Patterns and drivers of conifer regeneration following stand-replacing wildfire across western Cascadia

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A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington
2022

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Program Authorized to Offer Degree:
Environmental and Forest Sciences

University of Washington

Abstract

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Tree regeneration is a critical mechanism of forest resilience to stand-replacing wildfire. Post-fire tree regeneration dynamics have been relatively well-studied in historically fire-frequent forests across western North America, though are understudied within forests characterized by infrequent and severe fire regimes like those of the western Cascades in Washington and Oregon, USA (western Cascadia). Recent wildfire activity (2015-2020) in western Cascadia has provided a unique opportunity to address this knowledge gap. Here, we asked: how is post-fire conifer regeneration across western Cascadia affected by pre-fire stand age, burn-patch size, and topo-climatic conditions? We established 39 1-hectare long-term monitoring plots across strata of pre-fire stand age and forest zone in four wildfires in western Cascadia. At each plot, we collected data on post-fire conifer species composition and abundance. We used generalized linear models to test how conifer establishment rates (seedlings $ha^{-1}yr^{-1}$ above 10 cm) and regeneration rates (seedlings $ha^{-1}yr^{-1}$ of all heights) responded to pre-fire stand age/seral stage, distance to the nearest live seed source, and post-fire topo-climatic conditions. Conifer regeneration rates and tree species richness increased with pre-fire stand age/seral stage, regeneration rates decreased with greater distances to the nearest live seed source but were present out to 450 m, and establishment rates were greater in areas characterized by cooler and wetter macrosite (e.g. greater post-fire precipitation) and microsite (e.g., greater bryophyte ground cover) conditions. In general, initial seedling densities suggest that 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 per ha) in 82.1% and 64.1% of plots, respectively. Our study provides critical insight on the drivers of post-fire tree regeneration following stand-replacing wildfires in western Cascadia, and informs what factors are likely to support greater forest resilience to fire. Our findings can help inform land management strategies for post-fire responses which is of critical importance under the uncertainties of climate change and fire in infrequent, stand-replacing fire regimes.

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ACKNOWLEDGEMENTS

Brian Harvey – thank you for your unwavering support and encouragement, and for cultivating a supportive, collaborative, and fun lab culture. You are an incredible role model and I am grateful for the opportunity to grow as a scientist under your mentorship.

Harvey Lab – getting to work with each of you has made me a better person and scientist. Thank you for making the long days at the office or in the field in the heat/rain/brush/you-name-it an absolute blast.

Collaborators Daniel Donato and Josh Halofsky **–** I am grateful for your mentorship and support, and for your essential contributions, collaboration, and feedback to this research.

Committee members Brittany Johnson, Abigail Swann, and Daniel Donato – thank you for your thoughtful insight and feedback.

Field technicians 2019 to 2022 – This work is not possible without you! Thank you for your hard work, positive attitudes, and flexibility in the field. It was an honor getting to work with and know each of you.

My undergraduate advisors, Jonathan Martin and Erik Olson – thank you for your mentorship over the years and for the opportunity to pursue science as an undergraduate student. Your encouragement and guidance have played a huge role in where I am today, and I will always cherish those summer field days spent in the canopy.

Sam – thank you for your partnership and support over the years. Your curiosity, energy, and love has kept me grounded throughout the pandemic and graduate school.

Time spent in the field – for making me feel at home, inspiring curiosity and connection, and teaching me things that books and papers cannot.

Chapter 1

Patterns and drivers of conifer regeneration following stand-replacing wildfire across western Cascadia

1. Introduction

As climate warms and fire activity increases in many regions worldwide (e.g., Parks and Abatzoglou 2020; Collins et al. 2022), understanding how forests will be resilient to future fire is of growing importance and a priority of contemporary forest management and research. Resilience can be defined as the ability of an ecosystem to tolerate disturbance without transitioning to an alternative state (Walker et al. 2004). Effects of climate warming on forest resilience to fire in forests characterized by infrequent, stand-replacing wildfire (i.e., >90% fire-induced tree mortality) are not fully known, as the rarity of wildfire events limits information about the disturbance regime and post-fire recovery processes (Halofsky et al. 2020). Many infrequent, stand-replacing fire regimes are climate-limited, meaning fire-potential is constrained by climatic conditions rather than the availability of fuel (Meyn et al. 2007), and there is uncertainty in how continued climate warming and drying will affect frequency of wildfire events in these systems (e.g., Halofsky et al. 2020). Managing broadly for ‘forest resilience’ is often ambiguous and challenging without specific, quantifiable management targets (Greiner et al. 2020), especially in systems where information about fire is limited. Thus, determining and testing underlying mechanisms of forest resilience can reduce ambiguity and help land managers prepare for potential consequences of climate change.

One critical mechanism of forest resilience to stand-replacing wildfire is tree regeneration, which is influenced by biological legacies that persist from pre-fire conditions and support post-fire recovery (e.g., Foster et al. 1998; Turner et al. 1998; Franklin et al. 2002; Johnstone et al. 2016). Pre-fire stand conditions conceivably influence the potential abundance, species composition, and probability of persistence of legacies—including key components such as surviving trees or viable cones. One important legacy is the presence and abundance of viable seed, which is strongly influenced by stand age/seral stage and corresponding stand structure at the time of fire. For example, late-seral forests typically produce greater amounts of seed than younger forests (e.g., Viglas et al. 2013; Andrus et al. 2020) and can have greater seed dispersal distances from trees that are taller (e.g., Gill et al. 2020). Species composition and dominance of mature, cone-bearing individuals also changes throughout the sere of a forest (e.g., Andrus et al. 2020), which will influence available seed composition following a disturbance. Finally, stand structure will affect the probability of persistence of biological legacies that can be surviving individual trees. For example, a young forest that is homogenously dominated by dense, young trees is less likely to result in surviving individuals or cones relative to an old forest with heterogeneity in size, age, and spatial arrangement of trees. The oldest and largest individuals in an old stand are more likely to survive a fire and provide a seed source compared to younger individuals (e.g., Dunn and Bailey 2016).

Another key factor that influences tree regeneration is seed delivery into stand-replacing patches of wildfire, where access to a seed source is limited due to high fire-induced mortality and consumption of cones. Many coniferous tree species are obligate seeders that rely on wind-dispersed seed from adjacent live forest edges or adaptive traits such as serotiny (i.e., cones that seed bank in the canopy and open after fire) to re-establish (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 patch (e.g., Donato et al. 2009; Kemp et al. 2016; Harvey et al. 2016; Littlefield 2019).

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; Harvey et al. 2016; Hansen and Turner 2019). 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 moister aspects (Harvey et al. 2016; Hansen and Turner 2019, Littlefield 2019) or soil types better at retaining moisture (Donato et al. 2009) can provide refugia for seedlings against heat and drought stress.

Post-fire tree regeneration dynamics and some of the underlying mechanisms of resilience have been relatively well studied in ecosystems with moderate to frequent fire, but are less well understood in fire regimes characterized by infrequent and stand-replacing wildfire. Forests of the western Cascades of Washington and northwestern Oregon (hereafter referred to as ‘western Cascadia’) are a prime example of an infrequent, stand-replacing fire regime where insights about how forests respond to fire have been limited by relatively rare occurrences in the last century. Current understanding of fire regimes in this region suggest they are characterized by infrequent (>450-year fire return interval on average; Hemstrom and Franklin 1982, Agee 1993) and large (maximum wildfire events between 1,000,000 and 10,000,000 ha; Donato et al. 2020) wildfire events, with a high proportion of area being stand-replacing (Reilly et al. 2020). As such, most insights come from retrospective studies that infer fire size, fire frequency, and post-fire stand development pathways based on dendrochronological aging of forest stands (e.g., Hemstrom and Franklin 1982; Huff 1995; Fruend 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 individuals on site (usually <1000 years; Hemstrom and Franklin 1982), making it difficult to piece together a comprehensive long-term fire history in these forests that have a multi-century fire return interval (Agee 1993). In addition, insights about post-fire dynamics immediately following wildfire events are unable to be fully reconstructed from dendrochronological methods because of disappearing evidence over time. For example, evidence of the pre-fire stand conditions diminishes with increasing time since fire. Evidence of initial post-fire tree regeneration densities and species composition and processes that lead to survivorship through succession also cannot be reconstructed in retrospective studies.

Recent wildfire activity (2015-2020) in western Cascadia has provided a unique opportunity to study post-fire recovery processes immediately following the disturbance event, to better understand the drivers of post-fire tree regeneration in an infrequent, stand-replacing fire regime. 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 a changing climate and how that can affect fire and forest response in infrequent, severe fire regimes. We hypothesized that patterns of post-fire conifer regeneration abundance will be similar to those of other forested systems: specifically, increasing with closer distances to a live seed source and in topo-climatic conditions that mitigate drought stress (i.e., wetter and cooler conditions). We also expected higher regeneration abundance in older pre-fire stands, due to the increased probability of surviving individual tree legacies.

2. Methods

2.1 Study area

Western Cascadia includes all forested land west of the Cascade crest in Washington and northwestern Oregon characterized by historically infrequent (>450-year fire return intervals on average; Agee 1993) and stand replacing fire regimes (i.e., LANDFIRE fire regime groups IV and V; Rollins 2009; Barrett et al. 2010; Figure 1.1). These areas primarily fall within the rugged mountainous terrain of the Coast, Olympic, and Cascade Range. 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 1500 to 2500 mm per year, with up to 3800 mm per year in the coastal rain forest of the Olympic Peninsula. 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. At higher elevations, mean annual snowfall is much greater, ranging from 635 to 1270 cm the west Olympics and from 1000 to 1500 cm the western Cascades.

Forested communities at lower elevations primarily consist of the western hemlock (*Tsuga heterophylla*) zone, dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and western red cedar (*Thuja plicata*). The western hemlock zone is characterized by intermittent snow cover in the winter. 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 thrive 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 like western hemlock, western red cedar, 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., Tepley et al. 2014).

2.2 Sampled wildfires

We established 39 long-term monitoring plots across four wildfires that span from the Colombia River Gorge in Oregon to the North Cascades National Park in Washington, including the Goodell Creek (2015), Norse Peak (2017), Eagle Creek (2017), and Maple (2018) fires (Figure 1.1; Table 1.1). These wildfires ranged in size from 1,435 to 19,755 ha, and encompass elevations from 5 to 2,100 meters (Table 1.1).

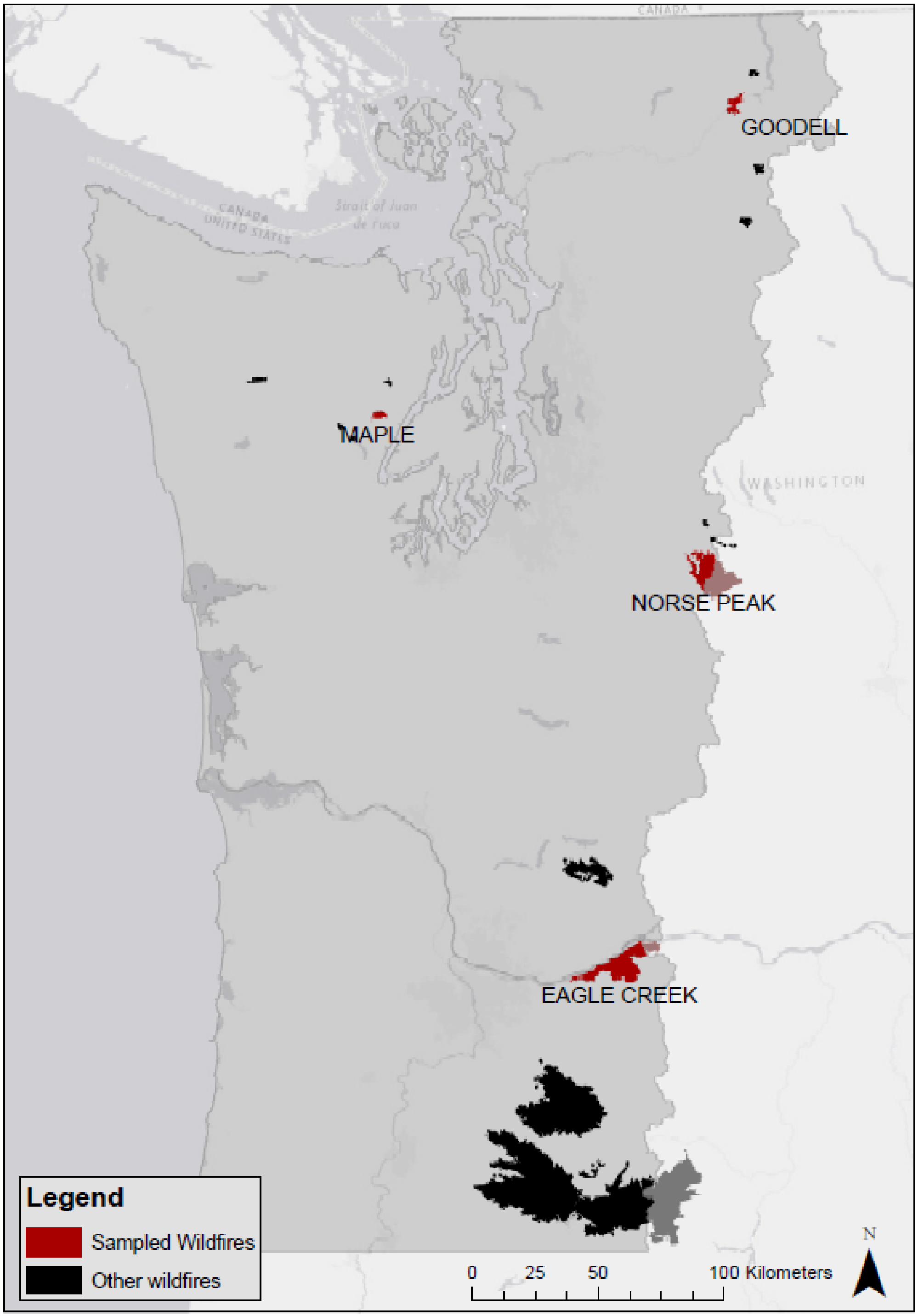

Figure 1.1 Western Cascadia study area with wildfire perimeters from 1986 – 2020 (source: Monitoring Trends in Burn Severity https://www.mtbs.gov/). Plots were established within the Goodell Creek (2015), Norse Peak (2017), Eagle Creek (2017), and Maple (2018) wildfires (colored in red).

Table 1.1 General information about the sampled wildfires in western Cascadia. Information on 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 to 1,600	North Cascades National Park	2020	8
Norse Peak	2017	8,936*	800 to 2,100	Mt Baker Snoqualmie-National Forest	2020	19
Eagle Creek	2017	19,755	5 to 1,400	Mt Hood National Forest and Colombia River Gorge National Scenic Area	2021	9
Maple	2018	1,435	160 to 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.

2.3 Data collection

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

Thirty-nine 1-ha plots were established within stand-replacing patches of wildfire (i.e., areas where overstory mortality exceeded 90%) across 2 strata of interest: forest zone (warm, lower elevation western hemlock zone and cold, higher elevation Pacific silver fir zone) and pre-fire stand age (young, mid seral, and late seral). Potential plot locations were first identified in ArcMap using spatial layers delineating burn severity, forest zone, and stand-age, then ground validated in the field. Forest zone was determined in the field using a forest zone key adapted from Van Pelt (2007) based on the pre-fire shade tolerant composition of the stand (Appendix A.2). If more than 10 percent of the shade tolerant component contained Pacific silver fir, the plot was assigned to the cold Pacific silver fir zone (hereafter referred to the 'cold forest zone'). If western hemlock was present and no other shade tolerant species exceeded 10 percent of the total shade tolerant basal area, then the stand was assigned to the warm western hemlock zone (hereafter referred to as the 'warm forest zone'). Pre-fire stand age was also assigned in the field using a stand development stage key from Van Pelt (2007), which estimates stand age by examining forest composition and structure. Each plot was assigned a pre-fire stand age of young, mid seral, and late seral (Appendix A.3). 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 and were structurally more developed than young stands, often originating 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 wildfire (~160-500+ years old). It is important to note that after stand-replacing fire, most tree stems from the pre-fire forest are still present and identifiable, allowing us to key out forest zone and pre-fire stand age in the field.

Burn severity, forest zone, and pre-fire stand age were consistent at the scale of each 1-ha (56.5 m radius) plot. Plots in the same strata (i.e., same forest zone and pre-fire stand age) were established at least 450 meters away from one another to reduce issues associated with spatial autocorrelation. Plot centers were established at least 100 meters away from a road or trail when possible to reduce the influence of human activities or edge effects (e.g., dispersal of invasive species or changes to light availability caused by the road clearing). We did not establish plots within areas that were salvage logged or planted and avoided placing our plots near streams, wetlands, or ephemeral creeks.

2.3.2 Field measurements

At each plot, we collected data on general stand characteristics, pre-fire stand structure, post-fire herb and shrub response, and post-fire conifer regeneration. General stand information was collected from plot center and included slope (degrees), aspect (degrees), and elevation (meters). Herb, shrub, and conifer regeneration surveys occurred within twelve subplots situated along four 24.5 m sub-cardinal transects (i.e., three subplots per transect; Appendix A.1). Percent cover of all herbaceous and woody plants was recorded within a 2 m radius at each of the twelve subplots. All plants were identified to the species level, except for the nominal groups of graminoids (Poaceae, Cyperaceae, and Juncaceae families collectively) and bryophytes (non-vascular seedless plants; e.g. mosses). Tall woody shrubs (Appendix A.4) received additional allometric measurements such as maximum height and number of stems in various basal diameter classes.

Post-fire conifer regeneration ≥ 10 cm tall was surveyed within a 3.5 m radius of subplot center. Species, height (cm), age (estimated by whorl counts and bud scars), and presence of any top damage (i.e., damage to the top of the leader that would obscure whorl counts or height) was recorded for each individual greater than 10 cm within the 3.5 m radius. Age estimation by counting whorls and bud-scars is a reliable estimate of age for young Douglas-fir, pines (*Pinus* spp.), and true firs (*Abies* spp) (e.g., Urza and Sibold 2013; Donato et al. 2016; Harvey et al. 2016). Whorl counts are unreliable for western hemlock and western red-cedar and thus were not recorded for these species. The total number of individuals < 10 cm tall of each species was tallied within a 0.5 m radius of subplot center for post-fire conifer regeneration.

2.4 Statistical analysis

We modeled the establishment and regeneration rates of conifer seedlings (seedlings ha^{-1} yr^{-1}) as a response to covariates related to pre-fire stand structure, burn patch size, and topo-climatic conditions. We define establishment rates as seedlings ha^{-1}yr^{-1} taller than 10 cm, which indicate conditions suitable for seedling survival and growth (i.e., seedlings that have resources to establish following germination). Regeneration rates are defined as the total seedlings ha^{-1}yr^{-1}

of all heights and better correspond to potential available seed input (i.e., areas with access to an available seed source and conditions suitable for germination). 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., Marsh et al. 2022).

Seedling ha^{-1}yr^{-1} was used to account for differences in time since fire across plots, which ranged from 3 to 5 years at time of sampling (Table 1.1). To calculate seedlings ha^{-1}yr^{-1}, the total number of seedlings in a plot 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 a standard approach in similar studies (e.g., Harvey et al. 2016).

Prior to developing models, we identified 6 target factors ecologically relevant to seedling establishment and survival that we wanted represented in our models: pre-fire stand structure, seed source availability, macroclimate setting, post-fire climatic conditions, topo-climatic conditions, and competition/microsite conditions. We gathered potential explanatory variables related to these target factors and assessed them for multicollinearity. Correlated variables with a Pearson’s correlation coefficient greater than 0.5 were identified and reduced to 1 by running parallel full models and choosing the variable that resulted in a better fit model based on the Akaike information criterion corrected for small sample size (AICc). For example, if 3 variables were highly correlated (i.e., Pearson’s correlation coefficient greater than 0.5), then 3 separate full models were run, each containing one of those correlated variables. The model that resulted in the lowest AICc indicated a better fit model, thus that model’s variable was chosen and the remaining 2 colinear variables were removed. Multicollinearity was also assessed following model fitting using the variation inflation factor (VIF) to ensure no variables were contributing to inflated parameter variance. Variables that resulted in a VIF greater than 2 were dropped from our models.

The final models contained eight explanatory variables: pre-fire stand age (young, mid seral, and late seral), distance to the nearest live seed source (m), forest zone (cold and warm), average 3-year post-fire standardized precipitation evapotranspiration index (SPEI), heat load index (HLI), topographic wetness index (TWI), vegetation percent cover, and bryophyte percent cover (Table 1.2 and Table 1.3). No transformations were required based on visual examination of histograms. Bryophyte percent cover, vegetation percent cover, pre-fire stand age, and forest zone were collected in the field. HLI, TWI, SPEI, and distance to the nearest live seed source were calculated or downloaded and are described in more detail below.

Heat load index (HLI) was calculated for each plot 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-meter resolution digital elevation model (DEM) input (source: United States Geological Survey https://www.usgs.gov/the-national-map-data-delivery). Topographic wetness index 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 of TWI indicate topographically 'drier' areas with less upslope accumulated flow.

We used the standardized precipitation evapotranspiration index (SPEI) downloaded from Climate Engine (https://app.climateengine.com/climateEngine) and sourced from gridMET (Abatzoglou 2013) 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 minimum SPEI values across the first three growing seasons following fire for each plot (i.e., calculated the average of minimum SPEI values for 1-year post-fire, 2 years post-fire, and 3 years post-fire). A negative SPEI value indicates 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.

Distance to the nearest live tree seed source (i.e., the nearest living clump of mature trees at least 1 ha in area) from plot center was measured in ArcMap 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 and a refugia density index (RDI; Downing et al. 2019). However, these alternative representations of live seed source did not perform as well in models as distance to nearest live seed source.

Table 1.2 Stand-scale (1-ha) range, mean, and median of quantitative explanatory variables (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 to 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 to 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
Average bryophyte % cover	Average percent cover of bryophytes (i.e., non-vascular plants), measured in the field.	0 to 64	14.88	7.92
Average vegetation % cover	Average percent cover of herbs and shrubs, measured in the field.	1 to 58	9.00	6.74
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 to 1,610.1	156.20	84.38

*SPEI = standardized precipitation evapotranspiration index

Table 1.3 Number of plots sampled within each strata of forest zone (warm, western hemlock forest zone or cold, Pacific silver fir forest zone) and pre-fire seral stage (young, mid seral, and late seral).

Strata	**Number of plots**
Warm forest zone	
Young	-
Mid	6
Late	18
Cold forest zone	
Young	3
Mid	5
Late	7
Total	39

2.4.2 Generalized linear models

We used generalized linear models (GLMs) with a negative binomial distribution and log link function to test the effect of pre-fire stand structure (pre-fire stand age), burn patch size (distance to the nearest live seed source), and topo-climatic conditions (forest zone, HLI, TWI, SPEI, bryophyte percent cover, and vegetation percent cover) on post-fire regeneration and establishment rates. 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 to allow for comparison of relative effect sizes across predictors and models (i.e., subtracting their means and dividing by their standard deviation). We used a p-value threshold of 0.05 to determine predictor variable significance in model outputs.

Best fit model selection was determined by comparing delta AICc among top-ranking models (note: the function 'dredge' from package MuMln in R was used to generate top-ranking models; https://www.rdocumentation.org/packages/MuMIn/versions/1.43.6/topics/dredge). 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 4 and 7 indicate considerably less support (Fabozzi et al. 2014) but were still examined during the model selection process.

No random effects were included in models. Model diagnostics were performed for models with and without a random effect of fire using the Diagnostics for Hierarchical Regression Models (DHARMa) package in R (https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html). Quantile residuals were equally distributed across fires, justifying the exclusion of a random effect of fire.

2.5 Comparing seedling densities to management standards

To compare initial post-fire seedling densities to forest practice management standards, we calculated the area occupancy (i.e., stocking) within plots based on presence of established seedlings among the twelve subplots. For each plot, we calculated the proportion of subplots occupied at a minimum density of 260 established seedlings per ha (i.e., at least 1 seedling present within each of the 3.5 m^2 subplots). We then averaged the plot-level area occupancy across the 39 plots. This metric provides a sense of how uniformly distributed seedlings are within a plot (i.e., are most seedlings clustered within a few subplots, or are they distributed across the entire stand).

We also calculated the proportion of plots (out of 39 plots) whose plot-level seedling density exceeded forest practice minimums of 470 seedlings per ha (Chapter 222-34-010 WAC). These forest practice minimums are seedling planting standards used by land management agencies following logging.

3. Results

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

Across all plots (hereafter referred to as ‘stands’), total seedling densities ranged from 22 to 264,067 seedlings ha^{-1} (median = 4,352, mean = 22,992; Table 1.4). Established seedling densities (i.e., seedlings greater than 10 cm tall) ranged from 22 to 51,449 seedlings ha^{-1} (median = 974, mean = 3,295; Table 1.4). On average, 72.2% of stand area was occupied at a minimum density of 260 established seedlings per ha (i.e., seedlings greater than10 cm tall; Table 1.4; Table 1.5; Appendix C.1). Total and established seedling densities exceeded forest practice minimum density thresholds of 470 seedlings per ha in 82.1% (32 out of 39) and 64.1% (25 out of 39) of stands, respectively (Appendix C.2).

On average, percent cover of bryophytes ranged from 0.1% to 67.8% across stands (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 C.3). Average maximum shrub height ranged from 0 to 1.3 m (median = 0.1 m, mean = 0.2m) (Appendix C.3).

3.2 Regeneration rates

Total regeneration rates ranged from 5 to 88,022 seedlings ha^{-1} yr^{-1} across stands (mean = 6,914, median = 1,068) and seedlings were present in 100% of stands (Table 1.5). Bryophyte percent cover, average 3-year post-fire SPEI, distance to a live seed source, and pre-fire stand age were included in the best fit model and were present in 100%, 42%, 54%, and 96% of top-ranking models with delta AICc values less than 7 (n= 24, Appendix B.1), respectively. Forest zone, TWI, and HLI were not included in the best fit model, occurring in 33%, 38%, and 42% of top-ranking models with delta AICc values less than 7 (Appendix B.1), respectively.

On average, regeneration rates increased by 84% for every 15% increase in bryophyte percent cover ($p = 0.027$, Appendix B.3; Figure 1.2) and decreased by 31% for every 100 m increase in distance to a live seed source ($p < 0.001$, Appendix B.3; Figure 1.2). Regeneration rates did not correspond with average 3-year post-fire SPEI ($p = 0.18$, Appendix B.3; Figure 1.2). Regeneration rates were greater in pre-fire late-seral stands than in pre-fire mid-seral stands, with pre-fire late-seral stands having 385% more seedlings ha^{-1} yr^{-1} than pre-fire mid-seral stands on average ($p = 0.017$, Appendix B.3; Figure 1.2). Regeneration rates in pre-fire young stands did not statistically differ from pre-fire mid-seral stands ($p = 0.20$; Appendix B.3; Figure 1.2).

Table 1.4 Summary description of regeneration and establishment densities (seedlings ha^{-1}) 3-5 years post-fire across plots, by species. Percent present indicates the percentage of plots that each species was present, out of 39 plots (e.g., Douglas-fir was present in 84.6% of plots). Area occupancy (%) represents the average percentage of area within a plot that was occupied at a minimum density of 260 seedlings ha^{-1}, where that species was present (e.g., in plots where Douglas-fir was present, it occupied 64.4% of subplots at a minimum density of 260 seedlings ha^{-1} on average).

	Regeneration Densities (total seedlings ha^{-1})				**Establishment Densities (seedlings ha^{-1} ≥ 10 cm)**					
Tree species	**Min – Max**	**Median**	**Mean**	**% Present**	**Min – Max**	**Median**	**Mean**	**% Present**	**Area Occupancy (%)**	**Mean Height (cm)**
All combined	22 – 264,067	4,352	22,992	100	22 – 51,449	974	3,295	100	72.2	16.6
Douglas-fir	0 – 42,610	736	3,831	84.6	0 – 27,695	238	1,410	84.6	64.1	17.2
Western hemlock	0 – 258,502	281	14,127	64.1	0 – 13,317	22	796	64.1	40.0	18.0
Noble fir	0 – 16,088	43	1,905	56.6	0 – 9,896	22	463	56.6	48.9	12.9
Pacific silver fir	0 – 3,205	0	284	30.8	0 – 671	0	39	30.8	25.7	12.2
Western red cedar	0 – 49,370	0	2,550	20.5	0 – 10,112	0	509	20.5	60.41	19.8
Lodgepole pine	0 – 1,667	0	76	17.9	0 – 1,667	0	76	17.9	45.2	45.4
Western white pine	0 – 1,083	0	28	2.6	0 – 22	0	<1	2.6	8.3	10.0
Subalpine fir	0 – 2,209	0	57	2.6	0 – 87	0	2	2.6	33.3	11.8
Engelmann spruce	0 – 1,061	0	27	2.6	-	-	-	2.6	-	-

Table 1.5 Summary description of regeneration and establishment rates (seedlings ha^{-1} yr^{-1}) 3-5 years post-fire across plots, by species. Percent present indicates the percentage of plots that each species was present, out of 39 plots (e.g., Douglas-fir was present in 84.6% of plots). Area occupancy (%) represents the average percentage of area within a plot that was occupied at a minimum density of 260 seedlings ha^{-1}, where that species was present (e.g., in plots where Douglas-fir was present, it occupied 64.4% of subplots at a minimum density of 260 seedlings ha^{-1} on average).

	Regeneration Densities (total seedlings ha^{-1})				**Establishment Densities (seedlings ha^{-1} ≥ 10 cm)**					
Tree species	**Min – Max**	**Median**	**Mean**	**% Present**	**Min – Max**	**Median**	**Mean**	**% Present**	**Area Occupancy (%)**	**Mean Height (cm)**
All combined	5 – 88,022	1,068	6,914	100	5 - 10,290	254	773	100	72.2	16.6
Douglas-fir	0-8,722	184	1,101	84.6	0 - 5,539	79	316	84.6	64.1	17.2
Western hemlock	0-86,168	72	4,524	64.1	4 - 2,663	33	268	64.1	40.0	18.0
Noble fir	0-5,363	11	600	56.6	0 - 2,474	7	131	56.6	48.9	12.9
Pacific silver fir	0-1,068	0	92	30.8	0 - 168	0	11	30.8	25.7	12.2
Western red cedar	0-9,874	0	597	20.5	0 - 2,022	0	127	20.5	60.41	19.8
Lodgepole pine	0-333	0	15	17.9	0 - 333	0	15	17.9	45.2	45.4
Western white pine	0-270	0	7	2.6	0-5	0	<1	2.6	8.3	10.0
Subalpine fir	0-736	0	19	2.6	0-29	0	1	2.6	33.3	11.8
Engelmann spruce	0-354	0	9	2.6	-	-	-	2.6	-	-

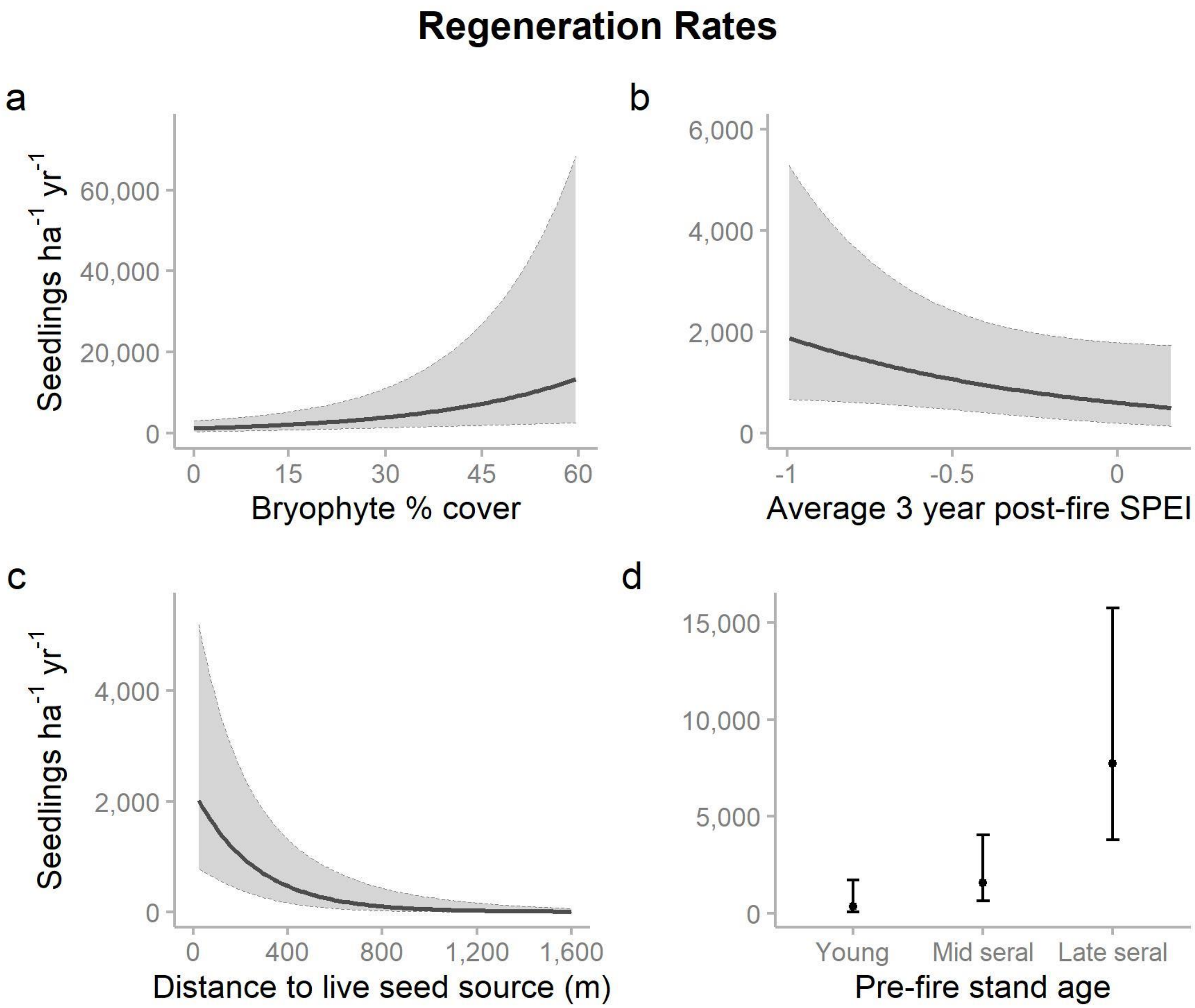

Figure 1.2 Effect of bryophyte percent cover (a), average 3-year post-fire SPEI (b), distance to live seed source (c), and pre-fire stand age (d) on regeneration rates (seedlings ha^{-1} yr^{-1} of any height) when all other model covariates are held constant at their median values. Shaded areas and error bars represent the 95% confidence intervals of predictions.

3.3 Establishment rates

Establishment rates ranged from 5 to 10,290 seedlings ha^{-1} yr^{-1} (mean = 773, median = 254; Table 1.5). Bryophyte percent cover, average 3-year post-fire SPEI, distance to a live seed source, forest zone, and pre-fire stand age appeared in 100%, 100%, 94%, 88%, and 53% of top-ranking models with delta AICc values less than 7 (n = 17, Appendix B.2), respectively, and were included in the best fit model. Vegetation percent cover, HLI, and TWI were not included in the best fit model and were present in 35% of top-ranking models with delta AICc values less than 7 ($n = 17$, Appendix B.2) and 0% of top-ranking models with delta AICc values less than 2.

On average, establishment rates increased by 200% for every 15% increase in bryophyte percent cover ($p < 0.001$, Appendix B.3; Figure 1.3) and increased by 170% for every 0.5 value increase in the average 3-year post-fire SPEI ($p < 0.001$, Appendix B.3; Figure 1.3). Establishment rates decreased by 25% for every 100 m increase in distance to a live seed source on average ($p < 0.001$, Appendix B.3; Figure 1.3).

Establishment rates were 174% greater in cold zone forests than warm zone forests on average ($p = 0.0045$; Appendix B.3; Figure 1.3). Establishment rates did not statistically differ between pre-fire young and mid-seral stands ($p = 0.22$; Appendix B.3; Figure 1.3). However, there was a suggestive difference between pre-fire late-seral and mid-seral stands, with pre-fire late-seral stands having 84% more seedlings ha^{-1} yr^{-1} relative to pre-fire mid-seral stands on average ($p = 0.06$; Appendix B.3; Figure 1.3).

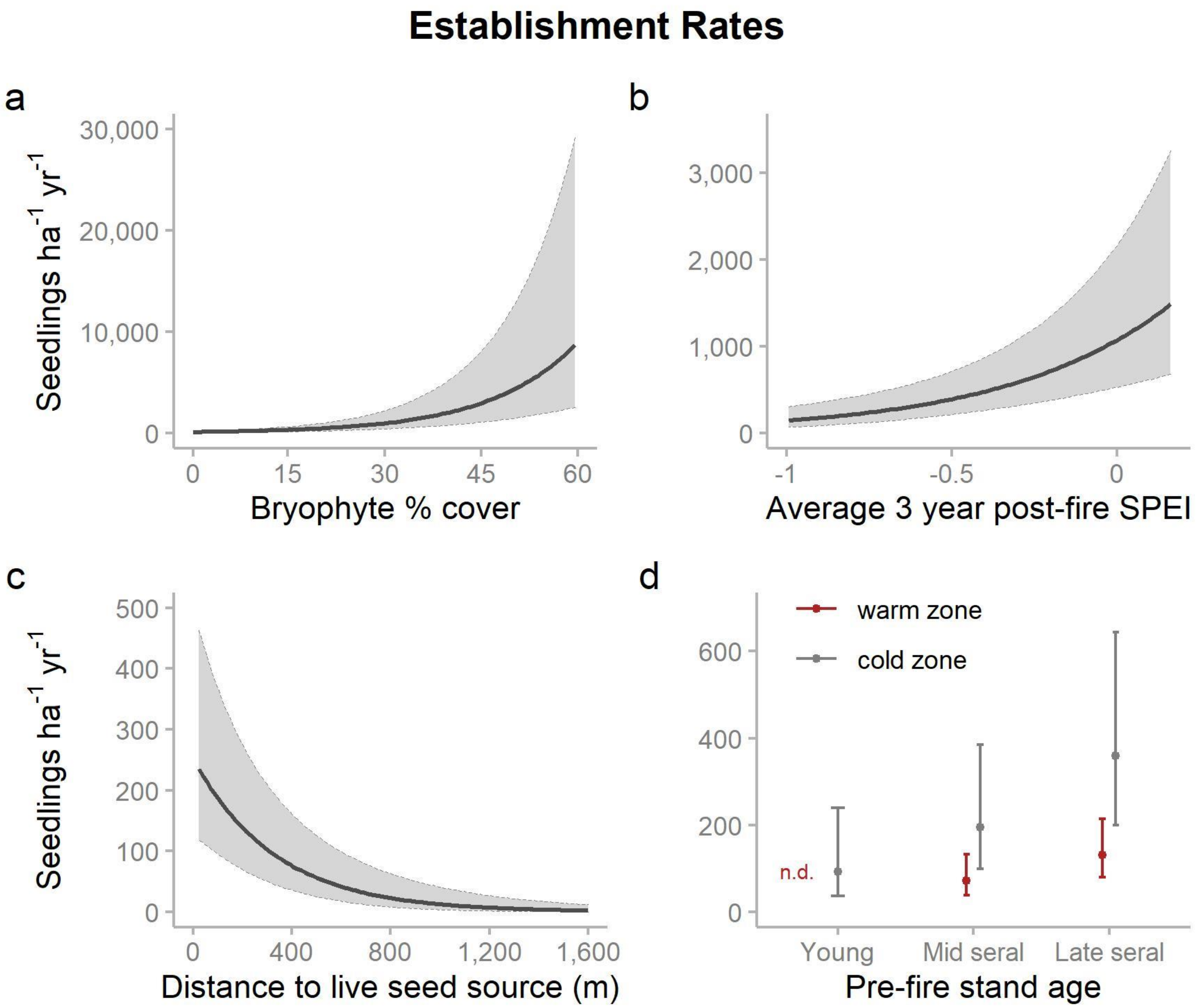

Figure 1.3 Effect of bryophyte percent cover (a), average 3-year post-fire SPEI (b), distance to live seed source (c), forest zone (d), and pre-fire stand age (d) on establishment rates (seedlings ha^{-1} yr^{-1} for seedlings reaching 10 cm in height) when all other model covariates are held constant at their median values. Shaded areas and error bars represent the 95% confidence interval of predictions. In panel d, "n.d." indicates no data as we did not have any plots that were young at the time of fire in the warm forest zone.

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

The relative effect of bryophyte percent cover was 78% greater for establishment rates than regeneration rates (Appendix B.3; Figure 1.4). Distance to live seed source had a 30% greater effect on regeneration rates relative to establishment rates (Figure 1.4). Forest zone and average

3-year post-fire SPEI were important predictor of establishment rates, but not regeneration rates (Appendix B.3; Figures 1.4). Pre-fire stand age corresponded more strongly with regeneration rates than with establishment rates (Appendix B.3; Figures 1.4).

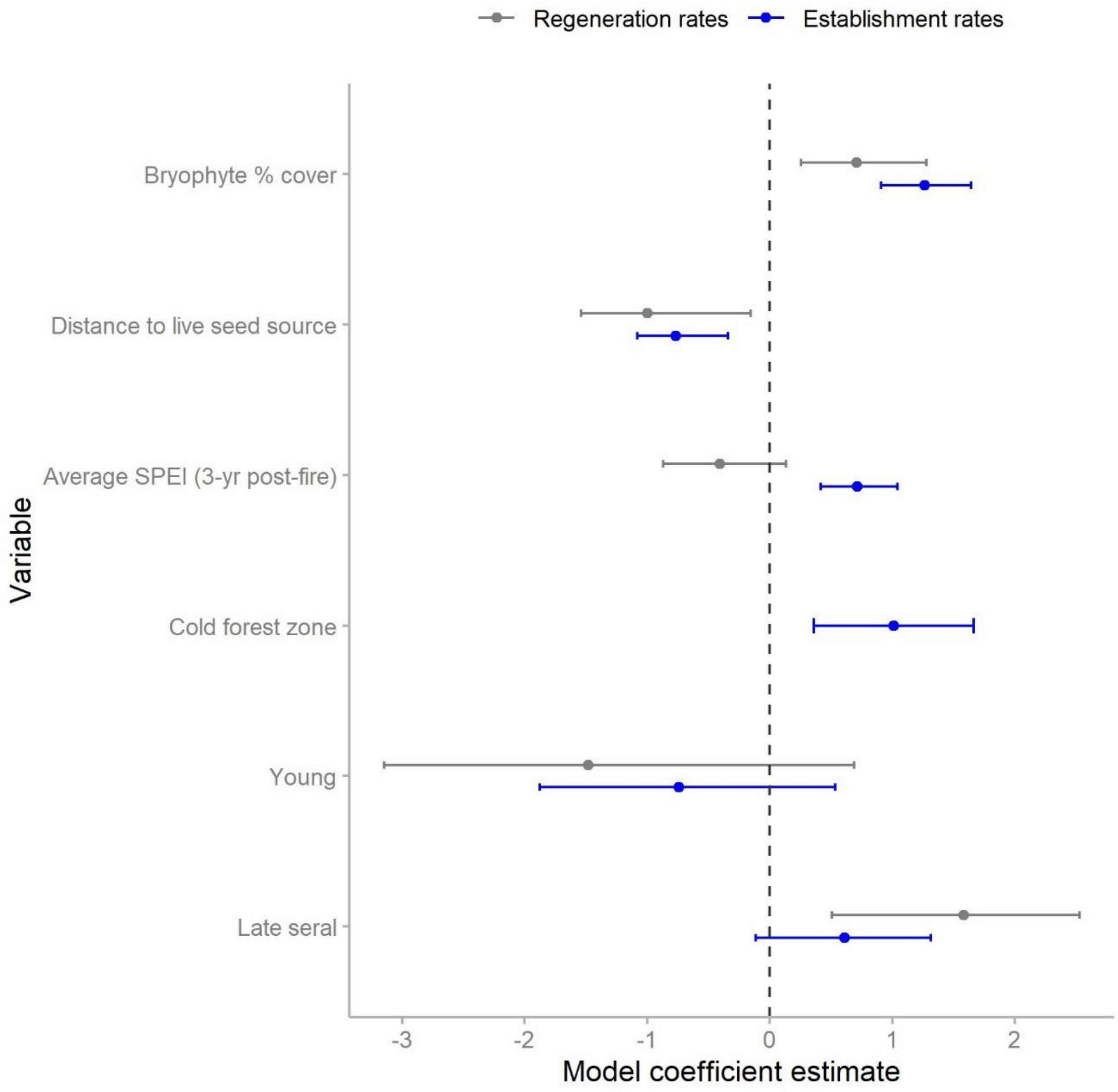

Figure 1.4 Model parameter coefficients for regeneration rates (gray) and establishment rates (blue) with 95% confidence intervals. All covariates in the models were scaled so that the relative effect sizes could be compared among covariates and between models.

3.5 Species composition across strata

A total of 9 conifer species were present across all stands (Table 1.4; Table 1.5). 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 red cedar (present in 20.5% of stands), and lodgepole pine (*Pinus contorta;* present in 17.9% of stands) (Table 1.4; Table 1.5). Western white pine (*Pinus monticola*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) were also present, but only in 2.6% of stands.

Among stands where species were present, Douglas-fir and western red cedar had the greatest area occupancy relative to other species, occupying 64.1% and 60.4% of stand area at a minimum density of 260 established seedlings per ha on average, respectively (Table 1.4). 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 a minimum density of 260 established seedlings per ha on average, respectively (Table 1.4).

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 species, followed by Douglas-fir (mean = 1,101, range = 0 – 8,722 seedlings ha^{-1} yr^{-1}), western red cedar (mean = 597, range = 0 – 9,874 seedlings ha^{-1} yr^{-1}), and noble fir (mean = 600, range = 0 – 5,363 seedlings ha^{-1} yr^{-1}) (Table 1.4; Table 1.5). Species abundance ranked similarly with establishment rates, though Douglas-fir had the greatest mean and range (mean = 316, range = 0 – 5,539 seedlings ha^{-1} yr^{-1}) while western hemlock had the second greatest (mean = 268, range = 0 – 2,663 seedlings ha^{-1} yr^{-1}).

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. 1.5). Similarly, Shannon diversity index (SDI) of conifer tree species was greatest is 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) (Figure 1.5).

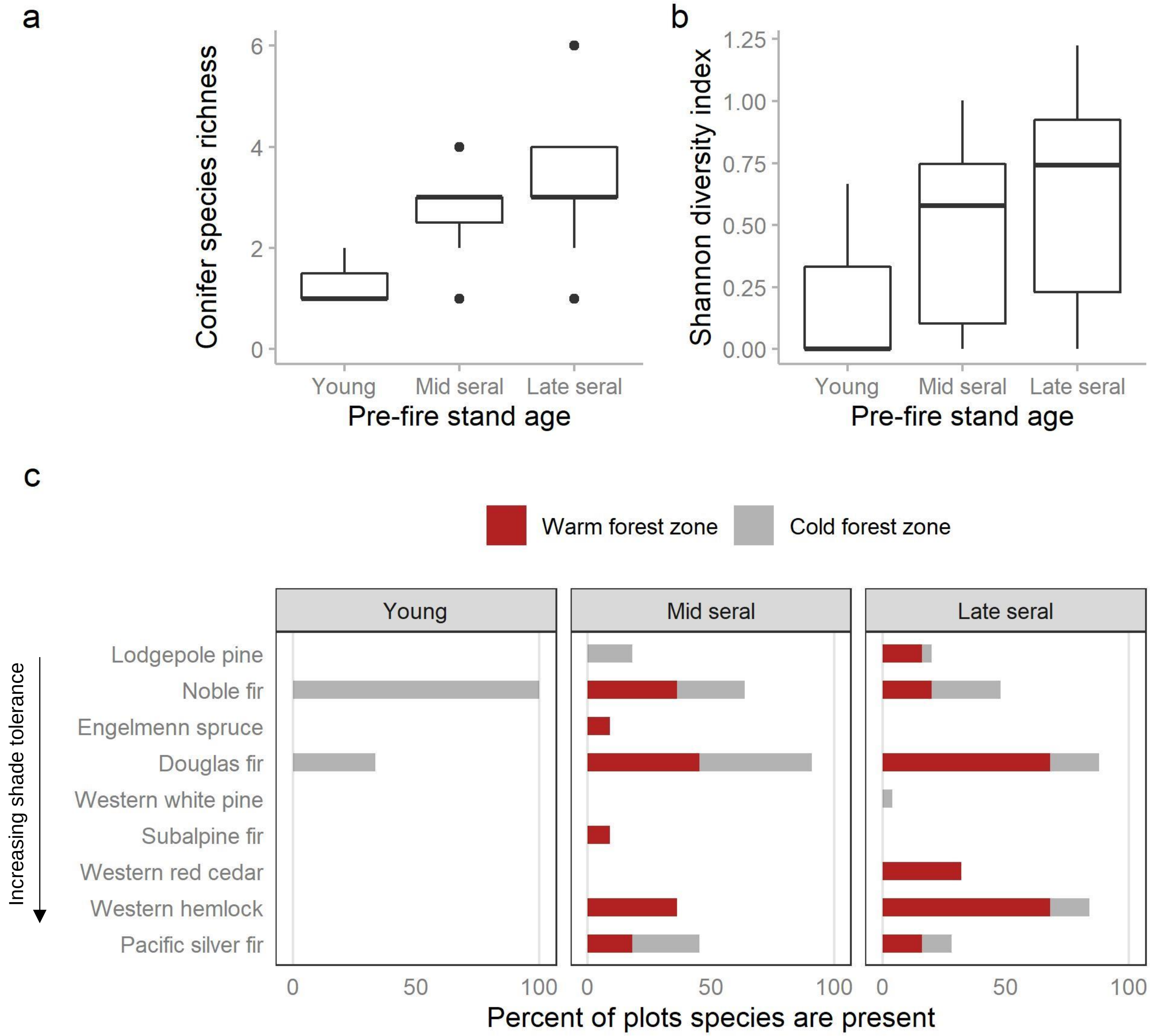

Figure 1.5 Conifer species richness (a), diversity (b), and plot occupancy across strata of pre-fire stand age and forest zone (c). In panel c, species are arranged from shade intolerant to shade tolerant (top to bottom; Minore 1979). These figures reflect total regeneration rates of all heights.

4. Discussion

Our study highlights how pre-fire stand age, burn patch size, and topo-climatic conditions affect post-fire regeneration dynamics within an infrequent, stand-replacing fire regime, and provides several key insights into mechanisms of forest resilience. First, we found that regeneration abundance and diversity increased with pre-fire stand age, suggesting forest resilience to stand-replacing fire is greater in older forests via increased seed availability. Second, the interior of large stand-replacing patches further away from a live seed source may be areas slower to regenerate and establish with trees. Last, 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 an infrequent, stand-replacing regime that can inform forest management amid the uncertainties of a changing climate.

4.1 Forest resilience to fire increases with pre-fire stand age via increased seed availability

Our finding that regeneration rates and conifer species diversity increased with pre-fire stand age highlight the importance of seed supply and diversity as a mechanism of post-fire forest resilience. In general, seed volume increases with stand age (Viglas et al. 2013; Andrus et al. 2020; Gill et al. 2020) and local and nearby seed dispersal is greater when the nearest live forest edge is older (Gill et al. 2020). This phenomenon could explain the increased diversity in post-fire species composition we observed in pre-fire late-seral stands (Table 1.5; Figure 1.5), as late-seral forests contain mature cone-bearing individuals of both shade tolerant and intolerant species (Van Pelt and Nadkarni 2004). Another potential explanation is that late-seral forests have a higher probability of retaining an in-situ seed source through survival of old and large, fire-resistant individuals (Keeton and Franklin 2005; Dunn and Bailey 2016). All of our sampled stands experienced greater than 90% fire-induced mortality by 3-5 years post-fire, though burn intensity and rates of delayed mortality were not known. Lower intensity fire could still result in mortality rates exceeding 90%, though may not consume cones in the upper canopy and may allow large, thick-barked species to survive long enough to put out a cone crop before dying. Larson and Franklin (2005) hypothesized the retention of a short-term canopy seed bank for Douglas-fir following fire in the western Cascades of Oregon, supported by previous observations of dense post-fire seedling abundance at distances up to 3 km from a live seed source (Gray and Franklin 1997). Because of the limited opportunity to study post-fire dynamics within infrequent fire regimes, information about short-term canopy seed banks and rates of delayed mortality following fire are limited in this system and is a valuable area of future research, as it may contribute to the underlying mechanism of increased regeneration rates in older stands.

Increased post-fire seedling abundance and diversity in pre-fire late-seral stands has important implications for future forest trajectories and managing forests for resilience amid a rapidly changing climate. First, our findings highlight the importance of late-seral forests (which are currently in deficit; Donato et al. 2020) and efforts to accelerate towards late-seral conditions in existing mid-seral forests (which are currently in excess; Donato et al. 2020). Climate warming and drying is expected to increase conditions associated with wildfire activity across western 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. Second, co-establishment of shade tolerant (e.g., western hemlock) and intolerant (e.g., Douglas-fir) species may accelerate aspects of structural forest development. For example, a multi-layered, vertically contiguous canopy is a key feature of late-seral forest structure, and is achieved through co-dominance of mature shade tolerant species that can regenerate continually in the understory in low-light 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 shade tolerant species growth release (Keeton and Franklin 2005). Post-fire stands with shade tolerant co-establishment also exhibit precocious complexity, sharing many aspects of structural complexity as late-seral stands immediately after fire like abundant coarse woody debris and snags, presence of shade tolerant and intolerant species, differentiated growth rates, and spatial heterogeneity (Donato et al. 2012). 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 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 often result in spatially and compositionally homogenous stands (e.g., Hayes et al. 2005) and do not reflect the full range of disturbance-created stand development pathways in the region (e.g., co-establishment; Donato et al. 2012; Tepley et al. 2014). Finally, our findings support retrospective dendrochronological observations of co-establishment in the region (e.g., Keeton and Franklin 2005; Tepley et al. 2013; Tepley et al. 2014). Our findings also 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. In summary, managing for late-seral conditions may confer resilience of forests to future wildfire by increasing regeneration rates and promoting heterogeneity in post-fire landscape structure, composition, and function.

Future research that tests underlying mechanisms of increased seed availability in older stands and effects of initial stand densities and composition on future successional outcomes through field studies and simulation modeling could provide valuable insight for future resilience to fire in western Cascadia. While we hypothesize that late-seral stands may have increased seed availability following stand-replacing fire, future research is needed to test this hypothesis and assess the source of increased seed availability using seed traps in the field (e.g., Gill et al. 2020). Understanding whether increased seed availability is a result of age of the nearest live forest edge (e.g., Gill et al. 2020) or retention of an in-situ seed source (suggested by Larson and Franklin 2005) has important implications for management, especially within the interior of large, stand-replacing patches of wildfire where distance to a live forest edge exceeds maximum dispersal distances. In addition, our data provides information on regeneration abundance and composition across a range of pre-fire stand ages and forest zones which was previously limited. Simulation modeling using the range of post-fire regeneration responses observed in this study could help further inform how pre-fire stand age affects long-term successional trajectories and stand development pathways (e.g., Hansen et al. 2018).

Finally, continued monitoring could inform how shade intolerant conifers, shade tolerant conifers, and shrubs/hardwoods interact over time. At 3-5 years post-fire, average shrub percent cover and maximum height was relatively low across stands (mean shrub percent cover of 2.7%

and mean maximum shrub height of 0.2 m; Appendix C.3), and average total vegetation percent cover (i.e., combined percent 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; Swanson et al. 2011) which may have contrasting effects on shade intolerant versus tolerant conifer species. For example, shade intolerant species are typically faster-growing and may have a competitive advantage if they are able to keep up or outpace shrub growth. However, shade intolerant species that are unable to outpace growth of shrubs may be outcompeted due to light limitations from the shade cast by shrubs. In contrast, shade tolerant species typically have slower growth rates but may be better equipped to withstand the shade cast by shrubs. These dynamics are difficult to assess at 3-5 years post-fire, but our data provide a baseline that can be compared to in future monitoring.

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. These findings are consistent with post-fire regeneration studies in dry and subalpine forest systems (e.g., Donato et al. 2009; Kemp et al. 2016; Harvey et al. 2016) and are ecologically intuitive as most coniferous species of the western Cascades are obligate seeders and non-serotinous, meaning they rely 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 450 meters (Figure 1.2). This may be explained by surviving individual trees, the retention of an in-situ seed source (see discussion in 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).

One key implication of our findings is that the interior of large, stand-replacing patches of wildfire where conifers are slower to establish could be areas to consider planting or prioritizing management of complex early-seral habitat. Complex early seral is the ‘pre-forest’ stage of forest development following a stand-replacing disturbance and before forest 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., DellaSala et al. 2014, Swanson et al. 2011, Swanson et al. 2014). In the western Cascades, complex early seral conditions are scarcer and in greater deficit than late-seral conditions (Donato et al. 2020) due to a history of logging followed by planting, which aims to accelerate conditions towards canopy closure for maximum timber yield. Given that total initial seedling densities appear to be naturally regenerating above forest practice minimum densities in 82% of our stands (Appendix C.2), areas that are slower to regenerate like far distances to live seed source could be prime candidate areas to manage for complex early seral conditions.

Larger wildfire events that burn under more extreme weather events likely result in larger patches of stand-replacing wildfire and further distances to live seed source in the interior of those patches (e.g., Reilly et al. 2020). The wildfires we sampled were relatively small compared to what is considered to be the upper range of wildfire sizes in western Cascadia (Donato et al. 2020; Reilly et al. 2020). For example, the Yacolt fire burned ~180,000 ha of forest in 1902 (Reilly et al. 2020) and more recently, the 2020 wildfire complexes in western Oregon burned ~146,000 ha (Riverside, Beachie Creek, and Lionshead Fires). In our study, most stands were within 450 meters from 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 meters of a live seed source; Appendix D.1). Future research studying post-fire regeneration response at further distances to a live seed source is underway (https://www.fs.usda.gov/pnw/groups/west-side-fire-and-climate-adaptation-research-initiative) 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 increased in cooler and wetter conditions across scales

Higher establishment rates within the cold forest 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 conspecifics (e.g., Bell et al. 2014), especially following stand-replacing disturbance (e.g., Dobrowski et al. 2015). Regeneration rates did not differ substantially between cold and warm forest zones, though establishment rates were 174% greater in the cold forest zone, suggesting that cold forests had more favorable conditions for seedling survival and growth. Cold forests occur at higher elevations and are characterized by cooler temperatures, increased precipitation, and persistent winter snow cover, relative to the warm forest zone (Franklin and Dyrness 1973) which may mitigate seedling drought-stress. Establishment rates also increased with average 3-year post-fire SPEI, suggesting increased seedling survival when post-fire climatic years were wetter on average. It is important to note that across stands, SPEI values ranged from -1.07 to 0.19 (Table 1.2). SPEI values between -1 and 1 are within normal, while values below -1 indicate drought. Our results suggest that stands that had values closer to 0 had higher establishment rates than those verging on a mild drought (i.e., values closer to -1).

Finally, bryophyte percent cover appeared to provide microsite conditions suitable for seedling germination and establishment potentially through reduced soil water loss and erosion. Bryophytes associated with disturbance, like 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; Silva et al. 2019; Grover et al. 2020), increasing water infiltration (Grover et al. 2020), aiding in recovery of soil microbial communities (Garcia-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. For example, regeneration and establishment rates were strongly associated with higher bryophyte cover in the Goodell Creek burn (n= 8 of our sample plots), which is characterized by shallow depth to bedrock and poorly developed soils (Franklin and Dyrness 1973). In many of our stands, most soil had been completely consumed and ground cover was mostly made up of cobbles and boulders. In areas where mineral soil is not readily available, bryophytes colonizing rocks may provide an important germination substrate.

The relationship between bryophyte percent cover and increased establishment rates could be partially affected by our sampling design, or may be correlative as opposed to causal. We standardized establishment rates across fires by dividing seedling densities by time since fire, following established protocols (e.g., Harvey et al. 2016). Doing so assumes a constant establishment rate across years, whereas post-fire establishment is dynamic from year to year. While we don’t believe this approach is consequential to the interpretations of our findings, it is important to keep in mind when interpreting results. Goodell Creek, for example, was sampled 5 years post-fire and had the strongest relationship between establishment rates and bryophyte percent cover, which could reflect an actual relationship or could be an artifact of there being more time for seedlings in that fire to grow and exceed 10 cm height. Additionally, we did not incorporate any predictor variables related to below ground dynamics (e.g., soil texture, soil burn severity, mycorrhizal relationships) in our models which are likely an important factor influencing seedling establishment following fire, especially with respect to bryophyte cover (i.e., interactions between below ground dynamics and bryophytes may influence microsite conditions that affect seedling establishment). In sum, future research is needed to further investigate the relationship between bryophyte percent cover and increased regeneration and establishment of conifer seedlings in this and other regions.

Our findings can help inform predictions about how and where post-fire recovery 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 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 per ha) by 3-5 years post-fire in 82.1% and 64.1% of stands, respectively (Appendix C.2). This suggests that climate warming and drying has yet to substantially limit post-fire tree regeneration in western Cascadia, as has been documented in some dry, water-limited forests where uncharacteristically severe fire and a drier post-fire environment has led to regeneration failure near lower treelines (Stevens-Rumman et al. 2017). 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. However, continued monitoring and research is needed to better understand at what point climate warming and drying may ultimately affect post-fire tree regeneration in a fire regime adapted to large, stand replacing wildfires, which is currently uncertain (Halofsky et al. 2020).

While these findings provide initial insights into what factors influence seedling survival in the immediate 3 to 5-year post-fire window, post-fire conifer establishment dynamics commonly continue over a period of 40 to 100+ years in the western Cascades based on retrospective dendrochronological studies and can exhibit multiple stand development pathways (e.g., Winter et al. 2002; Fruend et al. 2014; Tepley et al. 2013). Given establishment dynamics play out over longer time scales, continued monitoring is needed to better understand the nuances of establishment drivers following fire and how climate change may affect recovery across different stand development pathways. Our findings suggest stand-replacing patches in the western Cascades are currently recovering in ways similar to as they have in the past. In essence, there is evidence to suggest that the ingredients necessary for forest recovery (i.e., abundant and diverse regeneration) are present, putting stand-replacing patches on a trajectory towards forest resilience. This contrasts with findings in other ecoregions and fire regime groups, 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; Stevens-Rumann et al. 2018; Stevens-Rumann and Morgan 2019). Despite initial evidence of a trajectory towards forest resilience, continued monitoring is needed and these data can provide a baseline that future assessments can be compared to as climate warming and drying continues.

Conclusion

Effects of climate warming and drying on forest resilience to fire are poorly understood in infrequent, stand-replacing fire regimes where information about the disturbance regime and recovery processes are limited (Halofsky et al. 2020). Our findings provide critical insights into post-fire regeneration dynamics in western Cascadia and have important implications for forest management. In sum, we found that forest resilience to severe wildfire in western Cascadia (1) increased with pre-fire stand age, (2) decreased with further distances to a live seed source, and (3) was bolstered by cooler and wetter macro- and micro-site conditions. Our findings highlight the importance of structural complexity in late seral forests, and their importance for supporting forest resilience to severe fire.

Acknowledgements

This research is part of a broad, collaborative effort across agencies and partners to better understand the drivers, characteristics, and indicators of post-fire resilience in western Cascadia. Special thanks to the Climate Adaptation and Science Center and PNW West Side Fire Initiative for funding this research. Thanks to field crew technicians from 2019 (S. Burrington, H. Jayasekera, N. Lau, M. McNorvell, H. Wilson), 2020 (B. Hagedorn, M. Mahmoud, M. McNorvell, S. Patton, M. Stone, M. Todd, S. Vieira), 2021 (A. Brown, E. Burres, F. Dezza-Parada, D. Graham, S. Kruzka, A. MacKinnon, M. Shetreat-Klein, C. Zinke), and 2022 (E. Aosved, M. Elbrecht, N. Katz, C. Rolfson, L. Taylor-Manning) whose hard work made this research possible.

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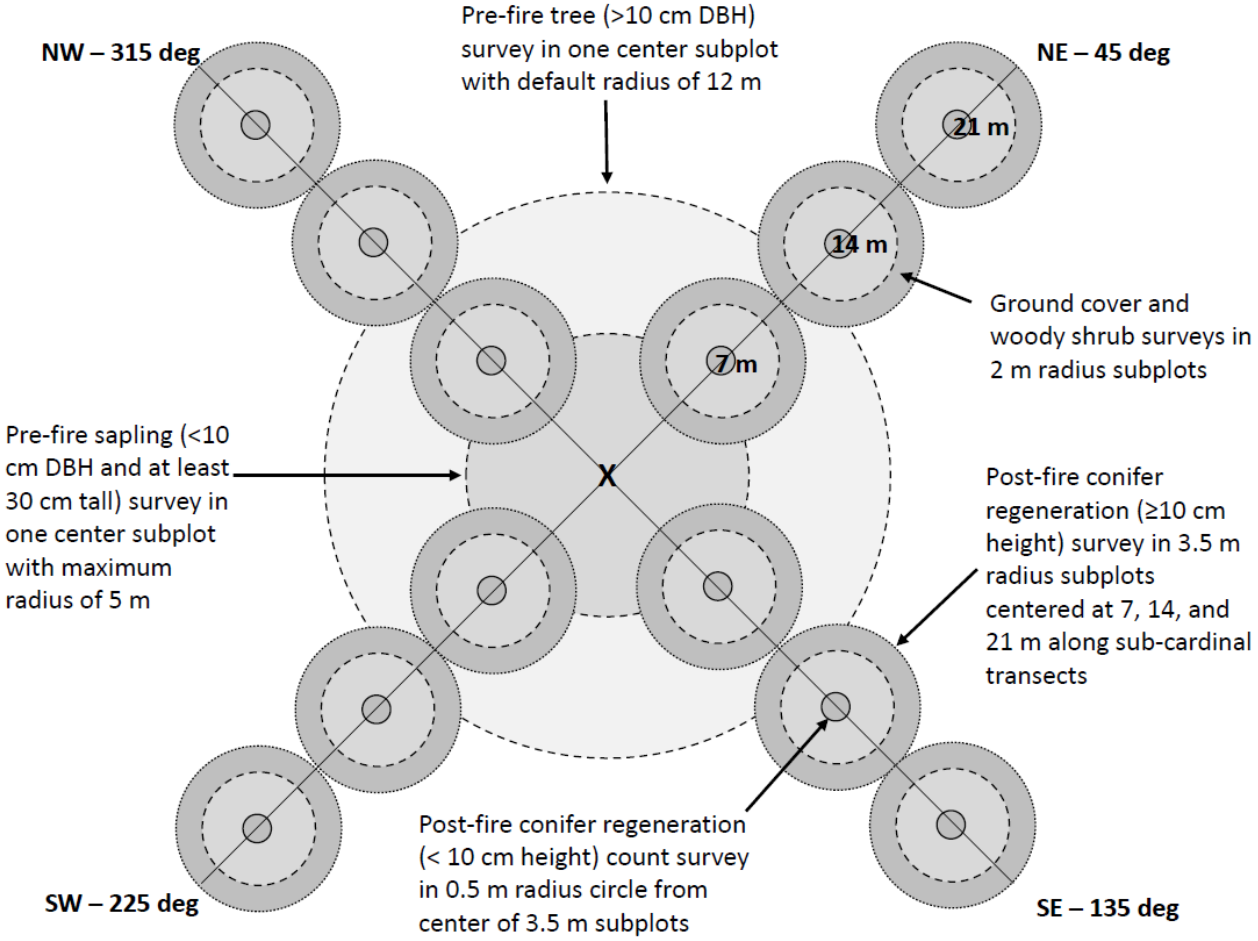
Appendix A: Plot Establishment



Appendix A.1 Plot layout design for collecting post-fire vegetation and conifer response.

Appendix A.2 The key used to determine forest zone and type.

Key out forest zone based on species composition at the 1-ha scale. ***Note: If you are sampling at Norse Peak, replace 10% with 20% for questions 2 through 5.***

- Is there >10% Douglas-fir in the shade tolerant component?
    - If yes, do not sample
    - If no, go to below
- Is there >10% subalpine fir in the shade tolerant component?
    - If yes, do not sample
    - If no, go to below
- Is there >10% mountain hemlock in the shade tolerant component?
    - If yes, sample – its COLD (*Tsuga mertensiana)*
    - If no, go to below
- Is there >10% Pacific silver fir in the shade tolerant component?
    - If yes, sample – its COLD (*Abies amabilis)*
    - If no, go to below
- Is there >10% western hemlock in the shade tolerant component?
    - If yes, sample – its WARM (*Tsuga heterophylla*)
    - If no, re-check above or abort the plot.

Appendix A.3 Summary of how Van Pelt (2007) stand developmental stages were lumped into young, mid, and late seral.

Van Pelt Stage	Pre-fire Stand Age
Cohort Establishment	*Not sampled*
Canopy Closure	Young
Biomass Accumulation /Stem Exclusion	Mid seral
Maturation I	Mid seral
Maturation II	Late seral
Vertical Diversification	Late seral
Horizontal Diversification	Late seral

Appendix A.4 Tall woody shrub species that received individual measurements of maximum height and tallies of stem basal diameters within the 2-meter radius circular subplots.

Scientific name	**Common name**
Acer spp.	Maple species
Alnus spp.	Alder species
Amelanchier alnifolia	Serviceberry (Saskatoon)
Arbutus menziesii	Pacific madrone
Arctostaphylos spp. (except *uva-ursi* or *nevadensis*)	Manzanita species
Ceanothus sanguineus	Redstem ceanothus
Ceanothus velutinus	Snowbrush
Chrysolepis chrysophylla	Chinquapin
Cladothamnus pyroliflorus	Copperbush
Cornus nutallii	Pacific dogwood
Cornus stolonifera	Red-osier dogwood
Corylus cornuta	Beaked hazelnut
Crataegus douglasii	Black hawthorn
Cytisus scoparius	Scotch broom
Fraxinus spp.	Ash species
Holodiscus discolor	Oceanspray
Lonicera spp.	Twinflower (honeysuckle)
Malus fusca	Pacific crabapple
Menziesia ferruginea	False huckleberry
Oemleria cerasiformis	Indian plum
Philadelphus lewisii	Mock orange
Physocarpus capitatus	Pacific ninebark
Populus spp.	Cottonwood/aspen
Prunus spp.	Cherry species
Quercus spp.	Oak species
Rhamnus purshiana	Cascara
Rhododendron spp.	Rhododendron, azalea species
Ribes spp.	Currant/gooseberry species
Rosa spp.	Rose species
Salix spp.	Willow species
Sambucus spp.	Elderberry species
Sorbus spp.	Mountain ash species
Spiraea douglasii	Steeplebush
Symphoricarpos albus	Common snowberry
Vaccinium spp.	Huckleberry species
Viburnum spp.	Cranberry species

Appendix B: Model Summary

Appendix B.1 Dredge model outputs for the full model with regeneration rate (total seedlings ha^{-1} yr^{-1}) as the response variable. Models with delta AICc values less than 2 are highlighted in gray.

Intercept	SPEI	Bryophyte % Cover	Forest Zone	HLI	Seed source Distance	Seral Stage	TWI	df	logLik	AICc	delta	weight
7.07	-	0.81	-	-	-1.04	+	-	6	-349.52	713.67	**0.00**	0.18
7.16	-0.41	0.71	-	-	-1.00	+	-	7	-348.40	714.42	**0.75**	0.13
6.92	-	0.83	-	-	-1.13	+	0.29	7	-348.99	715.60	**1.92**	0.07
7.05	-	0.77	-	-	-	+	-	5	-351.92	715.67	**1.99**	0.07
7.14	-	0.94	-	0.43	-	+	-	6	-350.80	716.22	2.54	0.05
7.10	-	0.92	-	0.20	-0.91	+	-	7	-349.32	716.24	2.57	0.05
7.11	-0.39	0.68	-	-	-	+	-	6	-350.88	716.38	2.70	0.05
7.13	-	0.77	+	-	-1.05	+	-	7	-349.44	716.50	2.83	0.04
7.06	-0.37	0.73	-	-	-1.07	+	0.21	8	-348.15	717.09	3.42	0.03
7.16	-0.38	0.76	-	0.09	-0.96	+	-	8	-348.36	717.52	3.85	0.03
7.17	-0.41	0.71	+	-	-1.00	+	-	8	-348.40	717.61	3.94	0.03
7.05	-	0.75	+	-	-1.18	+	0.36	8	-348.64	718.09	4.41	0.02
6.96	-	0.78	-	-	-	+	0.16	6	-351.74	718.11	4.44	0.02
7.15	-0.28	0.83	-	0.33	-	+	-	7	-350.27	718.15	4.48	0.02
7.11	-	0.73	+	-	-	+	-	6	-351.87	718.36	4.69	0.02
6.95	-	0.90	-	0.13	-1.04	+	0.26	8	-348.91	718.63	4.95	0.02
7.21	-	0.90	+	0.43	-	+	-	7	-350.72	719.05	5.38	0.01
7.09	-	0.94	-	0.41	-	+	0.09	7	-350.74	719.09	5.42	0.01
7.16	-	0.87	+	0.20	-0.92	+	-	8	-349.22	719.24	5.57	0.01
7.07	-0.38	0.68	-	-	-	+	0.09	7	-350.83	719.27	5.59	0.01
7.11	-0.40	0.68	+	-	-	+	-	7	-350.88	719.36	5.69	0.01
8.43	-	1.44	-	0.82	-	-	-	4	-355.56	720.30	6.62	0.01
7.11	-0.33	0.70	+	-	-1.09	+	0.24	9	-348.09	720.39	6.71	0.01
7.06	-0.36	0.75	-	0.04	-1.04	+	0.20	9	-348.14	720.48	6.81	0.01

Appendix B.2 Dredge model outputs for the full model with establishment rate (seedlings ha^{-1} yr^{-1} above 10 cm) as the response variable. Models with delta AICc values less than 2 are highlighted in gray.

Intercept	SPEI	Bryophyte % Cover	Forest Zone	HLI	Seed source Distance	Seral Stage	TWI	Vegetation % Cover	df	logLik	AICc	delta	weight
4.95	0.71	1.26	+	-	-0.77	+	-	-	8	-258.10	537.01	0.00	0.24
5.34	0.73	1.46	+	-	-0.81	-	-	-	6	-261.27	537.17	0.16	0.22
5.33	0.76	1.52	+	0.14	-0.81	-	-	-	7	-260.82	539.26	2.25	0.08
5.32	0.74	1.49	+	-	-0.77	-	-	-0.15	7	-260.86	539.33	2.32	0.08
4.95	0.68	1.25	+	-	-0.71	+	-0.11	-	9	-257.88	539.97	2.96	0.05
5.34	0.73	1.45	+	-	-0.80	-	-0.02	-	7	-261.27	540.15	3.14	0.05
4.96	0.70	1.25	+	-	-0.78	+	-	0.05	9	-258.06	540.34	3.33	0.05
4.95	0.71	1.25	+	-0.02	-0.77	+	-	-	9	-258.09	540.40	3.39	0.04
5.31	0.77	1.55	+	0.14	-0.77	-	-	-0.15	8	-260.39	541.58	4.57	0.02
5.16	0.84	0.99	-	-	-0.89	+	-	-	7	-262.24	542.10	5.09	0.02
5.32	0.75	1.52	+	0.15	-0.78	-	-0.05	-	8	-260.77	542.34	5.33	0.02
5.31	0.74	1.49	+	-	-0.76	-	-0.02	-0.15	8	-260.85	542.50	5.49	0.02
4.80	0.65	1.31	+	-	-	+	-	-	7	-262.71	543.03	6.02	0.01
5.82	0.77	1.18	-	-	-0.92	-	-	-	5	-265.65	543.12	6.11	0.01
4.96	0.66	1.22	+	-	-0.72	+	-0.13	0.08	10	-257.77	543.41	6.40	0.01
4.95	0.68	1.25	+	0.00	-0.71	+	-0.11	-	10	-257.88	543.62	6.61	0.01
4.95	0.69	1.21	+	-0.05	-0.79	+	-	0.07	10	-258.03	543.91	6.90	0.01

Appendix B.3 Coefficient estimates, standard error (SE), 95% confidence intervals, and p-values for parameters in the best fit model for regeneration rates (left) and establishment rates (right).

	Regeneration Rates (total seedlings ha^{-1} yr^{-1})				**Establishment Rates (seedlings ha^{-1} yr^{-1} ≥ 10cm)**			
Parameter	**Estimate**	**SE**	**95% Confidence Interval**	**P-Value**	**Estimate**	**SE**	**95% Confidence Interval**	**P-Value**
Intercept	7.16	0.51	[6.44, 8.10]	2.1e-15	4.95	0.28	[4.43, 5.54]	<2e-16
Bryophyte % cover	0.71	0.31	[0.26, 1.28]	0.027	1.26	0.16	[0.91, 1.64]	7.78e-09
Average 3-yr post-fire SPEI	-0.41	0.30	[-0.87, 0.13]	0.18	0.71	0.14	[0.42, 1.04]	3.79e-05
Distance to seed source	-1.0	0.27	[-1.54, -0.16]	0.00080	-0.77	0.14	[-1.08, -0.34]	5.26e-06
Forest zone (cold)	-	-	-	-	1.01	0.33	[0.36, 1.67]	0.0045
Pre-fire stand age (young)	-1.48	1.13	[-3.15, 0.69]	0.20	-0.74	0.59	[-1.88, 0.53]	0.22
Pre-fire stand age (late seral)	1.58	0.63	[0.51, 2.53]	0.017	0.61	0.31	[-0.12, 1.31]	0.06

Appendix C: Management Stocking Density Standards and Vegetation Response

Appendix C.1 Summary description of area occupancy (i.e., stocking) by species which describes the percentage of area within a plot that was occupied at a minimum density of 260 seedlings ha^{-1}. Area occupancy for individual species was calculated only among plots where those species were present (e.g., in plots where western hemlock was present, it occupied 40.0% of stand area at a minimum density of 260 seedlings per ha^{-1} on average).

	Established Seedlings (i.e., seedlings ≥ 10 cm)		
	Min – Max	Median	Mean
All combined	8.3 – 100	83.3	72.2
Douglas-fir	8.3 – 100	75.0	64.1
Western hemlock	8.3 – 100	33.3	40.0
Noble fir	8.3 – 100	45.8	48.9
Pacific silver fir	8.3 – 91.7	16.7	25.7
Western red cedar	8.3 – 100	66.7	60.4
Lodgepole pine	8.3 – 100	33.3	45.2
Western white pine	8.3 – 8.3	8.3	8.3
Subalpine fir	33.3 – 33.3	33.3	33.3
Engelmann spruce	-	-	-

Appendix C.2 Proportion of plots (out of 39 plots) that exceed forest practice minimum density thresholds of 470 seedlings per ha (190 seedlings per acre) and 865 seedlings per ha (350 seedlings per acre).

Threshold	**Total seedlings (seedlings of all heights)**	**Established Seedlings (seedlings ≥ 10 cm)**
470 trees per ha	82.05 %	64.10 %
865 trees per ha	79.49 %	53.85 %

Appendix C.3 Summary description of average plot-level percent cover (%) of bryophytes, graminoids, herbs, and shrubs. Average plot-level maximum height (m) summaries for tall woody shrubs are also included.

	Plot-Level Percent Cover (%)			**Plot-Level Maximum Height (m)**		
	Min-Max	**Median**	**Mean**	**Min-Max**	**Median**	**Mean**
Bryophytes	0.1 – 67.8	10.9	17.8	-	-	-
Graminoids	0 – 42.9	0.1	1.3	-	-	-
Herbs	0.1 – 29.6	1.7	2.7	-	-	-
Shrubs	0.1 – 19.2	0.6	2.7	0 – 1.3	0.1	0.2

Appendix C: Distance to Nearest Live Seed Source

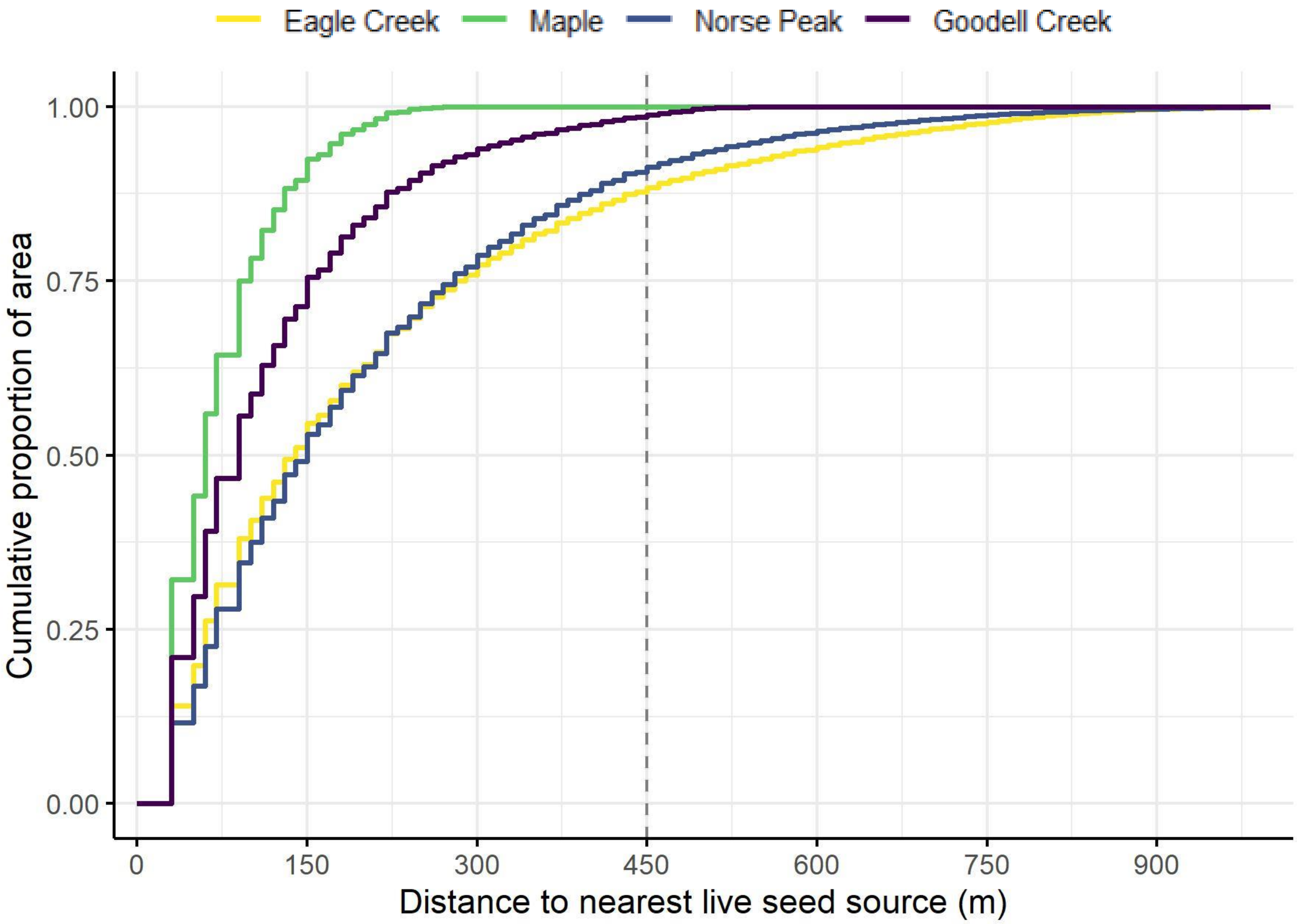


Figure C.1 Empirical cumulative density function curves of distance to the nearest live seed source for each sampled wildfire. Live seed source is defined as forested area that burned at less than stand-replacing burn severity based on RdNBR thresholds (forested versus non-forested area defined by LANDFIRE). Data source*: M. Buonanduci*, unpublished data.