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Tree mortality and structural change following mixed-severity fire in *Pseudotsuga* forests of Oregon's western Cascades, USA

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ABSTRACT

Mixed-severity fires are increasingly recognized as common in *Pseudotsuga* forests of the Pacific Northwest and may be an important mechanism for developing or maintaining their structural diversity and complexity. Questions remain about how tree mortality varies and forest structure is altered across the disturbance gradient imposed by these fires. Therefore, we sampled live and dead trees at 45–1.0 ha plots, each with four 0.10 ha nested subplots, stratified across an unburned, low, moderate and high-severity fire gradient. Burned plots were primarily sampled 10 and 22 years post-fire, except three plots sampled four years post-fire. We estimated probability of mortality for fire-tolerant (Douglas-fir, incense-cedar, sugar pine) and fire-intolerant (western hemlock, western redcedar, true fir) trees from 5079 samples. The probability of mortality varied across all species and fire-severity classes, but the greatest difference was observed between fire-tolerant and fire-intolerant functional groups. Probability of mortality decreased with increasing DBH for all species except western hemlock that did not increase its fire resistance with increasing size. Some large, fire-tolerant trees survived high-severity fire but only in 31% of our plots. Snag fall and fragmentation was estimated for trees killed by the fire from 2746 sampled snags and logs 10 and 22 years post-fire. The proportion of snags fallen decreased with increasing DBH for all species, and was positively correlated with fire severity, except for Douglas-fir that had a higher proportion felled following low-severity fire. Snag fragmentation rates were positively correlated with DBH and fire severity for all species. Individual tree and snag estimates were scaled to plot-level structural attributes and contrasted by their coefficient of variation within- and among-plots from unburned to moderate-severity, as well as across all sampled conditions. Structural attributes varied more within- than among-plots, likely a result of patchy mortality that increased with fire severity. Although vertical and horizontal structural diversity increased at sub-hectare scales, the highest variability occurred for all structural attributes when compared across all sampled conditions. We conclude that the range of fire effects imposed by mixed-severity fire is important in creating structural diversity in *Pseudotsuga* forests of the Pacific Northwest and should be promoted through progressive fire management programs aimed at maintaining this forest's fire regime now and in the future.

1. 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; Franklin and MacMahon, 2000; Harmon et al., 1986). Surviving trees and fire-created coarse wood are variously distributed through space and time, supporting a diverse array of flora and fauna as well as ecosystem processes controlled by the availability and abundance of these resources (Odum, 1969; Turner et al., 2003). For example, surviving trees provide refugia for species reliant on crowns for nesting (Bond et al., 2009), remain a seed source for propagating the next generation forest (Seidl et al., 2014), and support below-ground mycorrhizal symbionts that increase water and nutrient acquisition of legacy and regenerating vegetation (Louma et al., 2006; Simard, 2009). Fire-created coarse wood provides 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, surviving trees and fire-created coarse wood can provide ecological functions for several hundred years post-fire depending on mortality, snag dynamics and the decay or combustion of the coarse wood.

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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).

Mixed-severity fires may be more common and ecologically important than suggested by commonly-used successional models for *Pseudotsuga* forests (e.g., Franklin et al., 2002; Oliver and Larson, 1996). 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 to 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.

Methodologies have been developed to quantify fire severity using remotely sensed data first acquired in 1984 (Key and Benson, 2005; Miller and Thode, 2007). Several fires have burned with mixed-severity effects in western Oregon's *Pseudotsuga* forests in recent decades (Kushla and Ripple, 1997; MTBS, 2011). These fires offer the opportunity to assess near-term fire effects on forest structure and composition in response to a fire severity gradient, so we can better understand how mixed-severity fires impact these forests and potentially contribute to their structural diversity. Specifically, we sought to quantify the following in response to a mixed-severity fire gradient: (1) mortality by tree species and DBH, (2) variation in stand-level live and dead structural attributes, (3) fall and fragmentation of fire-created snags by species and DBH, and (4) variation in horizontal structural diversity at multiple scales.

2. Methods

2.1. Study area

Pseudotsuga forests of western Oregon's central Cascades are dominant from 500 to 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 the North/South Umpqua River watershed divide (43°43′36.8688″ N). The climate is typical of maritime conditions with cool, wet winters and warm, dry summers. Precipitation ranges from 1339 to 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 (PRISM, 2014, www.prismclimate.org). Temperature increases and precipitation decreases slightly from north to south in our study area. Douglas-fir, sugar pine (*Pinus lambertiana*) and incense-cedar (*Calocedrus decurrens*) are common fire-tolerant tree species and western hemlock, western redcedar (*Thuja plicata*), white fir (*Abies concolor*), grand fir (*Abies grandis*), and Pacific yew (*Taxus brevifolia*) are common fire-intolerant tree species. Giant chinkapin (*Chrysolepis chrysophylla*), 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 garrayana*) 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.

2.2. Sampling design

Several large fires burned a total of 76,746 ha within our study between 1987 and 2014 (Fig. 1). 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 3723 ha, respectively. We include additional plots from the 2009 Tumblebug Fire (4 years post-fire) that burned 5900 ha. The average proportion of low, moderate and high-severity fire effects for all large fires (i.e., >400 ha) within our study area are provided in Fig. 2.

We randomly located six sample plots within each of three fire-severity classes (i.e., low, moderate, high) at two time-since-fire periods (10 and 22 years post-fire). An additional six sample plots were placed in unburned stands as a reference group. We also sampled three plots (one in each severity class) in a fire that burned four years prior before our second field season ended. MTBS very low and low classes were combined into a single stratification layer. 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 maps created by the Monitoring Trends in Burn Severity program that derive thresholds by comparing the differenced normalized burn ratio (dNBR) to Composite Burn Index field data (Key and Benson, 2005; MTBS, 2011). Sampling was constrained to mature or old-growth (M/OG) *Pseudotsuga* forests by evaluating agency GIS databases that include 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 high-severity fire for >100 years. Only the southerly aspect of the Warner Fire was sampled so forest type and climatic conditions remained comparable across fire sites.

2.3. Field measurements

We sampled surviving trees and snags within 1-ha circular plots at four nested subplots. Subplot one was centered on the plot and

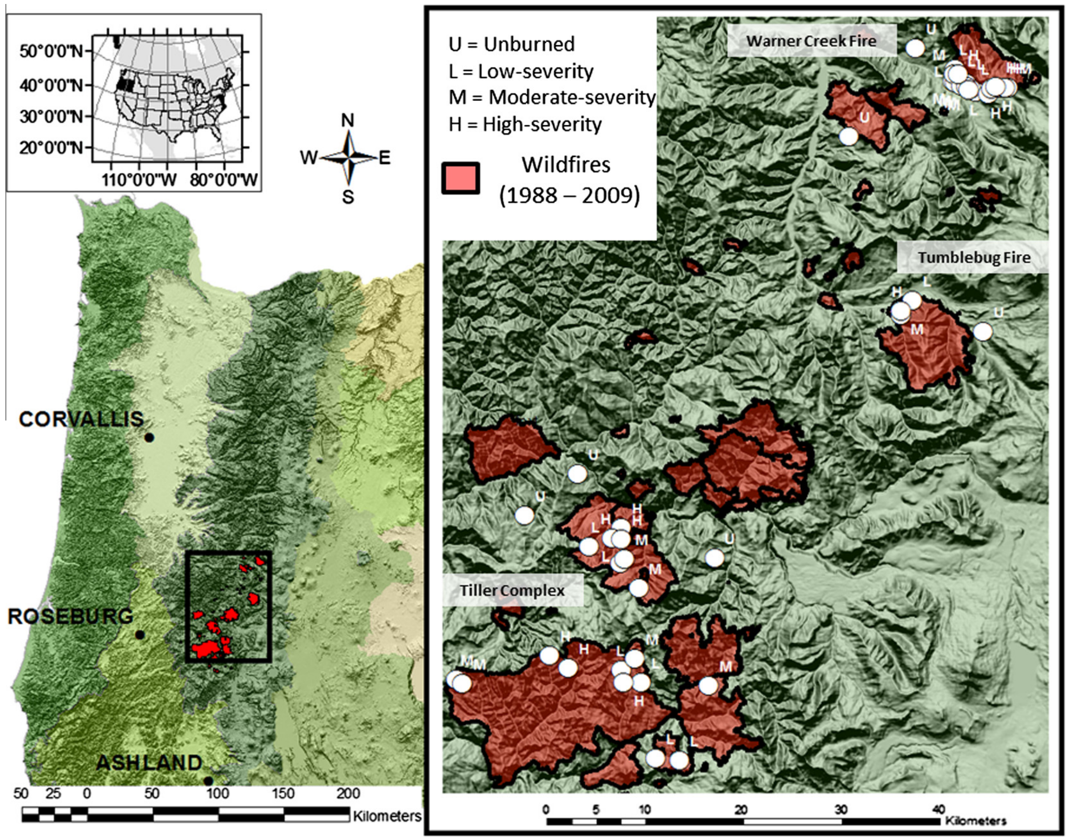

Fig. 1. A map depicting fire extents and plot locations across our study area in western Oregon's central Cascade Range.

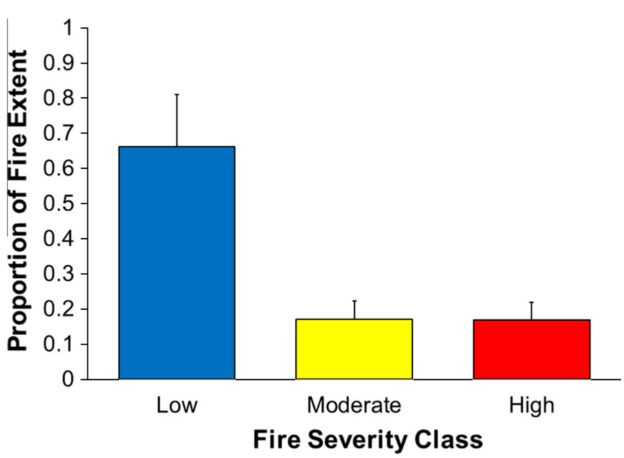

Fig. 2. A figure depicting the mean and standard deviation for fire severity classes from 11 large fires that burned within our study area. Estimates were derived from dNBR and classified by the MTBS program (MTBS, 2011). We combined the very low and low classes in this study.

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 fire-created snags >70 cm DBH were sampled within the 1-ha plot to capture large, spatially dispersed individuals. We recorded species, DBH (cm), total height (m), crown base height (m) and percent bole scorch for all surviving trees. We recorded species, DBH, condition (i.e. standing whole, standing broken, fallen), height, percent bark, percent bole scorch and decay class for all snags. 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 <2 m in height were considered fallen. Pre-fire snags were visually identified and separated from fire-created snags when bole sapwood was partially consumed or converted to charcoal (suggests lack of bark and advanced enough decay to support partial combustion). 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).

Downed coarse wood (logs) were sampled along five transects using a planar intercept method (De Vries, 1973). Logs included any woody detritus >7.62 cm in diameter. We recorded species, decay class, diameter at point of intersection and visually identified pre-fire coarse wood as we did for snags. 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.

2.4. Statistical analyses

Fire severity is commonly defined as the proportion of live biomass killed or combusted by a fire, and typically refers to tree mortality in forests (Keeley, 2009). Since MTBS fire severity classes are based on the Composite Burn Index, we estimated tree mortality from our plot data for each fire severity class. We accomplished this by reconstructing pre-fire live basal area and trees ha^{-1} for all plots, and then estimated their proportional change at the time of sampling. Reconstructed estimates were also used to evaluate if pre-fire differences might confound our results. 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).

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). 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. We tested two-way and three-way interactions among species, fire severity class and DBH in our analyses. Models with interaction terms would not converge for fire-tolerant species, even after trying several optimization methods and increasing the maximum number of optimization iterations. Plot was included as a random effect to account for positive correlations among residuals resulting from spatial autocorrelation within a plot. Sample size and descriptive statistics for this analysis are provided in Table 1. We included unburned plots in this analysis for a general assessment of the species and size-classes most susceptible to death from causes other than fire in this forest type.

The proportion of snags fallen and fragmented (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 these models would not converge. We focus on cumulative effects at 10 and 22 years post-fire for snag analyses and therefore did not include data from our four year post-fire site. We also estimated snag height following fragmentation (i.e., top breakage) using a linear mixed model. Again, plot was included as a random effect to account for positive correlations among residuals resulting from spatial autocorrelation within a plot. We estimated the half-lives (i.e. proportion $\geqslant 0.50$) for all species and diameter classes and report the largest DBH by species reaching this point by 10–22 years post-fire.

Surviving trees and snags 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 ($m^2\ ha^{-1}$), tree density (ha^{-1}), quadratic mean diameter (QMD) in centimeters, mean crown base height (CBH) in meters, snag basal area ($m^2\ ha^{-1}$) and snag density (ha^{-1}) as important vertical attributes of forest structure. Plot-level log volume, cover and diameter were estimated using equations developed by De Vries (1973). We used the coefficient of variation (CV) to test within- and among-plot variability for several structural attributes and severity metrics. We contrasted the CV at multiple scales to discern which scale variability was dominantly expressed. The CV for live structural attributes following high-severity fire was not included in this analysis because many plots had zero values making results from this test statistic spurious. 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).

3. Results

3.1. Reconstructed forest structure and fire severity

Pre-fire basal area and forest density did not differ significantly by fire severity classes at an $\alpha \leqslant 0.05$ (Table 2). Reconstructed basal area and forest density averaged 66.5 $m^2\ ha^{-1}$ (SD = 16.4) and 591.4 trees ha^{-1} (SD = 484.9) across all plots, respectively. Similarly, unburned plots averaged 69.2 $m^2\ ha^{-1}$ of live basal area

Table 1
Sample size and diameter distributions for dominant conifer species analyzed for probability of mortality and the proportion of snags fallen or fragmented.

Species	Probability of mortality			Probability of snag fall			Probability of snag fragmentation		
	DBH (cm)			DBH (cm)			DBH (cm)		
	N	Mean (SD)	Range	*N*	Mean (SD)	Range	*N*	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
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 ($m^2\ ha^{-1}$)	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 ($m^2\ ha^{-1}$)	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 ($m^2\ ha^{-1}$)	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)

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

Table 3
Regression coefficients and error estimates for predicting the probability of mortality for fire-tolerant and fire-intolerant trees.

Independent variable	Estimate	Std. error	*z*-value	Pr(>|z|)
Fire-tolerant trees				
(Intercept)	0.713	0.454	1.569	0.1167
DBH (cm)	−0.029	0.002	−18.047	<0.0001
Incense-cedar	−0.627	0.190	−3.295	0.0010
Sugar pine	0.817	0.205	3.983	<0.0001
Low-severity	0.350	0.534	0.655	0.5127
Moderate-severity	1.249	0.532	2.346	0.0190
High-severity	6.289	0.600	10.482	<0.0001
		Variance	Std. dev.	
Random effect	Plot	1.087	1.042	
Fire-intolerant trees				
(Intercept)	−1.932	0.310	−6.229	<0.0001
DBH (cm)	−0.002	0.008	−0.199	0.8425
True fir	0.870	0.370	2.349	0.0189
Western redcedar	0.973	0.465	2.096	0.0361
Low-severity	2.684	0.243	11.041	<0.0001
Moderate-severity	3.810	0.322	11.816	<0.0001
DBH ∗ true fir	−0.030	0.010	−2.922	0.0035
DBH ∗ western redcedar	−0.019	0.009	−1.980	0.0477
		Variance	Std. dev.	
Random effect	Plot	0.024	0.155	

Note: Fire-tolerant reference group is Douglas-fir in unburned forests; fire-intolerant reference group is western hemlock in unburned forests.

and 722 trees ha^{-1}. We observed some evidence of lower basal area and density within our high-severity plots, which was partially driven by two moderate-severity plots having >2000 pre-fire small diameter (<10 cm) hardwood and conifer trees. Additionally, small diameter snags that had fallen and decayed or were buried at our high-severity plots may have been missed during sampling despite our efforts to find them. The observed differences weren't large enough to bias our results by much, especially since they were most likely a result of missed small diameter snags in the high-severity plots that typically had 100% mortality.

Our stratified sampling based on dNBR and MTBS classification captured a gradient in tree-based fire severity (Table 2). 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). 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% to 97.4% basal area mortality.

3.2. Tree mortality

We estimated probability of mortality for six conifer species from 5079 samples (Fig. 3). We observed statistical differences among species within fire-tolerance groups, as well as across *a priori* fire severity classes, and in response to DBH (Table 3). 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 $\alpha \leqslant 0.05$. 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 1.008–1.032, *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 0.987–1.017, *p*-value = 0.84250).

The probability of mortality varied by species and included the interaction between species and DBH for fire-intolerant trees (Fig. 3). 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 (Fig. 3). Western redcedar had the highest probability of mortality among all fire-intolerant species until its DBH exceeded 52 cm, at

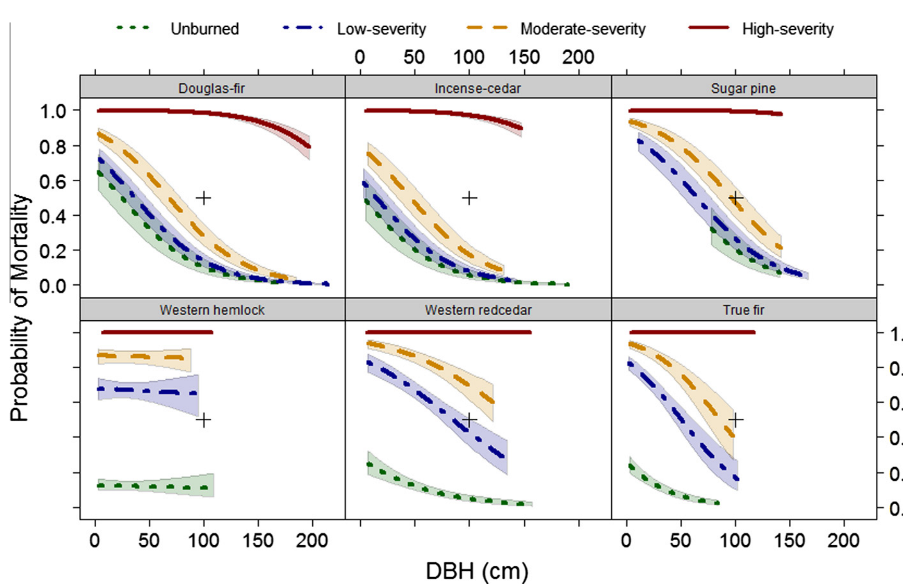

Fig. 3. Conditional probability of mortality with standard deviations (shaded regions) by species, DBH and fire severity. Fire-tolerant trees are depicted in the top row and fire-intolerant trees in the bottom. + is included for visual comparison and indicates a 100 cm DBH tree with a 0.50 probability of mortality.

Table 4
Regression coefficients and error estimates for predicting the proportion of snags fallen.

Independent variable	Estimate	Std. error	*z*-value	Pr(>|*z*|)
(Intercept)	0.429	0.368	1.165	0.2441
DBH (cm)	−0.012	0.004	−3.174	0.0015
True fir	0.197	0.407	0.484	0.6283
Incense-cedar	−1.138	0.617	−1.843	0.0654
Sugar pine	0.786	0.840	0.936	0.3490
Western redcedar	−2.796	0.647	−4.322	<0.0001
Western hemlock	−0.345	0.528	−0.653	0.5137
High-severity	−0.019	0.503	−0.037	0.9705
Moderate-severity	0.005	0.493	0.010	0.9923
DBH ∗ true fir	−0.014	0.012	−1.169	0.2422
DBH ∗ incense-cedar	0.007	0.009	0.789	0.4299
DBH ∗ sugar pine	−0.023	0.010	−2.368	0.0179
DBH ∗ western redcedar	0.013	0.008	1.534	0.1251
DBH ∗ western hemlock	−0.010	0.010	−0.978	0.3280
DBH ∗ high-severity	−0.021	0.005	−4.132	<0.0001
DBH ∗ moderate-severity	−0.013	0.005	−2.408	0.0160
True fir ∗ high-severity	0.687	0.747	0.919	0.3580
Incense-cedar ∗ high-severity	1.190	0.689	1.726	0.0844
Sugar pine ∗ high-severity	1.575	0.901	1.748	0.0805
Western redcedar ∗ high-severity	1.619	0.673	2.406	0.0161
Western hemlock ∗ high-severity	1.785	0.545	3.273	0.0011
True fir ∗ moderate-severity	1.182	0.651	1.815	0.0695
Incense-cedar ∗ moderate-severity	−0.345	0.797	−0.432	0.6655
Sugar pine ∗ moderate-severity	1.529	0.739	2.068	0.0386
Western redcedar ∗ moderate-severity	1.025	0.651	1.576	0.1151
Western hemlock ∗ moderate-severity	1.448	0.817	1.772	0.0764
		Variance	Std. dev.	
Random effect	Plot	0.8599	0.9273	

Note: The reference group is Douglas-fir following low-severity fire.

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 (Fig. 3). 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 general representation of background mortality for these species. Fortunately, the observed trends responded as expected given the relative shade-tolerance of our sampled species.

3.3. Snag dynamics

Snag fall was influenced by fire severity, species, and DBH as well as interactions among these factors (Table 4). We tested plot level environmental variables for statistical significance, but none were significant at an $\alpha \leqslant 0.05$. 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 (Fig. 4). 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 (Table 5). 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 (Fig. 5). 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,

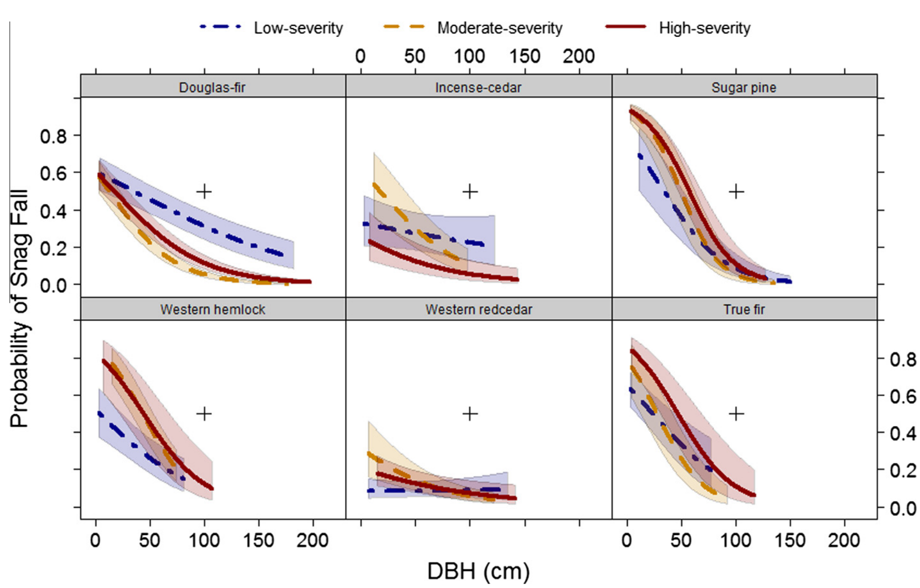

Fig. 4. Proportion of fallen snags and standard deviations (shaded regions) across the fire severity gradient. Fire-tolerant trees are depicted in the top row and fire-intolerant trees in the bottom. + is included for visual comparison and indicates a 100 cm DBH and proportion of 0.50.

Table 5
Regression coefficients and error estimates for predicting the proportion of snags fragmented.

Independent variables	Estimate	Std. error	*z*-value	Pr(>|z|)
(Intercept)	−0.990	0.398	−2.489	0.0128
DBH (cm)	0.010	0.003	3.874	0.0001
True fir	−4.125	1.562	−2.642	0.0082
Incense-cedar	0.330	0.580	0.568	0.5699
Sugar pine	−1.073	1.067	−1.005	0.3147
Western redcedar	−3.435	0.652	−5.270	<0.0001
Western hemlock	−0.075	0.786	−0.096	0.9238
High-severity	0.942	0.441	2.136	0.0326
Moderate-severity	−0.070	0.447	−0.157	0.8752
DBH * true fir	0.102	0.037	2.778	0.0055
DBH * incense-cedar	−0.002	0.008	−0.293	0.7695
DBH * sugar pine	−0.003	0.012	−0.250	0.8029
DBH * western redcedar	0.006	0.008	0.759	0.4479
DBH * western hemlock	0.022	0.017	1.281	0.2003
		Variance	Std. dev.	
Random effect	Plot	0.8695	0.9325	

Note: The reference group is Douglas-fir following low-severity 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 − 3.7 01433 (1.206324) ∗ 22 Yrs 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 (Fig. 6). 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.

3.4. Forest structure

Plot-level live structural attributes varied significantly across our fire severity gradient (Fig. 7). Pairwise comparisons of live basal area among all fire severity classes were significantly different at an $\alpha \leqslant 0.05$. 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.

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 6). 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.

4. Discussion

4.1. Mixed-severity fire and forest structure

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). We did not attempt to quantify fire regimes but rather view our observed

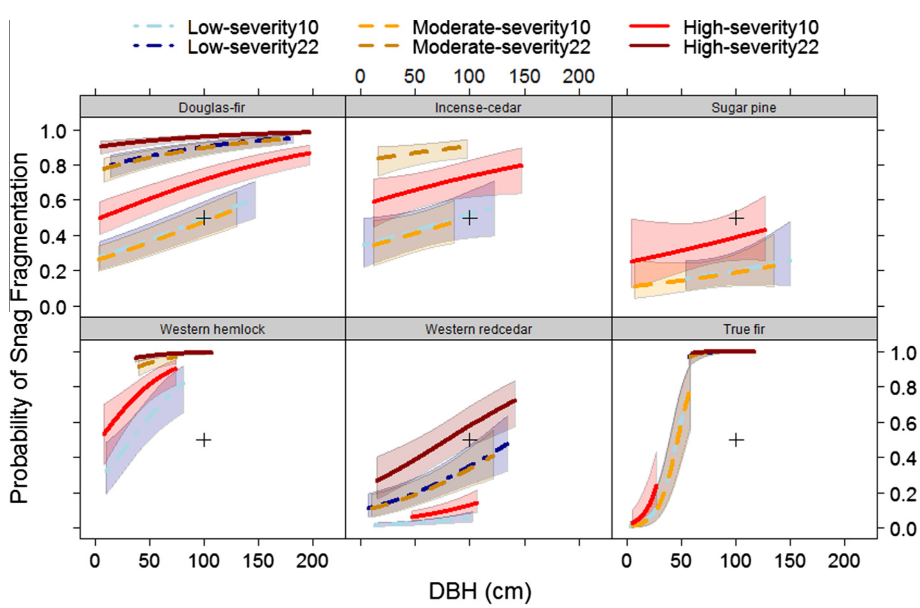

Fig. 5. Proportion of fragmented snags and standard deviations (shaded regions) across the fire severity gradient. Fire-tolerant trees are depicted in the top row and fire-intolerant trees in the bottom. + is included for visual comparison and indicates a 100 cm DBH and proportion of 0.50.

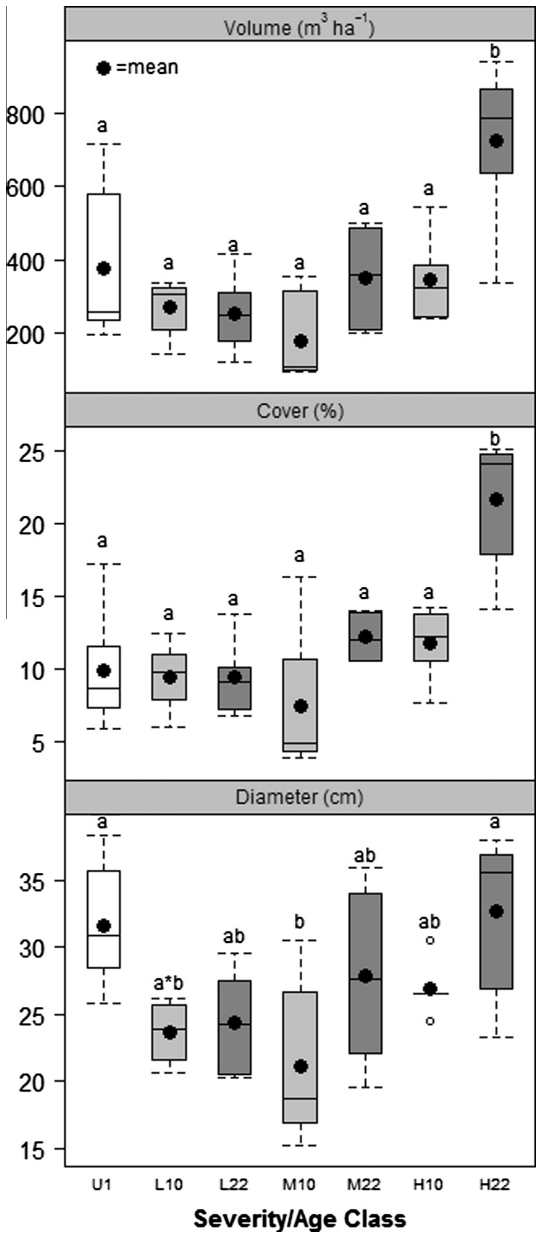

Fig. 6. Volume, cover and mean diameter of logs by fire severity and number of years post-fire. No statistical differences were observed by groups except for the high-severity class 22 years post-fire. The distribution of logs by severity class conforms to our results for snag fall and fragmentation. U = unburned, L = low-severity, M = moderate-severity, H = high-severity, 10 = 10 year post-fire site, 22 = 22 years post-fire site.

fire effects as the most recent fire-induced structural alteration in a long history of forest development. We believe this is a reasonable interpretation because fire suppression began approximately 100 years prior to sampling and may have only been effective beginning mid-twentieth century (Agee, 1993). This fire suppression period is shorter than historic mean fire return intervals for these forests, especially since historic fire-free periods extended beyond two centuries (Morrison and Swanson, 1990). Additionally, the average proportion of non-high severity fire was similar between our sampled fires and reconstructed estimates (Morrison and Swanson, 1990; Tepley et al., 2013), suggesting there has not been an observable increase in fire effects due to fire suppression or climate change in these forests. Therefore, our estimates at the individual-tree and plot-scale likely represent historic fire effects and strengthen the evidence that fires have and continue to burn with mixed-severity in *Pseudotsuga* forests of western Oregon's central Cascades.

Wildfires are commonly defined as discrete disturbance events that restructure forests by altering the abundance and distribution of live and dead biological legacies (Pickett and White, 1985). The size-distribution, species composition, and post-fire dynamics of surviving trees and fire-created coarse wood, as well as interactions among them, are significant determinants of habitat quality for many species (Fontaine et al., 2009; Hutto, 1995). Sub-hectare spatial variation in surviving trees results from small-scale patches of mortality (Boyden et al., 2005; Knapp and Keeley, 2006). Mortality patch-size appears to increase with increasing fire severity, varying the abundance and size-distribution of surviving trees and snags across the mixed-severity fire gradient. Surviving trees provide refugia for species reliant on crowns for nesting, and influence understory vegetation response which also contributes to habitat for many avian species (Bond et al., 2009; Cahall and Hayes, 2009; Franklin and MacMahon, 2000). Concurrently, the fire-created snags provide habitat structures for nesting, roosting and foraging (Saab et al., 2005; Spies et al., 1988). In fact, despite live structural diversity being reduced following high-severity fire, the early-seral vegetation response concurrent with the high abundance of snags creates a distinct habitat condition beneficial to many species (Swanson et al., 2010). Since structural diversity was highest across the full distribution of sampled fire effects, it is reasonable to hypothesize that mixed-severity fire enhances biodiversity within *Pseudotsuga* forests (Martin and Sapsis, 1992; Hansen et al., 1991). This includes the adjacent unburned forest, as well as unburned islands within the fire boundary, because they contain valuable biological resources and refugia for some species and contribute to the regeneration of the burned area (Eberhart and Woodard, 1987; Seidl et al., 2014).

Snags eventually transition to logs by falling or fragmenting, providing habitat structures for mammals and many invertebrate species (Harmon et al., 1986). The rate of fall and fragmentation varies by species, DBH and fire severity in *Pseudotsuga* forests (Brown et al., 2013). Interestingly, snag fall decreases with increasing DBH while snag fragmentation increases with increasing DBH. This is likely a result of larger diameter trees being taller and having a greater sail area and crown weight, making them more susceptible to applied forces from wind (Dunn and Bailey, 2015). Concurrently, as snags fragment they become more stable and therefore have a lower likelihood of falling (Dunn and Bailey, 2012). The lack of wind exposure, and therefore fragmentation, in low-severity plots likely contributed to Douglas-fir having a greater likelihood of falling at these plots relative to other sampled conditions (Fig. 4). We suspect snags continued to fall between 10 and 22 years post-fire, as observed by Brown et al. (2013), but the variability in our data exceeded any discernible trend across this time period.

Fire's legacy persists for centuries as disturbed ecosystems respond and take advantage of newly available resources (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 as subdominant individuals respond to 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, creating alternative successional trajectories (Tepley et al., 2013). For example, low-severity fire retains a relatively high abundance of fire-intolerant trees with a competitive

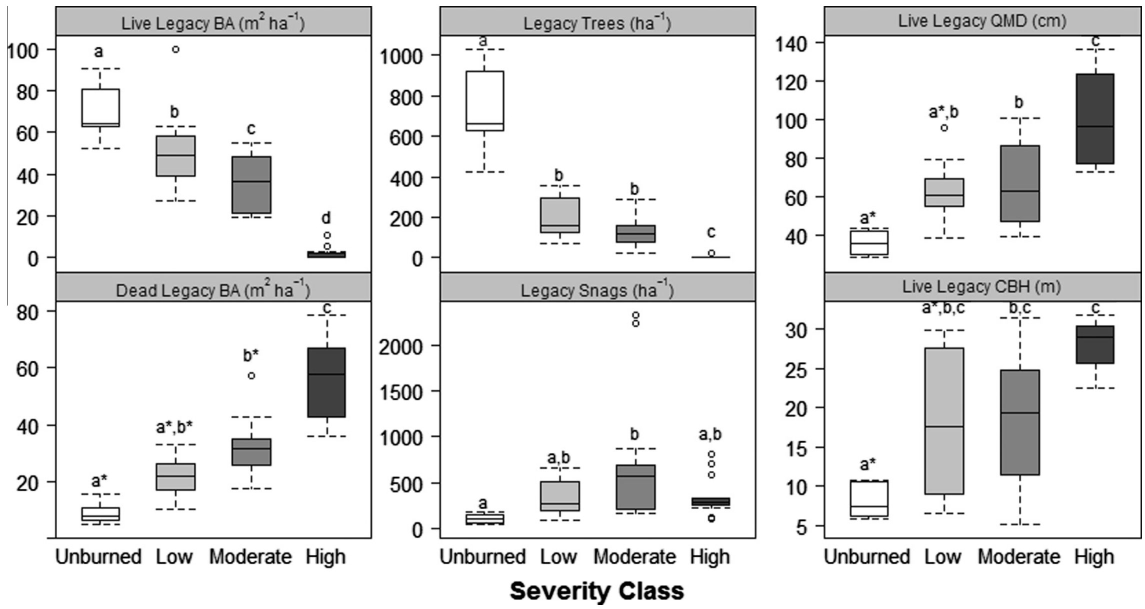

Fig. 7. Figure depicting plot-level structural attributes across our fire severity gradient. We observed significant differences in forest structure commensurate with fire severity classes, although low and moderate-severity conditions show little difference in some metrics. Lower case letters indicate statistically different pair-wise comparisons at and $\alpha \leqslant 0.05$.

Table 6
Within and among-plot coefficients of variation (CV) for structural attributes and severity metrics.

Attribute	Severity class								Burned
	Unburned		Low		Moderate		High		
	Within	Among	Within	Among	Within	Among	Within	Among	Landscape
	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

Note: CV 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 $\alpha \leqslant 0.05$, except those with an asterisk indicating a statistical difference at an $\alpha \leqslant 0.10$.

advantage to fill overstory gaps while simultaneously enhancing their probability of regenerating a new cohort. Moderate-severity fire has increasingly patchy mortality that significantly reduces the abundance of surviving trees, resulting in spatially diverse microclimates with varying amounts of light, water and nutrient resources. Both fire-tolerant and intolerant trees are retained as a seed source to facilitate the establishment of both fire-tolerant and intolerant species (Larson and Franklin, 2005; Tepley et al., 2014). High-severity fire kills 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 composition for centuries (Freund et al., 2014).

Vertical and horizontal structural diversity is an important attribute of M/OG *Pseudotsuga* forests in the western Cascades (Franklin et al., 1981). Vertical diversification has been purported to develop as small-scale disturbances 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 also facilitates horizontal diversification (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 this forest type (Weisberg, 2004). This effect is most exemplified by moderate-severity fire where sub-hectare patches of high-severity fire occur within broader moderate-severity conditions (Fig. 8). A fire typically burns an entire stand so light infiltration is greater than observed following individual or small group mortality by other mechanisms, influencing the establishment of a diverse understory (Van Pelt and Franklin, 2000). Vertical diversification will develop over time as a new cohort establishes, with varying composition and abundance, in response to the mixed-severity fire gradient. Mixed-severity fire also increases horizontal structural diversity across landscapes as the forest transitions among various levels of fire-severity, creating a complex mosaic of forest conditions with near and long-term structural and compositional variation that may be important to the resilience of these ecosystems.

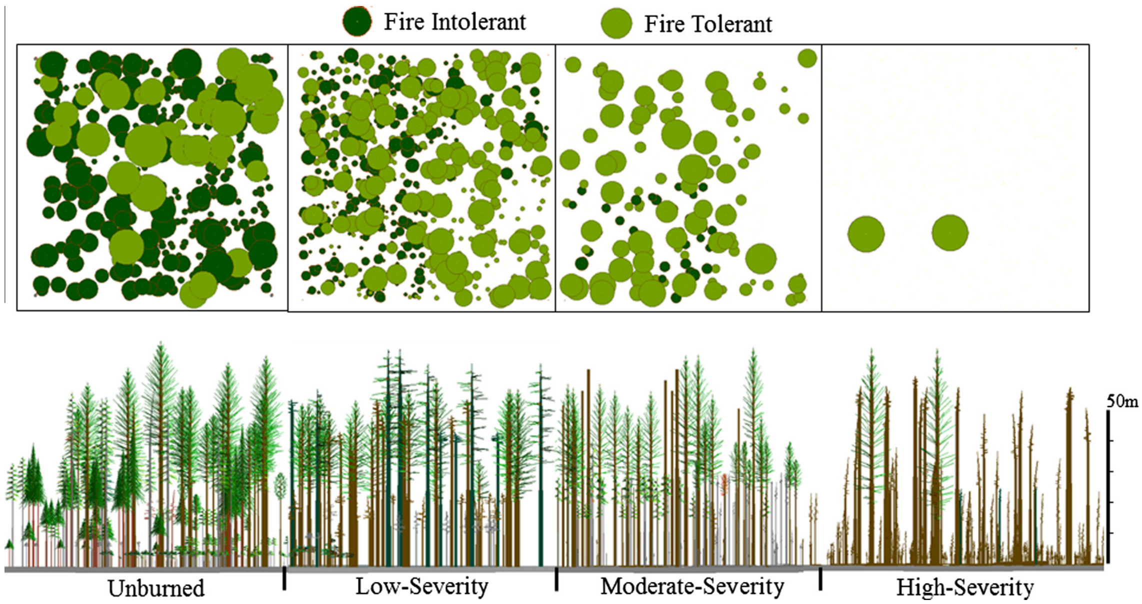

Fig. 8. A figure depicting post-fire structural conditions across our sampled fire-severity gradient. Each severity class is depicted from our sample data and varies in pre-fire composition and diameter distribution. The top panel is an overhead view and the bottom is the profile view of the same sample plot. The sizes of the circles are positively correlated with tree heights. Trees are spatially located randomly within each quadrant of the top panel, but each quadrant was populated from one of four subplots so they depict sub-hectare variation in fire effects. Although each fire 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).

Fire is an important ecosystem process in *Pseudotsuga* forests and recent interests in early-seral habitats suggests a transition to viewing fire as an important ecosystem process (Franklin and Johnson, 2012; Swanson et al., 2010). 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 accounted for >70% of the burned area in this study and historical reconstructions (Morrison and Swanson, 1990; Tepley et al., 2013). 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). We must account for both the near and long-term ecological effects of mixed-severity fire, especially when considering how contemporary fires interact with ecosystem services. As fire management programs adapt to the increasing trends in fire extent (Littell et al., 2009), and realize that managing large fires will be necessary to meet land management objectives (North et al., 2012), positive valuation of the 'ecological work' derived from mixed-severity fire becomes increasingly important.

4.2. Limitations

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., 2012). 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.

5. Conclusions

Mixed-severity fire effects are the cumulative response of interactions between fire intensity and individual tree resistance to mortality. We observed significant variation in tree mortality by species and DBH across a fire severity gradient in *Pseudotsuga* forests (Fig. 3). Autecological traits promoting fire-resistance and shade-tolerance appear inversely related in this forest type. Tree mortality creates coarse wood that provides structural resources valuable to many wildlife species, but their abundance and size-distribution also depend on the biological controls of fire severity. Coarse wood dynamics are subsequently dependent on species, DBH and fire severity. Low-severity may decrease vertical structural diversity for several decades by killing trees species that formed a sub-canopy layer. As fire severity increases vertical and horizontal structural diversity increase, except for live structure metrics following high-severity fire (Fig. 8). Combined, near-term mixed-severity fire effects increase structural diversity within these forests as some sites return to similar pre-fire conditions while others follow an alternate successional trajectory. Fire's legacy persists for decades or centuries as the ecosystem responds to newly available light, water and nutrient resources (Seidl et al., 2014).

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).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.01.031.

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