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Assessing uncertainty in forecasts of refugia for Joshua trees using high-density distribution data

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Abstract

Joshua trees (*Yucca brevifolia* and *Yucca jaegeriana*) are iconic, foundational species of the Mojave and Sonoran Deserts in North America. Due to their ecosystem importance, long generation times, and low resilience to disturbance, these hybridizing sister species are increasingly the focus of conservation efforts. Predicting Joshua tree responses to impending climate variability, along with the extent of suitable future habitat and/or climate refugia, is critical to ongoing management planning. Previous modeling efforts have been hampered by incomplete distribution data and are now out-of-date with the most recent global climate projections. We used a high-resolution, field-validated distributional database of nearly complete presence and absence records, along with a simulation of dispersal, to project Joshua tree distributions into future time periods and Coupled Model Intercomparison Project phase 6 (CMIP6) emissions scenarios. Overall, our models predict widespread habitat loss with limited availability of newly suitable habitat. Under the highest emissions scenario (SSP5–8.5), we project that up to 80% of current habitat may become unsuitable by 2100. Even so, our models predict a larger area of potential refugia than some previous efforts, particularly in the southern parts of the range, where we project persistent refugia through 2100. We also found a non-negligible influence of baseline climate period (the period used to represent "current" climate) on predicted future habitat probabilities. Simulations of dispersal based on the Joshua tree's limited capacity suggest that over 25% of suitable future habitat could be inaccessible, while much of the remaining future habitat area consists of refugia within the upper elevations of the species' current range. An increasing frequency of wildfire appears to be the greatest rangewide threat to future suitable habitat for Joshua trees, followed by renewable energy development. Over 80% of future suitable habitat occurs on federally managed lands, including up to 47% within Bureau of Land Management-administered areas and 15% within National Park Service units.

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dispersal, disturbance, Joshua trees, refugia, renewable energy, species distribution model, wildfire, *Yucca brevifolia*, *Yucca jaegeriana*

INTRODUCTION

The Mojave and Sonoran Deserts of North America are biodiversity hotspots, supporting hundreds of endemic species and multiple plant community types found nowhere else (Walker & Landau, 2018). Many native plants in these regions are adapted to a narrow range of environmental conditions, making them vulnerable to rapid changes such as surface disturbances and greater climate variability (Miller et al., 2009). In particular, long-lived desert species with life histories characterized by slow growth and rare seedling establishment are notoriously slow to recover from disturbance (Shryock et al., 2014). Higher temperatures, altered precipitation patterns (Seager et al., 2007), increased frequency of extreme drought (Dai, 2013), and amplified El Niño Southern Oscillation patterns (Cai et al., 2015) could fundamentally alter ecosystem processes within the Desert Southwest and shift or decrease habitat for numerous endemic species (Brown et al., 1997). The past 20 years were the driest in over 1200 years for southwestern North America (Williams et al., 2022). Moreover, changing temperature and precipitation patterns may interact with other factors, particularly invasive species-driven wildfires (Fusco et al., 2019) and land use change (Guo et al., 2018), to threaten native communities poorly adapted to such conditions. Predicting how desert species will respond to increased drought and temperature extremes expected for the southwestern United States features heavily in conservation planning across government agencies, tribes, and non-profit organizations. Utility-scale renewable energy development in this region, including solar and wind projects, also has the potential to impact habitat for numerous species (Bureau of Land Management, 2024; Smith et al., 2023). Hence, landscape development planning may benefit from knowledge of critical habitat for important native species, including locations of climate refugia.

Joshua trees (*Yucca brevifolia* and *Yucca jaegeriana*) are iconic, tree-like monocots that occur naturally in the Mojave and northwestern Sonoran Deserts (Spaulding, 1990; Van Devender, 1990). Once extending farther south into Mexico, the species' ranges contracted northward with climatic warming during the late Pleistocene (Smith et al., 2011; Van Devender, 1990). Although the western (*Y. brevifolia*) and eastern (*Y. jaegeriana*) Joshua trees occupy similar habitats in terms of climate and substrates (Esque et al., 2023), genetic divergence is maintained through an obligate pollinator mutualism (Godsoe et al., 2008; Yoder et al., 2013). Joshua trees are generally the tallest species in the sparse desert plant communities they inhabit, often co-occurring with smaller shrubs such as creosotebush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), or blackbrush (*Coleogyne ramosissima*), among many other species (Keeler-Wolf, 2007). The tree-like yuccas provide shelter and food for a number of wildlife species (Borchert & DeFalco, 2016). Given their broad ecosystem importance and iconic cultural status, Joshua trees are the focus of ongoing conservation efforts: the western Joshua tree was recently afforded protection in California under the Western Joshua Tree Conservation Act (State of California, 2023) but listing for both species was deemed unwarranted under the Endangered Species Act by the U.S. Fish and Wildlife Service (USFWS, 2023). A growing literature concerning the demography, establishment, and disturbance response of Joshua trees highlights potential vulnerabilities of populations to changing temperature and precipitation patterns and recent wildfire, threats which may be exacerbated by habitat loss (Smith et al., 2023; Sweet et al., 2019; Wilkening et al., 2020). Joshua trees are already restricted to cooler and moister upland sites within the Mojave Desert ecoregion as a whole (Esque et al., 2023) and have limited means for dispersal (Lenz, 2001; Vander Wall et al., 2006; Waitman et al., 2012), such that their ability to shift their distributions to track the changing climate may be limited (Cole et al., 2011; Dole et al., 2003).

As with other long-lived species, Joshua trees may be vulnerable to rapid changes in the environment because their long generation times, estimated to be from 50 to 70 years by Esque et al. (2015) for the western Joshua tree (*Y. brevifolia*)—although similar growth rates have been reported for the eastern Joshua tree (*Y. jaegeriana*; Comanor & Clark, 2000; Gilliland et al., 2006)—would likely slow demographic responses or adaptation to rapidly changing conditions. Seeding experiments with the eastern Joshua tree have shown that the climatic conditions for successful establishment are narrow and that their survival requires a deep root system that may require 95 days to develop (Lenz, 2001; Simpson, 1975). Although Joshua trees can germinate across a range of seasons, those that emerge with cool late spring rains are not likely to survive the high temperatures of the arid foresummer in June because they have little time to

accumulate resources and develop roots toward establishment. In contrast, seedlings that emerge during a strong summer monsoon have a higher likelihood of establishment because of the subsequent more reliable cool and wet winter rainfall period providing sufficient time for establishment (Reynolds et al., 2012). Moreover, following establishment, seedling and pre-reproductive Joshua trees are far more susceptible to drought, herbivory, and fire-caused mortality (DeFalco et al., 2010; Esque et al., 2015) than larger Joshua trees. Rising winter minimum temperatures, reduced summer precipitation, and increased recurrence of multi-year drought (Dai, 2013) could challenge the ability of Joshua tree populations to regenerate by seed rather than clonally. Among other threats, wildfires driven by invasive annual grasses such as red brome (*Bromus rubens* L.; Brooks et al., 2004) and cheatgrass (*Bromus tectorum* L.; Balch et al., 2013) have increasingly damaged Joshua tree populations, particularly since 2005 (Brooks & Matchett, 2006). Moreover, invasive grasses may become dominant within once-burned desert landscapes, increasing the likelihood of repeat burns (Klinger & Brooks, 2017). Joshua trees are often killed outright by wildfire (DeFalco et al., 2010), and the species does not maintain a long-term seedbank that could survive high soil temperatures experienced during wildfire (Esque et al., 2010; Reynolds et al., 2012). They are also unlikely to disperse back into disturbed areas with regularity, as seeds are largely eaten (Borchert & DeFalco, 2016) and dispersed only short distances by seed-caching rodents (Vander Wall et al., 2006; Waitman et al., 2012). Burned desert areas frequently have far fewer shrubs to provide microsites for seedling establishment, further reducing recruitment in those areas compared to unburned areas. Long-term observational studies have consistently indicated slow recovery times for disturbed Joshua tree woodlands (reviewed in Abella, 2010). Joshua trees also rely on an obligate mutualism with yucca moths for pollination, and the response of the yucca moths to climate variability, wildfire, or other disturbances could also prove limiting to the species resiliency (Godsoe et al., 2009).

Species distribution models (SDMs), which predict habitat probabilities for a species of interest based on environmental covariates at known occurrences, are a primary means of predicting species-level responses to various climate scenarios, although several caveats apply to their interpretation. In this approach, SDMs are fit to current day or "baseline period" climate and subsequently predicted into the same or broader areas using climate variables projected into future time periods and/or emissions scenarios, such as those from the Coupled Model Intercomparison Project phase 6 (CMIP6) representative concentration pathways corresponding to the 6th IPCC Assessment Report (IPCC, 2021). From the habitat probabilities resulting from SDMs, reflecting all potential suitable future habitat, climate refugia can be further defined as areas of predicted suitable future habitat that intersect with currently occupied habitat (in situ refugia from a "no-dispersal" scenario; sensu Ashcroft, 2010) or areas of suitable future habitat that are likely to be accessible through ordinary means of dispersal (ex situ refugia; sensu Ashcroft, 2010). The latter requires pairing SDMs with a model of partial dispersal incorporating aspects of the species biology and life history; for plants, this might include generation times, propagule dispersal mechanism and distance (Bateman et al., 2013; Engler et al., 2012). A less frequently applied interpretation of climate refugia, at least in terms of individual species distributions, includes areas that are buffered from climate variability due to microtopographic features that moderate temperatures or increase soil moisture, or areas in proximity to large water bodies (Morelli et al., 2016). However, identifying refugia at this microscale is beyond the scope of most SDMs, which rely on climate projections that are typically downscaled at coarser resolutions (1–10 km^2), and hence may be considered "macrorefugia" (Morelli et al., 2020).

An important caveat to the SDM approach is that these correlative models often do not account for biases that may limit model transferability to novel environments (Dormann et al., 2012), such as lag effects due to species demographic processes (Fordham et al., 2012; Svenning & Sandel, 2013), intraspecific variation arising from local adaptation (Jay et al., 2012), biotic interactions with non-focal species (Briscoe et al., 2019), microtopographic effects not well captured by the scale of environmental data used in modeling (Ashcroft, 2010), or difficulties with predicting into non-analog future environments (Williams & Jackson, 2007). However, correlative SDM approaches implicitly account for mechanisms controlling species distributions and have shown similar accuracy to mechanistic models incorporating population dynamics (Fordham et al., 2018), making them useful to inform conservation planning (Franklin, 2023). Moreover, habitat extrapolations from SDMs can be improved by incorporating simulations of species dispersal, which can include aspects of the species demography in relation to habitat suitability through space and time (e.g., Engler et al., 2012; Inman et al., 2016, 2022), thereby helping to avoid overprediction of future suitable habitat when no constraints on dispersal are assumed ("full dispersal" scenarios sensu Bateman et al., 2013). Incorporating realistic estimates of species dispersal is particularly beneficial in predicting responses to climate variability (Franklin, 2010), given that species vary in their capacity to migrate toward newly suitable habitat due to life-history traits and other species-specific factors, such

as the degree of local habitat fragmentation and biogeographic barriers or conduits to dispersal (Bateman et al., 2013).

There have been multiple efforts to project climate refugia for Joshua trees, throughout the whole (Cole et al., 2011; Dole et al., 2003) or portions of their ranges (Barrows & Murphy-Mariscal, 2012; Sweet et al., 2019). These efforts have been inconsistent with respect to the predicted extent of future suitable habitat, particularly in the southern portion of the range, where local and rangewide models have alternatively predicted persistence or extirpation, respectively. Moreover, previous models have not attempted to simulate dispersal, instead considering only fixed distances (Cole et al., 2011) or no-dispersal scenarios (Sweet et al., 2019). However, recent developments afford a new opportunity to model future habitat for Joshua trees with potentially greater accuracy: by pairing observation-based satellite surveys with extensive field validation, Esque et al. (2023) reproduce the ranges of both species of Joshua trees with near complete accuracy and high spatial precision (500 m^2). Here, we pair this novel occurrence dataset with updated future climate scenarios from the Coupled Model Intercomparison Projects of the IPCC sixth assessment report (CMIP6; Eyring et al., 2016; Lee et al., 2021), and a life-history based model of dispersal capacity (Engler et al., 2012) to predict future suitable habitat and climate refugia for Joshua trees with potentially greater accuracy than previous efforts. The use of new high-resolution occurrence data allows us to avoid several biases inherent to SDMs. By reproducing the entire range without relying solely on ground observations or herbarium specimens, the dataset avoids spatial selection bias due to inconsistent or incomplete sampling (Fourcade et al., 2014; Phillips et al., 2009). Moreover, by using extensive absence points generated from the margins of the species range, we remove biases which can occur from pseudo-absence selection in presence-only models (Lobo & Tognelli, 2011; VanDer Wall et al., 2009). Our models also include remotely sensed vegetation and edaphic properties, along with topographic metrics, which can improve accuracy relative to models incorporating climate alone (Velazco et al., 2017). Finally, given that aspects of Joshua tree's demography and dispersal potential are fairly well established, we incorporate a simulation of dispersal capabilities to better reflect future habitat accessibility.

Our objectives for the current work are threefold: (1) to develop new predictions for Joshua tree's future habitat suitability and in situ versus ex situ climate refugia based on high resolution range mapping, updated future climate assessments, and dispersal capacity; (2) to assess the variability in our forecasts due to emissions scenario, future time period, and baseline or "current day" climate period; and (3) to evaluate threats to future suitable habitat and refugia due to urbanization, renewable energy development, and wildfire, along with the land management status of these areas.

METHODS

Study area and species

The western (*Y. brevifolia*) and eastern (*Y. jaegeriana*) Joshua trees occupy mid-elevation mixed scrub and woodland habitats of the Mojave and Arizona Upland of the Sonoran warm desert ecoregions. The two species currently occupy approximately 32,000 km^2 of habitat based on an extensive remote-sensing and field-validated survey (Esque et al., 2023), including a narrow hybrid zone where the species' ranges overlap in the central Mojave Desert. Genetic isolation between Joshua tree species is thought to be maintained by an obligate mutualism with their respective pollinators—sister species of yucca moths with obligate seed-feeding larvae (Godsoe et al., 2008; Lenz, 2007; Pellmyr & Segraves, 2003), although this may not be the only mechanism (Royer et al., 2020). Habitat for the two Joshua tree species is similar in terms of overall aridity, annual precipitation (MAP approximately 200 mm), and annual temperature profiles (MAT approximately 16°C). However, *Y. jaegeriana* experiences a more bimodal precipitation pattern with increased summer/fall rainfall and slightly higher summer temperatures (Esque et al., 2023).

Present-day distribution

We represented the present-day distribution of Joshua trees with a previously developed, high resolution SDM, which is detailed in Esque et al. (2023). In brief, occurrences for this model were based on a visual grid search of high-resolution satellite imagery throughout the potential range of both Joshua tree species, along with extensive field validation and re-evaluation of imagery in grid cells to refine the final set of presences and absences. Field validation indicated that these techniques reproduce the range with little error. We then used random forest (RF) models (r package "ranger" v. 0.12.1; Wright & Ziegler, 2017) fit to the presence/absence records to extrapolate into areas known to support Joshua trees, but with obscured satellite imagery (e.g., Department of Defense lands). The final RF SDM comprised a weighted, model-averaged ensemble of eight candidate models assessed via spatial cross-validation (R package "blockCV" v2.1.4.; Valavi et al., 2019), with an

average AUC of 0.87 (on independently withheld data). A range of environmental variables were used to fit the RF models, including climate, topography, and remotely sensed vegetation and edaphic properties (Table 1). We chose a combined RF model, rather than individual species models, to represent the range of both Joshua trees because cross-validation performance was similar and between-model SDs in spatial predictions were

TABLE 1 Covariates used to fit habitat models (species distribution models) in current and future climate.

Covariate	Abbreviation	Description
Climate		
Annual heat/moisture index	AHM	Mean annual temperature in Celsius divided by mean annual precipitation in millimeters (MAT + 10)/(MAP/1000).
Mean annual precipitation	MAP	Average annual precipitation received during the climatic normal period.
Mean annual temperature	MAT	Average of the monthly temperature averages for the climatic normal period.
Precipitation ratio	P_{ratio}	Ratio of summer to winter precipitation.
Precipitation seasonality	PCV	CV in monthly precipitation totals for the normal period.
Summer maximum temperature	SMT	Average maximum temperature from June to August, based on the climatic normal period.
Summer Precipitation	SP	Average total precipitation received from May to October, based on the climatic normal period.
Temperature range	T_{range}	Difference between winter minimum temperature and summer maximum temperature.
Temperature seasonality	TSD	SD of the monthly mean temperatures.
Winter minimum temperature	WMT	Average minimum temperature from December to February, based on the climatic normal period.
Winter precipitation	WP	Average total precipitation received from November to April, based on the climatic normal period.
Satellite		
Climatic moisture deficit	CMD	A modified Thornthwaite-Mather climatic water-balance model (sensu Lutz et al., 2010) was used to calculate annual estimates of actual evapotranspiration (AET) and deficit between 1916 and 2005 at the 30 arc second resolution (Dobrowski et al., 2013).
NDVI amplitude	AMP	Maximum increase in canopy photosynthetic activity above the baseline. Derived from MODIS satellite bands.
NDVI maximum	Maxn	Normalized Difference Vegetation Index (NDVI) at the maximum level of photosynthetic activity in the canopy. Derived from MODIS satellite bands.
Sandy soils	Sand	Amount of soil surface texture in g/kg containing sand particle size (0–5 cm depth).
Topography		
Heat load index	HLI	Aspect/slope transformation index from McCune and Keon (2002), representing the range in heat load from coolest (northeast slope) to warmest (southwest slope).
Slope	Slope	Derived from a 30 m DEM and upscaled to 500 m resolution.
Topographic position	TPI	Steady state wetness index expressed as a function of slope and upstream contributing area (Moore et al., 1993). Derived from a 30 m DEM and upscaled to 500 m resolution.

Note: All variables were derived at a 500 m^2 spatial resolution using the North American Datum of 1983, UTM zone 11N (EPSG: 26911). Precipitation and temperature layers were created using ClimateNA v. 7.3 (Wang et al., 2016), which downscales PRISM data (Daly et al., 2008) and corrects for elevational variation. Satellite metrics incorporating data from the moderate-resolution imaging spectroradiometer (MODIS) satellite were averaged across 17 years (2003–2020) to represent a norm for the study region (NDVI amplitude and maximum—USGS eMODIS Remote Sensing Phenology, https://doi.org//10.5066/F7PC30G1). Soil surface texture was downloaded and mosaicked from the SoilGrids 2.0 web portal (Poggio et al., 2021). Topographic metrics were calculated by aggregating a 30 m digital elevation model (DEM) to 500 m × 500 m resolution (U.S. Geological Survey 3D elevation program, available from: https://www.usgs.gov/the-national-map-data-delivery).

improved (Esque et al., 2023). For spatial overlays, the current distribution was represented by a hybrid model combining the validated survey data with RF extrapolations into areas with obscured satellite imagery.

Future habitat projections

We predicted future suitable habitat by fitting RF models to current time period (hereafter "baseline period") climate variables, and then predicting the models on the same climate covariates defined for future climate periods, while holding all non-climate variables constant. As with the present-day SDM, model-averaging procedures were used to take a weighted average of model predictions across cross validation runs for each candidate future climate model, and among the candidate models (see Esque et al., 2023). It can be difficult to select a baseline climate period to represent the "current conditions" for a long-lived, slow-growing species such as the Joshua tree, and this ambiguity may lead to differences in forecasts of future habitat (e.g., Cole et al., 2011). For this reason, we compared multiple baseline periods to determine whether this choice impacted future suitable habitat projections (Table 2). We also compared three different emissions pathways defined in the IPCC AR6 report (Lee et al., 2021), representing the upper (SSP5–8.5), lower (SSP2–4.5), and medium-range (SSP3–7.0) bounds of potential emissions levels. For each pathway, we used the average from an ensemble of eight global circulation models (GCMs) as defined by Mahony et al. (2022) such that projections would remain consistent with the IPCC's "very likely" range of equilibrium climate sensitivity. Finally, we also compared three different future time periods along each emissions pathway, including near-term (2021–2040), midcentury (2041–2070), and late century (2071–2100) scenarios (Table 2). All climate data were derived on a 500×500 m resolution raster using ClimateNA v. 7.3 (Wang et al., 2016), which downscales PRISM climate data (Daly et al., 2008) using a local regression approach to correct for elevational variation for both baseline and future time periods (Mahony et al., 2022). Overall, we calculated future-projected SDMS for 30 combinations of baseline period, emissions scenario, and future time period. For each future projected SDM, we defined "future suitable habitat" as areas with habitat probabilities above the probability threshold used to classify habitat in the current-period SDM. This threshold was determined with the R package "dismo" (version 1.3-5; Hijmans et al., 2021) using a 90% sensitivity cutoff.

TABLE 2 Climate baseline periods (representing current conditions), future time periods, and emissions scenarios selected for modeling Joshua tree distributions.

Baseline periods	Future periods	Emissions scenarios (CMIP6)
1940–2000	2021–2040	SSP2–4.5
1970–2000	2041–2070	SSP3–7.0
1980–2010	2071–2100	SSP5–8.5
1990–2020	...	...

Note: Emissions scenarios correspond to the Coupled Model Intercomparison Project phase 6 (CMIP6) representative concentration pathways, as defined in the 6th IPCC Assessment Report (IPCC, 2021).

Uncertainty in forecasts of future suitable habitat

We used two methods to partition the variability in future habitat predictions due to baseline period, future time period, and emissions pathway. First, we calculated the overall estimated extent of future suitable habitat in square kilometers predicted by each of the 30 scenarios for use as a response variable. We then fit a three-way ANOVA without replication in R v. 4.1.3 (R Core Team, 2022) with baseline period, emissions pathway, and future time period as predictors, along with their interactions. This approach enables us to partition the SSs into the total percentage of variability explained by each predictor.

Second, we followed an approach proposed by Diniz-Filho et al. (2009) to conduct a spatial analysis of the uncertainty in forecasts of future habitat. Similar to the above, this method uses a multi-way ANOVA to partition the sources of variability in habitat probabilities. However, rather than using an overall sum of the predicted habitat area, we overlaid the 30 SDMs and conducted ANOVAs separately for each grid cell location. For each cell, we extracted the SSs attributable to each main effect and interaction, expressed as a percentage of the total. We then mapped these percentages to visualize the sources of variability in predictions through space.

Dispersal and refugia

Joshua trees do not possess a long-distance dispersal mechanism (their large seeds are dispersed short distances by seed-caching rodents; Vander Wall et al., 2006; Waitman et al., 2012), and do not appear to establish new individuals far beyond existing stands (Esque et al., 2023), likely due to infrequent recruitment and long generation times (Esque et al., 2015; Reynolds et al., 2012). Given these constraints, we chose to create dispersal-constrained scenarios for the future habitat SDMs, which may provide a more realistic range of outcomes. To simulate dispersal, we used a cellular-automaton approach following Engler

et al. (2012) and implemented in the R package MigClim (version 1.6, implemented in R version 3.5.2). In this approach, dispersal from cell to cell is controlled by multiple parameters, including: the habitat probability of grid cells for annual time steps and for future time period, termed "habitat change steps," which incorporate new SDMs reflecting successive future time periods (here, using the 2021–2040, 2041–2070, and 2071–2100 SDMs); P_{DISP}, a vector of probabilities defining the likelihood of dispersing from each grid cell to the next farthest cell from a focal occupied cell; and P_{PROP}, reflecting both the initial time to maturity (in annual dispersal steps), and the probability distribution determining propagule establishment from initial to full maturity age (e.g., when probability reaches 100%). Hence, P_{PROP} is a function of time since a cell is initially colonized in the simulation, representing the increasing ability of larger plants to produce propagules. Given that Joshua trees rarely disperse, we chose conservative values for these thresholds. We set the habitat suitability threshold to 0.462 (corresponding to 90% model sensitivity) with an annual time step, an initial plant maturity age of 30, and full maturity age of 70 (Esque et al., 2015). We allowed 30 annual time steps between each habitat change step in the MigClim simulation—2021, 2041, and 2071 SDMs—such that the final results indicated potential dispersal by 2041 (early century), 2071 (midcentury), or by 2100 (late century). The dispersal kernal P_{DISP} was set to [0.8, 0.05, 0.001], giving a high probability of a propagule moving one grid cell (e.g., 500 m^2) during the maturity phase, but low probability of moving up to three grid cells (1.5 km). Finally, we simulated the propagule production potential probabilities, P_{PROP}, using a beta distribution with shape parameters $\alpha = 2$ and $\beta = 5$ (rbeta function in the R "stats" package), resulting in an increasing probability of propagule production as colonized cells reached 70 annual time steps. The overall simulation was repeated 100 times for each climate scenario (SSP2–4.5, SSP3–7.0, and SSP5–8.5), with the results averaged between runs. Cells that could be colonized within the time frame of the simulations, but that did not intersect with currently occupied habitat, were considered to be accessible future habitat or "ex situ refugia," while current habitat that remained suitable and occupied throughout the simulation was considered to be "in situ" refugia. Henceforth, we term the spatial overlay of ex situ and in situ refugia for each emissions level/future time period scenario to be the total "accessible refugia" available to the species for that scenario.

Vulnerability and conservation status

We conducted an overlay analysis to determine the extent to which future suitable habitat, along with in situ and ex situ refugia, might be vulnerable to different types of disturbance and/or development, as well as the land management status of these areas. Spatial overlays were performed using the R package "terra" (version 1.5–34; Hijmans, 2022) at a spatial resolution of 500 m^2, corresponding to the SDM cell size. In some cases where existing spatial layers were insufficient, we created applicable layers through heads-up digitizing of Google Earth imagery in ArcGIS Pro. Disturbance categories we investigated included wildfire, urban development, renewable energy projects such as wind and solar power installations, agriculture, mineral resource extraction, roads, and railways.

Wildfire boundaries were downloaded from the USGS Monitoring Trends in Burn Severity database (https://www.mtbs.gov; Eidenshink et al., 2007), with the exception of the recent York fire (2023), which we digitized using the difference in Landsat normalized burn ratio from two cloud-free Landsat 9 scenes collected immediately before and after the wildfire. The MTBS database contains wildfires mapped from Landsat imagery that were larger than 4 km^2 and occurred after 1984 (when Landsat became available). Additionally, we assessed wildfire risk in Joshua tree habitat within the Mojave Desert portion of the range using an ignition probability layer from Klinger et al. (2021), who used fire history, climate, and remotely sensed vegetation indices to model ignition risk. Urban areas were delineated based on the 2019 National Land Cover Database impervious surfaces product (NLCD; Dewitz et al., 2021, https://doi.org/10.5066/P9KZCM54). Roads were represented by the U.S. Census Bureau Tiger Line shapefiles database (U.S. Census Bureau, 2023) and categorized according to type (highways, major and secondary roads, dirt roads). For other surface impacts, we combined existing information with hand-digitization, including for cultivated areas, mineral resource facilities, solar and wind energy installations. For example, we used mining and renewable energy point shapefiles from the North American Cooperation on Energy Information, Mapping Data available through the ESRI Living Atlas (https://open.canada.ca/data/en/dataset/aae6619f-f9f3-435d-bc32-42decd58b674) to aid in the search and creation of polygons for wind energy installations, as well as the roads leading to the windmills, solar farms or installations, and any mineral mining operations. For agricultural areas, we combined the NLCD "Cultivated Crops" and "Pasture Hay" layers with polygons digitized in Google Earth around agricultural areas not already covered by the NLCD layer. We also included verified renewable energy rights-of-way (ROW) from the U.S. Bureau of Land Management CA State Office, along with developable solar energy areas designated in the 2012 Western Solar

Plan (https://blmsolar.anl.gov/solar-peis), the California 2016 Desert Renewable Energy Conservation Plan (DRECP, 2015), and the 2013 Arizona Restoration Design Energy Project (RDEP; https://blmsolar.anl.gov/rdep). Finally, we evaluated proposed solar development alternatives from the 2023/2024 Draft Utility-Scale Solar Energy Development Programmatic Environmental Impact Statement (Bureau of Land Management, 2024), which would open new areas for solar energy project applications on BLM lands across 11 western states.

Apart from disturbance, we investigated the land management status of areas considered to be future suitable habitat and/or climate refugia. Presumably, Joshua tree habitat on federal lands, particularly those administered by the Bureau of Land Management (BLM), National Park Service (NPS), U.S. Fish and Wildlife Service (FWS), and certain Department of Defense (DOD) buffer areas, affords greater protection from future threats than private lands due to agency specific conservation objectives and partnerships in conjunction with the Western Joshua Tree Conservation Act, strong public interest, and laws such as the National Environmental Policy Act. Administrative boundaries were downloaded from the respective agencies and from the National Atlas of the United States (http://nationalmap.gov).

RESULTS

Future habitat projections

SDM predictions indicated considerable loss of suitable habitat across all future climate scenarios. Habitat loss was not concentrated in any one portion of the range (Figure 1A). The area of predicted future suitable habitat decreased linearly with time period from the 2021–2040 to the 2071–2100 future periods (Figure 2). The SSP5–8.5 (high emissions) scenario resulted in the largest habitat loss, while habitat loss under the low-emissions SSP2–4.5 scenario was considerably lower, and habitat loss under the SSP3–7.0 emissions scenario was intermediate. Overall, we project that the sister Joshua tree species could lose from 45% to 70% of their current range by 2070 and from 60% to 80% by 2100 (Figure 2; Appendix S1: Table S1), depending on the emissions scenario. Additional uncertainty could arise from the species ability to adapt or cope with future climate conditions, or to disperse to ex situ refugia as they become climatically suitable. Even in the highest emissions scenario for the period 2071–2100 (SSP5–8.5), however, our models do not predict total extirpation within any one portion of the range, including in the southernmost extent.

We also observed variation in future projections between models fit using different baseline climate periods to represent "current" conditions, but this variation was not consistent: no one baseline period consistently predicted the most or least area of future suitable habitat across emissions scenarios or future time periods. However, the 1940–2000 baseline had slightly better metrics than other baselines when fitted to the occurrence dataset (Table 3), and future projections fitted to this baseline period showed greater future suitable habitat area in the 2021–2040 and 2041–2070 periods, although not in the 2071–2100 period.

Areas projected to be future suitable habitat are typically higher in elevation, wetter, and cooler than current habitat on average (Figure 1B). However, future suitable habitat largely overlaps with current habitat in the upper elevations of the sister species' ranges (Appendix S1: Table S1), such that much of the future suitable habitat can be considered in situ refugia. For example, current habitat modeled with the 1940–2000 climate baseline contained approximately 70% of the future suitable habitat for 2041–2070 (SSP3–7.0 emissions scenario) and 60% of the future suitable habitat for 2071–2100. In situ refugia within the southernmost portion of the range are largely restricted to currently occupied higher elevation populations, with limited opportunity for upward migration. In contrast, future suitable habitat outside of current habitat is predicted northward of the current range for the western Joshua tree, and upward in elevation along the Hualapai Mountains for the eastern Joshua tree.

Uncertainty in forecasts of future habitat

At the aggregate level, future climate period explained approximately 70% of the variation in predicted future suitable habitat area across the combinations of scenarios (Appendix S1: Table S2). Emissions level was also influential, explaining 25% of the overall variation. Baseline period explained only 1% of the variation in total future suitable habitat area predicted.

However, results differed at the level of individual grid cell probabilities, particularly for grid cells with lower habitat probability values (Figure 3). In portions of the range with low predicted habitat probabilities (0–0.3), baseline climate period tended to explain the most variation in habitat probabilities among overlaid grid cells. Conversely, where current habitat probability values were higher (>0.3) and particularly in suitable habitat, future climate period explained the most variation across overlaid grid cells, followed by baseline. Overall, our findings suggest that using different baseline climate periods to represent "current" climate when projecting to a future period does impact results, but to a lesser extent than the

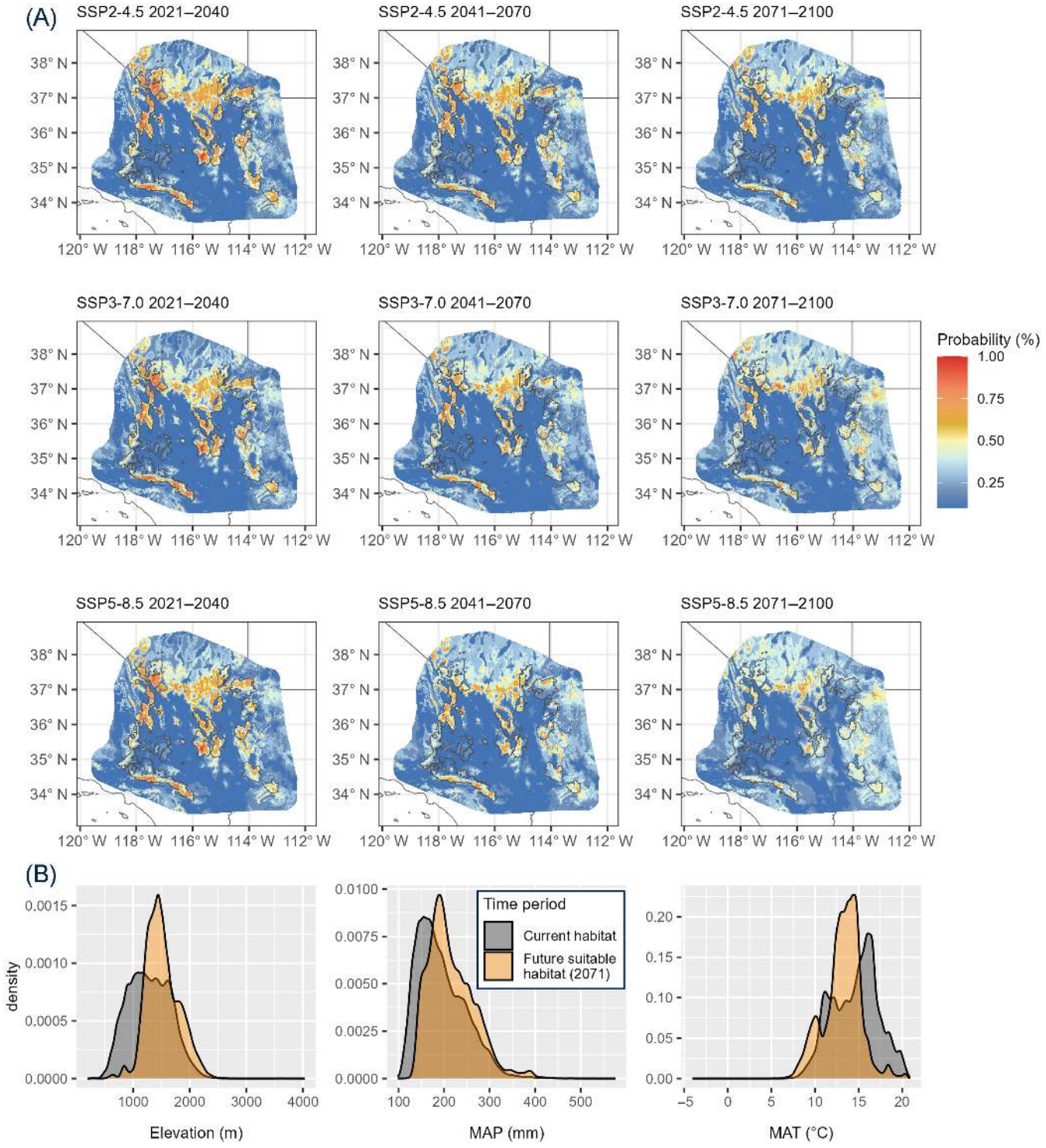


FIGURE 1 Projected future habitat probabilities for Joshua tree populations based on random forest models of presence and absence distribution data. (A) Panels are ordered by emissions scenario (rows) and future time period (columns). Plots show models first fit to the 1940–2000 climate baseline period and subsequently projected into future climate periods. (B) Density graphs contrast current habitat with future suitable habitat under the SSP3–7.0 2071–2100 scenario in terms of the current conditions at these sites for several variables. MAT, mean annual temperature; MAP, mean annual precipitation.

choice of future time period or emissions level (Figure 3), particularly for high habitat probability areas.

However, effects of baseline climate period were non-negligible. For the SSP3–7.0 emission scenarios, area of future suitable habitat ranged from 16,149 to 18,486 km^2 for 2041–2070 depending on the baseline climate period, and from 10,776 to 11,574 km^2 for 2071–2100 (Appendix S1: Table S1). Similarly, for the SSP5–8.5

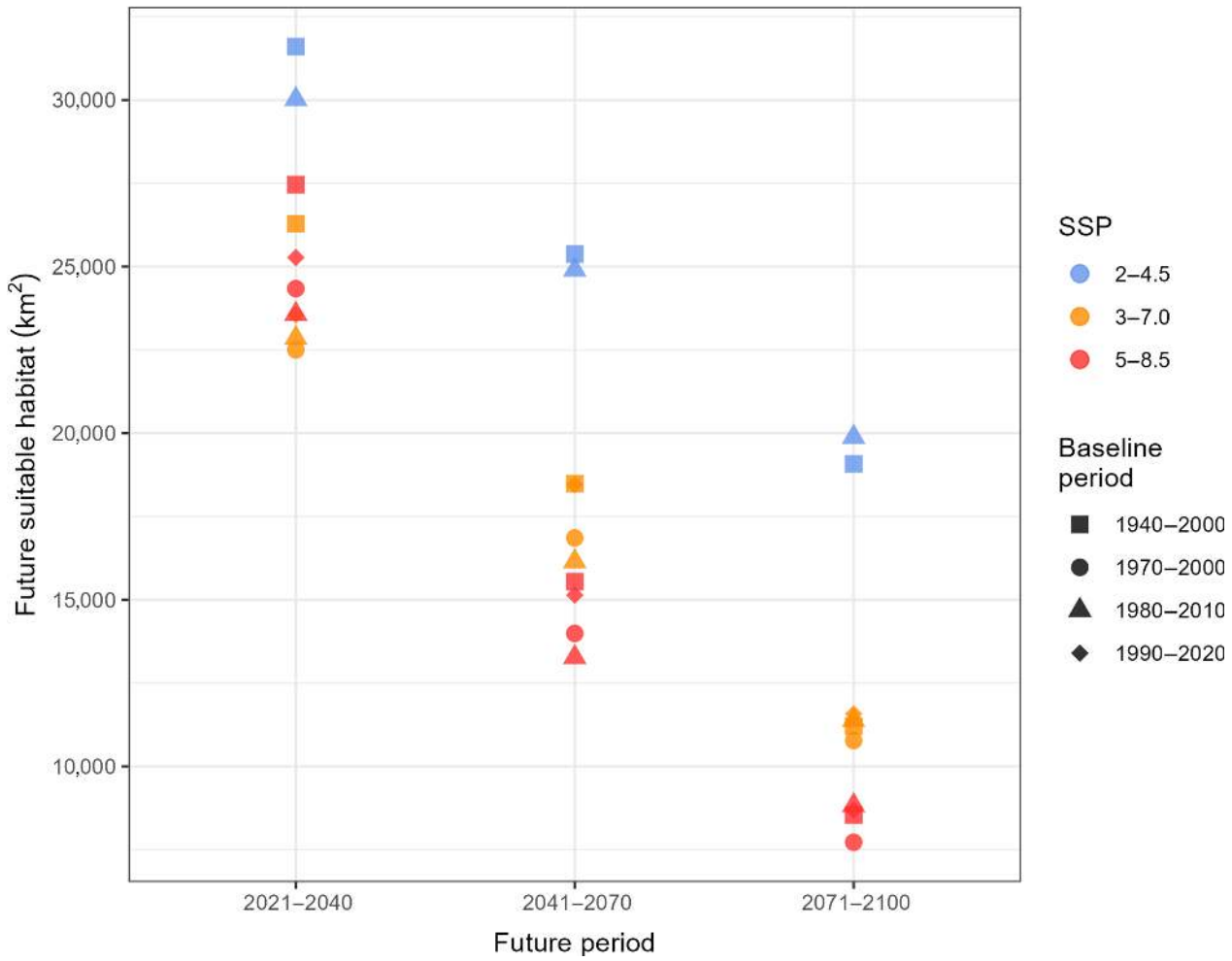


FIGURE 2 Area of Joshua tree future suitable habitat from models fit to different climate baseline periods, future time periods, and emissions scenarios (SSP).

scenario, future suitable habitat area ranged from 13,274 to 15,541 km^2 in 2041–2070 and from 7721 to 8825 km^2 in 2071–2100, depending on the baseline climate period used to fit the current conditions model. Based on these results, we created new layers for each emission and time period combination by averaging probabilities across the different baseline periods, referred to hereafter as "baseline mean" layers. In comparison to the individual SDMs, these layers are meant to bound the uncertainty due to "current climate" conditions by representing the consensus habitat probability among SDMs fit to different baseline periods. SDs across baselines for each emissions/future time period combination are displayed in the supplement (Appendix S1: Figure S1). We use the baseline mean layers for spatial overlays and simulations of dispersal.

TABLE 3 Average random forest model performance over model baseline periods (the climate normal period used to represent the "present day" or current conditions in species distribution models), based on spatial cross validation of independently withheld data subsets.

Baseline period	Average AUC	Average TSS
1940–2000	0.8703	0.5810
1970–2000	0.8698	0.5773
1980–2010	0.8681	0.5757
1990–2020	0.8688	0.5769

Note: Metrics include the area under the receiver operating characteristic curve (AUC; Fielding & Bell, 1997) and the true skill statistic (TSS; Allouche et al., 2006).

Dispersal and refugia

Projected accessible climate refugia for Joshua trees occurred predominantly at the upper elevations within current habitat, constituting in situ refugia. Hence, our simulations of potential dispersal to new habitat indicated that approximately 19.5% of potentially suitable future habitat may be inaccessible to Joshua trees by ordinary dispersal from 2041 to 2070, and 22.6% from

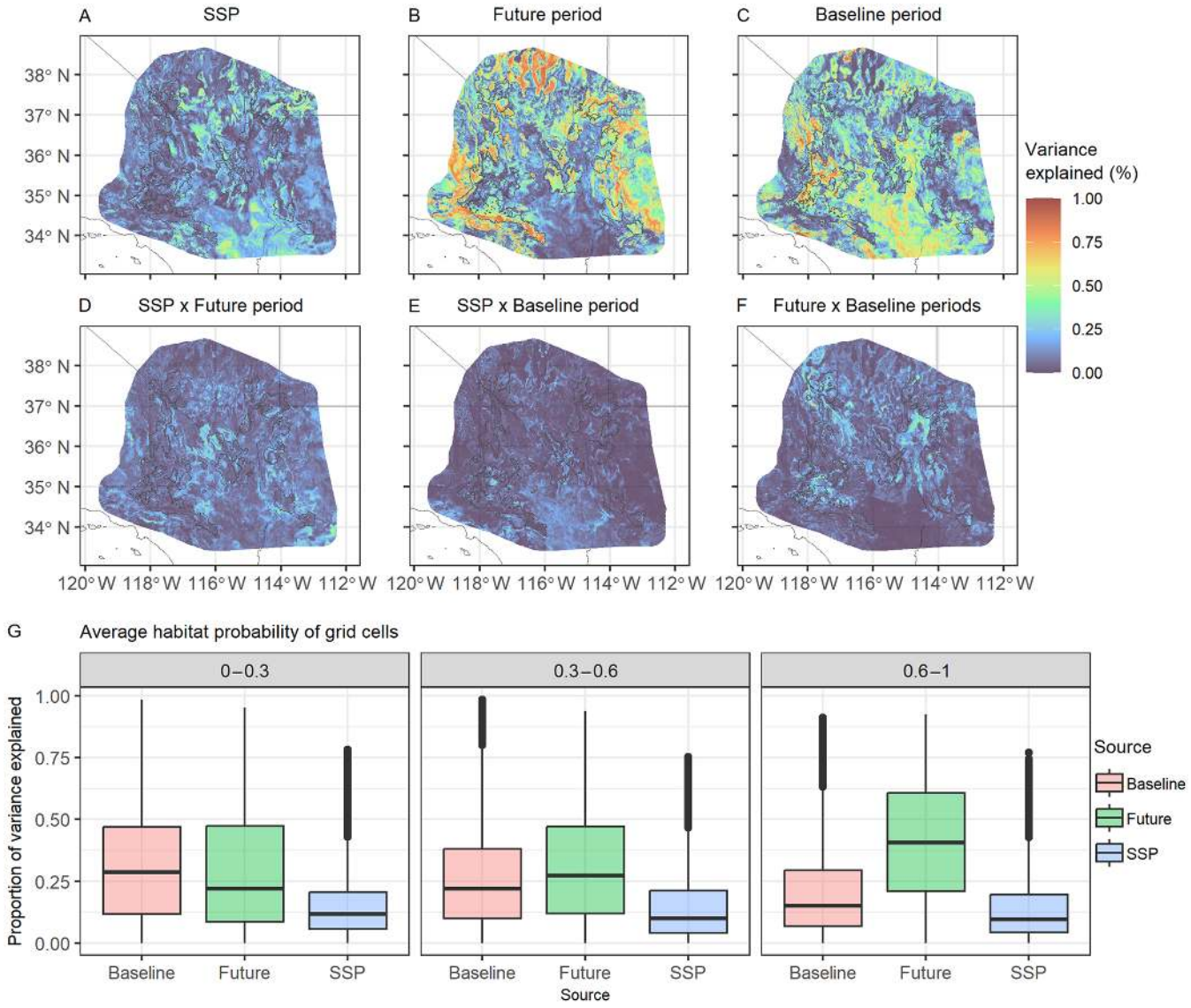


FIGURE 3 Partition of grid cell level variation in habitat probabilities due to (A) emissions scenario, (B) future time period, and (C) baseline climate period, along with their interactions (D–F). Variance explained is based on the SSs from three-way ANOVA without replication fit to each grid cell across 30 stacked habitat models. (G) Boxplots show the manner in which the proportion of variance in habitat probabilities (median, 25th and 75th percentiles, 1.5 × the interquartile range, and outliers) changes among grid cells grouped according to their initial habitat probability values in current climate.

2071 to 2100, under the SSP2–4.5 emissions scenario (Figure 4). For the higher emission SSP5–8.5 scenario, we found that 27.4% of suitable future habitat may be inaccessible to dispersal by 2041–2070 and 44.1% by 2071–2100. In general, the amount of accessible refugia decreased with higher emissions levels and with later future time periods, as the area of total future suitable habitat decreased. Overall, our simulations project that by 2100, approximately 14,411 km^2 of future suitable habitat may remain accessible refugia under the SSP2–4.5 scenario, and 4463 km^2 under the SSP5–8.5 scenario (Figure 4). The area of future suitable habitat, in situ refugia, and ex situ refugia for each of the baseline mean layers is provided in the supplement (Appendix S1: Table S3).

Vulnerability and land management status

Vulnerability

Joshua trees face multiple threats across their range (Figure 5). Based on spatial overlays, we found that wildfires have impacted the largest area of potential future

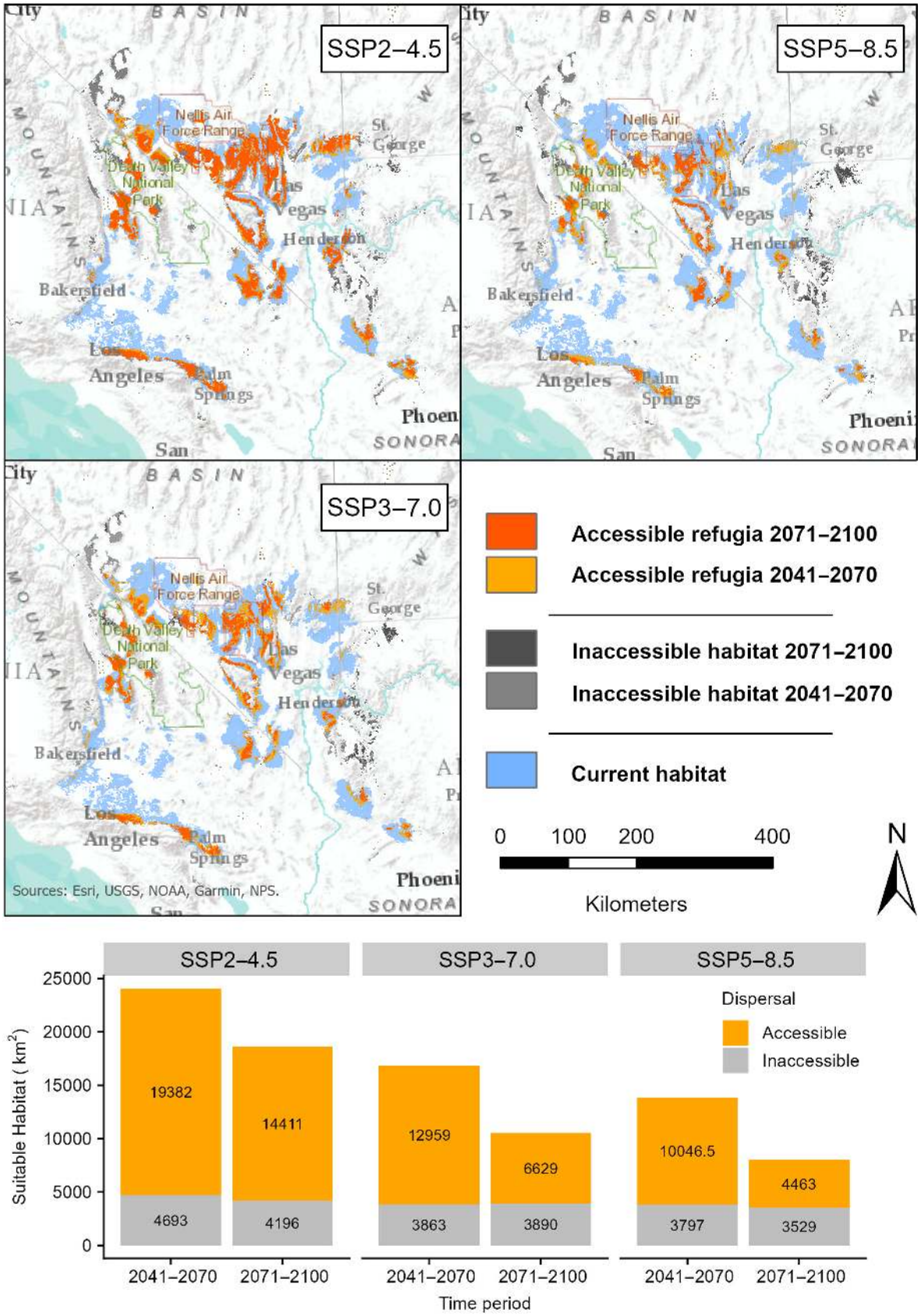


FIGURE 4 Legend on next page.

suitable habitat (Table 4, Figure 6A,B). This includes approximately 13.7% of accessible refugia under the SSP3–7.0 2021–2040 scenario (2540 km^2), 13% of accessible refugia under the SSP3–7.0 2041–2070 scenario (1688 km^2), and approximately 12.5% of the SSP3–7.0 2071–2100 accessible refugia that have burned since 1984 (830 km^2). While we do not quantify fire severity, these wildfires—drawn from the MTBS database—were all sufficiently large to spread beyond several square kilometers. Within only the Mojave Desert portion of the Joshua tree range, we found that future habitat probabilities were significantly positively correlated with wildfire ignition risk probabilities (derived from the model in Klinger et al., 2021) across all scenarios. Positive correlations were highest for 2071–2100 future habitat probabilities, averaging $r = 0.44$ across SSP5–8.5 baseline scenarios, $r = 0.42$ across SSP3–7.0 baselines, and $r = 0.39$ across SSP2–4.5 baseline scenarios. Across all scenarios, we found that 25%–30% of future suitable habitat occurred in higher wildfire ignition risk areas (Figure 6C). Other threats to future suitable habitat were more limited in spatial area (Table 4). In aggregate, the different classes of roads and rails intersect up to 255 km^2 of accessible refugia, depending on the scenario, while low-density development accounts for up to 118 km^2 (NLCD development classes include roads within developed areas). Existing renewable energy and mining facilities (including CA BLM rights-of-way) currently intersect up to 49 km^2 of early-century (2021–2040) accessible refugia. Up to an additional 12 km^2 of accessible refugia could be impacted by planned renewable energy development under the 2016 DRECP and 2012 BLM Western Solar Plan designations. However, updated land designations under the 2023/2024 Draft Solar Programmatic EIS have the potential to open a substantial area of Joshua tree future suitable habitat and accessible refugia to permit applications (Table 4; Appendix S1: Figure S2). Under Alternative 1, which includes resource-based exclusions alone, from 3311 to 5198 km^2 of 2021–2040 accessible refugia could be open for solar applications depending on the emissions scenario (constituting 18%–21% of the total accessible refugia; Table 4), compared to 142–252 km^2 of 2021–2040 accessible refugia under Alternative 5 (approximately 1% of the total accessible refugia). From 8% to 17% of late-century 2071–2100 accessible refugia could be open to applications under Alternative 1, or 0.5%–1% under Alternative 5.

Land management

The majority of future suitable habitat for Joshua trees occurs on federal lands, while approximately 10% occurs on private lands and 4% on state or county owned lands (Table 5; Figure 7). Of the future suitable habitat on federal lands, the majority occurs on BLM-administered areas (from 40% to 46% depending on the future scenario), while NPS and DOD each manage approximately 15% of the total future suitable habitat area. Smaller areas of potential future habitat occur on USFWS and USFS-administered lands, with each agency managing approximately 5% of the future suitable habitat area.

DISCUSSION

Understanding the Joshua tree's potential for long-term persistence through future suitable habitat and climate refugia is critical to ongoing conservation efforts and is of strong public interest due to the species' iconic status. Similar to alpine plants and other mountain species (Rumpf et al., 2018), Joshua trees are already restricted to cooler and moister sites within the desert ecoregions they inhabit (Esque et al., 2023), reducing their dispersal potential largely to the higher elevation desert ranges, potentially in competition with other species (Geppert et al., 2023). Here, we sought to provide a critical evaluation of potential in situ and ex situ refugia for Joshua trees in relation to updated CMIP6 climate models (Lee et al., 2021), management plans such as the Western Joshua Tree Conservation Plan (California Department of Fish and Wildlife, 2024) and the Draft Utility-Scale Solar Energy Development Programmatic Environmental Impact Statement (Bureau of Land Management, 2024), and threats including increasing wildfire frequency (Balch et al., 2013; DeFalco et al., 2010) and surface disturbances. Drawing from the most complete, high-resolution, and contemporary occurrence dataset yet available, we use RF SDMs to predict the distribution of potential Joshua tree habitat and climate refugia up to the year 2100. Overall, our models project substantial loss of habitat for Joshua trees by the late 21st century, particularly for populations in lower elevation, more arid sites. Under our projections, the area of future suitable habitat could contract by more than 80% relative to current habitat under the highest

FIGURE 4 Accessibility of future suitable habitat for Joshua trees based on simulated dispersal. Simulations were conducted with the baseline mean habitat layers for each emission scenario/future time period combination. Bar graphs show the total area determined to be either accessible refugia (in situ refugia overlapping with current habitat, along with ex situ refugia reached during the simulated dispersal) or inaccessible future suitable habitat for each scenario.

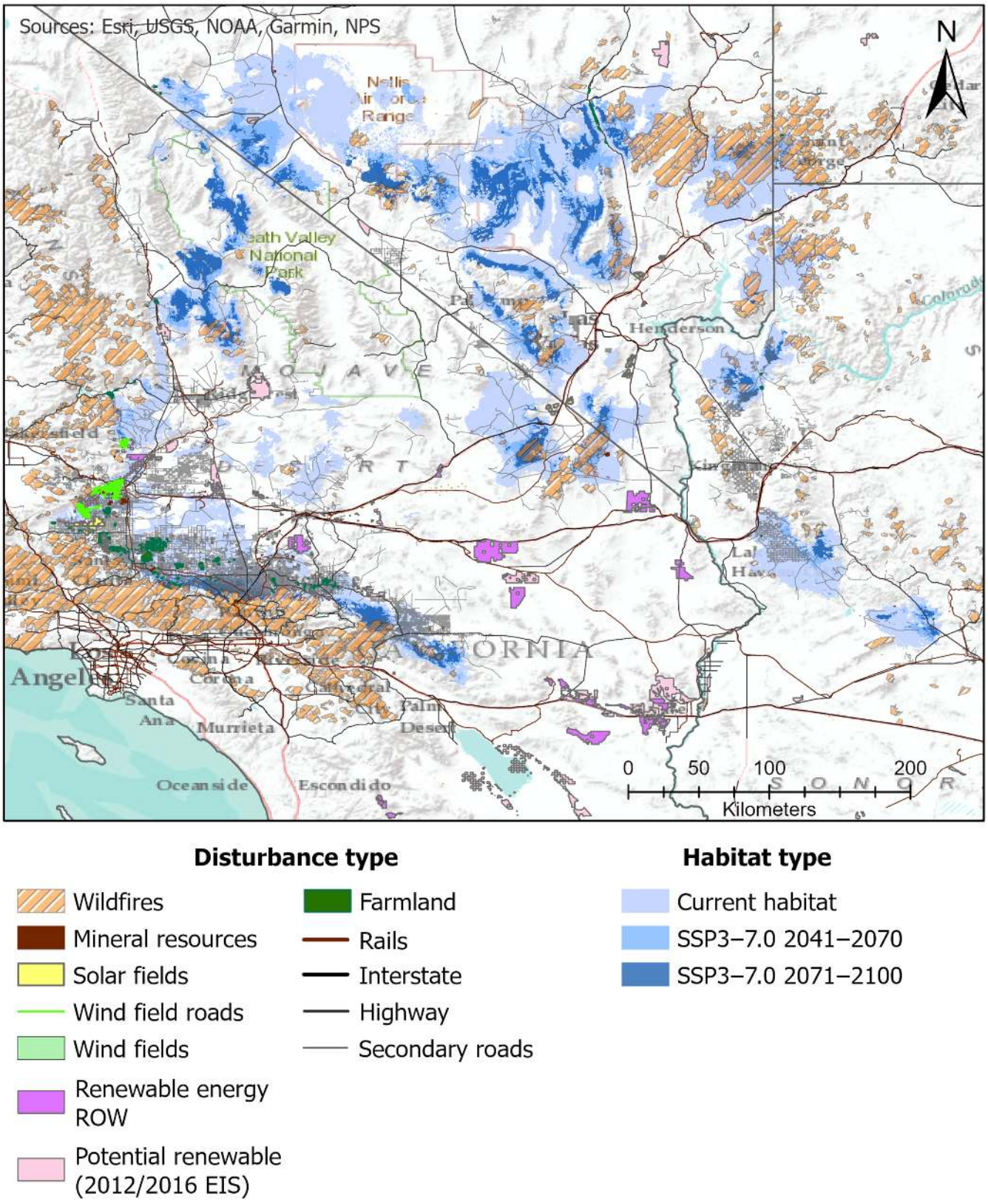


FIGURE 5 Overlay of current Joshua tree habitat and accessible climate refugia with existing and planned energy development, transportation corridors, urbanization, and large wildfires since 1984. "Renewable energy (ROW)" indicate rights-of-way for energy granted by the U.S. Bureau of Land Management (BLM) in California. Potential renewables refer to areas designated as "developable" under the 2012 Western Solar Plan, the 2016 Desert Renewable Energy Conservation Plan (DRECP), or the 2013 Restoration Design Energy Project (RDEP).

TABLE 4 Area in square kilometers of future suitable habitat and accessible climate refugia for Joshua trees intersected by different categories of disturbance, including renewable energy, wildfire, transportation infrastructure, and urbanization.

		SSP2–4.5			SSP3–7.0			SSP5–8.5		
Disturbance type	**Current**[a]	**2040**	**2070**	**2100**	**2040**	**2070**	**2100**	**2040**	**2070**	**2100**
Accessible refugia										
Energy										
Mining	52.72	28.38	18.40	13.06	27.56	10.30	4.43	26.85	8.59	4.64
Solar	35.62	1.06	0.45	0.32	0.83	0.32	0.14	0.69	0.32	0.00
Wind	9.34	0.49	0.14	0.01	0.71	0.18	0.01	0.54	0.11	0.00
Existing ROW (CA)	85.21	16.21	6.95	2.72	19.45	8.58	0.69	17.52	3.19	0.00
Developable (2012 WSP[b])	76.75	27.42	12.09	1.26	15.16	2.48	0.00	25.04	0.88	0.00
2024 DEIS[c]										
Alt. 1	8299.00	5198.06	3912.16	2462.91	3311.56	2202.02	871.12	3635.52	1527.92	519.43
Alt. 2	5389.03	3312.34	2433.34	1542.31	1972.29	1231.24	520.68	2235.66	916.18	311.46
Alt. 3	3633.28	2314.88	1765.97	1134.30	1336.06	884.43	402.92	1557.55	693.98	230.76
Alt. 4	747.32	325.38	232.55	164.50	182.86	122.27	70.65	222.21	108.27	22.47
Alt. 5	565.73	251.67	179.24	121.95	141.86	93.84	56.75	171.40	84.82	19.72
Wildfire	4457.62	2957.36	2393.89	1779.67	2539.95	1688.35	830.32	2650.97	1382.30	470.21
Road/rails										
Highways/interstate	37.99	13.33	9.45	4.99	10.24	5.51	2.12	10.61	4.38	1.57
Paved roads	384.44	162.95	129.80	92.89	149.45	104.92	53.20	148.95	88.28	25.94
Dirt roads	161.12	77.36	61.32	45.60	58.31	39.48	20.31	61.54	32.32	13.97
Railways	3.86	1.18	0.87	0.36	1.02	0.54	0.20	1.00	0.40	0.03
Urbanization										
NLCD[d] open	533.81	225.04	183.96	136.74	212.04	155.90	85.93	209.20	135.62	39.32
NLCD low	233.38	118.21	96.85	66.99	112.73	84.66	39.26	112.36	70.82	15.76
NLCD high	19.66	7.88	5.25	2.98	7.16	4.31	1.46	7.16	3.16	0.61
Future suitable habitat										
Energy										
Mining	...	28.38	18.40	13.06	29.58	12.20	4.43	28.84	9.49	4.64
Solar	...	1.06	0.45	0.45	2.14	0.38	0.20	1.32	0.32	0.00
Wind	...	0.49	0.14	0.01	1.00	0.28	0.01	0.75	0.14	0.00
Existing ROW (CA)	...	16.21	6.95	2.72	22.56	11.38	0.69	18.99	4.11	0.00
Developable (2012 WSP[b])	...	27.42	12.09	1.26	18.32	2.51	0.00	25.42	0.88	0.00
2024 DEIS[c]										
Alt. 1	...	6805.82	5410.50	3814.55	4295.47	3429.94	1995.92	4857.40	2574.28	1412.59
Alt. 2	...	4212.46	3178.16	2186.84	2585.85	1737.66	1038.16	3009.24	1360.32	826.37
Alt. 3	...	3074.91	2377.39	1663.83	1842.81	1293.49	814.80	2197.81	1062.22	589.09
Alt. 4	...	454.25	360.80	287.24	338.62	215.93	142.51	409.16	195.81	86.58
Alt. 5	...	365.39	277.65	218.77	265.26	165.95	122.59	316.46	154.35	82.53
Wildfire	...	3290.40	2690.67	2062.78	2978.97	1942.92	1218.73	3154.95	1630.01	858.73
Road/rails										
Highways/interstate	...	20.56	16.80	11.11	19.54	11.03	7.26	19.91	9.50	6.93
Paved roads	...	178.02	146.75	109.13	179.14	123.87	66.78	181.00	105.39	34.31

(Continues)

TABLE 4 (Continued)

Disturbance type	Current[a]	SSP2–4.5			SSP3–7.0			SSP5–8.5		
		2040	2070	2100	2040	2070	2100	2040	2070	2100
Dirt roads	...	86.52	68.79	52.43	71.77	46.97	26.98	75.63	40.08	19.21
Railways	...	2.03	1.65	0.70	2.15	1.06	0.35	2.06	0.88	0.09
Urbanization										
NLCD[d] open	...	261.27	225.57	177.25	273.37	195.89	116.09	274.69	172.34	62.53
NLCD low	...	135.00	111.97	77.32	145.20	99.81	47.55	144.39	84.98	21.93
NLCD high	...	15.58	12.39	6.09	21.42	9.79	3.21	21.35	8.25	2.39

Note: Columns are separated based on emission scenarios (SSP) and future time periods: 2040 (2021–2040), 2070 (2041–2070), 2100 (2071–2100). Calculations are based on the baseline mean habitat layers. "Accessible refugia" refers to the models constrained by simulated dispersal, constituting both in situ and ex situ refugia.

Abbreviation: ROW, rights-of-way.

[a]The species current habitat.

[b]Refers to the 2012 Western Solar Plan EIS.

[c]Refers to the 2023–2024 Draft Utility Scale Solar Programmatic EIS.

[d]NLCD refers to the National Land Cover Database (Dewitz et al., 2021).

emissions scenario (SSP5–8.5), or by nearly 60% under moderate emissions (SSP2–4.5), by the year 2100. Our models do not well align with a previous rangewide prediction (Cole et al., 2011) indicating complete habitat loss for southern populations. Rather, we find persistent future suitable habitat throughout the current range of both Joshua tree species that will likely constitute accessible in situ or ex situ refugia based on simulated dispersal, including in the southernmost populations of *Y. brevifolia* and *Y. jaegeriana*. Hence, our results are consistent with previous fine-scale studies from southern *Y. brevifolia* populations (Barrows & Murphy-Mariscal, 2012; Sweet et al., 2019), which also projected persistent end-of-century refugia in southern populations.

One obvious drawback to our approach is that correlative SDMs do not account for demographic processes (apart from our simulated dispersal parameters) that could introduce lag effects in the way populations respond to changing climate, particularly at their leading and trailing edges (Svenning & Sandel, 2013). In reality, demographic and biotic processes will markedly influence the rate at which populations respond to changing climate. While our simulated dispersal scenarios attempt to account for the interplay between propagule movement, generation times, and spatiotemporal shifts in habitat suitability, other processes will likely impact the capacity for Joshua trees to spread into newly suitable habitat: frequency of favorable climate conditions needed to induce mass reproduction and germination (Borchert & DeFalco, 2016; Reynolds et al., 2012), reduced survival among pre-reproductive Joshua trees (Esque et al., 2015), plant-pollinator interactions (Smith et al., 2011), competition with existing vegetation, and edaphic conditions. Conversely, persistence of Joshua trees at the trailing edge of their distributions will be influenced by adult survival as climate becomes increasingly unsuitable. Severe drought has the potential to induce mortality even in larger Joshua trees and may interact with other stressors such as wildfire or herbivory to reduce populations in these areas (DeFalco et al., 2010; Esque et al., 2003). Over time, long-surviving individuals may persist in environments that are no longer climatically suitable for recruitment of seedlings, as potentially observed in the southern range margins (Sweet et al., 2019), or in favorable microsites due to local topographic variation occurring at a finer scale than modeled. The pace of demographic changes could therefore obscure the extent of accessible climate refugia beyond the time periods used to represent future climate in our models. Our results are likely better interpreted as reflecting regions where Joshua tree populations can be at equilibrium with the future climate regime—that is, where recruitment and survival would likely be sustainable at the population scale, based on contemporary climate associations.

Predicting species range shifts into novel climates carries inherent uncertainty stemming from both the underlying future climate models (IPCC, 2021) and from issues of transferability into novel environments (Dormann et al., 2012). We chose to bound the climate variability in our forecasts by using an 8-model GCM ensemble selected to represent the "very likely" range of warming from the IPCC 6th assessment report (Mahony et al., 2022) and downscaled to a high resolution in ClimateNA (Wang et al., 2016). Focusing on individual climate models would likely have increased the range of

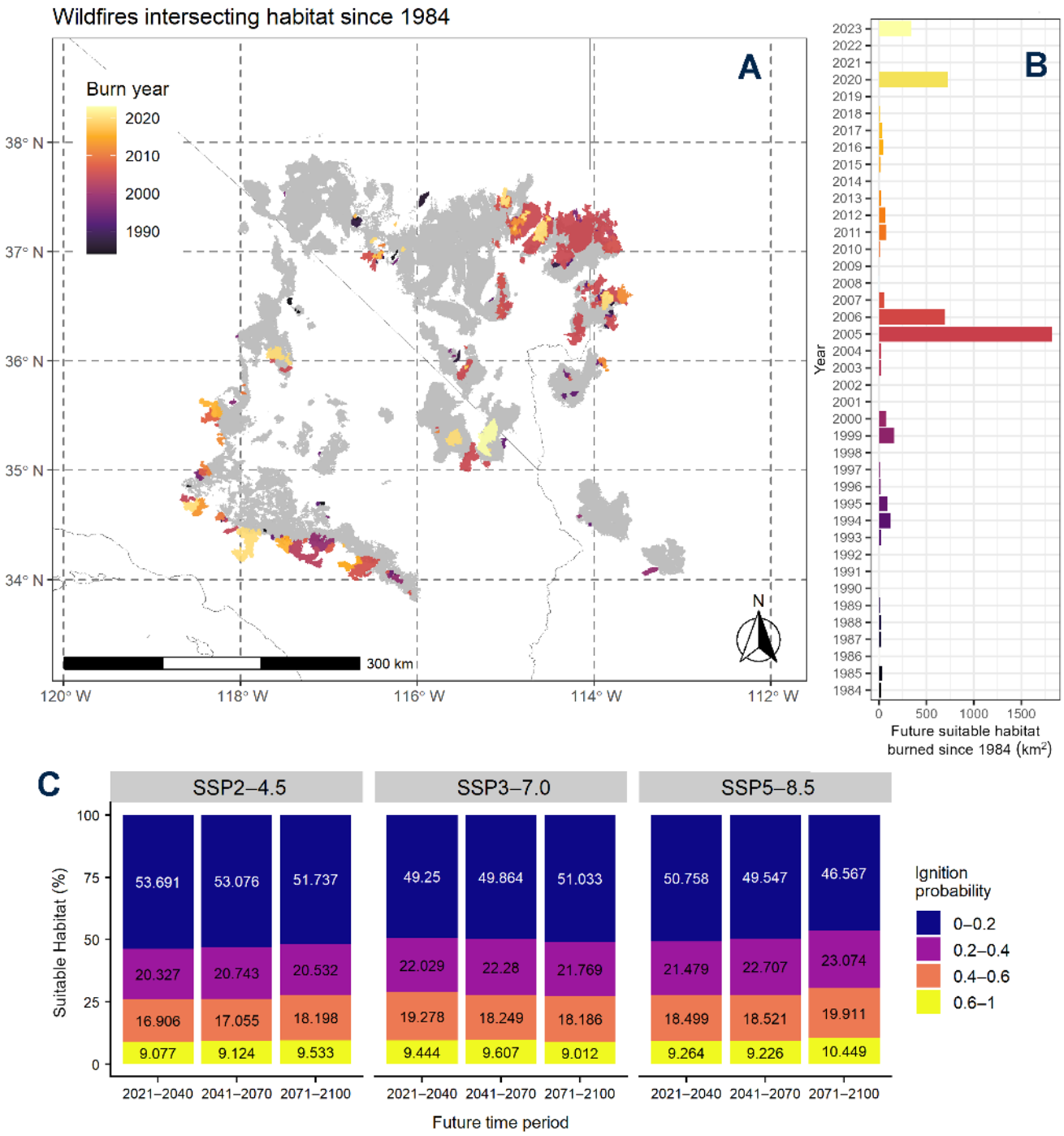


FIGURE 6 (A) Map of large wildfires occurring since 1984 in current Joshua tree habitat based on the Monitoring Trends in Burn Severity database (MTBS), and (B) the area of future suitable habitat burned by year, including future habitat identified jointly across all future species distribution model (SDM) scenarios. Additionally, (C) bar charts show the percentage of future suitable habitat occurring in different wildfire ignition risk probability classes, based on the model in Klinger et al. (2021).

variability in our forecasts, most notably by incorporating wider variation in summer precipitation changes over North America, which is still a large source of uncertainty across climate models (the 8-model ensemble forecast a 6% to 13% decrease in summer precipitation, which is not as extreme as in some individual models; Mahony et al., 2022). Additional simulations incorporating a greater range of outcomes in future climate predictions could be a focus for future work; however, we expect to see greater benefit by developing models incorporating

TABLE 5 Percentages of Joshua tree future suitable habitat under different land management jurisdictions.

		SSP2–4.5			SSP3–7.0			SSP5–8.5		
Ownership	**Current**	**2040**	**2070**	**2100**	**2040**	**2070**	**2100**	**2040**	**2070**	**2100**
Federal										
NPS	8.8	13.5	14.7	14.7	15.3	14.5	16.6	15	16.9	14.5
BLM	46.3	46	43.5	40.6	43.3	41.5	38.8	44.1	39.5	39.8
DOD	19	15.5	15.6	17.4	13.4	15.8	15.7	14.4	12.8	16.9
DOE	3.8	4.6	5.2	5.6	3.8	4	3.1	4.3	3.6	3.1
FWS	4.5	5.6	6.1	6.1	5.8	6.2	4.5	5.8	6	2.8
USFS	1.1	2.1	2.4	2.8	2.5	3.3	3.8	2.3	3.5	5.2
Other										
State	2	3.1	2.8	2.6	3.7	2.9	3.5	2.7	4.4	4.3
Private	14.5	9.1	9.2	9.1	12	11	10.5	11.3	11.8	8.3
Tribal	0.01	0.3	0.5	1.2	0.2	0.8	3.5	0.2	1.5	5.3

Abbreviations: BLM, U.S. Bureau of Land Management; DOD, U.S. Department of Defense; DOE, Department of Energy; FWS, U.S. Fish and Wildlife Service; NPS, U.S. National Park Service; USFS, U.S. Forest Service.

mechanistic relationships and recent demographic trends. Our predictions based on the 8-model GCM ensemble show that emissions scenario and future time period generate wide variation in the extent of predicted climate refugia, yet, in every scenario, we project substantial decreases in the Joshua tree's future habitat suitability. Moreover, our results align with expectations: the amount of future suitable habitat decreased with increasing emissions (from SSP2–4.5 to SSP5–8.5) and more distant time periods (from 2041 to 2100).

A point of uncertainty that may warrant further scrutiny concerns the influence of baseline climate period on future projections (i.e., the reference time period used as a basis of comparison against future time periods when forward-projecting SDMs). Although future time period and emissions scenario were more influential, we still found that the choice of baseline period influenced the extent of predicted suitable habitat by over 2000 km^2 in many scenarios. Effects were most prominent at the level of individual grid cell probabilities in areas of low to moderate habitat suitability (Figure 3). Further, no consistent ranking emerged between baseline periods and total predicted future habitat. The 1940–2000 baseline models predicted the most future suitable habitat for 2021–2040 and 2041–2070 (Table 3, Figure 2), but were surprisingly similar to the 1990–2020 baseline. Given these somewhat inconsistent results, we chose to average over the variability across baselines by creating mean probability layers for use in spatial overlays. Another valid approach could have been to construct agreement surfaces where grid cells reflect the number of models predicting future suitable habitat. From both a statistical and ecological perspective, our results highlight the need to carefully consider the time period used to represent baseline climate conditions when forecasting to future time periods. For very long-lived species, this decision may be challenging as baseline periods may not pertain equally to the oldest or youngest individuals in a population, and climate conditions supporting survival may differ from those enabling reproduction. Our approach of comparing different baselines may be well suited for such circumstances.

A large proportion of the future suitable habitat we predict overlaps with existing Joshua tree populations and hence constitutes in situ refugia (Appendix S1: Table S1), typically occurring at the upper elevational margins and in cooler/moister sites (Figure 1B). However, outside of existing populations, our simulations of dispersal project that over 20%—and potentially up to 40%—of the newly suitable future habitat will be inaccessible to Joshua trees. The proportion of inaccessible habitat is also projected to increase with time, as some midcentury habitat becomes unsuitable by end-of-century in our predictions. In part, these results are due to the stringent constraints we applied in the MigClim simulation—restricting time to first reproduction to 30 years and limiting the number of 500 m^2 grid cells propagules could potentially disperse to three (albeit with very low probabilities of movement beyond one grid cell). However, the parameters we selected are in keeping with observations of Joshua tree seed dispersal (Vander Wall et al., 2006; Waitman et al., 2012), generation times (Esque et al., 2015), rapid loss of seed germinability after a single growing season (Reynolds et al., 2012; Waitman et al., 2012), and the lack of evidence for longer distance dispersal observed during

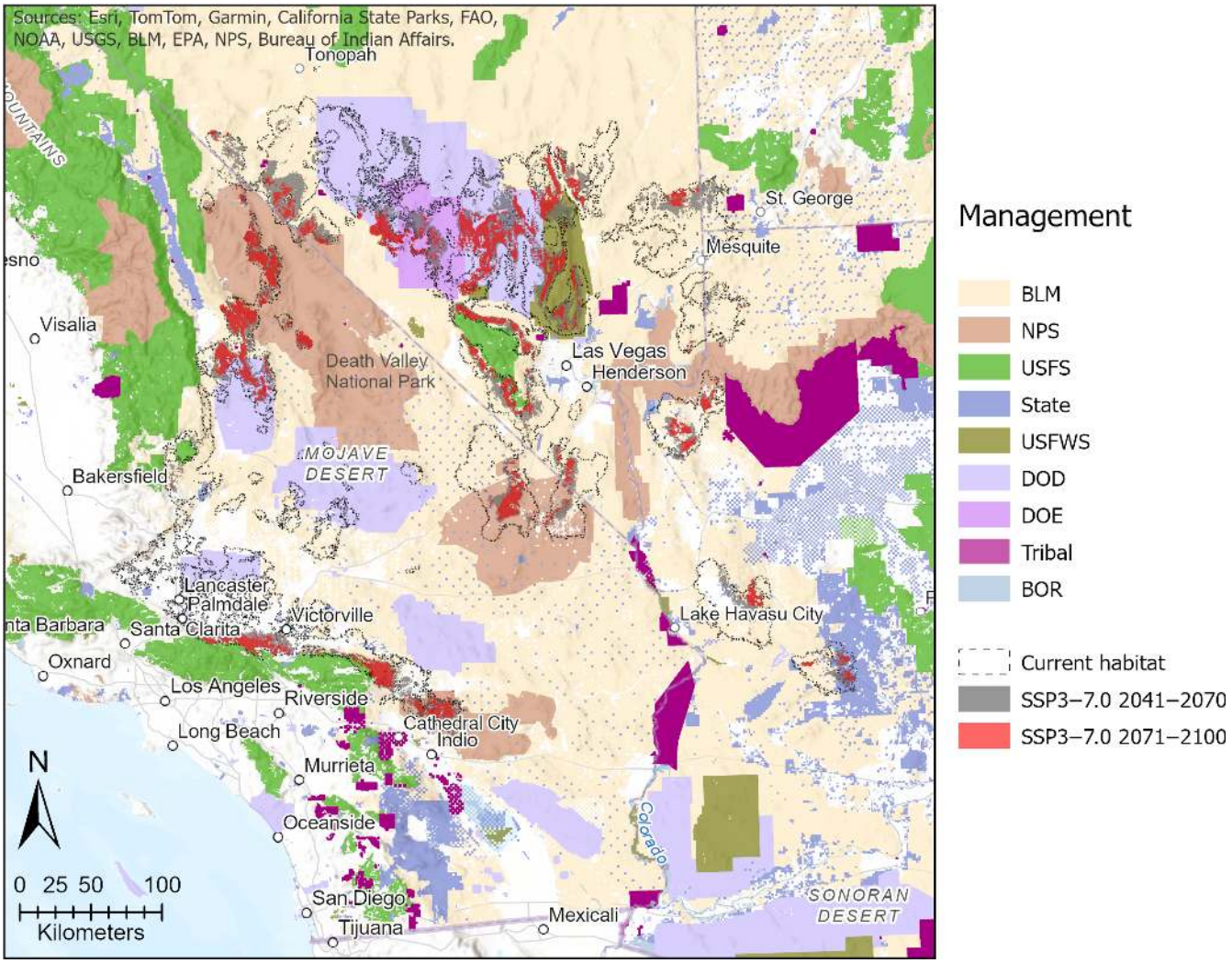


FIGURE 7 Land management status of areas intersecting Joshua tree's current habitat and accessible climate refugia for two future time periods (2041–2070, 2071–2100) under the SSP3–7.0 emissions scenario. BLM, Bureau of Land Management; BOR, Bureau of Reclamation; DOD, certain Department of Defense; DOE, Department of Energy; NPS, National Park Service; USFWS, U.S. Fish and Wildlife Service.

our recent large-scale range mapping efforts (Esque et al., 2023) in which Joshua trees located more than 500 m from existing stands were extremely rare. It is unlikely that Joshua trees will be able to disperse beyond the accessible refugia identified in our dispersal-constrained scenarios, leaving several thousand square kilometers of climatically suitable habitat unoccupied without management intervention to introduce trees to new areas. However, effectively seeding desert vegetation is notoriously difficult due to unpredictable climate, granivores, and local adaptation (Custer et al., 2022; DeFalco et al., 2012; Scoles-Sciulla et al., 2014), and field trials have shown young Joshua trees are susceptible to herbivory (Esque et al., 2015; Reynolds et al., 2012; Waitman et al., 2012). Hence, efforts to assist Joshua tree dispersal into unoccupied future suitable habitat would likely be met with considerable environmental challenges.

The persistence of Joshua trees within accessible refugia will also depend on the intensity of internal and external threats, particularly wildfires. The Mojave Desert is not a fire-adapted ecosystem, but invasive species have promoted an increasing fire regime over the last several decades (Brooks et al., 2004; Brooks & Matchett, 2006). In the last few years alone, thousands of acres of potentially accessible refugia have burned within the Mojave National Preserve in the Cima Dome and York Fires (Figure 5). Overall, we estimate that several thousand square kilometers of future suitable habitat have burned in the last several decades, with much of these burns occurring after 2005 (Figure 6). Apart from increased climate variability, wildfire appears to be the single greatest threat to Joshua tree's persistence. The continued spread of invasive annual grasses within the Mojave Desert (*B. rubens* L., *B. tectorum* L.) threatens

to increase fire frequency, particularly in areas that have already burned (Underwood et al., 2019). Comparing our results to a recent model of future wildfire ignition risk (Klinger et al., 2021), we find that a large proportion of future suitable habitat for Joshua trees occurs in higher ignition risk categories, with a probability of future ignitions greater than 40% (Figure 5). Wildfire risk may be higher for the eastern Joshua tree (*Y. jaegeriana*), as the increased summer precipitation in the eastern Mojave is linked with increased cover of C4 grasses and higher wildfire potential due to this fuel source (McAuliffe, 2016; Tagestad et al., 2016). Although Joshua trees are capable of resprouting after wildfire given favorable climatic conditions, the majority of individuals are killed outright, and the species does not maintain a long-term viable seedbank (DeFalco et al., 2010; St. Clair et al., 2022). Hence, while burned Joshua tree refugia would likely retain their suitability to support Joshua tree populations, the pace of natural recovery for burned desert vegetation communities is decadal (Engel & Abella, 2011). Attempts to reduce wildfire risk or restore burned Joshua tree stands could be crucial for the long-term persistence of Joshua trees.

Governmental policy has favored development of utility scale renewable energy facilities within portions of the Mojave and Sonoran Deserts in order to increase energy production and reduce greenhouse gas emissions (Federal Register, 2021; U.S. House of Representatives, 2020). Knowledge of species' current and future habitat requirements in relation to planned footprints for energy projects fills a critical need in managers' ability to balance clean energy development with conserving habitat for at-risk species. Based on our projections and available data on solar development, we find that potential impacts to Joshua tree's future suitable habitat and accessible refugia within lands considered "developable" for renewable energy under the 2012 Western Solar Plan and 2016 Desert Renewable Energy Conservation Plan are currently restricted to the western Joshua tree (*Y. brevifolia*) and include 15.2–27.4 km^2 of accessible early century (2021–2040) refugia, and 1–12 km^2 of accessible midcentury (2041–2070) refugia, depending on the emissions scenario (Table 4). In contrast, the 2023/2024 Draft Programmatic Environmental Impact Statement for Utility-Scale Solar Energy Development (Bureau of Land Management, 2024) could affect both the western and eastern (*Y. jaegeriana*) Joshua trees, opening large amounts of habitat to solar development applications. However, there is wide variation among alternative management plans considered in the document. Under Alternative 1 of the BLM Draft Environmental Impact Statement, up to 21% of early-century accessible refugia could be open to solar applications, and up to 17% of late century accessible refugia. Conversely, Alternatives 4 and 5 would pose fewer risks, as these alternatives open less than 20% of the available lands in Alternative 1 to solar applications. In these scenarios, up to 325 km^2 of early century accessible refugia, or 164 km^2 of late-century accessible refugia, could be impacted by future solar installations (~0.5%–1% of the total refugia). It should be noted that our spatial overlays do not account for site-specific management plans in the development of renewable energy facilities that might alleviate impacts to Joshua trees. We also do not account for future projects on private lands. Finally, impacts to existing populations outside of the areas predicted to be accessible refugia, and to populations in lower elevation early-century refugia versus those in late-century refugia, are likely not independent. Populations shifting in response to changing temperature and precipitation patterns tend to infill as they move upslope (Rumpf et al., 2018), such that lower elevation, declining populations may serve as a source of propagules, pollinator nourishment, and genetic diversity for spatially connected, viable refugial populations. Presumably, these benefits could continue for as long as adult Joshua trees are able to persist in habitats of declining suitability for Joshua trees.

Projects currently underway to obtain demographic data for Joshua tree populations will enable the development of coupled SDM-population models and/or demographic distribution models (see Briscoe et al., 2019), which could better account for spatially explicit demographic trends and lag effects in predicting future Joshua tree population dynamics. However, the future habitat models developed here provide a baseline with which to develop management strategies for sustaining—and in some cases restoring—climate refugia for Joshua trees. Despite the resource conflicts noted above, we find that over 80% of future suitable Joshua tree habitat occurs on lands owned and managed by various federal agencies (Table 5), including over 47% on BLM-administered lands and 15% within National Parks.

AUTHOR CONTRIBUTIONS

Todd C. Esque and Lesley A. DeFalco conceived the project and secured funding. Gabrielle A. Berry contributed to spatial layer development. Daniel F. Shryock performed the analysis and wrote the initial manuscript. All authors provided comments on previous versions of the manuscript and contributed to the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Shryock et al., 2025) are available from the U.S. Geological Survey ScienceBase-Catalog: https://doi.org/10.5066/P1I6UGOB.

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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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