



Wildfire severity and postfire salvage harvest effects on long-term forest regeneration

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Abstract. Following a wildfire, regeneration to forest can take decades to centuries and is no longer assured in many western U.S. environments given escalating wildfire severity and warming trends. After large fire years, managers prioritize where to allocate scarce planting resources, often with limited information on the factors that drive successful forest establishment. Where occurring, long-term effects of postfire salvage operations can increase uncertainty of establishment. Here, we collected field data on postfire regeneration patterns within 13- to 28-yr-old burned patches in eastern Washington State. Across 248 plots, we sampled tree stems <4 m height using a factorial design that considered (1) fire severity, moderate vs. high severity; (2) salvage harvesting, salvaged vs. no management; and (3) potential vegetation type (PVT), sample resides in a dry, moist, or cold mixed-conifer forest environment. We found that regeneration was abundant throughout the study region, with a median of 4414 (IQR 19,618) stems/ha across all plots. Only 15% of plots fell below minimum timber production stocking standards (350 trees/ha), and <2% of plots were unstocked. Densities were generally highest in high-severity patches and following salvage harvesting, although high variability among plots and across sites led to variable significance for these factors. Post hoc analyses suggested that mild postfire weather conditions may have reduced water stress on tree establishment and early growth, contributing to overall high stem densities. Douglas fir was the most abundant species, particularly in moderate-severity patches, followed by ponderosa pine, lodgepole pine, western larch, and Engelmann spruce. Generalized additive models (GAMs) revealed species-level climatic tolerances and seed dispersal limits that portend future challenges to regeneration with expected future climate warming and increased fire activity. Postfire regeneration will occur on sites with adequate seed sources within their climatic tolerances.

Key words: climatic tolerance; Douglas fir; dry forest; high severity; lodgepole pine; ponderosa pine; regeneration; resilience; salvage harvest; seed dispersal; western larch; wildfire.

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INTRODUCTION

Wildfires are integral in shaping ecosystems across the western United States, and large wildfire years have increased markedly in recent years (Stephens 2005, Miller et al. 2009, Westerling 2016), along with the size of stand-replacing (syn. high-severity) fire patches (O'Connor et al. 2014, Stevens et al. 2017). Given the large extent of the landscape currently recovering from fire, much uncertainty exists regarding the development of future forest canopies, particularly after moderate- and high-severity fires. Of special concern are forests that were historically dominated by low- and mixed-severity fires; ecosystems that are less well-adapted to the effects of large-scale and severe wildfires (Perry et al. 2011, Hessburg et al. 1999, 2016).

Seedling establishment delays result from lengthy dispersal gradients within large high-severity patches and the effects of these long distances on conifer species that rely on wind or animal seed dissemination. Replacing conifers in these areas are species well-adapted to fire, with the ability to resprout (Lawes and Clarke 2011, Pausas et al. 2016), or that depend on fire to germinate seeds stored in soils (Schwilk and Ackerly 2001, Keeley et al. 2011). In the western United States, few coniferous species regenerate through adventitious sprouting or by serotinous cones, suggesting that hardwood trees, shrubs, and other nonforest species may be favored in large stand-replacement patches (Lydersen and North 2012, Tepley et al. 2017). This, in turn, may lead to shifts in dominant species or physiognomic conditions (Romme et al. 1998, Odion et al. 2010) that can last for decades to centuries.

Regeneration failures are documented where postfire conditions were unfavorable to tree establishment and survival (Coop et al. 2016, Stevens-Rumann et al. 2018), and studies suggest that systems can persist in alternative nonforest states (Odion et al. 2010) or landscape traps (Lindenmayer et al. 2011). Where nonforest communities (e.g., grasslands, shrublands, and savannahs) establish after disturbance, their dominance can self-regulate through feedbacks with future reburns to the detriment of conifer establishment (Odion et al. 2010, Coop et al. 2016, Coppoletta et al. 2016). For example, short fire-return intervals favored shrubland

vegetation in the Klamath Mountains due to their high flammability and the inability of conifer seedlings to survive recurrent severe fires (Odion et al. 2010). While early seral patches are important components of western landscapes (Swanson et al. 2011), large contiguous patches can negatively influence plant and animal habitat and dispersal networks, distribution of future fire severity patch sizes, and forest regeneration (Hessburg et al. 2015, 2019). Where these patches occur following uncharacteristically large and severe wildfires, accelerating tree establishment and regrowth of conifers may be desirable for habitat restoration, erosion control, water quality, carbon sequestration, or other ecosystem services.

Postfire recovery is influenced by biotic and abiotic factors operating across multiple spatial and temporal scales. Recovery is contingent upon local viable seed source, favorable seedbed conditions, limited interspecific competition, favorable long-term climate, and near-term post-fire weather conditions (Larson and Franklin, 2005, Harvey et al. 2016, Kemp et al. 2016). Broad environmental gradients of western U.S. mountain ranges can significantly influence forest regeneration, with moist and cool environments favoring abundant regeneration, while arid conditions present challenges for seedling establishment and growth (Dodson and Root 2013, Savage et al. 2013, Tepley et al. 2017). For example, Dodson and Root (2013) showed significant increases in postfire regeneration density along a broad elevational gradient in eastern Oregon; tree establishment at low elevations was unlikely due to elevated evaporative demands. However, within environments, local variations in topography and edaphic properties can create favorable microsites for regeneration (Donato et al. 2009). Similarly, periods of benign weather following fire can provide opportunities for trees to regenerate (Littlefield 2019). However, long-term regeneration success is not guaranteed, particularly where trees develop at the edge of their physiological tolerance (Parks et al. 2019). Understanding the conditions conducive to regeneration and factors that limit long-term success is key to postfire management, especially as the climate changes (Tepley et al. 2017).

Management can foster the development of forest vegetation through planting, mechanical

removals, prescribed burning, and soil scarification to expose mineral soil (Shive et al. 2013, Stevens et al. 2014). However, current trends in burned area are outpacing the ability of some managers to mitigate the worst impacts of severe wildfires (North et al. 2019). After large fire years, managers prioritize the allocation of scarce resources, often with limited information on factors that drive forest establishment (Calkin et al. 2005). There is therefore a critical need to document long-term postfire regeneration dynamics across diverse biophysical settings and to predict where interventions are needed to improve successes.

In addition to promoting forest regeneration, postfire management responses in the western United States can include salvage harvest (Lindenmayer et al. 2012, Leverkus et al. 2018). Objectives of salvage harvest operations have traditionally been to extract economically valuable trees to recoup some of the timber value lost to the fire and offset costs of reforestation. Salvage harvesting has also been used to remove smaller trees that had encroached during the period of fire exclusion and would later serve as fuel for future reburns (Peterson et al. 2015). Still, much debate exists regarding the ecological consequences of salvage harvests on tree regeneration and other aspects of forest recovery (Sessions et al. 2004, Donato et al. 2006, Lindenmayer and Noss 2006). Ground disturbance from salvage operations can reduce competition from grass, forb, and shrub species, scarify soils to create a mineral seedbed for conifer establishment, and reduce fire hazard in the near and long term (Fraver et al. 2011, Ritchie et al. 2013). However, these same operations can cause extensive mortality to regeneration at a time when it may be vulnerable to mechanical damage (Donato et al. 2006), and some evidence shows salvage without follow-up prescribed burning concentrates surface fuels (McIver and Ottmar 2007), elevating the likelihood of future high-severity fire (Donato et al. 2006, Thompson et al. 2007). Careful comparisons of postfire vegetation development in salvaged and non-salvaged harvested patches, while controlling for fire severity and biophysical setting, can provide helpful insights into the potential usefulness of salvage harvests to the postfire environment.

Forest regeneration is a long-term process that depends on post-disturbance climate and weather conditions, the variability in physiological traits and life history strategies of regenerating species, and on the environmental context for regeneration (Coop and Schoettle 2009, Coop et al. 2010, Donato et al. 2016, Malone et al. 2018, Stevens-Rumann et al. 2018). Inter- and intraspecific competition and facilitation can affect establishment and growth and mortality processes, which in turn can influence forest recovery timing and future stand dynamics. As a consequence, assessments of short-term (e.g., 1–5 yr) postfire vegetation dynamics may not represent long-term establishment trends (Coop and Schoettle 2009). In this study, we evaluated long-term (15–30 yr) postfire trends on public lands in north-central and northeastern Washington State, across a gradient of biophysical conditions and postfire management (NEWFire). We established field plots within moderate- and high-severity fire patches that burned from 1984 to 2003. Our research questions were as follows:

1. What is the effect of fire severity on tree density and species composition 15–30 yr post-fire?
2. Does postfire salvage logging influence regeneration density and composition?
3. Do these influences vary by potential vegetation type?
4. What are key drivers of regeneration, and do they vary among tree species?

Finally, we placed our results within a broader climatic context of postfire regeneration studies conducted in the western United States: We compared regeneration densities across a climatic space that included our data and those of Stevens-Rumann et al. (2018), who compiled a multi-regional dataset from 1485 sites and 52 wildfires that burned across the U.S. Rocky Mountains.

METHODS

Study area description

Our study area focused on state and federal lands within the boundaries of National Forests (NF) in eastern Washington State, including the

northern half of the Okanogan-Wenatchee NF (ONF), located in the Eastern Cascades Section (M242C), and the western half of the Colville NF (CNF), located in the Okanogan Highlands Section (M333A; Bailey 1995; Figs. 1, 2), and including National Park Service, and Washington State Department of Fish and Wildlife, and Department of Natural Resources lands. These two Bailey Sections (hereafter, ecoregions) contain similar biophysical settings, climatic regimes, and vegetation types, which range from shrub-steppe and sparse woodland communities at lower elevations to subalpine forests and parklands at the highest elevations. Our sample sites focused on three classes of mixed-conifer forest—dry, moist, and cold-dry, which were derived from U.S. Forest Service potential vegetation maps and classifications (Table 1). These types were chosen because they occupy a range of climatic conditions that vary in the evaporative demand placed on tree establishment and growth, represent the majority of forest landscapes, are regularly influenced by wildfires, and are the focus of postfire management (Stine et al. 2014, Hessburg et al. 2016).

Following site selection (see section, Field methods), differences in climatic conditions at sampled locations across the two NFs were apparent, although overlap existed in both mean annual temperature and mean annual precipitation (Fig. 3). Plots within the CNF were located within a relatively compact climatic space compared to those of the ONF; temperatures were generally cooler, but precipitation levels were within the interquartile range of conditions of the ONF plots. For these reasons, we later test for potential differences in species' responses (see *Mixed-effect generalized additive modeling*).

Field site stratification

Our experimental design included three main factors: (1) fire severity (moderate or high), (2) postfire salvage logging (without post-harvest planting) or no postfire management, and (3) potential vegetation type (PVT, dry mixed-conifer, moist mixed-conifer, or cold-dry forest; Tables 2, 3).

The selection of potential field plots proceeded as follows: A 30-m grid of points was overlaid across the northern half of the ONF and eastern half of the CNF within a geographical

information system (GIS). Sample sites were retained if they satisfied 6 criteria: They were (1) within a fire perimeter that occurred prior to 2007, (2) >30 m inside a fire severity patch of moderate or higher severity (see *Fire severity*), (3) within a dry mixed, moist mixed, or cold-dry conifer type, (4) within an area of recent LiDAR acquisition, (5) within 3 km of a road, and (6) suitable for sampling after evaluation with aerial photography. Table 2 describes the datasets that were used for this stratification.

Our selection protocol resulted in a universe of 166,822 potential sample plots. We used a stratified random sampling design to create a complete matrix of the 12 experimental strata (Tables 2, 3). Twenty-five sample plots within 12 bins were randomly located across NF lands, for a total of 300 target sample locations to complete the 3 (PVT) \times 2 (severity) \times 2 (salvage) study design. A replacement plot list was also developed in the event plots were abandoned for logistical reasons or misclassification (see *Field rejection criteria*).

Field methods

Field rejection criteria.—Field crews would reject sample locations for significant safety risks, if 10% or more of the site was in an active or inactive stream bed, or where either planting or pre-commercial thinning was conducted. If the site met any of the rejection criteria, a replacement was located 30 m away using a randomized azimuth. If the relocated site was also rejected, the site was abandoned. This process resulted in 248 plots in the final frame; of these, 146 were located on the CNF and 102 on the ONF (Table 3). Final sample plots were located within fires that burned in 1988 (29 yr prior to sampling), 1994 (23 yr), 2001 (16 yr), and 2003 (14 yr; Table 4).

Plot design and field measurements.—We recorded measurements of overstory trees and tallied young trees and non-tree vegetation cover within sampled plots (Table 5). A fixed 16 m radius circular plot (Appendix S1: Fig. S1) was spatially referenced at plot center using a high-accuracy GPS unit (Javad Triumph 2 GNSS receivers collecting GPS and GLONASS L1 and L2 data). Global positioning data were collected for 15–30 minutes, in one-second epochs. These data were later post-processed using Javad Justin software (V2.122.160.95). Within the 16-m plot, four

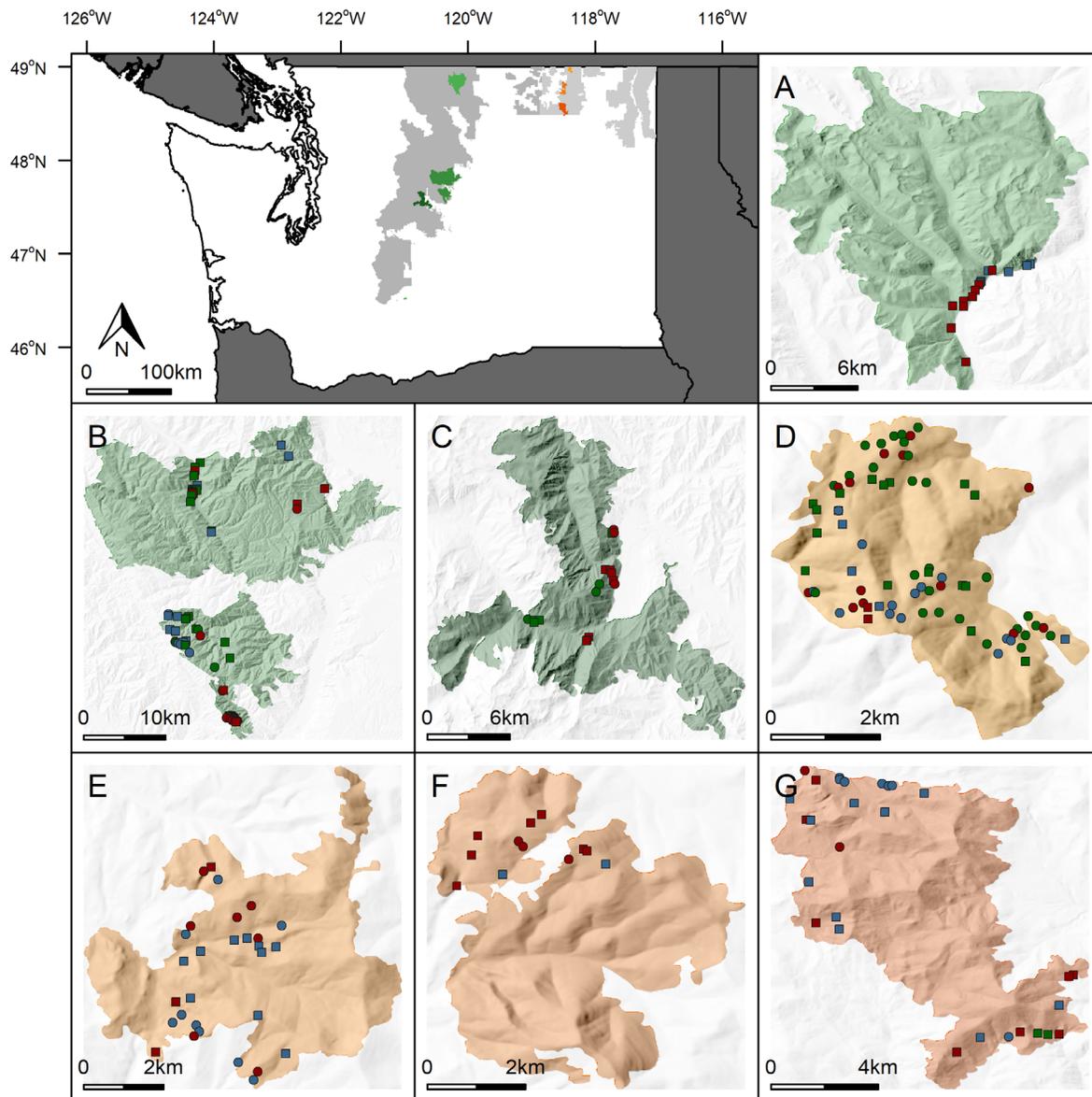


Fig. 1. Study proximity map, fire perimeters, and plot locations within the Okanogan-Wenatchee (dark gray, green shaded fires) and Colville National Forests (light gray, orange shaded fires) in central Washington State. Study plot colors indicate forest type (red, dry forest; green, moist forest; blue, cold forest). Plot shapes indicate postfire management applied (squares, salvage harvest; circles, no management).

subplots were established at cardinal directions, where tree regeneration (stems < 4 m height) was tallied by species and height class (<1, 1–2, 2–4 m heights). Plots varied in size depending on a prior assessment of regeneration density. Where regeneration density was high, plot sizes were reduced to reduce survey time. Subplots

varied in size from 16×0.5 m (0.0008 ha; $n = 36$), 16×2 m (0.0032 ha; $n = 120$) to the full 16-m circle (0.08 ha; $n = 92$). We did not age regenerating trees as the time required to do so was prohibitive for our sample size (see below). The <4 m height cutoff designating postfire tree regeneration was determined during a

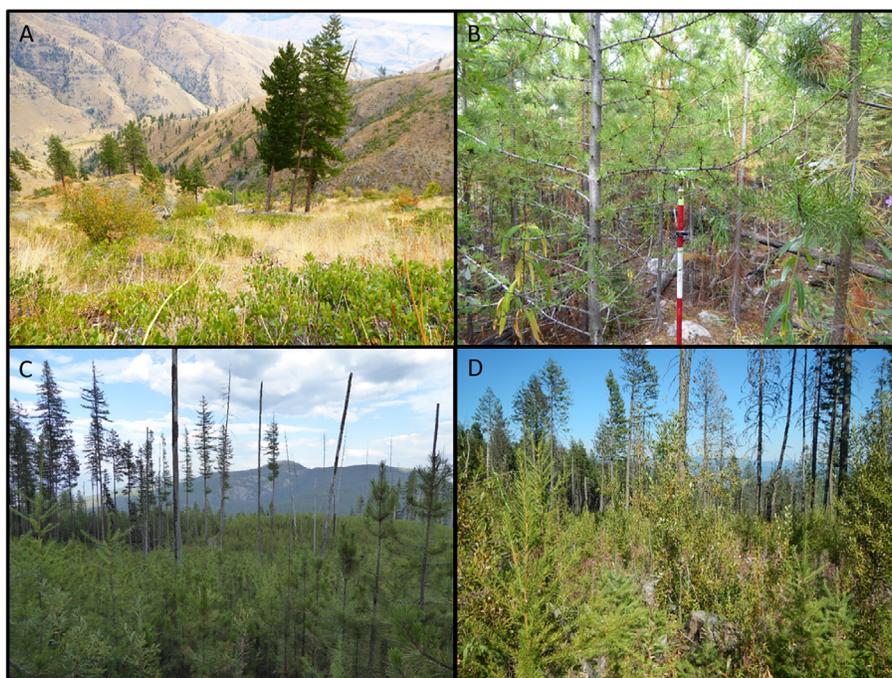


Fig. 2. Plot photographs from (A) a moderate-severity fire in dry mixed-conifer forest with salvage harvesting, (B) a high-severity fire in moist mixed-conifer forest with no postfire management, (C) a high-severity fire in a cold-dry forest with salvage harvesting, and (D) a moderate-severity fire in moist mixed-conifer forest with salvage harvesting.

Table 1. Summary of potential vegetation groups (PVGs) within the eastern Washington study area, their dominant coniferous species, and 30-yr climate normals.

PVG	USFS PVT†	Dominant species	MAT‡	MAP‡	DEF‡,§	AET‡,§
Dry mixed-conifer	Dry Douglas fir Dry mixed-conifer Ponderosa pine	<i>Pinus ponderosa</i>	6.6 [5.3, 7.8]	667 [536, 828]	290 [212, 337]	255 [235, 283]
		<i>Pseudotsuga menziesii</i>				
		<i>Abies grandis</i>				
		<i>Pinus contorta</i>				
Moist mixed-conifer	Moist mixed-conifer Cedar/Hemlock	<i>Pseudotsuga menziesii</i>	6.5 [5.6, 7.2]	884 [773, 942]	270 [207, 301]	258 [237, 285]
		<i>Pinus ponderosa</i>				
		<i>Abies grandis</i>				
		<i>Thuja plicata</i>				
		<i>Tsuga heterophylla</i>				
		<i>Pinus contorta</i>				
Cold-dry conifer	Mtn hemlock—cold/dry Subalpine fir—cold/dry	<i>Pinus contorta</i>	3.7 [2.8, 4.6]	848 [710, 1023]	148 [121, 226]	266 [233, 317]
		<i>Abies lasiocarpa</i>				
		<i>Tsuga mertensiana</i>				
		<i>Tsuga heterophylla</i>				
		<i>Pseudotsuga menziesii</i>				

Notes: Climate variables are mean annual temperature (MAT; °C), mean annual precipitation (MAP; mm), annual climatic water deficit (DEF; mm), and annual evapotranspiration (ET; mm), for the period 1981–2010. Quantiles are P₅₀ [P₂₅, P₇₅].

† See Table 2.1 in Burcsu et al. (2014) for detailed descriptions of each PVT.

‡ PRISM Climate Group 2013.

§ Jeronimo et al. (2019).

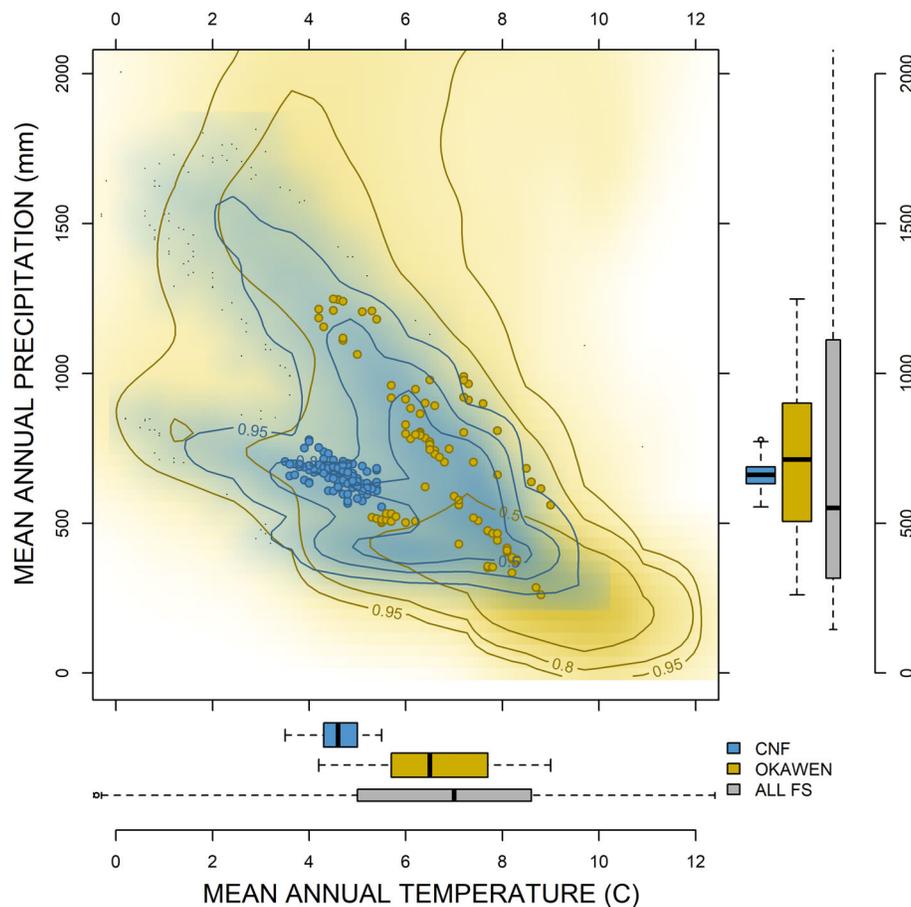


Fig. 3. Comparison of the climatic space sampled within the Colville (CNF, blue filled circles) and ONFs (OKAWEN, gold-filled circles) compared to the environmental conditions within the perimeter of the sampled wildfires (shading), and the conditions present across the entire NFs (contour lines). Climate conditions were estimated using 1-km resolution, 30-yr climate normals for mean annual temperature and precipitation, for the years 1961–1990. Shading represents the smoothed density within the scatterplot for all 1-km raster grid cells in the 11 sampled fires. Contour lines represent the 95th, 80th, and 50th percentile conditions across each NF. Boxplots show the quartiles of the sampled plots within each NF.

reconnaissance of field sites, which showed that surviving pre-fire trees generally exceeded this height, and trees below this height had established postfire. However, we recognize that on some of the older fires and more productive sites, some trees may have grown taller than the 4-m cutoff, and therefore, our sample may underestimate postfire regeneration densities.

Geospatial data

Fire severity.—Fire perimeters were mapped using the 30-m resolution Monitoring Trends in

Burn Severity (MTBS; mtbs.gov) database. Fires that were >404 ha and that burned between 1984 and 2015 were considered for sampling. Fire severity was measured using the relativized delta normalized burn ratio (RdNBR; Miller and Thode 2007) and then reclassified into unburned (RdNBR values 1–99), low (100–234), moderate (235–649), and high (>649)-severity burn classes following Haugo et al. (2019). These burn severity classifications represent values more closely tied to the study area (Cansler and McKenzie 2014, Reilly et al. 2017), rather than those of

Table 2. Description of datasets used to select sample points.

Dataset	Description	Citations
Fire severity	Fire severity rasters for small fires (≤ 404 ha) and large fires (> 404 ha) were classified into fire severity classes	Cansler and McKenzie (2014) Haugo et al. (2019)
Management history	Forest operations were classified into salvage harvesting, other mechanical treatments, planting, and surface fuel treatments based on the U.S. Forest Service FACTS database	US Forest Service FACTS [†] Washington State DNR GIS Open Data platform [‡]
Potential vegetation group (PVG)	U.S. Forest Service Region 6 PVT raster was used to classify the study area into a continuous raster of potential vegetation groups (PVG). The PVT raster was created from a crosswalk with a previously generated 60-m resolution plant associate group raster	Burcsu et al. (2014)
Road network	Combined road network layers from the U.S. Forest Service, Washington State Department of Transportation County Roads, and U.S. Census Bureau TIGER 2016 road data [#] and performed a geographic buffer analysis to identify all sample plots within 3 km of a road	US Forest Service Roads [§] Department of Transportation Roads [¶] TIGER roads [#]
Google Earth screening	Initial screening of plots used Google Earth imagery to eliminate plots located on a road or streambed, with evidence of potential hazards, or those with apparent fire severity misclassification	

[†] <https://data.fs.usda.gov/geodata/edw/datasets.php>

[‡] <http://data-wadnr.opendata.arcgis.com/>

[§] https://data.fs.usda.gov/geodata/webapps/EDW_DataExtract/

[¶] <https://www.wsdot.wa.gov/mapsdata/geodatacatalog/default.htm>

[#] <https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>

Miller and Thode (2007), which were optimized for the Sierra Nevada. A 3×3 focal smoothing was used on the classified fire severity raster, which eliminated all cells within 30 m of a fire severity patch edge, thus eliminating possible edge effects.

Topography.—We obtained a 1/3 arc-second (~ 10 m) digital elevation model (DEM) from the National Elevation Dataset (<http://ned.usgs.gov/>), and re-projected the elevation data to 30-m resolution using bilinear interpolation. With the 30-m DEM, we then developed aspect, slope, topographic roughness, and topographic position indices using the terrain function within the raster package in R (Hijmans 2019).

Climate and climate variability.—Climate data for each sample plot were obtained using the desktop application climateWNA (Wang et al. 2012, 2016). The application produces downscaled PRISM climate data (PRISM Climate Group 2013) including climate normals (1981–2010) and annual summaries for a variety of metrics. Downscaling in climateWNA is achieved using

bilinear interpolation of baseline climate data of the four nearest grid cells, and a lapse rate-based elevation adjustment detailed in Wang et al. (2012).

Mean annual temperature (MAT) and precipitation (MAP) were used to represent long-term climate. We elected to use these over other measures of productivity (e.g., actual evapotranspiration or climatic moisture deficit) because we found that MAT was highly correlated ($r = 0.932$) with climatic moisture deficit (CMD), and because MAT and MAP, while components of water balance calculations, are more readily interpreted. We did not use seasonal or monthly variables as most were highly correlated with annual values, and because timing of precipitation and seasonal warming/cooling trends were generally similar across the sample plots.

Annual climate variability was calculated at each sample location using climateWNA across the years 1965–2016. At each location, the time series of each variable was first converted to percentiles, and the average percentile was then

Table 3. Sample sizes for 12 strata sampled on National Forests in eastern Washington State.

Fire name by year	Dry forest				Moist forest				Cold forest			
	Salvage		None		Salvage		None		Salvage		None	
	Mod†	High	Mod	High	Mod	High	Mod	High	Mod	High	Mod	High
1988												
Dinkelman	4	6	1	1	6	5	4	4	1	4	2	4
Sherman	2	0	3	2	0	0	0	0	0	0	0	1
White Mountain	1	1	3	4	0	0	1	1	5	1	5	4
1994												
Copper Butte	7	0	2	1	0	0	0	0	7	2	6	4
Hatchery Complex (Hatchery)	2	0	0	0	0	0	1	0	0	0	0	0
Hatchery Complex (Rat)	1	0	4	2	2	1	4	0	0	0	0	0
Tyee Creek	1	1	4	5	0	0	7	5	0	0	3	1
2001												
Mt. Leona Complex	1	0	0	2	0	0	0	0	0	0	1	0
Sleepy Complex (Sleepy)	0	0	0	1	0	0	0	0	0	1	1	0
2003												
Fawn Peak Complex (Farewell)	0	0	5	4	0	0	0	0	0	0	2	4
Middle Fork	0	0	0	0	0	1	0	0	0	0	0	0
Togo Mountain	3	10	0	2	13	14	8	8	4	9	2	3
Total	22	18	22	24	21	21	25	18	17	17	22	21

† Mod designates moderate-severity fire; high is high-severity fire.

Table 4. Characteristics of fires sampled on National Forest lands eastern Washington State.

Year	Colville NF	N	Okanogan-Wenatchee NF		Total
			N	Total	
1988	White Mountain	26	Dinkelman	42	76
	Sherman	8			
1994	Copper Butte	29	Tyee Creek	27	73
			Hatchery Complex	17	
2001	Mt. Leona Complex	4			7
	Sleepy Complex	3			
2003	Togo Mountain	76	Fawn Peak Complex	15	92
			Middle Fork	1	
Total		146		102	

calculated for the 1- to 3-yr postfire period. These methods were similar to those of Harvey et al. (2016) and Stevens-Rumann et al. (2018), who used z-scores (standard deviations from the mean) across a 30-yr climate record. In our study, correlations between average 1- to 3-yr postfire climate z-scores and percentiles were >0.96 for each of the four variables, across the 248 sampled sites. We chose a >50-yr record to capture long-

term trends in climate, encompassing years of both cool and warm phases of the Pacific Decadal Oscillation (Mantua and Hare 2002).

Mixed-effect generalized additive modeling

We used a mixed-effect generalized additive modeling (GAM) approach to identify (1) significance among experimental design factors (fire severity, salvage/no salvage, and PVT) while accounting for (2) significant environmental covariates of regeneration density, (3) potential interactions between environmental cofactors and NF membership, and (4) a random effect of plot membership within individual fires. The use of GAM over generalized linear models allowed for the use of smoothing splines to account for nonlinearities between regeneration density and other model covariates. Mixed-effect GAMs were successfully used by Kemp et al. (2019) who studied postfire regeneration density across dry mixed-conifer forests of the Northern Rocky Mountains, USA.

Data related to topographic features of the plots, overstory structure, distance to nearest overstory tree, postfire percentile weather conditions, and climate variables were attributed to each plot. GAMs were used to model total regeneration density, large conifer (2–4 m) stems only,

Table 5. Field data collected by vegetation stratum.

Stratum	Sampling area	Attributes measured
Overstory tree (live and dead, >4 m height)	16 m radius	All: species, diameter at breast height (dbh), status (alive/dead), decay class (1–5, Cline et al. 1980) Subset (3–9 trees): tree height, total crown ratio, and compacted crown ratio
Seed tree	N/A	Distance to the nearest mature seed-bearing tree alive and reproductive prior to fire for each species represented in the tree regeneration tally. Distance >400 m was recorded as 450 m
Tree regeneration (<4 m height)	Small: four, 16 × 0.5 m; medium: four, 16 × 2 m; large: one, 16 m radius	Four belt transects, arranged in cardinal directions originating from plot center (small and medium). Belt transect widths were modified for each plot to ensure a plot included 10–50 stems. All live regeneration with two or more years of apparent growth was tallied by species and height class
Non-tree vegetation	2 × 5 m	One subplot was superimposed directly over the center of each of the four seedling/sapling belt transects For each non-tree category present, percent cover, mean, and maximum height were assessed

and for Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), and Engelmann spruce (*Picea engelmannii*), separately. Models were developed in the *mgcv* package v1.8.30 (Wood 2011) within R v3.5.3 (R Core Team 2019). Thin plate splines were used to represent semi-parametric smoothing terms in the GAM models. The dimensions of all smoothed terms were set at 10, which defined the upper limit on the degrees of freedom associated with the smoothing parameters. This dimensionality allowed us to observe nonlinearities that emerged from response–predictor relationships without significant model overfitting. Overfitting was further reduced by using (1) restricted maximum likelihood estimation (RMLE), which penalizes overfitting of smooth parameter estimates and produces more stable parameter estimates compared to other methods Wood (2011), and (2) regularization, which adds an extra penalty to superfluous terms allowing estimates to converge toward zero, thereby minimizing their influence on model performance.

Regeneration density response variables exhibited non-Gaussian distributions and were log-transformed prior to modeling. Following log-transformation, a Shapiro-Wilk test showed significant deviations from a normal distribution in total regeneration density ($W = 0.980$, $P = 0.002$) and all other response variables ($P < 0.001$). Other distributions were also tested (i.e., log-normal and gamma), but these provided inferior fits

to the Gaussian distribution based on visual inspection of quantile-comparison plots.

A restricted set of nine cofactors was selected from a larger set of potential predictors in a separate random forest (RF) analysis (Appendix S2). Backwards elimination was conducted across species models, whereby predictors with the lowest variable importance were removed from the model until out-of-bag R^2 values were within 10% of the maximum for that model. Final variables selected from each RF species model were combined into a final set of predictors that were then used across all GAM models. Correlation pairs plots are shown in Appendix S1: Figs. S2–S4, and variability in climate normals and variability across fires is presented in Appendix S1: Table S1.

GAM models were first run with the full set of (1) experimental design factors (fire severity class, PVT, salvage/non-salvage, and NF membership), (2) then with a restricted set of nine environmental cofactors, and (3) with a random effect for fire membership. To test for differences in species' responses to the nine cofactors across NF ownerships, each of the nine cofactors included an interaction with NF membership, which developed separate smoothing parameters for ONF and CNF. Model selection then proceeded by (1) removing all nonsignificant ($P > 0.05$) design factors and (2) using AIC to sequentially remove cofactors and their interactions with NF membership. For the latter step, inclusion of the NF variable indicated that the

regeneration response to a cofactor was sufficiently different to warrant separate smoothing terms for each NF (i.e., the AIC was lower for the more complex model), while its removal indicated no difference in regeneration response to the cofactor.

RESULTS

Regeneration was abundant across the entire study area (Fig. 4). Median regeneration density across the 248 sampled plots was 4414 stems/ha, with lower and upper quartile values of 733 and 20,352, respectively (Table 6). Only four plots (1.6%) had no regeneration present, 17 plots (6.9%) had <100 stems/ha, and 37 (15%) had <350 stems/ha; the latter of which represents a minimum acceptable stocking level by the

Washington State Department of Natural Resources, which is similar to minimum stocking standards on NF lands (Tepley et al. 2017). When only large conifer regeneration was considered (2–4 m height), median density was 687 stems/ha (IQR: 3919 stems/ha), and only 24 plots (9.7%) recorded no large conifer regeneration.

Douglas fir was the dominant regenerating species, representing 37% of stems across all size classes (Appendix S1: Fig. S5). Lodgepole pine and ponderosa pine each comprised ~15% of the regeneration, and Engelmann spruce and western larch represented ~10%. Douglas fir was present on >94% of plots with a median density of 1367 stems/ha, when present (Table 6). Ponderosa pine and Engelmann spruce were present on 40% of plots and had median densities of 243 and 1250 stems/ha where present, respectively.

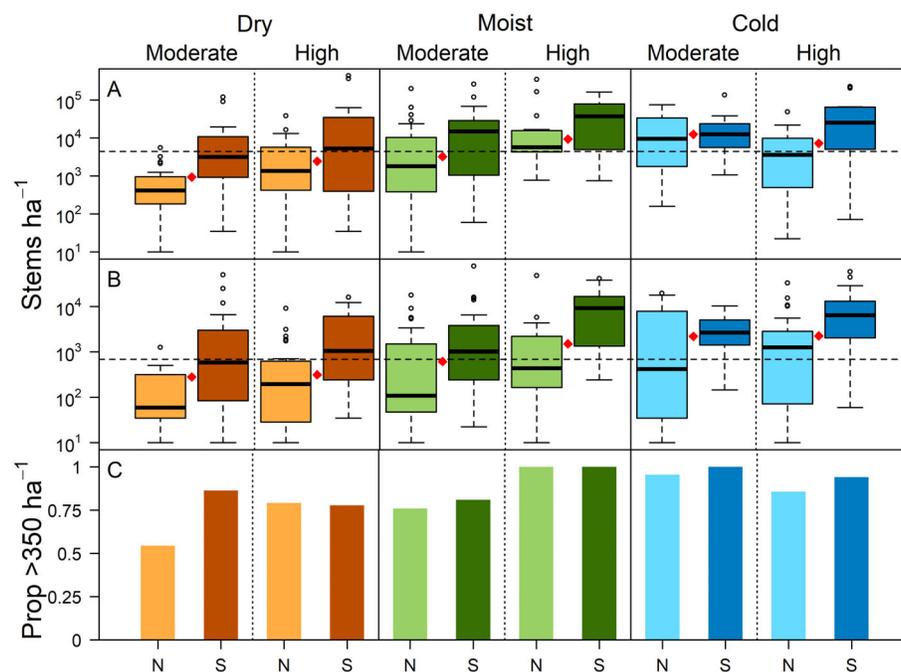


Fig. 4. Boxplots depicting postfire tree regeneration density by management treatment, burn severity, and forest type for (A) all regenerating stems, (B) tall conifer (2–4 m height) stems, and (C) barplots showing the proportion of plots within each sample stratum with >350 stems/ha. Acronyms are N, no salvage treatment; and S, salvage harvested. Dashed horizontal lines in (A) and (B) represent median densities across all plots. Box-and-whisker plots were constructed using the default boxplot function in the R graphics package, and boxes represent the 25th, 50th, and 75th percentiles. Whiskers extend to the most extreme data point no further than $(1.5 \times \text{IQR}) + 75\text{th percentile}$ or $(1.5 \times \text{IQR}) - 25\text{th percentile}$, and points represent data outside those ranges. Red diamonds in boxplots indicate median densities for the respective forest type and burn severity class summarized across management treatments. Moderate and high refer to fire severity. Sample sizes can be found in Table 3.

Table 6. Percent occurrence and quantile estimates of regeneration densities for the main species encountered with the 248 sample plots.

Species	Percent of plots	Where present		
		P_{25}	P_{50}	P_{75}
All species	98.4	895.2	4648.4	21171.9
Douglas fir	94.4	315.2	1367.2	4062.5
Ponderosa pine	40.7	49.7	243.4	937.5
Lodgepole pine	54.4	156.3	634.1	7695.3
Western larch	53.3	390.6	2031.3	7578.1
Engelmann spruce	44.0	234.4	1250.0	9062.5

Note: Quantiles were calculated for all plots where regeneration for that species was present and represented the 25th (P_{25}), median (P_{50}), and 75th (P_{75}) percentile classes.

Similarly, lodgepole pine and western larch occupied ~50% of plots at median densities of 634 and 2031 stems/ha where present, respectively (Table 6).

Lack of self-replacement when a species was present in the overstory (i.e., for trees >4 m height) was low. Lack of lodgepole pine regeneration occurred in 17.2% of plots, where it was present in the overstory; ponderosa pine, 14.7%; western larch, 5.3%; and Douglas fir, 2.0%.

Differences in density and species composition were apparent across NFs. Median regeneration density was more than 10-fold greater in the CNF plots (12,343 stems/ha) compared to ONF plots (932 stems/ha), and regeneration failures were not observed on any CNF plot. Trends were similar when only large conifer regeneration was considered (CNF: 2422 stems/ha; ONF: 180 stems/ha). Ponderosa pine was the dominant species in ONF plots (representing 39% of regenerating stems), particularly in dry forest types (44%), but was a minor component in CNF plots (2%). Douglas fir was the second most abundant species in ONF plots (36%), and it dominated in CNF plots (39%). In the latter case, Douglas fir was most prominent in dry forest (55%) and moderate-severity patches (49%), and least common in moist forest (20%) and high-severity patches (27%). Fig. 3 shows a high degree of overlap in climatic space within the CNF and ONFs, both across the NFs (contour lines) and within sampled fire boundaries (shading). However, sampled plots on the ONF spanned broader precipitation and temperature gradients than those on the CNF, where plots were generally located in cooler and moderately drier environments.

Effects of fire severity on regeneration

Coefficient estimates for fire severity indicated that tree density was generally higher in moderate-severity patches, except for large conifer and lodgepole pine regeneration, which were more abundant in high-severity patches (Fig. 5). However, the main effect of fire severity was only significant for lodgepole pine and Douglas fir, after accounting for other cofactors. Lodgepole pine exhibited significantly higher density on high-severity plots ($P = 0.015$), and GAM models predicted a nearly 10-fold increase in density compared to moderate-severity plots (Fig. 5). On average, lodgepole pine represented 21% of regenerating stems in high-severity versus 6.8% in moderate-severity patches (Appendix S1: Fig. S5). Model results for Douglas fir were equivocal; while the coefficient estimate indicated that moderate-severity fire led to greater Douglas fir regeneration density ($B = 0.276$, $P = 0.048$), model predictions showed slightly higher densities within high-severity patches (Fig. 5). A significant interaction between fire severity and forest type indicated that moderate-severity fire increased densities in cold forest, but decreased them in dry and moist mixed-conifer forests (Fig. 5). Overall, Douglas fir dominance was greatest in moderate-severity patches: 44% vs. 30% of stems in high-severity plots.

Distance from seedlings to mature canopy trees varied between high- and moderate-severity fire plots. For moderate-severity plots, median distance from plot center to the nearest canopy tree was 7.9 m (3.4, 19.5 m) compared to 67.7 m (30.0, 139.8 m) for all high-severity plots.

Effects of salvage logging on regeneration densities

The main effect of postfire salvage was significant ($F = 11.05$, $P = 0.001$; Fig. 5). Mean regeneration densities were 2.5 times greater on salvaged versus non-salvaged plots. A significant interaction was found between salvage treatments and NF land status ($F = 13.11$, $P = 0.000$). On the CNF, mean density on salvage plots was 51,859 stems/ha compared to 21,095 stems/ha for non-salvaged plots. On the ONF, mean density was greater on non-salvaged plots, 6747 vs. 2574 stems/ha (salvaged). Similar trends were found for large conifer regeneration (Fig. 5).

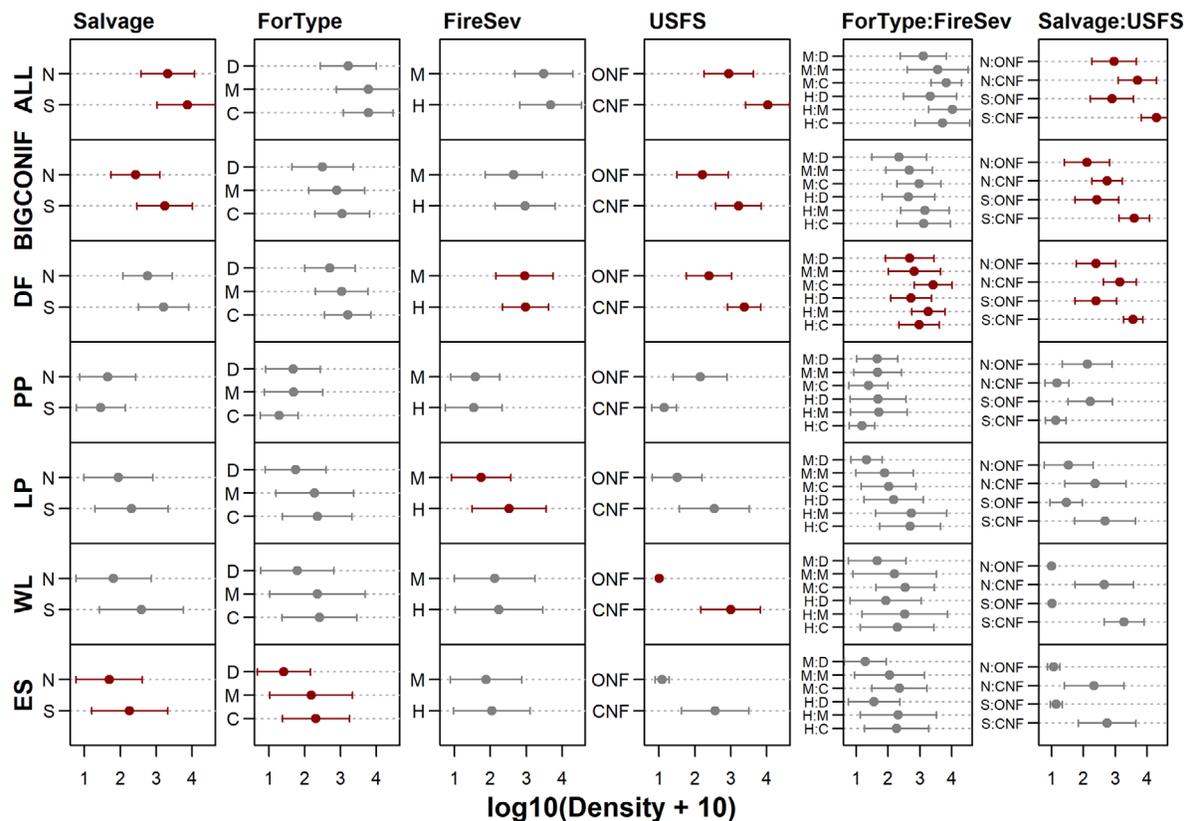


Fig. 5. Fixed effect results from generalized additive models (GAMs) used to identify significant main and interaction effects for study strata included in our study design. Study strata included postfire salvage harvesting (salvage [S], no management [N]), forest type (dry mixed [D], moist mixed [M], and cold-dry [C] conifer), and fire severity (moderate [M], high [H]). U.S. Forest Service membership (Okanogan-Wenatchee [ONF] and Colville [CNF] National Forest). Mean and standard deviations from GAM predictions are represented by dots represent bars, respectively. Significant effects (red) and nonsignificant (gray) effects are shown. Models were developed for all species combined (ALL), large conifer regeneration (2–4 m height, BIGCONIF), Douglas fir (DF), ponderosa pine (PP), lodgepole pine (LP), western larch (WL), and Engelmann spruce (ES).

Regeneration density was highest on salvaged plots for all species except ponderosa pine, and the main effect of salvage was significant large conifer ($F = 37.87$, $P < 0.001$) and Engelmann spruce ($F = 4.78$, $P = 0.030$) regeneration. Mean spruce density was more than twice as abundant on salvaged (5037 stems/ha) vs non-salvaged (2314 stems/ha) plots. Douglas fir exhibited a significant interaction between salvage and NF status ($F = 6.00$, $P = 0.015$), where only small differences in regeneration density were observed on the ONF, but on the CNF, density increased nearly twofold after salvage harvesting. A similar result was identified for all species

combined. Overall, species composition was similar for salvaged and non-salvaged plots (Appendix S1: Fig. S5).

Effects of forest type on regeneration densities

Regeneration density generally increased from dry to moist to cold forest types, but the main effect of forest type was significant only for Engelmann spruce ($F = 7.45$, $P = 0.001$). Ponderosa pine was one exception to this trend, where the highest densities occurred on dry forest plots.

With respect to percent composition, Douglas fir was the most abundant species across forest types, where percent composition ranged from

46% in dry mixed-conifer, 39% in cold forest, and 27% in moist mixed-conifer types (Appendix S1: Fig. S5). Ponderosa pine was the second most dominant species in dry and moist mixed-conifer forest (~20%), but as expected, was a minor component of cold forests (5%). Ponderosa pine was only present on 14% of plots on the CNF compared to 79% of plots on the ONF. Lodgepole pine was most dominant on moist and (15%) cold (18%) forest plots, but as expected, only represented 8% of stems on dry forest plots. On the ONF, lodgepole was mostly associated with cold-dry forest plots (73% of plots) compared to dry and moist mixed-conifer (23% of plots), but was present on ~75% of all plots across forest types on the CNF. Similar trends were exhibited by Engelmann spruce, where percent composition was 5, 12, and 15% on dry, moist, and cold forest plots, respectively. Western larch represented ~10% of stems across all forest types and was almost exclusively found in CNF plots.

Environmental cofactors

GAM modeling revealed key species-level tolerances to environmental gradients and differences in regeneration responses within the two NFs. Regeneration densities were more responsive to climatic gradients on the CNF than on the ONF despite a broader sampling of gradients on the latter NF (Figs. 3, 6).

Regeneration density generally declined with increasing mean annual temperature (30-yr normal), and this trend was most apparent on the CNF (Fig. 6). Mean annual temperature was significant for all species but ponderosa pine. Large conifer regeneration showed a significant negative trend with mean annual temperature for ONF but not CNF plots. Both Douglas fir and western larch showed slight but significant declines in regeneration density between 5° and 8°C, but Engelmann spruce showed an increase in regeneration density within this same range.

Regeneration density mostly increased with increasing mean annual precipitation (MAP), but significance for this variable varied by species. On the ONF, Douglas fir regeneration increased with increasing MAP, while ponderosa pine exhibited a unimodal response with maximum densities occurring near 800 mm (Fig. 6). Density of lodgepole pine and Engelmann spruce showed a positive relationship with MAP on the

CNF, while total, large conifer, and western larch regeneration density did not exhibit a significant correlation with MAP on either NF.

Postfire (1–3 yr) weather conditions were generally cooler and wetter than the 1965–2016 average across the sampled fire locations (Fig. 7). Median MAT was below the 50th percentile, and median MAP was at the 72nd percentile. Only one-third of plots experienced MAP below the 50th percentile. Median moisture deficit was at the 22nd percentile, with a few outlier plots experiencing deficits above the 50th percentile (Fig. 7). A negative relationship was found between postfire percentile temperature and years since fire ($r = -0.961$; Fig. 8), indicating that postfire MAT increased over time such that warmer conditions were experienced in more recent fires compared to older fires.

Postfire weather variables were significant drivers of regeneration density, and percentile conditions were generally cooler and moister in the 1- to 3-yr period after the fires than for the >50-yr climate record (Fig. 7). The regeneration response to postfire temperatures (i.e., 3-yr mean temperatures) varied across NFs, with a positive relationship on the CNF and a negative or neutral relationship on the ONF (Fig. 6). Increases in postfire precipitation led to increased regeneration density on both NFs for all species combined, large conifer, and Douglas fir regeneration, and no other significant trends were identified. Trends were not significant for ponderosa pine for either postfire temperature or precipitation.

A significant positive relationship between transformed aspect and regeneration density was identified for all species but lodgepole pine, which showed a positive but nonsignificant relationship. For most species, the lowest densities occurred on neutral aspects (i.e., southeast and northwest, ~0.5) as compared to harsher southwestern slopes. Ponderosa pine density peaked across a wide range of aspects, and density declined only on southwest-facing slopes.

The influence of residual overstory characteristics on regeneration varied by species, but density generally increased with increasing conspecific overstory basal area (BA). Total regeneration density showed a unimodal response to overstory BA, where density peaked at around 30 to 40 m²/ha on the ONF, but no

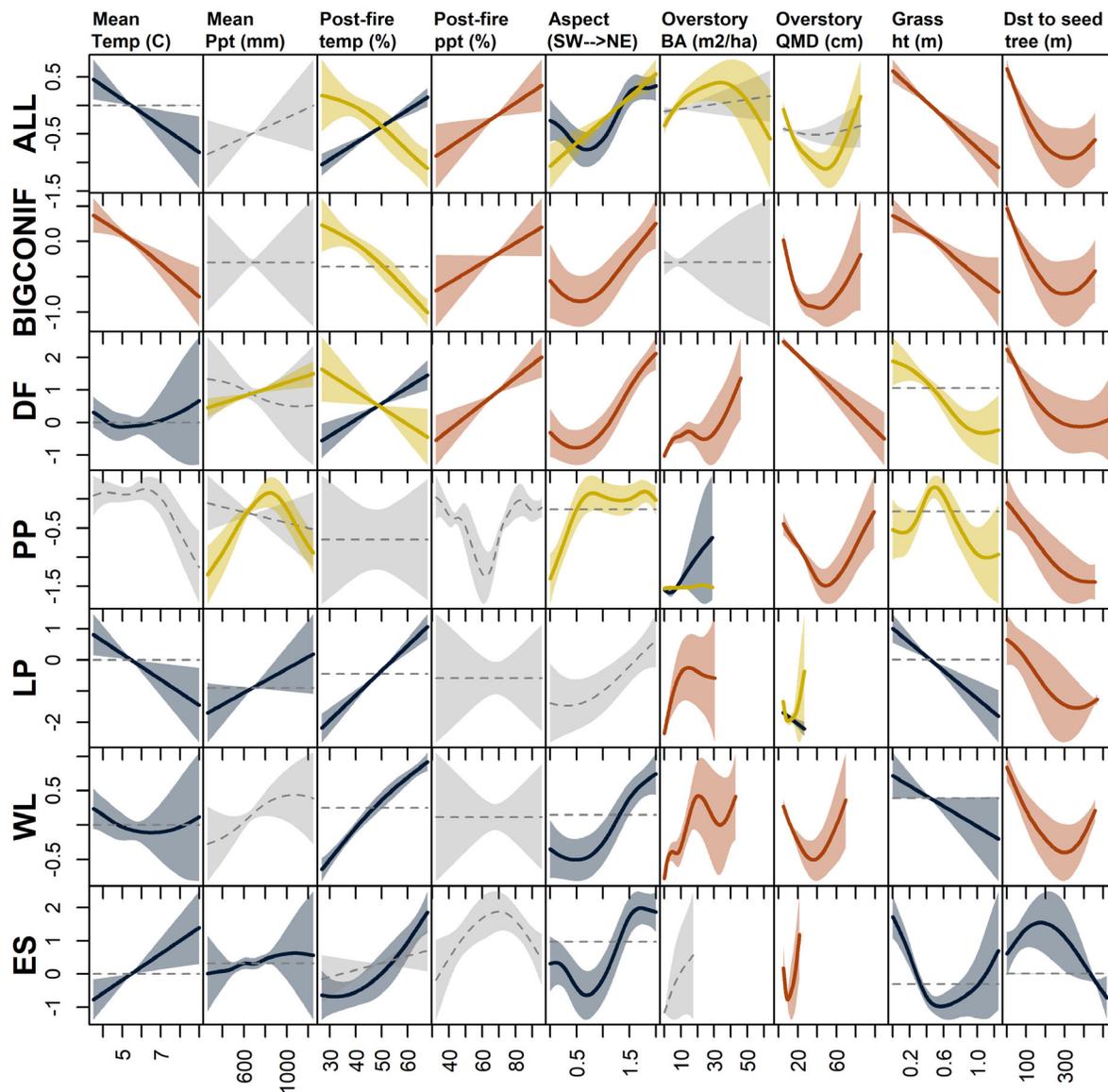


Fig. 6. Smoothed effects from generalized additive models (GAMs). Significant effects are shown for Colville NF (blue), Okanogan-Wenatchee NF (gold), both NF combined (red), or no significance (gray). Variables were first submitted to the GAM with a USFS interaction term, and model complexity was reduced by selecting the model with the lowest AIC score by first removing the USFS interaction and then the smoothed term all together. See Fig. 5 for species definitions. % refers to percentile annual climate conditions.

significant response was apparent on the CNF. Large conifer and Engelmann spruce regeneration both exhibited a nonsignificant relationship with overstory BA. Overstory conspecific quadratic mean diameter (QMD) followed a U-shaped distribution with peak regeneration density, where overstory QMDs were at their lowest or

highest observed for that species. Douglas fir was an exception to this rule though, and regeneration density declined linearly with increasing overstory Douglas fir diameter. U-shaped distributions for overstory QMDs likely resulted from our 4 m height cutoff separating regenerating from overstory trees.

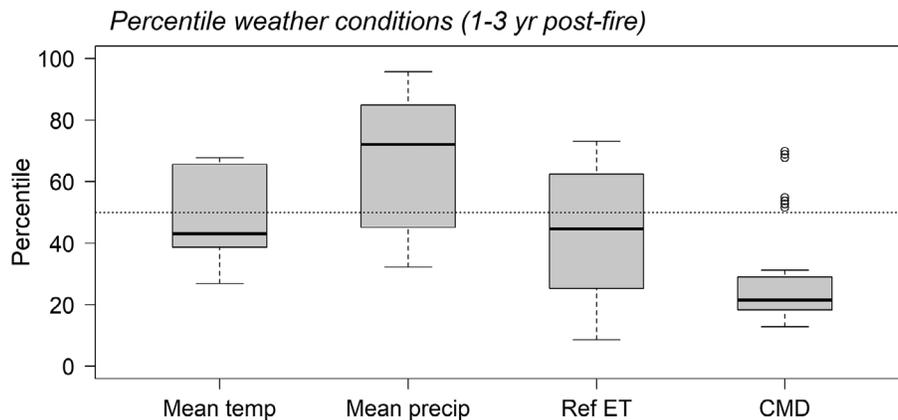


Fig. 7. Mean percentile postfire (1–3 yr) weather conditions for sampled points ($n = 248$). Ref ET is reference evapotranspiration, and CMD is climatic moisture deficit.

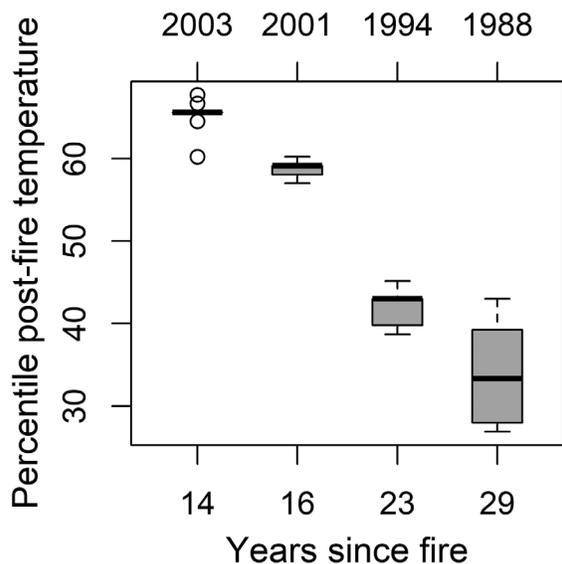


Fig. 8. Relationship between percentile postfire temperature conditions and the number of years between the fire and field sampling in 2017. Pearson's correlation coefficient between the continuous values of these variables was -0.961 . Boxplots were constructed following the description in Fig. 4.

Distance to seed tree was a significant determinant of regeneration density for all species. Regeneration density declined with increasing distance to seed trees up until 200–300 m, where this effect leveled off. Engelmann spruce was exceptional to this trend, showing an inhibition response; density increased from 0 to 200 m and declined thereafter.

Apparent competition from grass also influenced regeneration density, with most coniferous species displaying a negative linear relationship with maximum grass height. Ponderosa pine density, however, increased to a maximum grass height of 0.6 m and decreased with taller grass. Engelmann spruce showed a U-shaped trend, where density was lowest for maximum grass heights near 0.6 m.

Comparison with Stevens-Rumann et al. (2018)

To put our study within a broader context, we compared our results with a recent meta-analysis of postfire regeneration in the U.S. Rocky Mountains by Stevens-Rumann et al. (2018; hereafter, CSR). To begin, we subset the CSR and our datasets to match fire year (1988–2003) and temperature–precipitation data space, which resulted in a sample size of 253 for the CSR and 206 for our data (Fig. 9A). With the reduced datasets, we found that regeneration density was higher and failure rates lower in our study compared to CSR (Figs. 9B, C, E). Within the subsets (as described above), the CSR study included 55% of plots with tree density ≤ 350 stems/ha compared to only 12% of our study plots. Regeneration failure occurred in 31% of the CSR plots and 1.5% of our study plots (Figs. 9B, C). The reduced CSR data included dry ponderosa pine, dry mixed-conifer, and moist mixed-conifer forest types, which showed regeneration failure rates of 52% ($n = 126$), 22% ($n = 50$), and 1% ($n = 77$), respectively. All the dry ponderosa pine forest types

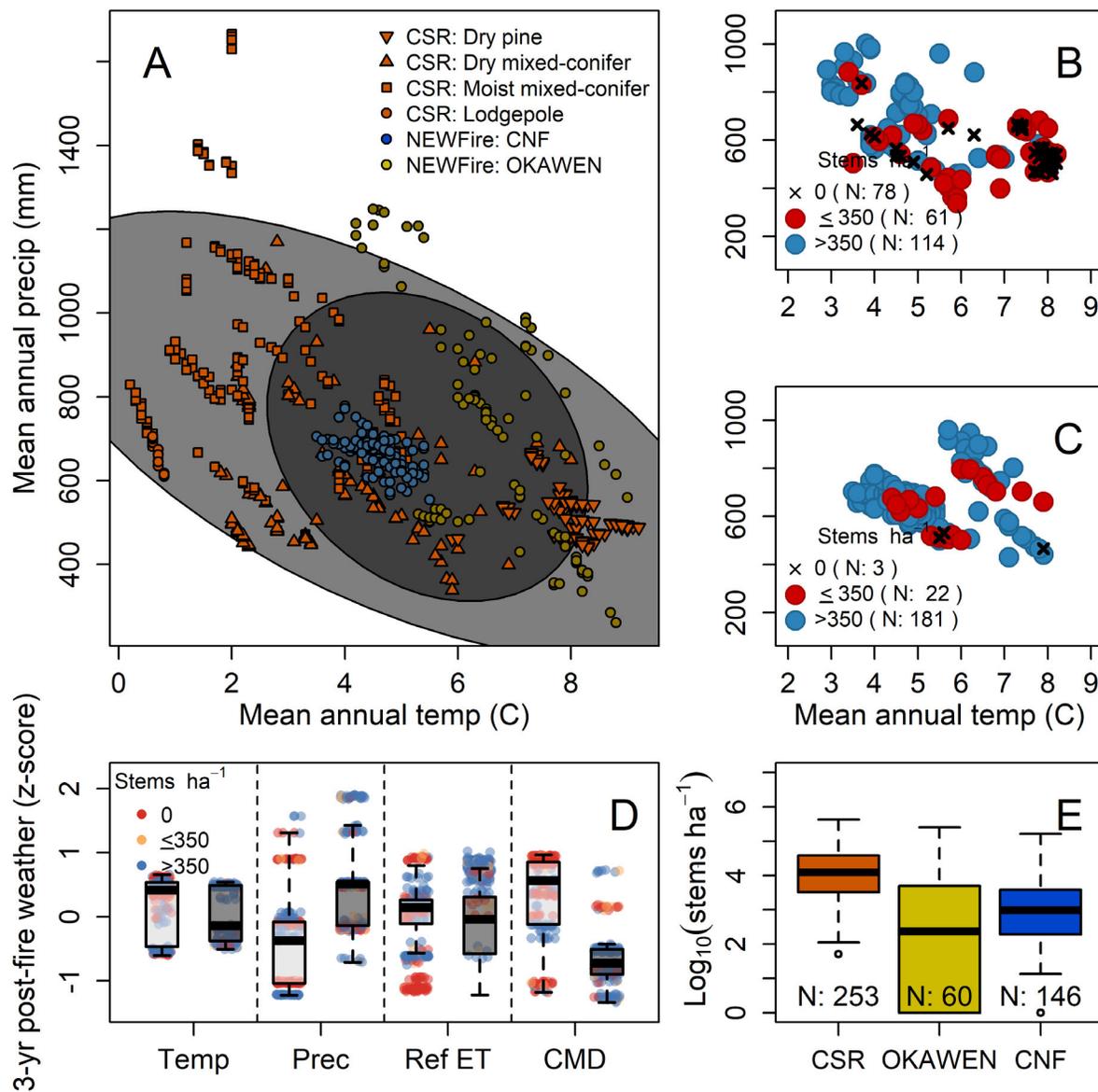


Fig. 9. Comparison between the current study (NEWFIRE) and those of Stevens-Rumann et al. (2018; hereafter, CSR) that burned within the same time frame (1988–2003). (A) Distribution of study plots in climate space. Data ellipses represent the normal 90% for each dataset. (B) Distribution of CSR plots zoomed in to the overlap area in (A). (C) Distribution of NEWFire plots zoomed in to the overlap area in (A). (D) Three-year postfire weather (z-scores) for CSR (left, white boxes) and NEWFIRE (right, gray boxes). Scatterplots represent regeneration density at each plot. (E) Boxplot of regeneration densities for CSR and NEWFIRE within the CNF (CNF) and ONF (OKAWEN).

were sampled in the Colorado Front Range, and these plots represented 85% of all failures reported in the reduced CSR dataset.

We note too in the CSR dataset that postfire annual moisture deficits were significantly

greater over the 2000–2015 period as compared to 1985–1999 period. Their results suggested that increasingly unfavorable postfire growing conditions corresponded with lower seedling densities and increased regeneration failure. Furthermore,

they suggested that many of the driest forest plots already occurred at the edge of their climatic tolerance and were thus prone to conversion to nonforest after fires.

DISCUSSION

Recent studies of natural regeneration after large and severe wildfires in the western United States suggest that forests may not be regenerating across many burned landscapes (Stevens-Rumann et al. 2018, Davis et al. 2019, Stevens-Rumann and Morgan 2019). In Washington State alone, a total of 1.3 million ha have burned between 2009 and 2018, creating uncertainty regarding the future trajectories of previously forested landscapes. We surveyed regeneration in northeastern Washington State across two broad environmental gradients to quantify 15- to 30-year trends in postfire regeneration. Approximately 85% of our sample plots were well-stocked (>350 stems/ha), and over two-thirds had >1000 stems/ha. High variability in regenerated tree size, stocking density, and species composition was observed among fire severity, salvage harvesting, and forest PVT, but few incidences of regeneration failure were observed. Biophysical controls on regeneration densities were apparent and highlighted species-level tolerances to climatic gradients and postfire weather conditions, as well as seed dispersal limitations.

Long-term climate effects on postfire regeneration

Climate is a primary top-down driver of vegetation community structure and composition. Climate contributes controls on variability in life-form and species dominance, which are a function of individual tolerances to temperature, precipitation, and solar radiative forcing. For example, in the Front Range of Colorado, Chambers et al. (2016) found postfire tree recruitment was hindered by high temperatures, low precipitation, and moisture deficit associated with low elevation sites. Dodson and Root (2013) similarly found conifer regeneration was limited at lower elevations by climatic moisture stress following the 2002 Eyerly Fire in eastern Oregon (Dodson and Root 2013). Similar results have been found in other parts of the U.S. Rocky Mountains (Chambers et al. 2016, Donato et al. 2016, Urza and Sibold 2017) and central Sierra Nevada

(Collins and Roller 2013, Welch et al. 2016). In many of these studied areas, authors have either observed or predicted near-term transitions to alternative nonforest states, a trend that is projected to increase under future warming (McDowell and Allen 2015).

The geographic region studied here represents the northeastern Cascades and Okanogan Highlands, which are poorly represented in the postfire regeneration literature (Stevens-Rumann and Morgan 2019), and which are well within the climate and environmental space of the dominant coniferous species of the region (Appendix S1: Fig. S6). Within this context, long-term trends from our study demonstrate that postfire regeneration was adequate to forest recovery across the sampled forest types, even following severe fire. Furthermore, this regeneration has survived through a recent 116-week drought in central and eastern Washington (January 2014–March 2016; obtained from the U.S. Drought Portal <https://www.drought.gov/drought/states/washington>; Svoboda et al. 2015).

Nonetheless, a certain amount of caution is advised when interpreting the high levels of regeneration reported in our study. Our results do not purport that postfire regeneration will be abundant after future fires in north-central Washington or in similar locations that occupy similar climatic niches. The intent of our study was to better understand the mechanisms that drive postfire tree regeneration in an effort to help managers understand where to focus replanting efforts after future fires. Tree regeneration patterns will likely change in the future under a warming climate and well-documented increases in the amount and patch sizes of high-severity fires. However, the variability in regeneration density and species composition that we observed across the climatic and fire severity conditions provides clues to what we might expect going forward.

Another important consideration for our study was the use of a 4 m height cutoff to designate postfire regeneration. We did not use destructive sampling or bud scar counts to resolve establishment dates for each tallied stem (Davis et al. 2019, Littlefield 2019, Stevens-Rumann and Morgan 2019), and therefore, the 4-m cutoff was used because it was easily employed in the field and was based on preliminary reconnaissance of the

sites. However, it is likely that we underestimated postfire regeneration as some stems >4 m were likely present across the study domain. No evidence of a systematic bias in our estimates exists, and given the overwhelming abundance of regeneration found in our study, our conclusions regarding observed effects of fire severity, salvage, and forest type are supported by the data.

Mean annual temperature (MAT) was a leading predictor in our GAMs after variable reduction and was significant for all species but ponderosa pine. A sharp decline in regeneration abundance was observed for most species, particularly for regeneration on the CNF (Fig. 6). The environment sampled on the CNF was notably cooler than the sampled area on the ONF, suggesting that the higher densities observed under these more benign climate conditions could shift under future climates. In the Pacific Northwest, temperatures will likely increase by 2.4°C (RCP 4.5)–3.2°C (RCP 8.5) by mid-century (Snover et al. 2013), and our models predict a median reduction in regeneration density of nearly 2000 stems/ha within this MAT range. In a similar study, Tepley et al. (2017) predicted that under a RCP 8.5 warming scenario half of the area currently capable of supporting mixed-conifer/mixed-evergreen forests will be at risk of low recruitment by the end of the century in the Klamath Mountains.

While forest type was included as a factor in our study design, it was not a significant variable for any species, with the exception of Engelmann spruce. This was due in large part to the inclusion of the environmental cofactors in the GAMs. Regeneration abundance was more directly controlled by environmental gradients, and our results apply across the sampled PVTs. Due to complex topography and strong temperature and precipitation gradients, forested watersheds in central and eastern Washington generally contain a blend of dry, moist, and cold forests. These three forest types have different historical fire regimes, forest development patterns, climate, and tree species mixes that have different seed production and dispersal strategies. Postfire regeneration can thus differ as well. Most fires, even small ones, burn across all of these forest types. Thus, managers need to understand how postfire regeneration will differ in different parts

of a fire and by severity patch size. While these three PVTs represent a gradient of conditions, they are useful for communicating differences to managers.

Postfire weather variability

Temporal variability in climate forcing over both the short- and long-term can affect site suitability for a given species, particularly after disturbances, where regeneration is most vulnerable to fluctuations in precipitation and temperature. The abundant regeneration observed in our study appears due, in part, to more benign postfire weather conditions. Median precipitation was well above the long-term average (72nd percentile), while temperature (43rd) and moisture deficit (22nd) were well below normal, suggesting that postfire establishment was unimpeded by water stress during critical regeneration years. Within this range of conditions, most species in our study favored warmer and moister conditions in the years following fire. However, the response to postfire temperature differed across NFs, with most species exhibiting a positive relationship with postfire temperature on the cooler CNF plots and a negative relationship on the warmer ONF plots. These results underscore the observation that regeneration response to environmental conditions is site-, species-, and postfire climate-specific. Western larch showed the greatest sensitivity to postfire temperature conditions, showing a distinct positive trend with postfire temperature, and this was the leading variable in the GAM ($F = 22.97$, $P < 0.001$). However, caution should be taken when interpreting the postfire temperature results given the high correlation with time since fire (i.e., percentile postfire temperatures increased as time since fire increased). Higher predicted regeneration densities for more recent fires could be the result of less accumulated time for density-dependent mortality, competitive exclusion, and other potential mortality agents to affect abundance. The fact that we saw a similar decline in regeneration abundance for large conifer regeneration on the ONF suggests that higher postfire temperatures on these plots limited regeneration. Regenerating stems of this size likely have surpassed mortality related to early establishment and may be a better indicator of postfire weather effects on regeneration abundance.

In comparison, Stevens-Rumann et al. (2018) showed declines in regeneration relative to pre-fire densities, particularly for fires after 2000. The authors attribute these findings to significantly greater annual moisture deficits in recent years, particularly for dry forests at the edge of their climatic tolerances. Accordingly, when we subset the data from Stevens-Rumann to match the climatic space and temporal range of our fires, regeneration failures in their study were generally clustered near the warmest temperatures sampled (i.e., $>7^{\circ}\text{C}$), which corresponded with dry ponderosa pine types sampled exclusively in the Colorado Front Range. Plots with $\text{MAT} > 7^{\circ}\text{C}$ were not well represented in our dataset—only 18% of our plots had $\text{MAT} > 7^{\circ}\text{C}$, all of which fell on the ONF. Previous studies in this region show that mild postfire conditions with moderate temperatures and high precipitation favor episodic ponderosa pine regeneration events (League and Veblen 2006, Keyes and González 2015, Rother and Veblen 2017). These studies show abundant ponderosa pine regeneration is contingent upon coherence of benign post-fire weather and prolific cone production by residual ponderosa pines. In our study, ponderosa pine was an exceptional species with regard to its environmental (in)tolerance; it was neither sensitive to MAT nor postfire weather conditions and was abundant in nearly all topographic settings but southwest-facing. A significant relationship between ponderosa pine density and MAP suggested that recruitment peaked around 800 mm, which was well within the range of conditions present on most NF lands in eastern Washington (Fig. 3). In this context, ponderosa pine will have significant opportunity to occupy new sites (excluding low elevation sites) as the climate warms in eastern Washington.

At higher elevation sites, regeneration is limited by cold-induced photoinhibition and frost damage and regeneration is therefore favored under warmer and wetter conditions (Harvey et al. 2016, Urza and Sibold 2017). Interactions among climate variables and disturbances make predictions of future vegetation dynamics highly uncertain, particularly where facets of future projected climate have counteracting effects on species (e.g., lodgepole pine regeneration favors lower precipitation but is limited by warm temperatures; Urza and Sibold 2017). Future

projections of precipitation in the Pacific Northwest show high year-to-year variability and increased summer drying (Snover et al. 2013). Given the sensitivity shown by most species sampled here to fluctuations in postfire temperature and precipitation, our results suggest that high variability in future seasonal and annual weather may lead to challenges for the establishment and growth of dominant tree species in the region.

Fire severity and distance to seed source

Much uncertainty in postfire vegetation dynamics derives from the total area and non-random spatial distribution of large, high-severity patches (Stevens et al. 2017), and from the interpretation of actual tree mortality from the spectral changes of pre-fire and postfire Landsat data (Furniss et al. 2019, 2020). Large patches pose particular challenges for most conifers, which rely on seed dispersal over relatively short distances (Collins et al. 2017). High-severity fires can also influence microclimate and soil properties, as well as encourage the establishment and growth of shrub species. Historically, most wildfires in the region burned more frequently and at low to moderate severity creating a heterogeneous patchwork of forest successional stages across the landscape (Perry et al. 2011, Stevens et al. 2017). Furthermore, even within areas interpreted as burned through Landsat-derived analysis, small ($1\text{--}100\text{ m}^2$) unburned patches in low- to moderate-severity fires would have provided increased survivorship of saplings within the burned matrix (Meddens et al. 2016, Blomdahl et al. 2019). Large high-severity patches, while accounting for most of the area burned, were less common in most environments, and viable conifer seed sources were generally in close proximity for regenerating the post-disturbance landscape (Hessburg et al. 2007, Stevens et al. 2017). To the extent that these large high-severity patches lacked even small unburned areas within them, seed dispersal distances would be longer. Long distance to a reliable seed source can impede regeneration, favoring long-term dominance of ruderal or nonforest species (Haire and McGarigal 2010), or species with serotinous cones, such as lodgepole pine. Seed dispersal limitations for conifers in the western United States are well known (Clark et al. 1999, Welch et al. 2016, Haffey et al.

2018) and confirmed by our study. Littlefield (2019) showed significant declines in juveniles at distances >75 m one decade after stand-replacing fire in eastern Washington. This was similar to the median distance to seed tree observed on high-severity plots in our study (68 m). Distance to seed tree was an important predictor variable for most species in GAM models, and regeneration abundance clearly declined as a function of distance to seed source, for all species.

Lodgepole pine regeneration favored high severity in our study (Appendix S1: Fig. S6). It is a serotinous species in this region and, therefore, less dependent upon wind dispersal compared with other conifers. When postfire weather is favorable, lodgepole pine regenerates at very high densities in high-severity patches, even when few or no seed trees survive (Turner et al. 2003). In our study, only 12% of plots were within 60 m of a lodgepole pine seed tree, and only 17% had lodgepole pine residuals within the maximum distance (450 m) measured in the field, suggesting that establishment was less dependent on wind-dispersed seed rain and more likely associated with serotiny. Consistent with our GAM model results (Fig. 6), lodgepole generally does not disperse at distances >60 m (Lotan 1976). This suggests that seed rain from surviving non-serotinous trees may play a role, albeit a lesser one.

Severity was not a significant factor determining regeneration densities of either western larch or Engelmann spruce (Fig. 5). Both species have lightweight, wind-dispersed seeds that can travel long distances (>250 m; Burns and Honkala, 1990). Engelmann spruce seedlings are sensitive to excessive solar radiation, but are capable of regenerating in the shade of standing dead trees and logs. Western larch seedlings are susceptible to high soil temperatures and drought. Where viable seed sources were readily available in proximity (<200–300 m), limits on regeneration success were most likely related to prevailing postfire climate conditions and availability of favorable microsites.

Salvage harvesting

Given the scale and severity of wildfires across the western United States, land management agencies are tasked with restoring desired surface fuel levels in the postfire landscape and

recouping lost economic value, while minimizing potential negative impacts to aquatic and terrestrial habitats (Beschta et al. 2004). Salvage harvesting can have both positive and negative ecological effects depending on the objectives, scale, and intensity (McIver and Starr 2001, Beschta et al. 2004, Keyser et al. 2009). It can impede successful regeneration by physically injuring or burying established young seedlings, altering seedbeds through surface fuel deposition, and reducing or eliminating viable seed sources following harvest (Donato et al. 2006, Greene et al. 2006, Keyser et al. 2009). Alternatively, soil disturbances related to harvests can improve seedbeds for conifer establishment by exposing mineral soil (Greene et al. 2006), reducing shrub and herbaceous cover, and disrupting hydrophobic soils (McIver and Starr 2001). Effects of salvage harvesting on coarse woody debris accumulation and subsequent fire behavior are mixed and are a function of fire severity, postfire forest structural characteristics, and time since fire (Ritchie et al. 2013, Dunn and Bailey 2015).

Our results show a neutral to slightly positive effect of salvage logging on total regeneration density >15 yr after fires. The positive salvage response was more prevalent on the CNF, where suitable climate and postfire weather conditions combined with exposed mineral soils. It is not clear why this effect was less apparent on the ONF, but it may be either due to warmer mean temperatures on these plots inhibiting regeneration across salvaged and unmanaged plots alike, or due to relative differences in salvage harvest operations.

A possible explanation for increased regeneration abundance on salvage harvested plots may be related to our site selection criteria, which included only salvage harvested sites with no planting. The National Forest Management Act (NFMA 1976) requires that salvage harvested forests on NF lands be certified as stocked within 5 yr of harvesting, which necessitates subsequent tree planting where natural regeneration does not meet stocking requirements (North et al. 2019). Thus, salvaged sites with tree densities below minimum stocking may be rare in this region. However, in the central Sierras, Collins and Roller (2013) found that salvaged sites without planting exhibited the lowest regeneration

densities compared to no treatment and salvage followed by planting. In their study, postfire treatment was the leading variable explaining *Pinus* spp. regeneration densities. In our study, we excluded sites where planting had occurred to assess natural regeneration potential after fires. Thus, our results do not provide evidence that salvage harvests increase tree regeneration across all environments. Regeneration densities in our study were generally quite high and more than sufficient for forest recovery, with or without salvage. Our results do, however, demonstrate that higher levels of natural regeneration occur on salvaged sites when seed source is available, postfire weather is favorable, and harvest operations do not negatively affect soil. Moreover, our results confirm that under the evaluated conditions, salvage harvesting does not categorically impede long-term forest regeneration and postfire resilience.

Management implications

The great majority of plots measured in this study are on a successional trajectory toward an overly dense forest condition. Little evidence of complete regeneration failure was apparent for the postfire landscapes of our study area, suggesting that nonforest vegetation did not significantly inhibit tree regeneration, establishment, or growth across the sampled environmental gradients. However, the applicability of our results to future fires is less clear. We found that postfire weather in our study was favorable for tree regeneration for the fires we studied. In contrast, postfire weather for more recent fires has much hotter and drier compared to the previous 30 yr, and the prospects of warmer and drier future conditions are clear. In a recent detailed assessment of the climatic drivers of postfire regeneration across much of the western United States, Davis et al. (2019) found that certain seasonal and annual climate variables have recently crossed key physiological tolerances relevant to successful Douglas fir and ponderosa pine regeneration. The authors suggested that future climate change may lead to ecosystem transitions to nonforest types in some affected forests.

Our results suggest that successful regeneration for different coniferous species will be contingent upon synchrony between sufficient seed crops from mature surviving trees, and a

favorable 2- to 5-yr period when temperature and precipitation levels are moderate and within seedling tolerances. However, this does not preclude subsequent drought-induced die-off events. While climate projections indicate an overall trend toward warmer and drier conditions, there will still likely be periods of more favorable climate for tree regeneration due to multi-annual climatic oscillations in ENSO and the PDO. However, seed dispersal limitations will likely increase as the size and severity of fires continue to increase, particularly for species that are primarily wind-dispersed. Planting may be used to foster the development of these species within burned areas, where long distances to mature canopy trees exist (North et al. 2019), and where projected MAT and MAP conditions are deemed suitable to successful tree regeneration and ongoing forest development. However, in areas that are less than suitable for conifer establishment, managers might consider avoiding replanting and allowing a smooth transition to nonforest conditions. Likewise, where MAT and MAP suggest changes in site suitability for certain conifers, managers might also consider assisting in these transitions by replanting species that will be better adapted to the shifting conditions (North et al. 2019, Stevens-Rumann et al. 2019, Stevens-Rumann and Morgan 2019).

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