

Mixed-Severity Fire and Salvage Logging in Dry Forests of Oregon's Western Cascades

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Abstract

Interest in PNW forests is shifting from a focus on old-growth forests alone to include the ecological value and processes of early-seral communities. However, focusing on the alpha and omega states of a linear successional model does not account for the suite of conditions derived from mixed-severity fire common in many forests. There has also been a continued interest in salvage logging as fire extent continues to increase in these forests. Therefore, examining the effects of mixed-severity fire and salvage logging on forest structure, the generator of early-seral and other vegetation communities, and tree regeneration communities has become critical. To do so, we sampled forest structure (1000 m² circular plots), understory vegetation (100 m² plots) and tree regeneration (100 m² plots) at 216 co-located plots stratified across unburned, low, moderate, high-severity and salvaged logged conditions 10 and 22-years post-fire on the west slope of Oregon's Cascade Mountains. We quantified the probability of mortality by tree species and cumulative effects of individual tree mortality on forest structure across the fire severity gradient and following salvage logging. We then investigated understory vegetation response to these post-fire and management conditions, as well as variability in tree regeneration. Our results presented in this report suggest mixed-severity fire is functionally important to *Pseudotsuga* forests of the PNW as it increases structural and compositional diversity in both the near and long-term. Despite increasing fire extent across much of the western U.S. and concerns regarding the resilience of many forests, our study highlights the benefits contemporary fires have on many ecological processes and supports the expansion of beneficial fire across these landscapes as society shifts towards learning to live with fire.

Introduction

Structurally diverse Douglas-fir/western hemlock (*Pseudotsuga menziesii/Tsuga heterophylla*, hereafter referred to as *Pseudotsuga* forests) forests have been the focus of conservation efforts for decades following extensive timber harvesting and declining populations of species reliant on them (Swanson and Franklin, 1992). These forests are found extensively throughout the western Cascade Range of the Pacific Northwest (PNW) and wildfires have played an important role in their structure and function. Episodic, stand-replacing fires occurring at intervals from 200 – 300 years have dominated perceptions of fire regimes in this forest type (Agee, 1993). These stand-replacing fires are inferred to have created the initial structural 'palette' by initiating the next generation forest. Over time, tree mortality at smaller spatial scales (e.g., windthrow, root rot pockets, density-dependent mortality) dominated the disturbance-induced change that vertically and horizontally diversified forest structure (Franklin et al., 2002). This fire regime and developmental pathway may dominate *Pseudotsuga* forests of the north Cascades, but there is evidence of an alternative developmental pathway as fire regimes vary along a south-north latitudinal gradient within the Cascades of the PNW (Weisberg and Swanson, 2003).

Several fire-history and age-structure studies in western Oregon's central Cascades have described mixed-severity fire in this forest type (Means, 1982, 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). Mean fire return intervals ranged from 95-150 years, although fire frequency was highly variable depending on local topographic and climate effects (Morrison and Swanson, 1990). These fire history and forest developmental studies relied heavily on age cohorts, having to infer disturbance processes from existing patterns in forest structure (Tepley et al., 2013). While highly beneficial because they capture long-term forest development, these methodologies are confounded by the cumulative effects of subsequent disturbance, loss of information and limited understanding of near-term effects. Therefore, questions remain about how mixed-severity fire initially restructures these forests and facilitates vertical and horizontal structural diversity.

Fire ecology in forested ecosystems has typically emphasized the interaction between disturbance regimes, tree composition and age-structure, and successional development (Pickett and White, 1985). This focus and the reliance on dendrochronology inherently exclude more ephemeral ecosystem responses to fire, such as understory vegetation development that may be as valuable to the ecosystem as broader successional processes. For example, understory vegetation species in early-seral forests are primary producers contributing to ecosystem energetics and food webs (Campbell and Donato, 2014), they

interact with forest structure to provide additional wildlife habitat attributes (Hagar, 2007), and directly make up, or indirectly support, much of the biodiversity in forest environments (Halpern and Spies, 1995; Reilly et al. 2006). Therefore, fire's functional role in forested ecosystems should also be characterized by near-term ecological responses that directly contribute to or influence many ecosystem attributes and processes (Odum, 1969; Hansen et al., 1991, Spies, 1998; Turner, 2010).

Understory vegetation has demonstrated differential response to variation in fire regimes, most commonly associated with fire frequency or magnitude (Wright and Heinselman, 1973; Huston, 1979). High-frequency, low-severity fires maintain biological communities in a pseudo steady-state or successional stage by mediating overstory density and promoting dominance of fire-resilient species (Weaver, 1943; Landers et al., 1995; Heyerdahl et al. 2001; Drewa et al., 2002; Zenner 2005). Lowfrequency, high-severity fire stimulates diverse early-seral vegetation communities otherwise excluded by dominance of long-lived overstory species (Swanson et al., 2010). These alternative response strategies manifest from interactions among direct and indirect fire effects that interrupt or terminate an individuals' life cycle, impact above and belowground reproductive tissues, consume or stimulate seedbanks, and alter the distribution of overstory trees and their competitive or facilitative interaction with understory vegetation (Bond and van Wilgen, 1996; Gray and Spies, 1997; Sugihara et al., 2006; Peterson and Reich, 2008). Over time, terrestrial vegetation can adapt to these selective pressures as fire functions as a limiting, regulating or stimulating ecological force (Noble and Slayter, 1981; Bond and Keeley, 2005; Keeley et al., 2011). We hypothesized vegetation would exhibit a more diverse response to a mixedseverity fire gradient than just early-seral and old-growth communities that have received greater research and management attention (Halpern, 1988; Franklin and Spies, 1991; Swanson et al., 2010, 2014; Dodson et al., 2012; Franklin and Johnson, 2012; Campbell and Donato, 2014).

Three fire regime types are typically described by commonly used classification systems (Agee 1993). The structure and composition of forests with unaltered disturbance regimes are the expression of the functional traits of available tree species and these disturbance regimes. High-frequency, low-severity fires are chronic disturbances that mediate overstory density and promote dominance of fire-tolerant species such as longleaf and ponderosa pine forests (Weaver, 1943; Landers et al., 1995; Heyerdahl et al. 2001; Drewa et al., 2002; Zenner 2005). Low-frequency, high-severity fires are episodic disturbances promoting dominance of species with resilience mechanisms (e.g., fire-serotiny) capable of responding to stand-replacing events, such as lodgepole and jack pine forests of North America (McCune, 1988; Clark, 1991). Mixed-severity (a.k.a. moderate-severity) fire regimes are the third fire-vegetation interaction, but are arguably the least understood regime type in forest systems despite increasing evidence they historically were more common than initially observed (Baker and Ehle, 2001; Perry et al. 2011; Tepley

et al., 2013; Tepley and Veblen, 2015; Reilly et al., in review). Vegetation interactions with mixed-severity fire regimes may exhibit characteristics of both chronic and episodic disturbance across a landscape, or an alternative interaction not currently recognized or readily understood (Perry et al., 2011, Halofsky et al., 2011).

The Intermediate Disturbance Hypothesis (IDH) provides a theoretical framework for a fire-vegetation interaction that could be emblematic of mixed-severity fire regimes (Connell, 1973). In theory, the highest biodiversity within an ecosystem is derived from moderate frequency or magnitudes of disturbance. By definition, mixed-severity fire regimes exhibit a gradient in fire effects but are generally hypothesized to have the greatest proportion of area burning with moderate severity (Agee, 1993); conditions often thought of as mixed-severity at small spatial scales. Fires burning more frequently or with higher severity within these ecosystems would result in lower diversity because of local extinction of species not adapted to frequent fires (Engbar et al., 2014). Alternatively, fires burning less frequently or at lower severity would also result in lower diversity as species are competitively excluded by long-lived, fire-intolerant individuals. These disturbance-driven effects should be expressed in overstory tree composition and regeneration dynamics in ecosystems dominated by a mixed-severity fire regime, despite the current lack of evidence supporting the IDH in forest ecosystems. We hypothesized tree regeneration diversity would be highest following moderate-severity fire, and that regeneration communities would differentiate along a disturbance gradient.

The reliance on dry-forest ecosystems with limited tree species to describe mixed-severity fire regimes may contribute to the lack of evidence supporting a fire-vegetation interaction specific to mixed-severity fire regimes. In addition, fire regimes in most dry forest systems have been highly altered, requiring the use of dendrochronology to infer disturbance processes from fire history and existing patterns of age structure and composition. This prevents direct observation of fire effects on existing forest structure and tree regeneration that contributes to current and future structural complexity. Fortunately, there are opportunities to investigate mixed-severity fire regimes in the more mesic Douglas-fir/western hemlock forests (*Pseudotsuga menziesii/Tsuga heterophylla*, hereafter referred to as *Pseudotsuga* forests) of the Pacific Northwest (PNW). These forests have a more abundant tree species pool and a mixed-severity fire regime that has not deviated significantly from their mean fire return interval (Means, 1982; Morrison and Swanson, 1990; Kushla and Ripple, 1997; Weisberg, 2004; Tepley et al., 2013; Dunn and Bailey, 2016; Reilly et al., *in review*). Therefore, we leveraged several fires burning between 10 and 22-years prior to sampling to quantify mixed-severity fire effects on forest structure, understory vegetation and tree regeneration response to those conditions, and the impacts of salvage logging on these ecological attributes.

Methods

Study Area

Pseudotsuga forests are one of the most widely distributed forest types in the PNW. Several fire-history and age-structure studies in western Oregon's central Cascades have described mixed-severity fire regimes in this forest type (Means, 1982; Morrison and Swanson, 1990; Weisberg and Swanson, 2003; Weisberg, 2004; Tepley et al., 2013). Mean fire return intervals ranged from 95-150 years with effects spanning a disturbance gradient from low to high-severity (Means, 1982; Morrison and Swanson, 1990; Weisberg, 2004). Low and 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 effects still observed in contemporary fires (Kushla and Ripple, 1997; Dunn and Bailey, 2016; Reilly et al., *in press*).

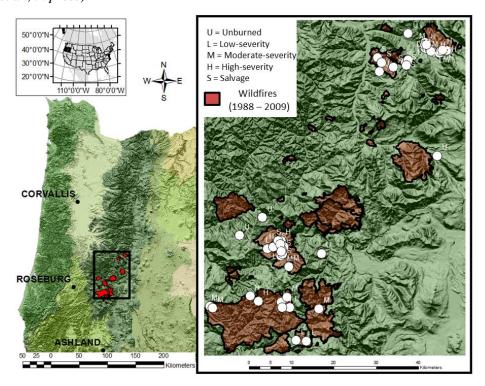


Figure 1: A map depicting fire extents and plot locations across our study area in western Oregon's central Cascade Range.

Pseudotsuga forests of western Oregon's 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 focused our sampling in fires 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) capturing much of the 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 oC in August, to 4.3 oC in December, and average minimum temperatures range from 9.1 oC in August to -2.8 oC 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 (*Pseudotsuga menziesii* (Mirb.) Franco), sugar pine (*Pinus lambertiana* Dougl.) and incense-cedar (*Calocedrus decurrens* (Torr.) Florin) are common fire-tolerant tree species and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), grand fir (*Abies grandis* (Donn ex D. Don) Lindl.), and Pacific yew (*Taxus brevifolia* Nutt.) are common fire-intolerant tree species in these forests. Giant chinkapin (*Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmqvist), bigleaf maple (*Acer macrophyllum* Pursh), Pacific madrone (*Arbutus menziesii* Pursh) and Pacific dogwood (*Cornus nuttallii* Audubon ex Torr. & A. Gray) are common hardwood associates. The potential vegetation type transitions to silver fir (*Abies amabilis* (Dougl. Ex Loud.) Dougl. Ex Forbes) and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) at higher elevations, with dry Douglas-fir, Oregon white oak (*Quercus garryana* Dougl. ex Hook) and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests occurring at lower elevations.

Sampling Design

Several large fires burned a total of 76,746 ha within our study area between 1987 and 2014 (Figure 1), but 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. We randomly located six plots with four nested subplots (sample unit) within each of three fire-severity classes (i.e., low, moderate, high) and salvage logged stands at two time-since-fire periods (10 and 22-years post-fire). An additional six plots were placed in unburned stands as a reference group. 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 classes were identified from resampled maps (to 90x90 m pixels to more closely align with plot size) initially created by the Monitoring Trends in Burn Severity program. This program derives thresholds by relating the differenced normalized burn ratio (dNBR) to Composite Burn Index field data (Key and Benson, 2005, MTBS, 2014). Sampling was constrained to mature or old-growth

(M/OG) *Pseudotsuga* forests (prior to most recent fire) by evaluating agency GIS databases that included stand age, direct anthropogenic disturbance, and 100 years of documented fire history. We also evaluated sample plots in the field for multi-storied conditions or the presence of >70 cm DBH trees. The reliability of fire history records diminishes as one progresses back in time, but are confident that we only sampled M/OG forests in this study that did not experience fire or harvest for > 100 years. Only the southerly aspect of the Warner Fire was sampled so that forest type and climatic conditions remained comparable across fire sites.

Overstory Attributes

We sampled surviving trees and snags in four nested subplots within 1-ha circular plots. Subplot one was centered on the plot and subplot two was centered 36.6 m away along a random azimuth. Subplots three and four were centered systematically at 36.6 m from plot center at an azimuth of 120 and 240 degrees from the azimuth between subplots one and two. Surviving trees and standing or fallen coarse wood 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 surviving trees or snags >70 cm DBH were sampled within the 1-ha plot to capture large, spatially dispersed individuals for plot-level averages. We recorded species, DBH, total height and crown base height for all surviving trees. We recorded species, DBH, condition (i.e. standing whole, standing broken, fallen), height, and percent combustion of sapwood or heartwood on snags. Pre-fire snags were visually identified and separated from fire-created snags when bole sapwood was partially combusted or converted to charcoal because this suggests a lack of bark and decay advanced enough to support partial combustion at the time of the fire.

We reconstructed pre-fire live basal area (m² ha¹) and stems per hectare (# ha¹) as the sum of current surviving tree estimates and sampled snags or logs. We quantified post-fire tree basal area, density, quadratic mean diameter (QMD), and canopy base height (CBH) for live trees at the time of sampling. We differenced pre- and post-fire estimates to quantify observed fire severity at each plot and subplot for use in analyses. Estimates were made at the subplot and plot-level to evaluate the influence of overstory structure on understory vegetation at both scales. We used linear mixed-models to test differences among severity classes 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 were sampled for individual species at four 100 m^2 (10 x 10 m) plots centered at our tree/snag subplots. These vegetation plots were the units of measure for all understory vegetation analyses. We visually estimated cover for individual shrub and subshrub species, but combined ferns, graminoids, forbs and moss into individual functional groups to facilitate more rapid sampling and reduce the influence of highly ephemeral species potentially more abundant 10-years post-fire than 22-years post-fire. 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 for statistical analyses. 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 particularly when a species exceeded 25% cover. We considered species present in unburned plots as 'residual' and those found only within burned plots as 'colonizers' (a.k.a. invaders) (Dyrness, 1973). 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 tallest two height classes were considered dominant seedlings and all regenerating trees > 2.54 cm DBH were considered saplings for analyses.

Tree regeneration

Tree seedlings were sampled at 100 m2 (10 x 10 m) plots centered on the forest structure subplots. Each plot was partitioned into quadrants and seedlings (i.e., any regenerating tree species <2.54 cm DBH) were tallied by species in the following height classes: 1-50 cm, >50-150 cm, >150 cm. Regenerating trees >2.54 cm DBH were considered saplings in burned plots and sampled according to our tree structure protocol. Surviving saplings were separated from regenerating trees by evaluating each tree for evidence of bole or crown scorch. Live trees $\leq 10 \text{cm}$ DBH in unburned plots were considered regenerating trees for these conditions. White fir transitions to grand fir along a latitudinal gradient within our study area and are known to hybridize, so we combined them into a composite Abies species.

Key Findings

Our stratified sampling based on dNBR and MTBS classification captured a gradient in tree-based fire severity. 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. Basal area mortality at moderate-severity plots was 16.2% (SE = 3.8) higher than low-severity plots, with only 17.3% (SE = 4.3) more tree ha⁻¹ killed. 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, even though this only represented a 20.9% (SE = 4.3) increase in tree ha⁻¹ mortality. Only 31% of our high-severity plots had surviving trees, which ranged from 76.6% - 97.4% basal area mortality.

Tree Mortality

We estimated probability of mortality for six conifer species from 5,079 samples. We observed statistical differences among species within fire-tolerance groups, as well as across *a priori* fire severity classes, and in response to DBH. We tested plot-level environmental variables (i.e., elevation, slope, aspect, latitude, and heat load) and number of years post-fire for statistical significance, but none were significant at an $\alpha \le 0.05$. DBH ranged from < 4.0 to > 100 cm for all tree species, though fire-tolerant trees (dominated by Douglas-fir) had a broader range and higher average DBH than fire-intolerant trees. The probability of mortality for all fire-tolerant trees decreased by 1.03 times (95% confidence interval (CI) of 1.026 - 1.032) for each centimeter increase in DBH. True firs responded similarly to increasing DBH, (estimate = 1.03, 95% CI of 1.017 - 1.048, p-value < 0.0001), but this factor was not as influential for western redcedar (mean = 1.020, 95% CI of 1.008 to 1.032, p-value < 0.0001). 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).

The probability of mortality varied by species and included the interaction between species and DBH for fire-intolerant trees. Incense-cedar had the lowest probability of mortality for fire-tolerant species, 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 for Douglas-fir and sugar pine than incense-cedar, respectively. Western hemlock had the lowest probability of mortality for fire-intolerant trees <30 cm DBH, but true fir trees transitioned to having the lowest probability of mortality thereafter. Western redcedar had the highest probability of mortality among all fire-intolerant species until its DBH exceeded 52 cm, at which point it exhibited a lower probability of mortality than western hemlock.

As expected, the probability of mortality increased with increasing fire severity classification. While this is typically assumed, including fire severity class as a factor in our analysis allowed us to directly test the significance and magnitude of this effect. We've included unburned plots in this analysis but their timing of mortality was not specifically identified. We did not observe insect outbreaks or

significant mortality from pathogens, over 97% of the sampled snags were in decay classes three or less (Cline et al., 1980), and 51.1% were still standing. This suggests these trees likely died within the past three decades dominantly from competition, but this remains uncertain so these estimates are best viewed as a basic representation of background mortality for these species. Fortunately, the observed trends responded as expected given the relative shade-tolerance of out sampled species, and their stand dominance indicated by DBH.

Snag Dynamics

Snag fall was influenced by fire severity, species, and DBH as well as interactions among these factors. We tested plot level environmental variables for statistical significance, but none were significant at an $\alpha \le 0.05$. We did not observe a statistical difference between the proportion of snags fallen between our 10 or 22-years post-fire sites, so we report the cumulative proportion of snags fallen together. We observed variation among species within a severity class, but error bars overlapped for many species so these differences were not always significant. The proportion of snags felled by 10-22-years post-fire decreased with increasing DBH for all species. The proportion of fallen snags increased with increasing fire severity with the exception of Douglas-fir, that had a higher proportion felled following low-severity fire after accounting for the effect of DBH. Sugar pine snags had the highest proportion felled across all fire severity classes, and western redcedar and incense-cedar were the least likely to fall. Overall, snag DBH and species influenced their transition to logs, but the proportion fallen by 10-22 years post-fire depended on fire severity.

Snag fragmentation was influenced by species, DBH, fire severity class and time-since-fire, with a statistical interaction occurring between fire severity and species. Not all species of snags were sampled at each time-since-fire period or severity class, and the diameter distribution varied with species and severity class. Proportion of snags fragmented by 10 or 22-years post-fire was positively correlated with DBH and fire severity for all species, although low and moderate-severity plots were not statistically different. 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 height of fragmented snags by 22 years post-fire could be estimated by the equation: Height (m) = 4.183237 (1.069606) + 0.171947 (0.009519)*DBH - 3.701433 (1.206324)*22Yrs Post-fire. This regression equation only accounted for a small proportion of observed variation (marginal $R^2 = 0.27$ and conditional $R^2 = 0.35$).

We observed little difference in log metrics by severity class except for differences between unburned and high-severity plots 22-years post-fire. Increased snag fragmentation between 10 and 22-years post-fire, especially following high-severity fire, contributed to this increase as snags transitioned to logs. We expect differences by severity class to increase over time because a greater abundance of larger diameter snags were present in higher severity classes and will continue to fall and fragment into the future.

Forest Structure

Plot-level live structural attributes varied significantly across our fire severity gradient (Figure 2). Pairwise comparisons of live basal area among all fire severity classes were significantly different at an $\alpha \leq 0.05$. We also observed significant differences among live trees ha⁻¹, except between low- and moderate-severity classes. Basal area of snags was inversely correlated with estimates for surviving trees, but differences among fire severity classes were not as significant. Snag density was highly variable and didn't exhibit a statistically significant difference among fire-severity classes. Quadratic mean diameter (QMD) and mean crown base height (CBH) were positively correlated with fire severity class as incrementally larger trees were killed. Only the largest, fire-tolerant trees survived high-severity fire and therefore these sites had the largest QMD and CBH for surviving trees.

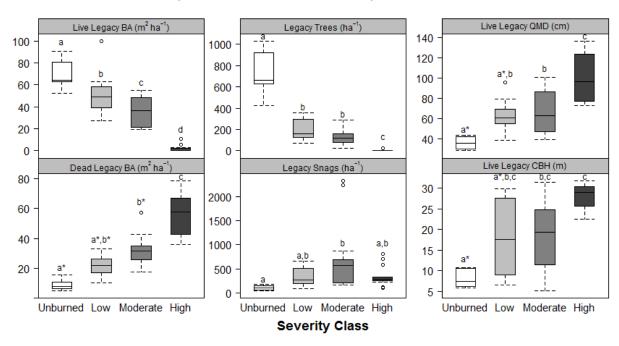


Figure 2: Figure depicting plot-level structural attributes across our fire severity gradient. We observed significant differences in forest structure commensurate with fire severity classes, although low and

moderate-severity conditions show little difference in some metrics. Lower case letters indicate statistically different pair-wise comparisons at and $\alpha \le 0.05$.

Live and dead structural attributes varied more within than among plots for each fire severity class, although variation was highest when plots were evaluated across all conditions (Table 1). Average within-plot CV for tree basal area and density were positively correlated with fire severity and increased more between low and moderate-severity than unburned and low-severity plots. In contrast, average within-plot CV for snag basal area and density generally decreased with increasing fire severity. The higher within-plot CV values observed for snag basal area in unburned forests were likely a function of the relatively low abundance of snags in this condition, making the CV estimate sensitive to large individuals. The CV was similar among plots within each fire-severity class, suggesting plot-level estimates were equally variable within a severity class. The greatest variation was observed when all plots were evaluated together (i.e., landscape scale) except snag basal area, suggesting total variation was more than the subparts (i.e., individual severity classes). Structural attributes were more homogeneous following high-severity fire because a large proportion of these plots had 100% mortality.

Table 1: Coefficient of variation by severity class at multiple scales.

Severity Class									
	Unbur	ned	Low		Moderate		High		Burned
	Within	Among	Within	Among	Within	Among	Within	Among	Landscape
Attribute	Mean (SD)	Mean	Mean (SD)	Mean	Mean (SD)	Mean	Mean (SD)	Mean	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

Understory Species Response

Wildfire increased the total number of species present in our sample by 100% as colonizers mixed with residual species. *Vaccinium membranaceum* was observed in 1 unburned plot, but we considered it a colonizer species as previously observed following clearcut harvesting in this region (Halpern and Lutz, 2013). A total of 46 understory species/functional groups were identified, but only 36 were common enough (i.e. present in >5% of our plots) to be used in our community analyses (Table 2). Neither residual nor colonizers responded consistently across our sampled fire severity gradient, so we classified each into one of three disturbance response-groups (Figure 3). These groups (i.e. disturbance-sensitive, disturbance-stimulated, and disturbance-amplified) represent dominant disturbance response-curves resulting from direct fire effects, intra-species competition, and tolerance to changes in microclimatic conditions.

Disturbance-sensitive species comprised 22% of all sampled species or functional groups, all of which declined in relative abundance with increased fire severity. Local (plot-level) extirpation of individual disturbance-sensitive species likely occurred, but none were extirpated entirely from a fire severity class. Approximately 43% of all residual species were disturbance-sensitive, including the common shade-tolerant species *Acer circinatum*, *Rhododendron macrophyllum*, and *Corylus cornuta*. Several residual low-shrubs were also disturbance-sensitive, including *Berberis nervosa* and *Gaultheria shallon*.

Table 2: Sampled species list with classification as residual or colonizer species, response type and relative abundance value by observed fire severity class.

and retained assurance variety observed	· · · · · · · · · · · · · · · · · · ·	Response Veg.		Relative abundance (%)				
Species/functional group	Identifier	type	type	unburned	low	moderate	high	
Acer circinatum Pursh	ACCI	sensitive	residual	44	11	23	22	
Chimaphila umbellata (L.) W.P.C. Barton	CHUM	sensitive	residual	66	4	24	6	
Corylus cornuta Marshall	COCO	sensitive	residual	55	5	31	9	
Gaultheria shallon Pursh	GASH	sensitive	residual	45	22	25	8	
Berberis nervosa Pursh	BENE	sensitive	residual	39	16	19	25	
Moss	MOSS	sensitive	residual	51	25	15	9	
Rhododendron macrophyllum D. Don	RHMA	sensitive	residual	46	15	31	8	
Rubus nivalis Douglas ex Hook.	RUNI	sensitive	residual	60	3	11	26	
Vaccinium parvifolium Sm.	VAPA	sensitive	residual	43	8	21	28	
Arctostaphylos columbiana Piper	ARCO	stimulated	colonizer	0	7	61	33	
Chrysolepis chrysophylla (Douglas ex Hook.) Hjelmq.	CHCH	stimulated	residual	2	26	42	31	
Ferns	FERN	stimulated	residual	9	29	38	24	
Linnaea borealis L.	LIBO	stimulated	residual	36	4	43	18	
Rhamnus purshiana DC.	RHPU	stimulated	colonizer	0	42	52	7	
Ribes sanguineum Pursh	RISA	stimulated	colonizer	0	40	27	34	
Rosa spp.	ROSA	stimulated	residual	21	26	27	26	
Ceanothus integerrimus Hook. & Arn.	CEIN	amplified	colonizer	0	23	23	54	
Ceanothus sanguineus Pursh	CESA	amplified	colonizer	0	10	43	46	
Ceanothus velutinus Douglas ex Hook.	CEVE	amplified	colonizer	0	0	5	95	
Forbs	FORB	amplified	residual	7	24	29	40	
Garrya fremontii Torr.	GAFR	amplified	colonizer	0	6	13	81	
Graminoids	GRAM	amplified	residual	7	14	14	64	
Holodiscus discolor (Pursh) Maxim.	HODI	amplified	residual	4	23	29	44	
Mahonia aquifolium (Pursh) Nutt.	BEAQ	amplified	residual	1	26	19	54	
Paxistima myrsinites (Pursh) Raf.	PAMY	amplified	residual	8	5	7	80	
Prunus emarginata (Douglas) Eaton	PREM	amplified	colonizer	0	0	0	100	
Ribes divaricatum Douglas	RIDI	amplified	colonizer	0	24	23	54	
Ribes roezlii Regel	RIRO	amplified	colonizer	0	0	14	86	
Rubus leucodermis Douglas ex Torr. & A. Gray	RULE	amplified	colonizer	0	2	9	89	
Rubus parviflorus Nutt.	RUPA	amplified	residual	1	4	38	57	
Rubus ursinus Cham. & Schltdl.	RUUR	amplified	residual	3	5	17	75	
Salix scouleriana Barratt ex Hook.	SASC	amplified	colonizer	0	13	15	73	
Symphoricarpos mollis Nutt.	SYMO	amplified	residual	14	17	24	45	
Toxicodendron diversilobum (Torr. & A. Gray) Green	TODI	amplified	colonizer	0	23	0	77	
Vaccinium membranaceum Douglas ex Torr.	VAME	amplified	colonizer	4	5	40	51	
Whipplea modesta Torr.	WHMO	amplified	residual	5	28	24	43	
Rare species (occurred in <5% of plots)	Se	Severity association						
Oemleria cerasiformis	OECE	unburned	residual	100	0	0	0	
(Torr. & A. Gray ex Hook. & Arn.) J.W. Landon								
Chimaphila menziesii (D. Don) Spreng.	CHME	low	colonizer	0	100	0	0	
Cytisus scoparius (L.) Link	CYSC	moderate	colonizer	0	0	100	0	
Lonicera ciliosa (Pursh) Poir. ex DC.	LOCI	low/moderate	colonizer	0	38	38	24	
Philadelphus lewisii Pursh	PHLE	moderate	colonizer	0	5	95	0	
Acer glabrum Torr.	ACGL	high	colonizer	0	0	0	100	
Amelanchier alnifolia (Nutt.) Nutt. ex M. Roem.	AMAL	high	colonizer	0	35	0	65	
Gaultheria ovatifolia A. Gray	GAOV	high	colonizer	0	49	0	51	
Sambucus nigra L.	SANI	high	colonizer	0	0	0	100	
Sambucus racemosa L.	SARA	high	colonizer	0	0	44	56	

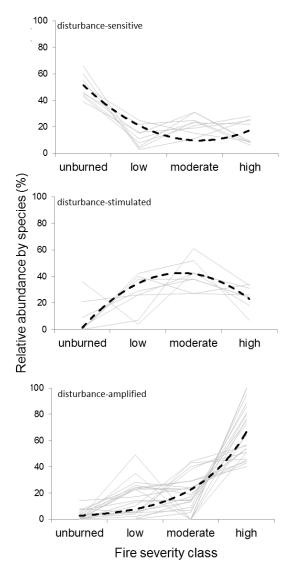


Figure 3: Three dominant disturbance response-curves were observed across a fire severity gradient for common understory species and functional groups. Fire severity was based on the proportion of observed overstory basal area mortality at the time of sampling. Grey lines are the relative abundance of individual species or functional groups, and the black line was fitted to the mean across all species within a response type to depict the dominant trend.

Disturbance-stimulated species responded positively to fire occurrence, but their greatest relative abundance was observed following low or moderate-severity fire (Figure 3). This response-group included 24% of all sampled species, of which 36% were residual and 64% were colonizers. These included residual species such as *Chrysolepis chrysophylla* or *ferns* that are tolerant of both shady and open environments, but may experience increased mortality following high-severity fire and therefore have reduced vegetative propagation. Moderately fire-tolerant, these species may rely on both resprouting

and soil seedbanks to take advantage of newly available resources and reduced competition to increase in relative abundance (Morgan and Neuenschwander, 1988; Stickney et al., 2000; Harrod et al., 2007). Colonizers such as *Arctostaphylos columbiana* and *Ribes sanguineum* responded positively to fire, but also exhibited a decrease in abundance as severity increased from moderate to high 10 and 22-years post-fire.

The relative abundance of many understory species increased markedly with increasing fire severity, exhibiting what we considered a disturbance-amplified response (Figure 3). This response-group included 54% of all sampled species (36% and 64% residuals and colonizers, respectively), or 70% of all colonizers and 39% 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 combined as functional groups fitting this response type. Many of these species germinate from long-lived soil seedbanks and are highly competitive in open conditions. Additionally, many produce soft mast consumed by avian species that further support their colonization or expansion post-fire (McComb, 2008; Campbell and Donato, 2014). The majority of species commonly associated with early-seral communities exhibited a disturbance-amplified response and dominated these highly-disturbed sites.

Understory Community Response

We identified five different understory communities across our disturbance gradient within the Tiller Complex (Figure 4a). Plots within these 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. $A \ge 0.10$) except for the two moderate-disturbance communities. 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 $R^2 = 0.711$. Axis 1 was positively correlated with fire severity as estimated by multiple factors. The most significant biophysical factor associated with axis 2 was elevation.

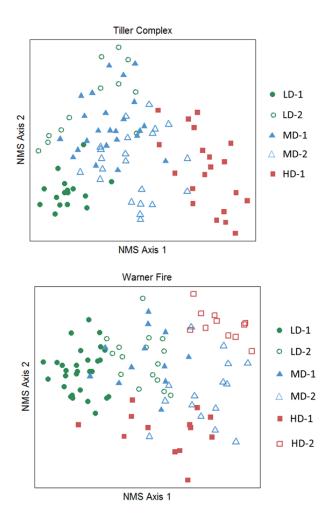


Figure 4: Ordination of vegetation communities along axes 1 and 2, of a 3-dimensional solution, from non-metric multidimensional scaling. Axis 1 dominantly represents the sampled disturbance severity gradient, with increasing severity from left to right, for both fire sites. Axis 2 was most closely associated with elevation for both fire sites.

Six understory communities were identified across our disturbance gradient within the Warner Fire (Figure 4b). 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. 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 the disturbance gradient, but mixed significantly with elevation and other biophysical factors. Elevation was again the most significant biophysical factor influencing separation along axis 2.

Both biological and physical factors influenced community response to mixed-severity fire (Figure 5). The benefit of our random forest analysis was that it ranked all biophysical factors by their relative importance in classifying plots into a vegetation group, which cannot be determined from ordination axes alone. 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 correlated or non-influential factors. Only four biophysical factors were retained as important at the Tiller Complex (Figure 5), improving classification accuracy to an 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%. Plot-level surviving overstory basal area was the most important biophysical factor influencing post-fire understory community response at both fires. Variation in subplot-level surviving overstory basal area, pre-fire basal area, and the abundance of dominant regenerating trees were other important biological factors (Figure 5). Elevation was the only important physical-related factor influencing community response in our analysis. One of our least influential factors was a priori severity class as defined from remote sensing, suggesting the ecological resolution of this metric is coarse and additional information is necessary to quantify the ecological effects of fire.

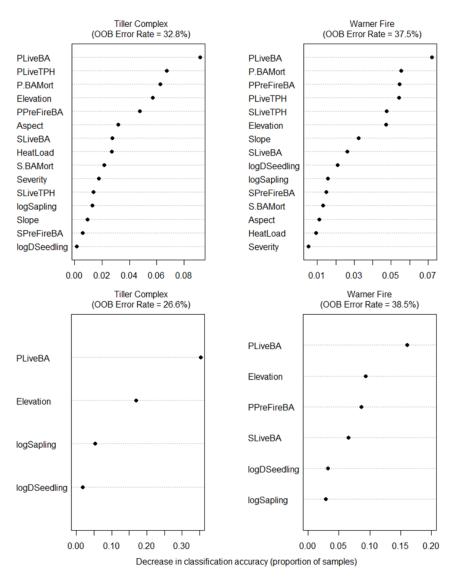


Figure 5: Biophysical factors influencing vegetation communities ranked by their importance measure estimated from the ensemble model random forest. The graphs on the top depict all biophysical factors considered in this analysis and those on the bottom depict the dominant factors determined using a manual stepwise selection procedure with the criteria that the out-of-bag classification error rate was either reduced or remained within 1% of our initial estimate.

Tree Regeneration

Fire increased regeneration abundance relative to unburned forests except at sites experiencing very low severity where basal area mortality did not exceed observed mortality from other agents (Figure 6). Abundance was most closely associated with fire severity estimated at the 1-ha plot scale, and exhibited a nonlinear response. Our estimates suggest the highest median regeneration abundance

followed moderate-severity fire, with the highest observed abundance between 25% - 50% basal area mortality. The absolute maximum estimates observed at any regeneration plot was 81,500 trees ha⁻¹ at the Tiller Complex experiencing 31% basal area mortality at the 1-ha plot-scale, and 72,500 and 73,800 trees ha⁻¹ at the Warner Fire following 36% and 100% basal area mortality, respectively. These estimates were much greater than the maximum of 8,300 trees ha⁻¹ observed in unburned forests. No other biophysical factors were statistically correlated with regeneration abundance after accounting for fire severity.

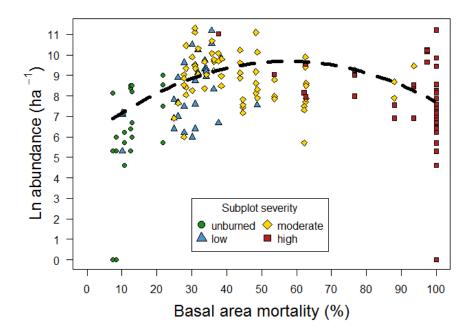


Figure 6: Correlation of the natural logarithm of total tree regeneration abundance with observed basal area mortality at the full plot-scale 10 and 22-years post-fire. No statistical difference was observed between the fires sites. Symbols and colors reflect observed subplot fire severity (basal area mortality) within each plot to demonstrate the sub-hectare variation. Unburned = no fire-induced mortality, low <25%, moderate = 25-75%, and high >75%.

Species richness of regenerating trees was statistically correlated with fire severity at the 1-ha plot-scale, exhibiting a nonlinear trend similar to regeneration abundance (Figure 7). On average, species richness was highest following moderate-severity fire, increasing to an average of four species regenerating in each regeneration plot from approximately two species in the least disturbed forests (Figure 3). As severity increased beyond moderate levels, richness declined on average to two species following 100% basal area mortality. The absolute maximum richness observed was at a plot with approximately 80% basal area mortality, although this plot was an outlier (Figure 7). In general, the highest species richness was observed between 25% and 50% basal area mortality where six to seven

species were commonly observed. All but two of the 13 regenerating tree species sampled were present in both fires. The exceptions were ponderosa pine, only observed in five regeneration plots (moderate and high-severity only) at the Tiller Complex, and Pacific silver fir that was only observed at three regeneration plots (high-severity plots only) in the Warner Fire around 1300 m elevation. 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, sugar pine and grand/white fir were commonly encountered regenerating conifers.

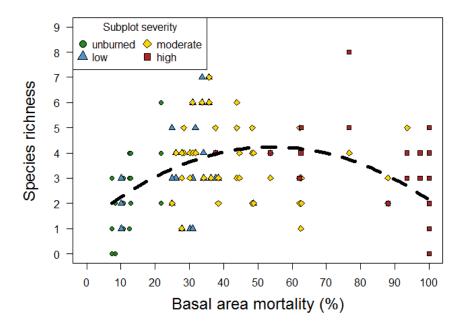


Figure 7: Figure depicting tree species richness as a function of plot-level basal area mortality. Dashed line represents average estimates across the continuous disturbance gradient and exhibits highest average values following moderate-severity fire, providing evidence for the Intermediate Disturbance Hypothesis.

Regeneration communities varied significantly across the fire severity gradient and our time since fire sites. The overall chance-corrected within-group agreement among the six regeneration groups was A = 0.197 (p-value <0.0001). The strength of the compositional difference varied by specific pairwise comparisons, but all were statistically different except high-severity at Tiller Complex and high-severity sites with dry edaphic conditions at Warner Fire. The two regeneration communities following high-severity fire at Warner Fire had the strongest compositional differences of all pairwise comparisons. The relative abundance of shade-tolerant tree species decreased with increasing fire severity, except for the prevalence of a high abundance of western hemlock following high-severity fire at moist sites in the Warner Fire (Figure 8).

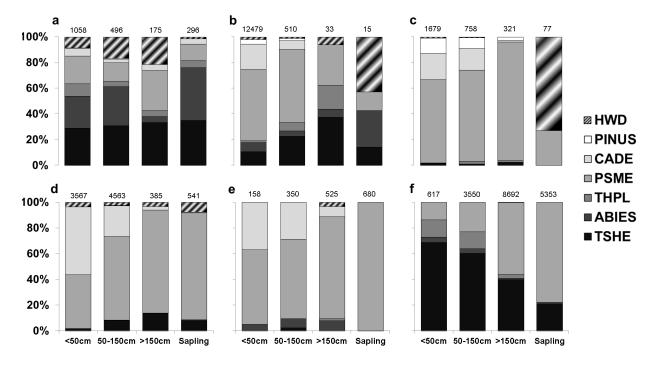


Figure 8: Regeneration composition by height class across a mixed-severity fire gradient at two timesince fire sites: a) unburned forests, b) mixed-severity 10 years post-fire, c) high-severity 10 years post-fire, d) mixed-severity 22 years post-fire, e) dry high-severity sites 22 years post-fire, and f) and wet high-severity sites 22 years post-fire. HWD = hardwoods, PINUS = pine species, CADE = incense-cedar, PSME = Douglas-fir, THPL= western redcedar, ABIES = true fir species, TSHE = western hemlock.

The spatial distribution of regenerating trees varied by species across the fire severity gradient (Figure 9). Unburned forest had the highest percent (39%) of quadrants without any regenerating trees, although the majority of these plots were fully occupied by overstory trees. The Tiller Complex lacked regenerating trees in 4% and 27% of the quadrants 10 years after mixed-severity and high-severity fire effects, respectively. At the Warner Fire, regenerating trees were not present in 11% and 16% of the quadrants following mixed-severity and high-severity fire effects, respectively. When we considered a larger spatial scale (i.e., 10 x 10 m), only three unburned regeneration plots and two high-severity regeneration plots at the Tiller Complex lacked regenerating trees. In general, conifers and hardwoods were more spatially frequent following mixed-severity fire at both fire sites relative to unburned forests high-severity fire area, except some shade-tolerant species regenerating well in unburned forests and at wet edaphic sites in the Warner Fire. Overall, Douglas-fir had the greatest spatial distribution of all species at both fire sites.

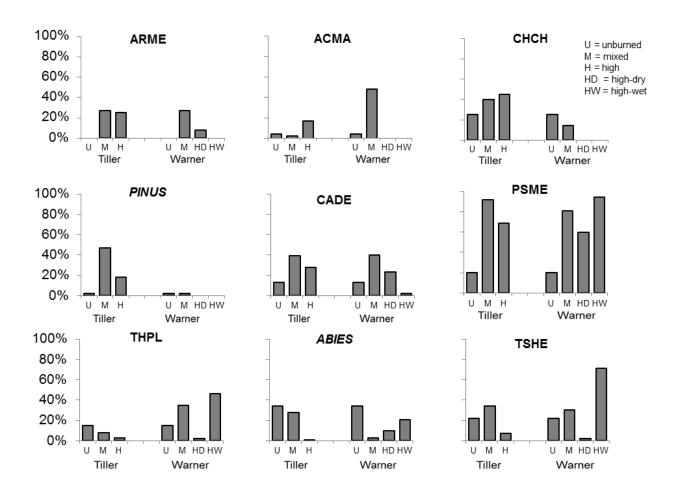


Figure 9: Frequency of quadrants where individual species were present. The dominant difference in regeneration response among these fires was a decrease in the presence of *Pinus* species at Warner Fire, and abundant shade-tolerant species following high-severity fire at the Warner Fire. CADE = incensecedar, PSME = Douglas-fir, TSHE = western hemlock, THPL= western redcedar, TABR = Pacific yew, ABIES = true fir species, and PINUS = all pine species.

Salvage Logging

Our salvage logging analyses focused on comparisons between high-severity fire and salvage sites only, except when unburned conditions were included to investigate changes associated with disturbance. We did this because salvage logging did not represent a continuous disturbance gradient as observed with increasing fire severity. Additionally, salvage operations focus primarily on sites burned at high severity because of concerns regarding fire effects at this magnitude of disturbance.

Forest Structure

Salvage logging focuses on removal of dead trees primarily to utilize the economic value quickly lost to decay. Variation in the abundance of snags and logs becomes the primary near-term effect these operations have on post-fire forest structure following high-severity fire. We reconstructed pre-fire basal area for our sample plots burned at high-severity or salvage logged, and then contrasted basal area at 10 or 22-years post-fire when sampled (Figure 10). We also contrasted log volume derived from the line intercept method and volume calculations (de Vries, 1973). Unsurprisingly, salvage logging decreased the abundance of snags at both 10 and 22-year post-fire sites. Over time, legacy snag dynamics did not appear to vary by management strategy as snags continued to fragment and fall at similar rates. This resulted in an accumulation of logs, with a more significant separation after 22-years post-fire. This appeared to occur for two reasons: 1) the proportion of snags salvaged 10-years post-fire was less than we observed at our 22-year post-fire site, and 2) follow-up treatments (e.g. site preparation via burning) was more intensive at our 22-year post-fire site, reducing the abundance of cull logs or tree tops within these stands relative to the less intensive salvage operations we observed at our 10-year post-fire site. While temporal trend lines are represented by a straight line, snag dynamics are log accumulations likely develop along non-linear trends (Dunn and Bailey, 2015), but we do not have a higher temporal resolution in our sampling to confirm these trends.

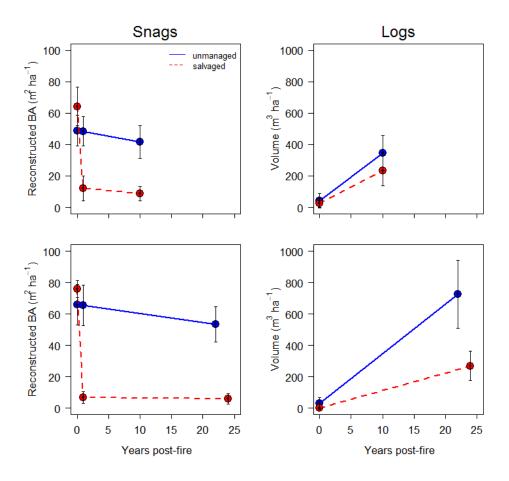


Figure 10: Figure depicting the variation in snag and log abundance by post-fire management strategy at our 10-year post-fire site (top row) and 22-year post-fire site (bottom row).

Understory Vegetation

No statistically significant variation among understory vegetation communities was observed between salvaged and unmanaged sites at our 10-year post-fire site. However, we did observe differentiation in vegetation communities at our 22-year post-fire site, but much of this was attributed to differences in elevation among the sites (Figure 11). At the Tiller Complex, overall plots within these a priori groups were more closely associated than expected by chance (combined A = 0.113 p-value <0.001), with high-severity and salvaged communities being significantly separated in multi-dimensional space (i.e. $A \ge 0.10$) from unburned forests but weak variation between unmanaged and salvaged logged sites (A = 0.012, p-value = 0.035). At the Warner Fire, overall plots within these a priori groups were more closely associated than expected by chance (combined A = 0.117 p-value <0.001), with high-severity and salvaged communities being significantly separated in multi-dimensional space (i.e. $A \ge 0.10$) from unburned forests but we observed less, but statistically significant, variation between

unmanaged and salvaged logged sites (A = 0.073, p-value <0.0001). Our ordination resulted in a 3-axes solution for both time-since-fire sites. Axis 1 was positively correlated with fire severity as estimated by multiple factors and the most significant biophysical factor associated with axis 2 was elevation.

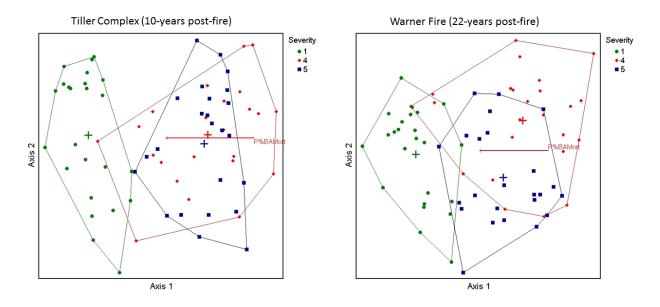
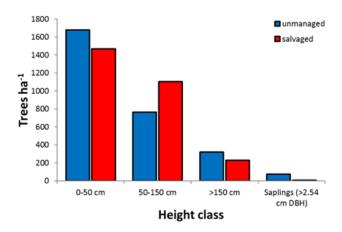


Figure 11: Ordination of understory vegetation communities in unburned forests, unmanaged high-severity plots, and salvage logged high-severity plots. Vegetation communities at high-severity and salvaged plots departed significantly from unburned forests, but did not differentiate among salvaged and unmanaged plots at either 10 and 22-years post-fire. The dominate gradient captured along axis 1 for both sites was fire severity, with axis 2 dominantly representing an elevation gradient.

Tree Regeneration

Tree regeneration dynamics varied among salvaged and unmanaged stands, particularly at our 22-year post-fire site. Our two sampled salvaged sites varied operationally, with the 22-year post-fire site representing a more intensively managed post-fire site as more snags were removed and site preparation with subsequent precommercial thinning occurring approximately 15 years post-treatment in some of the stands. The abundance of trees by height classes were very similar at the Tiller Complex except for the largest size-class, where less intensive silviculture was applied (Figure 12). This suggests neither a negative or positive impact was observed between these management strategies, despite evidence from other post-fire sites (Donato et al., 2006, 2009). However, salvaged sites exhibited lower abundances of regenerating trees in the two tallest size-classes suggesting either an intentional or unintentional negative correlation with post-fire management on regeneration abundance.

Tiller Complex (10-years post-fire)



Warner Fire (22-years post-fire)

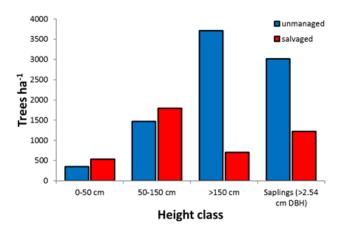


Figure 12: A figure contrasting the abundance of regenerating trees by size-class in unmanaged and salvaged sites at the Tiller Complex and Warner Fire. Tiller Complex represents a less intensive post-fire management strategy relative to the Warner Fire.

Post-fire regeneration communities did not vary significantly at the Tiller Complex, but differentiated at the Warner Fire (Figure 13). There were two notable differences at the Warner Fire. First, a high number of shade tolerant species were observed in all height classes in unmanaged sites at the Warner Fire. These shade tolerant species were rare at the salvaged sites within the Shady Beach fire used to contrast unmanaged and slavaged sites. This may have occurred because of slight elevation differences among the sampled plots, as well as vegetation treatments and precommercial thinning targeting these less commercial species. The other observed difference was the reforestation with ponderosa pine at several sampled plots. We could not identify why this species was chosen for reforestation because the agency records were destroyed, but potentially it was done because the post-treatment sites were hotter

and drier than typical sites and ponderosa pine is more tolerant of these conditions. Regardless the reason, these stands represent and unique community not observed in other post-fire sites. However, natural ponderosa pine stands do exist within the Middle Fork of the Willamette River Watershed so they are not completely planted outside their potential ecological amplitude within the western Cascades of Oregon.

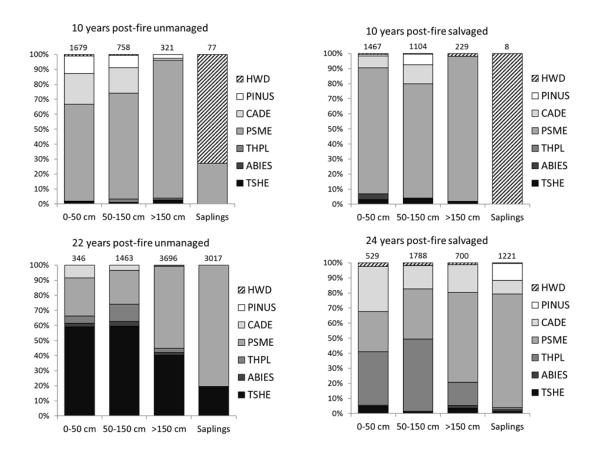


Figure 13: Regeneration composition by height class at unmanaged and salvaged sites. Top row is for the Tiller Complex (10-years post-fire) and bottom row represents the Warner Fire (22/24–years post-fire).

We investigated tree regeneration dynamics further at our 20+ years post-fire site by quantifying attributes of the saplings sampled at these sites (Figure 14). We did this because salvage logging and silviculture objectives tend to focus on improving regeneration of commercial species and shortening harvest rotations. One of the most noticeable differences observed was in the total number of saplings sampled. Unmanaged stands had a greater distribution in abundance as well as over 1000 more regenerating trees ha⁻¹ on average. However, the quadratic mean diameter averaged closs to 10 cm more at salvaged sites relative to unmanaged sites. Similarly, the average height of regenerating trees at the salvaged sites was about 2 m taller, and the average basal area was higher at salvage logged sites as a result of the larger sized trees. This suggests, that while salvage logging may reduce total regeneration

abundance, intensive silviculture can accelarate the growth of regenerating trees and potentially reduce harvest rotation if that is the primary management goal in these burned forests.

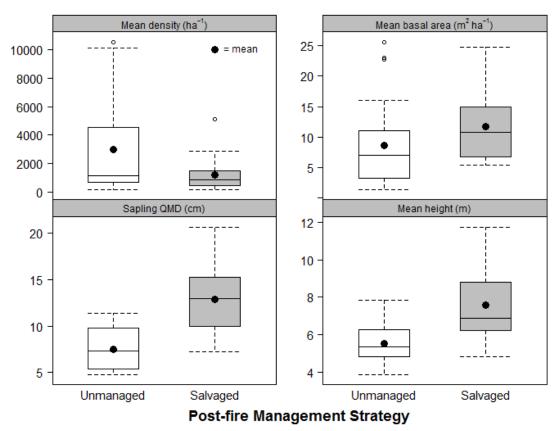


Figure 14: Contrasting metrics of regenerating saplings in unmanaged and salvaged stands 22+ years post-fire. We only contrasted these metrics for the older fires because there was not a large abundance of saplings at the Tiller Complex when sampled.

Management Implications

Mixed-severity fire provides an important ecological function in *Pseudotsuga* forests of western Oregon's central Cascades. Fire return intervals vary significantly in space and time, but can be as short at 95 years (Morrison and Swanson, 1990). These forests may not have missed a fire cycle, but are within or approaching their historic return interval and therefore fire's ecological function can be maintained if fires are allowed to burn. This may be particularly important in young or mid-seral forests regenerating following high-severity fire and currently lack vertical and horizontal structural diversity (Freund et al., 2015); conditions that could be accelerated by low and moderate-severity fire. Of course, some mid-seral forests naturally lack structural diversity while others may develop it through other pathways (Pollock et al., 2012). Despite the potential for low-severity and high-severity fire to homogenize certain aspects of vertical and horizontal structural diversity, these conditions are part of a continuous natural successional

cycle in *Pseudotsuga* forests. These forests regenerate and utilize available growing space within decades, and the various structural conditions created by mixed-severity fire result in different successional pathways that may retain landscape-scale structural diversity for a century or more (Tepley et al., 2013, 2014). Mixed-severity fire may increase the resilience of these forests by diversifying landscapes, so landscape management plans should incorporate the distribution of conditions we have presented so they manage within the bounds of historical disturbance regimes (Cissel et al., 1999). Additionally, decisions regarding wildfire response should consider the near and long-term ecological benefits that mixed-severity fire has on forest structure, and weigh them against the any negative consequences so that mixed-severity fires can continue to burn and provide their historic ecosystem service (North et al., 2012).

Vegetation response to wildfires can provide evidence that supports interpretations of their ecological impacts and the resilience of these ecosystems. We observed multiple understory vegetation communities across each fire severity class, suggesting the diversity in post-fire conditions is not adequately represented by fire severity maps because they do not provide the ecological resolution necessary to predict understory vegetation response (Miller and Thode, 2007; Halofsky and Hibbs, 2008; Keeley, 2009; Morgan et al., 2014; Reilly et al., in review). This effect can be partially attributed to the abundance of surviving trees being more important than proportion killed; an effect observed in our study even though we limited variation in pre-fire forest conditions. This effect would likely be more evident in younger forests with lower pre-fire basal area, where 20% mortality (low-severity) in a forest with 20 m² ha-1 tree basal area would likely result in a post-disturbance community similar to those observed following moderate or high-severity fire. Integrating pre-fire spatial data and fire-severity estimates to produce legacy maps of surviving trees, and incorporating this into a predictive model, could provide a more complete picture of the post-fire environment as shown in our example provided in Figure 15 that clearly demonstrate the increased variability of the post-fire environment. Legacy and response maps may be better for assessing post-fire vegetation resilience, wildlife habitat conditions, or ecosystem productivity by providing a more comprehensive picture of the post-fire environment. These maps offer a better assessment of the future successional trajectory of these burned landscapes (Seidl et al., 2015) than can be derived from commonly used fire severity maps and should be given greater focus in future landscape-scale ecological research.

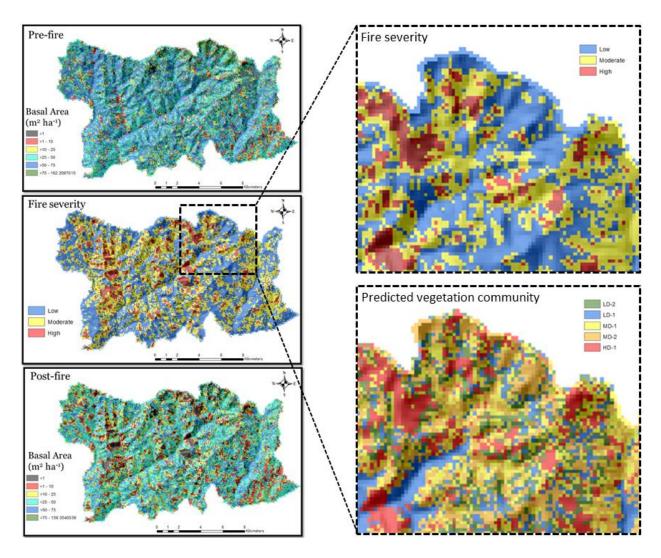


Figure 15: An example provided to display the complexities of the post-fire understory vegetation response and how the use of surviving overstory basal area can be used to provide an alternative perspective of the post-fire environment.

Mixed-severity fire resulted in diverse understory vegetation responses at the population and community level of organization. Native understory species exhibited three distinct response-curves to increasing fire 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). Species richness increased by 100% in our sample following mixed-severity fire, and was negatively correlated with surviving overstory basal area and elevation. Individual species response-curves led to community assemblages that varied distinctly across our mixed-severity disturbance gradient (Figure 4). Mixed-severity fire also resulted in varying abundances and size-class distributions of surviving trees and snags, promoting structural complexity and interactions with understory vegetation

that are likely used by many faunal species and communities (Cahall and Hayes, 2009, Fontaine et al., 2009; Fontaine et al., 2012). These communities and their development over time define the heterogeneity created by mixed-severity fires and provide valuable information for assessing ecosystem resilience to fire; however, researchers need to incorporate additional information (e.g., pre-fire basal area) into landscape-scale assessments of burned landscapes to better understand the ecological impacts of these events.

We observed negative and positive responses to salvage logging depending on the ecological attribute of concern. Unsurprisingly, forest structure was altered at both salvaged sites relative to unmanaged high-severity sites as snags were felled and removed offsite. This has consequences on both near and long-term wildlife habitat, carbon stores and soil development. However, economic utilization of this material has important social benefits and this should be weighed against these negative effects. Similarly, salvage logging appears to reduce the number of regenerating trees and can alter the composition of the regenerating trees. These effects can have negative consequences that extend through the development of the next generation forest that may last for centuries. However, if the production of harvestable material is the primary objective of the disturbed land, then salvage logging and intensive silviculture could promote a more rapid accumulation of commercially viable trees. The varied response highlights the importance of establish well-defined land management objectives well in advance of a disturbance.

We focused primarily on specific post-fire conditions and subsequent understory vegetation and regeneration response, but there are other aspects of moderate-interval, mixed-severity fires in Pseudotsuga forests to consider. Low and moderate-severity fires create large snags while retaining large live trees that can become snags in a later fire at a moderate interval of 100 years or less (Dunn and Bailey, 2016). High-severity fire may result in a temporal disconnection of several hundred years in the availability of these structures as forests regenerate over multiple decades, grow into large trees and reburn (Freund et al. 2014; Tepley et al., 2014). Variation in forest conditions over multiple, low and moderate-severity events result in greater continuity of live and dead forest structures across space and time. Concurrently, mixed-severity fire promotes significant variability in understory vegetation response with implications on population and community sustainability as propagules are produced and stored in seedbanks or disseminated to other disturbed areas. By 22-years post-fire, we observed the beginning stages of successional transition as regenerating trees began to influence understory communities through competitive exclusion (Halpern and Lutz, 2013). Subsequent mixed-severity fires in M/OG forests may be necessary to maintain temporal and spatial continuity in understory vegetation communities and structural conditions across broad landscapes, with subsequent reburn in the future likely necessary to maintain viable populations of colonizing species and habitat resources within these burned areas.

Promoting fire as a natural process, and understanding the importance of mixed-severity fire in *Pseudotsuga* forests could lead to the long-term development and maintenance of resilient forest landscapes in this broadly distributed forest type of the PNW.

Mixed-severity fire regimes are arguably the least understood regime type in forest systems. These fire regimes are functionally important to the development of structural complexity in *Pseudotsuga* forests of the PNW. Contemporary fires continue to burn with severity distributions similar to those found historically (Kushla and Ripple, 1997; Tepley et al., 2014; Dunn and Bailey, 2016), and can still provide beneficial effects if allowed to burn across these 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 which can affect available seedbanks. Strategies should be developed to facilitate the incorporation of mixed-severity fire effects into landscape management plans as a means to promote and maintain structural complexity at stand and landscape-scales (Cissel et al., 1999).

Future Research Needs

Using contemporary fires and fire severity estimates to draw inferences about historic spatial patterns is inhibited by the legacy of past management activities because of their influence on tree composition and size-distribution. Tree mortality is an expression of fire intensity against tree autecological traits that promote resistance to fire-induced mortality (Brown and Smith, 2000, Woolley et al., 2013). We observed significant variation in individual tree mortality by species and DBH, which has implications on the proportion of mortality (i.e., fire severity) as well as the surviving overstory community (Belote et al., 2015). Trees within managed stands of even-aged, single species plantations are likely to respond more uniformly to fire than stands with mixed composition or diameter distributions. Therefore, fires occurring in these stands would result in a different spatial pattern of mortality than might have occurred under historic conditions.

Assuming one fire regime for the entire distribution of a forest type could lead to a spurious understanding of disturbance processes and forest dynamics. For example, there is evidence that *Pseudotsuga* forests transition from a low or mixed to a high-severity fire regime along a south-north gradient in the Cascades (Weisberg and Swanson, 2003). Compositional and developmental trajectories differ by the magnitude or frequency of wildfires, with cumulative effects differentiating the structure and composition of these forests (Tepley et al., 2013, 2014, Zenner, 2005). As the length of fire seasons and large fire extent increases across much of the western U.S. (Westerling et al., 2006, Littell et al., 2009), fire severity has increased in many forests types raising concerns regarding the future condition and resilience of affected forests (Miller et al., 2009). Identifying a departure in fire regimes requires, at

minimum, and understanding of the frequency and severity of historical and contemporary wildfires. Pseudotsuga forests have typically been viewed as having a high-severity fire regime (Agee, 1993), yet Pseudotsuga forests within our study area are increasingly recognized as having a mixed-severity fire regime. The old paradigm would view a contemporary fire dominated by high-severity fire as similar to historical fires, despite actually being departed. Therefore, site specific historical and contemporary wildfire data is necessary to prevent the over-application of one fire regime to an entire forest type.

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Deliverables

Deliverable Proposed	Description	Delivery
Dissertation	PhD Dissertation, OSU	Completed June, 2015
Manuscripts	Multiple manuscripts from	1 accepted in 2016
	dissertation chapters	1 currently in review
Local Forest	Presentation of results to	Completed June, 2015
Presentations	Willamette and Umpqua National	
	Forests	
Conference	Present results at regional, national,	Following presentations have been
Presentations	or international meetings	given:
		Dunn, CJ, Bailey, JD. May 2014. Scale-Dependent Vegetation Response to a Mixed-Severity Disturbance Gradient. Large Wildland Fires Conference. Missoula, MT.
		• Dunn, CJ , Reilly, MJ, Bailey, JD. Nov. 2015. Improving fire severity maps to assess forest resilience: Tree survival is more important than mortality for vegetation response to mixed-severity fire. AFE 6 th International Fire Congress, San Antonio, TX. AFE 6 th International Fire Congress, San Antonio, TX.
		Bailey, JD, Dunn, CJ . April 2016. Impacts of Post-fire Salvage Harvesting on Early-seral Ecosystems in Western Oregon. 5 th International Fire Behavior and Fuels Conference, Portland, OR.