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RESEARCH ARTICLE

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,

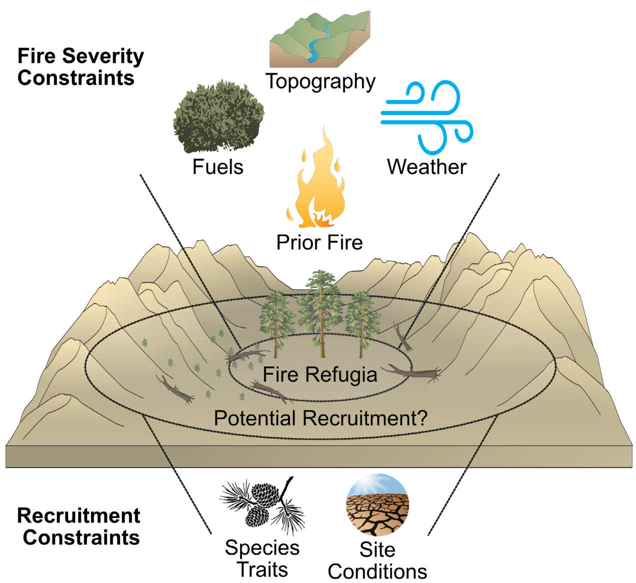

FIGURE 1 A summary of factors influencing forest resilience to wildfire. Fire severity is influenced by fuels, topography, and weather conditions during burning, as well as the effects of prior fires. For obligate seeders, post-fire tree recruitment is then constrained by seed availability and environmental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

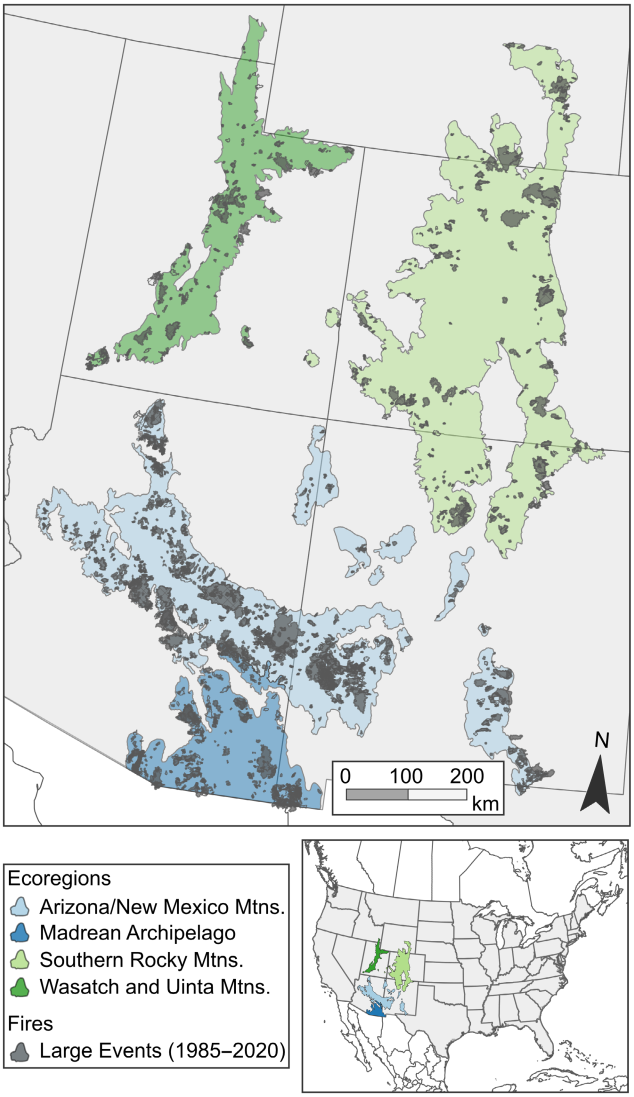

FIGURE 2 Study area, included EPA Level III ecoregions (EPA, 2021), and the locations of large (>404 ha) fire events that occurred from 1985 to 2020 (Eidenshink et al., 2007) throughout the southwestern US.

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.

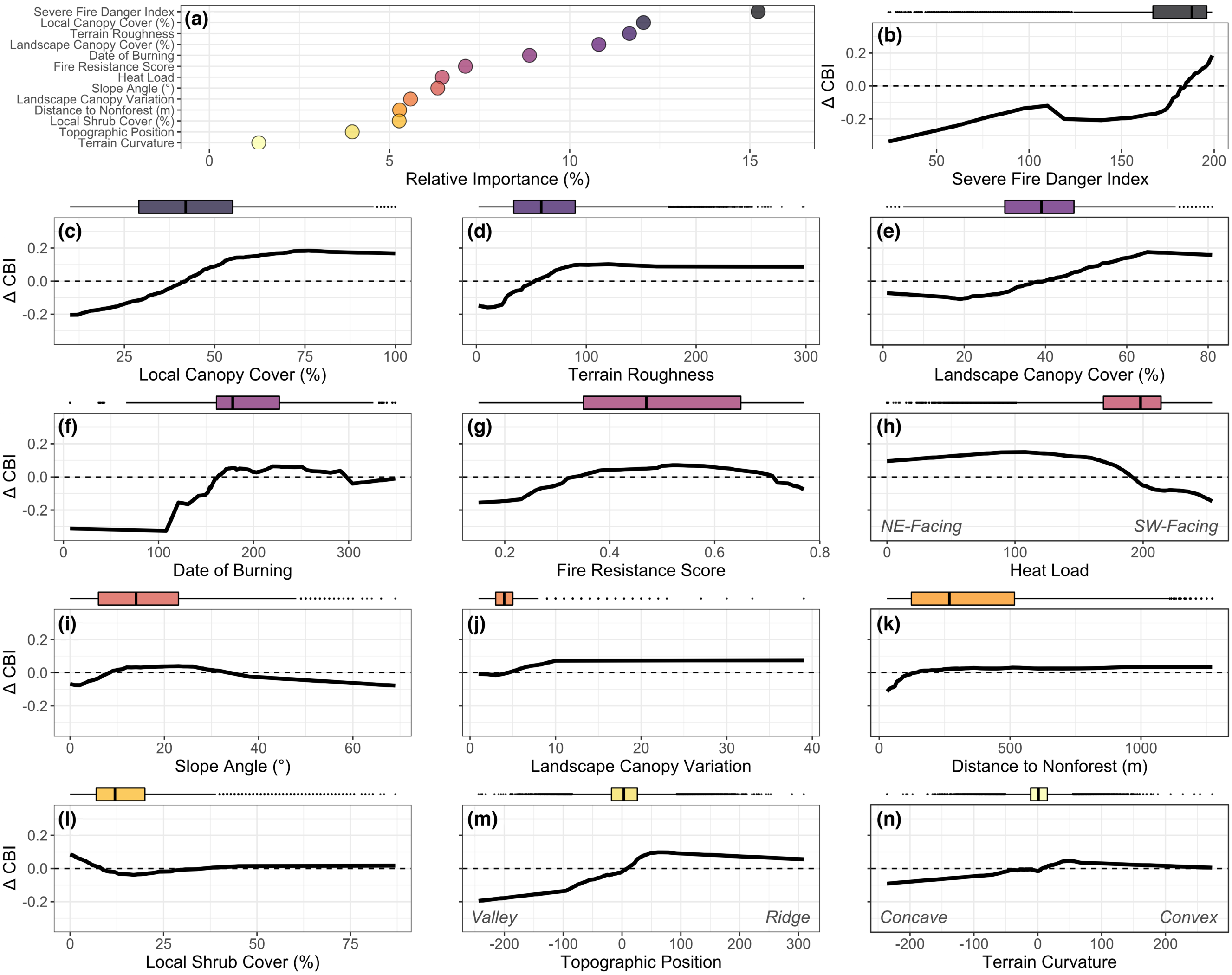

FIGURE 3 Results of the random forest model predicting fire severity (CBI; Composite Burn Index) in locations that burned once in the study period. Panel (a) shows the relative importance of predictors included in the final model using the permutation-based mean decrease in accuracy statistic. Panels (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.

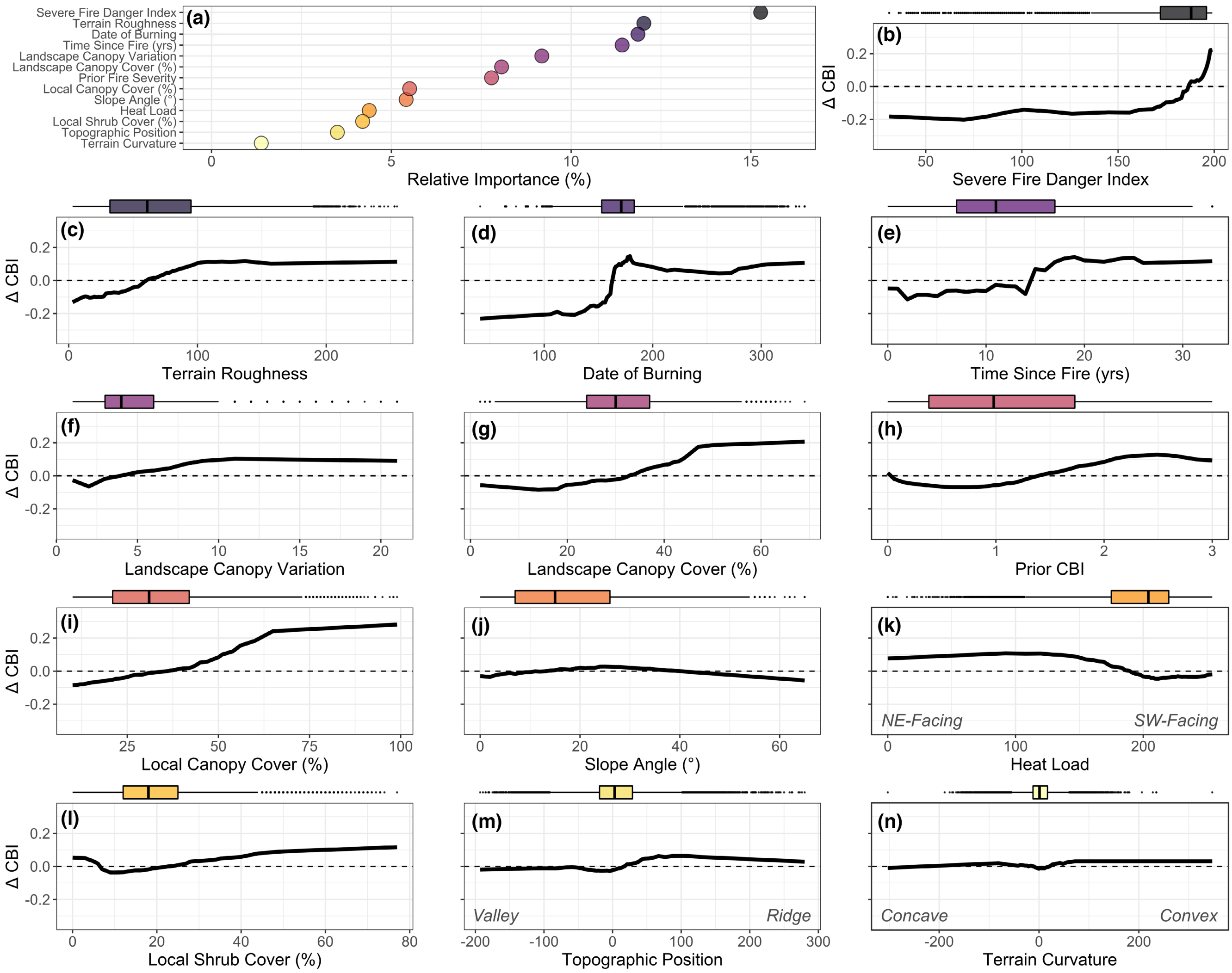

FIGURE 4 Results of the Random Forest model predicting fire severity (CBI; Composite Burn Index) in locations that burned twice in the study period. Panel (a) shows the relative importance (*x*-axis) of predictors (*y*-axis) included in the final model using the permutation-based mean decrease in accuracy 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).

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.

3.2 | (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).

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

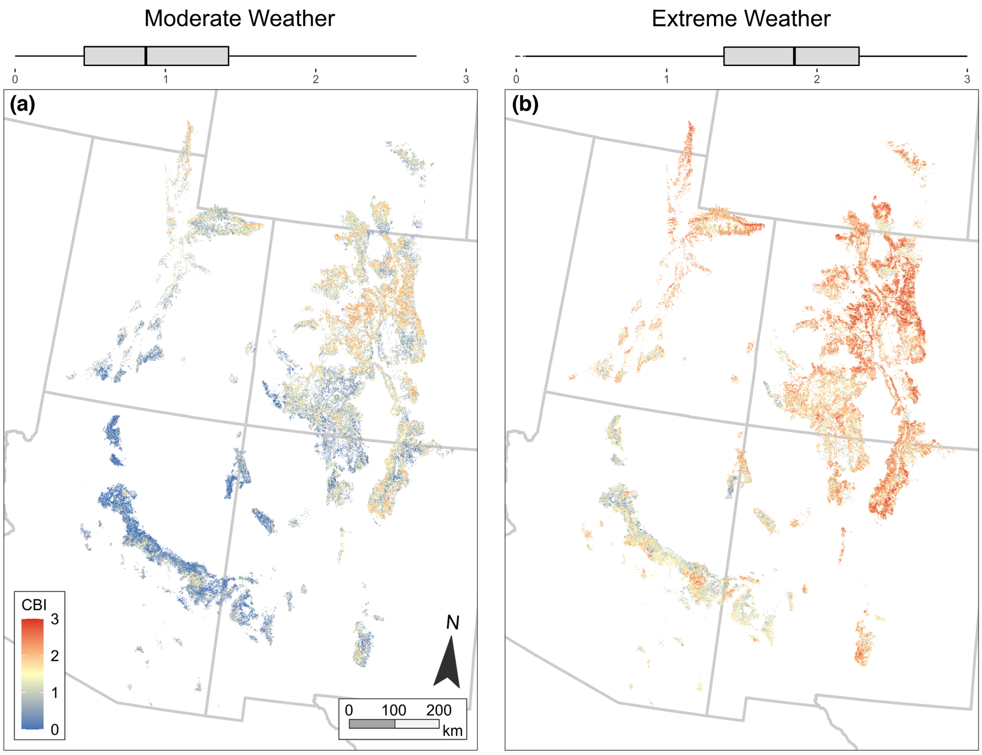

FIGURE 5 Predicted fire severity (CBI; Composite Burn Index) throughout upland conifer forests of the southwestern US based on 2021 fuels conditions, existing topography, and two fire weather scenarios. Moderate (a) fire weather conditions were based on 75th percentile daily weather (i.e., Severe Fire 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

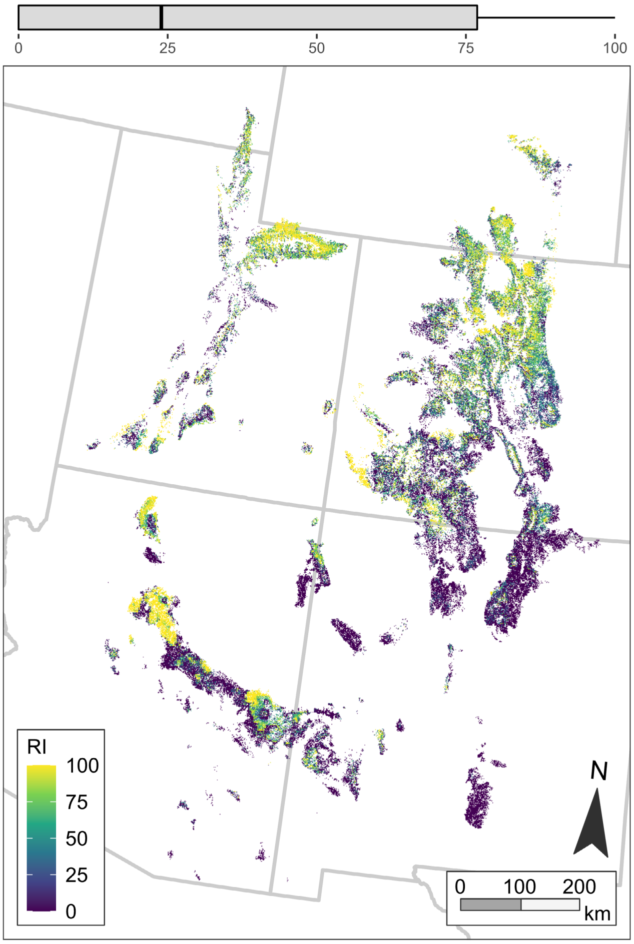

FIGURE 6 Predicted values of the recruitment index (RI) throughout upland conifer forests of the southwestern US, with higher values indicating a greater potential for post-fire recruitment. Boxplot at the top shows the distribution of predicted RI values across the study area.

the effects of climate-driven forest transformations. Forests below 40% canopy cover and those within 100 m 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

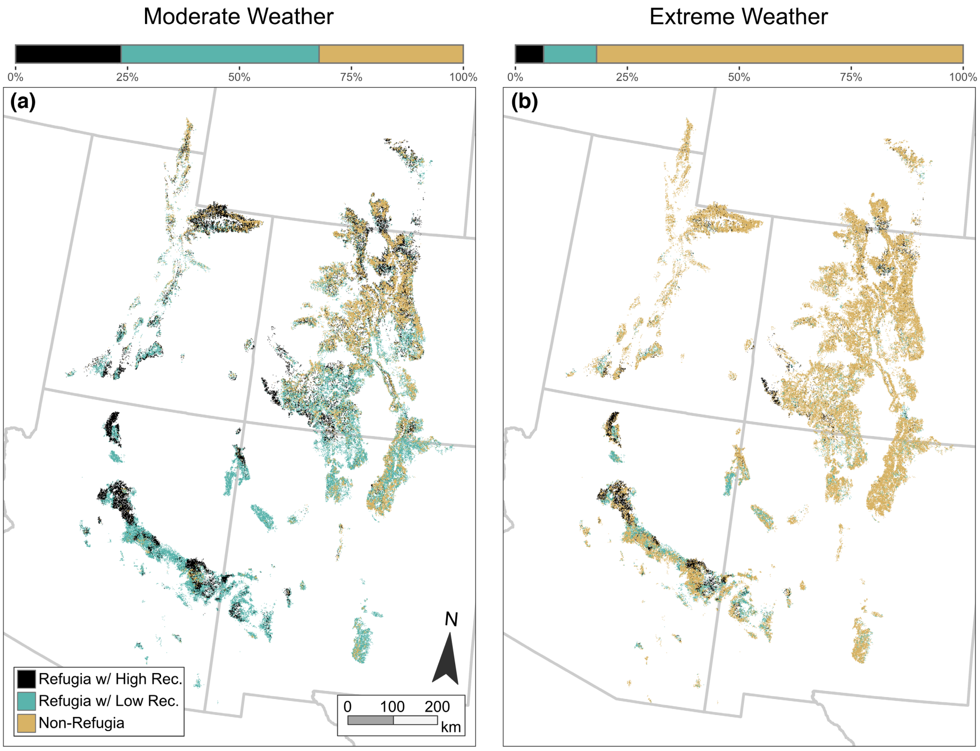

FIGURE 7 Predicted locations of fire refugia throughout upland conifer forests of the southwestern US based on moderate (a) and extreme (b) fire weather. "Refugia with high recruitment" are sites with low predicted fire severity and a high recruitment index (i.e., a high ability to support conifer forest 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

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

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Supplementary Information

Appendix S1: Summaries of Species Traits for Dominant Conifers in the Study Area

Table S1.1: A summary of typical elevational zones, relative fire resistance, pre-1900s fire regimes, and plant traits related to fire resistance for each of the six species included in this study.

Species	**Elevational Range**	**Fire Resistance Score**[1]	**MFRI (years)**[2]	**Traits Influencing Fire Resistance/ Susceptibility**[3]
Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Mayr] Franco)	Low to Intermediate	0.49	5 - 100+	Thin resin-filled bark in younger trees, thin corky bark in older trees is offset by low-growing branches. Shallow lateral roots. Mistletoe brooms can lead to fuel accumulations and ladder fuels contributing to crown fires.
Engelmann spruce (*Picea engelmannii* var. *engelmannii* Parry ex Engelm. and var. *mexicana* [Martínez] Silba; also called Mexican spruce)	High	0.26	90 - 350+	Thin bark, shallow roots, low-growing branches, tendency to grow in dense stands, moderately flammable foliage, heavy lichen growth. High fuel loading from accumulated needles can lead to crown fires.
Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson)	Low to Intermediate	0.39	20 - 200+	Thin bark, but occasionally fire resistant in open stands; lichen accumulation on older trees. High fuel buildup due to mistletoe, snow breakage, windthrow and bark beetles. Generally deep rooting system.
Ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.)	Intermediate to High	0.77	1 - 50+	Open crowns, self-pruning branches, thick and relatively non-flammable bark, thick bud scales and tight needle bunches, high foliar moisture, deep rooting habit.

Subalpine fir (*Abies lasiocarpa* var. *lasiocarpa* [Hook.] Nutt. and var. *arizonica* [Merriam] Lemmon; also called corkbark fir	High	0.31	90 - 350+	Thin bark, shallow roots, low growing branches, tendency to grow in dense stands, highly flammable foliage, moderate to heavy lichen growth. High fuel loads under trees can lead to crown fires.
White fir (*Abies concolor* var. *concolor* [Gordon & Glend.] Lindl. ex Hildebr)	Low to Intermediate	0.43	5 - 200+	Thin bark, resin blisters and drooping lower branches in young trees; Self pruning and thick bark in older trees, offset by heavy lichen growth and shallow roots.

1: Fire resistance scores (FRS) were derived from Stevens et al. (2020), who combined a range of plant traits related to resistance and flammability into a single numerical value ranging from 0 to 1. Higher values are indicative of greater fire resistance.
2: Mean fire return intervals were obtained from the USDA Fire Effects Information System (FEIS), summarizing existing knowledge for each tree species (*USDA Forest Service, Fire Effects Information System (FEIS)*, 2022).
3: Plant traits were summarized from synthesis papers and public data sources (Baker, 2009; Burns & Honkala, 1990; Stevens et al., 2020; *USDA Forest Service, Fire Effects Information System (FEIS)*, 2022).

Table S1.2: Relative drought tolerance, shade tolerance, common regeneration traits, dispersal mechanisms, and requirements for seed germination for each of the six conifer species included in this study.

Species	**Drought Tolerance**[1]	**Shade Tolerance**[1]	**Regeneration Traits**[1]	**Dispersal Mechanisms**	**Seed Germination**[1]
Douglas-fir	Moderate	Moderate	Most trees produce cones at >12 cm DBH (40 years) (Rodman, Veblen, et al., 2021) .	Wind and animals. Most dispersal within 120 m of a live tree (Kemp et al., 2016; McCaughey et al., 1986).	Most germination occurs within 150 days of seedfall, but seeds remain viable for 1 or occasionally 2 years.
Engelmann spruce	Low	Moderate to High	Most trees begin to produce cones at sizes > 5 cm DBH (ca. 25 years) (Andrus, Harvey, et al., 2020); layering near timberline.	Wind. Most dispersal < 150 m from live trees (Gill et al., 2020; McCaughey et al., 1986).	Germinates 2-3 weeks after snowmelt, but can emerge following summer rains or in the second year.
Lodgepole pine	Moderate	Low	Starts producing seed at ca. 5-15 years (Turner et al., 2007). Individual trees have predominately open or closed (serotinous) cones at later ages. Serotinous genotype often produces open cones up until ~ 60 years and then closed cones after. Closed cones can stay on the tree and remain viable for 40 years or more (Rhoades et al., 2022).	Wind, serotiny, and animals. Most dispersal within 60 m of live (non-serotinous) or recently burned (serotinous) trees (Gill et al., 2020; McCaughey et al., 1986).	Requires light but not stratification. Germinates following snowmelt in spring or early summer.

Ponderosa pine	High	Low	Most trees produce cones at >18 cm DBH (50 years). Seed production is episodic at tree- and stand-scales (Krannitz & Duralia, 2004; Rodman, Veblen, et al., 2021; Wion et al., 2021).	Wind and animals. Most dispersal within 90 m of a live tree (Chambers et al., 2016; Kemp et al., 2016; McCaughey et al., 1986).	Cold-moist stratification not required.
Subalpine fir	Low	High	Most trees begin to produce cones at sizes > 7 cm DBH (ca. 30 years) (Andrus, Harvey, et al., 2020); Layering can occur at high elevations.	Wind. Most dispersal < 150 m from live trees (McCaughey et al., 1986).	Cold-moist stratification required; germinates in spring.
White fir	Moderate	Moderate to High	Cones produced around 20-50 years.	Wind. Most dispersal < 150 m from live trees (McCaughey et al., 1986).	Cold-moist stratification required.

1: Where not otherwise indicated, information was derived from species summaries in FEIS and Silvics NA (Burns & Honkala, 1990; *USDA Forest Service, Fire Effects Information System (FEIS)*, 2022)

Appendix S2: Correcting for Bias in Random Forest Predictions of Fire Severity

Regression predictions from Random Forests and other tree-based statistical learning algorithms can be prone to bias towards the mean (Belitz & Stackelberg, 2021; Parks et al., 2019; Zhang & Lu, 2012). This occurs because tree-based predictions are made using averages of subsets of the data (Breiman et al., 1984), which can push predicted values towards the mean of the response variable. Because Random Forests are an ensemble of many individual tree-based models (i.e., classification and regression trees), they can also be prone to such biases. We were interested in accurate predictions across a range of fire severities (i.e., the Composite Burn Index; CBI), therefore we performed a bias correction of predicted values. Specifically, we used a *Z*-score matching method described in Rodman et al. (2021) to match the mean and variance of predicted values with observed data. Similar transformations have been employed to correct bias in climate datasets and harmonize the distributions of differing data types (Bouwer et al., 2004; Flint & Flint, 2012). This transformation is based on the following equation:

Equation S2.1:

$$\hat{y}_{corrected} = \left(\left(\frac{\hat{y}_{uncorrected} - \mu_{rf}}{\sigma_{rf}}\right) * \ \sigma_{obs}\right) + \mu_{obs}$$

where $\hat{y}_{uncorrected}$ and $\hat{y}_{corrected}$ are the predicted values of CBI at a given sample point, before and after bias correction, respectively. Likewise, μ_{rf} and μ_{obs} are the means and σ_{rf} and σ_{obs} are the standard deviations of RF-predicted and observed values of fire severity across all sample points in out-of-bag data. We applied this formula to predictions made in one-fire and reburn models separately because of differences in the training datasets. Values used in each formula are provided in Table S2.1. Following bias correction, any values outside of the typical range of CBI (i.e., [0, 3]) were truncated to [0, 3] as follows:

Equation S2.2:

$$f(\hat{y}_{corrected}) = \begin{cases} 0 & if \quad \hat{y}_{corrected} < 0 \\ x & if \quad 0 \leq \hat{y}_{corrected} \leq 3 \\ 3 & if \quad \hat{y}_{corrected} > 3 \end{cases}$$

Table S2.1: Values used in bias correction (Eq. S2.1) for Random Forest predictions of fire severity.

	μ_{rf}	μ_{obs}	σ_{rf}	σ_{obs}
One-fire model	1.449001	1.450123	0.5217355	0.9614945
Reburn model	0.9581118	0.9564298	0.5216691	0.8038882

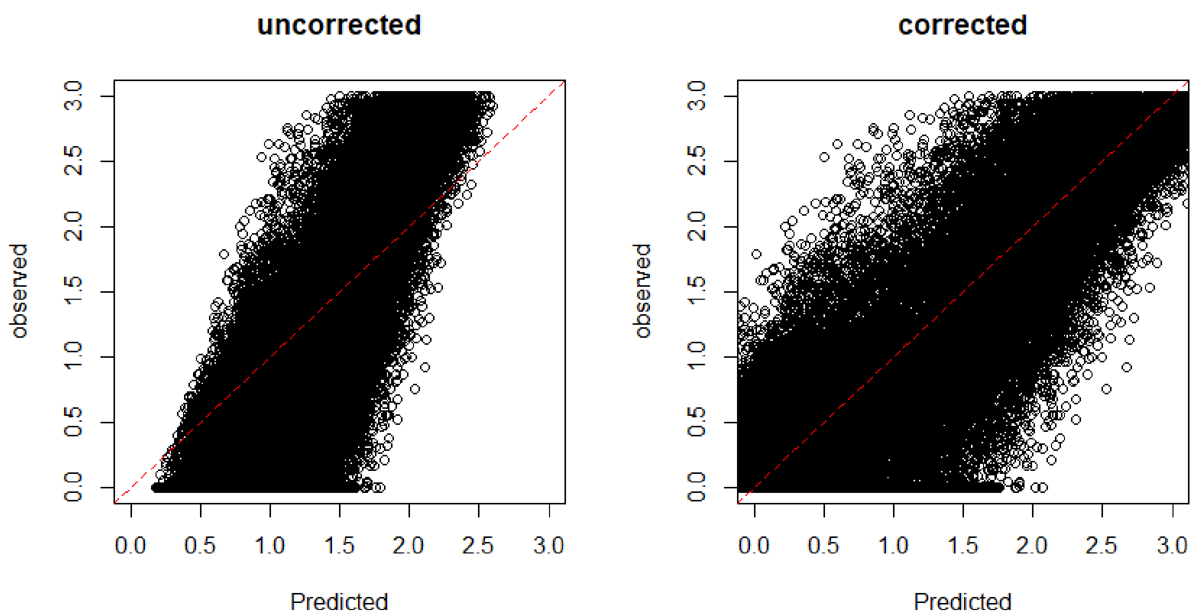

Figure S2.1: Results of bias correction for Random Forest-based predictions of fire severity (CBI; composite burn index) across recent (1985-2020) fires in the Southwest U.S. Uncorrected values (left) show predicted values of fire severity in the out-of-bag sample in the "one-fire model" (i.e., locations with only one large fire from 1985 to 2020). Corrected values (right) show predicted values of fire severity after applying Equation S2.1 and coefficients from Table S2.1. Red dashed lines show a 1:1 line of observed vs predicted values, and deviations from the slope of this line indicate prediction bias at the extremes.

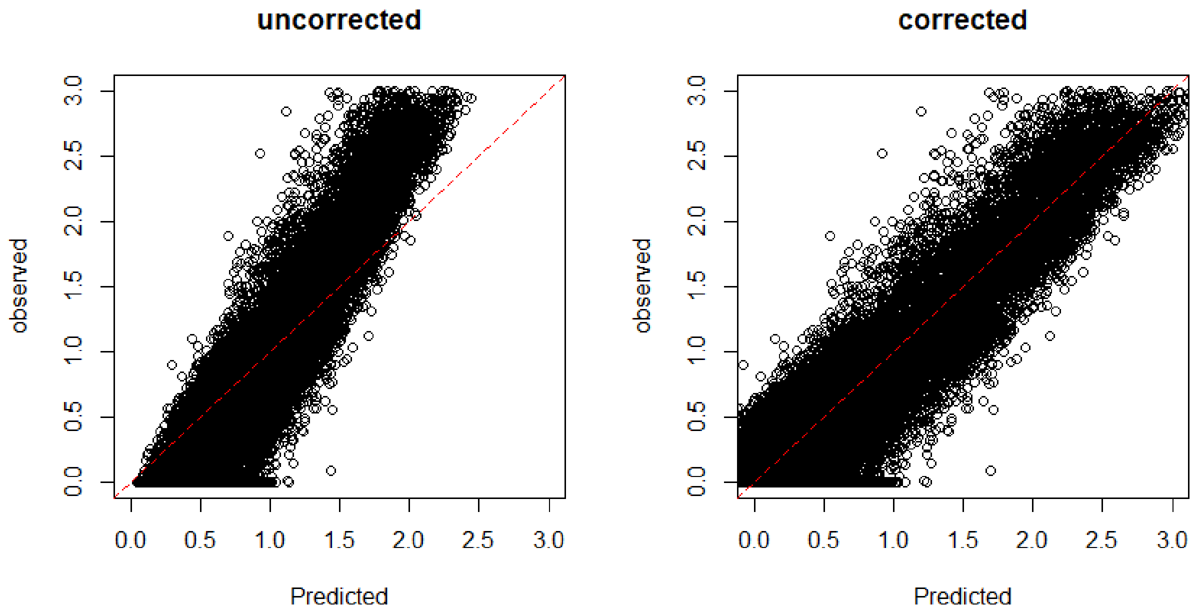

Figure S2.2: Results of bias correction for Random Forest-based predictions of fire severity (CBI; composite burn index) across recent (1985-2020) fires in the Southwest U.S. Uncorrected values (left) show predicted values of fire severity in the out-of-bag sample in the “reburn model” (i.e., locations with two large fires from 1985 to 2020). Corrected values (right) show predicted values of fire severity after applying Equation S2.1 and coefficients from Table S2.1. Red dashed lines show a 1:1 line of observed vs predicted values, and deviations from the slope of this line indicate prediction bias at the extremes.

Appendix S3: Modeling Post-Fire Recruitment Potential and Developing the Recruitment Index

To quantify the potential for existing forest communities to support post-fire recruitment across the region, we used ecological niche models for post-fire tree seedlings from Davis et al. (2023), who synthesized tree regeneration data from over 10,000 field plots throughout recently burned forests of the western United States (Table S3.1). Davis et al. (2023) developed binomial (logit link) generalized linear mixed models of recruitment probability for each of the six dominant conifer species in our study area based on biophysical variables, including average climate, post-fire drought stress, topography, fire severity, and seed source availability. While models were largely unchanged from those described in Davis et al. (2023), we replaced original topographic variables (i.e., 90-m spatial resolution) with 30-m topographic variables to better incorporate fine-scale topographic effects that are known to influence tree recruitment in this region (Andrus, Hart, et al., 2020; Rodman et al., 2020). Refitting models with these finer-scale spatial covariates slightly changed accuracy metrics and classification thresholds for each species, thus we summarize new models in Table S3.1.

We used these models to develop regionwide 30-m maps of post-fire recruitment probability for each of the six conifer species included in our study (Figs. S3.1-S3.7). In developing these maps, we used measured climate conditions between 2001 and 2020, a period of extreme drought stress and an analog for near-term future conditions (Williams et al., 2022). Because we were interested in the potential for refugia to facilitate recovery in adjacent high-severity areas, we used high fire severity values (i.e., relativized burn ratio [RBR] of 400; Parks et al., 2014) with the availability of a nearby seed tree (i.e., 30-m distance to seed tree) and moderate amounts of surviving canopy cover (i.e., mean cover of 12.3% in the a 300-m surrounding radius; the median surrounding tree cover of 'high-severity' plots in Davis et al.

[2023] throughout our study area). While we used CBI in our fire severity models, RBR was used here because it was used in the original models of Davis et al. (2023); RBR is strongly related to CBI (Parks et al., 2019) .

Our regionwide predictive maps give the probability of at least 100 trees ha^{-1} of a given species establishing within 10 years of fire occurrence, assuming high fire severity, the availability of a nearby seed source, recent climate conditions, and existing topography at each site. We then used species-specific probability thresholds that maximized the sum of sensitivity and specificity (i.e., the true skill statistic [TSS]) to classify each 30-m pixel as "recruitment present" or "recruitment absent" for subsequent processing (Table S3.1; Fig. S3.1-S3.7). After developing binary species maps, we then used raster-based focal statistics to summarize tree species recruitment maps in the local neighborhood around each pixel, thereby converting pixel-based estimates of recruitment presence into a local neighborhood metric describing the suitability for recruitment in the landscape around each pixel (Fig. S3.1). To do so, we developed species-specific dispersal kernels to quantify landscape suitability based on the distance-squared-weighted refugia density metric of Coop et al. (2019), with a center cell weight of 0 (thereby quantifying recruitment potential in the landscape around a pixel, rather than the pixel itself). Our variation of this metric quantifies the focal sum of "presence" pixels for the recruitment of a given species, with pixels in a focal window weighted by the inverse of the squared distance from the focal refugia pixel. Because different tree species can disperse at different distances based on seed size and shape (McCaughey et al., 1986) which influences pattern of post-fire recruitment (Kemp et al., 2016), we used different window sizes for each species map, with heavier-seeded pines (e.g., lodgepole pine at 60 m, and ponderosa pine at 90 m) having smaller window sizes than Douglas-fir (120 m), Engelmann spruce (120 m), and true firs (e.g., subalpine fir at 150 m, white fir at 150 m). All species values were scaled from 0 to 100 to ensure a consistent range despite differences in window sizes. Finally, we calculated a recruitment index (RI) as the weighted sum of all individual species maps, with weights based on the relative dominance (i.e., the proportion of total basal area [BA] for the six focal species) in each 30-m pixel (Fig. S3.1-S3.7). RI, ranging 0-100, summarizes the extent to which existing forest communities align with environmental conditions for post-fire recruitment in the surrounding landscape, and how well a surviving patch of forest might facilitate recovery into adjacent severely burned areas.

Table S3.1: Final statistical models, sample sizes, accuracy metrics, and probability thresholds to define presence/absence in predicting post-fire tree recruitment for each species. In “Model Predictors”, terms in “Poly(term, n)” are polynomial terms, where n gives the order of the polynomial, terms in “(1|term)” give random intercepts included in the final models, and “offset()” accounts for the probability of presence given sampling effort (i.e., plot sizes). Pairs of variables connected by “*” are bivariate interaction terms. Sample sizes (No. Plots and No. Fires) give the number of unique plot locations and fires included in data used to train each model. AUC (area under the receiver operating curve) is a measure of agreement in binary classifiers (e.g., presence/absence), where values range 0-1 with 1 indicating perfect agreement across a range of classification thresholds. AUC (full) shows the AUC value for the model when using the full dataset, and AUC (cv) shows the AUC value when comparing model predictions to withheld data in spatially stratified cross-validation. The “Presence/Absence” threshold identifies the probability cutoff that maximizes the sum of sensitivity and specificity for a given species (i.e., the True Skill Statistic; TSS); this threshold was used when developing maps of the recruitment index (RI; Appendix S3).

Species Name	**Species Code**	**Model Predictors**	**No. Plots**	**No. Fires**	**AUC (full)**	**AUC (cv)**	**Presence/Absence Threshold**
Douglas-fir	PSME	Pre-fire disturbance type, Poly(Heat Load Index [HLI], 2), Years since fire, Distance to seed source, Mean post-fire tree cover within 300 m radius, Species variety, Average Climatic Water Deficit (CWD) in the driest month, Relativized Burn Ratio (RBR) * Minimum growing season CWD in 5 years after fire, RBR * Maximum growing season CWD in 5 years after fire, offset(log(Plot size)), (1 | Fire Name)	6,015	274	0.74	0.74	0.29
Engelmann spruce	PIEN	Pre-fire disturbance type, Years since fire, Mean post-fire tree cover within 300 m radius, Poly(RBR, 2), Distance to seed source, Poly(HLI, 2), Topographic Position Index (TPI), Poly(Minimum growing season CWD in 5 years after fire, 2), Average Climatic Water Deficit (CWD) in the driest month, offset(log(Plot size)), (1 | Fire Name)	1,514	138	0.73	0.70	0.54
Lodgepole pine	PICO	Pre-fire disturbance type, Years since fire, Maximum growing season precipitation in five years after fire * TPI, Poly(HLI, 2), Distance to seed source, Mean post-fire tree cover within	3,251	181	0.79	0.75	0.52

		300 m radius, RBR * lodgepole variety, def30_gs_gm, poly(Maximum growing season CWD in 5 years after fire, 2), RBR * Maximum growing season precipitation in 5 years after fire, offset(log(Plot size)), (1 | Fire Name)					
Ponderosa pine	PIPO	Pre-fire disturbance type, Years since fire, HLI, Distance to seed source, Species variety * Poly(Mean post-fire tree cover within 300 m radius, 2), Species variety * RBR, Average CWD in the driest month, Maximum growing season CWD in 5 years after fire * RBR, poly(Maximum growing season precipitation in 5 years after fire, 2), offset(log(Plot size)), (1 | Fire Name)	7,719	276	0.70	0.69	0.22
Subalpine fir	ABLA	Pre-fire disturbance type, Years since fire, Poly(HLI, 2), Distance to seed source, RBR, Average CWD in the driest month, Poly(Maximum growing season CWD in 5 years after fire, 2) * Mean post-fire tree cover within 300 m radius, offset(log(Plot size)), (1 | Fire Name)	2,174	139	0.81	0.78	0.13
White fir	ABCO	Pre-fire disturbance type, Years since fire, Poly(HLI, 2), TPI, Distance to seed source, Species variety, RBR, Mean post-fire tree cover within 300 m radius * Minimum summer vapor pressure deficit (VPD) in 5 years after fire, Average annual CWD, offset(log(Plot size)), (1 | Fire Name)	3,846	192	0.73	0.70	0.30

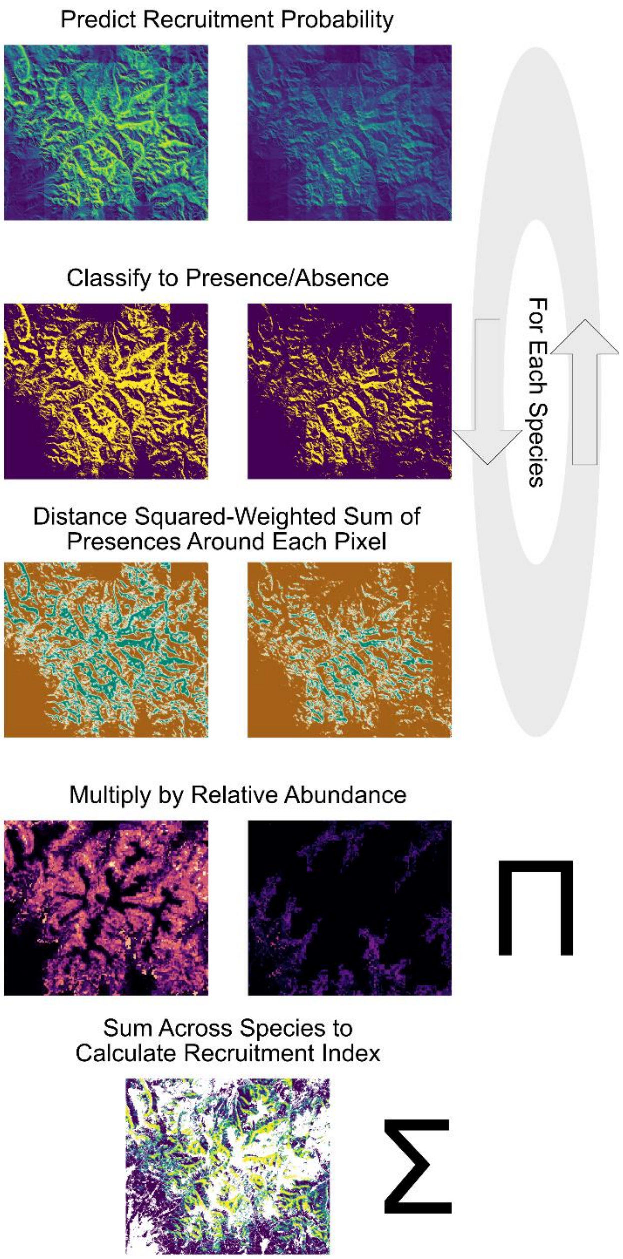

Figure S3.1: A summary of the methods used to calculate the recruitment index (RI) in upland forests of the southwestern United States. For each of the six dominant conifers, we predicted post-fire recruitment probability, classified these probabilities into likely presence/absence of recruitment based on thresholds in Table S3.1, and calculated the distance-squared-weighted sum of presence values around each pixel (restricted to pixels within the dispersal distance of a given species). We then calculated RI as the weighted sum across all species, with weights based on relative abundance of each species in a given pixel.

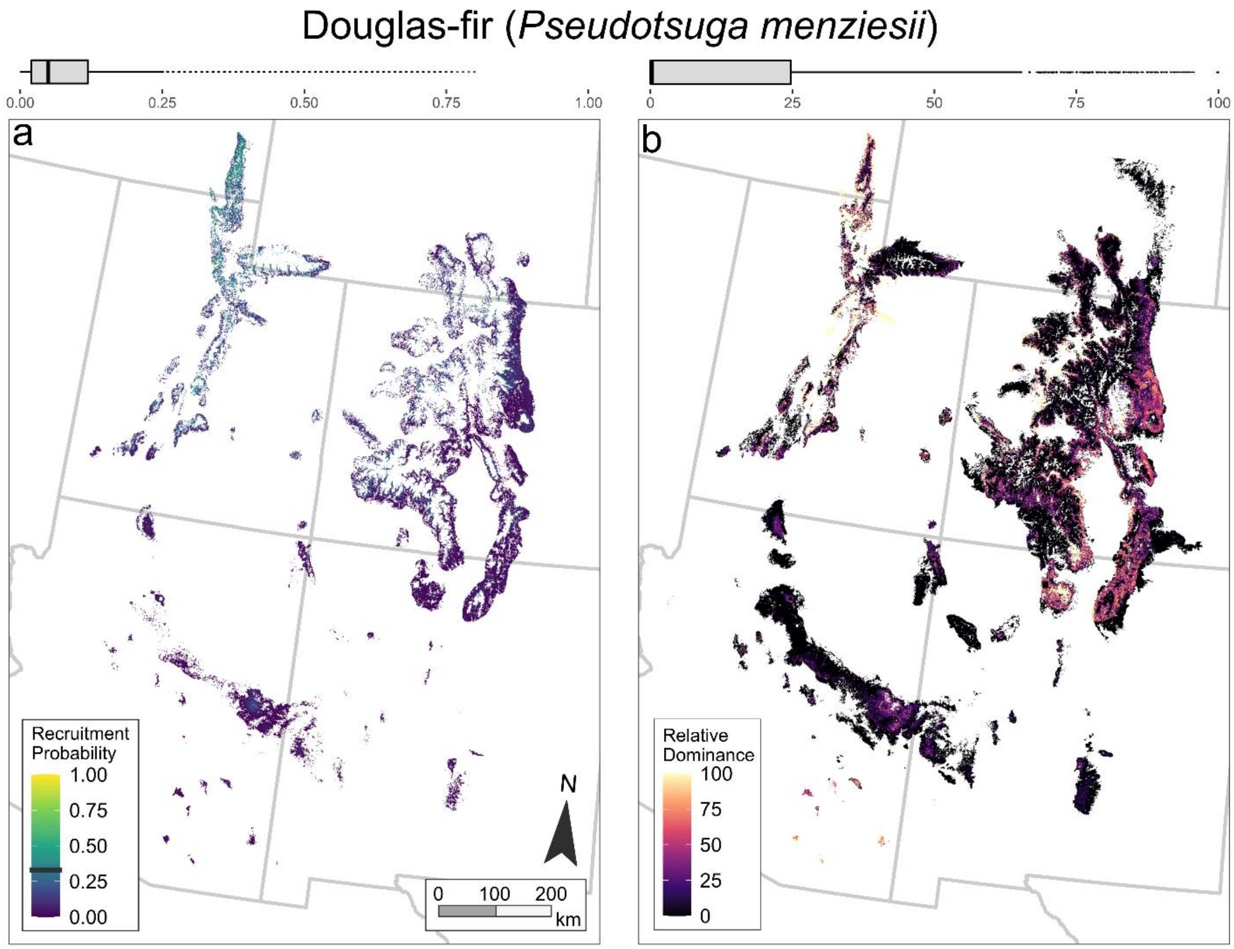

Figure S3.2: Probability of post-fire recruitment (a) and relative dominance (i.e., percentage of total community basal area) (b) for Douglas-fir throughout the Southwest US. Recruitment predictions (a) were restricted to areas with at least 1 m^2 ha^{-1} from the corresponding species (i.e., panel (b)) and give the probability of at least 100 seedlings ha^{-1} establishing within ten years of fire occurrence, assuming high-severity fire but the availability of a nearby seed source. Species basal area maps used in (b) were obtained from Wilson et al., (2013). The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1.

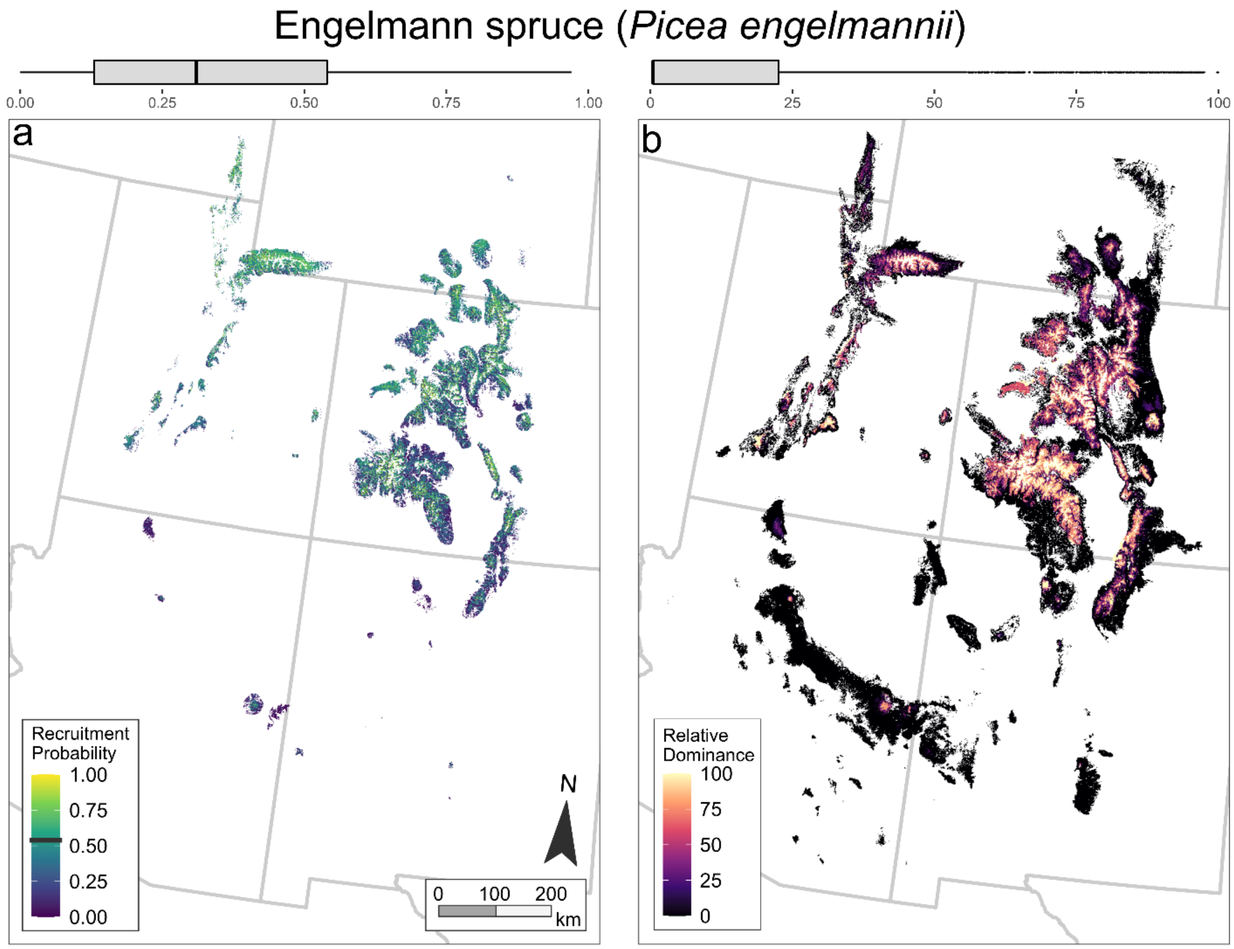

Figure S3.3: Probability of post-fire recruitment (a) and relative dominance (i.e., percentage of total community basal area) (b) for Engelmann spruce throughout the Southwest US. Recruitment predictions (a) were restricted to areas with at least 1 m^2 ha^{-1} from the corresponding species (i.e., panel (b)) and give the probability of at least 100 seedlings ha^{-1} establishing within ten years of fire occurrence, assuming high-severity fire but the availability of a nearby seed source. Species basal area maps used in (b) were obtained from Wilson et al., (2013). The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1.

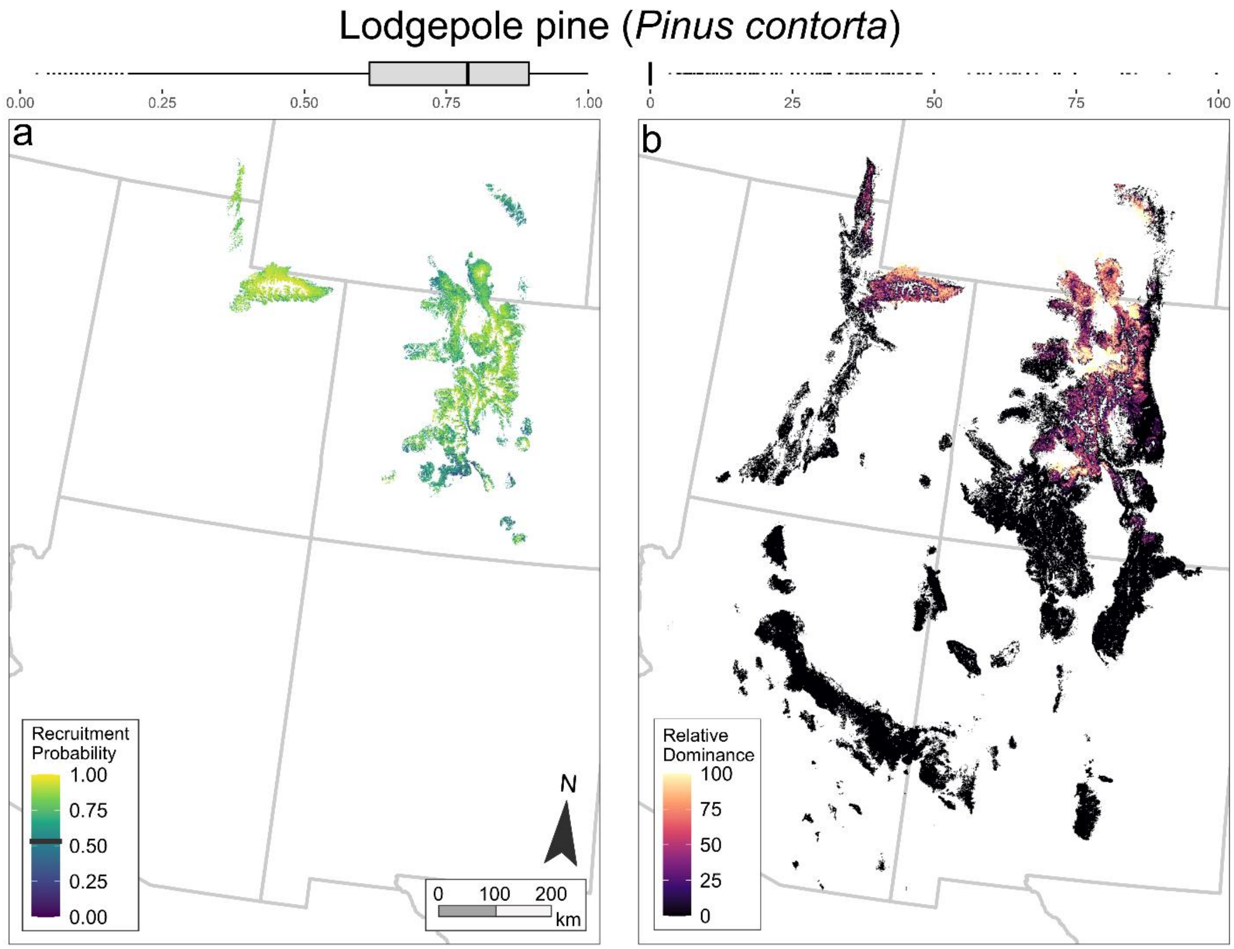

Figure S3.4: Probability of post-fire recruitment (a) and relative dominance (i.e., percentage of total community basal area) (b) for lodgepole pine throughout the Southwest US. Recruitment predictions (a) were restricted to areas with at least 1 m^2 ha^{-1} from the corresponding species (i.e., panel (b)) and give the probability of at least 100 seedlings ha^{-1} establishing within ten years of fire occurrence, assuming high-severity fire but the availability of a nearby seed source. Species basal area maps used in (b) were obtained from Wilson et al., (2013). Note that lodgepole pine is partially serotinous, and does not need live seed trees for post-fire establishment in many areas. The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1.

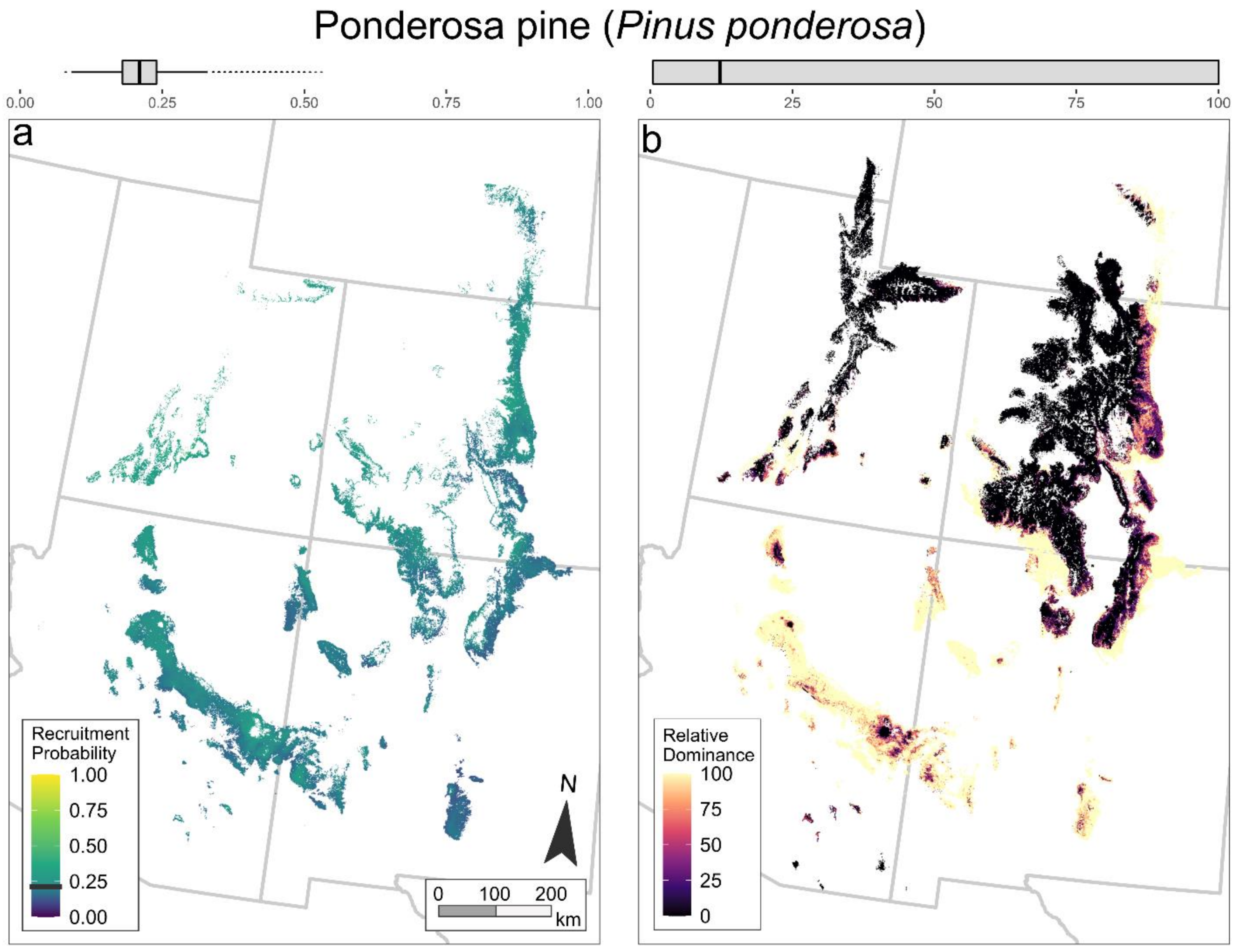

Figure S3.5: Probability of post-fire recruitment (a) and relative dominance (i.e., percentage of total community basal area) (b) for ponderosa pine throughout the Southwest US. Recruitment predictions (a) were restricted to areas with at least 1 m^2 ha^{-1} from the corresponding species (i.e., panel (b)) and give the probability of at least 100 seedlings ha^{-1} establishing within ten years of fire occurrence, assuming high-severity fire but the availability of a nearby seed source. Species basal area maps used in (b) were obtained from Wilson et al., (2013). The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1.

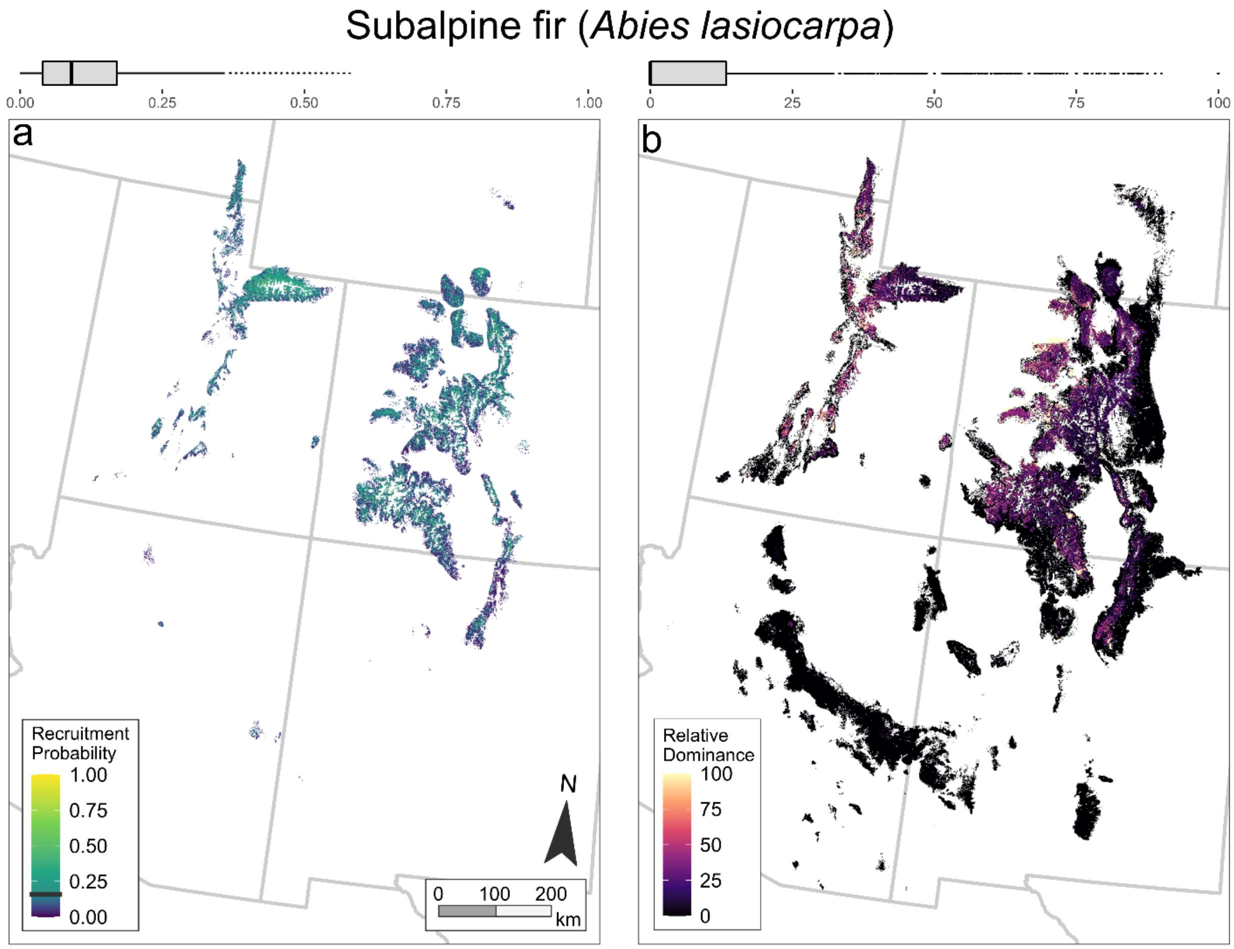

Figure S3.6: Probability of post-fire recruitment (a) and relative dominance (i.e., percentage of total community basal area) (b) for subalpine fir throughout the Southwest US. Recruitment predictions (a) were restricted to areas with at least 1 m^2 ha^{-1} from the corresponding species (i.e., panel (b)) and give the probability of at least 100 seedlings ha^{-1} establishing within ten years of fire occurrence, assuming high-severity fire but the availability of a nearby seed source. Species basal area maps used in (b) were obtained from Wilson et al., (2013). The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1.

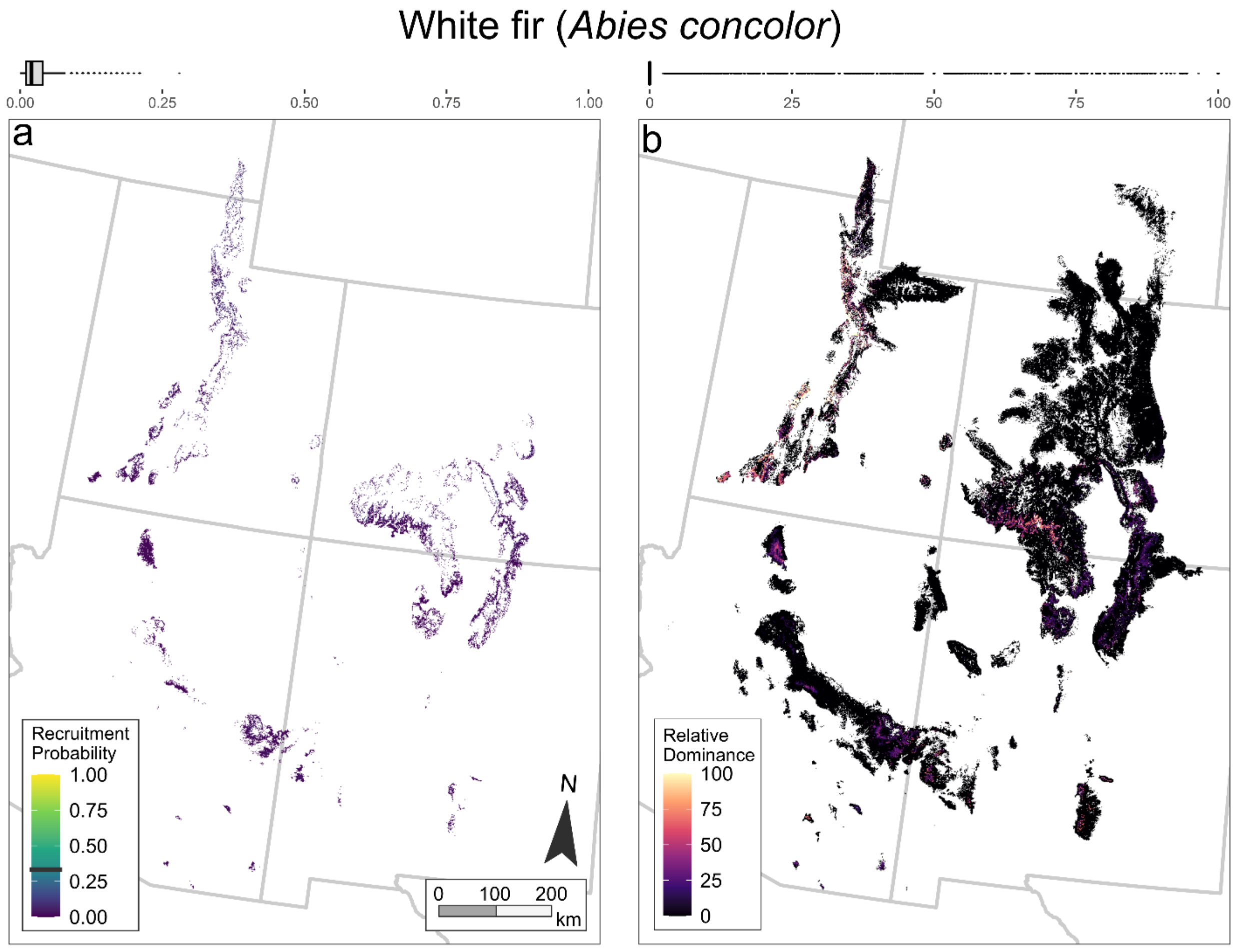

Figure S3.7: Probability of post-fire recruitment (a) and relative dominance (i.e., percentage of total community basal area) (b) for white fir throughout the Southwest US. Recruitment predictions (a) were restricted to areas with at least 1 m^2 ha^{-1} of the corresponding species (i.e., panel (b)) and give the probability of at least 100 seedlings ha^{-1} establishing within ten years of fire occurrence, assuming high-severity fire but the availability of a nearby seed source. Species basal area maps used in (b) were obtained from Wilson et al., (2013). The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1.

<u>Appendix S4: Quantifying Uncertainty in Regionwide Predictions</u>

Methods: Mapping and Summarizing Predictive Uncertainty

To describe and visualize uncertainty in our predictions of fire severity (i.e., CBI; composite burn index), post-fire recruitment, and the locations of potential refugia, we developed pointwise prediction intervals of fire severity and post-fire recruitment throughout the study area. We then propagated this uncertainty throughout the same analytical process used to develop the recruitment index (RI; Appendix S3) and map potential refugia. Because models of fire severity (Random Forests) and post-fire recruitment (generalized linear mixed models) were developed using different statistical frameworks, methods of calculating these prediction intervals differed among models. For models of fire severity, we used quantile regression forests, a variation of Random Forests that can predict the conditional distribution of a response, and a common method of developing prediction intervals (Meinshausen, 2006). We used these models to predict the 15.9th (i.e., lower) and 84.1st quantiles (i.e., upper) of the conditional distribution of fire severity within each 30-m pixel (Fig. S4.1). We selected these quantiles because they approximate the mean ± one standard deviation in a standard normal distribution, and were consistent with the width of prediction intervals in our recruitment predictions. For models of recruitment probability of each tree species, we mapped the standard error of prediction for each 30-m pixel using the 'glmmTMB' package in R (Brooks et al., 2017), following Davis et al. (2023). On the logit scale, we added and subtracted the standard error of the prediction from the predicted population-level mean value, and then converted these values to the scale of the response (i.e., probabilities of 0-1) using the inverse logit transformation (Figs. S4.2-S4.7). All prediction intervals can be interpreted as containing ca. 68.2% of likely outcomes based on the underlying data and the findings from our models. Variation in the width of these intervals is shown in the rightmost columns of Figs. S4.1-4.7, and demonstrates variation in model uncertainty throughout the study area.

Next, we used prediction intervals of recruitment probability for each species to calculate lower and upper bounds of the recruitment index (RI) (Fig. S4.8). We did this following similar methods to the calculation of RI described in the Appendix S3 and Fig. S3.1, but by replacing the population-level mean probabilities of each species with the lower and upper values of the prediction interval. Thus, the lower bound of the RI indicates assumes that all species had a lower probability of recruitment than expected (i.e., mean probability minus one standard error of prediction), whereas the "upper" bound of the RI indicates the opposite – that all species had a higher probability of recruitment than expected (i.e., mean probability plus one standard error of prediction). Variation in RI, calculated as the difference between these two bounds, is shown in Fig. S4.8c.

Finally, we mapped the locations of potential refugia by incorporating predictive uncertainty from both fire severity and recruitment models using two possible scenarios bracketing the range of likely outcomes (Fig. S4.9). The first (i.e., "lower") scenario assumed that fire severity was greater than expected (i.e., 84.1st percentile) across the entire study area, while the RI was lower than expected (i.e., 15.9th percentile of each species' recruitment probability). In other words, this scenario assumes that conditions for the formation and maintenance of refugia, and their ability to support recruitment, are worse than might be expected given the model results and underlying data throughout the study area. The second scenario (i.e., "upper") serves as an alternative in which fire severity was lower than expected (i.e., 15.9th percentile) and the RI was higher than expected (i.e., 84.1st percentile). Thus, the upper scenario represents an optimistic view of fire refugia and their ability to support post-fire recruitment. We compared these two scenarios by identifying pixels that were assigned to the same refugia class in each map (i.e., “areas of agreement”).

Results: Spatial Variation in Uncertainty of Model Predictions

Uncertainty in predictions of fire severity, species-specific recruitment probability, RI, and potential refugia varied markedly throughout the study area. Overall, prediction intervals of fire severity were fairly wide (Fig. S4.1), despite the promising performance of the model in spatially stratified cross-validation (Table 3 in the main text). We interpret this to mean that predictions of central tendency (i.e., the conditional mean) for fire severity are fairly reliable, but the width of prediction intervals also highlights the stochastic and complex nature of fire behavior, beyond what could be easily described using the spatial datasets considered here. Variation in the width of prediction intervals across the study area also demonstrates that there is greater uncertainty and scenarios than others. For example, under moderate weather conditions, much of the Arizona/New Mexico Mountains is predicted to be unburned, or burn at low to moderate severity (i.e., CBI < 2.25) with relatively high certainty when compared to other portions of the study area (Fig. S4.1c). Likewise, areas that have experienced recent fire (i.e., 2020 fires in northern Colorado and southern Wyoming), have greater certainty under moderate conditions, highlighting their importance as fire breaks during moderate weather. In contrast, areas with greater certainty under extreme fire weather tended to be dense-canopied, higher-elevation forests in the Southern Rocky Mountains (Fig. S4.1c). Thus, it can be stated with greater certainty that such areas are likely to burn at moderate to high severity (i.e., CBI > 1.25) under extreme weather than other forests throughout the study area.

In comparison to models of fire severity, models of recruitment probability had relatively narrow prediction intervals (Figs. S4.2-S4.7), though a direct comparison is difficult given differences in underlying statistical methods, and the nature of the response variable (i.e., continuous vs. binary). However, because of the comparatively narrow prediction intervals for many species, RI values in “lower” and “upper” scenarios did not substantially differ throughout much of the study area (Fig. S4.8). A notable exception is in central Arizona, where predicted RI values were relatively high (Fig. 6 in the main text; Fig. S4.8, Table S4.1), but also had high uncertainty relative to many other portions of the region (Fig. S4.8c). Many of these areas are dominated by ponderosa pine, and predicted post-fire recruitment in this area is close to the statistical threshold that separates likely presence and absence for the species (Fig. S3.5). Thus, a reduction of one standard error of the prediction for this species puts many 30-m pixels below the threshold for species presence (Table S3.1), which in turn reduces the community-weighted recruitment index in central Arizona. In contrast, areas with dominance by other tree species show comparatively greater certainty in RI values.

The locations of potential refugia in lower and upper scenarios illustrate notable uncertainty, as well as some generalizable trends (Fig. S4.9). Altering RI and fire severity using values from their prediction intervals lead to important changes in the amount and distribution of refugia with high recruitment, refugia with low recruitment, and non-refugia. Under moderate weather, 8.7% of total study area shows class agreement between the lower and upper scenarios (Fig. S4.9c), of which 99.5% was either refugia with high recruitment (25.7%) or refugia with low recruitment (73.8%), and less than 0.5% were non-refugia. Under extreme weather, 17.5% of the total study area exhibited class agreement between lower and upper scenarios, primarily (99.7%) in “non-refugia”, with only 0.3% in refugia with low or high recruitment. Thus, predicted locations of refugia are more certain under moderate weather conditions, whereas the predicted locations of non-refugia are more certain under extreme weather conditions.

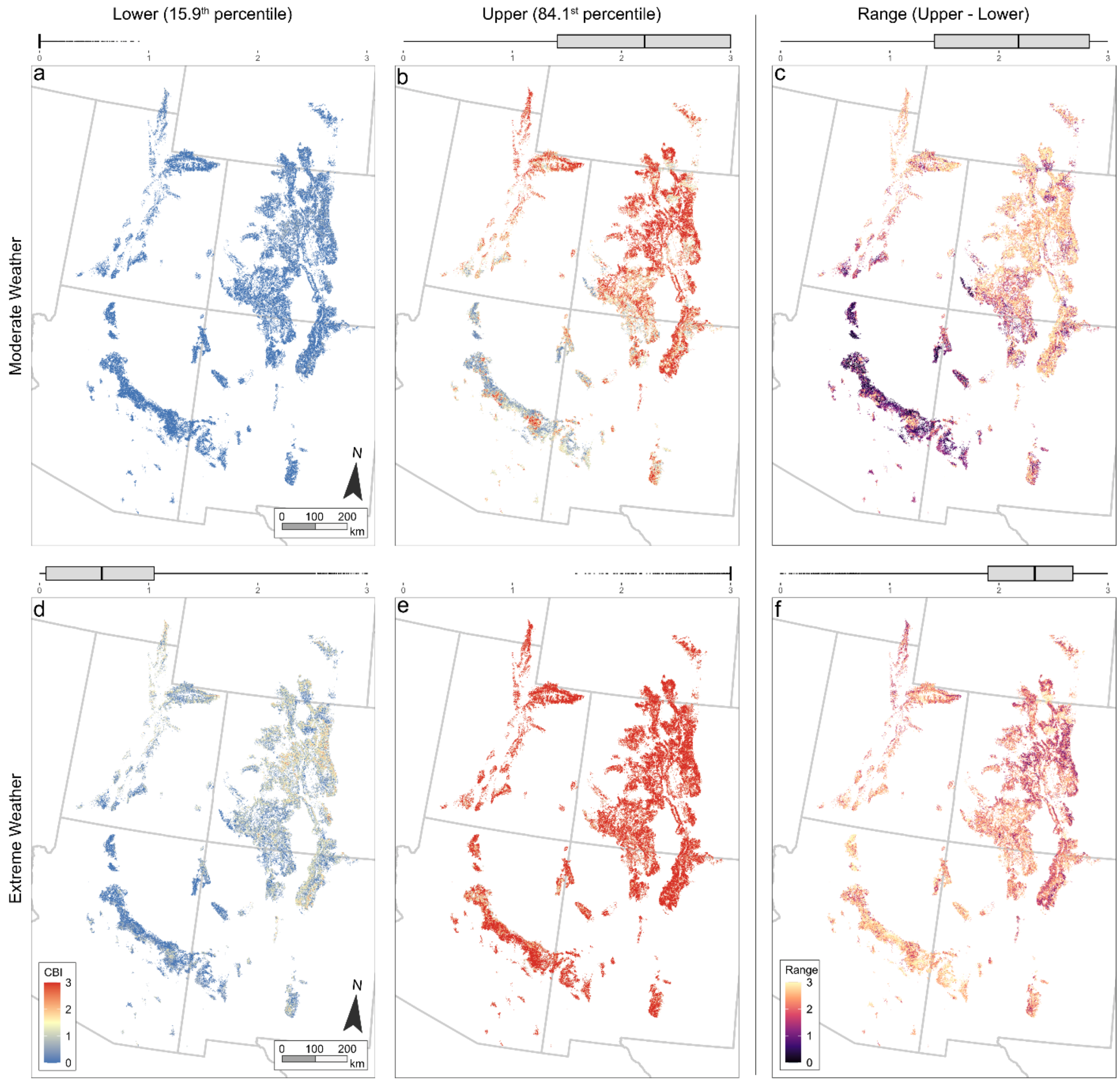

Figure S4.1: Uncertainty in predictions from models of fire severity (i.e., CBI) presented in Figs. 3-5 in the main text. Panels (a, d) give the "lower" bounds of the prediction interval (i.e., the 15.9th percentile), panels (b, e) give the "upper" bounds of the prediction interval (i.e., the 84.1st percentile). Predictions were made using quantile regression forests, with percentiles for lower and upper bounds selected to approximate the mean ± one standard error of the prediction. Panels (c, f) show the width of the prediction interval (i.e., upper minus lower bounds), with brighter areas having comparatively greater uncertainty. Boxplots above each panel summarize regionwide values within each map.

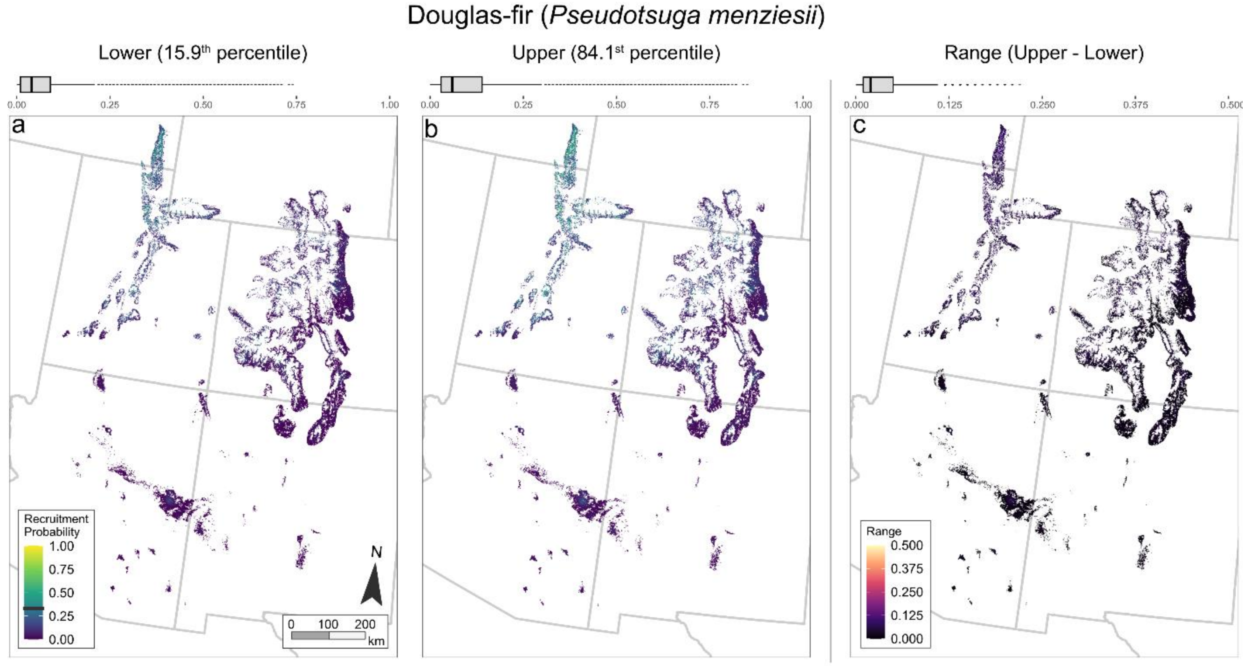

Figure S4.2: Uncertainty in predictions from the model of post-fire Douglas-fir recruitment probability, presented in Table S3.1 and Fig. S3.2. Panel (a) gives the "lower" bounds of the prediction interval (i.e., the 15.9th percentile; mean minus one standard error of the prediction) and panel (b) gives the "upper" bounds of the prediction interval (84.1st percentile; i.e., mean plus one standard error of the prediction). Panel (c) shows the width of the prediction interval (i.e., upper minus lower), with brighter areas having comparatively greater uncertainty. Maps were restricted to areas with at least 1 m^2 ha^{-1} of the corresponding species. The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1. Boxplots above each panel summarize regionwide values within each map.

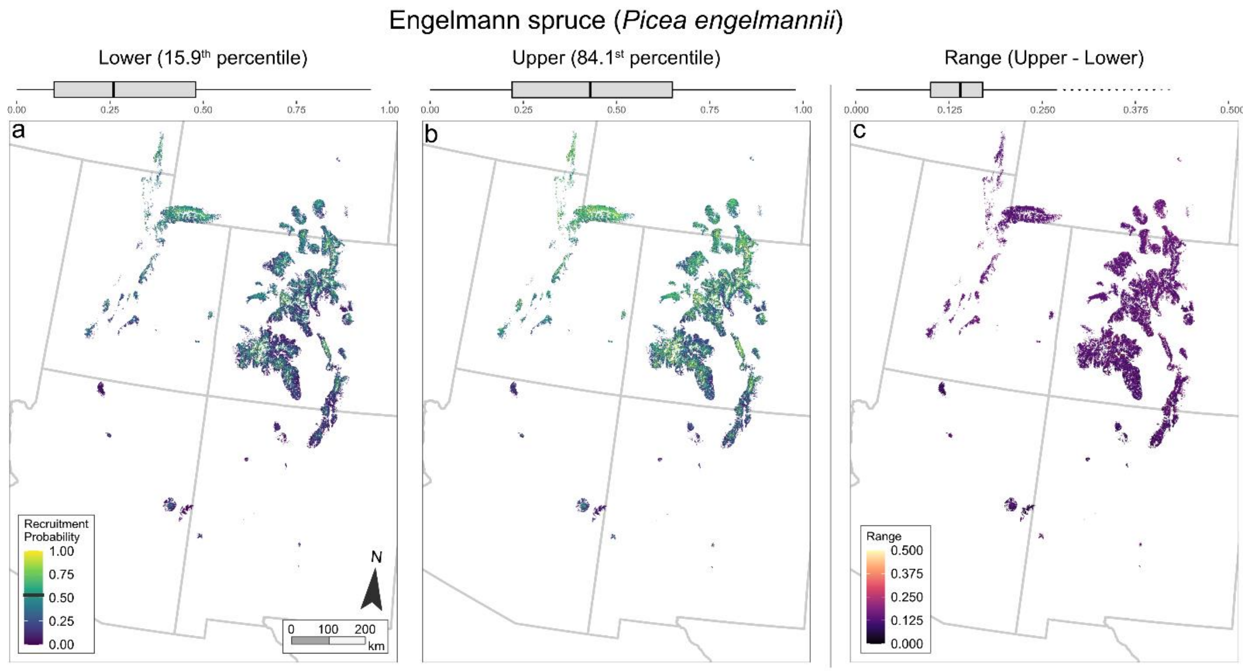

Figure S4.3: Uncertainty in predictions from the model of post-fire Engelmann spruce recruitment probability, presented in Table S3.1 and Fig. S3.3. Panel (a) gives the “lower” bounds of the prediction interval (i.e., the 15.9th percentile; mean minus one standard error of the prediction) and panel (b) gives the “upper” bounds of the prediction interval (84.1st percentile; i.e., mean plus one standard error of the prediction). Panel (c) shows the width of the prediction interval (i.e., upper minus lower), with brighter areas having comparatively greater uncertainty. Maps were restricted to areas with at least 1 m^2 ha^{-1} of the corresponding species. The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1. Boxplots above each panel summarize regionwide values within each map.

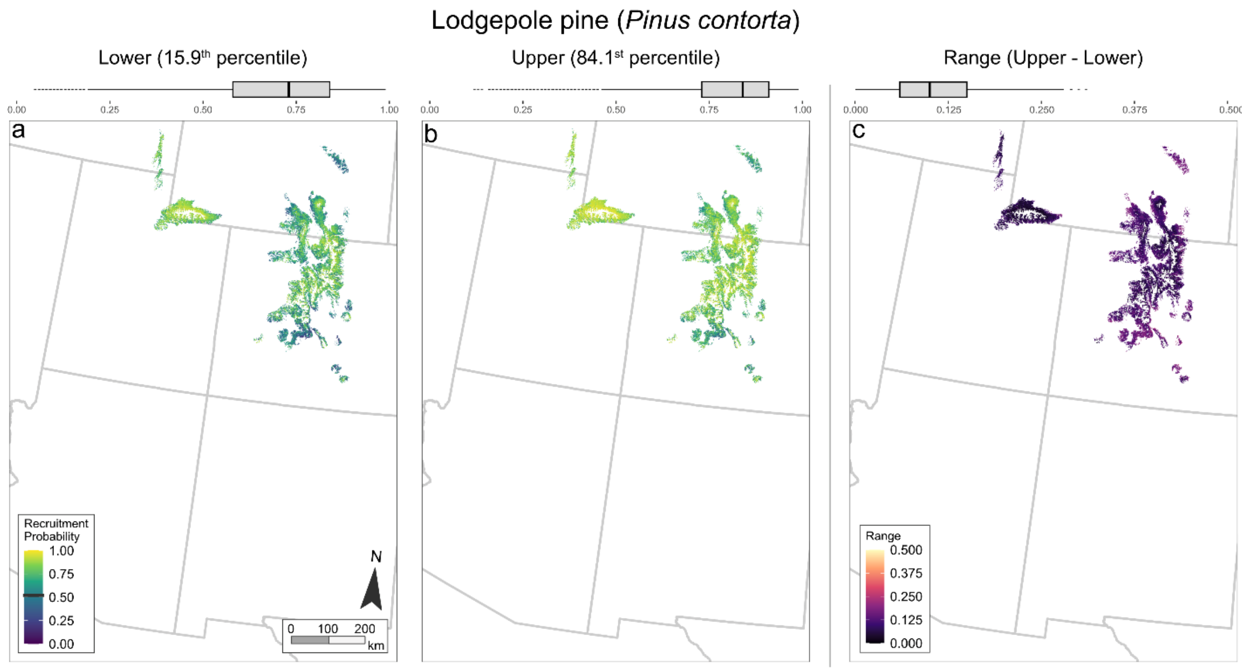

Figure S4.4: Uncertainty in predictions from the model of post-fire lodgepole pine recruitment probability, presented in Table S3.1 and Fig. S3.4. Panel (a) gives the “lower” bounds of the prediction interval (i.e., the 15.9th percentile; mean minus one standard error of the prediction) and panel (b) gives the “upper” bounds of the prediction interval (84.1st percentile; i.e., mean plus one standard error of the prediction). Panel (c) shows the width of the prediction interval (i.e., upper minus lower), with brighter areas having comparatively greater uncertainty. Maps were restricted to areas with at least 1 m^2 ha^{-1} of the corresponding species. The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1. Boxplots above each panel summarize regionwide values within each map.

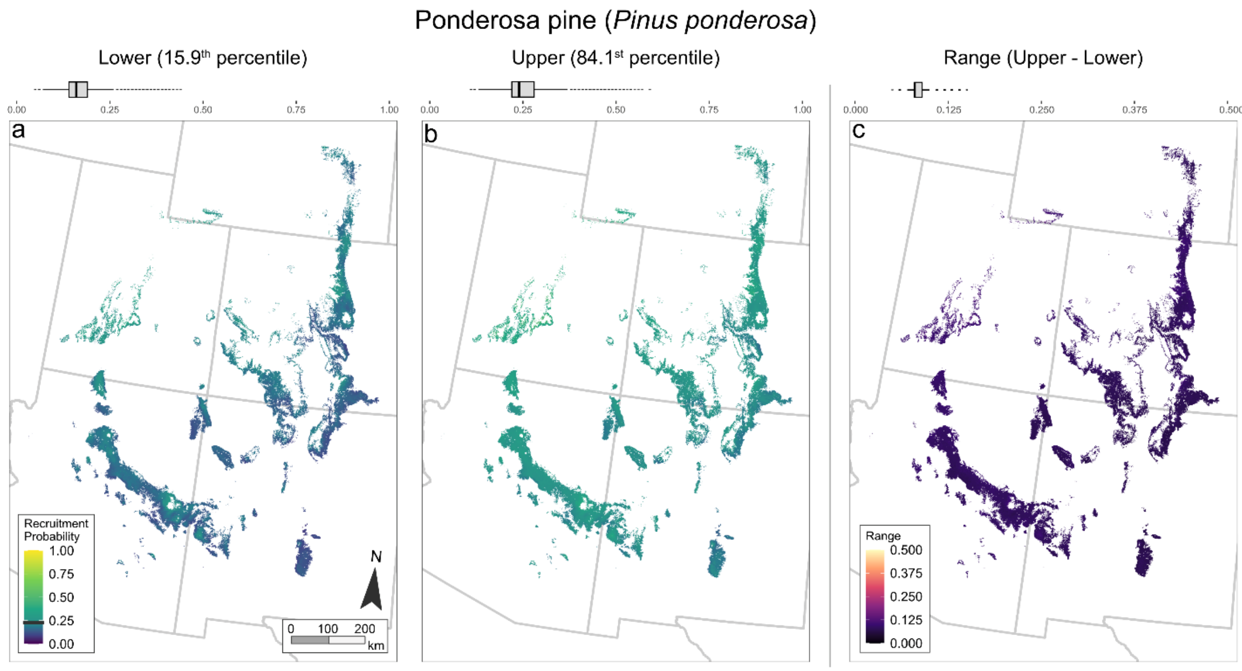

Figure S4.5: Uncertainty in predictions from the model of post-fire ponderosa pine recruitment probability, presented in Table S3.1 and Fig. S3.5. Panel (a) gives the "lower" bounds of the prediction interval (i.e., the 15.9th percentile; mean minus one standard error of the prediction) and panel (b) gives the "upper" bounds of the prediction interval (84.1st percentile; i.e., mean plus one standard error of the prediction). Panel (c) shows the width of the prediction interval (i.e., upper minus lower), with brighter areas having comparatively greater uncertainty. Maps were restricted to areas with at least 1 m^2 ha^{-1} of the corresponding species. The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1. Boxplots above each panel summarize regionwide values within each map.

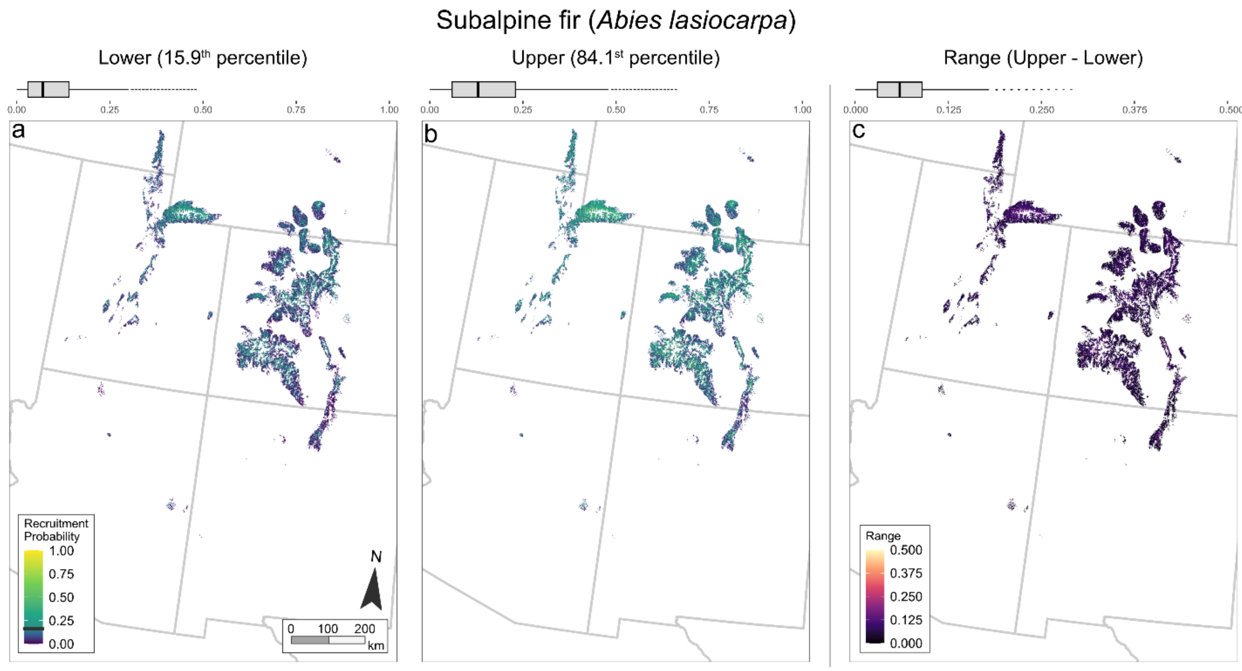

Figure S4.6: Uncertainty in predictions from the model of post-fire subalpine fir recruitment probability, presented in Table S3.1 and Fig. S3.6. Panel (a) gives the “lower” bounds of the prediction interval (i.e., the 15.9th percentile; mean minus one standard error of the prediction) and panel (b) gives the “upper” bounds of the prediction interval (84.1st percentile; i.e., mean plus one standard error of the prediction). Panel (c) shows the width of the prediction interval (i.e., upper minus lower), with brighter areas having comparatively greater uncertainty. Maps were restricted to areas with at least 1 m^2 ha^{-1} of the corresponding species. The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1. Boxplots above each panel summarize regionwide values within each map.

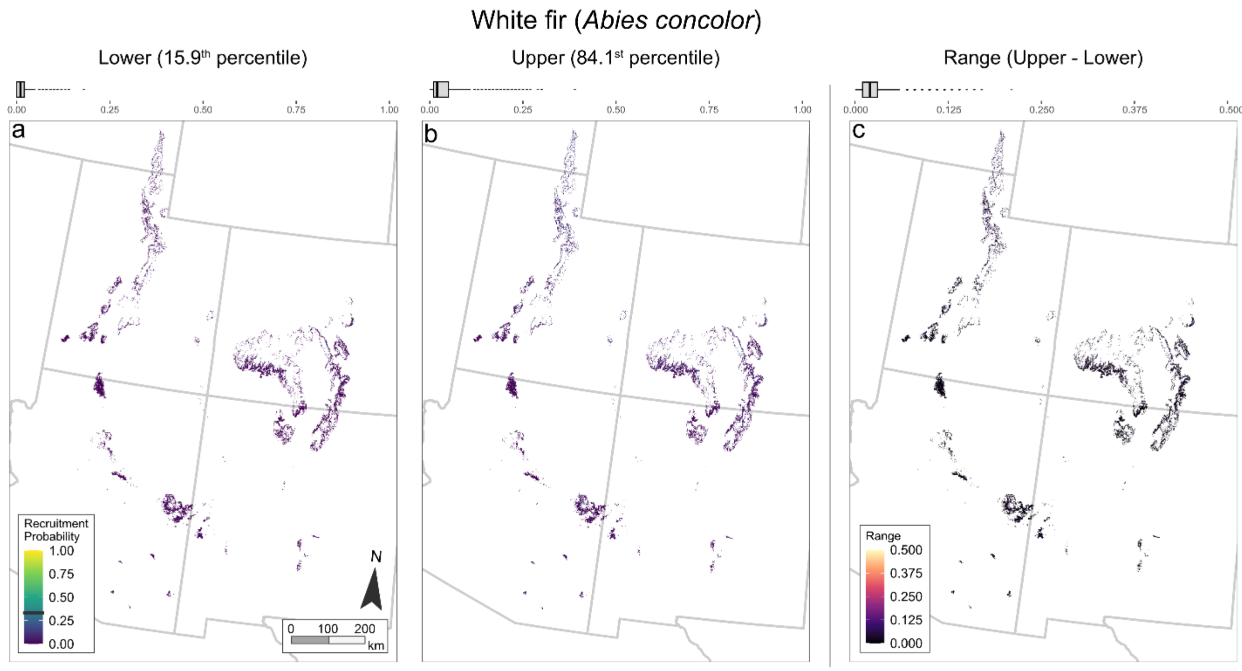

Figure S4.7: Uncertainty in predictions from the model of post-fire white fir recruitment probability, presented in Table S3.1 and Fig. S3.7. Panel (a) gives the "lower" bounds of the prediction interval (i.e., the 15.9th percentile; mean minus one standard error of the prediction) and panel (b) gives the "upper" bounds of the prediction interval (84.1st percentile; i.e., mean plus one standard error of the prediction). Panel (c) shows the width of the prediction interval (i.e., upper minus lower), with brighter areas having comparatively greater uncertainty. Maps were restricted to areas with at least 1 m^2 ha^{-1} of the corresponding species. The black horizontal line in the legend of (a) shows the probability threshold that best separates presence and absence in Table S3.1. Boxplots above each panel summarize regionwide values within each map.

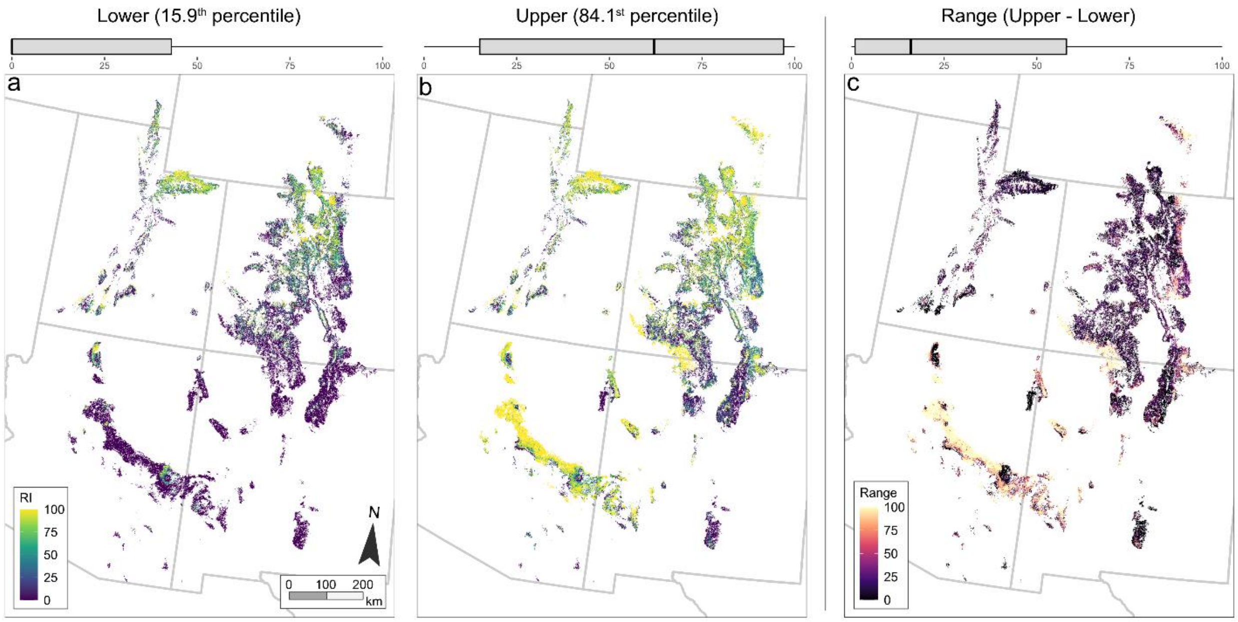

Figure S4.8: Uncertainty in predictions of the recruitment index (RI), presented in Fig. 6 of the main text. Panel (a) gives RI calculated using the lower bounds of the prediction interval for each tree species (i.e., panel [a] maps in Figs. S4.2-4.7), whereas panel (b) gives RI calculated using the upper bounds for each species (i.e., panel [b] maps in Figs. S4.2-4.7). Panel (c) shows the width of the prediction interval (i.e., upper minus lower bounds), with brighter areas having comparatively greater uncertainty. Boxplots above each panel summarize regionwide values within each map.

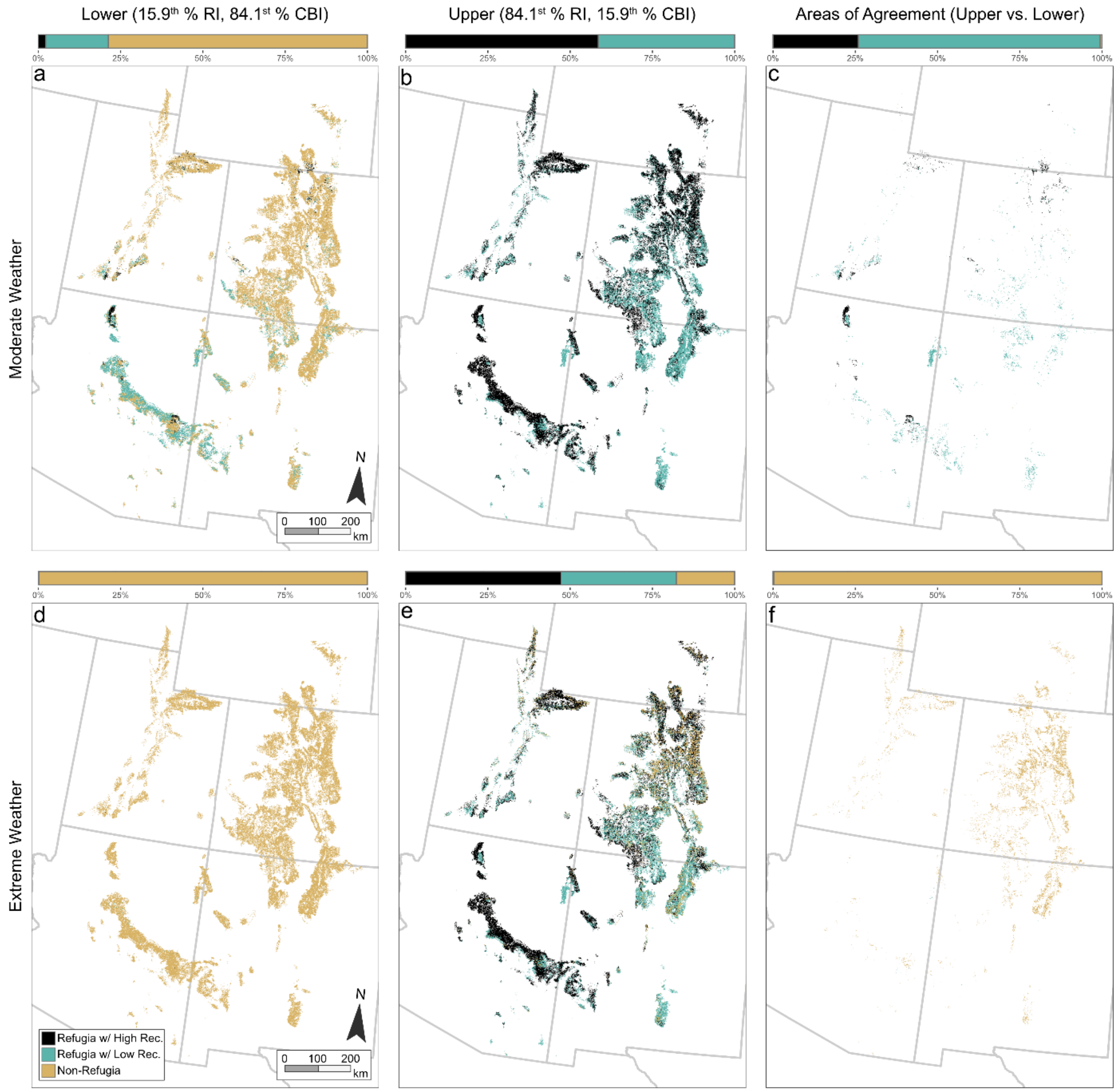

Figure S4.9: Spatially explicit uncertainty of the locations of refugia with high recruitment, refugia with low recruitment, and non-refugia, presented in Fig. 7 of the main text. Panels (a, d) give potential refugia locations calculated using the upper bounds of fire severity (i.e., CBI, composite burn index; Fig. S4.1a) under each fire weather scenario, and lower bounds of the recruitment index (i.e., RI; Fig. S4.8a), whereas panels (b, e) give the locations of potential refugia using the lower bounds of fire severity (Fig. S4.1b) under each fire weather scenario, and upper bounds of the recruitment index (Fig. S4.8b). Panels (c, f) show locations of agreement between lower and upper panels, and have comparatively greater certainty. Boxplots above each panel summarize regionwide values within each map.

Table S4.1: Predicted values of fire severity (CBI; Fig. 5 in main text and Fig. S4.1) and the recruitment index (RI; Fig. 6 in main text and Fig. S4.8) across upland conifer forests of the southwestern US. Numbers before parentheses are the mean predicted value within each EPA Level III ecoregion (EPA, 2021). Parenthetical values are the mean width of pointwise prediction intervals in Figs. S4.1c (left column), S4.1f (middle column) and S4.8c (right column), approximately two standard errors of the prediction.

Ecoregion	Fire Severity – Moderate Weather	Fire Severity – Extreme Weather	Recruitment Index
Arizona/New Mexico Mountains	0.46 (1.23)	1.41 (2.51)	29.15 (60.78)
Madrean Archipelago	0.76 (1.61)	1.53 (2.46)	6.98 (16.11)
Southern Rocky Mountains	1.13 (2.32)	1.98 (2.16)	38.04 (25.09)
Wasatch and Uinta Mountains	0.96 (2.21)	1.90 (2.24)	55.33 (13.62)
Overall	0.94 (2.03)	1.83 (2.25)	37.9 (32.4)

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