

Congruence between future distribution models and empirical data for an iconic species at Joshua Tree National Park

LYNN C. SWEET ^{1,†} TYLER GREEN,² JAMES G. C. HEINTZ,¹ NEIL FRAKES,³ NICOLAS GRAVER,²
JEFF S. RANGITSCH,² JANE E. RODGERS,³ SCOTT HEACOX,¹ AND CAMERON W. BARROWS¹

¹Center for Conservation Biology, University of California, Riverside, 75-080 Frank Sinatra Drive, Palm Desert, California 92211 USA

²Great Basin Institute, Reno, Nevada 89511 USA

³Joshua Tree National Park, Twentynine Palms, California 92277 USA

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Abstract. U.S. national parks protect a natural heritage of global significance; those parks, especially those in the arid southwest, are threatened by climate change. Identifying climate refugia within our national parks using not only statistical models, but also validating predictions using robust field data should provide focus for managers in their stewardship of parks' biological resources. In the region surrounding Joshua Tree National Park (JTNP), which straddles the Colorado and Mojave deserts in southern California, previous research has predicted the widespread demise of its namesake iconic species, the Joshua tree (*Yucca brevifolia*) due to climate change. In order to assess whether climate refugia exist for Joshua trees in the future at JTNP, we employed both field measurements and statistical models. We used current distribution point data together with historic climate data, to match conditions when the existing Joshua trees established, in order to predict the distribution of continuously suitable conditions (refugia) at the end-of-century. While the high and moderate mitigation could result in refugia for approximately 19% and 14% of the original area within JTNP, respectively, the business-as-usual scenario indicated an almost complete elimination of Joshua trees from the park. In order to validate model predictions, using teams of community scientists, we measured the demographic patterns of Joshua tree stands from low to upper elevations within JTNP. Recruitment within stands shows a strong concordance with modeled climate refugia; high-recruiting stands were within or closer to modeled refugia and in areas with lower climatic water deficit, higher precipitation, and lower maximum temperature than low-recruiting stands. These findings most importantly indicate the importance of regional to global mitigation strategies for carbon emissions, as reflected in the difference between maintenance of refugia vs. an almost complete elimination of the species from the park by the end-of-century. This also underscores the need to protect areas predicted to support refugia from multiple management threats. Rather than an ominous prediction of extinction, climate refugia provide land stewards with targets for focusing protective management, giving desert biodiversity places to weather the future.

Key words: citizen science; climate change; community science; conservation; Joshua trees; Mojave Desert; plant distribution; recruitment; refugia; species distribution modeling.

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† **E-mail:** lynn.sweet@ucr.edu

INTRODUCTION

In North American deserts, rising temperatures coupled with prolonged drought may have already resulted in levels of aridity exceeding those since the medieval warming period and have likely also exceeded the warming during that period (Woodhouse et al. 2010). Severe droughts are likely to become the norm as modern climate change continues to develop (Cook et al. 2015, Prein et al. 2016). Notable and striking declines in bird communities, attributed to climate change, are already evident in the Mojave Desert (Iknayan and Beissinger 2018). Within this region of the United States, the National Park System has set aside examples of wilderness and biodiversity, protecting a natural heritage of global significance; climate change threatens these natural riches, especially for those parks in the arctic and desert regions (Gonzalez et al. 2018). This outlook for U.S. desert national parks is dire; however, while it is impossible for park managers to tackle the primary sources of climate change directly, if managers can identify, verify, and protect features that buffer against the effects of a warming and drier climate, there might be a somewhat more optimistic future (Gonzalez et al. 2018).

Those climate-buffering features, which may include higher elevations, north-facing slopes, canyons or ravines that capture and hold water, cool air drainages, or even regions of higher species and genetic diversity (Harrison and Noss 2017), are spatially discrete areas that are collectively identified as climate refugia (Morelli et al. 2016). Species distribution models (SDMs) have been used extensively in conservation biogeography to correlate the physical and climatic environment in which species are found to predict their distribution on the landscape currently and under climate change (Guisan and Zimmermann 2000, Franklin 2009). Models using past and current climate metrics, coupled with future climate predictions, forecast species responses to climate changes. If there is an overlap between modeled current or historic species distributions and those predicted in a future climate scenario, those areas of overlap may be potential climate refugia.

Validating modeled climate response is a critical, yet often neglected, step in the identification

and management of climate refugia (Morelli et al. 2016). Without validations, SDMs, and the locations of potential climate refugia, remain hypotheses (Jarnevich et al. 2015). Here, we demonstrate how demographic metrics can provide this information and empower park managers to not only identify species or natural community-specific climate refugia but also target monitoring efforts to see whether these predictions bear out on the ground. This allows prioritization for preserving and managing those identified refugial areas to reduce the effects of other, non-climate-related stressors. Our focus here is identifying the existence and extent of potential climate refugia for an iconic Mojave Desert species, the Joshua tree (*Yucca brevifolia* Engelm.), within Joshua Tree National Park (JTNP).

Joshua Tree National Park straddles the lower elevation Colorado and higher elevation Mojave Deserts in southern California. Evidence from paleo-biological records indicates that Joshua trees, among many species, have shifted their distribution since the Pleistocene, when they were more broadly distributed in the southwestern United States (Smith et al. 2011). Today, Joshua trees occur in a jagged continuous band across the western Mojave Desert and in fragmented populations to the north and east (Cole et al. 2011); the occurrence of Joshua trees within JTNP defines the current southern extent of the Mojave Desert before it transitions into the Colorado Desert within the park. While the ecotone between these deserts has shifted during glacial and inter-glacial cycles, as a whole, it is believed to have been quite stable since the end of the Pleistocene (Holmgren et al. 2010). Perhaps because of their iconic and keystone status, Joshua trees have received considerable attention with respect to their sensitivity to climate change. Dole et al. (2003), in an early species distribution modeling effort at 10 km resolution, predicted sharp declines in suitable habitat over the range. Cole et al. (2011), using broad-scale modeling at a 1- and 4-km resolution, showed widespread elimination of Joshua trees from most of their current distribution, including JTNP. Both of these studies were based on distribution information encompassing the full range of the species and two proposed ecotypes: the

eastern Joshua tree (*Y. brevifolia* Engelm. var. *jaegeriana* McKelvey) and the western Joshua tree (*Y. brevifolia* Engelm. var. *brevifolia*; McKelvey 1947; see Lenz 2007 for discussion of differences between the two forms). Following on that study, Barrows and Murphy-Mariscal (2012), using a finer scale, a more restricted extent focusing on populations of the western Joshua tree, and a uniform maximum temperature increase of 3°C, predicted persistence of JTNP Joshua trees, but within an area that was just 10% of their current distribution. Others have examined key components of Joshua tree demography, such as survivorship following fires, juvenile growth, pollination, fruit production, and seed predation, all within a climate change context (DeFalco et al. 2010, Esque et al. 2015, Borchert and DeFalco 2016, Harrower and Gilbert 2018).

Published models of Joshua trees (Dole et al. 2003, Cole et al. 2011, Barrows and Murphy-Mariscal 2012) all agree on a substantial climate-related decline in suitable area for this species across the Mojave Desert, but differ in their predictions for the most southern populations at JTNP. Since these earlier efforts, better, downscaled climate data have become available not only for historic time periods, but for many future scenarios (Flint et al. 2013, Flint and Flint 2014). There are also more complete distribution point records available through community science (also known as citizen science) efforts, facilitating the construction of better SDMs. As complex landscapes harbor topography that is lost in coarse-scale maps, here we seek to improve on past efforts by using finer scale data. In addition, the newer downscaled climate data (Intergovernmental Panel on Climate Change [IPCC], the Coupled Model Intercomparison Project 5 [CMIP5]) allows us to predict the distribution of the Joshua trees under high, moderate, and no carbon emissions mitigation scenarios.

Large, long-lived species, such as Joshua trees, have an advantage over short-lived species, as they can weather year-to-year variation and short-term droughts (Morris et al. 2008). Still, long-term persistence, especially over the time reflected in climate change estimates, depends on where and when species reproduce, recruit, and establish on a landscape. Other studies have found differences between the adult distribution and the distribution of juveniles or seedlings on

the landscape (McLaughlin and Zavaleta 2012, Bell et al. 2014). Since the establishment stage of trees and other perennial species is a vulnerable and important stage (Cavender-Bares and Bazzaz 2000), the density of seedlings in a given area can provide early indications of future distribution shifts (Kullman 2002, Lenoir et al. 2009, Vitasse et al. 2012).

In order to study the future distribution of Joshua trees at JTNP, therefore, a field-based assessment of current recruitment patterns may be foretelling of changes in the population of Joshua trees on the landscape. Joshua tree annual survivorship is age- and precipitation-dependent; low precipitation levels have an inordinate negative impact on survivorship of smaller plants (Esque et al. 2015, DeFalco et al. 2010). With the levels of increased aridity that this region has already experienced (Woodhouse et al. 2010), it follows that demographic shifts in Joshua trees should be apparent. The occurrence of young, healthy Joshua trees can therefore provide an empirical validation for modeled predictions of where climate refugia have already started to become established today.

By combining finer scale topographic and climate datasets, using more refined climate models and a more comprehensive set of Joshua tree location data, our objective was to construct SDMs to forecast this species' response to multiple future climate scenarios. Then, with the aid of volunteer community scientists, we collected Joshua tree demographic data across their range within the park. We aimed to identify the existence and extent of potential Joshua tree climate refugia and validate this prediction using empirical demographic data on Joshua tree recruitment along a gradient that falls within and outside modeled refugia.

MATERIALS AND METHODS

Study area

The study was located in JTNP (1238 mi², 34°0' N, 116°12' W) in southern California, USA. The community of Joshua Tree, California (station elevation 829 m), on the northern edge of the park, has a mean annual temperature (MAT) of 18.6°C and a mean annual precipitation (MAP) of 119 mm (of which approximately 18% falls during the summer months). Eagle

Mountain (station elevation 296 m), at the southeastern end of the park, has a MAT of 23.1°C, and a MAP of 93 mm (of which approximately 26% falls during the summer months; Western Regional Climate Center [WRCC] 2018). The park encompasses a suite of arid to semi-arid vegetation types and climates, generally grouped into the Colorado Desert Zone at the south and eastern portions, the Mojave Desert Zone at the north and western end, as well as within upper elevation sites, and a so-called transition zone in between, in which species are intermixed to various degrees. The overall study, conceptualized in 2013 and implemented beginning in 2014, was designed as a framework for monitoring vegetation and animal community changes across the park (for study background, design and details, see Barrows et al. 2014). The study sites within JTNP consist of 27 nine-hectare macroplots placed in a stratified pattern to be evenly distributed across the elevation gradient covered by these three zones. The macroplots were placed non-randomly to avoid areas with evidence of fire, areas that were not reasonably and safely accessible on foot by volunteers, boulder piles, areas that were highly non-uniform in topography and vegetation across the 9 ha, and areas that were heavily impacted by visitor use (trampling, roads, paths). Since the study inception, we have added several macroplots beyond the park boundary, of which one was used for this study, a site on land owned by Mojave Desert Land Trust (MDLT) 5 km north of the park, which contains transition zone vegetation and is similar in climate to the West Entrance macroplot. Here, we focus on the subset of 14 macroplots containing Joshua trees (Table 1).

Field data collection

During 2016–2017, teams of professional biologists together with community scientist volunteers completed full counts of all live Joshua trees within the 14 macroplots where this species occurs. Macroplots were censused using a walking inventory navigating with the use of GPS units, covered generally in 25-m swaths by small teams of 3–5 individuals. We recorded locations for each Joshua tree (using either a Trimble Juno GPS or a Garmin GPS). As a proxy for age of Joshua trees (see Gilliland et al. 2006 and Esque et al. 2015 for discussion), teams measured

Table 1. Approximate location, elevation, and determined vegetation zone for each of the study macroplots containing Joshua trees within Joshua Tree National Park and vicinity, southern California, USA.

Macroplot name	Elevation (m)	UTM Easting (NAD 83)	UTM Northing (NAD 83)	Vegetation zone
Eureka Peak (EUP)	1651	560000	3766000	Mojave
Key's View (KEV)	1536	576000	3754500	Mojave
Queen Mountain West (QMW)	1488	581500	3768000	Mojave
Upper Covington (UPC)	1487	565000	3763000	Mojave
Lost Horse Valley (LHV)	1392	576500	3757000	Mojave
Sheep Pass (SHP)	1369	581500	3763000	Mojave
Split Rock Trail (SRT)	1328	586500	3763500	Mojave
Hi-View Nature Trail (HVT)	1295	555500	3770500	Mojave
Black Rock Canyon (BRC)	1268	556500	3770000	Mojave
Lost Horse Road (LHR)	1248	574500	3765000	Transition
Pleasant Valley (PLV)	1237	588500	3747000	Transition
West Entrance (WEN)	1134	568500	3771500	Transition
Geotour Tank (GTT)	1080	585000	3754500	Transition
MDLT Sec 33 (MDL)	972	558500	3776500	Transition

height to the tallest part of the crown (along the axis of the trunk for trees that were leaning), living condition (a qualitative, categorical rating scale for overall plant condition from 2 (few shoots alive) to 5 (most shoots alive), and number of clonal sprouts on all living trees that we encountered within the macroplots. Similar to Esque et al. (2015), we differentiated between individuals that arose from sexual as opposed to asexual reproduction, taking measurements and counting only the former. We considered all

sprouts within 2 m of another Joshua tree to be clonal reproduction from the older individual, rather than offspring from sexual reproduction (seedlings). Consistent efforts were made to search for seedlings and young plants within nurse plants (shrubs) across macroplots.

Species distribution modeling

In order to predict the current Joshua tree distribution, we used the species distribution modeling platform, Maxent (v 3.4.1; Phillips et al. 2006) to develop relationships between Joshua tree presence points and a database of nine environmental variables including climate, topography, and soil characteristics. Maxent was run using data representing historic Joshua tree distribution and conditions to produce a prediction of the extent of historic habitat suitability, and we then used the same model with current and future climate variables to predict habitat suitability in the future. For the development of the base (historic) model, the following settings were used: The jackknife function was used to measure variable importance; response curves were created; the regularization multiplier was set to 1; 500 iterations were performed; and Maxent used a total of 11,142 presence points and pseudo-absences drawn from the background for this presence-only model. The area under the receiver operating characteristic plot (AUC) was used to assess the model performance, which is a measure based on the sensitivity and specificity performance of the model when predicting presence points. The AUC quantifies this relationship on a scale between 0.5 (no better than random prediction) and 1.0 (perfect performance; Fielding and Bell 1997). Percent variable contribution to the final model and permutation importance (difference in the model AUC when the variable is randomly changed; see Phillips et al. 2006 for explanation) were used as indicators of variable importance.

The presence record dataset consisted of a previously produced dataset of presences within JTNP (Barrows and Murphy-Mariscal 2012), observations from targeted surveys by JTNP professional staff, and iNaturalist research-grade observations with <50 m recorded precision, resulting in a dataset of 1747 observations (of which 1163 presence records were used for training in Maxent) over an area of approximately

2000 km². We assumed some bias in the sampling, as the crowd-sourced dataset was concentrated in recreational areas. However, both the previously developed point dataset and the JTNP surveys were targeted by professional staff to locate and describe stands of Joshua trees throughout the range of the Joshua tree, including remote areas within the park.

We used a downscaled climate variable dataset (2014 Basin Characterization Model [BCM], Flint and Flint 2014; <http://climate.calcommons.org/dataset/2014-CA-BCM>) at 270-m initial resolution, in addition to a physical topography dataset developed from various public datasets using ArcGIS Spatial Analyst (ESRI 2018; Table 2). All variables were projected to a uniform projection (NAD 83 UTM Zone 11N) and resampled to a 180-m resolution using bilinear interpolation in ArcGIS. As the vast majority of observations were of trees >1 m in height, these trees were presumed to be >30 yr old (using the calculations of Esque et al. 2015), and so they would have established prior to 1980. Therefore, the climate variables used to develop the model were the climate data from the period 1951–1980 rather than the later 1981–2010 period (which we then used in a second time-step and used as a projected dataset in Maxent). The future climate scenarios onto which the model was projected were the end-of-century (2070–2099) CMIP5 MIROC RCP 4.5, 6.0, and 8.5 emissions scenarios, representing CO₂ emissions under highly mitigated, moderately mitigated, and unmitigated scenarios, respectively. Changes in climate variables from the base Historic (1951–1980) to more recent Historic (1981–2010) and Future (2070–2099) under the three scenarios calculated in Spatial Analyst using the Zonal Statistics Tool for the area encompassing Joshua trees data points within the modeling extent. We calculated refugia as the area of overlap between Maxent cloglog format output (scale 0–1, higher values have higher predicted suitability) values of >0.4 for both the historically suitable area and the future identified suitable areas, respectively. The geographic area of interest used for calculating Joshua tree persistence was the JTNP and a 5-km buffer.

Field and model output analysis

Joshua tree demographic data were summarized using R version 3.4.2 (R Core Team 2018).

Table 2. Variables used in the creation of the Maxent species distribution model for Joshua trees within the vicinity of Joshua Tree National Park.

Variable	Description	Original data source	Units
Soil: Percent Sand	Percent sand content of soils	SSURGO and STATSGO2 (USDA NRCS 2012)	% Volume
Slope	Median slope value from a 18 × 18 neighborhood of 10 m cells where slope is given in degrees above horizontal	NED 10 m DEM; Digital elevation data from the United States Geological Survey—National Elevation Dataset	Degrees
Northness	Cosine of the circular aspect variable value in radians, multiplied by the slope	NED 10 m DEM; Digital elevation data from the United States Geological Survey—National Elevation Dataset	Unitless
Eastness	Sine of the circular aspect variable value in radians, multiplied by the slope	NED 10 m DEM; Digital elevation data from the United States Geological Survey—National Elevation Dataset	Unitless
Ruggedness	Median value from a 18 × 18 neighborhood of Sappington analysis results based on a 3 × 3 neighborhood of 10 m cells	NED 10 m DEM; Digital elevation data from the United States Geological Survey—National Elevation Dataset	Unitless
Climatic water deficit	Average climatic water deficit for the 30 yr period. Potential (PET) minus actual (AET) evapotranspiration based on PRISM 800 m data. Resampled to 180 m using bilinear interpolation	2014 California BCM (Basin Characterization Model) Downscaled Climate and Hydrology. 30-yr Summaries (Flint and Flint 2014)	mm
Precipitation, Annual	Average annual precipitation during the 30-yr period from the BCM and resampled to 180 m using bilinear interpolation	2014 California BCM (Basin Characterization Model) Downscaled Climate and Hydrology. 30-yr Summaries (Flint and Flint 2014)	mm
Minimum temperature, Coldest quarter	Average minimum monthly temperature occurring during period December through February during each 30-yr period from the BCM and resampled to 180 m using bilinear interpolation	2014 California BCM (Basin Characterization Model) Downscaled Climate and Hydrology. 30-yr Summaries (Flint and Flint 2014)	°C
Maximum temperature, Warmest quarter	Average maximum monthly temperature occurring during period December through February during each 30-yr period from the BCM and resampled to 180 m using bilinear interpolation	2014 California BCM (Basin Characterization Model) Downscaled Climate and Hydrology. 30-yr Summaries (Flint and Flint 2014)	°C

Using height as a proxy for age, we identified juvenile individuals as those below a height of 60 cm, likely about 10–20 yr in age (using the calculations of Esque et al. 2015 for MAP = 120 mm/yr) but which were pre-reproductive (trees may flower starting at 200 cm height; N. Frakes, N. Graver, and T. Green, *unpublished data*). We tallied the number of living trees per macroplot and the number of juvenile trees under 60 cm. The distance from the center of each macroplot to the area identified as refugia under the most mitigated scenario (MIROC RCP 4.5) was calculated using the Near tool in ArcGIS for the refugia raster converted to a polygon. The approximate area of historic fires, circa 1890s to 2018, within the park was drawn from California's Fire Resources Assessment Program (FRAP, data available at: <http://frap.fire.ca.gov/data/frapgisdata-subset>), and the area of intersection

with the modeled refugia was calculated using ArcGIS.

This study was meant to be spatially explicit in nature, comparing relative rates of recruitment within and outside predicted refugia, and we have not found an estimate for local replacement rates necessary for population sustainability. Therefore, we used a density metric (number of juvenile trees per area) and considered a large gradient of Joshua tree abundance to identify areas of higher recruitment relative to other areas within the park. While this analysis did not fully assess the long-term viability of the populations at the 14 macroplots, to contrast the study areas and compare them with the predicted area of refugia, therefore, macroplots were categorized in one of two groups: High-recruiting macroplots were assigned as those that exceeded the mean value of juvenile individuals per macroplot (density) for the study, and low-

recruiting macroplots were below the mean. A two-sample Welch's *t* test was used to assess the differences between the distance to refugia in the high-recruiting and low-recruiting macroplots. We extracted elevation and the UTM Easting coordinate from each of the raster centroids for the refugia areas, and likewise, extracted climate and other variables represented in the raster variable dataset for the center of each macroplot.

RESULTS

Historic and future suitable habitat

Training data for the model Maxent model had an AUC value of 0.927. The variable that both contributed highest to the model and had the highest permutation importance was annual precipitation. Maximum and minimum temperature contributed highly to the model, but both were <7% in terms of permutation importance. Slope and climatic water deficit (CWD) both had slightly higher permutation importance than either of the temperature variables. All macroplots were within the predicted historic suitable area for Joshua trees (Fig. 1a). The refugia predicted to support Joshua trees under the three future climate scenarios are shown in Fig. 1b–d. All of the three future climate scenarios showed large-scale reduction in the suitable areas at end-of-century (Table 3). The MIROC 4.5 and 6.0 scenarios, representing moderately high and moderate mitigation indicated refugia for 18.6% and 13.9% of the original occupied area, respectively. However, the so-called business-as-usual scenario, 8.5, indicated an almost complete elimination of Joshua trees from the area of interest, though some areas to the northwest, in the San Bernardino Mountains, were predicted to support small areas of refugia (Appendix S1). The area of overlap of the refugia under RCP 4.5 and historic fires was over 6000 ha or approximately 49.9% (Fig. 2). This overlap area primarily covered lower and central portions of the modeled refugia, and less so the upper elevations of the refugia.

The future climate scenarios onto which the model was projected were the end-of-century (2070–2099) MIROC RCP 4.5, 6.0, and 8.5 scenarios, which correspond to changes in climate summarized in Table 3. The historic-to-current changes indicate a very slight increase in precipitation over the range of Joshua trees, together

with an increase in minimum and maximum temperature, as well as CWD. The future scenarios predicted a 3–5°C increase in maximum summer temperature, and a 2°C to almost 4°C increase in minimum winter temperatures, a decrease in precipitation, and an increase in CWD.

High-recruiting vs. low-recruiting stands

The total number of live Joshua trees per macroplot ranged from 48 to 562 trees per 9 ha (5.3–62.4 trees/ha). The mean number of juvenile trees <60 cm was 27.5, and the mean number of adults >60 cm was 266.9. The macroplots ranged from 0 to 77 juvenile individuals per macroplot, representing 0–20% of the trees present (mean 9%). Only three individuals smaller than 20 cm in height were counted, and the tallest three individuals were over 900 cm (minimum 9, maximum 989, mean 281, median 365). Based on point location values extracted from the mapping dataset, high-recruiting macroplots had significantly higher annual precipitation, and marginally significantly lower CWD and maximum temperature of the warmest quarter (Table 4). High-recruiting macroplots (macroplots exceeding 27.5 juvenile trees per macroplot) were geographically differentiated from low-recruiting macroplots in that they were located either within or significantly closer to predicted future refugia than low-recruiting macroplots (Table 4; Fig. 3a). When we plotted temperature and precipitation for refugia areas together with macroplots, there was considerable correspondence between the high-recruiting macroplots and the refugia (Fig. 3b). The highest macroplot, at Eureka Peak, though it was located within the area of predicted refugia, was not a high-recruiting macroplot. Conversely, although High View Trail and Black Rock Canyon were high recruiting, they were just outside the plotted area of refugia. Finally, the Lost Horse Valley macroplot was within the area of refugia; however, the macroplot was below the mean value for recruitment.

DISCUSSION

Planning for climate change-precipitated shifts in the ranges of plant (and animal) species distributions is of foremost importance for conservation and natural lands management (Thuiller et al. 2008). Species distribution modeling is one

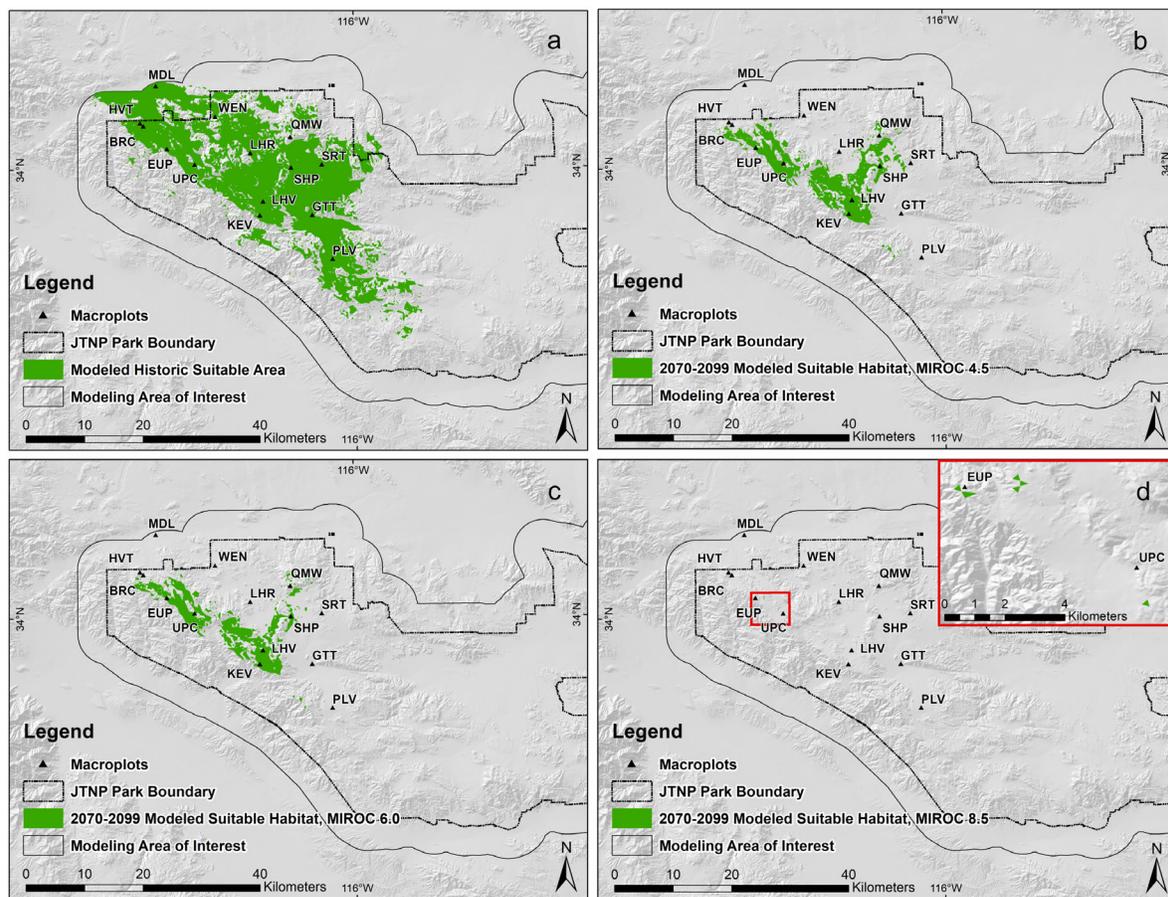


Fig. 1. (a–d). Model of historically suitable habitat (a) and end-of-century refugia for Joshua trees (*Yucca brevifolia*) at Joshua Tree National Park using Maxent. Modeled refugia are the area of overlap between current and future suitable habitat under 3 representation concentration pathways (RCPs) in the MIROC model: RCP 4.5 (b), 6.0 (c), and 8.5 (d, with inset to display the modeled area).

Table 3. The changes in amount of suitable area for Joshua trees in the vicinity of Joshua Tree National Park (Maxent modeled suitable refugia), and climate departure from the historic models (2014 Basin Characterization Model dataset; Flint and Flint 2014) to the periods indicated, under three representation pathways in the MIROC model – indicates the baseline.

Period	Suitable area (ha)	Percentage of range	Max Temp, Warmest quarter, °C (SD)	Min Temp, Coolest quarter, °C (SD)	Annual precipitation (mm) (SD)	Climatic water deficit (mm) (SD)
Historic 1951–1980	65,022	100	–	–	–	–
Historic 1981–2010	8715	13.4	+0.46 (0.10)	+0.63 (0.10)	+18 (7.4)	+36 (10)
Future refugia 2070–2099 (MIROC 4.5)	12,089	18.6	+2.98 (0.29)	+2.20 (0.23)	–79 (31)	+123 (20)
Future refugia 2070–2099 (MIROC 6.0)	9053	13.9	+3.3 (0.29)	+2.4 (0.23)	–67 (29)	+122 (21)
Future refugia 2070–2099 (MIROC 8.5)	15	0.02	+5.0 (0.29)	+3.70 (0.23)	–84 (32)	+186 (28)

Note: SD, standard deviation.

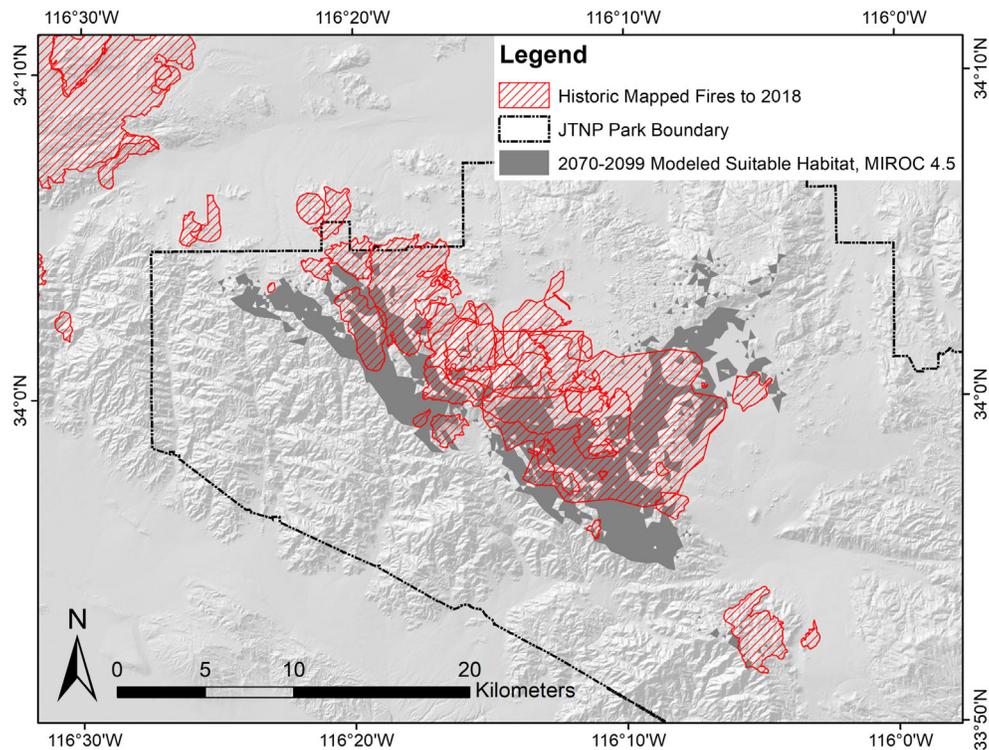


Fig. 2. Distribution of modeled end-of-century Joshua tree (*Yucca brevifolia*) refugia under MIROC 4.5 (gray), and mapped historic fires (hashed fill) within Joshua Tree National Park (FRAP data, available at: <http://frap.fire.ca.gov/data/frapgisdata-subset>).

tool within a suite of useful research in this area (Dawson et al. 2011, Franklin et al. 2016), which offers ever-more precise predictions of the future for many species of concern (Newbold 2010, Franklin 2013, Franklin et al. 2013). Several studies have tested future species distribution models against other measured plant responses over space, for example, remaining green canopy (Navarro et al. 2019) and tree growth and mortality from inventory data (Lloret et al. 2013). McLaughlin and Zavaleta (2012) and McLaughlin et al. (2014) compared life-stage sensitivities along similar lines to this approach, but also did not assess full population viability at each location; however, a study by Pironon et al. (2015) did incorporate demographic analysis for several species of herbs, where they were able to collect a full suite of sampling data (fecundity, inter-annual survival). Studying the density of tree recruitment, we found early indications of a shift in recruitment for this long-lived species, even with the modest climate changes that have

occurred from the thirty-year period 1950–1980 to the following thirty-year period. If recruitment patterns portend the future distribution of adults on the landscape, this type of analysis allows a glimpse into changes that may occur even before those outlined in the modeled future scenarios. Our results provide a striking estimate of what may happen if business-as-usual policies that affect carbon emissions are to continue. These findings are meant to not only demonstrate what is occurring and may occur in a broad sense, but also provide concrete, actionable data to park management for in situ conservation of species.

Measuring the demographic characteristics of Joshua tree populations across a series of large (9 ha) macroplots provided a valuable inventory of density and size of individuals across a range of occurrence of the Joshua tree. The macroplots represented a wide range of densities, especially of juveniles, with one macroplot containing none at all, to more than 70 juveniles. While recruitment for this species may be infrequent due to

Table 4. Mean values (SD) of the variables extracted from the climate (2014 Basin Characterization Model dataset; Flint and Flint 2014) and physical dataset for the macroplot locations in the Joshua tree (*Yucca brevifolia*) “high-recruiting” ($n = 6$) and “low-recruiting” ($n = 8$) macroplots within the vicinity of Joshua Tree National Park.

Variable	High-recruiting macroplot	Low-recruiting macroplot	<i>P</i> value
Elevation (m)	1407 (112)	1255 (209)	0.11
Climatic water deficit (mm) (SD)	1067 (56)	1144 (99)	0.09
Annual precipitation (mm) (SD)	273 (22)	235 (38)	0.04*
Min Temp, Coolest quarter, °C (SD)	0.01 (0.63)	0.77 (1.14)	0.14
Max Temp, Warmest quarter, °C (SD)	31.4 (0.77)	33.7 (1.59)	0.06
Mean distance to refugia (m)	233 (365)	2871 (2531)	0.02*

Notes: SD, standard deviation. High-recruiting macroplots had > mean density of juveniles (>27.5/ha). * indicates $P < 0.05$.

multiple factors (Reynolds et al. 2012), this study as well as the study of Barrows and Murphy-Mariscal (2012) found many trees under 1 m (presumably younger than approximately 20–30 yr by the calculations of Esque et al. 2015) in height across the park. Our western (similar to St. Clair and Hoines 2018) and upper elevation (similar to DeFalco et al. 2010) macroplots generally showed higher densities of Joshua trees and higher survival of young trees, respectively. The majority of those counted as juveniles here were tall enough to have survived the early, precarious seed to early seedling transition (generally higher survivorship for Joshua trees over 30 cm, see Esque et al. 2015), and so these patterns should be reflective of those that support adult populations. The correspondence between the modeled area of refugia and the density of recruitment is not surprising—the factors that allow for recruitment (lower CWD, higher precipitation), especially in a desert environment, also differentiated, on a landscape scale, the areas supporting Joshua trees within the park, as seen in the SDM variable importance estimation. Features not reflected in the model, such as rockiness, or competing, dense vegetation could also explain departures from expected numbers of juveniles within a macroplot. Certainly, the latter is an area that needs exploration, for this and many species (Liang et al. 2018). This type of on-the-ground measurement of recruitment and density should be an integral part of not only validating the modeling effort but also of adaptive management for parks.

Prior research has predicted major declines in the amount of area that will support Joshua trees (Cole et al. 2011, Barrows and Murphy-Mariscal 2012). The current study, showing a range of

outcomes tied to human greenhouse gas emissions, benefited from a more rigorous distribution dataset from community science (iNaturalist) and those data provided by targeted JTNP surveys, and from fine-scale detailed climate data from the 2014 BCM (Flint and Flint 2014), providing a more nuanced prediction of changes across the landscape. Additionally, the hydrologic variable CWD, reflecting the degree of dry-down over the season (sensu Stephenson 1998), has been shown to be especially helpful in predicting suitability for other plant species (Lutz et al. 2010) and especially for seedling recruitment (Davis et al. 2016). In fact, accounting for such hydrologic variables may explain seemingly anomalous patterns of species shifts (Crimmins et al. 2011). Moreover, we were able to pinpoint differences in these variables on the ground between sites that were high recruiting vs. those that were not showing a lower deficit in high-recruiting areas.

Not surprisingly, much of the area of identified refugia occurs in the upper elevation and more westerly areas of JTNP. This is consistent with other findings that this species may not be reproducing in areas where temperatures are higher (St. Clair and Hoines 2018), and with other studies showing distributional shifts in desert vegetation toward higher elevations (Kelly and Goulden 2008). These areas experience higher precipitation and cooler temperatures, which have historically been more broadly distributed and are expected to contract within the park boundary and elsewhere. In addition, there may exist additional areas of refugia at or near these elevations within the park and beyond; our modeling scale was likely still too coarse to fully reflect potential topo-climatic refugia or

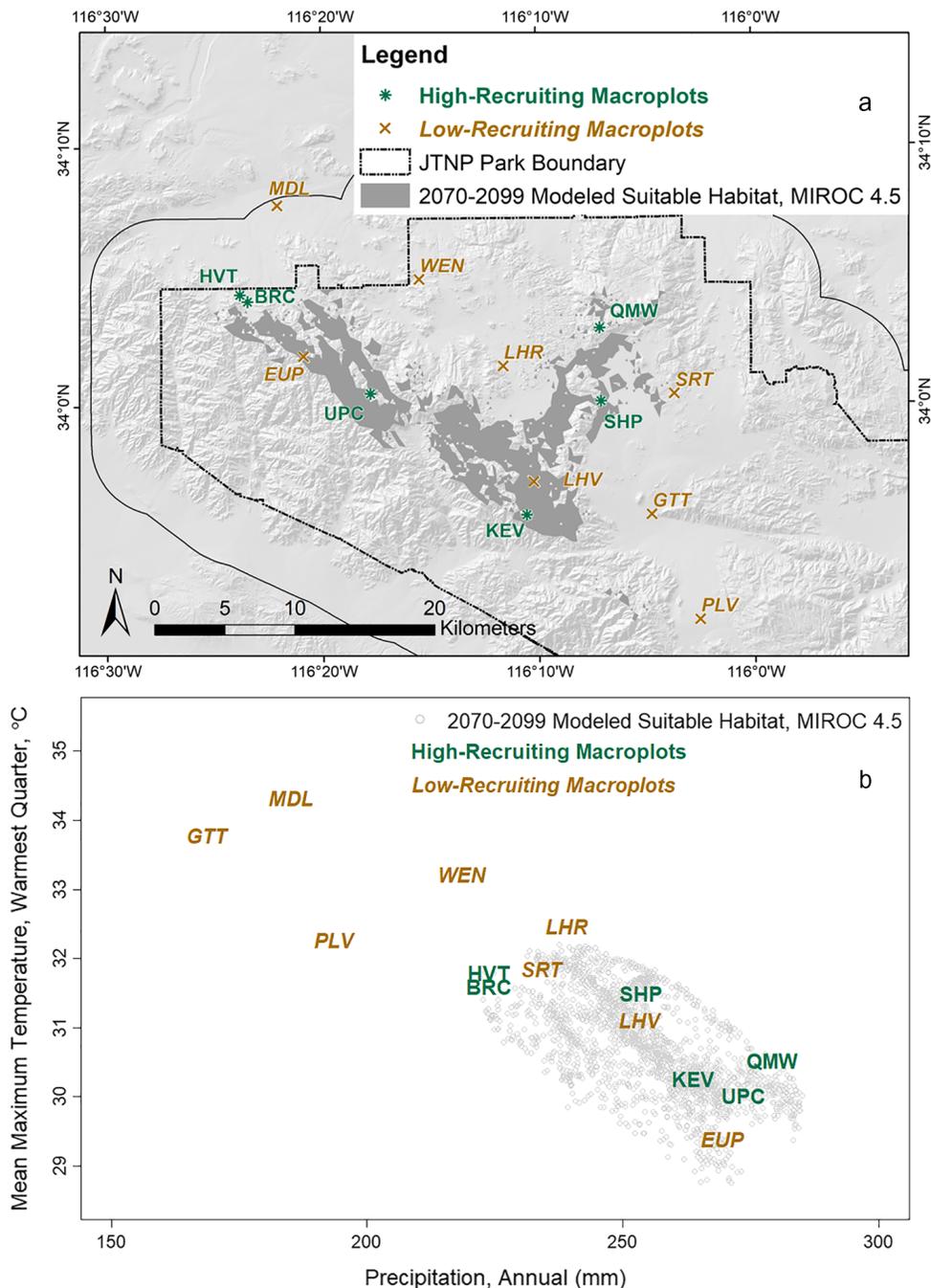


Fig. 3. Modeled refugia (gray) under the MIROC RCP 4.5 scenario at end-of-century for Joshua trees (*Yucca brevifolia*) within the vicinity of Joshua Tree National Park together with sampled macroplots indicated as either high recruiting (>mean juvenile density, in green) or low recruiting (<mean juvenile density, gold, italic). The map (a) shows the distribution of the refugia and macroplots in geographic space, and the right-hand plot (b) shows the distribution of both according to extracted historic (1951–1980) values for mean annual precipitation and mean maximum temperature of the warmest quarter from the 2014 Basin Characterization Model dataset (Flint and Flint 2014).

hydrologic refugia (McLaughlin et al. 2017) on the landscape that may also buffer the effects of climate changes (Randin et al. 2009, Ackerly et al. 2010, Davis et al. 2016). In addition, there may be other localized hydrologically induced refugia for this species below the level of resolution of the model, such as areas with a high cover of boulders that sheet water in specific areas, allowing for locally high soil water content (C. W. Barrows, *personal observation*). These microrefugia (sensu Rull 2009, Dobrowski 2011) may additionally act as stepping-stones or seeds for species migration into areas that are not currently occupied (Hannah et al. 2014) but that are suitable in the future. Conversely, there may be some areas that are mapped as suitable habitat and/or refugia in which the current dominant vegetation may exclude Joshua trees. The highest elevation macroplot, Eureka Peak, though modeled as refugia, is not a high-recruiting macroplot and is currently dominated by oaks and pines, though it does contain some Joshua trees. The RCP 8.5 model indicates that this may become a key area of refugia for Joshua trees (Fig. 1d).

Because assisted migration is a contentious issue, especially in a national park, our goal here was to inform management with the most robust available predictions, focusing on areas where the species occurs already. Given the known limitations of SDMs with regard to biotic interactions and other problems (Guisan and Thuiller 2005), validated in situ refugia provide a higher level of confidence regarding providing the essential resources for species and their commensal associates. Currently unoccupied, entirely new habitat cannot provide that same confidence. We assumed that the dispersal abilities of this species, small mammals being the likely dispersal vector (Vander Wall et al. 2006), are somewhat limited. That limited ability to track a rapidly changing climate, together with a long time to reproductive maturity and the timescale reflected in these end-of-century models, indicates threats to persistence of Joshua trees may worsen, unless the buffering abilities of climate refugia are sufficient to sustain populations. Therefore, we focused on areas of refugia for the species, occurring toward the leading edge of the current species' distribution within the park (relevant to in situ conservation efforts), rather than the entirety of future suitable habitat (areas relevant

to assisted migration). While a lack of recruitment or increases in mortality of such iconic species at the trailing edge of the range (hotter, drier lower elevations) at JTNP may be distressing to land managers, there may be little that can be done to mitigate these effects without intensive management (but for counter-argument, see Hannah et al. 2014: Box 1). This said, the importance of trailing-edge populations is an understudied area, and these populations may be important to long-term genetic diversity in species by harboring genetic information for weathering hotter and drier conditions (Hampe and Petit 2005). Nevertheless, we argue that currently occupied climate refugia are most relevant to the conservation of the species for the next 50 yr, and perhaps longer. Since these refugia are also subject to threats such as fire and invasive species, management efforts aimed at reducing these threats provide on-the-ground actions that increase the likelihood that these areas will sustain this iconic species.

As we have shown, approximately one-half of the park's Joshua tree refugia, as currently mapped, have already burned (Fig. 2), and Joshua trees show high post-fire mortality (DeFalco et al. 2010). It should be noted that the burn area polygons in the FRAP database were likely simplified; with the exception of the Lost Horse Road macroplot, which had a light burn at one end, we did not see any evidence of fire on the rest of the macroplots. The threat of wildfire is exacerbated due to the spread of exotic grasses causing an increase in burn severity and frequency (Brown and Minnich 1986, Brooks 1999, Brooks and Esque 2002, Brooks and Matchett 2006). The areas mapped as Joshua tree refugia, which are found at higher elevation wetter areas, also tend to have the highest covers of invasive annual grasses. In response, JTNP has already used the previously mapped Joshua tree refugia identified in Barrows and Murphy-Mariscal (2012), taking novel and aggressive management actions such as establishing fuel breaks around refugia, controlling invasive annual grasses using mechanical and chemical treatments. In addition, JTNP provides actionable guidance to the Fire Resource Advisors pertaining to the ecological sensitivity and appropriate fire responses in these areas. This said, Brooks and Matchett (2006) postulated that fire regimes at upper

elevations in the Mojave Desert may be dictated more by woody fuels than invasive grasses, though this needs to be assessed for JTNP, where invasive grasses, especially *Bromus* spp., persist into the upper elevation modeled refugia (N. Frakes, *unpublished data*).

Recruitment, survival of populations, and certainly migration of the species will be affected by factors such as the availability of pollinators, dispersers, seed and seedling predators and other mutualisms on the landscape (Araújo and Luoto 2007, Esque et al. 2015). These aspects of species biology are not necessarily congruent; for example, patterns of success such as fruit production do not necessarily align with geographic patterns of demographic metrics for Joshua trees. Recent research into pollination ecology has shown a peak in pollination (by the obligate pollinator, the yucca moth; Pellmyr and Segraves 2003) and fruit set in areas on the lower end of the area of refugia generally identified here (Harrower and Gilbert 2018). This is consistent with other findings that have shown that higher temperatures across a geographic gradient positively affected fruit set due to moth activity, whereas patterns in tree density showed the opposite pattern (St. Clair and Hoinés 2018). Findings such as these demonstrate the importance of accounting for other relevant trophic relationships when predicting climate change effects on species—as in here where the complexities of invertebrate biology have a significant effect on seed set, and therefore potentially recruitment and dispersal patterns. Joshua trees may reproduce clonally, however, and patterns of sexual and clonal reproduction have not yet been investigated. As such, most seedlings of Joshua trees occur beneath nurse shrubs, which buffer the young seedlings from extreme temperatures and browsing, and further dispersal of the species may depend on the persistence of certain co-occurring vegetation, similar to other species in arid ecosystems (Gómez-Aparicio et al. 2004, Quero et al. 2011). This also illustrates why burns that clear the shrub layer present a particular challenge for recovery of this species.

While species distribution models/habitat suitability metrics are increasingly easy to create for both current conditions and future conditions, significant uncertainty exists in these predictions: due to differences between available GCMs (Flint

and Flint 2012) especially with respect to precipitation (Thorne et al. 2015), the lack of fine-scale soil data over much of the United States, the transferability of climate envelopes across time and space, and the accuracy of the species occurrence data among other concerns (Elith et al. 2006). Therefore, while we may treat these models with some confidence in the direction and magnitude of expected changes, we must also look for ways to assess the on-the-ground veracity of the predictions. Notably, these predictions differ from those of both Barrows and Murphy-Mariscal (2012) and Cole et al. (2011), which is likely due to (1) finer scale climate data (Barrows and Murphy-Mariscal 2012, resampled from 800 m PRISM data), (2) different future climate scenarios used, and (3) better and more dense information about Joshua tree presence, especially from the aforementioned targeted lower elevation surveys by JTNP resource staff. Certainly, modeling at range edges is greatly benefited by information from a southern boundary.

Long-term, large geographic scale inventory and monitoring projects that document density and recruitment patterns are invaluable resources for testing distribution model output, and these have been used to assess whether predicted changes are occurring, or whether species are able to migrate as expected (Zhu et al. 2012, Bell et al. 2014, Serra-Diaz et al. 2016). Although coarse-scale, long-term projects are useful for many species (Franklin et al. 2017), their utility for more narrowly distributed species or for specific information along range edges may be limited. Studies such as the present one, built on a framework from specific regional management questions (Barrows et al. 2014), can give specific and actionable data for adaptive management in parks.

CONCLUSIONS

Within Joshua tree refugia, plant and animal communities are nevertheless still vulnerable to multiple threats beyond the threat of climate change. These threats include anthropogenic nitrogen deposition from the LA basin, which bolsters the growth of invasive species, in turn increasing fire risk (Allen et al. 2009). Additionally, park staff must manage to reduce direct impacts of visitor use, changes in predator

abundance (Iknayan and Beissinger 2018), and off-highway vehicle activity. While the threat of global climate change is not something that can be mitigated locally, managing these additional threats within specific areas is more tractable for park managers. Our findings most importantly indicate the importance of regional to global mitigation strategies for carbon emissions, as reflected in the difference between maintenance of refugial areas for Joshua trees vs. an almost complete elimination of Joshua trees by the end-of-century.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2763/full>