


Where and why do conifer forests persist in refugia through multiple fire events?

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Abstract

Changing wildfire regimes are causing rapid shifts in forests worldwide. In particular, forested landscapes that burn repeatedly in relatively quick succession may be at risk of conversion when pre-fire vegetation cannot recover between fires. Fire refugia (areas that burn less frequently or severely than the surrounding landscape) support post-fire ecosystem recovery and the persistence of vulnerable species in fire-prone landscapes. Observed and projected fire-induced forest losses highlight the need to understand where and why forests persist in refugia through multiple fires. This research need is particularly acute in the Klamath-Siskiyou ecoregion of southwest Oregon and north-west California, USA, where expected increases in fire activity and climate warming may result in the loss of up to one-third of the region's conifer forests, which are the most diverse in western North America. Here, we leverage recent advances in fire progression mapping and weather interpolation, in conjunction with a novel application of satellite smoke imagery, to model the key controls on fire refugia occurrence and persistence through one, two, and three fire events over a 32-year period. Hotter-than-average fire weather was associated with lower refugia probability and higher fire severity. Refugia that persisted through three fire events appeared to be partially entrained by landscape features that offered protection from fire, suggesting that topographic variability may be an important stabilizing factor as forests pass through successive fire filters. In addition, smoke density strongly influenced fire effects, with fire refugia more likely to occur when smoke was moderate or dense in the morning, a relationship attributable to reduced incoming solar radiation resulting from smoke shading. Results from this study could inform management strategies designed to protect fire-resistant portions of biologically and topographically diverse landscapes.

KEYWORDS

forest loss, forest resilience, Klamath-Siskiyou ecoregion, reburn, refugia, wildfire

1 | INTRODUCTION

Wildfire frequency and severity shape ecosystems, affecting biodiversity and ecosystem services across the globe. In recent decades, increasing fire extent and severity have raised concerns about forest

decline and type conversions (Boer et al., 2020; Coop et al., 2020; Parks & Abatzoglou, 2020). Wildfire-driven conversions of forest to alternative states can occur when high-severity fire overwhelms species' fire-adaptive traits at local and landscape scales (Johnstone et al., 2016; Whitman et al., 2019). In some cases, repeat burning,

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also referred to as “reburn” or “short-interval fire” (Buma et al., 2020; Prichard et al., 2017), can result in forest loss when species’ resistance (ability to remain relatively unchanged by fire) and resilience (ability to recover following fire) mechanisms are overwhelmed (Bowman et al., 2014; Holz et al., 2015; Turner et al., 2019). In contrast, some places persist as forest when surrounding areas burn at higher frequency and/or severity, and these “fire refugia” are important features of landscapes where high-severity reburn is increasing (Collins et al., 2019; Coop et al., 2020). Understanding the biophysical drivers that support fire refugia in forests worldwide contributes to the growing toolbox supporting adaptation in response to global change (Krawchuk et al., 2020).

Fire refugia are areas that burn less frequently or severely than the surrounding landscape—where dominant elements of pre-fire vegetation, like trees, persist relatively unaltered (Krawchuk et al., 2016; Meddens et al., 2018). Fire refugia (hereafter, “refugia”) can support post-fire ecosystem recovery and the persistence of vulnerable species in fire-prone landscapes (Landesmann & Morales, 2018; Robinson et al., 2013; Schwilk & Keeley, 2006). Although repeat burning and disturbance refugia have become important research foci in recent years (Buma et al., 2020; Krawchuk et al., 2020), relatively little is known about where and why refugia persist as they pass through successive fire filters (but see Martinez et al., 2019). Conceptually, refugia occur and endure along a gradient ranging from transient refugia that survive a single fire event to persistent refugia that change relatively little through multiple fire events (Meddens et al., 2018). Refugia are more likely to be transient when they arise due to stochastic weather and fire behavior conditions unique to an individual fire event (Berry et al., 2015; Robinson et al., 2013). Refugia also occur due to less dynamic factors such as fuel arrangement and availability, as well as relatively immutable topographic features such as rocky outcrops with discontinuous fuels (Adie et al., 2017; Landesmann et al., 2015), and landscape depressions, cold-air pools, and poleward-facing aspects where high fuel moistures limit fire intensity (Leonard et al., 2014; Román-Cuesta et al., 2009; Wilkin et al., 2016). These more enduring features may lend support to persistent refugia. However, refugia may be more likely to “wink out” after a period of fire exclusion (Downing et al., 2020), or during severe fire weather conditions (Kolden et al., 2017).

The Klamath-Siskiyou ecoregion of northwest California and southwestern Oregon provides an ideal natural laboratory to study the drivers of refugia occurrence and persistence. The Klamath-Siskiyou (hereafter, “K-S”) is a biodiversity hotspot that supports more conifer species than any other region in western North America (Cheng, 2004; Whittaker, 1960). Between 1985 and 2017, approximately 200,000 ha burned twice, and 18,000 ha burned three times (Figure 1). K-S conifer forests are vulnerable to loss through repeat burning and a phenomenon known as “interval squeeze” or “immaturity risk” (Enright et al., 2015; Keeley et al., 1999). High-severity burned conifer forests in the K-S typically convert to shrubland or hardwood forest (McCord et al., 2020; Odion et al., 2010). This early-seral conversion is perpetuated when repeat burning kills regenerating conifers before seedlings have overtopped competing

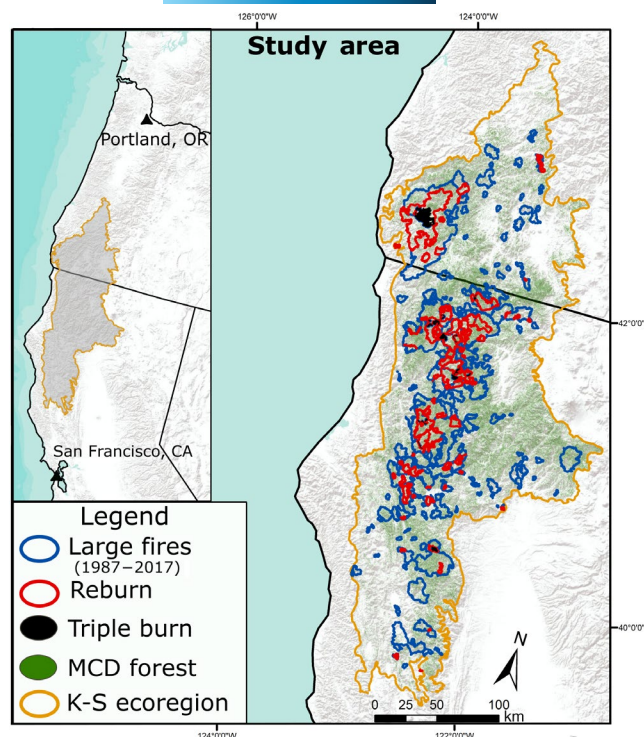


FIGURE 1 Map of the Klamath-Siskiyou (K-S) ecoregion study area in southwest Oregon and northwest California, United States. Fire perimeters are from the Monitoring Trends in Burn Severity (MTBS) program (<https://www.mtbs.gov>). Areas burned twice during the Landsat era are “Reburn,” areas burned three times are “Triple burn.” Mature, conifer-dominated (MCD) forest was identified using pre-fire composition and structure data based on gradient nearest neighbor (GNN) imputation (Ohmann et al., 2012)

vegetation, developed resistance to fire, and/or become reproductively mature (Tepley et al., 2017). Fire has been an important ecological process in the K-S for millennia (Colombaroli & Gavin, 2010; Mohr et al., 2000), historically contributing to the maintenance of patchy, heterogeneous landscapes composed of conifer and hardwood forests, shrublands, and grasslands (Odion et al., 2004). However, hotter and drier climatic conditions and a lack of surviving post-fire seed sources undermine the ability of conifer forests to recover following high-severity fire (Tepley et al., 2017). Climate warming is expected to increase fire frequency in the K-S (Davis et al., 2017), and repeat burning is projected to convert about one-third of the region’s conifer forest to shrublands or hardwood forest by the end of the century (Serra-Diaz et al., 2018). In some cases, these conversions may provide ecosystem benefits where early-seral communities have declined because of afforestation resulting from fire suppression (Knight et al., 2020). In others, widespread conifer forest loss may result in undesirable impacts to biodiversity, carbon storage, and timber supplies (Miller et al., 2018).

Identifying the areas most likely to persist as forest through wildfire requires landscape-scale assessments of the factors that drive fire behavior and severity: topography, fuels, and weather. Topography influences fire behavior directly as the physical template across which fire burns (Rothermel, 1972) and indirectly

by mediating fuel and vegetation characteristics and fine-scale weather and climate (Kane et al., 2015; Wilkin et al., 2016). Low-severity fire effects in the K-S have been associated with lower elevations that are less likely to burn severely in head fire originating from lower slope positions (Estes et al., 2017; Grabinski et al., 2017), as well as north-facing aspects where fuel moistures are elevated due to lower incoming solar radiation (Alexander et al., 2006; Taylor & Skinner, 2003). Fuel influences fire behavior as a function of its composition, structure, and arrangement, all of which reflect underlying biophysical gradients and disturbance history (Agee, 1993). Conifer stands composed of larger trees in the K-S tend to burn at lower severities than shrublands and hardwood forests (Grabinski et al., 2017; Odion et al., 2004; Thompson & Spies, 2009), although these relationships vary with species composition and associated flammability (Perry et al., 2011). Top-down weather factors such as temperature, wind, and humidity influence fire behavior as well as the availability of fuels to burn. Fire severity in the K-S is strongly mediated by fire weather conditions during moderate conditions (Estes et al., 2017), but even more so when severe conditions override other fuel and topographic controls (Thompson & Spies, 2009).

Smoke is another factor that may influence fire severity and refugia patterns. Temperature inversions under stable air masses concentrate smoke at lower elevations in mountainous landscapes like the K-S (Robock, 1988), where fire-atmospheric feedback mechanisms can result in persistent inversions that last for days or weeks (Kochanski et al., 2019). Beneath inversions, wind speeds are lower due to reduced vertical mixing, and temperatures are cooler due to the scattering and absorption of incoming solar radiation; above inversions, temperatures are elevated when smoke aerosols are sufficiently dense to absorb radiation and radiate heat into the atmosphere (Kochanski et al., 2019). These effects are known as “smoke shading” (Lareau & Clements, 2015). Researchers in the K-S have reported reduced fire severity below smoke inversions relative to what would be expected in the absence of an inversion (Estes et al., 2017; Miller et al., 2012; Taylor et al., 2009). However, no research to date has directly quantified the influence of smoke density on fire effects in the K-S or elsewhere.

Here we explore the effects of repeat burning on refugia by addressing the following question: where and why do conifer forests persist in refugia through multiple fire events? We leverage recent advances in fire mapping and weather interpolation—combined with a novel application of satellite-based smoke imagery—to undertake a broadscale retrospective analysis of fire severity through multiple fire events in the K-S. We focus on mature, conifer-dominated (MCD) forests because these ecosystems are vulnerable to projected changes in climate and fire regimes, and because shrublands and hardwood forests respond differently to repeat burning due to their resprouting ability. Specifically, we evaluate the effects and relative importance of topography, fuels, and weather factors on the probability of MCD refugia (1) forming during an initial fire, (2) persisting through a reburn, and (3) persisting through a triple burn. By examining the similarities and differences among these three scenarios, we elucidate the dominant controls of refugia occurrence and

persistence in an ecosystem at risk of widespread fire- and climate-induced forest loss.

2 | MATERIALS AND METHODS

2.1 | Study area

The Klamath-Siskiyou ecoregion (Figure 1) is a topographically and geologically varied landscape that supports globally important biodiversity (Olson et al., 2012). The 48,400 km² study area is generally characterized by a Mediterranean climate with cool, wet winters and warm, dry summers. Strong west to east temperature and precipitation gradients and complex mountainous topography result in substantial climatic variability (Skinner et al., 2006). Mean annual temperature averages 11.5°C; mean annual precipitation averages 1491 mm (PRISM, 2020). Thunderstorms are common during the summer months, and lightning-caused fires account for most of the area burned in the region over the last half century (Skinner et al., 2006).

Fire was frequent in much of the K-S during the centuries prior to European colonization. Conifer forests at low and middle elevations burned every 5–20 years on average, while upper elevations and riparian areas burned somewhat less frequently (Metlen et al., 2018; Skinner, 2003; Stuart & Salazar, 2000; Taylor & Skinner, 1998, 2003). Pre-colonization fires, including cultural burning by tribal communities, were characterized by a mixed-severity regime that supported exceptionally diverse mosaics of forests, shrublands, and grasslands (Halofsky et al., 2011; Metlen et al., 2018; Taylor & Skinner, 1998). Institutionalized fire suppression began in the early 20th century, and by the 1940s these efforts had radically reduced fire frequencies (Metlen et al., 2018; Stuart & Salazar, 2000; Taylor & Skinner, 1998, 2003). The relative absence of fire has resulted in widespread afforestation and densification, increased fuel accumulations, and compositional shifts toward more fire-sensitive species (Knight et al., 2020; Perry et al., 2011; Taylor & Skinner, 2003). Prolonged fire-free periods may have occurred in the region historically (Colombaroli & Gavin, 2010). However, modern fire exclusion and resultant changes to fuels, in conjunction with longer fire seasons and more extreme fire weather (Abatzoglou & Williams, 2016; Westerling, 2016), appear to be driving increases in fire extent, frequency, and severity (Dennison et al., 2014; Steel et al., 2018).

Contemporary MCD forests in the K-S are dominated by Douglas-fir (*Pseudotsuga menziesii*) with lesser amounts of white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), incense-cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), and Jeffrey pine (*Pinus jeffreyi*; Appendix S1). These species do not resprout when top-killed by fire, requiring seeds dispersed from surviving (or very recently living) trees to regenerate. In contrast, less common serotinous or semi-serotinous species in the region, such as knobcone pine (*Pinus attenuata*), can reproduce following high-severity fire from in situ seed sources.

Common hardwood tree species such as tanoak (*Notholithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), canyon live oak

(*Quercus chrysolepis*), and chinkapin (*Chrysolepis chrysophylla*) resprout prolifically following fire and are widespread, subdominant tree species in MCD forests (Donato et al., 2009). Common resprouting sclerophyll shrub genera include *Arcostaphylos* and *Ceanothus*, some species of which also recruit abundantly from soil seedbanks following fire (Knapp et al., 2012; Odion et al., 2010).

2.2 | Analysis overview

We developed three statistical models of refugia probability in MCD forests, constrained by the temporal availability of fire severity and fuels data from Landsat imagery (since 1984) and fire weather and smoke data associated with MODIS imagery (since 2002): (1) The *initial fire* model examines refugia probability in MCD forests that burned for the first time as early as 2002 and subsequently re-burned. (2) The *reburn* model examines refugia probability in MCD forests that persisted through an initial fire event as refugia as early as 1985 and reburned after 2001. (3) The *triple burn* model examines refugia probability in MCD forests that persisted through both an initial and reburn fire event as refugia and burned for a third time after 2001.

2.3 | Mapping MCD fire refugia

Once, twice, and triple burned areas were identified using fire perimeter data acquired from the Monitoring Trends in Burn Severity (MTBS) large fire (>400 ha) database (<https://www.mtbs.gov>; Eidenshink et al., 2007). Following Meigs and Krawchuk (2018), we created fire severity maps using the relative differenced normalized burn ratio (RdNBR; Miller & Thode, 2007) in 2-year intervals (fire year ± 1 year) from 30 m Landsat time series fitted with the LandTrendr algorithm (Kennedy et al., 2010). Image processing was conducted in Google Earth Engine (Gorelick et al., 2017). Refugia were identified as locations displaying little or no fire-induced spectral change (Collins et al., 2019; Kolden et al., 2012), based on a refugia threshold of RdNBR ≤ 166 from Meigs and Krawchuk (2018) corresponding to $\leq 10\%$ tree basal area mortality (Reilly et al., 2017). This RdNBR threshold reliably identified refugia for field plots located in our study area (overall classification accuracy = 85%, Appendix S2). Here, fire refugia are referred to as follows: (1) *initial* refugia from a single fire, (2) *transient* refugia that do not persist through reburn, (3) *persistent* refugia that survive reburn, and (4) *super-persistent* refugia that survive triple burn (Figure 2).

We identified MCD forest from existing pre-fire composition and structure maps developed using gradient nearest neighbor (GNN) imputation (Ohmann et al., 2012). GNN maps combine Landsat time series and forest inventory data ($n = 17,000$) to impute plot-level forest structure and composition attributes. We classified areas with an old-growth structural index of 80 years or greater as mature forest (Davis et al., 2015). We identified areas containing >50% basal area of live conifer trees ≥ 2.5 cm diameter at breast height as conifer

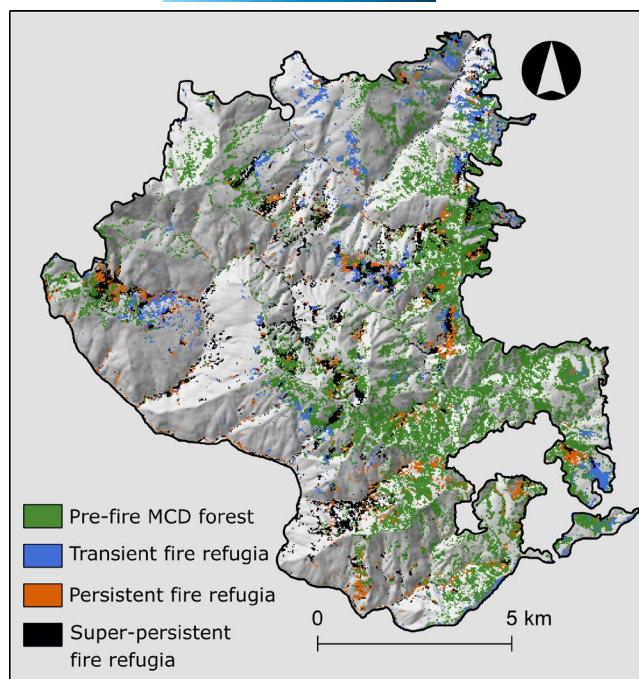


FIGURE 2 Maps of mature conifer-dominated (MCD) forest and MCD fire refugia extent in a triple burned area. The amount of relatively intact MCD forest progressively eroded over multiple fire events. Colors represent fire refugia that persisted through one (transient, blue), two (persistent, orange), and three (super-persistent, black) fire events

forest. We classified MCD forest using maps produced for the year prior to initial fire.

We generated random samples of 30 m pixels for our three statistical models of refugia probability. Following Zald and Dunn (2018), we imposed a 200 m inter-plot minimum distance constraint to reduce the potential for spatial autocorrelation. For the initial fire model ($n = 15,568$), we sampled only areas that were MCD forest in the year prior to fire. For the reburn ($n = 33,196$) and triple burn ($n = 2156$) models, we constrained sampling to MCD forest that was also classified as refugia in previous fires. We used 50% of each sample for model fitting and 50% for model validation. The sampling process for each was independent, and ultimately <1% of sampled pixels were included in more than one model.

2.4 | Predictor variables: Fuels, topography, weather, prior fire, and smoke

We assessed pre-fire fuels using transformed Landsat imagery and GNN forest structure data (Table 1). We utilized the three Tasseled Cap (TC) indices—brightness, greenness, and wetness—which are transformations of original Landsat bands that capture the three major axes of spectral variation (Masek et al., 2008). Previous studies in the US Pacific Northwest have demonstrated that TC indices are useful for capturing variability in conifer forests

TABLE 1 Predictor variables for boosted regression tree (BRT) analysis

| Variable | Description | Source |
|----------------------------|--|--------------------------|
| Weather | | |
| Maximum temperature | Z-scores from temporally normalized daily maximum temperature | Abatzoglou (2013) |
| Morning smoke | Aerosol optical depth, a measure of atmospheric smoke from MODIS satellite imagery | Lyapustin et al. (2018) |
| Topography | | |
| Elevation | m | DEM; Farr et al. (2007) |
| Slope | degrees | DEM |
| Aspect | Beers transformed, 0 = southwest, 1 = northwest/southeast, 2 = northeast (unitless) | Beers et al. (1966), DEM |
| TPI | Low values represent valleys, high values represent ridges, unitless (300 m) | Weiss (2001), DEM |
| SWI | Increases with potential soil wetness, influences vegetation moisture, composition, and structure (unitless) | Olaya (2004), DEM |
| Fuel | | |
| Brightness (TC1) | Axis 1 from Tasseled Cap transformation, from LandTrendr imagery (unitless) | Crist (1985) |
| Greenness (TC2) | Axis 2 from Tasseled Cap transformation, from LandTrendr imagery (unitless) | Crist (1985) |
| Wetness (TC3) | Axis 3 from Tasseled Cap transformation, from LandTrendr imagery (unitless) | Crist (1985) |
| QMD | Quadratic mean diameter based on GNN imputation mapping (cm) | Ohmann et al. (2012) |
| TPH | Stand density based on GNN imputation mapping (trees ha ⁻¹) | Ohmann et al. (2012) |
| Biomass | Biomass based on GNN imputation mapping (kg ha ⁻¹) | Ohmann et al. (2012) |
| Refugia focal ^a | Neighborhood amount of fire refugia cells within a 300 m radius | |
| TSIF ^a | 1–30, time since initial fire, derived from MTBS large fire database (years) | |
| TSR ^b | 2–23, time since reburn, derived from MTBS large fire database (years) | |
| Initial FS ^a | RdNBR fire severity based on Landsat satellite mapping (unitless) | Miller and Thode (2007) |
| Reburn FS ^b | RdNBR fire severity based on Landsat satellite mapping (unitless) | Miller and Thode (2007) |

TPI, topographic position index; SWI, soil wetness index; GNN, gradient nearest neighbor; DEM, digital elevation model. The response variable for all BRT modeling is a binary classification (refugia or non-refugia) of burn severity derived from Landsat satellite data (see Section 2).

^aVariable included only in the reburn and triple fire models.

^bVariable included only in the triple fire model.

(Cohen et al., 2001; Thompson et al., 2007) and for identifying refugia (Meddens et al., 2016). We represented live fuel loading, stand structure, and fuel arrangement using GNN estimates of biomass, quadratic mean diameter, and stand density.

We derived five terrain metrics to investigate the influence of topography on refugia probability: elevation, slope, aspect, soil wetness, and topographic position (Table 1). These variables were selected from a larger suite of topographic metrics based on a collinearity threshold ($|r| > 0.7$ Appendix S1; Dormann et al., 2013). We chose the spatial scale at which to calculate topographic position (300 m) based on the explanatory power of different window sizes from exploratory analyses. Terrain metrics were calculated based on a 30 m digital elevation model using the raster (Hijmans, 2020) and RSAGA (Brenning, 2008) packages in the R statistical computing environment (R Core Team, 2020).

We accounted for the influence of previous fire on refugia probability with time since fire derived from MTBS fire perimeter data and previous fire severity data from Landsat-derived RdNBR values. To evaluate how surrounding patterns of refugia influence the probability of local refugia persistence, we created a refugia focal index that is the sum of MCD refugia cells within a 300 m radius, which

was based on the explanatory power of different window sizes from initial modeling. Low and high values represent neighborhoods where refugia are sparse and abundant, respectively.

We characterized daily fire weather conditions using interpolated maximum temperature data. We chose maximum temperature because it was the most robust meteorological variable in exploratory analyses (where we also assessed minimum relative humidity and energy release component). Each sample pixel was assigned a day-of-burn date from daily fire progression maps derived from MODIS hotspot fire detection (Parks, 2014). We then extracted day-of-burn maximum temperature values from interpolated, moderate-resolution (~4 km) meteorological grids (gridMET, <https://www.climatologylab.org/gridmet.html>; Abatzoglou, 2013). To account for substantial regional temperature variability, we converted raw data to temporally normalized z-scores based on fire season climate normals (June 1st to September 30th, 1979–2018). A z-score less than or greater than zero represents a below-average or above-average maximum temperature for a specific location, respectively.

We quantified wildfire smoke using MODIS aerosol optical depth (hereafter, “smoke”) data from the Multi-Angle Implementation of

Atmospheric Correction algorithm (MAIAC). MAIAC produces daily smoke data using a physical atmospheric-surface model and stored spectral, spatial, and thermal signatures for 1 km gridded cells (Lyapustin et al., 2018). We restricted our analysis to data from the morning overpass (TERRA satellite) because we were interested in the influence of latent smoke likely trapped by thermal inversions rather than smoke from active fires during the peak afternoon burn period (Figure 3). Because smoke data were sometimes not available for our entire study area each day (depending on satellite orbit paths), we temporally averaged (day-of-burn ± 2 days) smoke imagery to produce region-wide maps. This temporal smoothing is consistent with the uncertainty associated with day-of-burn estimates from MODIS hotspot data (Parks, 2014). Additionally, the MAIAC algorithm is sometimes unable to retrieve smoke data in and around actively burning fires when smoke is particularly dense (David et al., 2018; Superczynski et al., 2017). Because these missing data were non-random and more likely to be associated with active fires in our study area, we interpolated smoke values for these locations using an inverse distance-weighted approach. Interpolated values were only assigned to areas where raw smoke data were absent. We conducted all MAIAC data processing and interpolation using Google Earth Engine.

Fire activity above an inversion layer may be elevated due to higher temperature and lower relative humidity relative to conditions below the inversion or conditions in the absence of an inversion (Robock, 1988; Sharples, 2009). To account for this effect, we adopted a 1300 m elevation threshold developed by Estes et al. (2017) based on K-S weather station data and input from local land managers. Following interpolation, locations >1300 m were assigned a smoke value of zero based on the assumption that smoke at these elevations was more likely to be the product of actively burning fire rather than latent smoke settled beneath inversions.

2.5 | Modeling fire refugia probability

We modeled refugia probability as a binary response (refugia, non-refugia) using Boosted Regression Trees (BRT). BRT models are well-suited to ecological modeling because they allow for interactions and are relatively insensitive to collinearity and outliers (Dormann et al., 2013; Elith et al., 2008). Several recent studies have successfully used BRT to model complex, nonlinear relationships between biophysical factors and fire severity (e.g., Krawchuk et al., 2016; Meigs et al., 2020; Zald & Dunn, 2018).

Models shared the same suite of topographic, fuel, and weather variables (Table 1). Our reburn and triple burn models also included the refugia focal index, time since initial fire, and initial fire severity. The triple burn model further included time since reburn and reburn fire severity.

We also fit submodels for each variable category to evaluate the relative importance of fuels, weather, and topography. We included time since fire and prior fire severity in the fuels submodels because these factors primarily influence fuel reaccumulation between fires (Coppoletta et al., 2016). The refugia focal index was included in the reduced fuel submodels because it can be interpreted as a measure of neighborhood fuel composition and structure. Morning smoke was included in the weather submodels.

BRT model runs were parameterized following Krawchuk et al. (2016) using random subsets of the data to produce a minimum of 1000 trees (learning rate = 0.001, tree complexity = 5, bag fraction = 0.5). We evaluated model performance based on two criteria: (1) cross-validated percentage deviance explained and (2) area under the curve of the receiver operating characteristic (hereafter "AUC") from both cross-validation and independent validation datasets. AUC is a synthetic metric that evaluates model sensitivity and specificity to assess the capacity to correctly predict the presence or absence of refugia. We interpreted AUC values to indicate fair

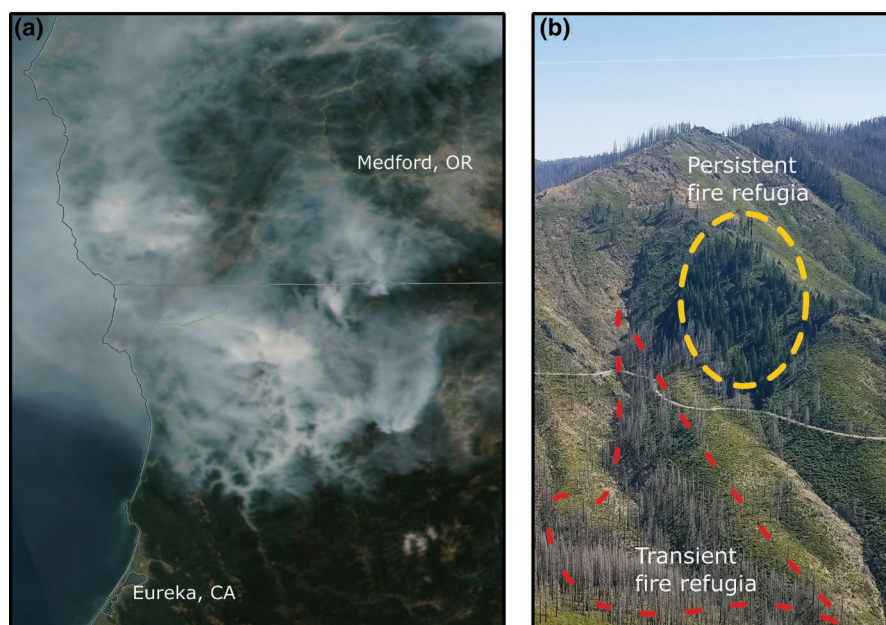


FIGURE 3 (a) MODIS Terra true color imagery from the morning of August 26, 2017 shows morning smoke concentrated in the Klamath and Salmon River drainages, likely due to the presence of a thermal inversion. (b) Transient (red) and persistent (yellow) refugia from the 1987 Fort Copper and 2017 Abney fires. The relatively long (30 years) period since initial fire may have reduced the probability of more initial fire refugia persisting through reburn

(>0.6–0.7), good (>0.7–0.8), very good (>0.8–0.9), or excellent (>0.9) model performance (Krawchuk et al., 2016; Meigs et al., 2020). We quantified the relative influence of each variable to identify the factors that most strongly control refugia probability, and we used partial dependence plots to examine the effect of predictor variables on refugia probability after accounting for all other variables in the model. We assessed interactive effects of predictor variables on refugia probability using three-dimensional surface plots (Appendix S2), presenting results for a subset with the strongest interactions in each model. BRT modeling was performed using the *gbm* (Greenwell et al., 2020) and *dismo* (Hijmans et al., 2020) R packages.

3 | RESULTS

3.1 | Initial fire refugia

Refugia accounted for 31% (9590 ha) of the total 30,953 ha of MCD forest in 25 fires that burned for the first time between 2002 and 2015. Overall model performance was good (Table 2). The weather submodel explained more variation than either the fuels or topography submodels. Maximum temperature was the single most important variable and displayed a strongly negative relationship with refugia probability (Figure 4). Low elevations were positively associated with refugia, whereas intermediate elevations had the lowest probability of refugia. The association between morning smoke and refugia probability was strongly positive. Refugia probability was positively associated with TC wetness and topographic soil wetness and negatively associated with TC brightness. Refugia were less likely to occur on convex landforms and in very high-density stands with small diameter trees. Morning smoke had the strongest positive effect on refugia probability when maximum temperatures were much higher than average (Appendix S2: Figure 1).

3.2 | Reburn: persistent refugia

Persistent refugia accounted for 45% (20,349 ha) of the 45,788 ha of reburned MCD refugia within 105 reburns (unique combinations of first and second fire events). Overall model performance was good (Table 2). The fuels submodel, which included time since initial fire and initial fire severity, explained more variation than either the topography or weather submodels. The single most important variable was time since initial fire, which was generally negatively associated with persistent refugia probability (Figure 5). Consistent with the initial fire model, reburn refugia probability was positively associated with TC wetness and negatively associated with maximum temperature, topographic position, and TC brightness. Persistent refugia probability was highest when refugia initially burned at very low severity ($RdNBR \approx 25$). The relationship between reburn refugia probability and morning smoke was less influential and hump shaped; probabilities were highest at moderate smoke levels. In contrast to the initial fire model, refugia probability was positively associated with elevation, but elevation was substantially less influential than in other models. Locations with a higher density of neighboring refugia (higher refugia focal values) were more likely to persist through reburn as refugia than locations where nearby refugia were sparse or absent (low refugia focal values). Very low initial fire severity had a substantial positive effect on refugia probability within 20 years of initial fire but had little effect in older fires (Appendix S2: Figure 4).

3.3 | Triple burn: super-persistent refugia

Super-persistent refugia accounted for 73% (1347 ha) of the 1851 ha of MCD reburn refugia within 16 triple burn events (unique combinations of first, second, and third fire events). Overall model performance was good (Table 2). The weather submodel explained less

TABLE 2 Overall deviance explained, mean ROC, and variables with the greatest relative influence for full and reduced initial fire, reburn, and triple burn models. Columns V1, V2, and V3 represent the first, second, and third most influential variables, respectively, in each model. Variables are defined in Table 1

| Model | Variable class | CV Dev. Expl. | CV ROC | Valid. ROC | V1 | V2 | V3 |
|--------------|----------------|---------------|--------|------------|-----------------|------------|-----------|
| Initial fire | Topography | 9% | 0.68 | 0.68 | Elevation | SWI | TPI |
| | Fuels | 14% | 0.71 | 0.71 | TPH | QMD | Wetness |
| | Weather | 18% | 0.76 | 0.63 | TMax | Smoke | NA |
| | Full model | 26% | 0.80 | 0.73 | TMax | Elevation | Smoke |
| Reburn | Topography | 2% | 0.59 | 0.59 | TPI | Elevation | Slope |
| | Fuels | 9% | 0.68 | 0.69 | Time since fire | Initial FS | Wetness |
| | Weather | 6% | 0.64 | 0.61 | TMax | Smoke | NA |
| | Full model | 14% | 0.72 | 0.70 | Time since fire | TMax | Wetness |
| Triple burn | Topography | 19% | 0.68 | 0.70 | Elevation | Aspect | TPI |
| | Fuels | 26% | 0.72 | 0.74 | Reburn FS | Wetness | TSR |
| | Weather | 18% | 0.69 | 0.62 | TMax | Smoke | NA |
| | Full model | 34% | 0.73 | 0.76 | TMax | Wetness | Reburn FS |

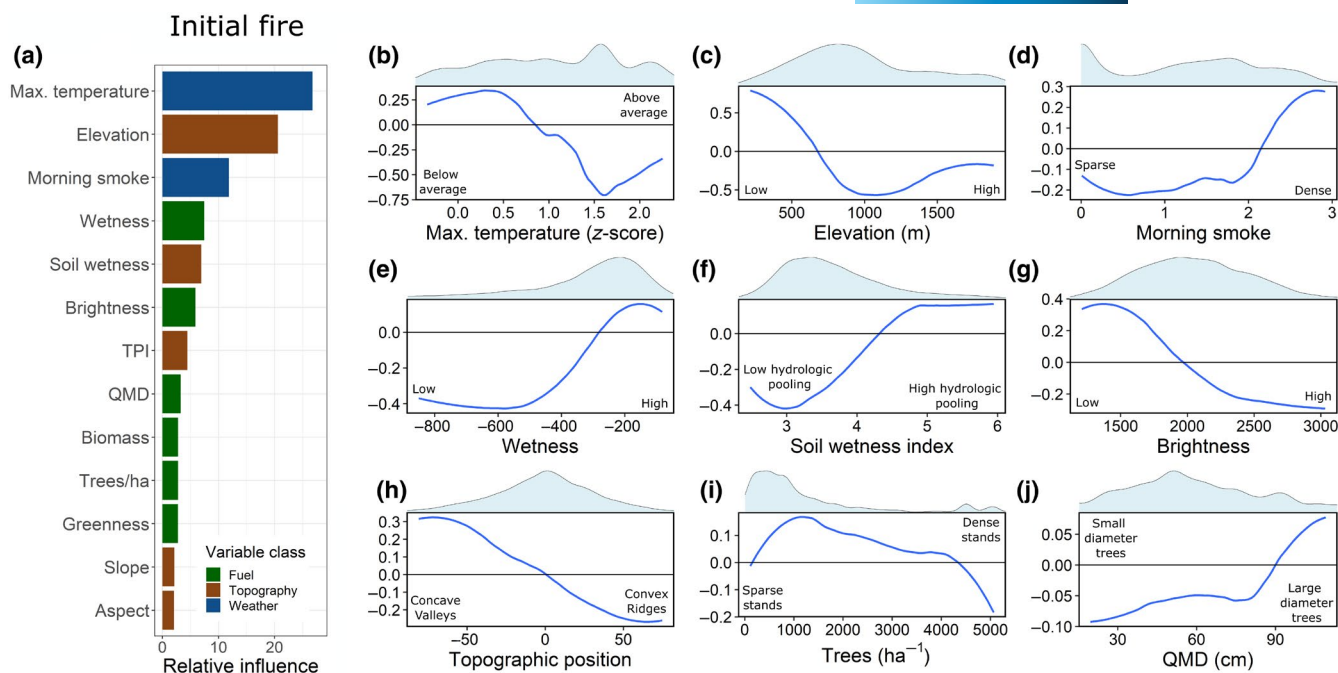


FIGURE 4 The relative influence for variables included in the initial fire model, color-coded by variable class. (a) Variables with the highest relative influence values most strongly affected fire refugia probability. (b–j) Partial dependence plots for the top nine model predictors in order of decreasing relative influence. Note that the scales vary on the y-axes, which represent the logit probability of fire refugia after accounting for the influence of other predictor variables. Values on the x-axis are bound by the 1% and 99% sample quantiles of the observed data to reduce the influence of very rare observations resulting in predictions that distort the representation of modeled relationships. Density plots above each panel represent the distribution of observed values for each variable. Partial dependence plots for less influential model variables can be found in Appendix S1

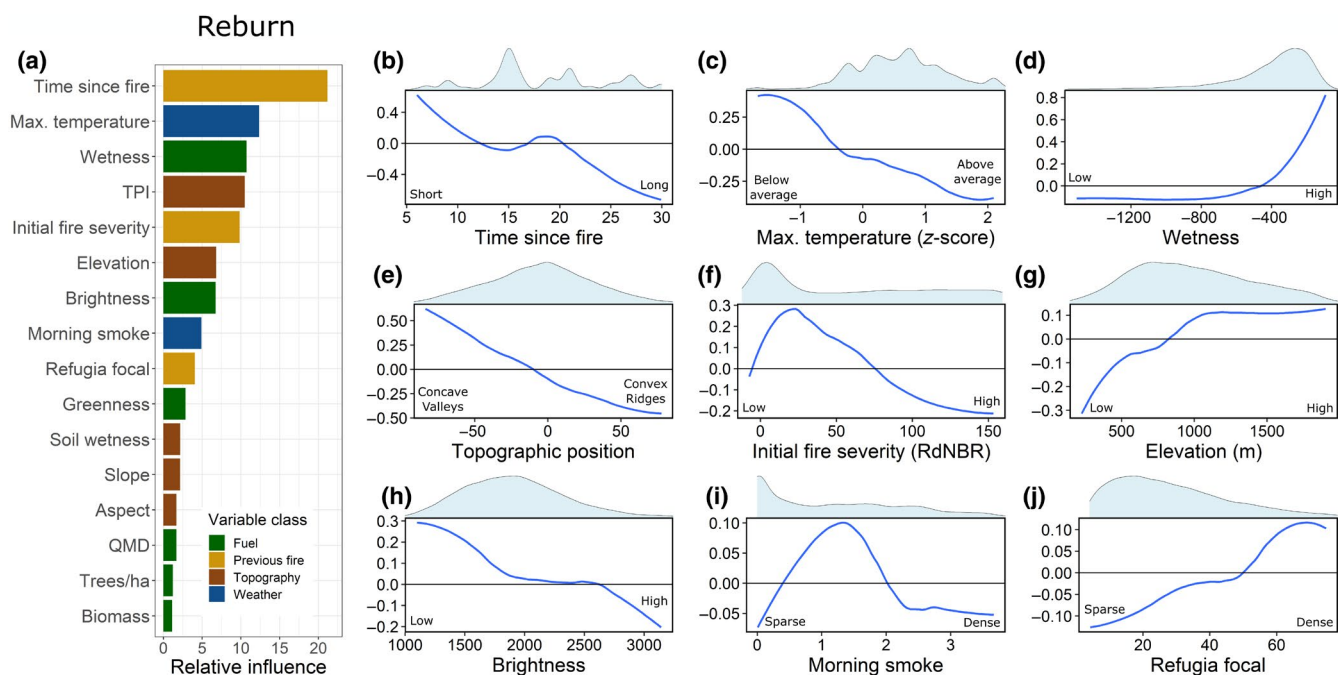


FIGURE 5 The relative influence for variables included in the reburn model, color-coded according to variable class. (a) Variables with the highest relative influence values most strongly affected fire refugia probability. (b–j) Partial dependence plots for the top nine model predictors in order of decreasing relative influence. Note that the scales vary on the y-axes, which represent the logit probability of fire refugia after accounting for the influence of other predictor variables. Values on the x-axis are bound by the 1% and 99% sample quantiles of the observed data to reduce the influence of very rare observations resulting in predictions that distort the representation of modeled relationships. Density plots above each panel represent the distribution of observed values for each variable. Partial dependence plots for less influential model variables can be found in Appendix S1

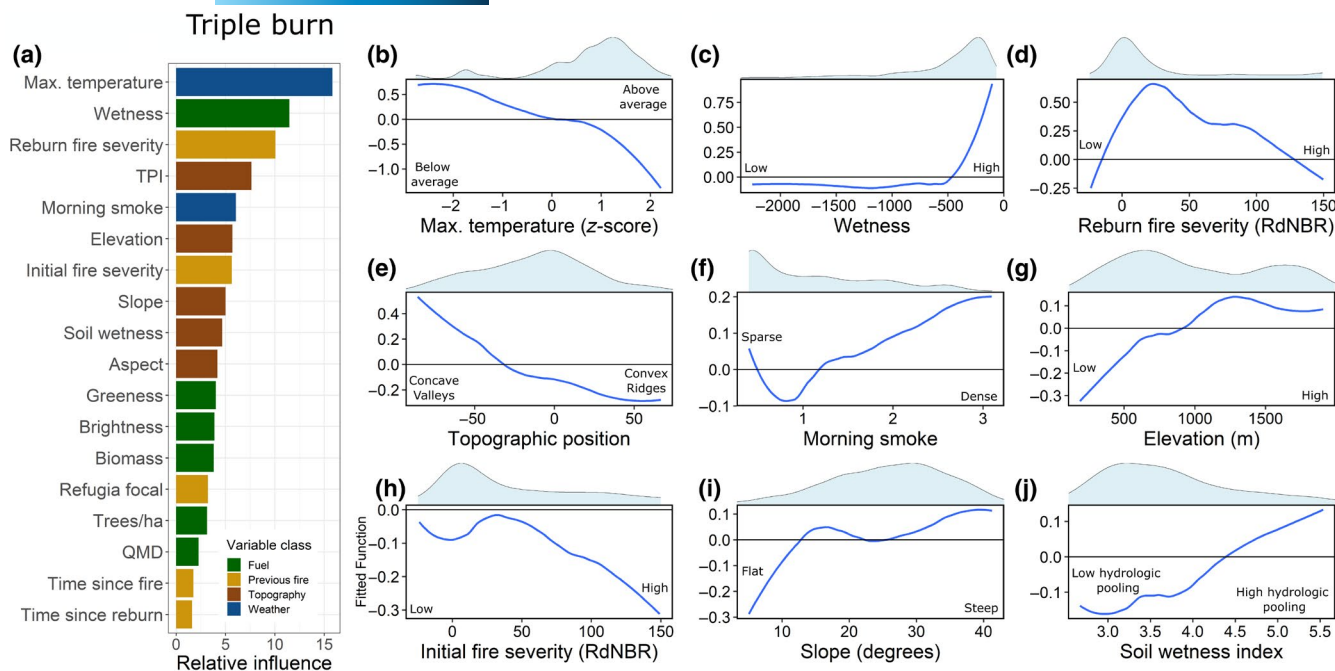


FIGURE 6 (a) The relative influence for variables included in the Triple model, color-coded according to variable class. (a) Variables with the highest relative influence values most strongly affected fire refugia probability. (b–j) Partial dependence plots for the top nine model predictors in order of decreasing relative influence. Note that the scales vary on the y-axes, which represent the logit probability of fire refugia after accounting for the influence of other predictor variables. Values on the x-axis are bound by the 1% and 99% sample quantiles of the observed data to reduce the influence of very rare observations resulting in predictions that distort the representation of modeled relationships. Density plots above each panel represent the distribution of observed values for each variable. Partial dependence plots for less influential model variables can be found in Appendix S1

variability in the data than either the fuels or topography models. Substantially more variation was explained in the triple burn topography submodel (19%) than in the initial fire (9%) or reburn (2%) models, and five of the 10 most influential variables in the triple burn model were topographic. The three most important variables were maximum temperature, TC wetness, and elevation, all of which demonstrated associations that were fairly consistent with the reburn model results (Figure 6). Super-persistent refugia probability was positively associated with moderate to steep slopes, dense morning smoke, and areas with high potential hydrologic pooling. Consistent with the reburn model, the probability of super-persistent refugia peaked in concave topographic positions where previous fire burned at very low severity ($RdNBR \approx 25$). Concave landforms had a substantial positive effect on refugia probability when temperatures were well above average (Appendix S2: Figure 7).

4 | DISCUSSION

We reveal key factors influencing the persistence of forests in refugia across a highly fire-prone biodiversity hotspot, and highlight that some refugia appear to build up resistance as they pass through multiple fire filters. The distribution of refugia was nonrandom and shaped by multiple weather, topographic, and fuel factors. Hotter-than-average fire weather was associated with lower refugia occurrence and persistence, an indication that climate warming may be a

mechanism responsible for refugia loss. Moderate to dense morning smoke—likely associated with temperature inversions—had a strong positive effect on refugia probability, particularly when temperatures were above average. The atmospheric conditions conducive to persistent inversions in the K-S have become considerably less common over the past century, which may be weakening a key mechanism of refugia persistence (Johnstone & Dawson, 2010). Super-persistent refugia appear to be at least partially entrained by landscape features that offer protection from fire, suggesting that topographic variability is an important stabilizing factor for the distribution of mature conifer forest as fire activity increases.

Our results demonstrate that repeat burning decreases the abundance of refugia within fire perimeters, which is a key control on post-fire regeneration for tree species reliant on surviving individuals for seed sources (Coop et al., 2019). Increasing fire activity and decreasing post-fire regeneration rates associated with climate warming may be compounded when these same climatic conditions manifest as severe fire weather resulting in the loss of refugia and the seed sources they contain (Abatzoglou & Williams, 2016; Rodman et al., 2020). Observed and projected fire-induced shifts in the K-S are similar to those increasingly documented in forests worldwide. Montane forests in the US Rocky Mountains, eucalypt forests in Australia, conifer forests in the boreal zone, and others are vulnerable to short fire-free intervals and slow post-fire regeneration following high-mortality events (Bowman et al., 2014; Turner et al., 2019; Whitman et al., 2019). Although

fire-induced forest loss is a major concern globally, increasing fire activity and reductions in mature forest types can also have ecological benefits. In the K-S, moderate- or high-severity fire resulting in the loss of MCD forest may positively contribute to the restoration of the historical forest and non-forest patch mosaic, and support early-seral species like knobcone pine that rely on periodic high-severity fire to maintain their ranges (Reilly et al., 2019).

Some refugia appeared to become increasingly fire resistant as MCD forest passed through multiple fire filters. The percentage of area that persisted as refugia increased by approximately 50% between initial fire (31%), reburn (45%), and triple burn (73%). Increasing resistance to fire over successive fire events is likely the product of a combination of factors observed in other forest ecosystems, including the progressive restriction of persistent refugia into more fire-resistant landscape positions (Wood et al., 2011), as well as the self-limiting effect of short fire intervals (Coppoletta et al., 2016; Parks et al., 2014).

Topography was an important control on the distribution of super-persistent refugia, a result consistent with the influence of terrain on refugia occurrence and persistence in a wide variety of forests in North and South America, Africa, Europe, and Australia (Adie et al., 2017; Collins et al., 2019; Krawchuk et al., 2016; Landesmann et al., 2015; Román-Cuesta et al., 2009). As we found here, refugia in forest ecosystems are frequently associated with concave landforms (e.g., gullies) in wetter settings where fuels are moister and less available to burn (Leonard et al., 2014). The relatively strong topographic signal detected in our triple burn model provides evidence that contemporary repeat burning may strengthen the feedbacks between underlying topoedaphic templates and fire severity (Kane et al., 2015; Martinez et al., 2019). The stability of these feedbacks in the K-S and elsewhere may have historically contributed to the development of old forest structure (Camp et al., 1997), the persistence of fire-sensitive species in topographic refugia (Schwilk & Keeley, 2006), and the maintenance of early-seral communities dependent on recurrent high-severity fire (Odion et al., 2010). The lack of a stronger topographic signal in our reburn models may be due in part to critical fire weather (79% of reburn samples burned on hotter-than-average days), which can reduce the influence of topography and decrease the predictability of refugia (Collins et al., 2019; Krawchuk et al., 2016). It is also possible that the muted effect of topography in the initial fire and reburn models may be related to a homogenizing effect of fire suppression, as prior studies report that topography did not strongly influence reburn fire severity where fire had been reintroduced after a prolonged period of exclusion (Coppoletta et al., 2016; Thompson & Spies, 2009).

The strong influence of prior fire severity was somewhat unexpected given that our reburn and triple burn analyses were constrained to a narrow range of prior fire effects ($RdNBR \leq 166$), although generally similar self-reinforcing behavior has been reported in prior studies (Collins et al., 2009; Grabinski et al., 2017; Harris & Taylor, 2017). It is unlikely that very light burning in refugia

meaningfully shifted forest composition and structure back toward the less dense, more fire-resistant norms that historically characterized much of the region's conifer forests (Knight et al., 2020; Taylor & Skinner, 1998, 2003). However, very low-severity fire in refugia may have provided an optimal balance between reducing surface fuels while minimizing overstory tree mortality, thereby inhibiting post-fire shrub or hardwood responses and reinforcing a structure more resistant to canopy-killing fire effects.

Our finding that refugia persistence is negatively associated with time since prior fire is consistent with studies reporting lower reburn severity with shorter fire return intervals (Collins et al., 2009; Parks et al., 2014), and the importance of time since fire as a mediator of fire effects in forest ecosystems globally (Collins et al., 2019; Héon et al., 2014; Prichard et al., 2017). Time since fire is generally interpreted as a proxy for fuel accumulation (Coppoletta et al., 2016), a process that rapidly (5–10 years) diminishes the self-limiting effect of fire in the K-S (Donato et al., 2013). Refugia persistence through reburn was most probable at short fire intervals (<20 years), which is consistent with historic norms reconstructed from dendrochronological evidence (Taylor & Skinner, 1998, 2003). A small decrease in the probability of refugia persistence at 15 years since fire in the reburn model (Figure 5b) corresponds to the interval between the most widespread fire years in the region (1987–2002–2017). This suggests that longer-term or larger-scale phenomenon (e.g., multi-year drought) unaccounted for here may contribute to both widespread fire activity as well as refugia loss.

Given the relatively small degree of fire-induced change in refugia, the importance of time since fire may reflect neighborhood effects, as fuels—particularly resprouting shrubs and hardwoods—rapidly reaccumulate in surrounding higher-severity burned areas. This interpretation is supported by our finding that refugia were positively associated with more contiguous patches of intact conifer forest (lower TC brightness) and neighborhoods with larger amounts of surrounding refugia (higher refugia focal values). Closed canopy forests in the K-S tend to burn at lower severity than shrublands (Grabinski et al., 2017; Odion et al., 2004; Thompson & Spies, 2009), and high-severity fire may have had a greater propensity to spread into small, isolated refugia embedded in a more pyrophilic matrix.

Smoke density strongly influenced refugia probability, illustrating an important negative feedback loop between fire and its effects. Refugia were more likely to occur when smoke was moderate to dense in the morning, a relationship attributable to reduced incoming solar radiation resulting from smoke shading beneath temperature inversions. Smoke density was negatively associated with elevation (irrespective of the 1300 m threshold), and the strong influence of smoke on refugia probability could be considered both a topographic and atmospheric effect. Our results corroborate prior observations and the findings from the only other study that has quantified the influence of smoke on fire effects using presence/absence methods that differ substantially from ours (Estes et al., 2017). There is some indication that fire-atmosphere feedbacks that

promote refugia persistence may be weakening as the atmospheric conditions (e.g., strong subsidence) responsible for persistent inversions in the K-S have become substantially less common over the last century (Johnstone & Dawson, 2010).

Multiple assumptions and sources of uncertainty influence our capacity to quantify drivers of refugia probability. The 30 m grain of Landsat-based vegetation (GNN) and severity (RdNBR) data cannot detect very small yet ecologically important patches of MCD forest and refugia (Blomdahl et al., 2019; Coop et al., 2019), and our methods were not designed to account for delayed (>1 year) mortality that likely influenced long-term refugia pattern dynamics. Additionally, satellite data are unable to reliably detect fire-induced change below tree canopies that may have influenced repeat burning dynamics in refugia (Kolden et al., 2012; Meddens et al., 2016). We recognize that our 10% basal area mortality threshold for refugia is somewhat arbitrary—there may be substantial differences in the ecological importance and persistence of refugia defined based on different thresholds (e.g., truly unburned). Although GNN data were not developed for applications in moderate- and high-severity burned landscapes (Bell et al., 2015), we assume that the GNN maps imputed from generally unburned inventory plots are appropriate in the context of MCD refugia with minimal fire-induced change. Future research could leverage additional post-fire field data, including observations in refugia, to better understand the structural and compositional conditions that promote persistence. Another limitation of our study is that we did not account for the effects of fires which occurred prior to 1984 when Landsat data acquisition began. Pre-Landsat fires almost certainly introduced variability we were unable to capture directly in our models, but we believe it is unlikely that much of our study area burned at high severity in the several decades prior to 1984 because we constrained our analysis to mature (>80 years old) conifer-dominated forest.

As far as we know, our integration of satellite smoke imagery into fire effects models is the first such effort its kind, but there are undoubtedly opportunities to improve on this approach. We did not explicitly include wind and atmospheric stability in our models, and future work could attempt to distinguish between the effects of inversions themselves (stable atmosphere, calm winds) and the effects of smoke shading. Smoke plume height (Lyapustin et al., 2020) and remote weather station data could be combined with smoke imagery to definitively ascribe the effects we report here to thermal inversions. Lastly, future research could evaluate if our results are generalizable to other fire-prone regions with complex terrain and where thermal inversions occur.

5 | CONCLUSION

Refugia are ecologically important components of heterogeneous fire severity mosaics. Topographic settings associated with enduring fire refugia support the persistence of vegetation communities like conifer forests in the K-S that are particularly vulnerable to changing climate–fire interactions (Berry et al., 2015; Collins et al., 2019).

Observed and projected increases in both global forest fire activity (Andela et al., 2017) and reburns in western US forests (Buma et al., 2020) highlight the need to better understand the top-down and bottom-up controls on refugia occurrence and persistence. We found that pattern–process relationships shift in relative importance as landscapes pass through successive fire filters, and repeat burning appears to amplify the effect of terrain features. If similar dynamics operate in other forest communities, topographic templates could form the basis of management strategies designed to protect and restore the most fire-resistant portions of vulnerable forests in a wide variety of ecosystems.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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