FINAL REPORT

Impacts of burn severity, microclimate, and soil properties on initial post-fire tree regeneration

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List of Abbreviations/Acronyms

VPD – Vapor Pressure Deficit
USFS – United States Forest Service
PP – Propagule Pressure
DSS – Distance to Seed Source
DEF – Climatic water deficit
HLI – Heat Load Index
RMSE – Root Mean Square Error
PSME – *Pseudotsuga menziesii* (Douglas-fir)
LAOC – *Larix occidentalis* (Western larch)
PICO – *Pinus contorta* (Lodgepole pine)

Keywords

Climate, Fire Severity, Fire Effects, Post-fire Recovery, Microclimate, Environmental Gradient, Mixed-Conifer Forest, Rocky Mountains, Seedling Regeneration, Seedling Mortality, Soil Nitrogen

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1. Abstract

Climate warming and increased frequency and severity of wildfires have the potential to undermine forest resilience to wildfires. Species demography implies that vegetation responses to fires depend on a series of population filters, including adult survival, seed availability, germination, establishment, and survival; the impacts of these varying filters will ultimately determine post-fire forest trajectories. The objectives of this study were to (1) assess how fires affect biologically-relevant microclimate conditions; and (2) evaluate the relative influence of seed availability, microclimate, and fire effects (on overstory, understory, and soil conditions) on post-fire seedling demography. This study was conducted in two large, lightning-ignited wildfires from the regionally extensive fire season of 2017 in northern Rocky Mountain mixed-conifer and subalpine forests. Conifer seedling density, survival, and growth were tracked in the first three years post-fire in 69 plots spanning environmental and fire severity gradients, and microclimate conditions were measured in a subset of those plots. We found that sites burned at high severity had, on average, 3.7 °C higher daily maximum temperatures and 0.81 kPa higher daily maximum VPD compared with adjacent unburned forest. In addition, we found that seedling regeneration was abundant, with a median density of 2,633 ha^{-1}. Variables describing seed availability, microclimate, overstory fire severity, understory vegetation, and soil nitrogen availability accounted for 75% of the variability in seedling density among plots. The robust regeneration observed in this case is likely due, in part, to moderate post-fire climate conditions, which supported high annual survivorship rates exceeding 50%. Our results highlight the importance of fine-scale heterogeneity in fire effects for supporting post-fire tree regeneration, which alter microclimate conditions and create diverse microsite environments for seedlings. These results reveal the importance of residual structures in burned areas to buffer microclimate conditions, and they highlight future research needs to identify favorable microsites for reforestation efforts, particularly as the climate warms. This study contributes to an improved understanding of the mechanisms of forest resilience to wildfires and demonstrates the utility of a demographic perspective for anticipating forest responses to future wildfires under changing environmental conditions.

2. Objectives

The objective of this work was to address key uncertainties about the drivers of early post-fire seedling regeneration across environmental gradients in the northern Rocky Mountains, a region experiencing increasing fire activity (Littell et al. 2009, Westerling 2016) and reduced tree regeneration in recent decades (Stevens-Rumann et al. 2018). Our goals were to:

1. Quantify how moderate- and high-severity wildfire impact microclimate conditions across biophysical gradients.
2. Evaluate the relative influence of different aspects of fire severity, including impacts on seed availability, microclimate, and overstory, understory, and soil conditions, on post-fire conifer seedling demography.

We successfully met the above objectives. We developed datasets of microclimate and soil nitrogen availability over the first two growing seasons post-fire, as well as conifer seedling annual recruitment, survivorship, and height growth over the first three years post-fire. We used these data to quantify fire effects on microclimate, and to elucidate the influence of microsite factors on early post-fire seedling regeneration. The results of Objective 1 are published in Wolf et al. (2021) and briefly described here, and the results of Objective 2 are in preparation for publication and presented in detail in this report.

This research directly addressed the topic area of fire effects and post-fire recovery and is relevant to the management of fire-prone forests. Clarifying the role of microsite conditions in post-fire seedling recruitment provides useful information for managers in planning reforestation activities. Further, supporting landscape resilience to fire is a core management goal under the National Cohesive Wildland Fire Management Strategy (Wildland Fire Executive Council 2014). This research also contributes to an improved understanding of the mechanisms of forest resilience to wildfires, which could aid efforts to anticipate and mitigate the impacts of rising temperatures and more frequent fire in Western forests.

3. Background

Forest ecosystems and the services they provide are changing due to the combined impacts of warmer, drier climate conditions and increased wildfire frequency and severity resulting from anthropogenic climate change and past land use and management policies (van Mantgem et al. 2013, Westerling 2016, Abatzoglou and Williams 2016, McKenzie and Littell 2017, Holden et al. 2018, Parks and Abatzoglou 2020). Post-fire tree regeneration is a critical stage of community re-organization affecting forest composition and structure over decades or longer (Turner et al. 2016, Urza and Sibold 2017). In the western U.S., reduced tree regeneration after fires has been documented in a variety of forest ecosystems in recent years (Stevens-Rumann et al. 2018, Andrus et al. 2018, Turner et al. 2019, Rodman et al. 2020a), a trend which is expected to continue under climate warming (Kemp et al. 2019, Davis et al. 2020).

A demographic framework can be applied to address the challenge of understanding the dominant controls of forest trajectories after wildfires (Davis et al. 2018). This framework emphasizes that tree regeneration is the net result of seed dispersal and seedling germination, establishment, and survival over multiple years after a fire, which in turn depends on a suite of biotic and abiotic factors that create filters at each demographic stage (Fig. 1). These demographic processes have rarely been quantified for western conifer species after wildfires, and the relative importance of the controls at each stage of community reorganization are untested. A more detailed understanding of the mechanisms governing post-fire regeneration is needed to be able to anticipate circumstances in which forests may be resilient or not to future fires, and why.

A well-developed body of evidence highlights the importance of seed availability and favorable climate conditions for post-fire tree regeneration (e.g., Kemp et al. 2016, Harvey et al. 2016, Davis et al. 2019b, Stevens-Rumann and Morgan 2019). However, the impacts of fire severity on local microclimates have rarely been quantified. Regional climate trends are mediated both by local topography (Dobrowski 2011) and vegetation (Zellweger et al. 2020) to create microclimate conditions. With greater aridity and fire activity leading to reduced canopy cover and evapotranspiration, microclimatic buffering will decline in fire-affected areas (Davis et al. 2019a, Wolf et al. 2021). Thus, climate and fire severity interact to determine the post-fire conditions experienced by seedlings, and greater exposure to microclimatic extremes in high-severity patches compared with areas of lower adult mortality could alter regeneration patterns.

In addition, fire plays an important role in providing opportunities for regeneration through increased availability of resources such as light, soil nutrients, and seed beds, with many shade-intolerant seed-obligate conifer species dependent on fire for reproduction (York et al. 2003, Ehle and Baker 2003, Johnstone and Chapin 2006, Moghaddas et al. 2008, Steed and Goeking 2020).

While the effects of seed availability and climate variability on regeneration are generally well-documented, responses to these additional aspects of fire severity are more varied among species and challenging to tease apart (Urza and Sibold 2017, Korb et al. 2019, Rodman et al. 2020b). For example, high-severity fire results in more stressful (i.e., warm-dry) microclimate conditions which could inhibit regeneration, as well as reduced organic layer depth and a pulse of nutrient availability (e.g., Turner et al. 2007), which could enhance regeneration (Dzwonko et al. 2015). These changes have contrasting effects on seedling recruitment and typically covary with propagule availability (Brown et al. 2015), complicating interpretations of the effects of fire severity on regeneration at the microsite scale.

The potential for increased fire frequency and severity highlights the pressing need to understand mechanisms of forest resilience to wildfires, and how they differ among species and across environmental and fire severity gradients. We use an ecologically-based sampling approach to quantify the impacts of wildfire on microclimate conditions and evaluate the dominant controls of post-fire seedling regeneration in mixed-conifer and lower subalpine forests of the Northern Rockies. We monitored microclimate and tracked seedlings in two wildfires in western Montana over several years post-fire, and estimated rates of seedling establishment,

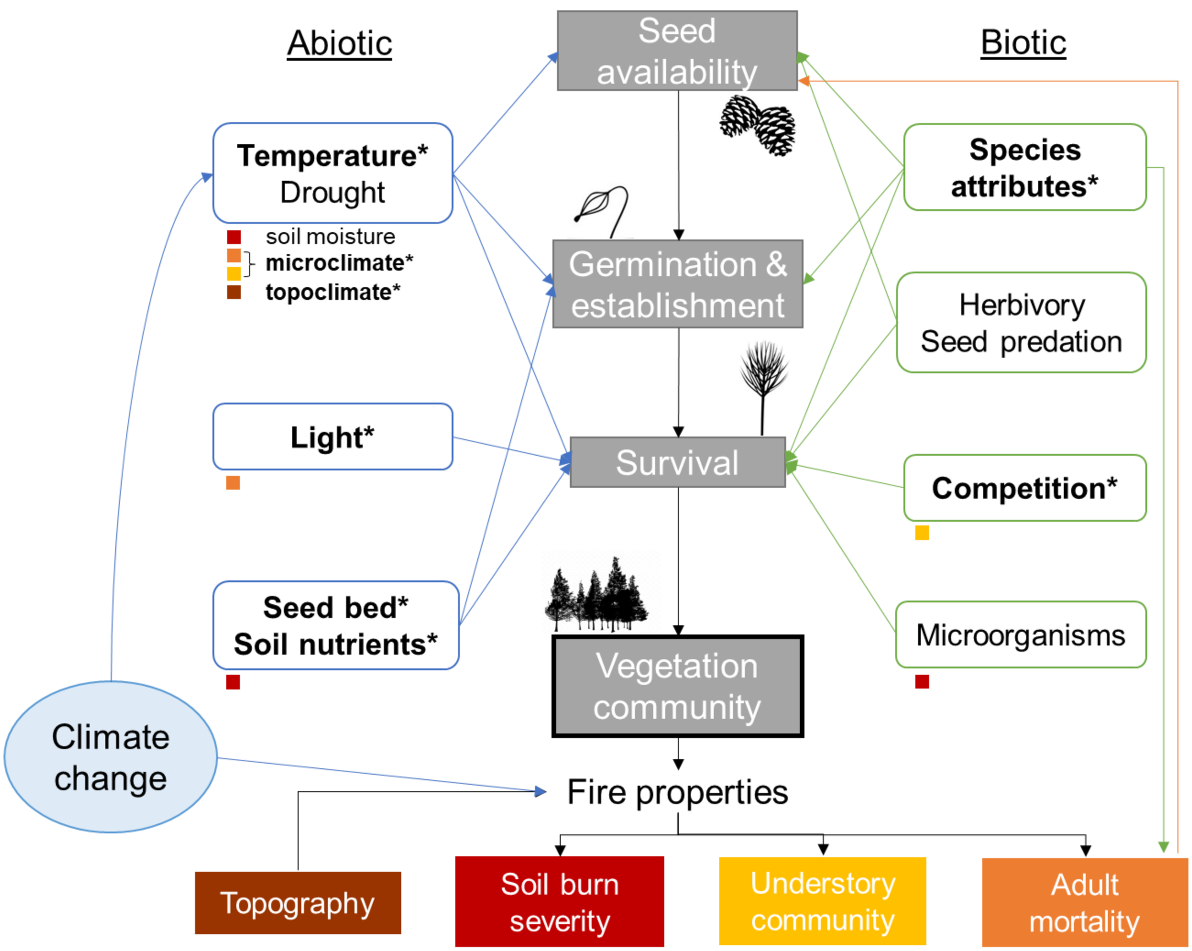

Figure 1. Conceptual figure of the abiotic and biotic controls of seed-obligate conifer regeneration and how they are affected by fire, adapted from Davis et al. (2018). Climate change is expected to increase growing-season temperatures and aridity, and increase the frequency of fire and the proportion of high-severity fire. Factors that are bold with asterisks are accounted for (directly or indirectly) in this study.

survival, and growth in study sites stratified by topographical position and fire severity to capture a range of abiotic and biotic conditions. This study informs expectations of forest responses to the combined impacts of climate warming and changing fire regimes and highlights potential avenues of forest resilience.

4. Materials and methods

To address our first research question (see above), we monitored microclimate in burned and unburned plots to quantify the impacts of moderate- and high-severity fire on below-canopy atmospheric conditions. To address our second research question, we quantified early post-fire seedling demography in these and additional study plots to elucidate the relative importance of controls of tree regeneration at each demographic stage and to test how conifer regeneration is influenced by fire severity through microclimate and overstory, understory, and soil conditions.

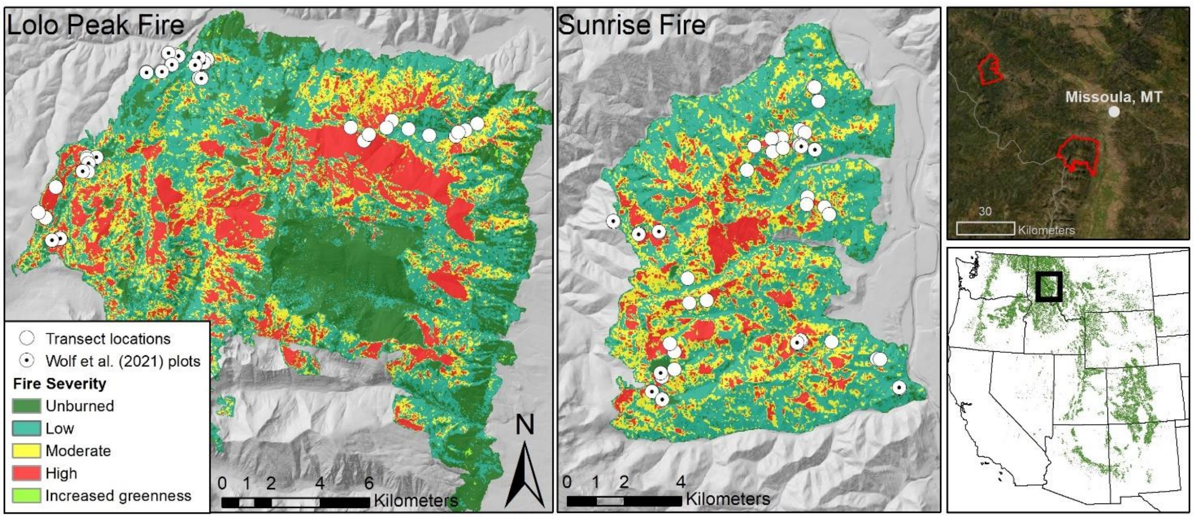

Figure 2. Map of study area and sample sites in the Lolo Peak (n = 35 transects) and Sunrise (n = 34) fires. Sample sites include those that are unique to this study (white circles) and those which also have microclimate measurements published in Wolf et al. (2021) (white circles with black dots). Fire severity classifications are from the Monitoring Trends in Burn Severity project (MTBS 2019), and satellite imagery is from Esri. The green area in the lower right panel delineates the extent of Rocky Mountain forest cover, as defined by LANDFIRE's National Vegetation Classification product (landfire.gov).

4.1. Study area and site selection

We sampled in two large wildfires in the Bitterroot Mountains of Montana (Fig. 2). The Lolo Peak and Sunrise fires burned across c. 22,000 and 11,000 ha, respectively, from July to September, 2017, with 15-20% of the area classified as high-severity fire (MTBS 2019). The study area spans forests dominated by ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and western larch (*Larix occidentalis*) at low to mid elevations (i.e., <1500 m) and xeric aspects, as well as forests dominated by lodgepole pine (*Pinus contorta var. latifolia*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) at mid to high elevations (c. 1500 - 2200 m). Fireweed (*Epilobium angustifolium*) is often dominant in recently burned sites. Soils are primarily gravelly, well-drained inceptisols derived from volcanic ash overlying metasedimentary, granitic, or mica schist parent material (Bailey 1995, Soil Survey Staff 2017). Mean annual temperature averaged 5.1 °C and total annual precipitation averaged 986 mm across the study sites from 1981-2010, with 22% of precipitation occurring during the growing season of June to September (PRISM Climate Group 2015).

We sampled seedling demography in 69 plots spanning biophysical and fire severity gradients, a subset of 46 of which also had microclimate measurements. Sites were stratified by elevation (low [1000-1500 m] and high [1500-2000 m]), aspect (northern [315-45°] and southern [135-225°]), and fire severity (unburned, moderate, high). Potential study areas were identified in using USFS Burned Area Reflectance Classification soil burn severity maps (30-m resolution), and exact sampling locations were randomly identified in a geographic information system to satisfy selection criteria (Wolf et al. 2021). Planting by USFS overlapped with seven plots; however, planted seedlings were initially easily distinguishable from natural regeneration based on size, and were marked to maintain that distinction and excluded from analyses.

4.2. Field measurements

Plots were sampled in the first three years after the fires (2018 - 2020) to measure aspects of seeding demography, microclimate conditions, and soil nutrients. Seedling density, overstory tree density (defined as all trees >1.37 m height), and live and dead basal area were measured within 60-m-long belt transects that varied from 1 to 10 m in width, depending on the number of seedlings present. We grouped seedlings of *Abies grandis* and *A. lasiocarpa* together in our analyses because *A. grandis* was present in low numbers, and distinguishing between germinant seedlings of these species was not always possible. Seedlings are defined as having established after the 2017 fires; burned sites were selected to have near-complete surface fire to minimize errors counting seedlings that established pre-fire, but counts in unburned sites rely on age estimates. Seedling age was estimated based on height, presence of cotyledons, and bud scars (Urza and Sibold 2013). We focus our analyses on total seedling density in the final sampling year in burned sites (pooling seedlings of all ages) to minimize uncertainty from age estimates (Hankin et al. 2018).

Within each transect, 6-10 permanent 1-m^2 subplots were marked using stakes for repeat sampling. Live and dead canopy cover and the distance to the nearest live tree were measured at each subplot, and ocular ground cover measurements were taken to estimate cover of bare ground or rock, litter, coarse woody debris, moss or lichen, forbs, grasses, and shrubs to the nearest five percent. We monitored individual seedlings within 2-10 subplots, with the goal of tracking 10-100 seedlings per plot. Seedlings were marked and height was measured to track annual survivorship and vertical growth.

4.3. Microclimate measurements

To characterize post-fire microclimate conditions experienced by seedlings, we deployed sensors in a subset of 15 plots in 2018 and 40 plots in 2019. Sensors recorded near-ground atmospheric temperature and relative humidity from June to September. Hourly data were used to calculate daily maximum temperature (°C) and vapor pressure deficit (VPD, kPa) in each plot. We used these data in two ways. First, to evaluate the effects of fire on microclimate, we compared microclimate in burned (n=22) and unburned (n=11) plots (Wolf et al. 2021). These data were used to calculate the difference in daily maximum temperature and VPD between paired burned and unburned plots in similar biophysical settings, as a metric of the impact of moderate- and high-severity fire on near-ground microclimate conditions. Secondly, we used all microclimate data from 2019 (n = 40 plots) to develop microclimate metrics as predictors of post-fire seedling demography (Table 1). To extrapolate beyond the subset of plots with field microclimate measurements, we used linear mixed effects models to predict daily microclimate conditions in all plots over the three study years. Daily predictions were aggregated to the absolute (T_{max}) and the average (T_{avg}) maximum daily temperature over the growing season in each plot and year, to match the temporal scale of seedling regeneration data.

4.4. Seed availability, topoclimate, and fire severity metrics

We used two metrics of seed availability: field-measured distance to seed source (*DSS*), and a distance-weighted propagule pressure metric (*PP*) based on post-fire satellite imagery (Table 1) which captured variability in the abundance of potential seed trees. Presence of live trees after fire was identified visually in 10 m by 10 m grid cells within a 200 m radius circle centered on each plot, using post-fire images from ESRI (0.5-m resolution) or NAIP (1-m resolution). To account for declining seed dispersal with greater distance from a seed source, live tree cover was weighted (i.e., 1/meters from plot center) using methods from Coop et al. (2019).

We used a suite of long-term climate metrics with fine spatial resolution (<1-km) to characterize the biophysical setting of each plot (Table 1). Heat load index (*HLI*), calculated at 1/3 arc-second resolution, integrates the effects of aspect, slope, and latitude into a unitless index of potential solar heating (McCune & Keon (2002)). Water balance was represented by climatic water deficit (*DEF*, mm), averaged for 1981-2015 from a downscaled (250-m) climate product described by Holden et al. (2016, 2018). Annual precipitation (ppt_{ann}, mm) and growing-season precipitation (ppt_{JJAS}, mm) were averaged for 1981-2015 from ClimateWNA , which interpolates 800-m PRISM grids and adjusts for elevation to generate scale-free climate data (Wang et al. 2016).

We developed continuous metrics of fire severity at each plot, by using a PCA to summarize a suite of field measurements of fire effects as described by Wolf et al. (2021). We interpreted the first two principal components to reflect distinct aspects of fire severity, and use these as predictor variables in statistical models of seedling density (Table 1). We interpret PCA Axis 1 (*Axis1*) as a metric of overstory fire effects, with positive values associated with high tree mortality and scorch height. We interpret PCA Axis 2 (*Axis2*) as a metric of understory conditions, with positive values associated with high bare ground cover and negative values associated with high moss and forb cover.

To quantify soil nitrogen availability, we used field-incubated resin capsules and measured soil inorganic N concentration in the first and second year after fire. Soil samples were collected at meter 0, 30, and 60 of each transect in August-September of 2018 and again in 2019. We deployed mesh capsules containing ion-exchange resin (Unibest, Walla Walla, WA, USA), which adsorb ammonium (NH_4^+) and nitrate (NO_3^-) ions in soil solution (Binkley and Matson 1983), to obtain a time-integrated measure of inorganic nitrogen availability. These were placed at c. 5-cm depth in the mineral soil at meter 0, 30, and 60 of each plot in August-September 2018, and were allowed to incubate in the field until June 2019 to capture post-thaw N mineralization. See Wolf et al. (in prep) for detailed methods.

Table 1. Predictors used in statistical models of seedling regeneration.

Category	Subcategory	Variable	Units	Description
Seed availability	Seed source proximity	*PP_dWt*		Propagule pressure, defined as distance-weighted live tree cover in a 200-m radius around plot center.
		DSS	m	Plot-averaged distance to the nearest live tree of any species, measured in the field.
		BA_{Spp}*_L*		Live basal area of focal species, used only in species-specific models.
	Serotiny	BA_{PICO}		Plot-averaged basal area of *P. contorta*, used as a proxy for potential release of serotinous cones. Used only in all-species and PICO models.
	Forest type	$Spp_{present}$	1/0	Binary: 1 if focal species is present in overstory or as a seed source, 0 otherwise. Used only in species-specific models.
Climate	Topography	*HLI*		Unitless index of potential solar heating.
	Precipitation	*ppt_ann*	mm	35-year average annual precipitation.
		ppt_JJAS	mm	35-year average growing-season precipitation.
		ppt_pf	mm	2-year postfire average growing-season precipitation.
	Water balance	*DEF*	mm	35-year average climatic water deficit (250 m).
	Microclimate	T_{max} T_{avg}	°C °C	Modeled post-fire absolute maximum JJAS temperature. Modeled post-fire average daily maximum temperature.
Fire effects	Overstory	*Axis1*		First principle component of field measurements describing fire severity, with positive values reflecting greater overstory mortality and loss of live canopy cover.
		dnbr		Satellite-derived metric of fire severity.
		Canopy	%	Live + dead canopy cover, averaged to plot scale for models of whole-plot seedling counts.
	Understory	*Axis2*		Second principle component of field measurements describing fire severity, with positive values reflecting greater bare ground cover and negative values reflecting greater moss and forb cover.
		Cover	%	Six variables describing ground cover in subplots of different vegetation types (Moss, Forb, Grass, Shrub), coarse woody debris (Wood), and bare ground (Bare), which are averaged to plot scale for models of whole-plot seedling counts.
	Soil	*soilN* *NO3* *NH4*	µg N day^{-1}	Three variables describing resin-capsule inorganic nitrogen (NO_3, NH_4, or total), an integrated measure of nitrogen availability in years 1-2 post-fire.

4.5. Statistical analyses

4.5.1. Objective 1: Quantifying effects of fire on microclimate

To quantify the effects of fire on microclimate conditions, we built statistical models of the differences in daily maximum temperature (ΔT_{max}) and VPD (ΔV_{max}) between paired burned and unburned plots. We modeled ΔT_{max} and ΔV_{max} as a function of ambient temperature, topoclimate metrics (*DEF* and *HLI*), field-based fire severity metrics (*Axis1* and *Axis2*), and the difference in canopy cover between the paired burned and unburned site (ΔCanopy), using linear mixed-effects models. As a proxy for ambient temperature, we used 4-km resolution GridMET daily maximum temperature data (Abatzoglou 2013). We tested the addition of quadratic terms and two-way interaction terms, and selected models to balance parsimony with model skill. Model skill was measured using leave-one-out cross-validated root-mean-square-error (RMSE).

4.5.2. Objective 2: Evaluating controls of post-fire seedling demography

To evaluate the relative influence of controls of post-fire regeneration, we built statistical models of total seedling density in the third year after fire in burned plots, as well as annual recruitment, survivorship, and height. We conducted model selection to obtain a best-fit model for each demographic stage and species (all species, *P. contorta*, *P. menziesii*, and *L. occidentalis*). We used negative binomial generalized linear mixed effects models with a log link for seedling density and annual recruitment models. For seedling survivorship, we used binomial mixed effects models with a logit link, and for seedling height, we built a generalized linear mixed model using a gamma distribution. We grouped fixed-effects predictors into three broad categories describing controls of post-fire regeneration: seed availability, climate, and fire severity, each of which included subcategories of correlated variables (Table 1). To find a best-fit model, we first identified the set of predictors (one from each subcategory in Table 1) that minimized AICc, and then conducted further model selection. To test the influence of seed availability, microclimate, and fire severity on seedling density, we compared models containing subsets of predictors. Model fit was evaluated using pseudo-R^2 values and *k-fold* cross-validated spearman correlations between observed and predicted values (ρ).

5. Results and discussion

5.1. Quantifying effects of wildfire on microclimate

Differences in temperature and VPD between paired burned and unburned plots in similar biophysical settings varied diurnally and throughout the season (Wolf et al. 2021), and were typically largest when ambient temperatures were high (e.g., during the hottest part of the day). Averaged across the season, daily maximum temperature was 2.6 ± 2.7 °C (standard deviation) higher in burned than in unburned plots, and daily maximum VPD was 0.52 ± 0.54 kPa (30%) higher. Comparing unburned plots with those classified as high-severity, differences in average daily maximum temperature and VPD were 3.7 ± 2.4 °C and 0.81 ± 0.40 kPa, respectively, and reached maxima of 12.8 °C and 4.7 kPa. These differences between burned and unburned forest

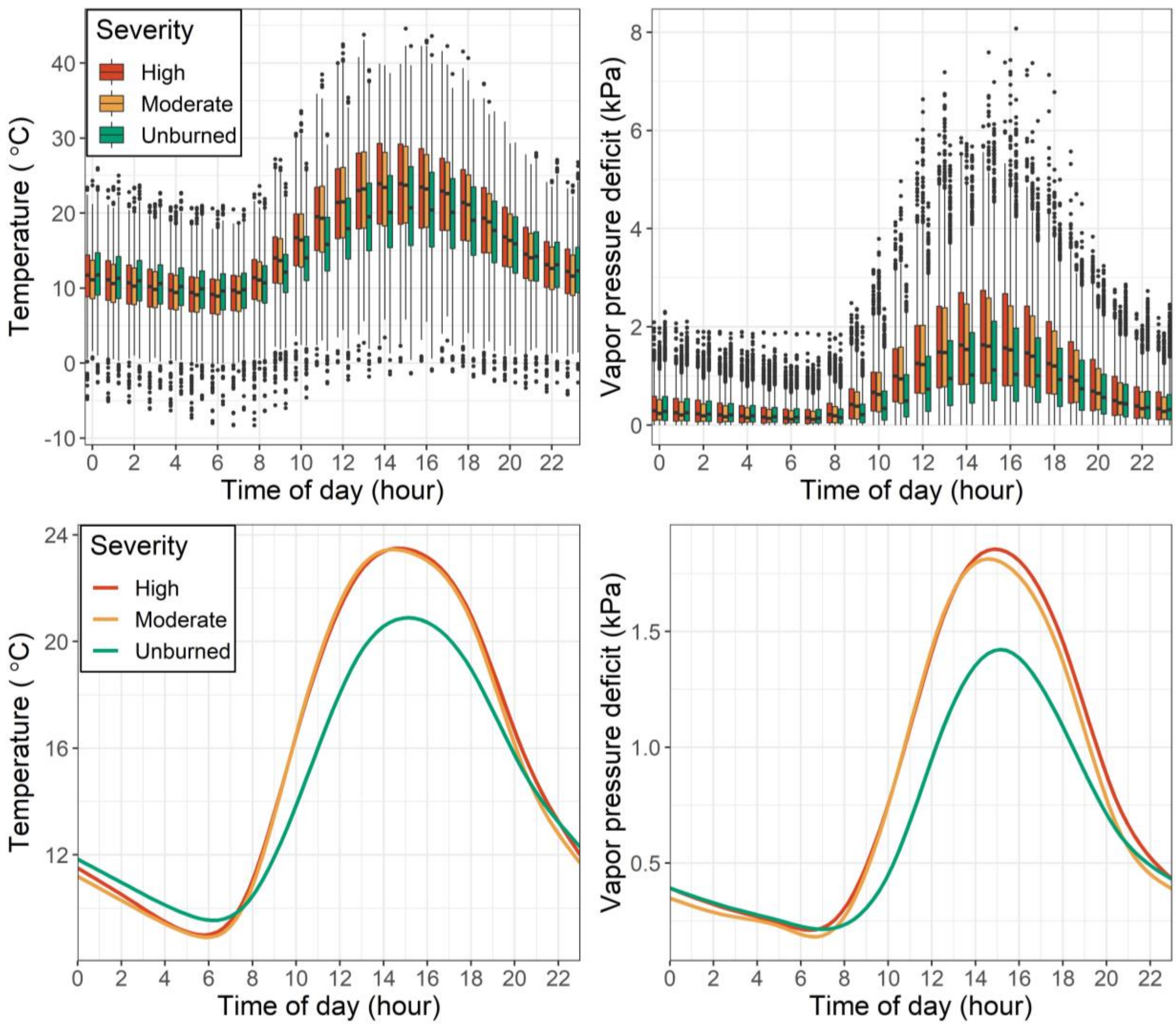

Figure 3. Daily microclimate conditions grouped by fire severity classes. Diurnal variability in VPD (kPa) and temperature (°C) across all sensors and years, aggregated to hourly timesteps and displayed using boxplots (top panel), and smoothed by time of day (*mgcv* package in R) (bottom panel). Sensors are grouped by fire severity classifications (high, moderate, unburned) based on field measurements. The difference in daily maxima between paired burned and unburned plots was calculated and used in further analyses as a measure of the effect of fire on microclimate conditions in each plot. From Wolf et al. (2021).

are likely due to increased surface radiation intensity, reduced evaporative cooling, and increased sensible heating in the post-fire environment (Liu 2005, e.g., Chambers 2005, Liu et al. 2019), and are consistent with studies documenting increased air temperature or VPD after fires (Ripley and Archibold 1999, Ma et al. 2010, Bello-Rodríguez et al. 2019). Further, the magnitude of these changes in microclimate conditions are large enough to be biologically meaningful for plants. For example, wildfire effects on microclimate may be one mechanism driving a post-fire shift in understory species composition toward warm-adapted taxa in some western forests (Stevens et al. 2015), and conifer seedlings are vulnerable to mortality through desiccation with increases in air temperatures similar to those observed here (Rother et al. 2015).

Our statistical models for the differences in daily maximum temperature (ΔT_{max}) and VPD (ΔV_{max}) between paired burned and unburned plots revealed that the effects of fire on microclimate conditions depended on canopy cover, biophysical setting, and fire severity. ΔT_{max} values at each plot were best explained by the difference in canopy cover from the unburned plot (ΔCanopy), the ambient temperature ($T_{max}A$), long-term climatic water deficit (*DEF*), potential solar heating (*HLI*), understory conditions (*Axis2*), and interaction terms among these variables, with an average cross-validated RMSE of 2.50 °C ± 0.90. Similarly, ΔV_{max} was best explained by ΔCanopy and an interaction between $T_{max}A$ and *DEF*, with an average cross-validated RMSE of 0.62 kPa ± 0.25.

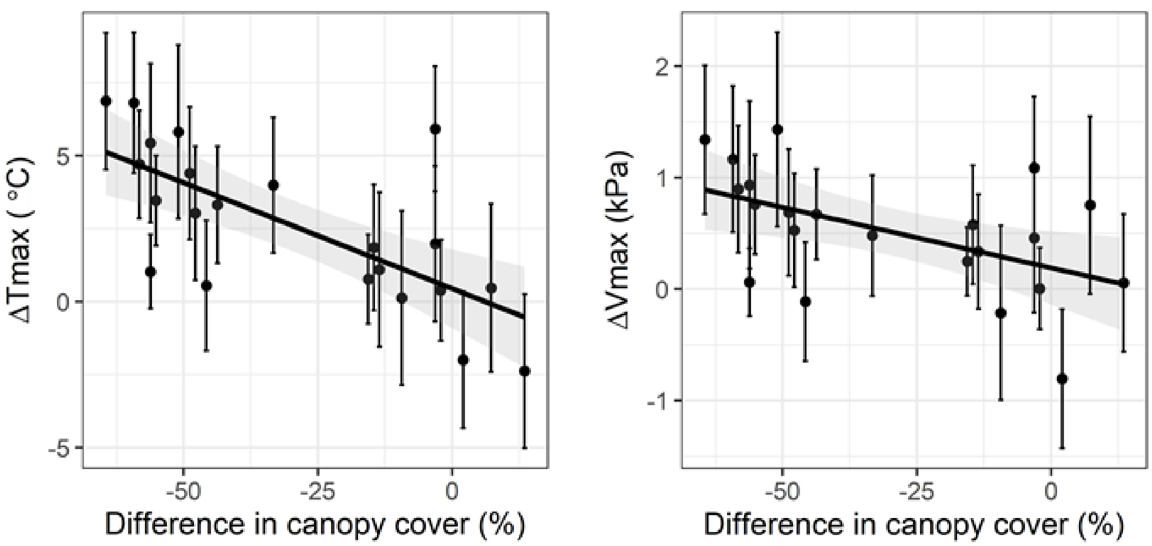

Figure 4. Changes in microclimate with varying canopy cover. Bivariate relationship between the difference in canopy cover above the sensor in paired burned and unburned plots (ΔCanopy, x-axis) and ΔT_{max} (top panel), and ΔV_{max} (bottom panel). Positive ΔT_{max} and ΔV_{max} values indicate warmer/drier conditions in the burned plot than the unburned plot, and negative ΔCanopy values indicate less canopy cover in the burned plot than the unburned plot. Plot averages ± two standard errors are shown, as well as a simple linear fit with 95% confidence intervals (shaded bands). From Wolf et al. (2021).

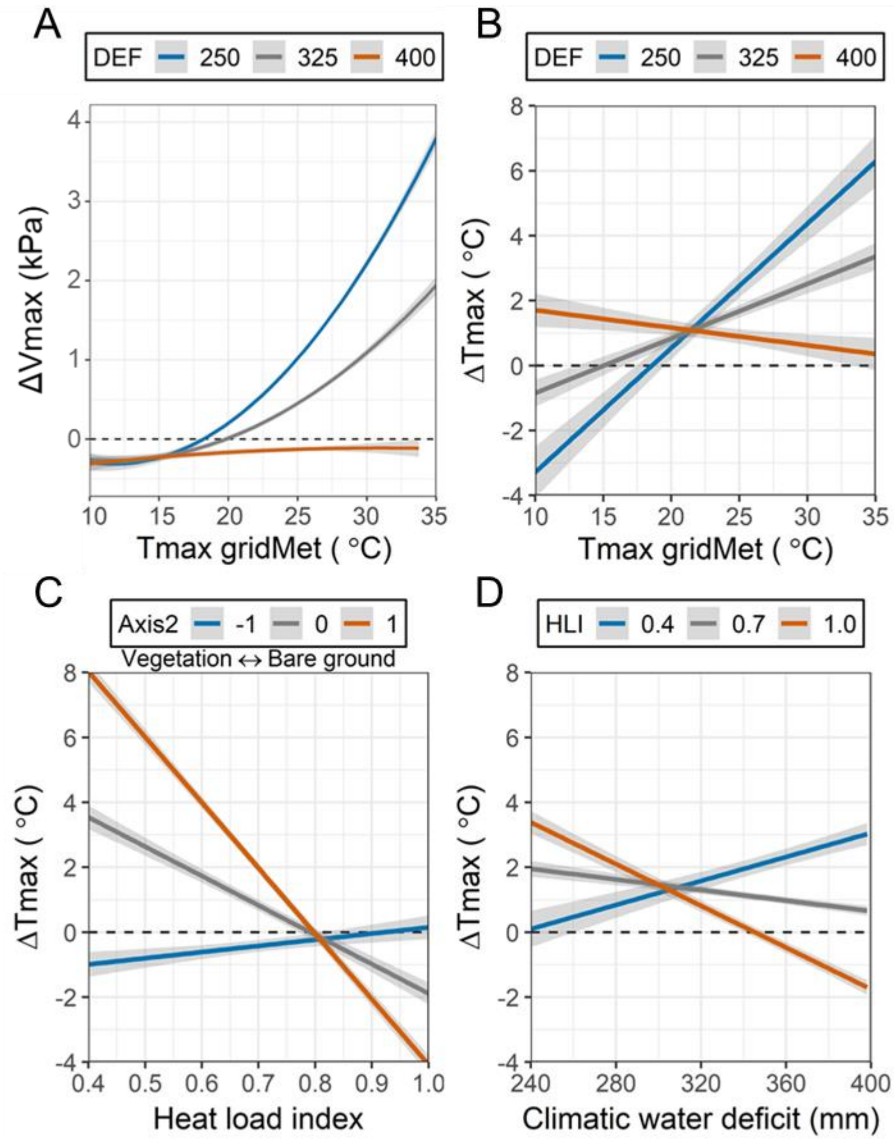

Figure 5. Influence of ambient temperature, site climate, and fire severity on predicted changes in microclimate. Model predictions of ΔV_{max} and ΔT_{max} after controlling for differences in canopy cover between paired burned and unburned plots, where higher ΔV_{max} and ΔT_{max} values indicate higher VPD and temperature, respectively, in the burned plot. Trends in predicted ΔV_{max} and ΔT_{max} are graphed against ambient weather (Tmax gridMet) for varying levels of climatic water deficit (DEF, mm) (top panel), and trends in predicted ΔT_{max} are graphed to show the effects of additional interaction terms among DEF, heat load index (HLI), and ground cover (Axis2) (bottom panel). High DEF indicates lower long-term moisture availability. Negative Axis2 values indicate greater understory vegetation cover, while positive values indicate greater bare ground cover. High HLI indicates higher potential solar heating. Shaded bands show 95% confidence intervals. Modified from Wolf et al. (2021).

Burned and unburned sites with larger differences in canopy cover tended to have larger differences in temperature and VPD (Fig. 4). This supports the interpretation that the effects of fire on microclimate vary across fire severity gradients, with areas of greater canopy loss having larger changes in microclimate compared with adjacent unburned forest, and is consistent with studies that demonstrate a strong influence of canopy cover on microclimatic buffering (e.g., Rambo and North 2009, Suggitt et al. 2011, von Arx et al. 2013, Davis et al. 2019a). In addition, given that total (live and dead) canopy cover was an important predictor in our statistical models, our results highlight the importance of residual dead trees in providing shade and regulating near-ground microclimate conditions after fire (Fontaine et al. 2010, Hoecker et al. 2020).

In addition to canopy cover, our statistical models imply that fire severity also affects microclimate through its impacts on understory cover, which interacts with topography to influence temperature extremes (Fig. 5). Maximum temperatures tended to be higher at sites with more bare ground and less understory vegetation, perhaps due to differences in albedo and evapotranspiration affecting the surface energy balance (Liu 2005, Tsuyuzaki et al. 2009). This finding implies that microclimatic extremes will attenuate over time after fire as vegetation reestablishes.

Our findings also reveal that the effect of wildfire on microclimate depends strongly on the biophysical setting. Sites with high long-term climatic water availability (i.e., low *DEF*) experienced larger fire-caused changes in microclimate (Fig. 5). Forests in warm-dry biophysical settings, such as at low elevations and on south-facing slopes, have less capacity to buffer microclimatic extremes due to lower water availability to support evaporative cooling and lower vegetation productivity. Thus, the effects of fire have a relatively smaller impact on microclimate conditions in warm-dry sites compared with cool-mesic forests where canopy loss due to fire strongly impacts understory microclimates. This suggests that we may be underestimating the potential impacts of fire-caused changes in microclimate conditions in cool-moist settings, which could push conditions closer to climatic limits for tree regeneration (Andrus et al. 2018, Davis et al. 2019b). These impacts are most pronounced under warm ambient temperatures (Fig. 5) and could increase the exposure of understory plants and tree seedlings to microclimatic extremes.

Our study thus documents substantial impacts wildfire on microclimatic extremes in forest ecosystems, quantifying changes that are biologically meaningful for plants. Our results reveal that these impacts vary significantly based not only on ambient conditions and fire severity, but also on the biophysical context of a site, including long-term climatic water deficit.

5.2. Evaluating controls of post-fire seedling demography

5.2.1. Evidence of forest resilience to wildfires

Regeneration was abundant by the third year after fire, with a median density of 2,633 seedlings per hectare among all plots (IQR 750 to 7500 ha^{-1}). All burned plots (n=47) had at least one live seedling, with four plots (8.5%) having densities less than 100 ha^{-1}, and 12 plots (26%) having densities greater than 10,000 ha^{-1}. Seedling densities were significantly greater in burned than unburned sites on average for *P. contorta*, *P. ponderosa*, and *L. occidentalis*. Comparing post-fire seedling densities with reconstructed pre-fire tree densities, two-thirds of burned plots were at or above replacement density three years after the fire, and 53% had twice the pre-fire density (Fig. 6), with post-fire species composition generally reflecting pre-fire composition. High rates of annual recruitment and survivorship (median 66% survival) in burned plots over the first three years contributed to post-fire regeneration, with higher survival, on average, in burned than unburned plots (Fig. 7).

The robust regeneration found in our study sites contrasts recent observations of declines in conifer regeneration (Harvey et al. 2016, Donato et al. 2016, Stevens-Rumann et al. 2018, Andrus et al. 2018, Davis et al. 2019b). Seed availability may help explain the robust regeneration observed in this study, due to the fact that all plots were within 100 m of a seed source, the distance from live trees at which seed dispersal is limited (Kemp et al. 2016, Littlefield 2019, Carlson et al. 2020). However, only about 12% and 8% of the area of the Lolo Peak and Sunrise fires, respectively, were greater than 100 m from a non-severe patch (Holden et al. 2021). This spatial distribution of seed availability is consistent with a random subset of 30 similar large fires in the northern Rocky Mountains, which averaged 14% of burned area >100 m from non-severe patches. Further, of the area far from live seed sources, 91% and 56% in the Lolo Peak and Sunrise fires, respectively, are within the elevational range of *P. contorta*. Thus, even within large fires, not all high-severity patches are seed-limited, and a majority of burned

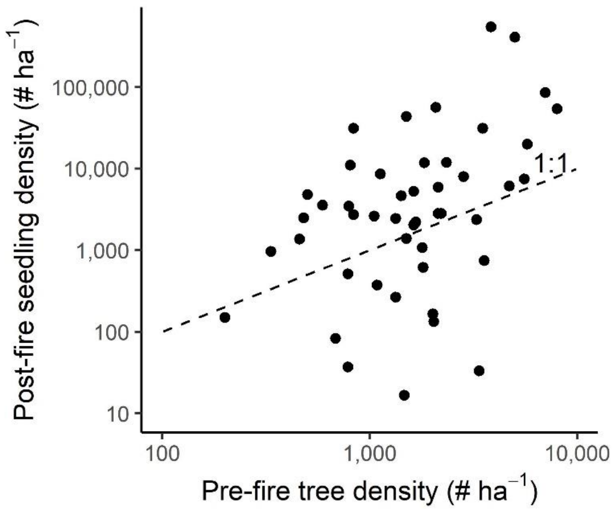

Figure 6. Comparison between pre- and post-fire tree densities in burned plots. Total seedling density in year 3 after fire plotted against reconstructed pre-fire mature tree density for all burned plots (n = 47). The dashed line shows a 1:1 relationship, where plots on or above that line have at least as many seedlings present after fire to replace adult trees present before fire.

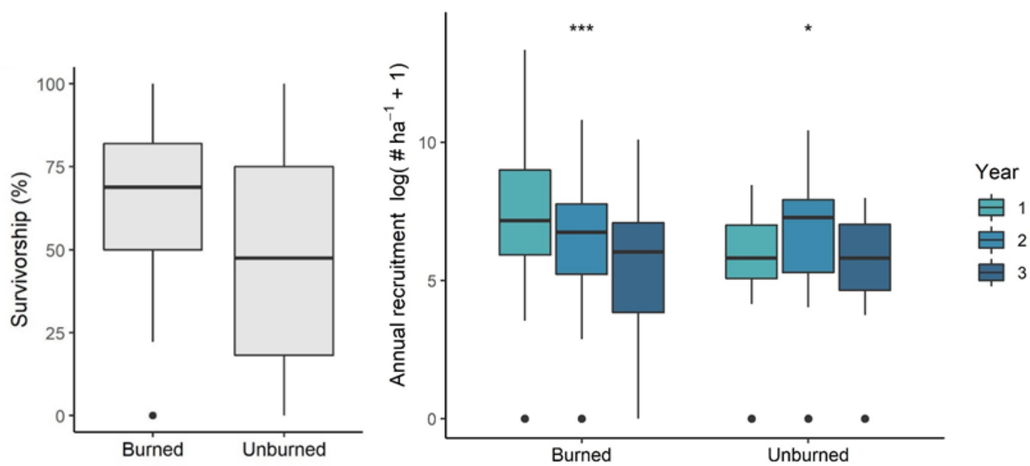

Figure 7. Seedling survivorship and annual recruitment in burned and unburned plots. Estimates of total seedling survivorship over the first three years post-fire (left) and annual recruitment of germination-year seedlings, identified based on the presence of cotyledons (right), in burned (n = 47) and unburned plots (n = 22). Significance of paired nonparametric Friedman tests evaluating differences in recruitment among years are shown for burned and unburned plots (* p<0.05, ** p<0.01, *** p<0.001). Annual recruitment was significantly greater in burned than unburned plots only in the first year after fire.

area typically has the potential for seed availability to support regeneration through dispersal from surviving trees or release from serotinous cones.

We also attribute our finding of abundant regeneration, in part, to moderate post-fire climate conditions in the three study years. Growing-season (Jun-Sept) daily maximum temperatures in 2018-2020 averaged 0.3 °C (0.21 sd) above, and precipitation 32 mm (0.63 sd) below, the 1981-2020 mean in Missoula, MT (WRCC 2021). Although our data represent a narrow range of climate variability, we highlight that declining regeneration is not yet pervasive in all contexts (Littlefield 2019, Povak et al. 2020). Given initial regeneration, these forests will likely develop similar stand characteristics to pre-fire conditions, providing an important example of how forests can be resilient to wildfires.

These findings further emphasize the role that fire plays in stimulating conifer regeneration. A statistical model of seedling density across all plots (burned and unburned) predicted an increase in density of nearly 600% with a one standard deviation increase in overstory fire severity (*Axis1*), implying that, after accounting for seed availability, regeneration was higher in burned forest. This pattern reflects higher seedling survivorship in burned than unburned plots on average and greater annual recruitment in the first year after fire (Fig. 7), and is likely attributable to increased resource availability in burned areas (e.g., Clemente et al. 2005). For example, fire increased light availability, with 30% lower median total canopy cover in burned than unburned plots ($p < 0.001$, $W = 101$, $n = 69$), and greater moss cover (150%) and reduced litter cover (71%) in burned plots, which was likely associated with improved root access to stable moisture in mineral soil (Stein and Kimberling 2003, Johnstone and Chapin 2006). In addition, fire increased nitrogen availability, with median 93% greater resin-sorbed nitrogen in burned relative to unburned plots in similar biophysical settings, and three-fold greater total soil inorganic N content one year after fire (Fig. 8), consistent with a widely-observed short-term N pulse after fire (Wan et al. 2001, Smithwick et al. 2005, Gundale et al.

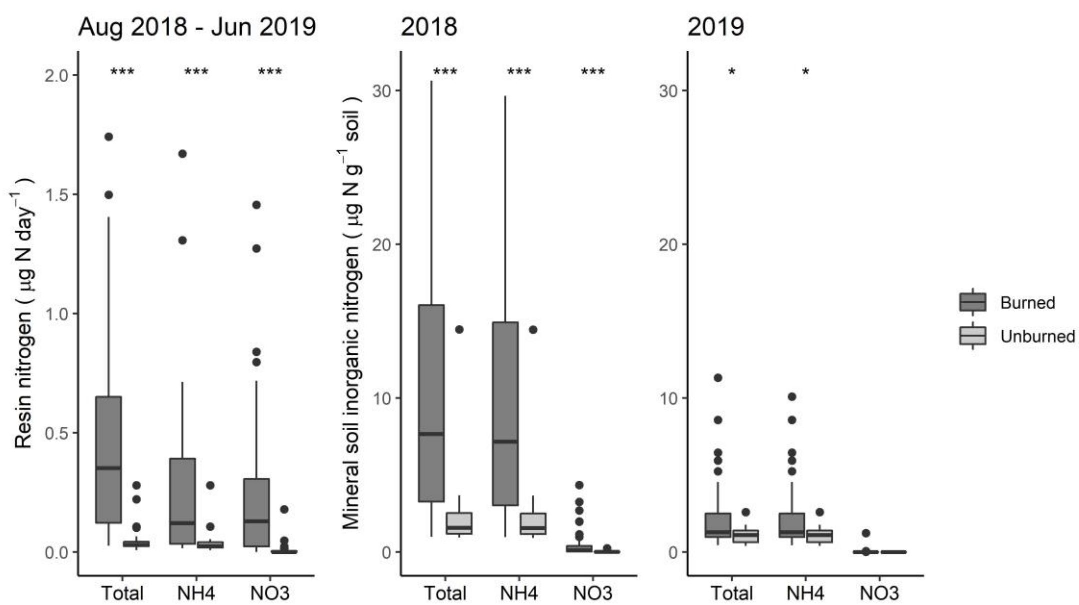

Figure 8. Measurements of soil nitrogen availability, measured using field-incubated resin capsules (left), and mineral soil inorganic nitrogen concentration in the first- and second-year post-fire (right). Statistical significance of nonparametric Wilcoxon rank-sum tests comparing burned and unburned soils are reported (* p<0.05, ** p<0.01, *** p<0.001).

2005, Turner et al. 2007). This increased resource availability apparently created favorable conditions for seedlings in burned sites.

5.2.2. *Controls of post-fire seedling regeneration*

The best-fit model for total seedling density in burned sites accounted for 75% of the variability among sites, and cross-validated well (ρ = 0.63). This model revealed a strong positive relationship of seedling density with BA_{PICO} and a negative relationship with *DSS*, representing seed availability, a negative relationship with T_{max}, representing microclimate, and effects of *Axis1*, *Axis2*, and *soilN*, representing distinct aspects of fire severity (Fig. 9). Seedling density increased with higher overstory fire severity (*Axis1*) and higher moss and forb cover and less bare ground cover (*Axis2*), and, contrary to expectation, decreased with greater soil nitrogen availability (*soilN*).

Among species, positive relationships of seedling density with seed availability and negative relationships with warm, dry climate were consistent, although the specific variables retained and their relative influence on species density differed (Fig. 10). In particular, the effects of fire severity metrics were not uniform among species. Predictors of regeneration also differed slightly between burned and unburned forest. Similar to burned plots, seedling density in unburned plots had a negative relationship with *DSS* and canopy cover and a positive relationship with moss cover, but density in unburned plots increased with *soilN*, suggesting that regeneration in unburned forest is limited by light availability and soil nutrients. Differing effects in burned and unburned forest imply that there is some optimal level of fire-caused canopy opening and nitrogen supply that supports regeneration, beyond which more severe impacts could be inhibitory.

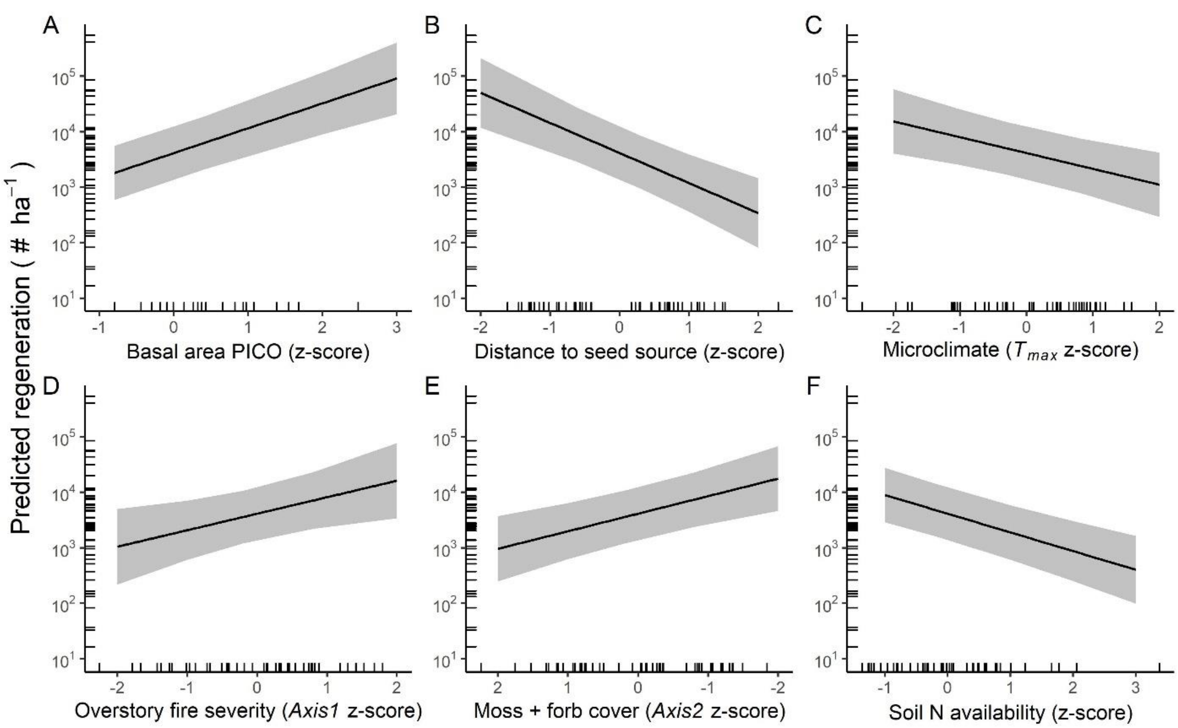

Figure 9. Influence of seed availability, microclimate, and fire severity on seedling regeneration. Partial effects plots for model of total seedling density in burned plots, with 95% confidence intervals.

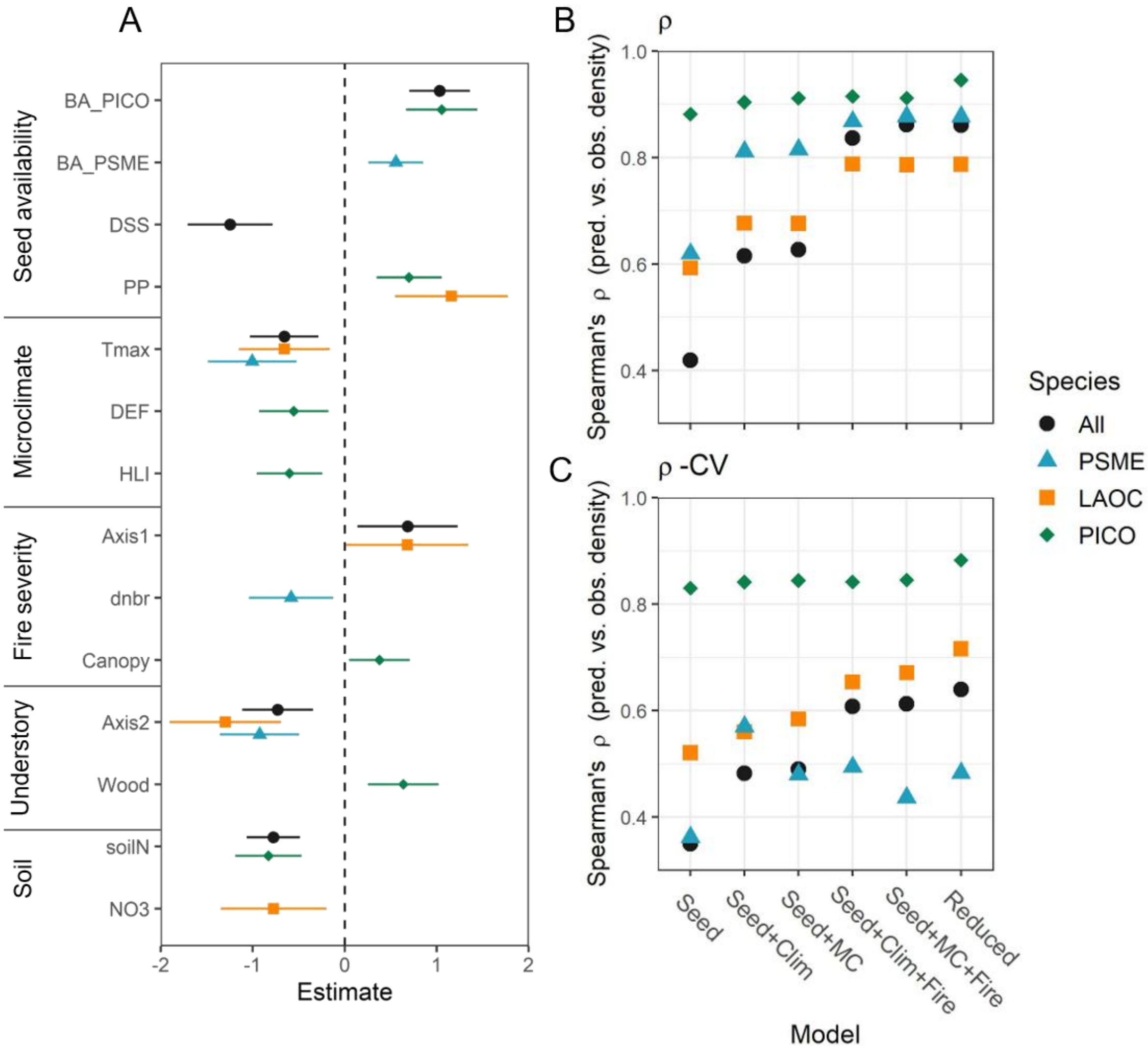

Figure 10. Comparison of the relative influence of variables describing seed availability, climate, and fire severity on post-fire seedling regeneration. Seedling density in the third year after fire in burned plots (n = 47) was modeled for all species and individual species: *P. menziesii* (PSME), *L. occidentalis* (LAOC), *P. contorta* (PICO). Predictors are grouped into categories describing seed availability ("Seed"), site climate ("Clim") or microclimate ("MC"), and fire effects ("Fire"), including overstory fire severity, understory cover, and soil nitrogen availability (Table 1). ***A:*** Estimates of main effects and 95% confidence intervals for reduced (best-fit) models. ***B, C:*** Measures of model fit, including the correlation between observed and predicted values (A), and cross-validation results (B), for models including subsets of predictors (e.g., the "Seed+MC" model includes seed-availability and microclimate variables as predictors of seedling density), to compare their relative influence.

Our findings highlight the primary importance of seed availability for post-fire tree regeneration (Fig. 9, 10), consistent with prior understanding (Stevens-Rumann and Morgan 2019). Variables describing seed availability explained 50% of the total variability in seedling densities among plots, with greater seedling density in sites closer to live seed sources and at sites with a greater component of *P. contorta* in the overstory (BA_{PICO}), representing a proxy for seeds from serotinous cones. *P. contorta* had the highest median (25,270 ha^{-1}) and maximum (>500,000 ha^{-1}) post-fire density of any species.

Our results also highlight the dependence of seedling regeneration and survival on microclimate conditions. After accounting for seed availability, variables describing the biophysical setting and post-fire microclimate provided significant additional explanatory power (marginal R^2 = 64%), consistent with the understanding that juvenile conifers are vulnerable to desiccation or heat-induced mortality from warm, dry atmospheric or soil conditions (Kolb and Robberecht 1996, Johnson et al. 2011). Seedling density in year three, annual recruitment, and seedling survivorship were all higher in relatively cool-wet sites (Fig. 9, 11, 12), and seedling survival was most sensitive to climate in young seedlings (Fig. 12A), highlighting that germination-year climate conditions create the strongest mortality filter on post-fire regeneration. This implies that fire-induced canopy loss may amplify the impacts of climate warming on regeneration by increasing exposure to warm-dry extremes (Zellweger et al. 2020), particularly in relatively cool-wet forests where canopy loss has a larger absolute effect on microclimate (Davis et al. 2019a, Wolf et al. 2021).

Despite the importance of microclimate, our models also did an excellent job predicting post-fire seedling density based on metrics describing biophysical setting and fire severity (Fig. 10), suggesting that water balance metrics largely capture spatial variability in microclimate conditions. Our results thus support the utility of predictive models based on fine-scale (250 m resolution) gridded climate data to inform management decisions (e.g., Holden et al. 2021).

Our results further reveal the multifaceted impacts of fire severity on seedling recruitment and survival through its influence on microsite factors not captured by satellite metrics. After accounting for seed availability and climate, variables describing fire severity substantially improved model fit (marginal R^2 = 78%), with contrasting effects of different aspects of fire severity (Fig. 9, 10). For example, seedling density increased with overstory fire severity (*Axis1*). This implies that while some remaining canopy cover, even dead, supports regeneration through microclimatic buffering, overstory mortality also supports regeneration, through greater light availability, or perhaps through increased soil moisture due to reduced canopy interception and evapotranspiration (Ma et al. 2010, Cardenas and Kanarek 2014, Kolb et al. 2020, Hill and Ex 2020). Responses to this trade-off vary among species (Chen 1997, Hill and Ex 2020). For instance, *P. menziesii* regeneration was greater at low fire severity, with a stronger negative effect of microclimate on regeneration than other species (Fig. 10), implying a preference for cooler, more shaded environments consistent with its high shade-tolerance compared to *P. contorta*, *L. occidentalis*, or *P. ponderosa* (Minore 1979, Rodman et al. 2020b).

Our results also highlight how burn mosaics with heterogeneous fire effects promote forest resilience by creating diverse understory environments and microsites for regeneration. Total, *P. menziesii*, and *L. occidentalis* seedling densities (Fig. 10) and survival and growth (Fig. 11C, 12B) were higher in sites with greater moss and forb cover and less bare ground cover, likely representing a proxy for surface soil moisture or less competition from shrubs and grasses (Wagner et al. 1989, Pinto et al. 2012, North et al. 2019, Kolb et al. 2020, Carlson et al. 2020). Additionally, more bare soil may be associated with high surface temperatures or vulnerability to erosion (Certini 2005). Coarse wood cover also has a nurse effect on seedling regeneration through microclimatic buffering (Pettit et al. 2019, Hill and Ex 2020); although we found that this was only significant for *P. contorta*, forbs could play a similar role, particularly in warm-dry sites (Fig. 11; Maher and Germino 2006, Korb et al. 2019). While high-severity plots had higher bare ground ($\rho = 0.67$, $p < 0.001$, $n = 47$) and lower forb cover ($\rho = -0.49$, $p < 0.001$, $n = 47$),

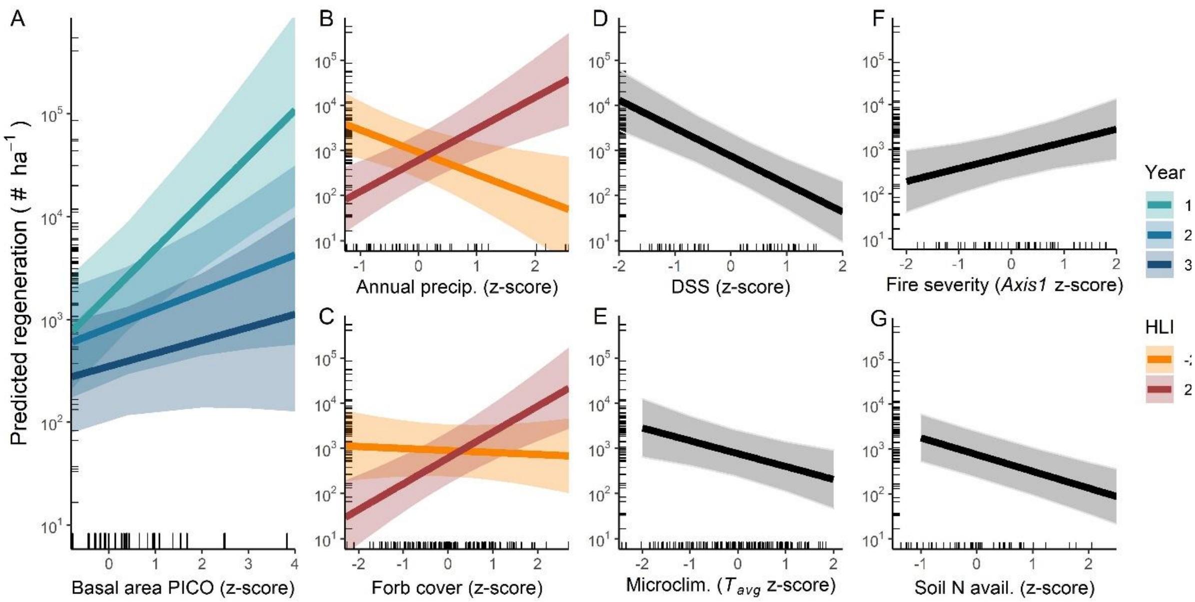

Figure 11. Controls of annual seedling recruitment. Partial effects plots for best-fit model of annual seedling recruitment of germination-year seedlings (identified based on the presence of cotyledons) of all species in burned plots, with 95% confidence intervals.

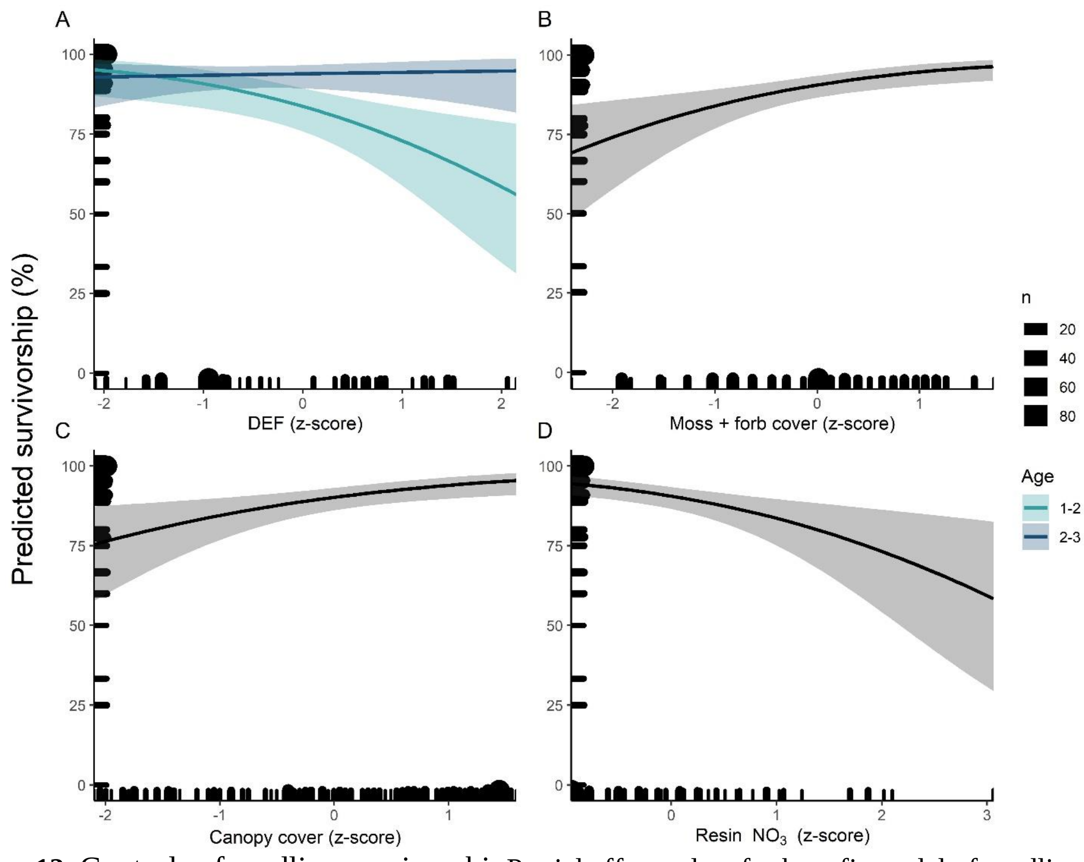

Figure 12. Controls of seedling survivorshipPartial effects plots for best-fit model of seedling survivorship in year three after fire (all species), with 95% confidence intervals. Marker sizes indicate the number of seedlings represented in the survivorship estimate from each plot (n).

moss and coarse wood cover did not differ with fire severity, suggesting that high-severity patches can harbor favorable below-canopy microsites. Still, while it was not observed here, our results anticipate that very severe fire which consumes coarse wood and burns down to mineral soil (e.g., Turner et al. 2019) would inhibit regeneration.

In contrast to expectation, our results suggest that soil nitrogen availability inhibits seedling recruitment and survival (Fig. 11G, 12D), ultimately limiting regeneration (Fig. 9F). Seedling survival declined with higher nitrate availability (Fig. 12), suggesting that high post-fire N supply (Fig. 8) likely exceeded seedling demand (Romme et al. 2009), and may stimulate aboveground growth without commensurate root development, potentially inhibiting drought resistance and survival (Isaac and Hopkins 1937, Bensend 1943, Ingestad 1962, Kitchen 1966, Nilsen 1995). Alternatively, soil heating could elevate soil inorganic nitrogen and cause a suite of other changes (e.g., Fig. 1) that we did not account for but which impact regeneration. For example, soil water repellence and reduced interception can enhance erosion (Shakesby and Doerr 2006); anecdotally, we observed root exposure or burial of seedlings in some high-severity sites. Biotic effects, such as reduced mycorrhizal abundance and diversity (Taudière et al. 2017), could also impact seedling survival and growth (Miller et al. 1998, Hasselquist et al. 2005, Peay et al. 2012). Additional research is needed to evaluate how the effects of fire on soil physical properties, biogeochemical processes, and biota over short and long timescales (DeLuca and Sala 2006, Ferrenberg et al. 2013, Pellegrini et al. 2018, Bowd et al. 2019, Dove et al. 2020) influence seedling physiology and demography.

5.2.3. Seedling demographic stages: annual recruitment, survivorship, & height growth

Annual recruitment in burned sites declined over time after fire, with significantly greater recruitment in the first year (median 1292 ha^{-1}) compared to the second (median 850 ha^{-1}) and third (median 417 ha^{-1}) years after fire ($p < 0.05$; Fig. 7). Annual recruitment was largely influenced by the same variables governing total seedling density after three years (Fig. 11). Positive effects of precipitation on annual recruitment in sites with high solar exposure (Fig. 11B) points to an optimal, relatively warm and wet environment, perhaps reflecting areas of high overlap in species ranges. Declining recruitment by year three highlights the relevance of initial post-fire regeneration to longer-term forest trajectories, particularly for *P. contorta* (Fig. 11A). Serotinous *P. contorta* regenerates immediately after fire and can have wide variation in density (Turner et al. 2004, Harvey et al. 2016), affecting stand structure and function for decades to centuries (Kashian et al. 2005, Smithwick et al. 2009, Turner et al. 2016). This suggests the potential for vulnerability to drought during this critical regeneration window (Piñol and Sala 2000, Petrie et al. 2016, Hansen and Turner 2019), although dense initial regeneration could allow for stand replacement even with high mortality rates.

Recruitment of *P. ponderosa* was low (median 17 ha^{-1} yr^{-1}, IQR 0-100) and declined after the first year despite moderate climate. This is, in part, attributable to higher mortality of seedlings in warm-dry sites (Fig. 12A) where *P. ponderosa* is most prevalent. However, even in these sites, *P. ponderosa* recruitment was low compared to co-occurring *P. menziesii* (median 17 ha^{-1} yr^{-1}, IQR 16-576). This is perhaps due to a lack of mast years during the sampling window, which occur every 3-8 years and depend on climate conditions (Keyes et al. 2015). *P. ponderosa* recruitment will likely increase in subsequent years with greater seed production, but will eventually decline as the canopy fills in (Ehle and Baker 2003); only 6% of *P. ponderosa* seedlings were observed in unburned sites. This highlights important post-fire contingencies of climate and timing of seed production (Rodman et al. 2020b).

Seedling survival was high in the first three years after fire, with median 66% (IQR 46 – 82%) total survivorship across all plots. This exceeds estimates of less than 50% survival of seeded and planted seedlings under field conditions from other studies (Stein and Kimberling 2003, Shepperd et al. 2006, Keyes et al. 2007, 2009, Pinto et al. 2012, Kolb et al. 2020, Hill and Ex 2020, Hoecker et al. 2020), likely due in part to moderate climate conditions in the sampling years (Chen 1997, Pinto et al. 2011, Rother et al. 2015). In addition, by sampling annually, we did not fully capture high rates of germination-year mortality (Stein and Kimberling 2003, Keyes et al. 2007), although we observed that survival increased with seedling age.

Survivorship in burned plots from the second to third year after fire was positively related to seedling age, canopy cover (*Canopy*, subplot scale), and total moss and forb cover (*Moss+Forb*, subplot scale), and negatively related to *DEF* and resin nitrate (*NO3*), with a model AUC of 0.77 (Fig. 12). The negative effect of warm-dry site climate on survival was more pronounced for seedlings from their first to second year than older seedlings (Fig. 12A), consistent with greater vulnerability to desiccation during root and vascular development in young seedlings (Stein and Kimberling 2003, Johnson et al. 2011, Miller and Johnson 2017). Nevertheless, severe drought years can cause high mortality in older seedlings (Kolb et al. 2020), such that long-term survival remains uncertain and will depend on climatic extremes.

Height growth varied significantly among species (Fig. 13). *P. ponderosa* had the greatest height of germination-year seedlings (median 5.8 cm, IQR 4.6 – 6.5) and *P. engelmannii* had the smallest initial height (median 1.7 cm, IQR 1.3 – 2.1), while all other species averaged 2.0 to 3.3 cm. *L. occidentalis* tended to grow fastest, with median height of 11.5 cm (IQR 8 – 18 cm) at age three and a maximum of 42 cm. Expected seedling height in burned plots in the third year after fire related positively to moss and forb cover and microclimate conditions (T_{avg}) (Fig. 13). Differing growth rates depending on microclimate conditions (Fig. 13C) likely reflects the prevalence of fast-growing species (e.g., *L. occidentalis*) in relatively warm-dry sites, but could also imply higher survival of larger individuals under stressful (i.e., warm-dry) microclimate conditions. Additional research is needed to link height growth, microclimate, and survival.

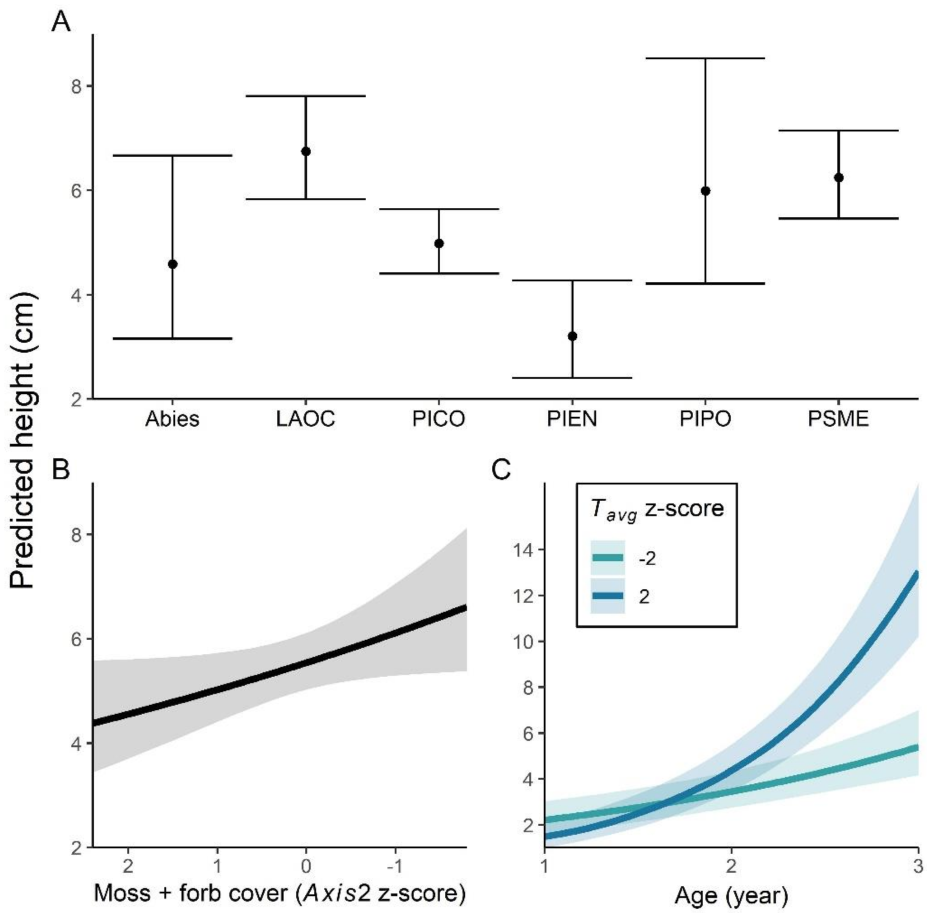

Fig. 13. Controls of seedling growth.Partial effects plot for best-fit model of seedling height in year 3 after fire, with 95% confidence intervals.

5.3. Limitations

Several limitations to this study highlight priorities for future research. Most critically, the resilience seen in these forests could be undermined by a severe heat or drought event in subsequent years causing additional seedling mortality. Future research should investigate changes in climate sensitivity as seedlings age, to assess the likelihood of mortality-causing climate events over time after fire. Further, our interpretations are limited to a relatively narrow range of conditions in mixed-conifer and lower subalpine forests of the northern Rocky Mountains, but may be representative of how regeneration occurs under moderate climate conditions after similar large fires. In addition, we were unable to quantify soil moisture or temperature, which are important aspects of microclimate that can be impacted by fire and can influence seedling regeneration (Petrie et al. 2016, Pettit et al. 2019, Hill and Ex 2020, Hoecker et al. 2020). Regeneration was likely also influenced by other factors that we did not measure, including seed predation, herbivory, and soil properties (Fig. 1), highlighting priorities for future research into fire effects on surface soil moisture and other soil conditions relevant to seedlings. Despite these limitations, our findings demonstrate the utility of a demographic framework predicting the dominant controls of post-fire regeneration, and further highlight the importance of heterogeneity in fire effects to generate favorable microsites for seedlings.

5.4. Science delivery

Two refereed journal articles will come from this project. Wolf et al. (2021), focused on quantifying the effects of wildfire on microclimate conditions (Objective 1, see above), was published in *Ecosphere* in May, 2021. A second manuscript, focused on evaluating controls of early post-fire seedling demography (Objective 2), is in preparation for publication and will be submitted shortly after submission of this final report.

The results of this project were presented in a webinar to the Northern Rockies Fire Science Network on 9/22/21, titled “Wildfire effects on microclimate conditions and seedling regeneration in Northern Rockies mixed-conifer forests”. A research brief is under development in collaboration with the Northern Rockies Fire Science Network and will be published this year. Additional science delivery activities included a presentation at the Ecological Society of America meeting in August 2020, a public talk at the Stevensville, MT, public library in June 2019, and a lecture in “The Future of Forests” teacher workshop presented through the University of Colorado Boulder CIRES outreach program in July 2021. Student investigator Wolf is also involved in outreach through the SkypeAScientist program, and has spoken with six K-12 classes throughout the country about this project and fire science more generally.

The data collected in this project are being incorporated into a West-wide analysis of post-fire regeneration led by co-PI Kimberley Davis in collaboration with The Nature Conservancy. We will also use these data to help validate the RegenMapper tool co-developed by the USFS and University of Montana researchers, which provides spatial predictions of the probability of conifer regeneration in recent fires and is being used by the USFS Region 1 to inform reforestation efforts.

6. Conclusions and Implications for Management and Future Research

Our results quantify the substantial impacts of fire on understory microclimate conditions, which vary across biophysical and fire-severity gradients. We found that fire increases microclimatic extremes, with the largest impacts in areas of greater canopy loss, in relatively cool-wet biophysical settings, and in days and seasons when ambient temperatures are high. Our results further reveal the relative importance of drivers of post-fire regeneration, including fire effects on microclimate and microsite factors that influence seedling recruitment, survival, and growth. We were able to explain 75% of the variability in post-fire tree regeneration based on seed availability, microclimate conditions, and fire effects on overstory, understory, and soil conditions, with fine-scale heterogeneity in fire severity playing an important role in creating diverse microsites to support regeneration. These findings provide an example of how forests can be resilient to contemporary fire activity, and contribute to an understanding of how forest scientists and managers can anticipate forest responses to future wildfires under changing environmental conditions.

Warmer and drier climate conditions in this century (McKenzie and Littell 2017, Ficklin and Novick 2017) have the potential to undermine the forest resilience observed in this study. As ambient temperatures increase and increased high-severity fire removes canopy buffering, burned areas will be exposed to greater climate and microclimate extremes. For example, our statistical model predicts that an increase in microclimate temperatures by 2 °C above the average observed in our sites would result in a decline in total seedling densities of approximately 26%. Further, more frequent and severe fires (Westerling 2016, Parks and Abatzoglou 2020) would reduce seed availability in large patches. We note, however, that within similar fires over the past decades, only 0-33% of burned areas are more than 100 m from a live tree. We can thus expect some reduction in post-fire tree regeneration under future conditions in these mixed-conifer and lower subalpine forests of the northern Rocky Mountains.

Our findings also highlight the potential for changes in forest composition, given differences in species responses to seed availability, climatic, and fire severity variables (Fig. 10). For example, our results highlight cone serotiny as one mechanism of forest resilience (Fig. 9A, 11A), with abundant *P. contorta* regeneration likely except where fire intervals are short (e.g., <20 years; Hansen et al. 2018). In addition, *L. occidentalis* regenerates well in areas of high overstory fire severity (Fig. 10A) and grows rapidly (Fig. 13), and may be well-suited to take advantage of open, disturbed areas (Steed and Goeking 2020). Wildfires thus have the potential to catalyze shifts in species composition in zones of overlapping species distributions, creating opportunities for mixed-conifer and lower subalpine forests to adjust to changing climate.

Finally, our results reveal the diversity of microsite habitats that support regeneration. We show that herbaceous plants and dead wood (standing or debris) contribute to microclimatic buffering (Fig. 4, 5), and that regeneration depends on different aspects of fire severity (Fig. 9, 10). This suggests that heterogeneity in pre-fire forest structure, fire effects, and understory communities have the potential to create microrefugia for regeneration even within areas of stand-replacing fire. Based on these findings, we expect that forest loss would be largely restricted to large high-severity patches lacking serotinous *P. contorta*, short-interval fires, or areas of exceptionally severe burning with stressful microclimatic and soil conditions (Turner et al. 2019, Hoecker et al. 2020).

We highlight several opportunities for management to increase forest resilience to wildfires based on these results. Retention of standing dead trees support natural regeneration through microclimatic buffering. Our findings support the utility of fuels treatments and managed wildfire use in low- and mixed-severity fire regimes to promote diversity in patch size and fire severity (Hessburg et al. 2016, Stephens et al. 2020), which supports regeneration through seed provision and microclimatic buffering (Coop et al. 2019). These benefits are most likely to manifest in relatively cool-moist settings (e.g., north-facing slopes) with greater water availability to support buffering (von Arx et al. 2013, Davis et al. 2019a, Wolf et al. 2021), and under moderate fire weather in protected topographic positions (Krawchuk et al. 2016). While such refugia may similarly promote resilience in subalpine forests with high-severity fire regimes, fuels management is not feasible nor effective in those systems (Halofsky et al. 2018).

Our findings also support the utility of post-fire reforestation efforts to facilitate forest resilience where seed sources are lacking, and suggest that survival would be highest in cool-wet topographical settings, with mosses, forbs, and some canopy cover, even dead, to provide microclimatic buffering, and in microsites with relatively low soil burn severity (Fig. 9). Uncertainty in the mechanisms underlying these relationships, and the degree to which they are similar for natural regeneration and planted seedlings, highlight topics for future research. In addition, our results highlight that planted seedlings are not subject to the strong germination-year mortality filter. Planting might be possible in high-severity areas with relatively unfavorable warm-dry microclimates for natural regeneration (Shepperd et al. 2006, North et al. 2019), and flexibility in selecting a relatively moist year for planting could facilitate root establishment in marginal areas (Pinto et al. 2012), particularly in sites with relatively low shrub density to compete with seedlings (Gray et al. 2005) as in most of our plots. Additional research is needed to evaluate differences in early survival and microsite preferences of natural and planted seedlings.

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Appendix B. List of Completed Scientific/Technical Publications/Science Delivery Products

Articles in peer-reviewed journals, with project supported personnel in bold

Wolf KD, **Higuera PE**, **Davis KT**, Dobrowski SZ. (2021) Wildfire impacts on forest microclimate vary with biophysical context. Ecosphere 12: e03467.

Technical reports

Wolf KD, **Davis KT**, **Higuera PE**. (*in preparation*). Wildfire effects on microclimate conditions and seedling regeneration in Northern Rockies mixed-conifer forests. Northern Rockies Fire Science Network Research Brief.

Graduate thesis

Wolf KD. (*in progress, anticipated 2022*) Interactions among climate, fire, and ecosystem processes across multiple spatial and temporal scales in Rocky Mountain subalpine forests. PhD Dissertation, Systems Ecology, University of Montana.

Presentations/webinars/other outreach/science delivery materials

Wolf KD. (2021). Wildfire effects on microclimate conditions and seedling regeneration in Northern Rockies mixed-conifer forests. Northern Rockies Fire Science Network Webinar. https://www.youtube.com/watch?v=wxRAOWiVGkY&t=1s

Wolf KD, **Davis KT**, **Higuera PE.** 2020. Burn severity, microclimate, and species composition drive post-fire tree regeneration in the first two growing seasons following wildfires in the northern Rocky Mountains. - Ecol. Soc. Am. Annu. Meet. #83375: Contributed Talk.

Davis KT and **Wolf KD** (2021) Post-fire regeneration in a changing climate. Invited presentation in The Future of Forests Teacher Workshop hosted by CIRES Education & Outreach, virtual.

Davis KT and **Wolf KD** (2019). Forests and fire in a changing climate. Public presentation at the North Valley Public Library, Stevensville, MT.

Appendix C. Metadata

This project produced a dataset containing annual seedling density, survival, and growth data over the first three years following the fires (2018-2020) in 69 plots, with associated plot data (slope aspect, fire severity, tree density, canopy cover, understory vegetation cover by life form, seed source information), soil data, and microclimate data. The refereed journal article utilizing this dataset is in preparation for publication and will be submitted shortly after submission of this final report. The metadata have been submitted to JFSP along with this report, and we plan to make the data available through Dryad after the manuscript is published under the following doi: 10.5061/dryad.9s4mw6mhj.

Additional microclimate data produced by this project are currently available online. This project produced a dataset containing hourly near-ground atmospheric temperature and vapor pressure deficit over the first two growing seasons following the fire (June-September, plus or minus one month) in 33 plots in two large wildfires from 2017. These microclimate data are stored along with associated plot data and climate data in an ecological archive through Dryad:

Wolf, Kyra (2021), Data from: Wildfire impacts on forest microclimate vary with biophysical context, Dryad, Dataset, https://doi.org/10.5061/dryad.47d7wm3c6