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Refuge-yeah or refuge-nah? Predicting locations of forest resistance and recruitment in a fiery world

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Abstract

Climate warming, land use change, and altered fire regimes are driving ecological transformations that can have critical effects on Earth's biota. Fire refugia—locations that are burned less frequently or severely than their surroundings—may act as sites of relative stability during this period of rapid change by being resistant to fire and supporting post-fire recovery in adjacent areas. Because of their value to forest ecosystem persistence, there is an urgent need to anticipate where refugia are most likely to be found and where they align with environmental conditions that support post-fire tree recruitment. Using biophysical predictors and patterns of burn severity from 1180 recent fire events, we mapped the locations of potential fire refugia across upland conifer forests in the southwestern United States (US) (99,428 km^2 of forest area), a region that is highly vulnerable to fire-driven transformation. We found that low pre-fire forest cover, flat slopes or topographic concavities, moderate weather conditions, spring-season burning, and areas affected by low- to moderate-severity fire within the previous 15 years were most commonly associated with refugia. Based on current (i.e., 2021) conditions, we predicted that 67.6% and 18.1% of conifer forests in our study area would contain refugia under moderate and extreme fire weather, respectively. However, potential refugia were 36.4% (moderate weather) and 31.2% (extreme weather) more common across forests that experienced recent fires, supporting the increased use of prescribed and resource objective fires during moderate weather conditions to promote fire-resistant landscapes. When overlaid with models of tree recruitment, 23.2% (moderate weather) and 6.4% (extreme weather) of forests were classified as refugia with a high potential to support post-fire recruitment in the surrounding landscape. These locations may be disproportionately valuable for ecosystem sustainability, providing habitat for fire-sensitive species and maintaining forest persistence in an increasingly fire-prone world.

KEYWORDS
climate vulnerability, disturbance refugia, ecological resilience, fire severity, fire-driven transformations, post-fire tree recruitment, southwestern United States

1 | INTRODUCTION

Climate change, human land use, and altered fuels complexes are modifying fire regimes and reshaping forest ecosystems worldwide (Arias et al., 2021; Balch et al., 2017; Clarke et al., 2022; Hartmann et al., 2022). Shifting climate conditions, combined with severe fire activity, can overwhelm forest resilience processes (e.g., survival and recruitment) and drive rapid ecological reorganization (Falk et al., 2022; Johnstone et al., 2016). Forests dominated by coniferous obligate seeders (i.e., cone-bearing trees that reproduce only from seed) may be particularly vulnerable to fire-driven transformations towards non-forest cover (e.g., shrubland or grassland), with potential effects on carbon storage, nutrient cycling, biodiversity, and other important ecosystem services (Guiterman et al., 2022; Hessburg et al., 2019). Fire-driven transformations can occur when (1) severe fires eliminate seed-bearing trees in large patches that exceed typical seed dispersal distances, (2) fires occur at sites or in time periods where regeneration is limited by environmental conditions, or (3) increases in fire frequency (e.g., severe, short-interval reburns) exceed the ability of local species to establish, reach fire-tolerant sizes, and/or reach reproductive maturity (Coop et al., 2020; Enright et al., 2015). However, the rate and magnitude of fire-driven ecosystem changes will not play out uniformly across landscapes and species' ranges but will depend on the suite of factors that influence fire severity and species' environmental tolerances. Locations where current forests are buffered from altered fire regimes and climate change are critical to sustaining forest biota and ecosystem functions over upcoming decades, and may also facilitate species migration and adaptation over longer time scales (Jump & Peñuelas, 2005; Krawchuk et al., 2020; Morelli et al., 2020). Accordingly, identifying such locations will be valuable for predicting and mitigating the effects of fire-driven transformations in forested ecosystems.

Resilience, or the ability of systems to withstand and persist through disturbance, is controlled by both resistance and recovery mechanisms (Albrich et al., 2020; Hodgson et al., 2015; Holling, 1973). Fire refugia are defined as locations that are disturbed less frequently or less severely by fire than their surroundings (Camp et al., 1997; Krawchuk et al., 2020; Meddens et al., 2018). Because these locations embody resistance to change and can also promote post-fire recovery in the surrounding landscape, they can serve as key elements of forest resilience in the context of a warming and more fire-prone world. Fire refugia have been identified across varying temporal and spatial scales, ranging from locations of tree survival after a single fire (Chapman et al., 2020), to forest stands that remain stable through multiple fire events (Downing et al., 2021). Here, we seek to identify forested (i.e., ≥10% canopy cover) sites that are likely to be skipped (i.e., unburned islands) or burned at low severity within future fire events, a definition that is broadly relevant to a range of forest ecosystems (Meddens et al., 2018).

Unburned and low-severity areas can make up 40% or more of a given fire event (Kolden et al., 2012; Krawchuk et al., 2016). However, predicting the locations of such areas in future events is challenging because individual fires can be shaped by a wide range of factors such as fuels, topography, weather, past fire effects, and their interactions (Figure 1). For example, vegetation structure, composition, and spatial pattern can influence fire behavior at a range of spatial scales, and open-canopied forests might be expected to have greater fire resistance (Finney, 2001; Koontz et al., 2020; Yocom et al., 2022). Refugia are also more likely to be found in valley bottoms and sheltered topographic settings that are skipped during periods of active fire behavior (Estes et al., 2017; Meigs et al., 2020). Weather is an important driver of fire behavior that can interact with fuels and topography; forests burning under moderate weather conditions (e.g., low wind speeds, cool temperatures) may be more likely to contain refugia (Chapman et al., 2020; Collins et al., 2019; Downing et al., 2021). Across many forests of the western United States (US), large fires have been shown to reduce subsequent fire occurrence or severity for 10 years or more (Buma et al., 2020; Harris et al., 2021; Stevens-Rumann et al., 2016), though these effects can vary based on local plant community traits and the severity of the initial fire (Coppoletta et al., 2016; Tepley et al., 2018). A range of individual factors influence fire severity and the locations of refugia, but there is a pressing need to understand how these factors interact with regeneration processes to shape the resilience of today's forest ecosystems.

While refugia play an important role in post-fire tree recruitment by providing critical seed sources (Chambers et al., 2016; Coop et al., 2019; Kemp et al., 2016) and buffering microclimatic conditions (Carlson et al., 2021; Wooten et al., 2022), recruitment adjacent to refugia is also likely to vary based on biophysical conditions and individual species' climatic tolerances (Figure 1). For successful recruitment, seed dispersal must occur in sites that can support germination and longer-term seedling survival (Grubb, 1977; Rodman,

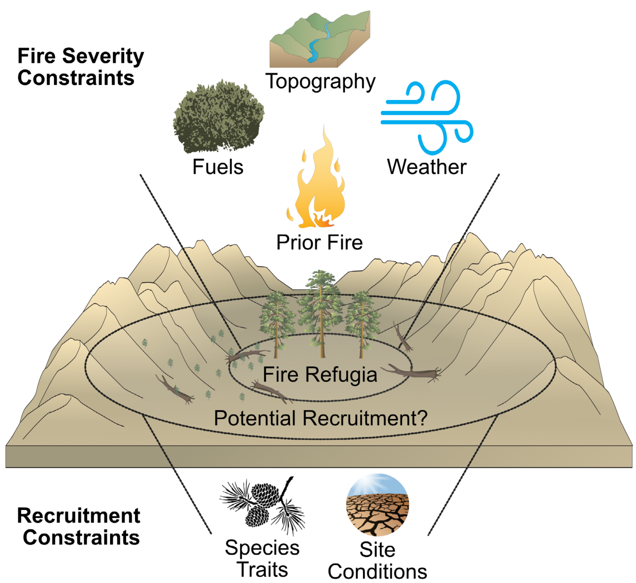

FIGURE 1 A summary of factors influencing forest resilience to wildfire. Fire severity is influenced by fuels, topography, and weather conditions during burning, as well as the effects of prior fires. For obligate seeders, post-fire tree recruitment is then constrained by seed availability and environmental conditions.

Veblen, Chapman, et al., 2020). However, a warming climate is already altering site suitability for post-fire conifer recruitment (Davis et al., 2023; Korb et al., 2019; Stevens-Rumann et al., 2018). Even in close proximity to seed sources, tree regeneration is often limited at dry sites or when fires are followed by drought events (Guz et al., 2021; Harvey et al., 2016; Rodman, Veblen, Battaglia, et al., 2020). More broadly, many western US forests are in a state of disequilibrium with current and near-term-future climate due to the rapid pace of environmental change over the past century (Gray & Hamann, 2013; Parks, Dobrowski, et al., 2019). Furthermore, within any given tree species, seedlings are more climatically sensitive than large trees (Bell et al., 2014; Dobrowski et al., 2015). Thus, it is unlikely that all refugia will facilitate post-fire forest recruitment because locations with surviving trees may not consistently align with conditions necessary for post-fire tree regeneration of the existing tree species.

Identifying refugia that are likely to facilitate tree recruitment in the surrounding landscape is particularly valuable in forests of the southwestern US, which are highly vulnerable to the effects of a changing climate (Thorne et al., 2018; Triepke et al., 2019). Forests in this region have recently experienced increases in both fire severity and annual area burned (Higuera et al., 2021; Parks & Abatzoglou, 2020; Singleton et al., 2019), as well as some of the driest conditions since at least 800 CE (Williams et al., 2022). Indeed, shifting wildfire regimes and climate warming have already driven forest transformations across southwestern US ecosystems (Guiterman et al., 2022; Stevens et al., 2021), with further increases expected in the future (Davis et al., 2020; Parks, Dobrowski, et al., 2019; Rodman, Veblen, Battaglia, et al., 2020). Management strategies such as mechanical thinning (i.e., using mechanized equipment to remove tree biomass), prescribed fire, resource objective fire (i.e., allowing lightning-ignited fires to burn without aggressive suppression), and post-fire reforestation are increasingly used to offset the effects of a changing climate and altered fire activity on southwestern US forests (Huffman et al., 2020; North et al., 2015; Stevens et al., 2021). The explicit incorporation of fire refugia into the planning of such strategies is new, yet promising (Krawchuk et al., 2020; Martinez et al., 2019; Stevens et al., 2021). For example, locations of potential refugia might be used to conserve habitat and maintain connectivity for fire-sensitive species (Andrus et al., 2021; Landesmann & Morales, 2018; Robinson et al., 2014) or considered as essential elements that influence the outcomes of larger fuel treatments (Pradhan et al., 2023; Wilkin et al., 2016). After over a century of fire exclusion, fire is now regarded as a key tool to promote resilient social-ecological systems (North et al., 2021; Schoennagel et al., 2017). Predictions of refugia could also play a crucial role in fire management decisions by identifying sites, seasons, and weather conditions in which fire might be most effectively utilized.

Here, we use remotely sensed severity data from 1180 fires, in combination with gridded biophysical predictors, to better understand the factors that influence patterns of fire severity in the southwestern US. We then use these models to map the locations of potential refugia throughout all upland conifer forests in the region. Finally, we overlay potential refugia with species-specific maps of post-fire conifer recruitment developed in a recent, west-wide synthesis (Davis et al., 2023) to identify refugia that are best aligned with environmental conditions that support post-fire recruitment. Specifically, we asked: *(Q1) What fuel characteristics, topographic factors, weather conditions, and prior fire effects best predict fire severity within large (>404 ha), recent fires (i.e., 2002–2020) in the southwestern US? (Q2) Based on empirical models of fire severity from Q1 and current (i.e., 2021) landscape conditions, where are likely locations of unburned or low-severity fire areas (i.e., refugia) in southwestern US forests? (Q3) Where are environmental conditions most suitable for post-fire tree recruitment of existing forest communities? (Q4) Where are potential fire refugia most likely to support post-fire tree recruitment?* Answering these questions will help to predict fire-driven forest transformations in a climatically vulnerable region and an era of accelerating fire activity.

2 | METHODS

2.1 | Study area, climate, and vegetation

Our study area included upland conifer forest ecosystems of the southwestern US, within EPA Level III Ecoregions 19, 21, 23, and 79 (Figure 2). Climate in the study area is generally semi-arid and continental, with maximum July temperatures from 15.9 to 34.5°C (mean = 24.6°C), January minimum temperatures from −21.3 to 3.6°C (mean = −10.4°C), and total precipitation from 231 to 1918 mm year^{-1} (mean = 637 mm year^{-1}) (PRISM Climate Group, Oregon State University, 2022). Average temperatures decline and precipitation levels increase with both elevation and latitude. The North American monsoon (i.e., rainfall from July to September) provides 7.6%–59.3% (mean = 31.5%) of annual precipitation, with higher percentages in the southern and eastern portions of the study area.

Typical tree species in the study area include Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Mayr] Franco), Engelmann spruce (*Picea engelmannii* var. *engelmannii* Parry ex Engelm. and var. *mexicana* [Martínez] Silba; also called Mexican spruce), lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson), ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.), subalpine fir (*Abies lasiocarpa* var. *lasiocarpa* [Hook.] Nutt. and var. *arizonica* [Merriam] Lemmon; also called corkbark fir), and white fir (*Abies concolor* var. *concolor* [Gordon & Glend.] Lindl. ex Hildebr). Though other trees are also present, these species comprise 72.9% of the total tree basal area throughout our study area (Wilson et al., 2013) and are those for which post-fire recruitment data were most widely available (Davis et al., 2023). Thus, we focused on forests including at least one of these species for our analyses (Little, 1971; Rollins, 2009; Wilson et al., 2013). The relative dominance of these species varies across abiotic gradients (Figures S3.2–S3.7), with pine-oak (i.e., *Quercus* spp.) forests and pure stands of ponderosa pine occupying the driest sites, often intergrading with Douglas-fir and white fir in wetter areas. Lodgepole pine is commonly found at intermediate

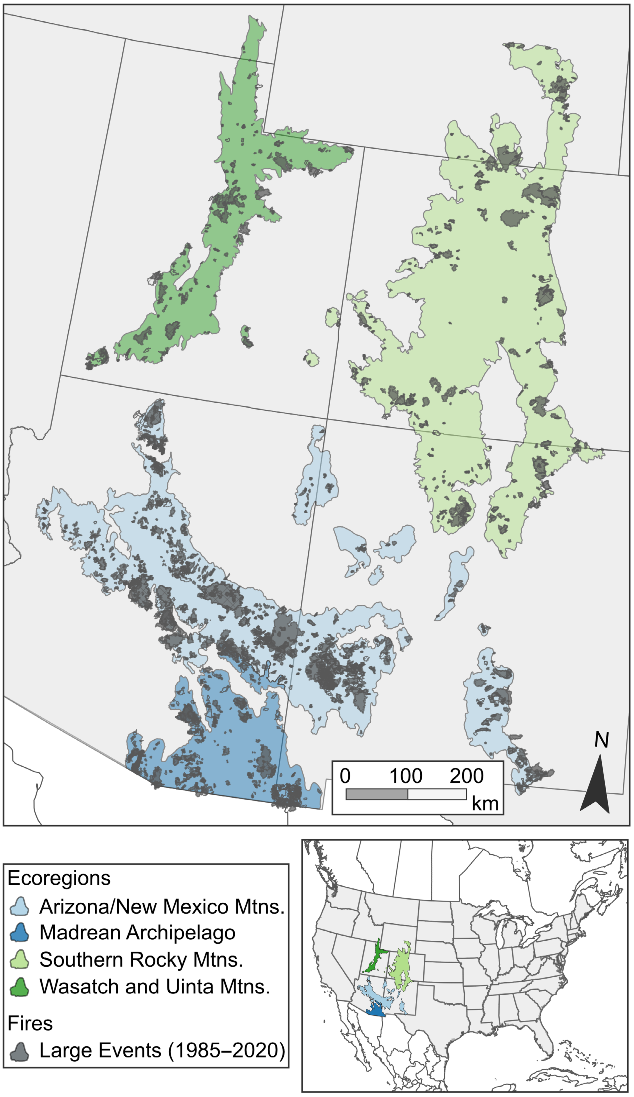

FIGURE 2 Study area, included EPA Level III ecoregions (EPA, 2021), and the locations of large (>404 ha) fire events that occurred from 1985 to 2020 (Eidenshink et al., 2007) throughout the southwestern US.

to high elevations at the northern end of the study area, typically forming even-aged cohorts that established following severe fires or extensive logging activity in the past 200 years (Sibold et al., 2006). Engelmann spruce and subalpine fir often co-dominate at higher elevations (O'Connor et al., 2017; Peet, 1981; Veblen, 1986).

These tree species have a range of strategies to persist in the fire-prone southwestern US (Appendix S1). Due to thick bark, relatively deep roots, and an open branch structure, lower-elevation species (e.g., ponderosa pine and Douglas-fir) are typically more resistant to fire than are high-elevation species (e.g., Engelmann spruce and subalpine fir) that occupy wetter sites with infrequent fire occurrence (Baker, 2009; Stevens et al., 2020). Lodgepole pine has low to moderate fire resistance but can quickly recolonize areas following severe fire due to partial serotiny, where closed cones found on some individuals open following fire and can trigger prolific tree regeneration (Tinker et al., 1994; Turner et al., 2007). On average, lodgepole pine (<10 years), Engelmann spruce (25 years), and subalpine fir (30 years) can become reproductively mature early in life under open, post-fire conditions (Andrus et al., 2020; Turner et al., 2007), whereas Douglas-fir (40 years) and ponderosa pine (50 years) may take longer to bear cones (Rodman, Veblen, et al., 2021). Though wind, water, and animals all play important roles in post-fire seed dispersal, most seedling establishment for these species occurs close to reproductively mature trees (Table 1).

2.2 | Overview of analyses

To answer our research questions, we performed analyses in the following steps (detailed descriptions of each step are provided in subsections below). First, we developed statistical models to describe relationships between remotely sensed patterns of fire severity and biophysical predictors within past fire events (*Q1*). We then used these models with regionwide data to map potential fire severity throughout upland conifer forests in the study area and identify sites that were most likely to be unburned or burn at low severity (i.e., refugia) under different weather conditions (*Q2*). Next, we developed maps of environmental suitability for post-fire recruitment throughout the study area using empirical models for each of the six most common conifer species (*Q3*). Finally, we overlaid maps of potential refugia from *Q2* and potential recruitment from *Q3* to identify refugia that were most likely to facilitate recruitment of existing tree species into adjacent areas (*Q4*). Information from past fires (*Q1*) was restricted to upland conifer forests—as defined by LANDFIRE Environmental Site Potential data (Rollins, 2009), species range maps (Little, 1971), and >1 $m^2 ha^{-1}$ combined basal area of our focal tree species early in the study period (Wilson et al., 2013)—that burned from 2002 to 2020, with ≥10% tree canopy cover in the year before the fire (Jones et al., 2018). Regionwide predictive maps (*Q2*–*Q4*) were similarly restricted to upland conifer forests, but also constrained to areas with ≥10% canopy cover in 2021, for a total mapped area of 99,428 km^2.

2.3 | Q1, fire severity data

We obtained perimeters for all large (>404 ha) fire events that occurred from 1985 to 2020 from the Monitoring Trends in Burn Severity (MTBS) program (Eidenshink et al., 2007). While our analyses focused on fires that occurred from 2002 to 2020 ($n = 1180$), earlier fires (i.e., 1985–2001; $n = 634$) were included to describe prior fire effects following Downing et al. (2021). The majority of the 1180 recent fires in our study area were wildfires (75.1% of all events; 91.1% of the total burned area), with the remaining events classified as prescribed fire (17.7% of events; 5.5% of area), resource objective fire (2.5% of events; 1.9% of area), or unknown (4.7% of events; 1.6% of area). To describe fire activity under a range of weather conditions and suppression strategies, thereby ensuring a representative sample for use in predictive models, we retained all incident types in our analyses. To quantify fire severity at a 30-m resolution in each

TABLE 1 Descriptions of the six focal tree species in this study, including elevational zone in which they are most commonly found, fire resistance (i.e., the ability of trees to tolerate and survive fire), serotiny (i.e., fire-adapted canopy seedbanks), and post-fire dispersal distances.

Species	Elevational range	Fire resistance	Serotiny	Typical dispersal distance
Douglas-fir (15.1%)	Low to Intermediate	0.49	No	<120 m from live trees (Kemp et al., 2016; McCaughey et al., 1986; Rodman, Veblen, Chapman, et al., 2020)
Engelmann spruce (20.0%)	High	0.26	No	<150 m from live trees (Gill et al., 2020; McCaughey et al., 1986)
Ponderosa pine (38.5%)	Low to Intermediate	0.77	No	<90 m from live trees (Chambers et al., 2016; Kemp et al., 2016; McCaughey et al., 1986)
Lodgepole pine (16.1%)	Intermediate to High	0.39	Partial (Tinker et al., 1994)	<60 m of live (non-serotinous) or recently burned (serotinous) trees (Gill et al., 2020; Kemp et al., 2016; McCaughey et al., 1986)
Subalpine fir (7.1%)	High	0.31	No	<150 m from live trees (Gill et al., 2020; McCaughey et al., 1986)
White fir (3.2%)	Low to Intermediate	0.43	No	<150 m from live trees (McCaughey et al., 1986)

Note: Fire resistance scores range from 0 (lowest fire resistance) to 1 (highest fire resistance) based on flammability and fire-adaptive traits (Stevens et al., 2020). Percentages of the study area dominated by each species (Wilson et al., 2013) are provided in parentheses after species names.

event, we developed raster maps of the bias-corrected composite burn index (CBI) following Parks, Holsinger, et al. (2019). This procedure maps CBI within each fire using statistical models developed from field-derived CBI data collected in 263 fires across a range of forest types in North America; predictors in this model include Landsat-derived spectral indices, latitude, and 1981–2010 annual average climatic water deficit. The CBI, a continuous index ranging 0 (unburned) to 3 (highest severity) (Key & Benson, 2006), was treated as a response variable in subsequent statistical analyses.

2.4 | Q1 and Q2, predictors of fire severity

To characterize the influence of fuels on fire severity, we used vegetation conditions in the year prior to a fire from the Rangeland Analysis Platform (RAP) (Jones et al., 2018) (Table 2). We summarized RAP data within each 30-m pixel, as well as a 910-m radius surrounding each pixel, an extent that approximates the median daily spread rate in recent large fire events throughout the western US (Coop et al., 2022). Within each fire perimeter, we used RAP to describe pre-fire canopy cover, the mean and coefficient of variation of canopy cover in the surrounding area (i.e., 910-m radius), the distance (m) to the closest pixel with less than 10% canopy cover (i.e., nonforest), and pre-fire shrub cover. We described forest composition using the Fire Resistance Score (FRS), a community-weighted index that uses measured species traits from western US conifers (e.g., flammability, bark thickness) to estimate fire resistance of a community (Stevens et al., 2020).

To describe differing aspects of topography that might influence fire severity (Table 2), we used ca. 10-m digital elevation models (USGS, 2021) to calculate slope angle, roughness (i.e., the standard deviation of elevation), topographic position (Weiss, 2001), and mean curvature (Safanelli et al., 2020). We also obtained the continuous heat load index from Theobald et al. (2015). For roughness and topographic position, we used a 910-m radius circular window to describe neighborhood effects. For curvature, we used a 90-m window to describe local terrain shape.

To quantify the effects of fire weather on severity, we developed two metrics to describe daily weather conditions and fire seasonality. We first calculated the Severe Fire Danger Index (SFDI), a derived metric that combines different elements of fire weather and flammability (i.e., daily temperature, humidity, wind speed, and fuel moisture) into a single daily value (Jolly et al., 2019) (Table 2). We obtained values of Energy Release Component and Burning Index, components of SFDI, from the GridMET database (Abatzoglou, 2013). Daily SFDI was developed as a continuous index ranging from 2 (least extreme fire weather) to 200 (most extreme fire weather), with values relative to the long-term climatology (all days 1979–2020) within each 4-km pixel. Following Parks et al. (2014), we developed 30-m date of burning (DOB) maps for each fire by interpolating moderate resolution imaging spectroradiometer (MODIS) and visible infrared imaging radiometer suite (VIIRS) active fire detections. We assigned fire detections occurring between midnight and 6 am to the previous day following Coop et al. (2022). We used DOB maps to extract daily SFDI values for each burned 30-m pixel and to quantify the potential effects of seasonality on fire severity. FRS (250 m), topography (10 m), and SFDI (4 km) data were resampled and aligned to 30-m fire severity grids using "average" resampling, which limits changes in data values (GDAL—Geospatial Data Abstraction Library, 2020). For areas with two overlapping fire events in the same 30-m pixel, we extracted severity in the initial event as well as time between fires to describe prior fire effects (Table 2).

2.5 | Q1 and Q2, predicting and mapping fire severity

We developed two Random Forest (RF) (Breiman, 2001) models to predict fire severity in 30-m pixels that were within (1) *a single large*

TABLE 2 List of spatial datasets tested to predict fire severity during large recent fire events in the southwestern US, original data resolution, methods of calculation, and their rationale for inclusion.

Category	Variable	Spatial/temporal resolution	Methods	Rationale
Fuels	Local Canopy Cover	30 m/Annual	Percent forest cover in a 30-m pixel in the year before fire occurrence (Jones et al., 2018)	Local forest structure influences fuel availability and crowning potential (Stephens et al., 2009)
	Landscape Canopy Cover	30 m/Annual	Mean forest cover within a 910-m radius surrounding a pixel in the year before the fire (Jones et al., 2018)	As a contagious process, fire severity and spread are influenced by forest structure in the surrounding landscape (Finney, 2001)
	Landscape Canopy Variation	30 m/Annual	Standard deviation of forest cover within a 910-m radius surrounding a pixel in the year before the fire (Jones et al., 2018)	Heterogeneous forest conditions on local to landscape scales may influence fire severity by breaking up canopy fuel continuity (Koontz et al., 2020; Reynolds et al., 2013)
	Distance to Treeless Area	30 m/Annual	Distance from a given pixel to the closest pixel with less than 10% canopy cover (Jones et al., 2018)	Proximity to meadows or open areas may reduce the potential for tree mortality during fire (Chapman et al., 2020)
	Shrub Cover	30 m/Annual	Percent shrub cover in a 30-m pixel in the year before the fire (Jones et al., 2018)	Flammable shrubs can influence fuel complexes and the potential for tree survival during fire (Coppoletta et al., 2016; Paritsis et al., 2015)
	Fire Resistance Score (FRS)	250 m/Time-Invariant	Relative fire resistance of a forest community based on measured species traits (e.g., bark thickness, flammability) (Stevens et al., 2020)	Tree species range widely in fire resistance and have differential susceptibility under similar burning conditions (Baker, 2009; Stevens et al., 2020)
Topography	Slope	10 m/Time-Invariant	Slope angle of a pixel, in degrees based on digital elevation model (USGS, 2021)	Slope angle influences fire spread rates through convective pre-heating, with lower severity expected on flat slopes (Rothermel, 1972)
	Terrain Roughness	10 m/Time-Invariant	The standard deviation of elevation (USGS, 2021) in a 910-m radius surrounding each pixel	Areas with high roughness are more often characterized by infrequent or mixed-severity fire regimes (Stambaugh & Guyette, 2008)
	Topographic Position	10 m/Time-Invariant	The elevation of a pixel minus the mean elevation in a 910-m radius surrounding area (Weiss, 2001)	Ridgetops are often prone to high-severity fire, whereas valley bottoms are commonly fire skips (Estes et al., 2017; Meigs et al., 2020)
	Heat Load	10 m/Time-Invariant	An index of terrain-driven solar heating, which combines slope, aspect, and latitude (Theobald et al., 2015)	Aspect can influence vegetation types and fuel moisture, helping to form local refugia (Camp et al., 1997)
	Terrain Curvature	10 m/Time-Invariant	Mean concavity/convexity of a local neighborhood along axes parallel and perpendicular to the slope (Safanelli et al., 2020)	Local slope curvature influences soil moisture and exposure, which have the potential to influence fire severity (Bigler et al., 2005; Viedma et al., 2015)
Weather	Date of Burning (DOB)	30 m/Daily	Calculated using interpolation of thermal anomalies from Moderate Resolution Imaging Spectroradiometer (MODIS) and Visible Infrared Imaging Radiometer Suite (VIIRS) active fire detections following (Parks, 2014)	The season of fire occurrence is related to both weather and the phenology of plant communities, which may influence fire severity (Miller et al., 2019; Ritter et al., 2023)
	Severe Fire Danger Index (SFDI)	30 m/Daily	Describes weather conditions and fuel moisture during the burn date in a pixel, relative to the long-term (i.e., 1979–2020) climatology at a site (Jolly et al., 2019)	Fire weather is a key driver of fire behavior, with extreme weather sometimes overriding the influence of local fuels and terrain (Collins et al., 2019; Krawchuk et al., 2016)
Prior Fire	Time Since Fire	30 m/Annual	The number of years since the last recorded fire in a pixel (Eidenshink et al., 2007)	The time since last fire can either enhance or buffer communities against fire through positive or negative fire feedbacks (Buma et al., 2020; Kitzberger et al., 2016)
	Prior Composite Burn Index	30 m/Annual	The severity of the last recorded fire in a pixel following Parks, Holsinger, et al. (2019)	Prior fire severity can enhance or buffer subsequent fire severity depending on fuel profiles and flammability (Coppoletta et al., 2016; Tepley et al., 2018)

fire event (hereafter 'one-fire' model), or (2) *in two large fire events* (hereafter 'reburn' model). In the one-fire model, we considered pixels that were located within the boundary of one fire perimeter from 2002 to 2020, with no other recorded fires, and used potential predictors related to fuels, topography, and weather. In the reburn model, we considered pixels within exactly two fires—at least one fire from 2002 to 2020 and one preceding fire as early as 1985—and used predictors related to fuels, topography, weather, and prior fire effects. Too few areas were within the intersections of three or more fires in our study area and timeframe (188,815 ha; 3.7% of total fire area) to develop a generalizable model for areas with multiple reburns.

To obtain training data for each RF model, we used a stratified sampling approach to extract fire severity and biophysical predictors at point locations throughout the study area. Our strata were based on fire ID, ecoregion, fire severity (unburned or low [CBI < 1.25], moderate [1.25 ≤ CBI < 2.25], or high [CBI ≥ 2.25]; Miller & Thode, 2007), and community fire resistance (low [FRS < 33rd percentile], moderate [FRS ≥33rd and <66th percentile] and high [FRS ≥66th percentile]). While we attempted to maintain a balanced sample across strata, some strata were so uncommon (e.g., low FRS in fires that primarily burned in ponderosa pine) that the overall sample is unbalanced, though it is broadly representative of burned areas throughout the study area. To limit the effects of fires for which we had no data on prior severity, we excluded areas that burned in 1984 (preceding the time period of our CBI maps), in fire events that were too small to be included in the MTBS dataset (e.g., within NIFC fire perimeters <404 ha; NIFC, 2022) or with more than two fire occurrences since 1985. We also restricted sampling to upland conifer forests with at least 10% canopy cover in the year before the fire. We extracted separate samples to inform each RF model, with 36,227 points (0.1% sample) from 547 fire events in one-fire areas, and 20,769 points (0.3% sample) from 481 unique combinations of fires in reburn areas. Though we did not use a minimum spacing between sampled points, we used spatial cross-validation to limit the effects of spatial autocorrelation on variable selection and accuracy assessment (see below).

Using sampled data, we fit RF models of fire severity using the 'ranger' (Wright & Ziegler, 2017) and 'spatialRF' (Benito, 2021) packages in R (R Core Team, 2021). These data showed no evidence of multicollinearity of predictors based on a variance inflation factor cutoff of 5. From an initial set of predictors (Table 2), we selected final predictors for each RF model using a two-stage variable selection approach. First, we used recursive feature elimination to remove variables with low relative importance and little influence on overall predictive accuracy (Kuhn et al., 2019). Next, we used 30-fold spatially stratified cross-validation (Benito, 2021) to remove any variables that reduced model accuracy when predicting to new fires and areas, thereby ensuring generalizable models for regionwide predictions (Meyer et al., 2019). After identifying final predictor variables, we tuned models using spatially stratified cross-validation to optimize the number of predictors to select at each tree split (i.e., 'mtry'), and the number of samples included in each terminal node (i.e., 'min.node.size'). To summarize the effects of final variables in each model, we calculated relative variable importance (i.e., the permutation-based mean decrease in accuracy statistic, scaled to sum to 100) (Wright & Ziegler, 2017) and developed accumulated local effects plots, which illustrate the effect of each variable on predicted values of the response (Molnar et al., 2018). We summarized model accuracy using Pearson's correlation coefficient (*r*) and the root-mean-square error between observed and predicted values of fire severity in (1) the out-of-bag dataset created during model fitting and (2) in 30-fold spatially stratified cross validation. Because RF regression predictions can be biased towards the mean of the response variable (Belitz & Stackelberg, 2021), we applied a bias correction to RF-predicted values following Rodman, Andrus, et al. (2021) (Appendix S2).

To map potential fire refugia throughout upland conifer forests in the study area, we used final RF models to develop 30-m predictions of fire severity based on topography, 2021 fuels, and moderate and severe fire weather scenarios. We defined moderate fire weather as having an SFDI value of 150 (i.e., the 75th percentile of daily weather in a pixel) and a burn date of May 1st. We defined severe fire weather as an SFDI value of 198 (i.e., 99th percentile of daily weather in a pixel) and a burn date of July 1st, spanning the range of conditions under which large fires typically burn in our study area. For areas without any recorded fires from 1985 to 2020 in the MTBS dataset, we predicted fire severity using the one-fire model, and for areas with at least one prior fire event (i.e., 15.7% of the final study area), we used the reburn model.

2.6 | Q3, quantifying environmental suitability for recruitment

To describe environmental suitability for the recruitment of existing forest communities, we developed a community weighted recruitment index (RI) (Appendix S3; Figure S3.1). First, we used statistical models from Davis et al. (2023) to make 30-m regionwide predictions of post-fire recruitment probability for each of the six focal conifer species based on recent (i.e., 2001–2020) climate, and existing topography. To account for the effects of variables unrelated to environmental suitability in our predictions (Table S3.1), we assumed that high-severity fire occurred in a given 30-m pixel, but that seed was available following Rodman, Veblen, Battaglia, et al. (2020). Next, we used the distance-squared-weighted density metric of Coop et al. (2019) to summarize recruitment predictions in the area around each potential refugia pixel, with window sizes for each species based on typical dispersal distances (Appendix S3; Table 1). Finally, we calculated RI as the weighted sum of individual species recruitment maps, with weights based on species' relative abundances (Wilson et al., 2013). RI, ranging from 0 (poor conditions) to 100 (excellent conditions), is a continuous metric that estimates how well a locally resistant fire refugium might facilitate tree recruitment in the surrounding landscape.

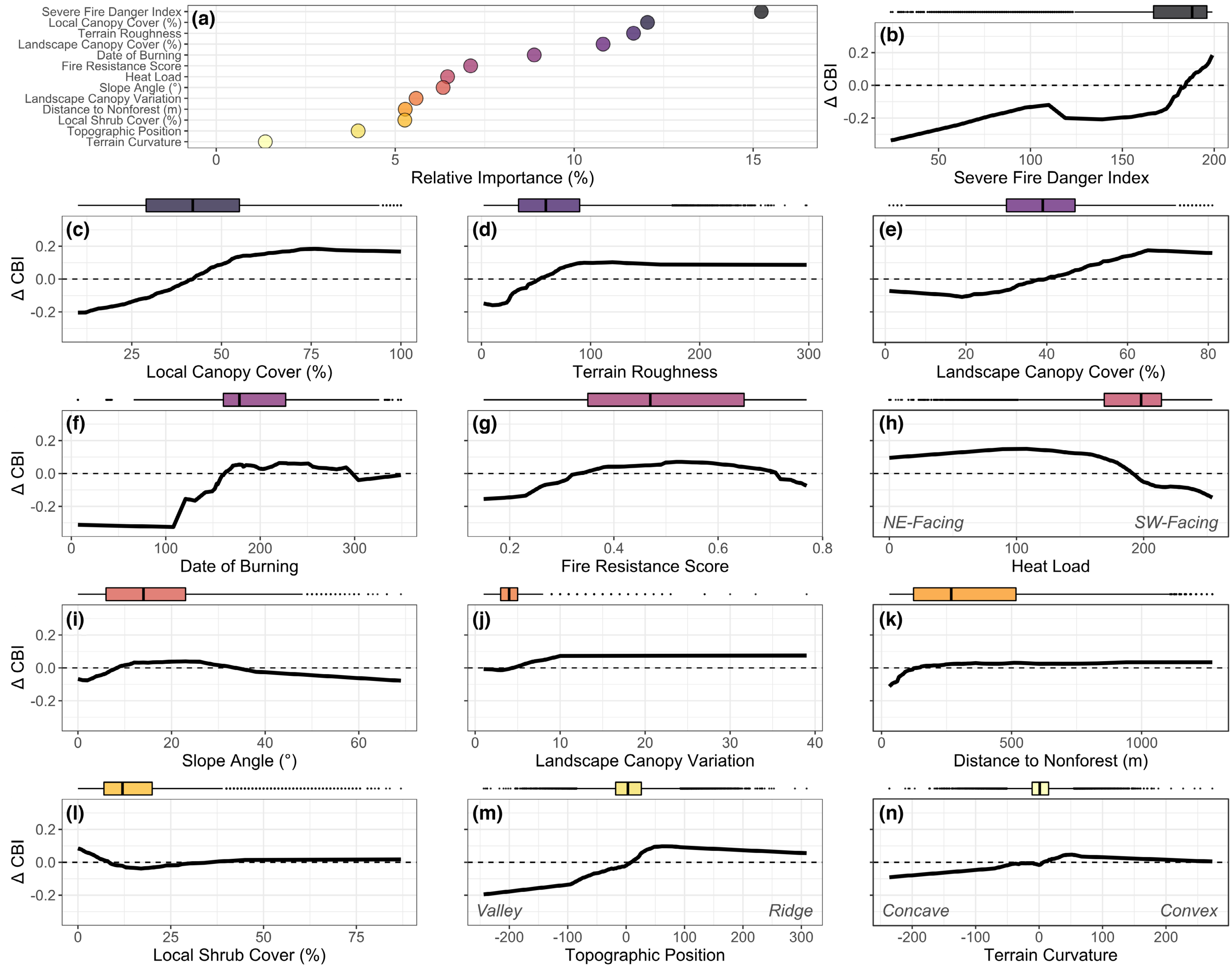

FIGURE 3 Results of the random forest model predicting fire severity (CBI; Composite Burn Index) in locations that burned once in the study period. Panel (a) shows the relative importance of predictors included in the final model using the permutation-based mean decrease in accuracy statistic. Panels (b–n), sorted by relative importance of each predictor, are accumulated local effect plots showing predicted changes in fire severity (*y*-axis) across the range of each predictor (*x*-axis), after accounting for the effects of other predictors in the model. Where solid black lines are above the dashed line in (b–n), values of a given predictor are associated with a higher fire severity, while values below the dashed line indicate a relationship with lower fire severity. Boxplots above panels (b–n) show the range of sampled values for each predictor.

2.7 | Q4, identifying refugia that support conifer tree recruitment

To identify refugia with a high potential to facilitate post-fire recruitment, we overlaid maps of predicted fire severity (under moderate and severe fire weather, separately) and RI as follows. First, we classified potential fire refugia as 30-m pixels with predicted fire severity of unburned or low in regionwide maps (i.e., CBI values <1.25; Miller & Thode, 2007). Next, because RI is a new metric with no empirical threshold of what constitutes high or low values, we used k-means cluster analysis of all 30-m pixels in the study area to split RI values into two relatively distinct groups (low [<46] and high [≥46]). We then classified pixels as "refugia with high recruitment" (i.e., CBI < 1.25 and RI ≥ 46), "refugia with low recruitment" (i.e., CBI < 1.25 and RI < 46), or "non-refugia" (i.e., CBI ≥ 1.25) under each fire weather scenario.

2.8 | Q2–Q4, quantifying uncertainty in predictions of fire severity, recruitment, and refugia

Major uncertainty exists in predicting forest ecosystem dynamics across regional extents. To quantify and map this uncertainty, we developed pointwise prediction intervals (i.e., mean ± 1 standard error of prediction) using models of fire severity and species-specific post-fire recruitment probability. Using these prediction intervals, we then propagated uncertainty throughout the same processing steps involved in developing maps of potential refugia under "upper" (i.e., lower than expected fire severity and higher than expected recruitment) and "lower" scenarios (i.e., higher than expected fire severity and lower than expected recruitment). We present abbreviated results of these uncertainty analyses in the main text, and additional analyses and figures in Appendix S4.

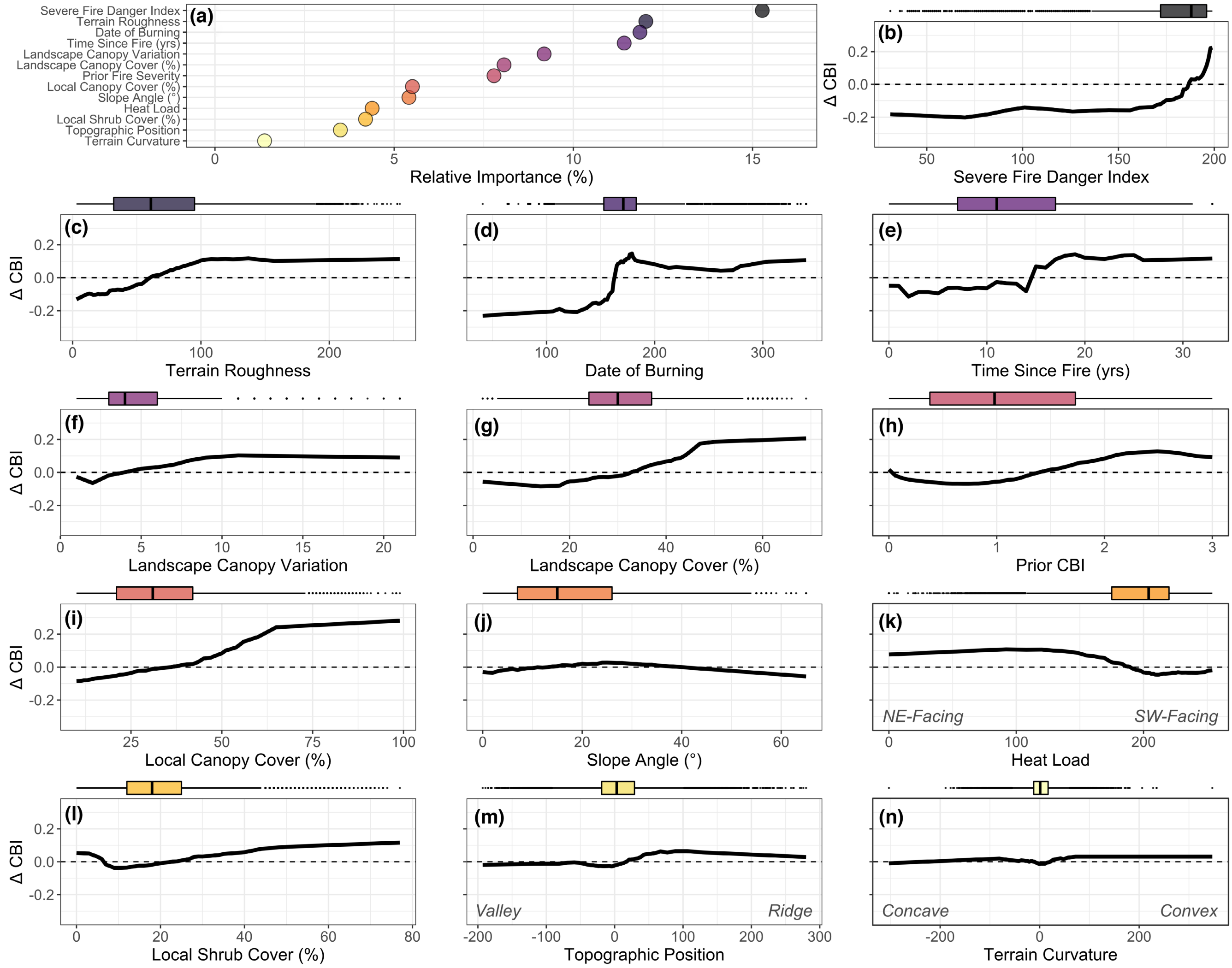

FIGURE 4 Results of the Random Forest model predicting fire severity (CBI; Composite Burn Index) in locations that burned twice in the study period. Panel (a) shows the relative importance (*x*-axis) of predictors (*y*-axis) included in the final model using the permutation-based mean decrease in accuracy statistic. Panels (b–n), sorted by relative importance of each predictor, are accumulated local effect plots showing predicted changes in fire severity (*y*-axis) across the range of each predictor (*x*-axis), after accounting for the effects of other predictors in the model. Where solid black lines are above the dashed line in (b–n), values of a given predictor are associated with a higher fire severity, while values below the dashed line indicate a relationship with lower fire severity. Boxplots above panels (b–n) show the range of sampled values for each predictor.

3 | RESULTS

3.1 | (Q1) What fuel characteristics, topographic factors, weather conditions, and prior fire effects best predict fire severity within large (>404 ha), recent fires (i.e., 2002–2020) in the southwestern US?

Pre-fire fuels were the most important group of predictors in the fire severity models, comprising 38% (one-fire) and 27% (reburn) of total variable importance. Fire severity was positively associated with both local- and landscape-scale canopy cover, with notable increases in severity above 30%–40% cover (Figures 3c,e and 4g,i). Similarly, distance to nonforest had a positive relationship with fire severity, where forests within 100 m of nonforest areas had lower fire severity in the one-fire model (Figure 3k), though this term was excluded from the reburn model. Canopy cover variation had a positive relationship with fire severity in each model (Figures 3j and 4f). Pre-fire shrub cover had contrasting effects on fire severity in the one-fire and reburn models. In the one-fire model, low shrub cover was associated with higher fire severity, though the relationship was relatively weak (Figure 3l); in the reburn model, fire severity increased when shrub cover exceeded 10% (Figure 4l). The FRS, an indicator of forest community resistance to fire, was non-linearly related to fire severity. In the one-fire model, severity was typically greatest with FRS values of 0.4 to 0.6 (Figure 3g). Low FRS values may be indicative of cold, wet areas that are more likely to remain unburned within larger perimeters, whereas high values represent communities composed of thick-barked and fire-tolerant conifers.

Overall, topographic predictors accounted for 30% and 27% of the total variable importance in the one-fire and reburn models, respectively. Of these predictors, terrain roughness had the strongest relationship with severity in each model, with sites located in more variable topographic settings tending to burn at higher severity (Figures 3d and 4c). Positive values of topographic position (Figures 3m and 4m) and curvature (Figures 3n and 4n), representing ridgetops and outwardly convex slopes, respectively, were also associated with higher fire severities in each model. Likewise, slopes between 10 and 30 degrees tended to burn at higher severity than did flat areas or extremely steep slopes (Figures 3i and 4j). Finally, southwest-facing slopes (i.e., high heat load values) burned at lower severities than did northeast-facing slopes (Figures 3h and 4k).

Weather variables were also key drivers of severity in recent fires throughout our study area, accounting for 24% and 27% of total variable importance in the one-fire and reburn models, respectively (Figures 3 and 4). SFDI was the top individual predictor of fire severity in each model (Figures 3a and 4a), and severity increased substantially when SFDI exceeded the 90th percentile at a given site (i.e., >180) (Figures 3b and 4b). Likewise, DOB was among the best predictors of fire severity, ranking fifth (one-fire) and third (reburn) in terms of relative importance in each model (Figures 3a and 4a). Spring-season fires (i.e., prior to June 1st; DOB < 151) typically burned at lower severities than did summer or fall fires (Figures 3f and 4d).

Prior fire effects accounted for 19% of total variable importance in the reburn model (Figure 4a). Time since fire was the highest ranking predictor in this group, where fire severity was reduced for up to 15 years after an initial fire event (Figure 4e). Prior CBI had a complex non-linear effect on fire severity, where low- to moderate-severity events (CBI < 1.5) had the greatest buffering effect (Figure 4h). Though time since fire and prior CBI were related to severity in reburns, sampled areas within reburns had lower severities overall (mean CBI = 0.96) than did first-entry fires (mean CBI = 1.45), indicating a consistent buffering effect of past fire. Final one-fire and reburn models performed well in cross-validation, and were deemed adequate for regionwide predictions (Table 3).

3.2 | (Q2) Based on empirical models of fire severity from Q1 and current (i.e., 2021) conditions, where are predicted locations refugia?

Predicted fire severity differed widely between the two weather scenarios, with mean CBI values of 0.94 under moderate weather (Figure 5a), as compared to 1.83 under extreme weather (Figure 5b). Overall, predicted severities were highest in the northern portion of the study area, and lowest in the southern portion, likely due to more abundant past fire activity (Figure 2) and lower forest cover in the South (Figure 5; Table S4.1). Potential refugia (i.e., areas with predicted CBI < 1.25) comprised 67.6% of forests in the study area under moderate weather conditions, and 18.1% under extreme weather. Recent (i.e., 1985–2020) large fires played an important role in the predicted locations of refugia. Under moderate weather, 98.4% of areas within recent fires were predicted refugia, as compared to 61.9% of recently unburned areas. Likewise, under extreme weather, 44.4% of areas within recent fires were identified as potential refugia, as compared to just 13.2% of unburned areas. There was notable uncertainty in predictive maps of fire severity, likely due to the stochastic factors and fine-scale processes influencing fire behavior in our training data, as well as the high-variance nature of base learners (i.e., individual trees) within RF models (Figure S4.1; Table S4.1).

TABLE 3 Accuracy metrics from final Random Forest models used to predict fire severity in forests of the southwestern US that experienced one (i.e., one-fire) and two (i.e., reburn) large fires.

	Accuracy metric	
Model	**Pearson's *r***	**RMSE**
One-fire	0.58 (0.38)	0.78 (0.85)
Reburn	0.69 (0.46)	0.58 (0.75)

Note: Accuracy metrics were calculated on out-of-bag data during model fitting and in 30-fold spatially-stratified cross-validation, which are presented before parentheses and inside of parentheses, respectively.

Abbreviation: RMSE, root-mean-square error.

3.3 | (Q3) Where are environmental conditions most suitable for post-fire tree recruitment of current tree species?

Values of the RI, which describes the extent to which surviving trees might facilitate post-fire recruitment in the surrounding landscape, also varied across the study area (Figure 6). In general, recruitment probabilities were highest at intermediate to wet portions of each species' range, such as at higher elevations and latitudes (Figures S3.2–S3.7). Indeed, mean RI values were highest and had comparatively greater certainty in the northern ecoregions (Table S4.1). Mean RI across the study area was 37.9, with 39.7% of the total area classified as having high recruitment potential (RI ≥ 46). In comparison to maps of fire severity, there was greater certainty in predictions of recruitment probability and RI, but uncertainty was relatively high in the Arizona/New Mexico Mountains, where recruitment conditions are marginal for the dominant tree species (Figures S4.2–S4.8; Table S4.1).

3.4 | (Q4) Where are fire refugia most likely to support post-fire tree recruitment?

Refugia with high recruitment (i.e., CBI < 1.25 and RI ≥ 46)—sites that were predicted to resist fire and also support recruitment into

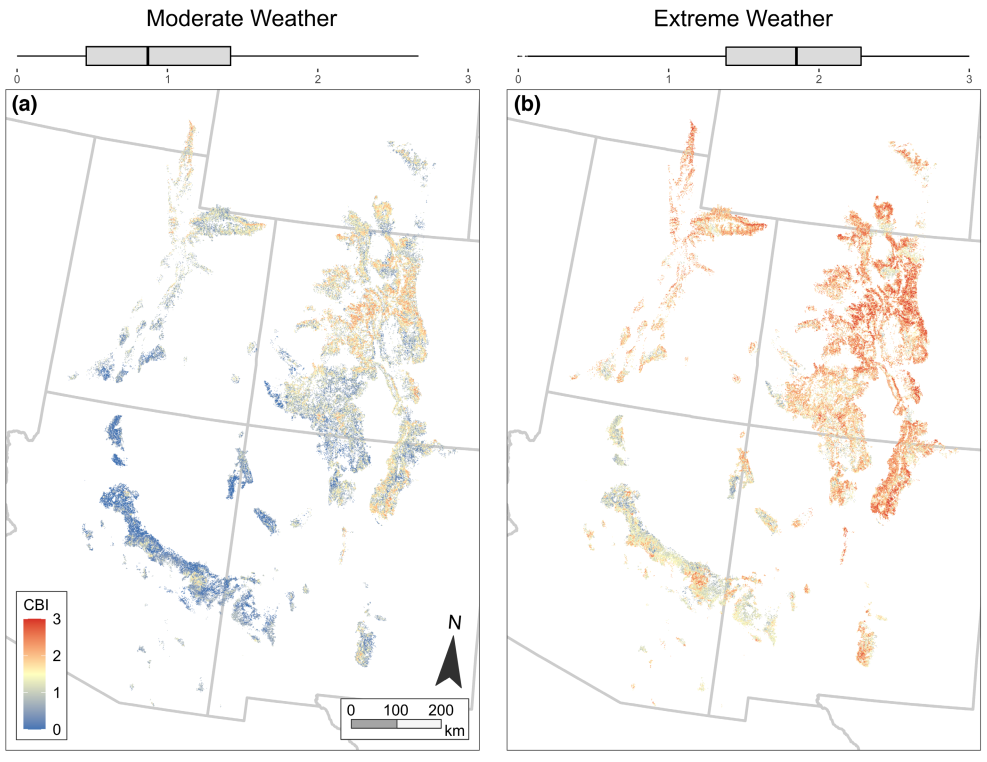

FIGURE 5 Predicted fire severity (CBI; Composite Burn Index) throughout upland conifer forests of the southwestern US based on 2021 fuels conditions, existing topography, and two fire weather scenarios. Moderate (a) fire weather conditions were based on 75th percentile daily weather (i.e., Severe Fire Danger Index [SFDI] value of 150) and a burn date of May 1. Extreme (b) fire weather conditions were based on 99th percentile of daily weather (i.e., SFDI of 198) and a burn date of July 1. Boxplots above each panel show the distribution of predicted fire severity values across the study area. CBI values <1.25 were predicted to be unburned or low-severity areas (i.e., refugia).

adjacent areas—were located in 23.2% of the study area under moderate weather conditions (Figure 7a) as opposed to just 6.4% under extreme weather (Figure 7b). Likewise, refugia with low recruitment (i.e., CBI < 1.25 and RI < 46) were more widespread under moderate weather (44.4% of the study area) than under extreme weather (11.7%) throughout the study area. Though southern ecoregions (i.e., Arizona/New Mexico Mountains and Madrean Archipelago) had lower average RIs when compared to northern ecoregions, they were also predicted to burn at lower severity (Figures 5 and 6; Table S4.1). In combination, these factors led to slightly higher percentages of predicted refugia in the southern ecoregions, particularly under extreme fire weather (Figure 7; Table 4). However, predictions of refugia had relatively high uncertainty across the study area, primarily due to uncertainty in predictions of fire severity (Figure S4.9; Table S4.1).

4 | DISCUSSION

Forests worldwide are becoming increasingly vulnerable to fire-driven transformations (Hartmann et al., 2022; Seidl & Turner, 2022). Indeed, shifting fire regimes, combined with limited post-fire tree recruitment, may reshape the coniferous forests that are emblematic of many western US landscapes (Coop et al., 2020). The present study contributes to the understanding of fire-driven transformations by helping to identify forested sites across the southwestern US that may be locally resistant to fire (i.e., refugia) and facilitate post-fire tree recruitment in the surrounding landscape. This is the first empirical study to predict both fire severity and post-fire recruitment across a broad range of forest types and ecoregions, helping to assess vulnerability to fire-driven forest transformations across a diversity of landscapes. Our results demonstrate that (1) fuels, topography, and weather were all useful predictors of fire severity throughout the study area, (2) initial fires can meaningfully reduce the severity of reburns, with the strongest effects when the initial fire occurred at low or moderate severity and reburns occurred within 15 years, (3) post-fire recruitment potential varied according to community composition and the environmental tolerances of individual tree species, but was generally greatest in the northern ecoregions, and (4) refugia with a high potential to support recruitment represented a relatively small percentage of the study area, but these areas are likely to play an important role in forest ecosystem dynamics over upcoming decades.

4.1 | Factors influencing fire severity

Fuels played a critical role in the severity of recent large fires in our study area, and such information may help to anticipate and mitigate

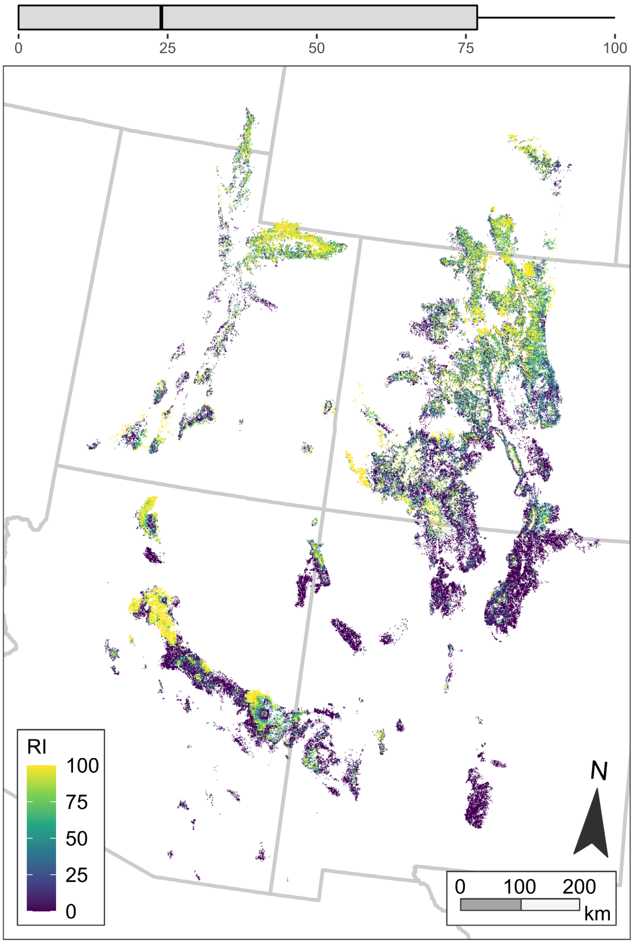

FIGURE 6 Predicted values of the recruitment index (RI) throughout upland conifer forests of the southwestern US, with higher values indicating a greater potential for post-fire recruitment. Boxplot at the top shows the distribution of predicted RI values across the study area.

the effects of climate-driven forest transformations. Forests below 40% canopy cover and those within 100m of non-forest areas (e.g., meadows) were most likely to be unburned or burn at low severity, suggesting that low-density forests interspersed with open areas are particularly resistant to fire. These findings align with prior research illustrating the importance of pre-fire vegetation (Parks et al., 2018; Taylor et al., 2021) and low-density savannas (Chapman et al., 2020) in shaping landscape-scale patterns of fire severity. Fuels are one side of the fire behavior triangle (i.e., fuels, topography, and weather) that can be most feasibly altered by humans, using activities such as mechanical thinning and/or prescribed fire. These management activities can be utilized for a range of purposes, including the protection of communities and infrastructure or the restoration of degraded systems (Schoennagel et al., 2017; Stephens et al., 2021). Dense stand conditions and high-severity fire are an inherent component of some southwestern US ecosystems, such as cold/mesic forests found at high elevations (Baker & Veblen, 1990; Romme & Knight, 1981), where fuels reduction can be valuable to protect important human infrastructure (e.g., reservoirs, houses), but is not necessarily congruent with restoration objectives (Schoennagel et al., 2004). In contrast, ponderosa pine-dominated forests comprise roughly 39% of our study area (Wilson et al., 2013) and are where strategic thinning and burning are more likely to accomplish both restoration and fuels reduction objectives (Stephens et al., 2021). Thus, while active management to reduce fuels may help to buffer some ecosystems from fire-driven forest transformations in the near term, such activities must also be considered in the context of both societal needs and the natural disturbance regime of the system (Allen et al., 2002).

Topography is an important determinant of both vegetation patterns and fire behavior, and topographic variation was linked to fire severity across our study area. Fire severity increased with terrain roughness and topographic position, peaking on moderately steep slopes, ridges, and areas with rugged topography, findings that are consistent with prior studies in the western US (Camp et al., 1997; Chapman et al., 2020; Krawchuk et al., 2016). Valley bottoms and topographic concavities afforded the greatest reductions in fire severity, where fire spread and severity may be diminished by reduced wind speeds, shallower slopes, higher levels of soil moisture, and cooler temperatures associated with thermal inversions and smoke (Bradstock et al., 2010; Downing et al., 2021; Romme & Knight, 1981). Indeed, the importance of such settings in moderating fire severity and promoting fire refugia has been demonstrated over a wide range of ecosystems and spatiotemporal scales (Collins et al., 2012; Haire et al., 2017; Leonard et al., 2014; Robinson et al., 2014). Heat load was also a useful predictor of fire severity, with southwest-facing aspects showing a greater potential for refugia. In our study area, southwesterly slopes tend to be warmer and drier, with more open canopies and grassy understories that can support frequent, lower-severity fire (Margolis et al., 2022). As highlighted by our uncertainty analyses (Appendix S4) and prior research (Kolden et al., 2017), the locations of surviving trees after any given fire may be heavily shaped by stochastic processes; however, refugia that persist through multiple fire events are increasingly likely to owe their existence to deterministic processes including protection afforded by topographic factors that impede crown fire transition and spread (Downing et al., 2021). Accordingly, associations between refugia and topography may become both stronger and more predictable as more fires eliminate susceptible forest patches from the landscape, and over longer time frames as fire-sensitive vegetation becomes restricted to the most protected locations (Krawchuk et al., 2020; Wood et al., 2011).

Daily fire weather and the DOB were two of the strongest individual predictors of fire severity in our study area, and we found that areas that burned under moderate weather conditions (SFDI < 90th percentile) and in the spring season (DOB < 151) were most often associated with refugia. These findings were unrelated to differences in fire incident types among seasons. For example, prescribed fires and resource objective fires, which typically burn at lower severities than wildfires (Huffman et al., 2017), represented 12.5% of all fire events in the summer and fall (DOB ≥ 151) as compared to just 5.5% of events in the spring (DOB < 151) (Eidenshink et al., 2007). Fire weather has been a strong predictor of severity and the presence of refugia across a diversity

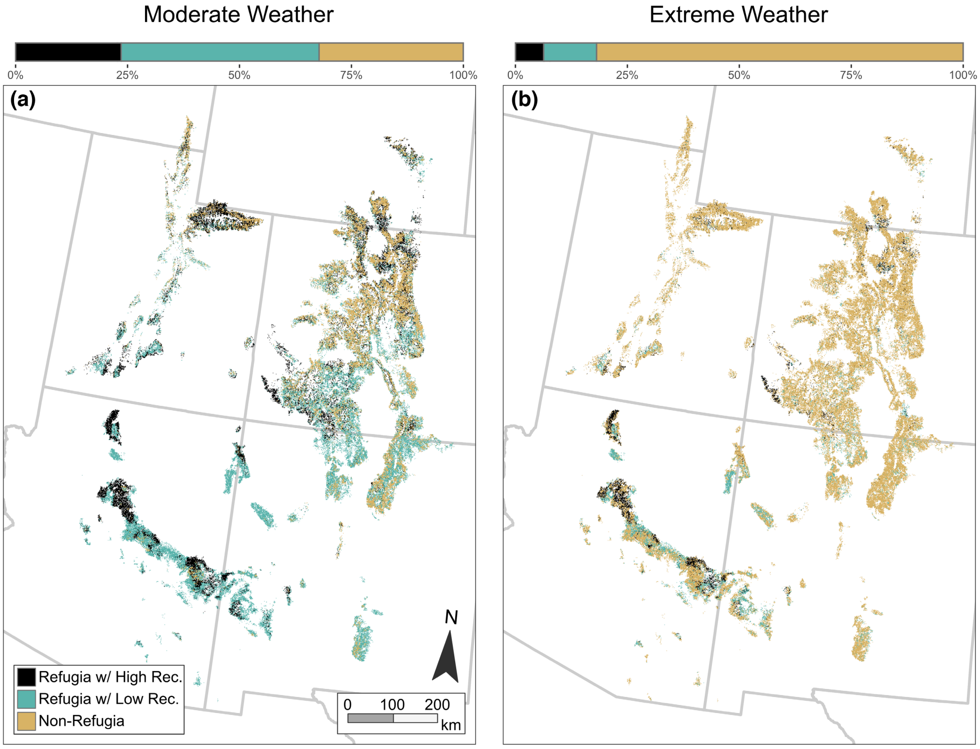

FIGURE 7 Predicted locations of fire refugia throughout upland conifer forests of the southwestern US based on moderate (a) and extreme (b) fire weather. "Refugia with high recruitment" are sites with low predicted fire severity and a high recruitment index (i.e., a high ability to support conifer forest recruitment into adjacent, severely burned areas), whereas refugia with low recruitment have low predicted fire severity and low recruitment indices. "Non-refugia" were predicted to burn at moderate or high fire severity. Stacked bar graphs above each panel give the percentage of the study area in each category.

TABLE 4 Percentages of 2021 upland conifer forests within each EPA Level III ecoregion (EPA, 2021) classified as refugia with high recruitment (i.e., predicted CBI [Composite Burn Index] < 1.25 and RI [Recruitment Index] ≥ 46), and refugia with low recruitment (i.e., CBI < 1.25 and RI < 46), under moderate and extreme fire weather scenarios.

	Moderate weather		Extreme weather	
Ecoregion	Refugia w/ high recruitment	Refugia w/ low recruitment	Refugia w/ high recruitment	Refugia w/ low recruitment
Arizona/New Mexico Mountains	28.8% (66.8)	64.7% (24.8)	14.1% (68.6)	26.3% (27.4)
Madrean Archipelago	6.0% (20.3)	88.4% (53.0)	2.8% (19.7)	23.8% (76.0)
Southern Rocky Mountains	18.2% (51.5)	38.5% (39.7)	3.6% (38.1)	6.9% (38.7)
Wasatch and Uinta Mountains	38.1% (61.5)	32.3% (27.4)	5.4% (52.7)	6.5% (29.8)
Overall	23.2% (56.3)	44.4% (22.4)	6.4% (47.3)	11.7% (35.0)

Note: Numbers in parentheses are estimates of uncertainty (i.e., the range of percentage estimates given prediction error in underlying CBI and RI maps) surrounding these percentages, as described in Appendix S4 and Figure S4.9, with higher values showing comparatively greater uncertainty.

of ecosystems, from the southern Rocky Mountains (Chapman et al., 2020) to the Pacific Northwest US (Krawchuk et al., 2016; Meigs et al., 2020; Taylor et al., 2021) and southeastern Australia (Collins et al., 2019). While there has been substantial research regarding fire weather, comparatively little is known about the broad-scale relationships between seasonality and fire severity. Still, one observational study of prescribed fire suggests that spring burns may be less severe than summer or fall burns in the Southwest (Ritter et al., 2023). Though weather and seasonality are often related, fire seasonality is likely to have a wide range of additional effects on plant communities due to intra-annual differences in physiological and demographic processes (Miller et al., 2019). Humans modify the fire season through accidental ignitions (Balch et al., 2017) and through management activities that can target periods of mild weather (e.g., prescribed fire or resource objective wildfire) (Huffman et al., 2020; Ryan et al., 2013; Young et al., 2020). For example, while summer is the natural wildfire season of many western US forests, prescribed and managed fires are more commonly used in the shoulder seasons (i.e., spring and fall) (Ryan et al., 2013; Young et al., 2020). Our results indicate that the expanded use of such strategies under moderate weather conditions and in the spring season is likely to promote low- and moderate-severity fire throughout the southwestern US.

4.2 | Fire as a management tool

Fires are a keystone process in western US conifer forests, which have developed fire-adaptive traits over millions of years of evolutionary history (Keeley & Pausas, 2022). After an extended period of fire exclusion in many western US landscapes (Hagmann et al., 2021), a majority of fires are still actively suppressed due to existing government policies and potential risks to infrastructure (North et al., 2015). However, there is an increasing recognition that restoration of fire is critical for developing climate-resilient forests and human communities (North et al., 2021; Schoennagel et al., 2017; Young et al., 2020). Our results highlight the importance of prior fires in reducing subsequent fire severity and promoting refugia, reinforcing the value of fire as a key management tool. Indeed, our predictive maps indicated that fire refugia were 36.4% (under moderate weather) and 31.2% (extreme weather) more common across forested areas with at least one large, recent fire (i.e., 1985–2020), as compared to recently unburned forests, illustrating that fire plays a critical role in promoting and maintaining fire-resistant landscapes.

Though prior burning may have positive or negative effects on fire severity depending on site productivity and the traits of local vegetation communities (Coppoletta et al., 2016; Taylor et al., 2021; Tepley et al., 2018), the consistent buffering effects of fire observed in the present study are similar to those found across many coniferous forests of the Intermountain West (Parks et al., 2014; Walker et al., 2018; Yocom et al., 2022). We also found that the strongest buffering effects of fires occur within 15 years of initial fire occurrence and when initial fires burned at low to moderate severity (i.e., CBI < 1.5). A 15-year buffering effect is within the range of 1 to 30 years reported by other studies of fire severity and spread (Buma et al., 2020; Cansler et al., 2022; Parks et al., 2014; Stevens-Rumann et al., 2016; Yocom et al., 2019); beyond this time, the effects of the initial fire may wane due to surface fuel accumulation. Likewise, the comparatively greater buffering effects of low- to moderate-severity fire might be attributed to increases in coarse wood (Roccaforte et al., 2012; Stevens et al., 2021) or resprouting vegetation following high-severity fire (Coop et al., 2016; Guiterman et al., 2018). Indeed, the cover of shrubs, many of which are resprouting angiosperms in this region, had a positive effect on fire severity in our reburn model. Overall, fires with the greatest ability to reduce subsequent fire severity may be those that reduce live fuels, but do not lead to substantial increases in coarse wood or a strong vegetative resprouting response (Huffman et al., 2020; Hunter et al., 2011). Fire will play an increasingly important role in forest management throughout the western US over upcoming decades (DellaSala et al., 2022); as such, mitigating fire-driven forest transformations will require identifying weather windows, topographic settings, and fuels conditions in which both prescribed fire and natural ignitions can be most effectively utilized to achieve management goals (North et al., 2021).

4.3 | Constraints on post-fire recruitment

Building off a west-wide synthesis of post-fire regeneration data (Davis et al., 2023), we leveraged extensive field inventories (i.e., >10,000 individual plots) and species-specific models of recruitment probability to predict forest community-level responses to wildfire. Overall, recruitment potential varied regionally, with higher average recruitment in Colorado and Utah when compared to Arizona and New Mexico. Similarly, other studies have identified substantial recruitment limitations in dry forests of Arizona and New Mexico (Guiterman et al., 2022; Haffey et al., 2018) and comparatively greater recruitment to the north and west (Davis et al., 2020; Hoecker & Turner, 2022; Vanderhoof et al., 2020), due to differences in both environmental conditions and tree species composition. Recruitment is a key indicator of forest resilience to wildfire, and it is valuable to consider this process in tandem with fire severity when assessing vulnerability to forest transformations (Coop et al., 2020; Savage et al., 2013). As many western US conifers are obligate seeders, seed availability acts as a primary filter of recruitment (Chambers et al., 2016; Kemp et al., 2016; Rodman, Veblen, Chapman, et al., 2020). Seed availability can be influenced by both high-severity patch sizes and the presence or abundance of seed-bearing trees (Chapman et al., 2020; Gill et al., 2020; Stevens et al., 2017). However, even in locations where seeds are available, existing forest communities are not always in alignment with local environmental conditions (Davis et al., 2019; Rodman, Veblen, Chapman, et al., 2020; Stevens-Rumann et al., 2018). Our newly developed RI, which combines dispersal characteristics of the constituent species and environmental conditions in the surrounding landscape, highlights many of these potential limitations to conifer recruitment and helps to identify refugia that can support post-fire tree recruitment in adjacent, severely-burned areas.

4.4 | Potential fire refugia across the southwestern US

Patterns of fire severity and post-fire recruitment are driven by different sets of factors in southwestern US conifer forests, but the intersection of these factors has critical implications for the resilience of forest communities (Coop et al., 2020; Davis et al., 2020). For example, fire severity is strongly influenced by fuels and daily weather (Cansler et al., 2022; Parks et al., 2018), whereas post-fire recruitment is more commonly limited by seasonal, annual, or average climate conditions of a site (Davis et al., 2019; Guz et al., 2021; Rodman, Veblen, Battaglia, et al., 2020). Overall, we predicted that 67.6% (under moderate weather) and 18.1% (under extreme weather) of the study area were potential refugia (i.e., CBI < 1.25), and 39.7% of the study area had high recruitment potential. However, when overlaying maps of fire severity and recruitment, just 23.2% (moderate weather) and 6.4% (extreme weather) of the study area was refugia with a high potential to support recruitment in the surrounding landscape. Though these sites represent a small fraction of the region, it is important to note that such areas act as potential centers of nucleation and dispersal that can affect a much larger area (Coop et al., 2019). Fire refugia also contribute to the maintenance of community components and ecosystem functions, such as by providing critical habitat for fire-sensitive plant and animal species (Andrus et al., 2021; Downing et al., 2019; Landesmann & Morales, 2018; Robinson et al., 2014). These habitat patches, nested within larger networks, could be relatively buffered from near-term changes in climate and allow for both migration and in-situ adaptation in a period of rapid change (Haire et al., 2022; Morelli et al., 2020). Thus, refugia with high recruitment potential are disproportionately valuable in conifer forests of the southwestern US, a region that is especially vulnerable to fire-driven forest conversions (Davis et al., 2020; Parks, Dobrowski, et al., 2019).

Additional research is needed into how management activities (e.g., mechanical thinning, prescribed fire, resource objective fires) might foster and maintain fire refugia in the region (Stevens et al., 2021), and how networks of potential refugia might interact to facilitate the persistence of fire-sensitive species (e.g., Mexican spotted owl; *Strix occidentalis lucida*) (Jones et al., 2022). Identifying the locations and drivers of potential fire refugia, as done in the present study, is a first step towards building this new knowledge. However, our findings also point unequivocally toward two management strategies that can support and maintain refugia by reducing the likelihood of severe fire: (1) reducing canopy cover and creating heterogeneous fuels conditions using mechanical thinning where it is ecologically appropriate and socially acceptable, and (2) utilizing additional prescribed and lightning-ignited fires under moderate fire weather to mitigate the effects of future fire activity under more extreme conditions when suppression is ineffective. Where feasible, these activities may help to resist fire-driven ecosystem transformations in portions of the southwestern US.

4.5 | Study limitations and directions for future research

Factors such as serotiny, animal-mediated dispersal, the limited extent of reburns in our study area, and uncertainty in predictions may complicate models of refugia presented here. Several studies have found weak or inconsistent relationships between lodgepole pine establishment and distances to live trees due to partial serotiny in the species (Hoecker & Turner, 2022; Kemp et al., 2016; Urza & Sibold, 2017). However, even for lodgepole pine, there is concern that severe, short-interval reburns could overwhelm forest resilience due to a lack of trees bearing serotinous seeds in young post-fire stands (Gill et al., 2020; Turner et al., 2019). Refugia may remain valuable, even for this exceptionally fire-adapted species, by buffering trees against the effects of severe, short-interval reburns and maintaining available seed sources on the landscape. Long-distance dispersal events, likely facilitated by animals, have been noted in both montane and subalpine forests throughout the study area (Coop & Schoettle, 2009; Owen et al., 2017). Thus, the influence of fire refugia may extend well beyond the wind- and water-driven dispersal distances that we considered when calculating RI. Across the Southwest, areas with three or more fires were comparatively rare (i.e., 3.7% of the total burned area). Multiple reburns at a site may have additive or multiplicative effects (Downing et al., 2021; Hunter et al., 2011) that we could not adequately quantify throughout our study area due to the limited sample area. Additional research is needed to better understand the interactions of fuels, topography, weather, and prior-fire effects in areas with multiple reburns, which are likely to become increasingly common in the coming decades. Further, though the study period includes some of the driest conditions in the last thousand years (Williams et al., 2022), we note that the spatial overlap between contemporary forest composition and regeneration likelihood is expected to contract under future climate, and fire activity is likely to continue to increase (Coop et al., 2020; Davis et al., 2023). Finally, there was sizable uncertainty in some of our predictions, likely due to the stochastic and locally specific nature of individual fire behavior (Appendix S4). Some of these uncertainties may be unavoidable when working with empirical models and broad-scale spatial datasets. However, we hope that this work will provide a foundation that future research can build upon, as more sophisticated statistical approaches (e.g., deep learning) and detailed spatial datasets become increasingly common in ecological research.

5 | CONCLUSION

Here, we used empirical models of fire severity and post-fire recruitment, developed from over 1000 unique fire events and 10,000 post-fire field plots, to identify potential fire refugia across ca. 100,000 km^2 of forest area throughout the southwestern US. Because refugia are relatively buffered from fire-driven ecosystem transformations, they may help to "flatten the curve" during a period of rapid environmental change (Krawchuk et al., 2020; Morelli et al., 2020). However, these effects are likely to be most pronounced in areas where conditions promoting resistance to fire align with environmental conditions supporting post-fire tree recruitment, as identified in the present study. Anticipating ecological transformation in this era of uncertainty is challenging, yet critical for human adaptation to change (McDowell et al., 2020; Seidl & Turner, 2022). For example, potential fire refugia, which represent areas of relative stability, may help in outlining protected habitat networks for fire-sensitive or forest-obligate species that require particular forest structural or compositional conditions. Likewise, active forest management (e.g., mechanical treatments, prescribed fire, resource objective fires, and post-fire replanting) may work with the locations of potential refugia to help reinforce and expand refugial networks and maintain critical ecosystem services provided by forest ecosystems. Importantly, this study illustrates that open-canopied forests and fires burning under moderate weather conditions may promote and maintain refugia. Conversely, our results also suggest that aggressive suppression strategies which extinguish fires under moderate weather conditions will lead to continued increases in fuel accumulation, reduce the potential for fire refugia under more extreme conditions in which fires cannot be suppressed, and threaten the longer-term sustainability of southwestern US forests. Fire, as a dominant terrestrial disturbance (Bowman et al., 2009), will act as a major driver of ecological transformations across Earth's forests, and refugia will play an integral role in resilience to such transformations.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and R code used to process, analyze, or visualize data in this study are available through Data Dryad (Rodman et al., 2023). Spatial data can also be viewed using the following web application: https://kylerodman-eri.users.earthengine.app/view/us-southwest-refugia.

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SUPPORTING INFORMATION

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