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ARTICLE

Ecology of Critical Zones

Montane springs provide regeneration refugia after high-severity wildfire

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Abstract

In the mountainous regions of the Western United States, increasing wildfire activity and climate change are putting forests at risk of regeneration failure and conversion to non-forests. During periods with unfavorable climatic conditions, locations that are suitable for post-fire tree regeneration (regeneration refugia) may be essential for forest recovery. These refugia could provide scattered islands of recovering forest from which broader forest recovery may be facilitated. Spring ecosystems provide cool and wet microsites relative to the surrounding landscape and may act as regeneration refugia, though few studies have investigated their influence on post-fire regeneration. To address this knowledge gap, we quantified coniferous tree regeneration adjacent to and away from springs in mixed-conifer forests in a mountainous region of central Idaho, USA. Our research objectives were to (1) quantify post-fire conifer density near and away from springs, (2) assess the relative importance of distance to a spring compared with other biophysical factors important to post-fire regeneration, and (3) examine the temporal trends of post-fire seedling establishment near and away from springs. In areas burned at high severity from fires in 1988, 2000, and 2006, we sampled transects at 27 springs for the count, age, and height of extant conifer seedlings, as well as topographic factors and distance to surviving seed source. We modeled the relative effects of distance to a spring, topographic variables (slope, heat load index, elevation), post-fire climate, and distance to surviving seed source for the two dominant species, Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*), using a generalized linear mixed-effects model. Our study revealed that proximity to springs resulted in higher conifer density and earlier establishment after high-severity wildfire when conditions for available seeds and topography were also met. Our results demonstrate that springs are important and previously undescribed regeneration refugia with landscape-scale implications for post-fire forest recovery in increasingly water-limited environments. Springs are relatively abundant features of montane landscapes and may offer continued regeneration refugia for post-fire recovery into the future, but additional springs mapping and hydroclimatic considerations are needed.

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KEYWORDS
conifer regeneration, fire ecology, groundwater, groundwater-dependent ecosystems, refugia, regeneration refugia, spring ecosystems, wildfire

INTRODUCTION

More frequent and larger high-severity wildfires followed by hot and dry post-fire climate conditions are leading to decreased post-fire tree regeneration or regeneration failure in many forested landscapes in the Western United States (Coop et al., 2020; Ellis et al., 2022; Kemp et al., 2019; Parks & Abatzoglou, 2020; Rother et al., 2015; Stevens-Rumann et al., 2018; Westerling et al., 2011). Reduced regeneration not only has negative implications for carbon storage, wildlife, and economic stability, but is also pushing ecosystems toward a tipping point resulting in ecosystem transitions from forests to non-forests (Coop et al., 2020; Johnstone et al., 2016; Stevens-Rumann et al., 2022). Understanding how forests are changing over time, and the drivers of successful regeneration after disturbances like wildfire is critical to forward-looking forest management (Vose et al., 2018).

Successful forest regeneration for many conifer species in the Western United States following wildfire is initially influenced by the spatial patterns of burn severity and resulting biological legacies (i.e., surviving seed sources) (Rodman et al., 2023). Many conifers are obligate seeders that depend on wind and/or animal dispersal (Neale & Wheeler, 2019), and have dispersal-distance thresholds limited by distance to surviving seed source (Kemp et al., 2016; Laughlin et al., 2023; Littlefield, 2019). In contrast, species like lodgepole pine (*Pinus contorta*) possess serotinous cones that open with fire and generally reestablish to pre-fire densities following high-severity wildfire (Guz et al., 2021; Lotan, 1976), unless fire return intervals are too frequent (<20 years) or the site conditions are unsupportive (Hansen et al., 2018).

When seeds are available, inadequate site conditions influenced by post-fire climate (e.g., moisture deficit) and local topography and geology may limit seedling establishment (Andrus et al., 2022; Davis et al., 2018, 2023; Marshall et al., 2023; Stevens-Rumann & Morgan, 2019). Microsite conditions such as soil moisture, humidity, and temperature are important limitations on conifer establishment success following wildfire (Hill et al., 2024; Marshall et al., 2023; Webb et al., 2023; Wolf et al., 2021). Previous research shows that higher post-fire conifer densities are typically found on wetter and cooler aspects and in topo-edaphic settings that are more mesic (e.g., see Harvey et al., 2016; Marshall et al., 2023). Alternatively, limited soil moisture and high surface temperatures can hinder establishment, potentially leading to establishment failure or tree mortality due to embolism (Allen et al., 2010; Johnson et al., 2011; Maher & Germino, 2006). Similarly, biologic controls on microsite conditions such as canopy cover may hinder seedling establishment due to competition for resources (e.g., light, nutrients, and water) (Andrus et al., 2022) or may improve seedling survival by reducing local vapor pressure deficit and providing protection from direct solar radiation (Davis et al., 2019a; Will et al., 2013; Wolf et al., 2021). Thus, successful post-fire regeneration is a function of both seed availability and site conditions conducive to establishment.

While seed availability is the first filter on successful post-fire regeneration, microsite conditions are a critical secondary control and more research is needed to understand the distribution of suitable microsite conditions and their interaction with surviving seed sources (Brodersen et al., 2019; Rodman et al., 2023; Stevens-Rumann & Morgan, 2019). Therefore, we introduce the term "regeneration refugia" to describe locations with inherent site conditions that support an increased likelihood of plant population recovery after fire compared with the surrounding landscape. Importantly, these refugia may provide scattered islands of recovering forest from which broader forest recovery may be facilitated (Figure 1). Regeneration refugia are unique from other refugia types (e.g., disturbance or climate change refugia) since they are not necessarily resistant to disturbance or climatic pressure (Krawchuk et al., 2020) but describe a biophysical context conducive to regeneration compared with their surroundings.

Within the framework of regeneration refugia (Figure 1), mesic sites such as spring ecosystems may function as such refugia (Tsinnajinnie et al., 2021). Spatially distributed based on underlying geology, springs are locations on the landscape where the aquifer meets the Earth's surface and expels groundwater (Stevens et al., 2021). Springs are especially important in arid and semi-arid regions of the Western United States where their cool and wet environment provide refugia from dry and hot conditions and result in increased biological productivity, diversity, and resilience to perturbations relative to the surrounding landscape (Murphy et al., 2015; Springer et al., 2015; Tsinnajinnie et al., 2021). Previous studies have demonstrated the refugial

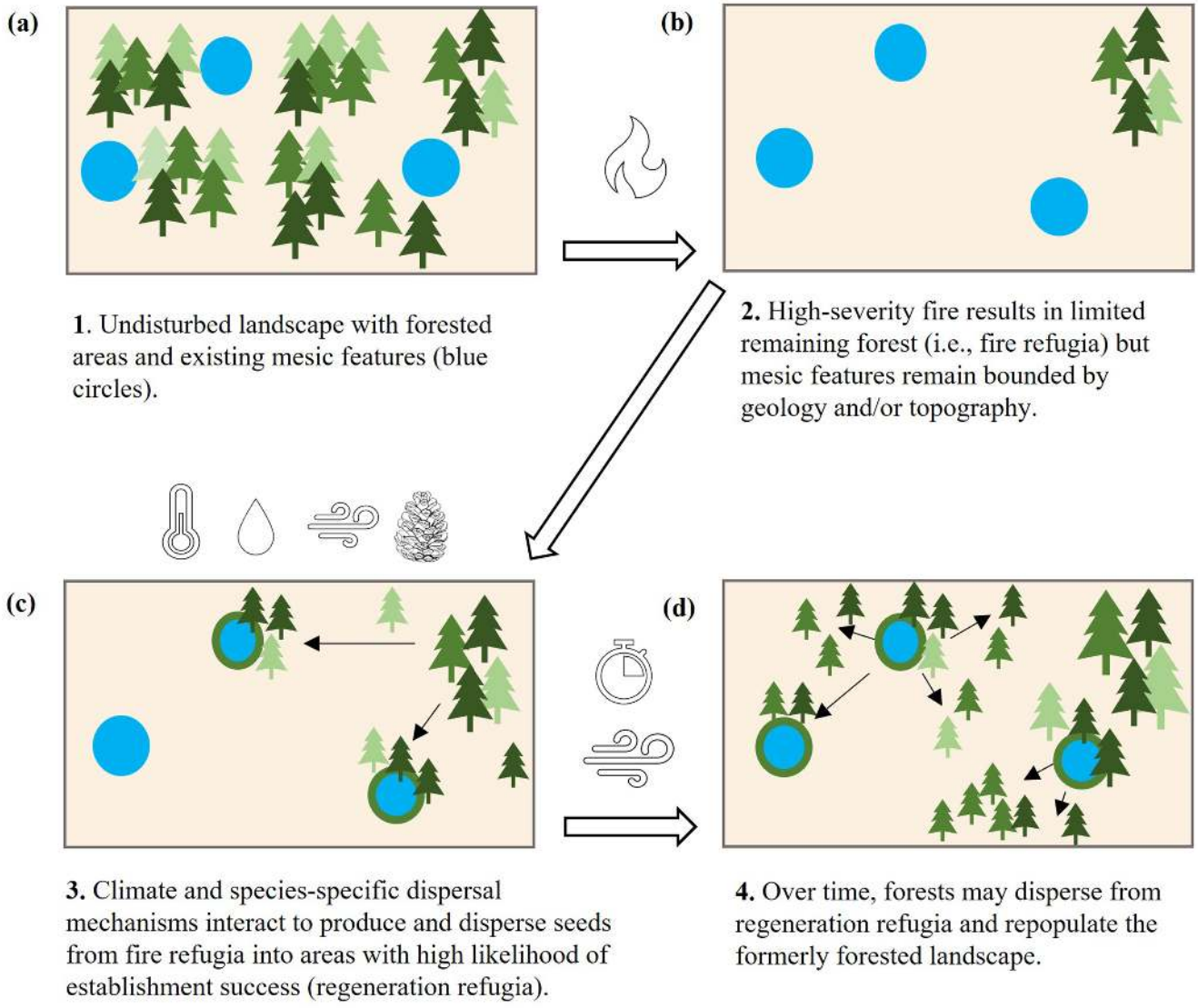


FIGURE 1 Conceptual functionality of regeneration refugia in a post-high-severity fire landscape. (a) An undisturbed forested landscape with mesic or hydric landscape features undergoes a high-severity fire leaving limited surviving trees that resisted the fire (fire refugia: Meddens et al., 2018), (b) but mesic or hydric features (e.g., springs) remain bounded by geology and/or topography. (c) Climate and species-specific dispersal mechanisms (e.g., wind or serotiny) interact to produce and disperse seeds from fire refugia into areas with high likelihood of establishment success (regeneration refugia). Over time, (d) trees may disperse from regeneration refugia and repopulate the formerly forested landscape.

function of springs in past periods of climate change (Murphy et al., 2015) and during drought (Fuchs et al., 2019), but few studies have investigated the role of springs in forest recovery after wildfire (Tsinnajinnie et al., 2021).

Springs could potentially function as regeneration refugia for conifers after wildfire through several mechanisms. For example, the increased soil moisture at springs could reduce the soil burn severity during a wildfire and preserve seeds (biological legacies) and facilitate rapid regeneration, similar to observed post-fire resilience in other non-spring riparian areas (Dwire & Boone Kauffman, 2003; Halofsky & Hibbs, 2008, 2009). Persistent soil moisture also provides suitable conditions for seed germination and growth after a burn (Johnson et al., 2011; Marshall et al., 2023; Webb et al., 2023). Moreover, rapid regrowth of riparian vegetation around springs and continuously cold groundwater output creates a cooler microclimate relative to the surrounding landscape potentially sheltering seedlings from hot surface temperatures that could otherwise lead to stress or mortality (Davis et al., 2019b; Fuchs et al., 2019). Conversely, high spring flows resulting in dense riparian canopy cover and saturated soil or large seasonal or interannual variability in spring discharge could hinder the establishment of some

conifer species (Cartwright & Johnson, 2018; Halofsky & Hibbs, 2009).

Despite the alignment between conditions at springs and requirements for conifer regeneration in mixed-conifer forests, we know relatively little about the intersection between springs and post-fire conifer regeneration. Thus, our main research goal was to investigate whether springs provided post-fire regeneration refugia for conifers in a mountainous mixed-conifer setting in high-severity burned areas. Our research objectives were to (1) quantify post-fire conifer density near and away from springs, (2) assess the relative importance of distance to a spring compared with other biophysical factors important to post-fire regeneration, and (3) examine the temporal trends of post-fire seedling establishment near and away from springs. Springs are relatively abundant features in montane landscapes, and the results from our study could inform ecologically and spatially based post-fire management strategies where post-fire regeneration failure is a concern (Larson et al., 2022; North et al., 2019).

METHODS

Study area

Our study area was in the lower Big Creek drainage in central Idaho in the Frank Church River of No Return Wilderness (FCRNRW) (Figure 2). The FCRNRW is a 957,793-ha federally designated Wilderness area with minimal modern human development and management, including no post-fire management. This research was conducted within the Krassel District in the Payette National Forest and based out of the Taylor Wilderness Research Station, a remote research station owned and operated by the University of Idaho. The lower Big Creek drainage receives approximately 38 cm of annual precipitation with most of the precipitation occurring in the winter and spring months (gridMET; Abatzoglou, 2013). Lower Big Creek is characterized by an average January minimum temperature of approximately −10°C, while average July maximum temperature is 28°C. Minimal precipitation occurs in the summer months (June to September), averaging 10 cm (gridMET; Abatzoglou, 2013). The bedrock geology consists mainly of Diorite, Quartzite, and Granodiorite (Stewart et al., 2013). Dominant soil types include sandy and silty loam, but in steeply sloped areas (>30°) minimal or thin soil cover exists. However, increased soil cover and depth typically occurs near springs through greater organic decomposition from riparian vegetation.

Data were collected in the summer and fall of 2023 within the perimeters of three wildfires: the Golden fire (1988; 19,481 ha [48,138 acres]), the Dunce Creek fire (2006; 2777 ha [6863 acres]), and the Diamond Point Complex (2000; 109,816 ha [271,361 acres]) (Figure 2b; MTBS, 2023). The elevation of springs sampled ranged from 1200 to 2400 m and occur primarily in dry mixed-conifer (Douglas fir [*Pseudotsuga menziesii*] and ponderosa pine [*Pinus ponderosa*]), and some in moist lodgepole pine forest types (Payette National Forest, 2012). According to LANDFIRE data, historic fire return intervals in mixed conifer forests of the Northern Rocky Mountains typically are between 19 and 43 years and burn at low to moderate severity (USDA, 2012a). In lodgepole-dominated forests, the historical fire return interval is between 92 and 307 years, primarily characterized by stand-replacing burns (USDA, 2012b).

Site selection

Springs were selected based on field accessibility, location within a high-severity burn patch and evidence of pre-fire conifer presence (i.e., snags or downfall) (Appendix S1: Section S1). Springs that emerged near (~30 m) a perennial surface stream channel were excluded from the study to isolate the effect of the spring and avoid the potential influence of the surface-stream riparian area on post-fire forest recovery (Halofsky & Hibbs, 2009). Pre-classified overstory burn severity rasters were downloaded from the Monitoring Trends in Burn Severity (MTBS) interactive viewer (MTBS, 2023) that contain the differenced normalized burn ratio (dNBR) with defined severity classes (unburned, low, moderate, and high). Only springs that burned within high-severity burn patches were included in the study to assess regeneration in areas most at risk of regeneration failure and forest to non-forest conversion (Kemp et al., 2016; Stevens-Rumann et al., 2018).

Field sampling

Beginning from a point 20 m downslope from the spring emergence, we sampled two 40-m-long belt transects in opposing directions and perpendicular to the spring channel (Figure 3a). If the spring riparian area was visually estimated as small (<1000 m^2), we only sampled one pair of transects. For large springs (>1000 m^2), one additional pair of transects were sampled 20 m downslope from the first pair to account for the effect of a large

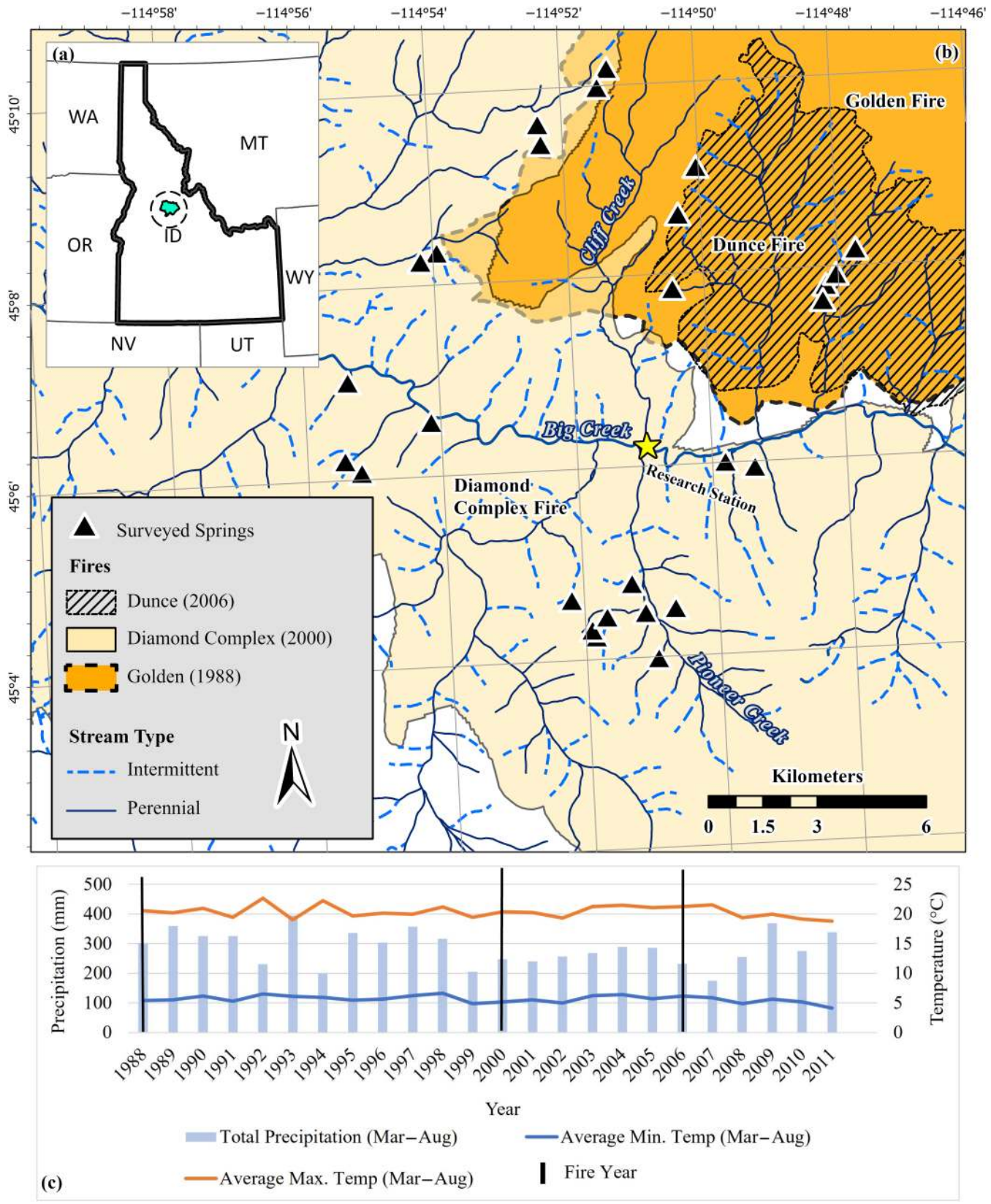


FIGURE 2 (a) Study area located in the Big Creek drainage in central Idaho, USA, and (b) location of surveyed springs surrounding Taylor Wilderness Research Station (Research Station) within relevant wildfire perimeters. (c) Post-fire climate (March to August total precipitation and March to August average maximum and minimum temperatures) during the study period with fire years marked in vertical black lines. Climate data from gridMET (Abatzoglou, 2013) downloaded from climatetoolbox.org. Streams spatial data from the National Hydrography Dataset (USGS, 2023).

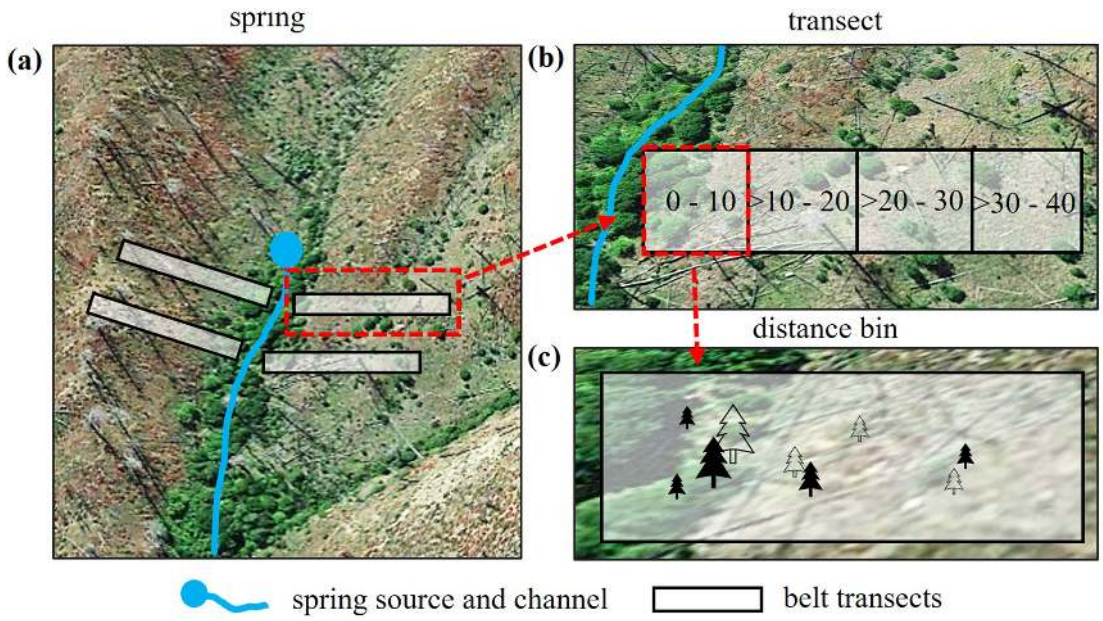


FIGURE 3 Study design with three levels of sampling including (a) the spring site, (b) transect level, and (c) distance bin level. (a) At each spring, two to four 40-m transects were laid out from the wetted edge of the spring channel perpendicular to the slope. (b) At each transect, distance to seed source, slope angle, and aspect were recorded. (c) At the distance bin level, tree count, height, and age were collected (satellite imagery from Google Earth 2016).

spring riparian area. Transect widths were determined prior to sampling and varied from 2.5 to 30 m depending on a visual estimate of tree density, similar to previous studies that used belt transects (Kemp et al., 2016; Stevens-Rumann et al., 2015). The belt transects were subdivided into four 10-m-long distance from spring bins (hereafter, distance bins) (Figure 3b). Within each distance bin, live conifer trees of all sizes were counted by species, and each tree's height measured using a laser range finder (Nikon Forestry Pro II) or meter stick (Figure 3c).

We also collected several biophysical parameters that affect post-fire forest recovery (Table 1). Distance to surviving seed source, which is a strong predictor of tree density, was measured at each transect. The horizontal distance to the ten nearest surviving conifer trees was measured from the center of each transect using a Nikon Forestry Pro II laser range finder and then averaged per transect (Kemp et al., 2016). Typically, surviving pre-fire seed-bearing trees were in mixed-species clusters or unburned forest edges (i.e., including Douglas fir) and we did not distinguish between species in our measurement of distance to seed source. To account for topographic controls on regeneration we also collected aspect (in degrees), slope using a clinometer (in degrees), and elevation of the spring site using a handheld GPS device (in meters) (Figure 3; Table 1). Aspect was measured on both the spring and transect scale (Figure 3) and used to calculate the heat load index (HLI).

To understand tree age demographics with distance from the spring, age was randomly subsampled across representative tree heights using bud scar counting or an increment borer depending on the diameter of the tree (>4 cm) (Speer, 2010; Urza & Sibold, 2013). When an increment borer was used, the tree was cored as close to the base of the tree as possible, and tree age was estimated as the number of annual growth rings (Speer, 2010). We modeled tree age as a function of height for all trees of the two dominant species (Douglas fir and lodgepole pine) (Miller et al., 2007). We compared average annual growth rate (height/age) across distance bins using a one-way ANOVA to check the validity of fitting models equally across all distance bins for each species but found no significant differences between the distance bins (Douglas fir, $p = 0.371$; lodgepole pine, $p = 0.158$; Appendix S1: Section S2). The height-to-age models were applied to all tree heights recorded to predict tree age (Appendix S1: Section S3). When the model predicted a 0 or negative tree age (<1% of trees), the age was changed to 1 year. Aging trees also allowed us to confirm that we only sampled trees that established post-fire (see *Results* and Appendix S1: Table S7).

We surveyed seven springs located within more than one fire perimeter (i.e., reburn; Figure 2). Based on the timing of seedling establishment, all seedlings appeared to establish after the second fire at reburned springs. Additionally, seedling density was not significantly different at reburned sites for either dominant species (Douglas

TABLE 1 Candidate predictor variables included in initial models.

Candidate predictor variable	Description	Data source	Measurement scale	Range	Mean (SD)	Median
Hydrological						
Distance to spring (m)	Distance to wetted spring channel edge measured with a transect tape in the field. Lower values indicate closest distance to a spring.	Field	Distance bin	5–35	18.7 (11.5)	15
Biological						
Distance to nearest surviving seed source (m)	Distance to nearest potential seed source that survived the fire (10 measurements per transect).	Field	Transect	50–500	249.2 (170.5)	206.9
Topography						
Slope (°)	Slope of the spring site and each transect.	Field	Spring and transect	7–33 (S); 2–37 (T)	21 (6.4) (S); 16.9 (9.2) (T)	23 (S) 17 (T)
Heat load index (HLI)[a]	Index indicating incident solar radiation based on aspect using equations from McCune and Keon (2002). Values closer to 0 indicate wetter and cooler topo-climate conditions (e.g., northwest-facing slopes), while values closer to 1 indicate warmer and drier topo-climate conditions (e.g., southeast-facing slopes).	Field	Spring and transect	0.001–0.99 (S); 0.007–0.99 (T)	0.40 (0.37) (S); 0.45 (0.34) (T)	0.30 (S); 0.47 (T)
Elevation (m)	Site elevation.	Field	Spring	1207–2387	1824.5 (345)	1762.5
Climate						
Average 5-year post-fire cumulative precipitation (Mar to Aug) (mm)	Average of cumulative precipitation at each spring site from Mar to Aug over the first 5 years post-fire.	PRISM[b]	Spring	202–525	282 (80)	267
Average 5-year post-fire seasonal maximum temperature (°C)	Average maximum air temperature at each spring site from Mar to Aug for the first 5 years post-fire.	PRISM	Spring	13–21	18 (2)	18

Note: S, spring; T, transect.
[a]McCune and Keon (2002).
[b]PRISM Climate Group (2024).

fir, $W = 3287$, $p = 0.9798$; lodgepole pine, $W = 1267.5$, $p = 0.8011$; Appendix S1: Section S7), suggesting minimal effects of reburns in our study. Thus, we excluded the effects of reburns in our analysis.

Climate predictors derived from spatial datasets

To account for the potential effect of climate on post-fire regeneration we, calculated several post-fire climate parameters (Table 1). For each spring, we calculated the average 5-year post-fire cumulative seasonal (March to August) precipitation and the average 5-year post-fire seasonal (March to August) maximum temperature using data derived from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) (PRISM Climate Group, 2024).

Data analysis

Effect of spring proximity versus biophysical and climate predictors on tree density

To understand whether proximity to a spring was a significant predictor of tree density compared with other

factors, we fit a generalized linear mixed-effect model (GLMM) with a negative binomial distribution and a log link ("glmmTMB" package in R; Brooks et al., 2017). We fit models for the two dominant tree species observed: (1) Douglas fir and (2) lodgepole pine. Our tree count data were overdispersed, which we handled using negative binomial distributions (Andrus et al., 2022; Kemp et al., 2016; Zuur et al., 2009).

The dependent variable for each model was tree count and an area offset term was also included in each model to account for varying sampled area (Zuur et al., 2009). Predictor variables were standardized to allow coefficient comparisons ($x - \text{mean}(x)/\text{SD}(x)$) (Gelman, 2008). For clearer model coefficient interpretation, distance bins were converted to a continuous variable by centering the distance value within each distance bin (e.g., a 0–10-m-bin was converted to 5 m). To account for the presence or absence of a tree species, when a particular tree species was present in one distance bin along a transect but was absent in another distance bin along the same transect, a count of "0" was added for that species in the distance bin it was absent from.

Transect within a spring were assigned as nested random effects in our Douglas fir model to account for multiple transects per spring and data collected at the distance bin level (Figure 3). When we fit the full random effects structure for lodgepole pine, the spring had a variance close to 0 which resulted in a singular fit. Thus, we only assigned transect as a random effect for our lodgepole pine model after calculating the intra-class correlation metric (ICC) to determine which random effect resulted in a better-fitted model.

All predictors were tested for collinearity using Spearman's rank tests and variables with a Spearman's $\rho > |0.5|$ were not included in the same model (Table 1; Appendix S1: Section S4). Elevation and distance to seed source were correlated for both species, likely due to the occurrence of large stand-replacing fires in high elevation zones in the study area. We decided to use distance to seed source for our Douglas fir model because it is a biological indicator of forest recovery likelihood. We chose elevation for our lodgepole pine model because distance to seed source may be less biologically relevant for lodgepole pine regeneration since it relies on serotinous cones (Despain, 2001; Lotan, 1976). Post-fire climate variables (average 5-year seasonal post-fire maximum temperature and precipitation) were highly correlated (Spearman's $\rho > |0.5|$) with each other and with elevation, so we iteratively fit separate models with each collinear variable and then used the Akaike information criterion (AIC; Akaike, 1974) to assess model fit (Appendix S1: Section S5). We selected our final model based on the lowest AIC (Fabozzi et al., 2014). In our lodgepole pine dataset, elevation was collinear with HLI and transect slope (Spearman's $\rho > |0.5|$), so we fit two models to predict post-fire lodgepole pine density and reported coefficient estimates for the two models in our results. Model performance for the final models were assessed using the "performance" package (Lüdecke et al., 2021). Model assumptions were tested using the Diagnostics for Hierarchical Regression Models (DHARMa) package (Hartig, 2022) (Appendix S1: Section S5).

Tree age and temporal trends with distance to a spring

Tree age with proximity to a spring is non-parametric and ordinal (distance bins), so we performed Kruskal–Wallis tests to assess differences in age among distance bins for both Douglas fir and lodgepole pine in each fire year (Hollander & Wolfe, 1973). If the Kruskal–Wallis test indicated significant differences ($\alpha = 0.05$) in age between distance bins, a post hoc pairwise test with a holm correction was performed to identify distance bins that differed significantly from each other using the kruskalmc() function in the "pgirmess" package in R (Giraudoux, 2024). Using our age data we also visualized and qualitatively described the temporal establishment patterns with distance to a spring following Harvey et al. (2016) and Stevens-Rumann et al. (2018). All analysis was done using R version 4.3.2 (R Core Team, 2023).

RESULTS

Tree density with distance from a spring

A total of 823 post-fire trees were counted and measured at all springs, including 521 Douglas fir, 261 lodgepole pine, 34 ponderosa pine, and 7 Engelmann spruce. Since 95% of the trees counted were Douglas fir or lodgepole pine, we focused on these two species in our analysis.

Generally, both Douglas fir and lodgepole pine density decreased with distance from the spring (Table 2; Figure 4). For Douglas fir, the highest densities were found within 0–10 m of the spring (42% of the overall tree density) (Table 2). Within the 0–10 m distance bin, Douglas fir had a 70% higher average density than the >10–20 m distance bin, and a 95% greater average density than the >30–40 m distance bin across the entire study area. Similarly, for lodgepole pine, the highest mean, median, and sum of tree density occurred within 0–10 m

TABLE 2 Summary of tree density (in number of trees per hectare) measured with distance to the spring for the two dominant tree species observed across all burned areas.

Species	Distance to the spring (m)	Tree density			Percentage of total[a]
		Mean	Median	Sum	
Douglas fir	0–10	562	200	33,150	42
	>10–20	269	0	16,150	21
	>20–30	291	0	17,150	22
	>30–40	199	0	11,950	15
Lodgepole pine	0–10	490	200	15,200	31
	>10–20	259	200	8800	18
	>20–30	321	0	10,900	22
	>30–40	406	0	13,800	28

[a]Percentage of total trees by species. Percentages were rounded to the nearest whole number.

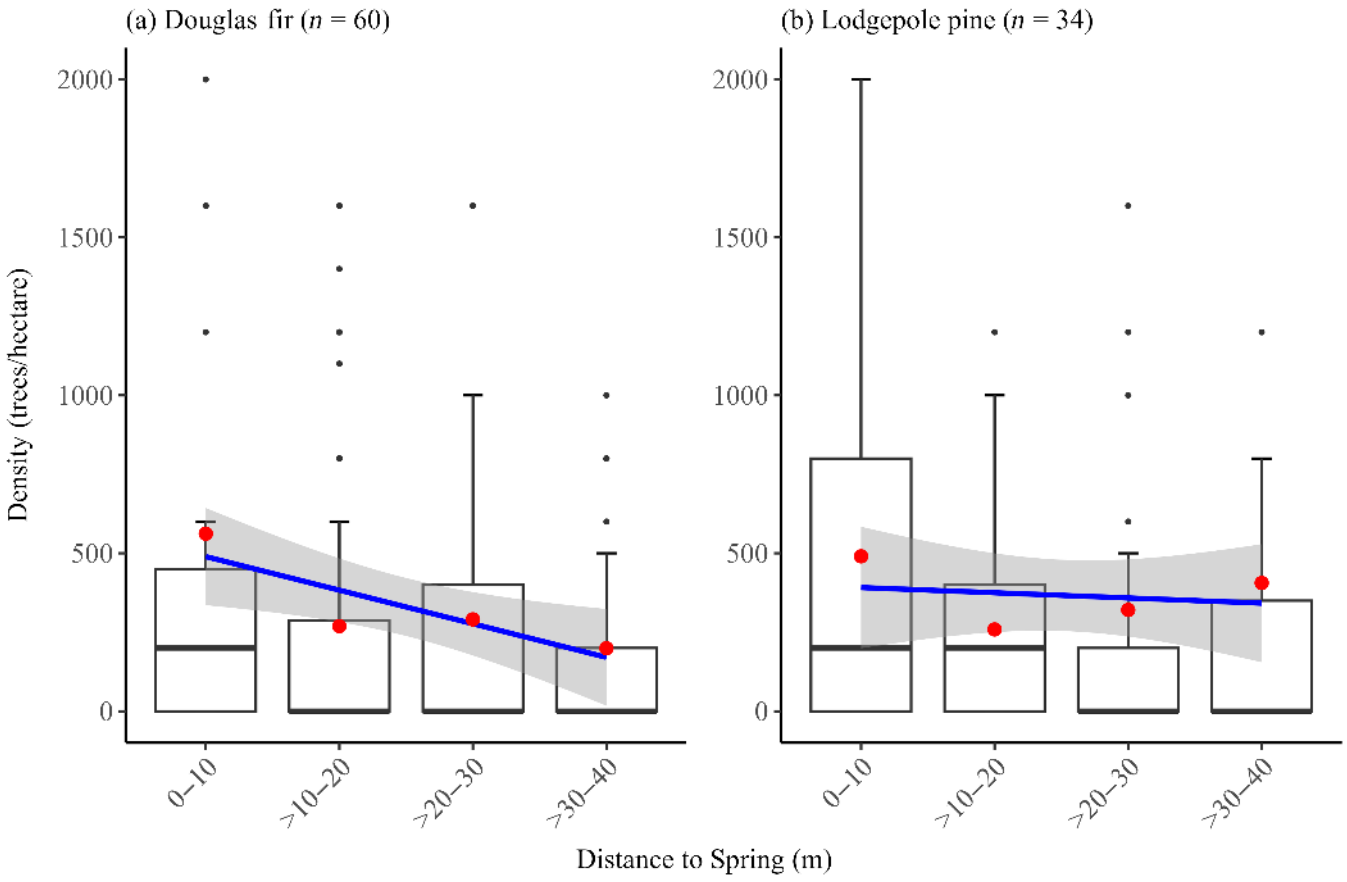


FIGURE 4 Tree density of (a) Douglas fir and (b) lodgepole pine trees with distance from a spring for each transect for all fires. Points represent outliers in the dataset, the solid black line within each boxplot represents the median, and the whiskers represent 1.5× the interquartile range. Red dots represent the mean density for each distance bin across all springs. A linear smoother was added with 95% CIs to better visualize the decrease in density with distance from the spring. There are density values for Douglas fir and lodgepole pine >2000 trees/ha not shown in the graph for clearer comparison among species. "n" is the number of transects.

of the spring (31% of the total across all burned areas) (Table 2; Figure 4b). The 0–10 m distance bin for lodgepole pine had a 62% greater average density compared with the >10–20 m distance bin, but only a 19% difference in average density compared to the >30–40 m distance bin.

Effects of distance to a spring and biophysical parameters on regeneration

Post-fire Douglas fir stem density model

In our Douglas fir model (Table 3), the distance to a spring was a significant predictor of Douglas fir density, and decreased with distance from the spring ($\beta = -0.30$, $p = 0.004$). Distance to seed source was the most significant predictor of Douglas fir density ($p = 0.0009$) (Table 4; Figures 5 and 6) and is associated with decreasing density with increasing distance from seed source ($\beta = -0.76$). Topographic factors (HLI, slope) were poor predictors of Douglas fir density (Table 4). Through our iterative model selection process, we found that average 5-year post-fire cumulative seasonal precipitation ($p = 0.47$) and post-fire maximum temperature ($p = 0.75$) did not have significant effects on Douglas fir density and were not included in the final model (Appendix S1: Section S5).

Post-fire lodgepole pine stem density models

In our lodgepole pine model (Table 3), the distance to the spring was a significant predictor of lodgepole pine density with decreasing density farther from springs ($\beta = -0.32$, $p = 0.018$) (Table 4; Figure 5). Elevation was the most significant predictor of post-fire lodgepole pine stem density ($p = 0.0069$) with increased lodgepole pine density with increasing elevation ($\beta = 0.8$) (Table 4; Figure 5). Additionally, lodgepole pine density increased significantly with HLI (spring) ($\beta = 0.55$, $p = 0.014$).

TABLE 3 Generalized linear mixed-effect model performance metrics for the negative binomial count models for both Douglas fir and lodgepole pine.

Model	R^{2}[a]	RMSE	ICC	Moran's *I*
Douglas fir	0.346	3.5	0.233	$I = -0.005$, $p = 0.62$
Lodgepole pine[b]	0.336	2.786	0.244	$I = -0.239$, $p = 0.28$

Note: Moran's *I* indicates spatial autocorrelation among residuals.
Abbreviation: ICC, interclass correlation coefficient; RMSE, Root Mean Square Error.
[a]Nakagawa and Schielzeth (2013).
[b]Model performance metrics reported from the non-elevation lodgepole pine model.

Tree age patterns near springs

Douglas fir

In all burned areas, Douglas fir median, mean, and max tree ages were higher in the 0–10 m distance bin relative to the other distance bins (Figure 7a; Appendix S1: Section S6). However, Kruskal–Wallis results suggested Douglas fir tree ages did not differ significantly between distance bins in the 1988 fire ($\chi^2 = 0.034$, df = 3, $p = 0.99$). For the 2000 and 2006 fires, Kruskal–Wallis results suggest significant differences in tree ages with distance from spring (2000 fire, $\chi^2 = 13.834$, df = 3, $p = 0.003$; 2006 fire, $\chi^2 = 13.141$, df = 3, $p = 0.004$). In the 2000 fire, Douglas fir tree ages are significantly older in the 0–10 m distance bin than in the >30–40 m distance bin ($p = 0.001$), but not between any other distance bin (Figure 7a; Appendix S1: Section S6). For the 2006 fire, Douglas fir tree ages are significantly older in the 0–10 m distance bin than in the >20–30 m distance bin ($p = 0.001$) but not between any other distance bins.

Lodgepole pine

For lodgepole pine trees, we found significant differences in age between distance bins but age with distance from spring was variable and produced no clear trend for

TABLE 4 Results from generalized linear mixed models for post-fire regeneration of Douglas fir and lodgepole pine.

	Douglas fir				Lodgepole pine			
Predictor variable	**Coef**	**SE**	***p***	**95% CI**	**Coef**	**SE**	***p***	**95% CI**
Distance to the spring	−0.30	0.10	0.004	−0.5, −0.09	−0.32	0.13	0.018	−0.58, −0.05
Transect HLI	−0.35	0.21	0.10	−0.76, 0.07	...	...	...	...
Spring HLI	...	...	...	...	0.55	0.22	0.014	0.11, 0.98
Distance to seed source	−0.76	0.23	0.0009	−1.2, −0.31	...	...	...	...
Transect slope	−0.20	0.20	0.30	−0.59, 0.18	−0.48	0.28	0.093	−1.0, 0.08
Elevation[a]	...	...	...	...	0.80	0.30	0.0069	0.22, 1.38

Abbreviation: HLI, heat load index.
[a]Elevation was correlated with spring HLI and transect slope for lodgepole pine thus were not included in the same model. A separate model was fitted that included elevation as a fixed effect, and its estimate reported here. All other variable coefficients were reported from the lodgepole pine non-elevation model.

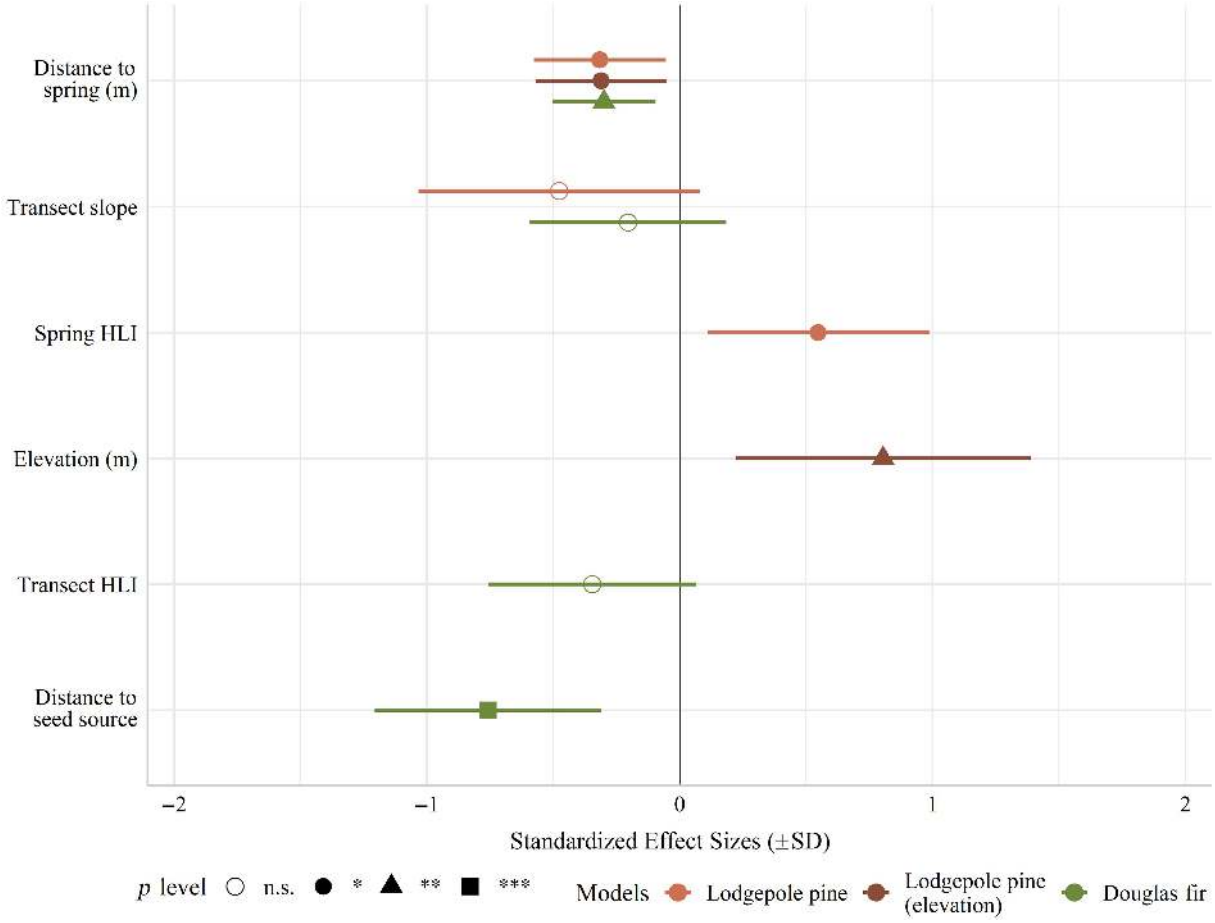


FIGURE 5 Results from the generalized linear mixed models, including standardized coefficient effect sizes (points) and 95% CIs (horizontal lines) on tree density (in number of trees per hectare) for the three models. Point shape indicates statistical significant level where "n.s." = not significant.

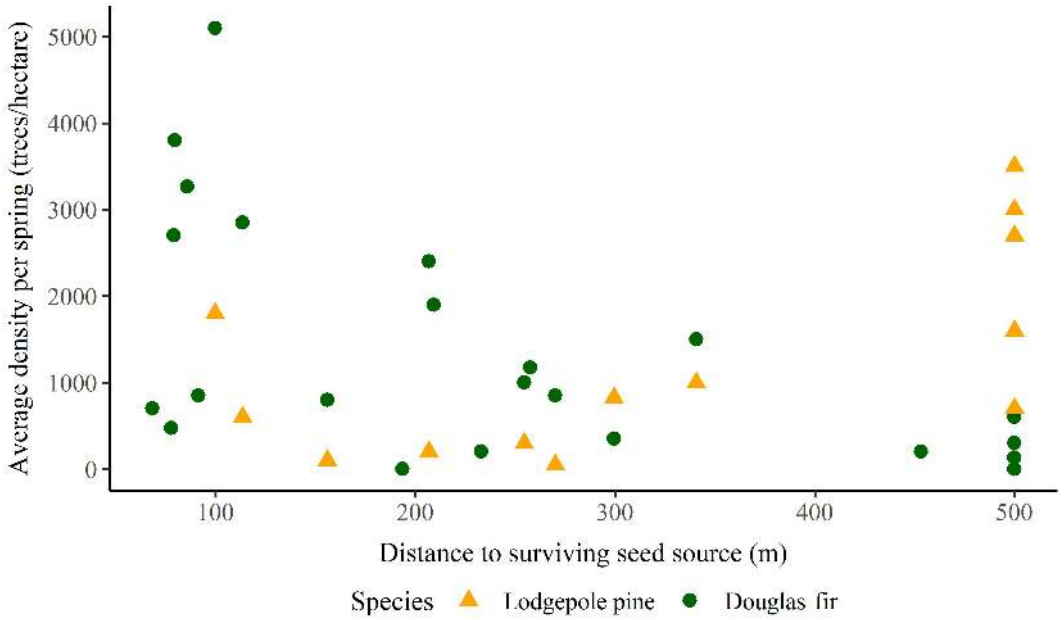


FIGURE 6 Relationship between distance to seed source and average density per spring for each species from field observations. When no surviving seed sources were observed, a default value of 500 m was assigned to a transect.

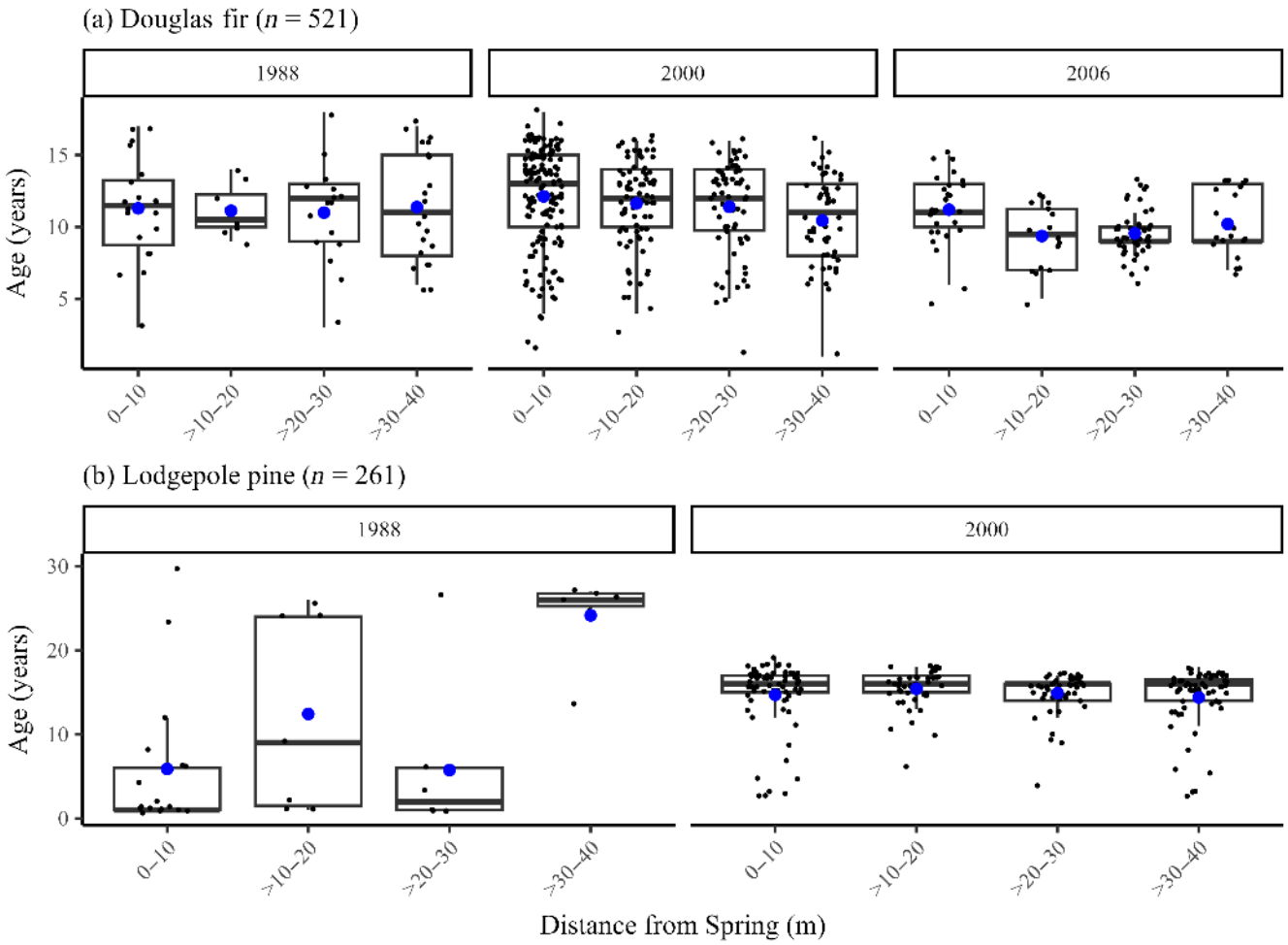


FIGURE 7 Age distributions of post-fire (a) Douglas fir and (b) lodgepole pine trees with distance from the spring by fire year listed above each panel. Solid black lines indicate the median, blue points indicate the mean, the box bounds indicate the 25th and 75th quantiles, and vertical bars indicate 1.5× the interquartile range. There was no lodgepole pine regeneration observed at springs in the 2006 fire.

either the 1988 or 2000 fire (Figure 7b; Appendix S1: Section S6). In the 1988 fire, tree ages are significantly older in the >30–40 m distance bin than in the 0–10 m and >20–30 m distance bins according to Kruskal–Wallis results ($\chi^2 = 12.138$, df = 3, $p = 0.007$) and post hoc pairwise comparisons ($p = 0.002$). No significant differences in tree ages exist in the 2000 fire among distance bins (Kruskal–Wallis: $\chi^2 = 4.7808$, df = 3, $p = 0.19$).

Temporal patterns of conifer regeneration near springs

Douglas fir

Qualitative assessment of post-fire regeneration trends suggested slightly earlier and more rapid initiation of Douglas fir regeneration closer to springs in the three fires (Figure 8a). Douglas fir regenerated in a large single pulse relatively soon after fire with the majority of regeneration occurring in the 0–10 distance bin. A second regeneration pulse occurred ~22 years post-fire, but regeneration is more evenly distributed across distance bins compared with the earlier regeneration pulse.

Lodgepole pine

Lodgepole pine regenerated in one large pulse starting several years after the fires (Figure 8b). Initially, lodgepole pine regenerated slightly earlier and in greater density closer to the spring post-fire, but over time, the rate and quantity of regeneration did not differ between distance bins. A small amount of continuous regeneration occurred over time, but the regeneration density was

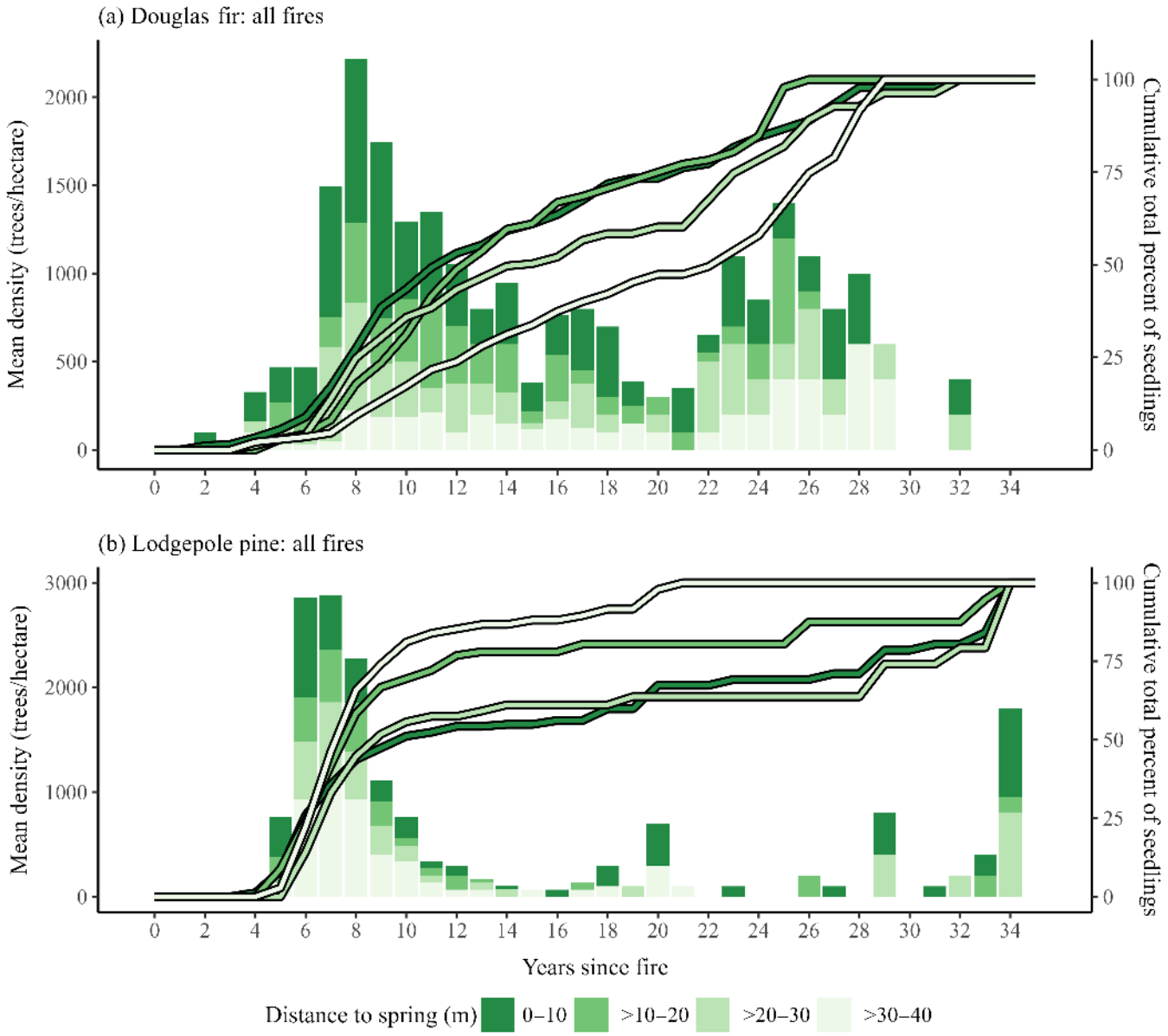


FIGURE 8 Temporal trends in (a) Douglas fir density and (b) lodgepole pine density in each post-fire year with distance from the spring (shades of green) aggregated across the three study fires. Data are the mean transect density by year and distance from the spring on the primary *y*-axis and the cumulative percent of total seedlings for each distance bin displayed on the secondary *y*-axis. Germination year was predicted from height-age models.

relatively low compared with the initial post-fire regeneration pulse.

DISCUSSION

Our findings indicated that proximity to springs significantly influenced the spatial pattern and temporal trend in conifer regeneration following high-severity wildfire in a mixed-conifer montane environment. Here, we discuss three key results from our study: (1) tree density decreased with greater distance from springs for Douglas fir and lodgepole pine, (2) modeled age data suggested that Douglas fir trees regenerated earlier after fire near springs compared withfarther away, and (3) distance to seed source and topographic variables were the primary predictors of regeneration near springs. Our study introduced springs as regeneration refugia for post-fire conifer establishment likely due to their cool and wet microsite conditions. We outline the implications of springs as regeneration refugia, future research directions, and post-fire management strategies.

Springs as regeneration refugia

Spatial regeneration patterns

Post-fire regeneration densities were higher for all species closer to springs across the study area (Figures 4 and 9a; Table 2) and all models indicated a negative relationship between distance to spring and tree density (Table 4; Figure 4). In addition, areas farther away from springs (>30–40 m) had a median density of 0 trees/ha compared with 200 trees/ha closer to springs (0–10 m), suggesting that regeneration failure may be more likely farther away from springs (Table 2). The inherent mesic site conditions at springs (cold and wet) likely led to the observed higher tree density and their functionality as regeneration refugia in our study area (McLaughlin et al., 2017). This assumption is consistent with findings from similar studies that linked cool and wet microsite conditions to higher Douglas fir and lodgepole pine regeneration (e.g., Andrus et al., 2018; Davis, Dobrowski, Higuera, et al., 2019; Hansen et al., 2018; Marshall et al., 2023; Petrie et al., 2016). Germinating seeds and seedlings are especially sensitive to surface and shallow soil moisture which can experience high daily variability driven by temperature and surrounding vegetation growth (i.e., transpiration) (Johnson et al., 2011; Will et al., 2013). The shallow water table near springs likely buffers seedlings from daily variability in soil moisture and plant available water and increases the likelihood of successful establishment.

It is well established that riparian areas are colder (air and surface temperature), have higher relative humidity (lower vapor pressure deficit), and more canopy cover compared with the surrounding environment (Dwire & Boone Kauffman, 2003; Eskelson et al., 2013; Rambo & North, 2008). These spring-riparian conditions could shelter seedlings from vascular tissue damage by direct solar radiation and embolism from high vapor pressure deficit, ultimately leading to higher post-fire seedling establishment (Figure 4; Table 2; Clark-Wolf et al., 2022; Davis et al., 2019a; Fuchs et al., 2019; Wolf et al., 2021). Buffering of harsh seedling establishment conditions at springs is also suggested by the minimal effect of HLI on post-fire Douglas fir density (Table 4). Conversely, dense hardwood riparian cover likely contributed to the observed low conifer density at some springs (Figure 9b; Halofsky & Hibbs, 2009) due to biological competition and limited light availability hindering seedling establishment (Hill et al., 2024). Overall, proximity to a spring is an indirect indication of cooler and more humid conditions, and is a likely explanation of the springs' functionality as regeneration refugia.

Temporal regeneration trends

Our results suggest that Douglas fir establish earlier and more rapidly closer to springs relative to further away (Figures 7 and 8). Differences in tree ages among distance bins have landscape-scale implications for forest resilience to disturbance. Stand age diversity leads to greater forest heterogeneity and resilience to disturbance (Johnstone et al., 2016). Furthermore, earlier establishment near springs suggests that springs could act as source populations for Douglas fir with the potential to



FIGURE 9 (a) Dense Douglas fir regeneration bordering a spring riparian area, and (b) dense riparian vegetation surrounding another spring with little conifer regeneration observed (photo credit: Grace Peven).

propagate outward into surrounding habitat and recolonize burned areas with trees (Coop et al., 2019).

Lodgepole pine initially established slightly earlier closer to springs after the three fires, but over time this trend dissipated, and trees established at similar rates across distance bins (Figure 8b). This initial trend is likely driven by a small number of early establishers in the 1988 fire since tree age distribution across distance bins was relatively similar at springs in the 2000 fire (Figure 7b). Over time, lodgepole pine continued to establish (likely by a non-serotinous seed source) in small numbers and resulted in higher cumulative density closer to springs (Table 2; Figure 4b). Higher cumulative density for both dominant tree species closer to springs implies that springs provide lasting (non-transient) regeneration refugia after fire.

The non-spring biophysical environment significantly limits regeneration

Regardless of whether a spring provided suitable establishment conditions (i.e., soil moisture, reduced surface temperature, etc.), distance to surviving seed source was the most significant factor in predicting post-fire Douglas fir density (Table 4; Figures 5 and 6). Distance to seed source is a well-known control on conifer regeneration following wildfire for non-serotinous species (Busby & Holz, 2022; Hansen et al., 2018; Harvey et al., 2016; Kemp et al., 2016; Laughlin et al., 2023). This finding also aligns with our conceptual framework (Figure 1), which suggests that the functionality of regeneration refugia is constrained by the availability of surviving seed sources. Likewise, sites with no nearby surviving seed sources had no or minimal post-fire Douglas fir regeneration (Figure 6). However, even some sites with nearby seed sources had low densities, which may be explained by physical dispersal barriers (e.g., hillslope direction or slope angle), variability in seed yield, and/or site conditions.

Not surprisingly, post-fire lodgepole pine density was limited by factors other than distance to seed source likely due to serotinous cones that open with fire (Figure 5; Kemp et al., 2016; Littlefield, 2019). Elevation was the most significant predictor of lodgepole pine density in our model, consistent with previous findings (Guz et al., 2021) (Table 4; Figure 5). An increase in elevation generally represents an increase in moisture availability and a decrease in air temperature. The large effect size of elevation ($\beta = 0.8$) compared with distance to a spring ($\beta = -0.32$) suggests that macro-climate controls on soil moisture may be more important than proximity to localized water sources (springs) for lodgepole pine regeneration. Similarly, our results indicated that lodgepole pine density increased with higher heat load (i.e., southwest facing slopes), which aligns with previous studies (Littlefield, 2019), and suggests that lodgepole pine is more temperature and light limited (i.e., photosynthetic photon flux density) than water limited in our study area (Williams et al., 1999).

As global climate change continues to increase surface temperature and moisture deficit, springs could become increasingly important regeneration refugia for Douglas fir at lower elevations. Conversely, rising temperatures might diminish the significance of springs for lodgepole pine, since they could benefit from increased temperatures in their preferred higher elevation zones (Guz et al., 2021; Hansen et al., 2018).

LIMITATIONS AND FUTURE RESEARCH DIRECTIONS

Our study was limited by the known distribution of springs across the study area. Thus, it was challenging to stratify sampling across topographic parameters important to regeneration (e.g., slope, geology, soil, etc.) and is likely why slope, for example, did not have a greater effect on regeneration (Table 4; median slope = 23° and SD = 7°). Additionally, locations like springs that predictably regenerate earlier and in higher quantities after wildfire could have greater resiliency to repeated disturbances (Holden et al., 2010), but is likely mediated by burn severity and disturbance frequency (Enright et al., 2015; Stevens-Rumann & Morgan, 2016). Future studies should investigate the role of springs in forest regeneration following repeated disturbances and samples across greater topographic variability.

Since our study surveyed springs that burned between 35 and 17 years ago we were unable to assess the early establishment dynamics and competition that are likely to occur soon after a fire (i.e., succession). It is possible that higher densities for both Douglas fir and lodgepole pine occurred immediately following wildfire near springs but rapid riparian vegetation regrowth, extreme weather conditions, or browsing by mammals could have led to a reduction in density (Bartos et al., 1994; Littlefield, 2019; Marshall et al., 2023; Tsinnajinnie et al., 2021). Additionally, the coarse spatial resolution of our climate data (4 km) and study timing (up to 35 years post-fire) is likely why maximum temperature or cumulative precipitation did not have significant effects on Douglas fir tree density in our preliminary model iterations (Appendix S1: Section S5). Future studies should consider surveying springs sooner and continuously post-fire to assess successional dynamics and destructive

sampling of seedlings where the exact establishment year can be obtained and tied to annual climate conditions (Hankin et al., 2018).

Little research has been conducted on the stability of spring discharge and spring response to climate change (Cartwright & Johnson, 2018; Weissinger et al., 2016). Depending on a spring's annual discharge stability, which will influence the water table depth and plant available water, springs could become ephemeral regeneration points, meaning that their capacity to support forest regeneration is transient or reduced over time (Cartwright et al., 2020; Davis et al., 2019b; Meddens et al., 2018). Linking post-fire tree establishment years to spring discharge stability could offer insights into the long-term capacity of springs as regeneration refugia.

MANAGEMENT AND POLICY IMPLICATIONS

In stand-replacing burns where surviving seed sources are absent, forest managers may consider replanting near springs to facilitate forest recovery. However, land managers should consider first prioritizing mapping springs since it is estimated that over 50% of springs are unmapped in the Western United States (Springer et al., 2008). Understanding the distribution of springs and prioritizing mapping could aid land managers in efficient and rapid post-fire restoration efforts. Additionally, identifying the distribution and landscape-scale influence of springs is a pressing and timely issue given the recent US Supreme Court decision that removed water bodies that were not "a continuous surface connection" from protection under the Clean Water Act (Sackett, 2023). Continuing the study of springs and demonstrating their importance for landscape-scale resilience (even when 'unconnected') is important for present and future policy decisions.

CONCLUSIONS

Here, we presented a novel investigation into the role of springs as regeneration refugia following high-severity fire in mixed conifer forests in central Idaho. This study revealed that proximity to springs, compared with surrounding upland habitat, resulted in higher conifer density and earlier establishment following wildfire when conditions for available seeds and topography were also met. These findings position spring ecosystems as important and previously undescribed regeneration refugia with landscape-scale implications for post-fire forest recovery in increasingly water-limited environments. Springs are relatively abundant features across montane landscapes and may offer continued regeneration refugia for post-fire recovery into the future, but additional springs mapping and hydroclimatic considerations are needed.

As climate change pushes variables important to regeneration (e.g., surface temperature and soil moisture), past thresholds for tree establishment, regeneration refugia are increasingly important to identify (Halofsky et al., 2020; Rodman et al., 2023). With hotter and drier climate conditions projected for the future, variables like distance to seed source are expected to become secondary controls on post-fire regeneration (Davis et al., 2023). Buffering against poor regeneration conditions in the context of climate change is increasingly critical for forest recovery. Future research should continue monitoring of springs and groundwater-dependent ecosystems in more recent fires to compare the relative effects of springs, post-fire climate, and biological controls on forest regeneration.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Peven, 2024) are available from Zenodo: 10.5281/zenodo.11659544.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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