ECOSPHERE

How does tree regeneration respond to mixed-severity fire in the western Oregon Cascades, USA?

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Abstract. Dendroecological studies of historical tree recruitment patterns suggest mixed-severity fire effects are common in Douglas-fir/western hemlock forests of the Pacific Northwest (PNW), USA, but empirical studies linking observed fire severity to tree regeneration response are needed to expand our understanding into the functional role of fire in this forest type. Recent increases in mixed-severity fires offered this opportunity, so we quantified the abundance, spatial distribution, species richness, and community composition of regenerating trees across a mixed-severity fire gradient (unburned–high-severity fire) 10 and 22 yr post-fire, and use our results to inform a discussion of fire's functional role in western Oregon Cascades Douglas-fir forests. Regeneration abundance was unimodal across the fire severity gradient such that the greatest mean abundance followed moderate-severity fire (25–75% basal area mortality). Similarly, the greatest number of species was present within the most 25-m^2 regeneration quadrants (most extensive distribution) following moderate-severity fire, relative to any other fire severity class. On average, species richness also exhibited a unimodal distribution across the severity gradient, increasing by 100% in stands that experienced moderate-severity fire relative to unburned forests or following high-severity fire, as predicted by the Intermediate Disturbance Hypothesis. Several distinct regeneration communities emerged across the fire severity gradient, including early seral tree communities indicative of those observed in initial and relay floristics successional models for this forest type. Most significantly, moderate-severity fire alters successional trajectories and facilitates the establishment of a more diverse tree regeneration community than observed following low- or high-severity fire. These communities are reflective of the diverse overstory communities commonly encountered throughout this forest type. The emergence of these diverse forests is unlikely to develop or persist in the absence of moderate-severity fire effects, and may be perpetuated longer by recurring moderate-severity fire relative to experiencing stand replacing fire. Therefore, moderate-severity fire may be the most functionally important fire effect in Douglas-fir forests and should be better represented in successional models and more prominent in ecologically based fire and forest management.

Key words: Cascade Mountains; Douglas-fir; fire effects; forest resilience; forest succession; mixed-severity fire; moderate-severity fire; tree regeneration.

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INTRODUCTION

Wildfires variously function as discrete events that alter ecosystem processes (Pickett and White 1985) or a distinct ecosystem process (Noble and Slatyer 1981, Agee 1993, Bond and van Wilgen 1996, Bond and Keeley 2005, Sugihara et al. 2006, Pausas and Keeley 2019). The degree to which fire functions in these capacities depends primarily on interactions between fire frequency, fire intensity, and the adaptive traits of the species pool. In forested ecosystems, discrete events are relatively easy to measure as fire severity (e.g., mortality of existing vegetation) and the ensuing ecosystem response. In contrast, observing fire as an ecosystem process is more difficult because one must identify an emergent property derived from compounding disturbance effects not ascribed to other ecosystems processes. The latter typically relies upon multiple lines of evidence quantifying long-term fire regime attributes and the resulting ecosystem structure and composition. Disentangling these differences and appropriately characterizing fire disturbance dynamics is necessary as discrete events guide ecological forestry or restoration actions, while emergent properties provide long-term goals and trajectories (Cissel et al. 1999, Franklin and Johnson 2012, Dunn 2018, Halofsky et al. 2018).

Dendroecological reconstructions and regeneration studies describe the ecological function of fire across North American conifer forests. Chronic fire disturbance (i.e., high frequency, low severity) promotes dominance of early seral, fire-resistant trees like ponderosa pine (*Pinus ponderosa*) or longleaf pine (*Pinus palustris*), and maintains an open, mixed-age forest structure (Platt et al. 1988, Landers et al. 1995, Zenner 2005, Merschel et al. 2014, Johnston 2017, Heyerdahl et al. 2019). Episodic fire disturbance (i.e., low frequency, high severity) promotes dominance of species with rapid regeneration mechanisms (e.g., serotiny), creates early seral habitats with high species diversity, and reinitiates a pioneering cohort with near- and long-term contributions to forest structure (Hemstrom and Franklin 1982, Fahnestock and Agee 1983, Dickman and Cook 1989, Franklin et al. 2002, Axelson et al. 2009, Kulakowski et al. 2012). Mixed-severity fire regimes are a third commonly referenced regime type, where diverse patch-size distributions and landscape-scale structural mosaics are recognized as ecologically important outcomes that vary in space and time (Baker and Ehle 2001, Fulé et al. 2003, Hessburg et al. 2005, Scholl and Taylor 2010, Halofsky et al. 2011, Perry et al. 2011, Tepley and Veblen 2015, Iniguez et al. 2016).

Douglas-fir/western hemlock forests (*Pseudotsuga menziesii* (Mirb.) Franco/*Tsuga heterophylla* (Raf.) Sarg., hereafter referred to as Douglas-fir forests) are one of the most widely distributed forest types in the Pacific Northwest (PNW), USA (Franklin and Dyrness 1988). Researchers often consider this forest type to be archetypal of an episodic disturbance regime (Fahnestock and Agee 1983, Franklin et al. 2002, Freund et al. 2014, Seidl et al. 2014, Halofsky et al. 2018). However, dendroecological investigations, direct observations of post-fire succession, and satellite derived burn severity maps suggest more complex disturbance processes may be prevalent both historically (Means 1982, Teensma 1987, Morrison and Swanson 1990, Weisberg 2004, Tepley et al. 2013) and contemporarily (Kushla and Ripple 1997, Dunn and Bailey 2016, Reilly and Spies 2016). Researchers increasingly accept that non-stand replacing fire may be the most common and functionally important fire effect in large portions of Douglas-fir forests (Tepley et al. 2013, Reilly et al. 2017). However, this perspective was derived from dendroecological studies that infer process from pattern and sometimes lack direct fire evidence (Morrison and Swanson 1990, Tepley et al. 2013, 2014), such that field observations of tree regeneration across a gradient in fire severity would provide valuable insights by directly linking this ecosystem response to observed fire effects.

Recent increases in large fire occurrence in the western Oregon Cascades provide new opportunities to observe Douglas-fir forest response to wildfires directly. Arguably, fire exclusion in these forests has not exceeded the range of variability in natural fire return intervals (50–150 yr; Means 1982, Morrison and Swanson 1990, Weisberg 2004, Spies et al. 2018). We concentrated on fires that burned >10 yr prior to sampling to capture regeneration dynamics more reflective of future successional trajectories than observations taken within the first couple years post-fire, especially since tree recruitment may lag for decades following fire (Tepley et al. 2013, Freund et al. 2014). Specifically, we quantified the abundance, distribution, species richness, and community composition of regenerating conifer and hardwood trees across a fire severity gradient from unburned to 100% basal area mortality. We use these results to inform a discussion on fire's functional role in western Oregon Cascades Douglas-fir forests.

METHODS

Study area

Douglas-fir forests of the western Oregon Cascade Mountains are typically found between 500 and 1300 m elevation from the State of Washington to the South Umpqua River Watershed in south-central Oregon (Franklin and Dyrness 1988). Regional climate is maritime influenced with cool wet winters and warm dry summers. Average annual 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. Temperature increases and precipitation decreases along a north–south climatic gradient in our study area (Daly et al. 2002; www.prismclimate.org). We focused our sampling in fires that burned within the Middle Fork of the Willamette River Watershed near Oakridge, Oregon (43°4′1.6032″ N) south to the North/South Umpqua River Watershed divide (43°43′36.8688″ N) near Tiller, Oregon. Fig. 1 depicts our sample plots, with the most northern plots placed ~10 miles east of Oakridge, Oregon, along Highway 58 and our most southern plots being ~25 miles east of Tiller, Oregon. This study area encompasses an area just south of the line where Agee (1993) hypothesized a transition in this forest's fire regime, and south to the southern extent of Douglas-fir/western hemlock forests based on U.S. Forest Service agency spatial databases (https://data.fs.usda.gov/geodata/).

Douglas-fir forests in our study area are compositionally diverse relative to other conifer forests in the western USA. Common shade-intolerant species include Douglas-fir, sugar pine (*Pinus lambertiana* Dougl.), and incense-cedar (*Calocedrus decurrens* (Torr.) Florin). Western hemlock, 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 commonly encountered shade-tolerant tree species. 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 western hemlock 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.

Study design

In 2012 and 2013, we located plots within and around the 2002 Tiller Complex and Apple fire (10 yr post-fire) on the Umpqua National Forest, and the 1991 Warner Fire (22 yr post-fire) on the Willamette National Forest (Fig. 1). Sampling was limited to mature or old-growth Douglas-fir forests that had not been logged or experienced fire within the past 120 yr, except the 1991 or 2002 fire events of interest, based on agency records and inspection for harvest activities at time of sampling. We used equal probability point sampling in ArcMap 10.0 (ESRI 2011) to randomly locate six, 1-ha plots within each of three fire severity classes (i.e., low, moderate, high) at the two time-since-fire sites. Plots within a severity class were constrained to be >400 m apart. Fire severity maps were resampled 90 × 90 m pixel maps, to more closely align with our plot size, created using the Landtrendr algorithm and published fire severity thresholds where low ≤25% basal area mortality (RdNBR < 235), moderate = 25–75% basal area mortality (RdNBR 235 to 649), and high ≥75% basal area mortality (RdNBR > 649; Reilly et al. 2017). An additional six 1-ha plots were located in unburned stands adjacent to our sampled fires as a reference group, for a total of 42 plots each containing four nested subplots as described below.

Fire severity and forest structure

We sampled surviving trees and coarse wood (snags and logs) in four nested subplots within our 1-ha circular plots, a layout based on the U.S. Forest Service Forest Inventory and Analysis plot design (Bechtold and Patterson 2005). We placed one subplot at plot center, and three additional subplots centered 36.6 m away oriented along a random azimuth, but with each subplot having

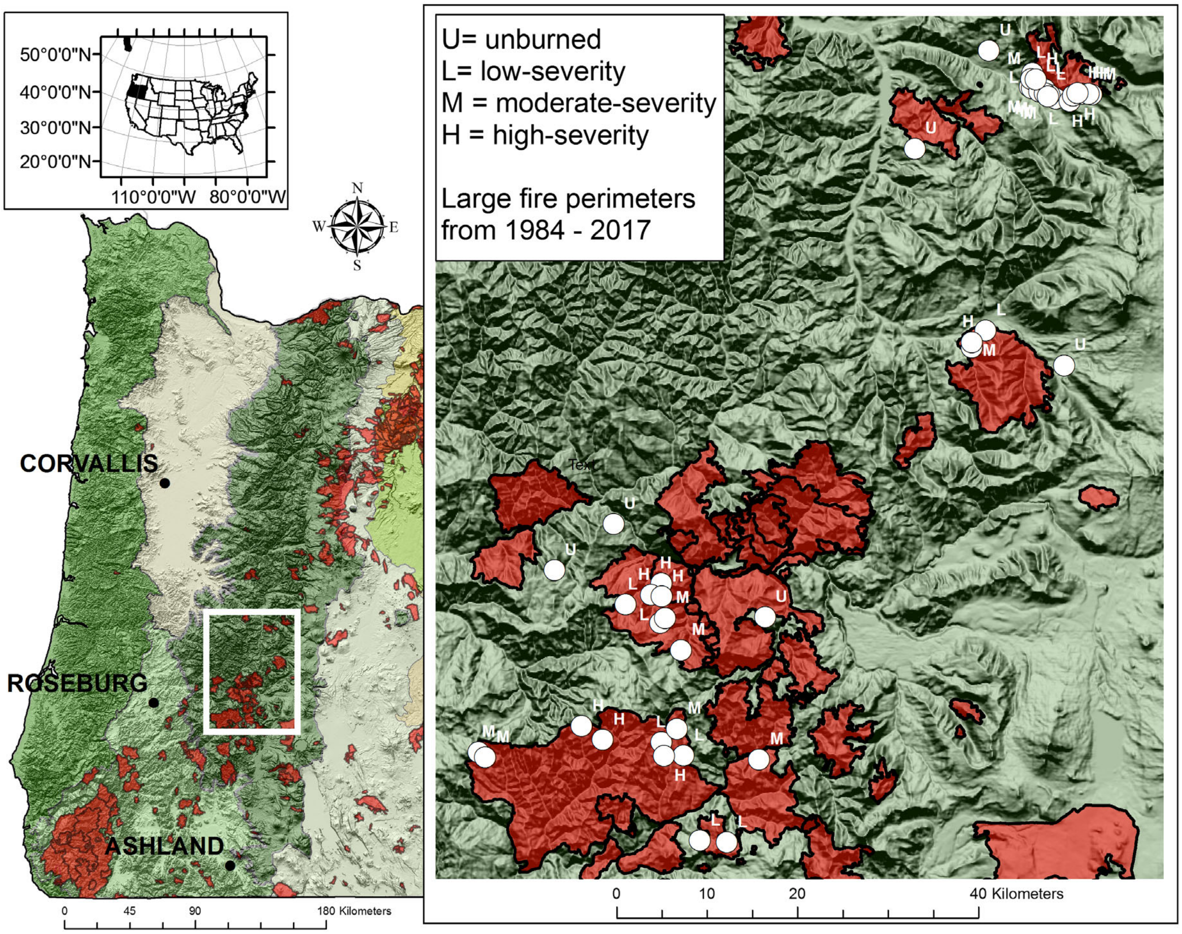

Fig. 1. A map depicting fire extent from 1984 to 2016, and the location of our 42 plots across our study area in western Oregon's Cascade Range. We only sampled tree regeneration 10 and 22 yr post-fire despite the extensive burned areas in more recent years. The bar chart represents the cumulative area of low-, moderate-, and high-severity fire from remotely sensed data capturing initial fire effects in mature and old-growth Douglas-fir/western hemlock forests.

120° of separation. Surviving trees and standing or fallen coarse wood >2.54–10.0 cm diameter at breast height (dbh, i.e., 1.37 m above ground) were sampled in a 5.64 m radius area (1/100th ha) in each subplot, >10.0–40.0 cm dbh within an 8.92 m radius area (1/40th ha), and >40 cm dbh at 17.84 m radius area (1/10th ha). For surviving trees, we recorded species, dbh, total height, and crown base height (cbh). For coarse wood, we recorded species, dbh, condition (i.e., standing intact, standing broken, fallen), height, and percent combustion of sapwood or heartwood. We also sampled trees and coarse wood >70 cm dbh across the entire 1-ha plot, recording the same information as in subplots, to capture large, spatially dispersed individuals for plot-level estimates. Sampling required systematic gridding for all trees and standing or downed coarse wood to reconstruct pre-fire forest conditions and observed basal area mortality. We visually identified pre-fire coarse wood and separated them from fire-created coarse wood when ≥5% of the bole sapwood was combusted or converted to charcoal (Dunn and Bailey 2012).

We summarized pre- and post-fire forest attributes at the plot and subplot level to describe the sampled fire severity gradient and for use as covariates in other analyses. We reconstructed pre-fire live basal area and tree density as the sum of current surviving trees and fire-created coarse wood, and quantified observed basal area mortality as the difference between live trees and dead trees killed by fire. We also differenced standing live basal area and standing coarse wood basal area in unburned plots to help us distinguish fire effects and subsequent regeneration responses that are distinct from other disturbance agents (e.g., insects, pathogens, drought, and density-dependent mortality). We summarize pre- and post-fire forest attributes by a priori severity classes at the subplot scale (low ≤ 25%, moderate = 25–75%, and high ≥ 75% basal area mortality) to demonstrate the gradient in fire effects captured by our sampling. We used linear mixed models to test differences among a priori severity classes with plot as a random effect to account for any positive correlations in residuals resulting from our nested plot design. Pairwise comparisons were adjusted for multiple comparisons using Tukey corrections in multcomp package of R (Torsten et al. 2008). For all regeneration analyses, we used continuous estimates of observed forest attributes (i.e., surviving basal area or proportion basal area mortality) because they are a direct measure not prone to errors associated with Landsat-based remote sensing estimates (Hoe et al. 2018).

Tree regeneration

We sampled regenerating trees as seedlings (regenerating trees ≤ 2.54 cm dbh) or saplings (post-fire regenerating trees > 2.54 cm dbh). We separated post-fire regenerating trees from survivors based on visual evidence, or lack thereof, of bole or crown scorch. Seedlings were sampled in square 10 × 10 m plots (seedling plots) centered on the four nested forest structure subplots. We partitioned each seedling plot into equal-area quadrants and counted seedlings by species in three height classes: 1–50, >50–150, and >150 cm. Saplings were sampled according to our forest structure protocol previously described. For unburned plots, we considered all live trees >2.54–10.0 cm dbh as regenerating saplings for comparison to burned plots. We combined white fir and grand fir into a composite *Abies* species because they hybridize and generally occupy the same ecological niche within our study area. We also combined ponderosa and sugar pine because of their relatively low abundance and similar shade tolerance.

We were interested in whether overstory competition (i.e., observed surviving basal area) or fire severity (i.e., observed percent basal area mortality) better predicted regeneration abundance after fire disturbance. In addition, we wanted to gain insights into the spatial scale of overstory influence on tree regeneration dynamics, so we evaluated overstory competition and fire severity at the 0.10-ha (i.e., subplot) and 1.0-ha (i.e., plot) scale. We observed high correlation between overstory competition and fire severity across these spatial scales, so these factors were included in separate statistical models with up to five additional plot-level environmental covariates (Table 1). The sample units were our seedling subplots for a total sample size of 168. We observed overdispersion with a Poisson distribution based on the ratio of *chi*-squared to residual degrees of freedom, so we used a generalized linear mixed-effects model with a negative binomial distribution and log link in the glmmADMB package of R (R Development Core Team 2008, Fournier et al. 2012). We included plot as a random effect to account for any positive correlations in residuals resulting from our nested plot design. We evaluated quadratic terms for overstory competition and fire severity at both spatial scales, and used stepwise model selection and Akaike Information Criterion (AIC) to select the final parsimonious model that best describes the drivers of regeneration abundance following fire disturbance.

We quantified the distribution of regenerating conifer trees as the frequency of occurrence of each species within quadrants (i.e., 5 × 5 m) at each seedling plot. This scale approximates regeneration stocking levels typical of forest management practices in the PNW (Tappeiner et al. 2015). We estimated frequency of hardwood trees at the 100-m^2 seedling plot-scale because giant chinkapin was originally sampled as a shrub at these same plots for other research questions. We sampled 96 frequency-quadrants in each a priori fire severity class and unburned forest condition, but combined plots into fire severity classes based on observed conditions using the thresholds of <25%, 25–75%, and >75% basal area mortality as low-, moderate-, and high-severity fire, respectively. According to our

Table 1. Covariates tested for correlation with regeneration abundance and richness.

Covariate	Units	Definition
Elevation	meters	Elevation can be considered a proxy for water balance and temperature differences
Slope	degrees	Water drainage, soil depth, heat exposure
Aspect	azimuth	Heat exposure, water balance
Heat load	unitless	Heat exposure, water balance
Plot-level surviving basal area	m^2/ha	Post-disturbance overstory competition at hectare scale
Plot-level surviving trees/ha	no./ha	Post-disturbance overstory competition at hectare scale
Plot-level basal area mortality	percent	Estimate of the release of resources previously excluded by overstory competition at hectare scale
Subplot-level pre-fire basal area	m^2/ha	Pre-disturbance overstory competition at 0.10-regeneration plot-scale
Subplot-level surviving trees/ha	m^2/ha	Post-disturbance overstory competition at 0.10-regeneration plot-scale
Subplot-level basal area mortality	percent	Estimate of the release of resources previously excluded by overstory competition at 0.10-regeneration plot-scale

plot-level reconstructed fire severity, only one plot (four subplots) remained in the low-severity class so we exclude this plot and severity class from frequency estimates. We analyzed each time-since-fire group (Tiller and Apple or Warner Creek) independently. We also separated dry and wet high-severity sites at the Warner Fire (12 seedling plots in each group) because of an abundance of regenerating western hemlock observed at toe of slopes with moister edaphic conditions at the Warner Creek Fire. This resulted in six distinct groups for comparative purposes.

We also quantified species richness (number of distinct species) of regenerating trees in response to the fire severity gradient using the same methodology as the abundance analysis. One exception was that we used a normal distribution in our generalized linear mixed-effects model after evaluating diagnostic plots for assumptions of normality (i.e., normal q-q plots) and equal variance (R Development Core Team 2008). Again, our final parsimonious model was the statistical model with the lowest AIC value, describing the drivers of species richness and the scale of influence that best predicts the observed response.

Community composition of regenerating trees can contribute further insights into the development of forests following disturbance. Therefore, we characterized regeneration communities across observed fire severity classes in the same categories described previously. We tested for compositional differences among our six groups (unburned, moderate-severity 10 yr post-fire, high-severity 10 yr post-fire, moderate-severity 22 yr post-fire, and high-severity wet and high-severity dry 22 yr post-fire) using a Multi-Response Permutation Procedure in PC-ORD (https://www.wildblueberrymedia.net/software). We used a Sorensen's (Bray-Curtis) distance measure and 5000 randomization tests to obtain the chance-corrected within-group agreement (*A*-statistic; Mielke and Berry 2001). We based this analysis on the seven most common conifer species because of their easily comparable functional traits and common occurrence as overstory trees in this forest type. Abundance values were log-transformed to reduce the effects of very large values and ubiquitous distribution of Douglas-fir (McCune et al. 2002). We tested for outlier plots (distance measure >2.5 standard deviations from the mean), but none were present, and report overall and pairwise comparisons of differences among these groups.

RESULTS

Fire severity and forest structure

There were no statistically significant differences between reconstructed pre-fire basal area or forest density based on a priori severity groups, at an alpha <0.05, when 10- and 22-yr post-fire sites were included in a single statistical model (Table 2). Reconstructed pre-fire basal area averaged 66.5 m^2/ha (standard deviation [SD] = 16.4) and reconstructed pre-fire forest

Table 2. Mean (standard deviation) of fire effects and forest structural attributes based on a priori fire severity classes at our sampled 10 and 22 yr post-fire sites.

		10 yr post-fire			22 yr post-fire		
Attribute	Unburned	Low	Moderate	High	Low	Moderate	High
Reconstructed tree basal area (m^2/ha)	69.2 (14.0)^{a}	69.4 (13.9)^{a,b}	57.4 (12.7)^{b}	51.2 (7.2)^{b}	75.2 (23.8)^{a}	77.1 (18.6)^{a}	67.2 (11.4)^{a}
Reconstructed tree density (trees/ha)	721.8 (216.4)^{a}	738.4 (216.5)^{b,a}	1306.9 (912.8)^{a}‡	444.4 (254.3)^{b}	364.7 (143.8)^{b}	369.7 (246.8)^{b}	228.2 (100.0)^{b}
Percent fire-induced basal area mortality (m^2/ha)	NA	36.4 (8.5)^{a}	50.3 (12.6)^{b,a}†	95.0 (9.4)^{c}	25.5 (7.8)^{a}	42.7 (12.7)^{b}	97.6 (4.8)^{c}
Percent fire mortality (trees/ha)	NA	70.5 (7.1)^{a}	84.6 (11.9)	99.2 (1.5)	49.2 (11.5)^{a}	71.5 (9.9)^{b}	99.6 (0.6)^{c}
Surviving tree basal area (m^2/ha)	69.2 (14.0)^{a}	42.7 (10.2)^{b}	28.1 (10.4)^{b}	2.3 (4.4)^{c}	56.6 (23.8)^{a}	44.0 (12.2)^{b,a}	1.3 (2.4)^{b}
Surviving tree density (trees/ha)	721.8 (216.4)^{a}	217.9 (92.5)^{b}	140.2 (48.3)^{c,b}	4.9 (10.6)^{d,c}	187.3 (102.6)^{b}	113.8 (97.2)^{b}	1.3 (2.1)^{b}
Surviving tree canopy base height (m)	8.0 (2.3)^{a}	9.2 (2.3)^{a}	12.4 (7.4)^{a}	27.2^{b}†	24.2 (5.0)^{b}	24.6 (5.0)^{b}	29.0^{b}†
Surviving tree quadratic mean diameter (cm)	35.9 (6.8)^{a}	52.1 (10.1)^{a}	52.5 (18.0)^{a}	91.7^{b}†	65.0 (11.0)^{b}	81.9 (21.4)^{b}	109.1^{c}†
Snag basal area (m^2/ha)	9.0 (3.9)^{a}	24.8 (8.2)^{b}	28.4 (9.4)^{b}	48.4 (9.4)^{c}	18.1 (6.2)^{a}	32.9 (13.2)^{b}	65.6 (12.9)^{c}
Snag density (trees/ha)	102.2 (50.6)^{a}	514.3 (145.0)^{a,b}	1165.7 (892.2)^{b}‡	439.2 (248.7)^{a,b}	169.2 (70.8)^{a}	252.4 (156.5)^{a}	226.3 (99.2)^{a}
Elevation (m)	774–1246	917–1174	938–1257	801–1183	764–1021	776–1308	1056–1301
Slope (°)	19.3 (3.9)	20.2 (1.1)	20.6 (6.9)	21.3 (3.7)	23.5 (6.5)	19.1 (6.4)	17.4 (3.0)
Heat load	0.90 (0.08)	0.78 (0.12)	0.89 (0.13)	0.86(0.12)	0.98 (0.04)	0.99 (0.02)	0.97 (0.02)

Notes: Lower case letters indicate statistically different estimates at an alpha ≤0.05.
† Estimated for live trees only.
‡ Includes two plots with a high abundance of <10 cm snags.

density averaged 591.4 trees/ha (SD = 484.9). However, when separated by time-since-fire groups (i.e., 10 or 22 yr post-fire), the Warner Creek Fire did not exhibit significant pre-fire differences among severity groups, but the Tiller Complex had statistically lower pre-fire basal area and tree densities in moderate and high-severity classes relative to unburned forests. As expected, tree mortality varied significantly across our sampled fire severity gradient with the largest increase in basal area mortality observed between moderate- and high-severity plots as incrementally larger trees died. Only 31% of all high-severity plots had surviving trees, ranging from 2.6% to 23.4% of pre-fire basal area. Live structural attributes also varied across our fire severity gradient at both fire sites, although pairwise comparisons of surviving tree basal area between the low and moderate-severity classes were not statistically different at an alpha ≤0.05. One key observation is that mortality generally exceeded our a priori threshold for low-severity fire (i.e., <25% basal area mortality) in all but one plot, most likely a result of delayed tree mortality (Ryan and Reinhardt 1988, Brown et al. 2013). For a more in-depth analysis of mortality and structural change in response to this fire severity gradient, refer to Dunn and Bailey (2016).

Tree regeneration

Regeneration abundance was best predicted by observed basal area mortality at the 1-ha plot-scale (Table 3). The highest mean regeneration

Table 3. Statistical summary from our analysis of regeneration abundance at the 0.10-ha regeneration plot and basal area mortality at the 1-ha plot-scale

Coefficient	Estimate	Standard error	z	Pr(>|z|)	Variance	Standard deviation
Intercept	6.0015	0.6048	9.92	<0.0001		
Basal area mortality (plot)	0.1281	0.0262	4.89	<0.0001		
Basal area mortality^2 (plot)	−0.0011	0.0002	−5.08	<0.0001		
Random effects (plot)						
Intercept					0.8201	0.9056
Negative binomial dispersion parameter	0.93385	0.10497				

Note: Akaike Information Criterion = 3264.8, Log-likelihood = −1627.38.

abundance resulted from moderate-severity fire, especially following 25–50% basal area mortality (Fig. 2). The highest abundance of regenerating trees observed was 81,500 trees/ha, following 31% basal area mortality at the Tiller Complex. We also observed 72,500 and 73,800 trees/ha at the Warner Fire following 36% and 100% basal area mortality, respectively. These estimates were much greater than the maximum of 8300 trees/ha observed in unburned forests. No additional environmental variables (elevation, slope, etc.) had statistically significant correlation with regeneration abundance after accounting for fire severity.

Moderate-severity fire resulted in the greatest distribution for the greatest number of species of

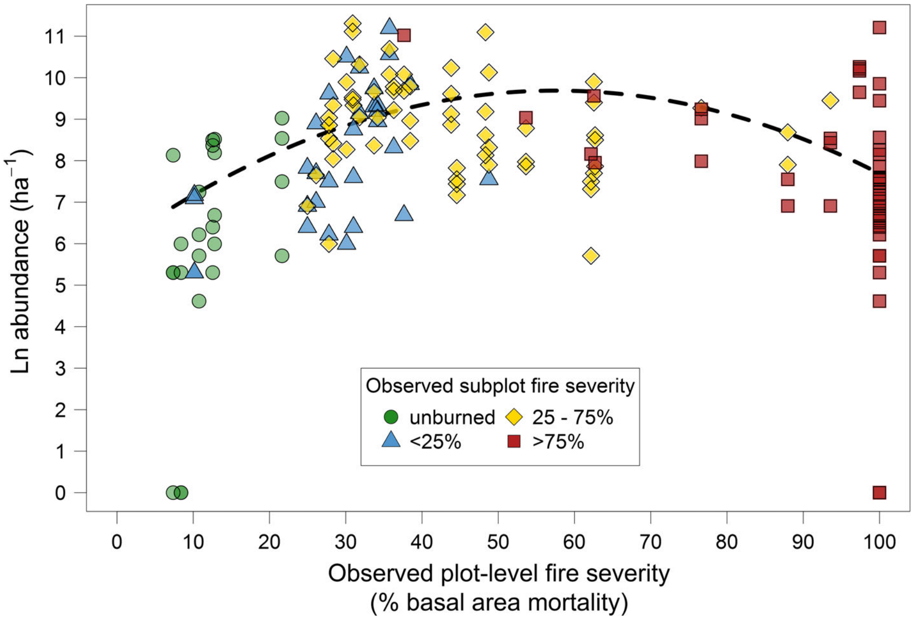

Fig. 2. Correlation of the natural logarithm of total tree regeneration abundance with observed basal area mortality at the 1-ha plot-scale. The dashed line represents the statistical relationship from our top model quantifying regeneration abundance at the nested 0.10-ha regeneration plot-scale in relation to observed basal area mortality at the 1-ha plot-scale. Points are observations of regeneration abundance at each of the four nested regeneration plots, and their color and shape schema represent the observed basal area mortality at the 0.10-ha scale. The x-axis represents basal area mortality at the 1-ha plot-scale. Most a priori low-severity plots transitioned to moderate-severity, most likely a result of delayed mortality, by the time we sampled these forests a decade or two after the fire.

any fire severity class considered (Fig. 3). Notable exceptions were some shade-tolerant species more frequently encountered in unburned forests and at moist edaphic sites in the Warner Fire. Overall, Douglas-fir had the greatest distribution of all species, consistent with its dominance within our study area, except at unburned sites where shade-tolerant species had higher frequency of occupancy. Regenerating trees occupied the majority of our 5 × 5 m quadrants across the fire severity gradient, although 39% of unburned quadrants lacked regenerating trees. Regenerating trees were absent in 4% and 27% of quadrants 10 yr after observed moderate- and high-severity fire effects, respectively. Similarly, 11% and 16% of quadrants lacked regenerating trees 22 yr after observed moderate- and high-severity fire effects, respectively. In many cases, overstory trees occupied the quadrants without regenerating trees. When we considered the full seedling plot-scale (i.e., 10 × 10 m), only three (6%) unburned and two (4%) high-severity plots at the Tiller Complex lacked regenerating trees 10 yr post-fire.

Species richness of regenerating trees was most strongly correlated with observed basal area mortality at the 1-ha plot-scale, including the quadratic term like our abundance estimates (Table 4). On average, species richness was highest following moderate-severity fire, with up to a 100% increase in mean richness relative to unburned forests or following high-severity fire (Fig. 4). On average, the highest species richness occurred between 25% and 50% basal area mortality, where we commonly observed six to seven species within a 100-m^2 area. The absolute maximum richness observed followed 80% basal area mortality, but this plot appears to be an outlier (Fig. 4). All but two of the 13 regenerating tree species sampled were present in both fires. The exceptions were ponderosa pine, only observed in five seedling plots (moderate- and high-severity only) at the Tiller Complex, and Pacific silver fir that was only observed at three seedling plots (high-severity plots only) in the Warner Fire at ~1300 m elevation. Pacific madrone, bigleaf maple, and giant chinkapin were commonly encountered hardwoods. Douglas-fir, western hemlock, incense-cedar, western redcedar, sugar pine, and grand/white fir were common regenerating conifers. Pacific yew and Pacific dogwood were rare relative to other species, but still present in these early post-fire environments.

Regeneration communities varied significantly across the fire severity gradient and our fire sites (Fig. 5). The overall chance-corrected within-group agreement among the six regeneration groups was $A = 0.197$ ($P < 0.0001$). The strength of the compositional difference varied by specific pairwise comparisons, but all were statistically different except high-severity sites at Tiller Complex and high-severity sites with dry edaphic conditions at Warner Fire (Table 5). However, some pairwise comparisons did not exhibit strong separation in community structure, assuming an A-statistics ≥ 0.10 is indicative of strong community separation. Interestingly, the two high-severity groups at Warner Fire had the strongest compositional differences of all pairwise comparisons. These regeneration communities develop from two broader species pools common to wet Douglas-fir forests to the north and dry Douglas-fir forests to the south, in what could be considered a broad ecotone forest. Shade-tolerant species such as western hemlock, true fir, western redcedar, and some hardwoods dominated regeneration in unburned forests (Fig. 5). Moderate-severity fire increases the abundance of shade-intolerant species, such as Douglas-fir, incense-cedar, and pine species without excluding the regenerating shade-tolerant species observed in unburned forests. Douglas-fir, incense-cedar, pine species, and resprouting hardwoods dominate areas burned at high-severity, largely excluding shade-tolerant species except for the prevalence of a high abundance of western hemlock following high-severity fire at moist sites in the Warner Fire. We discuss these communities and their relationship to forest succession in detail in the following section.

DISCUSSION

Despite an abundance of ecological literature describing Douglas-fir forests, there remains significant uncertainty regarding non-stand replacing fire, tree regeneration response to these conditions, and potential variation in the successional development of this forest type. Researchers and managers remain dominantly focused on high-severity fire effects in Douglas-fir forests

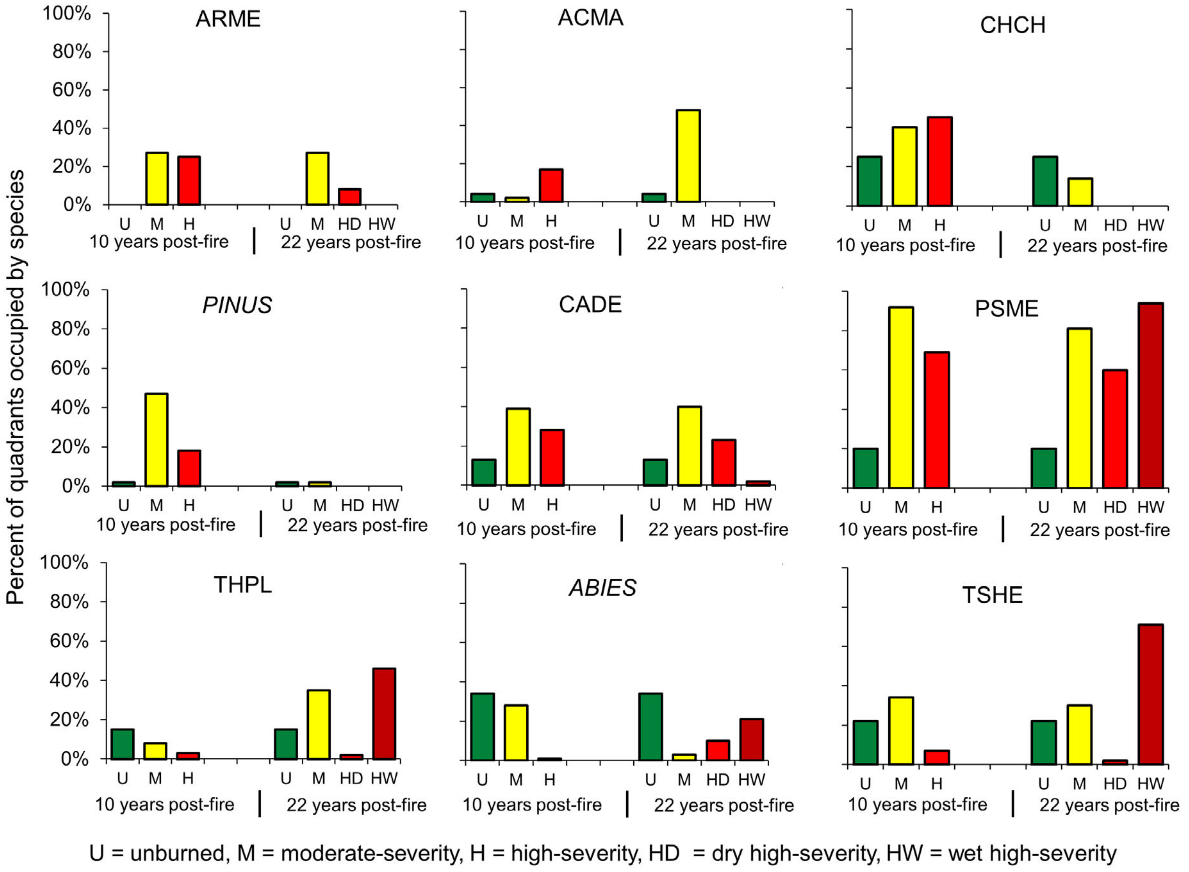

Fig. 3. Frequency of quadrants where individual species were present. The dominant difference in regeneration response among these fires was a decrease in the presence of *Pinus* species at Warner Fire, and abundant shade-tolerant species following high-severity fire at the Warner Fire. CADE, incense-cedar; PSME, Douglas-fir; TSHE, western hemlock; THPL, western redcedar; TABR, Pacific yew; ABIES, true fir species; and PINUS, all pine species.

Table 4. Statistical summary for correlation between species richness at the 0.10-ha regeneration plot and basal area mortality at the 1-ha plot-scale.

Coefficient	Estimate	Standard error	*t*	*P*	Standard deviation
Intercept	1.2479	0.6442	1.9372	0.0550	
Basal area mortality (plot)	0.1104	0.0279	3.9593	0.0003	
Basal area mortality^2 (plot)	−0.0010	0.0002	−4.3330	0.0001	
Random effects (plot)					
Intercept					1.0242
Residual					1.0332

Note: Akaike Information Criterion = 586.8, Log-likelihood = −288.4.

(Swanson et al. 2010, Franklin and Johnson 2012, Seidl et al. 2014, Parks et al. 2015) despite evidence suggesting Douglas-fir forests may exhibit a north–south gradient in fire regimes (Agee 1993, Halofsky et al. 2018). Oregon's Douglas-fir forests having moderate fire return intervals (ranging from 50 to 150 yr) and non-stand replacing disturbance accounting for the large

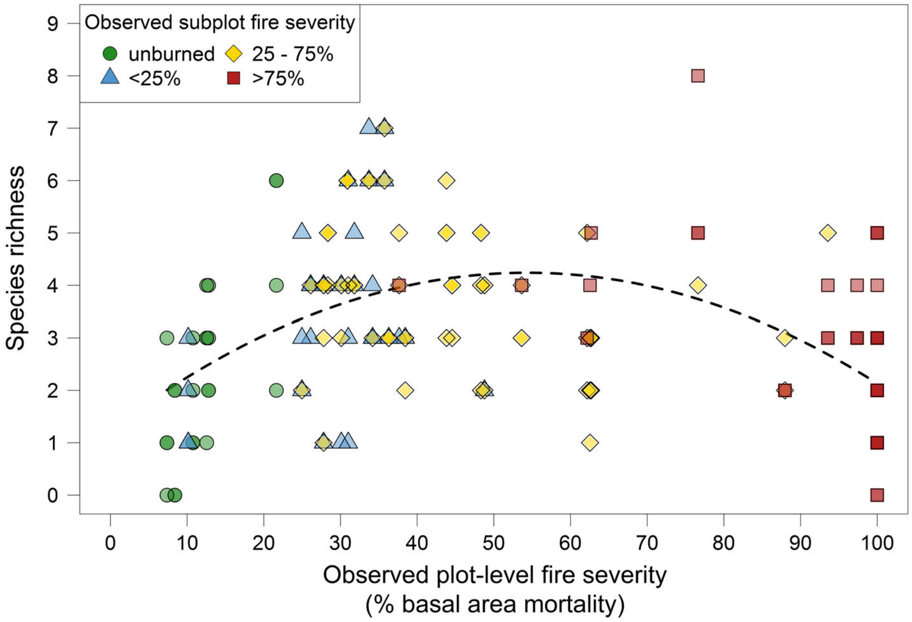

Fig. 4. Figure depicting the humped-shape response of tree species richness as a function of observed fire severity. The dashed line represents the mean statistical relationship from our final model quantifying mean species richness at the 0.10-ha regeneration plot-scale in relation to observed basal area mortality at the 1-ha plot-scale. Points are observations of species richness at each of the four nested regeneration plots, and their color and shape schema represents the observed basal area mortality at the 0.10-ha scale. The *x*-axis represents basal area mortality at the 1-ha plot-scale. Most a priori low-severity plots transitioned to moderate-severity, most likely a result of delayed mortality, by the time we sampled these forests a decade or two after the fire.

majority (>66%) of the burned area (Means 1982, Morrison and Swanson 1990, Weisberg 2004, Tepley et al. 2013, Reilly et al. 2017). Similar observations have been made in both field and remotely sensed assessments of contemporary fires (Kushla and Ripple 1997, Dunn and Bailey 2016, Reilly and Spies 2016, Reilly et al. 2017), including the 2017 Eagle Creek fire that burned along the Oregon and Washington border where initial fire affects 45% low severity, 22% moderate severity, and 33% high severity. In the following paragraphs, we discuss tree regeneration response to the gradient in fire severity and relate that response to research and theoretical models of successional development in this forest type.

Our intent is not to suggest that high-severity fire, and the development of early seral environments, are not an important component of disturbance dynamic in Douglas-fir forests. Rather, we want to place high-severity fire within the context of the broader fire severity gradient. High-severity fire resulted in distinct regeneration composition consistent with the commonly assumed relay floristics model (Egler 1954, Franklin et al. 2002). Lack of shade-tolerant conifers and hardwoods reduced regeneration diversity in plots that experienced high-severity fire (Fig. 4), while facilitating the rapid establishment and dominance of regenerating shade-intolerant species, especially Douglas-fir (Fig. 5). Douglas-fir's abundance and distribution suggests they will dominate stand dynamics for decades or longer (Fig. 3), until microclimatic conditions ameliorate (e.g., solar insolation, moisture stress) and shade-tolerant species increase in abundance (i.e., relay floristics) as death of the pioneering cohort commences (Tepley et al. 2014). However, within the distribution of conditions indicative of this successional model we observed significant variation in the starting point, including regeneration gaps and wide ranges in regeneration density (Fig. 3; Tappeiner et al. 1997, Poage and Tappeiner 2002, Winter et al. 2002, Donato et al. 2011, Freund

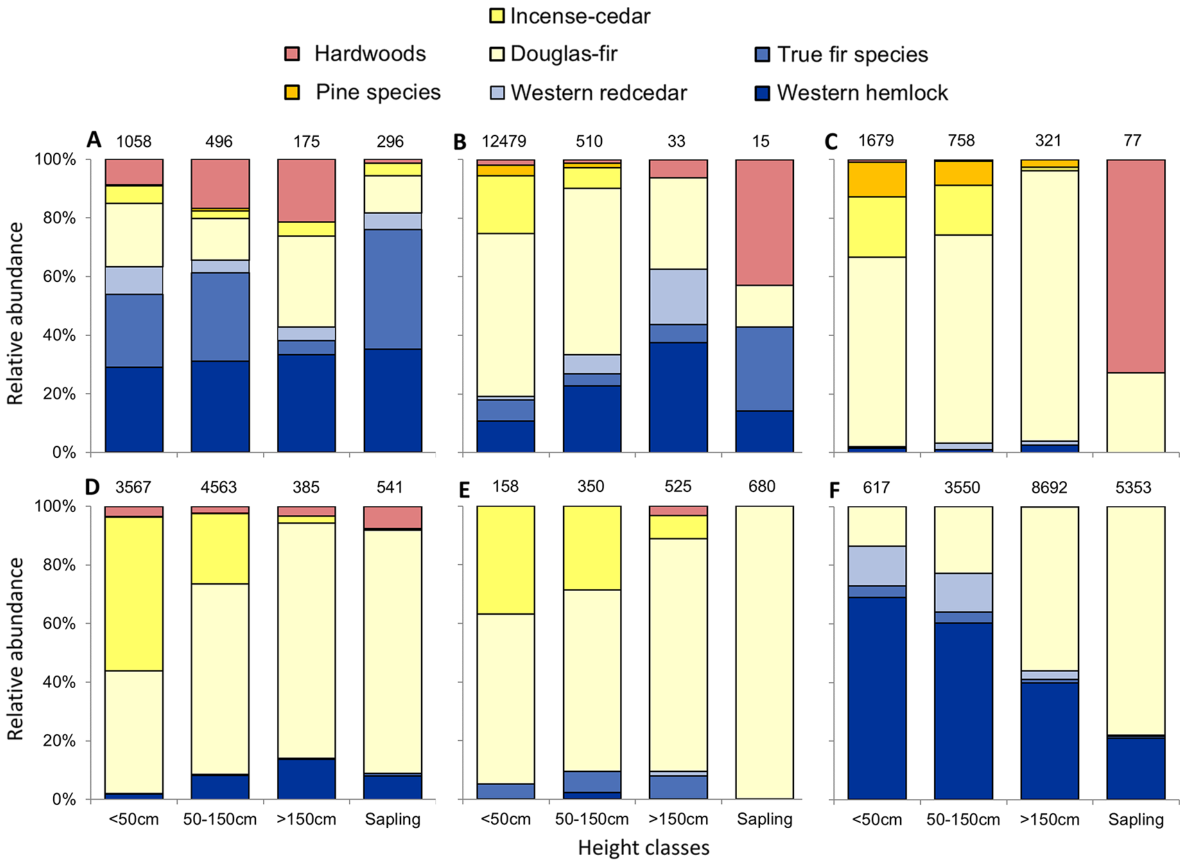

Fig. 5. Regeneration composition by height class in response to a fire severity gradient at two time-since fire sites. Bars demonstrate relative composition by height class, so we provide average abundance values by height class at the top of each bar. The smallest height class is the most abundant 10 yr post-fire, while taller height classes are the most abundant 22 yr post-fire suggesting regeneration in response to fire is declining by 22 yr post-fire. (A) Unburned forests, (B) moderate-severity 10 yr post-fire, (C) high-severity 10 yr post-fire, (D) moderate-severity 22 yr post-fire, (E) dry high-severity sites 22 yr post-fire, and (F) and wet high-severity sites 22 yr post-fire.

et al. 2014). These conditions and future trajectories will contribute to landscape-scale structural diversity and a broader distribution in the timing of structurally complex, old-growth forests.

Regeneration response to high-severity fire was not limited to the promotion of mono-specific stands of Douglas-fir (Fig. 5). Late seral species are sometimes present at stand initiation, exhibiting an initial floristics model of succession (Egler 1954). Research has shown western hemlock can immediately regenerate in high abundance following disturbance when soil moisture is high enough to offset higher transpirational demands common in post-disturbance landscapes (Isaac 1943). We observed this effect at toe-slopes within the Warner Fire landscape where western hemlock regenerated prolifically and reached sapling size by 22 yr post-fire (Fig. 5). The tolerance of western hemlock to shade and competition suggests this species will persist into later successional stages and likely become dominant earlier in succession than occurs under the relay floristics model (Tepley et al. 2014).

In contrast, a high abundance of surviving overstory trees competitively excludes most shade-intolerant tree species while facilitating the recruitment of late seral shade-tolerant trees (Fig. 5). These post-fire conditions were relatively

Table 5. Summary of our statistical results using a Multi-Response Permutation Procedure contrasting six groups, representative of post-fire regeneration communities observed across our fire severity gradient.

Severity/time-since-fire comparison	*T*-statistic	*A*-statistic	*P*
Unburned vs. Moderate 10 yr	−19.3809	0.1363	<0.0001
Unburned vs. High 10 yr	−17.1012	0.2089	<0.0001
Unburned vs. Moderate 22 yr	−18.5865	0.1375	<0.0001
Unburned vs. High-dry 22 yr	−12.3800	0.2124	<0.0001
Unburned vs. High-wet 22 yr	−7.9633	0.1267	<0.0001
Moderate 10 yr vs. High 10 yr	−12.1897	0.0880	<0.0001
Moderate 10 yr vs. Moderate 22 yr	−19.7311	0.1003	<0.0001
Moderate 10 yr vs. High-dry 22 yr	−14.2638	0.1243	<0.0001
Moderate 10 yr vs. High-wet 22 yr	−13.6319	0.1220	<0.0001
High 10 yr vs. Moderate 22 yr	−6.8225	0.0566	0.0002
High 10 yr vs. High-dry 22 yr	−0.9429	0.0169	0.1478
High 10 yr vs. High-wet 22 yr	−13.9875	0.2435	<0.0001
Moderate 22 yr vs. High-dry 22 yr	−6.5900	0.0671	0.0003
Moderate 22 yr vs. High-wet 22 yr	−7.7195	0.0769	0.0001
High-dry 22 yr vs. High-wet 22 yr	−10.9457	0.3083	0.0000

rare in our study area, with only 8.3% of our a priori low-severity plots exhibiting true low-severity effects (i.e., <25% basal area mortality; Table 2). The resulting ecological effects and subsequent regeneration abundance (Fig. 2) and diversity (Fig. 4) are largely indistinguishable from unburned forests. However, low-severity fire does produce a pulse of shade-tolerant cohorts, following a slow and sporadic recruitment from other disturbances that do not remove as much litter and duff, which may inhibit establishment of small seeded species. In contrast, endogenous or exogenous mortality mechanisms that create canopy gaps promote advanced regeneration as opposed to seedling regeneration as they slowly diversify forest structure over time (Whitmore 1989, Franklin and Van Pelt 2004, Meigs and Keeton 2018).

Moderate-severity fire receives less attention in research but are critical to consider in Douglas-fir forests, because fire-induced basal area mortality between 25% and 75% is the most abundant fire severity class, when delayed mortality is accounted for in stands that initially experienced low-severity fire (Ryan and Reinhardt 1988). Moderate-severity fire results in the most structurally diverse sub-hectare conditions of any severity class (Dunn and Bailey 2016), producing variable light and soil moisture conditions known to influence regeneration dynamics (Gray and Spies 1997, Zald et al. 2008). Coupled with surviving shade-tolerant and shade-intolerant trees as seed sources (Larson and Franklin 2005, Tepley et al. 2014), moderate-severity fire produces the most abundant, spatially distributed and diverse cohort of regenerating trees. This response is consistent with the theoretical response described by the Intermediate Disturbance Hypothesis (Connell 1978, Wilkinson 1999, Roxburgh et al. 2004) and appears functionally important for developing and maintaining the compositional diversity of these Douglas-fir forests.

Moderate-severity fire increases the pace and scale of near- and long-term structural complexity, which is a measure of the composition, relative abundance, and vertical and horizontal distribution of trees, snags, and logs (McElhinny et al. 2005). This three-dimensional structure is an important ecological attribute of forested ecosystems, often considered a surrogate for ecosystem biodiversity (Harmon et al. 1986, Spies and Franklin 1988, Franklin and Spies 1991, Hansen et al. 1991, McElhinny et al. 2006, Reilly and Spies 2015). Common successional models assume structural complexity increases slowly over time through small-scale endogenous or exogenous mortality mechanisms such as wind throw or root rot (Oliver and Larson 1996, Franklin et al. 2002). Our observations suggest an alternative pathway toward structural complexity exists. Moderate-severity fire results in the most structurally complex post-fire forest condition, at least for a couple decades following the incident (Dunn and Bailey 2016). Coupled with the increased abundance, spatial distribution, and diversity of fire-mediated understory reinitiation observed following moderate-severity fire (Figs. 2–4), there is a higher probability that structural complexity will increase into the future because of moderate-severity fire relative to the other post-fire structural conditions and regeneration response observed in this study. This successional model may explain the unexpected overstory communities (e.g., incense-cedar and western redcedar or sugar pine and western hemlock as co-dominant trees) observed regularly in our study area. Moderate-severity fire may also stimulate abundant hardwood tree regeneration and maintain species like sugar pine that are often rare following low-severity fire or in unburned forests (Atzet and Wheeler 1982). This increase in structural complexity and response diversity suggests moderate-severity fire increases forest resilience to disturbances like disease, insect, drought, and fire (Elmqvist et al. 2003). We define forest resilience as the capacity of this forest type to absorb disturbance and reorganize while undergoing change, such that it retains essentially the same function, structure, identity, and feedbacks (Walker et al. 2004). Forest resilience is enhanced by structural complexity and response diversity because species vary in their (1) probability of mortality from fire (Dunn et al. 2019), (2) growth rate following fire (Johnston et al. 2019), (3) tolerance to shade and drought (Niinemets and Valladares 2006), and (4) susceptibility to insects and disease (Agne et al. 2018). While our observations may be limited to the highly productive Douglas-fir forests we sampled, similar regeneration responses have been reported in moister forests at the northern reach or north of our study area despite having a less diverse species pool (Larson and Franklin 2005, Tepley et al. 2013).

We have described a gradient in fire-induced overstory mortality and the subsequent tree regeneration response to those conditions, and highlighted critical linkages between our observations and research on successional trajectories and overstory composition in this forest type. Douglas-fir forests burn with mixed-severity, consistent with changing perspectives in many, if not most, conifer forests of western North America (Agee and Krusemark 2001, Baker and Ehle 2001, Fulé et al. 2003, Hessburg et al. 2005, 2016, Scholl and Taylor 2010, Halofsky et al. 2011, Perry et al. 2011, Tepley and Veblen 2015, Iniguez et al. 2016, Reilly et al. 2017). While mixed-severity fire effects may be common in Douglas-fir forests, Agee (1993) proposed a moderate-severity fire regime for this forest type which is consistent with our observations of the most abundant overstory mortality class (Dunn and Bailey 2016) that facilitates a more abundant and diverse regeneration community. Building capacity to support more mixed-severity fire effects across landscapes is important (DellaSala et al. 2017), but the underlying goal should be to expand non-stand replacing fire to maintain ecosystem response diversity (Mori et al. 2013). This is especially important today because the rapid reorganization of vegetation communities in early post-disturbance environments can facilitate adaptation of forests to a changing climate, and moderate-severity fire effects appear to create the conditions most conducive to this adaptive change.

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