PETITION TO LIST THE Joshua tree (*Yucca brevifolia*) UNDER THE ENDANGERED SPECIES ACT

The Joshua tree (*Yucca brevifolia*) pictured on the 1987 U2 album cover of the same name. The tree fell around 2000. Photo: Wikimedia

Petition Submitted to the U.S. Secretary of the Interior Acting through the U.S. Fish and Wildlife Service

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INTRODUCTION

WildEarth Guardians (Guardians) respectfully requests that the Secretary of the Interior, acting through the U.S. Fish and Wildlife Service (Service) list the Joshua tree—either as a full species *(Yucca brevifolia)* or as two subspecies (*Y. b. brevifolia*, *Y. b. jaegeriana*)—as "threatened" under the U.S. Endangered Species Act (ESA) (16 U.S.C. §§ 1531-1544). WildEarth Guardians also requests that the Service designate critical habitat for the species or subspecies concurrent with listing.

Joshua trees exist in a precarious equilibrium. They have evolved a mutualistic relationship with yucca moths, on which they depend for pollination. They depend for seed dispersal on the vagaries of rodent caching. They require a narrow climate window to thrive. Lastly, Joshua trees are slow-growing, slow-reproducing plants and therefore respond very slowly to changes in their environment.

The delicate balance allowing Joshua trees to survive is being disrupted by several human-caused threats. Climate change is first among them; climate models indicate that by 2100, as much as 90% of Joshua tree habitat may disappear. Secondary and interacting threats include drought, pollution, invasive plants, and changing fire regimes.

These iconic trees are an irreplaceable part of the Mojave Desert and the American landscape. Because of their nature, efforts to save them must look to the future on a timescale of decades, if not centuries. We therefore urge the Service to take the long view and proactively conserve these incredible plants before they become endangered.

ENDANGERED SPECIES ACT AND IMPLEMENTING REGULATIONS

The ESA, 16 U.S.C. §§ 1531-1544, was enacted in 1973 "to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, [and] to provide a program for the conservation of such endangered species and threatened species." 16 U.S.C. § 1531(b). The protections of the ESA only apply to species that have been listed as endangered or threatened according to the provisions of the statute. The ESA delegates authority to determine whether a species should be listed as endangered or threatened to the Secretary of Interior, who has in turn delegated authority to the Director of the U.S. Fish & Wildlife Service. As defined in the ESA, an "endangered" species is one that is "in danger of extinction throughout all or a significant portion of its range." 16 U.S.C. § 1532(6); *see also* 16 U.S.C. § 533(a)(1). A "threatened species" is one that "is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." 16 U.S.C. § 1532(20). The Service must evaluate whether a species is threatened or endangered as a result of any of the five listing factors set forth in 16 U.S.C. § 1533(a)(1):

A. The present or threatened destruction, modification, or curtailment of its habitat or range;
B. Overutilization for commercial, recreational, scientific, or educational purposes;
C. Disease or predation;
D. The inadequacy of existing regulatory mechanisms; or
E. Other natural or manmade factors affecting its continued existence.

A taxon need only meet one of the listing criteria outlined in the ESA to qualify for federal listing. 50 C.F.R. § 424.11.

The Service is required to make these listing determinations "solely on the basis of the best scientific and commercial data available to [it] after conducting a review of the status of the species and after taking into account" existing efforts to protect the species without reference to the possible economic or other impacts of such a determination. 16 U.S.C. § 1533(b)(1)(A); 50 C.F.R. § 424.11(b). "The obvious purpose of [this requirement] is to ensure that the ESA not be implemented haphazardly, on the basis of speculation or surmise." *Bennett v. Spear*, 520 U.S. 154, 175 (1997). "Reliance upon the best available scientific data, as opposed to requiring absolute scientific certainty, 'is in keeping with congressional intent' that an agency 'take preventive measures' *before* a species is 'conclusively' headed for extinction." *Ctr. for Biological Diversity v. Lohn*, 296 F. Supp. 2d 1223, 1236 (W.D. Wash. 2003) (*emphasis in original*).

In making a listing determination, the Secretary must give consideration to species which have been "identified as in danger of extinction, or likely to become so within the foreseeable future, by any State agency or by any agency of a foreign nation that is responsible for the conservation of fish or wildlife or plants." 16 U.S.C. § 1533(b)(1)(B)(ii); *see also* 50 C.F.R. § 424.11(e) (stating that the fact that a species has been identified by any State agency as being in danger of extinction may constitute evidence that the species is endangered or threatened). Listing may be done at the initiative of the Secretary or in response to a petition. 16 U.S.C. § 1533(b)(3)(A).

In determining if a species should be listed as "threatened," the Service must consider whether it is likely to become an endangered species within the "foreseeable future." Courts have held that the definition of foreseeable future is species-specific, depending on the species' life history characteristics. In *Otter v. Salazar*, No. 1:11-cv-00358-CWD, 2012 WL 3257843 (D. Idaho Aug. 8, 2012) the court held that "the definition of foreseeable future is to be made on a species-by-species basis and through an analysis of the time frames applicable to the particular species at issue." *Id.* at 19. In *W. Watersheds Project v. Foss*, No. CV 04-168-MHW, 2005 WL 2002473, at 16 (Aug. 19, 2005) the court stated: "the definition of 'foreseeable future' may vary depending on the particular species." *Id.* In order to list a species as "threatened," the ESA only requires a showing that the species is likely to be in danger of extinction in the foreseeable future, not that it be at "high risk" of extinction. *Id.* at 17. As both the life span and the generation time of Joshua trees are long, it may take four to five decades to detect demographic changes in the population. We consider the timeframe of approximately 100 years discussed in this petition (*see* "Factor E: Climate change," *infra*) to be a reasonable definition of "foreseeable future" for this long-lived, slow-growing species. If anything, this timeframe is too short, but we are limited by the predictive ability of climate models.

After receiving a petition to list a species, the Secretary is required to determine "whether the petition presents substantial scientific or commercial information indicating that the petitioned action may be warranted." 16 U.S.C. § 1533(b)(3)(A). Such a finding is termed a "90-day finding." A "positive" 90-day finding leads to a status review and a determination whether the species will be listed, to be completed within twelve months. 16 U.S.C. §1533(b)(3)(B). A "negative" initial finding ends the listing process, and the ESA authorizes judicial review of such a finding. 16 U.S.C. § 1533(b)(3)(C)(ii). The applicable regulations define "substantial information," for purposes of consideration of petitions, as "that amount of information that would lead a reasonable person to believe that the measure proposed in the petition may be warranted." 50 C.F.R. § 424.14(b)(1).

The regulations further specify four factors to guide the Service's consideration on whether a particular listing petition provides "substantial" information:

i. Clearly indicates the administrative measure recommended and gives the scientific and any common name of the species involved;
ii. Contains detailed narrative justification for the recommended measure; describing, based on available information, past and present numbers and distribution of the species involved and any threats faced by the species;
iii. Provides information regarding the status of the species over all or significant portion of its range; and
iv. Is accompanied by appropriate supporting documentation in the form of bibliographic references, reprints of pertinent publications, copies of reports or letters from authorities, and maps. 50 C.F.R. §§ 424.14(b)(2)(i)-(iv).

Both the language of the regulation itself (by setting the "reasonable person" standard for substantial information) and the relevant case law underscore the point that the ESA does not require "conclusive evidence of a high probability of species extinction" in order to support a positive 90-day finding. *Ctr. for Biological Diversity v. Morgenweck*, 351 F. Supp. 2d 1137, 1140 (D. Colo. 2004); *see also Moden v. U.S. Fish & Wildlife Serv.*, 281 F. Supp. 2d 1193, 1203 (D. Or. 2003) (holding that the substantial information standard is defined in "non-stringent terms"). Rather, the courts have held that the ESA contemplates a "lesser standard by which a petitioner must simply show that the substantial information in the Petition demonstrates that listing of the species may be warranted." Morgenweck, 351 F. Supp. 2d, p. 1141 (*quoting* 16 U.S.C. § 1533(b)(3)(A)); *see also Ctr. for Biological Diversity v. Kempthorne*, No. C 06-04186 WHA, 2007 WL 163244 at 3 (N.D. Cal. Jan. 19, 2007) (holding that in issuing negative 90-day findings for two species of salamander, the Service "once again" erroneously applied "a more stringent standard" than that of the reasonable person).

CLASSIFICATION AND NOMENCLATURE

Common name. Common names for *Yucca brevifolia* include "Joshua tree" or more rarely "Joshuatree yucca" (Petrides, 1998, p. 383). *Y. b. jaegeriana* is known by the common names "Jaeger Joshua tree," "Jaeger's Joshua tree," or "eastern Joshua tree" (IT IS, 2015d). We refer to the full species as "Joshua tree" throughout this petition; subspecies will be referred to by their Latin names.

Taxonomy. The petitioned species is *Yucca brevifolia* (Engelm 1871). The full taxonomic classification is shown in Table 1. It is within the monotypic Clistocarpa section of the genus *Yucca*, defined by a spongy, indehiscent fruit (Pellmyr et al., 2007, p. 496). There are two generally accepted varieties of Joshua tree: *Y. b.* var. *brevifolia* and *Y. b.* var. *jaegeriana.* In the literature on Joshua trees, "variety" is generally used to refer to infraspecific groupings. In botanical taxonomy, "variety" is equivalent to "subspecies" as defined by the ESA (USFWS, 1978, p. 17,912; Haig et al., 2006, p. 1,589), so we use the term "subspecies" in this petition. Lenz (2007) divides the genus into two full species: *Y. brevifolia* and *Y. jaegeriana*. This division has not been universally adopted, and the two subspecies interbreed in the Tikaboo Valley contact zone in Nevada (Yoder et al., 2013, p. 2). For the purposes of this petition, we treat *Y. brevifolia* as a single species with two subspecies: *Y. b. brevifolia* and *Y. b. jaegeriana*. However, if the Service determines that *Y. b. brevifolia* and *Y. b. jaegeriana* are better treated as full species, we ask that this petition be considered a petition for each of the two full species, as the description and information for *Y. b. brevifolia* and *Y. b. jaegeriana* is equivalent to information on *Y. brevifolia* and *Y. jaegeriana,* respectively.

The subspecies *Y. b. herbertii* (J. M. Webber) Munz was described in 1959 based on production of off-sets from underground rootstocks; though occasionally mentioned in the literature, this subspecies has not been universally accepted (Lenz, 2007, pp. 98-99; *see also* ITIS, 2015c) and therefore will not be discussed further in this petition. There is mention of another subspecies, *Y. b. weberi*, in Maxwell (1971, p. 5), but this subspecies is not verified elsewhere and is most likely a synonym for *Y. b. herbertii*, so will not be discussed further.

Table 1. Taxonomy of *Yucca brevifolia* (ITIS 2015a-d).

Kingdom	Plantae
Division	Magnoliophyta
Class	Lilopsida
Order	Liliales
Family	Agavaceae
Genus	*Yucca*
Species	*brevifolia*
Subspecies	*brevifolia* *jaegeriana*

SPECIES DESCRIPTION

***Yucca brevifolia*: full species.** Joshua trees are monocotyledonous evergreen trees endemic to the Mojave Desert (Smith et al., 1983, p. 10). Joshua trees are “the tallest and most treelike of the yuccas,” and have the shortest leaves (Petrides, 1998, p. 383). Joshua trees can grow up to 70 feet tall, though trees over 40 feet are rare. Trunks are fibrous and the one- to two-inch-thick bark is soft and corklike. Young trees typically lack branches as they generally grow three to nine feet in height before branching. Branches are often seven to 20 feet or longer and fork at two- to three-foot intervals. Leaves are clustered in rosettes at the branch ends (Gucker, 2006, p. 5). Leaves are six to 13 inches (15-33 centimeters (cm)) long, 0.25 to 0.5 inch (0.64-1.3 cm) wide, flat above with fine-toothed edges, blue-green, and rigid (Petrides, 1998, p. 383, 385). They exhibit C_3 photosynthesis (Smith et al., 1983, p. 10), and “photosynthesis by *Y. brevifolia* is better adapted to the moderate temperatures of spring and fall than to the high temperatures of summer” (Smith et al., 1983, p. 16). The combination of “a moderate photosynthetic rate and a high leaf area index enables *Y. brevifolia* to exhibit substantial productivity during the winter-spring growth period” (Smith et al., 1983, p. 16).

Joshua trees are long-lived; one population near St. George, Utah, had an estimated median age of 89 years, and five percent of that population are expected to reach 383 years of age (Gilliland et al., 2006, p. 207). They have been described as “probably the oldest living things in the

American southwest desert," with large trees estimated to be up to 300 years old (Johnson, 1970, p. 99).

Figure 1. *Yucca brevifolia brevifolia* (a), *Y. b. jaegeriana* (b) (Godsoe et al., 2009, p. 595), and the two subspecies growing in sympatry in Tikaboo Valley, Nevada (bottom, *Y. b. brevifolia* on the left and *Y. b. jaegeriana* on the right. Image is reversed from its original orientation for consistency of presentation) (Starr et al., 2013, p. 2).

Y. b. brevifolia. The larger of the two subspecies grows on average 15 to 30 feet tall,[1] and the trunks of older trees can reach five feet in diameter (Figure 1a). The lowest branches are usually six to ten feet above the ground. Leaves are eight to 14 inches (20-36 cm) long and 0.375 to 0.5 inch (0.95-1.3 cm) wide (Benson & Darrow, 1981, p. 51).

The two subspecies are distinguished not only by physical characteristics, but also by range. *Y. b. brevifolia*, the western subspecies, occupies "plains and gravelly alluvial fans in the Mojavean Desert and just above it at 2,000 to 5,000 feet elevation [in] California from the Haiwee Reservoir south of Owens lake southward through the mountains along and in the Mojave Desert (but occasionally on the flats) to the Iron and Eagle mountains, Riverside County, and eastward to the Grapevine Mountains near Death Valley; Nevada from Goldfield, Esmerelda County, to

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[1] For consistency, meters have been converted to feet where found. Conversions between meters and feet have been rounded to the nearest 1, or to the nearest 10 if over 1,000. In some cases we leave the original measurement in meters for increased accuracy. All other conversions are given in parentheses and rounded as appropriate.

Lincoln and Clark counties; southwestern Utah; Arizona south of the Colorado River in Mohave County and southeastward to southwestern Yavapai County" (Benson & Darrow, 1981, p. 51).

Y. b. jaegeriana. The smaller, eastern subspecies is sometimes referred to as the "miniature Joshua tree" (Figure 1b). Trees are generally 9 to 15 feet tall, with trunks smaller than 15 inches (38 cm) in diameter. The lowest branches are usually within three feet of the ground, and leaves are 4 to 10 inches (10-25 cm) long and 0.25 to 0.375 inch (0.64-0.95 cm) wide (Benson & Darrow, 1981, p. 52). *Y. b. jaegeriana* are "[c]ommon on the hills and alluvial fans of the upper part of the Mojavean Desert at 2,500 to 4,500 feet elevation… [in] California east of Baker, to the Shadow, Kingston, Clark, and New York mountains in San Bernardino County; Nevada in Clark County; Arizona in northwesternmost Mohave County; southwesternmost Utah (Beaverdam Mountains)" (Benson & Darrow, 1981, p. 51).

Reproduction. Joshua trees reproduce sexually through seed production and sometimes asexually by rhizomes, branch sprouts, or basal sprouts (Gucker, 2006, p. 6, 8). Seed production is "periodic or rare" and "wet years" are suggested as best for flowering and fruit production (Gucker, 2006, p. 6). Joshua trees flower in mid-spring (Waitman et al., 2012, p. 2). "Joshua tree flowers occur in dense, heavy panicles that measure 8 to 20 inches (20-40 cm) long. Individual flowers are round to egg-shaped and measure 1 to 2 inches (2.5-5 cm) by 0.4 to 0.8 inch (1-2 cm) wide" (Gucker, 2006, p. 6, *internal citations omitted;* Figure 2).

Figure 2. Flowers of *Yucca brevifolia brevifolia* (left) and *Y. b. jaegeriana* (right). Six-inch ruler (Lenz, 2007, p. 101).

Joshua trees are fleshy- or baccate-fruited species; fruits are borne in tight clusters at the ends of branches (Lenz, 2001, p. 62). Fruits are indehiscent capsules, which become spongy and dry with age. Egg-shaped capsules are 2 to 4 inches (6-10 cm) long and approximately 2 inches (5 cm) in diameter. Fruits develop at the base of the inflorescence while the upper portion is still in flower. Mature fruits contain 30 to 50 seeds, which are flat to thickened with smooth to undulate surfaces. Seeds are 0.3 to 0.4 inch (7-11 millimeters (mm)) long (Gucker, 2006, p. 6, *internal citations omitted*).

At peak ripeness, the fleshy, moist mesocarp has a sugar content of up to 20%, and the fruits have softened so that the thin exocarp is easily broken. As time passes, the green mesocarp dries and becomes a granular white mass. As the fruits age, they may split along carpel lines or the exocarp may crack, releasing moisture so that the fruits eventually become hard, dry, spongy, grayish-green to tan or brown-colored bodies (Lenz, 2001, p. 62). "*The fruits never open spontaneously for the release of the enclosed seeds*" (Lenz, 2001, p. 62, *emphasis in original*), leading to considerable speculation about the species' seed dispersal mechanism (*see* "Seed dispersal," *infra*).

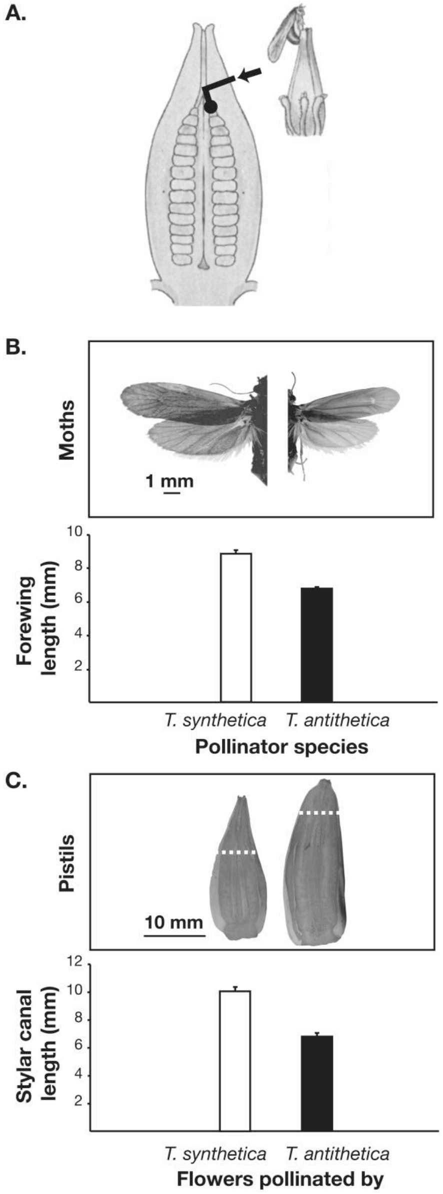

Figure 3. Mechanics of oviposition and phenotype matching in flowers and pollinators of *Yucca brevifolia*. A) Oviposition into a Joshua tree flower by a female moth and cross section of floral pistil showing the path taken by the moth's ovipositor, first cutting through the stylar wall and then pushing down the stylar canal to the ovules. B) Half-images of female *Tegeticula synthetica* (left) and *Tegeticula antithetica* (right), and a bar chart showing the mean and 95% confidence intervals for female forewing length (a standard index of overall body size) for each species. C) Cross-sectioned, stained pistils from Joshua trees in populations pollinated by *T. synthetica* and *T. antithetica,* respectively, with the lowest extent of their stylar canals (i.e., top of the column of ovules onto which the female moth oviposits) marked by dashed horizontal lines, and a bar chart showing the mean and 95% confidence intervals of stylar canal length for trees pollinated by each moth species. Trees pollinated by the larger *T. synthetica* have significantly longer stylar canals (P < 0.0001) (Godsoe et al., 2008, p. 817).

Pollination. Yuccas (Agavaceae) have an obligate pollination mutualism with yucca moths (Lepidoptera, Prodoxidae). The plants rely on adult moths for pollination, while the moth larvae feed on developing yucca seeds (Pellmyr, 2003, p. 36). The associations between yuccas and moths are relatively exclusive, often with a single pollinator species per plant species (Pellmyr, 2003, p. 36). Joshua trees are pollinated by *Tegeticula antithetica* and *T. synthetica* (Smith et al., 2009, p. 5,219).

Female yucca moths lays their eggs in Joshua tree flowers by inserting a flattened, blade-

> like ovipositor through the top of the wall of the floral pistil and down the stylar canal. Following oviposition, to ensure that the flower will develop and produce seeds for the offspring to eat, the moths deliberately pollinate the flower, placing pollen collected previously directly onto the floral stigma using uniquely-derived, tentacle-like mouthparts… The conflict between the plant's interests (minimizing the number of seeds lost to feeding by the moth's larvae) and the moth's interests (producing as many larvae as possible) sets up a coevolutionary tug-of-war between plant and pollinator that has shaped the evolutionary history of each. (Smith et al., 2009, p. 5,219, *internal citations omitted*)

Western *Y. b. brevifolia* are primarily pollinated by *T. synthetica,* while the eastern *Y. b. jaegeriana* are primarily pollinated by *T. antithetica,* with a small (~5 kilmoter- (km) wide) area of sympatry in the Tikaboo Valley of central Nevada (Yoder et al., 2013, p. 2). "[M]orphological studies have shown that Joshua trees pollinated by the two moth species differ significantly in both vegetative and floral features, with the greatest difference found in the length of the stylar canal—the path through which the female yucca moth inserts her ovipositor during oviposition" (Smith et al., 2009, p. 5,219, *internal citations omitted*). The moths also show differences in morphology. *T. antithetica* is smaller and has a shorter ovipositor; though it visits *Y. b. brevifolia* and *Y. b. jaegeriana* indiscriminately when both subspecies are present, it produces more larvae per oviposition event when laying eggs on the shorter-styled *Y. b. jaegeriana. T. synthetica,* which is larger and has a longer ovipositor, visits *Y. b. jaegeriana* rarely when both subspecies are present and does not appear to successfully produce larvae on the shorter-styled eastern trees. This is likely because *T. synthetica*'s larger ovipositor damages *Y. b. jaegeriana* flowers badly enough to induce abscission (shedding of the flower) (Smith et al., 2009, pp. 5,225-5,227; Figure 3).

Germination. In the laboratory, germination rates of Joshua tree seeds were typically 90 to 95%. During germination studies inside rodent exclosures, germination rates dropped to 14.8%, indicating that many viable seeds do not germinate (Vander Wall et al., 2006, p. 542). The cause of this low germination rate is unknown; under natural conditions, rodent predation, abiotic factors, soil invertebrates, or microbes may reduce germination. Seeds cached by rodents are more likely to germinate than seeds left at the soil surface. A study simulating rodent caches at various depths determined that seeds at the surface or buried 0.04 inch (0.1 cm) below the surface germinated a fraction of the time compared to seeds buried 0.4 to 1.2 inches (1-3 cm) below the surface (Waitman et al., 2012, p. 6). However, the germination rate of cached seeds is still very low; only three out of 836 seeds found in caches remained there until they germinated in the spring and established seedlings (Vander Wall et al., 2006, p. 542; this may be a lower rate than usual as the cited study took place during a period of drought). Seedlings are also more likely to emerge under shrub cover (Waitman et al., 2012, p. 6), supporting the findings of Bittingham and Walker (2000, p. 374) that "nurse plants" (which "ameliorate a stressful environment for seedlings of other plants") play an important role in successful Joshua tree germination:

> Recruitment of *Y. brevifolia* is largely dependent upon the existence of microclimates that occur under the canopies of perennial shrubs, most importantly *Coleogyne ramosissima.* The advantages of germination within the canopy of another plant include higher soil moisture, reduced insulation, reduced surface temperatures, reduced evapotranspirational

> demand, increased nutrients, reduced herbivory, and reduced wind desiccation. Disadvantages of germination under another plant may include competition for water if the adult plant has a near-surface root system, reduced [photosynthetically active radiation (PAR)] inhibiting carbon gain, and allelopathy. (Brittingham & Walker, 2000, p. 379)

Further supporting the importance of nurse plants, Esque et al. (2015, pp. 87-88) found that "[t]he position of pre-reproductive *Y. brevifolia* in relation to perennials significantly influenced survival time… Survivorship curves for [plants found at the edge of perennials versus plants well inside the drip line of associated perennials] clearly indicate greater mortality for canopy-edge plants during the first few years of monitoring."

"[R]ecruitment of *Y. brevifolia* requires a convergence of events, including fertilization by unique pollinators, seed dispersal and caching by rodents, and seedling emergence from a transient seed bank triggered by isolated late-summer rainfall. Alignment of these convergent events likely results in the successful establishment of new seedlings only a few times in a century" (Esque et al., 2015, p. 85). *Y. brevifolia* seeds have "frequent opportunities for germination," with "the greatest seedling emergence occur[ing] when rainfall events coincided with warm temperatures in September and April," (Reynolds et al. 2012, p. 1,652) but seedling survival is generally low. In studies from December 2008 to November 2010, 82% of the seedlings that emerged in September 2008 perished within the first 12 months, and only 5% survived until the end of the study. No seedlings that emerged in January or April 2010 survived for 12 months and only 3% of the seedlings that emerged in September 2009 survived at least until the conclusion of the study 16 months later (Reynolds et al. 2012, pp. 1,650-1,651).

> When compared to the climate record for our site, favorable precipitation conditions for seedling emergence occurred in about 68% of summers, which suggests that conditions conducive to emergence events might be more common than expected on the basis of our low detection of *Y. brevifolia* seedlings in the field. However, summer precipitation decreases on a southeast to northwest gradient across the entire range of *Y. brevifolia* and, thus, conditions conducive to emergence are expected to decline in frequency across that gradient in relation to less summer precipitation. This pattern implies that there are fewer opportunities of emergence in the far western Mojave Desert, and under the current climate regime *Y. brevifolia* in that area may be most vulnerable to demographic change resulting from low and infrequent recruitment and [sic] may already have occurred. (Reynolds et al. 2012, p. 1,652, *internal citations omitted*)

Germinability of seeds decreases over time. "Longevity of seeds in the soil declined by about 50% per year, which indicates that *Y. brevifolia* has little capacity for seed dormancy," and likely does not produce a consistent seed bank (Reynolds et al. 2012, p. 1,652).

Seed dispersal. There are several theories about the mechanism of Joshua tree seed dispersal, including wind dispersal, coevolution with now-extinct megaherbivores, and rodent activity. Wind is unlikely to effectively disperse Joshua tree seeds. In wind tunnels, it took strong winds of approximately 88 and 74 km/hour to move seeds and fruits, respectively, on a cobble substrate approximating typical natural conditions (Waitman et al., 2012, p. 4). Winds this high are rare in the Mojave Desert, compromising a maximum of 1.3% of wind speed observations (Waitman et al., 2012, p. 4).

Some researchers theorize that Joshua trees originally evolved to be dispersed by now-extinct megaherbivores, potentially proboscideans (elephant family), camelids, or ground sloths (Lenz, 2001, p. 66). Some researchers favor the Shasta ground sloth (*Nothrotheriops shastaensis*) as a seed dispersal vector (*e.g.* Cole et al., 2011) based on the presence of Joshua tree leaves, fruits, and seeds in fossilized ground sloth dung. However, Lenz (2001) dismisses ground sloths as influencing Joshua tree evolution as they appeared in Joshua tree range only long after arborescent yuccas were established in the region (p. 70), and Waitman et al. (2012) argue that dispersal by ground sloths was unlikely as most of the seeds found in sloth dung were damaged (p. 6). Others disagree with the megaherbivore theory entirely:

> [Scientists have] suggested that large, herbivorous mammals, perhaps extinct, may have dispersed the seeds of some yuccas in their feces, but there is no direct evidence to support this hypothesis, and the production of pods at variable heights ([7 to 33 feet] above the ground) by Joshua trees raises questions about coevolution with an obligate, non-climbing herbivore. Also, the seed coat of Joshua tree seeds is relatively thin. It seems unlikely that such seeds could be adapted for mastication and the severe treatment they would likely receive in a vertebrate gut. Available information suggests that seeds that are not harvested by seed-caching rodents probably have no chance of establishing a seedling. Although more research is needed, the indehiscent nature of Joshua tree fruits and the lack of an alternative means of seed dispersal suggest that seed-caching rodents may be required for Joshua tree seed dispersal. (Vander Wall et al., 2006, p. 543; *see also* Smith et al, 2011; Waitman et al., 2012)

Joshua tree seeds may have been dispersed historically by woodrats; Joshua tree remains were recovered from macrofossil woodrat middens in the western Mojave Desert and in Death Valley (Gucker, 2006, p. 15).

Regardless of historic mechanisms for seed dispersal, present-day Joshua tree seed dispersal is primarily via rodent caching. "The dismantling of yucca pods by rodents is very important because there is no other known mechanism for Joshua tree seeds to exit the indehiscent seed pods" (Vander Wall et al., 2006, p. 543). Rodent species that feed on and cache Joshua tree seeds include white-tailed antelope squirrels (*Ammospermophilus leucurus*), Merriam's kangaroo rats (*Dipodymus merriami*), canyon mice (*Peromyscus crinitus*), Mohave ground squirrels (*Xerospermophilus mohavensis*), and California ground squirrels (*Otospermophilus beecheyi*) (Vander Wall et al., 2006, p. 541-542; Gucker, 2006, p. 15).

Rodent dispersal, though necessary for Joshua tree reproduction, contributes to the low germination rate and limited migration capabilities of the trees. White tailed antelope squirrels and Merriam's kangaroo rats do not preferentially cache seeds under the shrub cover of potential nurse plants (Waitman et al., 2012, p. 5; Swartz et al., 2010, p. 1,265), and thus do not maximize germination or recruitment.[2]

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[2] Pale kangaroo mice (*Microdipodops pallidus*) and little pocket mice (*Perognathus longimembris*) cache seeds preferentially under shrubs (Swartz et al., 2010, p. 1,265), but neither species has been recorded caching Joshua tree seeds.

Another disadvantage of rodent seed dispersal is that it may depend on a fine balance between seed and rodent abundance:

> Scatter-hoarding as a dispersal syndrome is often dependent on masting; the production of large seed crops may be sufficient to satiate the appetite of granivorous animals. If scatter-hoarding rodents are satiated, the remaining seeds that have been hoarded are available to germinate. The quality of seed dispersal may thus be dependent on the overabundance of seed production… The rainfall and temperature conditions that favor seedling survival probably occur infrequently, making recruitment episodic. The relationship between Joshua trees and scatter-hoarding rodents is a mutualistic one; however, the relationship may be context dependent. Small seed crop size along with an overabundance of rodents may shift this interaction from mutualism toward seed predation by rodents. (Waitman et al., 2012, p. 6, *internal citations omitted*)

Lastly, dispersal distances are short. Vander Wall et al. (2006, p. 241) found that the mean maximum dispersal distance by rodents was 98 (±55) feet. However, the dynamics of dispersal distance are more complex than could be fully quantified in the study:

> Most yucca seeds reside at several different sites before finally being consumed or germinating, and removal of seeds from cache sites is not an accurate measure of seed predation. The recaching of seeds has important consequences for seed dispersal; as seeds are dispersed from original caches they may be moved further from the original source plant, split into additional caches, and moved to a greater variety of habitat. Because many seeds were moved from their original cache site and probably recached, our estimate of establishment from natural caches is likely to be an underestimate of true seedling establishment. We were unable to conduct extensive, repeated surveys of the areas around source plants, so many secondary (and tertiary) caches were probably missed, and the fate of these seeds is unknown. Also, some of the recached seeds were probably carried farther from the source plant, suggesting that maximum seed dispersal distances were probably greater than the mean maximum distance of [98 feet] recorded for primary caches. (Vander Wall et al., 2006, p. 542, *internal citations omitted*)

Researchers have recorded longer dispersal distances: “young or juvenile plants have been found as far as 495 feet (151 m) from a seed-producing plant in Los Angeles County. A maximum dispersal distance of 823 feet (251 m) was recorded in San Bernardino County” (Gucker 2006, p. 7). However it is unknown how common these events are, and “most long-distance dispersal events [for plants] may be so rare as to be nearly unpredictable” (Neilson et al., 205, p. 753). “Even given the possibility of long-range dispersal events, habitat fragmentation resulting from human land-use activities will have significant impact on the abilities of species to successfully disperse in response to changing climate conditions” (Shafer et al., 2001, p. 211). Joshua tree dispersal appears to be consistently slow. “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 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” (Cole et al., 2011, p. 145, *internal citations omitted*).

Fossil evidence from the Holocene indicates that Joshua tree migration rates were slow; -3 to 7 feet per year (-1 to 2 m/yr). This is similar to observed migration rates over the past 70 years. "Assuming that the secondary seed dispersal by the rodents moves seeds 40 m [131 ft] 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 [7 ft/yr] rate observed over the Holocene" (Cole et al., 2011, p. 142).

Due to their relatively short dispersal distances and low germination rates, it is difficult for these long-lived and slow-growing plants to colonize new habitats:

> During major and sudden climactic shifts, *Y. brevifolia* would be unable to "jump" to distant sites where conditions might be more favorable… Even if the species were able to make sizeable geographical leaps, it would be constrained by the over-ruling fact that in a single generation it could move only the distance a pollinating moth can fly. The reasoning being that although successfully colonizing a new area and reproducing asexually, the plants without aid of the pollinating moth would be unable to reproduce sexually and therefore unable to permanently hold new territory… [M]oths may fly as far as [380 feet]… [*Y. brevifolia*'s] resilience has permitted it to successfully endure past environmental revolutions and the [theorized] loss of its principal seed-dispersing agent, or agents. However, depending upon the intensity and duration of global warming its long-range survival may depend upon the availability of a refugia. (Lenz, 2001, p. 72)

Growth rate and maturity. "Being monocots, and therefore lacking in growth rings, Joshua trees are difficult to date" (Barrows & Murphy-Mariscal, 2012, p. 35). In Joshua Tree National Park, "a test study of unbranched [seedlings] showed a growth rate of 3 inches [7.6 cm] per year for the first 10 years and a scant 1.5 inches [3.8 cm] per year after that" (Keith, 1982, p. 42). Gucker (2006, p. 5) reports average growth rates ranging from 2.3 to 4.6 inches/year (5.9-11.7 cm/year).

> McKelvey (1938) estimated [Joshua trees'] vertical growth rate to be to be around [3 feet] in the first 6 years and then slowing down towards maturity and Gossard (1992) found that in Joshua Tree National Park their growth rate is slower, somewhere around 'two feet every ten years.' The Center for Arid Land Restoration reported seedling Joshua trees can grow 10-15 cm [4-6 inches] in their first year and then 2.5 cm/year [1 inch/yr] thereafter. Finally, Gilliland et al. (2006) reported a mean growth rate of 3.75 cm/year [1.5 inches/yr] for Joshua trees in southern Utah. (Barrows & Murphy-Mariscal, 2012, p. 35, *some internal citations omitted*).

The most recent study reports a "long-term mean annual growth rate of 3.12 ±1.96 cm [1.23 ±0.77 inches] over 22 [years]… Mean change in height between census periods was positively correlated with the amount of precipitation… summed across the census period" (Esque et al, 2015, p. 87). Joshua trees generally do not fruit until they reach a height of 8 feet (Cole et al., 2011, p. 137). The generation time of *Y. brevifolia* is probably more than 20 years (Dole et al., 2003, p. 144); Esque et al. (2015, p. 89) estimate a generation time of 50 to 70 years.

Gene flow and genetic diversity. Smith et al. (2008, p. 2,685) suggest that "there may not be intrinsic barriers to reproduction between different Joshua tree morphotypes, but… these

populations are maintained as evolutionarily distinct groups by pollinator specificity" (*see also* Starr et al., 2013; Yoder et al., 2013). Though the subspecies are differentiated genetically, there is "strong evidence for hybridization between subspecies" (Starr et al., 2013, p. 7).
There is "much greater [nuclear] gene flow moving from *Y. b. jaegeriana* into *Y. b. brevifolia* than vice versa" (Starr et el., 2013, p. 7), which is likely due in large part to the ability of *T. antithetica*, the primary pollinator of *Y. b. jaegeriana*, to pollinate both subspecies when they are present. This is supported by research on chloroplast DNA, which is maternally inherited through the seed:

> Analysis of DNA sequence data from the chloroplast… finds that although there is effectively no gene flow from *Y. b. jaegeriana* into *Y. b. brevifolia*, there appears to be ongoing movement of chloroplast genomes from *Y. b. brevifolia* into *Y. b. jaegeriana*. While the very low rate of sequence evolution in the chloroplast makes it difficult to distinguish contemporary gene flow from ancestral polymorphism, it is intriguing that this pattern of asymmetrical plastid introgression mirrors the differences in pollinator behavior. (Starr et al., 2013, p. 4, *internal citations omitted*)

Smith and colleagues speculated that the lower host fidelity in *T. antithetica* caused a chloroplast capture event (Starr et al., 2013, p. 4): "in order for the high levels of chloroplast introgression from west to east to be explained by nuclear gene flow, there must be significant pollinator mediated gene flow from east to west. Thus, we would predict that the eastern moth (*T. antithetica*) must visit and successfully pollinate western trees much more often than western moth (*T. synthetica*) pollinates eastern trees" (Smith et al., 2009, p. 5,220). This appears to be the case: "where the two pollinator species co-occur, a large, statistically significant fraction of trees appear to be of hybrid origin. In addition, genetic analyses indicate higher rates of nuclear gene flow from *Y. b. jaegeriana* into *Y. b. brevifolia*, which may explain the introgression of *Y. b. brevifolia* chloroplast genomes into *Y. b. jaegeriana*" (Starr et al., 2013, p. 4).

HABITAT REQUIREMENTS

Joshua trees inhabit the "Joshua tree series" of the Mojave desertscrub biome, where the Mojave Desert grades upslope along its periphery into cooler, moister vegetation (Turner, 1982, p. 165). Joshua tree may be co-dominant with "*Larrea, Coleogyne, Juniperus*, or *Carnegiea* at various places in its near-circular range around the margins of the [Mojave] Desert," and understory species are diverse (Turner, 1982, p. 166; *see also* Benson & Darrow, 1981, p. 8). Perennial grasses are often the dominant vegetation in Joshua tree stands (Gucker, 2006, p. 3). Joshua tree populations are not regularly distributed across the landscape, "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 desert rains by storing the briefly available near surface water collected through their extensive network of fibrous roots" (Cole et al., 2011, p. 137, *internal citations omitted*).

Soil. "Soils in Joshua tree habitats are silts, loams, and/or sands described as fine, loose, well drained, and/or gravelly. Joshua tree tolerates alkaline and saline soils" (Gucker, 2006, p. 9, *internal citations omitted*) and prefers "well-drained mesas or the slopes at the foot of desert ranges" (Maxwell, 1971, p. 4) where runoff is minimal (Turner, 1982, p. 166). "It is most often found on level flats or gentle slopes" (Rowlands, 1978, *cited in* Lenz, 2001, p. 61).

Elevation. Reports of the upper and lower elevation limits of Joshua trees vary, with a minimum of ~1,600 and a maximum of ~7,200 feet (Table 2).[3] Lower elevation limits increase in the northern areas of their distribution (Gucker, 2006, p. 8).

Successful seedling recruitment appears to be bounded by physiological limits of the plants at both low and high elevations:

> [L]owest percentages [of seedling recruitment] were at [3,280] and [3,940 feet], increasing to a maximum at [5,250 feet] (50%), then decreasing at [5,910] and [6,560 feet] (12%). Smith et al. (1983) concluded that low temperatures act as a constraint upon the range of *Y. brevifolia* at high elevations, while high temperatures recorded within the Mojave Desert were within its physiological capability. However, data gathered in the Sheep and Spring Mountain ranges indicate that low elevations did have sparse levels of seedling recruitment, while higher elevations had higher recruitment levels until a physiological point (perhaps a critical temperature) where they no longer occurred. (Brittingham & Walker, 2000, p. 380)

Table 2. Elevation range of Joshua trees (*adapted from* Gucker, 2006, p. 9)

State/region	*Elevation (feet)*
Arizona	Under 3,600
California	1,600-6,600
Death Valley	Above 5,600
Intermountain West	2,800-7,200
Mojave Desert	2,000-6,600
Nevada	3,600-6,900
Utah	2,620-5,610 (Welsh et al., 2003, p. 683)

Climate. Joshua trees are adapted to cold winters, hot summers, and little precipitation (Gucker, 2006, p. 8). "Climate is an important determinant of Joshua tree distribution, and the climactic requirements of the two subspecies are very similar across the many environments they both encounter" (Godsoe et al., 2009, p. 597). The plant as a whole "tolerates a broad range of temperatures, from -25 to 51 °C [-13 to 120 °F], and annual precipitation from 98 to 268 mm [3.9-10.6 inches]" (Lenz, 2001, p. 61). The plant's leaves are very hardy:

> *Y. brevifolia* can survive leaf temperatures well below 0 °C and above 50 °C [32 °F to 122 °F], with a lower tolerance… of approximately -11 °C [12 °F] and an upper tolerance of 59 °C [138 °F]. The respective tolerances of the photosynthetic apparatus… were -6

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[3] Elevation reports include: between 1,640 to 6,560 feet (Hickman 1993, p. 1,210); mostly "above 3,000 feet where cold winters allow an essential dormant period" (Keith, 1982, p. 42); 2,000 to 5,000 feet for *Y. b. brevifolia* and 2,500 to 4,500 feet for *Y. b. jaegeriana* (Benson & Darrow, 1981, pp. 51-52), 2,300 to 6,890 feet (Rowlands, 1978, *cited in* Gilliland et al., 2006, p. 202), 2,460 to 5,910 feet (Thomas et al., 2004, p. 245), "between [2,950 feet] and [5,910 feet] in the eastern and above [2,620 feet] in its western area" (Went, 1957, p. 172).

> °C [21 °F] and 57 °C [135 °F]… Although the low temperature tolerance of its leaves may limit its range at higher elevations, the leaves of *Y. brevifolia* are apparently able to tolerate even higher temperatures than it encounters in the field. (Smith et al., 1983, p. 16)

Despite their heat tolerance, Joshua trees are limited in range by a large set of environmental requirements, including temperature and precipitation. "High germinability within the first year and broad emergence of *Y. brevifolia* during periods of increased soil moisture and warm weather indicate adaptation to regular summer rainfall" (Reynolds et al., 2012, p. 1,652). The trees also require a specific temperature range. Climate models support limits on Joshua tree distribution from numerous climatic factors:

> 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 and are thus assumed to be reflected in the distribution of the species. (Cole et al., 2011, p. 143)

Went (1957) suggests that after *Y. brevifolia* has "reached a certain age the plant requires an annual cool-season exposure to low temperatures for optimal growth later in the warm season" (Turner, 1982, pp. 166-167). "When this *Yucca* is grown at lower altitudes, it survives well as a young plant, but grows poorly when older. From its distribution the impression was gained that it needs a yearly period of cold for proper growth" (Went, 1957, pp. 172-173). Went supported this hypothesis with laboratory experiments. "At the age of [3.5] years some [*Y. brevifolia*] plants were given a two-month cold treatment at 4 °C [39 °F] (16-hour photoperiod). During the cold period no growth took place but during the next two months more than double the number of new leaves developed when compared with plants which did not have the cold treatment" (Went, 1957, p. 173). The need for a cold period for optimal growth may explain Joshua trees' restriction to higher, cooler sites at the Mojave Desert periphery (Turner, 1982, p. 167).

GEOGRAPHIC DISTRIBUTION

Fossil record. During the Pleistocene,

> *Yucca brevifolia* had a more expansive distribution, occurring in middens as far south as Organ Pipe National Monument, as far north as the Armagosa Desert and Sheep Range of southern Nevada and as far east as the Waterman Mountains of southern Arizona, whereas its subsequent Holocene history has been one of contraction from the southern and eastern limits of its Pleistocene range [Figure 4]. Global warming may have a further,

> profound impact on the range of *Yucca brevifolia.* (Holmgren et al., 2009, pp. 10-11, *internal citations omitted*)

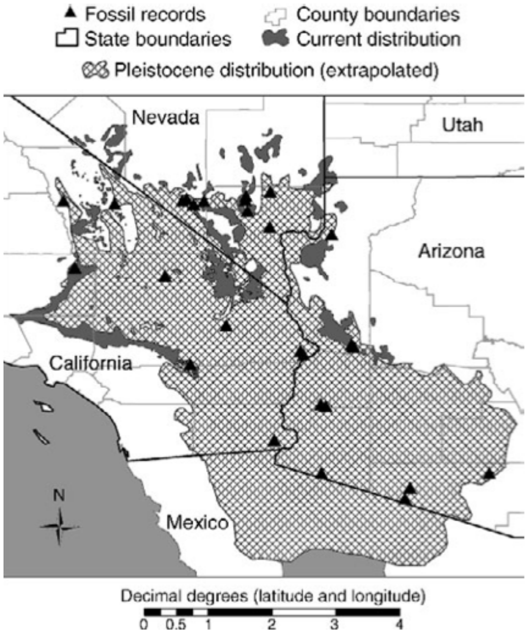

Figure 4. Current Joshua tree distribution contrasted to late Pleistocene (22,000 to 13,000 calendar year BP) fossil records, which were used to extrapolate a possible late Pleistocene range (Cole et al., 2011, p. 140).

The Pleistocene distribution was stable within the area now known as Joshua Tree National Park (JNTP), but that stability may not hold up under current climate stressors:

> One of the most notable trends in [the packrat midden record] is the relative stability of many species within JTNP, including the park's namesake *Yucca brevifolia*. Factors contributing to this stability likely include the lack of invasion by extralocal species during the late glacial and the early establishment and persistence of many desert scrub elements… [M]odeled potential climate ranges for species such as *Yucca brevifolia* suggest a future for plant populations at JTNP that stands in marked contrast to the past stability seen in the packrat midden record. (Holmgren et al., 2009, p. 13)

In order to model the potential impacts of climate change on Joshua trees, researchers have looked to similar climate shifts that happened in the past. "About 11,700 calendar years ago, temperatures rapidly increased as the Younger Dryas Period [of the Pleistocene] ended and the early Holocene began" (Cole et al., 2011, p. 138). This rapid warming event, which may have taken place over as little as 50 years, is the "most recent warming event of similar rate and magnitude to that projected for the near future" (Cole et al., 2011, p. 138-139, *internal citations omitted*). "Although the rapidly warming climate of the early Holocene would seem to have opened up vast new areas of potential [Joshua tree] range to the north, the fossil record does not record any significant northward expansion over the last 11,700 years" (Cole et al., 2011, p. 145, *internal citations omitted*).

> 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. (Cole et al., 2011, p. 145; *see* "Factor E: Climate change," *infra*)

One study indicates that Joshua trees may have shifted their range during glacial cycles without suffering population declines:

> Although palaeorecords clearly indicate that Joshua trees occurred over a much broader geographic area during the last glacial period, we found no indication of dramatic population declines in *Y. brevifolia* since the [last glacial maximum (LGM)]. The distribution models also suggest that the total potential distribution was either constant, or increased slightly between the LGM and today, and that habitat loss in the southern part of the Joshua tree's range was offset by the addition of new potential habitats in the north.[4] (Smith et al., 2011, p. 10, *internal citations omitted*)

Genetic data indicates that populations of both Joshua trees and their mutualistic moths increased concomitantly during the late Pleistocene, though Joshua tree range did not become significantly larger (Blatrix et al., 2013, p. 310). Explanations for signatures of population growth in the genetic data are uncertain, but the simplest explanation is that "large population expansions occurred prior to the end of the last glacial period," before the Holocene (Smith et al., 2011, p. 14). The implications of this information for the future of Joshua trees is uncertain; other models are not optimistic about the trees' ability to shift their range rapidly enough to keep pace with the current rate of climate change (*see* "Factor E: Climate change" *and* "Limited dispersal capabilities," *infra*).

Current range. The Joshua tree is endemic to the Mojave Desert, and is found "along almost the entire periphery of the [Mojave] where this biome grades upslope into cooler moister vegetation" (Turner, 1982, p. 165). It occupies desert grasslands and shrublands in California, southern Nevada, northwestern Arizona, and southeastern Utah (Cole et al., 2011, p. 137). *Y. b. brevifolia* occupies "plains and gravelly alluvial fans in the Mojavean Desert and just above it at 2,000 to 5,000 feet elevation [in] California from the Haiwee Reservoir south of Owens lake southward through the mountains along and in the Mojave Desert (but occasionally on the flats) to the Iron and Eagle mountains, Riverside County, and eastward to the Grapevine Mountains near Death Valley; Nevada from Goldfield, Esmerelda County, to Lincoln and Clark counties; southwestern Utah; Arizona south of the Colorado River in Mohave County and southeastward to southwestern Yavapai County" (Benson & Darrow, 1981, p. 51). *Y. b. jaegeriana* are "[c]ommon on the hills and alluvial fans of the upper part of the Mojavean Desert at 2,500 to 4,500 feet elevation… [in] California east of Baker, to the Shadow, Kingston, Clark, and New York mountains in San Bernardino County; Nevada in Clark County; Arizona in northwesternmost Mohave County; southwesternmost Utah (Beaverdam Mountains)" (Benson & Darrow, 1981, p. 51; Figures 5 & 6).

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[4] Note: "Distribution modeling reconstructs only the potential habitats that are likely to have been suitable given the climate; if dispersal limitation excluded trees from some potential habitat, either in the past or in the present, this difference would not be captured in the distribution modeling" (Smith et al., 2011, p.14).

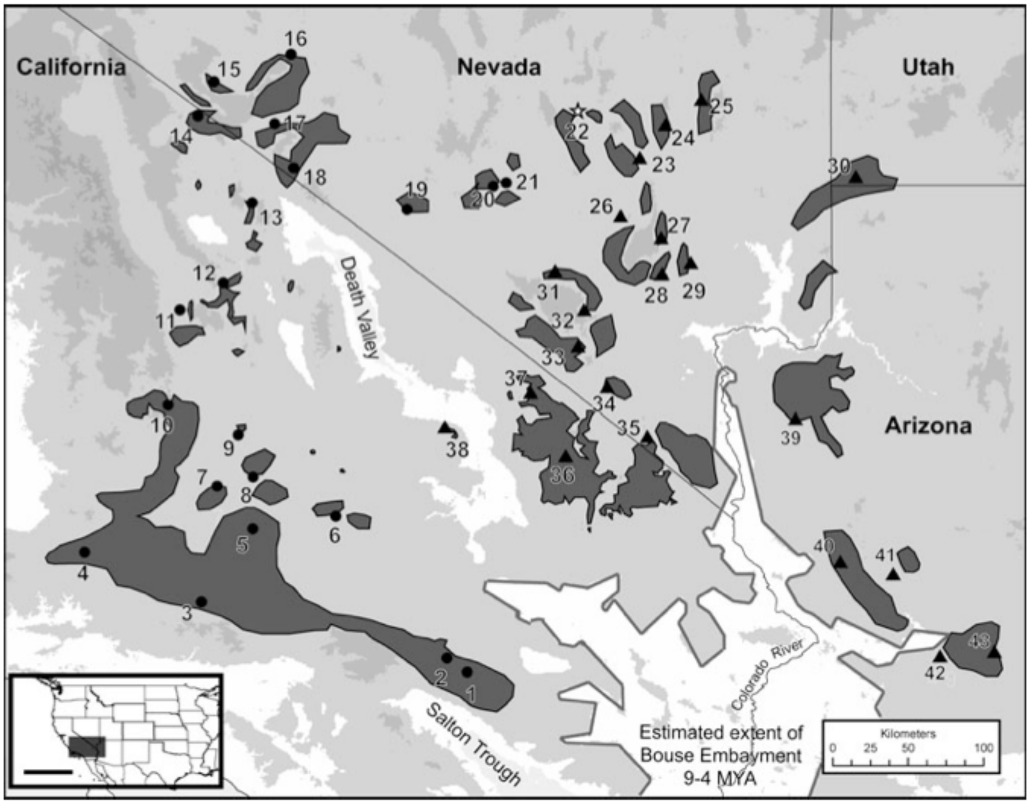

Figure 5. Range of *Yucca brevifolia* (shown as dark grey polygons). Circles indicate numbered study sites pollinated by *Tegeticula synthetica*; triangles indicate study sites pollinated by *T. antithetica.* The Tikaboo Valley population where the two species co-occur (22) is indicated by a star (Smith et al., 2008, p. 2,678).

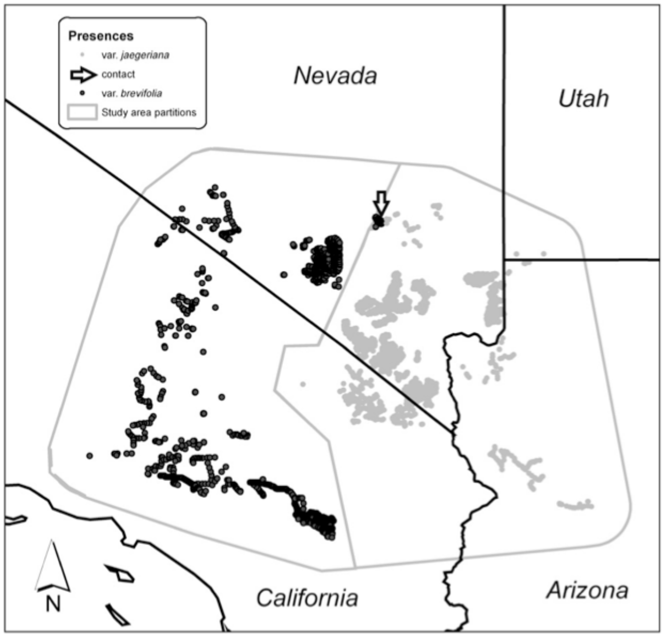

Figure 6. *Yucca brevifolia brevifolia* and *Y. b. jaegeriana* range (Godsoe et al., 2009, p. 590).

POPULATION STATUS: HISTORIC AND CURRENT

There are no population number or trend estimates available for the Joshua tree. From climate modeling, it appears that suitable habitat for successful recruitment has contracted since the early 1900s due to the +1 °C (+1.8 °F) change in mean high July temperatures since that time (Barrows & Murphy-Mariscal, 2012, p. 35; *see* "Factor E: Climate change: impacts on Joshua trees," *infra*).

NatureServe conservation status. When NatureServe last ranked the Joshua tree nationwide in 2003, it was deemed "N4:" apparently secure. However, this ranking is based on only three sources, and was last reviewed in 2003 (NatureServe, 2015a). Similarly, the rankings of the subspecies are based on one or two references and have not been updated since 2003 (NatureServe 2015b & 2015c).

NatureServe has not ranked the species by state in Arizona, California, or Nevada, most likely because state programs do not track it as a rare plant (Lazar, personal communication, July 22, 2014; NatureServe, 2015a, p. 2). Utah ranks the Joshua tree "S3S4:" vulnerable or apparently secure (NatureServe, 2015a, p. 2). An "S3" ranking of "vulnerable" would be appropriate for the species (Lazar, personal communication, July 22, 2014).

The California Native Plant Society (CNPS, 2015, p. 1) ranks the Joshua tree woodland alliance[5] as "S3" (vulnerable) in California using NatureServe's Network Core methodology (*see* Faber-Langendoen et al., 2012).

IDENTIFIED THREATS TO THE PETITIONED SPECIES: CRITERIA FOR LISTING

The Service must evaluate whether a species is "threatened" or "endangered" as a result of any of the five listing factors set forth in 16 U.S.C. § 1533(a)(1):

> A. The present or threatened destruction, modification, or curtailment of its habitat or range;
> B. Overutilization for commercial, recreational, scientific, or educational purposes;
> C. Disease or predation;
> D. The inadequacy of existing regulatory mechanisms; or
> E. Other natural or manmade factors affecting its continued existence.

(Factor A) The Present or Threatened Destruction, Modification, or Curtailment of Habitat or Range

Habitat loss is one of the major threats to the Joshua tree:

> Joshua tree… habitat includes all Mojave mid-elevation mixed scrub that supports Joshua trees, other Yucca species, and cactuses. The overriding conservation challenge associated with this habitat type is its long recovery time (150-200 years), meaning that

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[5] An "alliance" is defined as a "category of vegetation classification which describes repeating patterns of plants across a landscape. Each alliance is defined by plant species composition, and reflects the effects of local climate, soil, water, disturbance, and other environmental factors" (http://vegetation.cnps.org/whatsalliance).

> once habitat is destroyed, it is unlikely to be recovered within time frames relevant to ongoing conservation planning. Any loss of Joshua tree habitat should therefore be considered functionally irreversible, and should be avoided whenever possible. Of particular concern are invasive plants that increase vulnerability to fire (particularly red brome, *Bromus rubens*), and ignition of fires by humans. (GBBO, 2010, p. Hab-8-3)

Climate change. Joshua tree range shifts and contractions resulting from climate change are the most serious threat to this species in the foreseeable future. See "Factor E," *infra*, for a detailed discussion of climate change impacts.

Air pollution. "The western Mojave Desert is affected by air pollution generated in the Los Angeles air basin that moves inland with the predominant westerly winds. The pollution contains both oxidized and reduced forms of nitrogen (N), which are of concern because they are deposited on soil and plant surfaces and thus fertilize plants" (Allen et al., 2009, p. 2, *internal citations omitted*). Increased nitrogen deposition benefits non-native plants more than native plants, increasing their competitive advantage (Allen et al., 2009, pp. 16-17): "[r]esponses to N deposition in deserts include alterations of species composition, often increases in biomass of exotic species, and decreases in native species" (Allen & Geiser, 2011, p. 134). A study in Joshua Tree National Park observed N impacts to plants along the existing N gradient, which "did not reveal a clear relationship between non-native grass cover and soil N concentration." However, fertilizer experiments showed significant impacts, including increased non-native grass biomass (Allen et al., 2009, p. 15). Soils exposed to N pollutants accumulate N over time (Allen et al., 2009, p. 15), so continued pollution from the Los Angeles area will likely cause N levels to eventually reach detrimental levels. "[E]ven small yearly N increases, such as the 5 [kilogram/hectare (kg/ha)] over two years in this study, will eventually raise the level of soil N to values high enough to cause a significant increase in non-native grass biomass" (Allen et al., 2009, p. 16). "[L]ow-level N inputs on the west end of Joshua Tree National Park may have already accumulated enough N in surface soils (*e.g.*, 23 [micrograms/gram (µg/g)]) to affect non-native grass productivity. Characteristics intrinsic to local sites will determine to what extent non-native species will invade a site, but anthropogenically elevated N will cause a further imbalance if the invaders are nitrophilous and/or prolific seed producers" (Allen et al., 2009, p. 19). Non-native plants are linked to increased frequency and intensity of fire in the Mojave Desert, which threatens Joshua trees (*see* "Altered fire regimes and invasive weeds," *infra*). "Fires have become more frequent in the Mojave and Sonoran Deserts, and there may be a relationship between fire and increased grass biomass under enhanced N deposition. Fire risk, which was calculated as the probability of producing enough fine fuels to carry a fire (1 [ton per hectare] fine fuel), increased exponentially when deposition was above 3.0 kg N [per hectare per year]" (Allen & Geiser, 2011, p. 137, *internal citations omitted*).

Altered fires regimes and invasive weeds. "More frequent fires in the Mojave Desert are the result of the interaction of increased nitrogen deposition and the competitive advantage that nitrogen gives to invasive grasses such as red brome, *Bromus rubens*" (Barrows & Murphy-Mariscal, 2012, p. 30). The prevalence of non-native grasses and the associated changes in fire regimes are a serious threat to Joshua trees.

Non-native grasses, primarily red brome (*Bromus rubens*) and *Schismus* spp., are established and common in the Mojave Desert and compete with native grasses (Brooks, 2000, p. 93, 103).

"[B]iomass of alien annual plants is negatively correlated with biomass and species richness of native annuals, even when potential covarying factors such as disturbance and soil nutrient levels are accounted for… These alien grasses affect native desert annuals by promoting wildfires and possibly by competing with them for limiting resources such as nitrogen and water" (Brooks, 2000, p. 92, *internal citations omitted*).

Middle elevation shrubland[6] in the Mojave, where *Y. brevifolia* is one of the dominant plant species, is particularly susceptible to increased fire size following years of high rainfall. This is likely related to the "flush of non-native annual grasses, *Bromus rubens* in particular, that produces continuous fuelbeds following years of high rainfall" (Brooks & Matchett, 2006, p. 148). "The impact of fire on [Joshua tree] seedling and juvenile survival is particularly exacerbated because fires tend to track the same heavy precipitation years that are most suitable for *Y. brevifolia* emergence" (Esque et al., 2015, p. 90, *internal citations omitted*).

> Most fires and area burned between 1980 and 2004 occurred in the middle elevation ecological zone. This zone often has enough cover of native vegetation to carry fire, and likely experienced stand-replacing fires over long return intervals (4,100 years) in the past. However, the enhancement in fuel continuity that is provided by non-native annual grasses following years of high rainfall is enough to significantly increase the size of fires. (Brooks & Matchett, 2006, p. 158, *internal citations omitted*)

The replacement of perennial native grasses with non-native annual grasses has caused a shift in fire regimes away from stand-replacing fires over long return intervals and infrequent small fires to a regime of frequent large fires:

> [A]n invasive plant/fire regime cycle is probably establishing in the middle elevation, and to a much lesser degree the low elevation, shrubland zones of the Mojave Desert. The native fuels in these zones are near the tipping point between a fire regime characterized by infrequent small fires and one of frequent large fires. When non-native annual grasses are added to these fuel types, especially when they bridge the interspace fuel gaps between perennial shrubs and grasses, the transition between these alternative fire regime states is much more likely. Altered fire regimes appears to have occurred over broad expanses of middle elevation shrublands in the northeastern Mojave Desert… Repeated fires are typically followed by dominance of *Bromus* spp., *B. rubens* in particular, which can create fine fuelbeds capable of carrying fire again soon after burning. Some of these areas have reburned three times during the past 60 years. (Brooks & Matchett, 2006, p. 161-162)
>
> In the western Mojave desert of California, nonnative annual grasses (red brome, cheatgrass, and Mediterranean grasses (*Schismus* spp.)) and forbs (chiefly, cutleaf filaree (*Erodium cicutarium*)) may comprise over 50% of the biomass. Fires are more frequent, since these nonnative species have altered the fuel structure and subsequent fire behavior in what was a relatively fire-resistant landscape. Nonnative annual grass stems are

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[6] Middle elevation shruband is "typified by blackbrush (*Coleogyne ramosissima*) shrublands at its upper ectones phasing into mixed woody-scrub vegetation types dominated by creosotebush (*Larrea tridentata*) at its lower ecotones. Perennial grasses (*Achnatherum* spp., *Pleuraphis* spp.) and Joshua trees are often co-dominants with various shrub species" (Brooks and Matchett, 2006, p. 150).

> persistent, and nonnative litter decomposes slowly, providing fuel for frequent fires. Red brome contributed to substantial increases in fire frequency in the Mojave and Colorado deserts of California since the 1970s. From 1980 to 1995, 77% of the total [Bureau of land Management (BLM)]-managed Mojave Desert areas burned. Approximately 25% of the fires were started by lightning, while the other 75% were human caused. Most fires burned in the summer (May-September), and most fires in BLM-managed areas of the Colorado Desert burned along the Mojave Desert ecotone near Joshua Tree National Park. Fires were rare in Joshua Tree National Park until about 1965. Since the establishment of red brome and cheatgrass, fires have become more frequent and more severe. Before 1965 most lightning fires burned less than 0.25 acre (0.1 ha). In 1979 the Quail Mountain Fire burned 6,000 acres. In 1995, the Covington Fire burned 5,158 acres (2,087 ha), and 4 years later 13,894 acres (5,623 ha) of Joshua Tree National Park burned. (Gucker, 2006, p. 10, *internal citations omitted*)

"Fire has been historically infrequent in the Mojave Desert, and its increased prevalence caused by the invasion of non-native annual grasses is a major concern for land managers there" (Brooks & Matchett, 2006, p. 148; *see also* Vamstad & Rotenberry, 2010, p. 1,315) as it is causing a shift in the vegetation dynamics of the region. This shift is apparent at Joshua Tree National Park (JTNP):

> One of the principal management questions is the degree to which fire has played an ecological role along the elevation/vegetation gradient at JNTP. Except at the highest elevations, the natural vegetation is characterized by barren ground in between desert shrubs and cacti, which have little adaptation to fire. This has changed with invasion by non-native Mediterranean grasses such as *Bromus madritensis* var. *rubens, Bromus tectorum* and *Schismus*, which tend to connect the woodier fuels, especially following wet falls and early winters, and recover quickly after fire. With each subsequent fire the native plants vanish but these invasive grasses thicken and expand, fuelling ever larger and more frequent wildfires, inducing what has been called the "grass-fire cycle." Prior to 1965, fire records at the park suggest that most lightning-caused fires, which happened in May through September, seldom spread more than a few tens of [meters] from the strike. With the shift to a positive [Pacific Decadal Oscillation] Index and wetter winters, *Bromus madritensis* var. *rubens* spread dramatically and began fuelling large fires in both the Mojave and Sonoran Deserts. At JTNP, fires measuring in the thousands of acres burned in 1979, 1995, 1999 and 2006.[7] The increase in fire size and frequency could transform JTNP vegetation in a matter of decades. (Holmgren et al., 2009, pp. 5-6, *footnote added*)

"[R]apid changes in fire regimes, which lead to a greater prevalence of fire may be detrimental to native species. Changes in disturbance regimes that occur over short periods of time may exceed the potential for native species to evolve in response to them, and may lead to their extirpation from the affected region" (Brooks & Matchett, 2006, p. 149). More frequent fires will be detrimental to Joshua trees, as fire decreases survival:

> Five years after the Juniper Fire Complex of May 1999, approximately 80% of burned *Y. brevifolia* died compared with 26% in adjacent unburned sites. This high postfire

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[7] For background information, see http://www.nps.gov/jotr/naturescience/fireregime.htm.

> mortality of *Y. brevifolia* is consistent with other studies including 90% mortality six years after a 1978 fire in Lower Covington Flat at Joshua Tree National Park and 64-95% mortality at sites censused 1 to 47 [years] after fires in Mojave and Sonoran deserts of California. (DeFalco et al., 2010, p. 246, *internal citations omitted*)

Young sprouts whose "active meristems close to the ground are vulnerable to extreme fire temperatures and flames that consume whole plants" (DeFalco et al., 2010, p. 246) are most susceptible to mortality from fire, but fire impacts all age classes. "Survival of the larger unburned plants declined more slowly than smaller plants during the 5-year study, but immediate declines in survival were striking for all sizes of burned *Y. brevifolia*" (DeFalco et al., 2010, p. 244). Observations by researchers suggest that even large trees are susceptible to mortality from fire damage, with many scorched trees dying within five years (Thomas et al., 2004, p. 247). Low post-fire survival was exacerbated by drought (DeFalco et al., 2010, p. 246). "Mortality of seed-producing adults over expansive areas and loss of suitable establishment sites are important limitations to *Y. brevifolia's* recolonization after fires" (DeFalco et al., 2010, p. 249). *Y. brevifolia* are able to resprout post-fire, but this adaptation was only advantageous under favorable precipitation conditions:

> Webber (1953) suggested that *Y. brevifolia* is highly adapted to fire, and… speculated that *Y. brevifolia* sprouting is a successful means of repopulating disturbed sites. Our data indicate that *Y. brevifolia* sprouting can provide some advantage to survival only when precipitation is sufficient (*e.g.*, at higher-elevation sites or during wet years). Thus, sprouting of *Y. brevifolia* in the Mojave Desert presents an uncertain recovery strategy in postfire landscapes, especially in the face of herbivory and recurring low-precipitation years, and merits further long-term research attention. (DeFalco et al., 2010, pp. 247-248, *internal citations omitted*)

"The vegetation in Joshua tree woodlands is generally not adapted to fire, in part due to its lack of a previously documented fire regime and in part due to its slow recovery from fire" (Vamstad & Rotenberry, 2010, pp. 1,309-1,310). Fire impacts can last for decades:

> The recruitment of *Y. brevifolia* is a slow process even without the impediments introduced by accelerated fire-return intervals. At 13 burned sites in Joshua Tree National Park, few arboreal species recolonized even 47 [years] after a single fire. *Yucca brevifolia* re-established so slowly in comparison to other perennial species on plowed fields that after 70 [years] there were virtually no arboreal species on disturbed sites. A 20-year study of *Y. brevifolia* on three 0.1-ha plots in southern California found only two seedlings, both of which died within a year, though sample sizes were small for drawing demographic conclusions. After the 1999 fire in Joshua Tree National Park, burned sites were nearly denuded of shrub and perennial grass cover, and this postfire landscape lacked the safe sites beneath nurse plants necessary for *Y. brevifolia* seedlings to establish. (DeFalco et al., 2010, p. 249, *internal citations omitted*)
>
> The return of *Y. brevifolia* to prefire densities and demographic structure may take decades to centuries or be entirely unlikely, especially in light of potential changes to regional desert climate in combination with plant invasions and the potential for recurrence of subsequent fires. Even in the absence of the invasive species-driven fire

> regime, the ability of *Y. brevifolia* to contend with climate changes, as suitable establishment conditions vary through space and time, may be challenged. (Reynolds et al., 2012, p. 1,653, *internal citations omitted*)

In combination with range contractions from climate change, the shift in fire regimes could be deadly for the species: most of the climate refugia in Joshua Tree National Park identified via modeling were located in areas with some of the highest fire frequency of the Park (*see* "Factor E: Climate change," *infra*), leading researchers to believe that "[p]rotecting important climate refugia is a critical conservation strategy, but these areas will not protect Joshua trees very well unless the more proximate threat of wildfire catalyzed by invasive grasses, catalyzed by smog (nitrogen) drifting in from the Los Angeles Basin is addressed" (Barrows, personal communication, Sept. 3, 2014). "If a shortened fire cycle is realized in this ecosystem where fire returns on a cycle that does not allow for reestablishment of sub-shrub and/or long-lived perennial cover, fire may have the effect of arresting succession. It is therefore quite possible that the long term reestablishment of plants and animals in these habitats, with a shorter fire-return interval, may never return to a pre-burned condition" (Vamstad & Rotenberry, 2010, p. 1,315).

Grazing. In California, "[l]ivestock has heavily impacted many *Yucca brevifolia* woodlands. Grazing does not improve range conditions of their dry, harsh environment, and efforts to improve the range are expensive and yield few benefits" (CNPS, 2015, p. 7). "Grazing history has changed the fire regime by increasing non-native annual grasses" (Thomas et al., 2004, p. 247). There is little available information on grazing impacts to Joshua trees, but the Service should examine this potential threat as approximately 37% of current Joshua tree range overlaps active federal grazing allotments.[8]

(Factor B) Overutilization for commercial, recreational, scientific, or educational purposes

Though not specific to Joshua trees, collection of native plants is acknowledged as a problem in parts of Joshua tree range:

> Harvest and collection of native plant species may pose risks to vegetation communities across Arizona. Plants, especially succulents (including yuccas, ocotillo, saguaros, other cactus species, etc.), are illegally collected for use in landscaping or for illicit trade. Overharvest of long-lived species can lead to local or widespread extirpations. Not only do these activities degrade habitat quality, they may also cause changes in native fauna community composition and favor encroachment by nonnative species. (AZGFD, 2012, p. 85)

Collection is unlikely to rise to the level of a threat to the full species, but the Service should consider potential impacts in its finding.

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[8] Calculated by Kurt Menke, Bird's Eye View GIS, from data provided in Cole et al., 2003.

(Factor D) The Inadequacy of Existing Regulatory Mechanisms

Federal. No regulations exist to ameliorate the negative impacts of climate change, as the Service has acknowledged in its “warranted but precluded” finding for the meltwater lednian stonefly, which is primarily threatened by climate change:

> The United States is only now beginning to address global climate change through the regulatory process (*e.g.*, Clean Air Act). We have no information on what regulations may eventually be adopted, and when implemented, if they would address the changes in meltwater lednian stonefly habitat that are likely to occur in the foreseeable future. Consequently, we conclude that existing regulatory mechanisms are not adequate to address the threat of habitat loss and modification resulting from the environmental changes due to climate change to the meltwater lednian stonefly in the foreseeable future. (USFWS, 2011a, p. 18,694)

Joshua trees are protected from harvest on U.S. Forest Service and National Park Service lands, and a permit is required for collection on Bureau of Land Management lands (NDF, undated, p. 1). Federal lands provide some protection from development or urbanization for trees in projected climate refugia:

> [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.

Of the area with ownership data (75% of total area), BLM land contains the largest amount of current Joshua tree habitat (~42%), followed by National Park Service land (~14%) and private land (~5%).[9] No other land ownership type contains more than 4% of total habitat. Neither the BLM nor the Forest Service lists the Joshua tree as a “sensitive species” in any of the regions where it is found. Joshua trees are not listed as “threatened” or “endangered” federally or in any state within the species’ range.

Arizona. Both Joshua tree subspecies are “salvage protected restricted native plants;” they are “not included in the highly safeguarded category but are subject to damage by theft or vandalism” (ADOA, 2015, pp. 3-4), and can be collected only with a permit (AZGFD, 2015, p. 3).

California. The California Desert Native Plants Act prohibits harvesting of desert plants, including yucca, without a permit in Imperial, Inyo, Kern, Los Angeles, Mono, Riverside, San Bernardino, and San Diego Counties.[10]

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[9] Calculated by Kurt Menke, Bird’s Eye View GIS, from data provided in Cole et al., 2003.

[10] For the full provisions of the law, see: https://www.wildlife.ca.gov/Conservation/Plants/CA-Desert-Plant-Act

Nevada. *Y. brevifolia* is not included in the Nevada Natural Heritage Progam "At-risk (Tracked) Species" or "Watch Species" list.[11] Collecting requires a permit. "Digging up cactus and yucca on public or private land in Nevada is a regulated activity. On federal land owned by the [BLM], permits and tags are required. U.S. Forest Service and National Park Service do not allow harvest of native plants on their lands" (NDF, undated, p. 1).

The Great Basin Bird Observatory (GBBO), identifying threats to bird habitats in Nevada, identified seven conservation concerns for Joshua Tree habitat: 1) Change in precipitation and snowmelt related to climate change 2) Change in temperature related to climate change 3) Increased fire frequency or intensity 4) Invasive weeds 5) Urban, suburban, and industrial development 6) Motorized recreation 7) Livestock/wild horse and burro grazing (GBBO, 2010, p. Hab-8-3). Since Joshua tree stands in Nevada are not fully mapped yet, the GBBO recommends that:

> Clark County's Desert Conservation Program's current effort to map these habitats in Clark County be expanded into Nye and Esmeralda counties through a multi-agency inventory effort, and further that other Joshua tree mapping efforts underway by [the U.S. Geological Survey] be used to generate the best possible GIS maps of Joshua tree occurrence, density, and condition. Monitoring stand conditions and habitat loss will be critical for effective adaptive management efforts in light of climate change and increased fire frequency. Therefore, we recommend that a comprehensive monitoring plan for Joshua tree habitats, perhaps similar to forestry monitoring practices, be developed and implemented. (GBBO, 2010, p. Hab-8-6)

Utah. Joshua trees have no special conservation status in Utah.

In summary, there are few specific protections for Joshua trees. In some states they are protected from collecting; however, overutilization does not appear to be a serious threat. Other protections are attached to the land on which Joshua trees are found, providing limited insulation from certain types of development. However, no existing regulations assist in identifying and protecting climate refugia or otherwise address the threats of fire, invasive species, and climate change.

(Factor E) Other Natural or Man-made Factors Affecting its Continued Existence

Climate change. As described in "Habitat requirements: Climate," *supra*, despite being hardy desert plants, Joshua trees need a narrow range of environmental conditions to thrive. They can survive high temperatures, but drought decreases survivorship and recruitment. Extreme cold events limit the distribution of Joshua trees, though they need a period of cold to maximize growth. As we summarize below, it appears that the zones of appropriate climate will shift drastically in the foreseeable future due to climate change, likely faster than the trees can expand or shift their range.

The southwestern United States is a climate change "hotspot," and Joshua tree range may be close to the epicenter. "According to the 15-model consensus, the strongest U.S. hot spot by far stretches across the Southwest from southern California to west Texas and intensifies even more

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[11] For the complete lists, see http://heritage.nv.gov/species/lists.php.

over northern Mexico. By another statistical analysis technique, the American Southwest hot spot extends northward into Nevada, Utah, and Colorado" (Kerr, 2008, p. 909; Figure 7).

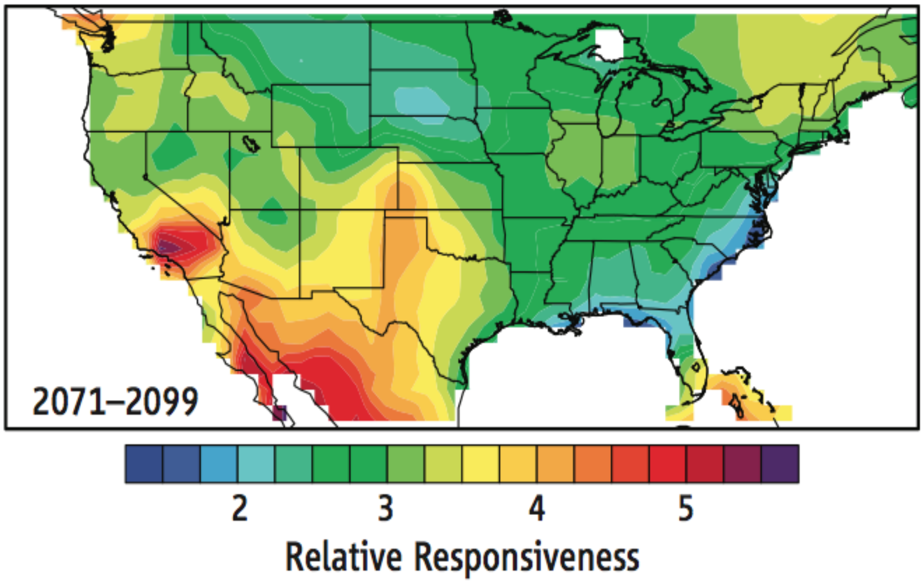

Figure 7. Combined models predict that the U.S. Southwest and northern Mexico will be most responsive in changing temperature and precipitation, as well as climate variability from year to year (reds and yellows), to climate change (Kerr, 2008, p. 909).

The Southwest is already feeling the impacts of climate change. "The predicted Southwest hot spot of climatic change looks much the same during the next 30 years as at the end of this century. And that future hot spot bears a strong resemblance to the drying and warming of the Southwest during the past decade or so" (Kerr, 2008, p. 909).

> Climate change is well under way in [the southwestern United States and northern Mexico] with clear trends of both warming and drying. This is partially a consequence of a northward shift in the track of winter and spring storms. Temperatures are expected to increase by 2.0 to 3.0 °C [3.6-5.4 °F] by 2050 and 2.2 to 5.5 °C [4.0-9.9 °F] by 2100, and spring precipitation is anticipated to decrease by 20 to 40% by the end of the century, but the contribution of summer monsoon remains uncertain. Monsoons have been delayed by approximately 10 [days] in northern Mexico over the last half century. Multiyear droughts are projected to increase by mid-century, with some persisting for a decade or more. In spite of this drying trend, flooding events are anticipated to increase in response to greater storm intensities falling on a larger proportion of bare soil. (Polley et al., 2013, p. 503, *internal citations omitted*)
>
> The current prognosis for global climate change impacts on the Southwest include fewer frost days; warmer temperatures; greater water demand by plants, animals, and people; and an increased frequency of extreme weather events (heat waves, droughts, and floods). Furthermore, warmer nights and projected declines in snow pack, coupled with earlier spring snow melt, will reduce water supply, lengthen the dry season, create conditions for drought and insect outbreaks, and increase the frequency and intensity of wildfires. Temperatures currently considered unusually high will occur more frequently. These

> model-based projections align with observations made in the region over the past decade. (Archer & Predick, 2008, p. 23)

Temperature. The Southwest "has heated up markedly in recent decades, and the period since 1950 has been hotter than any comparably long period in at least 600 years" (Garfin et al., 2014, p. 464). The National Climate Assessment predicts that regional annual average will "rise by 2.5 °F to 5.5 °F [1.4-3.0 °C] by 2041-2070 and by 5.5 °F to 9.5 °F [3.0-5.2 °C] by 2070-2099 with continued growth in global emissions (A2 emissions scenario), with the greatest increases in the summer and fall. If global emissions are substantially reduced (as in the B1 emissions scenario), projected temperature increases are 2.5 °F to 4.5 °F [1.4-2.5 °C] (2041-2070), and 3.5 °F to 5.5 °F [1.9-3.0 °C] (2070-2099)" (Figure 8). Other models project "a notable increase in annual mean temperature of +4.5 °C [8.1 °F] (Notaro et al., 2012, p. 1,370).

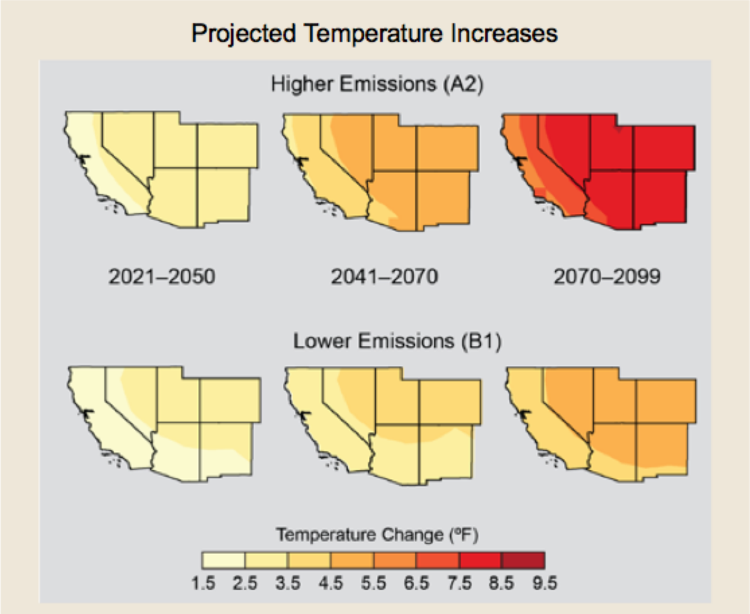

Figure 8. Maps show projected changes in average, as compared to 1971-1999. Top row shows projections assuming heat-trapping gas emissions continue to rise (A2). Bottom row shows projections assuming substantial reductions in emissions (B1) (Garfin et al., 2014, p. 464).

Precipitation. Climate models predict that "by the second half of the 21st century, the number and duration of extreme dry events increases markedly, with most of the projected dry spells lasting longer than five years and in three cases exceeding 150 months—more than 12 years… Composited over the 11 extreme drought years, the aggregate Southwest precipitation was reduced to 77% of its 1951-1999 average, April 1 snow water equivalent was reduced to 50%, and runoff was reduced to 63%" (Cayan et al., 2010, p. 21,273). Soil moisture is projected to decrease as a result of the precipitation deficit: by the end of the 21st century, "the soil moisture deficits range from 1.7 to more than 2 standard deviations below the mean" (Cayan et al., 2010, p. 21,274).

> Water inputs are expected to decline due to reduced precipitation. Water losses are also likely to increase due to elevated evapotranspiration rates at higher temperatures and greater run-off losses associated with increased frequencies of high intensity convectional

> storms. Urban expansion will also increase human demand for water and further reduce water availability for wildland ecosystems. (Archer & Predick, 2008, p. 25)

Projections of precipitation changes are less certain than temperature changes, but precipitation will become more variable and drought more extreme. "The one climate change-related precipitation prediction with broad model support is that rainfall will become more variable and droughts as well as wet periods will become more extreme. It is the intensity and duration of those projected droughts that are likely to drive much of the climate change-related shifts in suitable habitat within [the southwestern U.S.]" (Barrows & Murphy-Mariscal, 2012, p. 30). "Despite a small decrease in mean precipitation (-4%) during 2000-2100 under the A2 scenario, the frequency of extremely dry years is expected to increase substantially. During the 1953-1956 drought annual mean precipitation across the [southwestern United States] was only 25 cm [10 in]. According to the CMIP3 models, by 2070-2099 one in every five years will be characterized by 25 cm [10 inches] of annual precipitation or less, making such extreme drought a regular occurrence" (Notaro et al., 2012, p. 1,370).

"Rising temperatures will exacerbate droughts, along with their ecological impacts, through enhanced evapotranspirational demand" (Notaro et al., 2012, p. 1,366):

> Average summer-fall evaporative demand has been increasing steadily in recent decades of atmospheric warming, and it has been the highest on record since 2000. Recent research documents that summer-fall atmospheric evaporative demand is just as important as winter precipitation in stressing montane plants, and that this available water deficit has impacted Southwestern forests for centuries during periods of warming and/or drought. In fact, climate model projections of winter precipitation and summer-fall evaporative demand suggests that megadrought-type forest drought-stress conditions will exceed those of the megadroughts of the 1200s and 1500s on a regular basis by the 2050s, and that this condition has prevailed over about 30% of the past 13 years in the Southwest. (Brusca et al., 2013, p. 3,313)

"Future droughts are projected to be substantially hotter, and for major river basins such as the Colorado River Basin, drought is projected to become more frequent, intense, and longer lasting than in the historical record" (Garfin et al., 2014, p. 465). There is already evidence of decreased precipitation and increased drought. "From 1988 through 2012 desert regions of southeastern California experienced a 16% decrease in precipitation compared with the previous 25 year period (1963 through 1987)… The severity of drought was exacerbated by a rise in annual temperature of approximately 2 °C [3.6 °F] beginning in the late 1970s" (Cornett, 2014, p. 73).

"Drought and increased temperatures due to climate change have caused extensive tree death across the Southwest," (Garfin et al., 2014, p. 468) and Joshua trees are vulnerable to the same fate, particularly as juveniles. Juvenile Joshua trees lack the extensive root systems of adult trees and are therefore more vulnerable to drought. Seedlings germinating after a rainfall event must quickly develop root systems to survive the dry season. "[S]eedings of *Y. brevifolia* that can grow to 25 cm [9.8 inches] before the onset of drought will have the greatest probability of survival under differing climate scenarios" (Esque et al., 2015, p. 88; *see also* Reynolds et al., 2012, p. 1,652). "Although there are uncertainties as to how precipitation will respond with climate change, one scenario is that precipitation events may become more variable and seedlings may thus be required to endure extended drought periods; a feat which entirely depends on the length of drought and timing of rainfall events" (Murphy-Mariscal, personal communication, Sept. 3, 2014). "The rarity or absence of successful seedlings or saplings over recent decades in the southern portion of the Joshua tree range, 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" (Cole, 2011, p. 147, *internal citations omitted*). Decreasing precipitation and increasing periods of drought are likely to decrease Joshua tree recruitment and survival, as "climactic events have a strong influence on the early life stages of this species, whether directly through drought stress or indirectly by increased herbivory during drought conditions" (Esque et al., 2015, p. 89).

<u>Elevated CO_2 levels.</u> There is some evidence that elevated CO_2 levels could act to offset climate change impacts on Joshua trees by increasing low-temperature tolerance and seedling survival. However, the benefits from elevated CO_2 are limited and are likely cancelled out by threats such as drought, invasive species, and wildfire.

Experiments revealed that an elevated CO_2 environment enhanced low-temperature tolerance for three species of desert plant: *Yucca brevifolia, Y. shidigera*, and *Y. whipplei.* "In particular, [cellular survival of low-temperature treatment] was 1.6 °C [2.9 °F] lower for *Yucca brevifolia…* at 700 compared to 360 µmol [per mol] CO_2 and day/night glasshouse temperatures of 20/5 °C [68/41°F]" (Loik et al., 2000, p. 53).

> Enhanced low-temperature tolerance would potentiate a northward shift in distribution by about 350 km; the present-day northern limits of *Y. brevifolia* and *Y. schidigera* from near Beatty to Goldfield, NV, might shift as far as Winnemucca (approximately 40 °N latitude). Low-temperature tolerance was enhanced by exposure to lowered day/night air temperatures and elevated CO_2 for *Yucca brevifolia, Y. schidigera* and *Y. whipplei,* suggesting greater seedling survival during sub-zero air temperature events in the future. This portends enhanced seedling establishment and possibly changes in the distribution limits of these species. It is important to note that the potential for any climate- or atmospheric-induced enhancement of establishment and migration may be confounded by edaphic factors, biotic interactions, the presence of safe sites or nurse plants for seedling establishment, and the ability of seedlings to survive extreme drought and high temperatures in summer. In addition, large-scale processes, such as changes in surface albedo, precipitation, rain-to-snow ratios, and nutrient turnover rates, may be important for determining seedling and community responses to climate change. (Loik et al., 2000, p. 54, *internal citations omitted*)

Elevated CO_2 levels benefit Joshua trees less during drought years, and also disproportionately benefit non-native species. "Though elevated CO_2 levels can enhance new shoot production of native perennial shrubs, it does not enhance production in a drought year. Elevated CO_2 enhances the success of invasive annual grasses (*Bromus* spp.) in arid ecosystems, enhancing plant density, biomass and seed rain moreso than for native annuals" (Smith et al., 2012, pp. 80-81). Overall, "limited available data suggest increases in atmospheric CO_2 concentrations could promote Joshua tree seedling survival, and could result in an increase of this native species' range. However, [Joshua trees] are likely to decline in abundance if subjected to fires resulting from establishment of nonnative grasses" (Archer & Predick, 2008, p. 25).

<u>Range shifts.</u> "Ecosystem simulations under future climate scenarios suggest that the preferred ranges of many species could shift tens to hundreds of kilometers over only 50 to 100 years, nearly an order of magnitude faster than may have occurred since the last glaciation" (Neilson et al., 2005, p. 750). "[G]lobal warming has the potential to impose substantially higher migration rates than during post-glacial time," with large areas of the globe requiring migration rates of ≥1,000 m [3,280 ft] per [year] for plants to keep up with range shifts (Malcolm et al. 2002, pp. 844-845). This far exceeds the estimated migration rate for Joshua trees of ~2 m/year [7 ft/year], or even the optimistic projections of 22 to 33 m/year [72-108 ft/year] used in some modeling efforts (*see* Cole et al., 2011).

"[T]he Southwest is experiencing more rapid change in montane plant communities than most other regions of the world, as predicted by climate models" (Brusca et al., 2013, p. 3,314). Plants are already shifting their ranges. Studies of vegetation elevation transects in the Santa Catalina Mountains established in 1964 and revisited in 2011 indicate that "15 of the 27 most common plant species in the Catalinas have increased their lower elevational boundary, whereas four have increased their uppermost elevational boundary, and eight have decreased their upper elevation boundary" (Brusca et al., 2013, p. 3,312). "The mean lower elevation boundary of the 27 montane plants in our study is conservatively estimated to have risen at a mean rate of 27.6 m/decade [91 feet/decade], although this figure is somewhat abstract because we compare only two points in time, 49 years apart" (Brusca et al., 2013, p. 3,314).

> Sessile organisms, such as plants, are particularly susceptible to rapid climate change because they can only migrate during certain life stages. If climate conditions become unsuitable for a plant, potential migration to areas with a more suitable climate can only occur via the dispersal and establishment of the next generation of individuals. If the rate of climate change is too fast, plants will not be able to adjust quickly enough to changing conditions, resulting in extirpations and the extinction of species along with shifts in major patterns of species diversity. (Shafer et al., 2001, p. 200; *see* "Life history factors: Limited dispersal capabilities," *infra*)

<u>Impacts to Joshua trees.</u> These changes will almost certainly impact Joshua trees, as similar climate shifts have done in the past:

> 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. (Cole et al., 2011, p. 145)

A number of climate models predict range contractions and habitat loss for Joshua trees under future climate scenarios.[12] Shafer et al. (2001) examined potential changes in tree distribution

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[12] One exception is Notaro et al., 2012, who simulated a "general expansion in the range of yucca and oak species and contraction for pine and juniper species… during the 21st century… In contrast to the projections for the most abundant species, the threatened or endangered species that are listed as salvage restricted under Arizona native plant laws might benefit from climate change" (p. 1,382).

using three potential models. "Under each of the future climate scenarios, [*Yucca brevifolia*'s] potential range is fragmented and displaced northward and eastward" (Shafer et al., 2001, p. 211, Figure 9).

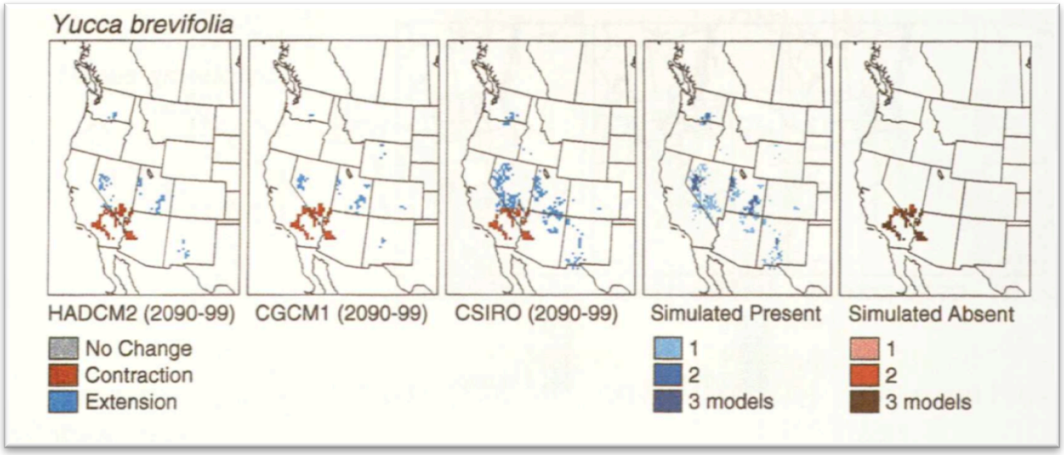


Figure 9. Comparison of observed Joshua tree distribution with future simulated distribution using climate scenarios for 2090-99 generated by the HADCM2, CGCM1, and CSIRO general circulation models (GCM) (left three columns). "No change" indicates where the species is observed at present and is simulated to occur under future climate conditions; "contraction" indicates where the species is observed at present but is simulated to be absent under future climate conditions; and "extension" indicates where the species is not observed at present but is simulated to occur under future climate conditions. Agreement among the future distributions of each species as simulated by the three GCM scenarios is displayed by showing for each grid point the number of model scenarios that simulate a species to be present or absent (right two columns). (Shafer et al., 2001, p. 210)

In a model of the potential impacts of doubled CO_2 concentrations on Joshua tree distribution, total area occupied decreased by 25%, the species persisted in only 24% of currently occupied cells, and "entire isolated populations were lost in the southeastern portion of the study area" (Dole et al., 2003, p. 141; Figure 10). When the model accounted for potential higher freezing tolerance of Joshua trees under doubled CO_2 conditions (*see* "Factor E: Elevated CO_2 levels," *supra*), these losses were offset somewhat with 29% of occupied cells remaining occupied (Dole et al., 2003, pp. 141-142). Both models showed a 262-foot decrease in the average elevation of occupied cells, and increases in potential habitat in Nevada, the southern San Joaquin Valley, west-north-west of Phoenix, AZ, and between Tehachapi and Barstow, CA (Dole et al., 2003, pp. 141-142). Conversely, Notaro et al. (2012, p. 1,378) predict "robust range expansion" for Joshua trees, however it is uncertain that Joshua trees will be able to take advantage of newly available habitat, or shift in elevation and range along with climate (*see* "Seed dispersal," *supra, and* "Life history factors: Limited dispersal capabilities," *infra*).

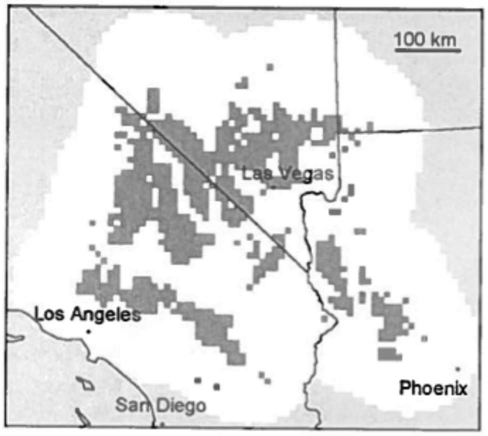


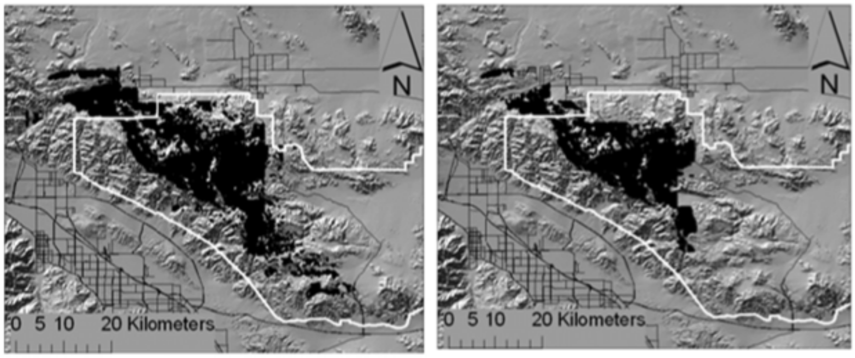
Figure 10. Current modeled distribution of Joshua trees. Comparing the current modeled distribution to doubled CO_2 scenarios showed only 24 to 29% of cells remaining occupied (Dole et al., 2003, pp. 139, 141).

A model comparing Joshua tree responses to future climate trends to the baseline interval of 1930-1969 (before the climate of the western United States began to trend distinctly warmer) "project[s] 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" (Cole et al., 2011, p. 143). These results are very similar to those of Shafer et al. (2001), except that Shafer et al.'s "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)" (Cole et al., 2011, p. 143).

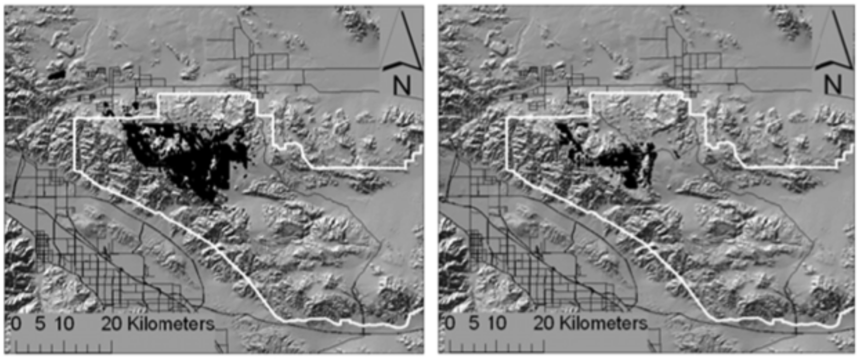
At a regional scale, "[f]ive individual [general circulation models] downscaled to ~4 km, one suite of 22 ~4-km models, and one ~1-km model, all project the future elimination of Joshua tree throughout most of the southern portions of its current range, with only perhaps 10% of existing stands remaining" (Cole et al., 2011, p. 148). Smaller-scale or more fine-grained modeling efforts are more optimistic, as they may "identify local adaptations and climate-change refugia, a perspective that may be lost with larger scale analyses" (Barrows & Murphy-Mariscal, 2012, p. 30). However, finer-scale models still show significant range contraction.

A study restricted to a "679,585 ha area including Joshua Tree National Park and a 10 km buffer surrounding the park" (Barrows & Murphy-Mariscal, 2012, p. 30), at the southern limit of Joshua tree range, modeled the impact of maximum July temperatures increased by 1 °C, 2 °C, or 3 °C (1.8 °F, 3.6 °F, or 5.4 °F).

> At a 1 °C [1.8 °F] increase in mean maximum July temperatures niche models retained 65-70% of their current areal extent. At an increase of 2 °C [3.6 °F] niche models retained 22-34% of their original distribution. At the final, most extreme simulated increase in summer maximum temperature (3 °C [5.4 °F]), Joshua trees retained 2-10% of their original distribution and were confined to an elevational range of approximately 600 m [1,970 feet] compared to their current +1000 m [3,280 feet] range. (Barrows & Murphy-Mariscal, 2012, p. 33)



Current niche model **+1°C niche model**



+2°C niche model **+3°C niche model**

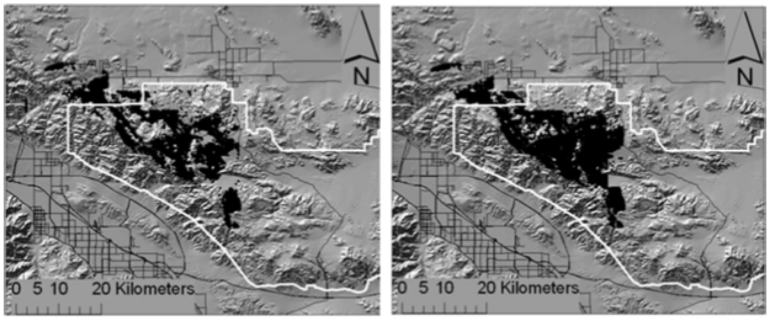
Figure 11. Adult Joshua tree niche models depicting the distribution of suitable habitat under current, +1°, +2°, and +3 °C (+1.8 °F, +3.6 °F, and +5.4 °F) mean maximum July temperature shifts. This niche model did not explicitly include precipitation as an independent variable, rather precipitation is included implicitly due to the high correlation between mean maximum July temperature and precipitation, and represents an intermediate level of modeled aridity (Barrows & Murphy-Mariscal, 2012, p. 33).

"Under the most severe climate scenario… there was a 90% reduction in [Joshua trees'] current distribution, nevertheless a refugium of suitable Joshua tree habitat still remained within JTNP" (Barrows & Murphy-Mariscal, 2012, p. 29; Figure 11). These refugia and others like them need to be identified and protected "as they are our best hope of maintaining any resemblance of our current biodiversity for future generations" (Barrows, personal communication, July 21, 2014).

"Mature Joshua trees are likely more resilient than seedlings or juveniles," and "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" (Cole et al., 2011, p. 147). Niche models show less habitat suitable for recruitment than is suitable for mature trees. The niche model for current juvenile habitat closely resembles the niche model for adult trees at a temperature increase of 1 °C (1.8 °F) (Figure 12). Ages of adult Joshua trees are difficult to estimate; in Barrows and Murphy-Mariscal's study site, most were probably >50-100 years old. They conclude:

> Our adult Joshua tree niche model… represented recruitment that occurred back into the early 1900s or earlier. Since that time there has been a roughly +1 °C [+1.8 °F] change in mean high July temperatures. Our niche model for more recent Joshua tree recruitment was substantially smaller and concentrated at higher elevations compared to our adult model; however our recent recruitment model was a near match, based on model

> perimeter and mean elevation, to our adult model with a +1 °C shift in mean maximum July temperatures. The shift in mean elevation between the current adult and juvenile Joshua tree model (60 m [197 feet]) is consistent with similar recent elevational shifts observed for a broad range of desert vegetation immediately south of JTNP. That closest model match coupled with the empirical +1 °C provides a level of model validation, consistent with a hypothesis that early levels of climate change may have already had an impact on Joshua tree recruitment. (Barrows & Murphy-Mariscal, 2012, p. 35, *internal citations omitted*).



Juvenile Joshua tree niche model **+1°C Adult Joshua tree niche model**

Figure 12. Juvenile Joshua tree niche model based on seedlings 630 centimeters in total height, compared to the adult niche model with a +1 °C (1.8 °F) shift. This niche model did not explicitly include precipitation as an independent variable, rather precipitation is included implicitly due to the high correlation between mean maximum July temperature and precipitation, and represents an intermediate level of modeled aridity (Barrows & Murphy-Mariscal, 2012, p. 34).

Small-scale population studies also show declines. Joshua trees declined at three sites in JTNP: numbers in the Lost Horse Valley study site declined 33% from 1990-2013, and “no new, young Joshua trees appeared during the study period” (Cornett, 2014, p. 72). “A second site at Upper Covington Flat showed a 16% decline in Joshua tree numbers from 1988 through 2008. A third site in Queen Valley showed a wildfire-assisted 73% decrease from 1990 through 2013” (Cornett, 2014, p. 73, *internal citations omitted*). This research is inconclusive because of the small sample size; in addition, it may take four to five decades of monitoring in order to detect population declines associated with climate change, as Joshua tree recruitment is pulsed and associated with relatively rare wet years, and seeing little recruitment for a decade may represent normal population cycles (Barrows, personal communication, July 21, 2014; *see also* “Germination,” *supra*). However, this study does support other climate models indicating Joshua trees may lose habitat and populations to climate change. Recruitment is low elsewhere as well: “survey results show minimal to no recent Joshua tree recruitment within the southern Mojave Desert in recent years” (Cole et al., 2011, p. 140, *internal citations omitted*). In contrast, Barrows & Murphy-Mariscal (2012, p. 35) report “considerable Joshua tree seedling recruitment” in core areas (refugia) of JNTP, though there was less successful reproduction and recruitment in peripheral areas at lower elevations in the eastern portions of JTNP at the edge of current Joshua tree distribution (Barrows, personal communications, July 21 and 22, 2014).

New demographic information will increase the accuracy of future models:

> Given the differential effects of climate and fire on *Y. brevifolia* of different sizes, future demographic modeling for this species will benefit from estimates of size- and age-

> specific survival rates. This approach will improve climate-based niche models by providing better estimates of populations growth and migration rates as the species advances along its leading edge and recedes along the trailing edge… Demographic models for this species must account for extended periods of increased survival punctuated by brief periods of high mortality to provide realistic population predictions for the changing regional climate. (Esque et al., 2015, p. 90)

Secondary impacts to Joshua trees from climate change could stem from "desert rodents foraging for moisture during times of drought, the necessity of low winter temperatures for flowering, fire, and any climatic effects upon the mutualistic moths which are required for pollination" (Cole et al., 2011, p. 146, *internal citations omitted; see also* "Factor E: Dependence on obligate pollinators," *infra*). Water stress leads to increased herbivory. "Between May 1989 and March 1990, 45% (24 of 53) of the *Y. brevifolia* were killed by [*Lepus*] *californicus* when precipitation was low, and by the end of August 1990, and additional 9 plants were consumed (total mortality=61%)" (Esque et al., 2015, p. 87).

If climate change impacts recruitment before it impacts mature trees, then by the time population declines in adults are detected, it may already be too late as recruitment in the area will have halted. "Because *Y. brevifolia* is long-lived, the current distribution of reproductive adults may mask the effects of recent changes in climate on recruitment and survival of seedlings and juveniles, which are more sensitive to the vagaries of desert conditions" (Esque et al., 2015, p. 90). Therefore it is unwise to wait another three decades for conclusive evidence of Joshua tree decline due to climate change. Rather, we should take action on the best available information.

> The science of climate change inevitably contains uncertainties partly because climatic and ecological systems are complex and the consequences of this unprecedented phenomenon will be expressed over long time frames. Despite these uncertainties, it would be irresponsible to ignore the cumulative evidence for climate change—both the current footprint and model projections—on the basis that the rates and magnitude of change are not fully known. Unfounded optimism regarding climatic consistency currently constrains our ability to anticipate and develop effective contingency plans for nominal weather variation, and this perspective will pose a challenge to the development of strategies for confronting climate change. (Polley et al., 2013, p. 493)

Vandalism. Joshua trees have suffered occasional vandalism. In the 1970s, Maxwell (1971, p. 5) noted that "some of the trees are being leveled to make way for housing tracts, and quite a number are destroyed by thoughtless human vandals." In California, "[e]xtensive vandalism has occurred in many areas" (CNPS, 2015, p. 7). Vandalism is unlikely to rise to the level of a threat to the full species, but the Service should consider potential impacts in its finding.

Life history factors. Projected changes in climate, and the subsequent range shifts of North American trees and shrubs, are large. "Changes of this magnitude would tend to have negative consequences for species that are rare, have narrow environmental tolerances, low dispersal rates, or are less competitive than other species" (Shafer et al., 2001, p. 212). Joshua trees are particularly susceptible to climate change and prone to extinction because of their limited dispersal capabilities and dependence on obligate pollinators.

Limited dispersal capabilities. Joshua trees are a slow-growing species that do not readily reproduce or migrate (*see* "Species description: Reproduction and dispersal," *supra*). As climate change shifts the boundaries of habitable Joshua tree range, the trees themselves may not be able to follow. "[O]bservation from past and current rates of migration were only ~2 m/year [7 ft/year]" (Cole et al., 2011, p. 145).

> [Joshua trees'] 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 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. (Cole et al., 2011, p. 145)

"In the worst case scenario, *Y. brevifolia* will migrate too slowly to fill potential new habitat, while much of its current range will become climatically unfavorable" (Dole et al., 2003, p. 144).

Cole et al. (2011) modeled projected climate change combined with migration rates of Joshua trees to show areas of potential natural migration over the next 60 to 90 years.

> [These areas] are shown at 2-km expansion outward from current populations, corresponding to a rate of 22 to 33 m/year [72-108 ft/year], in order to make these areas visible [Figure 13], although our observations for past and current rates of migration were only ~2 m/year [7 ft/year].[13] 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. (p. 145)

For whitebark pine (*Pinus albicaulis*), which has a similar generation time, the Service found that climate change would likely be too rapid for the species to adapt:

> Historical (paleoecological) evidence indicates that plant species have generally responded to past climate change through migration, and that adaptation to changing climate conditions is less likely to occur. Adaptation to a change in habitat conditions as a result of a changing climate is even more unlikely for *P. albicaulis,* given its very long generation time of approximately 60 years. The rate of latitudinal plant migration during past warming and cooling events is estimated to have been on the order of [328 feet] per year. Given the current and anticipated rates of global climate change, migration rates will potentially need to be substantially higher than those measured in historic pollen records to sustain the species over time. A migration rate of at least a magnitude higher ([3,280 feet] per year) is estimated to be necessary in order for tree species to be capable of tracking suitable habitats under projected warming trends. (USFWS, 2011b, p. 42,637, *internal citations omitted*)

"Several models project significant potential future expansion into new areas beyond the current range [of Joshua trees], but the species' historical and current rates of dispersal would seem to

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[13] For most plant species, migration distances over a century are too small to spatially resolve in most global vegetation models (Neilson et al., 2005, p. 752).

prevent natural expansion into these new areas" (Cole et al., 2011, p. 148). If new areas of suitable habitat are indeed created due to climate change, it is unlikely that Joshua trees will be able to make use of them through natural migration. "The relative isolation of many new areas of suitable bioclimactic habitat that are simulated under future climate scenarios, coupled with their small size, would make natural dispersal to these areas difficult for many species" (Shafer et al., 2001, p. 211)

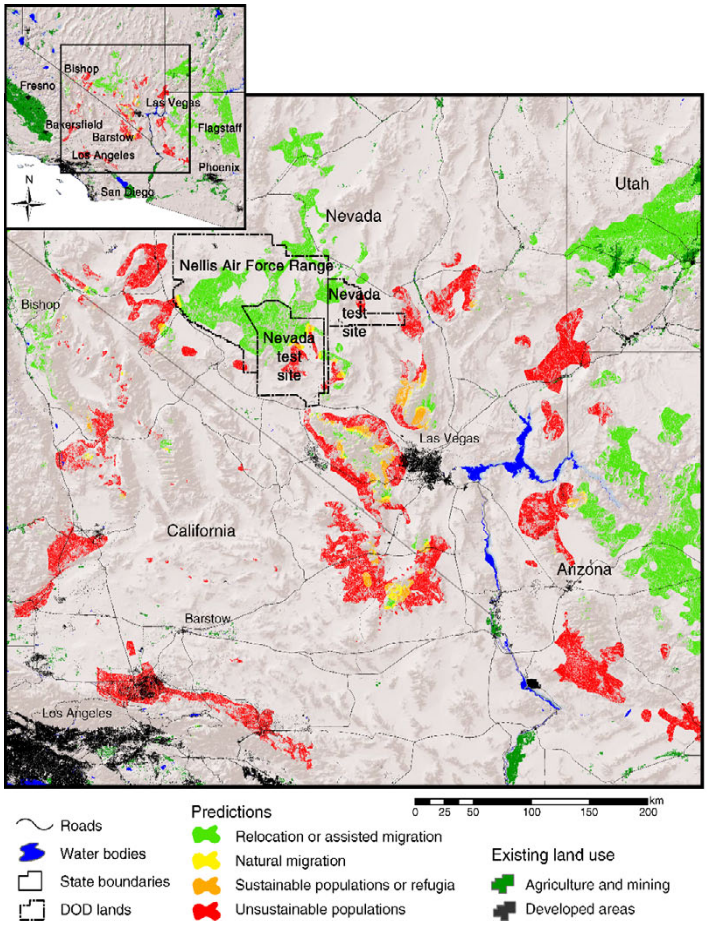

Figure 13. Areas where a majority (three of five) of climate models "predict existing Joshua tree populations with future climates unsuitable for survival (red), current populations with future climates favorable for Joshua tree persistence (orange), areas within 2 km of current populations with future 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)" (Cole et al., 2011, p. 146).

Cole et al. (2011) recommend investigating the possibility of assisted migration or relocation in order to establish new Joshua tree populations in new areas of favorable climate outside the natural migration range. Along the northern edge of the trees' range, populations may be expanding, and ongoing research is investigating "whether the trees' range is in fact expanding, and if so whether they may be able spread quickly enough to keep up with the changing climate" (James, 2014, p. 6).

Dependence on obligate pollinators. Climate impacts on Joshua trees may manifest themselves through effects on other species. Climate impacts "may not… 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" (Cole et al., 2011, p. 147).

"Obligatory interactions are expected to be particularly sensitive to climate change because the two partners may respond differently to changes but each still depends upon the other for its survival" (Blatrix et al., 2013, p. 307).

> The potential outcomes of abrupt climate changes can be predicted as follows. If the change is within the range of tolerance of both species, the interaction can persist but may be severely affected. Alternatively, the change can be out of the range of one of the interacting species. In this case, the outcome for both species will depend on whether or not the less affected species will be able to survive on its own until the more affected partner recovers. The outcome will thus depend on a combination of the following parameters: life-history traits of the two partners, duration of the climatic event, degree and nature of dependency between the partners, dispersal ability of the affected partner, and geographical extent of the event (which determines whether or not the affected partner will be able to recolonize empty host niches from source populations). (Blatrix et al., 2013, p. 311)

Because Joshua trees are entirely dependent on yucca moths for pollination, any impact on the moths will cascade to the trees, and vice versa. This makes them more vulnerable to synergistic impacts or abrupt climate changes (*infra*). Examples from similar mutualistic relationships illustrate this mechanism:

> Fig trees (more than 700 species in the genus *Ficus*) depend for their pollination on specific wasps (Agaonidae) that develop in a subset of the seeds. This nursery pollination mutualism is very similar to the one described above between *Yucca* trees and their *Tegeticula* moths. The two partners strictly depend on each other. The [El Niño-Southern Oscillation (ENSO)] event of 1997-1998 caused an extreme drought in Borneo, which caused the loss of leaves and fruits in several species of fig trees. The duration of the drought exceeded the lifespan of the pollinators, so that although the trees survived the drought, pollinators became locally extinct. Six months after the drought, pollinators had not yet recolonized and fertilized figs were absent. Similarly, Hurricane Andrew in 1992 caused the loss of leaves and fruits of a *Ficus* species in Florida, and caused presumably local extinction of the pollinator. However, in both cases, the long lifespan of the trees allowed recovery of the mutualism. Pollinating wasps, with short generation times and high dispersal capacities, spread from pockets where they had survived. Other organisms dependent on the fig/wasp mutualism may not have been so fortunate. Fig trees are considered keystone species in tropical ecosystems because many species directly rely on figs for food. The breakdown of the fig/fig wasp mutualism, even temporarily, may thus have dramatic consequences on local communities because production of figs depends on their pollination by fig wasps. (Blatrix et al., 2013, p. 312, *internal citations omitted*)

Human population growth. The population of the Southwest is expected to increase from 56 million to 94 million by 2050 (Garfin et al., 2014, p. 463). Human population growth will increase development and resource use pressures on the region. "Severe and sustained drought will stress water sources, already over-utilized in many areas, forcing increasing competition among farmers, energy producers, urban dwellers, and plant and animal life for the region's most precious resource" (Garfin et al., 2014, p. 463). "Humans have also highly altered and fragmented natural landscapes, affecting plant migration" (Neilson et al., 2005, p. 753).

Synergistic and cumulative impacts. The interaction of the threats described above creates more danger to Joshua trees than each threat acting alone. For example, invasive species increase fire risk during the climatic conditions when Joshua trees are most likely to sprout. Juvenile Joshua tree mortality is increased by drought and fire, which are exacerbated by climate change. The combination of increased fire risk, decreased precipitation, and increased temperature may have already significantly reduced the habitat suitable for Joshua tree recruitment.

> [P]redicted changes in the regional climate present novel threats to these desert plant communities. We expect that the greater frequency and amplitude of the rapid switches between El Niño wet phases that promote alien annual plant production followed by dry La Niña phases will continue to promote desert wildfires that injure and kill all size classes of *Y. brevifolia.* Future ENSO periods will likely favor a demographic shift toward taller, older *Y. brevifolia* populations. These shifts in stand structure due to drought- and fire-induced losses of smaller *Y. brevifolia* may prevail over plant responses that enhance survival such as freezing tolerance that facilitates plant migration as atmospheric CO_2 concentrations increase. Furthermore, given that the recruitment of *Y. brevifolia* seedlings is phenomenologically linked to the canopies of perennial shrubs and grasses during high precipitation years, greater frequency of recruitment failure on postfire landscapes will be detrimental to aging *Y. brevifolia* populations in the future. (DeFalco et al., 2010, p. 247, *internal citations omitted*)
>
> The altered fire regime in the Mojave Desert is not directly related to climate change; however it represents a threat to Joshua trees as well as the overall biodiversity of the region as desert species generally lack fire response adaptations… The current distribution of red brome with respect to Joshua trees indicates that its distribution would shift in response to climate change much the way Joshua trees would, continuing their current sympatry. The interaction between increased invasive grass-spread wildfires and a climate change-related increase in severe wildfire conditions will threaten the sustainability of Joshua trees, even within their JTNP refugia. Climate change may stress Joshua trees and inhibit their ability to survive wildfires, and it will certainly reduce the area of suitable habitat so that any fire will impact a larger proportion of the remaining Joshua tree population. (Barrows & Murphy-Mariscal, 2012, p. 35, *internal citations omitted*).

When combined with the Joshua trees' slow reproduction and limited dispersal capabilities, the various obstacles to Joshua tree survival and recruitment create a recipe for disaster. Other, less directly related factors, such as human population growth increasing pressure on natural resources in the Southwest or climate impacts to yucca moths, could also increase extinction risk. "Rather than climate change alone, it is likely that the interaction of climate and other environmental stressors may hasten the decline of native species" (Barrows & Murphy-Mariscal, 2012, p. 30).

> Traits such as ecological specialization and low population density act synergistically to elevate extinction risk above that expected from their additive contributions, because rarity itself imparts higher risk and specialization reduces the capacity of a species to adapt to habitat loss by shifting range or changing diet. Similarly, interactions between environmental factors and intrinsic characteristics make large-bodied, long-generation and low-fecundity species particularly predisposed to anthropogenic threats given their lower replacement rates. (Brook et al., 2008, p. 455, *internal citations omitted*)
>
> [O]nly by treating extinction as a synergistic process will predictions of risk for most species approximate reality, and conservation efforts therefore be effective. However challenging it is, policy to mitigate biodiversity loss must accept the need to manage multiple threatening processes simultaneously over longer terms. Habitat preservation, restoring degraded landscapes, maintaining or creating connectivity, avoiding overharvest, reducing fire risk and cutting carbon emissions have to be planned in unison. Otherwise, conservation actions which only tackle individual threats risk becoming half-measures which end in failure, due to uncontrolled cascading effects. (Brook et al., 2008, p. 459, *internal citations omitted*)

CONCLUSION AND REQUESTED DESIGNATION

WildEarth Guardians hereby petitions the U.S. Fish and Wildlife Service under the Department of Interior to list the Joshua tree (*Yucca brevifolia*) as a “threatened” species under the Endangered Species Act. Listing is warranted, given ongoing and future threats, most notably climate change. The Joshua tree is threatened by at least three of the five listing factors under the ESA: the present or threatened destruction, modification, or curtailment of its habitat or range; inadequate regulatory mechanisms; and other natural or manmade factors affecting its continued existence.

WildEarth Guardians requests that critical habitat be designated for the Joshua tree in occupied and unoccupied suitable habitat concurrent with final ESA listing. Designating critical habitat for this species will support its recovery and protect areas crucial to long-term survival of Joshua tree populations.

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