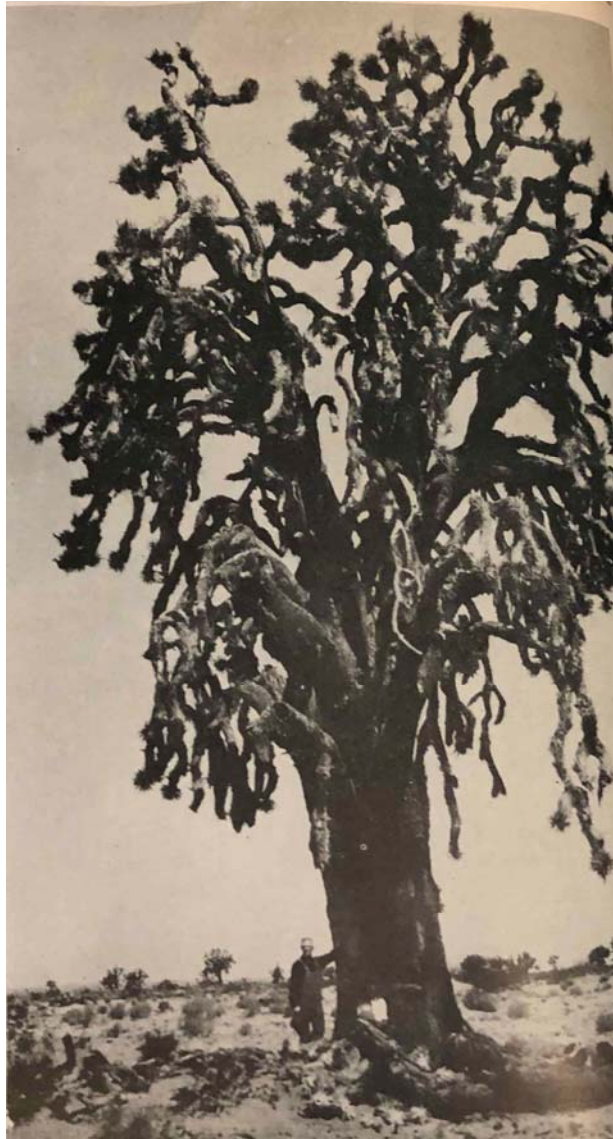


BEFORE THE CALIFORNIA FISH AND GAME COMMISSION

**A Petition to List the Western Joshua Tree (*Yucca brevifolia*) as
Threatened under the California Endangered Species Act (CESA)**



Center for Biological Diversity
October 15, 2019



Notice of Petition

For action pursuant to Section 670.1, Title 14, California Code of Regulations (CCR) and Division 3, Chapter 1.5, Article 2 of the California Fish and Game Code (Sections 2070 *et seq.*) relating to listing and delisting endangered and threatened species of plants and animals.

I. SPECIES BEING PETITIONED:

Species Name: Western Joshua tree (*Yucca brevifolia*) as either a full species, or as the subspecies *Yucca brevifolia brevifolia*.

II. RECOMMENDED ACTION: Listing as Threatened

The Center for Biological Diversity submits this petition to list the western Joshua tree (*Yucca brevifolia*) as Threatened pursuant to the California Endangered Species Act (California Fish and Game Code §§ 2050 *et seq.*, “CESA”). The western Joshua tree (*Yucca brevifolia*), long recognized as a subspecies or variety (*Yucca brevifolia brevifolia*), has recently been recognized as a full species distinct from its close relative, the eastern Joshua tree (*Yucca jaegeriana*).

This petition demonstrates that the western Joshua tree is eligible for and warrants listing under CESA based on the factors specified in the statute and implementing regulations. Specifically, the western Joshua tree meets the definition of a “threatened species” since it is “a native species or subspecies of a . . . plant that, although not presently threatened with extinction, is likely to become an endangered species in the foreseeable future in the absence of the special protection and management efforts” Cal. Fish & Game Code § 2067.

In the event the Commission determines that full-species taxonomy is not sufficiently established, petitioners request listing of the taxa as a subspecies/variety *Yucca brevifolia brevifolia*. Additionally, while petitioners believe that the western Joshua tree warrants protection under CESA throughout its range in California, in the event the Commission determines that it does not, the Commission must assess whether either of the two population clusters of the species (denoted as *Y. brevifolia* North [YUBR North] and *Y. brevifolia* South [YUBR South] in the petition) separately warrant listing as ecologically significant units (ESUs).

Cover photo of tallest (25 m) known *Yucca brevifolia* in western Antelope Valley in 1925 from Webber (1953). The tree was burned by vandals in 1930, generating outrage and sparking early desert protection efforts culminating in the 1936 creation of Joshua Tree National Monument.

III. AUTHOR OF PETITION:

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I hereby certify that, to the best of my knowledge, all statements made in this petition are true and complete.



Signature: _____ Date: 10/15/19

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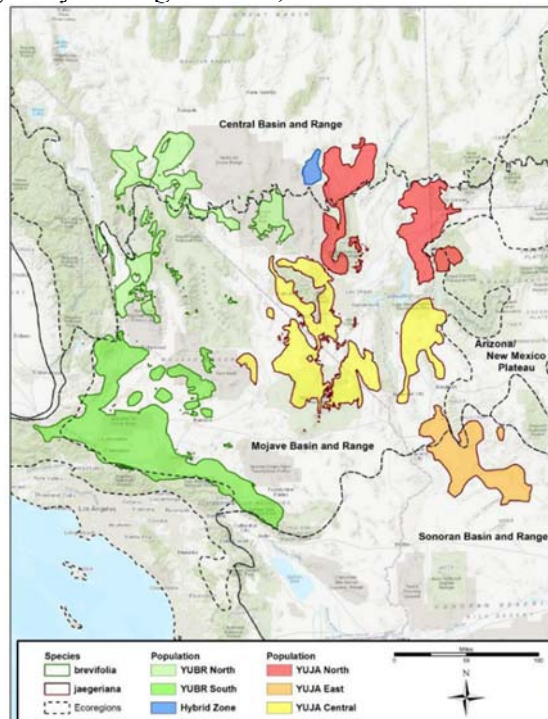
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Executive Summary

The Center for Biological Diversity submits this petition to list the western Joshua tree (*Yucca brevifolia*) as Threatened pursuant to the California Endangered Species Act (CESA). This petition demonstrates that the western Joshua tree is eligible for and warrants listing under CESA based on the factors specified in the statute and implementing regulations.

Under CESA, a “threatened species” is “a native species or subspecies of a ... plant that, although not presently threatened with extinction, is likely to become an endangered species in the foreseeable future in the absence of the special protection and management efforts...” A plant is an “endangered species” when it is “in serious danger of becoming extinct throughout all, or a significant portion, of its range due to one or more causes, including loss of habitat, change in habitat, overexploitation, predation, competition, or disease.” While the western Joshua tree is not at imminent risk of extinction, it faces significant and growing threats, primarily from climate change, that ultimately threaten the viability of the species in all or a significant portion of its range in California; it consequently meets the definition of a “threatened species.”

Long considered a single species with two subspecies or varieties, the Joshua tree has recently been recognized as comprised of two distinct species, the western Joshua tree (*Yucca brevifolia*) and the eastern Joshua tree (*Y. jaegeriana*). The two species are geographically separated, genetically and morphologically distinguishable, and have different obligate pollinators.



Both species occur in California, with the western Joshua tree having a boomerang-shaped range from Joshua Tree National Park, westward along the northern slopes of the San Bernardino and San Gabriel Mountains, through the Antelope Valley, northward along the eastern flanks of the southern Sierra Nevada and eastward to the edges of Death Valley National Park (green areas on

map). The eastern Joshua tree's range in California is centered in the Mojave National Preserve (yellow areas on map).

While both the western and eastern species of Joshua tree are of conservation concern, the fate of the western Joshua tree in California is particularly alarming, as recent studies indicate that the species' range is contracting at lower elevations, recruitment is limited, and mortality is increasing, all of which would likely reflect a population already starting to decline due to recent warming. Even greater changes are projected to occur over the coming decades.

Climate change represents an existential threat to western Joshua trees. Even in the absence of climate change, the convergence of factors necessary for recruitment results in successful establishment of new seedlings only a few times in a century. Such recruitment has already largely stopped at the drier, lower limits of the species' range. Prolonged droughts, which are projected to occur with greater frequency and intensity over the coming decades, will not only preclude recruitment across ever-greater areas of the species' range, but will lead to higher adult mortality, either directly due to temperature and moisture stress or indirectly due to increased herbivory from hungry rodents lacking alternative forage. Whether or not the species' pollinating moth will be able to keep pace with a changing climate is highly questionable. The Joshua tree's ability to colonize new habitat at higher elevations or latitudes is extremely limited and no such range expansion is yet occurring, even as the lower elevation and southern edge of its range is already contracting. And there is no safe refuge, as the higher elevation areas in which Joshua trees are projected to best be able to survive increasing temperatures and drying conditions are at great risk of fire due to the prevalence of invasive non-native grasses. Absent rapid and substantial reductions in GHG emissions *and* protection of habitat, the species will likely be extirpated from all or most of California by the end of the century.

In addition to climate change and fire, the western Joshua tree is threatened by habitat loss and degradation from other human activities. The portion of the species' range where management is most protective—Joshua Tree National Park—is also the area where the early impacts of climate change are already being felt most severely. Other areas of federal land that are home to the species are subject to poorly-regulated activities including off-road vehicle use, cattle grazing, power and pipeline rights-of-way and large-scale energy projects that consume or degrade habitat. And while much of the western Joshua tree's range is on public lands, approximately 40% of its range in California is on private land, of which only a tiny fraction is protected from development. Under current growth projections, virtually all of this habitat will be lost in the coming decades absent strengthened protection under the law.

The Joshua tree has long been the most iconic species of the Mojave Desert. Given the well-publicized threats facing the species in the face of climate change, it has recently become an emblem of our society's failure to address the climate crisis. But the Joshua tree is also uniquely situated to become an example of successful action to save a species threatened by climate change. Action taken in and by California to save the species can serve as a model for proactive climate adaptation efforts not just in California but around the world. Listing the species under CESA is not just a symbolically important act of California recognizing the threats the species faces from climate change, but also can serve as the impetus for meaningful management actions that can help ensure the species remains a living icon in perpetuity.

The Western Joshua Tree Warrants Listing as Threatened under the California Endangered Species Act (CESA)

1 Introduction

This petition summarizes the available scientific information regarding the taxonomy and natural history of the western Joshua tree (*Yucca brevifolia*), its distribution and abundance in California, population trends and threats, and discusses the limitations of existing management measures in protecting the species. As demonstrated below, western Joshua trees meet the criteria for protection as “threatened” under the California Endangered Species Act (CESA) and would benefit greatly from such protection.

2 Life History

2.1 Taxonomy

Joshua tree taxonomy has long been subject to some dispute and confusion. Often referenced as being within the Families Liliaceae or Agavaceae, under the molecular-based taxonomic system developed by the Angiosperm Phylogeny Group, the species is now considered as being within the Asparagaceae (AGP IV 2016; ITIS 2019).

The Joshua tree has until recently been treated by most authorities as a single species, *Yucca brevifolia* Engelm., comprised of two varieties or subspecies, *Yucca brevifolia brevifolia* (western Joshua tree) and *Yucca brevifolia jaegeriana* (eastern Joshua tree) (ITIS 2019).¹ The two forms are for the most part geographically separated, genetically and morphologically distinguishable, and have different obligate pollinators. The two forms may be the result of allopatric speciation, though some gene flow between them has been documented in a small area in Nevada (Yoder et al. 2013; Royer et al. 2016). Lenz (2007) believed the differences in flower and fruit morphology between *Y. b. brevifolia* and *Y. b. jaegeriana* as well as each having different obligate pollinators were sufficient to recognize *Y. b. jaegeriana* as a full species, *Y. jaegeriana*.

More recent studies focused on pollinator interactions have confirmed significant morphological differences in the styler canals of the flowers of the two forms, which correspond to differences in ovipositor length in their respective pollinators (Godsoe et al. 2008; Starr et al. 2013; Yoder et al. 2013). Smith et al. (2008) used genetic markers to determine that western and eastern Joshua trees likely diverged over 5 million years ago, which corresponds to the time when the Bouse Embayment, an extension of estuarine waters of the Gulf of California, extended into the Mojave, separating western and eastern areas (Pellmyr and Segraves 2003). Starr et al. (2013) and Yoder et al. (2013) also found genetic differentiation between the two forms but declined to recognize them as separate species.² Royer et al. (2016) expanded on these studies

¹ Other previously described subspecies/varieties including *Y.b. herberti*, *Y.b. weberi* and *Y.b. wolfei* are considered synonyms of *Y. brevifolia* (ITIS 2019; Wallace 2017).

² Yoder et al. (2013) noted that whether *Y. b. brevifolia* and *Y. b. jaegeriana* represent full species “is heavily dependent on the species concept we use to make that judgment.” Starr et al. (2013) noted that “[t]he validity of this

using molecular techniques and found “evidence for strong genome-wide patterns of divergence between the Joshua tree species” and noted their results “revealed extensive genetic differentiation between *Y. brevifolia* and *Y. jaegeriana*.” Royer et al. (2016) followed Lenz (2007) and recognized *Y. brevifolia* and *Y. jaegeriana* as full species.

Most recently, in a broad review of the science regarding Joshua trees, the U.S. Fish and Wildlife Service treated *Y. brevifolia* and *Y. jaegeriana* as separate species for purposes of federal Endangered Species Act (ESA) consideration (Wallace 2017; USFWS 2018; USFWS 2019).³ Petitioners follow Lenz (2007), Royer et al. (2016), Cole et al. (2017) and USFWS (2018) and treat *Y. brevifolia* and *Y. jaegeriana* as full species. However, since CESA provides for the protection of both species and subspecies, regardless of whether it is treated as a species (*Y. brevifolia*) or subspecies (*Y. b. brevifolia*), the western Joshua tree is eligible for and warrants listing under the statute.

2.2 Species Description⁴

The earliest known written description of the Joshua tree is an unflattering entry in the Fremont Report in which it was noted that “their stiff and ungraceful form makes them to the traveler the most repulsive tree in the vegetable kingdom . . .” (Fremont 1845). Over time, Joshua trees became increasingly more appreciated, with Griffin (1930) referring to them as “one of the outstanding plants of the desert,” Runyon (1930) characterizing them as “grotesque in the extreme...yet they are magnificent,” Little (1950) somewhat undecidedly calling them “picturesque or grotesque,” and Jaeger (1965) calling them “at once the most spectacular and most characteristic tree of the Mohave Desert.”

More technically, the Jepson Flora describes Joshua trees as follows:

Habit: Plant 1--15 m. *Stem:* erect, above ground, generally branched above, rosettes at tips, well above ground. *Leaf:* 15--35 cm, 0.7--1.5 cm wide, dark green, expanded base 2--4 cm, 4--5 cm wide, +- white, margins minute-serrate, yellow. *Inflorescence:* 3--5 dm, distal generally +- 1/2 exerted from rosettes. *Flower:* erect; perianth 4--7 cm, +- bell-shaped, parts lanceolate to oblong, +- fused at base, cream to +- green; filaments thick; pistil +- 3.5 cm. *Fruit:* capsule, spreading to erect in age, 6--8.5 cm, ellipsoid, dry, spongy, or leathery in youth. (Hess 2012).

Among the numerous natural history accounts of the Joshua tree, Gucker (2006), prepared for the U.S. Forest Service and readily available online,⁵ is among the most comprehensive. The following is largely adapted from Gucker (2006).

designation [two species] is not yet certain, and here, we conservatively refer to the two morphotypes as subspecies.”

³ As discussed *infra*, while the taxonomic and other life history discussions in USFWS (2018) represent a comprehensive summary of the available science, the threats analysis in the document is highly problematic and shows some evidence of political interference driving its ultimate conclusions.

⁴ Because the bulk the scientific literature cited in this petition treats Joshua trees as a single species without distinction between *Y. brevifolia* and *Y. jaegeriana*, this petition generally refers just to the “Joshua tree,” highlighting difference between the two taxa where appropriate.

The Joshua tree is a 5 to 20 meters tall, evergreen, tree-like plant. Trees exceeding 10 meters are rare. Tree size and growth form vary with site and climate conditions, as well as between the two species. *Y. brevifolia* typically have one main stout stem or trunk that measures 0.3 to 1 meter in diameter and have an expanded base. *Y. jaegeriana* typically have multiple stems. Trunks are fibrous, and the bark or periderm is soft and cork like. Bark plates measure 7.5 to 15 cm long and 2.5 to 5 cm in thickness. (Gucker 2006).



Figure 1. Western Joshua tree (*Yucca brevifolia*) and Easter Joshua tree (*Yucca jaegeriana*).

Older plants generally have extensive branching. Young trees typically lack branches and are covered with persistent reflexed leaves. Trees normally reach 1 to 3 meters tall before branching. Branches are 2 to 5 meters and fork at 0.5 to 1-meter intervals. Inner branches are typically erect, and outer branches can be horizontal or drooping. (Gucker 2006).

Leaves are clustered in rosettes at the branch ends. Clusters are commonly 0.3 to 1.5 meters long and 0.3 to 0.5 meters in diameter. Leaves are linear, needle shaped and measure 15 to 35 cm long by 0.7 to 1.5 cm wide, with enlarged bases attaching them to the branch. Leaf shape is slightly triangular and leaf margins are lined with small teeth. Spines measuring 7 to 12 mm occur at the leaf tips. Leaf clusters are longer (1-1.5 meters) on juvenile plants than on mature plants (0.3-1 meters). Outer leaf layers are thick and waxy to reduce water loss. Dead leaves are persistent and fold down, covering the branches and coating the trunks of young trees. (Gucker 2006).

Joshua tree flowers occur in dense, heavy panicles that measure 20 to 40 cm long. Individual flowers are round to egg shaped and measure 2.5 to 5 cm wide. Flowers have a musky scent, with the early botanist Trelease (1893) describing the smell as “so oppressive as to render

⁵ <https://www.fs.fed.us/database/feis/plants/tree/yucbre/all.html>

the flowers intolerable in a room.” Fruits are indehiscent capsules, which become spongy and dry with age. Egg-shaped capsules are 6 to 10 cm long and approximately 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 black seeds, which are flat to thickened with smooth to undulate surfaces. Seeds are 7 to 11 mm long. (Gucker 2006).



Figure 2. *Yucca brevifolia* fruit and seeds.

The two species of Joshua trees are morphologically distinguishable. *Y. jaegeriana* is sometimes referred to as dwarf Joshua tree as it is often smaller (3-6 meters tall), with shorter leaves (<22 cm) and shorter branches (0.7-1 meter) compared to *Y. brevifolia*. *Y. brevifolia* is less stocky, often 5 to 12 meters tall, with longer leaves (19-37 cm) and higher branches (2-3 meters above ground) compared to *Y. jaegeriana*. *Y. jaegeriana* displays true dichotomous branching while *Y. brevifolia* is not truly dichotomous. (Gucker 2006).

Lenz (2007) described the vegetative differences between the two species as follows:

Yucca brevifolia s.s. is arborescent with a distinct trunk and, usually, stout branches; *Y. jaegeriana* is generally smaller and branched from near the base, the branches somewhat slender. The two possess dissimilar patterns of branching, *Y. brevifolia* having pseudodichotomous (monopodial) branching; *Y. jaegeriana*, until flowering, has true dichotomous branching. The species differ in leaf length; *Y. brevifolia* having leaves 15–35 cm long, those of *Y. jaegeriana* 10–20 cm. Leaf length is variable, depending at least in part on environmental conditions. (internal citations omitted)

Additionally, Lenz (2007) noted the differences in flower morphology between *Y. brevifolia* and *Y. jaegeriana*:

Flowers of *Y. brevifolia* are nearly globular or depressed globular, the broadly ovate, fleshy, cream-colored perianth segments are strongly incurved, and the flowers never fully expand. Flowers of *Y. jaegeriana* are narrowly campanulate, conspicuously swollen at the base, somewhat constricted above, and the narrowly oblong perianth

segments are usually greenish, and recurved at their tips. The ovaries of *Y. brevifolia* are conical and taper from the base; those of *Y. jaegeriana* are lance-ovoid. Fruits of *Y. brevifolia* are ovoid to broadly ovoid; those of *Y. jaegeriana* are ellipsoid.



Figure 3: Flowers of *Y. brevifolia* (L) and *Y. jaegeriana* (R) above a 6” ruler. Source: Lenz 2007.

Studies on flower morphology in the context of pollination have concluded that the statistically greatest discernable difference between *Y. brevifolia* and *Y. jaegeriana* is in the length of the stylar canal—the path through which the female yucca moth inserts her ovipositor when laying eggs (Godsoe et al. 2008; Starr et al. 2013).

According to Warren et al. (2016), flower panicles grow primarily at the tips of branches that are oriented to the south, and when on branches that are not oriented in a southerly direction, the flower panicles themselves tend to bend or tilt toward the south. Such orientation may provide energetic and/or pollinator benefits (Warren et al. 2016).

2.3 *Reproduction and Growth*

Joshua trees reproduce both sexually and asexually, although patterns of sexual and clonal reproduction have not been thoroughly investigated (Sweet et al. 2019).

2.3.1 *Asexual reproduction*

Asexual reproduction is by rhizomes, branch sprouts, and/or basal sprouts. Rhizome production and clonal growth can be triggered by stem damage as well as certain environmental conditions. Dormant buds beneath the periderm may grow when older stems are bent or injured. Joshua trees with extensive rhizome growth and clonal form are typically shorter and have less branching than single-stemmed trees. In some cases, basal buds do not develop into distinct rhizomes, and stems grow adjacent to the main stem as sprouts. (Gucker 2006).

Some Joshua tree populations are largely if not entirely clonal, including in the Liebre Mountains and along the southern and western slopes of the Tehachapi Mountains. In these areas Joshua trees can occur in clumps nearly 30 feet (8 m) in diameter, with 30 to 40 trunk-like stems. A single clone in Gorman Creek was determined to occupy approximately one acre (0.4 ha) and was comprised of several hundred stems (Gucker 2006). Joshua trees with this growth form were previously classified as *Y. b. var. herbertii* (Webber 1953)(Figure 4) but are now known to be a clonal form of *Y. brevifolia* (ITIS 2019).



Figure 4: Type specimen of *Y. b. var. herbertii* in western Antelope Valley in 1946. Source: Webber (1953)

The extent of cloning apparently increases with increased elevation, with Joshua trees in low-elevation dry areas rarely forming more than 1 or 2 stems, but 2 to 3 stems are common, and some clumps are found, in higher, moister areas. A mix of temperature, high winds and abundant snowfall, as well as fire, may be the causal mechanisms of higher levels of Joshua tree cloning. (Gucker 2006). In a study following a large fire in Joshua Tree National Park in 1999, DeFalco et al. (2010) found that 33% of plants that were censused in burned areas sprouted from the root crown or stem after the fire compared with 15% in unburned areas. Recently, Harrower and Gilbert (2018) found enhanced clonality and lack of seedling recruitment on the lower elevation margins of the Joshua tree range in addition to the previously reported prevalence of cloning at higher elevation sites.

2.3.2 *Sexual reproduction*

Sexual reproduction of Joshua trees is by seed production. As described above, bisexual flowers occur in dense, heavy panicles that measure 20 to 40 cm long. Individual flowers are

round to egg shaped and measure 2.5 to 5 cm by 1 to 2 cm wide.

Esque et al. (2015) noted that while flowering has been observed in Joshua trees as small as 1 meter in some areas, trees that were over 30-years old at their study site had yet to flower. Flowering is considered episodic and rare, generally occurring only in wetter years (Gucker 2006). Reports differ on timing of flowering, with, for instance, Hess (2012) indicating April and May, Waitman et al. (2012) stating February through March, and Harrower and Gilbert (2018) indicating between February and April. Recently, Cornett (2018) reported an apparently unprecedented flowering event in November, following heavy October rains and warmer than usual temperatures immediately thereafter.

Irrespective of timing, Joshua tree flowers require insect pollination to produce seeds.

Pollination and seed production

Joshua tree, as with almost all yuccas, have an obligate pollination mutualism with yucca moths (Lepidoptera, Prodoxidae). Female moths carry pollen to Joshua tree flowers in specialized mouthparts, inject eggs into the floral ovaries using a bladelike ovipositor, and then actively apply pollen to the stigmatic surface to fertilize the flower. As a Joshua tree flower develops into a fruit, the moth eggs hatch and the emerging larvae eat a portion of the developing seeds. The moths are the sole pollinators of Joshua trees, and in turn, the Joshua tree seeds are the only food source for the moths (Pellmyr and Segraves 2003; Yoder et al. 2013).

Joshua trees are now known to be pollinated by two species of moth, *Tegeticula synthetica* and *T. antithetica*, the latter only described in 2003 by Pellmyr and Segraves. Outside of the narrow region in Nevada where *Y. brevifolia* and *Y. jaegeriana* are sympatric and hybridize, *T. synthetica* is the sole pollinator of *Y. brevifolia* and *T. antithetica* is the sole pollinator of *Y. jaegeriana*. While *T. synthetica* is about 30% larger than *T. antithetica*, the apparently more important difference in the two moths is the size of their ovipositors, with the difference in length of each matching the difference in the length of the stylar canal of their respective host plants, with the ovipositor of the western moth (*T. synthetica*) being about 50% larger than that of the eastern species (*T. antithetica*) (Pellmyr and Segraves 2003; Godsoe et al. 2008).⁶

The parallel differences between stylar canal length and ovipositor length between the two species of moths and two types of Joshua tree suggest that selection exerted by their pollinators is the best explanation for the morphological divergence of the trees. Since the female moth's ovipositor must be long enough to reach the ovules but not so long as to injure them, coevolution acting upon moth and tree should favor matching between the length of the moth's ovipositor and the flower's stylar canal (Godsoe et al. 2008; Yoder et al. 2013; Cole et al. 2017). Using molecular clock techniques, Pellmyr and Segraves (2003) concluded that the two moths diverged approximately 10 million years ago, while Smith et al. (2008) later determined that the split between the moth species likely occurred 1.14 million years ago.

⁶ In addition to the pollinating *Tegeticula* moths, bogus yucca moths of the sister genus *Prodoxus* also lay their eggs in Joshua tree flowers. Adult *Prodoxus* lack the specialized mouthparts used for pollination and the larvae feed on plant tissues other than seeds (Althoff et al. 2004).

Studies in Tikaboo Valley in Nevada where both the two moth species and the two types of Joshua trees are sympatric demonstrate that *T. antithetica* can successfully fertilize *Y. brevifolia* and reproduce in their fruits, but *T. synthetica* do not successfully rear larvae on *Y. jaegeriana* (Smith et al. 2009; Starr et al. 2013; Yoder et al. 2013). Consequently, gene flow is largely unidirectional, with flow from *Y. jaegeriana* into *Y. brevifolia* but not from *Y. brevifolia* into *Y. jaegeriana* (Starr et al. 2013).

Once pollinated, fruits form in early summer and seeds are mature in mid-summer (Waitman et al. 2012). Fruits are indehiscent capsules, which become spongy and dry with age. Egg-shaped capsules are 6 to 10 cm long and approximately 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 black seeds, which are flat to thickened with smooth to undulate surfaces. Seeds are 7 to 11 mm long. (Gucker 2006).

Seed predation and dispersal

While *Tegeticula* moths are necessary for pollination, their larvae are the first predators that Joshua tree seeds experience. In one study, the range of larvae per fruit was 0 to 6, with an average of 1.4. These larvae consumed or damaged 7% of seeds (Keeley et al. 1985). Borchert and DeFalco (2016) found much higher levels of larvae predation, with 19.5% damaged in a year of widespread fruiting and 42.8% damaged in a subsequent year of reduced flowering and fruiting. Seed production was more than 100 times greater in the first year of the study, leading the authors to speculate that Joshua trees may be a masting species.

Just as a portion of a Joshua tree's seed production goes to its pollinator, a large percentage of its seed production goes to its primary dispersers, various scatter-hoarding rodents. Among the current consumers (and likely dispersers) of Joshua tree seeds in California are the white-tailed antelope squirrel (*Ammospermophilus leucurus*), Mojave ground squirrel (*Xerospermophilus mohavensis*) and California ground squirrel (*Otospermophilus beecheyi*), all of which are known to climb Joshua trees to remove the fruits for later consumption and/or to eat through the desiccated fruits in situ to reach the seeds (Lenz 2001). Once fruits are on the ground, numerous other species will dismantle the fruits and eat and/or cache the seeds, including the round-tailed ground squirrel (*Xerospermophilus tereticaudus*), rock squirrel (*Otospermophilus variegatus*), Merriam's kangaroo rats (*Dipodymus merriami*), canyon mice (*Peromyscus crinitus*) and woodrats (*Neotoma sp.*) (Lenz 2001; Vander Wall et al. 2006; Waitman et al. 2012; Borchert and DeFalco 2016). Among these species, the white-tailed antelope squirrel and Merriam's kangaroo rats have been identified as the most frequent agents of seed removal and caching (Waitman et al. 2012; Borchert and DeFalco 2016).

Studies by Vander Wall et al. (2006), Waitman et al. (2012) and Borchert and DeFalco (2016) have all highlighted the importance of seed dispersal by scatter-hoarding rodents. In the study by Vander Wall et al. (2006), more than 99% of tracked seeds were removed by rodents from placement below Joshua trees, with 84% found in rodent caches at a mean maximum distance of 30 meters. Subsequent surveys found 46% of caches intact, 51% of caches missing entirely, a handful of caches largely empty but with a few remnant seeds below ground and

numerous new secondary caches established. Over the subsequent months, rodents ate most of the cached seeds. Ultimately, well under 1% of cached seeds were documented as eventually germinating from identified caches the following spring. Nevertheless, Vander Wall et al. (2006) concluded that “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,” and “that seeds that are not harvested by seed-caching rodents probably have no chance of establishing a seedling.”

While a rodent eats the vast majority of the seeds it removes from a Joshua tree fruit, it also acts as the primary seed disperser, moving seeds upwards of 50 meters from the source tree (Vander Wall et al. 2006; Waitman et al. 2012; Borchert and DeFalco 2016). Waitman et al. (2012) concluded that rodents not only disperse seeds, but also, via the act of caching them, increase the likelihood of germination as seeds that have been buried in soil have a much greater chance of establishing seedlings than those left on the soil surface. Consequently, the Joshua tree’s relationship with the predating rodent, which liberates its seeds from an otherwise inescapable pod, disperses them, and caches many where they have a higher chance of germination, may, as with the pollinating moth, be one of obligate mutualism (Vander Wall et al. 2006; Waitman et al. 2012).⁷

Waitman et al. (2012) also noted the limitations of the mutualistic relationship between Joshua trees and rodents, as it requires sufficient seed production such that the caching rodent collects more seeds than it can eat: “Small seed crop size along with an overabundance of rodents may shift this interaction from mutualism toward seed predation by rodents.” Given seed production is apparently greatest in wetter years, in drought years virtually all seeds may be consumed by rodents, resulting in no seedlings being produced that year.

While almost all authors recognize the current importance of rodent seed dispersal, several have hypothesized that the large effort in fruit production by Joshua trees without a specialized dispersal agent may indicate that current fruit production is an evolutionarily relict designed to attract a now extinct megaherbivore dispersal agent, with Cole et al. (2011) identifying ground sloths and Lenz (2001) suggesting Columbian mammoths. Cole et al. (2011) note that evidence supports “the concept that the species’ current mobility is constrained by the earlier extinction of the Shasta ground sloth and other possible seed vector(s).” However, Waitman et al. (2012) discount the role of the sloths in seed dispersal and conclude that “seed-caching rodents are responsible for seed dispersal today, and we suspect that they were an important, if not the sole, means of dispersal in the past.”

Additionally, several authors have identified wind as an important seed dispersal agent (e.g. Lenz 2001, citing earlier accounts), with Gucker (2006) noting that as fruits become overmature, skins crack and moisture is released, making fruits lighter and more easily wind dispersed, and that finding clumps of 2 or more seedlings is likely evidence that the dried fruits

⁷ However, unlike the Joshua tree’s relationship with *Tegeticula* moths, where both tree and moth absolutely need each other to successfully reproduce, the tree’s relationship with the rodent is more one-sided; the Joshua tree may be dependent upon the rodent to disperse its seeds, but the rodent – while certainly benefiting from the tree’s seeds – can generally subsist on other food sources in its absence.

were wind dispersed. The largest known modern dispersal distances for Joshua trees of 151 meters in the Antelope Valley and 251 meters in Lanfair Valley were recorded by Lenz (2001) and ascribed to wind. However, Waitman et al. (2012), based upon wind tunnel tests of fruits and seeds, discount wind dispersal of seeds as playing a significant role for Joshua tree reproduction.

As further discussed *infra*, whether by wind or rodents, seed dispersal of Joshua trees is generally considered quite limited, likely constraining the ability of the species to extend its range in response to changing conditions (Lenz 2001; Cole et al. 2011).

Germination and growth

In laboratory conditions, Joshua tree seeds germinate readily and do not require any pretreatment (Gucker 2006). Waitman et al. (2012) had germination rates of 99% on freshly harvested seeds, while other experiments had germination rates of 98% and 72% after 6 months and 1.5 years of storage, respectively (Gucker 2006).

Longevity of viable seeds in the soil seed bank is limited. Waitman et al. (2012) reported that “a small fraction of seeds” emerged the year following their experiment, indicating that in some circumstances viability is at least two years. Reynolds et al. (2012) observed that seeds in the ground “rapidly lost germinability through time. Longevity of seeds in the soil declined by about 50% per year, which indicates that *Y. brevifolia* has little capacity for seed dormancy.” Borchert and DeFalco (2016) noted that in most years when fruit production is enough to satiate predation by larvae and rodents, uneaten fruits may remain on the tree and “may function as a viable aerial seed bank well after fruit maturation,” since seed germinability is likely longer in an intact fruit than in the soil.

Notwithstanding very high laboratory germination rates, seedling production in the field is extremely low. Of the 1000 seeds tracked by Vander Wall et al. (2006), 836 were cached by rodents, but only three of these were documented to ultimately produce seedlings. Of seeds planted in artificial caches in enclosures that precluded rodent harvest, only 14.8% germinated (Vander Wall et al. 2006). In another enclosure study, Waitman et al. (2012) reported only 3.2% of cached seeds produced seedlings in the field, while 36% of pots in an artificial growing chamber produced seedlings. Buried seeds, both in the field and laboratory, were most likely to produce emergent seedlings when 1 to 3 cm deep, depths similar to the caches rodents were observed making (Waitman et al. 2012). Both Vander Wall et al. (2006) and Waitman et al. (2012) reported higher seedling emergence rates from caches under shrub cover. However, both studies also found that rodents cache seeds without regard to shrub cover.

Reynolds et al. (2012) described the climate conditions supporting emergence and postulated 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 may already have occurred.” Subsequent studies (*e.g.* Sweet et al. 2019) have demonstrated that this demographic change due to low recruitment is already underway.

Once a seedling emerges, it faces a long, arduous path to adulthood, with high mortality

until it exceeds 25 cm in height (Esque et al. 2015). Survival of seedlings requires periods of cool temperatures, little to no herbivory, summer rain, and some amount of yearly precipitation over a period of several years (USFWS 2018).

Growth rates are dependent on factors ranging from age, precipitation, presence of nurse plants, temperature and (at least in labs) photoperiod (Gucker 2006). Over the years various studies have indicated differing rates of growth. In one study in Joshua Tree National Park, unbranched seedlings grew at an average rate of 7.6 cm/year for the first 10 years and an average of 3.8 cm/year thereafter, with other studies showing annual growth rates of was 5.9 cm/year and 11.7 cm/year (Gucker 2006). More recently, Esque et al. (2015) measured a long-term mean annual growth rate of 3.12 ± 1.96 cm over 22 years and noted that long-term growth rates in other contemporaneous studies elsewhere in the Mojave were comparable.

Lab studies suggest that cold periods are required for optimal seedling growth, as 3-year old seedlings kept at 4 °C for 2 months produced twice as many new leaves after the cold treatment as seedlings without the cold treatment. Other lab experiments suggest that day length affects the growth of seedlings, with seedlings exposed to 10 hours of daylight producing the longest and most leaves, while seedlings grown in 16 hours of daylight produced the shortest and fewest leaves (Gucker 2006).

Perhaps the most important factor in seedling survival and growth is the presence of nurse plants. Several studies have found successful seedling emergence tied to shrub cover (Bittingham and Walker 2000; Vander Wall et al. 2006; Waitman et al. 2012), with blackbrush (*Coleogyne ramississima*) generally noted as the most important nurse plant. The benefits of a shrub canopy for a young Joshua tree include increased soil moisture, decreased insolation, reduced soil temperatures, decreased evapotranspiration, increased nutrients, decreased herbivory, and/or lower wind desiccation (Bittingham and Walker 2000; Gucker 2006).



Figure 5: Young Joshua tree emerging from nurse plant.

Once established, a Joshua tree is relatively long-lived. However, aging a Joshua tree or determining maximum lifespan is difficult as the plants lack annual growth rings. While one early report of a 20-meter tall Joshua tree estimated the plant to be 1000 years old (Little 1950), most early studies postulated that large trees can be 300 years old with an average life span of 150 years (Gucker 2006). More recent studies based on growth rate and long-term monitoring have reached similar conclusions. Gilliland et al. (2006), based upon growth rates generated from a 14-year census of a Joshua tree woodland, estimated that the oldest tree was 321 years, with mean age of trees of 62.2 years. Estimates based on observed patterns of survivorship produced similar results, with a median life expectancy of 89 years, with 5% of the population projected to reach 383 years. Esque et al. (2015) estimated a generation time of 50-70 years based on data collected during a 22-year study.

Summing up reproduction and recruitment by Joshua trees, Esque et al. (2015) highlighted the challenges Joshua trees face:

[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 successful establishment of new seedlings only a few times in a century. (internal citations omitted)

As further discussed *infra*, the Joshua tree's recruitment challenges make the species particularly vulnerable to climate change.

2.4 *Habitat Requirements*

Joshua trees occur in desert grasslands and shrublands in hot, dry sites on flats, mesas, bajadas, and gentle slopes in the Mojave Desert (Gucker 2006). Soils in Joshua tree habitats are silts, loams, and/or sands and variously described as fine, loose, well drained, and/or gravelly, while the plants can reportedly tolerate alkaline and saline soils (Gucker 2006). Cole et al. (2011) characterizes populations as discontinuous and reaching their highest density on the well-drained sandy to gravelly alluvial fans adjacent to desert mountain ranges.

Lenz (2001) reports that plants tolerate temperatures of -25°C to 51°C and annual precipitation ranges of 98 to 268 mm. According to USFWS (2018), the temperature range for western Joshua trees ranges from a low of -8.1°C to a mean summer high of 37.2°C and the species occurs in areas averaging more than 82 mm of rainfall and less than 738 mm of rainfall per year. Went (1957), based on field observations and laboratory experiments, noted that non-juvenile Joshua trees required annual exposure to low temperatures for optimal growth. Turner (1982) postulated that such a need for cold winter temperatures may explain why Joshua trees are largely limited to the higher and cooler periphery of the Mojave.

Temperature and precipitation are likely the prime constraints on the species, with Cole et al. (2011) noting 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.” Temperature and precipitation requirements are further discussed *infra* with regard to climate impacts on the species.

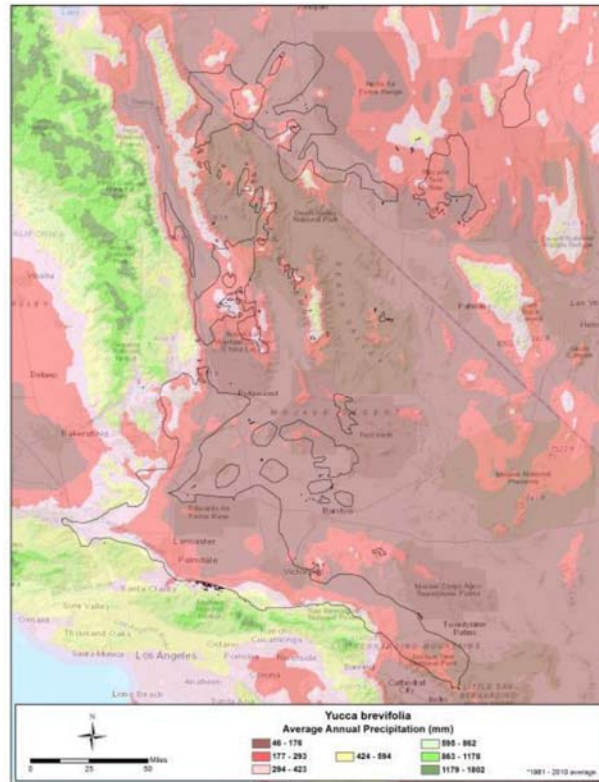


Figure 6. Average annual precipitation in range of *Y. brevifolia* (USFWS 2018).

The reported upper and lower elevation limits of Joshua trees vary significantly in the published literature (Gucker 2006). The recent Species Status Assessment by USFWS (2018) is based upon a comprehensive review of distribution records and describes the elevational range for *Y. brevifolia* as 750 meters (2461 ft) up to 2200 meters (7218 ft), and between 600 meters (1969 ft) and 2000 meters (6500 ft) for *Y. jaegeriana*.

Joshua trees are not restricted to any one desert scrub or xeric woodland community and can be found in many different plant alliances throughout their range (Turner 1982). For example, within Joshua Tree National Park, Harrower and Gilbert (2018) characterized their study area of Joshua trees as encompassing four broad eco-regional vegetation types: Sonoran–Colorado Desert scrub, Mojave–Sonoran creosote bush scrubland, Mojave mid-elevation desert, and pinyon–juniper woodland.

While Joshua tree habitat may not be limited by particular plant associations, as discussed *supra*, for successful reproduction and recruitment, Joshua trees require the presence of their obligate pollinator, rodents to disperse and cache seeds and nurse plants to shelter emerging seedlings.

3 Current and Historical Distribution

The current range of Joshua trees (both species)⁸ extends from northwestern Arizona to southwestern Utah west to southern Nevada and southeastern California at elevations between 600 and 2200 meters of elevation and between 34° to 38° latitude (USFWS 2018). The current range of the Joshua tree is but a small fraction of its range during the late Pleistocene.

Plant material from Shasta ground sloth dung and packrat middens indicates that during the Pleistocene the Joshua tree had a much larger southern distribution extending well into the Sonoran Desert, where its range may have encompassed La Paz, Maricopa, Pinal, Yuma, and Pima counties in Arizona; Imperial and Riverside counties in California; mainland Mexico; and northern Baja California, Mexico (Cole et al. 2011) (Figure 7).



Figure 7: Current and Pleistocene range of the Joshua tree. Source: USFWS (2018), based on Cole et al. (2011).

The Joshua tree's historical range contracted northward along the southern edge of its range as climates warmed at the start of the Holocene. As noted by Cole et al. (2011), this contraction was not matched by northward expansion:

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.

⁸ Because the split of Joshua trees into two species has only recently been recognized, much of the literature describing their past and present range does not explicitly distinguish between the two. The current range of *Y. brevifolia* is readily discernable from that of *Y. jaegeriana* and is described *infra*. However, while the historic range of Joshua trees is broadly known from subfossil records, the portion of that range that is ascribable to each species has yet to be determined.

Cole et al. (2011) ascribed the lack of northward expansion to the Joshua tree’s extremely limited dispersal ability, potentially a result of the extinction of the Shasta ground sloth which may have been a primary seed disperser for the species.

Since the end of the Pleistocene, the Joshua tree’s distribution has been remarkably stable throughout the Holocene into the present day (Cole et al. 2011; Holmgren et al. 2010).

There are currently five regional populations of Joshua trees distributed across the Mojave, southern Great Basin, and western Sonoran Deserts, with the vast majority of trees occurring within the Mojave.⁹ Of the five populations, two are of *Y. brevifolia* and three of *Y. jaegeriana*, with a sixth small hybrid population in Tikaboo Valley, Nevada. One of the *Y. brevifolia* populations is entirely in California (YUBR South in Figure 8), while the other is shared with Nevada (YUBR North in Figure 8). Only one of the three *Y. jaegeriana* populations occurs in California (primarily in the Mojave National Preserve), and this population is shared with Nevada and Arizona (YUJA Central in Figure 8) (USFWS 2018).

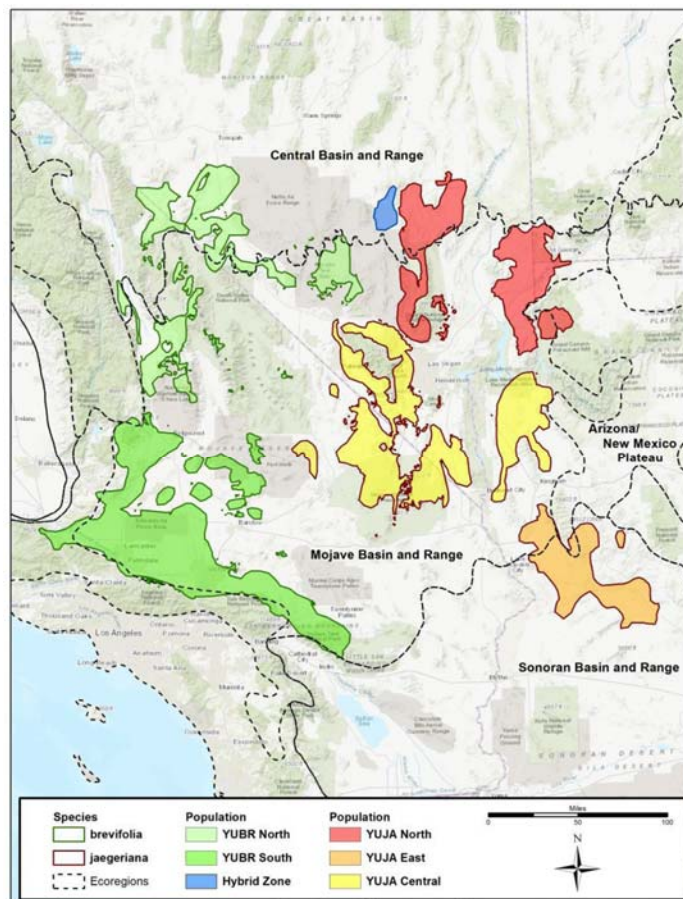


Figure 8. Current Joshua tree distribution. Source: USFWS 2018.

⁹ While numerous published studies have characterized the range of Joshua trees, USFWS (2018) is the most complete synthesis of range data; consequently, petitioners cite primary to that document in this section.

Y. brevifolia occurs almost exclusively in the Mojave Desert in unevenly distributed populations. A small portion of its northern extent occurs within the Great Basin Desert (Figure 8). The primary distinguishing feature of these two desert regions is the presence of creosote bush in the Mojave Desert and Sagebrush steppe in the Great Basin. The southern extent of *Y. brevifolia*'s range is in the Little San Bernardino Mountains of Joshua Tree National Park. The northern extent of its range is near Alkali, Nevada. The western extent is near the Hungry Valley State Vehicular Recreation Area near Gorman, California. The eastern extent of its range is in Tikaboo Valley, Nevada, where it co-occurs with *Y. jaegeriana* (USFWS 2018).

USFWS (2018), treats *Y. brevifolia* as comprised of two geographically separate populations, (YUBR) South and YUBR North.¹⁰ YUBR South is entirely within California. This population occurs within the area stretching from Joshua Tree National Park, north to Ridgecrest and Red Mountain. This area is comprised of alluvial plains, fans, and bajadas of the major valleys lying between scattered mountain ranges. On the southern and western edge of the population boundary, *Y. brevifolia* occurs in transitional areas characterized by higher elevations and more rainfall with semi-desert montane chaparral to pinyon-California juniper woodlands. There is some variation in vegetation from north to south, but the basins typically are dominated by creosote bush (*Larrea tridentate*) and white bursage (*Ambrosia dumosa*) and the higher elevations are characterized by junipers and pinyons (USFWS 2018).

In the YUBR South range, average annual rainfall varies between 82.4 mm and 738.1 mm and minimum temperatures range from -5.7°C at the upper elevational limit (2200 meters) to 4.8°C at the lower elevational limit (750 meters). Mean summer high temperature are between 23.4-37.2°C. Less than 10 percent of annual precipitation occurs in summer in most areas occupied by *Yucca brevifolia* (USFWS 2018).

The geographic area in which YUBR South is situated is comprised of 3.7 million acres, with just over 50% in private ownership, 48% federally owned, and just under 2% state, county and local owned (USFWS 2018). USFWS (2018) estimates that 3,255,088 acres of this area was suitable for Joshua trees based on soils and other habitat factors.¹¹ However, Joshua tree do not occupy the entirety of this area, as they can have a patchy and disjunct distribution. Notably, the Bureau of Land Management's (BLM's) calculation of Joshua tree woodland on lands under its jurisdiction is substantially less than this larger area estimated by USFWS (2018). USFWS (2018) mapped 841,220 acres within the area of YUBR South as on BLM lands. BLM (2006) itself calculated that only 3275 acres of "Joshua tree woodland" occur on its lands in the West Mojave Plan (WEMO) area, which includes all of YUBR South. While this extreme difference between the two estimates is partly attributable to Joshua trees occurring in other plant community types that occupy much larger areas (e.g. "blackbrush scrub" and "creosote bush scrub"), it does highlight that areas of dense concentrations of Joshua trees occupy a relatively small fraction of the larger mapped areas.

¹⁰ As discussed *infra*, each of these populations may constitute an evolutionarily significant unit (ESU).

¹¹ A peer reviewer of USFWS (2018) pointed out that "the potential distribution of Joshua tree under current climate conditions is vastly overestimated" (Smith 2018). This is discussed in greater detail in the section of the federal ESA listing decision, *infra*.

Additionally, the cities of Palmdale, Lancaster, Hesperia, Victorville, and Yucca Valley, as well as numerous smaller communities are within the mapped YUBR South area. While *Y. brevifolia* currently persists in the less-developed areas of these communities, it is absent from the more developed areas as well as the agricultural lands in the region. The Antelope Valley, where the largest of these cities are situated, is the area where the greatest habitat loss of *Y. brevifolia* has already occurred.

The YUBR North population occurs in the area north of Inyokern, along the west and north margins of Death Valley, to Goldfield, Nevada, and east to the Nevada Test Site. In contrast to the mostly creosote bush shrubland of the lower elevations in YUBR South, the vegetation of this higher and cooler zone includes single-leaf pinyon, juniper, and sagebrush. The elevation range of the species in this population is between 1500 and 2200 meters. Average annual rainfall varies between 95.8 mm and 429 mm, minimum temperatures range from -8.1 to 3.6°C, mean summer temperatures range between 20.4 and 36.3°C, and summer precipitation comprises up to a quarter of the mean annual precipitation (USFWS 2018).

In contrast to the area of YUBR South, which is majority private land, the area of YUBR North is overwhelmingly (96%) federal land (USFWS 2018). The approximately 2 million acres comprising the YUBR North area is about evenly split between California and Nevada. USFWS (2018) estimates that almost all of this area (1,941,701 acres) is suitable for Joshua trees.

4 Abundance and Population Trends

Due to the species' patchy distribution within its range, highly variable population density (4 to 840 trees per acre) and lack of range-wide population surveys, a reliable estimate of Joshua tree population size is not available (USFWS 2018). Similarly, no range-wide population trends have been documented. However, recent studies carried out in portions of the species' range indicate that density is negatively correlated with increasing temperature, the species range is contracting at lower elevations, recruitment is limited, and mortality is increasing, all of which would likely reflect a population already starting to decline.

DeFalco et al. (2010), in a study in Joshua Tree National Park, found that recent drought and fire had resulted in significant mortality of *Y. brevifolia* in the park. Five years after a fire, 80% of burned trees in the study area had died, with smaller trees (<1 m tall) dying more rapidly. But perhaps more surprising, DeFalco et al. (2010) found that unburned trees also had high mortality rates during the same study period (1999-2004), with 26% of unburned trees also dying. As with post-fire mortality, smaller trees died in the initial years of the drought with mid-size and larger trees showing effects in later years. Mortality was ascribed both to water stress itself, as well as herbivory by pocket gophers (*Thomomys bottae*), which likely turned to Joshua tree stems, roots and periderm as alternative food sources due to reduced herbaceous cover during the drought (DeFalco et al. 2010).

In a recent study, Harrower and Gilbert (2018) investigated various life-history parameters of Joshua trees in Joshua Tree National Park and found the "ratio of dead to living trees was greater at the lower elevations where the sites are warmer and drier than sites at higher elevation." Their results "suggest that the range of Joshua trees is contracting at the lower

elevations where there was no seedling recruitment and high tree mortality.” Harrower and Gilbert (2018) also note that Joshua trees “do not seem to be moving successfully into higher elevations,” potentially due to limitations on numbers of pollinating moths at these higher elevations. This finding is consistent with that of St. Clair and Hoines (2018) who found Joshua tree stand density negatively correlated with increasing temperature.

A series of small-scale studies in Joshua Tree National Park summarized in Cornett (2014) documented a 93% decline in Joshua tree abundance between 1990 and 2013 at one site, a 16% decline in Joshua tree numbers between 1988 and 2008 at second site, and a 73% decrease from 1990 through 2013 at a third site. Fire contributed to the decline at the third site, but even that site had declined by 18% prior to the fire. Cornett (2014) noted that declines at these three sites, which “represent a broad geographical sampling” of Joshua trees in the Park, and along with the documented mortality of some of the largest (and presumably oldest) trees in Park, “would seem to indicate *Yucca brevifolia* numbers are declining throughout the Park.”

Regardless of whether Joshua tree abundance is already declining, it is virtually certain that abundance will decline in the foreseeable future. The impacts of climate change, fire, habitat loss and other sources of mortality are discussed further below.

5 Factors Affecting Ability to Survive and Reproduce

As discussed in the Life History sections *supra*, Joshua tree survival and reproductive success is tied to multiple factors, many of which are influenced by climate. Importantly, survival varies greatly by size class, with relatively high survival among adults, but very high mortality rates for seedlings and smaller individuals (DeFalco et al. 2010; Esque et al. 2015). As noted by Esque et al. (2015), 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.” Consequently, while some impacts such as reduced recruitment may already be observable, impacts such as adult mortality and consequent population declines and range reductions may have a lag time before their presence is felt on the landscape (Svenning and Sandel 2013).

Among the factors affecting *Y. brevifolia*'s ability to survive and reproduce are predation, invasive species, wildfire, drought, climate change and habitat loss due to development. These factors are often related, synergistic, and collectively threaten the continued viability of the species.

5.1 Predation

Predation plays an important role in Joshua tree survival at every life stage. Before a seed even leaves a fruit, *Tegeticula* moth larvae eat a portion of the seeds, with Keeley et al. (1985) observing 7% of seeds in a fruit consumed or damaged (Keeley et al. 1985). Borchert and DeFalco (2016) found much higher levels of larvae predation, with 19.5% damaged in a year of widespread fruiting and 42.8% damaged in a subsequent year of reduced flowering and fruiting. Rodents then cache and ultimately consume the vast majority of seeds, with fewer than 1% of

seeds germinating (Vander Wall et al. 2006; Waitman et al. 2012; Borchert and DeFalco 2016). In drought years, virtually all seeds may be consumed by rodents, resulting in no seedlings being produced that year (Waitman et al. 2012).

Cattle have been documented grazing on the inflorescences of small Joshua trees. Lybbert and St. Clair (2017) documented floral herbivory by cows on *Yucca brevifolia* less than 2 m tall consumed 40% of inflorescences on their study plot. However, since the majority of Joshua trees flower above that 2 m threshold, only 6% of inflorescences overall were consumed by cattle. The fact that *Yucca brevifolia* evolved into a taller tree form than other yuccas might be a vestige of a growth-escape strategy to escape herbivory from a now extinct species, such as the Shasta ground sloth (Cole et al. 2011; Lybbert and St. Clair 2017).¹²

Drought years and fire also result in increased herbivory on seedlings and pre-reproductive Joshua trees (DeFalco et al. 2010; Esque et al. 2015), as the reduced availability of herbaceous forage forces small herbivores to use alternative food sources, including *Y. brevifolia* stems and leaves (DeFalco et al. 2010; Esque et al. 2015). DeFalco et al. (2010) found widespread evidence of tissue damage to Joshua trees in burned areas (28% of plants) from pocket gophers (*Thomomys bottae*), with lesser levels (16%) evident in unburned areas. Such damage occurred predominantly in lower elevation sites. In most areas Joshua tree survival rates dropped with evidence of rodent damage, with the effects most pronounced in burned areas.

In a separate study, Esque et al. (2015) found that herbivory by black-tailed jackrabbits (*L. californicus*) resulted in 55% mortality of pre-reproductive *Y. brevifolia* <25 cm tall on their study site in a single drought year. In addition to jackrabbits, Esque et al. (2015) documented damage to pre-reproductive plants from pocket gophers, white-tailed antelope squirrels (*Ammospermophilus leucurus*), and woodrats (*Neotoma sp.*).

While predation alone is likely not presently a threat to Joshua tree persistence, it can result in zero reproductive success in one or a sequence of dry years, as well as high mortality levels to seedlings and small plants (<25 cm tall), and even adults. This effect is magnified in areas that burn. Burned trees are likely physiologically more vulnerable to herbivore damage, while the lack of other herbaceous plants deprives young Joshua trees of nurse plants which shield them from herbivory. Moreover, jackrabbits, pocket gophers and other herbivores lack alternative food sources and turn to Joshua tree stems, roots and periderms for sustenance following such events (DeFalco et al. 2010; Esque et al. 2015). As discussed *infra*, both wildfire and droughts are predicted to increase in frequency and intensity in the coming decades, likely rendering the impacts of seed predation and herbivory on stressed and shrinking populations of Joshua trees more significant.

¹² Notably, cattle grazing can have significant impacts on other yuccas, with Lybbert and St. Clair (2017) documenting complete reproductive failure of *Y. baccata* and consequent apparent local extirpation of that species' pollinating moths on their study plot due to high levels of herbivory on the species' flowers by cows. *Y. baccata* is notably shorter than *Y. brevifolia* with its flowers within easy reach of cattle. The Joshua tree's evolutionary adaptation to survive sloth herbivory may have pre-adapted it to better survive cattle grazing.

5.2 Invasive species

Invasive plant species are widely established in the Mojave Desert throughout the range of *Yucca brevifolia*. And while invasive species represent a relatively small percentage of the flora, they represent a huge percentage of the biomass. Brooks and Berry (2006) found that in a high rainfall year (1995) nonnative annual species comprised 6% of the flora and 66% of the annual biomass, with those numbers increasing to 27% and 91% respectively in a low rainfall year (1999). The grasses red brome (*Bromus rubens*) and *Schismus* spp., along with the forb redstem fillaree/stork's bill (*Erodium cicutarium*) comprised 99% of the alien biomass. More recently, Sahara mustard (*Brassica tournefortii*) has spread into the Mojave, including into Joshua tree woodland (Frakes 2017; Brooks et al. 2018).



Figure 9: Carpet of desiccated invasive *Schismus* spp. between *Y. brevifolia*.

The abundance and diversity of alien species in the Mojave is positively correlated with disturbance, including livestock grazing, off-highway/off-road vehicle (OHV or ORV) use, fire, urbanization, roads, and agriculture. As summarized by Brooks and Berry (2006):

Alien annuals had high density, biomass, or cover near roads, in an area of OHV use compared to an area where OHV use was lower, in an area where both OHV use and grazing were present compared to an area where both disturbances had been excluded for at least 10 years, in two grazed areas compared with ungrazed areas, and in areas near livestock watering sites.... These studies indicate that species richness and biomass of alien annual plants are positively correlated with disturbance (internal citations omitted).

Invasive species are also aided by nitrogen deposition as a result of air pollution (Brooks 2003). As noted by Allen et al. (2009), 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” (internal citations omitted). Fertilization disproportionately benefits nonnative species leading to increased abundance and biomass of invasive species such as *Bromus rubens* and *Schismus* spp. (Brooks 2003; Allen et al. 2009; Allen et al. 2011; Bytnerowicz et al. 2016).

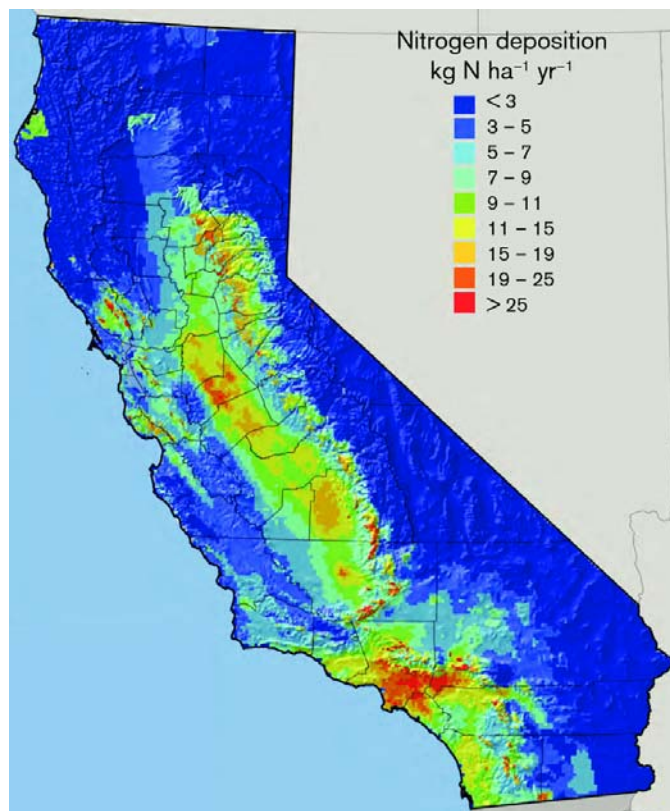


Figure 10: Map showing nitrogen deposition rates in California, with areas of high levels overlapping the range of YUBR South. Source: Bytnerowicz et al. 2016.

While the rapid spread of invasive species in the Mojave is resulting in competitive impacts on native annuals, and has also been demonstrated to have direct competitive impacts on native perennial species including creosote bush (*Larrea tridentata*) (DeFalco et al. 2007), direct competitive impacts of invasives on *Yucca brevifolia* have not been thoroughly studied. To the degree there is competition it would likely be most significant with emergent seedlings under nurse plants as this is the most vulnerable life stage of the Joshua tree (Reynolds et al. 2012).

The much bigger issue is that these invasive plants have altered fire dynamics, leading to larger and more frequent fires that are killing innumerable Joshua trees. As succinctly described by Barrows and Murphy-Mariscal (2012), “[m]ore 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*.” Similarly, Pardo et al. (2011) highlighted the dire consequences for *Y. brevifolia*: “In Joshua Tree National Park in southern California, N deposition favors the production of sufficient invasive grass biomass to sustain fires that threaten the survival of the namesake species.” As discussed below, the altered

fire regimes in the Mojave represent a significant threat to the Joshua tree at the individual and population level.



Figure 11: Fire-killed *Y. brevifolia* in a carpet of *Bromus rubens*.

5.3 Wildfires

Wildfire is one of the greatest threats to the persistence of *Yucca brevifolia*, particularly as the species' range contracts in the face of climate change and the frequency and severity of fire in the species' range increases (DeFalco et al. 2010; Holmgren et al. 2010; Vamstad and Rotenberry 2010; Cole et al. 2011; Barrows & Murphy-Mariscal 2012; Sweet et al. 2019).

5.3.1 Joshua tree response to fire

Some early researchers suggested that Joshua trees are well-adapted to fire due to the fact that damaged trees can resprout after fire (Webber 1953). Older adult trees are more fire resistant than younger trees as the apical meristems grow above the level of most ground fires while the flammable dead leaves on the main trunk that can facilitate fire spread into the crown are largely shed as the tree matures (Gunter 2006). And even if top-killed or damaged by fire, a Joshua tree can sprout from the root crown, rhizomes, and/or branches. Similarly, previous studies also found that Joshua trees can at least partially repopulate some burned areas via such sprouting (Loik et al. 2000a).

However, several longer-term studies have subsequently demonstrated that Joshua trees have relatively low post-fire survival, are slow to repopulate burned areas, and successful recruitment from resprouting requires sufficient precipitation in the years following fire (DeFalco et al. 2010; Vamstad and Rotenberry 2010; Abella et al. 2009).

As summarized by Brooks et al. (2018), “Yucca species such as Joshua tree and Mojave yucca (*Yucca schidigera*) often survive burning, but Joshua trees typically die within the first few years after fire due to drought and herbivory stress.” Moreover, Joshua trees are particularly vulnerable to fires as the “relatively small size and dense packing ratio of dead Joshua tree leaves compared with dead Mojave or banana yucca leaves increase the frequency at which they are completely burned and may explain why Joshua trees are more frequently killed by fire” (Brooks et al. 2018). It can take several decades before a Joshua tree sheds the dead leaves on its trunk, leaving the adult tree more fire resistant.

DeFalco et al. (2010) carried out a detailed study of Joshua tree survival in both burned and unburned areas of Joshua Tree National Park that paints a grim picture for species’ future in the face of increasing fire.

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 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 47yr after fires in Mojave and Sonoran deserts of California. Declining survival during the first year is attributed to immediate losses of small *Y. brevifolia* (< 1 m tall) whose active meristems close to the ground are vulnerable to extreme fire temperatures and flames that consume whole plants. As they age and grow taller, *Y. brevifolia* shed leaves from the trunk and are less likely to burn, unlike younger plants whose aging leaves are still attached and provide ladder fuel. Thus, taller plants likely sustained less proportional burn injury to the outer periderm tissue during the fire, and steep declines in this size class occurred only after the consecutive dry periods that began in the autumn months during 1999 and 2000 (internal citations omitted).¹³

Post-fire mortality in this study was likely the result of the interplay of drought and herbivory with fire. During the dry years subsequent to the fire, herbaceous plants were scarce, and pocket gophers (*Thomomys bottae*) gnawed the periderm and hollowed stems of *Y. brevifolia* causing many of them to topple. Pocket gopher damage reduced plant survivorship at low-elevation, unburned sites and diminished survival of burned plants in all but the driest site, which already had low survival (DeFalco et al. 2010).

The loss of *Y. brevifolia* was not only amplified by the lack of precipitation following the wildfire but also by herbivores that damaged burned plants. Herbaceous annual plants were scarce during the growing season following the 1999 fire, and many perennials were dormant due to low autumn through spring precipitation that triggers germination and breaks leaf dormancy. Widespread incidence of tissue damage by *T. bottae* in burned areas implies that the roots and periderm of *Y. brevifolia* that did not die immediately in the fire offered an

¹³ Noteworthy in the DeFalco et al. (2010) study is the fact that mortality of even unburned trees was high (26%) over the five years of their study. This was ascribed to a combination of drought stress and herbivory by pocket gophers. As discussed *infra*, such prolonged droughts are likely to be more frequent in a changing climate.

alternative succulent food source in denuded areas where shrubs and grasses were incinerated (DeFalco et al. 2010) (internal citations omitted).

DeFalco et al. (2010) observed that 33% of censused Joshua trees in burned areas sprouted from the root crown or stem after the fire. These are in line with other studies that found 25% of Joshua trees sprouting from the root crown after a 1978 fire (but with only 10% surviving five years later) and 28% sprouting from the root crown (and 2% from the stem) one year after a 1995 fire (Loik et al. 2000a).

Postfire sprouting prolonged Joshua tree survival in the DeFalco et al. (2010) study, but only at the wetter, high-elevation sites. As noted by DeFalco et al. (2010), “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.”

One area where Joshua trees may be more adapted to fire is along the far western edge of their range. As observed by Brooks et al. (2018),

Joshua tree populations along the extreme western edge of the desert bioregion near the Sierra Nevada and Transverse Ranges often resprout and survive more readily after fire than those further east. A cycle of relatively frequent fire and resprouting can result in short, dense clusters of Joshua tree clones, such as those found near Walker Pass, in the western end of the Antelope Valley, and in pinyon-juniper woodlands at ecotones with the Transverse Ranges such as Cajon Pass. High resprouting rates of Joshua trees in these areas may have evolved in local ecotypes that became adapted to shorter fire return intervals along the western desert ecotones than in other parts of the desert bioregion.¹⁴

Recruitment of new Joshua trees into burned areas is infrequent and slow. In one study no seedlings or saplings were observed in burned areas less than 10 years old, and fewer than 10 individuals per hectare were present on burned areas more than 40 years old in Joshua Tree National Park (Brooks et al. 2018). Another study found that Joshua trees were still rare on a site 65 years after a fire (Vamstad and Rotenberry 2010).

Among the factors inhibiting Joshua tree recolonization of burned sites are the lack of seeds due to mortality of seed-producing adults and the loss of suitable establishment sites due to the burning of nurse plants (DeFalco et al. 2010; Reynolds et al. 2012). Nurse plants in arid environments are known to moderate insolation, soil moisture, temperature, and humidity

¹⁴ Notably, the distinguishable clonal form of Joshua trees in these areas was once recognized as its own subspecies or variety, *Y.b. herbertii*, which is now considered a synonym of *Y. brevifolia* (Wallace 2017). Regardless of taxonomy, Joshua trees in these areas warrant special monitoring and protection as they may hold adaptations that make them particularly resilient in the face of increasing fires and climate change.

beneath their canopies and improve conditions for seedling establishment (Reynolds et al. 2012). Nurse plants also shield seedlings from herbivory (Esque et al. 2015).

Blackbrush (*Coleogyne ramosissima*) is one of the most important nurse plants for Joshua tree seedlings (Brittingham and Walker 2000) but is also one of the most vulnerable shrubs to fire (Brooks et al. 2018). Blackbrush are highly flammable, and once ignited tend to completely combust and are killed. Blackbrush stands can take centuries to recover, with the fastest documented recovery being on the order of 50 to 75 years (Brooks et al. 2018). Because of their extreme flammability and slow recovery, the mid-elevation zone dominated by blackbrush and home to Joshua trees is likely the most susceptible area to type conversion via the grass/fire cycle as a result of the arrival of non-native grasses (Brooks et al. 2018).

In the Joshua Tree National Park fire studied by Loik et al. (2000a), blackbrush was eliminated from the burned area with no signs of recovery. Loik et al. (2000a) postulated that “the time required for Joshua trees to begin recruitment via seeds will be delayed until *C. ramosissima* becomes re-established.”

As summarized by DeFalco et al. (2010), the “recruitment of *Y. brevifolia* is a slow process even without the impediments introduced by accelerated fire-return intervals.” And with such accelerated return intervals it may be impossible: “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” (Reynolds et al. 2012).

5.3.2 Increasing wildfire frequency and intensity in the Mojave

Large fires have been historically infrequent in Joshua tree woodlands, and the recent increase in fire size and frequency is partially due to invasion of exotic grasses, principally *Bromus* spp. and *Schismus* spp. (Brooks and Matchett, 2006; Vamstad and Rotenberry 2010; Klinger and Brooks 2017; Syphard et al. 2017; Brooks et al. 2018; Maloney et al. 2019).

Winters with relatively high amounts of precipitation produce an increase in biomass of native and especially non-native annual plants sufficient to carry fire in invaded habitats. The most dramatic changes have occurred in middle elevation shrublands dominated by creosote bush, blackbrush and Joshua trees. This zone is more susceptible than other areas of the Mojave Desert to increased fire size following years of high rainfall (Brooks and Matchett 2006).

The increase in fine, flashy fuel biomass from exotic plant species has increased the fire potential of these habitats sufficiently to allow for more frequent large fires than were carried by native vegetation alone (Brooks and Matchett 2006; Vamstad and Rotenberry 2010). The exotic grasses are of particular concern as they can form a continuous fuelbed for fire well into the hot, dry summer months and tend to not disarticulate as quickly as the native annual plants. While annuals, desiccated upright *Bromus* stems can be found on the landscape upwards of three years after senescence (Jurand and Abella 2013) and *Schismus* remnants can persist as fuel on the landscape for over a year (Brooks et al. 2018). Increased cover of invasive annual grass increases both the chance of a fire igniting and facilitates fire spread. This can both decrease the

time interval between the previous and subsequent fire as well as the extent of burning (Klinger and Brooks 2017).

Several recent reviews have documented fire frequency and extent in the Mojave over the past century (Tagestad et al. 2016; Syphard et al. 2017; Brooks et al. 2018). Each of these studies recognized that precipitation was a primary driver of fire frequency and extent, with wetter periods fostering the growth of invasive grasses which carry fire, and drier periods leading to fewer and smaller fires. Tagestad et al. (2016) summarized both short and long-term impacts of precipitation variation.

Long-term drought or above-average precipitation periods can have landscape-scale effects on the health and distribution of perennial plant species and the frequency and size of fires. Short-term increases in winter and summer precipitation can have an even greater effect on the likelihood of fire. High winter precipitation creates ephemeral flushes of herbaceous biomass resulting in continuous fuelbeds that promote the spread of fire. High summer precipitation brings thunderstorms with accompanying lightning and high winds which contribute to the ignition and spread of fires. Cumulative years of higher than normal precipitation also appear to have an effect on the potential for fire. This is especially a concern in areas invaded by annual grasses which exhibit a profound response to increased cool-season precipitation (internal citations omitted).

Particularly worrisome is that a sequence of wet years can lead to enormous fires, such as happened throughout the Mojave, including in the range of *Y. brevifolia* in 2005:

The 2005 Mojave Desert fire season, which burned an area equal to 132% of the total area that burned during the previous 25 years, was preceded by three extremely high precipitation years, suggesting that multiple years of high precipitation can have a cumulative effect on the accumulation of fuels (Tagestad et al. 2016).

According to Brooks et al. (2018), accounts by agency fire managers of the 2005 fires “indicate that these fires exhibited extreme fire behavior not previously observed in the Mojave Desert,” and they attributed this largely to continuous cover of taller than average red brome in the burn areas.

One consistent finding of recent California Desert fire studies is that fires are not evenly distributed by ecological zone or area, but that mid-elevation areas (the zone predominately occupied by Joshua trees) are particularly susceptible. Brooks et al. (2018) found, based upon fire data from 1972 to 2007, that “although fire occurrence across large parts of the warm deserts may be relatively low, they can be much higher and pose significant land management challenges in localized areas. The majority of fire area in the Mojave section of California occurred in the middle-elevation zone.” Brooks et al. (2018) also noted that in “the middle elevations of the Mojave Desert there was also evidence of a significant increase in annual fire area.”

Tagestad et al. (2016) similarly observed that between “1976 and 2010 there were 227 fires

in the Mojave Desert greater than 405 ha (1000 acres). These fires burned a total of 758,477 ha (1,874,230 acres) with most of the burned area occurring in the middle elevation zones receiving sufficient precipitation for growth of fuels.” Notably, blackbrush, a critical nurse plant for Joshua tree seedlings, experienced exceptional rates of burning, as “areas identified as historical blackbrush communities have experienced more multiple fires than all the other communities combined.”

Brooks et al. (2018) also found that fires in the California Desert “are clustered in regional hot spots where they are more frequent and burn more proportional area than desert-wide averages. These areas all occur in the Mojave ecological section, with one hot spot at the ecotone with the Colorado section in the vicinity of Joshua Tree National Park.” A recent mapping effort by Syphard et al. (2017) clearly shows that a disproportionate number of fires, including large fires, occur in the western Mojave range of *Y. brevifolia* (Figure 12).

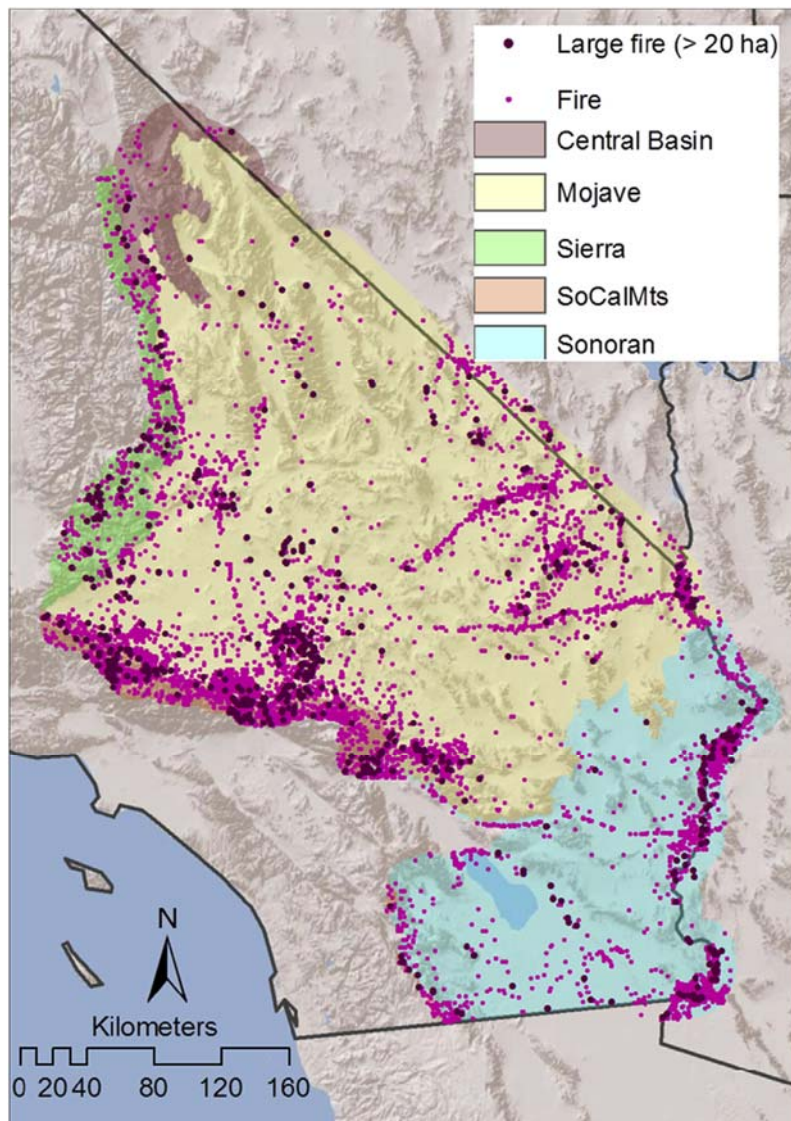


Figure 12. Fire occurrence between 1990-2010 in California Desert. Source: Syphard et al. (2019).

Fires in the Mojave are started by a mix of accidental and intentional human activities as well as lightning. Lightning frequency is higher in the desert than in any other California bioregion and is a significant source of fire (Brooks et al. 2018). Various studies have looked at the relationship of human caused versus lightning fires. One study found that the significant increase in fire frequency in the Mojave from 1980 to 1995 was associated with increased numbers of fires caused by humans, with the number of lightning-caused fires remaining constant. Although most human fires were small and started along roadsides, the less frequent large fires typically occurred in remote areas far from major roads and were started by lightning (Brooks et al. 2018). The influence of roads on fire ignitions is such that the outlines of Interstate Highways 5 and 40 can be discerned by the fire patterns reflected in the map in Figure 12.

Hopkins (2018), using data from Short (2017), tallied approximately 10,000 fires in the California desert from 1992 to 2015, and found that lightning accounted for only 10% of the fires, but 40% of the fires that burned more than 500 acres. Of the 90% that were human caused, equipment use was responsible for 22%, arson 8%, children 6%, smoking 5%, debris burning 5%, campfires 4%, and most of the remainder to unspecified miscellaneous causes.

A recent comprehensive analysis of fire records in the California Desert found that in “the Mojave, powerlines and other types of energy infrastructure (oil and gas wells, wind turbines, and power plants) were the most important anthropogenic land use contributors to large fires” (Syphard et al. 2017). The relationship between development and fire is also significant, with Syphard et al. (2019) warning that “[w]ith more fires occurring in close proximity to human infrastructure, there may also be devastating ecological impacts if development continues to grow farther into wildland vegetation.”

Fire fueled by invasive grasses is already significantly affecting Joshua tree woodlands. As Holmgren et al. (2010) summarized regarding conditions in Joshua Tree National Park (JTNP),

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 metres from the strike... [*B. 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. The increase in fire size and frequency could transform JTNP vegetation in a matter of decades.

The specific impacts of more frequent and intense fire on Joshua trees themselves are also significant. Esque et al. (2015) described these impacts:

Recent increases in fire frequency caused by invasive species throughout the range of *Y. brevifolia* have also affected all life stages of the species, and survival from intense fires is low even among large individuals. The impact of fire on seedling and juvenile survival is particularly exacerbated because fires tend to track the same

heavy precipitation years that are most suitable for *Y. brevifolia* seedling emergence (internal citations omitted).

Perhaps most importantly, areas identified as potential late-century climate refugia for *Y. brevifolia* are particularly vulnerable to fire, with over a third of the area identified as refugia by Barrows and Murphy-Mariscal (2012) burned between 1967 and 2012, and half the refugia identified under a moderate warming scenario by Sweet et al. (2019) burned as of 2018 (Figure 13).

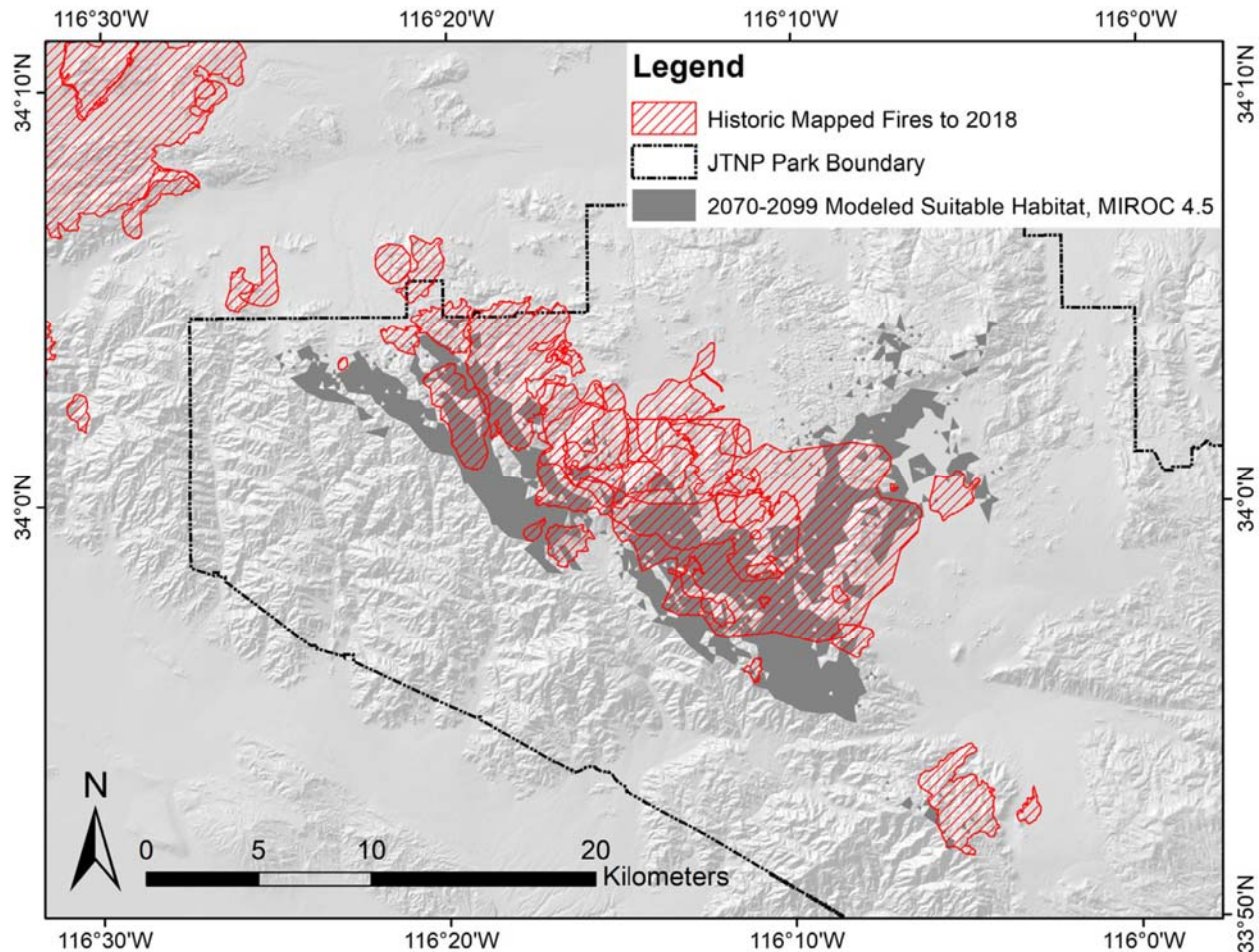


Figure 13. Historic fires in JTNP through 2018 in relation to modeled Joshua tree suitable habitat under a moderate warming scenario. Source: Sweet et al. (2019).

In sum, Joshua tree woodlands are generally not adapted to fire, and recover slowly, if at all (Abella et al. 2009; DeFalco et al. 2010; Vamstad and Rotenberry 2010; Brooks et al. 2018). Moreover, as noted by DeFalco et al. (2010), “the slower decline in survival for burned *Y. brevifolia* at the more mesic, high-elevation sites underscores the importance of postfire climate conditions on defining the demographic structure of recovering *Y. brevifolia* populations.” As discussed *infra*, a rapidly changing climate with greater heat stress and more intense droughts will make postfire recovery increasingly unlikely; and as fire increases in frequency and/or intensity, it will threaten the continued viability of ever-shrinking populations of *Y. brevifolia*.

5.4 Climate Change

Climate change represents the single greatest threat to the continued existence of *Yucca brevifolia*. Even under the most optimistic climate scenarios, western Joshua trees will be eliminated from significant portions of their range by the end of the century; under warming scenarios consistent with current domestic and global emissions trajectories, the species will likely be close to being functionally extinct in the wild in California by century's end (Dole et al. 2003; Cole et al. 2011; Sweet et al. 2019).

5.4.1 Current and projected climate change in the range of *Y. brevifolia*

A strong, international scientific consensus has established that human-caused climate change is causing widespread harms to human society and natural systems, and climate change threats are becoming increasingly dangerous. In a 2018 *Special Report on Global Warming of 1.5°C* from the Intergovernmental Panel on Climate Change (IPCC), the leading international scientific body for the assessment of climate change, describes the devastating harms that would occur at 2°C warming above pre-industrial levels, highlighting the necessity of limiting warming to 1.5°C to avoid catastrophic impacts to people and life on Earth (IPCC 2018). Average global temperature has already risen approximately 1°C (IPCC 2018).

In addition to warming, many other aspects of global climate are changing. Thousands of studies conducted by researchers around the world have documented changes in surface, atmospheric, and oceanic temperatures; melting glaciers; diminishing snow cover; shrinking sea ice; rising sea levels; ocean acidification; and increasing atmospheric water vapor (USGCRP 2017).

Climate change is increasing stress on species and ecosystems, causing changes in distribution, phenology, physiology, vital rates, genetics, ecosystem structure and processes, and increasing species extinction risk (Warren et al. 2011). A 2016 analysis found that climate-related local extinctions are already widespread and have occurred in hundreds of species, including almost half of the 976 species surveyed (Wiens 2016). A 2016 meta-analysis reported that climate change is already impacting 82% of key ecological processes that form the foundation of healthy ecosystems and on which humans depend for basic needs (Scheffers et al. 2016). The Mojave Desert in which the Joshua tree resides has already experienced many of these impacts, with, for example, bird occupancy and site-level species richness declining by about 50% over the past century (Iknayan and Beissinger 2018), and this decline linked to water stress related to increased cooling needs (Riddell et al. 2019).

Deserts have warmed and dried more rapidly over the last 50 years than other ecoregions, both globally and in the contiguous United States (USGCRP 2017). According to California's Fourth Climate Change Assessment: Inland Deserts Summary Report (Hopkins 2018), the California Desert has already experienced significant warming. Over the second half of the 20th century, daily maximum temperatures warmed by 0.4-0.7°F [0.22-0.39°C], comparing 1976-2005 with 1961-1990, and daily minimum temperatures warmed by 0.3-0.6 °F [0.17-0.33°C] over the same period.

Other studies have documented even greater warming in the range of the Joshua tree. The Washington Post, using NASA and NOAA county-level temperature datasets from 1895 to 2018, demonstrated that many areas of the United States have already had temperature increases well above the global average (Mufson et al. 2019).¹⁵ The four California counties in which *Y. brevifolia* occurs — San Bernardino, Los Angeles, Kern and Inyo — have already experienced average annual temperature increases of 1.9, 2.3, 1.7 and 2.3°C respectively.

Hopkins (2018) projects that daily maximum temperatures will increase by 5-6°F [2.8-3.3°C] for 2006-2039, by 6-10°F [3.3-5.6°C] for 2040-2069, and 8-14°F [4.4-7.8°C] for 2070-2100 on average for the region, with ranges depending on future greenhouse gas emissions (RCP 4.5 and RCP 8.5 scenarios). By the end of the century, the hottest day of the year is projected to rise by at least 6°F [3.3°C], and up to 9°F [5°C] on average. Extremely hot days, defined as temperatures >95°F [35°C], averaged 90 per year in the Mojave during the 1981-2000 period, and will increase to up to 141 days by the end of the century under RCP 8.5.

While temperature projections for the Mojave are unidirectional (it will be a lot hotter), precipitation projections are more complicated and divergent. For the suite of downscaled climate models used by Hopkins (2018), there is little projected change in average rainfall each year to the end of the century (<10%), even under different emissions scenarios. However, these projections show an increase in interannual variability, with reductions in minimum annual precipitation of up to 50% and increases in maximum annual precipitation of 40-65% by the end of the century, as well as an increase of winter precipitation (falling mainly in December, January, and February).

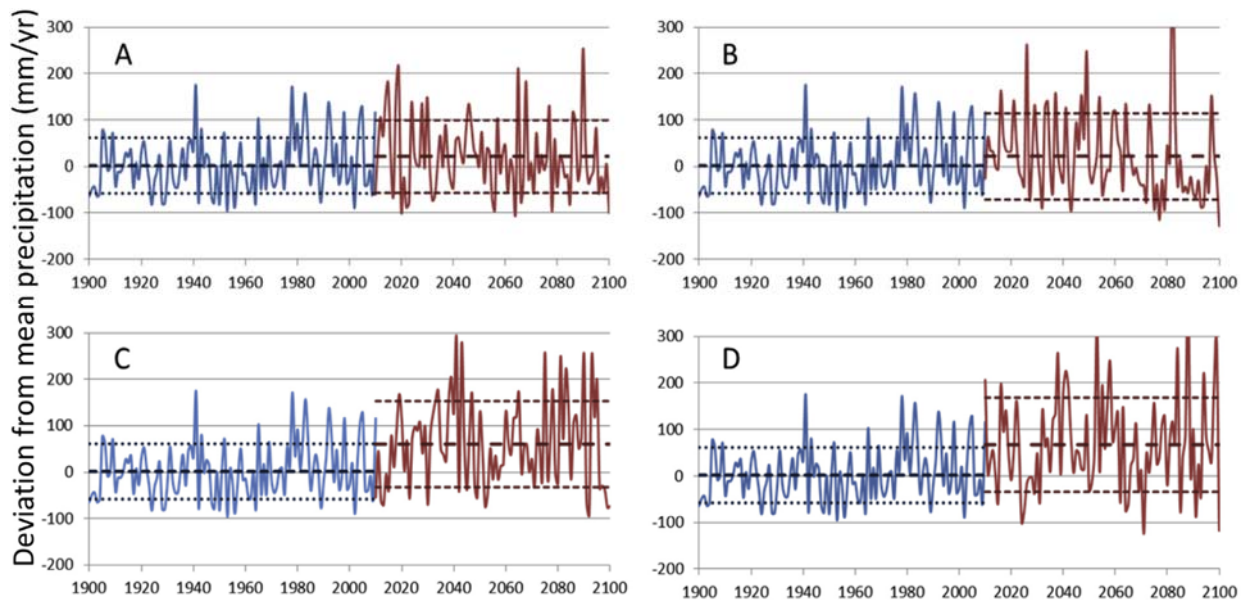


Figure 14: Plot of future modeled and historic precipitation in the Mojave Desert from global climate model/scenarios: A) GFDL/B1, B) GFDL/A2, C) IPSL/B1 and D) IPSL/A2. Source: Tagestad et al. (2016).

¹⁵ Available at <https://www.washingtonpost.com/graphics/2019/national/climate-environment/climate-change-america/>

Tagestad et al. (2016) came to similar conclusions, noting that “recent analysis of regional climate models over southwest North America indicate increased winter precipitation in the future within the Mojave ecoregion.” Tagestad et al. (2016), using climate models that best matched historic annual and seasonal precipitation records in the Mojave (GFDL_CM2.1 and IPSL_CM4), found that average annual precipitation is predicted to be higher than the historical average, although with greater annual and decadal variation, that there would be numerous, extended periods of high precipitation (Figure 14), and due to the invasive grass fueled link between winter precipitation and fire, concluded that “fire will be more prevalent in the Mojave Desert for many periods during the next century.”

In sum, average annual temperatures in the range of *Y. brevifolia* have already increased well over 1.5°C (Mufson et al. 2019), and daily maximum temperatures over the remainder of the 21st century under current emissions trajectories will increase by over 7°C (Hopkins 2018). Precipitation will increase in variability, with more extreme and prolonged droughts, while an overall increase in winter precipitation will foster more growth of invasive grasses, leading to more frequent and more intense fire (Hopkins 2018; Tagestad et al. 2016). Given Joshua trees are already suffering from the warming that has occurred to date, these additional changes pose a significant threat to the persistence of *Y. brevifolia* in California.

5.4.2 Climate change impacts on Joshua trees

Researchers have been raising the alarm about threats to the Joshua trees for decades. More than half a century ago, Webber (1953) stated of the species that “[r]egardless of the present wide distribution and large concentration of yuccas, its future appears very dim. This gloomy outlook is mainly due to the plant’s failure to reproduce and its destruction by man.” In 2000, Loik et al. (2000a) raised the specter of climate change, predicting that “[c]hanges in the local climate due to anthropogenic greenhouse gases may cause warming of the microclimate near the soil surface thereby precluding the future establishment of *Yucca brevifolia*.” A year later, Lenz (2001) noted that “Joshua trees in many areas appear physically stressed in all probability due to less than optimum growing conditions,” and speculated that “depending upon the intensity and duration of global warming its long-range survival may depend upon the availability of a refugium.”

Over the past 20 years, modeling of Joshua tree future distribution in a warming climate has become more sophisticated, has used more accurate and comprehensive distribution data, has produced projections at ever-finer spatial scales and has increasingly used field data to validate model performance. And while model projections of potential range expansion have varied greatly and have not distinguished between *Y. brevifolia* and *Y. jaegeriana*, every published modeling effort has predicted range contractions along the western edge of the Joshua tree’s range in California, which largely corresponds to the range of *Y. brevifolia* in the state. A review of these studies demonstrates that *Y. brevifolia* will face massive range contractions within the foreseeable future that threaten the continued viability of the species.

Thompson et al. (1998) published the first modeled projection of the future range of Joshua trees under changing climate conditions. Using data on temperatures and precipitation levels where the species is currently found, Thompson et al. (1998) calculated that Joshua tree potential

future habitat under doubled CO₂ conditions was almost 8-fold greater than present habitat, extending as far north as Washington state, south into Mexico and east into Texas. The modeling effort predicted retraction of range along its western edge in California. This study, which dealt with 16 different tree species, did not analyze other habitat variables or dispersal ability and used a model that poorly matched the current distribution of the species (e.g. the model predicted presence in the Coast Ranges under then current climate conditions).

Shafer et al. (2001) carried out a similar modeling effort looking at the future range of Joshua trees, finding that “[u]nder each of the future climate scenarios, its simulated potential range is fragmented and displaced northward and eastward.” The Shafer et al. (2001) study addressed 15 different species of trees, used three climate variables (mean temperature of the coldest month, growing degree days, and a moisture index) and a 25-km grid scale.¹⁶ Consequently, the results are coarse, but still roughly consistent with later modeling efforts (e.g. Cole et al. 2011), and most notably show almost complete extirpation of the species from California (Figure 15). The projected potential expanded range extending into northern Nevada and Utah as well as Washington state does not account for how the species might disperse into these new areas of potential habitat.

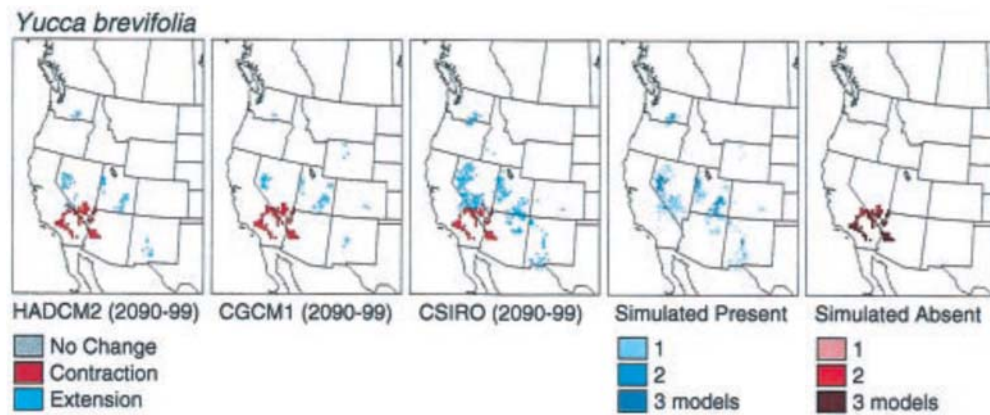


Figure 15: Modeled future range of Joshua Trees. Source: Shafer et al. (2001).

Dole et al. (2003) subsequently modeled future range for Joshua trees in a doubled CO₂ world, finding that “a considerable portion of the current range of *Y. brevifolia* will become climatically unfavorable for this species, but that significant amounts of new habitat may become available.” While Dole et al. (2003) did not take dispersal into account in the modeling, they noted that it would be a factor in real-world application, and 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) also noted a further potential limitation in the model which assumed “the distribution of *Y. brevifolia* is in equilibrium with current climate.” Significant subsequent research (e.g. Barrows and Murphy-Mariscal 2012; Harrower and Gilbert 2018; Sweet et al.

¹⁶ The current distribution data used to develop the model in Shafer et al. (2001) is also questionable as the paper states “*Yucca brevifolia* (Joshua tree) is found in the deserts of the southwest US and northwest Mexico.” The species has likely been absent from Mexico for thousands of years (Cole et al. 2011).

2019) has confirmed that at least in the southern part of its range, current climate conditions are already deleterious to Joshua tree survival and/or reproduction. Notwithstanding these model limitations, which almost certainly overestimate projected future habitat, modeled habitat loss is roughly congruent with the key results of Shafer et al. (2001) and Cole et al. (2011), with the species disappearing from 76% of its current range. Notably, much of the new area deemed climatically suitable for *Y. brevifolia* in California is developed agricultural land in the San Joaquin Valley and therefore highly unlikely to ever actually be occupied by the species.¹⁷

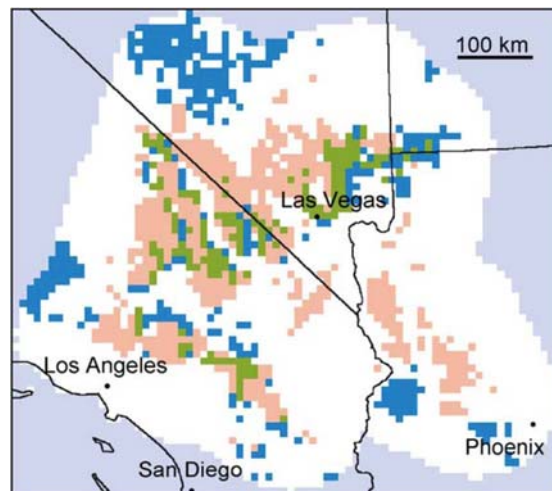


Figure 16: Modeled future range of Joshua Trees. Pink is lost range, green is maintained range and blue is expanded range. Source: Dole et al. (2003).

Cole et al. (2011) built a sophisticated species distribution model with climate and habitat variables derived from a comprehensive dataset of presence/absence data throughout the current range of the Joshua tree. Late Pleistocene and Holocene records were also compiled to generate a map of past distribution of the species. The study differed from previous models in its use of actual specific data points for presence and habitat variables for the species and the testing of the models to simulate the current range of the species.

Construction of an independent test data set of Joshua tree current presence and absence allowed the evaluation of multiple suitable climate models for Joshua tree. Model concordance was found to increase with the inclusion of measures of monthly temperature variability (maximum and minimum rather than just mean), finer spatial scale (~1 km rather than ~4 km), and applying a 40-year mid-20th-century baseline (1930–1969) climate rather than a 30-year late-20th century baseline (1970–1999).¹⁸

¹⁷ Dole et al. (2003) also modeled the impact of doubled CO₂ concentrations on the physiology of Joshua trees given there is some evidence that certain plant species are more resistant to freezing in high CO₂ conditions. Such modeling showed a 14% increase in projected new habitat and a slight increase (from 24% to 29%) of current habitat areas that would remain suitable. However, the authors recognized that the impacts of CO₂ induced warming were more significant than the physiological effects of CO₂ itself.

¹⁸ Cole et al. (2011) selected 1930 to 1969 as their climatic baseline period “because evidence suggests that Joshua tree recruitment was greater during this interval than during the latter part of the 20th century. For instance, survey results show minimal to no recent Joshua tree recruitment within the southern Mojave Desert in recent years, and

The methodology of Cole et al. (2011) consequently address many of the shortcomings of climate niche models that have been raised by some (Pearson and Dawson 2003; Fitzpatrick and Hargrove 2009).

All of the individual climate models, as well as an ensemble of 22 global circulation models (GCMs) utilized by Cole et al. (2011), project a severe (~90%) decline in the area of suitable climates for Joshua trees by 2070 to 2099, as the southern parts of its range becomes climatically unsuitable.

Cole et al. (2011) also modeled areas where the species could potentially naturally expand its range in the future, as well as areas that might be suitable for relocation or assisted migration (Figure 17).

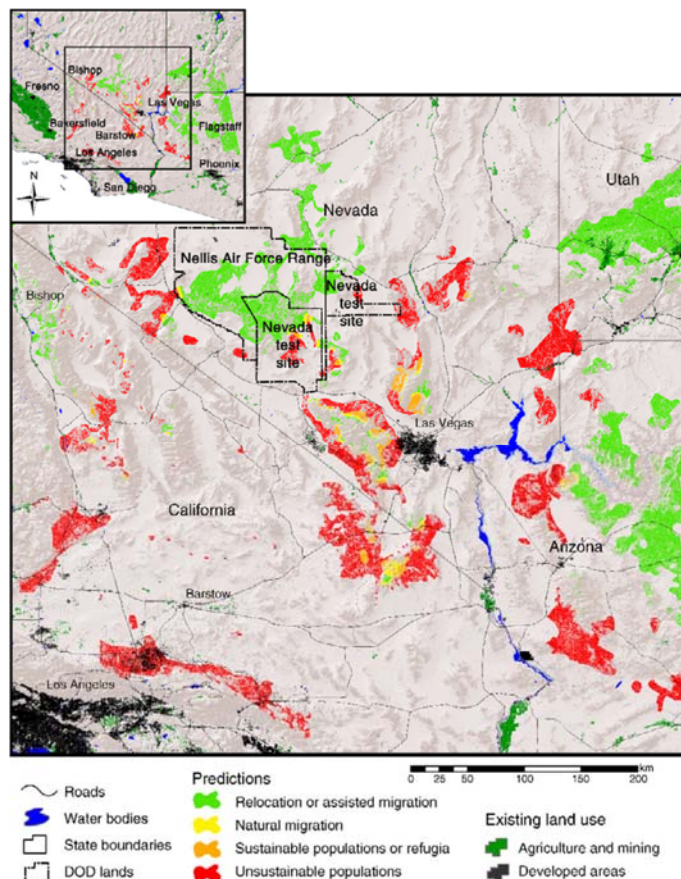


Figure 17. Areas with existing Joshua tree populations where a majority of the models used by Cole et al. (2011) predict future climates unsuitable for survival (red); current populations with future climates favorable for Joshua tree persistence (orange); areas within 2 km of current populations with 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). Source: Cole et al. (2011)

Joshua trees tall enough to be tallied in recent vegetation plots likely became established during this 1930–1969 interval or before.”

In determining potential natural expansion areas, Cole et al. (2011) looked at rates of migration discernable from paleontological data as well as from modern studies of seed dispersal by rodents. Such data reveals minimal actual northward range shift over the Holocene, corresponding to a migration rate of 2 meters a year. Similar migration rates could be calculated based on studies of rodent seed caching activity and Joshua tree generation time. Cole et al. (2011) postulated that their results “suggest that the species migrational capacities have been ineffective following the extinction of Pleistocene megaherbivores that may have acted as seed vectors, especially the Shasta ground sloth.” Given a 2-meters a year range expansion would total less than 200 meters by century’s end and would be largely invisible in any mapping effort, Cole et al. (2011) used “a generous estimate of potential natural migration of 2 km over the next 60 to 90 years” to designate areas of potential natural migration. This suggests that the colonization of mapped areas of natural migration might in fact also require assisted migration to occur in a meaningful timeframe.

Cole et al. (2011) summed up the relationship between the Joshua tree’s past, its present limited present dispersal abilities, and future projections to highlight the severe range contraction it will undergo in the coming decades.

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

Cole et al. (2011) do not predict the complete extirpation of Joshua trees from their current range, noting that the “results predict the survival of some natural Joshua tree populations throughout the next century, but most will be greatly reduced in area.” Importantly, because the authors modeled the Joshua tree present and future distribution as a single species, they did not distinguish between *Y. brevifolia* and *Y. jaegeriana*. From their mapping however, it appears that the majority of the areas for which Joshua trees are projected to persist are in the range of *Y. jaegeriana*. *Y. brevifolia* disappears almost entirely from its current range in California (Figure 17).¹⁹

¹⁹ A subsequent study by Notaro et al. (2012) included Joshua trees among 170 tree and shrub species for which they modeled projected range shifts by the end of the century. They noted that the projected northward shift of the species and decline in its southern range in response to warming was consistent with that described by Cole et al. (2011). However, unlike Cole et al. (2011), they did not consider dispersal ability in projecting range expansion and consequently concluded that the species would experience a “robust range expansion” of 143%. Importantly, their analysis was limited to the “Southwest United States” which did not include California. Consequently, regardless of other limitations of their analysis that may render the results suspect, the results shed no light on the future status of *Y. brevifolia* in California.

While the Cole et al. (2011) study looked at the future of Joshua trees throughout their range, Barrows and Murphy-Mariscal (2012) examined the status and fate of *Y. brevifolia* in Joshua Tree National Park (JTNP). The approach Barrows and Murphy-Mariscal (2012) took was one of niche modeling:

In lieu of local-scale predictions of how precipitation or temperature will shift, modeling the sensitivity of species to a gradient of climate change scenarios can provide insights as to potential effects of local-scale changes in temperature and precipitation. A useful tool in assessing species sensitivity to changing conditions is niche modeling which includes habitat variables, such as climate and terrain, in an attempt to assess the complex interaction of factors that constrain a species' distribution (internal citations omitted).

To assess the validity of the niche models, Barrows and Murphy-Mariscal (2012) used "citizen scientist" volunteers to collect Joshua tree recruitment data throughout their range in the park to determine whether modeled shifts in suitable habitat coupled with recent temperature increases approximate current demographic response patterns, specifically successful seedling recruitment. The key climate variable used was summer maximum temperature, which was changed incrementally by increasing mean maximum July temperature by 1°C, 2°C, and then 3°C.

Since the niche models were developed based on data of existing adult Joshua trees, the model projects the distribution of suitable habitat for the species when those individuals were recruited into the population, conditions when summer temperatures may have been up to 1°C cooler than current conditions. Shifting mean maximum summer temperatures upwards by 1°C, 2°C, and then 3°C resulted in modeled reductions in the extent of suitable habitat for Joshua trees of 30-35%, 66-78% and 90-98% respectively, depending upon the precipitation variables used.

The niche model Barrows and Murphy-Mariscal (2012) developed for juvenile Joshua trees (individuals 30 cm or less in height) based on their current distribution, resulted in a total suitable habitat area about half of that for adult trees. The juvenile model was a near match for the boundaries of the +1°C adult model. The match between the current juvenile model and the +1°C adult model provides some level of model validation consistent with the hypothesis that early levels of climate change may have already had an impact on Joshua tree recruitment. Put another way, adult Joshua trees in JTNP were recruited into the population under climate conditions where summer maximum temperature was approximately 1°C cooler than present; warming to date may not be fatal to established adult Joshua trees, but it has apparently already shrunk the area of suitable habitat for recruitment by half.²⁰

Barrows and Murphy-Mariscal (2012) contrasted their results to those of Dole et al. (2003)

²⁰ Barrows and Murphy-Mariscal (2012) noted that "we searched for but did not find any areas of non-fire related mortality of Joshua trees within JTNP." This seems at odds with DeFalco et al. (2010) who reported 26% mortality of unburned Joshua trees following drought in their study area in JTNP. A subsequent study by Harrower and Gilbert (2018) also documented significant non-fire mortality in the park, indicating that the current climate, at least at lower elevations, is already deleterious to adult Joshua trees.

and Cole et al. (2011), both of which indicated that similar expected levels of climate change would result in no suitable habitat for Joshua trees within the central or southern portions of their current distribution. Barrows and Murphy-Mariscal (2012) ascribed the differences as being due to the scales of analyses rather than differences in models or model assumptions, since finer-scale analysis can incorporate local adaptations as well as topographic-climate complexities that may provide refugia.

Barrows and Murphy-Mariscal (2012) declared their analysis “represents a more optimistic scenario than previously published models of climate change impacts on Joshua trees.” However, given their +3°C model found that Joshua tree range in the park could be curtailed by 90 to 98% and noted that red brome fueled wildfires could burn any remaining refugia, it is somewhat difficult to share their optimism. Moreover, Barrows and Murphy-Mariscal (2012) used a +3°C increase in summer maximum temperature as their “extreme” scenario, while Hopkins (2018) projects that summer maximum temperatures may hit that level before mid-century and may exceed +7°C by century’s end.

The most recent species distribution modeling effort for Joshua trees paints an even more concerning portrait of the species’ future. Sweet et al. (2019) sought to identify the existence and extent of potential climate refugia for *Yucca brevifolia* within JTNP. Similar to Barrows and Murphy-Mariscal (2012), this study developed species distribution models (SDMs) validated with field data:

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

Sweet et al. (2019) used the species distribution modeling platform Maxent to develop relationships between Joshua tree presence points and a database of nine environmental variables including minimum and maximum temperature, precipitation, climatic water deficit (CWD), topography, and soil characteristics. They used the end-of-century (2070–2099) CMIP5 MIROC RCP 4.5, 6.0, and 8.5 emissions scenarios, representing CO₂ emissions under highly mitigated, moderately mitigated, and unmitigated scenarios, respectively. The results showed loss of the vast majority of *Y. brevifolia* suitable habitat under all scenarios. Under the RCP 4.5 and 6.0 scenarios, 18.6% and 13.9% of current occupied areas remained as refugia. However, under the RCP 8.5 scenario, which is closest to current emissions trajectories, suitable habitat was almost completely eliminated, with only 15 ha, or 0.02% remaining as refugia (Figure 18).

As with those identified by Barrows and Murphy-Mariscal (2012), the refugia identified by Sweet et al. (2019) are in areas of high fire risk, with the authors noting that the “areas mapped as Joshua tree refugia, which are found at higher elevation wetter areas, also tend to have the highest covers of invasive annual grasses.” Approximately half of the refugia mapped under the

RCP 4.5 scenario have already experienced fire in recent decades. As discussed *supra*, fire fueled by invasive grasses is a significant source of Joshua tree mortality and creates conditions that delay or preclude recruitment, and therefore has the potential to diminish the effectiveness of any climate refugia for the species.

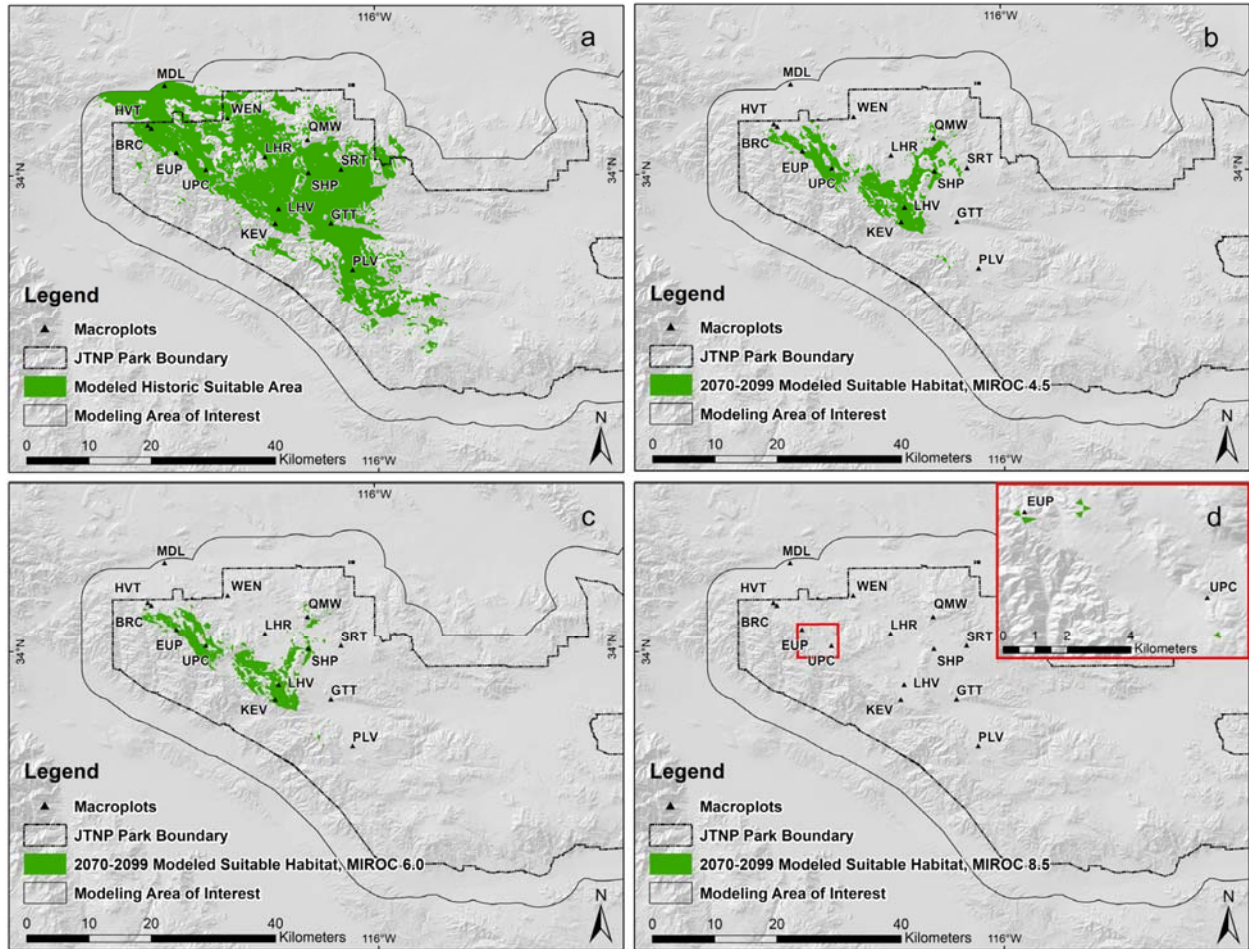


Figure 18: Map of historically suitable habitat (a) and end-of-century refugia for Joshua trees at JTNP. Modeled refugia are the area of overlap between current and future suitable habitat under 3 emission scenarios: RCP 4.5 (b), 6.0 (c), and 8.5 (d, with inset to display the modeled area). Source: Sweet et al. (2019).

The modeling results of Sweet et al. (2019) are similar to those of Barrows and Murphy-Mariscal (2012) in terms of overall trajectory and location of habitat loss in JTNP, but diverge in terms of how much area remains as refugia under their highest-warming scenarios. Barrows and Murphy-Mariscal (2012) projected between 2 and 10% of existing habitat would remain suitable in the park (916 to 4640 ha), while Sweet et al. (2019) projected only 0.02% would remain (15 ha). Sweet et al. (2019) ascribed the difference to finer scale habitat data, difference in climate scenarios used, and better and more dense information on Joshua tree presence. Put another way, the more detail we learn about the current status of Joshua trees, the bleaker their future appears.

Sweet et al. (2019) also used field data on distribution of juvenile trees (defined as smaller

than 60 cm) to validate their modeling results.²¹ They explained their rationale as follows:

Large, long-lived species, such as Joshua trees, have an advantage over short-lived species, as they can weather year-to-year variation and short-term droughts. Still, long-term persistence, especially over the time reflected in climate change estimates, depends on where and when species reproduce, recruit, and establish on a landscape. Other studies have found differences between the adult distribution and the distribution of juveniles or seedlings on the landscape. Since the establishment stage of trees and other perennial species is a vulnerable and important stage, the density of seedlings in a given area can provide early indications of future distribution shifts.

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

Sweet et al. (2019) categorized 14 nine-hectare macroplots throughout the park that contained Joshua trees as high or low-recruiting depending on whether the density of documented juveniles was above or below the mean. They found that high-recruiting macroplots had significantly higher annual precipitation, and marginally significantly lower climatic water deficit and maximum summer temperature. Importantly, high-recruiting macroplots were geographically differentiated from low-recruiting macroplots in that they were located either within or significantly closer to predicted future refugia than low-recruiting macroplots. Moreover, when temperature and precipitation for refugia areas were plotted together with macroplots, there was considerable correspondence between the high-recruiting macroplots and the refugia. This result, which validated modeled predictions, was “not surprising—the factors that allow for recruitment (lower CWD, higher precipitation), especially in a desert environment, also differentiated, on a landscape scale, the areas supporting Joshua trees within the park.”

Studying the density of tree recruitment, Sweet et al. (2019) found early indications of a shift in Joshua tree recruitment and noted that “[i]f recruitment patterns portend the future distribution of adults on the landscape, this type of analysis allows a glimpse into changes that may occur even before those outlined in the modeled future scenarios.”

The Sweet et al. (2019) analysis was designed “to inform management with the most robust available predictions, focusing on areas where the species occurs already.” These “occupied climate refugia are most relevant to the conservation of the species for the next 50 yr, and perhaps longer.” Proper management and protection of these areas is critical the persistence

²¹ Barrows and Murphy-Mariscal (2012) also used juvenile distribution to validate their models but used a 30 cm rather than 60 cm cutoff to define “juveniles”.

of *Y. brevifolia*: “Since these refugia are also subject to threats such as fire and invasive species, management efforts aimed at reducing these threats provide on-the-ground actions that increase the likelihood that these areas will sustain this iconic species.” Management and recovery actions are further discussed *infra*.

The species distribution modeling studies discussed above individually and collectively lay out a compelling warning about the difficult future facing *Y. brevifolia* in California. Two of those studies also looked at field data and concluded that recruitment of Joshua trees was *already* being hampered by warming (Barrows and Murphy-Mariscal 2012; Sweet et al. 2019).

Additionally, multiple other field studies documenting the *current* impacts of warming, drought, invasive species, fire and other impacts on Joshua tree survival and recruitment reinforce the findings of these modeling efforts. The more recent of these studies have specifically looked at such impacts in the context of climate change (*e.g.* DeFalco et al. 2010 [fire, drought and herbivory]; Reynolds et al. 2012 [seed germination and recruitment]; Esque et al. 2015 [recruitment and juvenile growth]; Borchert and DeFalco 2016 [reproduction, seed predation and dispersal]; Harrower and Gilbert 2018 [pollination]; St. Clair and Hoines 2018 [reproduction]). These studies and the documented impacts on *Y. brevifolia* are described in the sections on Reproduction, Abundance and Population Trends, and Factors Affecting Ability to Survive and Reproduce, *supra*.

Joshua tree persistence on the landscape is dependent not just on survival of Joshua trees themselves, but on successful recruitment, which is dependent upon their obligate pollinating moths, seed dispersing rodents and the presence of nurse plants. As summarized by Sweet et al. (2019), “[r]ecruitment, survival of populations, and certainly migration of the species will be affected by factors such as the availability of pollinators, dispersers, seed and seedling predators and other mutualisms on the landscape.” Climate change threatens to disrupt these essential relationships.

While multiple species can serve as its nurse plants, and a variety of rodents can act as seed dispersers, only a single species, *Tegeticula synthetica*, pollinates *Yucca brevifolia* in its California range (Pellmyr and Segraves 2003; Godsoe et al. 2008). And while clonal reproduction can prolong survival in certain locations and circumstances (DeFalco et al. 2010), ultimately long-term survival as a species likely requires the genetic diversity that sexual reproduction fosters (Harrower and Gilbert 2018). Consequently, the long-term viability of *Y. brevifolia* depends on maintaining its obligate mutualism relationship with *T. synthetica*.

A recent study by Harrower and Gilbert (2018) in JTNP sheds significant insight into the apparent fragility of the relationship between *Y. brevifolia* and *T. synthetica*. The authors succinctly lay out the problem:

Obligate mutualisms like the Joshua tree–yucca moth interaction are acutely sensitive to changes in climate. The interacting partners may respond differently, creating an asynchrony in species phenology that can lead to population decline and local extinction. Environmental changes that shift the outcome to fewer viable seeds or greater seed predation could be detrimental to both species. However, the climate

envelope within which this mutualism currently exists is narrow, and climate change effects in the Mojave Desert are expected to limit this envelope to only the highest elevations in Joshua Tree National Park (JTNP) within 90 yr, greatly reducing habitat with suitable climate and potentially extirpating the species from its namesake park (internal citations omitted).

Joshua trees are distributed across a 1200-m elevational range in JTNP from approximately 1000 m to 2200 m. Elevation gradients can serve as “natural experimental systems through systematic variation in abiotic and biotic factors,” and average daily summer temperature per site in the Harrower and Gilbert (2018) study declined steadily along the elevation gradient with the warmest site at 30.2°C and the coolest at 19.9°C. Harrower and Gilbert (2018) examined how the abundance of *Y. brevifolia* and *T. synthetica* varies by elevation and quantified how the outcome of the Joshua tree–yucca moth interaction shifts depending on the context of where it occurs and the impacts that may have on Joshua tree fitness.

The authors found a sharp dichotomy between intermediate elevation sites versus the highest and lowest sites. Tree abundance was highest at intermediate elevations, with a “marked peak at around 1250 m where the trees were numerous and large and produced many flowers; this peak coincided with a high abundance of moths, as well as high production of pods, seeds, fertile seeds, and seedlings that grew from seeds.” A positive relationship between moth abundance and successful sexual reproduction was found, with number of seedpods and fertile seeds per pod increasing with moth abundance. Moth abundance was significantly correlated with tree size, tree abundance, and number of flower panicles per tree, with larger trees having more panicles. These associations collectively indicate that reproductive success of both Joshua trees and yucca moths are greatest where the Joshua trees are abundant and vigorous, which currently is at intermediate elevations.

In stark contrast to intermediate elevation results, at the lowest and highest sites the number of dead Joshua trees peaked, while live trees were small and few and had few flowers, and no moths, seedpods, or seedlings were encountered. Reproduction was limited to clonal spread. Soil moisture was very low at the lower, warmer elevations and may have contributed to Joshua tree death. The authors noted that their observations were consistent with expectations from the models of Cole et al. (2011) and Barrows and Murphy-Mariscal (2012) and suggest that the range of Joshua trees is contracting at the lower elevations where there was no seedling recruitment and high tree mortality.

Harrower and Gilbert’s (2018) finding that at elevation extremes Joshua tree reproduction is almost exclusively clonal is consistent with previous accounts finding that Joshua tree clonality increases with elevation, but the lack of seedling recruitment and enhanced clonality at low elevations had not been previously reported. Trees produced flowers at both of the extremes, but no moths, fruit development, or seed set were observed in these areas. Consequently, the lack of seedlings could be explained by the lack of pollinators.

The presence of only clonal populations at the low and high ends of *Y. brevifolia* distribution has several very significant potential repercussions:

If trailing edge populations of (mostly clonal) Joshua trees are also those in the population that are best adapted to deal with the highest local temperatures, a lack of sexual outcrossing with populations at higher elevations could threaten overall species persistence due to reduced fitness of seedlings as the climate warms. Clones have reduced reproductive fitness, which could increase susceptibility to local extinction of the trees. The lack of pollinators, seed set, and seedlings at higher elevations suggests that Joshua trees are not currently expanding their range upslope (Harrower and Gilbert 2018) (internal citations omitted).

Harrower and Gilbert (2018) summarized the dilemma facing the *Y. brevifolia* and *T. synthetica* mutualism: “Joshua trees seem to be dying back at low elevations as predicted, but they do not seem to be moving successfully into higher elevations, where the mutualism is not successful.” Moths are absent at these higher elevations and it “remains to be seen if Joshua tree performance can improve at higher elevations and if it will be able to attract enough moths to successfully reproduce, or if moths can migrate to and survive at those locations.” Given “the survival of the species requires colonization of new habitats,” the current lack of a functioning pollination mutualism at the high elevation margins of the Joshua tree’s range raises serious doubts about the ability of the species to colonize new habitats, and ultimately to survive.²²

In sum, climate change represents an existential threat to *Y. brevifolia* in its California range. Even in the absence of climate change, the convergence of biotic and abiotic factors necessary for recruitment “results in successful establishment of new seedlings only a few times in a century” (Esque et al. 2015). Such recruitment has already largely stopped at the drier, lower limits of the species’ range (Barrows and Murphy-Mariscal 2012; Sweet et al. 2019). Prolonged droughts, which are projected to occur with greater frequency and intensity over the coming decades (Hopkins 2018), will not only preclude recruitment across ever-greater areas of the species’ range, but will lead to higher adult mortality, either directly due to temperature and moisture stress or indirectly due to increased herbivory from hungry rodents lacking alternative forage (DeFalco et al. 2010; Harrower and Gilbert 2018). Whether or not the species’ pollinating moth will be able to keep pace with a changing climate is highly-questionable (Harrower and Gilbert 2018). The Joshua tree’s ability to colonize new habitat at higher elevations or latitudes is extremely limited and no such range expansion is yet occurring, even as the lower elevation and southern edge of its range is already contracting (Cole et al. 2011; Harrower and Gilbert 2018). And there is no safe refuge, as the higher elevation areas in which Joshua trees are projected to best be able to survive increasing temperatures and drying conditions are at great risk of fire due to the prevalence of invasive grasses (Barrows and Murphy-Mariscal 2012; Sweet et al. 2019). Absent rapid and substantial reductions in GHG emissions *and* protection of habitat, the species will likely be extirpated from all or most of California by the end of the century.

²² Interestingly, certain higher elevation areas (but not the highest elevations) had the highest density of trees in the study, but very low moth abundance. These higher elevation sites were dominated by trees reproducing asexually. It is not clear whether moths are unable to thrive at these higher elevations or if the low numbers of flowers meant that location was unable to attract or support the moths. Harrower and Gilbert (2018) postulated that this elevation range, from 1500 to 1600 m, “where trees thrive but moths do not, may be an important transition zone for future work on the details of the Joshua tree–yucca moth climate mismatch.”

5.5 *Habitat Loss to Development*

While the overall outlook for *Y. brevifolia* is grim, the species has an advantage over many other climate-threatened species in that much of its habitat is at least nominally protected from other impacts. Its southernmost population is within the national park that bears its name, while some of its northernmost populations are in Death Valley National Park. As described in the Distribution section *supra*, YUBR North is 96% federal land, while, YUBR South is 48% federal land. Nevertheless, development presents a substantial threat to the species in a significant portion of its range.

Of the two *Y. brevifolia* populations, YUBR South has been the most impacted by human development and faces the greatest threats in its future. Over 50% of the land area comprising the habitat for this population is privately owned (USFWS 2018). The cities and towns of Apple Valley, Hesperia, Lancaster, Palmdale, Ridgecrest, Victorville, and Yucca Valley, along with many other smaller communities have been built in Joshua tree habitat in the YUBR South area. In recent decades these areas have grown rapidly, with the populations of Lancaster, Palmdale and Apple Valley all growing by approximately 36% between 2000 and 2018, Yucca Valley growing by 29.5% and Victorville by a staggering 93% during that same time period (SCAG 2019).

Human population growth in these areas and consequent loss of Joshua tree woodlands is expected to continue in the coming decades. The USFWS (2018), using the EPA's Integrated Climate and Land-Use Scenarios (ICLUS) modeling tool to predict future housing density growth in the range of the Joshua Tree, estimated that 41.6% of suitable habitat for *Y. brevifolia* in the YUBR South area would be lost to housing development by 2095 (Figure 19).²³ When combined with YUBR North, about a third of Joshua tree habitat would be lost for the species in California. Importantly, the ICLUS modeling done by USFWS only looks at housing density, not industrial, military or other development so likely represents an underestimate of development impacts.

In addition to urban growth, various other forms of development threaten Joshua tree habitat in California, including roads, highways, transmission lines, industrial facilities and large and small-scale renewable energy projects. While many of these impacts have been poorly quantified to date, according to USFWS (2018), renewable energy development has already resulted in the loss of 1.2% of mapped *Y. brevifolia* habitat, equating to about 68,000 acres. However, given USFWS included Nevada habitat in this calculation, while virtually all of the large-scale renewable energy development in the range of the species is in the YUBR South area, the actual total in California is likely closer to 2% of habitat lost to date. Under the Desert Renewable Energy Conservation Plan (DRECP) amendments to the California Desert Conservation Area (CDCA) Plan, of the 388,000 acres of development focus areas on BLM land subject to a streamlined review process to facilitate renewable energy development, approximately 50,000 acres fall within the mapped distribution for *Y. brevifolia* (USFWS 2018),

²³ In using the ICLUS model, USFWS (2018) ran development scenarios consistent with IPCC B1 and A2 climate scenarios. The 41.6% projection is from the A2 scenario which most closely matches current emissions trajectories. Under the lower-growth B1 scenario, 21.7% of YUBR South suitable habitat would be lost to housing development.

equating to more than 1% of additional habitat at risk from this type of development on federal lands and an unknown but potentially larger amount on private lands (Figure 19).²⁴

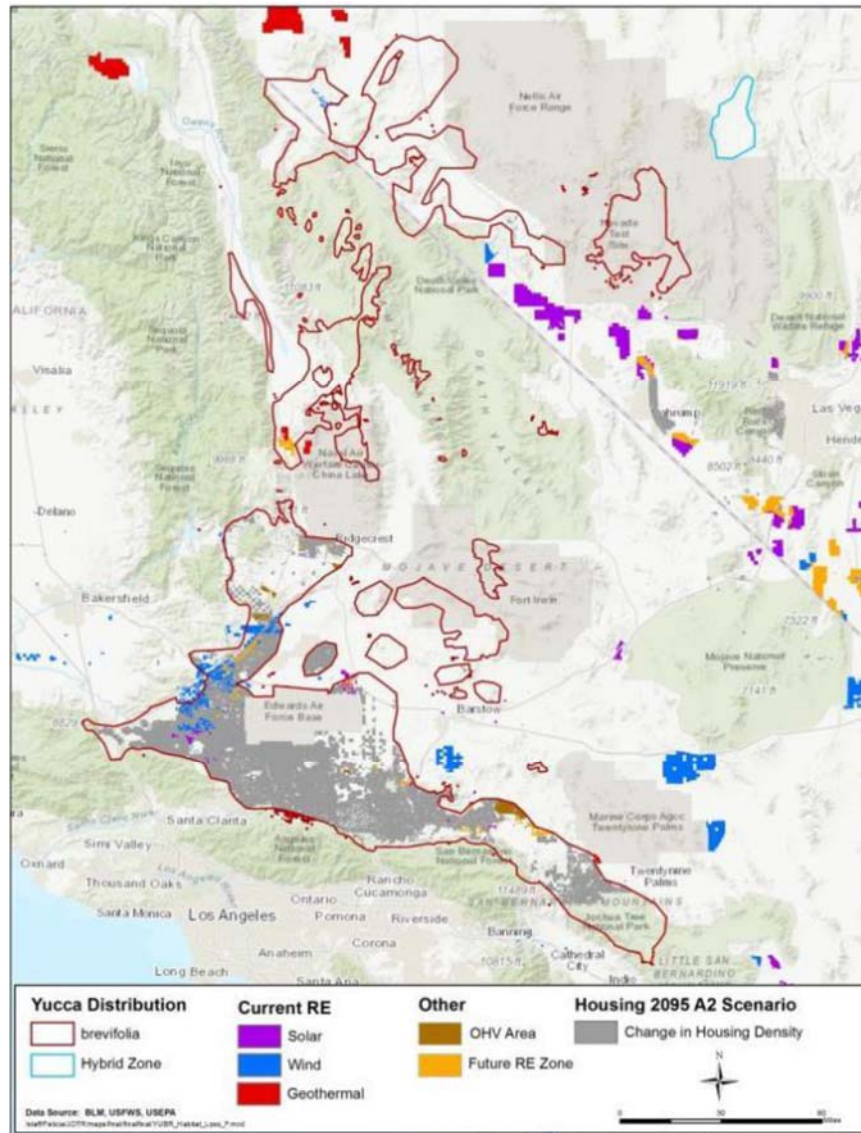


Figure 19: Map showing Joshua tree projected habitat loss due to urban growth, as well as current and projected habitat loss due to large-scale renewable energy projects. Source: USFWS (2018).

In sum, human development has already consumed hundreds of thousands of acres of habitat in the range of *Y. brevifolia*. Over the coming decades, over a million additional acres will be destroyed or degraded for housing, roads, energy projects and assorted other development (USFWS 2018). This large-scale loss or severe degradation of habitat is of conservation concern

²⁴ Notably, the Trump administration has initiated plans to roll back protections contained in the DRECP, which would likely subject additional areas of Joshua tree habitat to either renewable energy development or other forms of habitat degradation or destruction. <https://www.blm.gov/california/BLM-to-consider-changes-desert-renewable-energy-conservation-plan>.

for the species even absent the threats posed by climate change. However, given that *Y. brevifolia* in California will lose upwards of 90% of its range under likely climate scenarios, the added loss of habitat and the genetic resiliency and connectivity it provides will further push the species towards extirpation in California.

6 Degree and Immediacy of Threat

As demonstrated in the previous sections, the threats facing *Y. brevifolia* are severe and immediate. While extirpation is likely decades away, the species is already suffering the impacts of climate change, with recruitment failure and adult mortality at the hotter, lower elevation edges of its range (Barrows and Murphy-Mariscal 2012; Harrower and Gilbert 2018; Sweet et al. 2019). Moreover, the impacts of invasive grass fueled fire are already being felt, with approximately half of identified refugia areas in JTNP under moderate warming scenarios having burned in recent decades (Sweet et al. 2019). And perhaps most importantly, the impacts from current GHG emissions will continue to be felt for decades to come, with little time remaining to reduce such emissions before warming sufficient to drive *Y. brevifolia* to functional extinction becomes unavoidable. Consequently, while *Y. brevifolia* may not currently be “in serious danger of becoming extinct throughout all, or a significant portion, of its range,” it is certainly likely to become so “in the foreseeable future.” Cal. Fish & Game Code §§ 2062 & 2067.

7 Inadequacy of Existing Regulatory Mechanisms

No existing regulatory mechanism are currently in place at the international, national, state or local level that adequately address the threats facing *Y. brevifolia*.

7.1 Regulatory Mechanisms for Greenhouse Emissions Reductions

Given climate change is the greatest threat to the continued existence of the Joshua tree, ultimately the species cannot be saved absent global action to reduce such emissions. Unfortunately, such action is severely lacking in scale, speed and efficacy at all levels of government, both domestically and internationally.

The United States has contributed more to climate change than any other country. The U.S. is the world’s biggest cumulative emitter of greenhouse gas pollution, responsible for 25 percent of cumulative global CO₂ emissions since 1850, and is currently the world’s second highest emitter on an annual and per capita basis (Le Quéré et al. 2018). However, U.S. climate policy is wholly inadequate to meet the international Paris Agreement targets to avoid the worst dangers of climate change.

As summarized by the Fourth National Climate Assessment, efforts to mitigate greenhouse gas emissions do not approach the scale needed to avoid “substantial damages to the U.S. economy, environment, and human health and well-being over the coming decades”:

Climate-related risks will continue to grow without additional action. Decisions made today determine risk exposure for current and future generations and will either broaden or limit options to reduce the negative consequences of climate

change. While Americans are responding in ways that can bolster resilience and improve livelihoods, neither global efforts to mitigate the causes of climate change nor regional efforts to adapt to the impacts currently approach the scales needed to avoid substantial damages to the U.S. economy, environment, and human health and well-being over the coming decades (USGCRP 2018).

In 2016, the U.S. committed to holding the long-term global average temperature to well below 2°C and “to pursue efforts to limit the temperature increase to 1.5°C above pre-industrial levels” under the international Paris Agreement. Existing U.S. domestic laws including the Clean Air Act, Energy Policy and Conservation Act and others provide authority to executive branch agencies to require greenhouse gas emissions reductions from virtually all major sources in the U.S., sufficient to meet the Paris Agreement temperature commitment.

However, the Trump administration has focused on pushing through harmful rollbacks of federal climate policy, and federal agencies are either failing to implement or only partially implementing domestic law and policy mandating greenhouse gas reductions. Trump administration rollbacks of federal climate policy include rescinding the Climate Action Plan, repealing and replacing the Clean Power Plan, a plan to dramatically expand offshore oil drilling in all oceans along U.S. coast, an attempt to rescind the Obama-era withdrawal of offshore drilling in U.S. federal waters in most of the Arctic and parts of the Atlantic, lifting of the moratorium on new federal coal leases, weakening emissions standards for cars and light duty trucks, delaying the implementation of methane emissions standards for new and modified oil and gas facilities, and the intended withdrawal from the Paris Agreement.

As a result, current U.S. climate policy has been ranked as “critically insufficient” by an international team of climate policy experts and climate scientists who concluded in September 2019:

The Trump Administration has continued with its campaign to systematically walk back US federal climate policy. If it successfully implements all the proposed actions, greenhouse gas emissions projections for the year 2030 could increase by up to 400 MtCO_{2e} over what was projected when President Trump first took office. That’s almost as much as the entire state of California emitted in 2016 (CAT 2019).

To meet the carbon budget for keeping temperature rise below 1.5°C, most U.S. and global fossil fuels must remain undeveloped and fossil fuel production must be phased out globally within the next several decades (Rogelj et al. 2015). However, the U.S. is now the world’s largest oil and gas producer and third-largest coal producer (OCI 2019) due to U.S. policies that aggressively promote ever greater fossil fuel production. For example, in 2005, Congress exempted fracking from the Safe Drinking Water Act in legislation known as the “Halliburton Loophole.” Thereafter, fracking spread rapidly and facilitated a dramatic increase in U.S. natural gas and crude oil production (USEIA 2016). After Congress lifted the 40-year old crude oil export ban in December 2015, crude oil exports have skyrocketed and now hover at nearly three million barrels per day—about a quarter of all U.S. production (DiChristopher 2019). U.S. subsidies are also spurring fossil fuel production. A recent study assessing the impact of major federal and state subsidies on oil production found that these subsidies push nearly half of new

oil investments into profitability, potentially increasing U.S. oil production by 17 billion barrels over the next few decades (Erikson et al. 2017). In short, U.S. policy is incentivizing rather than reducing fossil fuel production.

And while U.S. policy and emissions are going in the wrong direction under the Trump administration, the rest of the world is doing little better. As summarized by CAT (2019), current policies, if actually implemented by all nations, will still result in over 3°C of warming, and even if all pledges and targets make pursuant to the Paris Agreement were met, warming would still be on the order of 2.6 to 2.9°C (Figure 20). This level is far above the 1.5°C threshold the world needs to stay below to avoid the worst impacts of climate change.

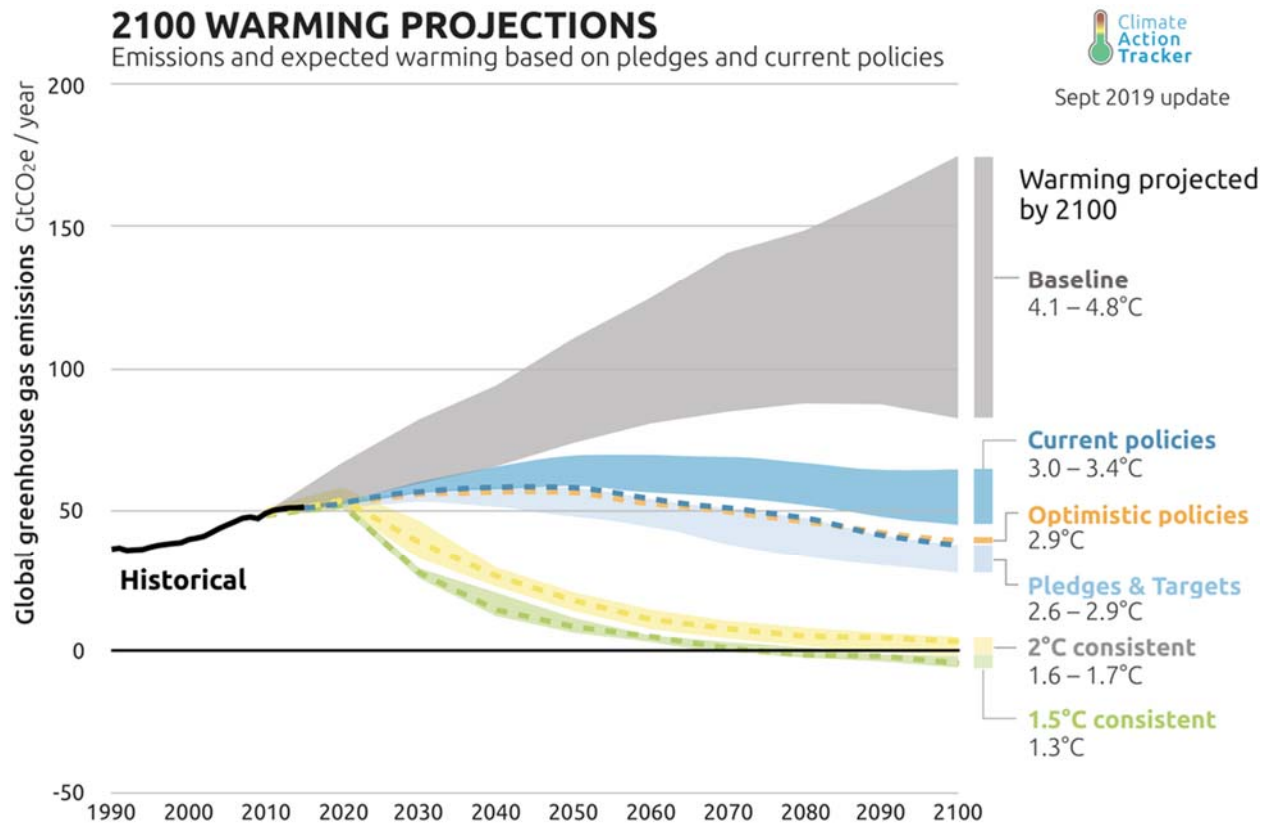


Figure 20: Graph showing mismatch between current emissions trajectories, international climate targets, and national policies and commitments. Source: CAT (2019).

In sum, both domestically and globally, government policies and commitments, not to mention actual actions, to avoid the worst impacts of climate change are woefully inadequate. These trends will lead to temperatures in the range of *Y. brevifolia* that are incompatible with reproduction and ultimately, survival of the species.

7.2 Mechanisms to protect habitat from fire, development and other threats

While the lack of effective regulatory mechanisms to address greenhouse pollution is largely determinative as to the question of whether *Y. brevifolia* qualifies for CESA protection,

mechanisms to protect the species from other threats are also insufficient.

7.2.1 Invasive species and fire

To date no legal, regulatory or management efforts have demonstrative effectiveness at addressing the severe threat that invasive species and consequent altered fire regimes pose to Joshua trees. While the National Park Service (NPS) has updated its fire management plans to address the increased threat of fire to the species, large fires continue to be a significant threat in JTNP (Sweet et al. 2019). Other areas in the species' range lack species-specific fire management plans. And while immediate suppression of fires in *Y. brevifolia* habitat can limit the spread of fires, protection of the species from fire ultimately requires invasive species management to reduce the fuel load. Given invasive species spread and abundance is linked to both disturbance (e.g. roads, ORVs, cows, urbanization) (Brooks and Berry 2006) and nitrogen deposition (Allen et al. 2009; Allen et al. 2011), each of these contributing factors will need to be addressed.

Disturbance is somewhat limited in the portions of the range of *Y. brevifolia* within national parks, but these areas harbor only approximately 10% of the species' current suitable range in California. The vast majority of the species' range in the state is on BLM, military and private lands that are not managed primarily for species protection and include activities such as ORV use, cattle grazing, military training, urban sprawl and activities that foster the spread of invasive species and/or the ignition of fires (USFWS 2018).

Notably, BLM recently (10/3/19) approved a Record of Decision for a vehicle route network in the West Mojave Planning Area, which encompasses the entire range of YUBR South and a portion of YUBR North. About a quarter of mapped Joshua tree habitat in YUBR South is on BLM land, while over half of YUBR North habitat is on BLM land. BLM approved an expansive ORV route network of 6000 miles of open vehicle routes in the plan area, ensuring that any public lands outside of wilderness will be highly fragmented, directly degrading habitat, exacerbating the spread of invasive species and increasing the number of human-caused ignitions (BLM 2019).

Nitrogen deposition impacts both disturbed and relatively undisturbed areas, with JTNP being one of the areas in the range of *Y. brevifolia* worst impacted by nitrogen deposition (Allen et al. 2011; Figure 10). As summarized by, Pardo et al. (2011), the threat is dire: "In Joshua Tree National Park in southern California, N deposition favors the production of sufficient invasive grass biomass to sustain fires that threaten the survival of the namesake species."

It is unlikely that nitrogen deposition will be adequately reduced throughout the range of *Y. brevifolia* for at least several decades, if ever. In the western areas of JTNP, nitrogen deposition is largely derived from nitric oxides (HNO₃) coming from automobile and powerplant pollution blown in from the greater Los Angeles area (Allen et al. 2009). In the eastern part of the park, deposition is largely from ammonia (NH₃) from local agricultural sources in the Coachella and Imperial Valleys (Allen et al. 2009). High rate of nitrogen deposition in the far western Mojave likely originate from a mix of smokestack and tailpipe pollution and agricultural sources in the San Joaquin Valley (Bytnerowicz et al. 2016). Even if California successfully decarbonizes its

vehicle fleet and power generation in the coming decades, nitrogen deposition from large-scale agriculture will likely continue to impact large areas of *Y. brevifolia* habitat for the foreseeable future.

Moreover, even if disturbance and nitrogen deposition are reduced and the further spread of invasive species can be curtailed, no fully-effective treatments currently exist to reduce or eliminate at a landscape scale the most pernicious invasive species (e.g. *Bromus* spp., *Schismus* spp., *Erodium cicutarium*), *Brassica tournefortii*) that have already become established in significant portions of the range of *Y. brevifolia* (Brooks et al. 2018).

7.2.2 Habitat loss and degradation

As discussed above, *Yucca brevifolia* stands to lose upwards of a third of its suitable habitat in California to development over the coming decades, including over 40% of its habitat in the YUBR South region. No existing state or federal regulatory mechanisms are currently operative in a manner that will meaningfully reduce this threat.

State and local mechanisms

A relatively small portion of the range of *Yucca brevifolia* occurs within California State Parks, including Red Rock Canyon State Park and Eastern Kern County Onyx Ranch State Vehicular Recreation Area in Kern County and Saddleback Butte State Park, Arthur B. Ripley Desert Woodland State Park, and Antelope Valley California Poppy Reserve in Los Angeles County. Collectively these make up less than 1% of the species range in the state (USFWS 2018). While these areas are protected from urban development and are generally to be managed for the protection of park resources, they alone are unlikely to prevent the decline and eventual extirpation of Joshua trees from the region. Saddleback Butte and Arthur B. Ripley Desert Woodland State Parks are small and isolated islands of protected habitat, comprised of approximately 3000 and 500 acres respectively. Antelope Valley California Poppy Reserve is approximately 1800 acres but contains only a few isolated clusters of Joshua trees. Red Rock Canyon State Park at approximately 27,000 acres is much more substantial in size, but is faced with many management challenges similar to adjacent BLM lands, particularly a proposed increase in ORV use in the Park. Similarly, the newly-created Eastern Kern County Onyx Ranch State Vehicular Recreation Area contains some Joshua tree woodland but is managed primarily for ORV use.²⁵ In any event, even if all other threats to *Y. brevifolia* in these parks were effectively managed, climate change and fire still threatened to extirpate the species from these parks over the coming decades.

The California Desert Native Plants Act, Cal. Food & Agricultural Code §§ 80001 – 80201, was passed “to protect California desert native plants from unlawful harvesting on both public and privately owned lands.” *Id.* at § 80002. Joshua trees are explicitly regulated under this provision. *Id.* at § 80073(a)(“yuccas”) & 80101(b)(1) (setting price for *Y. brevifolia* permits). The Act generally prohibits harvest of desert plants absent permits issued by the relevant county agricultural commissioner or sheriff. *Id.* at § 80073. Land clearing for agriculture and various

²⁵ Information on each of these parks is available at <https://www.parks.ca.gov/>.

other forms of development activities are generally exempted so long as the plants are not offered for sale and proper notice is given. *Id.* at § 80111. The statute also includes provisions designed to assure the survival and transplant of desert plants that are harvested pursuant to permits. *Id.* at § 80116. The Department of Fish and Wildlife is tasked with enforcing the statute. Cal. Fish & Game Code § 1925 (“The Department shall enforce the provisions of the California Desert Native Plants Act”).²⁶

Commercial collection was once seen as perhaps the greatest threat to the Joshua tree and other desert plants. As described in an early account about the threats commercial harvesters presented to the species in southern California, “As soon as they began to realize their beauty and unique character there began a wholesale foray into the desert to dig them up...At the present rate of destruction the cactus of the desert and the Joshua trees will be gone within two years” (Carr 1930). Various state and local laws and ordinances were ultimately passed to address this threat, including the California Desert Native Plants Act. While these measures have been largely effective at reducing the commercial harvest of Joshua trees, they have done little to slow the loss of habitat from agricultural conversion and development in the range of the species.

Among the local jurisdictions in the range of *Y. brevifolia* that currently have plant protection ordinances or other measures that nominally protect Joshua trees are Hesperia, Palmdale, Victorville, Yucca Valley, and Los Angeles and San Bernardino counties. While all of these provisions require consideration of Joshua tree retention in development plans, most exempt single-family homes and none act as an actual bar to tree removal, instead usually requiring transplantation, donation or making available for adoption trees removed from construction sites. *See, e.g.* Palmdale Municipal Code §§ 14.04.010 *et seq.* (requiring preservation of two Joshua trees per acre but allowing this metric to be met by donating removed trees to an offsite City-administered tree bank); Yucca Valley Ordinance 140 (allowing removal of Joshua trees for transplant if they interfere with “approved improvements or other ground disturbing activities” and “best efforts” are made to avoid the need to remove them).

The California Fish and Game Commission noted the inadequacy of these approaches when it adopted its California Policy for Native Plants in 2015:

The State’s policies and practices regarding native plants are in need of review and updating. More than 30 years ago state law focused on transplantation as a means of mitigating for listed plant species, however experience and numerous studies document that such practices are largely ineffectual over time and often damaging to species or population survival.²⁷

In sum, the California Desert Native Plants Act and similar local ordinances are, as recognized by the Commission, “largely ineffectual” at protecting imperiled plant species from habitat loss. These provisions may result in the near-term preservation of individual adult Joshua

²⁶ A similar statute, the Native Plant Protection Act provides comparable protections for “endangered or rare” native plants. Cal. Fish & Game Code §§ 1900-1913. The Joshua tree is not among the species regulated by this statute.

²⁷ Available at <https://fgc.ca.gov/About/Policies/Miscellaneous>.

trees in urban and suburban neighborhoods, but these areas are less likely to remain habitat long-term. Successful recruitment in such areas is likely constrained by lack of nurse plants and it remains highly uncertain whether pollinating moths will be able to persist with the resultant low Joshua tree densities (Harrower and Gilbert 2018)(“Having robust, dense, flowering trees is important to support and attract enough moths for successful seed set”). Consequently, these measures are inadequate to prevent extensive loss of Joshua tree habitat in the near-term and for the foreseeable future.

Other state statutes also are inadequate to protect Joshua trees from habitat loss. The California Environmental Quality Act (CEQA) is California’s landmark environmental law and establishes a state policy to prevent the “elimination of fish or wildlife species due to man’s activities, ensure that fish and wildlife populations do not drop below self-perpetuating levels, and preserve for future generations representations of all plant and animal communities....” Cal. Pub. Res. Code § 21001(c). Towards this end, state and local agencies are required to analyze and disclose the impacts of any discretionary decision or activity. CEQA contains a substantive mandate that agencies should not approve projects as proposed if there are feasible alternatives or mitigation measures which would substantially lessen the significant environmental effects of such projects. Cal. Pub. Res. Code § 21002.

CEQA requires a “mandatory finding of significance” if a project may “substantially reduce the number or restrict the range of an endangered, rare or threatened species.” Cal. Code Regs., tit. 14, § 15065(a)(1). CDFW has interpreted this provision to apply to species of special concern, which are species that are “experiencing, or formerly experienced, serious (noncyclical) population declines or range retractions (not reversed) that, if continued or resumed, could qualify it for State threatened or endangered status.”²⁸ CDFW further provides that species of special concern “should be considered during the environmental review process.” *Id.*; Cal. Code Regs., tit. 14, § 15380. Thus, a potentially substantial impact on a species of special concern, threatened species, or endangered species could be construed as “per se” significant under CEQA. *Vineyard Area Citizens for Responsible Growth, Inc. v. City of Rancho Cordova* (2007) 40 Cal.4th 412, 449. And under CEQA, when an effect is “significant,” the lead agency approving the project must make a finding that changes or alterations have been incorporated into the project to avoid or mitigate its significant impacts, or that such changes are within the responsibility of another agency, or that mitigation is infeasible. Cal. Pub. Res. Code § 21081(a). These provisions therefore provide some protections to species that are listed as species of special concern, threatened, or endangered.

However, Joshua trees are not listed as a species of special concern or as threatened or endangered, such that a project that has the potential to impact the species would not necessarily qualify as a “significant effect” under a lead agency’s interpretation of CEQA. In such case, CEQA’s substantive mandate to adopt all feasible alternatives or mitigation measures might not be triggered.

CEQA also requires a “mandatory finding of significance” if a project may “substantially

²⁸ California Department of Fish and Wildlife, *Species of Special Concern*, available at <https://www.wildlife.ca.gov/Conservation/SSC>.

reduce the habitat of a fish or wildlife species; cause a fish or wildlife population to drop below self-sustaining levels; threaten to eliminate a plant or animal community.” Cal. Code Regs., tit. 14, § 15065. Moreover, CEQA’s “Environmental Checklist” in Appendix G of the CEQA Guidelines characterizes a project’s effects as “significant” if the project would “[c]onflict with any local policies or ordinances protecting biological resources, such as a tree preservation policy or ordinance.”

While these provisions might theoretically offer some protection for Joshua trees, in practice they have not provided sufficient protection. Under CEQA, lead agencies have discretion to develop their own thresholds of significance. *East Sacramento Partnerships for a Livable City v. City of Sacramento* (2016) 5 Cal.App.5th 281, 300; Cal. Code Regs., tit. 14, § 15064(d). This allows local agencies—who are often under pressure from developers to approve projects—to make significance determinations that are inconsistent with independent scientific analysis, including CDFW’s analysis.

Even when a lead agency acknowledges that an effect is “significant,” CEQA allows a lead agency to adopt a “statement of overriding considerations” and approve a project if the agency finds that other factors outweigh the environmental costs of the project or that further mitigation is infeasible. Cal. Code Regs., tit. 14, § 15093(b); Cal. Pub. Res. Code § 21081. This means that even if a project may have a significant effect on a Joshua tree population, an agency could interpret CEQA as still allowing approval of the project. CEQA in practice is therefore inadequate to protect Joshua trees.

The Natural Community Conservation Planning Act is a voluntary conservation planning mechanism for proposed development projects within a planning area to avoid or minimize impacts to wildlife. Cal. Fish & Game Code §§ 2800-2835. The Act is designed to promote coordination among agencies and landowners to conserve unfragmented habitat areas and multihabitat management. Cal. Fish & Game Code § 2801(d).²⁹ The Act can also serve as a mechanism to authorize take of CESA listed species. *Id.* at § 2835.

There are no finalized Natural Community Conservation Plans (NCCPs) that cover the Joshua tree. One approved NCCP, the Coachella Valley MSHCP approaches the southern edge of the range of *Y. brevifolia* but does not include the species as a covered species. An NCCP that does overlap the range of the Joshua tree is the proposed Town of Apple Valley MSHCP.³⁰ This NCCP has been under development for several years with a planning agreement signed in 2017. However, *Y. brevifolia* is not on the proposed list of covered species for the NCCP. Previously, both the West Mojave Plan and the DRECP were intended to be joint plans covering both federal BLM lands and private lands subject to development, but each was ultimately implemented as a federal-only plan, neither of which treat the Joshua tree as a covered species. These plans are further discussed below. In sum, NCCPs may in the future provide some conservation benefit for Joshua trees, but have not done so to date and consequently cannot be considered as providing adequate protection in lieu of CESA listing.

²⁹ The NCCP Act is described on CDFW’s website at <https://www.wildlife.ca.gov/conservation/planning/NCCP>.

³⁰ Documents available at <https://www.wildlife.ca.gov/Conservation/Planning/NCCP/Plans/Apple-Valley-MSHCP>

Federal mechanisms

The primary federal regulatory mechanism with the potential to protect Joshua trees are management laws and plans governing federal lands. Almost all of the suitable habitat in YUBR north and half within YUBR South is on federal land. Consequently, management of these lands has an important role to play in determining the continued viability of Joshua trees in the state. As discussed above, approximately 10% of *Y. brevifolia* habitat is on NPS lands that are generally well-managed and should prevent significant habitat loss or degradation from activities such as ORV use, cattle grazing, road building or other forms of development. However, even within Death Valley National Park, the 86,400-acre Hunter Mountain Allotment is still active and overlaps with the range of *Y. brevifolia* in the park (NPS 2012). Nevertheless, these lands represent the best opportunities for active management measures to reduce the risk of fire and otherwise attempt to maintain *Y. brevifolia* on the landscape in the face of projected warming.

About 12 percent of the mapped distribution of the YUBR South population falls within military installations and a roughly comparable amount of the YUBR North population falls within such lands (USFWS 2018). The four bases in California with Joshua tree habitat - Edwards Air Force Base, Fort Irwin National Training Center, China Lake Naval Weapons Station and Twentynine Palms Marine Corps Air Ground Combat Center - have each developed Integrated Natural Resource Management Plans (INRMPs) pursuant to the Sikes Act, 6 U.S.C. §§ 670a-670o, that incorporate some avoidance and minimization measures that could reduce impacts to Joshua trees. These measures are summarized in USFWS (2018) and largely consist of avoidance where feasible and transplantation when conflicts are unavoidable. These measures largely mirror those required for private lands under state and local ordinances, which as discussed *supra*, are in the Commissions own words, “largely ineffectual.”

The majority of Joshua tree habitat on federal lands is on BLM lands. These areas are governed by the agency’s California Desert Conservation Area (CDCA) Plan as amended. The Northern and Eastern Mojave Plan (NEMO) area overlaps with most of the California range of the YUBR North populations and the West Mojave Plan (WEMO) area covers all of YUBR South and the southwestern portion on YUBR North. The 2016 Desert Renewable Energy Conservation Plan (DRECP) amendments cover the entirety of the species’ range in California. None of these plans provide adequate protection for *Y. brevifolia*. area

BLM’s NEMO plan does virtually nothing to specifically protect Joshua trees. The species is not mentioned in the Record of Decision (ROD) at all, and the only specific protection afforded to it is a prohibition on collecting downed trees for firewood (BLM 2002). Notably, Joshua tree protection is explicitly excluded from the plan’s measure to limit surface disturbance below certain thresholds:

It should be noted that some important plants, such as Joshua trees, which are important as an overstory plant but are not dominant, would not be a part of the evaluation trigger. Reestablishment of such plants could, of course, be a restoration requirement for a particular project, but they would not be used to trigger an evaluation for the purposes of reducing the cumulative disturbance total (BLM 2002).

In short, the NEMO plan was not designed with the intent of protecting Joshua trees, and the BLM apparently did not wish to have protection of the species act a barrier to any potential land-disturbing activities.

The WEMO plan is little better. As with NEMO, its ROD does not mention Joshua trees at all. The FEIS for the plan amendment was developed when the project was to also be a habitat conservation plan (HCP) covering private development in the plan area. In this context it discusses existing and proposed preservation of Joshua tree woodlands in the Antelope Valley by state and local entities, but the only specific conservation measure for Joshua trees that BLM itself takes is to prohibit harvesting of Joshua trees in designated conservation areas (BLM 2006). Given state law already prevents such harvest, this conservation measure is illusory. BLM approved the WEMO plan as a federal only plan with no HCP component. Under this alternative, BLM estimated that 54.1% of Joshua tree woodland habitat could be lost (BLM 2006).³¹

BLM recently completed an amendment to the WEMO plan dealing with vehicle routes (BLM 2019). Under this plan amendment, the route network is expanded to approximately 6000 miles of roads and trails open to ORVs. The ROD does not mention Joshua trees, the FSEIS does not meaningfully address impacts to Joshua trees, and the plan amendments do not add any specific measures to protect the species. Mentions of Joshua trees are cursory in the FSEIS, with for example, in a chart of subregions of the plan area, for one area BLM states that it “has an extensive Joshua Tree forest,” and immediately thereafter notes that “Gently terrain and good soils make ideal provide ideal OHV touring opportunities” [typos in original].³² In the ROD, BLM also reaffirms cattle grazing on all active allotments (BLM 2019). As discussed *supra*, invasive species and consequently fuel loads, and well as human-caused ignitions increase in areas subject to disturbance such as cattle grazing and ORV use (e.g. Brooks and Berry 2006). The recent plan amendment will both directly degrade Joshua tree habitat via increased vehicle use, while also indirectly exacerbating the conditions that lead to more frequent and more intense fires.

The more recent DRECP started as both a BLM plan and a state NCCP. Consequently, the environmental documents associated with it address the conservation of Joshua trees more directly than the overlapping BLM plans. However, the DRECP was ultimately adopted as a BLM-only plan, rendering much of the proposed broader conservation uncertain. Among the Joshua tree measures BLM adopted are an objective listed as “Conserve unique landscape features, important landforms, and rare or unique vegetation types identified within the BLM Decision Area, including...Areas of dense Joshua Tree woodland.” To meet this objective, the DRECP requires that for new actions, Joshua tree impacts are to be assessed in planning

³¹ As discussed in the Distribution section *supra*, “Joshua tree woodland” represents only a portion of the habitat types where the species occurs. However, it is the densest and highest quality habitat for the species.

³² The only other “analysis” of impacts to Joshua trees in the FSEIS, is an assertion repeated verbatim multiple time in the document that attempts to minimize harm from vehicles: “In remote or mountainous areas, most travel is confined to roads, so that the woodland communities (Joshua tree woodland, scrub oak, pinyon pine woodland, juniper woodland) suffer relatively fewer direct vehicle impacts” (BLM 2019).

decisions and “impacts to Joshua tree woodlands will be avoided to the maximum extent practicable, except for minor incursions” (BLM 2016).³³ In addition to the specific measures for Joshua trees, their habitat would likely gain better protection from various land designations made under the DRECP. However, the benefits for the species derived from the DRECP amendments to the CDCA Plan are in doubt, as the BLM announced that it was planning to revisit the conservation measures of the plan. See Notice of Intent to Amend the California Desert Conservation Area, Bakersfield, and Bishop Resource Management Plans and Prepare Associated Environmental Impact Statements or Environmental Assessments, 83 Fed. Reg. 4921 (February 2, 2018). That amendment process is currently ongoing.

In sum, outside of national parks and areas of congressionally designated wilderness, federal land management plans in the range of *Y. brevifolia*, if they address the species at all, at best provide for avoidance of harm to the extent “practicable” or “feasible.” Such protection is inadequate in the face of the difficulties the species will face in a rapidly changing climate.

8 USFWS’s Flawed Endangered Species Act Determination.

The strongest federal regulatory mechanism that could protect *Y. brevifolia* is the federal Endangered Species Act (ESA). However, on August 15, 2019 the USFWS found that listing Joshua trees (*Y. brevifolia* and *Y. jaegeriana*) throughout their multistate range was not warranted. Endangered and Threatened Wildlife and Plants; 12-Month Findings on Petitions to List Eight Species as Endangered or Threatened Species, 84 Fed. Reg. 41694 (August 15, 2019) (USFWS 2019). The finding was made in response to a 2015 petition by WildEarth Guardians seeking such listing.

While the 2018 species status assessment prepared by USFWS and relied upon by the agency in its decision is informative as to many aspects of Joshua tree taxonomy, natural history, distribution and threats, its conclusions are not at all determinative to the question of whether *Y. brevifolia* warrants listing under CESA. Most importantly, USFWS (2018) assessed whether Joshua Trees in their four-state range were threatened or endangered. And to the degree that the agency considered *Y. brevifolia* separately from *Y. jaegeriana*, it never examined the species’ status in just California, rather than California and Nevada combined. Under CESA, the only question is whether the species is imperiled in California. As both CDFW and the Commission have concluded—and appellate courts have upheld—the term “range” under CESA is construed to refer to the range of a species *within* California, not the worldwide range of the taxa. *California Forestry Assn. v. California Fish & Game Com.* (2007) 156 Cal.App.4th 1535, 1550-551.

Additionally, several of the analyses and conclusions contained in USFWS (2018) are flawed and served to downplay the threats and overstate the likely resilience of the species. For example, the agency used an upper “appropriate temperature range” for the species of 59°C (138°F). The same metric was used for all age classes, from seedlings to adults. This threshold

³³ DRECP documents are available at <https://eplanning.blm.gov/epl-front-office/eplanning/planAndProjectSite.do?methodName=dispatchToPatternPage¤tPageId=95675>

was based on a laboratory studies by Smith et al. (1983) in which detached leaves were placed in hot water for an hour and then examined for heat damage. The temperature at which a severed leaf demonstrates cell damage in a lab is a far different metric than the ambient temperature in which a Joshua tree can survive and successfully reproduce in the wild.³⁴ The temperature used by USFWS (2018) is higher than the hottest temperature (56.7°C; 134.1°F) ever measured on Earth. Notably, the highest lab air temperature that Smith et al. (1983) actually successfully reared Joshua trees was 45°C (113°F).³⁵

USFWS (2018) also downplays the risks of fire to *Y. brevifolia*. Using modeling to estimate invasive grass cover and link high coverage ratios (15-45%) as a proxy for increased fire frequency and severity, the agency estimated that approximately 1.4 percent of the YUBR South and 8.8 percent of the YUBR North current mapped distribution would be at risk in the next several decades. In contrast, Sweet et al. (2019) documented that half of the area of Joshua tree habitat in JTNP identified as refugia for the species under an RCP 4.5 pathway had already burned in recent decades. The total recent burn area in the park represents well over 10% of the current range of the species in the park and such fires are likely to increase within JTNP and throughout the range of the species.

Another severe limitation of USFWS (2018) is the complete discounting of species distribution modeling, which currently represents the best available science on the future status of the western Joshua tree. The agency admits that it did not carry out any such modeling, claiming that having quantitative information is somehow at odds with its goals in carrying out a status assessment.

We did not model future distribution based on predicted climate change scenarios. Instead, we used future scenarios to perform a qualitative evaluation of the impact of climate change on the current distribution. ... Our goal was to present information related to future climate outcomes, not to evaluate quantitative assessments of climate change on future Joshua tree distribution, therefore we did not construct ecological niche models (e. g., species distribution models) (USFWS 2018).

What USFWS claims it did in lieu of deploying ecological niche modeling was scenario planning, citing to Star et al. (2016) for its rationale.

Rather than focusing only on the most likely predictions, scenario planning identifies a range of possible future states. Scenarios are not predictions, and probabilities are not assigned to specific outcomes. By recognizing the limits of projections and acknowledging deep uncertainty, decision makers are not restricted to preparing for

³⁴ By way of comparison, according to industrial safety standards, a human can safely touch items as hot as 140°F without burning their hand, but prolonged exposure to air temperature of 140°F would lead to heat stress and ultimately be fatal.

³⁵ Among the various temperature ranges listed for the species in the wild, the highest is reported by Lenz (2001) as 51°C (124°F), which presumably corresponds to a one-time daily maximum temperature recorded somewhere in the species' range; this temperature is well above the average summer maximum of the hottest place in the United States, Furnace Creek in Death Valley (July average of 47°C (116°F)).

only one outcome, and can still act in the face of climate change while retaining flexibility.

USFWS (2018) also cites two older studies in an attempt to undermine the utility of such studies as well as the feasibility of doing them with regard to Joshua trees.³⁶

Furthermore, ecological niche models are often criticized for inaccurate projections of future occurrence (Fitzpatrick and Hargrove 2009, p. 2256). This is especially true for species where current distribution data are not extensive across the species range or information about physiological thresholds is lacking, such as Joshua tree (Pearson and Dawson 2003, p. 362). Given the absence of information about the adaptive capacity of Joshua tree, in combination with gaps in the occurrence data across the species' range, the probability of spurious conclusions seemed high.

The problems with USFWS's approach are many. First, USFWS did not *itself* need to model future distribution of Joshua trees, as this has already been done by multiple researchers, with Cole et al. (2011), Barrows and Murphy-Mariscal (2012) and Sweet et al. (2019) employing the most sophisticated of such efforts. Nowhere in USFWS (2018) is there even an acknowledgement that such modeling efforts have been undertaken and reported in these studies.³⁷

Second, while scenario planning may be useful in recovery planning or otherwise preparing for management responses to climate change, it has little utility in determining whether a species is "likely" to become endangered in the foreseeable future, as required by the ESA and CESA. 16 U.S.C. § 1532(20); Cal. Fish & Game Code § 2067 (ESA and CESA definitions of threatened species). In effect, USFWS (2018) is acknowledging that "[r]ather than focusing only on the most likely predictions" it instead applied a more nebulous framework that allowed it to "retain flexibility" and disregard not just the best available science, but also the plain language of the ESA.

Third, USFWS's reliance upon Pearson and Dawson (2003) and Fitzpatrick and Hargrove (2009) for its critique of ecological niche models is misplaced. The concerns raised by Pearson and Dawson (2003) and Fitzpatrick and Hargrove (2009) about the limitations of certain niche modeling efforts may be valid, but Cole et al. (2011), Barrows and Murphy-Mariscal (2012) and Sweet et al. (2019) all employed the measures raised by these earlier authors to improve the accuracy of their modeling, including, most importantly, validating their models against the current distribution of the species. Pearson and Dawson (2003) also note that information on dispersal abilities should also be included in modeling where possible, a factor clearly addressed in Cole et al. (2011).

³⁶Neither of these studies, nor Star et al. (2016), appear in the references section of USFWS (2018), indicating that they may have been added at the last-minute in an attempt to justify a legally and scientifically dubious conclusion.

³⁷Elsewhere in the document, USFWS (2018) cites to Cole et al. (2011) and Barrows and Murphy-Mariscal (2012) for other aspects of Joshua tree natural history or range. Sweet et al. (2019) had not been published at the time of USFWS (2018) but was released prior to the actual listing decision being published and should have factored into the final decision.

Additionally, the primary concern of Fitzpatrick and Hargrove (2009) is that climate change and future conditions will create novel environments with new species interactions, including many invasive species. This makes predictions about future species distribution less reliable, unless they account for such factors. But these concerns are addressed by Cole et al. (2011), Barrows and Murphy-Mariscal (2012) and Sweet et al. (2019) who examined the current and past status of *Y. brevifolia* across environmental gradients (elevation and latitude) and used increasingly finer-scale species distribution and climate data to refine their model outputs. Moreover, unlike USFWS who discarded such modeling entirely, Pearson and Dawson (2003) explicitly acknowledged the utility of such models: “In many cases, bioclimate envelope models provide perhaps the best available guide for policy making at the current time.” In the decade and half since this statement was published, such models have improved greatly and are even more useful for informing policy decisions.

Finally, USFWS’s failure to rely upon the published species distribution models was strongly criticized by one of the peer-reviewers of the status assessment.

[T]he assessment has not completed, and does not incorporate, a species distribution model, and thus draws invalid conclusions about future distributions under various climate change scenarios. Unfortunately, the problems are significant enough that the assessment’s conclusions are not scientifically sound, and should not be used for making a decision regarding whether to list Joshua trees under the ESA (Smith 2018).

Smith (2018) noted that species distribution models are the “accepted standard” for assessing future distribution of a species, described the finding of the various modeling efforts to date, compared these to the conclusions of the status assessment, and concluded that “[g]iven that the USFW assessment has not followed the conventional standards in the field for predicting future distributions, and makes predictions that are starkly different than those drawn by other workers making comparable model assumptions, I consider the assessment’s conclusions to be highly dubious.” Smith (2018) concluded with the recommendation that “[f]irst and foremost, the assessment simply MUST include a formal species distribution model.” (emphasis in original).

Smith (2018) also pointed out that the estimation of “suitable habitat” for Joshua trees was overstated in the status assessment.

[T]he way that ‘suitable habitat’ has been defined ignores important recent work on demographic trends in Joshua trees, with the result that the potential distribution of Joshua tree under current climate conditions is vastly overestimated.

Specifically, Smith (2018) pointed out USFWS (2018) had not taken into account climate change that has already occurred when it delineated such habitat.

In identifying the climate requirements for Joshua tree, the assessment uses the current distribution to determine suitable habitat... There are two significant, interrelated problems with these assumptions. First, the current distribution of Joshua

tree includes individuals who are hundreds of years old, and that became established during pre-industrial climate conditions when global average temperatures were a full degree cooler than they are today, and about 0.75 degrees cooler than the 30-year average. Indeed, it is well established that long-lived trees can persist as relict stands of moribund adults that exist outside the range of suitable habitats required for long term population persistence.

In the case of Joshua trees in particular, we have very compelling evidence that the current distribution of mature trees does not reflect the climate requirements for successful germination and seedling establishment. For example, extensive mapping studies in Joshua Tree National Park found that seedlings occur only in a fraction of the area occupied by adults, and that this area corresponds to the predicted distribution under a 2-degree warming scenario (Barrows and Murphy-Mariscal, 2012). That is, the suitable habitat for seedlings is much smaller, includes a narrower range of climates, than would be predicted based on adult presence data. Although the Barrows and Murphy-Mariscal study considered only a small portion of the geographic range of Joshua trees, other workers have found similar patterns across the Joshua trees range.

Smith (2018) concluded that these errors rendered the conclusions of the assessment unreliable: “I consider the current assessment to not be based on the best available science, and its conclusion have no valid scientific basis.” USFWS did not address either of the primary problems identified by Smith (2018) when it finalized the status assessment.

In sum, USFWS’s determination to not protect Joshua trees under the ESA should not, and legally cannot, be a basis to fail to protect *Y. brevifolia* under CESA.

9 The Western Joshua Tree Warrants Listing under CESA.

As detailed above, in conformance with the requirements of Cal. Code Regs., tit. 14, § 670.1, this petition presents scientific information regarding the western Joshua tree’s life history, population trend, range, distribution, abundance, kind of habitat necessary for survival, factors affecting the ability to survive and reproduce, degree and immediacy of threat, impact of existing management efforts, suggestions for future management, availability of sources and information, and detailed distribution maps.³⁸

That information clearly demonstrates that the western Joshua tree (*Yucca brevifolia*) is eligible for and warrants listing under CESA based on the factors specified in the statute and implementing regulations. While *Y. brevifolia* is not at imminent risk of extinction, it still faces significant and growing threats, primarily from climate change, that ultimately threaten the viability of the species in all or a significant portion of its range in California in the foreseeable future; it consequently meets the definition of a “threatened species.”

³⁸ Information on suggestions for future management and availability of sources and information are contained in the Management Recommendations and References sections *infra*.

Under CESA, a “threatened species” is “a native species or subspecies of a . . . plant that, although not presently threatened with extinction, is likely to become an endangered species in the foreseeable future in the absence of the special protection and management efforts” Cal. Fish & Game Code § 2067. A plant is an “endangered species” when it is “in serious danger of becoming extinct throughout all, or a significant portion, of its range due to one or more causes, including loss of habitat, change in habitat, overexploitation, predation, competition, or disease.” Cal. Fish & Game § 2062.

Moreover, CDFW has concluded—and appellate courts have upheld—that when determining whether a species is threatened or endangered under CESA, the term “range” is construed to refer to the range of a species or subspecies *within* California, not the worldwide range of the species or subspecies. *California Forestry Assn. v. California Fish & Game Com.* (2007) 156 Cal.App.4th 1535, 1550-551. This means that regardless of how *Y. brevifolia* may fair in Nevada, the Commission and CDFW can only consider the status and fate of the species in California.

Additionally, in determining the foreseeable future in the context of climate change, CDFW has treated the rest of the century as foreseeable.

In considering what the ‘foreseeable’ future is for climate change effects, the Department relied on climate change projections to the end of the 21st century, as described by the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2007). The IPCC models and projections have been thoroughly vetted and validated in the series of Assessment Reports produced over the past 12 years. The Department considers the climate change projections to be the best available information on global climate change (Bonham 2013).

As discussed in the climate sections above, absent rapid and substantial reductions in greenhouse gas emissions, the best available science demonstrates that by the end of this century *Y. brevifolia* will be extirpated from, at a minimum, a significant portion of its range in California. Any places it remains will be in small, isolated refugia. These areas, if any, will likely be populated with low numbers of non-reproductive adult trees, themselves threatened by fire. At such point, if not already extirpated from the state, the species will certainly be “in serious danger of becoming extinct throughout all, or a significant portion, of its range” in California and be an “endangered species.” Consequently, it is a “threatened species” today.

In the event the Commission determines that full-species taxonomy for the western Joshua tree is not sufficiently established, petitioners request listing of the taxa as a subspecies/variety *Yucca brevifolia brevifolia*. Additionally, while petitioners believe that the western Joshua tree warrants protection under CESA throughout its range in California, if the Commission determines that it does not warrant range-wide listing, the Commission must assess whether either of the two population clusters of the species, YUBR North and YUBR South separately warrant listing as ecologically significant units (ESUs).

The Commission and CDFW have long recognized that ESUs can be designated and listed under CESA, and this interpretation of CESA has been upheld by the courts. *See California*

Forestry Assn. v. California Fish & Game Com. (2007) 156 Cal.App.4th 1535, 1540 (“Consistent with the policy of the CESA, we will hold that the term ‘species or subspecies’ includes evolutionarily significant units”); *Central Coast Forest Assn. v. Fish & Game Com.* (2018) 18 Cal.App.5th 1191, 1197, fn. 4 [“CCFA IP”] (“An ESU is included within the term ‘species or subspecies’ in sections 2062 and 2067.”). While the ESU concept has primarily been applied to fish, the Commission recently listed an ESU of a mammal, the Pacific Fisher, as a “threatened species.” See 14 C.C.R. 670.5(b)(6)(J) (“Fisher (*Pekania pennant*) Southern Sierra Nevada Evolutionarily Significant Unit”). Moreover, unlike the federal ESA, where listing of distinct populations segments (DPSs), of which ESUs are subcategory, is restricted to vertebrate species (16 U.S.C. § 1532(16) (definition of “species”), the ESU concept under CESA has no such limitation and applies to all listable taxa, including plants.

The populations currently delineated as YUBR North and YUBR South have been recognized for over 40 years and recently confirmed by USFWS (2018).

Rowlands (1978, p. 72) subdivided the Joshua tree range into five regions based on differences in geographic distribution, varieties (i.e., species in this SSA), vegetation, and temperature and rainfall amounts. Based on these regions and more current distribution models (Cole *et al.* 2011, pp. 139–140), we delineated two populations of *Yucca brevifolia* [*Y. brevifolia* south (YUBR South) and *Y. brevifolia* north (YUBR North)], and three populations of *Y. jaegeriana* [*Y. jaegeriana* central (YUJA Central), *Y. jaegeriana* north (YUJA North), and *Y. jaegeriana* east (YUJA East)]. We added a sixth population, the Hybrid Zone in Tikaboo Valley, to distinguish the geographic area where both species, and their pollinators, come into contact between YUBR North and YUJA North.

The two *Y. brevifolia* populations are separated by a small gap in their range, with the northern edge of YUBR South reaching the southern parts of China Lake and the southern boundary of YUBR North reaching the northern edge of the base (Figure 8). USFWS (2018) characterizes YUBR North habitats as “somewhat drier and less diverse than YUBR South,” with the lower elevations of YUBR South comprised of mostly creosote bush shrubland, while YUBR North associated vegetation including single-leaf pinyon, juniper, and sagebrush. At its simplest, YUBR South occurs mostly in the creosote dominated Western Mojave while YUBR North occurs in the area where the Northern Mojave transitions to the Great Basin and sagebrush becomes more dominant. This significant difference in habitat between the two population is sufficient to recognize them as ESUs for separate evaluation in the event full species listing is ultimately not deemed warranted by the Commission.

10 Recommended Management and Recovery Actions

For all species imperiled due to the impending loss of their suitable habitat as a result of climate change, the most important recovery actions are those that lead to rapid and steep greenhouse gas emissions reductions so as to minimize the additional warming that will occur in the climate system. However, given inertia in both the climate system and society, significant additional warming is unavoidable even under the most optimistic climate scenarios. Species that are already showing the effects of warming will continue to suffer and decline. For many

narrowly-endemic species with limited dispersal capabilities we will soon reach a point where little else can be done other than ex situ conservation in captivity and/or via assisted migration. It is hard to be optimistic about the fate of such species, as they will likely be lost from the wild even under more moderate warming scenarios.

While the threats facing *Y. brevifolia* in the coming decades are dire, unlike more narrowly-endemic species, the species has the benefit of being long-lived, with a relatively large current distribution spread across elevational and latitudinal gradients, much of which is in protected areas. Consequently, if the species and its habitat are protected early from other threats, and with active management to enhance recruitment and survival, and potentially dispersal, the western Joshua tree has a realistic chance of persisting in the wild. In this context, recommendations for the management and recovery of the western Joshua tree are as follows:

1. The governor declares a climate emergency and takes all necessary action to set California on a path to full decarbonization of our economy by no later than 2045 (e.g. banning the sale of new fossil fuel vehicles by 2030 and requiring the generation of all electricity from carbon-free sources by 2030).
2. CDFW prepares a recovery plan for *Y. brevifolia* pursuant to Cal. Fish & Game Code § 2079.1.
3. CDFW works with local jurisdictions within the range of *Y. brevifolia* to develop NCCPs that protect from development all high-density Joshua tree habitat remaining on private lands.
4. The California Department of Parks and Recreation develops and implements management plans (including fire management plans) focused on Joshua tree protection for state park units within the range of *Y. brevifolia* (Red Rock Canyon State Park and Eastern Kern County Onyx Ranch State Vehicular Recreation Area in Kern County and Saddleback Butte State Park, Arthur B. Ripley Desert Woodland State Park and Antelope Valley California Poppy Reserve in Los Angeles County).
5. The California Department of Parks and Recreation seeks to acquire habitat to expand and connect existing state parks for protection and restoration of Joshua tree habitat.
6. CDFW expands its cooperative work with relevant federal agencies (NPS, DoD, BLM, USFWS) to better protect Joshua trees on federal land.
7. CDFW works with the University of California, California Invasive Plants Council and other institutions and agencies to develop effective measures to control the spread of invasive grasses in *Y. brevifolia* habitat.
8. CDFW works with CAL-FIRE to develop protocols for fire suppression activities within the range of *Y. brevifolia* that maximize protection of the species, while minimizing ground disturbance that may foster the spread of non-native grasses and other invasive species.
9. CDFW works with relevant entities to establish and maintain a seed bank of *Y. brevifolia* collected throughout the range of the species to ensure protection of its genetic diversity.
10. CDFW works with relevant entities to identify potential sites for assisted migration and develop protocols for carrying out such activities.

11 Conclusion

The Joshua tree has long been the most iconic species of the Mojave Desert. Given the well-publicized threats facing the species in the face of climate change, it has recently become an emblem of our society's failure to address the climate crisis. But the Joshua tree is also uniquely situated to become an example of successful action to save a species threatened by climate change. Action taken in and by California to save the species can serve as a model for proactive climate adaptation efforts not just in California but around the world. Listing the species under CESA is not just a symbolically important act of California recognizing the threats the species faces from climate change, but also can serve as the impetus for meaningful management actions that can help ensure the species remains a living icon in perpetuity.

12 References Cited

Copies of references cited in the petition are either linked to websites below or included as files on a disk accompanying a hard copy of the petition sent to the Commission.

Abella, S.R., E.C. Engel, C.L. Lund, J.E. Spencer. 2009) Early post-fire plant establishment on a Mojave Desert burn. *Madroño* 57(3):137-148.

Allen, E B. and L.H. Geiser. 2011. North American deserts. In L.H. Pardo, M.J. Robin-Abbott and C T. Driscoll (Eds.), *Assessment of Nitrogen Deposition Effects and Empirical Critical Loads of Nitrogen for Ecoregions of the United States* (pp. 133-142): General Technical Report NRS-80.

Allen, E.B., L.E. Rao, R.J. Steers, A. Bytnerowicz, and M.E. Fenn. 2009. Impacts of atmospheric nitrogen deposition on vegetation and soils at Joshua Tree National Park. *The Mojave Desert: Ecosystem Processes and Sustainability* (pp. 78–100). Las Vegas, NV: University of Nevada Press.

Althoff, D.M., K.A. Segraves, and J.P. Sparks. 2004. Characterizing the interaction between the bogus yucca moths and yuccas: do bogus yucca moths impact yucca reproductive success? *Oecologia* 140:321–327.

[APG] Angiosperm Phylogeny Group. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181 (1): 1–20.

Barrows, C.W. and M.L. Murphy-Mariscal. 2012. Modeling impacts of climate change on Joshua trees at their southern boundary: How scale impacts predictions. *Biological Conservation* 152:29–36.

Bonham 2013. Report to The Fish and Game Commission Status Review of the American Pika (*Ochotona princeps*) in California.

Borchert, M.I. and L.A. DeFalco. 2016. *Yucca brevifolia* fruit production, predispersal seed predation, and fruit removal by rodents during two years of contrasting reproduction. *American Journal of Botany* 03(5):830–836.

Brittingham, S. and L.R. Walker. 2000. Facilitation of *Yucca brevifolia* recruitment by Mojave Desert shrubs. *Western North American Naturalist* 60(4):374–383.

Brooks, M.L. 2003. Effects of increased soil nitrogen on the dominance of annual plants in the Mojave Desert. *Journal of Applied Ecology* 40:344-353.

Brooks, M.L. and K.H. Berry. 2006. Dominance and environmental correlates of alien annual plants in the Mojave Desert, USA. *Journal of Arid Environments* 67:100–124

Brooks, M.L. and J.R. Matchett. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980-2004. *Journal of Arid Environments* 67:148–164.

Brooks, M.L., Minnich, R.A., Matchett, J., 2018. Southeastern Deserts Bioregion. In *Fire in California's Ecosystems* 2nd Edition. University of California Press.

[BLM] Bureau of Land Management. 2002. Northern and Eastern Mojave Plan (NEMO). DOI-BLM-CA-D010-2002-0001-RMP-EIS (Northern and Eastern Mojave RMP Amendment).

<https://eplanning.blm.gov/epl-front-office/eplanning/planAndProjectSite.do?methodName=renderDefaultPlanOrProjectSite&projectId=73191>

[BLM] Bureau of Land Management. 2006. West Mojave Plan (WEMO). DOI-BLM-CA-D010-2003-0001-RMP-EIS (West Mojave RMP Amendment).

<https://eplanning.blm.gov/epl-front-office/eplanning/planAndProjectSite.do?methodName=renderDefaultPlanOrProjectSite&projectId=72544>

[BLM] Bureau of Land Management. 2016. Desert Renewable Energy Conservation Plan (DRECP). DOI-BLM-CA-D010-2014-0001-RMP-EIS (DRECP Amendment).

<https://eplanning.blm.gov/epl-front-office/eplanning/planAndProjectSite.do?methodName=dispatchToPatternPage¤tPageId=95675>

[BLM] Bureau of Land Management. 2019. West Mojave Route Network Project (WMRNP). DOI-BLM-CA-D080-2018-0008-EIS (West Mojave Route Network Project SEIS)

<https://eplanning.blm.gov/epl-front-office/eplanning/planAndProjectSite.do?methodName=dispatchToPatternPage¤tPageId=139661>

Bytnerowicz, A., Fenn, M.E., Allen, E.B., and Cisneros, R. 2016. Ecologically relevant atmospheric chemistry. In *Ecosystems of California*. Chapter 7. Edited by E. Zavaleta and H.A. Mooney. University of California Press, Berkeley, Calif. pp. 107–128.

Carr, H. 1930. *The Lancer*. Desert Magazine, July 1930. Pasadena, CA.

[CAT] Climate Action Tracker, USA. 2019. <http://climateactiontracker.org/countries/usa>. (updated version September 19, 2019).

- Cole, K.L., K. Ironside, J. Eischeid, G. Garfin, P.B. Duffy, and C. Toney. 2011. Past and ongoing shifts in Joshua tree distribution support future modeled range contraction. *Ecological Applications* 21(1):137–149.
- Cole, W.S., A.S. James, and C.I. Smith. 2017. First Recorded Observations of Pollination and Oviposition Behavior in *Tegeticula antithetica* (Lepidoptera: Prodoxidae) Suggest a Functional Basis for Coevolution with Joshua Tree (*Yucca*) Hosts. *Annals of the Entomological Society of America* 110(4):390–397.
- Comanor, P.L. and W.H. Clark. 2000. Preliminary growth rates and a proposed age-form classification for the Joshua tree, *Yucca brevifolia* (Agavaceae). *Haseltonia* 7:37-45.
- Cornett, J.W. 2014. Population dynamics of the Joshua tree (*Yucca brevifolia*): Twenty-three year analysis, Lost Horse Valley, Joshua Tree National Park. In R. E. Reynolds (Ed.), *Not a Drop Left to Drink* (pp. 71-73): California State University Desert Studies Center, 2014 Desert Symposium.
- Cornett, J.W. 2018. Joshua trees are blooming early in the desert. It's not a good thing — you can thank climate change. *DESERT* magazine. Jan. 30, 2019
- DiChristopher, T., *US crude oil exports hit a record last week at 3.6 million barrels a day*, CONSUMER NEWS AND BUSINESS CHANNEL, Feb. 21, 2019, available at: <https://www.cnbc.com/2019/02/21/us-crude-oil-exports-hit-a-record-high-last-week.html>.
- DeFalco, L.A., T.C. Esque, S.J. Scoles-Sciulla, and J. Rodgers. 2010. Desert wildfire and severe drought diminish survivorship of the long-lived Joshua tree (*Yucca brevifolia*; Agavaceae). *American Journal of Botany* 97(2):243–250.
- DeFalco, L.A., G.C.J. Fernandez, and R.S. Nowak. 2007. Variation in the establishment of a non-native annual grass influences competitive interactions with Mojave Desert perennials. *Biological Invasions* 9:293–307.
- Dole, K.P., M.E. Loik, and L.C. Sloan. 2003. The relative importance of climate change and the physiological effects of CO₂ on freezing tolerance for the future distribution of *Yucca brevifolia*. *Global and Planetary Change* 36:137–146.
- Engelmann, G. 1871. *Yucca brevifolia*, p. 496. In C. King, Report No. 5, Geological exploration of the fortieth parallel. Government Printing Office, Washington.
- Esque, T.C., P.A. Medica, D.F. Shrylock, L.A. DeFalco, R.H. Webb, and R.B. Hunter. 2015. Direct and indirect effects of environmental variability on growth and survivorship of pre-reproductive Joshua trees, *Yucca brevifolia* Engelm. (Agavaceae). *American Journal of Botany*. 102(1):85–91.
- Erickson, P., A. Down, M. Lazarus, and D. Koplow. 2017. Effect of subsidies to fossil fuel companies on United States crude oil production. *Nature Energy* 2:891-898.

- Fitzpatrick, M.C. and W.W. Hargrove. 2009. The projection of species distribution models and the problem of non-analog climate. *Biodiversity Conservation* 18:2255–2261
- Frakes, N. 2017. Invasive Plant Management at Joshua Tree National Park. Presentation at California Invasive Plant Council Symposium, October 2017.
- Fremont, J.C. 1845. Report of the Exploring Expedition to the Rocky Mountains in the Year 1842, and to Oregon and North California in the years 1843-44. 28th Congress, 2d Session. Gales and Seaton, Washington, D.C.
- Gilliland, K.D., N.J. Huntly, and J.E. Anderson. 2006. Age and population structure of Joshua trees (*Yucca brevifolia*) in the northwestern Mojave Desert. *Western North American Naturalist* 66:202–208.
- Godsoe, W., E. Strand, C.I. Smith, J.B. Yoder, T.C. Esque, and O. Pellmyr. 2009. Divergence in an obligate mutualism is not explained by divergent climatic factors. *New Phytologist* 183:589–599.
- Godsoe, W., J.B. Yoder, C.I. Smith, and O. Pellmyr. 2008. Coevolution and divergence in the Joshua tree/yucca moth mutualism. *The American Naturalist* 171(6):816–823.
- Griffin, H.E. 1930. Preserving California Desert Scenery. *Desert Magazine*, February 1930. Pasadena, CA.
- Gucker, C.L. 2006. *Yucca brevifolia*. In: Fire Effects Information System, U. S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/>.
- Harrower, J. and G. S. Gilbert. 2018. Context-dependent mutualisms in the Joshua tree–yucca moth system shift along a climate gradient. *Ecosphere* 9(9):e02439. 10.1002/ecs2.2439.
- Hess, W.J. 2012. *Yucca brevifolia*. In Jepson Flora Project (eds.) Jepson eFlora, http://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=48766 (accessed on October 13, 2019).
- Holmgren, C.A., J.L. Betancourt, and K.A. Rylander. 2010. A long-term vegetation history of the Mojave–Colorado Desert ecotone at Joshua Tree National Park. *Journal of Quaternary Science* 25(2) 222–236.
- Hopkins, F. (University of California, Riverside). 2018. Inland Deserts Summary Report. California’s Fourth Climate Change Assessment. Publication number: SUM-CCCA4-2018-008.
- Iknayan, K.J. and S.R. Beissinger. 2018. Collapse of a desert bird community over the past century driven by climate change. *Proc. Natl. Acad. Sci. U.S.A.* 115:8597–8602.

[ITIS] Integrated Taxonomic Information System. 2019. ITIS Database. [Online]. Available: <http://www.itis.gov/index.html>.

[IPCC] Intergovernmental Panel on Climate Change (IPCC). 2018. Global Warming of 1.5° C: An IPCC Special Report on the Impacts of Global Warming of 1.5° C Above Pre-industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty. Intergovernmental Panel on Climate Change. Available at: <http://www.ipcc.ch/report/sr15/>.

Jaeger, E. C. 1965. The California Desert. Stanford University Press. Stanford, California

Jurand, B.S. and S.R. Abella. 2013. Soil Seed Banks of the Exotic Annual Grass *Bromus rubens* on a Burned Desert Landscape. *Rangeland Ecology and Management*. 66:157–163.

Keeley, J.E. and A. Meyers. 1985. Effect of heat on seed germination of southwestern *Yucca* species. *The Southwestern Naturalist*. 30(2): 303-304.

Klinger, R. and M. Brooks. 2017. Alternative pathways to landscape transformation: invasive grasses, burn severity and fire frequency in arid ecosystems. *Journal of Ecology*. 105:1521–1533.

Lenz, L.W. 2001. Seed dispersal in *Yucca brevifolia* (Agavaceae) present and past, with consideration of the future of the species. *Aliso* 20:61–74.

Lenz, L.W. 2007. Reassessment of *Yucca brevifolia* and recognition of *Y. jaegeriana* as a distinct species. *Aliso: A Journal of Systematic and Evolutionary Botany* 24(1):97–104.

Le Quéré, C. et al. 2018. Global carbon budget 2018, 10 *Earth Syst. Sci. Data* 10:21412194.

Little, E. L. 1950. Southwestern trees: a guide to the native species of New Mexico and Arizona. Agricultural Handbook No. 9. Washington, DC: U.S. Department of Agriculture, Forest Service. 109 p.

Loik, M.E., C.D. St. Onge, and J. Rogers. 2000a. Post-fire recruitment of *Yucca brevifolia* and *Yucca schidigera* in Joshua Tree National Park, California. In J.E. Keeley, M. Baer-Keeley, and C.J. Fotheringham [eds.], *Second interface between ecology and land development in California*, 79 – 85. Open-File Report 00-62, U.S. Geological Survey, Sacramento, California, USA.

Loik, M.E., T.E. Huxman, E.P. Hamerlynck, and S.D. Smith. 2000b. Low temperature tolerance and cold acclimation for seedlings of three Mojave Desert *Yucca* species exposed to elevated CO₂. *Journal of Arid Environments*, 46(1):43–56.

Lybbert, A.H. and S.B. St. Clair. 2017. Wildfire and floral herbivory alter reproduction and pollinator mutualisms of *Yuccas* and *Yucca* moths. *Journal of Plant Ecology*. 10(5):851-858

Maloney, K.A., E.L. Mudrak, A. Fuentes-Ramirez, H. Parag, M. Schat, and C. Holzapfel. 2019. Increased fire risk in Mojave and Sonoran shrublands due to exotic species and extreme rainfall events. 10(2):e02592.

Mufson, S., C. Mooney, J. Eilperin, and J. Muyskens. 2019. 2°C: Beyond the Limit: Extreme climate change has arrived in America. Washington Post. <https://www.washingtonpost.com/graphics/2019/national/climate-environment/climate-change-america/>

National Park Service (NPS). 2012. Death Valley National Park Wilderness and Backcountry Stewardship Plan and Environmental Assessment. <https://parkplanning.nps.gov/showFile.cfm?projectID=23311&MIMEType=application%252Fpdf&filename=DEVA%5FWilderness%5F%5F%5FBackcountry%5FStewardship%5FPlan%2Epdf&sfid=139732>

Notaro, M., A. Mauss, and J.W. Williams. 2012. Projected vegetation changes for the American Southwest: Combined dynamic modeling and bioclimatic-envelope approach. *Ecological Applications* 22(4):1365–1388.

[OCI] Oil Change International, *Drilling Toward Disaster: Why U.S. Oil and Gas Expansion Is Incompatible with Climate Limits* (January 2019), <http://priceofoil.org/drilling-towards-disaster>.

Pardo, L.H., M.E. Fenn, C.L. Goodale, L.H. Geiser, C.T. Driscoll, E.B. Allen, J.S. Baron, R. Bobbink, W.D. Bowman, C.M. Clark, B. Emmett, F.S. Gilliam, T.L. Greaver, S.J. Hall, E.A. Lilleskov, L. Liu, J.A. Lynch, K.J. Nadelhoffer, S. S. Perakis, M.J. Robin-Abbott, J.L. Stoddard, K.C. Weathers, and R.L. Dennis. 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. *Ecological Applications* 21(8):3049–3082.

Pearson, R.G. and T.P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology & Biogeography* 12:361–371

Pellmyr, O. 2003. Yuccas, yucca moths, and coevolution: A review. *Annals of the Missouri Botanical Garden* 90(1):35–55.

Pellmyr, O. and K.A. Segraves. 2003. Pollinator divergence within an obligate mutualism: Two yucca moth species (Lepidoptera; Prodoxidae: *Tegeticula*) on the Joshua tree (*Yucca brevifolia*; Agavaceae). *Annals of the Entomological Society of America* 96:716–722.

Reynolds, M.B.J., L.A. DeFalco, and T.C. Esque. 2012. Short seed longevity, variable germination conditions and infrequent establishment events provide a narrow window for *Yucca brevifolia* (Agavaceae) recruitment. *American Journal of Botany* 99(10):1647–1654.

Riddell, E.A., K.J. Iknayana, B.O. Wolfc, B.S., and Steven R. Beissinger. 2019. Cooling requirements fueled the collapse of a desert bird community from climate change. *Proc. Natl. Acad. Sci. U.S.A.* <https://doi.org/10.1073/pnas.1908791116115>, 8597–8602.

- Rogelj, J., G. Luderer, R.C. Pietzker, E. Kriegler, M. Schaeffer, V. Krey, and K. Riahi. 2015. Energy system transformations for limiting end-of-century warming to below 1.5°C, 5 Nature Climate Change 519.
- Royer, A.M., M.A. Streisfeld, and C.I. Smith. 2016. Population genomics of divergence within an obligate pollination mutualism: Selection maintains differences between Joshua tree species. American Journal of Botany 03(10):1730–1741.
- Runyon, F.F. 1930. Our Natural Scenic Spots. Desert Magazine, July 1930. Pasadena, CA.
- Sanford, M.P. and N. Huntly. 2009. Selective herbivory by the desert woodrat (*Neotoma lepida*) on Joshua trees (*Yucca brevifolia*). Western North American Naturalist 69:165–170.
- Scheffers, B. R., L. De Meester, T.C.L. Bridge, A.A. Hoffmann, J.M. Pandolfi, R.T. Corlett, S.H.M. Butchart, P. Pearce-Kelly, K.M. Kovacs, D. Dudgeon, M. Pacifici, C. Rondinini, W.B. Foden, T. G. Martin, C. Mora, D. Bickford and J.E.M. Watson. 2016. The broad footprint of climate change from genes to biomes to people. Science 354:6313.
- Short, K.C., 2017. Spatial wildfire occurrence data for the United States, 1992-2015 [FPA_FOD_20170508]. 4th Edition. Fort Collins, CO: Forest Service Research Data Archive. <https://doi.org/10.2737/RDS-2013-0009.4>.
- Smith, C.I. 2018. Peer Review of USFWS Draft Species Status Assessment for Joshua Tree. Email comment, dated June 11, 2018.
- Smith, C.I., C.S. Drummond, W. Godsoe, J.B. Yoder, and O. Pellmyr. 2009. Host specificity and reproductive success of yucca moths (*Tegeticula* spp. Lepidoptera: Prodoxidae) mirror patterns of gene flow between host plant varieties of the Joshua tree (*Yucca brevifolia*: Agavaceae). Molecular Ecology 18:5218–5229.
- Smith C.I., O. Pellmyr, D.M. Althoff, M. Balcázar-Lara, J. Leebens-Mack, K.A. Segraves. 2008. Pattern and timing of diversification in *Yucca* (Agavaceae): specialized pollination does not escalate rates of diversification. Proceedings of the Royal Society of London, Series B: Biological Sciences 275:249–258.
- Smith, C.I., S. Tank, W. Godsoe, J. Levenick, E. Strand, T.C. Esque. 2011. Comparative phylogeography of a coevolved community: Concerted population expansions in Joshua trees and four yucca moths. PLoS One 6(10):1–18.
- Smith, C.I., W. Godsoe, S. Tank, J.B. Yoder, and O. Pellmyr. 2008. Distinguishing coevolution from covariance in an obligate pollination mutualism: Asynchronous divergence in Joshua tree and its pollinators. Evolution 62(10):2676–2687.
- Smith, S.D., T.L. Hartsock, and P.S. Nobel. 1983. Ecophysiology of *Yucca brevifolia*, an arborescent monocot of the Mojave Desert. Oecologia 60:10–17.

Smith, S.D., T.E. Huxman, S.F. Zitzer, T.N. Charlet, D.C. Housman, and J.S. Coleman. 2000. Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature* 408:79–82.

[SCAG] Southern California Association of Governments. 2019. Local Profiles. <http://www.scag.ca.gov/DataAndTools/Pages/LocalProfiles.aspx>

St. Clair, S.B. and J. Hoines. 2018. Reproductive ecology and stand structure of Joshua tree forests across climate gradients of the Mojave Desert. *PLoS ONE* 13(2): e0193248.

Star, J., E.L. Rowland, M.E. Black, C.A.F. Enquist, G. Garfin, C.H. Hoffman, H. Hartmann, K.L. Jacobs, R.H. Moss and A.M. Waple. 2016. Supporting adaptation decisions through scenario planning: Enabling the effective use of multiple methods. *Climate Risk Management*. 13:88-94.

Starr, T.N., K.E. Gadek, J.B. Yoder, R. Flatz, and C.I. Smith. 2013. Asymmetric hybridization and gene flow between Joshua trees (Agavaceae: *Yucca*) reflect differences in pollinator host specificity. *Molecular Ecology* 22(2):437-49.

Svenning, J.-C. and B. Sandel. 2013. Disequilibrium Vegetation Dynamics Under Future Climate Change. *American Journal of Botany* 100(7):1266–1286.

Sweet, L.C., T. Green, J.G.C. Heintz, N. Frakes, N. Graver, J.S. Rangitsch, J.E. Rodgers, S. Heacox, and C.W. Barrows. 2019. Congruence between future distribution models and empirical data for an iconic species at Joshua Tree National Park. *Ecosphere* 10(6):e02763/ecs2.2763.

Syphard, A.D., J.E. Keeley, and J.T. Abatzoglou. 2017. Trends and drivers of fire activity vary across California aridland ecosystems. *Journal of Arid Environments* 144:110–122.

Syphard, A D., H. Rustigian-romsos, M. Mann, E. Conlisk, M.A. Moritz, and D. Ackerly. 2019. The relative influence of climate and housing development on current and projected future fire patterns and structure loss across three California landscapes. *Global Environmental Change*, 56:41–55.

Tagestad J., M. Brooks, V. Cullinan, J. Downs, and R. Mckinley. 2016. Precipitation Regime Classification for the Mojave Desert: Implications for fire occurrence. *Journal of Arid Environments* 124:388–397.

Thompson, R.S., S.W. Hostetler, P.J. Bartlein, and K.H. Anderson. 1998. A Strategy for Assessing Potential Future Changes in Climate, Hydrology, and Vegetation in the Western United States. U.S. Geological Survey Circular 1153. United States Government Printing Office, Washington.

Trelease, W. 1893. Further Studies of Yuccas and Their Pollination. *Missouri Botanical Garden Annual Report*, Vol. 1893, pp. 181-226.

Turner, R.M. 1982. Mohave desert scrub. In D. Brown (Ed.), *Biotic Communities: Southwestern United States and Northwestern Mexico*. Salt Lake City, UT: University of Utah Press.

United Nations Framework Convention on Climate Change, Conference of the Parties Nov. 30-Dec. 11, 2015, Adoption of the Paris Agreement Art. 2, U.N. Doc. FCCC/CP/2015/L.9 (Dec. 12, 2015) (Paris Agreement).

[USEIA] U.S. Energy Information Administration. 2016. Hydraulically fractured wells provide two-thirds of U.S. natural gas production (May 5, 2016).
<https://www.eia.gov/todayinenergy/detail.php?id=26112>.

[USEIA] U.S. Energy Information Administration. 2016. Hydraulic fracturing accounts for about half of current U.S. crude oil production (March 15, 2016).
<https://www.eia.gov/todayinenergy/detail.php?id=25372>.

[EPA] U.S. Environmental Protection Agency. 2009. Land-Use Scenarios: National-Scale Housing-Density Scenarios Consistent with Climate Change Storylines (Final Report). U.S. Environmental Protection Agency, Washington, DC; EPA/600/R-08/076F. Available from the National Technical Information Service, Springfield, VA, and online at <http://www.epa.gov/ncea>.

[USFWS] U.S. Fish and Wildlife Service. 2018. Joshua Tree Species Status Assessment. Dated July 20, 2018. 113 pp. + Appendices A–C.

[USFWS] U.S. Fish and Wildlife Service. 2019. Endangered and Threatened Wildlife and Plants; 12-Month Findings on Petitions to List Eight Species as Endangered or Threatened Species, 84 Fed. Reg. 41694 (August 15, 2019).

[USGCRP] U.S. Global Change Research Program. 2017. Climate Science Special Report, Fourth National Climate Assessment, Volume I. <https://science2017.globalchange.gov/>.

[USGCRP] U.S. Global Change Research Program. 2018. Impacts, Risks, and Adaptation in the United States, Fourth National Climate Assessment, Volume II. <https://nca2018.globalchange.gov/>.

Vander Wall, S.B., T. Esque, D. Haines, M. Garnett, and B. Waitman. 2006. Joshua tree (*Yucca brevifolia*) seeds are dispersed by seed-caching rodents. *Ecoscience* 13:539–543.

Vamstad, M.S. and J.T. Rotenberry. 2010. Effects of fire on vegetation and small mammal communities in a Mojave Desert Joshua tree woodland. *J. Arid Environ.* 74, 1309–1318.

Waitman, B.A., S.B. Vander Wall, and T.C. Esque. 2012. Seed dispersal and seed fate in Joshua tree (*Yucca brevifolia*). *Journal of Arid Environments* 81:1–8.

Wallace, G. 2017. WEG 2015 petition to list *Yucca brevifolia*. U.S. Fish and Wildlife Service White Paper, 6 p. Carlsbad, CA.

Warren, R., J. Price, A. Fischlin, S. de la Nava Santos, and G. Midgley. 2011. Increasing impacts of climate change upon ecosystems with increasing global mean temperature rise. *Climatic Change* 106(2):141–177.

Warren, S.D, L.S. Baggett, and H. Warren. 2016. Directional Floral Orientation in Joshua Trees (*Yucca brevifolia*). *Western North American Naturalist* 76(3):374–378.

Webber, J.M. 1953. *Yuccas of the Southwest*. Agriculture Monograph No. 17. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.

[WEG] WildEarth Guardians. 2015. Petition to List the Joshua Tree (*Yucca brevifolia*) under the Endangered Species Act.

Went, F.W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. *Ecology* 29(3):242–253.

Went, F.W. 1957. The experimental control of plant growth. *Chronica Botanica* Volume 17. Waltham, MA: Chronica Botanica.

Wentz, J. & M.D. Gerrard, Persistent Regulations: A Detailed Assessment of the Trump Administration’s Efforts to Repeal Federal Climate Protections (2019), <http://columbiaclimatelaw.com/files/2019/06/Wentz-and-Gerrard-2019-06-Persistent-Regulations.pdf>.

Wiens, J. J. 2016. Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biology* 14(12):1–18.

Yoder, J.B., C.I. Smith, D.J. Rowley, R. Flatz, W. Godsoe, C. Drummond, and O. Pellmyr. 2013. Effects of gene flow on phenotype matching between two varieties of Joshua tree (*Yucca brevifolia*, Agavaceae) and their pollinators. *Journal of Evolutionary Biology* 26:1220–1233.