Final Report

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Patterns and drivers of post-fire tree regeneration across gradients of climate and burn severity in Eastern Washington

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Highlights

A survey of the patterns and drivers of post-fire tree regeneration was conducted 4-6 years post-fire across 325 plots located in 30 wildfires that occurred across eastern Washington between 2012 and 2017. Results indicate:

- Across forest zones, the 3-year period following recent fires had greater climatic moisture deficit (CMD) than the preceding 30-year average for every location. That is, all eastside sites are experiencing more droughty conditions than before.
- Post-fire tree density was highly variable (ranging from 0 to 161,200 trees per acre), was commonly abundant, and generally increased with closer proximity to seed sources. Densities generally were lowest in water-limited forest zones (e.g. dry and moist mixed conifer) and highest in energy-limited forest zones (e.g. cold and wet types).
- Distance to seed source was less important in water-limited forest zones than in energy-limited forest zones, where topo-climate constraints on seedling density appeared to be most important. Post-fire understory vegetation cover was associated with decreased post-fire seedling density in low-severity fire across forest zones but had varying relationships in moderate- or high-severity fire.
- Most burned sites may not need active reforestation to establish and maintain forest cover. Management efforts post-fire can target a) areas where sparse post-fire tree regeneration may need to be augmented by planting in focused portions of burned landscapes, and b) areas where super-abundant regeneration may call for pre-commercial thinning, prescribed fire, or other treatments to foster development of resilient forest structure.

Introduction

Post-fire tree regeneration is a critical mechanism of forest resilience and is potentially at risk in forests across the western US. While post-fire regeneration has received heightened attention in many forest regions, scant data exist to understand patterns of natural post-fire tree regeneration across environmental gradients in eastern Washington. With increases in fire activity occurring during a period of continued warming and drying, which is projected to continue into the future, understanding post-fire tree regeneration patterns in such contexts is needed to inform adaptive management strategies.

Objectives

In this study, we characterize post-fire tree regeneration across climate and topographic settings in eastern Washington and test how the influence of drivers of post-fire tree seedling density varies across these gradients. Measured 4-6 years post-fire, we collected data from 325 field plots distributed among 30 fires occurring between 2012 and 2017 that were stratified by forest zone (from water-limited dry and moist forests to energy-limited cold and wet forests), fire severity, and topographic setting. We asked three related questions about post-fire tree regeneration during a period of increasing warming and associated fire activity: 1) How do post-fire growing conditions in burned forests differ from climate norms in the three decades preceding fire in each location, and how do these differences vary among forest zones? 2) How does post-fire tree density and species composition vary across gradients of forest zone and fire severity, and where has post-fire tree regeneration yet to occur 4-6 years after fire? 3) How does the influence of drivers of post-fire seedling density (e.g., seed availability, topoclimate context, post-fire understory vegetation) vary across a gradient of water-limited to energy-limited forest zones?

Methods

Study Area and Design:

Our study area encompasses ecoregions east of the cascade crest in Washington, USA, including the North and South Cascades, the Columbia basin, and the Columbia Rocky Mountains and Okanagan Highlands in the northeast (Figure 1). This region is characterized by mixed-conifer forests that span a wide climate and elevation gradient (1500-6100 feet) with wet and cold subalpine forests at high elevations, moist mixed-conifer forests at mid elevations, and dry mixed-conifer forests at lower elevations (Agee 1996). In general, fire regimes vary intra-regionally by forest zone. Dry and moist forest zones have relatively frequent fire return intervals (~15-75 years) with predominantly low- to moderate-severity fire historically (Agee 1996). These forest zones are dominated by thick-barked fire-resistant conifer species (*Pinus ponderosa* and *Psuedotsuga menziesii)* that often survive surface fires. Cold subalpine and wet forests generally have infrequent fire return intervals (~75-300 years), with greater proportions of moderate- to high-severity fire (Agee 1996). These forest zones are dominated by thin-barked fire-sensitive conifer trees that are generally adapted to reproduce prolifically after high severity, stand replacing fire (*Pinus contorta, Tsuga heterophylla, Thuja plicata, Abies spp.*).

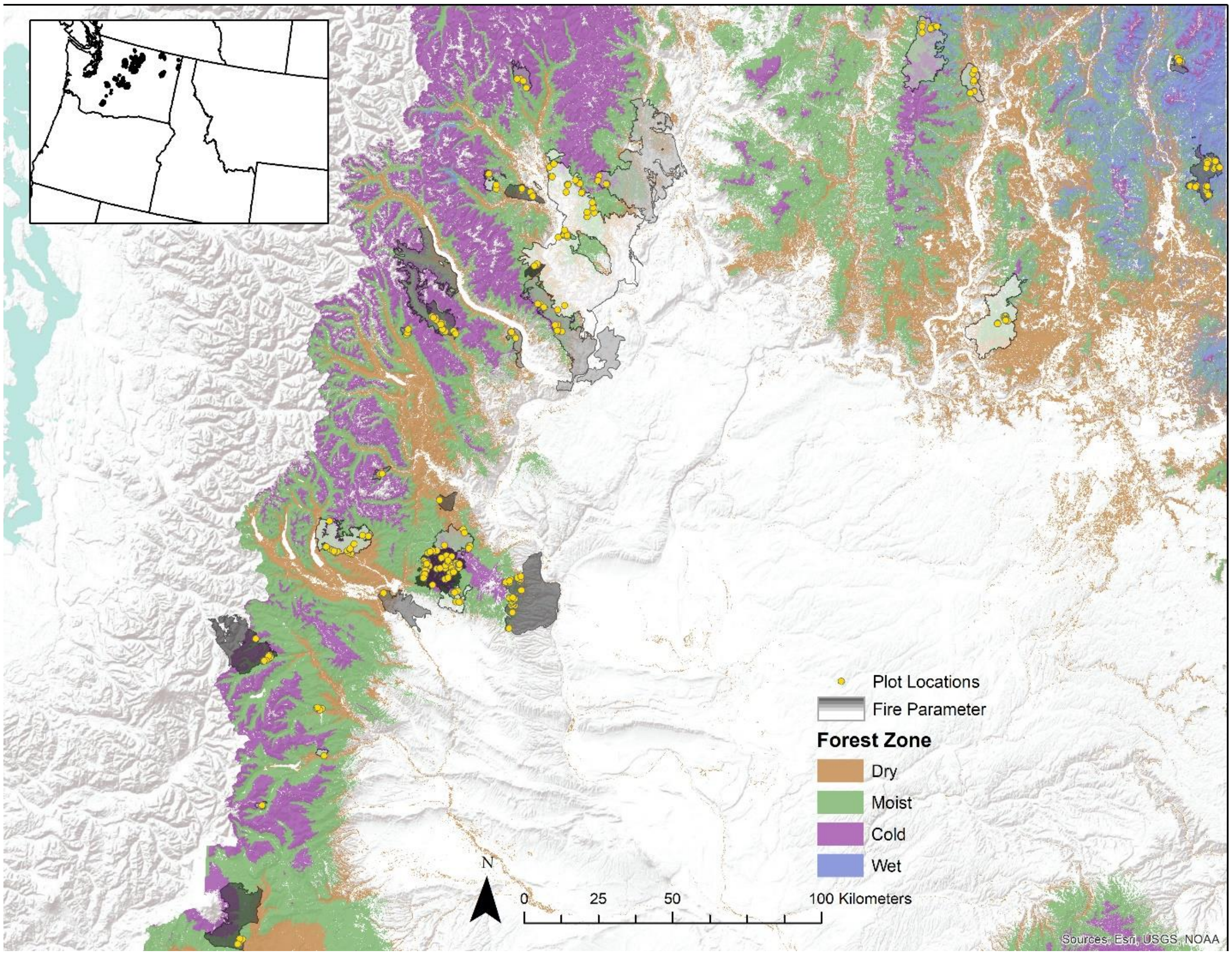

Figure 1: Locations of 325 plots within the 30 sample fires that burned between 2012-2017 across Eastern Washington (USA). Sites spanned gradients of climate, elevation, aspect, and fire severity. Plots were located across forest zone, which is a proxy for climate zone.

Sampling occurred within 30 large (>1000-acre) wildfires that burned between 2012 and 2017 on public forest lands east of the Cascade Crest in Washington, USA. We excluded areas that had less than 10% pre-fire forest cover or additional wildfires or management (e.g. post-fire logging, replanting, or re-burns) since the original fire event. Candidate plot locations were distributed randomly across key strata: three levels of burn severity and four ordinal forest zones arranged along a gradient from warm/dry to cool/wet (12 strata combinations). Maps of remotely-sensed burn severity (based on the difference normalized burn metric) were used as an initial stratification tool, but burn severity was assessed at each plot in the field by the percent overstory trees killed by fire as low severity (<30%), moderate severity, or high severity (>70%). Final plot selection was completed on the ground to determine if the above criteria was met. Within each factorial combination of forest zone and burn severity, plots were distributed across two aspect classes (NE or SW) to capture variability in local topographic setting. A total of 325 plots were sampled, with 6-22 plots in each of the 24 elevation/aspect/severity strata measured. Sampling was evenly distributed among fire years and randomly sampled 4-6 years post-fire in the years 2016-2021.

Field data collection:

We collected a suite of vegetation data in the field and examined several climate-related metrics (Table 1, see appendix for more method details).

Table 1: vegetation and climate-related data assessed for analysis.

Biological Attributes	Climate Attributes
Pre-fire stand structure • diameter at breast height (DBH) • tree species • live or dead status	*Drought Stress (climatic moisture deficit (CMD)* • 3-year post-fire plot average • 30-year pre-fire plot average
Distance to nearest patch of live trees	*Heat load index*
Post-fire understory vegetation • Percent cover of herbs, shrubs, and graminoids layer • Shrub height (cm)	*Soil available water capacity* *Latitude and longitude* *Day length*
Seedling density (trees <6 in [15 cm] DBH)	

Statistical Analysis

To characterize trends in post-fire climate conditions and pre-fire normal conditions (Q1), we compared 3-year post-fire plot CMD averages with pre-fire 30-year plot CMD averages for each forest zone. We also examined the average post-fire CMD departures and ranges relative to the 30-year pre-fire mean using z-scores (a measure of deviation). To test how post-fire tree seedling densities varied across gradients of forest zone and fire severity, and to determine where post-fire tree regeneration has yet to occur 4-6 years post-fire (Q2), we calculated the number of adult post-fire trees, number of post-fire seedlings, and adult post-fire trees + post-fire seedlings, with each also standardized to stems per acre.

We examined patterns of post-fire adult trees, seedlings, and both groups together across combinations of forest zone and fire severity. To understand how the influence of drivers of post-fire tree seedling density varied across a gradient of energy-limited to water-limited constraints (Q3) we constructed separate models for each unique combination of forest zone (dry, moist, cold, wet) and fire severity (low, moderate, high). Our candidate predictors of interest included a suite of variables defined by categories that have been found to impact post-fire successional processes (e.g., climate, seed source, topography, and vegetation interactions). Variables included in final model outputs were chosen to maximize model fitness across all model runs. Final predictor variables chosen fit within the categories mentioned above (Table 2).

Table 2: Predictor variables included in models of post-fire seedling density.

Variables of interest	Description
Seed Source	
Pre-fire Basal Area	pre-fire basal area of plot (ft^2 per acre)
Distance to Seed Source	distance to nearest seed source (ft; 2.5 acres of live trees)
Topoclimate	
Heat Load Index	(unitless) from 0 (coolest) to 1 (warmest)
Vegetation interactions	
Shrub Index	percent total shrub cover multiplied by mean shrub height
Graminoid Cover (%)	percent total graminoid cover

Results

Differences in post-fire growing conditions across forest zones (Q1)

Within plots across forest zones, the climate in the first 3 years post-fire was on average characterized by warmer and drier conditions (greater CMD) relative to 30-year pre-fire normal climate conditions (Figure 2). The magnitude of departure from 30-year pre-fire normals was generally greater in energy-limited forest zones (wet and cold forests) than in water-limited forest zones (moist and dry forests). Compared to 30-year pre-fire climate normals within plots for each forest zone, median post-fire CMD was 68% greater in wet forests, 50% greater in cold forests, 35% greater in moist forests, and 40% greater in dry forests (Figure 2). The absolute change in post-fire CMD was greatest in plots in dry and cold forest zones, with an increase of 1.57-in and 1.23-in, respectively. Moist forest CMD increased by 0.93-in and wet forest CMD increased by 0.79-in. Additionally, all plots across each forest zone had positive z-score values for 3-year post-fire plot CMD; i.e., a 3-year post-fire CMD that was greater than 30-year pre-fire averages for all plot locations (Figure 3). Along with an increase in average post-fire CMD, most years immediately following fire within each plot were characterized as warmer and drier than pre-fire normals. Specifically, 86% of individual post-fire years across all plots had a positive annual z-score value, with 64%, 85%, 82%, and 95% positive annual z score values for plots in wet, cold, moist, and dry forest zones (Figure 3), indicating that most post-fire years during the 3-year pulsed recruitment window were warmer and drier than the preceding 30-year period.

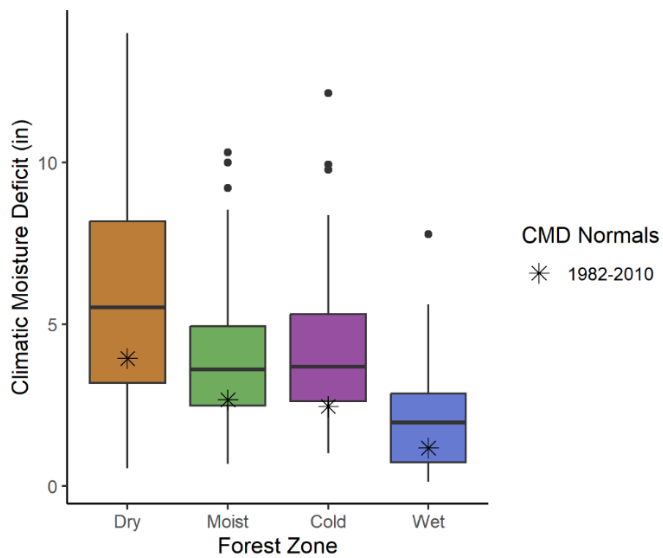

Figure 2: 3-year post-fire water year average of climatic moisture deficit by forest zone of the 325 plots sampled across 30 fires in eastern Washington (USA). In each boxplot, the center line represents the median response; lower and upper box boundaries represent 25th and 75th percentiles, while lower and upper error lines represent 10th and 90th percentiles, with circles falling outside of the percentiles. Asterisks indicate the 30-year pre-fire water year climatic moisture deficit normal from 1982-2010. All forest zones had median post-fire CMD well above the 30-year pre-fire normal, meaning the post-fire climate was warmer and drier than the 30-year pre-fire median value.

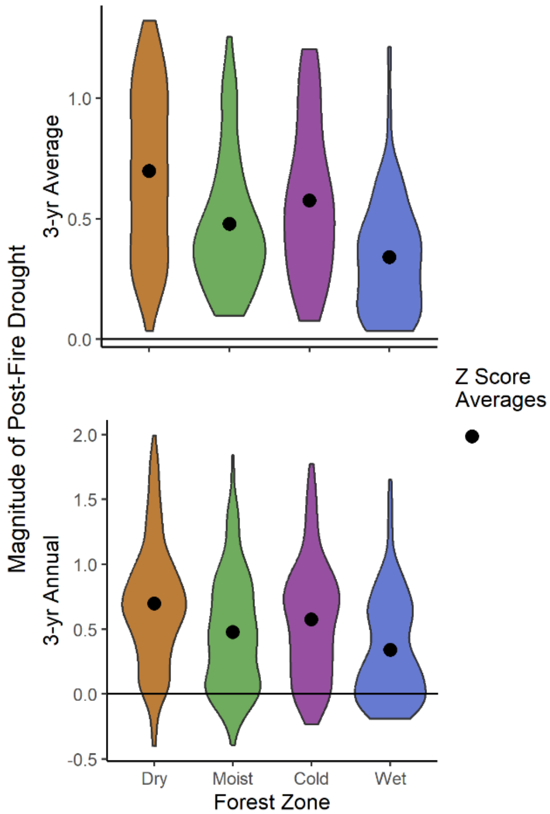

Figure 3: 3-year post-fire Z score averages of water year climatic moisture deficit (top) and the annual post-fire Z score average of water year climatic moisture deficit (bottom) by forest zone of the 325 plots sampled across 30 fires in eastern Washington (USA). The violin plot illustrates the distribution of values in the dataset with the width of the shaded area representing the proportion of the data located there. Points indicate the post-fire Z score average by forest zone.

Table 3: Summary of the mean, median, and range of post-fire live trees (adult trees) per acre, seedlings per acre, and live trees and seedlings per acre across forest zones and fire severity.

Trees per Acre

Fire Severity	Low Severity				Moderate Severity				High Severity			
Forest Zone	Mean	Median	Range	5th & 95th Percentile	Mean	Median	Range	5th & 95th Percentile	Mean	Median	Range	5th & 95th Percentile
Dry	373	152	0-1,619	0-1,261	211	66	0-1,1619	0-1,045	7	0	0-67	0-2,239
Moist	621	202	34-5,396	46-2,860	290	128	0-1,754	10-1,099	53	0	0-540	0-202
Cold	1,110	438	0-4,991	23-4,047	579	304	0-2,698	0-2,239	25	0	0-270	0-166
Wet	767	405	57-3,777	70-2,387	456	337	0-1,754	0-1,045	96	0	0-540	0-425

Seedlings per Acre

	Low Severity				Moderate Severity				High Severity			
Forest Zone	Mean	Median	Range	5th & 95th Percentile	Mean	Median	Range	5th & 95th Percentile	Mean	Median	Range	5th & 95th Percentile
Dry	3,754	937	0-35,073	0-20,308	2,508	485	0-38,580	0-9,572	495	23	0-9,847	0-1,639
Moist	4,210	742	0-40,199	5-16,410	4,127	860	0-36,826	0-15,600	3,657	31	0-55,442	0-10,876
Cold	3,969	674	0-23,876	57-16,322	7,960	1,652	0-86,198	2-28,005	6,097	1,821	0-39,255	12-25,441
Wet	16,488	4,138	135-157,423	280-61,040	16,488	6,340	996-130,444	1,505-53,284	28,972	14,232	29-90,650	83-84,229

Trees + Seedlings per Acre

	Low Severity				Moderate Severity				High Severity			
Forest Zone	Mean	Median	Range	5th & 95th Percentile	Mean	Median	Range	5th & 95th Percentile	Mean	Median	Range	5th & 95th Percentile
Dry	4,182	1,265	6-36,692	17-21,624	2,731	573	0-40,199	11-10,420	504	34	0-9,847	0-1,642
Moist	7,235	1,585	69-69,471	111-23,688	6,080	1,838	11-39,389	39-21,981	3,917	197	0-56,251	0-10,879
Cold	7,697	4,317	206-30,082	361-26,439	9,352	1,922	6-88,896	139-29,124	6,339	2,347	0-39,255	12-26,075
Wet	19,312	6,664	911-161,200	1,233-63,131	19,489	10,657	1,110-131,253	1,855-53,823	29,106	14,231	29-90,919	83-84,383

Post-fire tree density and species composition across gradients of forest zone and burn severity (Q2)

Post-fire live tree (surviving adult trees) and seedling density was highly variable overall, with density ranging from 0-161,200 trees per acre across all plots. Post-fire live tree and seedling density consistently decreased across the energy-limited to water-limited gradients of eastern Washington (i.e., from wet>cold>moist>dry forest zones; Table 3). The effects of fire severity on post-fire live tree and seedling density were variable across the forest zone gradient (Figure 4). Post-fire live tree and seedling density declined with greater fire severity in dry forests, whereas post-fire live tree and seedling density increased with greater fire severity in wet and cold forests; in moist forests, density was greatest in moderate severity fire and lower in low- and high-severity fire. Forest zone and fire severity interacted such that the difference between live tree and seedling densities among forest zones generally amplified with increasing fire severity. In low severity fire, median live tree and seedling density was 5.3x greater in wet forests than in dry forests. This difference increased in moderate-severity fire where median live tree and seedling density was 18.6x greater in wet forests than in dry forests and increased again in high severity-fire where median live tree and seedling density was 418.6x greater in wet forests than in dry forests (Figure 4, Table 3).

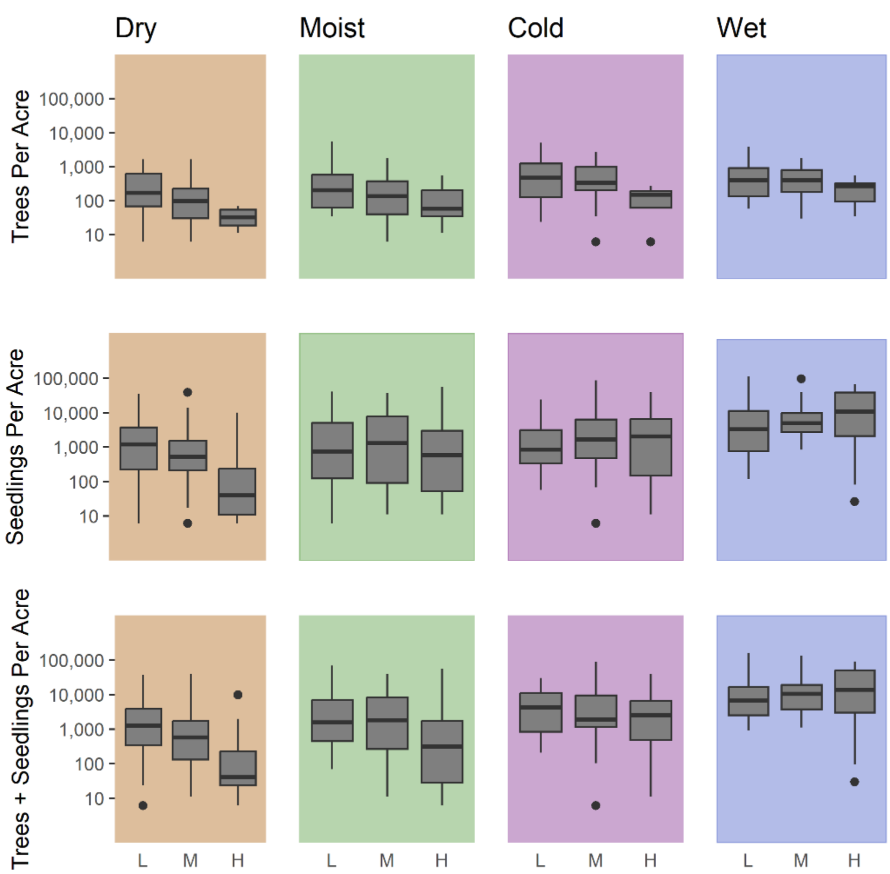

Figure 4: Post-fire trees (surviving adult trees; top), seedling densities (middle), and trees + seedlings (bottom) by forest zone and fire severity in eastern Washington (USA). Y axis log transformed for visualization. In each boxplot, the center line represents the median response within a forest zone and fire severity; lower and upper box boundaries represent 25th and 75th percentiles, while lower and upper error lines represent 10th and 90th percentiles, with circles falling outside of the percentiles.

Total post-fire live tree + seedling density was lower than pre-fire adult tree density in 27% of plots overall. The percentage of plots with lower post-fire live tree density than pre-fire adult tree density increased consistently from the energy-limited forest zones to water-limited forest zones (dry>moist>cold>wet forest zones) and with greater fire severity (high>moderate>low fire severity). Dry forests that burned at high severity had the lowest percentage of plots where post-fire live tree density met or exceeded pre-fire live tree density (19% of plots; Figure 5). This percentage increased to 36% for moist forest plots that burned at high severity and 70% for cold forest plots that burned at high severity. The wet forest zone had the greatest percentage of plots where post-fire live tree density met or exceeded pre-fire live tree density, with 96% (low-severity fire), 100% (moderate-severity fire), and 83% (high-severity fire).

Of the plots with post-fire live tree and seedling density less than pre-fire plot adult tree density (n=88), 84% (n=74) were in proximity (<492 ft [150 m]) to seed sources nearby provided by post-fire live trees; however 43% (3/7) and 33% (1/3) of cold and wet forest zones with post-fire live tree and seedling density less than pre-fire plot adult tree density had distance to seed source exceeding 1,000 ft. Though median pre-fire forest zone densities were 155, 573, 1,147, and 1,952 TPA for dry, moist, cold, and wet forest zones, respectively, plots with less than pre-fire adult tree densities had densities ranging from 0-69,471 TPA. Additionally, 53% of plots with less than pre-fire adult tree density had post-fire live overstory trees within the plot (47/88), indicative of available seed source on-site. Pre-fire stand composition in these locations was dominated by *Pinus ponderosa* and *Pseudotsuga menziesii*, with 66% of plots with >50% of pre-fire stem densities being either species.

Across all strata, 3% of plots had no seedlings or live trees present (0 TPA in 10/325 plots). The frequency of plots with 0 TPA increased from the energy limited to water limited forest zones (dry>moist>cold>wet), and with increasing fire severity (Figure 5b). Plots with 0 TPA did not occur in wet forest zones, and only occurred after high severity fire in moist and cold forest zones, where 9% (2/22) and 4% (1/23) of plots had 0 TPA. In the dry forests, plots with 0 TPA increased as fire severity increased, with 0%, 3% (1/31), and 19% (6/31) having 0 TPA in low, moderate, and high severity plots, respectively. Pre-fire density ranged from 0-108 TPA, with median density of 71 TPA. Of the 3% (n=10) of all plots with 0 TPA, three had distances to live seed sources >492 ft (150 m). Pre-fire stand composition in these areas were dominated by either *Pseudotsuga menziesii* and *Pinus ponderosa*, with at least half of the species composition in 9 out of the 10 plots being either species.

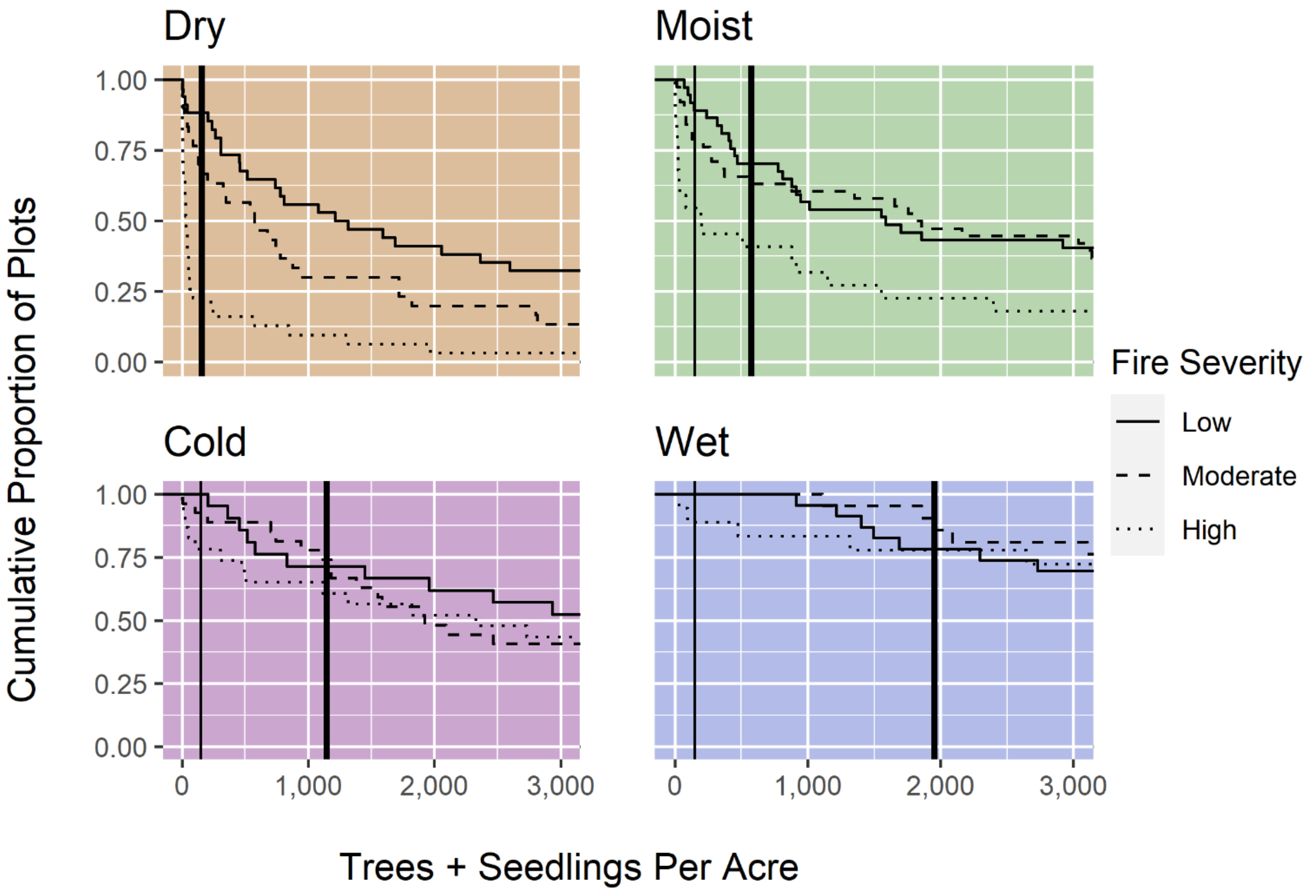

Figure 5: Cumulative distribution of tree (all surviving adult trees and seedlings) densities by fire severity across forest zones. Interested readers can find the proportion of plots exceeding whatever density threshold is most relevant for their purpose. The thin vertical line in each panel represents forest practice minima (150 TPA), while the thick vertical line represents the pre-fire median adult tree density in each forest zone. The portions of curves to the left of the thick vertical median line represent proportion of plots that are above pre-fire median tree densities.

The relative proportion of different tree species changed from pre-to-post fire across all strata, with changes often corresponding to differences in fire-adaptive traits among species (e.g., fire-resisting vs fire-sensitive species; Figure 6). Live tree density increased after fire in all forest zones, except in dry forests that burned at high-severity fire (Figure 6). The relative proportion of fire-resistant species such as *Pseudotsgua menziesii* and *Larix occidentalis* generally increased post-fire across zones, whereas the relative proportion of fire-sensitive species such as *Abies grandis* and *Abies lasiocarpa* generally decreased post-fire—particularly after high severity fire. The relative proportion of fire-resistant *Pinus ponderosa* was lower after fire across forest zones (Figure 6) and was never dominant (by density) across the forest zones it occupied pre- or post-fire. The relative density of *Pinus ponderosa* pre-fire was greatest in dry forests (20-44%) followed by moist forests (3-9%), and relatively rare in cold and wet forests. The relative proportion of *Pinus contorta*, which is adapted to establish prolifically via seed following stand-replacing fire, generally increased (ranging from 1 to 40% increases) with fire severity across all forest zones that it occupied. Fire-sensitive *Tsuga heterophylla* and *Thuja plicata* relative density pre- and post-fire was primarily limited to wet forests and exhibited varying responses to fire. In wet forests, the proportions of *Tsuga heterophylla* increased only in high severity fire (11%) and decreased in low- and moderate-severity fire (1-4%); whereas *Thuja plicata* increased in low- and moderate-severity fire (10% and 6% respectively) and decreased in high severity fire (19%).

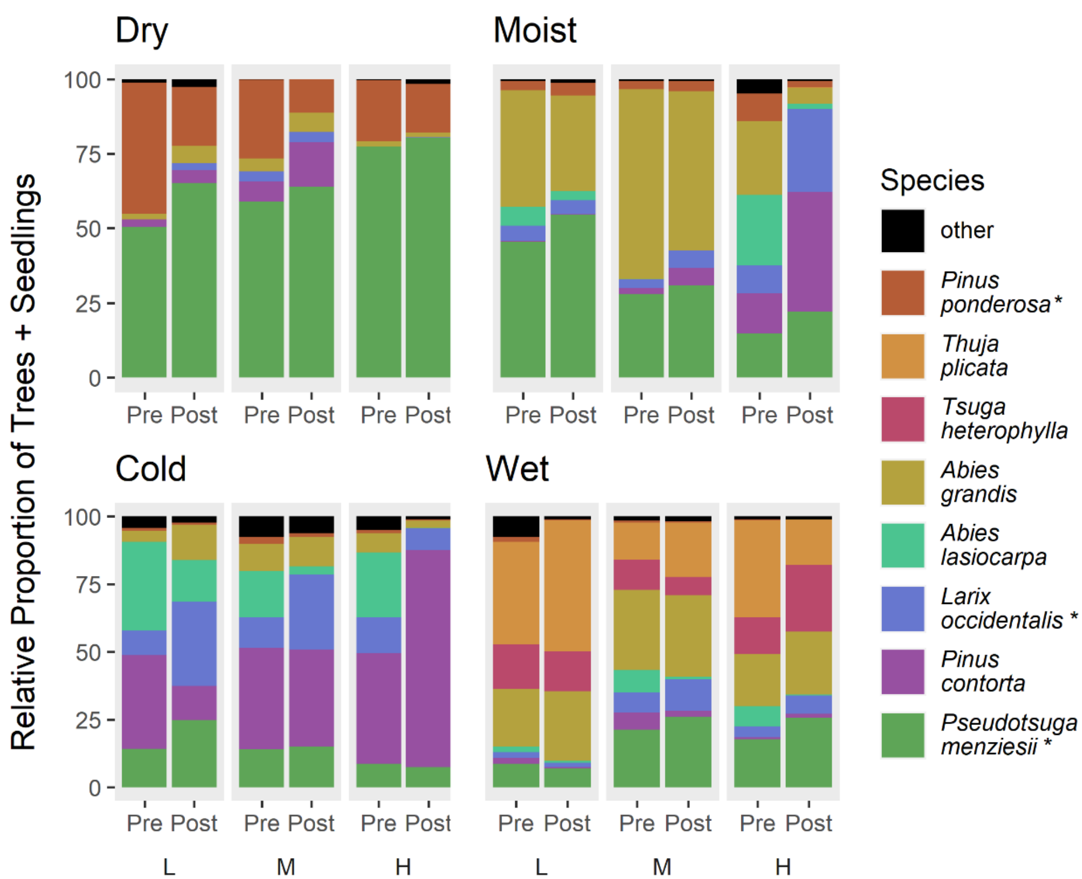

Figure 6: The proportion of pre-fire trees and seedling species (pre) and post-fire trees and seedlings (post) by forest zone and fire severity in eastern Washington (USA). Bars are colored by species in each forest zone and fire severity. The other category is composed of additional tree species not listed above (species: *Abies amabilis, Acer glabrum, Alnus rubra, Picea engelmannii, Pinus glauca, Pinus monticola, Populus balsamifera, Populus tremuloides, Tsuga meternsiana,* and unknown). Asterisk indicates species characterized as relatively more 'fire resistant'.

Drivers of post-fire seedling establishment across water- to energy-limited forest zones (Q3)

Post-fire seedling density was driven primarily by fire severity and forest zone, with nearly 60% of variance explained by these two factors. After accounting for forest zone and fire severity, the relative magnitude and direction of other drivers of seedling density varied across the gradient of water- to energy-limited forest zones, as well as across levels of burn severity (Figure 7).

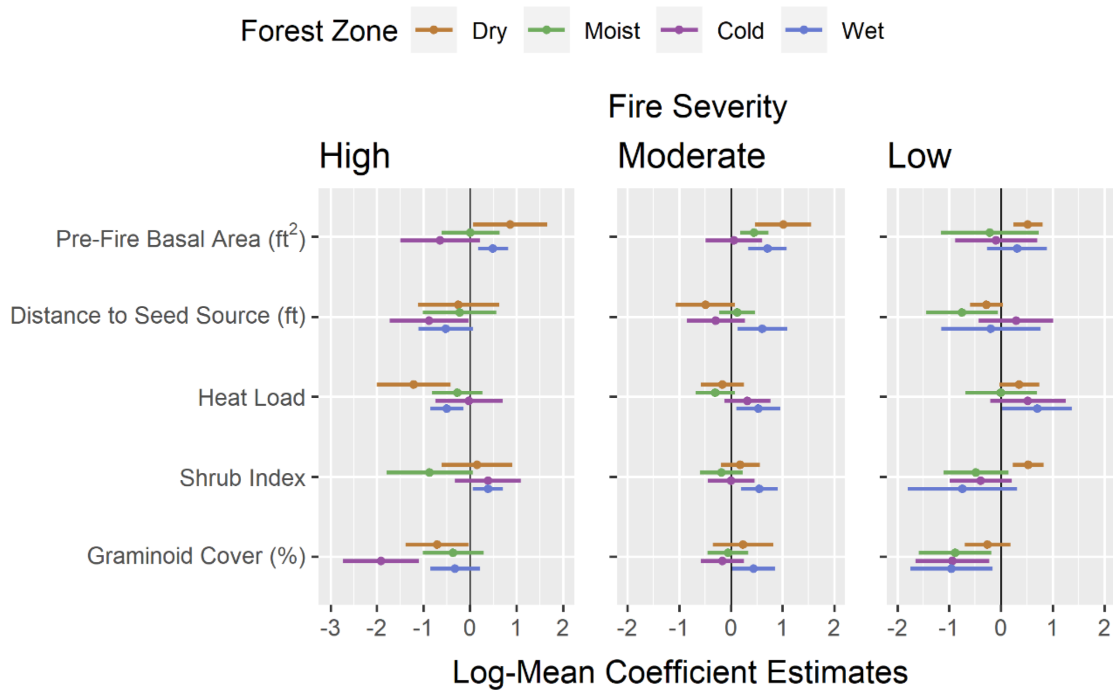

Figure 7: Fixed effects results examining relationships between post-fire seedling and individual parameters for each combination of fire severity and eastern WA forest zone. Each parameter is indicated by point estimate and colored by forest zone, with lines indicating 95% confidence intervals. The less overlap with the vertical zero line, the greater the confidence the parameter influences (positively or negatively) post-fire seedling densities. Positive and negative coefficients respectively reflect higher and lower post-fire seedling densities.

Seed Source and Delivery

Post-fire seedling density generally increased with greater pre-fire basal area (ft^2 per acre) within and among forest zones, with the strength of effects varying across strata (Figure 7). The dry forest zone was the only zone where post-fire seedling density consistently increased with pre-fire basal area across all levels of fire severity. In contrast, post-fire seedling density in cold forests had suggestive negative effects of pre-fire basal area in high-severity fire and no relationship in moderate- or low-severity fire. Post-fire seedling density increased with pre-fire basal area in moderate severity fire across all forest zones except cold forests.

Post-fire seedling density generally decreased with greater distance to the nearest seed source within and among forest zones, although the magnitude (and sometimes direction) of effects varied (Figure 7). In low-severity fire, post-fire seedling density decreased with greater distance to seed source in water-limited (dry and moist) forests but not in energy-limited (cold and wet) forests. This relationship flipped in high-severity fire, where post-fire seedling densities decreased with greater distance to seed source in energy-limited (cold and wet) forests but not in water-limited (dry and moist) forests. In moderate-severity fire, relationships were mixed such that post-fire seedling density decreased with greater distance to seed source for dry forests but increased with greater distance to seed source in wet forests; there was no evidence of an association in moist or cold forests.

Topoclimate

The relationship between post-fire seedling density and heat load index generally shifted from negative in high-severity fire to positive in low-severity fire. That is, in high-severity fire, northeastern slopes had higher post-fire seedling densities, whereas in low-severity fire, southwestern slopes had higher post-fire seedling densities. Across all forest zones the strongest change in magnitude and direction for this relationship was in dry and wet forest zones (Figure 7).

Post-fire Understory Vegetation

The relationship between post-fire seedling density and post-fire understory vegetation differed by plant life form (graminoids vs shrubs) among and within forest zones (Figure 7). Post-fire seedling densities consistently decreased with greater graminoid cover in low- and high-severity fire in most forest zones, whereas there were weaker and variable relationships in moderate-severity fire. The relationship between post-fire seedling density and shrubs was more variable, despite shrub cover increasing with increasing fire severity. In the dry forest zone, post-fire seedling density was positively related to shrub cover in low severity fire, and unrelated in moderate and high severity. Furthermore, post-fire mean shrub cover did not vary substantially in the dry forest zone (19%-17%). For the moist forest zone, there was a suggestive negative relationship between post-fire seedling density and shrubs in high and low-severity fire, with mean shrub cover varying (37% and 19%). In wet forests, this relationship flipped to positive in moderate- and high-severity fire. For cold forests, there was no strong relationship across fire severities, with minimal changes to mean shrub cover (21%-19%).

Key Takeaways

1. <u>Post-fire conditions in eastside forests are becoming drier relative to previous decades.</u> Across forest zones, the 3-year period following recent fires had greater climatic moisture deficit (CMD) than the preceding 30-year average for every location (and for 86% of individual post-fire years across plots). Despite wet and cold forests having the greatest percent increase in drought (68% and 50%), dry forests had the greatest magnitude and frequency of drought, with a raw increase of 1.57-in and 95% of post-fire years being warmer and drier than the 30 years preceding the fire.
2. <u>In much of the inland dry western US, trends of declining post-fire tree regeneration have been recorded. However, post-fire tree regeneration is generally common in our study area.</u> Recognizing seedling densities will decline with time, initial post-fire tree densities regularly exceeded pre-fire adult tree density across most major environmental gradients (forest zones, slope aspects, burn severities) in eastern Washington forests.
3. <u>In cold and wet forest zones, post-fire seedling densities were high.</u> Species known to either survive low- to moderate-severity fire or germinate immediately after fire were predominant (e.g. *Pinus contorta*, *Larix occidentalis*, *Tsuga heterophylla*, and *Thuja plicata*; (Agee 1996)). Of the cold sites with lower post-fire densities, pre-fire tree density was low with pre-fire basal area dominance of *Pinus ponderosa* or *Pseudotsuga menziesii*, and more than half of sites were >1000 ft from the nearest seed source.
4. <u>Dry forests are where post-fire tree regeneration is slow or yet-to-occur.</u> Post-fire drought conditions in water-limited forest zones (dry and moist forests) may be driving decreases in post-fire seedling establishment and plot occupancy. Despite available seed source from residual live trees nearby, only 19% and 36% of plots in dry and moist forests that burned at high severity met or exceeded pre-fire plot adult tree density.

5. Distance to seed source was less important in water-limited forest zones than in energy-limited forest zones. After high fire severity, seedling density in cold and wet forest zones declined with increasing distance to seed source. This relationship was not evident in water-limited forest zones (dry/moist forests) that historically experienced frequent low- to moderate-severity fire. In all high-fire severity plots across forest zones, approximately 50% of all sites were likely limited by dispersal distances (>492 feet [150 m] from the nearest seed source [Clark et al. 1999, Donato et al. 2016, Harvey et al. 2016]). These results imply that available seed source may not be the overriding limitation in post-fire tree regeneration in water-limited forest. Instead, post-fire tree regeneration in these locations may be more limited by stressful climate conditions.
6. Topoclimate constraints on seedling density appeared to be most important in warm and dry marginal forest locations. The strongest negative relationship between post-fire seedling density and heat load index was found in dry forests that burned at high-severity, where warmer and drier southwest aspects had lower post-fire seedling density. Establishment after stand-replacing fire may be primarily constrained by climate rather than seed availability in areas that are more water-limited, as the loss of the forest canopy results in increased exposure of the forest floor (Davis et al. 2019, Clark-Wolf et al. 2022), increasing temperature and drought stress on post-fire seedlings that is already high in sites with higher heat load.
7. Post-fire understory vegetation cover was associated with decreased post-fire seedling density in low-severity fire across forest zones but had varying relationships in moderate- or high-severity fire. The decrease in post-fire seedlings could be due to the presence of overstory trees and available post-fire seed sources for trees in low-severity sites, which may lead to competing vegetation being the primary limiting factor to subsequent seedling establishment. A similar pattern was found in cold forests after high-severity fire, where graminoid cover was found to negatively impact seedling density and could similarly be because of in-situ seed availability from serotinous *Pinus contorta*. Graminoid establishment after fire can be quite rapid and peak within the first few years after fire (Peppin et al. 2010, Andrus et al. 2022); this coincides with the peak of seedling establishment in the cold forest zone.

Management Considerations:

1. Most burned sites are regenerating sufficiently and meeting or exceeding pre-fire plot adult tree density after fire, as well as forest practices minima, meaning the default expectation can be that most burned sites will not need active reforestation to at least establish and maintain forest cover. Limited reforestation resources can be focused on the subset of contexts where regeneration appears to be most challenged (e.g. following high-severity fire in dry forests with southwestern aspects, or in other forest types when very distant from seed source), or where natural regeneration is not meeting other objectives such as desired species composition. Further, given the highly abundant regeneration in many sites, it may be just as important to allocate resources to treatments like pre-commercial thinning, mechanical fuel reduction, and prescribed fire to put regenerating forests on a trajectory toward resilient stand structure.
2. Pre-fire adult tree densities may not be a suitable benchmark for gauging post-fire minimum densities. Lower post-fire plot densities may not necessarily equate to regeneration success or failure, depending on site context. Pre-fire tree densities may be inflated due to higher modern pre-fire plot densities (as a result of the modern fire

suppression era) or deflated as our prefire density estimates likely underestimate contributions of small trees. Additionally, post-fire spatial and temporal heterogeneity of trees/seedlings, as well as inherent capacities and process rates in different forest types (e.g. low and slow regeneration in marginal dry forests), can be a useful consideration when weighing management intervention. Doing so can foster natural variability and heterogeneity inherent in inland forest landscapes. This consideration is especially important as management strategies continually adapt to global change.

3. Management strategies that promote post-fire resilience and decrease the impacts of climate change will only grow in importance. Site preparation, prescribed fire and thinning treatments may prove most beneficial in water-limited forest zones that need a longer recovery period post-fire or in areas that have uncharacteristically high post-fire regeneration; these treatments could mitigate the likelihood or impacts of future high severity fire, or insect and disease outbreaks. In areas where planting is not an option or climate is no longer suitable, strategies that facilitate passive forest re-assemblage or replacement could be considered (e.g., conversion to non-forest). In areas where passive management is not desirable, management strategies could focus on facilitating the movement of native populations that are more drought-tolerant and could be successful under the current disturbance regime.
4. These findings are necessarily most applicable to fires occurring during the timeframe we studied. As the climate continues to become warmer and drier, regeneration following future fires could deviate from the patterns observed here. However, given the high regeneration we observed, there is reason to expect that even with some degree of further climatic change, eastside forest cover may not (yet) be broadly threatened in the coming decades outside of existing dry forests toward the warm and dry margins.
5. A subsequent study is underway to evaluate potential regeneration failure following high-severity fire in marginal “trailing edge” sites near the low-elevation (warm/dry) ecotone between forest and non-forest.

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References

Agee, J. 1996. Fire Ecology of Pacific Northwest Forests. The Bark Beetles, Fuels, and Fire Bibliography.

Andrus, R. A., C. A. Droske, M. C. Franz, A. T. Hudak, L. B. Lentile, S. A. Lewis, P. Morgan, P. R. Robichaud, and A. J. H. Meddens. 2022. Spatial and temporal drivers of post-fire tree establishment and height growth in a managed forest landscape. Fire Ecology 18:29.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed Dispersal Near and Far: Patterns Across Temperate and Tropical Forests. Ecology 80:1475–1494.

Clark-Wolf, K., P. E. Higuera, and K. T. Davis. 2022. Conifer seedling demography reveals mechanisms of initial forest resilience to wildfires in the northern Rocky Mountains. Forest Ecology and Management 523:120487.

Davis, K. T., S. Z. Dobrowski, Z. A. Holden, P. E. Higuera, and J. T. Abatzoglou. 2019. Microclimatic buffering in forests of the future: the role of local water balance. Ecography 42:1–11.
Donato, D. C., B. J. Harvey, and M. G. Turner. 2016. Regeneration of montane forests 24 years after the 1988 Yellowstone fires: A fire-catalyzed shift in lower treelines? Ecosphere 7:e01410.
Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Global Ecology and Biogeography 25:655–669.
Peppin, D., P. Z. Fulé, C. H. Sieg, J. L. Beyers, and M. E. Hunter. 2010. Post-wildfire seeding in forests of the western United States: An evidence-based review. Forest Ecology and Management 260:573–586.

Appendix S1

Methods

Data Collection

Following established methods (Stevens-Rumann et al. 2015, Donato et al. 2016, Harvey et al. 2016), each plot consisted of a 0.17-acre circle (30-meter diameter) in which data were collected on physical site characteristics, pre-fire stand structure, burn severity, post-fire vegetation conditions, and post-fire trees (residual live trees and post-fire seedlings). Elevation (ft), slope (deg), and aspect (compass azimuth) were recorded from plot center and forest zone was characterized by plant association: dry (*Pinus ponderosa* and dry *Pseudotsuga menziesii* plant associations), moist (*Abies grandis/concolor* and moist *Pseudotsuga menziesii* plant associations), cold (*Abies lasiocarpa*, *Tsuga mertensiana*, and subalpine parkland plant associations) or wet (*Tsuga heterophylla* and *Abies amabilis* plant associations). Pre-fire stand structure was characterized by measuring diameter at breast height (DBH), species, and live/dead status of all pre-fire overstory trees (>6 inches [15 cm] DBH live, dead/standing or dead/fallen since fire) that were rooted in the plot. Distance to the nearest patch (>2.5 acre) of live and pre-fire mature tree(s) was measured from plot center with a laser rangefinder. If distance to nearest live tree patch could not be assessed in field (n=13), it was measured using aerial imagery (Google Earth Pro v.7.3). Additionally, we measured post-fire understory vegetation cover (percent cover of herbs, graminoids, and shrubs; plus shrub layer height) in four 6.5x16.4-ft (2x5 m) subplots, spaced 16.4-ft (5 m) from plot center in cardinal directions. For establishing tree seedlings (trees <6 in [15 cm] DBH), we recorded every individual in variable-sized subplots according to establishment density (per Kemp et al. 2016, Stevens-Rumman et al. 2015, Donato et al. 2016, Harvey et al. 2016). Default subplot size was four 6.5x49.2-ft (2x15 m) rectangular subplots (0.03 acre [120 m^2] total area) configured in cardinal directions. Subplot size was objectively decreased to four 1.6x49.2-ft (0.5x15 m) belt plots or increased to the entire 0.17-acre circular plot if visual inspection indicated >200 or <10 tree seedlings were captured in the default subplot size, respectively.

Post-fire Climate Conditions

We characterized post-fire climate conditions for each plot during the study period and compared post-fire climate to climate norms in the three decades preceding fire (1982-2010). Climate data were acquired from the desktop application climateWNA (Wang et al. 2012), which provides monthly and annual climate summaries of downscaled (0.62 miles [1 km]) climate variables from the PRISM climate dataset (PRISM Climate Group 2013). Downscaling is achieved using bilinear interpolation of baseline climate data of the four nearest grid cells, and a lapse rate-based elevation adjustment (see Wang et al. 2012 for details).

We calculated the annual cumulative water year climatic moisture deficit (CMD) for each year between 1982-2010 (referred to as 30-year pre-fire normal) using 0.62-mi (1-km) resolution estimates of precipitation and temperature (climateWNA), heat load index (McCune and Keon 2002), soil available water capacity (obtained from SSURGO at 3.93-in [100 mm] available water capacity depth; https://casoilresource.lawr.ucdavis.edu/), and day length. CMD can be thought of as an integrated measure of drought stress on plants. It is a biologically meaningful measure to assess the water balance at each site as it measures the amount of water by which potential evapotranspiration exceeds actual evapotranspiration (Stephenson 1990, 1998). Water balance has been found to be strongly correlated with vegetation distributions (Stephenson 1990, 1998), and has been widely adopted as a powerful explanatory variable for post-fire tree regeneration (e.g., Donato et al. 2016, Harvey et al. 2016, Stevens-Rumann et al. 2018, Davis et al. 2023). For each plot, we computed the 3-year water-year average CMD for the three years following fire and the 30-year water-year average CMD for the three decades preceding the fire. We quantified the 3-year post-fire average and 30-year pre-fire average CMD using a Thornthwaite-type water balance model following the equations provided in Lutz et al. (2010) using the Redmond (2022) CMD function in R (R Core Team 2022). We used the 3-year post-fire average as this window of time is often characterized as a period of pulsed establishment as competition with understory vegetation is low (Larson and Franklin 2005, Harvey et al. 2016, Stevens-Rumann et al. 2017).

Statistical Analysis

We used generalized linear models with a log-link (family = negative binomial) to account for overdispersed count data. With one model including all plots (n=325), we tested how post-fire seedling density patterns differed across combinations of forest zone and fire severity. We assessed the explanatory power of forest zone and fire severity by calculating ‘psuedo R^2’ utilizing R package *performance* (Lüdecke et al. 2021), as true R^2 for generalized linear models are not available (Zuur et al. 2009, Hilbe 2011). To compare the relative importance of factors driving post-fire seedling density across each combination of forest zone and level of burn severity, all predictor variables were included in all models. Each model was assessed for fit by plotting and calculating residual diagnostics utilizing R package *DHARMa* (Hartig 2022). The error structure, dispersion parameters, and residual diagnostics of model families were also compared by using Analysis of variance (ANOVA) to compare potential error families and a subsequent null model. All fixed effects were scaled and models were run using R package *glmmTMB* (Brooks et al. 2017). Fixed effect significance and importance was evaluated using the following α thresholds: strong evidence ($p < 0.01$); moderate evidence ($p < 0.05$); and weak/suggestive evidence ($p < 0.15$).

Table S1: All fires sampled in the study.

Sampling year(s)	Fire year	Fire Names (30)
2016-2018	2012	Table Mountain, Buckhorn, Peavine, Poison Canyon, Klone Peak, Taylor Bridge, Wild Rose, Chasmere, Basalt Peak
2017-2018	2013	Conrad Lake, Colockum Tarps
2018	2014	Carlton Complex, Upper Falls, Little Bridge, Snag Canyon, Duncan
2020-2021	2015	Renner, First Creek, Stickpin, Reach, Meeks Table, Carpenter Rd, Lime Belt, Cougar Creek, Tower, Wolverine, Twisp River
2021	2017	Jolly Mountain, Noisy Creek, Norse Peak

Table S2: Species codes and associated names for all species found in study.

Species Code	**Species**
PICO	*Pinus contorta*
LAOC	*Larix ocidentalis*
ABGR	*Abies grandis*
ABLA	*Abies lasiocarpa*
PSME	*Psuedotsuga menziesii*
PIPO	*Pinus ponderosa*
THPL	*Thuja plicata*
TSHE	*Tsuga heterafila*
Other	*Abies amabilis, Alnus rubra, Picea engelmannii, Pinus glauca, Pinus montícola, Populus balsamifera, Populus tremuloides, Tsuga meternsiana, and unknown conifer species*

Table S3: Sum of species abundance of pre-fire trees + seedlings per acre (top) and post-fire trees + seedlings per acre (all live trees and seedlings; bottom) by forest type and fire severity of fires sampled in eastern Washington (USA). Species are labeled utilizing their corresponding four letter species code.

Pre-Fire Trees per Acre												
Species Code	*Forest Type*											
	Dry			Moist			Cold			Wet		
	Fire Severity											
	L	M	H	L	M	H	L	M	H	L	M	H
abgr	381	884	172	48,020	66,426	4,761	2,767	5,650	2,327	9,952	15,664	9,597
abla	0	0	0	7,588	198	4,553	21,886	9,606	8,065	1,079	4,418	3,777
laoc	17	680	0	6,358	3,053	1,816	6,009	6,419	4,424	997	3,845	2,013
pico	540	1,355	0	220	1,928	2,563	23,131	20,978	13,670	997	3,372	366
pipo	9,190	5,335	2,063	3,673	2,836	1,770	703	1,422	439	809	405	135
psme	10,512	11,920	7,765	55,692	29,318	2,845	9,360	7,831	2,908	4,021	11,275	8,826
thpl	0	0	0	0	0	0	6	0	0	17,896	7,237	17,928
tshe	0	0	0	0	135	0	0	0	0	7,725	5,945	6,813
Other	242	39	29	888	674	933	2,861	4,249	1,670	3,599	844	557
Post-Fire Trees Per Acre												
abgr	8,196	5,241	258	86,023	123,488	4,677	20,986	27,519	3,811	114,337	123,537	121,494
abla	0	0	0	8,262	135	1,484	24,925	7,318	205	2,900	3,305	1,889
laoc	3,101	27,74	23	12,400	13,076	24,055	50,260	70,052	11,849	7,793	47,736	35,253
pico	6,138	12,377	0	372	13,384	34,443	20,165	90,293	116,719	1,801	8,713	7,751
pipo	28,107	92,95	2,534	11,009	7,810	1,805	1,479	3,765	809	1,147	1,720	0
psme	92,697	52,485	12,540	146,051	71,507	19,025	40,121	37,998	10,843	30,535	106,615	134,225
thpl	0	0	0	0	0	34	6	0	0	215,299	82,550	87,624
tshe	0	0	0	0	0	0	0	0	0	65,157	27,532	129,167
Other	3,811	34	263	3,570	1,675	652	3,700	15,513	1,572	5,165	7,560	6,498

References:

Brooks, M., K. Kristensen, K. van Benthem, A. Magnusson, C. Berg, A. Nielson, H. Skaug, M. Maechler, and B. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378-400. doi: 10.32614/RJ-2017-066.

Davis, K. T., M. D. Robles, K. B. Kemp, P. E. Higuera, T. Chapman, K. L. Metlen, J. L. Peeler, K. C. Rodman, T. Woolley, R. N. Addington, B. J. Buma, C. A. Cansler, M. J. Case, B. M. Collins, J. D. Coop, S. Z. Dobrowski, N. S. Gill, C. Haffey, L. B. Harris, B. J. Harvey, R. D. Haugo, M. D. Hurteau, D. Kulakowski, C. E. Littlefield, L. A. McCauley, N. Povak, K. L. Shive, E. Smith, J. T. Stevens, C. S. Stevens-Rumann, A. H. Taylor, A. J. Tepley, D. J. N. Young, R. A. Andrus, M. A. Battaglia, J. K. Berkey, S. U. Busby, A. R. Carlson, M. E. Chambers, E. K. Dodson, D. C. Donato, W. M. Downing, P. J. Fornwalt, J. S. Halofsky, A. Hoffman, A. Holz, J. M. Iniguez, M. A. Krawchuk, M. R. Kreider, A. J. Larson, G. W. Meigs, J. P. Roccaforte, M. T. Rother, H. Safford, M. Schaedel, J. S. Sibold, M. P. Singleton, M. G. Turner, A. K. Urza, K. D. Clark-Wolf, L. Yocom, J. B. Fontaine, and J. L. Campbell. 2023. Reduced fire severity offers near-term buffer to

climate-driven declines in conifer resilience across the western United States. Proceedings of the National Academy of Sciences 120:e2208120120.
Donato, D. C., B. J. Harvey, and M. G. Turner. 2016. Regeneration of montane forests 24 years after the 1988 Yellowstone fires: A fire-catalyzed shift in lower treelines? Ecosphere 7:e01410.
Hartig, F. 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models_. R package version 0.4.6, <https://CRAN.R-project.org/package=DHARMa>.
Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Global Ecology and Biogeography 25:655–669.
Hilbe, J. M. 2011. Negative Binomial Regression. Cambridge University Press.
Larson, A. J., and J. F. Franklin. 2005. Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. Forest Ecology and Management 218:25–36.
Lüdecke, D., M. Ben-Scachar, I. Patil, P. Wagoner, and D. Makowski. 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software, 6 (60) 3139. doi: 10.21105/joss.03139.
Lutz, J. A., J. W. van Wagtendonk, and J. F. Franklin. 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. Journal of Biogeography 37:936–950.
McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13:603–606.
R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
Redmond, M. 2022. CWD and AET function (Version V1.0.3). Zenodo. https://doi.org/10.5281/zenodo.6416352.
Stephenson, N. L. 1990. Climatic Control of Vegetation Distribution: The Role of the Water Balance. The American Naturalist 135:649–670.
Stephenson, N. L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. Journal of Biogeography 25:855–870.
Stevens-Rumann, C., P. Morgan, and C. Hoffman. 2015. Bark beetles and wildfires: How does forest recovery change with repeated disturbances in mixed conifer forests? Ecosphere 6:art100.
Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2017. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21:243–252.
Wang, T., A. Hamann, D. L. Spittlehouse, and T. Q. Murdock. 2012. ClimateWNA—High-Resolution Spatial Climate Data for Western North America. Journal of Applied Meteorology and Climatology 51:16–29.
Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.