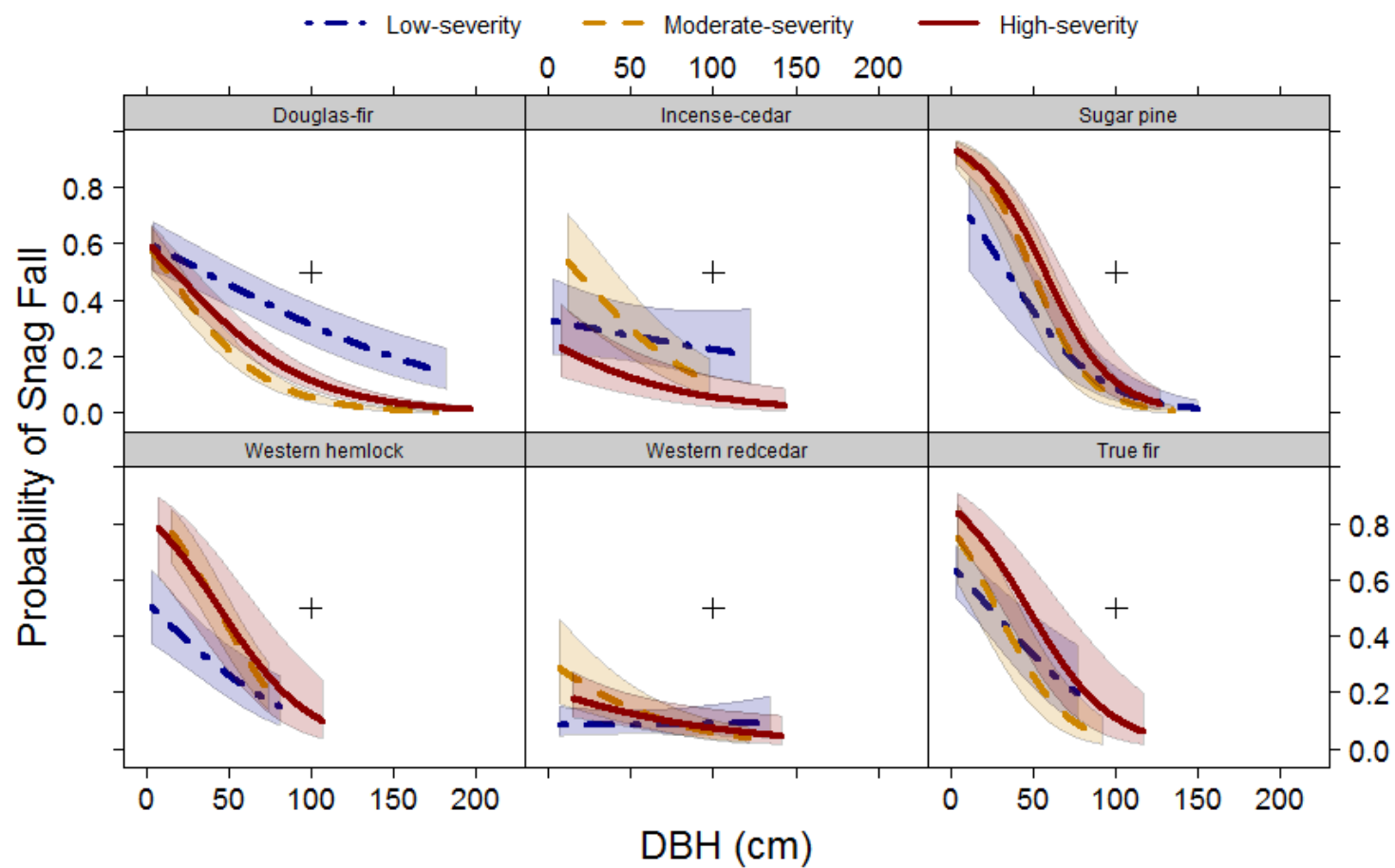


Figure 2.6: Conditional probabilities and standard deviations for estimating the probability of snag fall across a burn severity gradient. Fire-tolerant trees are depicted in the top row and fire-intolerant trees in the bottom. + was included for visual comparison and indicates a 100 cm DBH snag's half-life (i.e. probability of snag fall equal to 0.50).

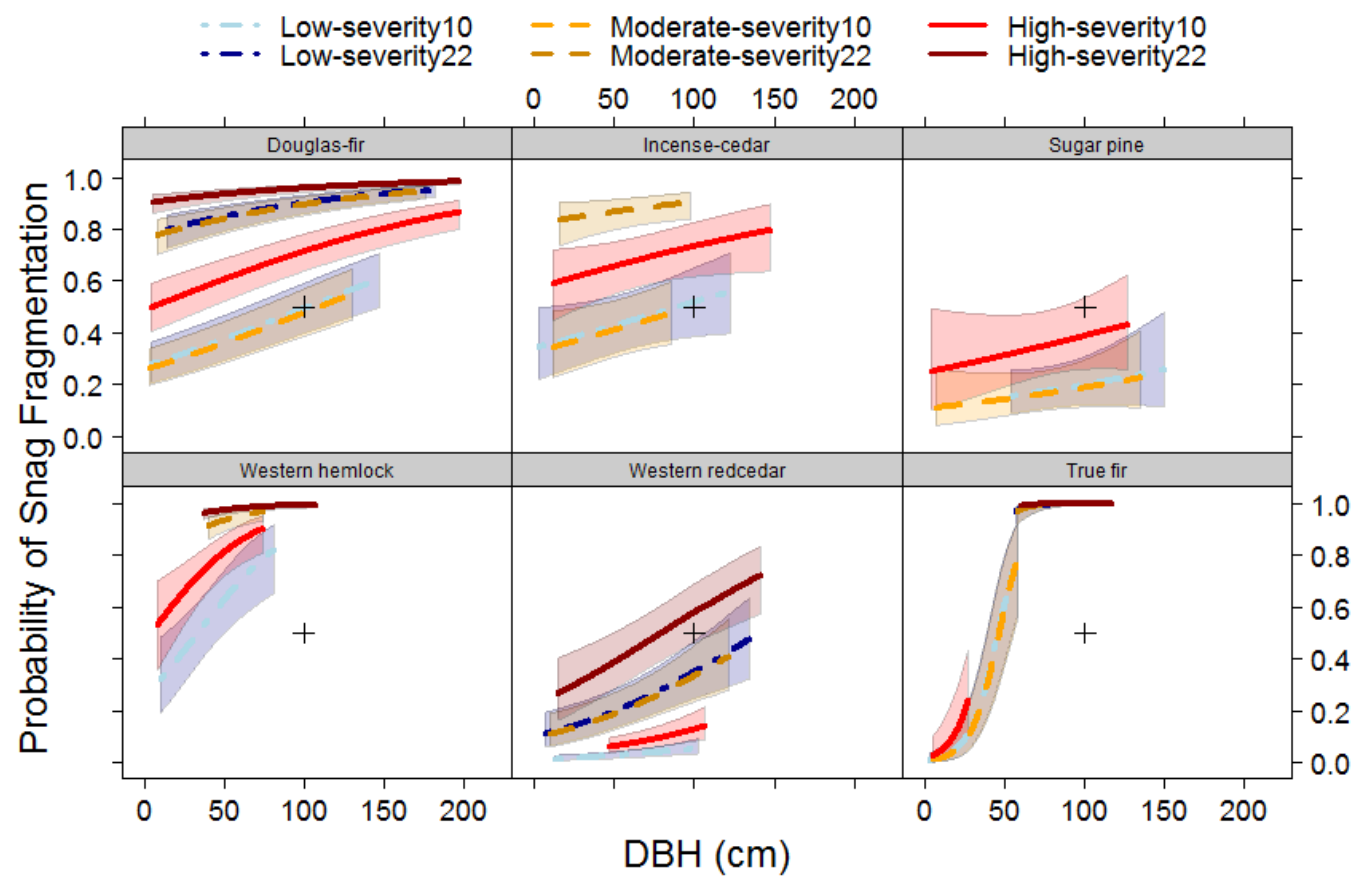


Figure 2.7: Conditional probabilities and standard deviations for estimating the probability of snag fragmentation across a burn severity gradient. Fire-tolerant trees are depicted in the top row and fire-intolerant trees in the bottom. + was included for visual comparison and indicates a 100 cm DBH snag with a 0.50 probability of being fragmented.

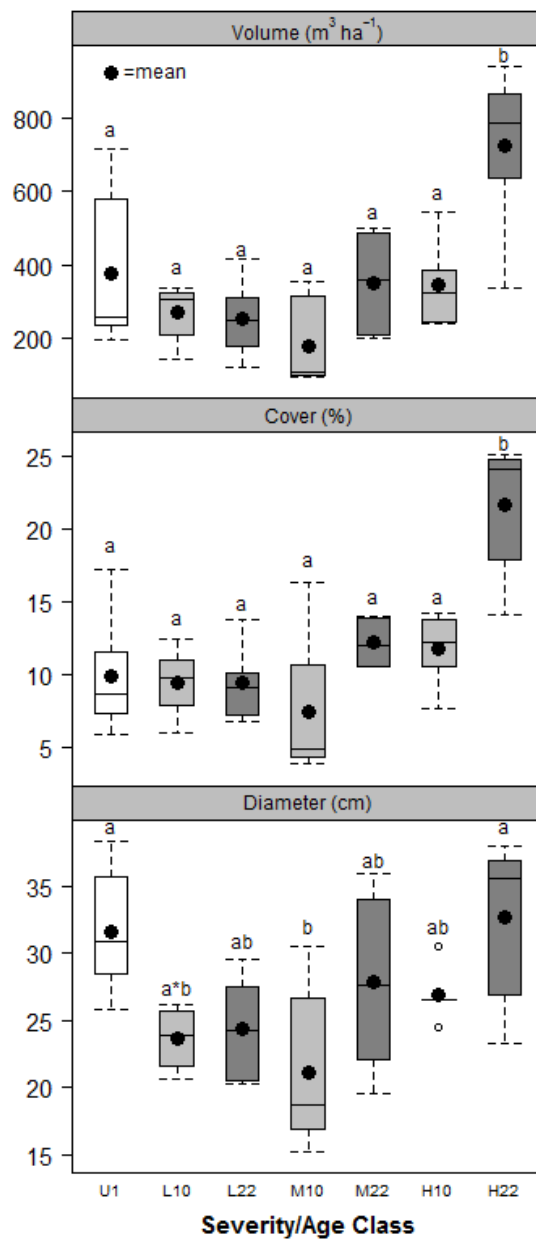


Figure 2.8: Dead biological legacies transition from snags to logs at varying rates dependent on size and local environmental conditions. The volume, cover and size of logs weren't statistically different by groups except for the high-severity class 22 years post-fire. The distribution of logs by severity class confirms our expected trends in snag fall and fragmentation. Accumulation will continue into the future, primarily in the moderate and high-severity classes since larger, more persistent snags were present in these classes.

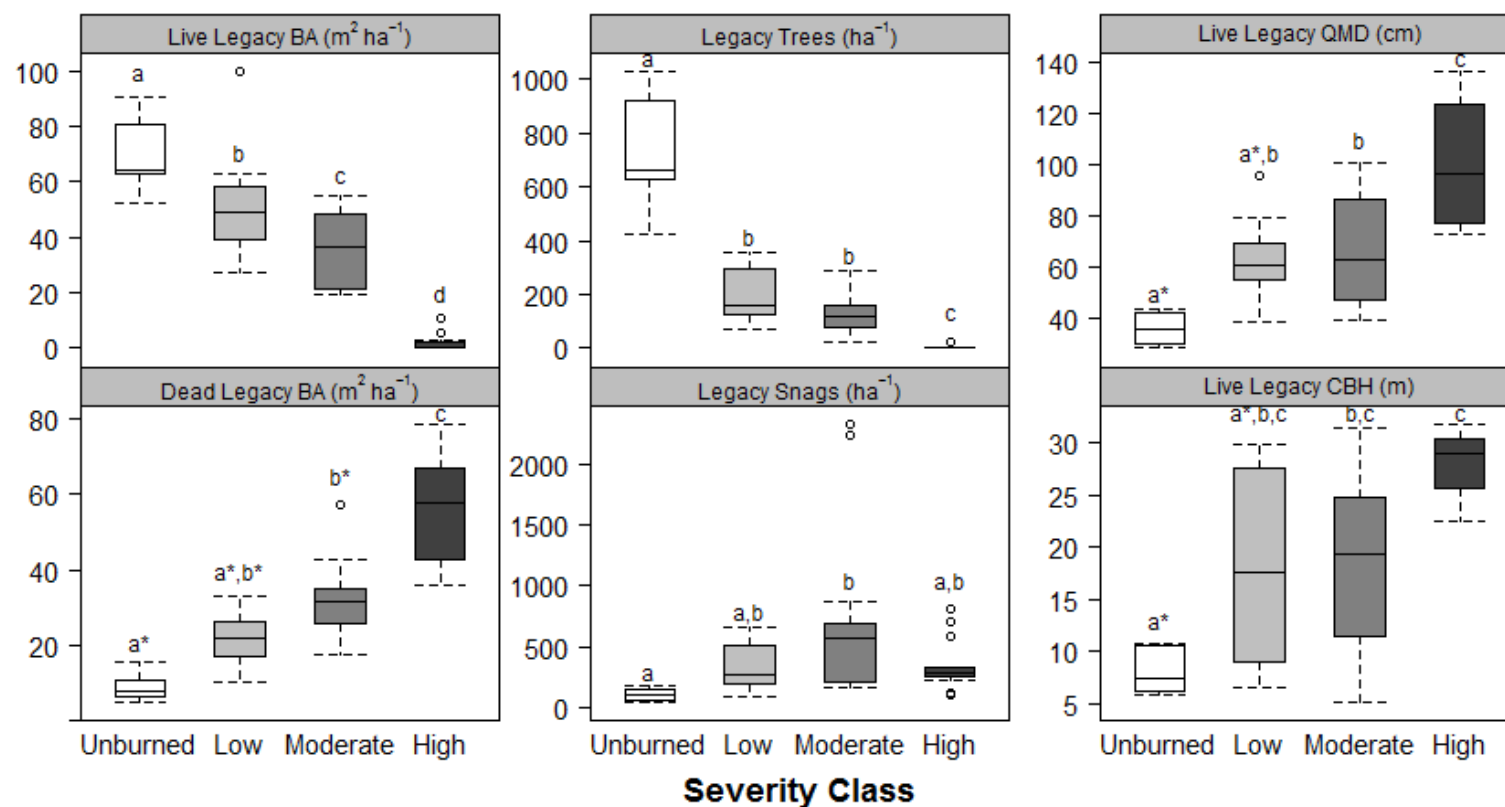


Figure 2.9: Figure depicting variation in forest structure across a fire severity gradient. Fire severity is often inferred from mortality or relative change from pre-fire conditions. Although related, the abundance of biological legacies may be more important metrics for understanding the future trajectory of the disturbed ecosystem. We observed significant differences in forest structure commensurate with fire severity classes, although low and moderate severity conditions show little difference in some metrics.

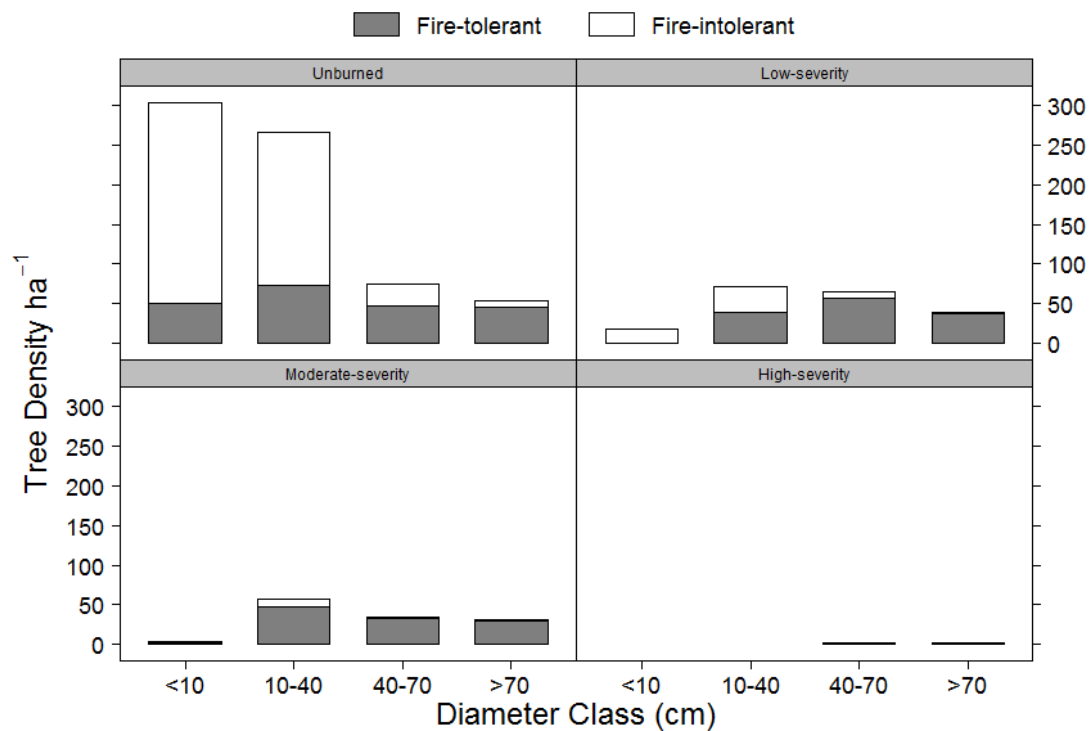


Figure 2.10: Density of fire-intolerant and tolerant trees varied by fire severity class and DBH. A greater proportion of both groups were lost as fire severity increased, with fire-intolerant species showing the greatest change.

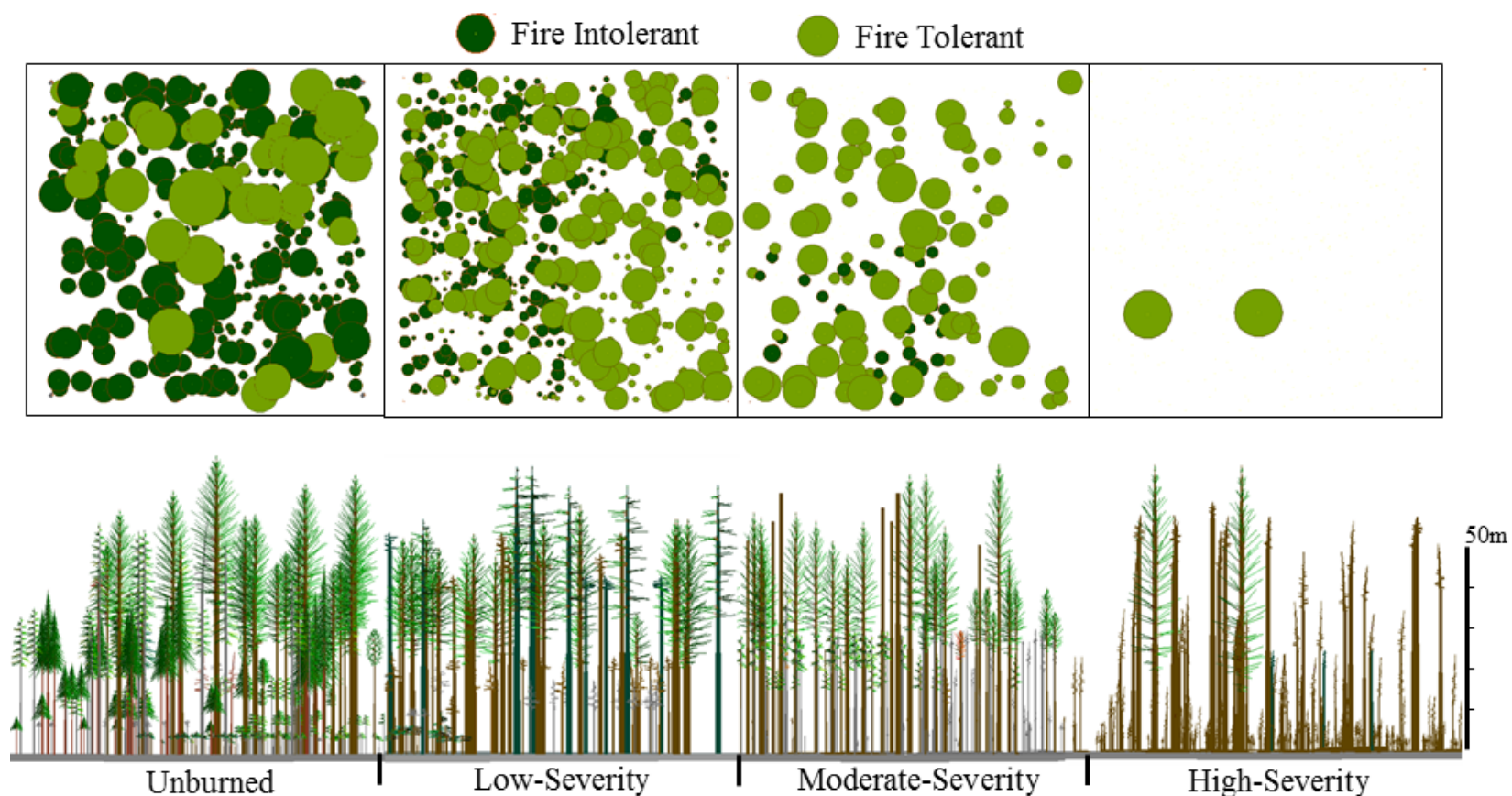


Figure 2.11: Profile and overhead depiction of four representative plots selected from our sample data set that span the burn severity gradient. The top panel is an overhead view and the bottom is the profile view of the same plots. Crown diameters in the top panel increase with increasing tree height. Each quadrant within a plot was populated from one of four subplots, therefore depicting the diversity of fire effects within a 1-ha plot. Trees are spatially located randomly within each quadrant. Although each burn severity class is represented by a different plot, dominant trends in mortality are evident. Both panels were created using the Stand Vegetation Simulator (McGaughey, 2004).

Tables

Table 2.1: Sample size and diameter distributions for dominant conifer species analyzed for probability of mortality, snag fall and snag fragmentation.

Probability of Mortality				Probability of Snag Fall			Probability of Snag Fragmentation		
Species	N	DBH (cm)		N	DBH (cm)		N	DBH (cm)	
		Mean (SD)	Range		Mean (SD)	Range		Mean (SD)	Range
Douglas-fir	3697	69.3 (36.6)	2.6 - 215.6	1977	61.2 (39.1)	2.6 - 196.7	1434	67.2 (39.3)	2.6 - 196.7
Incense cedar	246	64.3 (38.0)	3.3 - 189.5	113	61.9 (39.8)	3.3 - 189.5	82	65.1 (40.5)	3.3 - 189.5
Sugar pine	198	66.7 (42.2)	2.7 - 167.0	119	49.2 (40.0)	2.7 - 149.5	59	74.7 (36.9)	4.4 - 149.5
Western hemlock	366	32.5 (22.2)	2.6 - 108.6	214	34.5 (21.0)	2.7 - 108.6	134	32.3 (20.8)	2.9 - 107.4
Western redcedar	293	60.5 (31.9)	3.8 - 157.1	174	59.3 (33.4)	6.1 - 155.3	139	61.7 (34.2)	6.1 - 155.3
True fir	279	24.7 (24.0)	2.5 - 116.5	149	20.8 (23.8)	2.5 - 116.5	66	28.7 (30.2)	3.0 - 116.5

Table 2.2: Structural attributes and mortality metrics of plots summarized by fire severity class.

Attribute	Severity Class			
	Unburned	Low	Moderate	High
	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
N	6	13	13	13
Reconstructed BA ($\text{m}^2 \text{ha}^{-1}$)	69.2 (14.0)	71.9 (18.7)	67.4 (17.8)	58.8 (11.8)
Reconstructed Density (trees ha^{-1})	721.8 (216.4)	530.4 (257.5)	828.1 (771.4)**	355.4 (218.6)
Percent Mortality (BA)	N/A	30.7 (9.3)	46.9 (12.2)	96.6 (7.0)
Percent Mortality (trees ha^{-1})	N/A	61.2 (14.6)	78.5 (12.1)	99.4 (1.1)
Tree BA ($\text{m}^2 \text{ha}^{-1}$)	69.2 (14.0)	50.4 (18.3)	36.1 (13.1)	1.7 (3.3)
Tree Density (ha^{-1})	721.8 (216.4)	193.3 (96.5)	126.0 (71.4)	2.9 (7.3)
Tree CBH (m)	8.0 (2.3)	17.6 (8.8)	18.8 (8.5)	28.1 (3.9)*
Tree QMD (cm)	35.9 (6.8)	61.4 (15.5)	67.0 (23.3)	100.4 (28.8)*
Snag BA ($\text{m}^2 \text{ha}^{-1}$)	9.0 (3.9)	21.6 (7.4)	31.3 (11.0)	57.1 (13.4)
Snag Density (trees ha^{-1})	102.2 (50.6)	337.1 (202.2)	702.1 (742.3)**	353 (215.1)

Note: * Indicates values are from surviving trees only. **High values and standard deviations are inflated because of 2 plots with a high abundance of hardwood and conifer snags <10cm DBH. Without these plots the values would be 531.4 (290.5) and 413.7 (257.3) for reconstructed and snag density values, respectively.

Table 2.3: Equations and parameter estimates for predicting the probability of mortality by species and fire severity class.

Species	Severity Class	B_0 (SE)	B_1 (SE)	(cm)
Douglas-fir	Unburned ^a	$P_m = 1/1+\exp[-(0.712846 (0.454364) - 0.028776 (0.001594)^1 \times \text{DBH})]$		
	Low ^a	$P_m = 1/1+\exp[-(1.062651 (0.316966)^1 - 0.028776 (0.001594)^1 \times \text{DBH})]$		
	Moderate ^b	$P_m = 1/1+\exp[-(1.961745 (0.315265)^1 - 0.028776 (0.001594)^1 \times \text{DBH})]$		
	High ^c	$P_m = 1/1+\exp[-(7.001827 (0.440599)^1 - 0.028776 (0.001594)^1 \times \text{DBH})]$		
Incense cedar	Unburned ^d	$P_m = 1/1+\exp[-(0.085621 (0.482337) - 0.028776 (0.001594)^1 \times \text{DBH})]$		
	Low ^d	$P_m = 1/1+\exp[-(0.435336 (0.355696) - 0.028776 (0.001594)^1 \times \text{DBH})]$		
	Moderate ^e	$P_m = 1/1+\exp[-(1.334860 (0.355379)^1 - 0.028776 (0.001594)^1 \times \text{DBH})]$		
	High ^e	$P_m = 1/1+\exp[-(6.374756 (0.461739)^1 - 0.028776 (0.001594)^1 \times \text{DBH})]$		
Sugar Pine	Unburned ^f	$P_m = 1/1+\exp[-(1.529790 (0.504559)^1 - 0.028776 (0.001594)^1 \times \text{DBH})]$		
	Low ^f	$P_m = 1/1+\exp[-(1.879388 (0.379616)^1 - 0.028776 (0.001594)^1 \times \text{DBH})]$		
	Moderate ^g	$P_m = 1/1+\exp[-(2.811166 (0.377689)^1 - 0.028776 (0.001594)^1 \times \text{DBH})]$		
	High ^h	$P_m = 1/1+\exp[-(7.818823 (0.500890)^1 - 0.028776 (0.001594)^1 \times \text{DBH})]$		
Random Effects	Plot	1.087		
Western hemlock	Unburned ^a	$P_m = 1/1+\exp[-(-1.931852 (0.310115)^1 - 0.001508 (0.007592) \times \text{DBH})]$		
	Low ^b	$P_m = 1/1+\exp[-(0.752459 (0.300196)^1 - 0.001508 (0.007592) \times \text{DBH})]$		
	Moderate ^c	$P_m = 1/1+\exp[-(1.878655 (0.373014)^1 - 0.001508 (0.007592) \times \text{DBH})]$		
	High ^d	$P_m = 1$		
Western redcedar	Unburned ^e	$P_m = 1/1+\exp[-(-0.958377 (0.395420)^1 - 0.020168 (0.005907)^1 \times \text{DBH})]$		
	Low ^f	$P_m = 1/1+\exp[-(1.725829 (0.400211)^1 - 0.020168 (0.005907)^1 \times \text{DBH})]$		
	Moderate ^g	$P_m = 1/1+\exp[-(2.852097 (0.455235)^1 - 0.020168 (0.005907)^1 \times \text{DBH})]$		
	High ^d	$P_m = 1$		
True fir	Unburned ^e	$P_m = 1/1+\exp[-(-1.061895 (0.274031)^1 - 0.031914 (0.007617)^1 \times \text{DBH})]$		
	Low ^f	$P_m = 1/1+\exp[-(1.622450 (0.282901)^1 - 0.031914 (0.007617)^1 \times \text{DBH})]$		
	Moderate ^g	$P_m = 1/1+\exp[-(2.748583 (0.369551)^1 - 0.031914 (0.007617)^1 \times \text{DBH})]$		
	High ^d	$P_m = 1$		
Random Effects	Plot	0.02396		

Note: ¹ indicates an estimate is statistically different from zero at an $\alpha < 0.05$.

Lower case letters indicate statistically different groups within the fire tolerant and intolerant analyses.

Table 2.4: Equations and parameter estimates for predicting the probability of snag fall by species and fire severity class.

Species	Severity Class		B_0 (SE)	B_1 (SE)	(cm)
Douglas-fir	Low ^a	$P_m = 1/1+\exp[-($	0.428767 (0.368127)	$- 0.012156 (0.003830)^1$	$\times \text{DBH})]$
	Moderate ^b	$P_m = 1/1+\exp[-($	0.431363 (0.335028)	$- 0.024678 (0.003870)^1$	$\times \text{DBH})]$
	High ^b	$P_m = 1/1+\exp[-($	0.410145 (0.354327)	$- 0.03276 (0.003583)^1$	$\times \text{DBH})]$
Incense cedar	Low ^a	$P_m = 1/1+\exp[-($	-0.709501 (0.644998)	$- 0.05266 (0.008465)$	$\times \text{DBH})]$
	Moderate ^c	$P_m = 1/1+\exp[-($	-1.048708 (0.748345)	$- 0.017812 (0.009308)^1$	$\times \text{DBH})]$
	High ^b	$P_m = 1/1+\exp[-($	0.461632 (0.792229)	$- 0.025835 (0.008946)^1$	$\times \text{DBH})]$
Sugar Pine	Low ^d	$P_m = 1/1+\exp[-($	1.209906 (0.883112)	$- 0.035383 (0.010096)^1$	$\times \text{DBH})]$
	Moderate ^e	$P_m = 1/1+\exp[-($	2.748202 (0.599563) ¹	$- 0.048143 (0.009832)^1$	$\times \text{DBH})]$
	High ^e	$P_m = 1/1+\exp[-($	2.771240 (0.774857) ¹	$- 0.056168 (0.010260)^1$	$\times \text{DBH})]$
Western hemlock	Low ^{a,d}	$P_m = 1/1+\exp[-($	0.084172 (0.553908)	$- 0.022281 (0.010419)^1$	$\times \text{DBH})]$
	Moderate ^{b,e}	$P_m = 1/1+\exp[-($	1.519489 (0.858292)	$- 0.034502 (0.010937)^1$	$\times \text{DBH})]$
	High ^{c,e}	$P_m = 1/1+\exp[-($	1.824465 (0.651326) ¹	$- 0.042542 (0.010526)^1$	$\times \text{DBH})]$
Western redcedar	Low ^f	$P_m = 1/1+\exp[-($	-2.366788 (0.661292) ¹	$- 0.000465 (0.008179)$	$\times \text{DBH})]$
	Moderate ^c	$P_m = 1/1+\exp[-($	-1.309377 (0.598471) ¹	$- 0.012477 (0.008546)$	$\times \text{DBH})]$
	High ^{b,c}	$P_m = 1/1+\exp[-($	-0.766344 (0.789466)	$- 0.020105 (0.008565)^1$	$\times \text{DBH})]$
True fir	Low ^{a,d}	$P_m = 1/1+\exp[-($	0.625669 (0.429456)	$- 0.026292 (0.012057)^1$	$\times \text{DBH})]$
	Moderate ^e	$P_m = 1/1+\exp[-($	1.812684 (0.648868) ¹	$- 0.038834 (0.012464)^1$	$\times \text{DBH})]$
	High ^e	$P_m = 1/1+\exp[-($	1.294826 (0.779611)	$- 0.046866 (0.012397)^1$	$\times \text{DBH})]$
Random Effects	Plot		0.7988		

Note: ¹ indicates an estimate is statistically different from zero at an $\alpha < 0.05$.

Lower case letters indicate statistically different groups within the fire tolerant and intolerant analyses.

Table 2.5: Maximum DBH by species and fire severity class of snags with a half-life occurring by 10-22 years post-fire.

Species	Severity Class		
	Low	Moderate	High
Douglas-fir	36 cm	13 cm	18 cm
Incense-cedar	---	18 cm	---
Sugar pine	34 cm	49 cm	57 cm
Western hemlock	4 cm	43 cm	44 cm
Western redcedar	---	18 cm	---
True fir	24 cm	28 cm	47 cm

Table 2.6: Equations and parameter estimates for predicting probability of snag fragmentation by species and fire severity class.

Species	Severity Class		B ₀ (SE)	B ₁ (SE)	(cm)	B ₂ (SE)* - 22 Yrs Post-fire
Douglas-fir	Low ^a	$P_m = 1/1+\exp[-($	-0.99036 (0.39786) ¹	- 0.00970 (0.00251) ¹	x DBH	+ 2.23891(0.36573) ¹)]
	Moderate ^a	$P_m = 1/1+\exp[-($	-1.06058 (0.36999) ¹	- 0.00970 (0.00251) ¹	x DBH	+ 2.23891(0.36573) ¹)]
	High ^b	$P_m = 1/1+\exp[-($	-0.04836 (0.38276)	- 0.00970 (0.00251) ¹	x DBH	+ 2.23891(0.36573) ¹)]
Incense cedar	Low ^a	$P_m = 1/1+\exp[-($	-0.66082 (0.64234)	- 0.00736 (0.00766)	x DBH	+ 2.23891(0.36573) ¹)]
	Moderate ^a	$P_m = 1/1+\exp[-($	-0.73101 (0.64034)	- 0.00736 (0.00766)	x DBH	+ 2.23891(0.36573) ¹)]
	High ^b	$P_m = 1/1+\exp[-($	0.28117 (0.64531)	- 0.00736 (0.00766)	x DBH	+ 2.23891(0.36573) ¹)]
Sugar Pine	Low ^a	$P_m = 1/1+\exp[-($	-2.06378 (0.88311)	- 0.00667 (0.01194)	x DBH	+ 2.23891(0.36573) ¹)]
	Moderate ^a	$P_m = 1/1+\exp[-($	-2.13380(1.10546)	- 0.00667 (0.01194)	x DBH	+ 2.23891(0.36573) ¹)]
	High ^b	$P_m = 1/1+\exp[-($	-1.12166 (1.107155)	- 0.00667 (0.01194)	x DBH	+ 2.23891(0.36573) ¹)]
Western hemlock	Low ^a	$P_m = 1/1+\exp[-($	-1.06567 (0.81632)	- 0.03201 (0.01731)	x DBH	+ 2.23891(0.36573) ¹)]
	Moderate ^a	$P_m = 1/1+\exp[-($	-1.13584 (0.83591)	- 0.03201 (0.01731)	x DBH	+ 2.23891(0.36573) ¹)]
	High ^b	$P_m = 1/1+\exp[-($	-0.12366 (0.82931)	- 0.03201 (0.01731)	x DBH	+ 2.23891(0.36573) ¹)]
Western redcedar	Low ^c	$P_m = 1/1+\exp[-($	-4.42515 (0.71420) ¹	- 0.01563 (0.00750) ¹	x DBH	+ 2.23891(0.36573) ¹)]
	Moderate ^c	$P_m = 1/1+\exp[-($	-4.49536 (0.71133) ¹	- 0.01563 (0.00750) ¹	x DBH	+ 2.23891(0.36573) ¹)]
	High ^d	$P_m = 1/1+\exp[-($	-3.483102 (0.72161) ¹	- 0.01563 (0.00750) ¹	x DBH	+ 2.23891(0.36573) ¹)]
True fir	Low ^e	$P_m = 1/1+\exp[-($	-5.11481 (1.57382) ¹	- 0.11183 (0.03666) ¹	x DBH	+ 2.23891(0.36573) ¹)]
	Moderate ^e	$P_m = 1/1+\exp[-($	-5.18450 (1.58595) ¹	- 0.11183 (0.03666) ¹	x DBH	+ 2.23891(0.36573) ¹)]
	High ^f	$P_m = 1/1+\exp[-($	-4.17179 (1.58234) ¹	- 0.11183 (0.03666) ¹	x DBH	+ 2.23891(0.36573) ¹)]
Random Effects	Plot		0.8695			

Note: ¹ indicates an estimate is statistically different from zero at an $\alpha < 0.05$. Lower case letters indicate statistically different groups within the fire tolerant and intolerant analyses.

Table 2.7: Within and among-plot coefficients of variation for various structural attributes and severity metrics by fire severity class.

Attribute	Severity Class								Burned Landscape
	Unburned		Low		Moderate		High		
	Within Mean (SD)	Among Mean	Within Mean (SD)	Among Mean	Within Mean (SD)	Among Mean	Within Mean (SD)	Among Mean	
Tree BA (m ² ha ⁻¹)	27.8 (8.7) ^{a*}	20.2	31.6 (18.5) ^{a*}	36.3	49.9 (27.0) ^{a*}	36.2	N/A	N/A	95.3
Tree Density (ha ⁻¹)	42.2 (15.8) ^a	30	61.7 (19.7) ^{a,b}	49.9	81.5 (33.7) ^b	56.6	N/A	N/A	127.6
Tree CBH (m)	30.1 (16.7) ^a	28.1	26.7 (17.3) ^a	50.4	22.5 (10.9) ^{a**}	45	N/A	N/A	N/A
Tree QMD (cm)	17.4 (15.7) ^a	19	33.5 (18.1) ^a	25.3	25.2 (10.5) ^{a**}	34.8	N/A	N/A	N/A
Snag BA (m ² ha ⁻¹)	90.7 (30.9) ^a	42.8	65.6 (27.2) ^{a,b}	34.5	55.8 (20.9) ^b	35	24.0 (8.9) ^c	23.5	66.7
Snag Density (trees ha ⁻¹)	78.7 (38.4) ^a	49.5	54.4 (23.9) ^{a,b}	60	50.0 (26.3) ^{a,b}	105.7	41.0 (19.2) ^b	61	122.1
Tree BA Mortality (%)	N/A	N/A	48.4 (25.4) ^a	30.1	54.2 (24.9) ^{a,b}	26.1	6.1 (10.9) ^b	7.2	60.1
Tree Density Mortality (%)	N/A	N/A	28.8 (20.0) ^a	23.9	26.6 (20.6) ^{a,b}	15.4	1.7 (3.2) ^b	1.1	31.2

Note: Coefficient of variation wasn't calculated for the high burn severity class because 69% of the plots had 100% mortality. ** Indicates CV was estimated from subplots with legacy trees only. Lower case letters indicate significant groups at an alpha <0.05, except those with an asterisk indicating a statistical difference at an alpha <0.10.

CHAPTER 3: UNDERSTORY RESPONSE-DIVERSITY TO MIXED-SEVERITY FIRE IN *PSEUDOTSUGA* FORESTS OF OREGON'S WESTERN CASCADES, USA

Abstract

Mixed-severity fires are increasingly recognized in *Pseudotsuga* forests of the Pacific Northwest, yet understory vegetation response to mixed-severity fires has not been characterized even though the majority of vegetation diversity is found in these communities. Therefore, we sampled forest structure (1000 m² circular plots) and understory vegetation (100 m² plots) at 168 collocated plots stratified across unburned, low, moderate and high-severity conditions 10 years (Tiller Complex) and 22 years (Warner Fire) post-fire. We focused on shrub species, but sampled forbs, graminoids, ferns and moss as functional groups. Offsite colonization and fire stimulated soil seedbanks increased the total species richness from 23 to 46. The life-history strategies of residual and colonizing species resulted in three dominant species response-curves to the magnitude of disturbance: 1) 'disturbance-sensitive', when relative abundance was highest in unburned plots and continued to decline with increasing fire severity, 2) 'disturbance-stimulated', when relative abundance was highest following low or moderate-severity fire and 3) 'disturbance-amplified', when relative abundance increased with increasing fire severity. Residual and colonizing species assemblages promoted five or six distinct understory communities, dominantly driven by legacy tree basal area rather than the proportion of basal area killed. Understory communities were rarely associated with one disturbance severity class as fire refugia, variation in overstory and understory fire severity, and compensatory conditions offset fire effects. Early-seral habitats were the most different from unburned forests, but were not the only post-fire conditions important across these burned landscapes. Interactions among live and dead forest structures following low or moderate-severity fire, and the vegetation response to these conditions, are also unique to the post-fire landscape and likely important for various wildlife species. Therefore, if ecological forestry paradigms focus dominantly on creating old-growth structure or early-seral habitats, they might exclude important conditions that contribute to the landscape structural complexity created by mixed-severity fires.

Introduction

Fire is a dominant disturbance agent in forested ecosystems where it influences the distribution and structure of living and dead biological legacies (Bond and Keeley, 2005). Douglas-fir/western hemlock forests (*Pseudotsuga menziesii*/*Tsuga heterophylla*, hereto referred to as *Pseudotsuga* forests) of the Pacific Northwest (PNW) have typically been characterized as having a low-frequency, high-severity fire regime (Agee, 1993), where stand initiation is followed by a gradual transition to structurally complex, late-seral forests (Franklin et al., 2002). Increasingly, alternative successional trajectories are accepted for forested landscapes (Reilly et al., *in press*), especially when fire occurs at intervals shorter than the lifespan of the pioneering cohort (Zenner, 2005) or exhibits a gradient in fire effects (Perry et al., 2011). Several fire-history and age-structure studies in western Oregon's central Cascades have described mixed-severity fire in *Pseudotsuga* forests, with mean fire return intervals ranging from 95-150 years (Means, 1982, Morrison and Swanson, 1990, Tepley et al., 2013, Weisberg, 2004). Low or moderate-severity fire accounted for >70% of the burned area in at least two watersheds in Oregon's western Cascades during the 19th century (Morrison and Swanson, 1990), with similar results occurring in the more recent 1991 Warner Fire (Kushla and Ripple, 1997). Therefore, mixed-severity fires may be more common and ecologically important than previously suggested by commonly used successional models (Franklin et al., 2002).

Short and long-term ecological responses to disturbance have direct implications for wildlife habitat, biodiversity and ecosystem energetics (Hansen et al., 1991, Spies, 1998, Odum, 1969). Disturbance ecology in forested systems has emphasized the interaction between disturbance regimes, tree composition and age-structure, and successional development (Pickett and White, 1985). This perspective inherently excludes more ephemeral ecosystem responses, such as understory vegetation development that may be as important to the ecosystem as broader successional processes. For example, understory vegetation contributes to ecosystem energetics and food webs (Campbell and Donato, 2014), and interacts with forest structure to provide additional habitat attributes for many species (Hagar, 2007), and directly or indirectly supports much of the diversity in PNW forests

(Halpern and Spies, 1995). Therefore, the functional role of fire in forested ecosystems depends on both short and long-term ecological responses to disturbance regimes (Wright and Heinzelman, 1973, Turner, 2010).

Fire directly affects understory vegetation by interrupting or terminating an individuals' life cycle, impacting above and belowground reproductive tissues and consuming or stimulating seed banks (Bond and van Wilgen, 1996). Wildfires also indirectly influence understory vegetation by altering the distribution of legacy trees, which may competitively exclude some species while ameliorating microclimatic conditions for the benefit of others (Gray and Spies, 1997). The diverse life-history strategies and resilience mechanisms of native vegetation in the Cascade Mountains of Oregon suggest understory species would respond differently to the magnitude of a disturbance (Halpern, 1988). For example, *Rhododendron macrophyllum* or *Chrysolepis chrysophylla* are capable of resprouting after being top-killed, and therefore may respond rapidly in the post-fire environment (Halpern, 1989). Additionally, these species typically do better in shady environments so may be more prodigious following low or moderate-severity disturbance. Long-term studies investigating vegetation response to disturbance in *Pseudotsuga* forests have focused predominantly on high-severity disturbance, such as that induced by clearcut harvesting and broadcast burning (Dyrness, 1973, Halpern et al., 2013). Therefore, little is known about the response of understory vegetation to mixed-severity fire in these forests, even though understory vegetation response may be functionally important for maintaining resilient biological communities.

In this study, we examine the response-diversity of understory vegetation to recent mixed-severity fires in *Pseudotsuga* dominated forests of western Oregon's central Cascades. This area is an ideal place to investigate mixed-severity fire effects on understory vegetation in wet-forest environments for several reasons. First, multiple fires burned within these forests in 2002 and earlier, allowing us to investigate more persistent vegetation communities (i.e. those that follow the ruderal dominated vegetation community). Second, satellite derived fire severity maps are available for these fires, so we can stratify sampling to capture a disturbance gradient. Lastly, an 'ecological forestry' paradigm has been proposed for public lands management with the explicit intention to manage within the bounds of

natural disturbance regimes (Franklin and Johnson, 2012, Morrison and Swanson, 1990). Mixed-severity fire effects have not been explored extensively in this forest type, so our results will have direct implications on current and future management activities. Specifically, we asked the following questions: (1) Do individual species respond differently to variation in fire severity? (2) Does fire severity influence species assemblages such that discrete understory vegetation communities respond to the disturbance gradient?

Methods

Study Area

Pseudotsuga forests of western Oregon's central Cascades are dominant from 500 – 1300 meters elevation, extending from the State of Washington to the South Umpqua River Watershed (Franklin and Dyrness, 1988). We sampled fires in this forest type between the Middle Fork of the Willamette River Watershed near Oakridge, OR (43° 4' 1.6032" N), and south to the North/South Umpqua River Watershed divide (43° 43' 36.8688" N) to capture a productivity gradient in this forest type. The climate is typical of maritime conditions with cool, wet winters and warm, dry summers. Average annual precipitation ranges from 1339 – 1761 mm per annum, with ~75% falling from November through April. Average maximum temperatures range from 27.5 °C in August, to 4.3 °C in December, and average minimum temperatures range from 9.1 °C in August to -2.8 °C in December (Daly et al., 2002, www.prismclimate.org). There is a north-south climatic gradient such that temperatures increase and moisture decreases from north to south. Douglas-fir, sugar pine (*Pinus lambertiana*) and incense-cedar (*Calocedrus decurrens*) were common fire-tolerant tree species encountered in our study area. Western hemlock, western redcedar (*Thuja plicata*), white fir (*Abies concolor*), grand fir (*Abies grandis*), and Pacific yew (*Taxus brevifolia*) were common fire-intolerant tree species. Giant chinkapin (*Castanopsis chrysolepsis*), bigleaf maple (*Acer macrophyllum*), Pacific madrone (*Arbutus menziesii*) and Pacific dogwood (*Cornus nuttallii*) are common hardwood trees. The potential vegetation type transitions to silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) at higher elevations, with dry Douglas-fir, Oregon white oak (*Quercus garryana*) and ponderosa pine (*Pinus*

ponderosa) forests occurring at lower elevations. Douglas-fir and white fir forests are common at more southerly latitudes within and beyond our study area.

Sampling Design

Several large fires occurred within our study area during the past several decades, accounting for a total of 76,746 ha burned between 1987 and 2014 (Figure 3.1). Approximately 8,782 ha burned in 1987 and 1988, followed by 9,037 ha in 1996, 36,437 ha in 2002, and 20,049 ha burned in 2008 - 2009. The most recent fire, Deception Creek Complex, burned an additional 2,441 ha near Oakridge, OR in 2014. We concentrated our sampling within the 2002 Tiller Complex (10 years post-fire) and the 1991 Warner Fire (22 years post-fire), which burned 36,347 ha and 3,723 ha, respectively.

Sampling was constrained to mature/old-growth (M/OG) *Pseudotsuga* forests without evidence of direct anthropogenic disturbance or fire occurrence during the past 100 years of recorded fire history. We randomly located six clusters of four forest structure and regeneration plots (24 sample units), in each of three fire-severity classes (i.e. low, moderate, high), at both the Tiller Complex and Warner Fire. Only the south slope of the Warner Fire was sampled because climatic conditions, combined with the north aspect, developed much wetter forests (e.g., Pacific silver fir was often dominant) we considered different from our intended study area. An additional set of plot clusters were placed in unburned forests distributed across our study area as our reference condition (Figure 3.1). Plot clusters were randomly selected using equal probability point sampling in ArcMap 10.0 (ESRI Inc., 2011), with clusters constrained to be at least 400 m apart within a severity class. Fire severity was determined from maps derived by the Monitoring Trends in Burn Severity program (MTBS, 2011), and were intended to capture <25% basal area mortality (low-severity), 25 – 75% basal area mortality (moderate-severity), and >75% basal area mortality (high-severity).

Forest Structural Attributes

We sampled live and dead biological legacies (legacy trees and snags) within a 1-ha circular plot at four nested subplots. Standing and fallen trees and snags 2.54 – 10.0 cm diameter at breast height (DBH) were sampled in four 100 m² circular subplots, 10.0 – 40.0

cm DBH within four 250 m² circular subplots, and > 40 cm DBH at four 1000 m² circular subplots. All trees and snags >70 cm DBH were sampled within the full 1-ha plot to capture large, spatially disperse individuals. We recorded tree species, DBH (cm), total height (m), canopy base height (m), and noted whether the tree regenerated after the disturbance. Post-fire regenerating trees > 2.54 cm DBH were considered saplings. We recorded snag species, DBH and height, and then separated pre-fire snags from fire created snags when >5% of the bole sapwood was consumed or turned to charcoal. We reconstructed pre-fire live basal area and stems per hectare, and quantified post-fire tree basal area (m² ha⁻¹), density (ha⁻¹), quadratic mean diameter (QMD) in centimeters, and canopy base height (CBH) in meters. Estimates were made at the subplot and plot-level to compare the influence of forest structure on understory vegetation at these scales. We used linear mixed-models to test differences among groups because of our nested plot structure. Pair-wise comparisons were adjusted for multiple comparisons using Tukey corrections in multcomp package of R (Torsten et al., 2008).

Understory Vegetation

Understory shrub cover and regenerating tree abundance was collected for individual species at four 100 m² (10 x 10 m) plots centered at our tree/snag nested subplots. These understory vegetation plots were the units of measure for analyses. Regenerating trees were tallied by species in the following height classes: < 10cm, 10 – 50 cm, 50 – 100 cm, 100 – 150 cm, 150 – 200 cm, and > 200 cm. The top two height classes were considered dominant seedlings. We estimated cover for individual shrub and sub-shrub species, but combined ferns, graminoids, forbs and moss into individual functional groups. Cover estimates were placed into one of the following classes: trace, 0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, and >75% (Peet et al., 1998, Reilly et al., 2006). Cover classes were later converted to midpoint values within each class distribution. We used cover classes because of the potential for estimation error between sampling crews across years, as well the difficulty of determining cover values to the nearest percent when a species exceeded 50% cover. We considered species present in unburned plots as ‘residual’ and those found only within burned plots as ‘colonizers’ (aka invaders) (Dyrness, 1973).

Response-curves, presented as general trends of individual species or functional group across the disturbance gradient, were determined using indicator species analysis for the *a priori* fire severity classes (Dufrêne and Legendre, 1997). We quantified the relative abundance for each species or functional group, plotted their values across the sampled fire severity gradient, and then separated them into different response-groups depending on observed trends. An individual species or functional group was classified into one of three response groups: 1) 'disturbance-sensitive', when relative abundance was highest in unburned plots and continued to decline with increasing fire severity, 2) 'disturbance-stimulated', when relative abundance was highest following low or moderate-severity fire or 3) 'disturbance-amplified', when relative abundance increased with increasing fire severity. General response-curves were then fit to the average relative abundance across all species within a response-group.

We used hierarchical agglomerative cluster analysis to identify discrete understory communities based on our cover estimates (PCORD 6, 2015, McCune et al., 2002). We used a Sorensen (Bray-Curtis) distance measure with a flexible beta group linkage method where $\beta = -0.25$. We analyzed the Tiller Complex and Warner Fire individually to separate any confounding issues related to differences in site productivity or the number of years post-fire when they were sampled. We sought commonalities in community response to disturbance, as well as differences arising from other environmental gradients not explicitly targeted in our sampling design. Only two shrub species were unique to a sampling location; *Ribes divaricatum* was only found in Tiller Complex and *Rhamnus purshiana* was only found in the Warner Fire. Shrub abundance was generally higher in the Tiller Complex. We removed rare species occurring in <5% of plots, as well as two outlier plots in the Tiller Complex that had distance measures exceeding 3.0 standard deviations from the mean, resulting in a total of 96 (94 for Tiller Complex) plots for each analysis. The same unburned plots were used for each fire analysis. Group significance was evaluated using a Multi-response Permutation Procedure (MRPP) based on Sorensen's distance measure and 5000 randomization tests, obtaining the chance-corrected within-group agreement (A-statistic) (Mielke and Berry, 2001). We used non-metric multi-dimensional scaling (NMS) to display plots by community group (PCORD 6, 2015).

The number of discrete community groups was determined using several metrics from indicator species analysis (ISA), following methods by Dufrêne and Legendre (1997), as well as results from our MRPP. First, we averaged the ISA p-values across all species for 2 to 20 cluster analysis groups, as well as the p-values for the significant indicator species only. We also tallied the number of significant indicator species ($p \leq 0.05$) at each grouping level. Finally, we calculated the change in the A-statistic at each grouping level. We plotted the estimates and selected the number of groups based on a combination of low average p-values, local maxima of the number of significant indicator species, and an inflection in ΔA -statistic, suggesting a reduced marginal gain of within-group agreement as additional groups were added. We classified all communities as low-disturbance (LD), moderate-disturbance (MD) or high-disturbance (HD) communities based on their species composition and the distribution of *a priori* severity class plots represented in each community group.

The dominant biophysical factors influencing community group membership were determined using the permutation procedure randomForest (Liaw and Weiner, 2002). We used the mean decrease in classification accuracy as a measure of the importance of biophysical factors to membership in our community groups (Breiman, 2001). Random forest works by obtaining group membership of each out-of-bag (OOB) sample as predicted using a classification tree, and records the number of correctly classified plots. The importance of each biophysical variable was determined by permuting a given variable's values in the OOB sample, at which point group membership of the OOB samples were predicted again from the tree. The number of correctly classified plots after a permutation was subtracted from the original number of correctly classified plots, and then divided by the number of OOB samples for that tree. This produces the decrease in classification accuracy as a proportion of the plots and was repeated for each tree in the forest. The mean decrease in accuracy was defined as the average of these values over all trees in the forest. We reduced the total number of biophysical factors using a manual stepwise procedure with the criterion that our classification accuracy was not reduced by >1%. This allowed us to remove 'redundant' fire severity metrics and non-influential variables to obtain a more parsimonious set of factors influencing community response-diversity.

Results

Fire Severity and Forest Structure

There were no statistically significant differences between reconstructed pre-fire basal area and forest density at an $\alpha < 0.05$ when all plots were combined. Reconstructed basal area averaged $66.5 \text{ m}^2 \text{ ha}^{-1}$ ($\text{SD} = 16.4$) across all plots and reconstructed mean forest density averaged $591.4 \text{ trees ha}^{-1}$ ($\text{SD} = 484.9$). When reconstructed estimates were separated by fire site, the Tiller Complex had statistically lower pre-fire basal area and tree densities in the moderate and high-severity classes, relative to unburned conditions. The Warner Fire didn't exhibit significant differences across the severity gradient, but estimates were consistently higher than Tiller Complex due to differences in productivity and disturbance histories (Table 3.1). Combined, our sampling appeared to capture the variation in M/OG conditions across our study area.

Post-fire tree mortality varied significantly across our sampled fire severity gradient at both fire sites. The largest marginal increase in tree mortality (stems ha^{-1}) occurred between unburned and low-severity fires, given small tree mortality, but basal area mortality had the largest marginal increase moving from moderate to high-severity plots as incrementally larger trees were killed. Only 31% of all our high-severity plots retained legacy trees, ranging from 76.6% - 97.4% basal area mortality. Live structural attributes also varied across our fire severity gradient at both fire sites. Pairwise comparisons of legacy tree basal area between the low and moderate-severity classes weren't statistically different at an $\alpha < 0.05$, but did capture a gradient of increasing fire effects. Quadratic mean diameter and canopy base height were positively correlated with fire severity, as incrementally larger trees were killed and canopy ascension followed (Table 3.1).

Species Response to Disturbance

Wildfire increased the total number of species present in our sample as colonizers mixed with residual species (Table 3.3). We considered species present in unburned plots as 'residual' and those found only within burned plots as 'colonizers'. *Vaccinium membranaceum* was observed in 1 unburned plot, but we considered it a colonizer as observed following clearcut harvesting in this region (Halpern et al., 2013). A total of 46

understory species/functional groups were identified, but only 36 were frequent enough (i.e. present in >5% of our plots) to use in our analyses (Table 3.3). Of these, 22 (61%) were residual and the remaining 14 (39%) were colonizers. Neither residual nor colonizers responded consistently across our sampled fire severity gradient, so we classified each into one of three response-groups. These groups (i.e. disturbance-sensitive, disturbance-stimulated, disturbance-amplified) represent distinct disturbance response-curves (Figure 3.2) arising from direct fire effects, species competitive ability and tolerance to changes in microclimatic conditions.

Disturbance-sensitive species comprised 28% of our sampled species /functional groups and continued to decline in abundance with increasing fire severity. Local (plot-level) extirpation of individual disturbance-sensitive species was observed, but none were extirpated entirely from a fire severity class (see Appendix I). Approximately 46% of all residual species were disturbance-sensitive, including the common shade-tolerant species *Acer circinatum*, *Rhododendron macrophyllum*, and *Corylus cornuta* (Table 3.3). Several residual low-shrubs were also disturbance-sensitive, including *Mahonia nervosa*, *Gaultheria shallon* and *Linnea borealis*.

Disturbance-stimulated species responded positively to fire occurrence, but their greatest abundance occurred following low or moderate-severity fire. This response-group included 19% of all sampled species, of which 57% were residual and 43% were colonizers. These included residual species such as *Chrysolepis chrysophylla* that resprouted vigorously from basal buds, and ferns that regenerated rapidly from rhizomes to take advantage of newly available resources and reduced competition. Colonizers such as *Arctostaphylos columbiana* and *Vaccinium membranaceum* responded positively to fire, but appear to be poor competitors and therefore exhibited a decrease in abundance, relative to low or moderate-severity fire, following high-severity fire.

The majority of understory species increased with increasing fire severity, exhibiting what we considered a disturbance-amplified response-curve (Figure 3.2). This response-group included 53% of all sampled species (42% and 58% residuals and colonizers, respectively), which was 79% of all colonizers and 36% of all residuals. Graminoids were the only previously defined functional group with an amplified response, although nitrogen-fixers

(e.g., *Ceanothus spp.*) and soft-mast producing shrubs (e.g., *Ribes* and *Rubus spp.*) could be other functional groups fitting this response type. The majority of early-seral associates exhibited a disturbance-amplified response and dominated these highly-disturbed sites.

Response-Diversity of Understory Communities

We identified five discrete understory communities across our disturbance gradient within the Tiller Complex using a cluster dendrogram that had 1.56% chaining and retained 23.5% of the vegetation information at this grouping level. This approach reduced the number of vegetation communities to a comprehensible level while retaining the underlying disturbance and environmental gradients driving community response-diversity (Figure 3.3a). Plots within identified vegetation communities were more closely associated than expected by chance (combined $A = 0.211$ p-value < 0.001), with most groups being significantly separated in multi-dimensional space (i.e. $A \geq 0.10$) except for the two moderate-disturbance communities (Table 3.4). Our ordination resulted in a 3-axes solution with a cumulative coefficient-of-determination for the correlations between ordination distances and distances in the original n-dimensional space of $R^2 = 0.711$ (Figure 3.3). Axis 1 was positively correlated with our disturbance gradient (Appendix III). The most significant biophysical factor associated with axis 2 was elevation, but several factors were compressed onto all axes so they are imperfect measures of these gradients.

Six discrete understory communities were identified across our disturbance gradient within the Warner Fire (Figure 3.3); the cluster dendrogram had 1.72% chaining and retained 31.3% of the vegetation information at this grouping level. Plots within these vegetation communities were more closely associated than expected by chance ($A = 0.284$ p-value < 0.001), with most groups significantly separated in multi-dimensional space except a moderate and high-disturbance community (Figure 3.4). The cumulative coefficient of determination for the correlations between ordination distances and distances in the original n-dimensional space was $R^2 = 0.652$. Axis 1 was primarily associated with our disturbance gradient, but mixed significantly with elevation and other biophysical factors (Appendix IV). Elevation was again the most significant biophysical factor influencing separation along axis 2.

Biological and physical factors influenced vegetation community response to mixed-severity fire (Figure 3.4). The benefit of our random forest analysis was that it ranked biophysical factors by their relative importance in classifying plots into a vegetation group, which cannot be determined from ordination axes. The overall classification errors were 32.8% and 37.5% when all factors were included for the Tiller Complex and Warner Fire, respectively. The importance ranking of many variables changed as we reduced the number of redundant and non-influence factors. Only four biophysical factors were retained as important at the Tiller Complex (Figure 3.5), resulting in a decreased OOB classification error rate of 26.6%. Six biophysical factors were retained as important in the Warner Fire, which slightly increased our OOB classification error rate to 38.5%. Hectare-scale basal area of legacy trees had the greatest influence on classification of plots into the post-fire community groups at both fires. Variation in legacy tree basal area at the sub-hectare scale, pre-fire basal area, and the abundance of dominant regenerating trees were other important biological factors (Figure 3.4). Elevation was the only important physical factor influencing community response in our analysis, capturing variation in productivity from different moisture and temperature regimes.

Low-Disturbance Community Response

Low-disturbance communities were characterized by a high abundance of residual, disturbance-sensitive species (Figure 3.3). Several discrete LD communities were observed in our study, and each included plots from unburned and low or moderate-severity fire (Figure 3.6). One community was comprised of residual species only and had relatively low average understory cover (i.e. < 20%). This community developed from high pre-fire basal area and very low-severity fire that did not result in significant overstory mortality, competitively excluding understory vegetation. The second LD community type (LD-1 in Tiller complex, LD-2 in Warner Fire) was also dominated by residual, disturbance-sensitive species but averaged approximately 60% understory cover. Common residual species closely associated with these communities included the shade-tolerant species/functional groups *Linnaea borealis*, *Acer circinatum*, *Chimaphila umbellata* and moss (see Appendix VII and VII for other associates). These species are all closely associated with wet, shady environments occurring in old-

growth forests of the Pacific Northwest (Spies and Franklin, 1991). A third low-disturbance community type was observed in the Tiller Complex. This community was dominated by the residual, disturbance-sensitive and stimulated species *Chrysolepis chrysophylla* and *Rhododendron macrophyllum*. These species vigorously resprouted from belowground vegetative structures after being top-killed (Cromack et al., 1979), and therefore were capable of rapidly acquiring and utilizing newly available resources created by the fire.

Moderate-Disturbance Community Response

Moderate-disturbance (MD) communities were characterized by an increase in colonizers and disturbance-stimulated species, but retention of a significant proportion of disturbance-sensitive species (Figure 3.3). These three dominant species types assembled into communities with relatively equal abundance, although some MD communities were more closely associated with LD or HD communities depending on species composition (Tables 4 and 5). Some of the differences observed between MD communities were likely a function of the pre-fire community, especially as related to variations in moisture regimes (Dyrness, 1973). For example, vegetatively propagated species (e.g. basal sprouting, rhizomes) responded rapidly to moderate levels of disturbance (Halpern, 1988). This was most evident with *Chrysolepis chrysophylla* and ferns, but many disturbance-sensitive species like *Gaultheria shallon*, *Rhododendron macrophyllum* and *Acer circinatum* also vegetatively propagated and were present in moderate abundances within these communities. In general, the abundance of colonizers remained relatively low, most likely a result of competition inhibiting a more robust response. Although total understory cover typically increased with increasing fire severity, some moderate-disturbance communities had relatively low understory cover as fire-induced mortality and overstory competition excluded a more robust response.

High-Disturbance Community Response

High-disturbance communities significantly departed from those found in unburned forests, concurrent with the most significant change in forest structure (Figure 3.4). We identified one high-disturbance community at the Tiller Complex and two at the Warner Fire.

These communities were dominated by disturbance-amplified species (Figure 3.3), so the greatest total abundance of understory species was observed in this community type. *Ceanothus*, *Ribes* and *Rubus* spp. were commonly associated with these communities (Appendix VII and VIII). Elevation was an important factor driving high-disturbance species assemblages. The lower elevation, high-disturbance community (HD-1) at Warner Fire was more compositionally similar to the high-disturbance community at the Tiller Complex as elevation compensated for latitudinal effects on moisture and temperature regimes. As elevation increased, *Ceanothus velutinus* became the dominant species in these communities as other *Ceanothus* species dropped out of the community.

Discussion

Disturbance severity is typically quantified by the amount or proportion of live biomass loss (Keeley, 2009), but we found the magnitude of overstory mortality wasn't the most important factor influencing post-disturbance vegetation response (Figure 3.5). Instead, the abundance of legacy trees had a greater influence, which is related to, but does not necessarily proportional to trees killed. These legacy trees directly influence understory vegetation by: 1) competing with understory vegetation for light, water and nutrients, and 2) ameliorating microclimates, thereby favoring some species over others (Gray and Spies, 2004). Legacy trees also indirectly influence understory vegetation by increasing the abundance of regenerating trees (Seidl et al., 2014), which can quickly occupy disturbed sites (Larson and Franklin, 2005) and competitively exclude some species over time (Halpern et al., 2013). We observed these effects in our sample even though we limited variation in pre-fire forest density by only sampling M/OG forests, and would expect this to be more evident in younger forests with lower pre-fire basal area. For example, 20% mortality (low-severity) in a forest with $20 \text{ m}^2 \text{ ha}^{-1}$ tree basal area would likely result in a post-disturbance community similar to those observed following high-severity fire. Therefore, the abundance of live biological legacies has greater predictive power over the post-fire community than estimates of mortality and should be emphasized when assessing post-disturbance ecosystem resilience.

Life-history strategies are a significant factor driving the response-diversity of understory vegetation in this forest type (Halpern, 1989). Many residual species have resilience mechanisms (e.g. vegetative propagation from basal buds or belowground structures) that can facilitate rapid regeneration and dominance of the post-disturbance community (Dyrness, 1973). Disturbance-sensitive or stimulated species tend to vegetatively propagate from basal buds or root collars, and therefore respond well to low or moderate-severity fire. These species benefit directly from fire-induced mortality of competing understory vegetation, but also appear to benefit indirectly from live biological legacies inhibiting the rapid population expansion of disturbance-amplified species. Other residual species can propagate via rhizomes and continue to expand in abundance with increasing fire severity, likely aided by production of soft mast that are consumed and dispersed by faunal species (McComb, 2008). All residual species were found following high-severity fire and persist by their tolerance of these highly-competitive environments, waiting for the more ephemeral disturbance-amplified colonizers to decline as the forest transitions to mid-successional stages (Halpern et al., 2013).

Most colonizing shrubs maintain viable populations over long time periods by producing abundant soil seedbanks that remain viable for decades to centuries until scarified by heat or other mechanisms (Conard et al., 1985, Schoonmaker and McKee, 1988, Steen, 1966). This life-history strategy facilitates their rapid expansion post-fire by virtue of their presence onsite, which supports the ecological theory that initial floristics determines species presence or dominance. These colonizing species are typically excluded when regenerating trees reach canopy closure (Halpern et al., 2013), which may last for one to several centuries (Means, 1980, Morrison and Swanson, 1991, Weisberg, 2004). When canopy density remains open, colonizing species may persist for longer periods than otherwise expected by successional models (Halpern et al., 2013). Off-site colonization occurs in burned forests, and may be most abundance in *Ribes* and *Rubus* spp. that benefit from bird dispersal, but the relative contribution of varying regeneration mechanisms aren't fully understood at this time.

Understory communities are rarely associated with one disturbance-severity class for several reasons. First, we stratified fire-severity using remotely sensed data which is

inherently better at estimating fire effects on overstory trees than understory vegetation. Fire effects on overstory trees don't always correlate well with impacts to the forest floor or belowground resources (Halofsky and Hibbs, 2008). Fire effects on the forest floor have been shown to facilitate smaller scale variations in vegetation response (Dyrness, 1973, Halpern, 1988). Secondly, local fire refugia may prevent species mortality or minimize fire effects (Keeton and Franklin, 2004), thereby allowing them to survive the fire and sexually or asexually reproduce to increase in abundance later in successional development. This partially explains why we observed local extirpation of disturbance-sensitive species, without observing complete extirpation within a severity class. Lastly, compensatory conditions, or variation in site conditions that may result in similar ecological responses across landscapes, can exceed the influence of disturbance on community response (DeSiervo et al., 2015). The effect of compensatory conditions was evident in the relationship between altitude and elevation across our fire sites. High-disturbance communities at Tiller Complex were closely associated with high-disturbance communities at lower elevations within the Warner Fire. Elevation captured a gradient in moisture availability and temperature regimes, thereby compensating for the drier conditions observed at the Tiller Complex.

Combinations of living residual overstory structure and understory vegetation may be functionally important in forested ecosystems (Hagar, 2007, Saab et al., 2005). For example, structural diversity in old-growth *Pseudotsuga* forests promoted understory diversity, which in turn improved habitat quality for a larger abundance and diversity of faunal species (Carey, 1995, Franklin and Spies, 1991). Recently, early-seral forest conditions have become a prominent issue in management and conservation efforts in the PNW (Swanson et al., 2011) partially because this successional stage has distinct structural characteristics (e.g. high abundance of snags) important for many faunal species (Swanson et al., 2014, Hagar, 2007). These structures only provide a portion of the important habitat components because the early-seral vegetation communities also provide the greatest input of primary production as highly-palatable nitrogen rich leaves and soft mast, and therefore can support larger populations of secondary consumers (Campbell and Donato, 2014). Old-growth or early-seral structure-vegetation interactions don't include the distinct structure-vegetation interactions found following low or moderate-severity fire that may be equally

important. For example, moderate-severity fire retains large legacy trees while still promoting early-seral communities, although with less abundance than typically observed following stand-replacing fires. These live biological legacies are ecologically important components of ecosystems (Lutz et al., 2012), providing refuge for species reliant on crowns for nesting (Bond et al., 2009), retaining seed banks important for propagating the next generation forest (Seidl et al., 2014), and supporting belowground mycorrhizal symbionts that increase water and nutrient acquisition by legacy and regenerating vegetation (Louma et al., 2006, Simard, 2009). Snag densities are relatively high following moderate-severity fire, which provide habitat for primary and secondary cavity nesters (Raphael and White, 1984). Eventually dead biological legacies become logs and function as nurse logs for regenerating trees (Harmon and Franklin, 1989) as well as important structures for wildlife habitat (Harmon et al., 1986). Lastly, ungulates may utilize low or moderate-severity fire conditions for longer time periods than early-seral habitats. Although not as abundant as early-seral habitats, nitrogen fixing shrub species and graminoids increase in abundance following moderate-severity fire and therefore provide browse for ungulates. Concurrent with increased browsing resources, these post-fire conditions don't develop the dense shrub layers or the extremely abundant downed woody debris that occur in early-seral habitats after a decade of growth, which are visual impediments, inhibit travel, and elevate fear of predator encounters (Seager et al., 2013). The diverse structural conditions created by mixed-severity fire have ecological value and, therefore, the breadth of post-fire structural conditions should be considered equally valuable to ecosystem resilience.

The recognition that disturbance-induced or mediated forest structure is important for maintaining proper ecosystem function has prompted efforts to transition forest management in the Pacific Northwest towards an ecological forestry paradigm (Franklin and Johnson, 2012). Initial changes stemmed from old-growth forest conservation efforts stimulated by the scale and intensity these forests were being altered by harvesting (Swanson and Franklin, 1992). Silvicultural practices were explored for creating structurally diverse forests in stands previously altered by anthropogenic activities (Bailey and Tappeiner, 1998), and more recently through gap-thinning or variable density harvests (Dodson et al., 2012). These treatments also intend to develop functionally diverse understory communities

indicative of old-growth forests in the PNW (Ares et al., 2009, Bailey et al., 1998, Halpern et al., 2005). Recent interests in developing and conserving early-seral habitats have added group retention harvests to this ecological forestry paradigm (Swanson et al., 2010, Franklin and Johnson, 2012). Early and late-successional stages are two ecologically important conditions occurring in forests with a low-frequency, high-severity disturbance regime (Franklin et al., 2002). In forests that experience mixed-severity fires, such as *Pseudotsuga* forests of western Oregon's central Cascades, focusing on these stages of development excludes conditions created by low or moderate-severity fire that may also be functionally important. Managing for structural diversity beyond early and late-seral stages at broad scales aligns more appropriately with mixed-severity fire effects in *Pseudotsuga* forests of the Pacific Northwest. These diverse conditions are more likely to result in ecosystems resilient to rapid global environmental change and increased disturbance already observed today (Littell et al., 2009). While this would be best achieved by increasing the extent of mixed-severity fire, landscape management practices that attempt to mimic natural disturbance patterns may be the only practical means to achieve these goals (Cissel et al., 1999, Dodson et al., 2012).

Conclusions

Mixed-severity fire resulted in diverse understory vegetation responses at the population and community level of organization. These communities and their development over time define the heterogeneity following mixed-disturbances in these forests, as well as its resilience to fire. Native understory species exhibited three distinct response-curves to increasing disturbance severity: 1) disturbance-sensitive species decreased in abundance with increasing fire severity, 2) disturbance-stimulated species' abundance peaked following low or moderate-severity fire, and 3) disturbance-amplified species' abundance increased exponentially with increasing fire severity (Figure 3.2). Individual species response-curves led to community assemblages that varied distinctly across our mixed-severity disturbance gradient (Figure 3.4). These communities occurred with varying abundances of live and dead biological legacies, promoting structural complexity and interactions among structures that

are likely important to many faunal species and communities (Cahall and Hayes, 2009, Fontaine et al., 2009).

Characterizations of landscape-level fire severity typically rely on satellite derived estimates, dominantly capturing fire effects to overstory vegetation (Key and Benson, 2005, Miller and Thode, 2007). While these satellite-derived fire severity estimates did capture a gradient in understory species response, we did observe similar communities across multiple these classes as species life-history strategies interacted with the magnitude of the fire and biophysical factors across the landscape (Dyrness, 1973, Halpern, 1989, DeSiervo et al., 2015). Our observations also support the concept that severity is resource dependent, and what is high-severity for one resource might be optimal conditions for another. This is most exemplified in our study by early-seral forest conditions created by high-severity fire. These communities provide valuable habitat to many species (Swanson et al., 2014), are relatively rare on the landscape (Swanson et al., 2010), and contribute significantly to the energetics of these landscapes (Campbell and Donato, 2014). Promoting fire as a natural process, and understanding the value of mixed-severity fire in *Pseudotsuga* forests, could lead to the long-term development and maintenance of resilient forest landscapes.

Figures

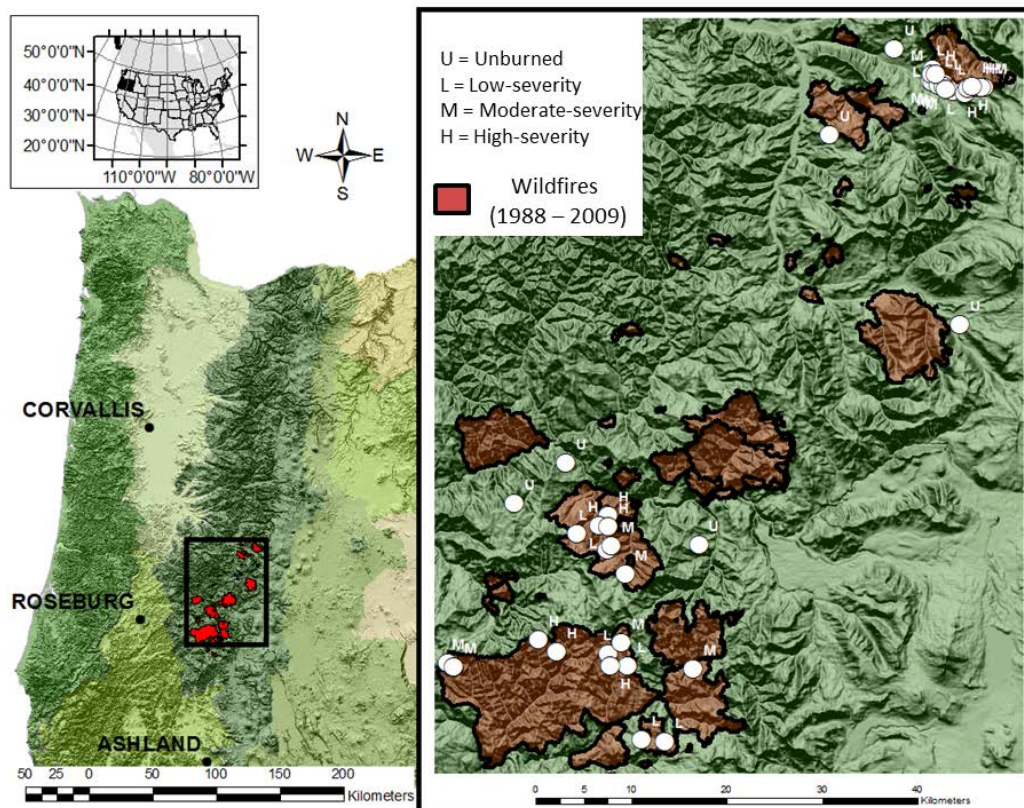


Figure 3.1: A map depicting fire extents and plot locations across our study area in Western Oregon's central Cascade Range.

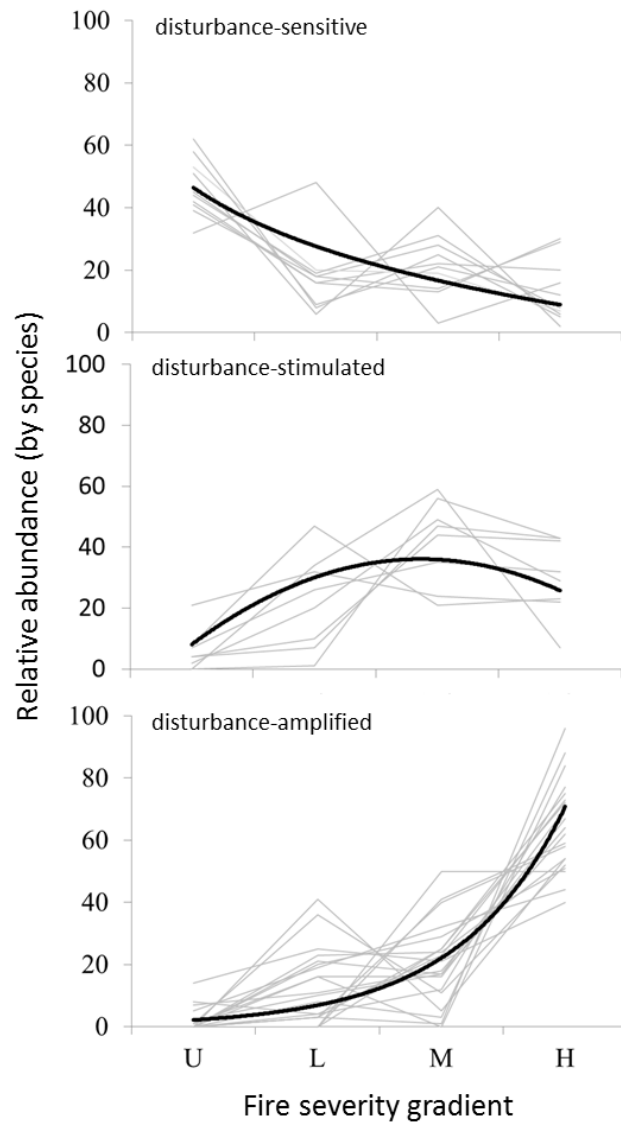


Figure 3.2: Three dominant disturbance response-curves were observed for common understory species or functional groups. Grey lines are observed values of relative abundance for individual species across a fire severity gradient, and the black line was fitted to the mean across all species within a response type to represent the dominant trend. U = unburned, L = low-severity fire, M = moderate-severity fire, and H= high-severity fire.

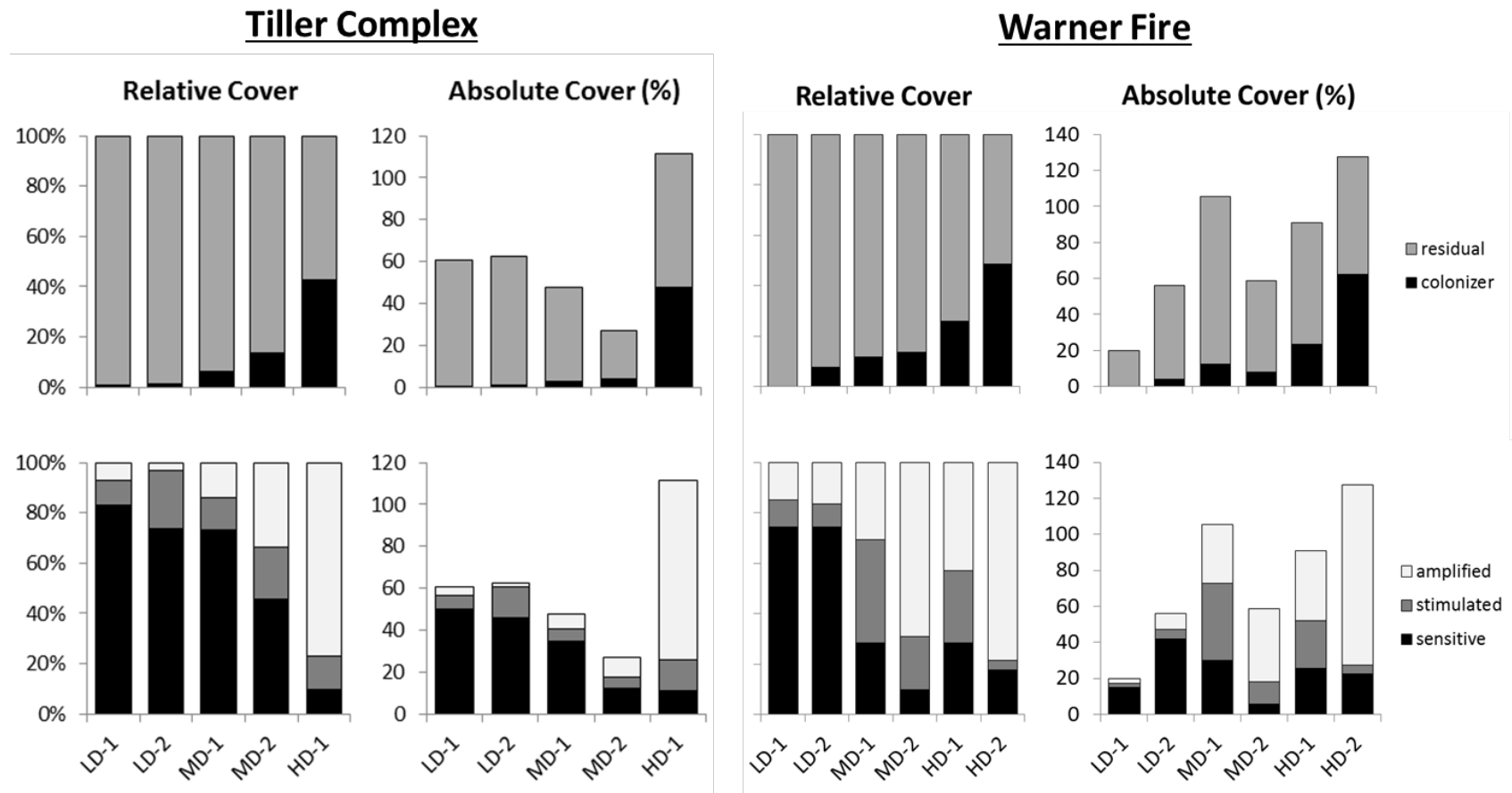


Figure 3.3: Distribution of species types and response-groups for dominant communities in the Tiller Complex and Warner Fire. Communities were classified as low, mixed or high-disturbance communities based on their species types and composition, as well as the distribution of *a priori* severity class plots included in the community.

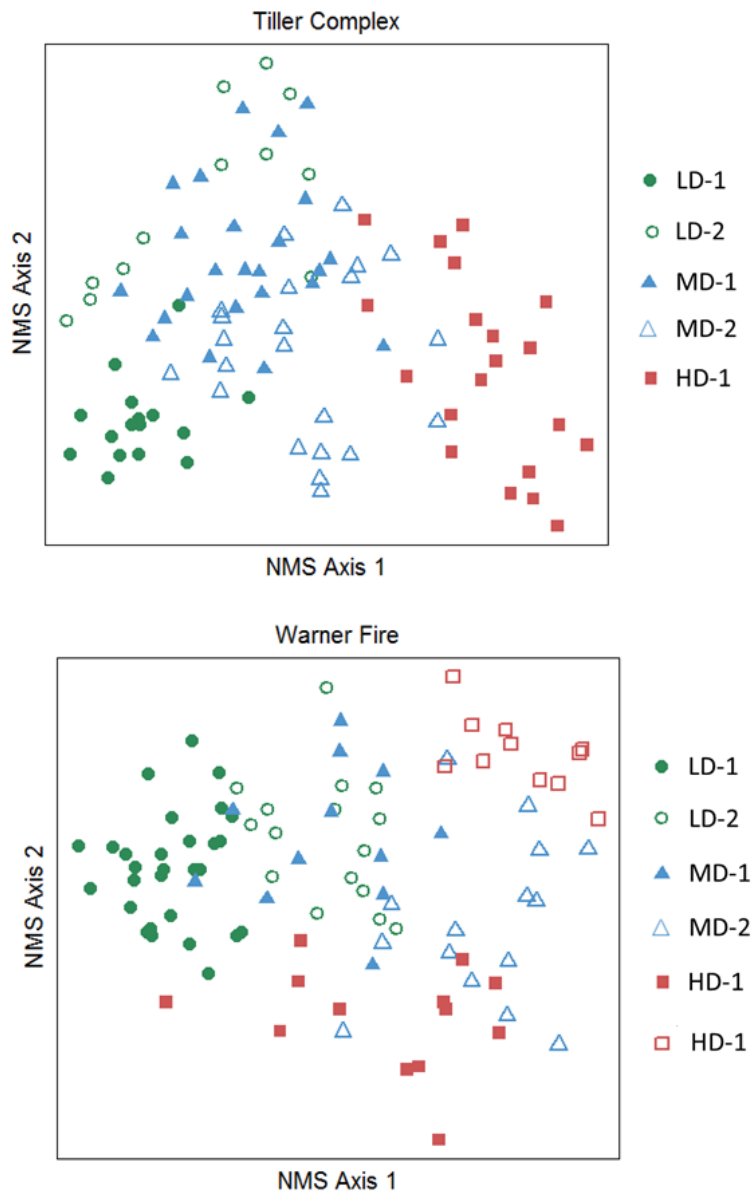


Figure 3.4: Depiction of vegetation communities along axes 1 and 2, of a 3-dimensional solution, from non-metric multidimensional scaling. Axis 1 dominantly represents the sampled disturbance severity gradient, with increasing severity from left to right, for both fire sites. Axis 2 was most closely associated with elevation for both fire sites.

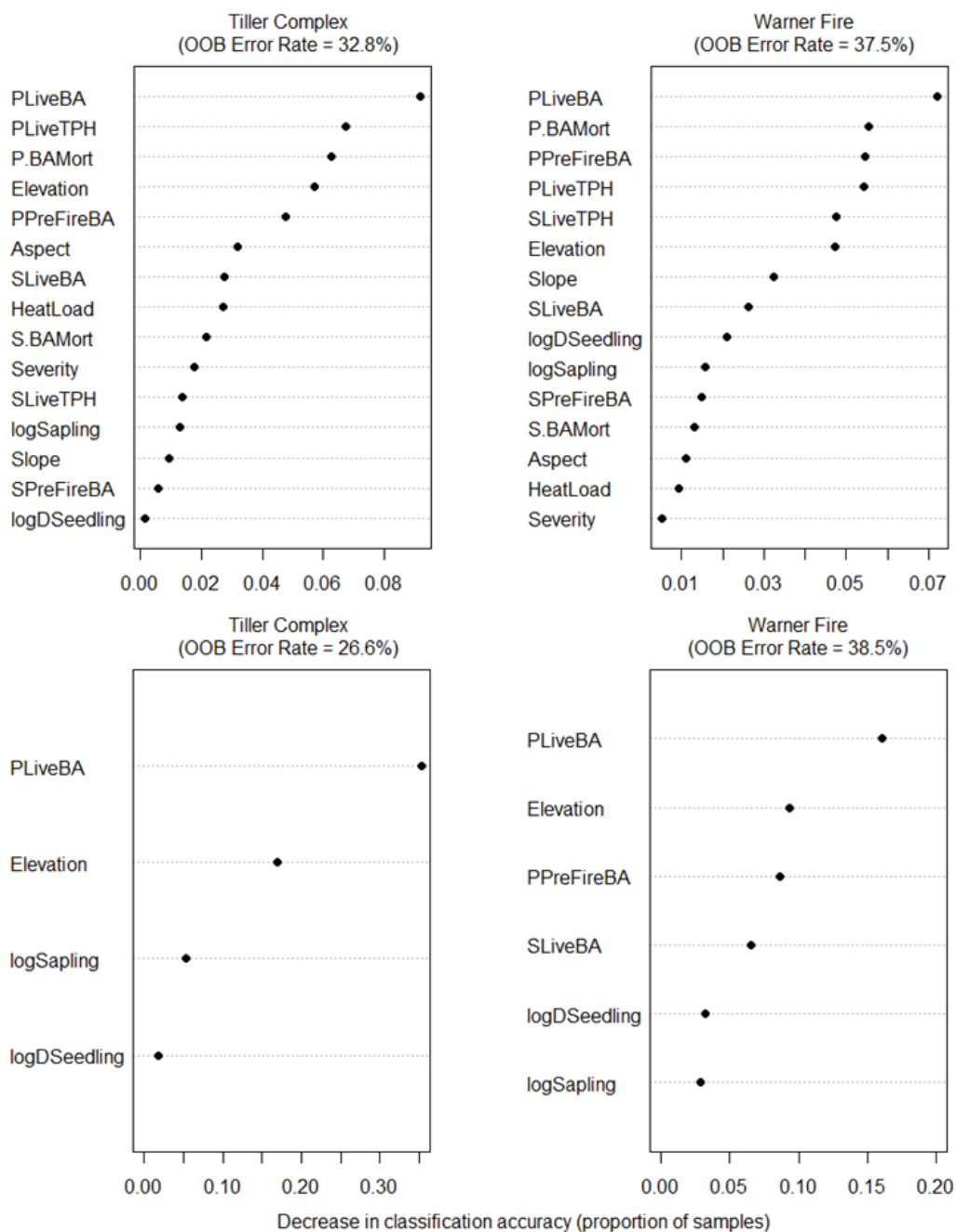


Figure 3.5: Ranked biophysical factors influencing vegetation communities by their importance measure estimated from the ensemble model random forest. The graphs on the top depict all biophysical factors considered in this analysis and those on the bottom depict the dominant factors determined using a manual stepwise selection procedure where the out-of-bag classification error rate was either reduced or remained within 1% of our initial estimate.

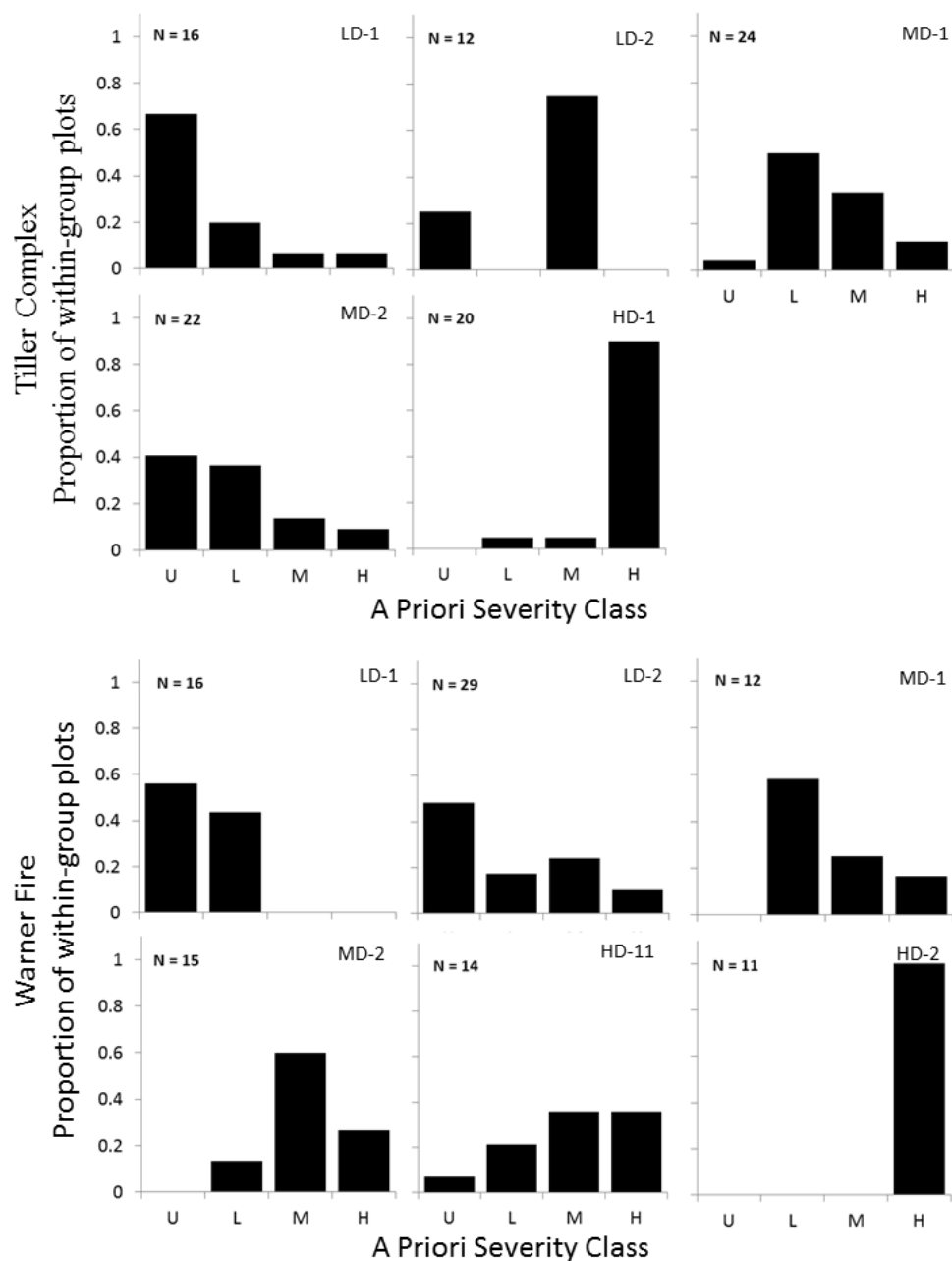


Figure 3.6: Distribution of a priori disturbance severity plots within each vegetation community for the Tiller Complex and Warner Fire. U = unburned, L = low-severity fire, M = moderate-severity fire, and H= high-severity fire.

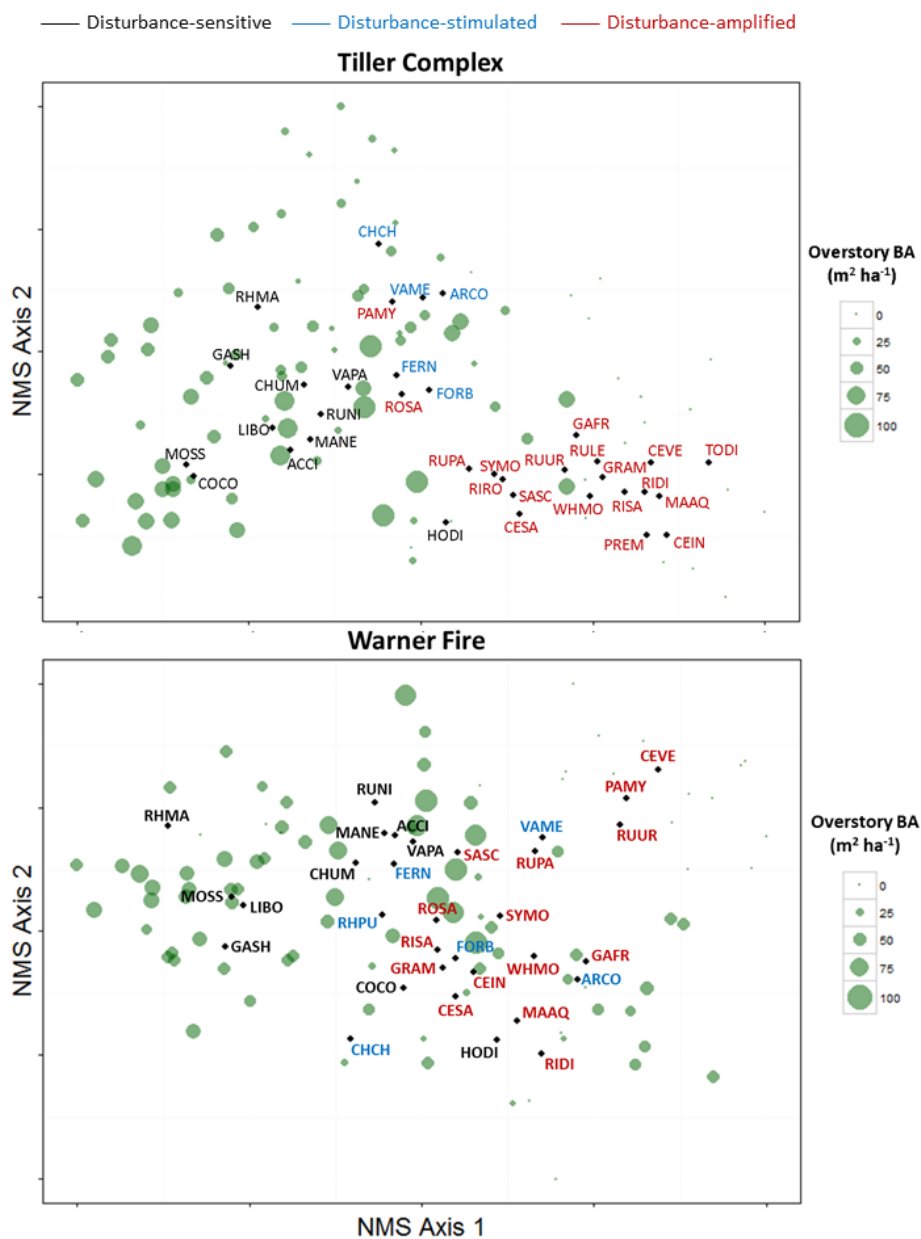


Figure 3.7: A depiction of individual species association with legacy tree basal area. Progression to the right of the graph represents increasing fire severity and a transition to early-seral vegetation communities. Disturbance-sensitive (black lettering), disturbance-stimulated (blue lettering) and disturbance-amplified (red lettering) species are displayed.

Tables

Table 3.1: A list of environmental variables included in our analysis investigating the dominant factors influencing shrub community structure across a mixed-severity fire gradient.

Variable	Definition	Units	Intended Gradient Captured by this Variable
Elevation	Altitude at plot center	meters	Elevation can be considered a proxy for water balance and temperature differences
Slope	Slope at plot center	degrees	Water drainage, soil depth, heat exposure.
Aspect	Dominant azimuth of the direction the plot was facing.	azimuth	Heat exposure, water balance
HeatLoad	Composite index capturing solar heating as a function of slope, aspect and latitude	unitless	Heat exposure, water balance
Severity	A priori severity class determined from dNBR estimates and MTBS classification thresholds	classes 1-5	Disturbance gradient
PPreFireBA	Reconstructed pre-fire plot-level basal area	m ² ha ⁻¹	Pre-disturbance overstory competition with vegetation community at hectare scale
PLiveBA	Plot-level legacy tree basal area	m ² ha ⁻¹	Post-disturbance overstory competition with vegetation community at hectare scale
PLiveTPH	Plot-level legacy tree abundance	# ha ⁻¹	Post-disturbance overstory competition with vegetation community at hectare scale
P.BAMort	Plot-level basal area mortality estimated from field measurements	percent	Estimate of the release of resources previously excluded by overstory competition at hectare scale
SPreFireBA	Reconstructed pre-fire subplot-level basal area	m ² ha ⁻¹	Pre-disturbance overstory competition with vegetation community at sub-hectare scale
SLiveBA	Subplot-level legacy tree basal area	m ² ha ⁻¹	Post-disturbance overstory competition with vegetation community at sub-hectare scale
S.BAMort	Subplot-level basal area mortality estimated from field measurements	percent	Estimate of the release of resources previously excluded by overstory competition at sub-hectare scale
logDSeeding	Abundance of dominant seedlings (seedlings >1.5 m height)	# ha ⁻¹ (log scale)	Competition effect of regenerating trees on understory shrub community at subplots
logSapling	Abundance of saplings (trees 2.54 - 10 cm DBH)	# ha ⁻¹ (log scale)	Competition effect of regenerating trees on understory shrub community at subplots

Table 3.2: Plot-level forest structural attributes for *a priori* disturbance severity classes for the Tiller Complex and Warner Fires.

<i>A Priori</i> Severity Classes by Fire Site							
Attribute	Unburned	Tiller Complex			Warner Fire		
		Low	Moderate	High	Low	Moderate	High
Reconstructed tree basal area (m ² ha ⁻¹)	69.2 (14.0) ^a	69.4 (13.9) ^{a,b}	57.4 (12.7) ^b	51.2 (7.2) ^b	75.2 (23.8) ^a	77.1 (18.6) ^a	67.2 (11.4) ^a
Reconstructed tree density (trees ha ⁻¹)	721.8 (216.4) ^a	738.4 (216.5) ^{b,a}	1306.9 (912.8) ^{a,**}	444.4 (254.3) ^b	364.7 (143.8) ^b	369.7 (246.8) ^b	228.2 (100.0) ^b
Percent fire mortality (BA)	NA	36.4 (8.5) ^a	50.3 (12.6) ^{b,a*}	95.0 (9.4) ^c	25.5 (7.8) ^a	42.7 (12.7) ^b	97.6 (4.8) ^c
Percent fire mortality (trees ha ⁻¹)	NA	70.5 (7.1) ^a	84.6 (11.9)	99.2 (1.5)	49.2 (11.5) ^a	71.5 (9.9) ^b	99.6 (0.6) ^c
Legacy tree basal area (m ² ha ⁻¹)	69.2 (14.0) ^a	42.7 (10.2) ^b	28.1 (10.4) ^b	2.3 (4.4) ^c	56.6 (23.8) ^a	44.0 (12.2) ^{b,a}	1.3 (2.4) ^b
Legacy tree density (trees ha ⁻¹)	721.8 (216.4) ^a	217.9 (92.5) ^b	140.2 (48.3) ^{c,b}	4.9 (10.6) ^{d,c}	187.3 (102.6) ^b	113.8 (97.2) ^b	1.3 (2.1) ^b
Legacy tree canopy base height (m)	8.0 (2.3) ^a	9.2 (2.3) ^a	12.4 (7.4) ^a	27.2 ^{b*}	24.2 (5.0) ^b	24.6 (5.0) ^b	29.0 ^{b*}
Legacy tree quadratic mean diameter (cm)	35.9 (6.8) ^a	52.1 (10.1) ^a	52.5 (18.0) ^a	91.7 ^{b*}	65.0 (11.0) ^b	81.9 (21.4) ^b	109.1 ^{c*}
Snag basal area (m ² ha ⁻¹)	9.0 (3.9) ^a	24.8 (8.2) ^b	28.4 (9.4) ^b	48.4 (9.4) ^c	18.1 (6.2) ^a	32.9 (13.2) ^b	65.6 (12.9) ^c
Snag density (trees ha ⁻¹)	102.2 (50.6) ^a	514.3 (145.0) ^{a,b}	1165.7 (892.2) ^{b,**}	439.2 (248.7) ^{a,b}	169.2 (70.8) ^a	252.4 (156.5) ^a	226.3 (99.2) ^a
Elevation (m)	774 - 1246	917-1174	938-1257	801-1183	764-1021	776-1308	1056-1301
Slope (degrees)	19.3 (3.9)	20.2 (1.1)	20.6 (6.9)	21.3 (3.7)	23.5 (6.5)	19.1 (6.4)	17.4 (3.0)
Heat load	0.90 (0.08)	0.78 (0.12)	0.89 (0.13)	0.86 (0.12)	0.98 (0.04)	0.99 (0.02)	0.97 (0.02)
Dominant seedlings - log scale (trees ha ⁻¹)	1.9 (2.6)	0.8 (1.9)	0.0	2.8 (2.7)	2.9 (3.6)	6.2 (2.9)	5.9 (3.0)
Saplings - log scale (trees ha ⁻¹)	5.7 (0.9)	0.4 (1.4)	0.5 (1.5)	1.8 (2.6)	1.9 (2.9)	4.3 (3.3)	7.3 (1.2)

*Estimated for live trees only. ** Includes two plots with a high abundance of <10 cm snags that skew these estimates.

Table 3.3: Species list identified as residual or colonizers following the fire, as well as their relative abundance response type to a mixed-severity fire gradient.

Species/functional group	Common name	Code	Type	Response Type (relative abundance)
<i>Ceanothus integerrimus</i>	deer brush	CEIN	colonizer	amplified
<i>Ceanothus sanguineus</i>	redstem ceanothus	CESA	colonizer	amplified
<i>Ceanothus velutinus</i>	snowbrush	CEVE	colonizer	amplified
<i>Garrya fremontii</i>	silk tassel	GAFR	colonizer	amplified
Graminoids	functional group	GRAM	residual	amplified
<i>Mahonia aquifolium</i>	Oregon-grape	MAAQ	residual	amplified
<i>Paxistima myrsinites</i>	Oregon boxleaf	PAMY	residual	amplified
<i>Prunus emarginata</i>	bitter cherry	PREM	colonizer	amplified
<i>Ribes divaricatum</i>	coast black gooseberry	RIDI	colonizer	amplified
<i>Ribes roezlii</i>	Sierra gooseberry	RIRO	colonizer	amplified
<i>Ribes sanguineum</i>	red-flowering currant	RISA	colonizer	amplified
<i>Rosa</i> spp.	rose species	ROSA	residual	amplified
<i>Rubus leucodermis</i>	blackcap raspberry	RULE	colonizer	amplified
<i>Rubus parviflorus</i>	thimbleberry	RUPA	residual	amplified
<i>Rubus ursinus</i>	trailing-blackberry	RUUR	residual	amplified
<i>Salix scouleriana</i>	Scouler's willow	SASC	colonizer	amplified
<i>Symphoricarpos mollis</i>	trailing snowberry	SYMO	residual	amplified
<i>Toxicodendron diversilobum</i>	poison oak	TODI	colonizer	amplified
<i>Whipplea modesta</i>	whipplevine	WHMO	residual	amplified
<i>Acer circinatum</i>	vine maple	ACCI	residual	sensitive
<i>Chimaphila umbellata</i>	prince's pine	CHUM	residual	sensitive
<i>Corylus cornuta</i>	beaked hazel	COCO	residual	sensitive
<i>Gaultheria shallon</i>	salal	GASH	residual	sensitive
<i>Linnaea borealis</i>	twinline	LIBO	residual	sensitive
<i>Mahonia nervosa</i>	drawf Oregon-grape	MANE	residual	sensitive
Moss	functional group	MOSS	residual	sensitive
<i>Rhododendron macrophyllum</i>	Pacific rhododendron	RHMA	residual	sensitive
<i>Rubus nivalis</i>	snow raspberry	RUNI	residual	sensitive
<i>Vaccinium parvifolium</i>	red huckleberry	VAPA	residual	sensitive
<i>Arctostaphylos columbiana</i>	hairy manzanita	ARCO	colonizer	stimulated
<i>Chrysolepis chrysophylla</i>	chinkapin	CHCH	residual	stimulated
Ferns	functional group	FERN	residual	stimulated
Forbs	functional group	FORB	residual	stimulated
<i>Holodiscus discolor</i>	ceano spray	HODI	residual	stimulated
<i>Rhamnus purshiana</i>	cascara	RHPU	colonizer	stimulated
<i>Vaccinium membranaceum</i>	thinleaf huckleberry	VAME	colonizer	stimulated
Rare species (occurred in <5% of plots)				Most abundant severity class
<i>Acer glabrum</i>	Douglas maple	ACGL	colonizer	high-severity
<i>Amelanchier alnifolia</i>	saskatoon (Pacific serviceberry)	AMAL	colonizer	high-severity
<i>Chimaphila menziesii</i>	little prince's pine	CHME	colonizer	low-severity
<i>Cytisus scoparius</i>	scotch broom	CYSC	colonizer	moderate-severity
<i>Gaultheria ovatifolia</i>	Western teaberry	GAOV	colonizer	high-severity
<i>Lonicera ciliosa</i>	orange honeysuckle	LOCI	colonizer	moderate-severity
<i>Oemleria cerasiformis</i>	Indian-plum	OECE	residual	unburned
<i>Philadelphus lewisii</i>	mock-orange	PHLE	colonizer	moderate-severity
<i>Sambucus nigra</i>	black elderberry	SANI	colonizer	high-severity
<i>Sambucus racemosa</i>	red elderberry	SARA	colonizer	high-severity

Table 3.4: Pair-wise comparisons of vegetation groups within the Tiller Complex from a multi-response permutation procedure; A-statistics ≥ 0.10 are typically considered to have significant group separation.

Group			T-Statistic	A-Statistic	p-value
Comparison					
LD-1	vs.	LD-2	-12.931	0.216	<0.001
LD-1	vs.	MD-1	-17.038	0.148	<0.001
LD-1	vs.	MD-2	-17.371	0.156	<0.001
LD-1	vs.	HD-1	-19.782	0.217	<0.001
LD-2	vs.	MD-1	-11.656	0.103	<0.001
LD-2	vs.	MD-2	-16.105	0.154	<0.001
LD-2	vs.	HD-1	-15.402	0.180	<0.001
MD-1	vs.	MD-2	-13.384	0.077	<0.001
MD-1	vs.	HD-1	-20.723	0.136	<0.001
MD-2	vs.	HD-1	-17.848	0.118	<0.001

Table 3.5: Pair-wise comparisons of vegetation communities within the Warner Fire from a multi-response permutation procedure; A-statistics ≥ 0.10 are typically considered to have significant group separation.

Group			T-Statistic	A-Statistic	p-value
Comparison					
LD-1	vs.	LD-2	-23.008	0.220	<0.001
LD-1	vs.	MD-1	-14.281	0.177	<0.001
LD-1	vs.	MD-2	-14.213	0.145	<0.001
LD-1	vs.	HD-1	-14.156	0.152	<0.001
LD-1	vs.	HD-2	-16.130	0.296	<0.001
LD-2	vs.	MD-1	-15.676	0.142	<0.001
LD-2	vs.	MD-2	-23.062	0.205	<0.001
LD-2	vs.	HD-1	-18.784	0.167	<0.001
LD-2	vs.	HD-2	-23.177	0.302	<0.001
MD-1	vs.	MD-2	-10.485	0.112	<0.001
MD-1	vs.	HD-1	-10.164	0.111	<0.001
MD-1	vs.	HD-2	-12.949	0.259	<0.001
MD-2	vs.	HD-1	-7.063	0.059	<0.001
MD-2	vs.	HD-2	-13.647	0.201	<0.001
HD-1	vs.	HD-2	-14.154	0.240	<0.001

CHAPTER 4: MIXED-SEVERITY FIRE AS A DRIVER OF REGENERATION DYNAMICS IN PSEUDOTSUGA FORESTS OF OREGON'S CENTRAL CASCADES, USA

Abstract

Mixed-severity fire regimes are increasingly recognized in *Pseudotsuga* forests of the Pacific Northwest, yet regeneration response to mixed-severity fires has not been characterized. Therefore, we sampled forest structure (1000 m² circular plots) and regeneration dynamics (100 m² plots) at 168 collocated plots stratified across unburned, low, moderate and high-severity conditions 10 years (Tiller Complex) and 22 years (Warner Fire) post-fire. The largest marginal increase in tree mortality (stems ha⁻¹) occurred between unburned and low-severity fires, given preferential mortality of small trees and shade-tolerant species, but basal area mortality had the largest marginal increase moving from moderate to high-severity. Pairwise comparisons of legacy tree basal area between low and moderate-severity weren't as significant as other comparisons, but did capture a gradient of increasing fire effects. Quadratic mean diameter and canopy base height were positively correlated with fire severity as incrementally larger trees were killed and canopy ascension followed. Regeneration density increased regardless of severity, relative to unburned forests (median density of 1,384 trees ha⁻¹), but the highest median density (16,220 trees ha⁻¹) followed low-severity fire at the Tiller Complex and moderate-severity fire (14,472 trees ha⁻¹) at Warner Fire. Plot-level average species richness was highest following these same fire severity classes, supporting the Intermediate Disturbance Hypothesis. Statistically distinct regeneration communities occurred across the fire severity gradient at both fire sites. The relative abundance of shade-tolerant tree species decreased as fire severity increased, except for a divergent response following stand-initiation at the Warner Fire. While divergent successional pathways were evident within a couple decades following stand-initiation, low or moderate-severity fires also modified successional trajectories and may be the most functionally important disturbance magnitude because it has the greatest potential to increase compositional and structural diversity. Incorporating mixed-severity fire effects into landscape management of *Pseudotsuga* forests could increase structural complexity at stand and landscape-scales.

Introduction

Structural complexity is an important ecological attribute of forested ecosystems (Hansen et al., 1991), and is often considered a surrogate for estimating biodiversity (McElhinny et al., 2006) and evaluating ecosystem services. Structural complexity is a measure of the composition, relative abundance, and vertical and horizontal distribution of various forest structures such as trees, snags and logs (McElhinny et al., 2005). The three-dimensional structure of forests is a reflection of disturbance history, forest development, and the dynamics of dead biological legacies (Franklin and Spies, 1991, Harmon et al., 1986, Spies and Franklin, 1988). Disturbances span multiple scales, from canopy gaps formed by individual or group tree mortality (Franklin and Van Pelt, 2004, Whitmore, 1989), to broader-scale wind and wildfire effects (Johnson and Miyanishi, 2007). Vegetation response to disturbances depends on their autecological traits and life history strategies (Halpern, 1989). The cumulative effects of natural disturbances diversify horizontal and vertical structure, increasing in complexity as forests transition to late seral stages (Franklin et al., 2002).

Wildfires are a dominant disturbance agent in forested ecosystems globally (Bond and Keeley, 2005). The long-term cumulative effects of wildfires are characterized by an ecosystem's fire regime, which quantifies the spatial and temporal attributes of historical fires, as well as their magnitude of effects (Sugihara et al., 2006). Fire frequency and severity (typically tree mortality) tend to be inversely related and are the most common attributes used to characterize fire regimes (Wright and Heinzelman, 1973). This classification leads to two dominant structural development pathways: 1) chronic-disturbance (high-frequency, low-severity) that mediates forest density and composition (Heyerdahl et al., 2001); and 2) episodic-disturbance (low-frequency, high-severity) where stand initiation is followed by a gradual transition to structurally complex, late-seral forests (Franklin et al., 2002, Zenner, 2005). These pathways don't account for mixed-severity fire, also common in many forested ecosystems, which exert a gradient in the magnitude of fire effects (Perry et al., 2011, Halofsky et al., 2011).

Douglas-fir/western hemlock forests (*Pseudotsuga menziesii*/*Tsuga heterophylla*, hereto referred to as *Pseudotsuga* forests) of the Pacific Northwest (PNW) are typically characterized as having an episodic-disturbance regime of low-frequency, high-severity fire (Agee, 1993). This disturbance regime has been challenged by recent fire-history and age-structure studies in

western Oregon's central Cascades that showed mean fire return intervals of 95-150 years and effects spanning a disturbance gradient from low to high-severity (Means, 1982, Morrison and Swanson, 1990, Weisberg, 2004). Non-stand replacing portions of these fires accounted for >70% of the burned area in at least two watersheds in Oregon's western Cascades during the 19th century (Morrison and Swanson, 1990), with similar results occurring in the more recent 1991 Warner Fire (Kushla and Ripple, 1997). Mixed-severity fires may be more common and ecologically important in these forests than previously suggested, contributing to the development of structural complexity indicative of old-growth forests in the PNW (Tepley et al., 2013).

Structural complexity may develop early in succession if forests are "born complex" (Donato et al., 2011); a condition that can persist for at least several decades following stand initiation (Halpern et al., 2013). The spatial variation and arrangement of regenerating trees in *Pseudotsuga* forests may occur in relatively low densities, followed by rapid tree growth and stands that do not transition through a competitive exclusion/biomass accumulation stage (Tappeiner et al., 1997, Poage and Tappeiner, 2002). Alternatively, these forests may develop from high densities of regenerating trees (Winter et al., 2000) that transition through stem exclusion on their path to structural complexity (Franklin et al., 2002). These divergent successional trajectories have been observed following stand-initiation in this and other forest types (Harvey and Holzman, 2014), but do not explicitly account for the lower-severity conditions common following mixed-severity fire (Tepley et al., 2014). The degree to which mixed-severity fire influences regeneration dynamics, as well its implications on successional development, remain largely unknown at this time.

In this study, we examine tree regeneration dynamics following mixed-severity fires in *Pseudotsuga* dominated forests of western Oregon's central Cascades. We had a unique opportunity to investigate regeneration dynamics following mixed-severity fire for several reasons. First, multiple fires burned within these forests in 2002 and earlier, allowing us to investigate a longer regeneration period than the initial flush immediately post-fire (Donato et al., 2009). Second, new satellite derived fire severity maps are available for these fires, so we can stratify sampling to explicitly capture a disturbance gradient. Lastly, mixed-severity fire effects have not been explored extensively in this forest type, so our results are timely for expanding our understanding of the development of these forests over time. Specifically, we

asked the following questions: (1) how does the magnitude of disturbance influence tree regeneration density, and (2) how does the magnitude of disturbance influence the composition of regenerating trees?

Methods

Study Area

Pseudotsuga forests of western Oregon's central Cascades are dominant from ~500 – 1300 m elevation, extending from the State of Washington to the South Umpqua River Watershed (Franklin and Dyrness, 1988). We sampled fires in this forest type between the Middle Fork of the Willamette River Watershed near Oakridge, OR (43° 4' 1.6032" N), and south straddling the divide of the North and South Umpqua River watersheds (43° 43' 36.8688" N). There is a north-south climatic gradient such that average temperatures increase and moisture decreases from north to south, so our sampling captured a productivity gradient in this forest type. The climate is typical of regional maritime conditions with cool, wet winters and warm, dry summers. Average annual precipitation ranges from 1339 – 1761 mm per annum, with ~75% falling from November through April. Average maximum temperatures ranged from 27.5 °C in August, to 4.3 °C in December, and average minimum temperatures ranged from 9.1 °C in August to -2.8 °C in December (Daly et al., 2002, www.prismclimate.org). Douglas-fir, sugar pine (*Pinus lambertiana*) and incense-cedar (*Calocedrus decurrens*) were common fire-tolerant tree species encountered in our study area. Western hemlock, western redcedar (*Thuja plicata*), white fir (*Abies concolor*), grand fir (*Abies grandis*), and Pacific yew (*Taxus brevifolia*) were common fire-intolerant tree species. Hardwoods were dominated by giant chinkapin (*Castanopsis chrysolepsis*), bigleaf maple (*Acer macrophyllum*), Pacific madrone (*Arbutus menziesii*) and Pacific dogwood (*Cornus nuttallii*). The potential vegetation type transitions to Pacific silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) at higher elevations, with climax Douglas-fir, Oregon white oak (*Quercus garryana*) and ponderosa pine (*Pinus ponderosa*) forests occurring at lower elevations and more southerly latitudes.

Sampling Design

Several large fires occurred within our study area during the past several decades, accounting for a total of 76,746 ha burned between 1987 and 2014 (Figure 4.1). Approximately 8,782 ha burned in 1987 and 1988, followed by 9,037 ha in 1996, 36,437 ha in 2002, and 20,049 ha burned in 2008 - 2009. The most recent fire, Deception Creek Complex, burned an additional 2,441 ha near Oakridge, OR in 2014. We concentrated our sampling within the 2002 Tiller Complex (10 years post-fire) and the 1991 Warner Fire (22 years post-fire), which burned 36,347 ha and 3,723 ha, respectively.

Sampling was constrained to mature/old-growth (M/OG) *Pseudotsuga* forests without evidence of direct anthropogenic disturbance. We randomly located six clusters of four forest structure and regeneration plots (24 sample units), in each of three fire-severity classes (i.e. low, moderate, high), at both the Tiller Complex and Warner Fire. An additional set of plot clusters were placed in unburned forests distributed across our study area as our reference condition (Figure 4.1). Plot clusters were randomly selected using equal probability point sampling in ArcMap 10.0 (ESRI, 2011), with clusters constrained to be at least 400 m apart within a severity class. Fire severity was determined from maps derived by the Monitoring Trends in Burn Severity program (MTBS, 2011), and were intended to capture <25% basal area mortality (low-severity), 25 – 75% basal area mortality (moderate-severity), and >75% basal area mortality (high-severity). Only the south slope of the Warner Fire was sampled because climatic conditions, combined with the north aspect, developed much wetter forests (e.g., Pacific silver fir was often dominant) we considered different from our intended study area.

Forest Structural Attributes

We sampled legacy trees and snags in nested, fixed radius plots. Standing and fallen trees or snags 2.54 – 10.0 cm diameter at breast height (DBH) were sampled in 100 m² circular plots, >10.0 – 40.0 cm DBH within 250 m² circular plots, and > 40 cm DBH at 1000 m² circular plots. We recorded tree species, DBH (cm), total height (m), canopy base height (m), and noted whether a tree regenerated before or after the fire. Post-fire regenerating trees >2.54 cm DBH were considered saplings. We recorded snag species, DBH and height, and then separated pre-fire snags from fire created snags when >5% of the bole sapwood was consumed or turned to

charcoal. We reconstructed pre-fire live basal area and stems per hectare, and quantified post-fire tree basal area ($\text{m}^2 \text{ha}^{-1}$), density (ha^{-1}), quadratic mean diameter (QMD) in centimeters, and canopy base height (CBH) in meters. Estimates were made at the plot-level to assess the influence of forest structure on regeneration response in relatively small patches. We used linear mixed-effects models to test differences among groups to account for any positive correlations in residuals resulting from our clustered plot design. All pair-wise comparisons were adjusted for multiple comparisons using Tukey corrections in multcomp package of R (Torsten et al., 2008).

Regeneration

Tree seedlings were sampled at 100 m^2 ($10 \times 10 \text{ m}$) plots centered on the forest structure plots. Each plot was partitioned into quadrants and seedlings (i.e., any regenerating tree species $<2.54 \text{ cm}$ DBH) were tallied by species in the following height classes: 1 – 50 cm, >50 – 150 cm, >150 cm. Regenerating trees $>2.54 \text{ cm}$ DBH were considered saplings in burned plots and sampled according to our legacy tree protocol. Live trees $\leq 10 \text{ cm}$ DBH in unburned plots were considered saplings for analyses. White fir transitioned to grand fir along a south-to-north gradient, but we combined them as a composite species since they hybridize.

We analyzed the density of regenerating trees (number ha^{-1}) by fire severity class using a generalized linear mixed-effects model in R (R Development Core Team, 2008), to account for any positive correlations in residuals resulting from our clustered plot design. We analyzed the Tiller Complex and Warner Fire separately because of the difference in time-since-fire when they were sampled. We utilized a negative binomial distribution in the glmmADMB package (Fournier et al., 2012) because there was significant overdispersion using a Poisson distribution. We tested for overdispersion using the ratio of *chi*-squared to residual degrees of freedom and found no evidence of overdispersion with the negative binomial distribution (ratio = 0.58 and 0.65 for the Tiller Complex and Warner Fire, respectively). We estimated total regeneration density as a function of fire severity (i.e. unburned, low-severity, moderate-severity and high-severity) and environmental variables (see chapter 2 for complete list) in our regression analysis to investigate the drivers of post-fire regeneration response. We accounted for multiple comparisons using Tukey methods when testing for differences among groups.

We estimated the spatial distribution of regenerating trees as the frequency of occurrence within quadrants (i.e. 5 x 5 m) at each plot. This scale approximates regeneration stocking levels (i.e., 5 x 5 m, or 16 ft. spacing) typical of forest management practices in the PNW (Tappeiner et al., 2015). We sampled 96 frequency-quadrants in each fire severity class and unburned forest condition. Frequencies were calculated as the percent of quadrants occupied by a regenerating tree, and were estimated for the seven most common conifer and four hardwood tree species.

We investigated differences in regeneration diversity across our fire severity gradient using two metrics: 1) average species richness by fire severity class, and 2) compositional differences in regeneration using a Multi-Response Permutation Procedure (MRPP) based on Sorensen's (Bray-Curtis) distance measure and 5000 randomization tests, obtaining the chance-corrected within-group agreement (A-statistic) (Mielke and Berry, 2001). Abundance values were log-transformed to reduce the effects of very large values for some species and plots (McCune and Grace, 2002). We also removed rare species occurring in <5% of plots, reducing the 13 sampled tree species to seven and five at the Tiller Complex and Warner Fire, respectively. We tested for outlier plots (distance measure >2.5 standard deviations from the mean), but none were present. The same unburned plots were used for comparisons in each fire analysis.

Results

Fire Severity and Forest Structure

There were no statistically significant differences between reconstructed pre-fire basal area and forest density at an alpha <0.05 when all plots were combined. Reconstructed basal area averaged $66.5 \text{ m}^2 \text{ ha}^{-1}$ (SD = 16.4) across all plots and reconstructed mean forest density averaged $591.4 \text{ trees ha}^{-1}$ (SD = 484.9). When reconstructed estimates were separated by fire site, the Tiller Complex had statistically lower pre-fire basal area and tree densities in the moderate and high-severity classes, relative to unburned conditions. The Warner Fire didn't exhibit significant differences across the severity gradient, but estimates were consistently higher than Tiller Complex due to differences in productivity and disturbance histories (Table

4.1). Combined, our sampling appeared to capture the variation in M/OG conditions across our study area.

Post-fire tree mortality varied significantly across our sampled fire severity gradient at both fire sites. The largest marginal increase in tree mortality (stems ha^{-1}) occurred between unburned and low-severity fires, given small tree mortality, but basal area mortality had the largest marginal increase moving from moderate to high-severity plots as incrementally larger trees were killed. Only 31% of all our high-severity plots retained legacy trees, ranging from 76.6% - 97.4% basal area mortality. Live structural attributes also varied across our fire severity gradient at both fire sites. Pairwise comparisons of legacy tree basal area between the low and moderate-severity classes weren't statistically different at an $\alpha < 0.05$, but did capture a gradient of increasing fire effects. Quadratic mean diameter and canopy base height were positively correlated with fire severity, as incrementally larger trees were killed and canopy ascension followed (Table 4.1).

Regeneration

Wildfire occurrence increased regeneration density regardless of severity, but was highest following low or moderate-severity fire (Table 4.2, Figure 4.2). The highest median density of regenerating trees (16,220 trees ha^{-1}) was observed following low-severity fire at the Tiller Complex, and following moderate-severity fire at the Warner Fire (14,472 trees ha^{-1}). These estimates were much greater than median densities in unburned forests (1,387 trees ha^{-1}). Regeneration abundance was not always statistically different by severity class, but the non-linear trend across the fire severity gradient was evident at both fire sites. No environmental variables were statistically correlated with regeneration abundance in our sample, after accounting for the effects of fire severity.

The frequency of plots with regenerating trees was dependent on species and fire severity (Figure 4.3). The unburned forest had the highest percent (39%) of quadrants without any regenerating trees. The Tiller Complex lacked regeneration in 2%, 5% and 27% of the quadrants 10 years after low, moderate and high-severity fire, respectively. At the Warner Fire, regenerating trees were not present in 19%, 2% and 16% of the quadrants following low, moderate and high-severity fire, respectively. When we considered a larger spatial scale (i.e., 10 x 10 m), only three unburned plots and two high-severity plots at the Tiller Complex lacked

regenerating trees. This suggests regeneration gaps are typically smaller than 25 m², but sometimes increase to 100 m² or greater. The seven most common conifer species typically occurred most frequently following low and moderate-severity fire at both fire sites, although some shade-tolerant species were more frequent in unburned forests. Overall, Douglas-fir was the most frequently encountered species at both fire sites (Figure 4.3).

Average species richness was highest following low or moderate-severity fire (Figure 4.4). All but two of the 13 regenerating tree species sampled were present in both fires. The exceptions were ponderosa pine, only observed in five plots (moderate and high-severity plots only) at the Tiller Complex, and Pacific silver fir that was only observed at three plots (high-severity plots only) in the Warner Fire. Pacific madrone, bigleaf maple, giant chinkapin and Pacific dogwood were commonly encountered hardwoods, but in much lower abundance than conifers. Douglas-fir, western hemlock, incense-cedar, western redcedar, Pacific yew, sugar pine and grand/white fir were commonly encountered conifer species.

Regeneration communities varied significantly across the fire severity gradient within both fires. The relative abundance of shade-tolerant tree species typically decreased as fire severity increased, except for a divergent response following stand-initiation at the Warner Fire (Figure 4.5). Therefore, we separated high-severity plots at the Warner Fire into two different groups (high-dry and high-wet) based on high densities of regenerating western hemlock trees. At the Tiller Complex, plots within our *a priori* fire severity classes were more closely associated than expected by chance (combined A = 0.209 p-value <0.001), with most severity classes significantly separated in multi-dimensional space (Table 4.3). The regeneration communities within the moderate and high-severity plots were more similar than other severity classes within this fire. Similarly, plots within our *a priori* fire severity class were more closely associated than expected by chance (combined A = 0.203 p-value <0.001), with most pairwise comparisons suggesting significant separation in multi-dimensional space (Table 4.3). The exceptions were that the low-severity group was not significantly different than the moderate-severity or high-dry groups. In the end, the two high-severity groups had the greatest dissimilarity. The relative abundance of shade-tolerant species decreased with increasing fire severity, as observed in the Tiller Complex, except for the high-severity, wet plots, where western hemlock was highly abundant.

Discussion

The abundance of post-fire legacy trees has greater influence on both regeneration density and diversity than the magnitude of mortality (Figures 2), even though disturbance severity is typically quantified by the amount or proportion of live biomass loss (Keeley, 2009). We observed this effect in our regeneration response even though we limited the potential variation in pre-fire forest density by only sampling M/OG forests. The highest density of regenerating trees followed low or moderate-severity fire with legacy tree basal area averaging 42.7 and 44.0 m² ha⁻¹ at the Tiller Complex and Warner Fire, respectively. These conditions occurred in different burn severity classes largely dependent on pre-fire forest density, although mortality exceeded expected losses at both fire sites. The result was overall mortality being more similar to the low end of moderate-severity, especially at the drier Tiller Complex (Table 4.1). Misclassification by the remote sensing techniques used to estimate fire severity (Miller and Thode, 2007) partially explains the higher mortality levels observed, but delayed mortality also contributes to these conditions. For example, approximately 55% of all trees living one year after burning died within 14 years, with higher severities experiencing a greater proportion of delayed mortality (Brown et al., 2013).

Legacy trees form the foundation for seed source and micro-climate conditions that drive future regeneration (Seidl et al., 2014), not the amount of mortality. Correlations between fire severity and regeneration response would differ substantially from our estimates when younger forests, with lower pre-fire basal area, burn. For example, 20% mortality (low-severity) in a forest with 20 m² ha⁻¹ tree basal area would likely induce a post-disturbance regeneration response more similar to those observed following high-severity fire, assuming seed sources were available. Quantifying the abundance of live biological legacies will therefore have greater predictive capacity for post-disturbance regeneration density and diversity, and should be emphasized when projecting future forest dynamics.

Regeneration Density

Pseudotsuga forests have resilience mechanisms that facilitate the rapid establishment of the next generation forest (Buma and Wessman, 2012). These resilience mechanisms persist as dormant biological legacies in the form of canopy seedbanks and basal or burl buds. Canopy

seedbanks are likely present on both trees and snags following mixed-severity fire, but legacy trees will produce significantly more seed during the protracted regeneration period of these forests (Tepley et al., 2014). A very abundant cone crop was reported in 1991 before the Warner Fire occurred, and since this fire burned in fall, seed production had likely reached its maximum abundance before the fire (Larson and Franklin, 2005). We observed similar regeneration densities at the Tiller Complex so an abundant cone crop may not be a significant determinant of post-fire regeneration density, unless one was produced in 2002 as well. Vegetative reproduction is an important regeneration strategy for several species of hardwood trees, so they were frequently encountered post-fire (Figure 4.6). Since hardwood trees are important components of early-seral habitats (Swanson et al., 2011), vegetative reproduction strategies are also important resilience mechanisms in these ecosystems.

The distribution of live and dead biological legacies, and their contribution to the post-fire seed bank, is a function of fire intensity interacting with pre-fire forest composition and tree diameter distributions. Individual species vary in their capacity to resist death by fire, increasing with increasing DBH (except western hemlock) as bark thickens and photosynthetic structures ascend (Dunn and Bailey, *in review*-Chapter 1). Canopy seedbanks from legacy trees and snags can lead to rapid regeneration immediately following fire in these forests (Brown et al., 2013). Snag seedbanks likely diminish within one or two years, and therefore legacy or offsite trees dominate seed sources relatively quickly following wildfire. Regeneration densities continued to increase in smaller height classes for at least ten years post-fire (Figure 4.5), suggesting legacy trees and offsite seed sources contribute more to forest establishment.

Regeneration cohorts in these ecosystems may be protracted over several decades post-disturbance (Freund et al., 2013, Tepley et al., 2014). We observed continued regeneration during the first two decades following mixed-severity fire. Assuming height is a surrogate for the age of regenerating trees, regeneration success was beginning to decline by 22 years post-fire (Figure 4.5). Regeneration density by height class exhibited a reverse-J shape, suggesting regenerating trees were still successfully germinating after 10 years of post-fire development. After 22 years of post-fire development, regeneration densities were highest in the 50 – 150 cm or >150 cm height classes, resulting in a hump-shaped size-class distribution consistent with an even-aged cohort following a stand-initiating disturbance (Tappeiner et al., 2015). These trends were consistent across all fire-severity classes except at the high-severity dry sites in the Warner

Fire, where density was greatest in the tallest height class (Figure 4.5). Therefore, our results also suggest tree regeneration can be protracted for at least two decades, but likely longer as lower density sites fill in, and overstory tree mortality continues (Van Mantgem et al., 2009).

Regeneration Composition

Species richness was highest following low or moderate-severity fire (Figure 4.4), supporting the Intermediate Disturbance Hypothesis (IDH) that theorizes intermediate levels of disturbance maximize species diversity (Connell, 1978, Roxburgh et al., 2004, Wilkinson, 1999). We observed the effects of both competitive exclusion and disturbance-induced local extinction at the low and high ends of our sampled disturbance gradient, respectively. This response appears to be driven by interactions among fire intensity, individual species autecological traits, and the resilience mechanisms described above. The selective pressure of mixed-severity fire may have developed various adaptive traits in trees of *Pseudotsuga* forests, promoting either their persistence or dominance following disturbance of varying magnitudes. Therefore, mixed-severity fire is fundamental to this ecosystem, especially with regards to the promotion and maintenance of tree species and structural diversity that was highest following the most common (i.e., covering the most fire area) disturbance magnitude of fires occurring in these forests – low or moderate-severity fire. Further research is needed to better understand how species autecological traits developed in response to mixed-severity fire, but over long time periods this is a plausible explanation of the unexpected species mixes (e.g., incense-cedar and western redcedar as co-dominant trees, sugar pine and western hemlock) observed regularly in our study area.

Conifer species of *Pseudotsuga* forests appear to have partitioned into two dominant groups, based on shade and fire tolerance, that respond differently to the ecological pressures of disturbance and competition (Givnish, 1988). The first group was dominated by western hemlock, true fir and western redcedar. These species are shade-tolerant and can persist as sub-dominant trees under conditions that competitively exclude shade-intolerant species (Figure 4.4). All conifer species were found to be regenerating in unburned forests, but the relative abundance of shade-tolerant species was positively correlated, while shade-intolerant species were negatively correlated, with size-class (Figure 4.4). Seedlings of all species appear capable of germinating under relatively intense competitive pressure from overstory trees, but do not

successfully recruit into larger size classes unless large enough canopy gaps are created by local disturbance (Gray and Spies, 1997). Shade-tolerant species also tend to be fire-intolerant (see Chapter 1), which is largely a function of bark thickness, although crown base height and rooting depth also influence their ability to resist fire (Brown et al., 2000). Therefore, seed source availability may partially drive the declining density of regenerating shade-tolerant, fire-sensitive species, and increasing density of shade-intolerant species, following higher severity fires (Chapter 1). Soil moisture conditions also influence post-fire conifer regeneration response (Zald et al., 2008). Western hemlock has been shown to regenerate in higher densities when soil moisture offsets increased transpirational demand in the post-disturbance environment (Isaac, 1948). We observed this effect following high-severity fire at Warner Fire; when soil moisture conditions were high, the site supported a high-density of regenerating hemlock trees (Figure 4.4). Although regenerating tree species were different at these sites, they did not increase diversity since Douglas-fir and western hemlock were so abundant other species could not compete for growing resources.

Shade-intolerant conifer species have adapted to disturbance regimes by developing autecological traits that increase their resistance to fire, while also being able to thrive in environments where the microclimate has transitioned to hotter and drier conditions (Chen et al., 1999). Sugar pine is the most shade intolerant conifer species present in these forests, but Douglas-fir and incense-cedar are also moderately shade-intolerant (Brown et al., 2000). These species responded positively to increasing fire severity, out-competing shade-tolerant species for available resources. Sugar pine was rare in lower-severity conditions and may need increased fire severity to successfully regenerate (Atzet and Wheeler, 1982). Douglas-fir and incense-cedar were abundant in moderate and high-severity conditions, although Douglas-fir appears to be the most flexible and resilient species to the variable post-fire conditions created by mixed-severity fire. Regeneration was prolific following higher severity conditions, but the local extinction of many shade-tolerant conifers or hardwoods reduced species richness in these forests, at least during early forest development.

Sexual reproduction and vegetative propagation are common regeneration strategies for hardwoods in *Pseudotsuga* forests. Pacific madrone, bigleaf maple, chinkapin and Pacific dogwood were commonly encountered hardwood trees. These species were present across all fire severity classes, although they were not frequently encountered in unburned forests (Figure

4.6). Maximum observed frequency of hardwood species followed low or moderate-severity fire, probably because lower intensity fires only top-killed these trees. Therefore, dormant buds on burls or root crowns, distinct to this tree functional group, are an important regeneration strategy and contributor to post-fire species richness (Lutz and Halpern, 2006, MacDonald and Tappeiner, 2002). These hardwood species also regenerate sexually, but soil seedbanks are unlikely to survive fire. Seed dispersal by animal and wind was likely the driving factor for their presence following severe fires that killed dormant basal or burl buds (Fonda, 2001). Hardwood abundance may peak early in forest development (Halpern et al., 2013) because of successional replacement, mechanical damage from falling snags, or other causes (Lutz and Halpern, 2006), so their contribution to structural complexity changes over time.

In summary, species richness was highest following low or moderate-severity fire because of interactions among several biophysical factors. First, individuals of each conifer species can survive low or moderate-severity fire, increasing the abundance and diversity of local seed sources. Secondly, many of the hardwoods resprout following top-kill, and therefore respond well to low and moderately severe fires that do not damage belowground reproductive structures. Lastly, low or moderate-severity fire increases the horizontal diversity of legacy trees and openings, also diversifying the microclimatic conditions that benefit various species. This may arise because of the presence of shaded area versus open gaps, hydraulic lifting and redistribution by legacy trees (Brooks et al., 2002), or smaller microsite variations created by fallen snags that further ameliorate the microclimate, or become nurse logs (Harmon and Franklin, 1989), and alter vegetation response (Gray and Spies, 1997). Regardless of the biophysical factors influencing the regeneration response at these sites, low or moderate-severity fire is functionally important for maintaining the compositional diversity of dominant trees in these forests.

Successional Relationships

Pseudotsuga forests exhibit significant variability in regeneration density at stand-initiation, supporting the hypothesis that forests can exhibit variable successional trajectories at this stage (Tappeiner et al., 1997; Donato et al., 2011). Densities were more variable at drier sites, like those found at the Tiller Complex or at dry sites in the Warner Fire. For example, over 25% of quadrants were not occupied by regenerating trees following high-severity fire in the

Tiller Complex, creating regeneration gaps and an irregular spatial distribution. Higher densities of regeneration at other quadrants suggest spatial-clumping also occurs at this young stage. Regeneration may take several decades to fully complete cohort establishment (Freund et al., 2014, Tepley et al., 2014), but intense competition from shrubs and the lack of local seed sources may inhibit the abundance of that establishment in later decades (Shatford et al., 2007). Some of this early structural complexity will persist into later stages of successional development (Sensenig et al., 2013, Halpern et al., 2013), but the direct influence on old-growth structural complexity remains unknown.

Divergent successional pathways were already evident within a couple decades following stand-initiation. We observed evidence of both “initial floristics” and “relay floristics” successional models proposed in this forest type (Tepley et al., 2014). Regeneration was dominated by shade-intolerant species in high enough abundance to dominate forest development following high-severity fire at both the Tiller Complex and Warner Fire (Figure 4.4). The lack of shade-tolerant species suggests they will establish later in succession as the microsite conditions ameliorate and other species are competitively excluded, transitioning to dominance as structural complexity increases with the death of the pioneering cohort (Franklin et al., 2002). In contrast, the initial floristics model was observed at the Warner Fire where western hemlock regenerated prolifically and reached the sapling size by 22 years post-fire. The tolerance of western hemlock to shade and competition suggests it is likely to persist into later successional stages and become dominant trees earlier in succession than occurs under the relay floristics model (Tepley et al., 2013).

Low or moderate-severity fires modify successional trajectories rather than resetting them to early-successional stages. Since low or moderate-severity fire facilitated the highest abundance and diversity of regenerating trees (Figure 4.2), these conditions likely contribute more to structural complexity than other fire effects. This response included conifer species that typically diverge along moisture gradients (e.g., incense-cedar, western redcedar), and abundant hardwoods that are important components of structural complexity in *Pseudotsuga* forests across successional development (Franklin and Spies, 1991, Halpern et al., 2013, Swanson et al., 2011). Therefore, at this scale, low or moderate-severity fire may be the most functionally important disturbance magnitude, with the greatest potential to increase structural complexity in *Pseudotsuga* forests.

Conclusions

The magnitude of fire-disturbance exerts significant influence over regeneration density and composition, with implications on immediate and long-term structural complexity. Unburned forests had the lowest median regeneration density across our sampled disturbance gradient, including the greatest number of quadrants without regenerating trees (Figures 2 and 3). Dense overstory trees competitively excluded regenerating trees, but facilitated the recruitment of shade-tolerant species into the higher size-classes (Figure 4.4). As canopy gaps form from individual tree or small group mortality, these species will have a competitive advantage to occupy the site and transition to sub-dominant or dominant trees. Wildfires increased regeneration densities across all severity classes, but low or moderate-severity fire had the greatest densities and highest species diversity across the disturbance gradient (Figure 4.2). This response was driven by resilience mechanisms that differed among conifers and hardwoods, which may be adaptive traits selected because of the long-term dynamics of moderate-interval, mixed-severity fires (i.e., 95-150 years). The combination of structural diversification resulting from fire-induced mortality (see Chapter 1), and the increased diversity in regeneration response, low or moderate-severity fire will likely promote more structurally complex forests. Stand-initiating fire exhibited divergent successional trajectories that increased the complexity of early-seral environments, further contributing to landscape level diversification of forest conditions.

Mixed-severity fires are functionally important to the development of structural complexity in *Pseudotsuga* forests of the PNW. These forests are often considered to have a low-frequency, high-severity disturbance regime, but mixed-severity fires occurred historically and may be more common and important than considered in traditional successional models (Franklin et al., 2002). Contemporary fires continue to burn with severity distributions similar to those found historically (Tepley et al., 2014, Kushla and Ripple, 1997), and therefore could have beneficial effects if promoted across landscapes. One limitation to accomplishing this is previously harvested stands that will respond differently to variation in fire intensities because their composition and diameter distributions have been altered. Strategies should be developed

to facilitate the incorporation of mixed-severity fire effects into landscape management as a means to promote structural complexity at stand and landscape-scales (Cissel et al., 1999).

Figures

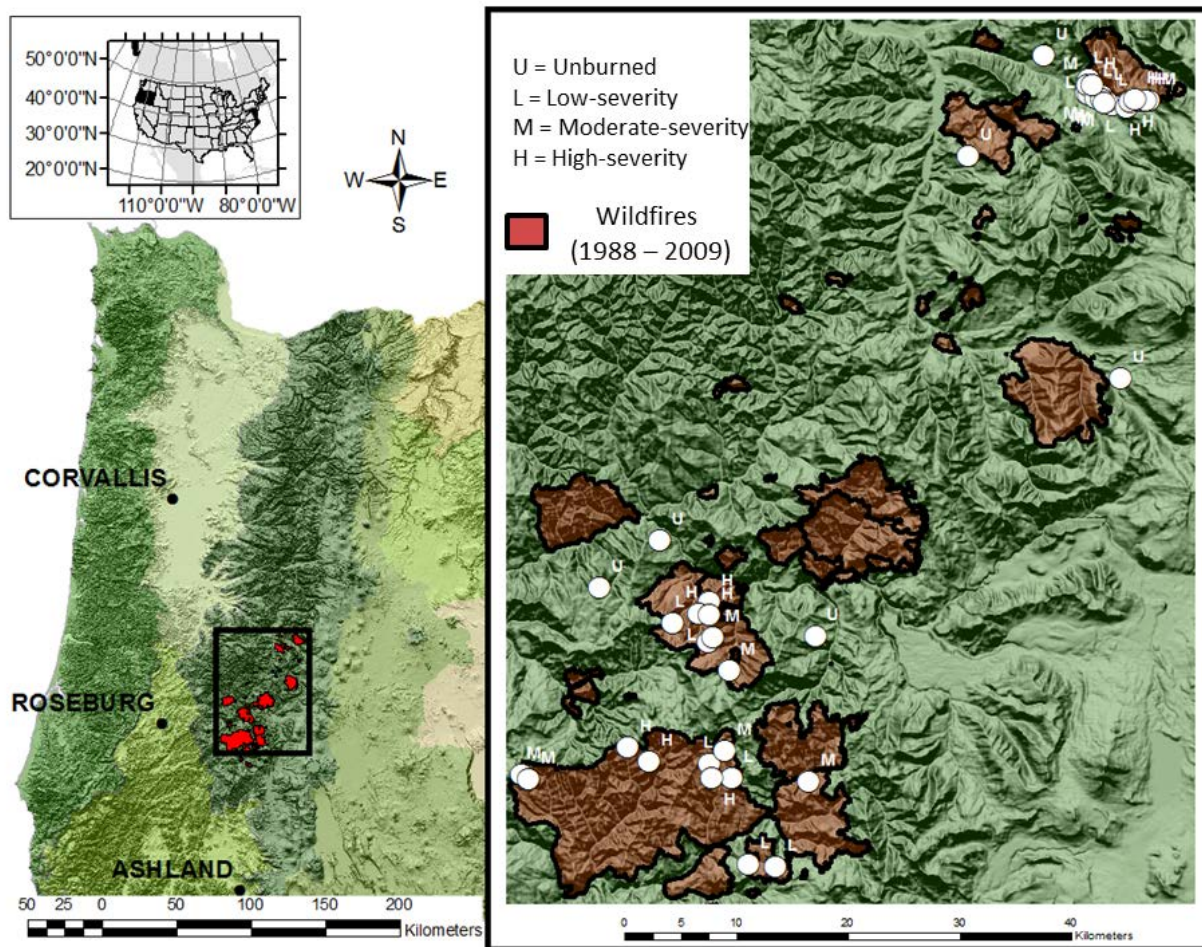


Figure 4.1: A map depicting fire extents and plot locations across our study area in Western Oregon's central Cascade Range.

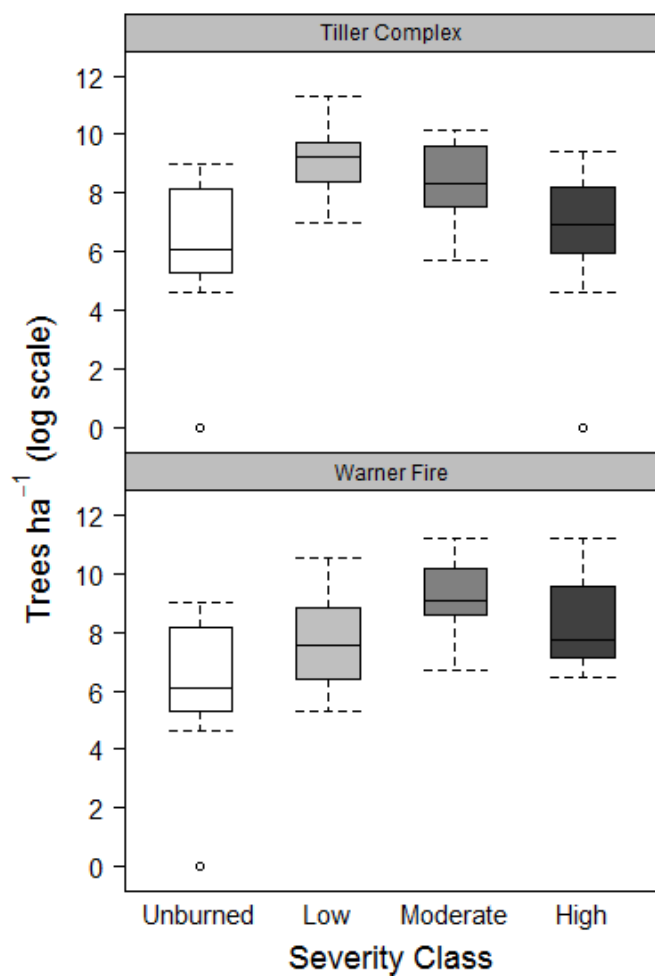


Figure 4.2: Total tree regeneration density by fire severity class in the Tiller Complex and Warner Fire.

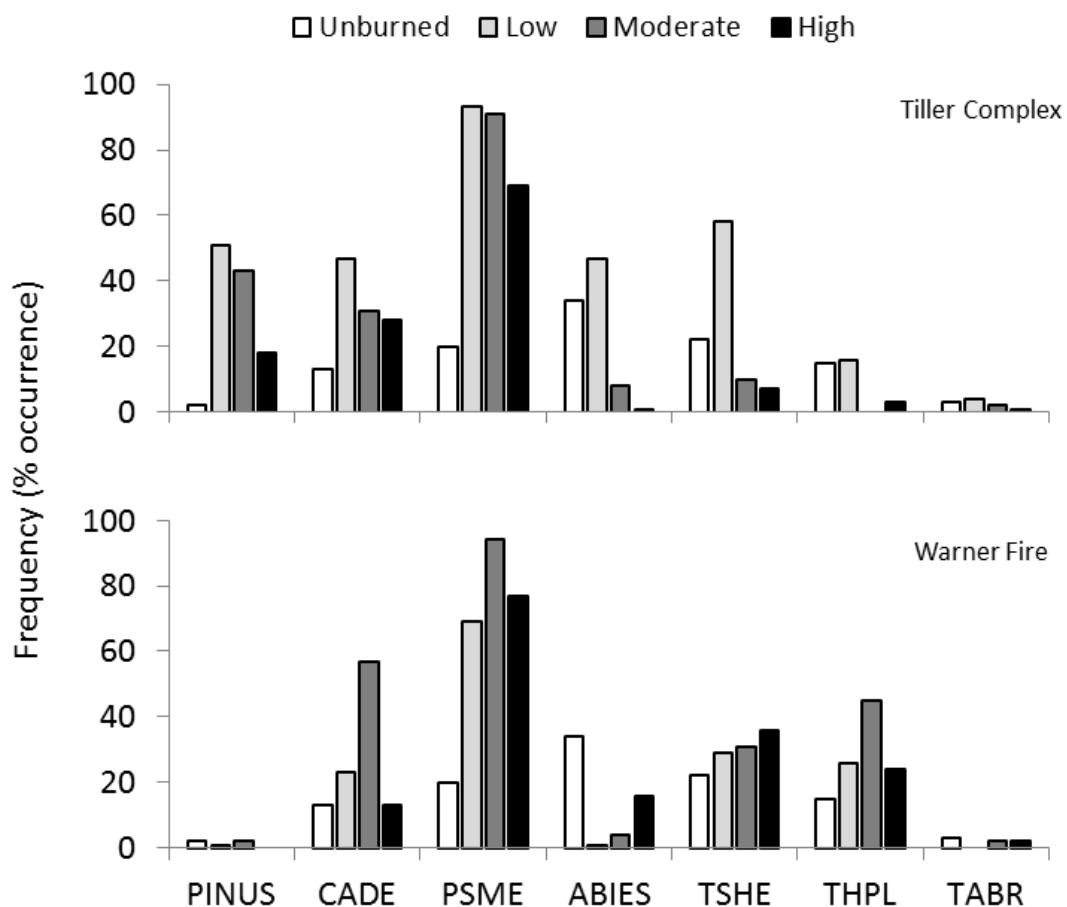


Figure 4.3: Frequency of quadrants where individual species were present. The dominant difference in regeneration response among these fires were a decrease in the presence of *Pinus* species at Warner Fire, and abundant shade-tolerant species following high-severity fire at the Warner Fire. CADE = incense-cedar, PSME = Douglas-fir, TSHE = western hemlock, THPL= western redcedar, TABR = Pacific yew, ABIES = true fir species, and PINUS = all pine species.

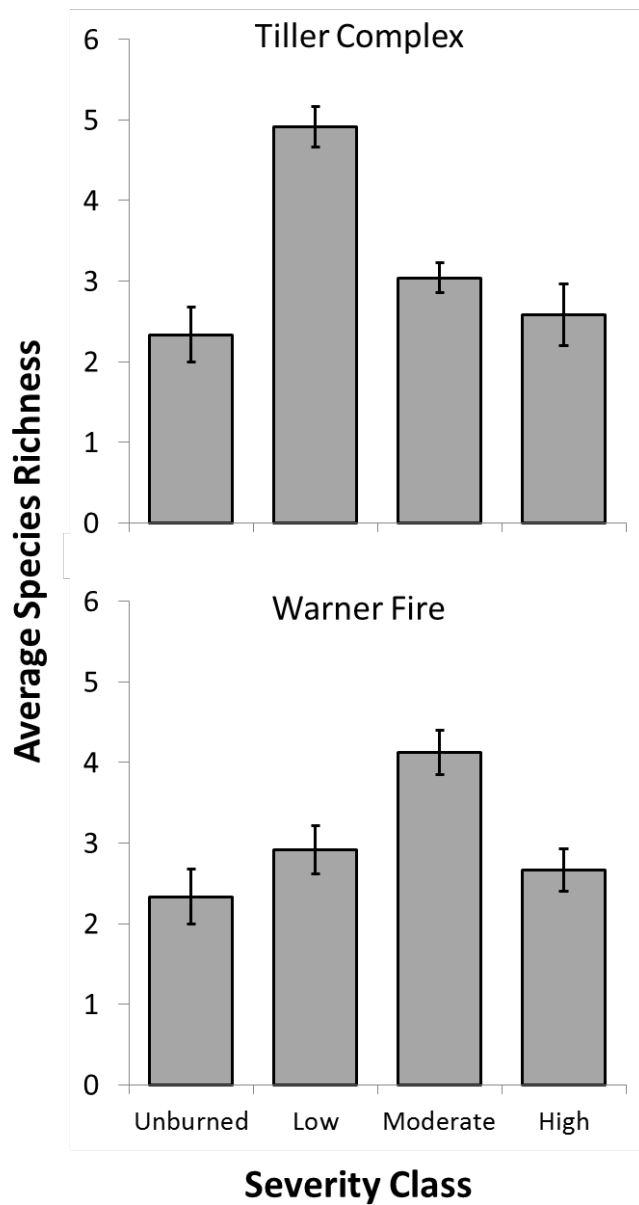


Figure 4.4: Average species richness and standard error bars of tree regeneration within sample plots across a mixed-severity fire gradient. Both fires exhibited a peak in richness following low or moderate-severity fire providing evidence for the Intermediate Disturbance Hypothesis.

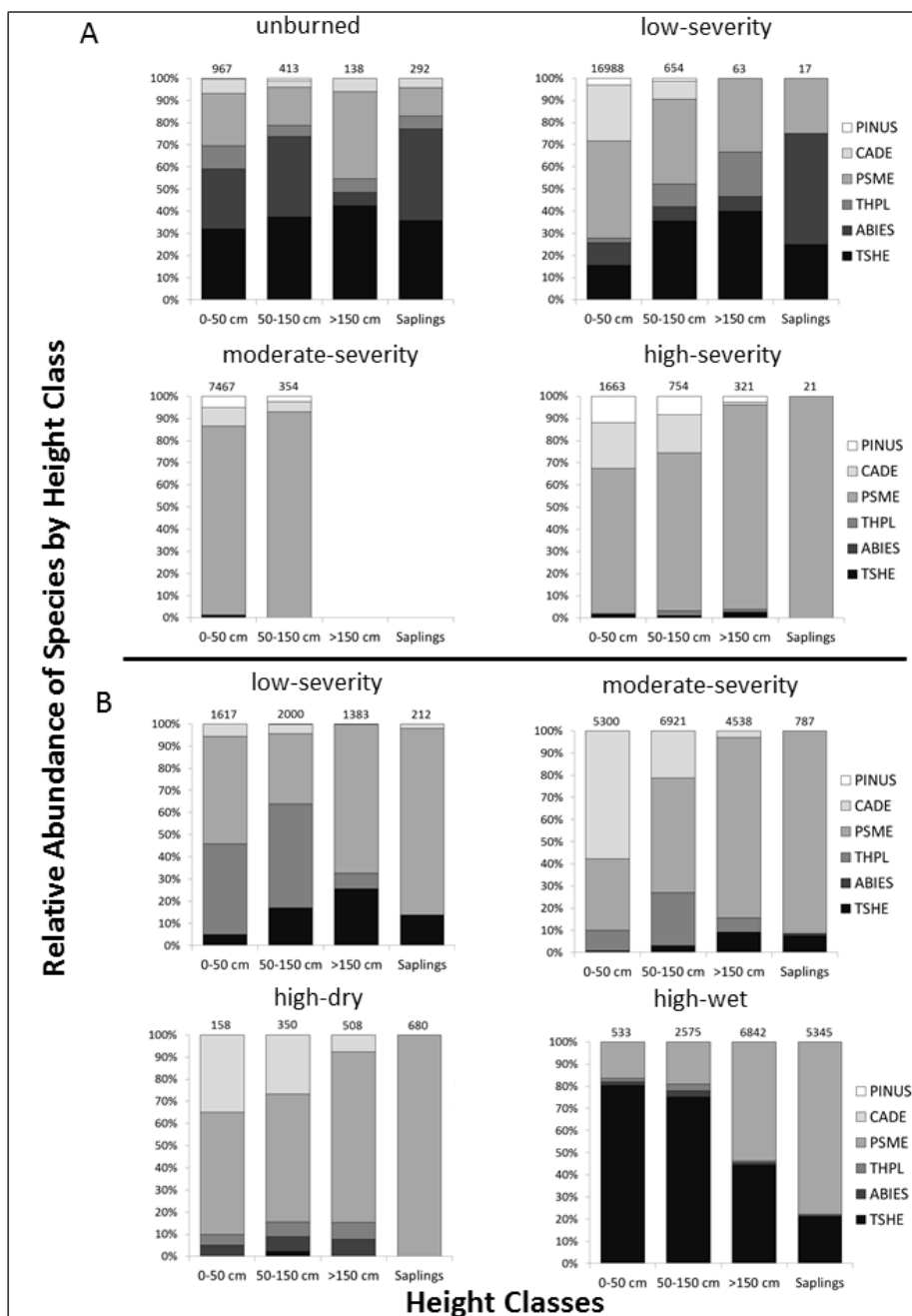


Figure 4.5: Regeneration composition by height class across a mixed-severity fire gradient: (A) unburned forests and conditions following the Tiller Complex, and (B) Warner Fire including the divergent developmental pathways following stand-initiation. Numbers provided on top of the bars were average regeneration densities for that height class. CADE = incense-cedar, PSME = Douglas-fir, TSHE = western hemlock, THPL= western redcedar, ABIES = true fir species, and PINUS = all pine species.

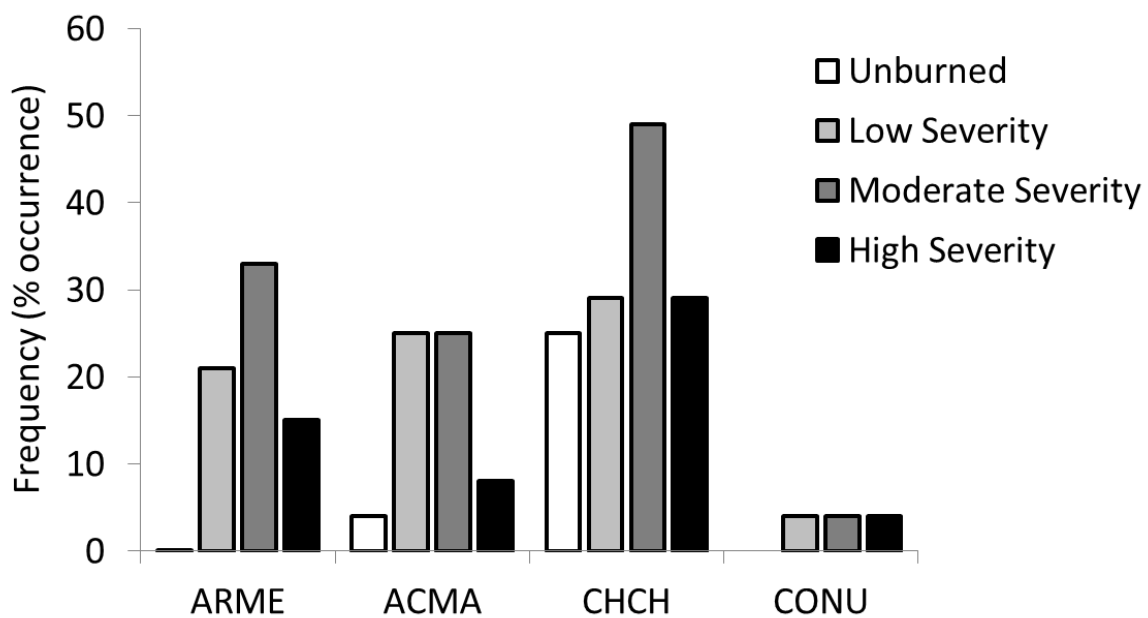


Figure 4.6: Frequency of occurrence of regenerating hardwood trees across a fire severity gradient at both fire sites. ARME = Pacific madrone, ACMA = bigleaf maple, CHCH = giant chinkapin, and CONU = Pacific dogwood.

Tables

Table 4.1: Mean (standard deviation) of forest structural attributes for *a priori* fire severity classes for the Tiller Complex and Warner Fires.

Attribute	<i>A Priori</i> Severity Classes by Fire Site						
	Unburned	Tiller Complex			Warner Fire		
		Low	Moderate	High	Low	Moderate	High
Reconstructed tree basal area (m ² ha ⁻¹)	69.2 (14.0) ^a	69.4 (13.9) ^{a,b}	57.4 (12.7) ^b	51.2 (7.2) ^b	75.2 (23.8) ^a	77.1 (18.6) ^a	67.2 (11.4) ^a
Reconstructed tree density (trees ha ⁻¹)	721.8 (216.4) ^a	738.4 (216.5) ^{b,a}	1306.9 (912.8) ^{a,**}	444.4 (254.3) ^b	364.7 (143.8) ^b	369.7 (246.8) ^b	228.2 (100.0) ^b
Percent fire mortality (BA)	NA	36.4 (8.5) ^a	50.3 (12.6) ^{b,a*}	95.0 (9.4) ^c	25.5 (7.8) ^a	42.7 (12.7) ^b	97.6 (4.8) ^c
Percent fire mortality (trees ha ⁻¹)	NA	70.5 (7.1) ^a	84.6 (11.9)	99.2 (1.5)	49.2 (11.5) ^a	71.5 (9.9) ^b	99.6 (0.6) ^c
Legacy tree basal area (m ² ha ⁻¹)	69.2 (14.0) ^a	42.7 (10.2) ^b	28.1 (10.4) ^b	2.3 (4.4) ^c	56.6 (23.8) ^a	44.0 (12.2) ^{b,a}	1.3 (2.4) ^b
Legacy tree density (trees ha ⁻¹)	721.8 (216.4) ^a	217.9 (92.5) ^b	140.2 (48.3) ^{c,b}	4.9 (10.6) ^{d,c}	187.3 (102.6) ^b	113.8 (97.2) ^b	1.3 (2.1) ^b
Legacy tree canopy base height (m)	8.0 (2.3) ^a	9.2 (2.3) ^a	12.4 (7.4) ^a	27.2 ^{b*}	24.2 (5.0) ^b	24.6 (5.0) ^b	29.0 ^{b*}
Legacy tree quadratic mean diameter (cm)	35.9 (6.8) ^a	52.1 (10.1) ^a	52.5 (18.0) ^a	91.7 ^{b*}	65.0 (11.0) ^b	81.9 (21.4) ^b	109.1 ^{c*}
Snag basal area (m ² ha ⁻¹)	9.0 (3.9) ^a	24.8 (8.2) ^b	28.4 (9.4) ^b	48.4 (9.4) ^c	18.1 (6.2) ^a	32.9 (13.2) ^b	65.6 (12.9) ^c
Snag density (trees ha ⁻¹)	102.2 (50.6) ^a	514.3 (145.0) ^{a,b}	1165.7 (892.2) ^{b,**}	439.2 (248.7) ^{a,b}	169.2 (70.8) ^a	252.4 (156.5) ^a	226.3 (99.2) ^a
Elevation (m)	774 -1246	917-1174	938-1257	801-1183	764-1021	776-1308	1056-1301
Slope (degrees)	19.3 (3.9)	20.2 (1.1)	20.6 (6.9)	21.3 (3.7)	23.5 (6.5)	19.1 (6.4)	17.4 (3.0)
Heat load	0.90 (0.08)	0.78 (0.12)	0.89 (0.13)	0.86(0.12)	0.98 (0.04)	0.99 (0.02)	0.97 (0.02)

Note: Lower case letters indicate statistically different estimates at an $\alpha \leq 0.05$. *Estimated for live trees only. ** Includes two plots with a high abundance of <10 cm snags that skew these estimates.

Table 4.2: Statistical summary from our analysis of regeneration densities at the Tiller Complex and Warner Fire.

Tiller Complex					
Severity Class	Estimate	Std. Error	LCL	UCL	p-value
Unburned^a	7.235	0.394	6.466	8.011	<0.001
Low^b	9.694	0.387	8.937	10.452	<0.001
Moderate^{c,b}	8.882	0.388	8.122	9.643	<0.001
High^{a,c}	7.555	0.394	6.784	8.327	<0.001

Warner Fire					
Severity Class	Estimate	Std. Error	LCL	UCL	p-value
Unburned^a	7.235	0.394	6.466	8.011	<0.001
Low^a	8.278	0.441	7.413	9.143	<0.001
Moderate^b	9.580	0.440	8.718	10.442	<0.001
High^{a,b}	8.629	0.444	7.760	9.498	<0.001

Note: LCL and UCL are upper and lower 95% confidence limits. Lower case letters next to severity classes indicate statistically different groups at an alpha <0.05 and adjustments for multiple comparisons.

Table 4.3: Statistical summary from our Multi-Response Permutation Procedure testing regeneration community differences across fire severity classes.

Severity Class			T-Statistic	A-Statistic	p-value
Comparison					
Tiller Complex					
Unburned	vs.	Low	-13.128	0.136	<0.001
Unburned	vs.	Moderate	-15.232	0.187	<0.001
Unburned	vs.	High	-17.101	0.209	<0.001
Low	vs.	Moderate	-9.271	0.095	<0.001
Low	vs.	High	-15.730	0.195	<0.001
Moderate	vs.	High	-4.477	0.051	0.002
Warner Fire					
Unburned	vs.	Low	-12.466	0.145	<0.001
Unburned	vs.	Moderate	-13.895	0.162	<0.001
Unburned	vs.	High-dry	-12.380	0.212	<0.001
Unburned	vs.	High-wet	-7.963	0.127	<0.001
Low	vs.	Moderate	-2.503	0.031	0.029
Low	vs.	High-dry	-3.092	0.053	0.014
Low	vs.	High-wet	-6.525	0.110	<0.001
Moderate	vs.	High-dry	-8.804	0.154	<0.001
Moderate	vs.	High-wet	-7.180	0.127	<0.001
High-dry	vs.	High-wet	-10.946	0.308	<0.001

CHAPTER 5: CONCLUSIONS

General Conclusions

Historically, *Pseudotsuga* forests were considered to have a low-frequency, high-severity disturbance regime, but mixed-severity fires were likely more common and more ecologically important than considered in traditional successional models (Franklin et al., 2002). Differences between fire effects among these fire regimes, the response of the ecosystem to the perturbation, and the successional trajectories created by mixed-severity fires are important to understand if the objective of public lands management is to maintain ecosystem resilience, especially in a period of such rapid global environmental change. In particular, one must consider whether or not the ecological consequences of these fires are different, or will become different, with global environmental change and other, more immediate anthropogenic disturbance. Our ability to observe and understand ecosystem change is reliant on our understanding of the past, and relating contemporary observations to historical trends. This study attempted to make an assessment of ecosystem response to contemporary mixed-severity fires, describing important fire effects and vegetative responses fundamentally different than would occur under a high-severity fire regime.

Mixed-severity fires are important to the development of structural complexity in *Pseudotsuga* forests in the near-term. We were able to quantify first order fire effects, or those effects directly attributed to the perturbation itself, in the form of mortality across species and size classes. The distribution of live and dead biological legacies was driven by fire intensity, variation in species resistance to mortality and the forest's seral state at the time of disturbance (Figure 2.5). Variation in fire effects initiated diverse structural changes that can provide habitat for various wildlife species, including species with preference for large legacy trees, large or high-densities of snags, or an abundance of logs. These structures provide immediately available habitat resources that may have been limited in the unburned forest. These resources can change relatively quickly with time, as snag fragmentation and fall occurs and coarse woody detritus decays. Therefore, habitat conditions can change quickly in response to the changes in these resources. This effect has certainly been observed in early-seral habitats as snags change quickly from hard snags to soft snags or logs.

Another near-term, and potentially ephemeral effect of mixed-severity fire, was a diverse understory response at the population and community level. Vegetation response was directly associated with the variable conditions created by mixed-severity fire in these forests, and was a direct reflection of the underlying environmental gradient created by the disturbance. Native understory species exhibited three distinct response-curves to increasing disturbance severity: 1) disturbance-sensitive species decreased in abundance with increasing fire severity, 2) disturbance-stimulated species' abundance peaked following low or moderate-severity fire, and 3) disturbance-amplified species' abundance increased exponentially with increasing fire severity (Figure 3.2). Individual species response-curves led to community assemblages that varied distinctly across our mixed-severity disturbance gradient (Figure 3.4). These communities occurred with varying abundances of live and dead biological legacies, promoting structural complexity with diverse vegetation resources (e.g., food sources such as soft mast production, high nitrogen content vegetation) likely important to many faunal species and communities (Cahall and Hayes, 2009, Fontaine et al., 2009).

Mixed-severity fires are also important to the development of long term structural complexity as their legacy persists for decades to centuries. This long-term legacy can be observed in vertical and horizontal structural diversity, as well as compositional changes. The magnitude of fire-disturbance exerts significant influence over regeneration density and composition. Unburned forests had the lowest regeneration densities as dense overstory trees competitively excluded regenerating trees, but these conditions did facilitate the recruitment of shade-tolerant species into the higher size-classes (Figure 4.4). As canopy gaps form from individual tree or small group mortality, these species will have a competitive advantage to occupy the site and transition to sub-dominant or dominant trees. Without disturbance, these forests would gradually transition from Douglas-fir dominance to western hemlock or true fir forests.

Wildfires increased regeneration densities across all severity classes, but low or moderate-severity fire had the greatest densities and highest species diversity (Figure 4.2). This response was driven by resilience mechanisms that differed among conifers and hardwoods, which may be adaptive traits selected because of the long-term dynamics of moderate-interval, mixed-severity fires (i.e., 95-150 years). Because of the combination of structural diversification resulting from fire-induced mortality (see Chapter 1), and the increased diversity in regeneration

response, low or moderate-severity fire will likely promote more structurally complex forests as they develop over time. Additionally, stand-initiating fire exhibited divergent successional trajectories that increased the complexity of early-seral environments, further contributing to landscape level diversification of forest conditions.

Mixed-severity fire has near and long-term ecological effects that, despite the rapid environmental change induced by these disturbances, are beneficial to the ecosystem and the species reliant on them. We are only beginning to understand how such diverse fire effects promote structurally complex, and biologically diverse, old-growth forests found across the PNW. Further investigation is needed to continue to build upon this knowledge, and may be more pertinent than ever, as rapid global environmental change will change forest dynamics. Our ability to observe these changes, and better understand their consequences, will be predicated on our knowledge of the past. Therefore, the opportunities to learn from historical forest development, and compare them to contemporary responses to fire, may be diminishing.

Future Considerations

Forest resilience may be jeopardized in the current age of rapid global environmental change. The ability of these ecosystems to absorb natural disturbances and respond similarly to historical conditions, thereby returning to a pre-disturbance state, may be inhibited by increased temperatures and evaporative demand, decreased precipitation, or an increase in natural and anthropogenic disturbances. Declines in the resilience of these forests may be observed through tree demography when increased mortality rates of existing trees, changes in growth rates, or changes in regeneration patterns indicate a shift towards new forest or state change. Fortunately, our data suggests the current successional trajectories of these post-disturbance ecosystems are still within the historical range of variability, so climate change effects haven't reached the point that no analog, or divergent, ecosystems are developing. Of course, we have not sampled all aspects of the ecosystem and therefore fragile components of these ecosystems may be changing without our knowledge.

There are fundamental challenges to observing fire effects and ecosystem response to disturbance. Some of this is a result of the scale of these disturbances and the difficulty in sampling their effects. Therefore, we often utilize landscape-scale fire severity maps derived from Landsat ETM satellite imagery. While these estimates offer some level of quantification of

fire effects, they may not capture the ecosystem response in great enough detail to allow us to assess the resilience of forested landscapes to disturbance. This is a result of these maps, and disturbance severity in general, being quantified by the amount or proportion of live biomass loss (Keeley, 2009). We found the magnitude of overstory mortality wasn't the most important factor influencing post-disturbance vegetation response, one aspect of ecosystem resilience (Figure 3.5). Instead, the abundance of legacy trees had a greater influence, which is related to, but does not necessarily proportional to the number of trees killed. These legacy trees directly influence understory vegetation by: 1) competing with understory vegetation for light, water and nutrients, and 2) ameliorating microclimates, thereby favoring some species over others (Gray and Spies, 2004). Legacy trees also indirectly influence understory vegetation by increasing the abundance of regenerating trees (Seidl et al., 2014), which can quickly occupy disturbed sites (Larson and Franklin, 2005) and competitively exclude some species over time (Halpern et al., 2013). Understanding whether or not these ecosystems remain resilient to contemporary fires is important if we want to restore disturbance processes to these ecosystems, as we transition towards planning for future resilience of these landscapes.

Promoting fire as a natural process, and understanding the value of mixed-severity fire in *Pseudotsuga* forests, could lead to the long-term development and maintenance of resilient forest landscapes. Recent interest in early-seral habitats suggests managers are realizing the importance of fire's functional role in restructuring these forests (Franklin and Johnson, 2012). Our observations also support the concept that severity is resource dependent, and what is high-severity for one resource might be optimal conditions for another. This is most exemplified in our study by early-seral forest conditions created by high-severity fire. These communities provide valuable habitat for many species (Swanson et al., 2014), are relatively rare on the landscape (Swanson et al., 2010), and contribute significantly to the energetics of these landscapes (Campbell and Donato, 2014). Unfortunately, conservation efforts that focus only on old-growth and early-seral forest conditions ignore the importance of mixed-severity fire, especially since low or moderate-severity fire accounts for >70% of the burned area (Kushla and Ripple, 1997, Morrison and Swanson, 1990). Additionally, the time period between the early-seral and old-growth conditions constitutes a large portion of a pioneering cohort's lifetime, exceeding estimated mean fire return intervals in nearby forests two or three fold (Morrison and Swanson, 1990).

Contemporary fires continue to burn with severity distributions similar to those found historically (Tepley et al., 2014, Kushla and Ripple, 1997), and therefore could have beneficial effects if promoted across landscapes. Since fire return intervals can be as short as 95 years in western Oregon's central Cascades (Morrison and Swanson, 1990), existing old-growth forests may have missed a fire cycle that could have short and long-term negative effects on ecosystem resilience. This is particularly important in mature forests without existing vertical and horizontal structural diversity; conditions that could be accelerated by low and moderate-severity fire. One limitation to returning fire to these landscapes is previously harvested stands will respond differently to fires because their species composition and diameter distributions have been significantly altered. Therefore, strategies should be developed to incorporate mixed-severity fire effects into landscape management as a means to promote increased structural complexity at the stand and landscape scale (Cissel et al., 1999).

We are continuing our research efforts within these same burned landscapes to include the effects of salvage logging on the structure and function of these ecosystems. Active management of post-fire environments is often pursued for economic purposes. Salvage logging and reforestation provide immediate economic benefits by utilizing live trees and snags as a timber resource. Additionally, the rapid establishment of commercially preferred tree species may reduce the time for a stand to reach its next harvest rotation, improving the long-term soil expectation value. Salvage logging and reforestation is an efficient and effective management strategy when economic return is the primary objective, but public lands are intended to provide additional benefits so economic gains must be weighed against other ecosystem impacts. In particular, salvage logging and reforestation following fire further alters stand structure by removing biological legacies, altering early seral forest habitat and potentially pushing the stand towards canopy closure more rapidly than naturally occurs. The degree to which salvaged logged sites differ from natural early seral habitat remains uncertain at this time.

We are also in the process of quantifying carbon pools and ecosystem productivity across the mixed-severity fire gradient. Although there are significant ecological benefits provided by the post-fire environment (including early-seral forest habitats), fire does reduce carbon stores and sequestration rates. Net ecosystem productivity (NEP) is the balance between heterotrophic respiration and net primary productivity. Fire alters NEP and total carbon pools primarily through pyrogenic emissions and biomass transfer from live to dead pools. As burn

severity increases, pyrogenic emissions increase and larger proportions of biomass are transferred from live to dead pools, increasing heterotrophic respiration and decreasing net primary productivity. Positive NEP recovery is dependent on the severity of the disturbance and the rate of vegetation growth and establishment during early seral forest succession, potentially taking several decades to achieve. These effects may inhibit returning fire to these forests if future carbon policy is directed at maximizing carbon sequestration and this overrides other ecological benefits derived from mixed-severity fire.

Investigating temporal trends in post-fire forest development following natural and anthropogenic disturbance is critical to understanding the ecological impacts of these disparate disturbance regimes. It shouldn't be surprising that conflicts may arise between ecosystem services. Ecological tradeoffs are inherent with change and are further complicated by human engagement with forest systems. System balance with anthropogenic engagement may be achieved across broad spatial and temporal scales, but determining how this is achieved should be founded in sound ecological theory and supported by scientific investigation.

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APPENDICES

Appendix I

Results from indicator species analysis as related to disturbance severity classes.

Species	Indicator Species			Relative Abundance					Relative Frequency				
	Maxgrp	Value	p*	MaxGrp	U	L	M	H	MaxGrp	U	L	M	H
Moss	U	53.3	0.00	U	53	20	19	7	L	100	100	94	81
<i>Acer circinatum</i>	U	28.3	0.02	U	42	16	22	20	U	67	35	42	38
<i>Linna borealis</i>	U	28.2	0.02	L	32	48	3	16	U	88	48	25	6
<i>Mahonia nervosa</i>	U	39	0.03	U	39	18	14	29	L	100	100	94	96
<i>Gaultheria shallon</i>	U	22.6	0.11	U	45	18	28	8	L	50	60	54	21
<i>Rhamnus purshiana</i>	U	16.5	0.18	M	0	34	59	7	M	0	17	27	4
<i>Vaccinium parvifolium</i>	U	13.7	0.21	U	41	16	13	30	U	33	23	27	29
<i>Corylus cornuta</i>	U	12.9	0.25	U	51	6	40	2	M	25	19	27	13
<i>Rubus nivalis</i>	U	7.3	0.35	U	58	9	21	12	H	13	6	8	13
<i>Chimaphila umbellata</i>	L	38.6	0.00	L	0	100	0	0	L	0	4	0	0
Ferns	L	40.4	0.02	L	8	47	21	23	L	54	85	71	77
<i>Rosa spp.</i>	L	20.1	0.44	L	21	32	24	22	U	75	63	50	52
<i>Rhododendron macrophyllum</i>	M	16.1	0.01	U	44	19	31	6	L	38	46	33	15
<i>Chrysopsis chrysophylla</i>	M	21.6	0.03	U	62	8	25	5	U	63	33	46	25
<i>Arctostaphylos columbiana</i>	M	20.9	0.05	M	0	1	56	43	M	0	19	38	23
<i>Holodiscus discolor</i>	M	17.4	0.19	M	4	10	44	42	M	25	29	40	29
Forbs	M	34.8	0.28	M	7	26	35	32	M	100	98	100	98
<i>Ceanothus velutinus</i>	H	59.9	0.00	H	0	3	1	96	H	0	21	15	63
<i>Rubus ursinus</i>	H	68.8	0.00	H	2	10	17	70	H	58	92	79	98
<i>Garrya fremontii</i>	H	28.6	0.00	H	0	3	25	72	H	0	8	13	40
<i>Rubus leucodermis</i>	H	33.2	0.00	H	0	8	3	88	H	0	13	4	38
<i>Prunus emarginata</i>	H	14.6	0.01	H	0	0	0	100	H	0	0	0	15
<i>Whipplea modesta</i>	H	40.2	0.01	H	5	19	32	44	H	67	79	77	92
<i>Paxistima myrsinites</i>	H	22.4	0.01	H	8	4	12	77	H	17	6	25	29
<i>Rubus parviflorus</i>	H	25.1	0.01	H	1	36	11	52	H	4	17	27	48
Graminoids	H	45.3	0.02	H	7	11	18	64	L	67	85	79	71
<i>Ceanothus sanguineus</i>	H	20.8	0.04	H	0	21	17	62	H	0	27	21	33
<i>Mahonia aquifolium</i>	H	13.9	0.04	H	1	16	16	67	H	4	17	15	21
<i>Toxicodendron diversilobum</i>	H	8.7	0.04	H	0	16	0	84	H	0	4	2	10
<i>Ribes roezlii</i>	H	9.1	0.05	H	0	4	23	73	H	0	4	6	13
<i>Ribes sanguineum</i>	H	13.5	0.05	H	0	41	5	54	H	0	21	8	25
<i>Ribes divaricatum</i>	H	10.8	0.09	H	0	3	40	58	H	0	6	13	19
<i>Ceanothus integrissimus</i>	H	15.7	0.16	H	0	23	24	54	M	0	29	40	29
<i>Vaccinium membranaceum</i>	H	10.7	0.23	M	4	7	47	43	H	4	10	21	25
<i>Symphoricarpos mollis</i>	H	12.4	0.88	H	14	25	21	40	U	46	38	42	31
<i>Salix scouleriana</i>	H	2.1	1.00	H	0	0	0	100	H	0	0	0	2
Rare species (occurred in <5% of plots)													
<i>Acer glabrum</i>	H	4.2	0.26	H	0	0	0	100	H	0	0	0	4
<i>Amelanchier alnifolia</i>	H	1.6	1.00	H	0	0	25	75	H	0	0	2	2
<i>Chimaphila menziesii</i>	L	4.2	0.27	M	2	20	49	29	M	17	33	44	19
<i>Cytisus scoparius</i>	M	2.1	1.00	M	0	0	100	0	M	0	0	2	0
<i>Gaultheria ovatifolia</i>	M	2.6	0.46	H	0	0	41	59	M	0	0	6	4
<i>Lonicera ciliosa</i>	M	1	1.00	M	0	25	50	25	H	0	2	2	2
<i>Oemleria cerasiformis</i>	U	4.2	0.15	U	100	0	0	0	U	4	0	0	0
<i>Philadelphus lewisii</i>	M	2	0.87	M	0	3	97	0	L	0	2	2	0
<i>Sambucus nigra</i>	H	1	1.00	H	0	0	50	50	H	0	0	2	2
<i>Sambucus racemosa</i>	H	17	0.05	H	0	20	29	51	H	0	27	21	33

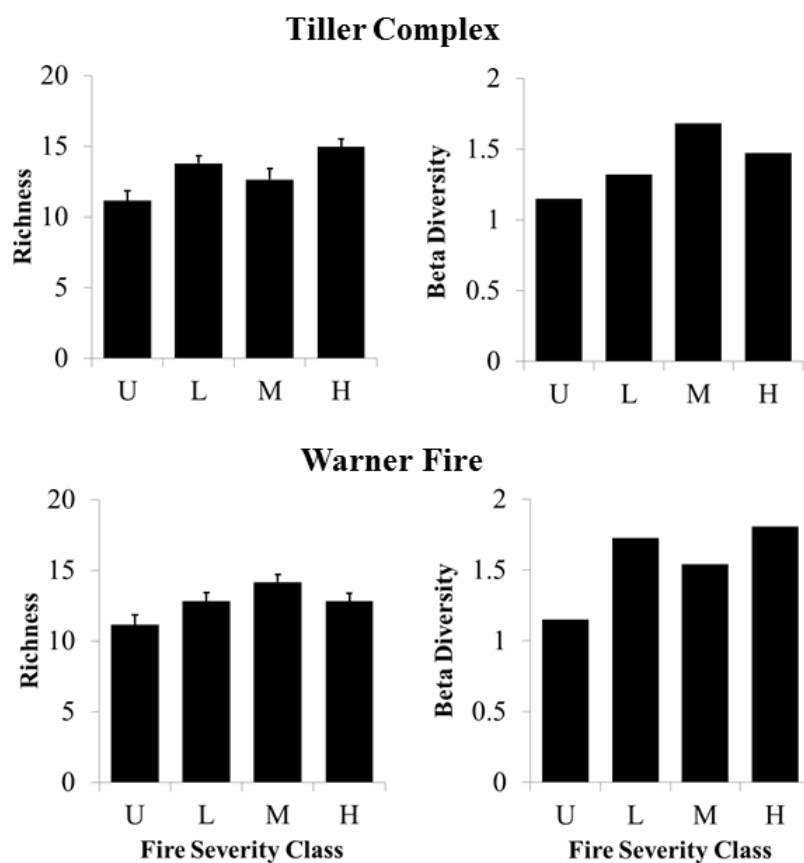
p* proportion of randomized trials with indicator value equal to or exceeding observed indicator value

Maxgrp = Group with maximum observed value

Relative frequency = % of plots in given group where each species was present

Relative abundance = average abundance of a given species in a group over the average abundance of that species in all plots, expressed as a percent

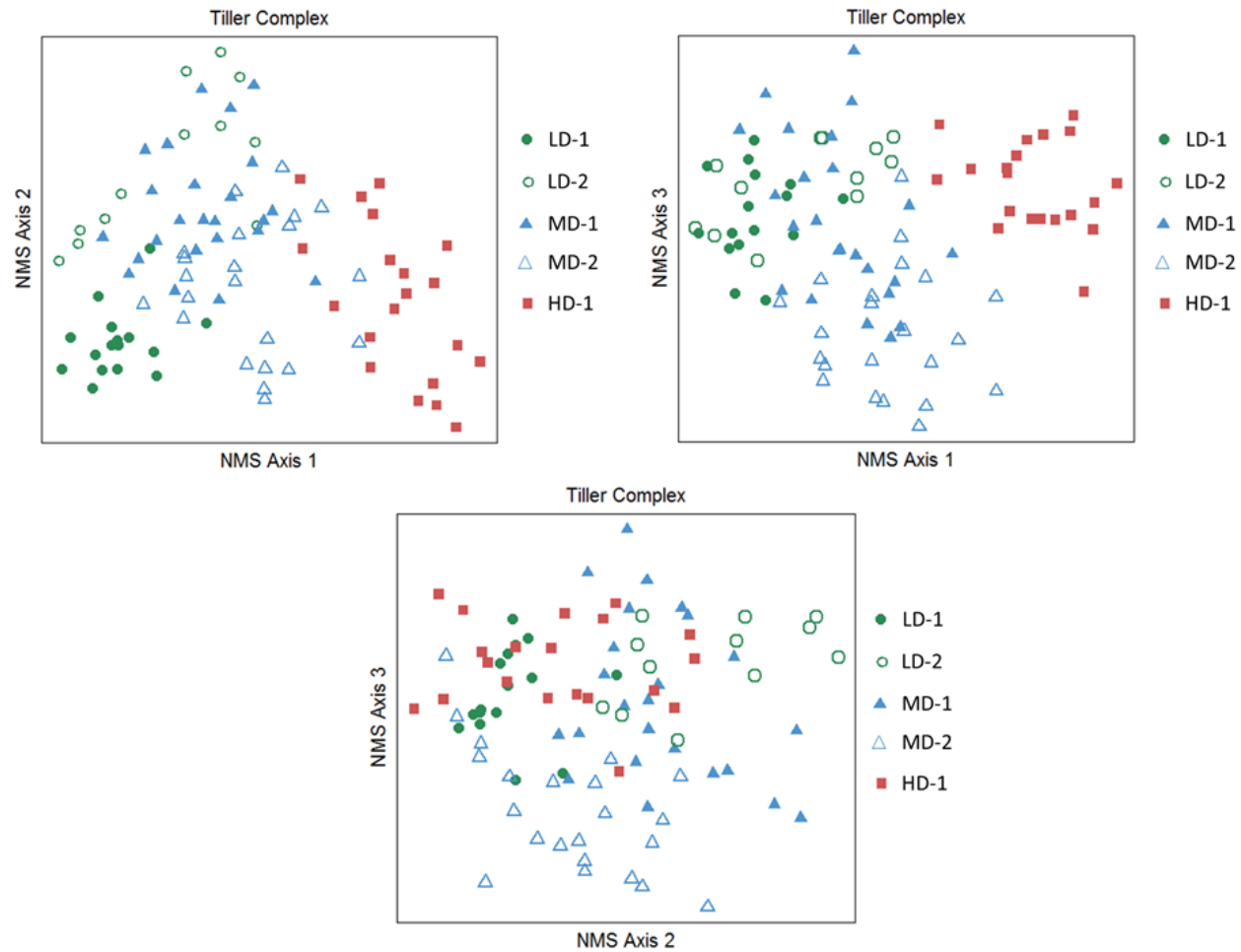
Appendix II



Species richness and Whitaker's beta diversity () by fire severity class for understory shrubs separated into samples obtained in the Tiller Complex and Warner Fire.

Appendix III

Tiller Complex NMS Plots for all axis combinations of a 3-dimensional solution.



Appendix IV

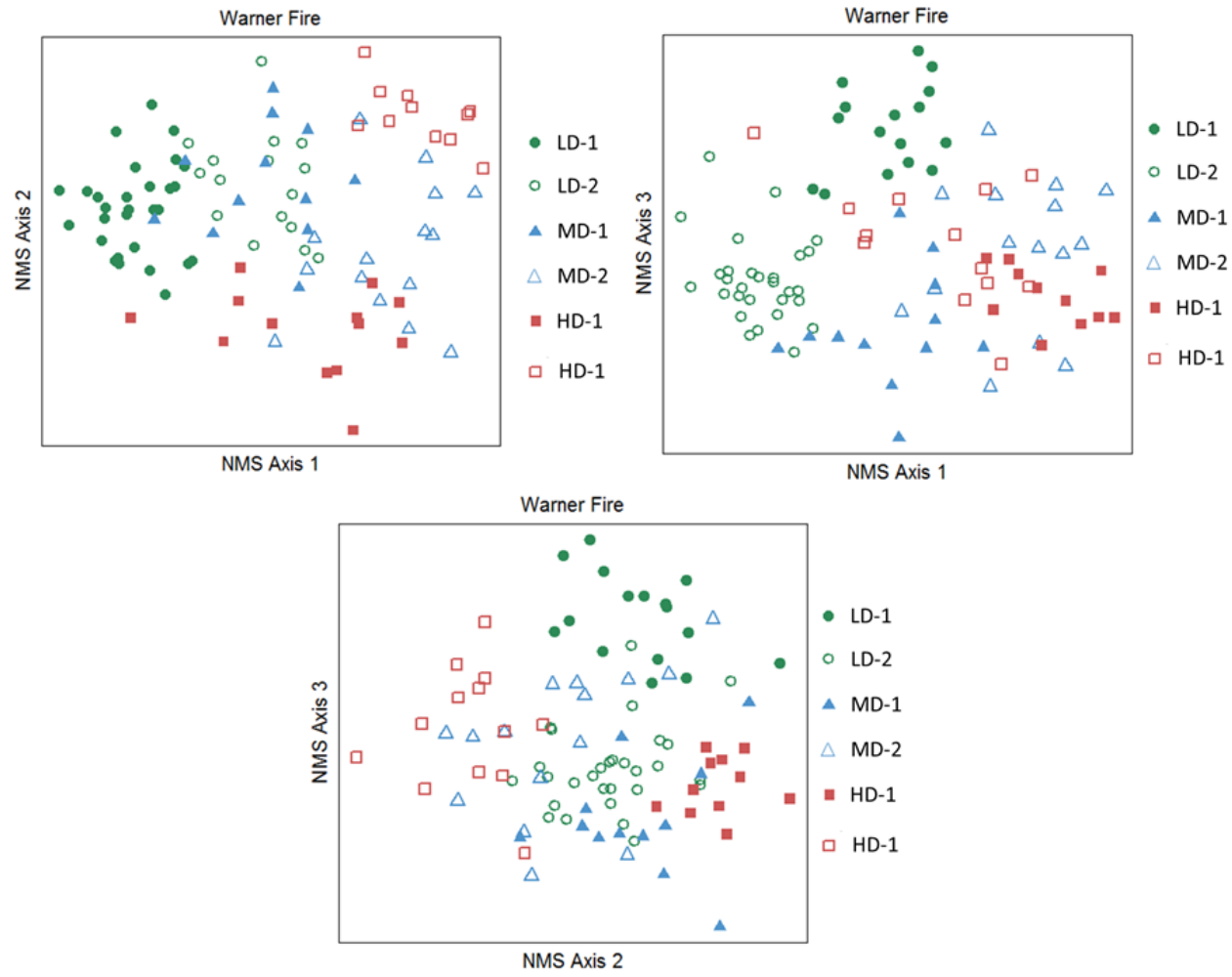
Ranked Pearson and Kendall correlations of biophysical factors for the 3-dimensional ordination axes within the Tiller Complex.

Variable	Axis 1			Axis 2			Axis 3		
	r	R ²	tau	r	R ²	tau	r	R ²	tau
P.BAMort	0.729	0.532	0.447	-0.069	0.005	0.049	0.355	0.126	0.248
S.BAMort	0.728	0.531	0.499	-0.135	0.018	-0.025	0.365	0.133	0.233
PLiveBA	-0.613	0.375	-0.451	-0.098	0.01	-0.096	-0.433	0.188	-0.27
PLiveTPH	-0.578	0.334	-0.421	-0.226	0.051	-0.075	-0.226	0.051	-0.199
SLiveBA	-0.559	0.313	-0.432	-0.046	0.002	-0.023	-0.452	0.204	-0.291
SLiveTPH	-0.486	0.236	-0.466	-0.229	0.053	-0.04	-0.308	0.095	-0.252
Slope	0.474	0.225	0.288	0.289	0.083	0.157	0.022	0	0.022
PPreFireBA	-0.338	0.114	-0.294	-0.236	0.056	-0.124	-0.415	0.172	-0.193
logSapling	-0.306	0.093	-0.255	-0.422	0.178	-0.326	-0.185	0.034	-0.144
Elevation	-0.03	0.001	0.058	0.556	0.309	0.356	-0.269	0.073	-0.162
SPreFireBA	-0.188	0.035	-0.13	-0.204	0.042	-0.132	-0.407	0.165	-0.244
Aspect	0.049	0.002	0.01	-0.117	0.014	-0.1	0.299	0.09	0.189
logDSeedling	0.251	0.063	0.144	-0.277	0.077	-0.225	0.158	0.025	0.122
HeatLoad	0.026	0.001	0.013	-0.107	0.011	-0.114	-0.002	0	0.01

Note: Bolded estimates represent Pearson correlations > 0.300 to highlight dominant biophysical factors.

Appendix V

Warner Fire NMS Plots for all axis combinations of a 3-dimensional solution.



Appendix VI

Ranked Pearson and Kendall correlations of biophysical factors for the 3-dimensional ordination axes within the Warner Fire.

Variable	Axis 1			Axis 2			Axis 3		
	r	R ²	tau	r	R ²	tau	r	R ²	tau
P.BAMort	0.610	0.372	0.419	0.047	0.002	-0.028	0.282	0.080	0.231
Elevation	0.556	0.309	0.352	0.319	0.101	0.230	-0.160	0.025	-0.074
PLiveTPH	-0.555	0.308	-0.456	0.186	0.035	0.009	-0.323	0.104	-0.209
S.BAMort	0.536	0.288	0.337	0.081	0.007	0.054	0.311	0.097	0.225
PLiveBA	-0.484	0.234	-0.392	0.022	0.000	0.024	-0.386	0.149	-0.192
SLiveTPH	-0.437	0.191	-0.406	0.148	0.022	-0.020	-0.277	0.077	-0.234
SLiveBA	-0.397	0.158	-0.304	-0.082	0.007	-0.108	-0.467	0.218	-0.278
SPreFireBA	0.013	0.000	-0.005	0.060	0.004	0.022	-0.398	0.158	-0.239
logDSeedling	0.075	0.006	0.055	-0.039	0.002	0.002	0.316	0.100	0.197
PPreFireBA	-0.027	0.001	-0.028	0.207	0.043	0.071	-0.375	0.141	-0.176
logSapling	0.102	0.010	0.114	0.269	0.072	0.180	0.076	0.006	0.058
Aspect	0.028	0.001	-0.204	-0.126	0.016	-0.089	0.202	0.041	0.107
Slope	0.253	0.064	0.230	-0.294	0.086	-0.202	0.093	0.009	0.090
HeatLoad	0.196	0.038	-0.004	-0.229	0.052	-0.280	0.258	0.067	0.111

Note: Bolded estimates represent Pearson correlations > 0.300 to highlight dominant biophysical factors.

Appendix VII

Tiller Complex communities indicator species analysis.

Species	Indicator Species			Relative Abundance						Relative Frequency					
	MaxGrp	Value	p*	MaxGrp	LD-1	LD-2	MD-1	MD-2	HD-1	MaxGrp	LD-1	LD-2	MD-1	MD-2	HD-1
<i>Corylus cornuta</i>	LD-1	35.6	0.0008	LD-1	95	0	0	1	5	LD-1	38	0	0	5	20
<i>Linnea borealis</i>	LD-1	58.3	0.0004	LD-1	72	5	14	9	0	LD-1	81	50	54	73	15
Ferns	LD-1	28.3	0.4453	HD-1	30	5	16	11	38	LD-1	94	33	67	59	70
<i>Acer circinatum</i>	LD-1	24.6	0.123	LD-1	56	6	8	13	17	LD-2	44	58	29	45	25
<i>Mahonia nervosa</i>	LD-1	39.4	0.0498	LD-1	39	10	11	22	17	MD-2	100	100	96	100	95
Moss	LD-1	73.3	0.0002	LD-1	73	12	7	7	1	MD-2	100	83	92	100	80
<i>Vaccinium parvifolium</i>	LD-1	14.8	0.4727	LD-1	40	14	13	9	25	HD-1	38	33	38	36	45
<i>Rhododendron macrophyllum</i>	LD-2	73.7	0.0002	LD-2	6	74	14	1	4	LD-2	50	100	83	27	25
<i>Vaccinium membranaceum</i>	LD-2	22.1	0.0318	LD-2	2	66	9	3	20	LD-2	13	33	17	5	20
<i>Chimaphila umbellata</i>	LD-2	45.2	0.0002	MD-2	16	33	10	35	7	LD-2	56	83	63	55	25
<i>Rubus nivalis</i>	LD-2	7.5	0.5639	MD-2	14	23	3	39	22	LD-2	6	33	8	9	5
<i>Paxistima myrsinites</i>	LD-2	9.6	0.5529	HD-1	2	29	16	10	43	LD-2	6	33	21	18	20
<i>Chrysolepis chrysophylla</i>	LD-2	27.5	0.1036	LD-2	5	60	8	1	26	HD-1	6	8	46	0	90
<i>Gaultheria shallon</i>	MD-1	51.5	0.0002	MD-1	31	15	51	1	1	MD-1	75	50	100	23	25
<i>Holodiscus discolor</i>	MD-2	11.1	0.5339	MD-2	13	1	2	61	22	LD-1	31	8	8	18	25
<i>Symphoricarpos mollis</i>	HD-1	19.6	0.1442	HD-1	24	0	5	14	56	LD-1	50	8	21	32	35
<i>Arctostaphylos columbiana</i>	HD-1	16.3	0.2192	HD-1	3	19	30	2	46	LD-2	19	42	33	9	35
<i>Ceanothus integerrimus</i>	HD-1	33.2	0.002	HD-1	0	0	2	15	83	LD-2	50	75	67	23	25
<i>Ceanothus sanguineus</i>	HD-1	13.1	0.1182	MD-2	0	0	0	56	44	HD-1	0	0	13	32	40
<i>Ceanothus velutinus</i>	HD-1	87.3	0.0002	HD-1	1	0	2	0	97	HD-1	0	0	0	9	30
Forbs	HD-1	34.8	0.2454	HD-1	15	19	17	14	35	HD-1	100	100	96	100	100
<i>Garrya fremontii</i>	HD-1	46.1	0.0004	HD-1	2	10	9	1	77	HD-1	6	8	21	5	60
Graminoids	HD-1	70.7	0.0002	HD-1	6	6	6	11	71	HD-1	88	42	92	68	100
<i>Mahonia aquifolium</i>	HD-1	25.2	0.0042	HD-1	1	0	3	11	84	HD-1	6	0	4	5	30
<i>Prunus emarginata</i>	HD-1	15.3	0.035	HD-1	0	0	0	23	77	HD-1	0	0	0	9	20
<i>Ribes divaricatum</i>	HD-1	28.4	0.0008	HD-1	5	0	0	0	95	HD-1	6	0	0	0	30
<i>Ribes roezlii</i>	HD-1	10.8	0.2022	HD-1	3	0	4	39	54	HD-1	6	0	8	18	20
<i>Ribes sanguineum</i>	HD-1	19.7	0.0224	HD-1	2	0	16	3	79	HD-1	6	0	13	9	25
<i>Rosa spp.</i>	HD-1	17.8	0.6857	HD-1	26	13	23	11	27	HD-1	63	58	58	55	65
<i>Rubus leucodermis</i>	HD-1	61.9	0.0002	HD-1	1	0	1	16	83	HD-1	13	0	8	23	75
<i>Rubus parviflorus</i>	HD-1	8.7	0.4113	HD-1	14	2	5	21	58	HD-1	13	8	4	9	15
<i>Rubus ursinus</i>	HD-1	75.4	0.0002	HD-1	4	3	11	7	75	HD-1	75	67	88	59	100
<i>Salix scouleriana</i>	HD-1	19.2	0.0788	HD-1	3	0	19	23	55	HD-1	13	0	29	9	35
<i>Toxicodendron diversilobum</i>	HD-1	20	0.005	HD-1	0	0	0	0	100	HD-1	0	0	0	0	20
<i>Whipplea modesta</i>	HD-1	76.7	0.0002	HD-1	6	1	5	11	77	HD-1	94	17	67	77	100

Appendix VIII

Warner Fire communities indicator species analysis.

Species	Indicator Species			Relative Abundance							Relative Frequency						
	MaxGrp	Value	p*	MaxGrp	LD-1	LD-2	MD-1	MD-2	HD-1	HD-2	MaxGrp	LD-1	LD-2	MD-1	MD-2	HD-1	HD-2
<i>Chimaphila umbellata</i>	LD-1	18.3	0.1874	HD-1	0	3	0	2	94	0	LD-1	44	34	0	33	15	27
<i>Gaultheria shallon</i>	LD-2	24	0.0908	HD-1	2	41	15	1	41	0	LD-2	25	59	50	13	54	0
<i>Linnea borealis</i>	LD-2	25.9	0.0362	LD-2	16	54	22	2	6	0	LD-1	50	48	8	13	31	0
Moss	LD-2	63.6	0.0002	LD-2	6	64	20	3	6	1	HD-1	100	100	100	87	100	82
<i>Rhododendron macrophyllum</i>	LD-2	24	0.0216	LD-2	13	87	1	0	0	0	LD-2	19	28	8	0	0	0
<i>Acer circinatum</i>	MD-1	23.1	0.2214	MD-1	5	24	40	6	0	26	HD-2	50	52	58	67	23	73
Ferns	MD-1	79.2	0.0002	MD-1	1	6	79	9	1	3	MD-1	50	83	100	87	69	91
<i>Mahonia nervosa</i>	MD-1	23.4	0.5851	HD-2	16	22	23	5	10	23	HD-1	100	97	100	100	100	91
<i>Rubus parviflorus</i>	MD-1	33.6	0.0194	MD-1	0	1	50	30	2	16	HD-2	0	31	67	60	15	82
<i>Salix scouleriana</i>	MD-2	13.3	0.3017	MD-2	0	16	27	33	2	23	MD-2	0	24	25	40	15	27
<i>Whipplea modesta</i>	MD-2	45.3	0.0006	MD-2	3	6	11	45	22	13	HD-2	69	76	75	100	92	100
<i>Arctostaphylos columbiana</i>	HD-1	23.7	0.049	HD-1	0	1	0	8	77	14	HD-1	0	7	0	13	31	27
<i>Ceanothus integerrimus</i>	HD-1	34.4	0.0044	HD-1	0	7	34	18	41	0	HD-1	0	28	33	40	85	0
<i>Ceanothus sanguineus</i>	HD-1	47.4	0.0002	HD-1	0	11	23	1	62	3	HD-1	0	31	67	20	77	9
<i>Chrysolepis chrysophylla</i>	HD-1	21.8	0.0952	LD-1	42	15	0	36	6	1	HD-1	0	17	8	7	23	0
<i>Corylus cornuta</i>	HD-1	45.5	0.0012	HD-1	0	23	2	1	74	0	HD-1	0	45	33	20	62	9
Forbs	HD-1	31.6	0.3319	HD-1	11	8	22	16	32	11	HD-1	100	97	100	100	100	100
<i>Garrya fremontii</i>	HD-1	7.7	0.4161	HD-1	0	1	0	10	50	39	MD-2	0	3	0	20	15	18
Graminoids	HD-1	34.2	0.0112	HD-1	8	11	22	19	37	4	HD-1	81	66	83	60	92	36
<i>Holodiscus discolor</i>	HD-1	57.3	0.0004	HD-1	0	3	12	21	62	2	HD-1	6	52	58	33	92	18
<i>Mahonia aquifolium</i>	HD-1	39.8	0.0002	HD-1	12	5	5	5	74	0	HD-1	25	10	8	13	54	0
<i>Rhamnus purshiana</i>	HD-1	26.1	0.0116	HD-1	0	22	28	8	42	0	HD-1	0	24	50	13	62	0
<i>Ribes divaricatum</i>	HD-1	12.9	0.175	HD-1	0	7	20	17	56	0	HD-1	0	14	8	13	23	0
<i>Ribes sanguineum</i>	HD-1	9.5	0.4681	HD-1	0	20	8	17	41	13	MD-2	0	17	17	27	23	9
<i>Rosa spp.</i>	HD-1	22.3	0.1526	HD-1	12	15	13	25	26	9	HD-1	69	62	42	60	85	45
<i>Symphoricarpos mollis</i>	HD-1	33.1	0.0358	HD-1	3	4	9	16	39	29	HD-1	44	38	58	47	85	36
<i>Ceanothus velutinus</i>	HD-2	92.5	0.0002	HD-2	0	0	2	5	0	93	HD-2	0	0	8	33	0	100
<i>Paxistima myrsinites</i>	HD-2	45.2	0.0004	HD-2	2	2	0	13	0	83	HD-2	6	14	0	40	0	55
<i>Rubus nivalis</i>	HD-2	12.4	0.2925	LD-1	59	6	0	1	0	34	HD-2	6	10	0	7	0	36
<i>Rubus ursinus</i>	HD-2	67	0.0002	HD-2	1	2	15	10	5	67	HD-2	50	83	100	93	92	100
<i>Vaccinium membranaceum</i>	HD-2	19	0.0494	MD-2	3	0	26	41	0	30	HD-2	6	0	8	27	0	64
<i>Vaccinium parvifolium</i>	HD-2	24.6	0.0142	HD-2	10	26	4	3	3	54	HD-2	13	21	17	7	8	45

