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Factors contributing to regeneration refugia in reburns, Lassen Volcanic National Park California, USA.

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ABSTRACT

Large wildland fires are becoming frequent in the western USA, and areas burned more than once (reburns) are increasingly common. Tree regeneration is a common metric used in post-fire forest management, yet investigations of regeneration fate through reburns are rare. Here, we examine factors that contribute to regeneration refugia, or locations in reburns that permit survival of tree regeneration through a reburn, and identify changes in biological legacies from earlier fires between 1984 and 2012 that could affect new post-reburn regeneration. We quantified post-fire tree regeneration and understory and fuel conditions in 2019 and 2021, and again in 2022 in Lassen Volcanic National Park, California, following the 2021 Dixie fire reburn. Regeneration persisted in almost 1/3 of 100 m^2 plots, with 19 % of all stems surviving the Dixie fire. Logistic regression models of regeneration refugia were developed considering both pre- and post-reburn conditions. A model of pre-reburn factors indicated the importance of landscape characteristics and legacies of previous fire, showing that regeneration persistence increased with slope, topographic wetness and pre-fire distance to forest, and decreased with previous fire severity. A full model including post-reburn factors indicated that fuel consumption was the most important determinant of regeneration refugia. However, legacy variables of distance to intact forest, fire severity, and pre-fire fuel load were also important, along with slope. Management action in reburn landscapes including fuel reduction at forest edges, in high severity burn areas, and on steep slopes may buffer regeneration refugia from fire effects in subsequent reburns.

1. Introduction

Large wildland fires are becoming more frequent in dry conifer forests in the western USA that have not burned in a century or more due to fire exclusion, and these forests are developing active fire regimes (Hessburg et al., 2019; Parks and Abatzoglou, 2020; Weber and Yadav, 2020; Taylor et al., 2021). Factors contributing to the increase in fire extent and severity in dry forests include high fuel loads caused by fire exclusion, forest management that removed fire resistant trees, abundant human ignitions, and difficulties in suppressing fire under extreme weather conditions (Hagmann et al., 2021, Kreider et al., 2024). Climate change, which increases fuel aridity, fire season length, and extreme fire weather, amplifies the potential for large wildfires (Abatzoglou and Williams, 2016; Williams et al., 2019; Coop et al., 2020). As area burned increases, repeat fires, or reburns, become more common and future forest characteristics become shaped by the biological legacies from previous fire effects (Collins et al., 2009; Johnstone et al., 2016; Coppoletta et al., 2016; Taylor et al., 2021). For example, reburn severity can be self-reinforcing, with a reburn burning at the same severity as the previous fire (Taylor et al., 2021). Determining how tree regeneration is affected by reburns is an important research need (Stevens-Rumann and Morgan, 2016; Turner et al., 2019), and requires an understanding of how legacies of past fires and reburn fire effects contribute to post-fire seedling regeneration, and persistence of regeneration through repeat fires.

Research on the effects of biological legacies has provided important understanding of controls on reburn tree seedling establishment and recruitment, and how that can influence future forest development

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(Franklin et al., 2000; Johnstone et al., 2016; Tepley et al., 2017; Turner et al., 2019; Harris et al., 2021a). Key factors tied to biological legacies include seed dispersal from surviving trees (Kemp et al., 2016; Gill et al., 2022; Davis et al., 2023); microclimatic conditions associated with canopy retention, understory vegetation cover and coarse woody debris (Clark-Wolf et al., 2022; Crockett and Hurteau, 2022); fire severity (Kemp et al., 2016; Busby et al., 2020; Harris et al., 2021a); soil nutrients and microbial communities (Clark-Wolf et al., 2022; Birch et al., 2025); competition of seedlings with understory plants, particularly fire-dependent shrubs (Collins and Roller, 2013; Shive et al., 2013; Lauvaux et al., 2016; Tubbesing et al., 2022); and time since fire (Turner et al., 2019; Busby et al., 2020; Niziolek et al., 2024). Yet, most inferences on controls of repeat fire effects on tree regeneration, and by extension post-fire vegetation development, rely on a space-for-time research design where sites with different initial conditions and disturbance histories are sampled and assumed to represent a time series of change at a single location. (Pickett, 1989). Challenges in reliably projecting temporal dynamics and forest structure with space-for-time substitutions can arise since the approach assumes everything but time since disturbance is identical among the spatial sampling sites (Damgaard, 2019; Kreyling, 2025).

Presence of tree regeneration is an important metric for post-fire forest management planning and decision-making (Stevens et al., 2021; Davis et al., 2023). Yet, research on the fate of regeneration through reburns using repeated field measurements is rare (e.g. Coop et al., 2016; Harris et al., 2021a). As fires become more frequent in dry conifer forests, persistence of tree regeneration through reburns may become an increasingly important influence on forest recovery. Laboratory experiments suggest that conifer seedlings can survive low-intensity surface fire, but that mortality increases rapidly with fire intensity, with similar responses among species (Smith et al., 2017, Steady et al., 2019). Therefore, fire intensity near each seedling as determined by fuels, terrain and weather should primarily determine seedling survival. Fire effects in reburns are time-dependent and related to both the characteristics of post-fire fuel recovery and legacy fuels from previous burns (Buma et al., 2020; Harris et al., 2021a; Jasperse et al., 2025). Generally, if reburns occur within a decade or two of a low-severity fire, resulting lower fuel loads may buffer fire effects (Harvey et al., 2016, Stevens-Rumann et al., 2016, Prichard et al., 2017; Taylor et al., 2021). On the other hand, high-severity fire may produce abundant coarse woody fuel and initiate a strong shrub response, facilitating high-severity reburns (Coppoletta et al., 2016; Lauvaux et al., 2016; Harris and Taylor, 2017; Taylor et al., 2022). Thus, reburns can kill regeneration, or permit advanced regeneration to persist in areas with limited fuels and fire effects and contribute to future canopy recovery (Fig. 1).

Here, we examine factors that contribute to regeneration refugia in reburns, and identify changes in biological legacies from earlier fires that could affect new post-fire regeneration in reburns after the 2021 Dixie fire in California. We use the term "regeneration refugia" to refer to locations in reburns that permit survival of tree regeneration through a reburn, as opposed to locations that support abundant post-fire seedling establishment (c.f. Peven et al., 2024). Our definition of fire refugia encompasses locally ($<$100 m^2) unburned or lightly burned patches within a burned matrix, consistent with longtime definitions of fire refugia (Camp et al., 1997, Meddens et al., 2018). The Dixie fire, the largest single fire in California history (374, 000 ha), burned through the perimeter of multiple fires in Lassen Volcanic National Park (LAVO) that occurred between 1984 and 2012. Fire effects and tree regeneration were first measured in field plots in LAVO in 2019 and 2021 (Harris et al., 2021a, b; Niziolek et al., 2024). The Dixie fire then burned over some of these plots, providing the rare opportunity to quantify and model Dixie fire effects on regeneration refugia in reburns and identify changes in factors that contributed to regeneration in previous reburns (e.g. Niziolek et al., 2024). Plots reburned in the Dixie fire were resampled in 2022.

We addressed the following research questions: 1) How frequent are regeneration refugia in reburns after a large wildfire? 2) Are regeneration refugia determined more by pre-fire fuel and vegetation conditions or landscape factors? 3) What role do legacy effects from past fires and Dixie fire reburn effects play in determining regeneration refugia? Before the Dixie fire, stocking of tree regeneration in reburns was strongly related to biological legacy factors that control seed dispersal and seedling establishment (e.g. distance to forest edge, time since fire), and terrain characteristics that influence topoclimate (e.g. elevation, aspect) and site conditions (Niziolek et al., 2024). Since fire-related legacy effects were important in earlier reburns, we hypothesized these legacy factors would contribute to presence of regeneration refugia after the Dixie fire. However, we anticipated that strong linkages between fuels, fire behavior, and fire intensity (Knapp and Keeley, 2006; Stephens and Finney, 2002) would make pre-fire fuel and vegetation conditions more important than legacy factors in determining occurrence of regeneration refugia.

Fig. 1. Tree regeneration that established after the Crater fire (1996) in 2021 before the Dixie Fire (a) and in 2022 after the 2021 Dixie fire (b). Canopy mortality from the Dixie Fire, in the background, increased distance to live forest edge from the plot center and was likely driven by high coarse woody surface fuel loads. Regeneration loss in the plot was limited due to discontinuous surface and live fuel loads, and very low fuel at the forest edge. Note the change in fuels and shrub mortality around the red fir seedling (red circle) which indicate Dixie fire activity near this surviving seedling. Seedlings and saplings in reburns may fare better in subsequent prescribed fires or wildfires where fuel loads remain patchy and low. Periods of low fuel loading and continuity following fire could be leveraged to create heterogeneous fuel and vegetation conditions that create regeneration refugia in reburns.

2. Methods

2.1. Study area

Post-fire regeneration persistence was evaluated in Lassen Volcanic National Park (LAVO, Fig. 2), a volcanic plateau punctuated by high volcanic peaks in the southern Cascades. Elevation in LAVO ranges from 1609 to 3187 m and forest zonation covaries with elevation and topoclimate (Parker, 1991; Taylor, 1995, 2000). Lower elevation forests are dominated by ponderosa pine (*Pinus ponderosa*) and Jeffery pine (*P. jeffreyi*), and mixed conifer forests of Jeffrey pine (*P. jeffreyi*) and white fir (*Abies concolor*) occur at higher elevation. Upper montane forests are comprised of red fir (*A. magnifica* var. *magnifica*), white fir (*A. concolor*), and western white pine (*P. monticola*). Lodgepole pine occupies low lying flats and moist depressions where cold air pooling impedes regeneration of other montane forest species. High elevation forests are dominated by mountain hemlock (*Tsuga mertensiana*) and whitebark pine (*P.albicaulis*) (Taylor, 1995). Trembling aspen (*Populus tremuloides*) occurs in persistently moist areas. The climate is Mediterranean, characterized by warm, dry summers and cold, wet winters. Average daily temperature ranges at Manzanita Lake, California (elevation 1780 m) in northwestern LAVO are −6.6 °C–5.0 °C in January and 7.5 °C–26.1 °C in July. Mean annual precipitation is 104 cm, but inter-annual variability is high. Most precipitation (>70 %) falls as snow between November and April.

2.2. Initial field sampling

This work is the result of an unplanned natural event, and we opportunistically resurveyed 145 field plots from three different projects with similar sampling protocols. Tree regeneration was assessed in 100 m^2 circular plots with the exception of 3 plots of 250 m^2 as detailed below, and in all cases a seedling was defined as 0.2–1.4 m tall and saplings as > 1.4 m tall and < 5 cm Diameter at Breast Height (DBH). Plots were initially sampled before the Dixie fire in 2019 and 2021 within the perimeters of eight fires that burned between 1984 and 2012, including three areas that burned twice before the Dixie fire (Fig. 2). Sample locations were restricted to areas inside fire perimeters, within 1.5 km of foot trails and roads, and with a minimum distance between plots of 300 m. A summary of field protocols is provided here, with full details in Pierce and Taylor (2011), Harris et al. (2021a), and Niziolek et al. (2024):

- Dataset 1 (Niziolek et al., 2024), n = 135 resurveyed plots, initially surveyed prior to the Dixie fire in 2021: Regeneration plots of 100 m^2 were established in areas of LAVO dry forests that had burned between 1984 and 2012. The DBH and species of all live trees (≥5 cm DBH) were assessed in the regeneration plots, as was the distance and direction from the plot center to the nearest cone bearing tree. In two 10 m^2 circular subplots, we estimated cover of shrubs, logs (>5 cm DBH), rocks (>10 cm in length), rock fragments (1–10 cm in length),

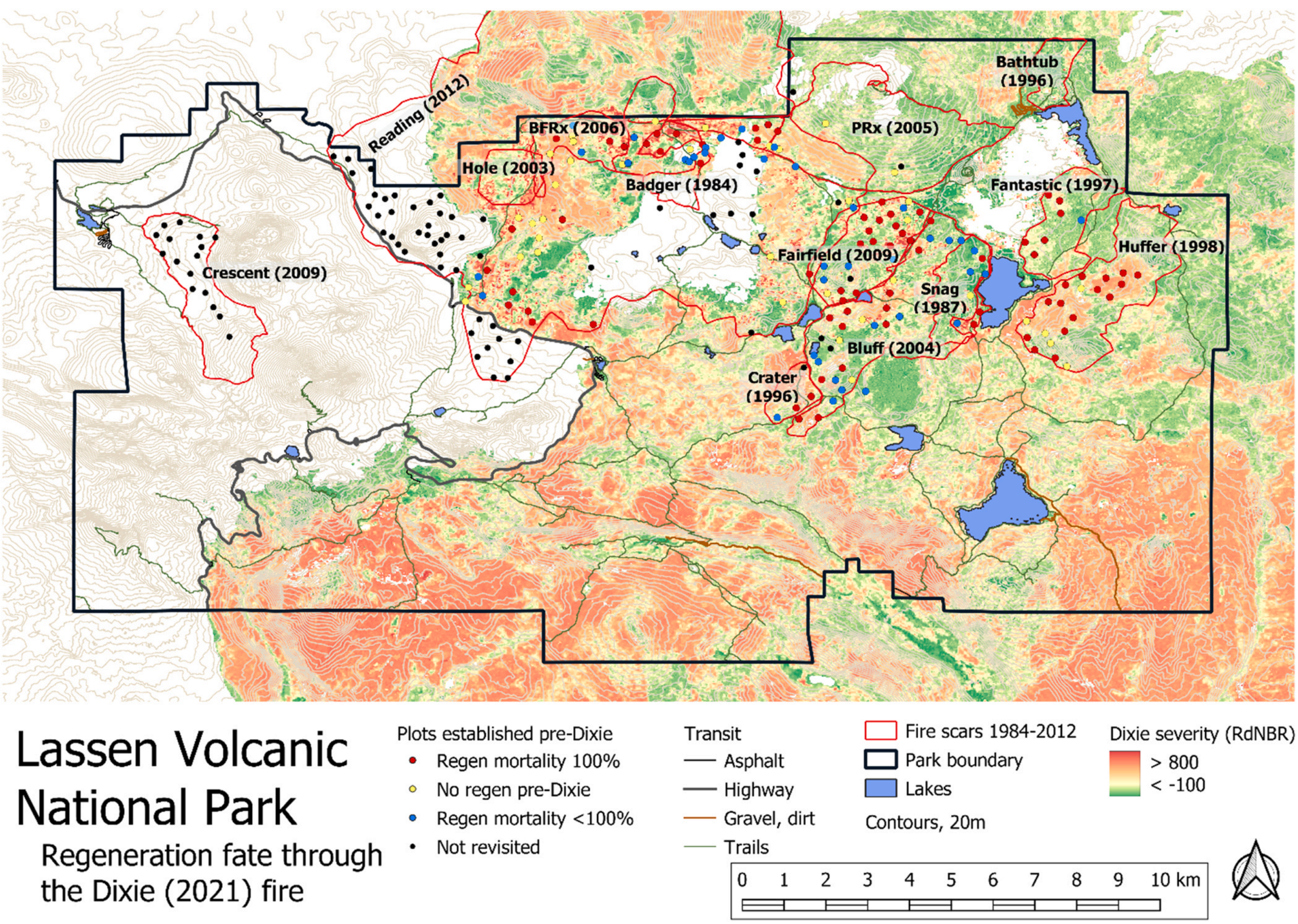

Fig. 2. Study area in Lassen Volcanic National Park showing fire history, location of plots, and severity of the 2021 Dixie fire. Names and parenthetical dates of fires are listed in bold black text along or overlapping the fire scar boundary; only fires > 400 ha for the period of analysis (1984-present) are displayed. Plot locations are indicated by circles; plot locations in black were sampled in 2019 or 2021 and not in 2022 because they were not reburned by the Dixie fire; plot locations in red had 100 % loss of conifer regeneration; plot locations in yellow had no regeneration prior to the Dixie fire; plot locations in blue were regeneration refugia that retained at least one stem of regeneration (100 stems ha^{-1}) after the Dixie fire.

forbs and grasses in one of seven cover classes: 0 %, < 1 %, 1–5 %, 6–25 %, 26–50 %, 51–75 %, and 76–100 %. Surface fuel load was estimated using the natural fuels photo series for the southern Cascade region (Blonski and Schramel, 1981). A photo series displays various levels of natural fuel loadings for forest types with different selected size classes that is calibrated with field based estimates of fuel size (time lag fuels), fuel mass, fuel volume, residue depth, and percent ground cover. Methods used in developing the photo series are described by Maxwell and Ward (1980).
- Dataset 2 (Harris et al., 2021a), n = 3 resurveyed plots, initially surveyed 2019: These plots had been burned in the 1984 Badger fire and again in the 2012 Reading fire, and followed the same protocols as those in Dataset 1 except that trees and tree regeneration were surveyed in 250 m^2 circular plots. Only three plots from this dataset were used in order to maintain the 300 m minimum distance between plots used for the regeneration plot set.
- Dataset 3 (unpublished), n = 7 resurveyed plots, initially surveyed 2019: Protocols were similar to those in Dataset 1 but differed in two ways. First, overstory trees (> 5 cm DBH) were surveyed in 500 m^2 circular plots. Second, given that the original goal of this project was to map surface fuels in the Reading fire (2012) scar, surface fuel loads were estimated from four 15.2 m long transects using the planar intercept method. Fuel loads were calculated following Brown (1974), using species-specific parameters developed for California forests (Van Wagdendonk et al., 1996, Van Wagtendonk et al., 1998).

2.3. Postfire resampling

Plots were resampled in 2022 after the 2021 Dixie Fire to identify legacy, terrain, and local factors that contribute to regeneration refugia. The Dixie fire burned over previously sampled reburn plots between August 9 and September 6, 2021. Only reburn plots inside the perimeter of the Dixie fire identified by satellite were resampled for this study. If, upon arrival at a plot location, fire effects from the Dixie fire (senescing needles, bark char, surface fuel consumption) were not evident within 50 m, we rejected the plot for sampling. We assessed percent of plot area burned at each location in categories < 15, 15–35, 35–65, 65–85, > 85 %; fifty-six plots were > 65 % burned in the Dixie, and only six < 15 %. Three of these showed no direct fire effects within the plot, but were retained because they represent fuel conditions occurring within the mapped fire footprint and are therefore important for understanding reburn effects in heterogeneous fuelscapes.

We resampled plots by replicating the original sampling protocols except that fuel consumption by the Dixie Fire was estimated using a combination of pre-Dixie Fire fuel load estimates and photographs before and after the Dixie Fire, since the photo series is not calibrated for use in recently burned areas. For Datasets 1 and 2 (n = 138 plots), percent reduction was estimated in the following categories: −15 % (negative loss, an increase in fuel load) to 0 %, 0–15 %, 15–35 %, 35–65 %, 65–85 %, > 85 % reduction in fuels. Post-fire fuel load in Mg ha^{-1} was then calculated from this percent loss estimate and pre-fire fuel load. For Dataset 3 (n = 7 plots), fuel consumption was calculated directly using the difference in pre-and post-fire measurements from fuel transects.

2.4. Geospatial layers

Terrain (e.g. elevation, slope, aspect) and Topographic Wetness Index (TWI) were calculated from digital elevation models from the National Elevation Dataset (NED, https://apps.nationalmap.gov/). NDVI change was calculated from late summer 2020 and 2022 LANDSAT TM imagery following the standard method NDVI = (NIR – Red) / (NIR + Red), and differenced.

We derived intact forest cover maps of the pre- and post-Dixie landscape from 1 m resolution National Agriculture Imagery Program (NAIP) imagery, as described by Niziolek and others (2024). Briefly, the Random Trees classifier (ESRI 2021) was applied to the NAIP imagery to define pixels as tree or non-tree subjects, a moving 30x30m window applied to classify areas of > /< 20 % forest cover, and an 8-neighbor query run to filter single and paired "tree" pixels. The result is a layer which identifies areas of > 20 % canopy cover ≥ 2700 m^2 (three neighboring pixels) in size. We measured distance from each plot to the nearest live forest edge before and following the Dixie fire.

Fire history and severity data were obtained from the Monitoring Trends in Burn Severity (MTBS) program (Eidenshink et al., 2007), except for the Dixie Fire severity map, which was provided by Harris et al. (2024) prior to MTBS data product release for the Dixie fire year. The MTBS program generates wildfire perimeters and burn severity maps. Relative differenced Normalized Burn Ratio (RdNBR) values were calculated from Landsat imagery, and burn severity was classified into categories (unchanged, low, moderate, high) using standard thresholds (Miller and Thode, 2007).

2.5. Vegetation and fuel change

We used nonparametric statistics to evaluate relationships between variables because most variables were nonnormally distributed. We applied Kruskal-Wallis tests to continuous variables, and Pearson's chi-squared tests to categorical and ordinal variables. When tests indicated significant differences between groups, Wilcoxon rank-sum tests with Benjamini-Hochberg corrections were used to identify where groups differed. For variables that were heavily zero-inflated, we applied permutation-based rank tests from the coin package in R, which preserves underlying data distribution and yields more accurate p-values than rank-based alone (Hothorn et al., 2008).

2.6. Factors contributing to regeneration refugia

Factors related to the probability of post-fire regeneration refugia after the Dixie fire reburn were modeled using logistic regression (Hosmer Jr et al., 2013). This analysis was performed using the 92 of the 145 100-m^2 plots in which regeneration had been present prior to the Dixie fire. Regeneration loss was defined as the complete loss of all conifers < 5 cm DBH from a plot, while regeneration refugia had at least one surviving stem < 5 cm DBH in a plot (i.e. seedling(s) and/or sapling (s)) after the Dixie fire. We fit two models; one using pre-reburn conditions ("pre-reburn model"), and one that additionally included post-reburn conditions and Dixie fire effects ("full model"). The rationale behind using two models is that the pre-reburn model is relevant to tree regeneration assessments in post-fire landscapes as managers contend with the increasing likelihood of reburns, whereas the full model offers a more detailed perspective on how reburn fire effects influence regeneration persistence.

Potential variables for the models were selected a priori based on their importance on pre-fire regeneration stocking and regeneration occurrence and the topographic setting, vegetation, fuels, and fire history of a plot (Niziolek et al., 2024). Variables considered for the pre-reburn model were: slope pitch, slope aspect, elevation, topographic wetness and position indices, time since last fire, previous RdNBR, number of past fires, fuel load, and distance to live forest. These same variables plus Dixie fire RdNBR (Miller et al., 2009), surface fuel mass loss, and NDVI change (White et al., 1996) from 2021 to 2022 were considered for the full model. We evaluated collinearity among all candidate predictor variables using Pearson correlation and variance inflation factors (VIFs). Variables with $r > 0.7$ or VIF > 5 were considered collinear. Candidate predictors showed low collinearity (all $r < 0.6$ and VIF < 3).

Final models were selected based on the lowest Akaike's Information Criterion (AIC, Akaike, 1974) using the function step AIC in the MASS package v. 7.3–58.1 in R. Note that selection using AIC may result in variables being included in a model that have $p > 0.05$ (Heinze et al., 2018). We took the approach of interpreting all variables retained in the models because we had ecological justification for including each variable, although we acknowledge that relationships with greater p-values have greater uncertainty (Shmueli, 2010). The Area Under the receiver operating characteristic Curve (AUC) was used to assess model accuracy. We tested for interaction terms between variables in the selected models based on our understanding of potential interaction effects on regeneration persistence (e.g. number of prior fires and fuel load). Interaction terms were removed if they were not significant, or negatively or neutrally contributed to model AUC; no interaction terms were included in the final models.

3. Results

A total of 145 previously burned plots were resampled after the Dixie fire in 2022, of which 92 had contained tree regeneration pre-reburn and 29 still contained live regeneration post-reburn. Field measured changes in surface condition largely followed change in satellite indices (i.e. RdNBR, change in NDVI); changes in fuel and vegetation were greatest (least) where satellite detected fire severity was highest (lowest) (Table 1).

Density of regeneration decreased after the Dixie fire in all fire severity classes, but the loss was greatest in moderate-severity plots (Table 1). Tree basal area and density similarly decreased across severity classes but the loss was significant only in moderate- and high-severity plots. Distance to forest also only increased significantly in plots burned at moderate- and high-severity (Table 1) with distances increasing by 134 % and 42 % after the Dixie fire, respectively. We note there was high variability in distances to forest edge within each severity class. Fuel mass was lost from all particle size classes with generally higher loss where Dixie fire severity was higher (Table 1). On the whole, Dixie fire severity (RdNBR 542 ± 599) was higher than the most recent previous fire (375 ± 318) in the plots we sampled.

3.1. Regeneration effects by species

In 2021, pre-reburn, we recorded a total of 3034 live seedlings and saplings across all species; in 2022 there were 574 (18.9 % persistence). Overall, seedlings and saplings experienced similar mortality ($p = 0.82$) from the Dixie Fire: 84 ± 32 % for seedlings and 84 ± 35 % for saplings (mean ± standard deviation among plots). Among species, survival varied widely (Fig. 3). Plot-level persistence of white fir stems averaged 10 ± 28 % for seedlings and 33 ± 47 % for saplings. Red fir seedlings and saplings persisted at 18 ± 35 % and 17 ± 41 %, respectively. Lodgepole showed the opposite trend, with 31 ± 41 % persistence of seedlings but only 18 ± 37 % for saplings. Jeffrey pine persistence was low across both size classes (7 ± 23 % and 6 ± 24 %). Western white pine showed little seedling persistence (4 ± 11 %) but relatively high sapling persistence (50 ± 71 %). Aspen had the highest overall survival (79 ± 30 % for seedlings, 50 ± 71 % for saplings), but this figure is impacted by resprouting following the Dixie fire and not necessarily persistence.

3.2. Models

The ninety-two plots which in 2021 had regeneration and burned in the Dixie fire were used to develop the reburn seedling refugia models. Regeneration persisted in 32 % ($n = 29$) of plots. The full model had greater accuracy (AUC =0.93) than the pre-reburn model (AUC=0.80). Both models included variables describing fire history, terrain, and fuels (Table 2).

3.3. Pre-reburn model

The pre-reburn model showed that likelihood of regeneration persistence increased with the number of prior fires, slope, topographic wetness, and distance from intact forest patches; it decreased with pre-fire fuel load and prior fire severity (Table 2, Fig. 4). Plots on steeper and moister sites, farther from forest edges, with lower surface fuel loads, and burned twice by previous fires rather than once were more favorable for regeneration persistence.

Table 1

Summary of vegetation and fuel conditions (mean ± one standard deviation) in all ($n = 145$) reburn plots sampled before ("pre-") and after ("post-") the Dixie fire. *p*-values in each severity class indicate results of paired Wilcox signed rank tests on change through the fire; the final p-value column indicates results of Kruskal-Wallis tests of differences in change through the Dixie fire by severity. Fine fuel mass is the sum of 1, 10, 100 h time lag fuels and coarse fuel mass is for 1000 h fuels.

Variable	Very low severity (n = 16) Dixie RdNBR < 0			Low severity (43) 0–314			Moderate severity (31) 314–641			High severity (55) > 641			Differences by class
	pre-	post-	*p*	pre-	post-	*p*	pre-	post-	*p*	pre-	post-	*p*	*p*
Seedlings ha^{-1}	1061 ± 2070	123 ± 249	.016	2509 ± 12317	997 ± 4861	< 0.001	2003 ± 4276	61 ± 156	< 0.001	1392 ± 2303	76 ± 237	< 0.001	0.003
RdNBR	238 ± 299	-177 ± 282	< 0.001	334 ± 349	177 ± 61	.003	374 ± 314	452 ± 89	0.18	458 ± 289	1126 ± 513	< 0.001	< 0.001
Surface fuel load (Mg ha^{-1})	24.2 ± 14.5	13.7 ± 8.2	< 0.001	25.0 ± 11.9	17.0 ± 9.1	< 0.001	26.9 ± 12.0	12.5 ± 8.4	< 0.001	25.9 ± 11.3	9.2 ± 8.5	< 0.001	< 0.001
Fine fuel load (Mg ha^{-1})	3.6 ± 1.9	2.4 ± 1.2	< 0.001	4.5 ± 2.0	3.2 ± 2.3	< 0.001	4.7 ± 2.4	2.0 ± 1.6	< 0.001	4.6 ± 2.1	1.5 ± 1.5	< 0.001	< 0.001
Coarse fuel load (Mg ha^{-1})	20.5 ± 13.5	11.2 ± 7.7	< 0.001	20.4 ± 10.9	13.7 ± 7.3	< 0.001	22.2 ± 11.1	10.4 ± 7.9	< 0.001	21.3 ± 10.0	7.7 ± 7.3	< 0.001	0.002
Distance to forest (m)	37.9 ± 61.4	47.1 ± 83.3	0.5	69.8 ± 81.1	80.6 ± 96.4	0.13	48.0 ± 63.8	70.4 ± 67.0	< 0.001	90.7 ± 87.0	165.7 ± 132.2	< 0.001	< 0.001
Tree basal area (m^2 $ha^{-1)}$)	18.2 ± 29.1	18.4 ± 29.4	0.3	16.8 ± 37.0	15.5 ± 37.0	0.2	14.0 ± 21.9	8.6 ± 18.8	.028	9.2 ± 27.4	2.1 ± 7.4	< 0.001	< 0.001
Tree density (stems $ha^{-1)}$)	153 ± 231	121 ± 221	0.5	119 ± 241	102 ± 226	0.4	134 ± 163	76 ± 121	0.002	105 ± 196	27 ± 79	< 0.001	0.016
Shrubs (% cover)	5.1 ± 8.0	6.1 ± 10.7	0.07	10.7 ± 12.5	8.6 ± 12.4	0.5	16.6 ± 19.0	6. ±11.8	< 0.001	11.8 ± 15.8	1.4 ± 3.0	< 0.001	< 0.001
Logs (% cover)	15.6 ± 13.6	5.4 ± 5.9	< 0.001	13.8 ± 11.3	9.0 ± 8.5	0.01	18.9 ± 13.8	10.1 ± 9.7	0.002	20.0 ± 15.4	9.4 ± 10.3	< 0.001	0.3

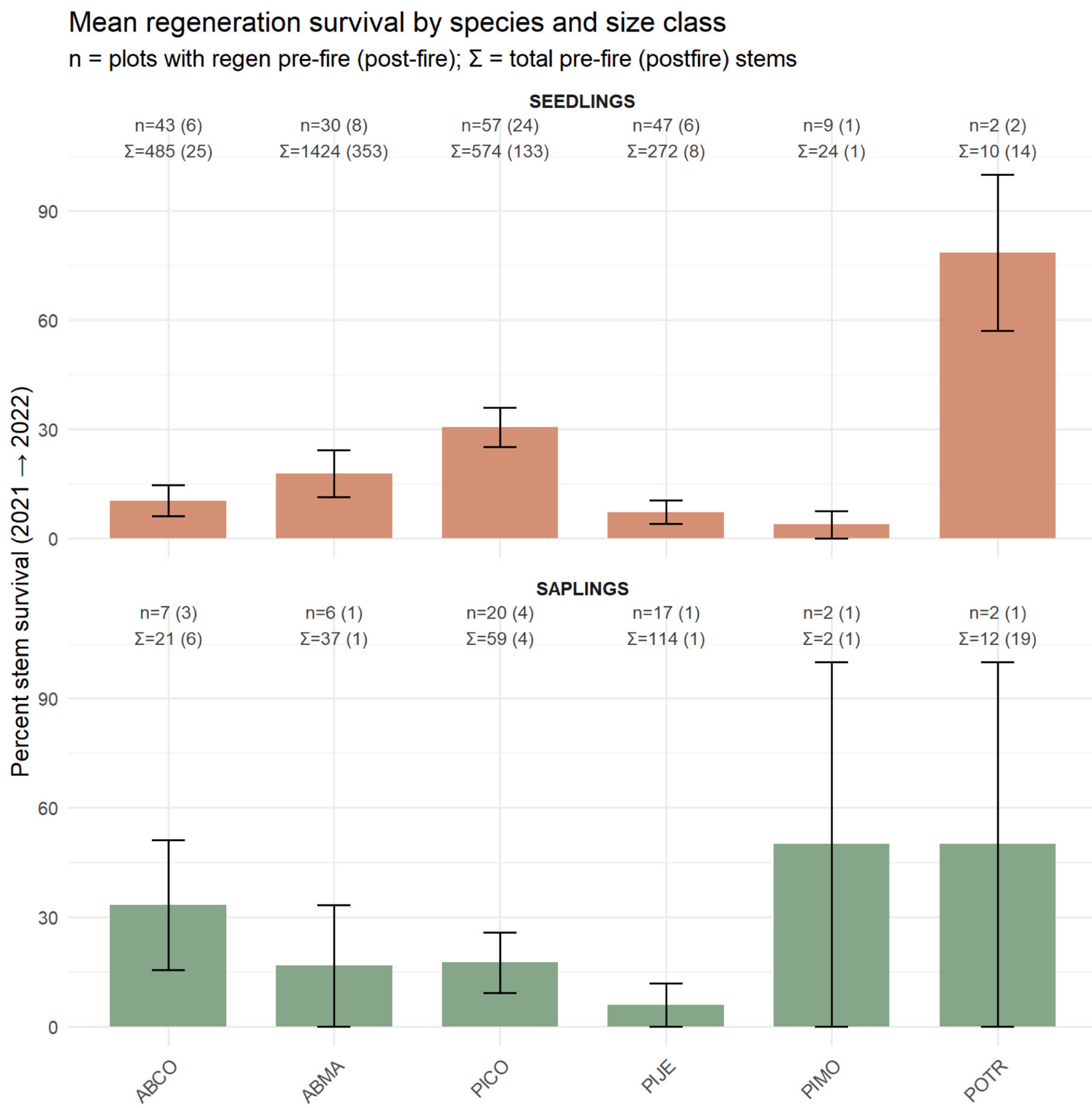

Fig. 3. Plot-level survival of seedlings and saplings by species. Error bars indicate one standard error around the mean. Frequency of occurrence in plots and number of stems are indicated above each bar. Species codes are: ABCO = *Abies concolor* (white fir), ABMA = *Abies magnifica* (red fir), PICO = *Pinus contorta* (lodgepole pine), PIJE = *Pinus jeffreyi* (Jeffrey pine), PIMO = *Pinus monticola* (western white pine) and POTR = *Populus tremuloides* (trembling aspen). Note that increases in trembling aspen stems through the fire is driven by resprouting behavior.

Table 2
Summary of logistic regression models predicting regeneration refugia.

	Pre-reburn model		Full model	
Variable	**Estimate**	***P***	**Estimate**	***P***
Intercept	-6.72		-3.34	
Distance to forest, pre-reburn (m)	0.017	0.003	0.032	0.002
Slope (°)	0.17	0.002	0.18	0.006
Pre-fire fuel load (Mg ha^{-1})	-0.04	0.103	0.097	0.045
Prior fire severity (RdNBR[a])	-0.0025	0.031	-0.002	0.161
Topographic wetness index	0.37	0.048		
Number of prior fires	1.75	0.059		
Fuel consumption (Mg ha^{-1})			-0.212	0.001
ΔNDVI[b], pre−post-fire			-37.45	0.009
Years since previous fire			0.37	0.090

[a] Relative differenced Normalized Burn Ratio
[b] Normalized Differenced Vegetation Index

3.4. Full model

The full model showed that regeneration persistence was positively related to slope, pre-fire surface fuel load, time since previous fire, and pre-reburn distance to intact forest while fuel consumption and greater change in NDVI had a negative effect on regeneration persistence (Table 2, Fig. 5). As in the pre-reburn model, plots on steeper slopes, farther from live forest edges, burned at lower severity in the previous fire and with lower pre-Dixie surface fuel loads were more likely to see regeneration persist. Regeneration was less likely to persist where fuel consumption and NDVI change through the Dixie fire were greatest.

4. Discussion

Our goal was to identify how frequent regeneration refugia in reburns were, and how legacy effects from past fires and landscape factors contribute to their occurrence. Reburns have become more common in the western USA since the mid-1980s with increased annual

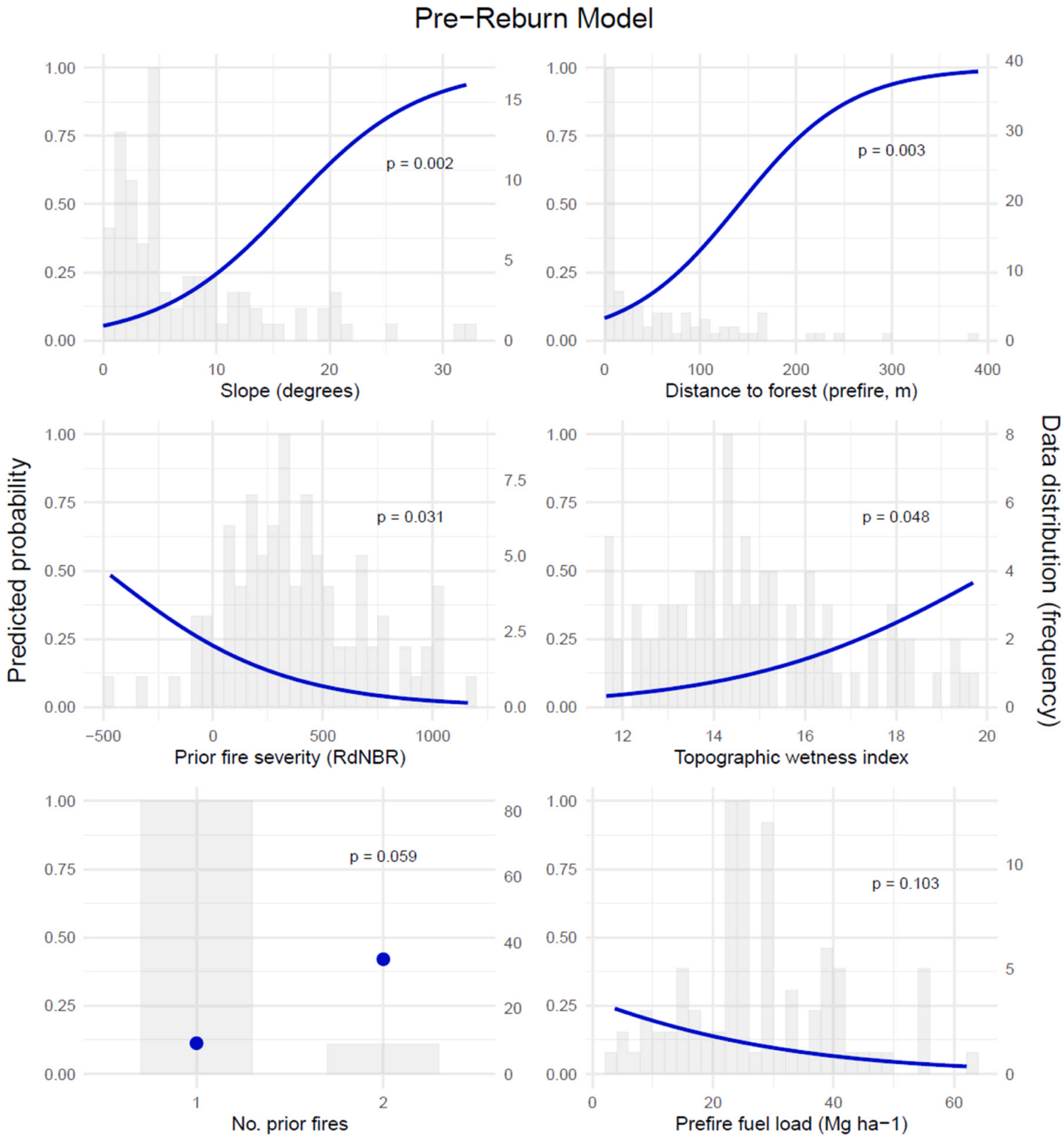

Fig. 4. Influence of individual variables on probability of regeneration persistence in the pre-reburn model. Variables are ordered from most (top left) to least (bottom right) important. Blue lines indicate modeled probability of regeneration persistence when all other variables are held constant at their median (or first factor level); grey bars indicate underlying data distribution.

area burned, and the occurrence of megafires. Consequently, there is a need to understand how persistence of regeneration through reburns contributes to future forest development. Regeneration refugia were moderately frequent after the Dixie fire reburn. Pre-reburn conditions contributing to regeneration persistence were terrain (slope, wetness), legacy effects (i.e. distance to previous live forest, previous fire severity, previous fire frequency) and fuel loading. An evaluation of post-fire conditions additionally showed the key contributions of fuel consumption and biomass change related to Dixie fire effects. Differences in the contribution of pre-and-post fire condition factors in reburns have implications for forest and fire management in dry forest landscapes where reburns are becoming more common.

4.1. Reburn regeneration refugia

Our study on regeneration persistence through reburns using repeat measurements showed that a subsequent reburn significantly reduces regeneration density and occurrence. Only 18.9 % of the individuals survived the Dixie fire reburn while frequency of persistence was 32 % at the plot level. Studies to compare our values of regeneration fate through reburns are scant, but data on seedling survival after a single fire are similar to our values. Small tree (>1 cm DBH and <10 cm DBH) survival was 9.5 % in a California mixed conifer forest after the 2013 Rim fire (Blomdahl et al., 2019), though survival was spatially variable. Seedling survival in small (> 1 m^2) unburned areas that represented 4.9 % of a 25 ha mapped area were almost an order of magnitude higher than in burned areas (63.4 % *vs.* 6.9 %). Survival in our reburn plots, which all had evidence of Dixie fire effects, is closer to the burned and overall survival values after the Rim fire. Areas with surviving small trees after the Rim fire (Blomdahl et al., 2019), and in some parts of the Dixie fire reburn, had post-fire regeneration density well above the defined seedling stocking minimum for southern cascade forests (435 stems ha^{-1}, Stein, 1981).

Areas unburned or lightly burned in wildfires or prescribed fires

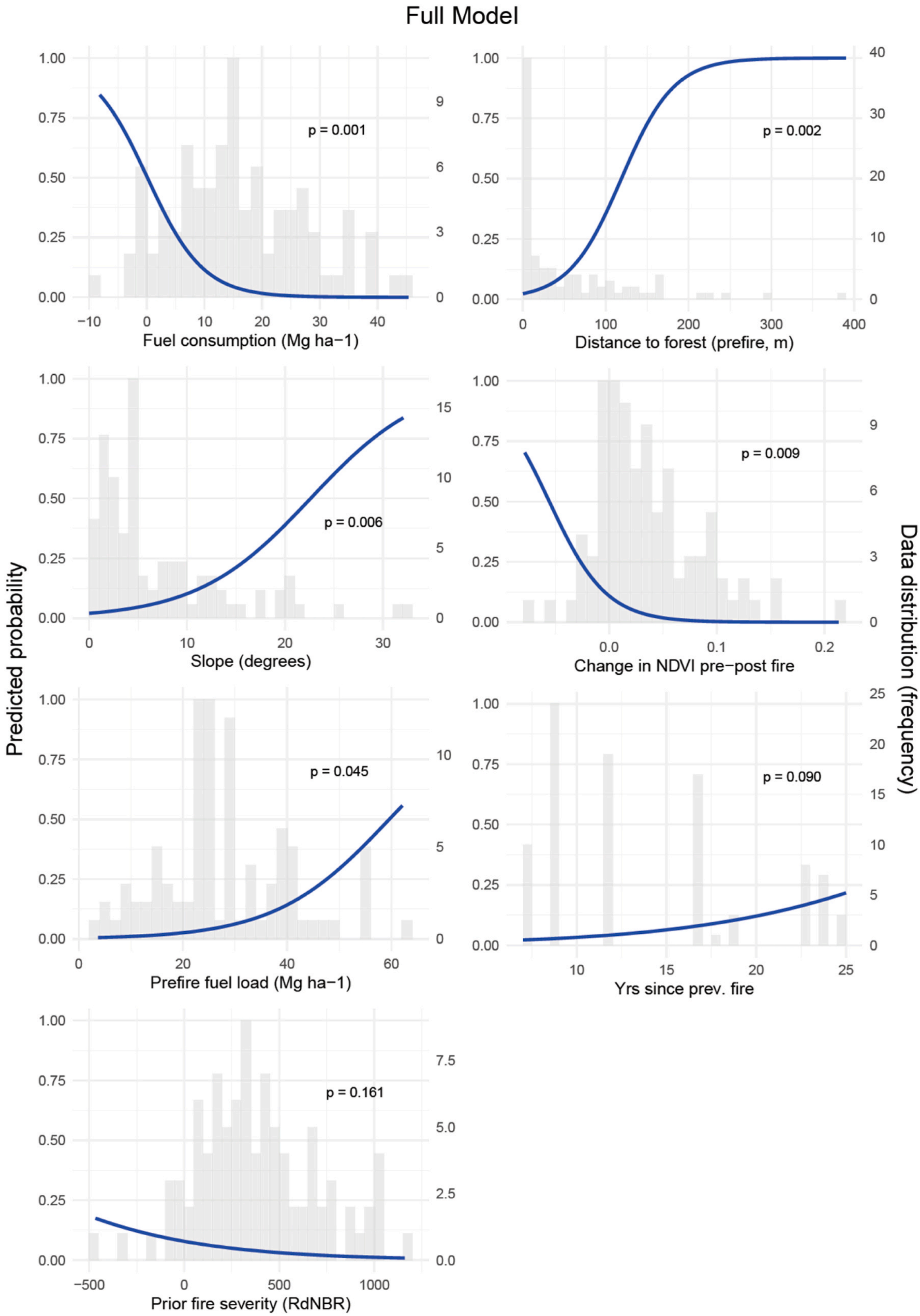

Fig. 5. Influence of individual variables on regeneration persistence in the full model including Dixie fire effects. Variables are ordered from most (top left) to least (bottom right) important. Blue lines indicate modeled probability of regeneration persistence when all other variables are held constant at their median; grey bars indicate underlying data distribution.

represent areas of potential regeneration refugia. Field measurement of unburned surfaces in late season prescribed fires in mixed conifer forest in California range from 5 % to 12 % (Knapp and Keeley, 2006; Blomdahl et al., 2019), a value similar to the frequency of unburned field plots (13 %) after wildfire in dry forests in eastern Oregon (Downing et al., 2020) and our values for regeneration refugia. Factors contributing to the occurrence and location of unburned surfaces include distance to a stream, Topographic Position Index (Dwire, Kauffman, 2003; Skinner et al., 2018), proportion of bare ground and rock, and burn season (Knapp and Keeley, 2006, Knapp et al., 2005), all of which would lower effective fuel continuity (Miller and Urban, 2000). Additional field efforts to quantify unburned area and regeneration refugia in burns, and reburns, are needed to fully evaluate their contribution to regeneration dynamics in reburn landscapes.

Interactions between repeated fire effects and species traits in the seedling/sapling pool can influence forest canopy composition over time (Keeley and Pausas, 2022). In the Dixie fire reburn there were overall differences in relative survival of seedlings and saplings of different species, though not always the expected differences. Jeffrey pine seedlings had lower relative survival than lodgepole pine, which was unexpected as bark, which confers heat resistance to fire (Agee, 1993), is much thicker in Jeffrey pine than lodgepole pine (Zeibig-Kichas et al., 2016). Jeffrey pine seedlings fared poorly (3 % survival) and so did white fir (5 % survival), which has thicker bark than all the other species except Jeffrey pine. However, experimental studies indicate that conifer seedling survival may not differ substantially among species because characteristics conferring resistance to fire such as thick bark have yet to fully develop (Smith et al., 2017; Steady et al., 2019). Our finding that sapling and seedling survival did not differ is inconsistent with past work demonstrating that persistence through prescribed fire increases with seedling height and sapling DBH (Battaglia et al., 2009). Overall, the highly variable reburn effects among the plots in our study may obscure effects of regeneration size and species on persistence. Our results also highlight the challenge of using fire-related traits to predict near term forest composition in reburns (e.g. Turner et al., 2019; Taylor et al., 2021; Jasperse et al., 2025).

4.2. Factors contributing to reburn regeneration refugia

4.2.1. Pre-reburn conditions

The pre-reburn model demonstrated the importance of both landscape factors and legacy fire characteristics. Slope was the most important pre-fire condition and likelihood of regeneration persistence was higher on steeper slopes. This is counter intuitive, as rate of spread and fire line intensity increase with slope (Rothermel, 1972; Ryan, 2002) and higher fire line intensities generate more severe fire effects (Ryan, 2002; Hood et al., 2018). However, in LAVO, steeper forested slopes are often punctuated with areas of rock outcrops that break up fuel continuity that reduces fire spread. High cover of bare ground and rock are known to impede fire spread and contribute to unburned surface area, at least in prescribed burns (Knapp and Keeley, 2006; Blomdahl et al., 2019).

Distance to forest edge in reburns was nearly as important as slope as a pre-fire factor. Probability of regeneration persistence was positively related to distance and increased markedly at distances > 100 m. This is at odds with probability of regeneration establishment, which is higher near forest edges where seed sources are more abundant (Niziolek et al., 2024). Persistence in reburns may be more likely farther from live forest due to fine fuel shadows; higher fine fuel loads generated by live canopy trees extend outward from the forest edge providing fuel continuity that increase the risk of subsequent fires burning at higher severity in and adjacent to live forest patches (Eskelson and Monleon, 2018; Moore et al., 2021; Stevens et al., 2021; Taylor et al., 2021). Higher severity fire at forest edges in reburns would reduce the probability of regeneration refugia near live forest edges. Other pre-reburn factors that affected fuels also influenced likelihood of regeneration persistence. Probability of persistence was higher when the previous burn was low in severity, site conditions were wet, and two fires preceded the Dixie fire reburn. These conditions would be likely to reduce fuels and increase surface fuel heterogeneity (prior low severity burn, two previous burns) or reduce fire spread due to high live and dead surface fuel moisture (wet riparian forest). The efficacy of the pre-reburn model and availability of geospatial data on fire history, terrain, and fuels (e.g. Rollins, 2009; Taylor et al., 2021) to quantify landscape factors suggests the pre-reburn model may have some capacity to predict regeneration persistence in future reburns.

4.2.2. Post reburn conditions

The full model that included post-reburn conditions highlights the importance of both live and dead fuel consumption (change in fuel load, NDVI), in addition to the terrain (slope), and legacy fire effects (distance to forest edge) factors identified in the pre-reburn model. Fuel consumption in plots (change in fuel load), and nearby (NDVI change), were the first and fourth most important variables affecting regeneration persistence. Fire effects are closely linked to fuel consumption, which is associated with fire-line intensity and flame length (Agee, 1993; Knapp and Keeley, 2006). Persistence was inversely related to fuel consumption; there was a higher likelihood when fuel consumption was < 10 %, and regeneration did not survive if consumption exceeded 30 %. NDVI change, a measure of live fuel change, had a similar inverse relationship and a higher likelihood of persistence with lower change. Pre-fire fuel load had a positive relationship with regeneration persistence, which is counter intuitive. This may be the case because large coarse woody debris (tree boles and branches) were the dominant fuel fraction in plots with a very high pre-fire fuel load, but finer surface fuels may have been insufficient for fire spread (e.g. Agee, 1981, 1993). Consequently, high pre-fire fuel loads may not contribute to area burned, particularly in reburns where fuel heterogeneity and continuity may be more important than loading in determining where fire spreads. We did not directly measure fuel continuity in our plots and fuel consumption may be a proxy for this variable in the post-fire conditions.

4.3. Limitations

Our study has several limitations. First, our evaluation of factors contributing to regeneration refugia were focused mainly on the obligate seeding conifers, the dominant life form in dry montane forests in California. Factors determining persistence for sprouting angiosperms which are common in some montane forests in California, such as the Klamath Mountains (Skinner et al., 2018), are likely very different. In LAVO, trembling aspen is locally abundant and co-occurs with conifers in areas of high soil moisture, and it sprouts vigorously after fire (Margolis and Farris, 2014; Niziolek et al., 2024). Consequently, location of aspen stands would likely be sufficient for predicting regeneration persistence through reburns. Second, our study was based on repeat measurements after an unplanned event that constrained the number plots, the number and characteristics of reburns, and the variables we could evaluate as contributing to regeneration persistence through reburns. Analyses of natural experiments such as wildfires face potential issues of pseudoreplication (Davies and Gray, 2015, van Mantgem et al., 2001), which we addressed by considering potential effects of dataset/prior fire identity in preliminary work and by examining multicollinearity among potential predictors. A more robust understanding of factors contributing to regeneration fate in reburns would likely come from analyses of a larger population of fires that capture a greater range of variability in terrain, landscape patterns of fire severity, and reburn fuel and vegetation characteristics known to influence forest dynamics (e.g. Collins et al., 2009; Taylor et al., 2021). An effort to immediately measure post-fire effects including fuels and tree regeneration in repeat prescribed fires and after repeat wildfires could generate sufficient data to evaluate more general models for predicting regeneration fate through reburns.

4.4. Conclusions and management implications

Both local and landscape factors controlled by terrain and legacy fire effects were important in identifying factors contributing to persistence of regeneration through reburns. The contribution of legacy fire effects in the pre-reburn and full model highlights their importance in contributing to regeneration refugia in reburn landscapes. Local fuel consumption had the strongest influence on persistence. It is important to note that some of the same legacy effects that promote post-fire seedling establishment and survival (e.g. shorter distances to live forest, higher cover of coarse woody debris) also reduce the probability of seedling/sapling persistence through a reburn. These potential trade-offs, between post-fire seedling establishment, and survival and vulnerability of regeneration through reburns, need further evaluation to understand how each contributes to forest recovery where landscape dynamics are increasingly driven by reburns.

Post-fire management decisions are informed by presence of tree regeneration, a key driver of near term forest recovery (Davis et al., 2023, Stevens et al., 2021). In LAVO, most forest occurs in designated Wilderness (75 %) where fire (prescribed, wildland) is the main tool used for fuels and vegetation management (National Park Service, 2006, 2022). Our models of regeneration persistence through reburns indicate that fuel reduction at forest edges (i.e. edge hardening) using prescribed fire could increase survival of natural regeneration through reburns (Stevens et al., 2021). Elevated coarse fuels at forest edges from trees killed by previous fires increase the risk of subsequent fires expanding areas of high severity fire effects adjacent to live forest patches (Collins et al., 2018; Lydersen et al., 2019; Taylor et al., 2021). Similarly, fire can be locally applied to large areas of coarse fuels in high severity patches to increase fuel heterogeneity and variability in fire effects in a reburn that could increase regeneration persistence. A landscape approach to managing fuels and future fire effects in reburn landscapes (Stevens et al., 2021) should increase both the immediate survival of regeneration refugia through reburns and development of conditions conducive to widespread post-fire natural regeneration (Stevens et al., 2021; Davis et al., 2023; Niziolek et al., 2024).

CRediT authorship contribution statement

Dani Niziolek: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Harris Lucas:** Writing – review & editing, Methodology. **Taylor Alan H:** Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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