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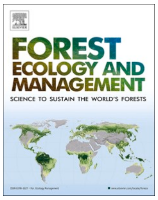

Patterns and drivers of early conifer regeneration following stand-replacing wildfire in Pacific Northwest (USA) temperate maritime forests

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ABSTRACT

Tree regeneration is a critical mechanism of forest resilience to stand-replacing wildfire (i.e., where fire results in >90 % tree mortality), and post-fire regeneration is a concern worldwide as the climate becomes warmer. Although post-fire tree regeneration has been relatively well-studied in fire-prone forests across western North America, it is less understood in fire regimes characterized by large patches of stand-replacing fire at long intervals, such as the nominally infrequent, high-severity fire regimes of the western Cascades of Washington and northern Oregon, USA (northwestern Cascadia) where some of world's highest-biomass forests reside. Recent wildfire activity (2015–2020) in northwestern Cascadia provides a unique opportunity to build understanding of the mechanisms underpinning forest resilience to fire, with implications for forest management and the myriad socio-ecological values associated with these landscapes. Here, we asked: how is post-fire conifer regeneration across northwestern Cascadia affected by pre-fire stand age, burn-patch size, and topo-climatic conditions? We established 39 1-ha long-term monitoring plots across four recent wildfires in northwestern Cascadia to measure post-fire conifer abundance and species composition. We used generalized linear models to test how rates of conifer regeneration (seedlings ha^{-1} yr^{-1} of all heights) and establishment (seedlings ha^{-1} yr^{-1} with heights >10 cm) respond to differences in pre-fire stand age/seral stage (young, mid-seral, late-seral), distance to the nearest live seed source, and post-fire topo-climate setting. In general, initial post-fire seedling densities suggest tree regeneration is abundant following stand-replacing fire in most areas across the region. For example, at 3–5 years post-fire, established seedlings were present in 100 % of plots, and regeneration and establishment levels exceeded state forest practices minimum density thresholds (470 seedlings ha^{-1}) in 82.1 % and 64.1 % of plots, respectively. Post-fire conifer regeneration and tree species richness were greater when pre-fire stand age was older, and was more dominated by shade tolerant species than when pre-fire stand age was younger. Regeneration decreased with farther distances to the nearest live seed source, though seedlings were still moderately abundant at distances as far as 400 m from edges of high-severity patches. Conifer establishment was greater in areas characterized by cooler and wetter macrosite (e.g., greater post-fire precipitation) and microsite (e.g., greater bryophyte ground cover) conditions. By providing information on the drivers and conditions in which land managers can expect natural regeneration to occur or not, our findings are directly relevant to pre- and post-fire forest management objectives under future climate and increased fire activity in systems structured in part by infrequent and severe wildfires.

Abbreviations: AICc, Akaike information criterion corrected for small sample size; ANOVA, analysis of variance; DEM, digital elevation model; DHARMa, diagnostics for hierarchical regression models; EDDI, evaporative demand drought index; ECDF, empirical cumulative density function; GLM, generalized linear model; gridMET, gridded surface meteorological dataset; HLI, heat load index; RDI, refugia density index; RdNBR, relativized differenced normalized burn ratio; SDI, Shannon diversity index; SPEI, standardized precipitation evapotranspiration index; TWI, topographic wetness index; VIF, variance inflation factor.

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1. Introduction

As climate warms and fire activity increases in many regions worldwide (e.g., Collins et al., 2022; Parks and Abatzoglou, 2020), understanding forest resilience to fire is essential to effectively managing forests for their ecological, economic, and cultural values (Davis et al., 2023). Resilience—the ability of an ecosystem to experience disturbance and return to a structurally and functionally state equivalent to the pre-disturbance ecosystem (Falk et al., 2022; Seidl and Turner, 2022; Walker et al., 2004)—is especially challenging to understand in forests in which large stand-replacing wildfires (i.e., >90 % fire-induced tree mortality) are known to occur at long intervals (i.e., stand-replacing fire rotations exceeding 200 years; Halofsky et al., 2018; Turner et al., 1998). Effects of climate warming on such systems are not well understood, as the rarity of major stand-replacing wildfire events limit information about the disturbance regime and post-fire recovery processes (Halofsky et al., 2020).

Many high-severity fire regimes that are characterized by the infrequent occurrence of large stand-replacing patches are climate-limited, meaning fire-potential is constrained by climatic conditions that affect fuel ignitability rather than the amount of fuel (Meyn et al., 2007). As such, in contrast to fuel-limited fire regimes, considerable uncertainty exists over how climate warming will affect the frequency of wildfire events and post-fire forest response in fuel-rich climate-limited systems (e.g., Halofsky et al., 2020). Managing broadly for forest resilience can be ambiguous and challenging without specific, quantifiable management targets (Greiner et al., 2020), especially in systems where information about fire is lacking. Thus, determining and testing underlying mechanisms of forest resilience to fire and other disturbances can reduce ambiguity and help land managers prepare for potential consequences of climate change (Johnstone et al., 2016).

One critical mechanism of forest resilience to stand-replacing wildfire is post-fire tree regeneration, which is partly influenced by biological legacies that persist from pre-fire conditions and support post-fire recovery (e.g., Foster et al., 1998; Franklin et al., 2002; Johnstone et al., 2016; Turner et al., 1998), such as seed trees that either survive fire or escape the most severe fire effects. Such seed source legacies may be strongly influenced by stand age/seral stage and corresponding stand structure at the time of fire. For example, young forests dominated by small, young, and densely arranged trees are less likely to result in surviving individuals or cones relative to an older forest with greater heterogeneity in size, age, and spatial arrangement of trees, the oldest and largest of which are more likely to survive fire (e.g., Dunn and Bailey, 2016). Other factors that may influence the persistence and composition of seed source legacies include the composition and dominance of cone-bearing trees at the time fire (e.g., Andrus et al., 2020), which change throughout the sere of a forest.

A second key factor influencing tree regeneration is seed delivery into stand-replacing patches of wildfire where seed source is limited due to tree mortality and consumption of cones. Many coniferous tree species are obligate seeders that rely on wind-dispersed seed from adjacent live forest edges or utilize adaptive traits such as serotiny (i.e., cones that seed bank in the canopy and open after fire) to re-establish tree presence (Neale and Wheeler, 2019). As such, for most non-serotinous species, seedling abundance decreases with greater distances to a live forest edge within the interior of a stand-replacing burn patch (e.g., Donato et al., 2009; Harvey et al., 2016; Kemp et al., 2016; Littlefield, 2019). Composition, structure, and topographic position of the nearest live forest edge may also influence seed volume and dispersal distances. For example, older stands typically produce a greater volume of seed and have greater dispersal distances from trees that are taller (e.g., Gill et al., 2021). In addition, the topographic position of the live forest edge relative to the stand-replacing burn patch (i.e., upslope versus downslope) may also affect dispersal distances (e.g., Gray and Spies, 1996).

Finally, once seed is present and germination occurs, successful tree regeneration relies on post-fire conditions suitable for seedling establishment and survival (e.g., sufficient moisture, light, and nutrients). Competition with fast-growing shrubs or herbs, heat stress, or drought stress can impede seedling survival (e.g., Donato et al., 2016; Hansen and Turner, 2019; Harvey et al., 2016) or facilitate survival in stressful conditions (Werner et al., 2019). Tree seedlings are particularly vulnerable to drought stress (e.g., Bell et al., 2014) and in some forested systems local topo-climatic factors such as cooler and wetter aspects (Hansen and Turner, 2019; Harvey et al., 2016; Littlefield, 2019) or soil types better at retaining moisture (Donato et al., 2009) can buffer seedlings against heat and drought stress.

Moist temperate forests of the western Cascades of Washington and northern Oregon (hereafter referred to as 'northwestern Cascadia') are a prime example of high-severity fire regimes that include large patches of stand-replacing fire occuring at infrequent intervals. Understanding of how these forests respond to fire has been limited by relatively rare fire occurrences in the last century, with few studies examining post-fire regeneration immediately following wildfire events (Larson and Franklin, 2005). Current understanding of fire regimes in this region suggests that forest ecosystems are characterized by a range of fire intervals/severities (Agee, 1993; Tepley et al., 2013), including the occurrence of infrequent (200 to >450-year fire return interval on average; Agee, 1993; Hemstrom and Franklin, 1982) and large (maximum area burned exceeding 1,000,000 ha; Donato et al., 2020) wildfire events with corresponding patches of high-severity fire (Reilly et al., 2022). As such, most insights come from retrospective studies that infer fire regime characteristics and post-fire stand establishment and development pathways using dendrochronological aging of forest stands (e.g., Freund et al., 2014; Hemstrom and Franklin, 1982; Huff, 1995; Winter et al., 2002). Insights from these studies suggest that the duration of conifer establishment (i.e., time from stand initiation to canopy closure) following stand replacing wildfire can range from 20 to 100+ years, depending on management intervention (e.g., planting), initial stand densities, and site conditions (Freund et al., 2014; Tepley et al., 2014; Winter et al., 2002). However, these approaches are limited in that they can only extend as far back as the longest living individual trees present (usually < 1000 years; Hemstrom and Franklin, 1982), making it difficult to piece together a comprehensive long-term fire history (Agee, 1993). In addition, information about pre-fire conditions (e.g., stand structure at the time of fire) and immediate post-fire dynamics (e.g., initial post-fire tree regeneration and processes that lead to survivorship through succession) are unable to be fully reconstructed from dendrochronological methods because of disappearing evidence over time.

Recent wildfire activity (2015–2020) in northwestern Cascadia has provided a unique opportunity to study post-fire recovery processes immediately following severe fire in a system structured in part by infrequent and large high-severity burn patches. Here, we asked: how is post-fire conifer regeneration in stand-replacing patches affected by pre-fire stand structure, burn-patch size, and topo-climatic conditions? This information is of increasing importance under the uncertainties of how a changing climate will affect fire and forest response in regimes influenced by infrequent severe fires, and will help inform what conditions land managers can and cannot rely on natural regeneration to meet their forest management objectives. We expected post-fire tree regeneration to be limited by seed availability, with post-fire seedling density, diversity, and relative dominance of shade-tolerant species increasing with pre-fire stand age, due to the increased probability and diversity of surviving individual tree legacies. We also expected post-fire seedling density to decrease with greater distances to a post-fire live seed source. Finally, we expected greater post-fire tree seedling establishment in topo-climatic conditions that mitigate drought stress (i.e., wetter and cooler conditions).

2. Methods

2.1. Study area

Northwestern Cascadia forests fall primarily within the rugged terrain of the Coast, Olympic, and Cascade mountain ranges, excluding the Puget Lowlands and Willamette Valley. Forests in northwestern Cascadia are highly productive and biomass-rich systems (Waring and Franklin, 1979). The region experiences a Mediterranean climate with mild, wet winters and warm, dry summers with most precipitation falling between October and April (Waring and Franklin, 1979). Total mean annual precipitation ranges from 1300 to 2500 mm per year, with up to 3600 mm per year in the coastal rain forest of the Olympic Peninsula (NOAA National Centers for Environmental Information, 2023). Mean annual snowfall at lower elevations can range from 25 to 76 cm in the west Olympic coast range and from 127 to 190 cm in the western Cascades (Western Regional Climate Center, 2023). At higher elevations, mean annual snowfall is much greater, ranging from 635 to 1270 cm in the west Olympics and from 1000 to 1500 cm in the western Cascades (Western Regional Climate Center, 2023).

Forested communities within northwestern Cascadia are differentiated in large part by snow cover persistence. At lower elevations where winter snow cover is intermittent, communities consist primarily of the western hemlock (*Tsuga heterophylla*) zone, dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and western redcedar (*Thuja plicata*). At higher elevations where snow cover is persistent through winter and into spring, forests transition to the Pacific silver fir (*Abies amabilis*) zone dominated by coniferous species adapted to cooler temperatures, increased snowfall, and a longer duration of snowpack. In the Pacific silver fir zone, the overstory is typically dominated by noble fir (*Abies procera*), Pacific silver fir, Douglas-fir, and western hemlock (Franklin and Dyrness, 1973). Douglas-fir and noble fir are shade-intolerant species that establish abundantly in post-disturbance environments and are typically present and dominant in the overstory from early to late succession (Franklin et al., 2002). Shade-tolerant species (e.g., western hemlock, western redcedar, and Pacific silver fir) are typically associated with later-seral conditions (Van Pelt and Nadkarni, 2004), though may be present earlier in succession if they co-establish with shade-intolerant species following a disturbance (e.g., Larson and Franklin, 2005; Tepley et al., 2014). Due to thick bark and pruning of lower branches, Douglas-fir and noble fir have greater fire resistance relative to more fire-sensitive local conifer species such as western hemlock, western redcedar, and Pacific silver fir (Agee, 1993; Minore, 1979).

2.2. Data collection

2.2.1. Sampled wildfires

We established 39 1-ha long-term monitoring plots three to five years post-fire across four wildfires spanning the Colombia River Gorge in Oregon (USA) to North Cascades National Park in Washington (USA) (Fig. 1). Fires include the Goodell Creek (2015), Norse Peak (2017), Eagle Creek (2017), and Maple (2018) fires (Fig. 1; Table 1), which range in size from 1435 to 17,666 ha and across elevations from 5 to 2100 m above sea level (Table 1).

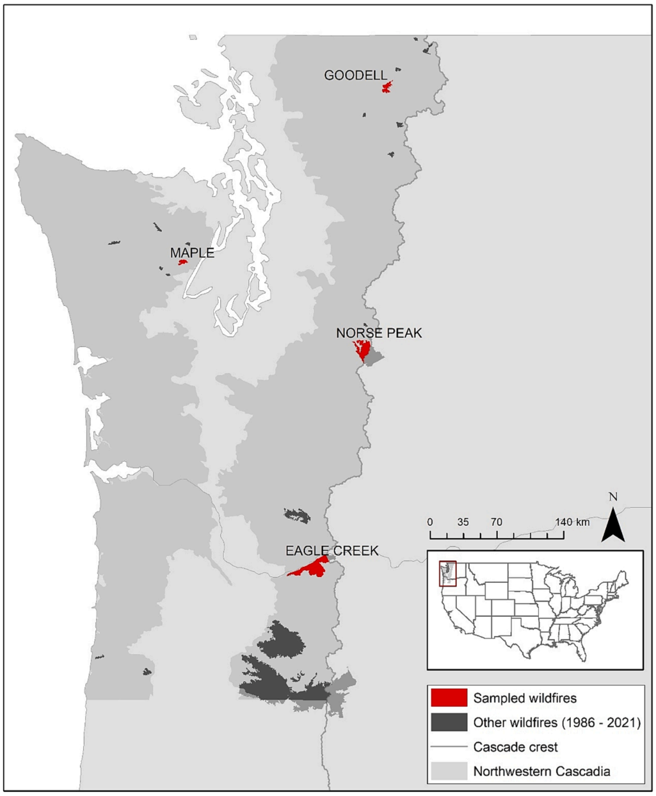

Fig. 1. Northwestern Cascadia study area map. Area burned in northwestern Cascadia from 1986 to 2021 (source: Monitoring Trends in Burn Severity https://www.mtbs.gov/). Long-term monitoring plots were established within the Goodell Creek (2015), Norse Peak (2017), Eagle Creek (2017), and Maple (2018) wildfires (colored in red).

2.2.2. Establishing plots across strata of forest zone and pre-fire stand age

All plots were established June through September 2019–2021 within stand-replacing patches of wildfire (i.e., areas where overstory tree mortality exceeded 90 %) stratified across two axes of interest: forest zone (lower elevation western hemlock zone and higher elevation Pacific silver fir zone) and pre-fire stand age (young, mid-seral, and late-seral). Potential plot locations were first identified remotely using spatial layers related to burn severity, forest zone, and stand-age with all accessible locations considered equally. Potential plot locations were ground validated by keying out forest zone, pre-fire stand age, and burn severity and then randomized locally using a random distance and azimuth to establish plot center. Forest zone and pre-fire stand age were determined in the field using regional keys adapted from Van Pelt (2007). Forest zone (western hemlock or Pacific silver fir zone) was determined from pre-fire shade tolerant abundance and composition of the stand (Appendix 1). We focused our sampling on these two forest zones since they occupy most of the forested land in the study region (Van Pelt, 2007) and are most relevant to forest land management. We excluded the Douglas-fir zone since these forests occur at warmer sites and are associated with a historically more frequent, mixed-severity fire regime relative to northwestern Cascadia (Franklin and Dyrness, 1973; Reilly et al., 2021). Pre-fire stand age was ascertained from a stand development stage assessment (a function of multiple attributes of forest composition and structure), and grouped into three classes: young, mid-seral, and late-seral (Van Pelt, 2007; Appendix 2). Young stands were forested plantations that originated following clear-cut logging in the late 1900s (~30–50 years old). Mid-seral stands originated following European colonization in the late 1800s to early 1900s and were structurally more developed than young stands, often initiating from wildfire disturbance or clear-cut logging (~70–150 years old). Late-seral stands ranged in age from around the time of European colonization to multi-century complex old-growth and originated following past wildfires (~160–500+ years old). Nearly all tree stems from the pre-fire forest were still present and identifiable following stand-replacing fire, making it possible to key out forest zone and pre-fire stand age in the field.

Burn severity, forest zone, and pre-fire stand age were consistent within each 1-ha (56.5 m radius) plot. Plots of the same strata (i.e., same forest zone and pre-fire stand age) were separated by at least 400 m to reduce spatial autocorrelation. Plot centers were established at least 100 m away from a road or trail when possible to limit the influence of

Table 1
Sampled wildfires in northwestern Cascadia. Area burned (ha) was sourced from Monitoring Trends in Burn Severity (https://www.mtbs.gov/).

Fire	Year Burned	Area Burned (ha)	Elevation (m)	Location	Year Sampled	Number of Plots
Goodell Creek	2015	2,681	140–1600	North Cascades National Park	2020	8
Norse Peak	2017	8,936*	800–2100	Mt Baker Snoqualmie-National Forest	2020	19
Eagle Creek	2017	17,666	5–1400	Mt Hood National Forest and Colombia River Gorge National Scenic Area	2021	9
Maple	2018	1,435	160–1170	Olympic National Forest	2021	3

*Norse Peak ignited in the eastern Cascades and spread west over the Cascade crest. This number reflects the forested area burned only on the west side of the Cascade crest. Total area burned including the eastern Cascades is 20,646 ha.

human activities or edge effects. We did not establish plots within areas that were salvage logged or planted post-fire, and avoided placing plots near streams, wetlands, or ephemeral creeks.

2.2.3. Field measurements of post-fire tree regeneration

At each plot (hereafter referred to as 'stand'), post-fire conifer regeneration surveys occurred within twelve circular subplots evenly distributed along four 24.5 m sub-cardinal transects (i.e., transects situated along azimuths of 45, 135, 225, and 315 degrees from plot center, with three subplots per transect). Within each subplot, post-fire conifer regeneration less than 10 cm tall of each species were tallied within a 0.5 m radius circle from subplot center and regeneration $\geq$10 cm tall of each species were tallied within a 3.5 m radius circle from subplot center.

We converted seedling density values to a rate (seedlings ha^{-1} yr^{-1}) to account for differences in time since fire across stands (Table 1). To calculate stand-level seedlings ha^{-1} yr^{-1}, the total number of seedlings in a stand was divided by total sampling area (ha) and time since fire (years), then rounded to the nearest integer. Standardizing seedling density to a rate of seedling establishment assumes a constant establishment rate across years and is an approach used to normalize across time that has been applied in similar studies (e.g., Harvey et al., 2016; see Appendix 3 and 4 for histograms of annual seedling recruitment).

Among total seedlings ha^{-1} yr^{-1}are many first-year seedlings in the cotyledon stage, for which expected survival rates are low (e.g., for some conifer species, an average survival rate of 20 %; Marsh et al., 2022). We therefore examined two different aspects of seedling abundance: regeneration rates and establishment rates. We define regeneration rates as the total seedlings ha^{-1} yr^{-1} of all heights, which represents potential available seed input (i.e., areas with access to an available seed source and conditions suitable for germination). Establishment rates are defined as seedlings ha^{-1} yr^{-1} taller than 10 cm, which better correspond to conditions suitable for seedling survival and growth (i.e., seedlings that have resources to establish following germination).

2.2.4. Field and remotely sensed explanatory variables

Based on established general ecological understanding of the system, we measured six factors relevant to seedling establishment and survival: pre-fire stand structure, seed source availability, macroclimate setting, post-fire climatic conditions, topo-climatic conditions, and competition/microsite conditions. Our final eight explanatory variables related to these factors included: pre-fire stand age (young, mid-seral, late-seral), distance to the nearest live seed source (i.e., the nearest living clump of mature trees at least 1 ha in area), forest zone (western hemlock versus Pacific silver fir), standardized precipitation evapotranspiration index (SPEI), heat load index (HLI), topographic wetness index (TWI), average vegetation percent cover, and average bryophyte percent cover (Table 2 and Table 3). Pre-fire stand age, forest zone, vegetation percent cover, bryophyte percent cover, and the variables to calculate HLI were collected in the field. Distance to the nearest live seed source, TWI, and SPEI were derived from publicly available geospatial datasets and are described in more detail below.

Table 2
Descriptive statistics for stand-scale (1-ha) quantitative explanatory variables used in modeling (n = 39).

Variable	Description	Range	Mean	Median
Heat load index	Index of incident radiation calculated using slope, aspect, and latitude. Values range from 0 (cooler topo-climatic conditions) to 1 (warmer topo-climatic conditions).	0.38–0.99	0.78	0.82
Topographic wetness index	Index of topographic controls on hydrologic processes, including soil moisture. Lower values indicate drier conditions; higher values indicate wetter conditions.	4.22–8.14	5.63	5.55
Average 3-year post-fire SPEI*	Index of growing season drought anomalies over a 180-day window. Values between −1 and 1 indicate relatively 'normal' conditions; values <-1 indicate drought; values > 1 indicate a wetter than normal growing season	−1.07 to 0.19	−0.66	−0.85
Bryophyte % cover	Average percent cover of bryophytes (i.e., non-vascular plants), measured in the field.	0–64	15	8
Vegetation % cover	Average percent cover of herbs and shrubs, measured in the field.	1–58	9	7
Distance to nearest live seed source (m)	Distance to nearest live clump of trees at least 1 ha in size, measured using NAIP** satellite imagery 2–3 years post-fire.	23.0–1610.1	156	84

*SPEI = standardized precipitation evapotranspiration index** NAIP = National American Imagery Program.

At each stand, we collected data on general stand characteristics, pre-fire stand age, forest zone, and post-fire herb and shrub response. General stand information was collected from the stand center and included slope (degrees), aspect (degrees), and elevation (meters). Pre-fire stand age and forest zone were keyed from stand center (see section 2.3.1). Percent cover of bryophytes and all herbaceous and woody plants was visually estimated within a 2 m radius at each of the twelve subplots.

Distance to the nearest live tree seed source from plot center was measured remotely using National Agriculture Imagery Program (NAIP) satellite imagery 2–3 years post-fire. We explored the use of other potential variables to represent an available tree seed source, including distance to the nearest live individual tree from plot center (i.e., center of 1-ha plot) and a refugia density index (RDI; Downing et al., 2019).

Table 3
Number of plots sampled within each stratum of forest zone (western hemlock zone or Pacific silver fir zone) and pre-fire seral stage (young, mid-seral, and late-seral).

Strata	Number of plots
Western hemlock zone	
Young	–
Mid-seral	6
Late-seral	17
Pacific silver fir zone	
Young	3
Mid-seral	5
Late-seral	8
Total	39

However, these alternative representations of live seed source did not perform as well in models as distance to nearest live seed source collected via aerial imagery based on comparisons of the Akaike information criterion corrected for small sample size (AICc; Bartoń, 2022).

We used the standardized precipitation evapotranspiration index (SPEI) downloaded from Climate Engine (https://app.climateengine.com/climateEngine) and sourced from gridMET (Abatzoglou, 2013) at a 4 km spatial resolution to represent post-fire climatic conditions in our statistical models. SPEI is a drought index that models the impact of precipitation and potential evapotranspiration on water demand and can be used to detect drought over varying temporal windows ranging from 1 to 48 months. We used a 180-day (6 month) window from April 1st to October 1st to detect post-fire climatic conditions during the growing season when drought is most consequential to seedling survival. We averaged the SPEI values across the first three growing seasons following fire for each stand (i.e., an average of three SPEI values representing 1, 2, and 3-years post-fire). Negative SPEI values indicate that the average growing season conditions in the first 3 years following fire were drier than normal; positive values indicate wetter than normal; and values close to 0 (i.e., between −1 and 1) indicate within normal. We explored the use of other drought indices, including evaporative demand drought index (EDDI), though these indices did not perform as well in models.

Heat load index (HLI) was calculated for each stand using the equation from McCune and Keon (2002) and provides an index of incident radiation with values that range from 0 to 1; lower values reflect cooler topo-climatic conditions (e.g., NE facing aspects) and higher values reflect warmer topo-climatic conditions (e.g., SW facing aspects). Aspect, slope, and latitude used in the HLI equation were collected in the field. Topographic wetness index (TWI) was calculated in ArcMap with a single direction flow model using a 30-m resolution digital elevation model (DEM) input (source: United States Geological Survey https://www.usgs.gov/the-national-map-data-delivery). TWI represents topographic controls on hydrological processes and provides a relative measure of accumulated water flow from upslope contributing area. Higher values of TWI indicate topographically 'wetter' areas with increased accumulated flow from upslope areas; lower values indicate topographically 'drier' areas with less upslope accumulated flow.

2.3. Statistical analysis

2.3.1. Explanatory variable selection

Prior to developing models, we assessed potential explanatory variables for multicollinearity. Initially, we started with multiple redundant variables related to our six target factors (i.e., pre-fire stand structure, seed source availability, macroclimate setting, post-fire climatic conditions, topo-climatic conditions, and competition/microsite conditions). Akaike information criterion corrected for small sample size (AICc; Bartoń, 2022) was used to identify the best variable among correlated variables with a Pearson's correlation coefficient greater than 0.6. For example, if three variables were highly correlated (i.e., Pearson's correlation coefficient greater than 0.6), then three separate full models were run, each containing one of those correlated variables. The model resulting in the lowest AICc indicated a better fit model, thus that model's variable was chosen, and the remaining two collinear variables were removed. Examples of redundant and correlated variables removed from the full model included average maximum shrub height (correlated with average vegetation percent cover), elevation (redundant with forest zone and correlated with average maximum shrub height and average vegetation percent cover), and distance to the nearest live individual tree (correlated with distance to the nearest live seed source). Multicollinearity was also assessed following model fitting using the variation inflation factor (VIF) (Fox and Weisberg, 2019) to ensure no variables were contributing to inflated parameter variance. Variables resulting in failed model convergence or a VIF greater than 2 were dropped from our models. No variable transformations were required based on visual examination of histograms.

2.3.2. Generalized linear models

We used generalized linear models (GLMs) with a negative binomial distribution and log link function (Venables and Ripley, 2002) to test the effect of pre-fire stand structure (pre-fire stand age), burn patch size (distance to the nearest live seed source), topo-climatic conditions (forest zone, HLI, TWI, SPEI), and competition/microsite conditions (bryophyte percent cover, and vegetation percent cover) on post-fire regeneration and establishment rates for all species combined. Poisson GLMs were fit and compared to negative binomial GLMs using a likelihood ratio test. In all model attempts, the negative binomial GLMs resulted in better model fit. Quantitative predictor variables were scaled prior to model fitting to allow for comparison of relative effect sizes across predictors and models (i.e., subtracting their means and dividing by their standard deviation). For coefficients in all models, we considered $P < 0.05$ as strong statistical support for effects and $P < 0.10$ as suggestive statistical support for effects.

Best fit model selection was determined by comparing delta AICc among top-ranking models generated using the function 'dredge' from the MuMIn package in R (Bartoń, 2022). Models with values of delta AICc less than 2 were considered to have substantial evidence in support of that model in addition to the best fit model (i.e., examined with equal weight to the best fit model; Fabozzi et al., 2014); values of delta AICc between 2 and 4 indicate some support; values between 4 and 7 indicates less support (Fabozzi et al., 2014) but were still examined during the model selection process. All variables with delta AICc values less than 2 were included in the best fit model, with the exception of TWI in the regeneration rates model due to its moderate correlation with distance to the nearest live seed source (i.e., a correlation coefficient of 0.53; Appendix 5). When deciding on final predictor variables to include in the best fit model, we also examined the proportion of top-ranking models with delta AICc values less than 7 for which each predictor variable was included.

Random effects were not included in models after running model diagnostics for models with and without a random effect of fire using the Diagnostics for Hierarchical Regression Models (DHARMa) package in R (Hartig and Lohse, 2022). DHARMa simulates new response data from the fitted model for each plot/observation, and then compares the actual response value to the empirical cumulative density function (ECDF) of simulated response values. A DHARMa residual is defined as the value of the ECDF of simulated response values at the observed response value (e.g., a residual of 0.5 indicates that 50 % of simulated response values were above and below the actual observed response). Quantile residuals were equally distributed across all fires in the establishment rates best fit model (Appendix 6b) and were distributed equally across all fires except for Goodell Creek in the regeneration rates best fit model (Appendix 6a). We ran a sensitivity analysis by removing Goodell Creek plots from our analysis to determine the effect on model outputs, which did not qualitatively change parameter estimates or significance (Appendix 7) which further justified the exclusion of fire as a random effect. In addition, the inclusion of a random effect is commonly not advised when there are fewer than 5 levels in a grouping factor (e.g., Crawley, 2002; Hodges, 2014).

2.4. Comparing seedling densities to management targets

To compare initial post-fire seedling densities to forest practice management targets, we calculated the area occupancy (i.e., stocking) within stands based on presence of established seedlings among the twelve subplots. For each stand, we calculated the proportion of the 12 subplots occupied at a minimum density of 260 established seedlings ha^{-1} (i.e., at least 1 seedling present within a 3.5 m radius subplot). This metric provides a sense of how uniformly distributed seedlings are within a stand (i.e., clustered within a few subplots vs. distributed across the entire stand). We also calculated the proportion of stands (out of 39 stands) whose plot-level seedling density exceeded forest practice minimum of 470 seedlings ha^{-1} (Chapter 222-34-010 WAC). These forest practice minima are stand-establishment standards used by land management agencies when regenerating stands following timber harvest in the region.

2.5. Species composition

To compare post-fire conifer species composition across pre-fire stand ages, we first calculated species richness and Shannon diversity index (SDI) at the stand scale and then performed a non-parametric Kruskal-Wallis rank sum test (R Core Team, 2022). Species richness was calculated by summing the total number of unique species present at each plot (i.e., across all twelve subplots). Shannon diversity index was calculated for each plot using the following equation:

$$SDI = -\sum_{i=1}^{S} p_i * \ln p_i$$

where S is the total number of species and p_i is the proportion of individuals belonging to the ith species. To determine which pre-fire stand ages differed from each other, we performed a Wilcoxon rank sum test (R Core Team, 2022).

To compare the relative abundance of shade-tolerant versus shade-intolerant post-fire conifer regeneration, we assigned each of our observed species as shade tolerant (Pacific silver fir, western hemlock, western redcedar, and subalpine fir) or intolerant (noble fir, Douglas-fir, lodgepole pine, Engelmann spruce, and western white pine; Minore, 1979). For each plot, we then calculated the percentage of total regeneration that was shade tolerant by dividing the count of shade-tolerant seedlings by the total number of seedlings.

3. Results

3.1. Seedling density and vegetation conditions at time of sampling (3–5 years post-fire)

Across all stands, regeneration densities (i.e., regeneration of all heights) ranged from 22 to 264,067 seedlings ha^{-1} (median = 4352, mean = 22,992; Table 4). Established seedling densities (i.e., seedlings ≥ 10 cm tall) ranged from 22 to 51,449 seedlings ha^{-1} (median = 974, mean = 3,295; Table 4). On average, 72.2 % of stand area was occupied at a minimum density of 260 established seedlings ha^{-1} (Table 4; Table 5). Regeneration and established seedling densities exceeded forest practice minimum density thresholds of 470 seedlings ha^{-1} in 82.1 % (32 out of 39) and 64.1 % (25 out of 39) of stands, respectively. There were no consistent patterns or conditions shared among stands with regeneration and established seedling densities below the forest practice minimum thresholds.

Across stands, average percent cover of bryophytes ranged from 0.1 % to 67.8 % (median = 10.9 %, mean = 17.8 %), graminoids ranged from 0.0 % to 42.9 % (median = 0.1 %, mean = 1.3 %), herbs ranged from 0.1 to 29.6 % (median = 1.7 %, mean = 2.7 %), and shrubs ranged from 0.1 % − 19.2 % (median = 0.6 %, mean = 2.7 %) (Appendix 8). Average maximum shrub height ranged from 0 to 1.3 m (median = 0.1 m, mean = 0.2 m) (Appendix 8).

3.2. Regeneration rates

Regeneration rates ranged from 5 to 88,022 seedlings ha^{-1} yr^{-1} across stands (median = 1068, mean = 6914) and seedlings were present in 100 % of stands (Table 5). Pre-fire stand age, distance to a live seed source, average 3-year post-fire SPEI, and bryophyte percent cover were included in the best fit model and were present in 96 %, 57 %, 43 %, and 100 % of top-ranking models with delta AICc values less than 7 (n = 23, Appendix 9), respectively. Forest zone, TWI, and HLI were not included in the best fit model, occurring in 30 %, 39 %, and 39 % of top-ranking models with delta AICc values less than 7, respectively (Appendix 9).

Regeneration rates were greater in pre-fire late-seral stands than in pre-fire mid-seral or pre-fire young stands, with pre-fire late-seral stands having 386 % more seedlings ha^{-1} yr^{-1} than pre-fire mid-seral stands on average (p = 0.002, Fig. 2a; Appendix 10). On average, regeneration rates doubled for every ~17 % increase in bryophyte percent cover (p = 0.004, Fig. 2d; Appendix 10) and decreased by 31 % for every 100 m increase in distance to a live seed source (p < 0.001, Fig. 2b; Appendix 10). Regeneration rates in pre-fire young stands did not statistically differ from pre-fire mid-seral stands (p = 0.10, Fig. 2a; Appendix 10). Regeneration rates did not correspond with average 3-year post-fire SPEI (p = 0.085, Fig. 2c; Appendix 10).

Table 4
Regeneration densities (seedlings ha^{-1}) and rates (seedlings ha^{-1} yr^{-1}) 3–5 years post-fire by species. Percent present indicates the percentage of stands that each species was present, out of 39 stands (e.g., Douglas-fir was present in 84.6 % of stands).

	Regeneration Densities (total seedlings ha^{-1})			Regeneration Rates (total seedlings ha^{-1} yr^{-1})			
Tree species	**Min – Max**	**Median**	**Mean**	**Min – Max**	**Median**	**Mean**	**% Present**
All combined	22 – 264,067	4,352	22,992	5 – 88,022	1,068	6,914	100.0
Douglas-fir	0 – 42,610	736	3,831	0–8,722	184	1,101	84.6
Western hemlock	0 – 258,502	281	14,127	0–86,168	72	4,524	64.1
Noble fir	0 – 16,088	43	1,905	0–5363	11	600	56.6
Pacific silver fir	0 – 3,205	0	284	0–1068	0	92	30.8
Western redcedar	0 – 49,370	0	2,550	0–9874	0	597	20.5
Lodgepole pine	0 – 1,667	0	76	0–333	0	15	17.9
Western white pine	0 – 1,083	0	28	0–270	0	7	2.6
Subalpine fir	0 – 2,209	0	57	0–736	0	19	2.6
Engelmann spruce	0 – 1,061	0	27	0–354	0	9	2.6

Table 5
Establishment densities (seedlings ha^{-1}) and rates (seedlings ha^{-1} yr^{-1}) 3–5 years post-fire by species. Percent present indicates the percentage of stands that each species was present, out of 39 stands (e.g., Douglas-fir was present in 84.6 % of stands). Area occupancy (%) represents the average percent area within a stand occupied at a minimum density of 260 seedlings ha^{-1} (i.e., at least one seedling per subplot). For example, in stands where Douglas-fir was present, it occupied 64.1 % of subplots at a minimum density of 260 seedlings ha^{-1} on average.

	Establishment Densities (seedlings ha^{-1} ≥ 10 cm height)			**Establishment Rates (seedlings ha^{-1} yr^{-1} ≥ 10 cm)**					
Tree species	**Min – Max**	**Median**	**Mean**	**Min – Max**	**Median**	**Mean**	**% Present**	**Area Occupancy (%)**	**Mean Height (cm)**
All combined	22 – 51,449	974	3,295	5–10,290	254	773	100.0	72.2	16.6
Douglas-fir	0 – 27,695	238	1,410	0–5,539	79	316	84.6	64.1	17.2
Western hemlock	0 – 13,317	22	796	0–2,663	33	268	64.1	40.0	18.0
Noble fir	0 – 9,896	22	463	0–2,474	7	131	56.6	48.9	12.9
Pacific silver fir	0 – 671	0	39	0–168	0	11	30.8	25.7	12.2
Western redcedar	0 – 10,112	0	509	0–2,022	0	127	20.5	60.4	19.8
Lodgepole pine	0 – 1,667	0	76	0–333	0	15	17.9	45.2	45.4
Western white pine	0 – 22	0	<1	0–5	0	<1	2.6	8.3	10.0
Subalpine fir	0 – 87	0	2	0–29	0	1	2.6	33.3	11.8
Engelmann spruce	–	–	–	–	–	–	–	–	–

Note: No Engelmann spruce seedlings greater than 10 cm tall were observed.

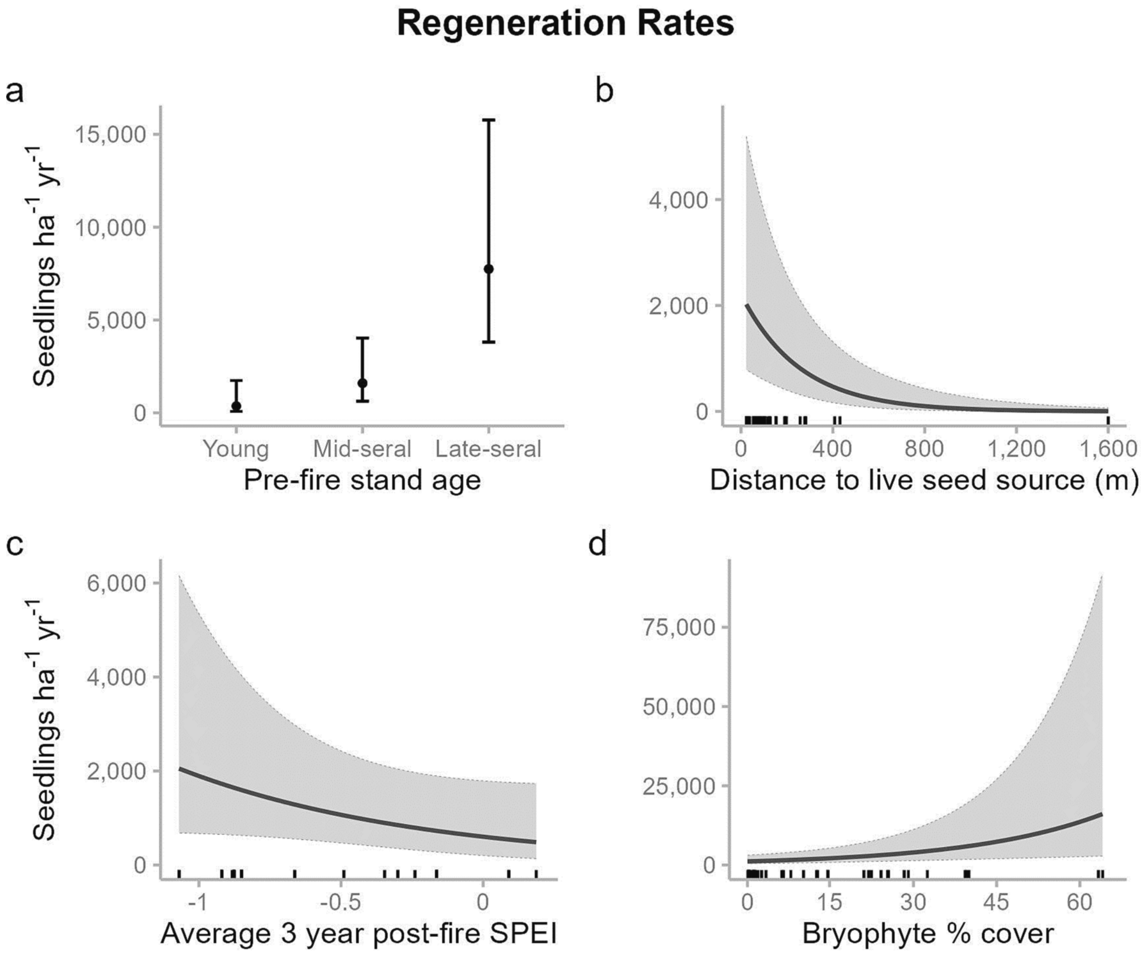

Fig. 2. Regeneration rates. Effect of (a) pre-fire stand age, (b) distance to live seed source, (c) average 3-year post-fire SPEI, and (d) bryophyte percent cover on post-fire regeneration rates (seedlings ha^{-1} yr^{-1} for seedlings of all heights) when all other model covariates are held constant at their median values. These covariates represent those included in the best fit model for regeneration rates. The lines represent the model predicted mean response; shaded areas and error bars represent the 95 % confidence intervals of predictions. Black tick marks on the x-axis represent plot values (n = 39) for each predictor variable in the dataset.

3.3. Establishment rates

Establishment rates ranged from 5 to 10,290 seedlings ha^{-1} yr^{-1} (median = 254, mean = 773; Table 5). Pre-fire stand age, forest zone, distance to a live seed source, average 3-year post-fire SPEI, and bryophyte percent cover appeared in 47 %, 88 %, 88 %, 100 %, and 100 % of top-ranking models with delta AICc values less than 7, respectively, and were included in the best fit model (n = 18, Appendix 11). Vegetation percent cover, HLI, and TWI were not included in the best fit model and were present in 29 %, 29 %, and 35 % of top-ranking models with delta AICc values less than 7, respectively.

On average, establishment rates doubled for every ~10 % increase in bryophyte percent cover ($p < 0.001$, Fig. 3d; Appendix 10). Although largely falling within the relatively ‘normal’ growing season drought range, establishment rates increased by 167 % for every 0.5 value increase in the average 3-year post-fire SPEI ($p < 0.001$, Fig. 3c; Appendix 10). Establishment rates decreased by 28 % for every 100 m increase in distance to a live seed source on average ($p < 0.001$, Fig. 3b; Appendix 10).

Establishment rates were 168 % greater in the Pacific silver fir zone than the western hemlock zone on average ($p = 0.001$, Fig. 3a; Appendix 10). There was a suggestive difference between pre-fire late-seral and mid-seral stands, with pre-fire late-seral stands having 79 % more seedlings ha^{-1} yr^{-1} relative to pre-fire mid-seral stands on average ($p = 0.06$, Fig. 3a; Appendix 10). Establishment rates did not statistically differ between pre-fire young and mid-seral stands ($p = 0.20$, Fig. 3a; Appendix 10).

3.4. Relative effect sizes of covariates between regeneration and establishment rate models

The relative effect size of pre-fire stand age corresponded more strongly with regeneration rates than with establishment rates (Fig. 4; Appendix 10). Distance to live seed source had a 30 % greater effect on regeneration rates relative to establishment rates (Fig. 4). The relative effect of bryophyte percent cover was 76 % greater for establishment rates than regeneration rates (Fig. 4; Appendix 10). Forest zone and average 3-year post-fire SPEI were important predictors of establishment rates, but not regeneration rates (Fig. 4; Appendix 10).

3.5. Species composition across strata

A total of nine conifer species were present across all stands (Table 4; Table 5). The most common tree species present were Douglas-fir (present in 84.6 % of stands), western hemlock (present in 64.1 % of stands), noble fir (present in 56.6 % of stands), Pacific silver fir (present in 30.8 % of stands), western redcedar (present in 20.5 % of stands), and lodgepole pine (*Pinus contorta*; present in 17.9 % of stands) (Table 4; Table 5). Western white pine (*Pinus monticola*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) were also present, but only in 2.6 % of stands.

Within stands where a given species was present, Douglas-fir and western redcedar had the greatest area occupancy relative to other species, occupying on average 64.1 % and 60.4 % of stand area at an average minimum density of 260 established seedlings ha^{-1}, respectively (Table 4; Appendix 12). Noble fir, lodgepole pine, western hemlock, subalpine fir, Pacific silver fir, and western white pine followed, occupying 48.9 %, 45.2 %, 40.0 %, 33.3 %, 25.7 %, and 8.3 % of stand area at an average minimum density of 260 established seedlings ha^{-1}, respectively (Table 4; Appendix 12).

Western hemlock had the greatest range (0 – 86,168 seedlings ha^{-1} yr^{-1}) and mean (4,524 seedlings ha^{-1} yr^{-1}) regeneration rates of any

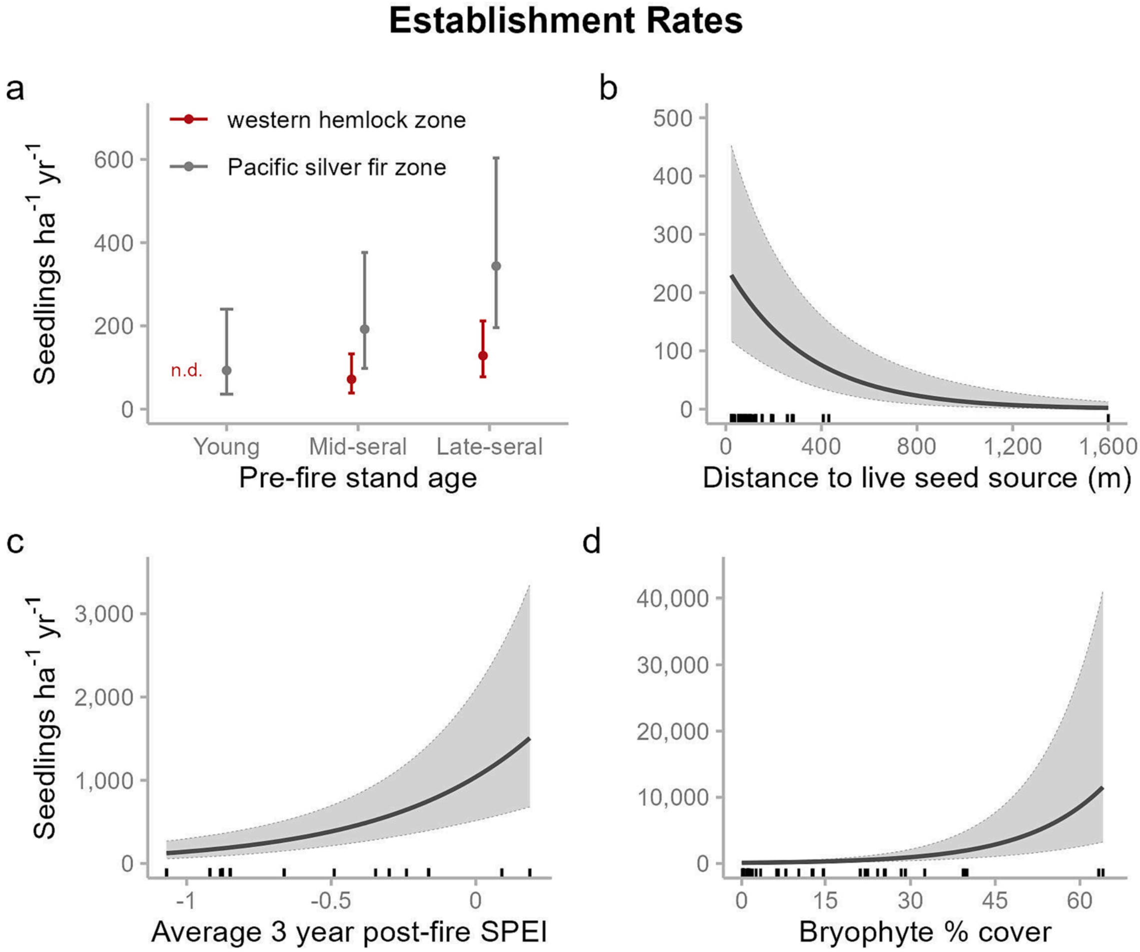

Fig. 3. Establishment rates. Effect of (a) pre-fire stand age, forest zone, (b) distance to live seed source, (c) average 3-year post-fire SPEI, and (d) bryophyte percent cover on post-fire establishment rates (seedlings ha^{-1} yr^{-1} for seedlings reaching 10 cm in height) when all other model covariates are held constant at their median values. These covariates represent those included in the best fit model for establishment rates. The lines represent the modeled predicted mean response; shaded areas and error bars represent the 95 % confidence intervals of predictions. Black tick marks on the x-axis represent plot values ($n = 39$) for each predictor variable in the dataset. In panel (a), “n.d.” indicates no data as we did not sample any plots that were young at the time of fire in the western hemlock zone.

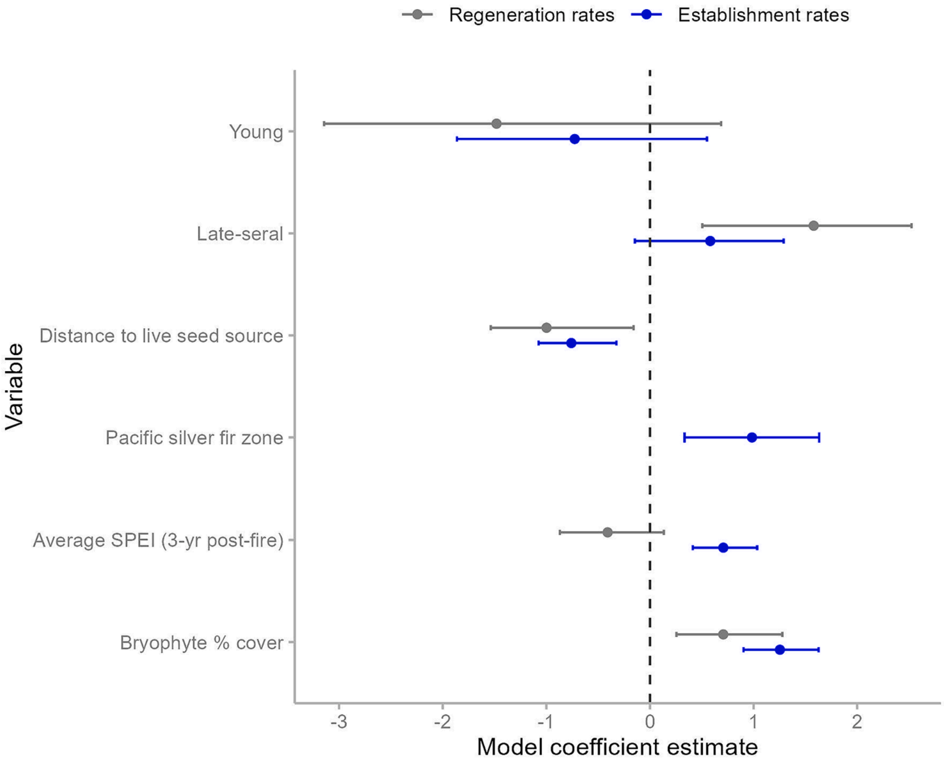

Fig. 4. Relative effect sizes of model predictors. Model parameter coefficients for post-fire regeneration rates (gray) and establishment rates (blue) with 95% confidence intervals. All covariates were scaled so that the relative effect sizes could be compared among covariates and between models. Note: parameter coefficients for young and late-seral stands are relative to the mid-seral stand intercept.

species (median = 72 seedlings ha^{-1} yr^{-1}), followed by Douglas-fir (mean = 1,101, median = 184, range = 0 – 8,722 seedlings ha^{-1} yr^{-1}), western redcedar (mean = 597, median = 0, range = 0 – 9,874 seedlings ha^{-1} yr^{-1}), and noble fir (mean = 600, median = 11, range = 0 – 5,363 seedlings ha^{-1} yr^{-1}) (Table 4; Table 5). Establishment rates per species ranked similarly with regeneration rates, though Douglas-fir had the greatest mean and range (mean = 316, median = 79, range = 0 – 5,539 seedlings ha^{-1} yr^{-1}) while western hemlock had the second greatest mean and range (mean = 268, median = 33, range = 0 – 2,663 seedlings ha^{-1} yr^{-1}).

Overall, post-fire conifer regeneration species diversity increased with pre-fire stand age ($p = 0.04$; Fig. 5). Conifer species richness was greatest in pre-fire late-seral stands (median = 3, range = 1–6 tree species), and decreased in pre-fire mid-seral (median = 3, range = 1 – 4 tree species) and pre-fire young stands (median = 1, range = 1–2 tree species) (Fig. 5a). Pairwise comparisons indicated suggestive statistical differences in species richness between pre-fire late-seral stands and young stands ($p = 0.05$; Appendix 13). Shannon diversity index of post-fire conifer tree species was greatest in pre-fire late-seral stands (median = 1.22, range = 0 – 0.74 SDI), followed by pre-fire mid-seral stands (median = 0.58, range = 0 – 1.0 SDI) and pre-fire young stands (median = 0, range = 0 – 0.67 SDI) (Fig. 5b), though there was weak support for statistically significant differences ($p = 0.10$). Co-establishment of shade intolerant and tolerant species was greatest in late-seral pre-fire stands but did not occur in young pre-fire stands (Fig. 5c; Fig. 5d). The proportion of regeneration abundance that was shade tolerant also was greatest in stands that were late-seral at the time of fire, relative to mid-seral stands (Fig. 5d).

4. Discussion

Our study highlights several important drivers of post-fire regeneration dynamics within a nominally infrequent, stand-replacing fire regime. First, we found regeneration abundance and diversity increased with pre-fire stand age, suggesting forest resilience to stand-replacing fire is greater in older forests due to biological legacies such as greater and more diverse seed availability. Second, the interior of large stand-replacing patches further away from a live seed source may be slower to re-establish as forest—though tree regeneration levels were surprisingly high within 400 m from a live forest edge. Last, while broadly robust, establishment rates were greater in cooler, wetter conditions which may highlight areas buffered from potential effects of climate warming and drying. These findings have important implications for understanding the mechanisms of forest resilience to severe fire in a system structured in part by such events and can inform forest management as the climate continues to warm and wildfire potential increases.

4.1. *Forest resilience to fire increases with pre-fire stand age and associated biological legacies*

Our finding that post-fire regeneration rates and conifer species diversity increased with pre-fire stand age highlights the importance of biological legacies in promoting seed supply and diversity as a mechanism of post-fire forest resilience. The structural complexity and heterogeneity exhibited by pre-fire late-seral stands may result in a wider range and increased persistence of potential seed source legacies from old and large fire-resistant individuals (Dunn and Bailey, 2016; Keeton and Franklin, 2005). For example, 5 out of the 6 stands with less than 100 % mortality were late-seral at the time of fire and most surviving individuals were large Douglas-fir trees greater than 100 cm diameter at breast height. All of our sampled stands experienced greater than 90 % fire-induced mortality by 3–5 years post-fire, though rates of delayed mortality were not known. Lower intensity fire could result in mortality rates exceeding 90 % without consuming cones in the upper canopy and may allow large, thick-barked species to survive long enough to produce and disperse a cone crop before dying. Retention of a short-term canopy seed bank following fire has been hypothesized for Douglas-fir in the

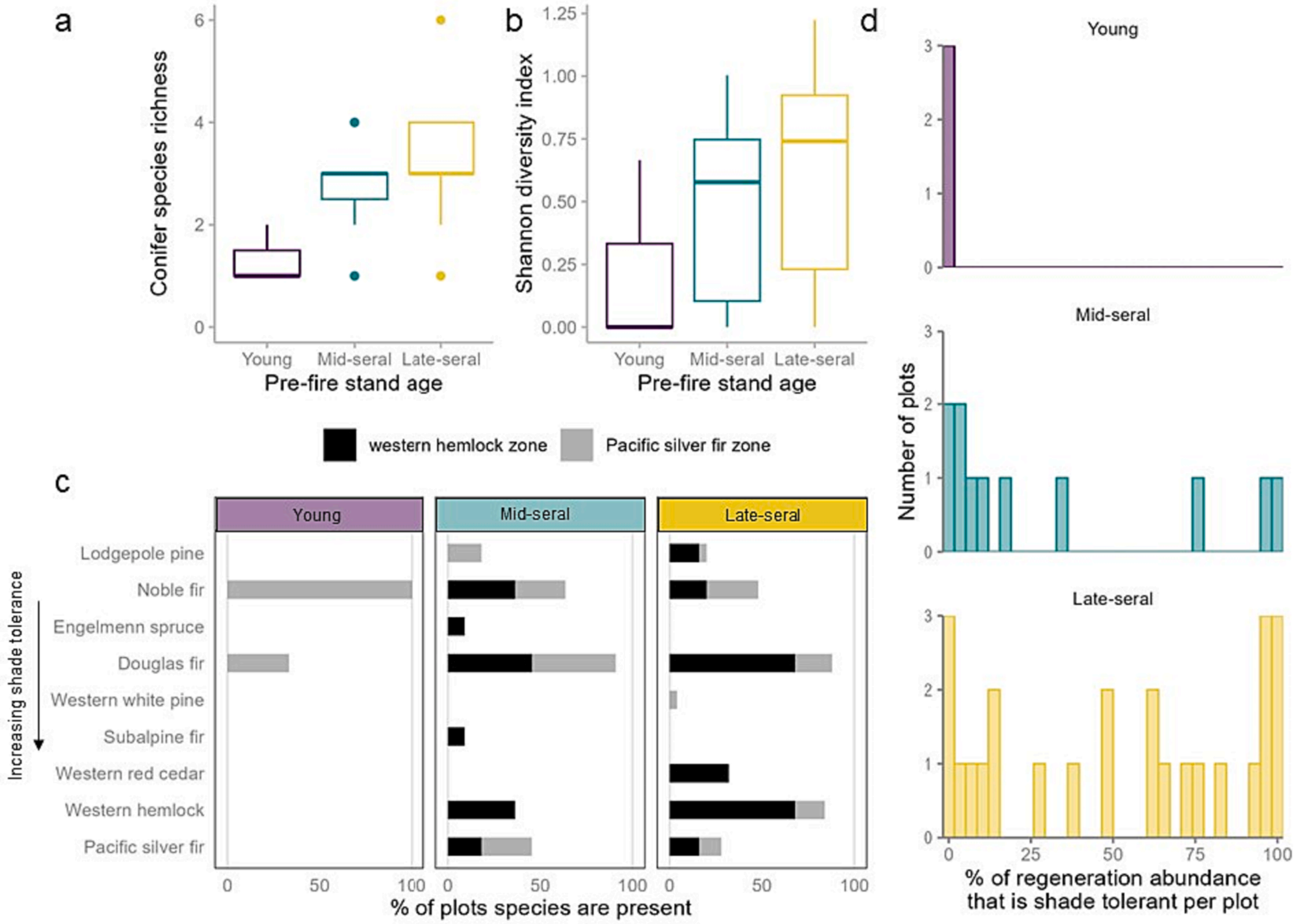

Fig. 5. Post-fire conifer regeneration composition. (a) Conifer species richness, (b) diversity (i.e., Shannon diversity index), (c) plot occupancy by species across pre-fire stand age and forest zone, and (d) histograms of plot-level shade tolerant regeneration abundance (%), including seedlings of all heights. In panels (a) and (b), the lower and upper hinges represent the 25th and 75th percentile values; the bolded horizontal line represents the median value; the upper and lower whiskers represent values from the hinge to the largest or smallest value no greater than 1.5x the interquartile range; points represent outlying values that extend beyond the whiskers. In panel (c), species are arranged from shade intolerant to shade tolerant (top to bottom; Minore, 1979).

western Cascades of Oregon (Larson and Franklin, 2005) and supported by previous observations of dense post-fire seedling abundance at distances up to 3 km from a live post-fire seed source (Gray and Franklin, 1997). Because of the limited opportunity to study post-fire dynamics following relatively rare stand-replacing fire events within infrequent fire regimes, information about short-term canopy seed banks and rates of delayed mortality following fire is understudied in this system and is a valuable area of future research, as it may contribute to the underlying mechanism of increased post-fire regeneration rates in older pre-fire stands.

Another potential explanation for increased regeneration rates in pre-fire late-seral stands is that the nearest post-fire live seed source was also more likely to be late-seral. In general, seed volume increases with stand age (Andrus et al., 2020; Gill et al., 2021; Viglas et al., 2013) and local and nearby seed dispersal is greater when the nearest live forest edge is older (Gill et al., 2021). Correspondingly, we observed greater diversity in post-fire conifer species composition in pre-fire late-seral stands (Table 5; Fig. 5), as late-seral forests contain mature cone-bearing individuals of both shade tolerant and intolerant species (Van Pelt and Nadkarni, 2004). Our finding of co-establishment of shade tolerant and intolerant species support retrospective dendrochronological observations in the region (e.g., Keeton and Franklin, 2005; Tepley et al., 2014, 2013) and build on those insights by providing information on potential drivers of co-establishment (i.e., increased potential for co-establishment as stand age and structural complexity increase), which has been difficult to do in retrospective studies due to loss of evidence of pre-disturbance stand conditions.

Greater post-fire seedling abundance and diversity in pre-fire late-seral stands has important implications for future forest trajectories and managing forests for resilience to wildfire. First, our findings highlight the importance of late-seral forests (which are currently in deficit across northwestern Cascadia; Donato et al., 2020) and efforts to accelerate stand structure towards late-seral conditions in existing mid-seral forests (which are currently in excess; Donato et al., 2020) in positioning the landscape for greater post-fire resilience. Climate warming and drying is expected to increase conditions associated with wildfire activity across northwestern Cascadia (Halofsky et al., 2020), and managing for late-seral forest conditions may confer resilience to fire by enhancing post-fire regeneration rates and diversity of post-fire species composition through the retention of biological legacies. Second, co-establishment of shade tolerant (e.g., western hemlock) and intolerant (e.g., Douglas-fir) species may accelerate aspects of forest structural development. For example, a multi-layered, vertically continuous canopy is a key feature of late-seral forest structure achieved through co-dominance of mature shade-tolerant species that can regenerate continually in low-light understory environments (Franklin et al., 2002). Co-establishment of shade-tolerant species after fire can increase the likelihood of a mature shade-tolerant seed source being present much earlier in succession relative to a mono-typic stand of shade-intolerant species like Douglas-fir, provided canopy gap opening processes allow for growth release of shade-tolerant species (Keeton and Franklin, 2005).

Shade tolerant co-establishment can contribute to precocious complexity (*sensu* Donato et al., 2012), wherein naturally regenerating post-disturbance stands exhibit many structural features typically associated with complex late-seral stands. Depending on the density of post-fire regeneration, these areas of co-establishment may exhibit structural complexity that persists through stand development (Donato et al., 2012), though continued monitoring is needed to test developmental pathways and trajectories in the future. The potential for accelerated structural development and increased heterogeneity in species composition and structure in co-established stands may support natural recovery of forests in stands that were late-seral at the time of fire, reducing the need for planting efforts. While planting efforts may be advantageous in areas managed for maximum timber yield, they can often result in spatially and compositionally homogenous stands (e.g., Hayes et al., 2005) and may not reflect the full range of disturbance-created stand development pathways in the region (e.g., co-establishment; Agee, 1993; Donato et al., 2012; Tepley et al., 2014).

Future field studies could build on our findings by exploring causal relationships between increased seed availability and stand age. While we hypothesize that late-seral stands may have increased seed availability following stand-replacing fire, research could test this hypothesis and assess the source of increased seed availability using seed traps in the field (e.g., Gill et al., 2021). For example, seed traps could be installed immediately following a wildfire event at far distances from a live seed source within stand-replacing burn patches where trees were killed immediately by fire via scorching (i.e., tree canopies are not consumed) or torching (i.e., tree canopies are consumed) to test for the hypothesis of a short-term canopy seed bank. Understanding whether increased seed availability is a result of age of the nearest live forest edge (e.g., Gill et al., 2021) or retention of an in-situ seed source (suggested by Larson and Franklin, 2005) would improve our understanding of forest resilience to fire in this system and inform prioritization of reforestation efforts, especially within the interior of large, stand-replacing patches of wildfire where distance to a live forest edge exceeds maximum dispersal distances (i.e., indicate what areas and conditions within stand-replacing patches are capable of regenerating naturally).

In addition, continued monitoring of recently burned stands could improve understanding of how shade-intolerant conifers, shade-tolerant conifers, hardwoods, and woody shrubs interact over time as establishment dynamics are likely to occur for multiple decades (Freund et al., 2014; Tepley et al., 2014; Winter et al., 2002). At 3–5 years post-fire, average shrub percent cover and maximum height were relatively low across stands (mean shrub percent cover of 2.7 % and mean maximum shrub height of 0.2 m; Appendix 8), and average total vegetation percent cover (i.e., combined cover of herbs, graminoids, and shrubs) was not a statistically significant predictor of regeneration or establishment rates. However, we expect shrub dominance and growth to increase rapidly with greater time since fire (i.e., shrubs are typically dominant during post-fire early-seral conditions; Brown et al., 2013; Swanson et al., 2011) which may have contrasting effects on shade intolerant versus tolerant conifer species based on differences in ability to withstand shade cast by shrubs or outpace shrub growth. These dynamics are difficult to assess only 3–5 years post-fire, but our data provide a baseline for comparisons in future monitoring work. In addition, continued monitoring and the establishment of additional plots would increase sample size and degrees of freedom that would allow for the exploration of interaction effects and development of species-specific models.

4.2. *Regeneration and establishment rates are limited by proximity to a live seed source*

Regeneration and establishment rates decreased with further distances to a live seed source, consistent with post-fire regeneration studies in dry, montane, subalpine, and boreal forest systems (e.g., Brown et al., 2015; Donato et al., 2016, 2009; Harvey et al., 2016; Kemp et al., 2016). This finding is ecologically intuitive as most coniferous species of the northwestern Cascades are obligate seeders and non-serotinous, meaning they rely primarily on wind-dispersed seed from adjacent live seed source (Neale and Wheeler, 2019). Despite regeneration rates decreasing with greater distances to a live seed source, regeneration was still relatively abundant at distances up to 400 m (Fig. 2), which greatly exceeds observations in other dry and subalpine systems where post-fire regeneration potential declines sharply after 75–150 m (e.g., Harvey et al., 2016; Kemp et al., 2016; Littlefield, 2019). This may be explained by surviving individual trees, the retention of an in-situ seed source (see section 4.1), or a result of long-distance wind dispersal events caused by updrafts or strong prevailing winds (e.g., Horn et al., 2001).

Given slower re-establishment of conifers within the interior of large, stand-replacing patches of wildfire, our findings suggest these could be areas to prioritize for either tree planting or management of complex early-seral habitat—depending on objectives. Complex early-seral habitat refers to the ‘pre-forest’ stage of forest development following a stand-replacing disturbance and before tree canopy closure, where herbs and shrubs dominate the post-disturbance vegetation (Swanson et al., 2011). Complex early-seral conditions host a high diversity of herbs, shrubs, insects, and wildlife and have important cultural and ecological value (e.g., Boyd, 1999; DellaSala et al., 2014; Swanson et al., 2014, Swanson et al., 2011). In the western Cascades, complex early-seral conditions are in greater deficit than late-seral conditions relative to the historical range of variation (Donato et al., 2020) due to a history of logging followed by prompt tree planting and site preparation, as well as a short duration relative to the treed condition. With total initial seedling densities naturally regenerating above forest practice minimum densities in 82 % of our stands, slower regenerating burned areas far from live seed sources could be prime candidates to manage for complex early-seral conditions as the establishment of trees is likely to be slower with lower initial seedling densities (Tepley et al., 2014).

Larger wildfire events that burn under more extreme weather conditions likely result in larger patches of stand-replacing wildfire and further distances to live seed source in the interior of those patches (e.g., (Buonanduci et al., 2023; Reilly et al., 2022). The wildfires we sampled were relatively small compared to what is considered to be the upper range of wildfire sizes in northwestern Cascadia (Donato et al., 2020; Reilly et al., 2022). For example, the 1902 Yacolt fire burned ~180,000 ha of forest in the northwestern Cascades and, more recently, the 2020 wildfire complexes in northwestern Oregon burned ~146,000 ha (Riverside, Beachie Creek, and Lionshead Fires) (Reilly et al., 2022). In our study, most stands were within 450 m of a live seed source (38 out of 39), which was largely a result of access constraints and the distribution of stand-replacing patch sizes (e.g., at least 88 % of stand-replacing area across our sampled wildfires were within 450 m of a live seed source; Appendix 14). Research studying post-fire regeneration response at further distances to a live seed source is underway within the 2020 wildfire complexes (https://www.fs.usda.gov/research/pnw/centers/wsfcari) and will help inform at what distance regeneration rates are severely limited. In addition, understanding how burn intensity and pre-fire stand age interact to affect the retention of an in-situ seed source can provide additional insights and implications for management of the interior of stand-replacing patches of wildfire (see section 4.1).

4.3. Post-fire conifer establishment was greater in cooler and wetter conditions across spatial scales

Higher establishment rates within the Pacific silver fir zone, a wetter post-fire climate, and increased bryophyte cover, suggest that seedling establishment and survival are bolstered by cooler and wetter macro- and microsite conditions. Conifers are particularly vulnerable to drought-stress at the seedling stage relative to their adult stage (e.g., Bell et al., 2014) especially following stand-replacing disturbance (e.g., Dobrowski et al., 2015) due to a warmer and drier microclimate (e.g., Chen et al., 1993). Although regeneration rates were generally robust and did not differ substantially between the Pacific silver fir and western hemlock zone, establishment rates were 174 % greater in the Pacific silver fir zone, suggesting that Pacific silver fir forests had more favorable conditions for seedling survival and growth. Pacific silver fir forests occur at higher elevations and are characterized by cooler temperatures, increased precipitation, and persistent winter snow cover, relative to the western hemlock zone (Franklin and Dyrness, 1973) which may mitigate seedling drought stress. Establishment rates also increased with average 3-year post-fire SPEI across forest zones, suggesting increased seedling survival when post-fire climatic years were wetter on average. Across stands, SPEI values ranged from −1.07 to 0.19 (Table 2), thus stands that had values closer to normal had higher establishment rates than those verging on a mild drought (i.e., values closer to −1). However, it is important to note that SPEI values were generally non-overlapping across fires (Appendix 15) and these results should be interpreted with caution as SPEI may be correlated with unmeasured predictors.

Bryophyte cover also appeared to provide microsite conditions suitable for seedling germination and establishment, potentially through reduced soil water loss and erosion. Bryophytes associated with disturbance, such as fire mosses (e.g., *Ceratodon purpureus*), can quickly colonize disturbed areas and have important effects on soil properties following fire by reducing soil erosion (Bu et al., 2015; Grover et al., 2020; Silva et al., 2019), increasing water infiltration (Grover et al., 2020), aiding in recovery of soil microbial communities (García-Carmona et al., 2022), and insulating soil which reduces soil temperatures (Park et al., 2018). In addition, bryophytes may be a favorable germination substrate in areas where access to mineral soil is limited such as talus slopes or rocky areas (e.g., regeneration abundance was strongly correlated with bryophyte cover in our Goodell Creek plots where cobble and boulders dominated the ground surface). It is also possible that the relationship between bryophytes and seedling establishment are correlative and potentially not causal (i.e., bryophytes may indicate better microsite conditions as opposed to providing them). Further research is needed to investigate the mechanistic relationship between bryophyte cover and increased regeneration and establishment of conifer seedlings within and beyond the region.

Our findings can help inform how and where post-fire response may be affected by climate warming and drying in the future. Despite establishment rates being greater in cooler/wetter conditions, initial seedling densities suggest that natural post-fire regeneration is abundant following stand-replacing fire in most areas across the region. For example, regeneration and establishment rates were above forest practice minimum density thresholds (i.e., 470 seedlings ha^{-1}) by 3–5 years post-fire in 82.1 % and 64.1 % of stands, respectively. This suggests that climate warming and drying has yet to substantially limit post-fire tree regeneration in northwestern Cascadia, in contrast to some dry, water-limited forests where uncharacteristically severe fire and a drier post-fire environment has led to regeneration failure near forest margins (Stevens-Rumann et al., 2018). Provided that establishment rates increased with cooler and wetter conditions, future climate-induced declines in post-fire regeneration may be buffered at higher elevations or microsites that mitigate drought stress. Additionally, warmer temperatures and reduced persistence of winter snowpack at higher elevations could also affect conifer species distribution, with lower elevation species like Douglas-fir and western hemlock becoming more abundant at higher elevations relative to Pacific silver fir. Continued monitoring and research is needed to better understand at what point climate warming and drying may ultimately affect post-fire tree regeneration in forest systems adapted to large, stand replacing wildfires (Halofsky et al., 2020).

While these findings provide initial insights into what factors influence seedling survival in the immediate 3–5-year post-fire window, retrospective dendrochronological studies suggest post-fire conifer establishment dynamics in the northwestern Cascades can occur over a period of 40–100+ years and can exhibit multiple stand development pathways (e.g., Freund et al., 2014; Tepley et al., 2013; Winter et al., 2002). Our findings suggest stand-replacing patches in northwestern Cascadia are currently recovering in similar ways as they have in the past and that the ingredients necessary for forest recovery (i.e., abundant and diverse regeneration) are present, indicating forests in northwestern Cascadia are currently resilient to stand replacing fire. This is generally consistent with findings in other subalpine and boreal forests charactered by infrequent and stand-replacing fire regimes (e.g., Baltzer et al., 2021; Harvey et al., 2016), however there is uncertainty and concern for how increasing frequency of severe fire and a warmer post-fire climate may alter outcomes in the future (e.g., Turner et al., 2019). Our findings contrast to post-fire regeneration dynamics other ecoregions and fire regimes, where changes to fire size, severity, or frequency in combination with a drier post-fire climate are leading to reduced regeneration densities, regeneration failure, and potential loss of forest resilience (e.g., conversion of forest to non-forest following stand-replacing fire in dry, historically fire-frequent forests; Coop et al., 2020; Stevens-Rumann et al., 2018; Stevens-Rumann and Morgan, 2019). Provided most areas are regenerating naturally at 3–5 years post-fire, broad scale post-fire planting efforts may not be necessary in areas not managed for maximum timber yield. Since establishment dynamics play out over longer time scales, continued monitoring is needed to better understand successional trajectories following fire and how climate change may affect recovery across different stand development pathways.

5. Conclusion

Effects of climate warming and drying on forest resilience to fire are poorly understood in nominally infrequent, stand-replacing fire regimes, where information about recovery processes is limited (Halofsky et al., 2020). Our findings provide critical insights into post-fire regeneration dynamics in northwestern Cascadia and have important implications for forest management. In sum, we found that forest resilience to severe wildfire in northwestern Cascadia (1) increased with pre-fire stand age, (2) decreased with further distances to a live seed source, though less so relative to other forested systems, and (3) was bolstered by cooler and wetter macro- and micro-site conditions.

Our findings highlight the importance of biological legacies and structural complexity in late-seral forests, and their importance for supporting forest resilience to stand-replacing wildfire. Management efforts to accelerate existing mid-seral conditions to late-seral conditions and allow for natural regeneration to occur in areas not managed for maximum timber yield may promote post-fire recovery by increasing heterogeneity in forest structure, composition, and function. Additionally, provided the regional deficit of complex early-seral habitat (Donato et al., 2020), areas that are currently slower to regenerate with trees post-fire (i.e., interior of stand-replacing patches) may be prime candidate areas to manage for complex early-seral habitat.

CRediT authorship contribution statement

Madison M. Laughlin: Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Liliana K. Rangel-Parra:** Data curation, Investigation, Writing – review & editing. **Jenna E.**

Morris: Data curation, Investigation, Writing – review & editing. **Daniel C. Donato:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Joshua S. Halofsky:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Brian J. Harvey:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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