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Past and ongoing shifts in Joshua tree distribution support future modeled range contraction

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Abstract. The future distribution of the Joshua tree (*Yucca brevifolia*) is projected by combining a geostatistical analysis of 20th-century climates over its current range, future modeled climates, and paleoecological data showing its response to a past similar climate change. As climate rapidly warmed ~11 700 years ago, the range of Joshua tree contracted, leaving only the populations near what had been its northernmost limit. Its ability to spread northward into new suitable habitats after this time may have been inhibited by the somewhat earlier extinction of megafaunal dispersers, especially the Shasta ground sloth. We applied a model of climate suitability for Joshua tree, developed from its 20th-century range and climates, to future climates modeled through a set of six individual general circulation models (GCM) and one suite of 22 models for the late 21st century. All distribution data, observed climate data, and future GCM results were scaled to spatial grids of ~1 km and ~4 km in order to facilitate application within this topographically complex region. All of the models project the future elimination of Joshua tree throughout most of the southern portions of its current range. Although estimates of future monthly precipitation differ between the models, these changes are outweighed by large increases in temperature common to all the models. Only a few populations within the current range are predicted to be sustainable. Several models project significant potential future expansion into new areas beyond the current range, but the species' historical and current rates of dispersal would seem to prevent natural expansion into these new areas. Several areas are predicted to be potential sites for relocation/assisted migration. This project demonstrates how information from paleoecology and modern ecology can be integrated in order to understand ongoing processes and future distributions.

Key words: climate change; climate effects modeling; extinct seed vectors; Joshua tree; Mohave Desert; plant migration; Yucca brevifolia.

INTRODUCTION

The Joshua tree enigma

The Joshua tree (*Yucca brevifolia* Engelm.), a giant yucca of the North American Mojave Desert, is known for its distinctive shape and height of up to 15 m (Fig. 1). It occupies desert grasslands and shrublands of the Mojave Desert of California, southern Nevada, northwestern Arizona, and southeastern Utah in the southwestern United States (Fig. 2). Joshua tree populations are discontinuous in their distributions, reaching their highest density on the well-drained sandy to gravelly alluvial fans adjacent to desert mountain ranges. Within dense stands, mature trees appear to be distributed across the landscape, rather than clustered together, especially at lower elevations. This pattern suggests that the mature trees might be able to take advantage of the infrequent rains by storing the briefly available near-surface water collected through their extensive network of fibrous roots (Gucker 2006).

Joshua tree presents several questions for evolutionary biologists, the first of which is its unusual height for a desert succulent. Fruiting generally does not begin until the individual has reached a height of around 2.5 m. Even its "dwarf" variety, *Yucca brevifolia* var. *jaegeriana*, typically reaches a height of 3–4 m (Benson and Darrow 1981). While a height of perhaps 1 m might allow the tree to escape high ground temperatures and the shading of adjacent plants, the selective advantage of a height exceeding 3 m is less clear. Greater height represents a large investment in supporting structure that also increases hydraulic resistance, lowering xylem water potential. The taller trees in this desert grassland may be more resistant to fire mortality (DeFalco et al.

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2010). It is also possible that the substantial stem of spongy tissue could facilitate water storage through dry seasons and years, similar to large arborescent cacti, although this has not been investigated.

Genetic studies support Joshua tree as the only member of section Clistocarpa; or yuccas with spongy and indehiscent seed pods (Pellmyr et al. 2007), which are actually large berries (Lenz 2001). While the capsules of smaller species break apart, releasing the seeds as they dry, Joshua tree and a few other large yuccas produce fleshy, indehiscent seed pods that are up to 10 times the mass of pods produced by the smaller species (Benson and Darrow 1981). The curious design of these seed pods led Lenz (2001) to speculate that its fruits were adapted for seed dispersal by now extinct megaherbivores (Janzen and Martin 1982).

Vander Wall et al. (2006) found that seed-caching rodents are capable of breaking open Joshua tree pods and caching the seeds. This, along with occasional spread of rhizomes (Guker 2006) could be the mechanism by which Joshua trees have persisted within their current populations and accomplished some colonization of adjacent areas.

Fossil Joshua tree and Shasta ground sloth.—The evidence of Pleistocene fossils of Joshua tree and the Shasta ground sloth (*Nothrotheriops shastensis* Sinclair) first became intertwined in the excavation of Gypsum Cave in southern Nevada in the 1930s (Harrington 1933). The poorly digested dung balls are almost entirely composed of the leaf fibers of Joshua tree (Fig. 1C), including abundant remains of fruits and seeds. The abundance of Joshua tree remains led the excavating paleontologist to proclaim that Joshua tree... "seems to have been a favorite food of the sloth" (Harrington 1933:193). Laudermilk and Munz (1934:33–34) also describe the yucca remains within the dung balls: "In addition to the fibers and epidermis, parts of the flower stalk, seed pods, and entire seeds also occur. In all cases where yucca seeds have been observed, these appear to be from *Yucca brevifolia*." They further describe the nature of the plant fossils in the dung balls as: "The material seems to have been poorly masticated, since large pieces of the wood stems of such plants as Atriplex and Ephedra, up to 3.5 cm long, are of common occurrence. The sharp tips of *Yucca brevifolia* and *Agave utahensis* also occur." Although we were unable to locate these original collections, a 40 000-year-old Joshua tree leaf discarded in the cave during these early excavations of the Pleistocene dung layers and collected much later is shown in Fig. 1C. Joshua tree no longer grows at Gypsum Cave, but survives just 20 km to the north at higher elevations.

Fossil records suggest that Joshua tree had a much larger geographic distribution during the latest Pleistocene. It is a more frequent component in fossil plant assemblages from packrat middens throughout the Mojave, Colorado, and Sonoran Deserts between 11 000 and 30 000 years ago than its current discontinuous range might suggest (Fig. 2; Appendix A). Its range suddenly contracted from the south as climates warmed at the start of the Holocene, leaving only what had been its northernmost populations.

The timing of the extinction of the Shasta ground sloth is well known due to dung deposits in caves that were continuously occupied throughout the latest Pleistocene. Radiocarbon dated dung balls from the top of the deposits show that this extinction occurred in continental North America about 12 900 calendar years ago (~11 000 radiocarbon year BP), or near the beginning of the cold Younger Dryas period. This extinction occurred somewhat later in other areas in a pattern suggesting a correlation with the rising populations of *Homo sapiens* (Steadman et al. 2005), although this period was also characterized by cooling climates which have recently become associated with a possible extraterrestrial impact 12 900 years ago (Firestone et al. 2007).

The most recent event of abrupt climate warming.—Future temperature increases for western North America are typically modeled to be between 3.5°C and 4°C over the next 60 to 90 years using the moderate A1B carbon emission scenario (Solomon et al. 2007). The effects of a past warming event of similar rate and magnitude could be used as an analog for the biological consequences of the future continental-scale climate warming (Cole 2010).

About 11 700 calendar years ago, temperatures rapidly increased as the Younger Dryas Period ended and the early Holocene began. Samples taken at a subannual resolution from the North Greenland Ice Core (NGRIP) suggest that this rapid warming may have started as a switch in climate mode occurring over only 1 to 3 years, initiating the warming over the subsequent 50 years (Steffensen et al. 2008). This rapid warming event is thought to have been caused by a sudden shift in the position of the Intertropical Convergence Zone, affecting widespread changes across the northern hemisphere such as increased moisture in Asian deserts (Steffensen et al. 2008). As a result, the timing of this change was likely to have been more-or-less synchronous throughout much of the northern Hemisphere (Alley 2000), although different regions experienced different magnitudes of change.

Regional records closer to the deserts of southwestern North America suggest that this warming had a magnitude of >4°C in winter minimum temperatures in the Grand Canyon (Cole and Arundel 2005) and a ~4°C increase in mean annual sea surface temperature off the coast of Northern California (Barron et al. 2004). Foraminiferal oxygen isotope values from a sea core in the Santa Barbara Basin (Hendy et al. 2002) also record this abrupt warming event around 11 700 years ago. This rapid warming event terminated the Pleistocene and was the beginning of the Holocene. It also was the most recent warming event of similar rate and magnitude to

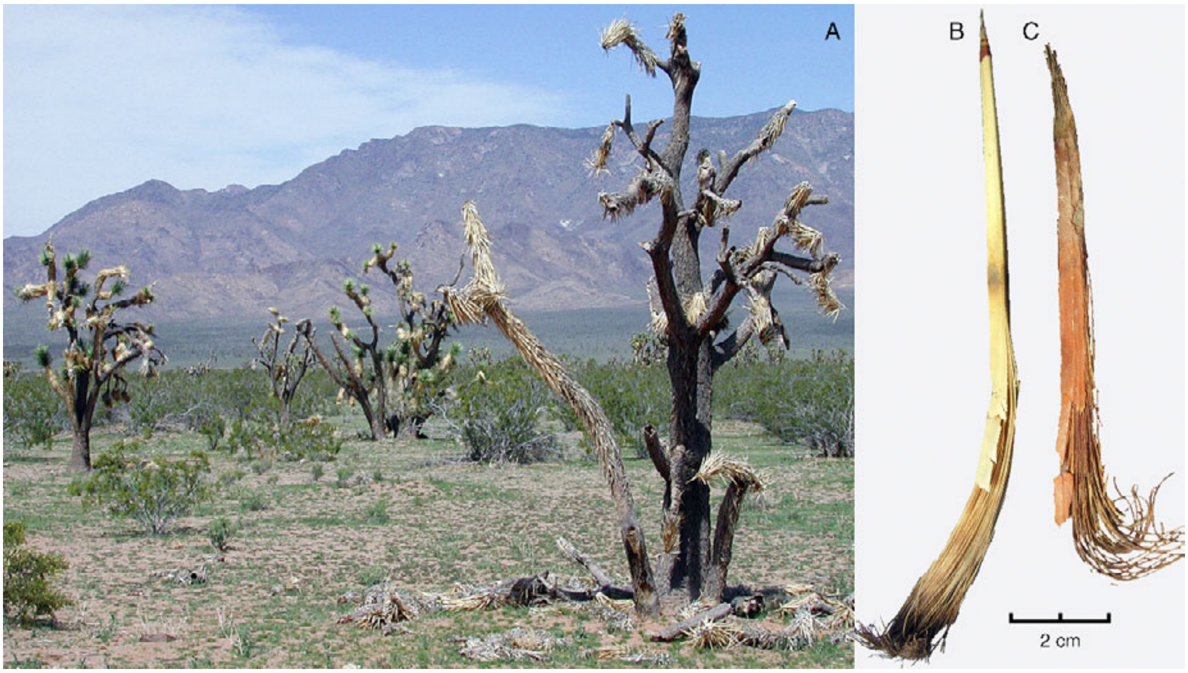

FIG. 1. (A) Joshua tree (*Yucca brevifolia*) woodland, Mojave County, Arizona, USA. This image, from April 2004, shows mortality resulting from several years of hot, dry climate. During 2003, this area received only 17% of its mean annual precipitation (2.6 of 15 cm), and the mean annual temperature was 2.2°C warmer than the long-term mean using measurements from the nearest climate station at Temple Bar, Arizona, USA. (B) Dried leaf from live tree, Clark County, Nevada, USA; (C) leaf from Pleistocene ground sloth dung layer, Gypsum Cave, Clark County, Nevada. This leaf has been radiocarbon dated at 40 000 ± 1200 yr BP (radiocarbon laboratory number WW7541).

that projected for the near future (Jackson and Overpeck 2000).

Modeling the response of Joshua tree to climate.—The climatic tolerances of a species (Shafer et al. 2001), sometimes referred to as its niche space (Jackson and Overpeck 2000), suitable climate space, climate window, or climate envelope, can be constructed by extracting the range of each climate variable across its range. But within the mountainous southwestern United States, climates are exceptionally spatially variable because of the extreme topography. As a result, extracting a species climate window from such a landscape requires a greater spatial detail than is typically available from population distribution maps or climate databases. To overcome these problems, we applied detailed observations of populations and fine-scale climate interpolations to a scale of ~4 km (2.5-arcmin).

Modeling the suitable climate for a species also requires distinguishing between parts of its range that are currently occupied from areas which from a climate perspective could potentially be occupied, but are not due to other reasons. Applying the terminology summarized by Jackson and Overpeck (2000), this is distinguishing between the species realized niche and its larger potential niche space. These areas of potential climate are unoccupied for a variety of reasons such as: the species' restricted capacity for colonization, historical events, substrate restrictions, current or past land use, geographic migration barriers, interactions with other species, and unmeasured climatic variables.

Predicting the consequences of a major climatic change on plant species population requires knowing both the plant's climate tolerances and how rapidly it can geographically shift in response to warming climates. Consequently, our models incorporate data from dispersal following the early Holocene warming as well as historical observations of the species movements.

METHODS

Past

The locations and ages of late Pleistocene Joshua trees from fossil packrat (*Neotoma* spp.) middens and Shasta ground sloth dung were compiled (Appendix A) and compared to Holocene records. Joshua tree fossils can be reliably identified in these deposits by its distinctive small, stiletto-like leaves with minutely denticulate margins (Fig. 1B, C), as well as fossil fruit pods and seeds.

Present

The geographic range and climatic tolerances of Joshua tree were derived using a compilation of presence and absence location data. Both presence and absences are recorded in plots contained within the LANDFIRE Reference Database (2007), the Central Mojave field data (Thomas et al. 2002), and the Beatly Plots (Webb et

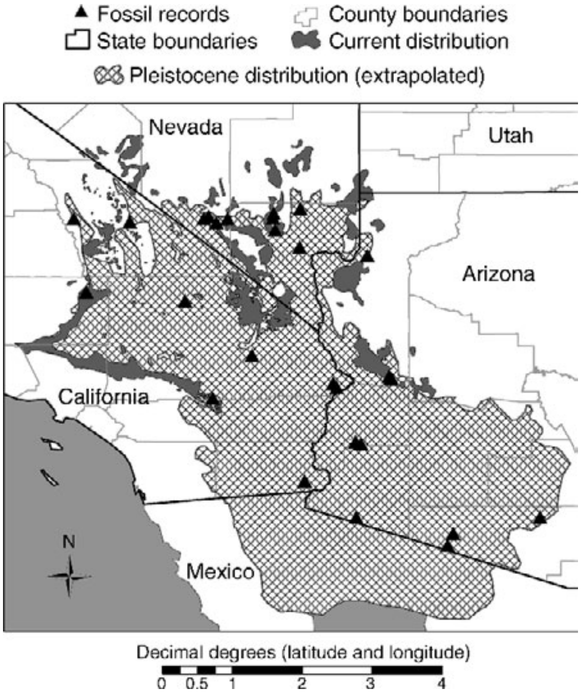

FIG. 2. Current likely distribution of Joshua tree (dark gray) is contrasted with its late Pleistocene (22 000–13 000 calendar years BP) fossil records of Joshua tree presence (dark triangles). Fossil absences (not shown) and presences were used to extrapolate a possible late Pleistocene range (crosshatched pattern) for Joshua tree assuming that areas with similar climates today to the modern locations of the fossils were also similar to them during the Pleistocene. These boundaries are speculative in some areas due to the scarcity of fossil records (southwestern California, USA; Gulf of California, Mexico). Abbreviations in the USA are: CA, California; NV, Nevada; UT, Utah; and AZ, Arizona.

al. 2003). Additional presence data were obtained from Rowlands (1978), and herbarium specimen location data provided by the participants of the Consortium of California Herbaria (*available online*).[9] Additional absence locations were generated from the Forest Inventory and Analysis National Incident Management System (NIMS) plot locations (Forest Inventory and Analysis Program 2008). This compilation of presence ($N = 991$) and absence ($N = 8079$) locations characterized the late-20th-century Joshua tree distribution (Appendix B).

In order to test the effects of climate grid resolution (~1 km vs. ~4 km), choice of monthly variables, and historical climate baseline on the effectiveness of the Joshua tree climate models, we compared many models, six of which are described in Table 1. We selected AD 1930 to 1969 to be our baseline climatic period because evidence suggests that Joshua tree recruitment was greater during this interval than during the latter part of the 20th century. For instance, survey results show minimal to no recent Joshua tree recruitment within the southern Mojave Desert in recent years (Commanor and Clark 2000; K. Cole, *personal observations*), and Joshua trees tall enough to be tallied in recent vegetation plots likely became established during this 1930–1969 interval or before. In addition, in the mid-1970s, the climate of the western United States began to trend distinctly warmer (Livezey et al. 2007), invalidating the assumption of climate normality following that time.

For each model, spatially important controlling climatic variables were analyzed using an analysis similar to that of Arundel (2005). The geographic extent of potential climate space was first determined using range of each climate variable within all the presence locations. Next, one variable at a time was withheld from the analysis to measure the resultant spatial expansion in the area of potential climate. Outliers, 1% of the extreme values in either tail of the variable range (2% of the locations), were removed to eliminate potential geo-referencing errors in species locations and errors created by small topographic features such as sharp ridges and deep ravines.

While Arundel (2005) ranked the climate variables in importance by the area of expansion of potential geographic range when each single variable was removed, we also considered the geographic distribution of the spatially constraining variables by selecting variables confining the species in all directions, producing a model that fits the presence/absence data well across the entire species range. Following the selection of constraining climatic variables, we developed probability surfaces using multiple logistic regression using all the available presence and absence location data as the dependent binary variable.

A model evaluation data set of 149 presence and 4354 absence locations was created using sources independent of the training data (Appendix B). Construction of this pseudo presence/absence gridded data set was required for this evaluation because of the high degree of spatial clustering of available plot data. This data set reduced spatial autocorrelation allowing the model performance to be evaluated equally across the landscape. The predictive abilities of each model could then be evaluated by the percentage of concordant and discordant pairs from among the 648 746 (149×4354) potential plot pairs. The suitable climate models with the highest percent of concordant pairs at both the ~1-km (30-arcsec) and ~4-km (2.5-arcmin) grid scales (model numbers 2 and 3; Table 1) were selected for further application to the future general circulation model (GCM) results.

Future downscaled GCM projections

To assess potential future changes in Joshua tree's suitable climate space we compared future projections from several GCM's for the late 21st century (2070–2099; ~$2 \times CO_2$). Five individual models and one ensemble of

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[9] ⟨http://ucjeps.berkeley.edu/consortium/⟩

48 runs of 22 models based upon the A1B carbon emission scenario were obtained from the Program for Climate Model Diagnosis and Intercomparison (PCMDI; AR4) archive (*available online*).[10] The five individual models used were: Hadley Center for Climate prediction (Hadgem1), Max Planck Institute for Meteorology (Mpi_echam5), CSIRO Atmospheric Research (Csiro_mk3), National Center for Atmospheric Research (Ncar_ccsm3), and Centre National de Recherches Météorologiques (Cnrm_cm3). They were selected because they represent a wide range of future moisture availability conditions for southwestern North America (Seager et al. 2007), and they all were ranked within the top half (of 22 models tested) for their ability to hindcast 20th-century precipitation seasonality within the southwestern U.S. deserts (Garfin et al. 2010). These models, especially the Hadgem1 and Mpi_echam5, outperformed most models in replicating the 1950 to 1999 AD geographic distribution of average seasonal precipitation (Garfin et al. 2010).

Results from an earlier, but higher resolution GCM, were also tested for comparison with the AR4 models. A run of NCAR's CCM3 (T170) global model of $2 \times CO_2$ climates generated global results on a ~75-km grid. These results were then downscaled for western North America to a ~1-km grid using the methods described in Cole et al. (2008*b*).

To find locations where a majority of the five ~4-km future suitable climate models agree, an 18% or greater probability threshold was selected for predicting suitable climate. These areas were then intersected where three or more of the models predict future climate suitable to Joshua tree. Using the current distribution map (Cole 2009), current populations falling outside of the area of agreement for future suitable climate (AAFSC) were designated as unsustainable. Current populations within the AAFSC were assigned as sustainable. Using a generous estimate of potential natural migration of 2 km over the next 60 to 90 years, areas within the AAFSC and 2 km or less from existing populations were designated as areas of potential natural migration. All remaining areas of the AAFSC were designated as areas of potential relocation or assisted migration. To further delineate suitable locations these areas were further confined to landforms that commonly support Joshua tree such as alluvial terraces, mesas, and gentle slopes (Gucker 2006). Landform classes were selected from Manis et al. (2001) for "nearly level plateaus or terrace" and "gently sloping ridges and hills" to further define the predicted areas to a 30-m resolution.

RESULTS

Past

In contrast to the alluvial terraces, mesas, and gentle slopes where Joshua trees are abundant (Gucker 2006), Pleistocene packrat middens are preserved in rockier habitats where middens are protected from moisture in caves or under alcoves. Yet despite sampling a less than optimal substrate, Joshua tree fossils have been found frequently in middens from across the Sonoran Desert of southern Arizona, the Colorado Desert of southern California, and the Mojave Desert of California, Nevada, and northwestern Arizona (Fig. 2; Appendix A). Because packrats typically collect items locally, these consistent fossil occurrences likely reflect a very predominant plant species, probably ubiquitous across the late Pleistocene Mojave and Sonoran deserts.

The current elevational range for Joshua tree is from 400 m to 1800 m (eFloras 2008). But between 22 000 and 11 700 years ago, fossil records document it within the lowest midden records at 245 m of the lower Colorado River valley (Cole 1986), to as high as its current maximum elevation at 1800 m in the Sheep Range of southern Nevada (Spaulding 1981). It possibly occurred at even lower elevations along the Gulf of California that are currently below sea level, as sea level was >80 m lower at that time (Fig. 2). After the Pleistocene to Holocene warming around 11 700 calendar years ago, the southern portions of the Joshua tree range rapidly contracted northward. By 8000 years ago, no fossil records are found to the south of, or down slope from, the current local limits of any stand.

Comparison of the few Holocene middens containing Joshua tree to its abundant Pleistocene records suggests minimal migrational change during the Holocene (Appendix A). But a few records could be used to infer movements from −10 to +35 km over the entire span of the Holocene (Appendix A). Thus, a range of possible northward Holocene migration rates could be −1 to 2 m/yr, much slower than any other species yet studied (McLachlan et al. 2005, Yansa 2006, Cole et al. 2008*b*). These results suggest that the species migrational capacities have been ineffective following the extinction of Pleistocene megaherbivores that may have acted as seed vectors, especially the Shasta ground sloth.

The low Holocene migration rates for Joshua tree are supported by observations of its movements within the last 70 years. In the southern part of its range, few had recolonized sites at Joshua Tree National Park 47 years after a fire or 70 years after a field was plowed (DeFalco et al. 2010). But near the northern end of its range in Nevada, Webb et al. (2003) document increases in the density of Joshua tree populations since 1963 from the numbers of distant mature Joshua trees in repeat photographs. At the northern periphery of the current range in the Inyo Mountains and Eureka Valley, California, mature Joshua trees are surrounded by frequent seedlings and saplings, typically within 30 m of an adult (K. Cole, *personal observation*; see Plate 1).

The increase in density in northern locations and absence of reproduction in southerly locations is further supported by the results from a previous study of permanent plots sampled in 1975, 1985, and 1995 at

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[10] ⟨http://www-pcmdi.llnl.gov⟩

TABLE 1. The effects of grid resolution, historical climate baseline period, and climate variables for six climate models suitable for Joshua trees (*Yucca brevifolia*).

Species model number	Grid resolution	Climate grids and baseline period	Model climate variables
1	~1 km (30 arcsec)	PRISM 1971–2000 normal	mean average monthly temperature and mean monthly precipitation
2	~1 km (30 arcsec)	ANUSPLIN 20th century	highest and lowest monthly mean temperatures over the period of record and mean monthly precipitation
3	~4 km (2.5 arcmin)	PRISM 1930–1969	extreme mean monthly temperature events and mean monthly precipitation
4	~4 km (2.5 arcmin)	PRISM 1930–1969	mean average monthly temperature and mean monthly precipitation
5	~4 km (2.5 arcmin)	PRISM 1930–1969	extreme mean monthly temperature events and maximum total precipitation
6	~4 km (2.5 arcmin)	Monthly P – PE 1930–1969	monthly total precipitation minus potential evapotranspiration

Notes: The models were evaluated by comparing the number of correct (concordant; the area under the Receiver Operating Characteristic curve) vs. incorrect (discordant) predictions from among 648 746 pairs of presence/absence locations (Appendix B) as reflected using a Somers' D statistic. A pair of observations is concordant if the observation with the observed response value of 1 has a higher predicted probability of being 1 based on the model, than the observation with the observed response of 0. A pair of observations is discordant if the observation with the observed response value of 1 has a lower predicted probability of being 1 based on the model, than the observation with the observed response of 0. Somers' $D = (\mathrm{nc} - \mathrm{nd})/(\mathrm{nc} + \mathrm{nd} + \mathrm{nt})$ where: nc is the number of concordant pairs, nd is the number of discordant pairs, and nt is the number of tied pairs. PRISM grids are from the PRISM Group, Oregon State University ⟨http://www.prismclimate.org⟩.

three locations across the distribution of Joshua tree. Comanor and Clark (2000) measured differences in growth rates between size classes and locations. The number of mature trees increased at all three locations. But the number of plants in the smaller size classes, seedlings and very young plants, differed across the populations. No plants in these size classes were observed in the two southerly study areas, near Victorville, California, and Kelso Dunes, California, USA. But at the most northerly location, the Nevada Test Site, five very young plants were observed in 1975. One of these plants survived to grow into a single-stemmed young plant, while the other four had died by 1995. One seedling was found at this northerly location in 1995; the only seedling found during this small study.

In the study of seed dispersal by seed-caching rodents within a southern Nevada Joshua tree stand, Vander Wall et al. (2006) found recent caches up to 30 m of the mature plant, and hypothesized that secondary caches could be carried up to 40 m. Almost all of the seeds in these caches were subsequently removed by granivorous rodents, such as deer mice (*Peromyscus* spp.), Merriam's kangaroo rat (*Dipodymys merriami*), packrats (*Neotoma* spp.), or white-tailed antelope squirrels (*Ammospermophilus leucurus*), but a small percentage (3 of 836) of the seeds from this study did successfully germinate. The fate of these resulting seedlings was not part of this study, but it is interesting to note that the area studied is among those with some of the highest probabilities of suitable climate for Joshua tree, both now and in the future.

The dispersal behavior from these seed-caching rodents over time (Vander Wall et al. 2006) could produce a slow migration rate similar to that observed in the Holocene fossil record. Assuming that the secondary seed dispersal by the rodents moves seeds 40 m from the source tree, and that each tree requires about 20 years to produce viable seed, then this combination would ultimately result in the 2 m/yr rate observed over the Holocene. This rate would likely increase and decrease during periods of favorable or unfavorable climate.

Present climate of Joshua tree

Our analysis of those climate variables that correlate with, as well as spatially confine (Arundel 2005), the modern occurrences of Joshua tree, allowed the development of suitable climate models from our ~1-km and ~4-km data sets of historical climate (Figs. 3A and 4A). The suite of suitable climate models (Table 1) show that monthly climate variables are useful for discriminating between where Joshua tree is present and where it is absent. All the models show acceptable to outstanding discrimination (Hosmer and Lemeshow 2000) using the evaluation data set.

The models using the entire 20th-century record or the 1930–1969 AD baseline period performed better than those using the most recent NOAA 1970 to 1999 normal values. The more detailed models run at the ~1-km grid also performed somewhat better than the ~4-km grid models. The model incorporating the moisture index (monthly precipitation – potential evaporation) rather than independent monthly temperature and precipitation variables performed the worst. The models incor-

TABLE 1. Extended.

Source of climate grids	Concordant pairs (%)	Discordant pairs (%)	Somers' *D*
PRISM Group	96.7	3.2	0.93
Cole et al. (2008*a*, *b*)	98.3	1.6	0.97
PRISM Group	97.9	2.0	0.96
PRISM Group	92.4	7.5	0.81
PRISM Group	97.4	2.5	0.95
calculated from variables available within the PRISM data set using the Hamon (1963) method	80.4	19.3	0.61

porating monthly temperature variability by using extreme high and low mean monthly values performed better than those simply using monthly mean values.

Suitable climate models number 2 and number 3 (Table 1) were selected as the best models for application of the ~1-km and ~4-km data sets. Both of these models seem to accurately describe the climatic basis for Joshua tree's present distribution. Because the spatial scale and available climate variables differed between the two data sets, a somewhat different suite of variables were combined to generate an optimal model from each data set. The ~1-km data set (Fig. 4A) was modeled by combining the mean precipitation of April, June, August, and December, extreme minimum temperature of January, and extreme maximum temperature of February. The ~4-km data set (Fig. 3A) incorporated mean precipitation of February, April, May, June, August, and December, minimum mean monthly temperature for February and December, and maximum mean monthly temperature for July and November.

The only region with a highly suitable climate and few presence plots are parts of southern to central Nevada. However, the region has few absence plots either, as much of it is occupied by defense department lands that have prevented plot measurements (Fig. 3A). Joshua tree is certainly present in places as suggested by the Natural Resources Management Plan for part of the area (Nellis Air Force Base 2007). But some of this region could also simply be unoccupied because of the species' restricted migration capacity.

The variables that rank the highest in the models suggest that the northern portion of Joshua tree's range is spatially limited by extreme winter cold events, but at lower elevations it is limited by extreme high temperature events in summer or winter. Mean precipitation patterns primarily limit the range from the east and west, as well as above and below its elevational range during various portions of the year. Low late-spring (April and May) precipitation seems to prevent Joshua tree from growing in lower elevation portions of the Mojave Desert. High winter rainfall or snow limit it from the higher elevations in some ranges of Nevada. The June drought period and the monsoon season, primarily in August, also appear to play an important part in limiting the distribution of Joshua tree in both the western and eastern portions of its range. We assume these limits are related to physiological limitations and are not coincidental. For example, seed germination experiments suggest germination is strongly controlled by temperature as well as seedling growth rates (Gucker 2006) and are thus assumed to be reflected in the distribution of the species.

Future Joshua tree range

All of the individual ~4-km GCMs and the ensemble of 22 GCMs project a severe decline in the area of suitable climates for Joshua tree by 2070 to 2099 AD, perhaps to as little as 10% of its current range, as the southern parts of its range becomes climatically unsuitable (Fig. 3B–G). The simulations, especially NCAR_ccsm3, and CNRM_cm3, portray broad future potential climates at higher elevations in the Sheep and Spring Ranges of southern Nevada and across the Nellis Air Force Range of south-central Nevada and across southern Utah. Some of the simulations suggest a potential new climate range spreading up the Owens Valley and Inyo and Panamint Mountains of California, as well as on the Hualapai Plateau of northernwestern Arizona.

Results from the ~1-km GCM (Fig. 4) are very similar to the ~4-km models across the southern portion of the Joshua tree range. It is also similar in many other areas, such as the greater potential across the Nellis Air Force Range of southwestern Nevada, and the Owens Valley of California.

The results obtained from the ~1-km model and each of the five ~4-km models from this study are also similar to those obtained earlier by Shafer et al. (2001). The methods applied by Shafer et al. (2001) differed in many respects, including: different GCMs, three climate variables (mean temperature of the coldest month, growing degree days, and a moisture index), a different historical baseline period (1951–1980), a different type of multivariate response surface, a different modern Joshua tree range map, all of which were projected onto a 25-km grid scale. Despite all of these differences, the results of Shafer et al. (2001) are very similar except that their future potential ranges expand much further to the north and east than those of the current effort. These differences are likely a result from the different grid scales used (1–4 km vs. 25 km).

As they are portrayed on Figs. 3 and 4, our models only estimate future areas of suitable climate from each individual model. They do not predict the future likely extent of Joshua tree populations until the species' migrational dynamics are considered. In order to

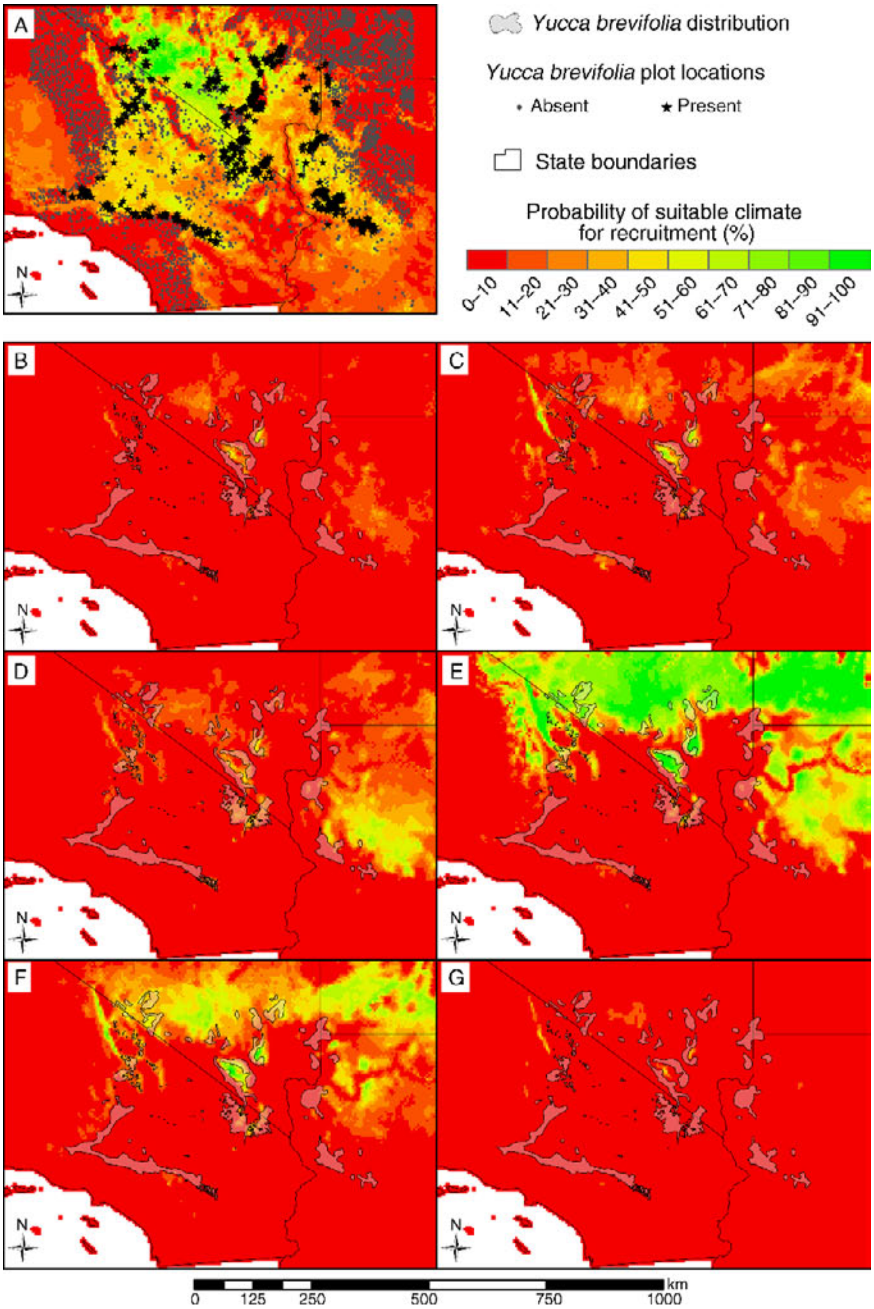

FIG. 3. (A) Suitable climate model for Joshua tree created with mid-20th-century (AD 1930–1969) PRISM mean precipitation variables and extreme mean monthly temperature events. (B–G) The Joshua tree future suitable climate model runs for late 21st century (AD 2070–2099 AD): (B) Hadgem1, (C) Mpi_echam5, (D) Csiro_mk3, (E) Ncar_ccsm3, (F) Cnrm_cm3, and (G) Ensemble (44 runs of 22 GCMs).

accomplish this and to consider the range of predictions from different models, the results of the five ~4-km models from this study were consolidated by combining the majority (three out of five) to project likely future Joshua tree potential climate (Fig. 5). These projections show where the majority of the models project current populations as unsustainable or sustainable under future climate scenarios. These models cannot project mortality of established individuals, only that certain populations are unsustainable through time either through direct mortality, or through an absence of successful reproduction.

New areas of potential climate on suitable landforms to support Joshua tree were then subdivided into areas of potential natural migration and areas with potential for assisted relocation. Areas with a potential for natural migration over the next 60 to 90 years are shown at 2-km expansion outward from current populations, corresponding to a rate of 22 to 33 m/year, in order to make these areas visible on Fig. 5, although our observations for past and current rates of migration were only ~2 m/year. The models project large areas of potential future habitat well outside of this range of natural migration, especially across the Nellis Air Force Base of southern Nevada (where it is likely already present), northwestern Arizona, and southwestern Utah.

DISCUSSION

Climatic tolerances for species in disequilibrium

Inferring species climate limits through geographic correlations between a current species range and recent climates relies on the assumption that the species is at least somewhat in geographic equilibrium with the baseline climate period used. That is, at least a portion of the species current range must be close to the geographic limit of each important variable comprising its suitable climate model. The greater the proportion of the species' range analyzed, the more likely this assumption is to be true because our observations of its realized niche will extend across the greatest portion of its potential niche space (Jackson and Overpeck 2000).

But the Joshua tree example used here does have an added complication in that its migrational capacity to respond to changing climates seems to be extremely limited. There are no historical records of Joshua tree invasions into new habitat and even few documented instances of recent seedling establishment. Although the rapidly warming climate of the early Holocene (Steffensen et al. 2008, Cole 2010) would seem to have opened up vast new areas of potential range to the north, the fossil record does not record any significant northward expansion over the last 11 700 years. These facts coalesce with morphological observations of the plant's indehiscent fruits and the abundance of fruits and seeds in fossil ground sloth dung to support the concept that the species' current mobility is constrained by the earlier extinction of the Shasta ground sloth and other possible seed vector(s) (Janzen and Martin 1982, Lenz 2001).

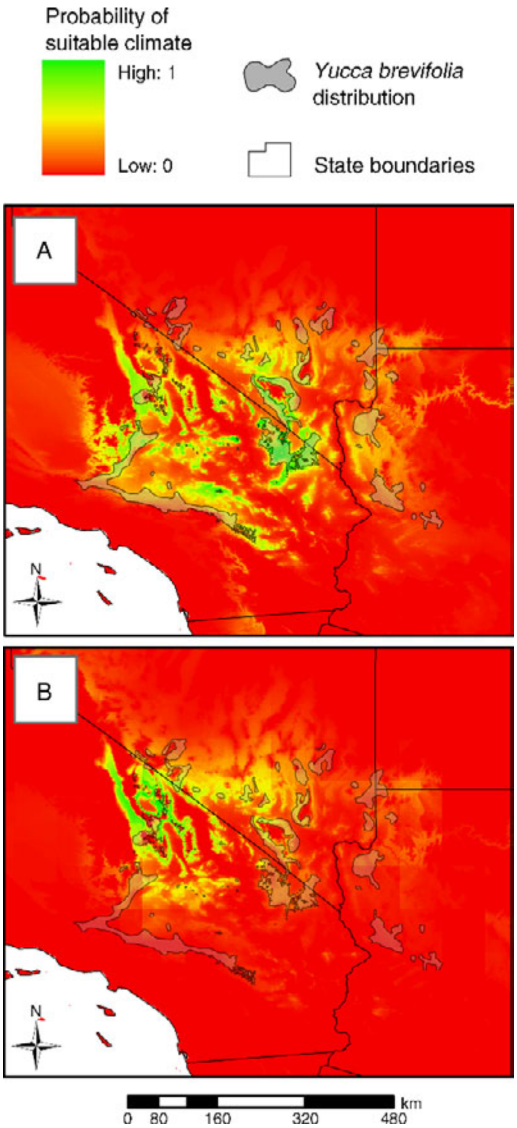

FIG. 4. (A) Suitable climate model for Joshua tree created with 20th-century ANUSPLIN mean precipitation variables and extreme mean monthly maximum and minimum temperature events (Cole et al. 2008*b*). (B) Future suitable climate model run from high-resolution (~75 km) late-21st-century projections downscaled to a ~1-km grid (Cole et al. 2008*b*).

Because of the constrained migrational capacity of Joshua tree, it is possible that our climate-window model underestimates its potential tolerance to colder temperatures. Populations could have prospered further north than its current range might suggest. This may be the case for other western tree species as well such as single-needle pinyon (*Pinus monophylla*; Cole et al. 2008*a*), especially because some may have not completely equilibrated to the warming over the last 150 years after the end of the little ice age. Because of this, it is possible that our model has underestimated the extent of potential areas for relocation throughout the Great Basin Desert regions of California, Nevada, and Utah. But this factor would be unlikely to mitigate the future predicted mortality of current southerly populations due to warmer temperatures.

The early Holocene retreat of Joshua tree to the northern periphery of its extensive Pleistocene range leaves little doubt that it is strongly influenced by rising temperatures. And its future movements, as modeled by these results, suggest a repeat of the pattern seen at the close of the Pleistocene, except starting from a much more restricted distribution. The results predict the survival of some natural Joshua tree populations throughout the next century, but most will be greatly reduced in area.

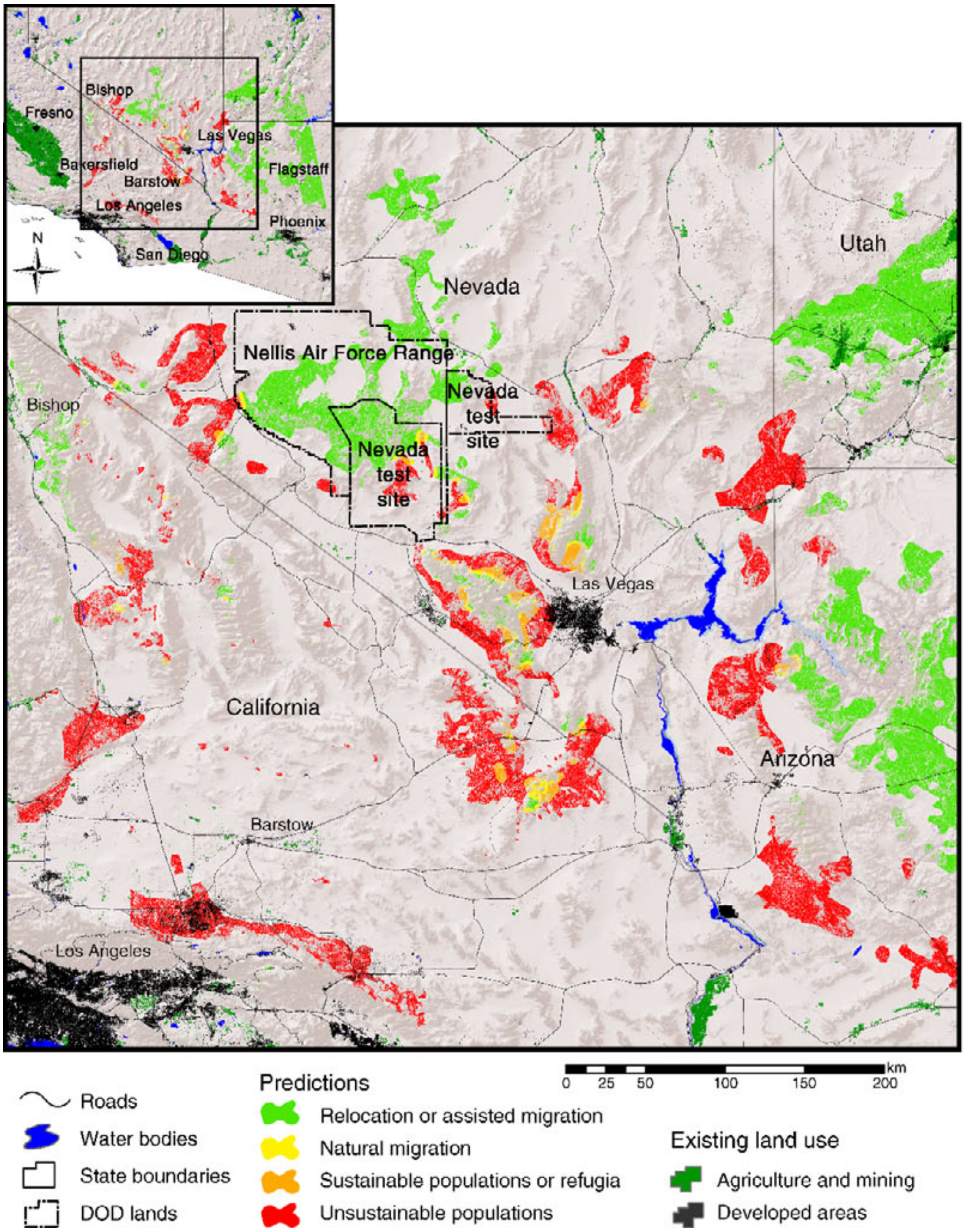

FIG. 5. Areas where a majority (three of five) of the models predict existing populations with future climates unsuitable for Joshua tree survival (red), current populations with future climates favorable for Joshua tree persistence (orange), areas within 2 km of current populations with future favorable climates and suitable substrates where natural migration could possibly occur (yellow), and protected areas with future favorable climates and suitable substrates where assisted migration might be possible (green). DOD stands for the U.S. Department of Defense.

Mechanisms of change

We have estimated the niche space for Joshua tree only from macrogeographic correlations between climate and populations. No inferences are made about the specific mechanisms through which climate affects the plants. Others have suggested more specific mechanisms such as: desert rodents foraging for moisture during times of drought (Esque et al. 2003), the necessity of low winter temperatures for flowering (Rundel and Gibson 1996), fire (DeFalco et al. 2010), and any climatic effects upon the mutualistic moths which are required for pollination (Pellmyr and

PLATE 1. Joshua tree saplings surrounding mature trees in the Inyo Mountains above Eureka Valley, California, USA. These saplings appear to be growing vigorously with leaves up to 35 cm long, unusual for a species named "brevi"-folia. Photo: K. L. Cole.

Segraves 2003). Extreme cold temperatures also may influence Joshua tree limits, and this effect could be moderated by future rising atmospheric CO_2 (Loik et al. 2000), although this is unlikely to be a factor in its decline in the warmest habitats. We believe that, because all of these mechanisms are ultimately a product of climate, these effects should all be incorporated within our modeled climatic window.

Because our model cannot directly address the specific mechanisms affecting Joshua tree varieties or genotypes at various localities, this remains an area for future research. Also, the life stage at which the species is limited cannot be determined using these techniques. Mature Joshua trees are likely more resilient than seedlings or juveniles. This effect may not even be a direct physiological control exerted on Joshua tree itself, as the species seed production is also dependent upon the survival of its mutualistic moth (Godsoe et al. 2008).

The rarity or absence of successful seedlings or saplings over recent decades in the southern portion of the Joshua tree range (Comanor and Clark 2000; K. Cole, *personal observation*), suggests that seedling success may be limited by successive years of high temperatures and/or low precipitation resulting in an excess of evapotranspirative stress at this life stage. Perhaps seedlings require several successive wet and/or cool years, and warmer desert sites below its current limit are beyond the limit of such periods. If this is the case, then modeling future climate variability would be essential for improving predictions as even the incorporation of monthly mean maxima and minima improved our model predictions.

Managed relocation

Although it is likely that some of these un-sampled areas with high levels of future climate potential, such as Nellis Air Force Base, are already occupied by Joshua tree, they could serve an important conservation function in the future. But other areas further from the current range in central Nevada, northwestern Arizona, and southwestern Utah could hold high potential for future relocation efforts, should such activities prove desirable and possible. Managed relocation, also known as assisted migration or assisted colonization, has become a controversial topic for conservation (Hoegh-Guldberg et al. 2008). Any future efforts toward managed relocation that do occur will become dependent upon downscaled model predictions like those shown in Fig. 5. Because these predictions have been downscaled to a landscape scale, land managers could apply these projections to specific parts of a protected area.

The landscape-scale models shown here also allow for a critical evaluation of model performance directly on the landscape prior to the start of any managed relocation efforts. Because of their downscaled projections, model performance can be tested at specific intervals in specific locations using repeat plot data. A climate/vegetation model could be applied using the actual measured climate trends over a test interval and compared to the model's predictions for such an interval. Once a model has proven the capacity to predict ongoing climate-driven vegetational changes within acceptable limits, then it may be sufficiently mature for application.

Fortunately for Joshua tree, a majority of the areas predicted to be sustainable, within migrational range, or potential assisted migration sites, are already on federal lands or other protected areas. Ninety-six percent (739 km^2 out of 772 km^2) of the area predicted to allow survival of current stands, and 91% (378 km^2 out of 414 km^2) of the area predicted within the range of natural migration are on Federal lands that are not expected to be at risk of development or urbanization. Further, 83% of the areas predicted as potential relocation sites (17 909 km^2 out of 21 578 km^2) occur on Federal lands.

CONCLUSIONS

As climate rapidly warmed at the start of the Holocene, the widely dispersed range of Joshua tree severely contracted from the south, leaving only the populations near what had been its northernmost limit. The Holocene and recent history of Joshua tree suggests that its migrational capacity may be severely limited. Its ability to spread northward into new suitable habitats during the Holocene may have been inhibited by the somewhat earlier extinction of its primary megafaunal dispersers, especially the Shasta ground sloth. Because GCM models project a climate warming of a similar pace and magnitude to that of the early Holocene over the next 60 to 90 years, Joshua tree could undergo a similar decline in its southernmost populations to that of the early Holocene.

Construction of an independent test data set of Joshua tree current presence and absence allowed the evaluation of multiple suitable climate models for Joshua tree. Model concordance was found to increase with the inclusion of measures of monthly temperature variability (maximum and minimum rather than just mean), finer spatial scale (~1 km rather than ~4 km), and applying a 40-year mid-20th-century baseline (1930–1969) climate rather than a 30-year late-20th-century baseline (1970–1999).

Five individual GCM models downscaled to ~4 km, one suite of 22 ~4-km models, and one ~1-km model, all project the future elimination of Joshua tree throughout most of the southern portions of its current range, with only perhaps 10% of existing stands remaining. Several models project significant potential future expansion into new areas beyond the current range, but the species' historical and current rates of dispersal would seem to prevent natural expansion into these new areas. Several regions are projected that could become potential sites for relocation/assisted migration, should such a policy be considered advisable and possible.

ACKNOWLEDGMENTS

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APPENDIX A

Fossil records documenting late Pleistocene Joshua tree distribution and Holocene migration rates (*Ecological Archives* A021-007-A1).

APPENDIX B

Creation of an independent, non-autocorrelated, evaluation data set (*Ecological Archives* A021-007-A2).