State of California
Natural Resources Agency
Department of Fish and Wildlife

REPORT TO THE FISH AND GAME COMMISSION
STATUS REVIEW OF WESTERN JOSHUA TREE (*Yucca brevifolia*)

March 2022


Western Joshua tree, photo by Jeb McKay Bjerke

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ABBREVIATIONS, ACRONYMS, AND TERMS

BLM – Bureau of Land Management
CCVI – Climate Change Vulnerability Index
CEQA – California Environmental Quality Act
CESA – California Endangered Species Act
CNDDB – California Natural Diversity Database
Commission – California Fish and Game Commission
Department – California Department of Fish and Wildlife
DNPA – California Desert Native Plants Act
ESA – Federal Endangered Species Act
et al. – “and others”
Ibid. – “in the same source”
Id. – “the same”
INRMP – Integrated natural resources management plan
IUCN – International Union for Conservation of Nature
NEPA – National Environmental Policy Act
NPPA – Native Plant Protection Act
ssp. – Subspecies
var. – Variety

EXECUTIVE SUMMARY

This Status Review is based on the best scientific information available to the California Department of Fish and Wildlife (Department) on western Joshua tree (*Yucca brevifolia* Engelm.) and serves as the basis for the California Department of Fish and Wildlife's (Department) recommendation to the California Fish and Game Commission (Commission) on whether to list the species as threatened under the California Endangered Species Act (CESA). On October 21, 2019, the Center for Biological Diversity submitted a petition to the Commission requesting that western Joshua tree be listed as a threatened species under CESA (Petition). At its scheduled public meeting on September 22, 2020, the Commission considered the Petition, and based in part on the Department's Petition evaluation and recommendation, found sufficient information exists to indicate the petitioned action may be warranted and accepted the Petition for consideration. Western Joshua tree was designated a candidate species on October 9, 2020, upon publication of the Commission's notice of its findings. This Status Review has also been independently reviewed by scientific peers.

Western Joshua tree is relatively widespread and abundant in California and is found in the Mojave Desert and Great Basin. Precipitation in these areas is low and oscillates between wetter and drier conditions over multi-year and multi-decade timescales. Sexual reproduction of western Joshua tree requires pollination by the moth species *Tegeticula synthetica,* and seed dispersal is facilitated by the scatter hoarding behavior of rodents. Several successive years of wet and/or cool conditions are then required to ensure seed germination and seedling survival. A western Joshua tree may require 30 to 50 or more years to reach reproductive maturity, and individual trees can survive for very long periods of time, perhaps over 150 years. The species is capable of asexual (clonal) reproduction which may allow individuals to survive indefinitely under appropriate conditions.

The population size and area occupied by western Joshua tree have declined since European settlement largely due to habitat modification and destruction, a trend that has continued to the present. Primary threats to the species are climate change, development and other human activities, and wildfire. Available species distribution models suggest that areas predicted to be suitable for western Joshua tree based on 20th century climate data will decline substantially through the end of the 21st century (2100) as a result of climate change, especially in the southern and lower elevational portions of its range. Predicted habitat for western Joshua tree based on 20th century climate conditions will likely remain in some areas at the end of the 21st century, and newly appear to the north and in higher elevation areas, although western Joshua tree is unlikely to colonize areas with newly suitable climate conditions quickly. The degree to which climate change will affect western Joshua tree populations will depend on both

the magnitude of climate change and the species' resilience to a changing climate. Predicted loss of areas of 20th century suitable climate conditions for western Joshua tree could result in an overall reduction in the number of new individuals added to the population or an increase in adult tree mortality, but the Department does not currently have information demonstrating that loss of areas with 20th century suitable climate conditions will result in impacts on existing populations that are severe enough to threaten to eliminate the species from a significant portion of its range by the end of the 21st century. The effects of development and other human activities will cause western Joshua tree habitat and populations to be lost, particularly in the southern part of the species' range, but many populations within the range of the species are protected from development, suggesting that a significant portion of the species' range will not be lost by development alone. Wildfire can also kill over half of western Joshua trees in areas that burn, and wildfire impacted approximately 2.5% of the species' range in each of the last two decades, but wildfire does not appear to result in loss of range, only lowering of abundance within the species' range.

There will be a substantial reduction in areas with 20th century suitable climate conditions for western Joshua tree by the end of the 21st century (2100), which is considered to be the foreseeable future for the purposes of this Status Review. This reduction in areas with 20th century suitable climate conditions in combination with other threats to the species is expected to have negative effects on the abundance of western Joshua tree and is substantial cause for concern. Nevertheless, western Joshua tree is currently abundant and widespread, which lessens the overall relative impact of the threats to the species, and substantially lowers the threat of extinction within the foreseeable future. Furthermore, the Department does not have the data to determine the extent to which climate changes that are expected to occur in the foreseeable future are likely to affect western Joshua tree range within California within this timeframe. While the Department recognizes the threats faced by the species, and the evidence presented in favor of the petitioned action, the scientific evidence that is currently possessed by the Department does not demonstrate that populations of the species are negatively trending in a way that would lead the Department to believe that the species is likely to be in serious danger of becoming extinct throughout all or a significant portion of its range in the foreseeable future.

The Department recommends that the Commission find that the recommended action to list western Joshua tree as a threatened species is not warranted.

INTRODUCTION

Species Being Reviewed

This Status Review addresses the plant *Yucca brevifolia* Engelm. For the purposes of this Status Review the term “western Joshua tree” shall mean the species *Yucca brevifolia* and the term “eastern Joshua tree” shall mean the species *Yucca jaegeriana* (McKelvey) L.W. Lenz. The more general term “Joshua tree” shall be used to mean both western Joshua tree and eastern Joshua tree collectively, or it may be used when the information presented is not known to be specific to one of the two species. Information that is specific to eastern Joshua tree is sometimes presented in this Status Review because it may be applicable to western Joshua tree or may provide relevant context. Additional information on the distinction between western Joshua tree and eastern Joshua tree is presented in the Taxonomy section of this Status Review.

Petition Evaluation Process

A petition to list the western Joshua tree (*Yucca brevifolia* Engelm.) as threatened under the California Endangered Species Act (CESA) was submitted to the Fish and Game Commission (Commission) on October 21, 2019 by the Center for Biological Diversity. Commission staff transmitted the petition to the Department of Fish and Wildlife (Department) pursuant to Fish and Game Code section 2073 on November 1, 2019 and published a formal notice of receipt of the petition on November 22, 2019 (Cal. Reg. Notice Register 2019, No. 47-Z, pp. 1592-1593). A petition to list or delist a species under CESA must include “information regarding the population trend, range, distribution, abundance, and life history of a species, the factors affecting the ability of the population to survive and reproduce, the degree and immediacy of the threat, the impact of existing management efforts, suggestions for future management, and the availability and sources of information. The petition shall also include information regarding the kind of habitat necessary for species survival, a detailed distribution map, and any other factors that the petitioner deems relevant” (Fish & G. Code, § 2072.3).

On March 11, 2020, the Department provided the Commission with its evaluation of the petition to assist the Commission in making a determination as to whether the petitioned action may be warranted based on the sufficiency of scientific information (Fish & G. Code, §§ 2073.5 & 2074.2; Cal. Code Regs., tit. 14, § 670.1, subds. (d) & (e)). By evaluating the information provided in the petition on its face and in relation to other relevant information the Department possessed or received relating to each of the relevant categories, the Department recommended to the Commission that the petition be accepted.

At its scheduled public meeting on September 22, 2020 by webinar/teleconference, the Commission considered the petition, the Department’s petition evaluation and recommendation, and comments received. The Commission found that sufficient information existed to indicate the petitioned action may be warranted and accepted the petition for consideration. Upon publication of the Commission's notice of its findings, western Joshua tree was designated a candidate species on October 9, 2020 (Cal. Reg. Notice Register 2020, No. 41-Z, p. 1349).

Status Review Overview

Following the Commission’s action to designate western Joshua tree a candidate species, the Department notified affected and interested parties and solicited data and comments on the petitioned action pursuant to Fish and Game Code section 2074.4 (see also Cal. Code Regs., tit. 14, § 670.1, subd. (f)(2)). Comments received are included in Appendix A of this report. The Department promptly commenced its review of the status of the species as required by Fish and Game Code section 2074.6, which has now concluded with this Status Review.

The review process included independent peer review of the draft Status Review by persons in the scientific/academic community acknowledged to be experts on subjects relevant to this Status Review and possessing the knowledge and expertise to critique the scientific validity of the Status Review contents. Appendix B contains the specific input provided to the Department by the individual peer reviewers, the Department’s written response to the input, and any amendments made to the Status Review (Fish & G. Code, § 2074.6; Cal. Code Regs., tit. 14, § 670.1, subd. (f)(2)). The Department does not have a duty or obligation to undertake independent studies or other assessments of western Joshua tree (Fish & G. Code, § 2074.8), and this Status Review is focused on presenting the relevant scientific information that was in the Department’s possession during preparation of this Status Review.

The Commission’s action designating western Joshua tree as a candidate species triggered the Department’s process for conducting a status review to inform the Commission’s decision on whether listing the species is warranted. At its scheduled public meeting on June 16, 2021 by webinar/teleconference, the Commission granted the Department a six-month extension to complete this Status Review and facilitate external peer review.

This Status Review report is not intended to be an exhaustive review of all published scientific literature relevant to western Joshua tree; rather, it is intended to summarize the key points from the best scientific information available relevant to the status of the species. This final report, based upon the best scientific information available to the Department, is informed by independent peer review of a draft report by scientists with expertise relevant to western Joshua tree. This review is intended to provide the Commission with the most current information on western Joshua tree and to serve as the basis for the Department's recommendation to the Commission on whether the petitioned action is warranted. The Status Review report also identifies habitat that may be essential to continued existence of the species and provides management recommendations for recovery of the species (Fish & G. Code, § 2074.6). Receipt of this report is to be placed on the agenda for the next available meeting of the Commission after delivery. At that time, the report will be made available to the public for a 30-day public comment period prior to the Commission taking any action on the petition.

BIOLOGY

Species Description

Western Joshua tree is a visually distinctive plant found in California's Mojave Desert and adjacent areas. The unique silhouette and tall stature of western Joshua tree relative to typical surrounding vegetation make it one of the most recognizable native plants of California deserts. Joshua tree has been utilized by Native American cultures for food, fiber, and other uses (Coville 1892, Stoffle et al. 1990, Fowler 1995, Small 2013, Gaughen pers. comm. 2020). Joshua tree landscapes are frequently represented in western art and culture (U2 1987, Bruno and Bruno 2017, Harrower 2019) and have become increasingly popular tourist destinations (NPS 2021). Joshua trees may also have medicinal properties (Patel 2012).

A summary of western Joshua tree's appearance and physical attributes was compiled from a number of sources, including scientific papers (Simpson 1975, Lenz 2007), botanical manuals (McKelvey 1938, Little 1950, Webber 1953, Hess and Robbins 1993, 2002, Alexander et al. 2008, Hess 2012), and the U.S. Forest Service's Fire Effects Information System (Gucker 2006).

Western Joshua tree is a woody evergreen plant, that can mature to heights of approximately 5 to 20 m (16 to 66 ft), although trees exceeding 10 m (33 ft) are rare (Cornett 1997). Western Joshua trees often have one main trunk that branches approximately one to three m (3 to 10 ft) above the ground, and older trees can have extensive branching and a large, rounded tree-like canopy. Western Joshua trees have a monopodial branching pattern, which means that after branching, one stem remains dominant, even though the branches may appear to be approximately equal in size. Branching of western Joshua tree typically occurs after an inflorescence is produced at the end of a stem, or after the growing tissue at the end of a stem (called the apical meristem) is otherwise damaged, such as by the yucca-boring weevil (*Scyphophorus yuccae*) (Jaeger 1965). Western Joshua trees typically produce two or three branches at the end of the stem after the apical meristem is damaged, but can produce up to five branches (Simpson 1975).

The leaves of western Joshua tree are narrowly tapered, 15 to 35 cm (5.9 to 13.8 in) long and 0.7 to 1.5 cm (0.3 to 0.6 in) wide with spiny tips, parallel veins, and expanded bases where they attach to the stem of the tree. The edges of the leaves are lined with minute teeth. The outer surface of the leaf has a thick and waxy coating to help reduce water loss. Leaves near the ends of stems tend to be oriented more vertically, while leaves that are lower tend to be oriented more horizontally, which may be an adaptation to optimize light utilization (Smith et al. 1983). The evergreen leaves of Joshua trees are used by the plant for many years, reducing the need to produce new biomass. Dead leaves can remain attached for a number of years, and fold down, concealing the younger stems and bark, contributing to western Joshua tree's distinctive shaggy appearance when viewed from a distance. Western Joshua trees produce woody stems via tissue called monocot cambium, but unlike many woody plants, the stems of western Joshua trees do not produce discernable secondary growth rings that may be used to precisely age plants (Barkley 1924, Simpson 1975, Zinkgraf et al. 2017, Jura-Morawiec et al. 2021). The soft, cork-like bark of western Joshua tree is visible after dead leaves fall from the stems of older plants.

Few observations of Joshua tree root systems are available. The root system of *Yucca* species was described as "deep and rather massive" by Crosswhite and Crosswhite (1984), but also described as shallow-rooted with little or no developed taproot system by Rundel and Gibson (1996). Gucker (2006) reports that mature Joshua trees may take advantage of infrequent rains by storing near-surface water collected through their extensive network of fibrous roots. Underground roots of eastern Joshua tree were observed 11 m (36 ft) away from what appeared to be the aboveground portion of the plant by Bowns (1973). Communities of fungi occur in association with western Joshua tree roots, forming mycorrhizal associations which may benefit western Joshua tree (Harrower and Gilbert 2021).

Some western Joshua trees grow in close groupings that are the result of asexual growth from underground stems called rhizomes; this growth form is more common at higher elevations (Rowlands 1978). When present, rhizomes grow horizontally and often produce sprouts approximately 1 to 3 m (3 to 10 ft) away from the parent plant (Gucker 2006); however, at higher elevations in the San Bernardino Mountains, sprouts as far as 5 m (16 ft) from parent plants have been observed (Borchert pers. comm. 2021). In areas where western Joshua tree exhibits abundant asexual growth, clumps of plants may form ring shapes when viewed from above, similar to the ring-shaped clumps found in other clonal plant species (Bonanomi et al. 2014).

Western Joshua trees produce a dense group of flowers at the ends of branches. These groups of flowers are arranged in panicles, which means that each group of flowers is branched, and the flowers that are near the base or outside of the group open before the flowers at the tip or close to the center. These panicles are approximately 20 to 40 cm (8 to 20 in) long, and tend to bend or tilt towards the south (Warren et al. 2016). Western Joshua tree panicles are composed of spherical-shaped generally cream-colored to greenish flowers, described by Trelease (1893) as having an "odor which is so oppressive as to render the flowers intolerable in a room," and described by Simpson (1975) as having a "strong, sweet, mushroom-like fragrance." Western Joshua tree flowers produce little if any nectar (Trelease 1893). The flowers of western Joshua tree have six perianth segments all resembling petals. These perianth segments are strongly incurved and never fully expand. Western Joshua tree flowers are bisexual, and have six male sexual parts called stamens, and one female sexual part called a pistil that has three ovary chambers. The stylar canal is the portion of a pistil that is used to transport genetic material from pollen to the ovules via pollen tubes. The length of the stylar canal of western Joshua tree pistils matches with the length of the organ that western Joshua tree's obligate pollinating moth, *Tegeticula synthetica*, uses to deposit eggs into the ovaries of western Joshua tree pistils.

After pollination, Joshua tree panicles develop into groups of approximately 2 to 30 fruits that are approximately 6 to 10 cm (2 to 4 in) long and approximately 5 cm (2 in) in diameter. Western Joshua tree seeds are thinly disc-shaped, generally black, and approximately 10 mm (0.39 in) in diameter (Figure 1). There are approximately 80 seeds in mature western Joshua tree fruits, and they are arranged in stacks (Borchert 2021). The fruits are spongy or leathery when young but become dry when mature and do not open to release seeds on their own. Fruits become brittle when dry, making it easier for animals or environmental influence to break open fruits and release the seeds.

Taxonomy

Under CESA, threatened and endangered species definitions include the description "…a native species or subspecies…" (Fish & G. Code, § 2062 and § 2067). The Legislature left the interpretation of what constitutes a "species or subspecies" under CESA to the Department and the Commission, the organizations responsible for providing the best scientific information and for making listing decisions, respectively. (*Cal. Forestry Assn. v. Cal. Fish and G. Com*. (2007) 156 Cal.App.4th 1535, 1548-49). In 2018, a California court of appeals decision determined that courts should give a "great deal of deference" to Commission listing determinations supported by Department scientific expertise (*Central Coast Forest Assn. v. Fish & G. Com*. (2018)

Figure 1: Western Joshua Tree Fruit with Seeds Consumed by Moth Larvae, photo by Jeb McKay Bjerke

18 Cal. App. 5th 1191, 1198-99). The Commission's authority to list necessarily includes discretion to determine what constitutes a species or subspecies (*Id*. at p. 1237).

Western Joshua tree (scientific name *Yucca brevifolia*) belongs to the group of flowering plants called monocots, which are characterized by having one embryonic leaf in their seeds, and often having leaves with parallel veins and flower parts that are in multiples of three. Within the monocots, Joshua tree has been placed in various plant families over the years, including the lily family (Liliaceae) and the agave family (Agavaceae). More recently, *Yucca* has been placed within an agave subfamily (Agavoideae) within a larger treatment of the asparagus family (Asparagaceae) (Chase et al. 2009, APG 2016, ITIS 2019).

There may be extensive traditional ecological knowledge of Joshua tree, however, the earliest recorded accounts known to the Department include a written description from 1844 (Fremont 1845) and an illustration from 1853 (Williamson 1853) which are discussed in more detail by Lenz (2007). The first scientific description of Joshua tree was in 1871 (Engelmann 1871, McKelvey 1938). The taxonomy of Joshua tree has subsequently been the subject of some dispute, and this dispute has largely focused on whether intraspecific taxa (additional taxonomic divisions within the species) exist, and if so, at what taxonomic rank those taxa should be recognized (i.e., variety, subspecies, or species). The history of this uncertainty has been described in various sources (McKelvey 1938, Lenz 2007, Jones and Goldrick 2015, Wallace 2017, USFWS 2018, Cummings 2019), and a summary of this history from these sources is presented below.

Two intraspecific taxa have been validly described since Engelmann's 1871 publication of the name *Yucca brevifolia*. *Yucca brevifolia* var. *herbertii* was described by Webber (1953) and included in Munz (1959), but this form is now understood to be a result of asexual growth of western Joshua tree from underground rhizomes, and this growth form is more common at higher elevations. *Yucca brevifolia* var. *herbertii* is therefore no longer recognized as a distinct taxon and is not discussed further in this Status Review.

Yucca brevifolia var. *jaegeriana* was first described by McKelvey (1938) and a number of sources have recognized this name since that time (Clokey 1951, McMinn 1951, Webber 1953, Munz 1959, Kearney and Peebles 1960, Rowlands 1978, Thorne et al. 1981, Kartesz 1987). The taxonomic rank of the name was recognized as a subspecies by Hochstätter (2001, 2002). Other sources, however, did not recognize the *jaegeriana* taxon to be distinct from *Yucca brevifolia* (Reveal 1977, Hess and Robbins 1993, 2002, McKinney and Hickman 1993, 2002, Hess 2012). As described by Wallace (2017), timing or oversight may have been the reason that the *jaegeriana* taxon was not recognized as distinct from *Yucca brevifolia* in the Flora of North America (Hess and Robbins 2002) or the second edition of the Jepson Manual (Hess 2012).

Lenz (2007) provided evidence that the *jaegeriana* taxon is distinct from *Yucca brevifolia*, and described *Yucca jaegeriana* as a species, highlighting differences in overall shape and form, branching, leaves, flowers, fruits, and different species of obligate pollinating moth. The pollinating moth for western Joshua tree is *Tegeticula* *synthetica* and the pollinating moth for eastern Joshua tree is *Tegeticula antithetica* (Pellmyr and Segraves 2003).

Since Lenz's work in 2007, a substantial amount of scientific attention has been directed towards understanding the coevolution of western Joshua tree, eastern Joshua tree, and their obligate pollinating moths, with much of this attention focused on a small area in Tikaboo Valley, Nevada where the two species co-occur, and hybridization has been observed (Pellmyr 2003; Smith et al. 2008b, 2008a, 2009, 2011, 2021; Godsoe et al. 2008, 2009, 2010; Starr et al. 2013, Yoder et al. 2013, Royer et al. 2016, 2020; Cole et al. 2017). Some of this work has revealed that the length of the stylar canals of western Joshua tree and eastern Joshua tree match the length of the organs that each of their respective pollinating moths use to deposit eggs into flower ovaries. Some of this scientific work has also provided information on the divergent selection pressures on these taxa that may have contributed to their evolution and speciation. Several researchers have examined genetic relationships between western Joshua tree and eastern Joshua tree (Starr et al. 2013, Yoder et al. 2013, Royer et al. 2016, Smith et al. 2021). Based on an analysis of single nucleotide polymorphisms, Royer et al. (2016) found that western Joshua tree and eastern Joshua tree are genetically distinct, and that natural selection is maintaining the differences between them. Smith et al. (2021) also found strong support for the conclusion that western Joshua tree and eastern Joshua tree are genetically distinct taxa.

In 2015, the U.S. Fish and Wildlife Service (USFWS) received a petition to list Joshua tree under the federal Endangered Species Act (federal ESA) (Jones and Goldrick 2015). In their Species Status Assessment, the USFWS considered both *Yucca jaegeriana* (eastern Joshua tree) and *Y. brevifolia* (western Joshua tree) as species for purposes of the federal ESA during consideration of that petition (Wallace 2017; USFWS 2018, 2019). The Petition submitted to the Commission includes a discussion of Joshua tree taxonomy and specifically requests that the Commission list western Joshua tree as threatened under CESA, regardless of the taxonomic rank into which the Commission classifies western Joshua tree. Based on the available scientific information, the Department considers western Joshua tree and eastern Joshua tree to be separate species (not subspecies of the same species) for the purposes of CESA and this Status Review.

The Petition states that western Joshua tree warrants protection under CESA throughout its range in California; however, the Petition also requests that the Commission assess whether either of two population clusters, denoted as *Y. brevifolia* North [YUBR North] and *Y. brevifolia* South [YUBR South], warrant listing separately as "ecologically significant units." In the 2018 Joshua tree Species Status Assessment, the USFWS treated these northern and southern population clusters as two geographically separate “populations” of western Joshua tree, and these two populations are discussed separately in much of the document (USFWS 2018). The distinction between the northern and southern populations in the USFWS Species Status Assessment appears to be based primarily on the distinct vegetational and climatic “regions” of western Joshua tree that were described and distinguished by Rowlands (1978).

A population of organisms considered distinct for conservation purposes based on scientific analysis of the reproductive isolation and genetic differences between population groups is eligible for listing under CESA (see *Cal. Forestry Assn. v. Cal. Fish and G.*, *supra*, 156 Cal.App.4th at 1535 [upholding the Commission’s listing of two evolutionarily significant units of Coho Salmon]. The Department has recognized that similar populations of a species can be grouped for efficient protection of genetic diversity (Id. at p. 1546-47). Further, genetic structure in populations is important because it fosters enhanced long-term stability (Id. at p. 1547). Genetic diversity spreads risk and supports redundancy in the case of catastrophes, provides a range of raw genetic materials that allow adaptation and increase the likelihood of persistence in the face of long-term environmental change, and leads to greater abundance (Ibid.).

The Department recognizes that genetic divergence among populations and genetic diversity within those populations are critical to species protection. Genetic divergence indicates the amount of time that population lineages have been separated. Effective conservation strategies often identify the most divergent clades in a group of lineages as key management units. Further, quantifying genetic diversity provides information on population health and indicates the extent to which populations have the capacity to adapt to changing conditions. While it can be difficult to determine when populations within species have sufficiently differentiated to be considered separate species or subspecies, a population-genetics approach using the fixation index F_{ST} is the most widely used summary measure of population divergence.

Recent studies suggest that western Joshua tree and eastern Joshua tree have a moderate degree of genetic differentiation and diverged approximately 100,000 to 200,000 years ago, which is considered a relatively recent divergence (Smith et al. 2021). The work by Smith et al. (2021) supports the conclusion that Joshua trees fall into two distinct groups (K=2) that correspond with western Joshua tree and eastern Joshua tree. Smith et al. (2021) does indicate there is genetic diversity among populations of western Joshua tree, particularly among populations in the southern and western extent of its range, and the Department also recognizes the vegetational and climatic differences between the northern and southern populations identified by Rowlands (1978). The Department also recognizes that populations of western Joshua tree in the southern part of its range generally face more serious threats than populations in the northern part of its range, as described in the Factors Affecting the

Ability to Survive and Reproduce section of this Status Review. Nevertheless, the Department does not currently have enough evidence of a clear genetic subdivision within western Joshua tree, that would support the differentiation of northern and southern populations as separate and discrete evolutionary significant units that would qualify them as separate "species or subspecies" under CESA. The genetic structure of western Joshua tree from north to south may instead be representative of a genetic cline, which is a continuous gradient of change in the genetic composition of populations within the range of the species that is associated with geography. Populations that are near each other are more genetically similar than populations that are farther away, but none appear fully isolated so as to be an evolutionary significant unit (Smith et al. 2021). Therefore, for purposes of this Status Review, the Department does not consider populations of western Joshua tree in the northern part of its range or the southern part of its range to be distinct "species or subspecies" under CESA.

The scientific understanding of the genetic diversity of Joshua tree will continue to improve with the completion of an ongoing project to assemble a Joshua tree reference genome.

Range and Distribution

Range is the general geographical area in which an organism occurs. For purposes of CESA and this Status Review, the range is the species' California range only (*Cal. Forestry Assn. v. Cal. Fish and Game Com.* (2007) 156 Cal.App.4th 1535, 1551), even though western Joshua tree extends into southern Nevada, reaching north to Alkali and east to Tikaboo Valley (USFWS 2018). Range is largely independent of species abundance, because population declines within an area do not necessarily change the overall geographical area in which an organism occurs. Species distribution describes the actual sites where individuals and populations of the species occur within the species' range.

Current Range

The California range of western Joshua tree is in southeastern California and covers much of the western half of the Mojave ecoregion (Figure 2) (USDA 2017). The southern and eastern extent of the species' range is at Joshua Tree National Park in San Bernardino County and the western extent of the species' range is near Gorman in Los Angeles County, where the species is found to the west of Interstate 5 (Figure 3). Within California, western Joshua trees extend to the north into Inyo County and occur within Death Valley National Park. The northernmost western Joshua trees are likely in the southeastern corner of Mono County near Fish Lake Valley, which is close to the California/Nevada border (Figure 3). Throughout California, substantial stands of

Figure 2: Western Joshua Tree Range and California Ecoregions

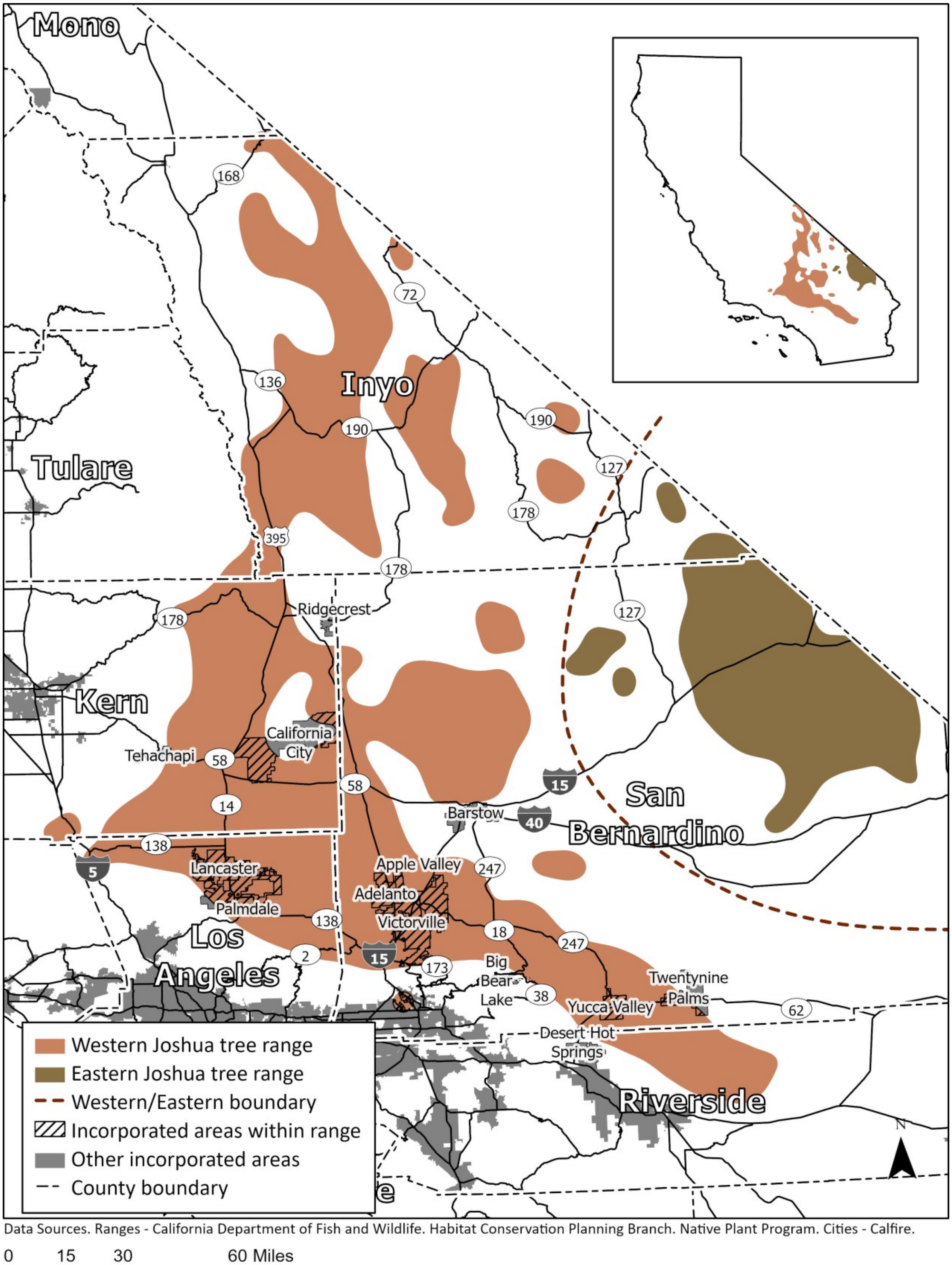

Figure 3: Joshua Tree Range in California

western Joshua tree were reported as high as 2,100 m (6,900 ft) and as low as 750 m (2,500 ft) elevation by Rowlands (1978), and individual trees can likely be found at elevations that are slightly higher or lower than this range. The western Joshua tree range shown in Figures 2 and 3 was developed using distribution information in the Department's possession during preparation of this Status Review, as described in the Current Distribution section of this Status Review.

Past Range

Fossil evidence indicates that Joshua tree was more widespread during the late Pleistocene period (22,000 to 13,000 years before present) (Cole et al. 2011). Joshua tree's range during the late Pleistocene period extended south of its present range farther into southern California and into Arizona, and likely also into northwestern Mexico (Rowlands 1978, Cole et al. 2011). Joshua tree's range suddenly contracted from the south as climates rapidly warmed approximately 11,700 years ago at the beginning of the Holocene period, and now only the northernmost Joshua tree populations remain (Cole et al. 2011). While Joshua tree's range contracted from the south as climates warmed, Cole et al. (2011) states that it also may have expanded very slowly to the north, and attributed this to very limited dispersal capabilities, which are discussed in more detail in the Seed Dispersal section of this Status Review. Smith et al. (2011) modeled historical range using 20th century suitable climate conditions to reconstruct a potential range of Joshua tree approximately 21,000 years before present during the last glacial maximum. The results of this modeling also suggested that Joshua trees formerly occupied a larger range in the southern Mojave Desert. Smith et al. (2011) suggested that loss of range in the southern part of Joshua tree's range between 21,000 years ago and the present may have been offset by the addition of new habitat in the north.

Current Distribution

Western Joshua tree is distributed in discontinuous populations in the Mojave Desert and in a portion of Great Basin Desert (Figure 2). Western Joshua tree is often noted as being abundant near the borders of the Mojave Desert in transition zones. The general distribution of Joshua tree has been described in various sources, and over time the understanding of western Joshua tree distribution has improved, with newer and larger datasets of presence points contributing to more accurate distribution maps.

The USFWS described the distribution of both western Joshua tree and eastern Joshua tree as part of a Species Status Assessment for the two species in 2018 and produced a distribution map as part of the assessment. The USFWS distribution map was based on several sources including Rowlands (1978); Cole et al. (2003, 2011); Webb et al.

(2003); the LANDFIRE Reference Database (2007); Godsoe et al. (2009); and other available databases (USFWS 2018).

The Department possesses vegetation maps that cover a large portion of the California deserts where western Joshua tree generally occurs. The Department's Vegetation Classification and Mapping Program (VegCAMP) uses a combination of aerial imagery and fieldwork to delineate polygons with similar vegetation and to categorize the polygons into vegetation types. In 2013, an effort was made to create a vegetation map that covers a large portion of the California deserts (CDFW and AIS 2013, Menke et al. 2013). The vegetation data from this project includes percent absolute cover of Joshua tree and in some instances only Joshua tree presence and absence data. A rigorous accuracy assessment of the mapped Joshua tree woodland (*Yucca brevifolia* vegetation alliance) was performed using field collected data and it was determined to be mapped with approximately 95% accuracy. This means that approximately 95% of field-verified, polygons mapped as Joshua tree woodland alliance were mapped correctly. While Joshua tree woodland alliance requires even cover of Joshua tree at ≥1% to be categorized as this alliance, the vegetation dataset has polygons recorded with <1% cover of Joshua tree as well as simple presence and absence data. This information was used to visualize the distribution and cover of western Joshua tree within the survey area (Figure 4). While Figure 4 is not a comprehensive representation of the distribution of western Joshua tree in California, it reflects the best information available to the Department on the cover and distribution of western Joshua tree.

The Department used publicly available vegetation mapping information (polygons) (Thomas 2002; Agri Chemical and Supply, Inc. 2008; NPS 2012; CDFW and USGS 2014; CDFW and Chico State University 2015; CDFW et al. 2017; CDFW 2019 a, b, c, d) combined with data from other sources including herbarium records, Calflora, and iNaturalist (points) to create the western Joshua tree range shown in Figures 2 and 3. The Department reviewed publicly-available point observations from herbaria, Calflora, and iNaturalist that appeared to be geographic outliers to ensure that incorrectly mapped and erroneous observations did not substantially expand the presumed range of the species. The Department did not include point observations for range mapping if photos demonstrated that the species was identified incorrectly, the observation was for a horticultural planting, or if the geographic location of the point observation was mapped incorrectly or was too imprecise for accurate mapping. Creating a range map with incomplete presence data can sometimes be misleading because the absence of data does not necessarily mean the absence of the species. Some of the observations used to produce the range map may also be old, particularly if they are based on herbarium records, and trees may no longer be present in some locations. Additionally, different buffer distances around data points can yield wildly different results for occupied areas. To create the general western Joshua tree range shown in Figures 2

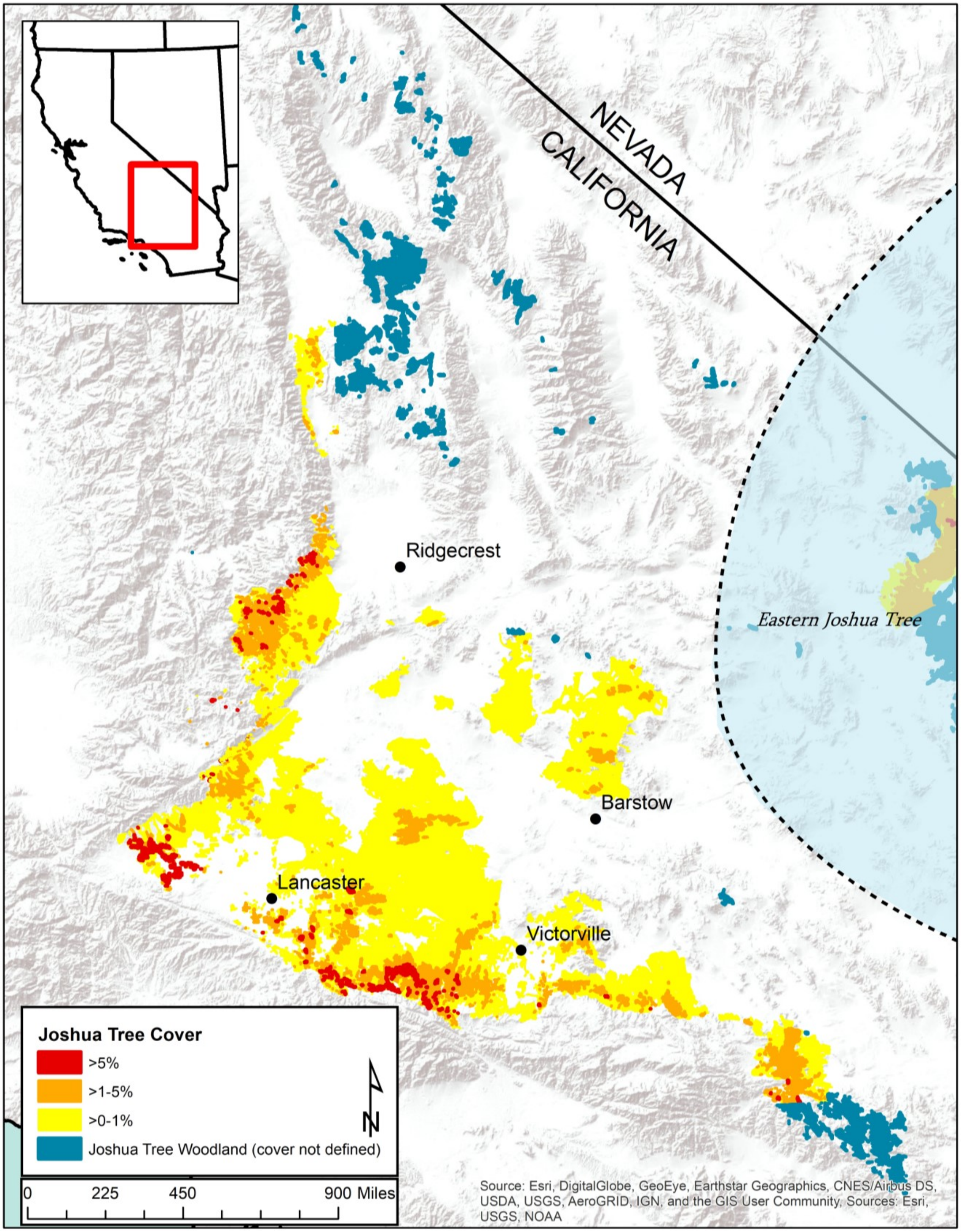

Figure 4: Joshua Tree Absolute Cover Classes (Data from Vegetation Maps)

and 3, the Department buffered presence locations, but did not use a specific buffer value, and instead used the data described above in a geographic information system exercise to extend the range polygons to closely follow known occurrence boundaries while eliminating small gaps between them.

The area occupied by the western Joshua tree range shown in Figures 2 and 3 is approximately 30,200 km^2 (11,660 mi^2); however, this is very likely an overestimation of the species distribution in California. If the point and polygon data used for the range are instead buffered by 0.2 km (0.12 mi) the distribution of the species in California would occupy 10,160 km^2 (3,920 mi^2) which is likely an underestimation of the actual distribution because populations represented only by points are likely larger than the buffered distance, and the Department does not have data for every location where western Joshua tree occurs. If each occupied area was reported as a point, with an average area of 0.59 km^2 (0.23 mi^2), and all point and polygon areas were additionally buffered by 0.2 km (0.12 mi), the distribution of western Joshua tree in California would be 13,880 km^2 (5,360 mi^2). To put these areas in perspective, the distribution of western Joshua tree is likely larger than the land area of the State of Connecticut, but smaller than the land area of the State of Hawaii. As part of its Species Status Assessment, the USFWS (2018) estimated that the distribution of western Joshua tree occupied an area of 22,823 km^2 (8,812 mi^2), but this estimate included areas outside of California. In an effort to estimate population size, WEST Inc. (2021a) used data from Cole et al. (2011) to report that western Joshua tree's distribution occupies 15,071 km^2 (5,819 mi^2), but WEST Inc. (2021b) later reported that this area was only for the southern part of the species' range, and the distribution in the northern and southern portions of the species' range together occupy an area of approximately 23,101 km^2 (8,919 mi^2), although this estimate likely includes areas outside of California.

The distributions of most plant species of conservation concern within California are documented in the Department's California Natural Diversity Database (CNDDB) (CDFW 2021a). The taxa that are tracked in the CNDDB are referred to as "elements." An "element occurrence" (occurrence) is a specific location where an element is known to occur. Occurrences are determined using a default separation distance of ¼ mi (0.4 km), meaning that if two populations of an element are separated by more than ¼ mi (0.4 km), the two populations will be considered separate occurrences (Bittman 2001, CDFW 2020). Prior to being designated a candidate species under CESA, western Joshua tree was not considered to be a plant species of conservation concern by the Department, and the species was therefore not tracked in the CNDDB. Although the Department has not begun tracking occurrences of western Joshua tree, initial estimates suggest that the number of western Joshua tree occurrences could total approximately 846 if it was tracked and mapped by the CNDDB using standard methodology. For comparison, the highest number of occurrences for a plant currently tracked by the Department in the CNDDB is 249 (CDFW 2021a). If western Joshua tree were tracked in the CNDDB, the number of occurrences would be much higher than any other plant element currently tracked in the database.

Scientific understanding of current western Joshua tree distribution is continuing to improve. Both remote sensing techniques using satellite imagery as described by Esque et al. (2020a) and citizen science applications such as iNaturalist are making it possible to develop a more detailed map of western Joshua tree distribution. These efforts nevertheless have limitations. Remote sensing techniques are most effective on western Joshua tree in lower-elevation areas where western Joshua trees are not surrounded by vegetation of similar height. Additionally, despite peer review of citizen science observations by other users, citizen science data frequently includes erroneous identification of species (including of western Joshua tree). Plants that may be confused with western Joshua tree are discussed in the Similar-looking Plants section of this Status Review.

Based on information available to the Department, western Joshua tree is relatively widespread across a large geographic area of southeastern California, western Joshua tree populations occupy relatively large areas within this geographic area, and the number of occurrences of western Joshua tree within California is very high compared with the number of occurrences for the approximately 1,700 plant species of conservation concern that are tracked and mapped by the Department’s CNDDB.

Life History

Flowering, Pollination, and Fruit Production

Mature western Joshua trees do not produce flowers every year, and flowering is thought to be episodic, possibly only occurring in wetter years; however, the conditions that lead to flowering are not well known (Gucker 2006, St. Clair and Hoines 2018). Western Joshua tree flowers have been reported between January and May, but flowering as early as November has also been observed (Hess 2012, Waitman et al. 2012, Cornett 2018a, 2018c, Harrower and Gilbert 2018, Barve et al. 2020, Brenskelle et al. 2021). Cold and dry conditions have been implicated for flowering that occurs relatively early in the flowering season (Brenskelle et al. 2021). In some years, many western Joshua trees produce flowers synchronously, leading to the production of large quantities of fruits and seeds in that year, which is part of a reproductive strategy called masting (Kelly and Sork 2002, Borchert and DeFalco 2016, St. Clair and Hoines 2018). A mast seeding reproductive strategy is beneficial for species whose seeds are dispersed by seed predators, because when more seeds are produced than predators can eat, the surviving seeds have a higher likelihood of establishing and developing into a reproductive adult (Kelly and Sork 2002). Large flowering events are relatively infrequent, perhaps only occurring once or twice per decade, and the environmental or other conditions that lead to large flowering and mast seeding events are currently unknown (Esque et al. 2010, DeFalco and Esque 2014, Borchert and DeFalco 2016).

Esque et al. (2015) reported that flowering may occur in Joshua trees that are as short as one meter, but that 30-year-old trees at their study site had yet to flower (a discussion of the relationship between plant height and age is presented in the Growth and Longevity section of this Status Review). Rowlands (1978) investigated the average height to first branching, which is likely indicative of the height at first flowering. The information presented in Rowlands (1978) from ten populations of western Joshua tree showed that the average height to first branching was between 1 and 1.5 m at the three northernmost populations examined, and the average height to first branching was between 2 and 2.5 m at more southern populations. Larger western Joshua trees tend to produce more flower clusters than smaller trees (Harrower and Gilbert 2018).

Joshua tree flowers require pollination to produce fruits. Most species in the genus *Yucca* are pollinated by a different species of yucca moth. Mutually-beneficial relationships between organisms are called mutualisms. Within California, western Joshua tree forms an obligate pollination mutualism with its specialized nocturnal pollinating yucca moth *T. synthetica*, and eastern Joshua tree forms an obligate pollination mutualism with its specialized pollinating yucca moth *T. antithetica* (Trelease 1893, Pellmyr and Segraves 2003). The interactions between *Yucca* species and yucca moths have captivated the attention of biologists for over 150 years, beginning with observations by George Engelmann and Charles Riley in the 1800s, and these interactions continue to be the subject of research (Riley 1873, Sheppard and Oliver 2004, Royer et al. 2020). In a letter, Charles Darwin (1874) once described the *Yucca*-yucca moth interaction mutualism as “the most wonderful case of fertilisation ever published.”

Western Joshua tree flower panicles create large, light-colored landing pads for *T. synthetica* moths to use, and residual heat in the flower panicles that were warmed by the sun during the day may provide a thermal reward for its nocturnal pollinating moths (Warren et al. 2016). Female *T. synthetica* moths have special tentacle-like mouth parts for collecting, transporting, and transferring western Joshua tree pollen (Cole et al. 2017). Female moths first gather a ball of western Joshua tree pollen with their mouth parts, next they oviposit eggs into the western Joshua tree flower, and finally the moths actively transfer pollen to a portion of the female sexual part of the flower called the stigma, ensuring that the flower will be fertilized (Pellmyr 2003, Cole et al. 2017). When ovipositing her eggs, a female yucca moth cuts through the ovary wall of a western Joshua tree flower so she can insert her ovipositor down the stylar canal to lay eggs near ovules that can eventually become seeds after the flower is fertilized (Cole et al.

2017). The moth eggs hatch within a few days and feed on developing seeds (Pellmyr 2003). By actively pollinating western Joshua tree flowers, female yucca moths can ensure that there will be a food source for their developing moth larvae. Both western Joshua trees and *T. synthetica* moths benefit from this interaction because each species is dependent on the other for a critical aspect of its sexual reproduction. In the late summer, moth larvae that developed within Joshua tree fruits fall to the ground below the tree, burrow into the ground, create a cocoon, and enter a period of suspended development called diapause (Pellmyr 2003). Yucca moth larvae are likely able to remain in diapause for several years before pupating into moths; the environmental or other cues that trigger this pupation are currently unknown (Riley 1892, Pellmyr 2003). The Department has very little information on the range of *T. synthetica*, however, any instance of non-clonal western Joshua tree recruitment is an indication that *T. synthetica* was present at the time the flower that produced the seed was pollinated.

After pollination, western Joshua tree fruits develop and seeds are produced. Borchert and DeFalco (2016) found that fruits may reach full size around late May, although seeds did not become black and capable of germination until approximately 14 days after they are full size. Fruits turn from pale green to a whitish light brown as they dry and may fall to the ground or into the leaves of the tree or remain attached to the panicle of the tree. As would be expected in a masting species, the amount of western Joshua tree seeds and fruits produced can be highly variable from year to year (Borchert and DeFalco 2016). Viable seed production by western Joshua tree may be limited more by pollen than other resources, and more seeds tend to be produced in areas with more *T. synthetica* moths (Harrower and Gilbert 2018). Within the vicinity of Joshua Tree National Park, Harrower and Gilbert (2018) found *T. synthetica* moths at elevations ranging from 1,049 m (3,442 ft) to 2,076 m (6,811 ft), but not at the lowest elevation study site that had western Joshua trees at 1,004 m (3,294 ft) or the highest elevation study site with western Joshua trees at 2,212 m (7,257 ft), however this was a short-term study conducted within one continuous western Joshua tree population, and additional are needed to determine whether the moth is present at higher or lower elevations.

<u>*Seed Dispersal*</u>

The primary current method of western Joshua tree seed dispersal is from the scatter-hoarding behavior of rodents who actively collect seeds from fruits in the canopies of trees and fruits and seeds that have fallen on the ground, and bury seeds in the soil relatively short distances away (Vander Wall et al. 2006, Waitman et al. 2012, Borchert 2016). Other methods and agents of seed dispersal such as wind, other mammals, birds (e.g., California scrub jay (*Aphelacoma californica*)), and extinct megaherbivores (e.g., giant sloths and relatives of elephants) have also been suggested in the scientific literature (McKelvey 1938, Lenz 2001, Borchert 2016). Rare long-distance dispersal events are likely important for plant migrations over large geographic scales (Clark et al. 1998). Rare long-distance dispersal events may have occurred for Joshua tree in the past and could still occur.

Lenz (2001) provided observations of apparent dispersal distances in areas that had been previously cleared of vegetation and left fallow at a population of western Joshua tree in the western portion of the Antelope Valley (Los Angeles County), and at a population of eastern Joshua tree in Lanfair Valley, California (San Bernardino County). Lenz (2001) found young plants (cluster of leaves, no stem) or juvenile plants (with stem but unflowered) in limited numbers as far as 151 m (495 ft) from potential seed donors in the Antelope Valley, and 251 m (823 ft) from potential seed donors in Lanfair Valley. Lenz (2001) did not explicitly test seed dispersal mechanisms but hypothesized that these dispersal events were the result of wind dispersal. However, the role of rodents in Joshua tree seed dispersal was not well understood at that time.

Joshua trees produce fruits that do not open when seeds are ripe and produce seeds with an undersized wing structure relative to seed mass, which are morphological characteristics that can indicate seed dispersal via scatter-hoarding rodents. Borchert (2016) used camera traps and affixed line to 208 western Joshua tree fruits and placed them under trees at two sites in the San Bernardino Mountains to observe and measure fruit dispersal. White-tailed antelope squirrel (*Ammospermophilus leucurus*) and kangaroo rats (*Dipodomys merriami* and *D. agilis*) were observed carrying fruits away from trees before dismantling them. The maximum distance that a fruit was moved was 46.9 m (154 ft), and the average dispersal distance was 6.4 m (21 ft) (Borchert 2016). White-tailed antelope squirrels were responsible for carrying away the most western Joshua tree fruits. Kangaroo rats readily collected loose western Joshua tree seeds from dishes (Borchert 2016). Other species observed interacting with western Joshua tree seeds and fruits included pocket mice (*Chaetodipus fallax* and *Perognathus longimembris*), pinyon mice (*Peromyscus trueii*), and California scrub jays (Borchert 2016).

Vander Wall et al. (2006) placed a total of 1,000 radioactively marked eastern Joshua tree seeds at the base of five different eastern Joshua trees (200 seeds per tree). Rodents removed 995 of the 1,000 seeds within two days, and researchers were able to find 67.7%–97.5% of the seed originally placed below each tree in seed caches at distances between 0.5 and 56.6 m (1.6 and 186 ft) away from where the seeds were originally placed. The average maximum dispersal distance was 30.0 m (98.4 ft). On a subsequent visit, Vander Wall et al. (2006) found that many of the seeds discovered in the seed caches on the previous visit were re-cached in secondary caches located between 0.2 and 32.2 m (0.7 and 106 ft) away from the original cache. Assuming seeds are sometimes re-cached in the same direction away from the source tree, results of the Vander Wall et al. (2006) study suggest that rodents may be capable of moving eastern Joshua tree seeds as far as 88.8 m (291 ft) away from a source plant (56.6 meters plus 32.2 meters). If entire fruits are first carried away from source trees by rodents, dispersal distance could be farther (Borchert 2016). The Vander Wall et al. (2006) study examined dispersal from only five source trees, and therefore may not demonstrate the maximum possible dispersal distances that seed caching rodents are capable of moving eastern Joshua tree seeds. In a subsequent study by Waitman et al. (2012) using camera traps, white-tailed antelope squirrels cached eastern Joshua trees seeds a mean distance of 21.3 ± 2.8 m (69.9 ± 9.2 ft) from the source tree, but only three trials were conducted, because the primary purpose of this treatment was for comparison with treatments involving rodents kept within an enclosure.

Waitman et al. (2012) also examined factors related to seed dispersal of eastern Joshua trees and found evidence that rodents are a factor causing eastern Joshua tree fruits to drop from the tree canopy at two study sites. Waitman et al. (2012) also placed a total of 160 eastern Joshua tree fruits on the ground and found that approximately 90% of these fruits were removed by ground-foraging rodents within approximately 15 days. Eastern Joshua tree seeds placed on the ground were also removed, but less rapidly than whole fruits. Waitman et al. (2012) also conducted experiments that involved placing a white-tailed antelope squirrel or Merriam’s kangaroo rat into a 10 by 10 m enclosure with 200 radioactively marked eastern Joshua tree seeds to study the scatter-hoarding behavior of these rodents, including the depth of seed caches, distance of caches from source trees, and whether seeds were cached in the open or under shrubs. Seed caches created by rodents in this study were buried at a mean depth of 12 ± 3 mm. One study suggested that scatter-hoarding rodents may preferentially place Joshua tree seeds under shrubs which would likely be beneficial for seedling emergence (Swartz et al. 2010), but Vander Wall et al. (2006) and Waitman et al. (2012) found that rodents do not appear to disperse eastern Joshua tree seeds with regard to shrub cover.

Using a wind tunnel, Waitman et al. (2012) also measured the wind speeds necessary to move eastern Joshua tree fruits and seeds on a sandy and a rocky substrate. Wind speeds required to move fruits was lower than wind speeds required to move seeds (31.9 ± 2.6 km/h and 43.6 ± 2.6 km/h, respectively on the sandy substrate). Wind speeds sufficient to move fruits and seeds on the rocky substrate averaged and 73.6 ± 4.8 km/h and 87.6 ± 5.5 km/h, respectively. Waitman et al. (2012) suggested fruits and seeds that do fall are unlikely to be carried far by wind and are instead much more likely to be gathered by rodents; therefore, wind is unlikely to be a primary mode of dispersal where rodents are present.

Although scatter hoarding rodents and Joshua trees are capable of a mutualistic relationship where both organisms benefit each other, in non-masting years when Joshua trees only produce a small number of seeds, an overabundance of rodents may consume all the seeds, resulting in a shift from a mutualistic relationship to a predatory relationship, and Joshua tree may not benefit from the relationship in these years (Waitman et al. 2012).

Joshua tree has been found to be a chief component in fossilized dung of the now-extinct Shasta ground sloth (*Nothrotheriops shastensis* Sinclair) that was found in a cave in southern Nevada (Harrington 1933, Laudermilk and Munz 1935, Cole et al. 2011). Poorly masticated fragments of Joshua tree up to 2 cm long were found in the dung, including sharp leaf tips, parts of the flower stalk and fruits, and entire seeds, although all seeds observed were split. Researchers have speculated that Joshua tree's large fruits may have been an adaptation for consumption by large mammals that are now extinct (Simpson 1975, Lenz 2001). In addition to extinct ground sloths, extinct long-necked members of Camelinae (relatives of camels and llamas) and extinct relatives of elephants in the order Proboscidea were present within the range of Joshua tree in the past. Extinct members of the order Proboscidea may have been capable of feeding on Joshua tree fruits via an elephant-like trunk, and elephants are known seed dispersers because they consume large quantities of material that is passed relatively undigested within a relatively short period of time (Lenz 2001 and citations therein). Shasta ground sloth and other megaherbivores became extinct approximately 12,900 years before present, perhaps due to rising populations of humans (Steadman et al. 2005) and/or a meteorite impact (Firestone et al. 2007). Joshua tree's height may have been an evolutionary strategy to elevate leaves, flowers, and fruits so they could not be reached by large herbivores (Lybbert and St. Clair 2017). Assuming that even a small proportion of Joshua tree seeds were capable of remaining viable in the dung of Shasta ground sloth or another extinct herbivore, Joshua tree may have been capable of more frequent longer-distance seed dispersal in the past. However; using genetic data, Smith et al. (2011) found no evidence of a change in the rate of Joshua tree dispersal corresponding with the timing of the extinctions of such herbivores, which would be expected were they important Joshua tree seed dispersers.

Seed Germination

While western Joshua tree seeds germinate readily under optimal conditions, seedling establishment is exceptionally rare (Reynolds et al. 2012), and few Joshua tree seedlings are observed in the field, particularly at lower elevations (Webber 1953, Wallace and Romney 1972, Comanor and Clark 2000, Esque et al. 2010).

Twenty-year-old western Joshua tree seeds stored at California Botanic Garden had 100% germination with no pretreatment and grown on agar in a germination chamber (Birker pers. comm. 2021). Other studies have reported similarly high Joshua tree germination success under controlled conditions (Wallace and Romney 1972, McCleary 1973, Gucker 2006, Alexander et al. 2008, Waitman et al. 2012). Seeds used for germination studies likely had high seed viability (ability to germinate) because obviously damaged seeds (as seen in Figure 1) would have been avoided during collection in the field.

While seed germination appears to be high under controlled conditions, seed viability decreases dramatically after dispersal in the wild. Reynolds et al. (2012) found that after one year in an underground cache, only 50%–68% of recovered eastern Joshua tree seeds were able to germinate, and after three years and four months in an underground cache, approximately 3% of recovered eastern Joshua tree seeds were able to germinate. This suggests that Joshua tree has limited capacity to maintain viable seeds in the soil for long periods of time. In mast years when fruit production is high enough to provide ample food for larvae and rodents, Borchert and DeFalco (2016) speculated that uneaten fruits in the tree canopy may function as an aerial seed bank, because seeds may remain viable for a longer duration when protected within fruits than loose in the soil.

Once western Joshua tree seeds have dispersed, they appear to be able to germinate any time after rain (Went 1948, Reynolds et al. 2012). Reynolds et al. (2012) examined several cohorts of artificially placed eastern Joshua tree seeds, and found that seedling emergence was greatest during spring and summer, when increased soil moisture was accompanied by warm soil temperatures, but seedlings were also able to emerge at other times of the year, suggesting some potential for adaptation to shifting conditions. McCleary (1973) tested four different eastern Joshua tree germination temperatures and found seed germination was fastest at 25°C.

Waitman et al. (2012) found that seed caching by rodents increased the likelihood of seedling emergence and seeds were most likely to produce seedlings when buried 1–3 cm (0.4–1.2 in) deep, and that seeds placed on the soil surface seldom germinated. Between August 2007 and September 2008, Waitman et al. (2012) found that only 133 of 2,880 artificial caches (4.6%) placed in the field produced seedlings and only 183 of the 5,760 seeds (3.2%) placed in those caches produced seedlings. Significantly more Joshua tree seedlings emerge from under shrubs than in the open (Vander Wall et al. 2006, Waitman et al. 2012, Reynolds et al. 2012). One study suggested that scatter-hoarding rodents may preferentially place seeds under shrubs which would likely be beneficial for seedling emergence (Swartz et al. 2010), but Vander Wall et al. (2006)

and Waitman et al. (2012) found that rodents do not appear to disperse eastern Joshua tree seeds with regard to shrub cover.

Establishment and Early Survival

The process by which individuals are added to a population is called recruitment. Recruitment of plants may be limited by the availability of seed and/or by other constraints on seedling establishment (Grubb 1977, Clark et al. 1999, 2007). Few experiments involving the addition of seeds to Joshua tree habitat have been conducted (Waitman et al. 2012, Reynolds et al. 2012), but results suggest that constraints on seedling establishment may be a critical factor limiting western Joshua tree recruitment. Following germination, several successive years of sufficiently wet and/or cool conditions are likely required for establishment of Joshua tree seedlings (Wallace and Romney 1972, Cole et al. 2011). Joshua tree seedlings and very young plants appear to require sufficient soil moisture to survive, periods of cold temperatures for optimal growth, and must not be consumed by herbivores (Went 1957, Esque et al. 2015). Of seedling cohorts monitored by Reynolds et al. (2012), seedlings emerging in September survived the longest, although approximately 90% of them died within one year. Esque et al. (2015) identified the seedling height of 25 cm as an important size class threshold because seedlings that attained this height before the onset of drought conditions had a much greater likelihood of longer-term survival than the seedlings that did not attain this height, none of which survived the study’s 22 year monitoring period.

Nurse plants appear to be critical habitat components for Joshua tree establishment (Waitman et al. 2012, Reynolds et al. 2012, Esque et al. 2015), likely by providing a microclimate with less direct sun, higher soil moisture, lower soil temperature, a reduction in water loss to the atmosphere, increased soil nutrients, and/or a reduction in the drying effects from wind (Holmgren et al. 1997, Brittingham and Walker 2000, Legras et al. 2010). Many plants with which Joshua trees co-occur including blackbrush (*Coleogyne ramosissima*) and creosote bush (*Larrea tridentata*) can act as nurse plants for Joshua tree seedlings by providing favorable conditions for seedling growth and survival, and perhaps some protection from small mammal herbivory (Loik et al. 2000b).

Harrower and Gilbert (2021) found that the presence of arbuscular mycorrhizal fungi in association with the roots of western Joshua tree seedlings generally appeared to have positive benefits for nitrogen absorption and plant biomass. Some species of arbuscular mycorrhizal fungi from low elevation areas in Joshua Tree National Park were found to have an initial negative impact on one- to three-month old western Joshua tree seedlings, but these associations became beneficial when seedlings were six-months old.

McCleary (1973) tested four different light cycles on young eastern Joshua tree plants and found that 10 hours of light and 14 hours of dark produced the highest average number of leaves, and the longest average total length of leaves per plant. Western Joshua tree seedlings were observed by Wallace and Romney (1972) to grow best at root temperatures near 18°C and without calcium carbonate ($CaCO_3$) in the soil.

Germination and emergence of perennial desert plants have been associated with infrequent weather events such as those associated with the El Niño–Southern Oscillation (Bowers 1997, Holmgren et al. 2006). Such events bring winter and early spring precipitation after seed germination and may be the conditions that are most conducive to establishment of western Joshua tree.

Esque et al. (2015) monitored a cohort of 53 western Joshua tree plants that were 5 to 6 years old for a period of 22 years at Yucca Flat, Nevada. These western Joshua trees had an average height of 21.5 cm when monitoring began in 1989, and the surviving 10 plants had an average height of approximately 1 meter in 2011. Most of the mortality was attributed to the plants being consumed by black-tailed jackrabbit (*Lepus californicus*) during drought years. DeFalco et al. (2010) monitored burned and unburned western Joshua trees for a five year period after a wildfire in Joshua Tree National Park, and found that plants that were less than approximately one meter (3.3 feet) were more vulnerable to drought, herbivory, and fire than larger size classes, which had a greater likelihood of survival. Harrower and Gilbert (2018) found considerable western Joshua tree seedling recruitment within Joshua Tree National Park at elevations around 1,300 m (4,300 ft), where trees were generally the biggest, and they produced the most flowers, fruits, and seeds.

Growth and Longevity

Smith et al. (1983) investigated the photosynthetic characteristics and transpiration (water loss through leaves) of western Joshua tree, and despite early assumptions to the contrary, found that western Joshua tree survives solely on the C_3 carbon fixation pathway, despite growing in arid areas where other photosynthetic pathways (e.g., C_4 and CAM) are sometimes utilized by plants as an adaptation to hot environments. Western Joshua tree is capable of controlling the stomata (openings for transfer of gases to and from the environment) of its leaves throughout the day and the year, which is an adaptation allowing it to control water loss and maintain its leaves during the summer and fall dry seasons (Smith et al. 1983). Because western Joshua tree's evergreen leaves are maintained for many years, there is a reduced need to produce new biomass. Western Joshua tree's moderate photosynthetic rate, arrangement of leaves, and high leaf area nevertheless also allow it to exhibit substantial photosynthetic productivity during the winter-spring growth period (Smith et al. 1983). Wallace and

Romney (1972) estimated that western Joshua trees at one site in Nevada produced about three sets of six leaf blades per growing tip per year but noted that six to eight sets of six blades were developed in 1969 due to the large amount of rain in that year. Like many desert plants, Joshua trees can survive with limited water by utilizing moisture reserves of intermediate and deep soils and moisture that is stored in leaves, trunk, and roots (Crosswhite and Crosswhite 1984). Although Joshua tree trunk diameter is generally expected to increase with time, the diameter of Joshua tree trunks has also been reported to decrease, perhaps as a result of drought (Phillips et al. 1980, Gilliland et al. 2006).

Western Joshua tree grows in height very slowly, and growth rates can vary based on location and other factors, but may be somewhat uniform in localized areas. Esque et al. (2015) monitored one site in Nevada over 22 years and found an average western Joshua tree growth rate of 3.12 cm in height per year. Comanor and Clark (2000) monitored three plots over 20 years (two with western Joshua tree and one with eastern Joshua tree) and found an average growth rate of approximately 4 cm per year. Gilliland et al. (2006) observed a growth rate of 3.75 cm per year at a population of eastern Joshua trees in Utah over a period of 14 years. Wallace and Romney (1972) estimated average western Joshua tree growth rates of about 1.5 cm per year at one site in Nevada. A growth rate of over 8 cm per year through approximately 17 years was observed in one tree near Rose Mine in the San Bernardino Mountains, which Rowlands (1978) reported as supporting clonal trees that are the tallest and fastest growing Joshua trees recorded in the southwest. Rowlands attributed this high growth rate to relatively high water availability coupled with deep sandy loam soil. Western Joshua tree growth rates as high as 14.3 cm per year were reported by McKelvey (1938). In one monitoring plot at Cima Dome in Mojave National Preserve, Cornett (2018b) found that annual height increase of eastern Joshua tree was moderately correlated with summer precipitation ($r = 0.53$, $P = 0.009$). Because Joshua tree does not produce clearly identifiable secondary growth rings in its wood, tree height is often used to approximate the age of the plants (Gilliland et al. 2006). Estimates for the ages of western Joshua trees are therefore dependent on the assumptions used for annual growth rate, and these estimates include a high level of uncertainty. Despite uncertainty, information on tree height can provide information about the demographic structure of Joshua tree populations, as described in the Demographic Information section of this Status Review. Went (1957) published data demonstrating that after Joshua tree has reached an age of approximately three years the plant requires exposure to low temperatures for optimal growth.

In areas outside of the distribution of *T. synthetica* moths, asexual reproduction is the only viable reproductive strategy for western Joshua tree. Asexual reproduction occurs from underground stems called rhizomes that grow horizontally and produce sprouts near the parent plant, resulting in plants with more than one main stem and clumps of plants growing together. Asexual reproduction may allow western Joshua tree individuals to survive for indefinite periods of time, because new sprouts create genetically identical clones of parent plants that may replace the parent plants after they have died, and this process can continue for many generations. The extent of asexual reproduction in Joshua tree populations increases with elevation (Simpson 1975, Rowlands 1978), and asexual reproduction has also been reported at lower elevations where sexual reproduction is not occurring (Harrower and Gilbert 2018), which is consistent with observations that asexual reproduction tends to be more frequent at the edges of plant species ranges (Silvertown 2008). The use of asexual growth for reproduction and survival by western Joshua tree may be an adaptation to higher elevations, harsher environmental conditions, or may be an adaptation to lower availability of yucca moths for pollination at these locations (Webber 1953, Rowlands 1978, Harrower and Gilbert 2018). As is the case with some relict species, the ability to reproduce asexually may extend the ability of western Joshua tree to persist in marginal climate conditions for very long periods of time. Western Joshua tree often resprouts after fire (Vogl 1967, Loik et al. 2000b, Gucker 2006, DeFalco et al. 2010), and like Joshua tree asexual growth, fire is also more frequent at higher elevation areas of the Mojave Desert (Brooks et al. 2018). DeFalco et al. (2010) found that resprouting of burned but still living western Joshua trees in Joshua Tree National Park generally prolonged the survival of burned plants five years after fire, compared with plants that did not resprout, but only at wetter, high-elevation sites. Abella et al. (2020) found resprouting to aid in eastern Joshua tree population persistence in areas that had previously burned, and therefore sprouting may be an important adaptation of Joshua tree to fire (Brooks et al. 2018). DeFalco et al. (2010) found that while sprouting may have increased survival of burned trees, sprouting in unburned trees may have negatively affected survival, suggesting that there is also a cost to sprouting, particularly during periods of low precipitation.

Assuming an average height of first flowering for western Joshua tree is approximately 2 m (6.6 ft), and an average growth rate for western Joshua tree is 4 cm (1.6 in) per year, the average time required for a germinated seed to reach reproductive maturity may be approximately 50 years, which appears to be consistent with the 50 to 70 years estimated by Esque et al. (2015). Western Joshua tree individuals that have reached reproductive maturity have high survivorship and are therefore likely to maintain reproductive potential for decades. Esque et al. (2020b) used an estimate of annual survival rate of 0.992 for eastern Joshua tree from one 14-year study (Gilliland et al. 2006) to calculate a generation length for western Joshua tree of approximately 185 years. Despite speculation that western Joshua tree may live for hundreds of years or even more than a thousand years, the maximum lifespan of western Joshua tree is unknown (Cornett 2006, Gilliland et al. 2006). If the average western Joshua tree lifespan becomes shorter than the generation length, populations will decline.

Summary of Important Life History Needs

Sexual recruitment of western Joshua trees requires a number of conditions to occur in succession; however, western Joshua trees are also capable of asexual growth for indeterminate periods of time, particularly at higher elevations, if the environmental conditions for survival and growth are maintained. Available information suggests that seed germination is most likely after large mast seeding events, which perhaps only occur once or twice per decade. The environmental or other conditions that lead to large simultaneous flowering events that result in mast seeding events are not currently known. Sexual reproduction requires the presence of western Joshua tree's obligate pollinating moth *T. synthetica*. The conditions that lead to the emergence and survival of *T. synthetica* moths are not currently known. After a mast seeding event, seed dispersal is facilitated by the scatter hoarding behavior of rodents, which results in burial of some western Joshua tree seeds at a soil depth suitable for germination and sometimes under a nurse plant that may aid in seedling survival. After burial of seeds, several successive years of sufficiently wet and/or cool conditions are likely required to ensure that seeds germinate, and that seedlings reach a sufficiently large size (perhaps at least 25 cm) before the arrival of a period of hotter and/or drier conditions. This period of several successive years of sufficiently wet and/or cool conditions must occur relatively soon after a mast seeding event, because western Joshua tree seeds do not remain viable in the soil for long periods of time. After a seedling has become established, it must survive a long period of time (perhaps 30-50+ years) to reach reproductive maturity. The minimum recruitment rate needed to keep populations of western Joshua tree from declining is not known (Wiegand et al. 2004).

Similar-looking Plants

Although Joshua tree is a distinctive plant, differentiating between western Joshua tree and eastern Joshua tree may be difficult, and there are several plant species known to occur within the range of western Joshua tree that look superficially similar to the species. In California, western Joshua tree and eastern Joshua tree do not co-occur.

Lenz (2007) described the differences between western Joshua tree and eastern Joshua tree, and highlighted differences in the overall shape and form, branching, leaves, flowers, fruits, and different species of obligate pollinating moth. Lenz provided photos showing visual differences between flowers, fruits, and entire trees, and provided the following key to differentiate between the two species:

Plants ca. 6–9 (–16) m tall, arborescent with distinct trunk and monopodial branching, branches stout; leaves 15–35 cm long; corollas cream-colored, globular to depressed globular, never opening fully; perianth segments broadly ovate, tightly incurved; fruits ovoid to broadly ovoid, rounded at tips; pollinator *Tegeticula synthetica*. CALIFORNIA, NEVADA: *Yucca brevifolia*

Plants ca. 3–6 (–9) m tall, stemless or with trunks, usually branching less than 1 m above ground, the branching dichotomous until flowering, irregular thereafter; branches relatively numerous, somewhat slender; leaves 10–20 cm long; corollas greenish to cream-colored, narrowly campanulate, conspicuously expanded at bases; perianth segments narrowly oblong, tips recurving; fruits ellipsoid, tapering at tips; pollinated by *Tegeticula antithetica*. ARIZONA, CALIFORNIA, NEVADA, UTAH: *Yucca jaegeriana*

There are two other species in the *Yucca* genus that occur in California: banana yucca (*Yucca baccata* var. *baccata*) and Mojave yucca (*Yucca schidigera*) (Hess 2012). Both of these species can look superficially similar to western Joshua tree but can be easily distinguished from Joshua tree by examining the edges of leaves: banana yucca and Mojave yucca have “fibrous-shredding” leave edges that peel off, while Joshua tree’s leaf edges do not peel off, and are slightly serrated when viewed up close.

HABITAT THAT MAY BE ESSENTIAL TO THE CONTINUED EXISTENCE OF THE SPECIES

Habitat for plants can often be described in terms of the other species they are found in association with (natural communities), the geology and soils in the area they grow, and the climate, hydrology, and other factors that support the species’ survival and reproduction. The Department’s preliminary identification of the habitat that may be essential to the continued existence of western Joshua tree includes habitat that fits the general descriptions provided below and that supports a relatively high density of western Joshua trees, supports relatively high recruitment of western Joshua trees from seed, and/or is predicted to remain suitable for the species in the future despite the effects of climate change.

Natural Communities

The Department uses *A Manual of California Vegetation*, Second Edition (Sawyer et al. 2009) to classify natural communities within California. Within this classification system Joshua tree is the defining species for the *Yucca brevifolia* vegetation alliance (Joshua tree woodland), which is within the Mojavean–Sonoran Desert Scrub vegetation macrogroup. Joshua tree woodland is classified as having Joshua trees evenly distributed at greater than or equal to one percent absolute cover, and with other trees such as California juniper (*Juniperus californica*), Utah juniper (*Juniperus osteosperma*), or single leaf pinyon (*Pinus monophyla*) with less than one percent absolute cover in the tree canopy (Thomas et al. 2004). Joshua tree woodlands have Joshua trees as emergent small trees over a shrub or grass layer with white bur-sage (*Ambrosia dumosa*), cheesebush (*Ambrosia salsola*), common sagebrush (*Artemisia tridentata*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), blackbrush (*Coleogyne ramosissima*), buckhorn cholla (*Cylindropuntia acanthocarpa* var. *acanthocarpa*), Nevada ephedra (*Ephedra nevadensis*), California buckwheat (*Eriogonum fasciculatum*), sticky snakeweed (*Gutierrezia microcephala*), winterfat (*Krascheninnikovia lanata*), creosote bush (*Larrea tridentata*), Anderson thornbush (*Lycium andersonii*), banana yucca, and Mojave yucca (CNPS 2021a).

While Joshua trees are the defining feature of Joshua tree woodland, Joshua trees may also be components of many other vegetation alliances within California (Table 1) (Rowlands 1978, Turner 1982, CNPS 2021a). Figure 4 shows the areas in California where vegetation has been mapped and where western Joshua tree has been recorded as present within one of three cover classes (>0%–1%, >1%–5%, and >5%). The darkest red areas in Figure 4 provide a rough approximation of the areas in California where the species is most abundant.

Rowlands (1978) found the largest Joshua trees in communities dominated by blackbrush, creosote bush, and big galleta grass (*Hilaria rigida*). Some researchers suggest that while Joshua tree may be the most obvious plant in an area visually due to its height and dramatic silhouette, understory species are often more dominant cover components of the natural communities where Joshua trees occur (Rowlands 1978, Turner 1982). Due to the variety of natural communities that western Joshua trees can be found in, they do not appear to require specific plant species assemblages to meet their critical life history needs.

Joshua tree seedlings are often found growing under the canopy of other woody shrubs and perennial plants which act as nurse plants for the seedlings and aid in their survival. Loik et al. (2000b) reports that blackbrush appears to be an important nurse plant for western Joshua tree in the Covington Flats area of Joshua Tree National Park. Brittingham and Walker (2000) found that a large majority of eastern Joshua tree seedlings in southern Nevada were found growing under the canopy of 16 different woody shrubs, with blackbrush appearing to be the most common nurse plant in the study area. Advantages of germination under the canopy of another plant likely include higher soil moisture, reduced exposure to direct sun, reduced surface temperatures, reduced evapotranspirational (water) demand, increased nutrients, reduced herbivory, and/or reduced wind desiccation. Brittingham and Walker (2000) found that eastern

Table 1: Vegetation alliances in California in which Joshua trees occur or may occur (CNPS 2021a). Table organized by primary lifeform followed by alliance scientific name.

Primary lifeform	Alliance scientific name	Alliance common name
Tree	*Chilopsis linearis - Psorothamnus spinosus*	Desert-willow - smoketree wash woodland
Tree	*Juniperus californica*	California juniper woodland
Tree	*Juniperus osteosperma*	Utah juniper woodland and forest
Tree	*Pinus sabiniana*	Foothill pine woodland
Tree	*Quercus lobata*	Valley oak woodland and forest
Tree	*Yucca brevifolia*	Joshua tree woodland
Shrub	*Ambrosia salsola - Bebbia juncea*	Cheesebush - sweetbush scrub
Shrub	*Coleogyne ramosissima*	Blackbrush scrub
Shrub	*Ephedra nevadensis - Lycium andersonii - Grayia spinosa*	Nevada joint fir – Anderson's boxthorn - spiny hop sage scrub
Shrub	*Ericameria nauseosa*	Rubber rabbitbrush scrub
Shrub	*Eriogonum fasciculatum - Bahiopsis parishii*	California buckwheat – Parish's goldeneye scrub
Shrub	*Gutierrezia sarothrae - Gutierrezia microcephala*	Snakeweed scrub
Shrub	*Larrea tridentata*	Creosote bush scrub
Shrub	*Larrea tridentata - Ambrosia dumosa*	Creosote bush - white bursage scrub
Shrub	*Menodora spinescens*	Spiny menodora scrub
Shrub	*Prunus fasciculata - Scutellaria mexicana*	Desert almond - Mexican bladdersage scrub
Shrub	*Purshia tridentata - Artemisia tridentata*	Bitter brush scrub
Shrub	*Yucca schidigera*	Mojave yucca scrub
Herb	*Hilaria jamesii*	James' galleta shrub-steppe
Herb	*Hilaria rigida*	Big galleta shrub-steppe
Herb	*Stipa speciosa*	Desert needlegrass grassland

Joshua tree recruitment occurred predominantly on the east and west sides of nurse shrubs and suggested that microclimates are important for seedling establishment.

Communities of fungi occur in soils and can sometimes form mutualisms with plants. Mycorrhizal fungi grow into plant roots and provide nutrients to the plant. Western Joshua tree has been shown to sometimes form mycorrhizal associations that may benefit western Joshua tree (Harrower and Gilbert 2021), but it is not known whether mycorrhizal associations are required for western Joshua recruitment. In a study of western Joshua tree across an elevational gradient in Joshua Tree National Park, Harrower and Gilbert (2021) found that mycorrhizal fungal communities change with elevation, and that mycorrhizal colonization of western Joshua tree roots decreased significantly at higher elevations. Natural communities that support the presence of western Joshua tree's obligate pollinating moth *T. synthetica* and that support populations of scatter-hoarding rodents for seed dispersal are likely important components of Joshua tree habitat, yet the specific characteristics of the natural communities that support these species that are important for the reproduction and dispersal of western Joshua tree are not currently known.

Geology and Soils

The origin and properties of bedrock materials and the tectonic history of the Mojave Desert and Great Basin regions are important components of the geology of these areas; however, most of the current desert landforms in the region are likely due to climatic changes during the last million years, erosion, and other processes within the past several thousand years (Stoffer 2004). Within the Mojave Desert and Great Basin regions, western Joshua trees occur on various landforms including gentle alluvial fans, bajadas, ridges, flats, mesas, and gentle to moderate slopes, often near the bases of mountains (Huning and Petersen 1973, Thomas et al. 2004, Gucker 2006). The highest densities of Joshua trees may be found on well-drained sandy to gravelly alluvial fans within and adjacent to mountains. In some areas where western Joshua trees are less common, such as Edwards Air Force Base, they may be restricted to areas that store sufficient groundwater, such as large sand dunes or along groundwater drainages (Charlton and Rundel 2017).

Water availability likely limits survival and reproduction of western Joshua trees, and therefore the water-retention capacity of the soil in a given area may be an important component of habitat for the species. Soil textures in Joshua tree habitat have been described as silts, loams, and/or sands, and variously described as fine, loose, well drained, and/or gravelly. Huning and Petersen (1973) collected a number of soil samples along transects within and outside of western Joshua tree habitat in California in an investigation of soil water potential. Huning and Petersen (1973) found western Joshua tree to occur more frequently in areas with bimodal soil textures (with both larger sand particles and smaller silty clay particles) that facilitate soil moisture retention than in areas with well-sorted soil (with soil particles tending to all be of similar size). Huning and Petersen (1973) reasoned that soil moisture is the limiting factor governing the distribution of western Joshua tree, and therefore when the amount of precipitation is a limiting factor for western Joshua tree survival, soil textures that retain moisture become an important habitat characteristic. Similarly, Huning and Petersen reported that western Joshua tree tends to not occur where the depth to bedrock is less than one meter because there is insufficient groundwater to support the Joshua trees in these locations. Western Joshua tree also appears to be unable to grow well in soils with a high clay content or other "extremes of composition" such as high volumes of coarse fragments (Huning and Petersen 1973, Borchert 2021). Wallace and Romney (1972) reported that western Joshua tree grows best at root temperatures near 18°C (64°F) and without calcium carbonate in the soil. Huning and Petersen (1973) found that soil pH, soil nutrients, and the age of soils (more modern soils versus soils from the Tertiary period) did not seem to be significant factors determining western Joshua tree distribution within their study area near Riverside, California.

Areas that collect water due to topography, subsurface bedrock, and/or soil structure could allow western Joshua tree to grow in some areas that may otherwise be too hot or too dry, and such areas could provide important refugia for the species in the future.

Climate, Hydrology and Other Factors

Climate in the Mojave Desert and southwestern Great Basin where western Joshua tree occurs consists of long, hot summers, mild winters, and low overall precipitation. The local climate in these regions varies primarily due to elevation and topography. Precipitation across the Mojave Desert region is highly variable from year to year and oscillates between wetter and drier conditions within multi-year and multi-decade timescales. While average climate may be associated with the physical condition, distribution, or population dynamics of many species, extreme climate may be equally if not more relevant for explaining these factors (Zimmermann et al. 2009, Siegmund et al. 2016, Germain and Lutz 2020, Stewart et al. 2021). Acclimation can affect the tolerances of many organisms, including plants, to extreme environmental conditions (Gerken et al. 2015, Nievola et al. 2017). Little information about the climate tolerances of western Joshua tree is known; however, some inferences and assumptions have been made by examining available information about average climatic conditions during all or a portion of the 20th century within the species' range. These assumptions have primarily been used for species distribution models, which are described in more detail in the Climate Change section of this Status Review. While examining 20th century suitable climate conditions within the known range of the species undoubtedly provides insight into the species' climate tolerances, average climate conditions from a single century (or portion thereof) are not entirely representative of the climate conditions and climate variability that western Joshua tree has endured in the past or can endure in the future.

Precipitation

As in many desert regions, the magnitude and seasonality of precipitation is a principal driver of ecosystem processes (Holmgren et al. 2006), and precipitation is likely a critical factor for understanding what constitutes western Joshua tree habitat. Precipitation provides water for plants to absorb immediately and may also replenish underground moisture that plants may utilize later in the season via roots. With extensive root systems and moisture stored in tissues, adult Joshua trees are somewhat resilient to periods with little precipitation. Juvenile Joshua trees and seedlings, on the other hand, cannot access deep groundwater and cannot store as much water in their tissues, and are therefore more dependent on regular precipitation for their establishment and survival. The intensity and duration of droughts and periods of relatively high precipitation are likely important factors in determining where western Joshua trees can survive and reproduce. Recent drought in the Mojave Desert, and the predicted effects of climate change in the region are discussed further in the Climate Change Regional Effects section of this Status Review.

In areas where western Joshua trees occur, precipitation is received in the form of rain and less frequently snow. Most precipitation occurs between October and April, and May and June are consistently dry, accounting for less than five percent of average annual precipitation (Hereford et al. 2004). Isolated thunderstorms are possible in summer (typically July-September), and more of these summer thunderstorms occur in the eastern part of the Mojave Desert than in the western part (Hereford et al. 2004). Precipitation across the Mojave Desert region is highly variable from year to year and oscillates between wetter and drier conditions within multi-year and multi-decade timescales. During the period of 1893 to 2001 annual precipitation averaged across the Mojave Desert region ranged from as low as 34 mm (1.3 in) in one year to as high as 310 mm (12.2 in) in another year, with an average annual precipitation across all 108 years of 137 mm (5.4 in) (Hereford et al. 2004, 2006). During the 108-year period studied, Hereford et al. (2006) and Tagestad et al. (2016) identified multi-year or multi-decade periods of drought or otherwise predominantly dry conditions with contrasting multi-year or multi-decade periods that had above average precipitation (Figure 5). Although the dataset presented by Hereford et al. (2004) (and shown in Figure 5 of this Status Review) ends in 2001, the early 21st century has been a period of predominately dry conditions in the Mojave Desert (Khatri-Chhetri et al. 2021). This interannual variation and longer-term oscillation of relatively wet and relatively dry conditions are likely the result of global-scale climate fluctuations including the El Niño-Southern

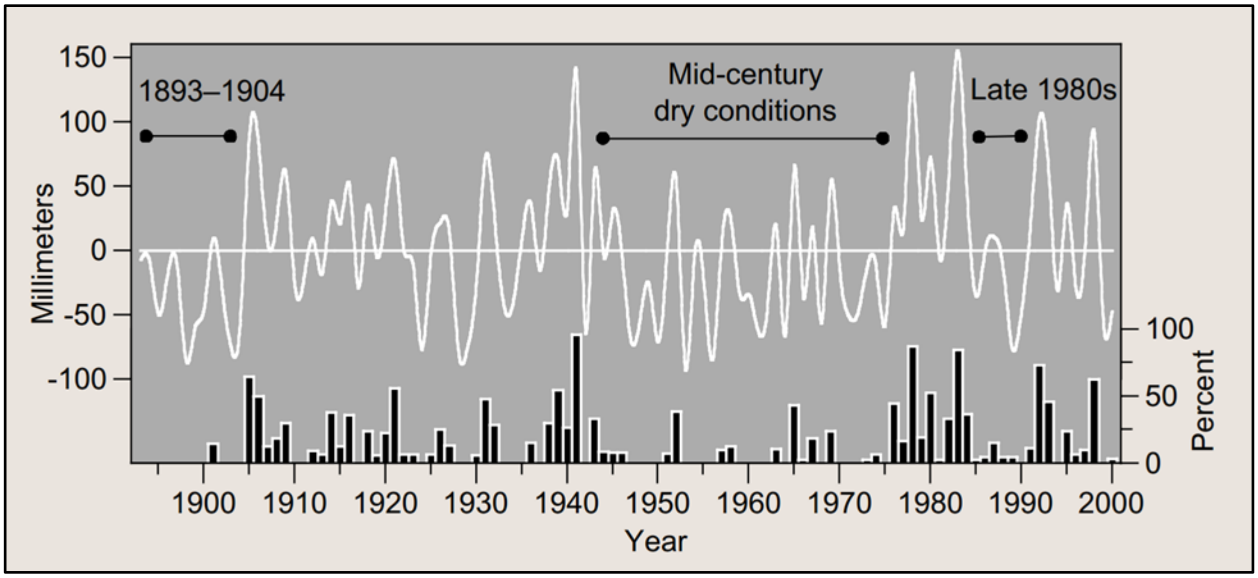

Figure 5: Average Deviation of Annual Precipitation in the Mojave Desert Region, 1893 to 2001 (Source: United States Geological Survey, Hereford et al. 2004).

Oscillation and the Pacific Decadal Oscillation (Cayan et al. 1998, McCabe and Dettinger 1999, Mantua and Hare 2002). The El Niño-Southern Oscillation may result in sea surface temperatures that may or may not result in anomalously wet or dry conditions across the Mojave. El Niño sea surface temperatures can often result in relatively wet winters, La Niña sea surface temperatures can often result in relatively dry winters, or there may be years that are considered neither El Niño nor La Niña. Analysis by Hereford et al. (2006) suggests that Mojave Desert precipitation oscillates between wetter and drier conditions irregularly, but with each successive wet winter event occurring an average of 4.8 years after the previous wet winter event. The Pacific Decadal Oscillation may also result in sea surface temperatures that result in decades-long periods of relatively wet or relatively dry conditions in the Mojave Desert, with each condition lasting for periods of two to three decades.

The timing and minimum amount of precipitation necessary for adult western Joshua tree survival, or for the germination and establishment of western Joshua tree seedlings is not currently known, but the available life history information suggests that seedlings require periods with regular precipitation to establish, and therefore it is likely that wet winter El Niño conditions, combined with longer-duration wet periods of the Pacific Decadal Oscillation provide the best chance for germination and establishment of western Joshua tree seedlings. In one monitoring plot at Cima Dome in Mojave National Preserve, Cornett (2018b) found that survivability (percentage of trees that survived since previous year) of eastern Joshua tree plants was moderately correlated with annual precipitation ($r = 0.51$, $P = 0.01$). Western Joshua tree is somewhat more abundant in the western Mojave Desert, where summer thunderstorms and precipitation are less common, and therefore western Joshua trees in the western Mojave Desert receive a greater proportion of their annual precipitation in the winter (Hereford et al. 2006). The amount of precipitation required for western Joshua tree likely varies depending on life history stage, and is also likely dependent upon a multitude of contributing factors including soil texture, ambient temperatures, local topography, elevation, and the presence and cover of other plants.

Climatic water deficit is a metric that has been correlated with vegetation distribution across many spatial scales, can be used to quantify the drought stress on plants in an area, and is generally considered to be a much more biologically meaningful metric than precipitation alone (Stephenson 1998). Climatic water deficit is defined as the amount of water that could have evaporated or been utilized by plants in an area (this is called potential evapotranspiration), minus the water that actually evaporated or was utilized by plants in an area (actual evapotranspiration). These metrics are less intuitive to understand than precipitation and temperature on their own, but they are affected by several abiotic factors that are important for plants, including soils, and the slopes and aspects of terrain, in addition to the timing and durations of precipitation, temperature, and solar radiation. Low elevation warm desert areas tend to have high climatic water deficits, and these deficits often decrease with increasing elevation.

Precise information on the climatic water deficits that western Joshua trees are able to tolerate, and the timing and amount of precipitation necessary for western Joshua trees to establish and survive are not directly known and are likely dependent on a number of factors. Nevertheless, some inferences may be made by examining available information on previous climatic conditions within the known range of the species. Much of the species distribution modeling work for western Joshua tree discussed in the Species Distribution Models section of this Status Report utilizes information on 20th century suitable climate conditions to make assumptions regarding the conditions necessary for western Joshua tree survival and establishment in the future.

High Temperatures

Smith et al. (1983) tested the thermal tolerances of western Joshua tree by subjecting leaves to temperature treatments, with results suggesting that the high temperature limit is 57°C (135°F), at which point photosynthetic functions are impacted. Although such high air temperatures are not expected to occur in areas with western Joshua tree in the foreseeable future, thermal tolerances in laboratory settings are different than thermal tolerances in the natural environment, which are confounded by a number of factors including but not limited to duration of exposure, water availability, and exposure to wind. High temperature alone may not be a direct physiological limit on western Joshua tree survival, but extreme high temperatures may nevertheless limit the distribution of the species, perhaps by contributing to climatic water deficit of an area, and other physiological stresses, particularly water stress, and therefore high temperatures likely limit the distribution of western Joshua tree indirectly.

St. Clair and Hoines (2018) found positive correlations between temperature and Joshua tree flower and seed production, suggesting that warming may positively affect Joshua tree reproduction. However, increased seed production would also depend on adequate pollination by *T. synthetica* under warmer climatic conditions. St. Clair and Hoines (2018) also found negative relationships between temperature and Joshua tree stand density, and suggested that there may be potential constraints of warmer temperatures on establishment success. Reynolds et al. (2012) found greatest seedling emergence occurred during spring and summer when warm soil temperatures were accompanied by increased soil moisture.

<u>*Low Temperatures*</u>

Smith et al. (1983) found the low temperature thermal tolerance of western Joshua tree to be approximately -6°C (21°F), which is a temperature that is reached in some areas of western Joshua tree's range, and may therefore be a limit on the distribution of the species in colder and higher elevation areas. Went (1957) published data demonstrating that after a Joshua tree has reached a certain age the plant requires exposure to low temperatures for optimal growth. This suggests that while extreme cold may be a limit on distribution, cold winter periods may be an important component for Joshua tree growth (Turner 1982).

Loik et al. (2000a) examined the effects of approximately doubled carbon dioxide (CO_2) levels (similar to what is expected globally at the end of the 21st century) and low temperatures on Joshua tree seedlings, and found that low-temperature tolerance was enhanced for Joshua tree seedlings maintained in the elevated CO_2 environment. Loik et al. (2000a) found that western Joshua tree seedlings that were acclimatized to low temperatures were better able to survive extreme low temperature events. Dole et al. (2003) utilized the work of Loik et al. (2000a) by incorporating the effects of elevated CO_2 levels on low temperature tolerance into a species distribution model for Joshua tree, which is discussed under the Species Distribution Models section of this Status Review.

ABUNDANCE AND TRENDS IN CALIFORNIA

Abundance

For the purposes of this Status Review abundance is defined as the number of individuals that are present overall, and density is the number of individuals that are present per unit of area. Western Joshua tree is currently relatively abundant in

California. Plant abundance can be quantified via a complete census of plants or estimated via statistical sampling. It is challenging to accurately estimate the size of plant populations that are patchy, occur at varying densities, or that occur over large geographical areas, and the western Joshua tree population has all of these characteristics. Estimates of the abundance of western Joshua tree therefore have a high amount of uncertainty associated with them.

As shown in Figures 2 and 3, western Joshua tree is widespread in the western Mojave Desert, and its range extends north into the southwestern Great Basin. Based on vegetation mapping data possessed by the Department, and as described in the Current Distribution section of this Status Review, western Joshua tree woodland could occupy an area within California of approximately 10,160 km^2 (3,920 mi^2) to 13,880 km^2 (5,360 mi^2), and additional areas that are not currently mapped could have lower densities of western Joshua trees, increasing the area occupied by the species. The USFWS (2018) estimated that the area occupied by western Joshua tree was 22,823 km^2 (8,812 mi^2), but this estimate included areas outside of California. WEST Inc. (2021a) used data from Cole et al. (2011) to report the area occupied by western Joshua tree as 15,071 km^2 (5,819 mi^2), but WEST Inc. (2021b) later reported that this estimate was only for the southern part of the species' range, and the northern and southern portions of the species' range together occupy an area of approximately 23,101 km^2 (8,919 mi^2), although this combined area likely includes areas outside of California. Within the areas occupied by western Joshua tree, the density of individuals varies widely. Some areas of the Mojave Desert have scattered Joshua trees at very low densities, while other areas have dense stands of trees.

WEST Inc. (2021a) used an analysis of aerial imagery to estimate the density of western Joshua trees within the species' southern range, and corrected for undercounting using density data from areas that were censused for western Joshua tree as part of renewable energy projects. WEST Inc. (2021a) used similar methods to separately estimate the density of western Joshua trees near the edges (± 5 km) of the area evaluated. This was done in an effort to make a more accurate estimate since the perimeter of the species' range was expected to have a generally lower density of plants than other portions of the range. WEST Inc. (2021a) estimated an overall western Joshua tree density of 4.27 to 7.04 trees per ha (95% confidence) within its southern range. Although the estimate from WEST Inc. (2021a) is only for the southern range of the species, it is likely the most accurate estimate of overall western Joshua tree density available. WEST Inc. (2021b) later revised their estimation methods to account for the effects of historical wildfire, but WEST Inc. did not provide the revised density estimates.

More localized estimates of western Joshua tree population density have also been made, ranging from 3.2 to 280 western Joshua trees per hectare. Esque et al. (2010)

examined 50 random plots containing at least one Joshua tree in Joshua Tree National Park and 50 random plots containing at least one Joshua tree in Death Valley National Park and found high variability in western Joshua tree density. Esque et al. (2010) reported an average density of 95.2 western Joshua trees per ha in Joshua Tree National Park and an average density of 62 Joshua trees per ha in Death Valley National Park. St. Clair and Hoines (2018) collected demographic information from ten different Joshua tree sites distributed across the Mojave Desert. Five of the sites were within the range of western Joshua tree, and three of those were within California. Western Joshua tree population density varied by more than an order of magnitude from 20 trees per ha in the eastern portion of Joshua Tree National Park to 280 trees per ha at Walker Pass, California. The average density of the five western Joshua tree sites studied by St. Clair and Hoines (2018) was 140 trees per ha. Rowlands (1978) recorded densities of Joshua trees at 21 stands throughout the range of eastern and western Joshua tree. Eight of these sites were within the range of western Joshua tree, and these had an average density of 81 trees per ha. It is unlikely that the density data from St. Clair and Hoines (2018) and Rowlands (1978) were intended to be representative of the entire California range of western Joshua tree, particularly areas with very low densities of trees. Sweet et al. (2019) reported densities of western Joshua tree at 14 nine-hectare macroplots within and near Joshua Tree National Park in 2016 and 2017, which were highly variable and ranged from 5.3 to 62.4 trees per ha. Densities of 3.2 and 33.9 western Joshua trees per ha have been reported to the Department at a preserve near Red Rock Canyon State Park and a preserve east of the North Haiwee Reservoir, respectively (Natural Resources Group, Inc. 2021). Despite the limitations of the estimates described above, they do provide information on possible densities of western Joshua tree.

Estimates indicate that the abundance of western Joshua tree is currently relatively high, but there is high uncertainty in estimates of population size due to both the uncertainty of density estimates, and uncertainty regarding how much area is occupied by the species. Assuming that the average density of western Joshua trees in all age classes in California is between 4.27 and 7.04 trees per ha (427 to 704 trees per km^2) (WEST Inc. 2021a), and the area occupied by western Joshua tree in California is between 10,160 km^2 and 13,880 km^2 (see Current Distribution section of this Status Review), there could be between 4.3 million and 9.8 million western Joshua trees in California (all age classes). An analysis by WEST Inc. (2021a) concluded that there are between 6.5 million and 10.6 million western Joshua trees, but this estimate appears to have only been for the southern part of the species’ range and did not take into account population reductions due to wildfires within the previous 100 years (WEST Inc. 2021b).

The Department also made a separate estimate of the number of adult western Joshua trees within California via stratified random sampling of aerial imagery. The resolution of the aerial imagery used (Google 2021) varied and we were unable to accurately recognize and count short and unbranched trees via aerial imagery, and no ground-truthing was conducted. The Department's estimates are therefore representative of taller adult trees, and not representative of all western Joshua trees like the density estimates previously described in this section of the Status Review. We randomly placed 150 circular 4-ha sampling plots entirely within mapped vegetation polygons containing western Joshua tree in California. We stratified these 150 sampling plots (50 per strata) within vegetation polygons with three different cover classes of western Joshua tree (>0%-1%, >1%-5%, and >5%) as identified on vegetation maps possessed by the Department. Cover class information was not available for 8% of the mapped area containing western Joshua tree and we had difficulty discerning individual trees in areas with abundant clonal growth. Based on the Department's stratified random sampling estimates, the average sample density across all areas and cover classes was approximately 3.1 to 3.5 adult western Joshua trees per ha (95% statistical confidence based on the methods in Elzinga et al. (1998)). Applying this estimate of adult western Joshua tree density to an estimated range of area that could be occupied by western Joshua tree within California (10,160 km^2 to 13,880 km^2) suggests that there could be between 3.1 million and 4.9 million adult western Joshua trees in California that are discernable via aerial imagery.

Population Trends

This section of the Status Review provides information on population trends of western Joshua tree from the past to the present. Discussion of western Joshua tree population trends that may occur in the future is provided in the Factors Affecting the Ability to Survive and Reproduce section of this Status Review. Population trends may be measured directly, inferred from demographic information, or indirectly inferred from fossil evidence or environmental impacts that have occurred in the past. Population trends can be an important predictor for extinction risk (O'Grady et al. 2004). Based on the available information, the Department concludes that development and other human activities which began with European settlement during and before the 19th century have resulted in the greatest decline in the number of western Joshua trees in California. Available information on Joshua tree population trends prior to European settlement is provided in the following section.

Inferred Long-term Trends

Genetic signatures suggest that western Joshua tree had a large population growth and range expansion into the Sonoran and Great Basin deserts from the Mojave Desert beginning about 200,000 years before present (Smith et al. 2011). Studies have made contradictory conclusions about Joshua tree's population trend over the past 20,000 years. Fossil evidence indicates that Joshua tree was more widespread during the late Pleistocene period (22,000 to 13,000 years before present) than it is today, with its range at that time extending south of its present range farther into southern California and Arizona, and likely also into northwestern Mexico, however a larger range does not necessarily mean that abundance was also higher (Rowlands 1978, Holmgren et al. 2010, Cole et al. 2011, Smith et al. 2011). Cole et al. (2011) noted that after a rapid warming of approximately 4°C in winter minimum temperatures in the Grand Canyon and 4°C increase in mean annual sea surface temperature off the coast of Northern California over an approximately 50-year period at the beginning of the Holocene period (approximately 11,700 years ago), available fossil records suggest that the range of Joshua tree contracted from the south over the following 3,700 years until the current southern range extent was reached. The apparent reduction in Joshua tree range from the late Pleistocene period to modern times suggests the population trend of Joshua tree across its entire range has been in decline. However, Smith et al. (2011) found no indication of dramatic Joshua tree population declines since the last glacial maximum approximately 21,000 years before present and suggested that habitat loss in the southern part of the Joshua tree's range may have been offset by the addition of new habitat in the north.

More recently, populations of western Joshua tree within California have declined following European settlement of the Mojave Desert region, primarily due to habitat loss and degradation related to agricultural conversion and development. It is difficult to quantify the magnitude of this population decline because there has been no long-term range-wide population monitoring, and the distribution of western Joshua tree prior to European settlement is not completely known. Nevertheless, western Joshua trees were removed from the Mojave Desert region as a result of human activities and continue to be removed to this day. Prior to 1920 and ending in the 1980s, much of the western portion of the Antelope Valley was utilized for alfalfa production (Borge 2018; Historic Aerials 2021), likely resulting in a widespread decline of western Joshua tree individuals as the desert was cleared for agricultural use. Figure 4 shows conspicuous areas where western Joshua tree is absent from western Antelope Valley and near the metropolitan areas of Palmdale and Lancaster, and these areas approximately overlap the same locations as current and historical agricultural activity and developed land use. These areas likely supported substantially more western Joshua trees in the past, as did other population centers and agricultural areas in western Joshua tree's range, such as Victorville, Hesperia, and Yucca Valley. Based on historic aerial imagery from the mid-20th century (Historic Aerials 2021) and presumed general distribution of western Joshua trees prior to European settlement, the Department estimates that approximately 30% of the habitat occupied by western Joshua tree in California may have been modified between European settlement and the present. While the historical densities of western Joshua tree in the areas of agricultural conversion and development are not known, the loss in number of individuals may have been somewhat proportional to the area of habitat lost. Information from aerial photography and the United States Geological Survey National Land Cover Database also show continuing land development within western Joshua tree habitat in the cities of Palmdale, Lancaster, Yucca Valley, Joshua Tree, Twentynine Palms, Victorville, Hesperia, and Apple Valley from 1984 to 2021, with many fragmented and isolated blocks of open space likely containing western Joshua tree (Krantz pers. comm. 2021, Appendix B). Despite the loss of a substantial number of western Joshua tree individuals from habitat loss since European settlement, the range (general geographical area in which the species occurs) in California appears to have remained more or less unchanged, with fragmented populations remaining in Antelope Valley and near the metropolitan areas of Palmdale and Lancaster, and dense stands remaining to the west of the areas presumed to have suffered the most serious historical habitat loss (see Figure 4). Habitat fragmentation is discussed further in the Development and Other Human Activities section of this Status Review.

Photographic evidence has shown various changes to western Joshua tree populations that are unrelated to direct tree removal and habitat loss. Historical photographs have been used to compare current and past conditions of western Joshua trees in some areas of California and Nevada (Cornett 1998), and a number of photographic monitoring plots were also established in Nevada in 1964 (Webb et al. 2003). Photo monitoring provides a view into the past that can be used to make direct comparisons, and photos have shown a range of changes to western Joshua tree populations including mortality of individuals, increases in individual plant size and number of branches, changes in vegetation composition, and migration into areas that appeared to be previously unoccupied (Wallace and Romney 1972, Webb et al. 2003). While localized observations from repeat photo monitoring can provide insights, they are not necessarily representative of landscape-wide trends.

Direct Population Monitoring

Recruitment is rare for many perennial plants in the Mojave Desert (Cody 2000), which provides a challenge for direct population monitoring. In addition to rare recruitment, western Joshua tree has a long generation time (see the Growth and Longevity section of this Status Review), and plants are long-lived. As a result, the population dynamics for western Joshua tree take place over long timescales and monitoring them directly requires planning and a long-term perspective. Very little long-term monitoring data for western Joshua tree is currently available. The quantitative monitoring data that are available span less than one full generation of the long-lived species (few monitoring efforts have reported data spanning a period greater than 30 years), and provide only a narrow view of population dynamics. Furthermore, the available long-term monitoring efforts for western Joshua tree lack replication and typically consist of only one small (typically 1 ha) plot per location without any replicates that would allow the results to be extrapolated to larger areas. Population trends from available direct population monitoring of western Joshua tree are not uniform, but several plots have shown declines in abundance, and little recruitment in plots has been observed. Trends in recruitment are discussed in more detail in the Demographic Information section of this Status Review.

Early monitoring plots were established, and data were collected from several locations within Joshua Tree National Park in the 1970s; however, attempts by Joshua Tree National Park staff to revisit and recollect data from these plots has not been possible because staff have been unable to replicate the original methods to collect comparable data (Frakes 2017b, Frakes pers. comm. 2021).

Comanor and Clark (2000) collected monitoring data from 1975 to 1995 from three circular 0.1-ha plots containing Joshua trees, but only two of these three plots had western Joshua tree and only one of those plots was in California. That plot was near Victorville at a relatively low elevation of 875 m (2,870 ft). Over the monitoring period from 1975 to 1995, the number of western Joshua trees in the Victorville plot remained the same (21 plants), and no recruitment was evident (Comanor and Clark 2000). Similarly, the number of Joshua trees in the other two plots examined by Comanor and Clark (2000) remained largely unchanged over the 20-year monitoring period.

Cornett (2009, 2012, 2013, 2014, 2016, 2020) established 1 ha monitoring plots in the late 1980s and mid-1990s at different western Joshua tree populations in the Mojave Desert and began collecting periodic data on western Joshua trees within those plots, with monitoring results spanning between 18 and 23 years. Western Joshua tree population declines were observed at the monitoring plot in Saddleback Butte State Park (Cornett 2016), Red Rocks Canyon State Park (Cornett 2020), and in the three monitoring plots within Joshua Tree National Park (Cornett 2009, 2012, 2014). The western Joshua tree population increased at the monitoring plot at Lee Flat in Death Valley National Park (Cornett 2013).

DeFalco et al. (2010) monitored western Joshua tree at five pairs of burned and unburned sites in Joshua Tree National Park from 1999 to 2004, to study post-fire effects. DeFalco et al. (2010) found that plants in burned plots declined by 80% at the end of the study, and plants in unburned plots declined by 26%, with drought likely increasing the decline in both burned and unburned plots during the monitoring period.

Barrios and Watts (2017) conducted a geographic information system (GIS) analysis of western Joshua tree population trends on Edwards Air Force Base from 1992 to 2015, focusing on area occupied by western Joshua trees as a proxy for the number of trees.

The report identified 18,673 ha (46,142 ac) as containing Joshua trees in 1992, 28,408 ha (70,198 ac) containing Joshua trees in 2008, and 32,508 ha (80,329 ac) as containing Joshua trees in 2015; however, the resolution of methods used for quantifying the number of trees improved greatly over time; 1992 (photogrammetry) methods were substantially different than the methods used in 2008 (LIDAR with 1.0-meter spot spacing) and in 2015 (LIDAR with 0.33-meter spot spacing). The different methodologies used, the known life history characteristics of the species, and a number of other factors identified by Barrios and Watts (2017) cast significant doubt on the validity of the reported 74% expansion of area occupied by western Joshua tree at Edwards Air Force Base between 1992 and 2015. This increase in area occupied may instead be better explained by technological advances that substantially increased the ability to detect western Joshua trees.

Gilliland et al. (2006) monitored a group of eastern Joshua trees by collecting demographic data from 77 trees at two-year intervals from 1987 through 2001. During the 14 years of the study, 8 of the 77 trees died, and Gilliland et al. (2006) did not report the establishment of any new eastern Joshua trees.

Several additional efforts to monitor Joshua tree populations have been initiated more recently and are discussed in the Management Efforts section of this Status Review. These monitoring efforts will likely provide additional direct population monitoring data in the future.

Demographic Information

The demographics of western Joshua tree are closely tied to the life history requirements of the species which are described in the Life History section of the Status Review. Important components in the life history of western Joshua tree include seed production, dispersal, and germination, seedling establishment, plant growth, sexual reproduction, asexual reproduction, long-term survival, and mortality of individuals. If comprehensive demographic data are available, it may be possible to use those data to provide insight into both the past and possible future demographic structure and size of populations (Brook et al. 2000). Demographic data can also be used to conduct population viability analyses to assess risk of extinction for populations or species (Chaudhary and Oli 2020), however no population viability analyses have been published for western Joshua tree. Demographic data that are not comprehensive nor collected in a systematic randomized sample should not be used to make statistical inferences about western Joshua tree populations on a larger population or species-wide scale. The Department does not currently have data on mortality levels of western Joshua tree across its range and similarly does not have data on the amount of recruitment that may be needed to maintain populations of western Joshua tree. Mortality and recruitment likely vary with the location and density of populations.

Because the Department does not have demographic data on current levels of mortality and recruitment and does not have data on the minimum amount of recruitment needed to maintain populations, many of the conclusions presented below on future population trends are somewhat speculative. Nevertheless, demographic information from the studies and other sources described in this Status Review provides the best available evaluation of western Joshua tree population trends in the late-20th century and may provide insight into possible future demographic structure and size of western Joshua tree populations.

Given the relatively long lifespan of western Joshua tree, the window for western Joshua tree reproduction is many decades long, and with the high abundance of existing populations the species may also be able to recruit a high number of individuals during favorable conditions, such as during multi-year or multi-decade periods of above-average precipitation described in the Precipitation section of this Status Review. On the other hand, multi-year or multi-decade periods of below-average precipitation in the future could also lead to periods of low recruitment and high mortality of adults. If recruitment does not keep pace with mortality, population sizes will decline.

Tree height is the most practical character to use for estimating Joshua tree age, and data from tree height surveys at a single point in time can provide insight into the current demographic structure of an area, an estimate of when trees were recruited into the population, and the trend of the population based on the relative numbers of plants in different Joshua tree age cohorts. Populations of Joshua trees that are increasing or sustainable at current population levels would be expected to have high numbers of young plants, decreasing numbers of older plants, and relatively few very old plants.

Although tree height is the best proxy to use for tree age, there are some limitations. The smallest size class is often underestimated because seedlings that are obscured beneath the canopies of other plants are very difficult to see, and researchers often note the difficulty in finding Joshua tree seedlings (Webber 1953, Wallace and Romney 1972, Comanor and Clark 2000, Esque et al. 2010, Reynolds et al. 2012). This limitation makes it problematic to utilize tree height data to identify relatively recent trends involving seedling establishment and early growth. It is therefore difficult in the short term to detect both periods of high seedling establishment and periods where little or no seedling establishment is taking place. Furthermore, the abundance of the youngest class of long-lived plants such as western Joshua tree are expected to fluctuate because seedling establishment is episodic. Nevertheless, seedlings that may initially be difficult to detect eventually become tall enough to be easily seen, with Cornett (2013) suggesting that it may take a minimum of three years for seedlings to become readily detectable. As trees get older, growth rates are affected by microhabitat and other factors, and distinct cohorts of trees that germinated near the same time may become less well-defined by height.

The Department does not possess a comprehensive random field sample of western Joshua tree heights across the species' range in California, and therefore the overall demographic trend of western Joshua tree in California is not currently known. The Department has, however, received western Joshua tree height information that is related to recently proposed development projects, and information that has been published or summarized in various scientific papers and reports. Demographic information based on western Joshua tree height from various locations is discussed in the following paragraphs and summarized at the end of this section.

In 2007, the National Park Service and U.S. Geological Survey established 50 randomly-placed 0.25 ha monitoring plots within the range of western Joshua tree in both Joshua Tree National Park and Death Valley National Park to collect initial demographic data and eventually monitor long-term trends of the species (Esque et al. 2010). The National Park Service and U.S. Geological Survey also established plots on National Park Service land within the range of eastern Joshua tree. The size distribution of Joshua trees reported in Esque et al. (2010) was aggregated among sampling locations within the range of both western Joshua tree and eastern Joshua tree and is typical of what would be expected for sustainable or increasing populations of long-lived plant species, e.g., generally large numbers of plants in the smaller size classes, moderate numbers of middle-sized plants, and greatly reduced numbers of the largest and oldest plants. Based on the information presented by Esque et al. (2010), which does not isolate height data on western Joshua tree by National Park Service Unit, Joshua tree populations on National Park Service lands appear to be sustainable, with large numbers of trees in younger age classes that may be able to replace the number of trees in the larger height classes, even if many of these smaller plants die.(see data specific to Joshua Tree National Park from St. Clair and Hoines (2018)). For a development project near the city of Hesperia, the Department also received western Joshua tree height data (Figure 6) showing a size distribution that is similar to the results presented by Esque et al. (2010), typical of what would be expected for a sustainable or increasing population of a long-lived plant species. The smallest 0-0.5 m height category of Figure 6 may represent a recent decline in seedling establishment, and/or it may be partially the result of underestimating seedlings, as discussed earlier in this section; however, the large numbers of trees in the younger age classes may still be able to replace the number of trees in the larger height classes, even if many of these smaller plants die.

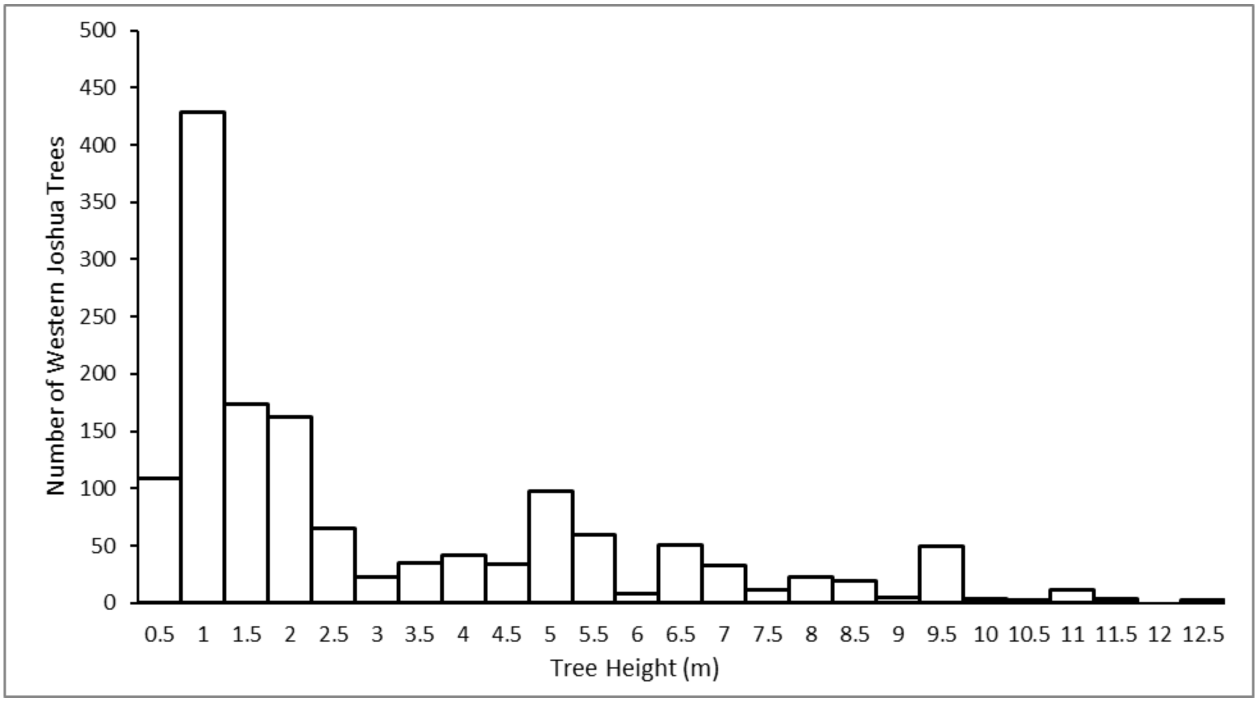

Figure 6: Heights of western Joshua trees in 2021 at a development project site near Hesperia (unpublished data from incidental take permit application to the Department)

The Department also aggregated western Joshua trees size class data reported for 11 recent solar energy development project sites in Kern County. Three broad size classes were reported for 222,073 western Joshua trees. Forty-four percent of trees were less than 1 m tall, 55% of trees were between 1 and 5 m tall, and 1% of trees were 5 m or greater in height. While these data are not as detailed as the height data presented in Figures 6, 7, and 8, the aggregated demographic structure in the form of tree height from these 11 project sites appears to be representative of relatively sustainable populations of western Joshua tree, with nearly half of the trees measuring under one meter tall, suggesting that they established in the early 1990s. The Department also received size class information for western Joshua trees at a preserve near Red Rock Canyon State Park which appears to be representative of a relatively sustainable population of western Joshua trees, with 83 percent of the trees measuring under one meter tall, suggesting that they established in the early 1990s (Natural Resources Group, Inc. 2021). The Department also received size class information for western Joshua trees at a development project site west of Adelanto and a mining project south of Lucerne Valley that appear to be representative of relatively sustainable populations of western Joshua tree. The demographic structure reported by Gilliland et al. (2006) for eastern Joshua tree was also broadly similar to that reported by Esque et al. (2010), with more trees in younger, smaller size classes than in older and larger size classes.

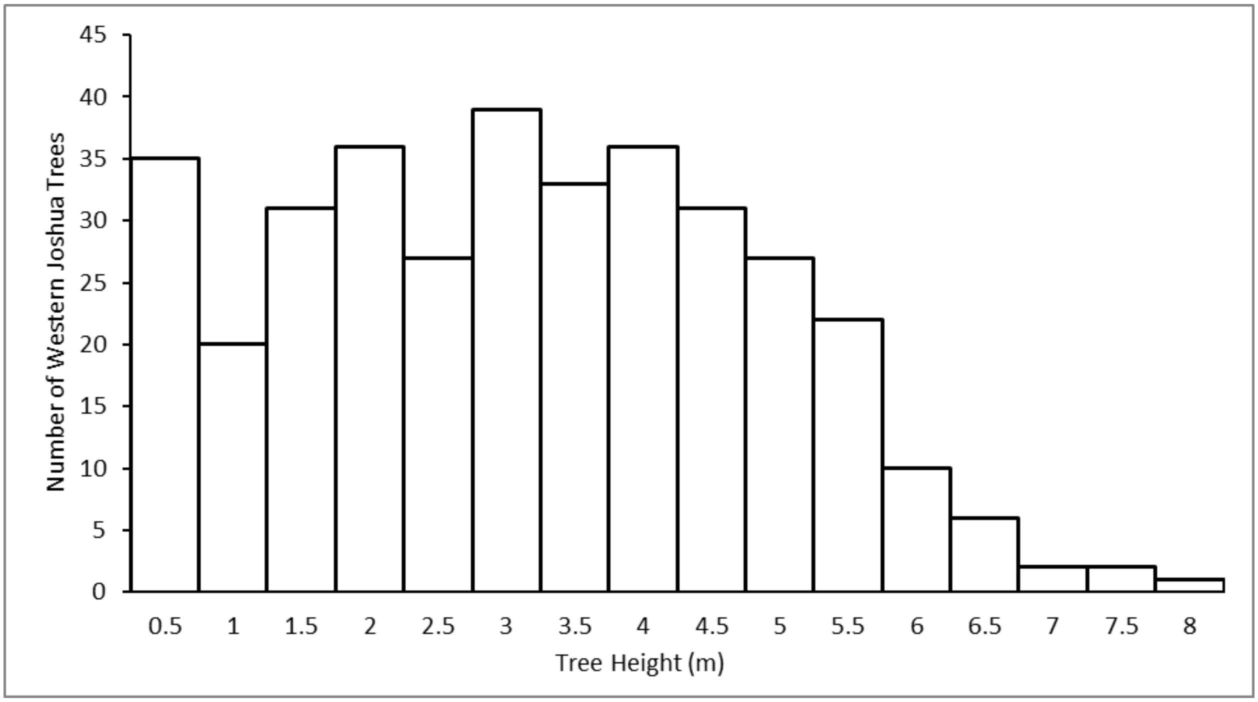

Figure 7: Heights of western Joshua trees in 2013 from three sampling locations in California (data from St. Clair and Hoines (2018))

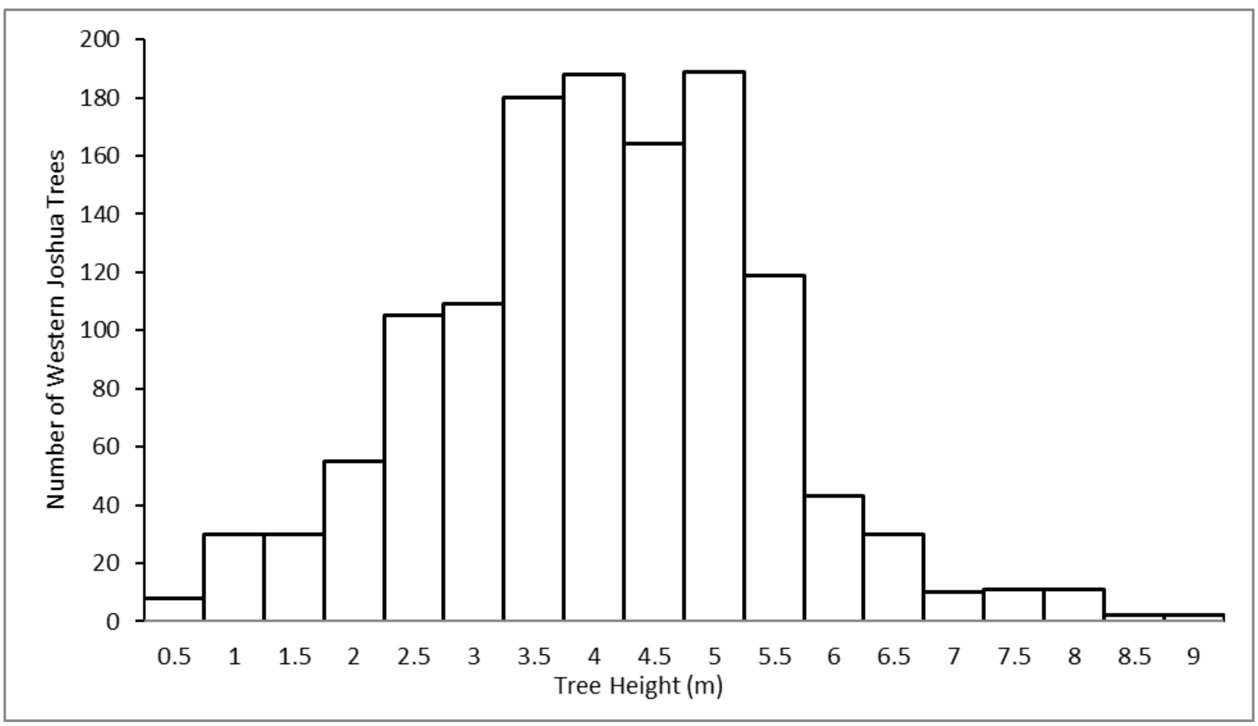

Figure 8: Heights of western Joshua trees at six development project sites near the cities of Palmdale and Lancaster in 2021 (unpublished data from incidental take permit applications sent to the Department)

A Joshua tree height dataset was made available by St. Clair and Hoines (2018) that consists of demographic information randomly collected from ten different Joshua tree sites distributed across the Mojave Desert. At each site, data were collected from 20 trees at each of six transects that were placed at one km intervals, so that 120 trees were sampled at each site. Five of the sites were within the range of western Joshua tree, and three of those were within California (Walker Pass, western Joshua Tree National Park, and eastern Joshua Tree National Park). While these three sites are not representative of the entire California range of western Joshua tree, they do provide a small sample of demographic data. The height of western Joshua tree at the three sites within the California range of western Joshua tree is presented in Figure 7. Unlike the tree height data shown in Figure 6 and the tree height data reported by Esque et al. (2010), St. Clair and Hoines (2018) found relatively fewer western Joshua trees in the younger (i.e., shorter tree height) categories, meaning there would need to be less mortality among the younger trees for them to be able to replace the older trees (there are fewer trees in the 0-0.5 m height class than the 2.5-3 m height class, which has the highest number of trees in Figure 7). Of the three western Joshua tree sites evaluated by St. Clair and Hoines (2018) in California, the eastern Joshua Tree National Park site had the lowest recruitment and the Walker Pass site had the highest recruitment. Assuming an average growth rate of 3-4 cm per year (Comanor and Clark 2000, Gilliland et al. 2006, Esque et al. 2015), these data from Clair and Hoines (2018) suggest a decline in western Joshua tree establishment since perhaps the 1950s. This decline may have been due, in part, to the mid-20th century dry conditions illustrated in Figure 5 and other factors discussed in this Status Review. The demographic structure of Joshua tree populations sampled by St. Clair and Hoines (2018) does not appear to be as sustainable as that reported for lands managed by the National Park Service; nevertheless, western Joshua trees have continued to establish within California in recent decades. The Department also received size class information for western Joshua trees at a preserve in southwestern Inyo County that is somewhat similar to the size class information shown in Figure 7, suggesting a decline in western Joshua tree establishment at that preserve since perhaps the 1950s (Natural Resources Group, Inc. 2021).

WEST Inc. (2021a) used an analysis of aerial imagery from the National Agriculture Imagery Program combined with and corrected by field data from solar energy development project sites to estimate the number of western Joshua trees in the southern portion of the species' range in three broad size classes. The estimate by WEST Inc. (2021a) indicated that 21% of western Joshua trees were less than 1 m tall, 58% of trees were between 1 and 5 m tall, and 21% of trees were 5 m or greater in height. These estimates of tree height include uncertainty because they are statistically estimated and not direct counts of plants in the field. The estimate of trees in the smallest, less than 1 m tall size class has the highest amount of uncertainty due, in part, to the difficulty in discerning them via aerial imagery, and therefore the number of plants in the smallest size class may have been underestimated. Furthermore, the size classes reported by WEST Inc. (2021a) are not as detailed as the height data presented in Figures 6, 7, and 8. Unlike the tree height data shown in Figure 6, reported by Esque et al. (2010), and reported for 11 recent solar energy development project sites in Kern County, the estimates provided by WEST Inc. (2021a) had fewer western Joshua trees in the youngest size class of less than 1 m tall. Fewer western Joshua trees in the youngest size classes suggests that an overall decline in western Joshua tree establishment may have taken place in the southern portion of the species' range since at least the early 1990s and perhaps earlier, but western Joshua trees have nevertheless continued to establish.

Contrasting further with the information presented in Figure 6 and presented by Esque et al. (2010), western Joshua tree height data from six development project sites near urban areas of Palmdale and Lancaster in Los Angeles County were reported to the Department in 2021 and are presented in Figure 8. Again, assuming an average growth rate of 3-4 cm per year, these data suggest that relatively few western Joshua trees have established at these sites since perhaps the 1950s, and establishment has continued to decrease since that time. While this decrease may have been due, in part, to mid-20th century dry conditions illustrated in Figure 5, environmental degradation related to urban and agricultural development may have disrupted an important aspect of western Joshua tree life history (see the Summary of Important Life History Needs section of this Status Review) which contributed to the reduced ability of western Joshua tree populations to establish new plants at these project sites in recent decades.

With an increasing number of monitoring plots being established for Joshua tree and other desert vegetation (see the Management Efforts section of this Status Review), the understanding of western Joshua tree recruitment, mortality, population trends, and demographic structure is expected to improve substantially in the coming decades, improving understanding of the status of the species.

Summary of Demographic Information

Based on the information available to the Department, local populations of western Joshua tree are currently exhibiting short-term demographic trends ranging from apparent increase or stability to apparent decline, but there does not appear to be a uniform range-wide trend. Data from WEST Inc. (2021a) suggests that there may be an overall declining trend in western Joshua tree establishment in the southern portion of the species' range in recent decades; however, this interpretation of the data may not be accurate due to the methods used for the study and the high uncertainty in estimating the abundance of the youngest size class. Populations of western Joshua tree are showing signs of drastic short-term decline in recruitment at six development project sites near the cities of Palmdale and Lancaster in the southwestern part of the species' range. More gradual decline in recruitment can be seen at the three locations in California sampled by St. Clair and Hoines (2018), which includes two locations in Joshua Tree National Park in the southern part of the species' range, and at a preserve in southwestern Inyo County. Populations appear to be experiencing stable short-term recruitment levels at various locations throughout the species' range, including at a development project site near Hesperia (Figure 6), another development project site west of Adelanto, a mining project site south of Lucerne Valley, several solar energy development project sites in Kern County, a preserve near Red Rocks Canyon State Park, and lands managed by the National Park Service as reported by Esque et al. (2010). The recent demographic trend information available to the Department suggests that density or extent of some populations may decline by the end of the 21st century (2100), but due to continuing recruitment, high abundance, widespread distribution, and the longevity of the species, the available demographic data does not currently suggest that western Joshua tree is likely to be at risk of disappearing from a significant portion of its range during this timeframe.

FACTORS AFFECTING THE ABILITY TO SURVIVE AND REPRODUCE

Large Population Size and Widespread Distribution

As described in the Range and Distribution and Abundance Sections of this Status Review, western Joshua tree is widespread and abundant in California. The abundance and widespread distribution of western Joshua tree within California are significant factors affecting the ability of the species to survive and reproduce. The smaller a species' range, the higher the probability that disturbances and environmental changes will affect a large enough portion of the species' range to jeopardize its persistence. Species with large ranges therefore tend to be less vulnerable to extinction from disturbances, environmental changes, random events, and other threats than species with more limited ranges (Purvis et al. 2000, Harris and Pimm 2007, Gaston and Fuller 2009, Pimm et al. 2014, Leão et al. 2014, Newbold et al. 2018, Silva et al. 2019, Enquist et al. 2019, Staude et al. 2020).

Population size and trends are also important predictors for extinction risk (Shaffer 1981, Pimm et al. 1988, O'Grady et al. 2004). Populations with high abundance can suffer substantial losses and still remain viable. Species with large populations that occupy large environmentally variable regions also generally have higher genetic diversity than species restricted to smaller areas and, therefore, avoid many problems of smaller populations (Ellstrand and Elam 1993, Reed 2005, Hobohm 2014). Populations with high levels of genetic diversity are less likely to require rapid evolutionary adaptation or migration to more suitable locations in order to persist in the face of climate change. Populations containing more genetic variability are more likely to contain traits that are beneficial under changing conditions, increasing the likelihood of persistence in their current range (Hoffmann et al. 2005, Hoffmann and Sgro 2011, Stotz et al. 2021). Western Joshua tree's current range, distribution, and abundance are all evidence that the species has been able to adapt to or endure the range of climate conditions and climate variability that has occurred within the species' range since the late Pleistocene period (22,000 to 13,000 years before present), although the species' range shifted during this time, as described in the Inferred Long-term Trends section of this Status Review.

In assessing whether western Joshua tree should be listed under the federal ESA (16 U.S.C. §§ 1531-1544), the USFWS (2018, 2019) concluded that western Joshua tree has a relatively large population and distribution that covers a range of elevations with differing climatic conditions and soil types, and concluded that western Joshua tree had: (1) a high capacity to withstand or recover from stochastic disturbance events (resilience); (2) the ability to recover from catastrophic events (redundancy); and (3) ability to adapt to changing conditions (representation) as those terms are defined by Smith et al. (2018), however the USFWS findings for Joshua tree were set aside and remanded to the USFWS for reconsideration in 2021 as described in the Federal Endangered Species Act section of this Status Review.

The concept that widespread and abundant species are less vulnerable to extinction is also reflected in the methodologies used by international nonprofit organizations to objectively rank the vulnerability to extinction of species throughout the world. The two most widely used approaches for assessing the conservation status of species in North America are NatureServe's assessments which prioritize rarity in assessing extinction risk and the International Union for Conservation of Nature (IUCN) Red List which places a higher emphasis on trends (Frances et al. 2018). NatureServe considers the abundance and distribution of species, or rarity, to be more than twice as important as threats in assessing the conservation status of a species (Faber-Langendoen et al. 2012). The IUCN uses any of several criteria to assess and rank the status of species under their Red List, including: (A) significant population size reduction, (B) significant reduction in geographic range, (C) small population size and decline, (D) very small or restricted population, or (E) a quantitative analysis demonstrating probability of extinction (Mace et al. 2008, IUCN 2012). The abundance and distribution of many widespread species excludes them from consideration under many of the IUCN Red List criteria listed above unless significant declines have been observed or quantitative analysis demonstrates a probability of extinction within 100 years or less.

Climate Change

It is unequivocal that human influence has warmed the atmosphere, ocean, and land, and widespread and rapid changes in the atmosphere, ocean, cryosphere, and biosphere have occurred (IPCC 2014, 2021). Global surface temperature will continue to increase until at least the mid-21st century under all emissions scenarios considered by the Intergovernmental Panel on Climate Change, and global warming of 1.5°C and 2°C will be exceeded during the 21st century unless deep reductions in emissions occur in the coming decades (Schwalm et al. 2020, IPCC 2021). While projected changes in climate may benefit some species, experimental and empirical evidence indicates that climate change is negatively impacting species and natural systems across the globe (Parmesan and Yohe 2003, Parmesan 2006, Scheffers et al. 2016), is increasing extinction risk (Warren et al. 2011, Nic Lughadha et al. 2020), and has already caused local extinction of some species (Wiens 2016). California's physical and biological systems have already been affected by climate change (Office of Environmental Health Hazard Assessment 2018, Iknayan and Beissinger 2018, Riddell et al. 2019). According to the California Global Warming Solutions Act of 2006, climate change is now considered one of the greatest threats to California's ecosystems, and over the 21st century, climate change will alter the fundamental character, production, and distribution of the ecosystems in California and elsewhere (Snyder et al. 2002, Snyder and Sloan 2005, California Energy Commission 2009, Shaw et al. 2011, Notaro et al. 2012, Garfin et al. 2013, Bedsworth et al. 2018). Climate change is a major challenge to the conservation of California's biological resources, and it will amplify existing threats and create new threats to natural systems.

Species distribution modeling efforts that have been conducted for Joshua tree so far and much of the climate change science available to the Department focus their predictions on conditions at the end of the 21st century (2100). Due to the high uncertainty in projecting the pace and magnitude of climate change and other threats in the 22nd century (after 2100), and the lack of available scientific information that contemplates such timeframes for the species, the Department cannot yet consider the range of the species in the 22nd century to be foreseeable. For the purposes of this Status Review, the Department considers the foreseeable future to be through the end of the 21st century (2100).

Regional Effects

Studies indicate that by the end of the 21st century California's climate will be considerably warmer than it is today, precipitation will become more variable, droughts will become more frequent, heavy precipitation events will become more intense, more winter precipitation will fall as rain instead of snow, snowpack will melt earlier in the year, and snowpack will be diminished (Leung et al. 2004, Hayhoe et al. 2004, Mote et al. 2005, Knowles et al. 2006, Garfin et al. 2013, Bedsworth et al. 2018, He et al. 2018). California is also vulnerable to climate fluctuations because it derives a large percentage of its water supply from a small number of large winter storms. These storms arise from “atmospheric rivers” which are long and narrow corridors of enhanced water vapor that are often associated with a low-level jet stream of an extratropical cyclone (Dettinger 2011, Dettinger et al. 2011).

The Mojave Desert and other regions of California where western Joshua trees grow are expected to become significantly hotter by the end of the 21st century, with daily average high temperatures in the Inland Deserts Region (all of Imperial County and the desert portions of Riverside and San Bernardino Counties) projected to increase by up to 4.5°C to 8°C (8°F to 14°F) at the end of the 21st century depending on future greenhouse gas emissions (Hopkins 2018), an increase that is greater than most other areas of California (He et al. 2018). Higher temperatures will exacerbate water stress on a region that is already limited by water availability. In areas supporting western Joshua tree the number of days with freezing temperatures is expected to go down (Sun et al. 2015).

Precipitation in areas with western Joshua tree is low, and highly variable from year to year, and this variability is projected to increase in the coming decades, with extreme droughts and extreme precipitation events both becoming more common (Hopkins 2018). The effects that climate change will have on overall average annual precipitation within the range of western Joshua tree is still uncertain, and projections suggest that there may be only slight changes, even under different emission scenarios (Allen and Luptowitz 2017, Hopkins 2018, He et al. 2018), or an overall drying pattern (Seager and Vecchi 2010), however water availability may nevertheless decrease as a result of increased temperatures and more precipitation falling as rain instead of snow. An analysis by Gonzalez (2019) found that approximately half of climate models evaluated project increased precipitation in Joshua Tree National Park at the end of the 21st century, and approximately half of the models project decreased precipitation, although higher predicted temperatures would tend to increase aridity. The Mojave Desert receives most of its average annual precipitation between October and April; however, a substantial amount of summer precipitation is also possible in the form of thunderstorms, with more summer precipitation falling in the eastern part of the Mojave Desert than in the western part (Hereford et al. 2004). According to some climate models, average winter precipitation (falling mainly in December, January, and February) may increase in the region (Allen and Luptowitz 2017), however, average precipitation from summer thunderstorms may decrease (Pascale et al. 2017). A 2021 study by Khatri-Chhetri et al. (2021) found that the Mojave Desert region is experiencing more frequent and severe drought conditions in recent years. In this study, both precipitation and temperature data were used in calculating the Standardized Precipitation Evapotranspiration Index (SPEI) which served as a proxy for drought. SPEI values from 1950 to 1999 were compared to SPEI values from 2000 to 2015 and it was shown that plant communities in the Mojave Desert experienced more drought stress during the 2000 to 2015 time period than the 1950-1999 time period. Based on this data, the authors concluded that the frequency and severity of dry periods are increasing in the 21st century. There may also be a slight reduction in wildfire ignitions due to lightning as a result of the reduced number of thunderstorms, although whether this will have any effect on wildfire risk is not known. Effects of climate change on oscillations between wetter and drier conditions within multi-year and multi-decade timescales are uncertain.

Direct Effects

The climatic conditions across western Joshua tree's range have already changed and will continue to change as a result of ongoing global greenhouse gas emissions. The Department expects that some of the effects of climate change described in the Regional Effects section of this Status Review (e.g., increased temperatures and decreased total water availability locally) will likely contribute to a decline in populations of western Joshua tree within California through the end of the 21st century; however, the extent to which the negative effects of climate change will impact the species' range, distribution, density, abundance, life history, and demographics as described in this Status Review in this timeframe is less clear. The primary reasons for the expected decline of populations of western Joshua tree within California may be the incremental contribution of climate change to high intensity and longer duration droughts, coupled with extreme high temperatures during the summer months, which may have direct physiological effects on western Joshua tree plants. These effects of climate change will likely reduce western Joshua tree seedling recruitment, and to a lesser extent also increase adult western Joshua tree mortality, leading to population declines as recruitment does not keep pace with mortality. Climate change may also contribute to the decline of populations of western Joshua tree via other more indirect mechanisms, including increased impacts from small mammals during drought, reduced growth due to lack of low winter temperatures, increases in fire activity, or effects on pollinating moths, which are discussed in more detail in the Indirect and Cumulative Effects, Wildfire, and Herbivory and Predation sections of this Status Review.

While the available evidence predicts that areas with suitable climate conditions based on 20th century climate data for western Joshua tree within California will decline substantially through the end of the 21st century (2100) due to climate change (exposure to climate change is high), the Department does not have data on the extent to which these changes to the climate conditions are likely to affect the demographics (e.g., recruitment and mortality) of the species throughout its range in the foreseeable future. Without data on the extent to which climate change is likely to affect western Joshua tree demographics through the end of the 21st century (2100), the Department does not have the data to conclude that climate change will likely result in a significant reduction of the species' range during this timeframe. The most direct evidence of climate change affecting the range of Joshua tree comes from Cole et al. (2011). Cole et al. (2011) noted that after a rapid warming of approximately 4°C in winter minimum temperatures in the Grand Canyon and 4°C increase in mean annual sea surface temperature off the coast of Northern California over an approximately 50-year period at the beginning of the Holocene period (approximately 11,700 years ago), available fossil records suggest that the range of Joshua tree contracted from the south over the following 3,700 years until the current southern range extent was reached. For this reason, the Department expects that any declines in abundance or changes in range of western Joshua tree that are caused by climate change may occur very slowly.

Western Joshua tree currently occupies a highly variable environment and some areas of climate refugia are expected to remain throughout the species' range in the foreseeable future, even at its southern trailing edge (Barrows and Murphy-Mariscal 2012, Sweet et al. 2019, Barrows et al. 2020). Because western Joshua tree evolved in a highly variable environment, the species may also have some resilience to a changing climate, particularly at the warmer and drier extents of its range. Species responses to increased climate variability are likely to be complex, and may be difficult to predict (Vázquez et al. 2017).

Based upon the information in the Life History and Climate, Hydrology and Other Factors sections of this Status Review, recruitment of western Joshua tree seedlings requires a number of conditions to occur in succession, notably the conditions leading to large mast seeding events, followed by several successive years of sufficiently wet and/or cool conditions so that seeds can germinate, and seedlings can reach a sufficiently large size before the arrival of a period of hotter and/or drier conditions. This suggests that western Joshua tree seedlings and juveniles may be particularly vulnerable to warming and droughts from climate change. Increasing summer temperatures and related water stress that are expected to occur by the end of the 21st century likely mean that recruitment of western Joshua tree seedlings will occur less frequently in many areas, and as a result, populations of western Joshua trees in these areas will decline in size over time. Declines due to reduced seedling recruitment will likely be most severe in areas of western Joshua tree's range that are already near the thermal and water stress tolerance limits for recruitment, such as at hotter, low-elevation areas. St. Clair and Hoines (2018) found significant positive relationships between temperature and Joshua tree flower and seed production, suggesting that Joshua trees have higher reproduction when temperatures are warmer; however, St. Clair and

Hoines (2018) also found negative relationships between temperature and Joshua tree stand density, and suggested that there may be potential constraints of warmer temperatures on establishment success. Despite concerns of lack of western Joshua tree seedling recruitment at low elevation areas within Joshua Tree National Park, Frakes (2017a) reported the presence of Joshua trees that were less than 50 cm (20 in) tall in 500 x 500 m (1,640 x 1,640 ft) monitoring plots across the entire elevation gradient in which the species occurs in the park, including the three lowest elevation plots. Due to the relatively long lifespan of western Joshua tree, and the species' ability to reproduce asexually, adult western Joshua trees may be able to persist on the landscape for long periods of time, even if they are not able to recruit new individuals into the population through sexual reproduction. As described in the Demographic Information section of this Status Review, it may be possible to use demographic information on western Joshua tree to identify areas where seedling recruitment in recent decades does not appear to be sufficient to maintain current population levels. A random field sample of western Joshua tree demographic information across the species' range could perhaps be used to correlate declines in recruitment with areas most severely affected by climate warming that has already occurred, however, such work has not been completed (discussions of work by Barrows and Murphy-Mariscal (2012) and Sweet et al. (2019) are in the Species Distribution Models section of this Status Review).

As described in the Precipitation section of this Status Review the timing and minimum amount of precipitation necessary for adult western Joshua tree survival is not currently known, but increasing summer temperatures and related water stress may negatively affect adult western Joshua trees in some areas, or even cause them to die, particularly during periods of extended drought. In instances where increasing summer temperatures and related water stress are not severe enough to result in direct mortality of established adult Joshua trees, this water stress may nevertheless reduce the ability of the adult trees to grow or reproduce asexually or limit the resources available to produce flowers and mature fruits for sexual reproduction. In 2016 and 2017, Frakes (2017b) collected data in Joshua Tree National Park on the health of live western Joshua trees and the number of trees that appeared to have died within the previous five years (i.e., recent mortality rate). Frakes (2017b) acknowledged there was likely some error in their ability to visually assess when a western Joshua tree had died, and some may have died more than five years earlier. Frakes (2017b) reported that across the 12 500 x 500 m (1,640 x 1,640 ft) plots, most live Joshua trees appeared robust or moderately healthy, but the estimated recent mortality rates ranged from 4% to 57% over five years, and the mortality rates across all 12 plots averaged together was 20% over five years. Drought from 2012 to 2016 was hypothesized to have contributed to the recent mortality. Harrower and Gilbert (2018) collected western Joshua tree demographic data at 11 sampling sites along a 1,200 m (3,900 ft) elevational gradient in

Joshua Tree National Park in 2016 and 2017, and found that the number of dead western Joshua trees was greatest at the highest elevation sampling site at 2,212 m (7,257 ft) and at the lowest elevation sampling site at 1,004 m (3,294 ft). Harrower and Gilbert (2018) suggested that this observation at the lowest elevation sampling site was consistent with expectations from species distribution models (Cole et al. 2011, Barrows and Murphy-Mariscal 2012), which are discussed in more detail in the Species Distribution Models section of this Status Review. Changes in CO_2 concentrations can affect the rate of chemical reactions in plants, and Huxman et al. (1998) found evidence that elevated CO_2 conditions may help offset high-temperature stress in a coastal *Yucca* species, but not Joshua tree.

There may be a time delay between the time when an area becomes no longer suitable for a species (crossing an extinction threshold) and when that species is no longer present, (Tilman et al. 1994, Kuussaari et al. 2009, van Mantgem et al. 2009, Svenning and Sandel 2013, Figueiredo et al. 2019). Extinction processes often occur with a time delay and populations living close to their extinction threshold might survive for long periods of time despite local extinction being inevitable (Hanski and Ovaskainen 2002, Lindborg and Eriksson 2004, Helm et al. 2006, Vellend et al. 2006, Malanson 2008, Cronk 2016). Because western Joshua tree is a long-lived species, adults could persist for decades or longer in areas that are no longer suitable for recruitment, or recruitment may continue, but at rates that are ultimately insufficient to maintain the species. Although these areas may be occupied, the presence of western Joshua tree may merely represent a delayed local extinction. The ability of western Joshua tree to reproduce asexually may extend the ability of the species to persist within its range for very long periods of time, and delay local extinction for centuries or millennia, or perhaps preserve it as a relict species from an earlier climate. The ability of western Joshua tree to reproduce asexually and the episodic nature of western Joshua tree recruitment may also mask the ability to determine whether populations have passed a local extinction threshold. Due to the lack of basic demographic information for western Joshua tree, such as mortality rates, sexual and asexual recruitment rates, and fluctuations of those rates over long timescales, and the lack of information on how these factors affect abundance, the Department does not currently have a way to determine if populations are likely subject to a delayed local extinction or not. The Department therefore does not currently have any information showing that western Joshua tree populations are experiencing delayed local extinction.

Migration may help some species respond to climate change (Neilson et al. 2005); however, western Joshua tree may not be able to naturally colonize areas of newly suitable climate quickly or at all due to species traits (e.g., slow growth and limited dispersal ability) and other factors such as geology, soils, land use, and existing natural communities in newly suitable climates. Nevertheless, while the direct effects of climate change are likely to result in the decline of populations at hotter, lower-elevation areas due to adult mortality and reduced recruitment of seedlings, climate change could also allow for the expansion of western Joshua tree into areas that were previously too cold or perhaps too wet to support the species. Smith et al. (1983) found the low temperature thermal tolerance of western Joshua tree to be approximately -6°C (21°F). As the climate warms, areas at higher elevations and higher latitudes that were sometimes below this low temperature thermal tolerance, but that were otherwise suitable for western Joshua tree, may become suitable for the species. Loik et al. (2000a) further examined the effects of low temperatures and elevated CO_2 levels on Joshua tree seedlings, and found that low-temperature tolerance was enhanced for Joshua tree seedlings maintained in an elevated CO_2 environment, which suggests that western Joshua tree populations that experience extreme low temperature events may receive a survival benefit from elevated CO_2 conditions that are expected in the future, further expanding the ability of the species to occupy colder areas. Newly suitable climates could therefore become populated by western Joshua tree, assuming that western Joshua tree is able to disperse into those areas. Trends since the beginning of the Holocene period approximately 11,700 years ago (Cole et al. 2011) suggest that natural colonization of areas that become suitable for western Joshua tree in the future would take place very slowly, however, dispersal facilitated by humans (assisted migration) could accelerate colonization.

Species Distribution Models

Efforts to predict effects of global climate change on the future range and distribution of species can be conducted using species distribution models (Elith and Leathwick 2009), which may also identify important areas of climate change refugia where species may persist (Barrows et al. 2020). These efforts usually involve inputting relevant geographic data into computer software, identifying variables that appear to influence the distribution of a species at one time period, and then using the climate variables expected in the future under climate change scenarios to generate a prediction of where climate conditions that supported the species during the historical period could be expected to persist in the future. Spatial data layers used for species distribution models ideally include a large set of biotic and abiotic variables hypothesized to have a major effect on the distribution of the species, and temporally matched data on climate and species distribution (e.g., abundance, presence-absence, presence only). The species distribution models for Joshua tree discussed below model suitable climate conditions using climate data from 30- to 100-year timespans from the 20th century, combined with past or current species distributions and sometimes other biotic or abiotic variables to project potential future species distributions.

Species distribution models have substantial inherent limitations (described near the end of this section), but despite their limitations, species distribution models are useful ways to anticipate how climate change may affect species distributions in the future, and can provide a useful first approximation of the direction and magnitude of potential impacts of climate change on species range (Ackerly et al. 2010). Furthermore, species distribution models gain power if they incorporate large sets of validated observations, and because western Joshua tree is so visually distinctive and well-observed, it is a good species for species distribution modeling applications. While species distribution models can help identify areas where climate conditions will likely depart from historical climate conditions (i.e. exposure), they cannot predict how and when a species will respond to that change in climate (i.e., sensitivity, or whether the climate change will cause the species to disappear from affected areas, and when that may occur) (Dawson et al. 2011). Uncertainty in species distribution modeling results could mean that a species' exposure to climate change is either higher or lower than models predict.

Seven Joshua tree species distribution modeling efforts that assess possible future distributions have been published, and five of them consider western Joshua tree and eastern Joshua tree collectively as one species across their entire range (Thompson et al. 1998, Shafer et al. 2001, Dole et al. 2003, Cole et al. 2011, Thomas et al. 2012). Two of the species distribution modeling efforts are specific to western Joshua tree, but only examine climate changes within Joshua Tree National Park and the surrounding vicinity (Barrows and Murphy-Mariscal 2012, Sweet et al. 2019). The Department is not aware of any species distribution modeling efforts that are specifically focused on the California range of western Joshua tree. The Department did not independently produce a species distribution model to predict the effects of global climate change on the future range and distribution of western Joshua tree within California as a part of this Status Review, but did assess the vulnerability of western Joshua tree to climate change using the NatureServe Climate Change Vulnerability Index (CCVI) Version 3.02 (NatureServe 2016, CDFW 2021b).

The species distribution modeling efforts that have been conducted for Joshua tree suggest that climate change could cause substantial reductions in areas with 20th century suitable climate conditions for the species at the southern parts of western Joshua tree's range, including within Joshua Tree National Park. These species distribution modeling efforts also suggest that substantial additional areas of 20th century suitable climate conditions may become available for western Joshua tree to the north, particularly in Nevada (outside of the scope of CESA) but also in some parts of eastern California, although the species is unlikely to naturally colonize these areas in the foreseeable future. There is also evidence that areas of 20th century suitable climate will remain within the species' range at the end of the 21st century, including within Joshua Tree National Park. While species distribution models are useful in suggesting that a shift in the potential range of the species will take place sometime in the future, the effects of climate change on the population dynamics or current populations of western Joshua tree in the foreseeable future are unknown. The negative effects of western Joshua tree exposure to climate change within the foreseeable future could perhaps be very severe, resulting in a loss of significant range, or perhaps they will be less severe, resulting in lowered abundance without significant range loss. Due in large part to the lack of information on western Joshua tree's sensitivity to climate change (see the Direct Effects section of this Status Review), in combination with resiliency of the species due to its high abundance and widespread distribution (as discussed in the Large Population Size and Widespread Distribution section of this Status Review), the Department does not currently have enough information to conclude that climate change is likely to cause western Joshua tree to become in serious danger of disappearing from a significant portion of its range in the foreseeable future (prior to 2100). While the Department does not currently foresee that the species is likely become in serious danger of reductions in a significant portion of its range in the foreseeable future, western Joshua tree populations within the areas that will be most severely impacted by climate change may nevertheless experience declines in density and distribution. Species distribution modeling efforts for western Joshua tree are discussed in more detail in the following sections.

<u>Range-wide Models</u>

The most useful range-wide species distribution modeling effort for this Status Review is Cole et al. (2011), which analyzes the entire range of western Joshua tree (lumped with eastern Joshua tree), uses climate variables at a relatively fine scale (1-km and 4-km grids), considers some climate variables at a monthly scale rather than annually, utilizes baseline climate conditions that may be somewhat more representative of what the species experienced during its evolution than other models produced for the species (the entire 20th century record and 1930-1969), and involved six different species distribution models and compared their results. The models developed by Cole et al. (2011) that most accurately describe how climate is correlated with Joshua tree's present distribution included variables such as average precipitation, extreme high and low temperatures, and average high and low temperatures in certain months. Based on these species distribution models, Cole et al. (2011) suggested that the northern portion of Joshua tree's range is spatially limited by extreme winter cold, but at lower elevations it is limited by extreme high temperature in summer or winter. The species distribution models also suggest that average precipitation patterns limit the range of Joshua trees on the east and west edges of its distribution, as well as above and below its elevational range during portions of the year. Cole et al. (2011) explains that low precipitation in April and May seems to prevent Joshua tree from growing at lower elevations, and high winter rainfall or snow limit it from the higher elevations in some ranges of Nevada. Cole et al. (2011) also suggested that the June drought period and summer thunderstorm season may be important in limiting the distribution of Joshua tree to the east and to the west.

Cole et al. (2011) provides a map product showing how one of their suitable climate models for Joshua tree compares with current distribution presence points. While there is rough concordance between many of the Joshua tree presence points and the model results, the Cole et al. (2011) model of baseline conditions also shows many areas that were predicted to be highly suitable but that do not support the species, along with many areas that were predicted to have low suitability but that nevertheless do support the species. This demonstrates that while species distribution models have utility for providing a useful first approximation of the direction and magnitude of potential impacts of climate change on species range, no model is perfect, and all models should be used with caution until tested with independent validation (Lee-Yaw et al. 2021). Even under baseline conditions, current species distribution models can only partially explain observed species distribution patterns and range. When species distribution models can only partially explain observed species distribution patterns and range, and are not strengthened with demographic data that agrees with model predictions, predictions of species distributions in the future become very speculative.

Based on the variety of models and scenarios analyzed, Cole et al. (2011) concludes that as much as 90% of the area with 20th century suitable climate conditions within Joshua tree's range is predicted to disappear by 2070-2099. Areas of 20th century suitable climate conditions are predicted to be lost throughout most of the southern portions of Joshua tree's current range (Cole et al. 2011).

Cole et al. (2011) also compared the projected loss of suitable Joshua tree climate with a climate-related contraction of Joshua tree's range from the south that occurred as the climate rapidly warmed approximately 11,700 years ago, at the beginning of the Holocene period. Joshua tree now only occurs at the northern periphery of its late-Pleistocene range, and this contraction may have occurred over a period of approximately 3,700 years. Cole et al. (2011) points out that while suitable climate may shift with warming, Joshua tree is a poor long-distance disperser, and based on historical migration rates, and current information on dispersal distances via seed-caching small rodents (Vander Wall et al. 2006, Waitman et al. 2012, Reynolds et al. 2012), Joshua tree may only be capable of migrating at a rate of perhaps two meters per year. This suggests that the species may have a difficult time naturally keeping pace with projected shifts in suitable climate conditions.

Thompson et al. (1998) modeled the range-wide response of Joshua tree to climate as forced by doubled CO_2 concentrations, along with the responses of 15 other common trees and shrubs of the western United States. Thompson et al. (1998) used a somewhat coarse 15-km grid, a range map from 1976, and climate data from a 30-year period as the baseline (dates of the 30-year period were not reported), with average January and July temperature and precipitation data for the analysis. The model of Joshua tree distribution prepared by Thompson et al. (1998) projects a reduction of historically suitable Joshua tree climate conditions at the western edge of its range, near Antelope Valley and to the north, but also projects a significant expansion of suitable climate conditions for Joshua tree in many directions into Mexico, Texas, and Washington. The model prepared by Thompson et al. (1998), poorly matches the current observed distribution of Joshua tree, which calls into question the modeling methodology and/or the assumptions used.

Shafer et al. (2001) modeled range-wide shifts in mid-20th century climate conditions within the range of Joshua tree and 76 other North American tree and shrub species in response to climate change by 2090–2099, assuming a one percent per year compound increase in greenhouse gases and using three different future climate change scenarios. Shafer et al. (2001) used a somewhat coarse 25-km grid, a range map from 1976, and climate data from a 30 year period (1951–1980) as the baseline, with (1) the average temperature of the coldest month, (2) a sum of the number of °C that was over 5°C on days that were warmer than 5°C, and (3) a moisture index similar to climatic water deficit for the analyses (climatic water deficit is discussed in the Precipitation section of this Status Review). All three future climate change scenarios used by Shafer et al. (2001) produced what appears to be near complete elimination of 1951–1980 suitable climate conditions from the southern portion of western Joshua tree's range by the year 2099, and also substantial expansion of 1951–1980 suitable climate conditions to the north and to the east into Nevada, Arizona and Utah, but also as far away as New Mexico, Wyoming, and Washington (outside of the scope of CESA). Unlike some of the other species distribution modeling efforts discussed, Shafer et al. (2001) did not perform checks of their model parameters by using 1951–1980 suitable climate conditions to assess how well their model accurately predicts the current distribution of Joshua tree, which calls into question the modeling methods used and therefore the accuracy of model predictions.

Dole et al. (2003) modeled the range-wide response of areas predicted to be suitable for Joshua tree based on late-20th century climate conditions under doubled CO_2 conditions, while also taking into account increased tolerance of extreme cold temperatures that could be expected to occur with increased CO_2 conditions (Loik et al. 2000a). Dole et al. (2003) used a relatively coarse grid-based distribution map for the current range of the species. Dole et al. (2003) used temperature data from a 30-year period (1961–1990) as the baseline for the species distribution model, and the climate variables used were January precipitation, July precipitation, annual precipitation, January average daily minimum temperature, July average daily maximum temperature, and July average temperature. All data layers used for the analysis were resampled to a 10-km grid. The results of the Dole et al. (2003) species distribution model under doubled CO_2 conditions show an overall 9% decrease in the number of grid cells with predicted late-20th century suitable climate conditions across the entire range, with 29% of grid cells retaining suitable climate conditions, and the remaining grid cells representing either loss or expansion of suitable climate conditions (percentages of loss and expansion were not reported). While the Dole et al. (2003) model predicted that some areas of late-20th century suitable climate conditions could become unsuitable in the future, grid cells of suitable climate conditions remained in substantial portions of the species' range, including in the southern portion. The model also projected new areas with late-20th century suitable climate conditions in the Mojave Desert, north of the current distribution limit in Nevada (outside of the scope of CESA), in the Owens Valley, in the Panamint and Inyo Mountains of California, and also in the southern San Joaquin Valley which is currently under intensive agricultural land use. The Dole et al. (2003) species distribution model broadly overestimates the ability of Joshua tree to disperse into new areas, but nevertheless identifies several areas where late-20th century suitable climate conditions for western Joshua tree would persist in California under doubled CO_2 conditions.

Thomas et al. (2012) used a Maxent-based approach to model range-wide response of Joshua tree and 165 other southwestern United States plant species to climate change using Intergovernmental Panel on Climate Change emission scenarios B1, A1B, and A2 for two time periods: 2040 to 2069 and 2070 to 2100. Maxent is a species distribution modeling package that uses a set of environmental (e.g., climatic) grids and georeferenced occurrence localities to express a probability distribution where each grid cell has a predicted suitability of conditions for the species (Phillips et al. 2021). Thomas et al. (2012) used species presence data from 30 different field studies, with occurrence records translated to the center of 843.5 m^2 grid cells. Monthly and annual average precipitation and temperature (minimum and maximum) from the years 1971–2000 were used as the baseline climate conditions. The areas modeled to be suitable for species using late-20th century suitable climate conditions were compared with the areas modeled to be suitable for species under the different emissions scenarios to assess climate vulnerability. Thomas et al. (2012) found that all 166 species evaluated were predicted to lose areas with 20th century suitable climate conditions under the scenarios evaluated, with substantial reductions in areas with 20th century suitable climate conditions for Joshua tree at the southern parts of its range, and substantial additional areas of 20th century suitable climate conditions becoming available to the north, particularly in Nevada.

Species distribution models for eastern Joshua tree have also predicted shifts in historically suitable climate. In an analysis of potential impacts of climate change on vegetation in Arizona, New Mexico, Utah, and Colorado, Notaro et al. (2012) used Maxent to produce species distribution models for 170 tree and shrub species, including eastern Joshua tree. Similar to the results from other Joshua tree species distribution modeling efforts, Notaro et al. (2012) projected a reduction in areas with historically suitable eastern Joshua tree climate conditions in the southern part of its range, and a substantial expansion of areas with historically suitable climate conditions to the north.

Joshua Tree National Park Models

Barrows and Murphy-Mariscal (2012) used a finer-scale species distribution modeling approach, focusing only on western Joshua tree within and near Joshua Tree National Park under scenarios of 1°C, 2°C and 3°C increases in maximum July temperatures, and precipitation scenarios of 25 mm less precipitation per 1°C of warming, no change in precipitation, and a model that does not use precipitation. All three warming scenarios are less severe than the warming that is generally expected to occur in the Mojave Desert by the end of the 21st century (Hopkins 2018). Using western Joshua tree location data from the National Park Service augmented with additional location data from researchers and citizen scientists, Barrows and Murphy-Mariscal (2012) utilized 30 years of July temperature data and average annual precipitation data from 1971-2000 and abiotic variables related to topography and soil to develop several species distribution models. The model that performed the best in predicting current western Joshua tree location data was selected and used to project the distribution of adult western Joshua tree in the future under different precipitation and warming scenarios. Rather than predicting the complete elimination of areas with late-20th century suitable climate conditions for western Joshua tree in Joshua Tree National Park, the model developed and selected by Barrows and Murphy-Mariscal (2012) predicted that approximately 10% of the current distribution of western Joshua tree within Joshua Tree National Park would retain late 20th century suitable climate conditions for adult trees under a +3°C warming with little change in average annual precipitation. Although climate models do not agree on whether there will be a decrease in precipitation, Barrows and Murphy-Mariscal (2012) predicted that approximately 2% of the current distribution of western Joshua tree within Joshua Tree National Park would retain late-20th century suitable climate conditions for adult trees under a +3°C warming scenario with a 75 mm decrease in annual precipitation. Barrows and Murphy-Mariscal (2012) also found that with a temperature increase of 1°C to 3°C, the areas with late-20th century suitable climate conditions for western Joshua tree are expected to shift upward in elevation in Joshua Tree National Park, but because western Joshua tree already occupies the highest elevation areas within Joshua Tree National Park, there will be a net loss of areas with late-20th century suitable climate conditions within Joshua Tree National Park.

Barrows and Murphy-Mariscal (2012) also developed a species distribution model for juvenile western Joshua trees less than 30 cm in height, representing the most recent cohort of juvenile western Joshua trees within Joshua Tree National Park. When areas suitable for juvenile western Joshua trees were modeled using late-20th century climate conditions, the area predicted to be suitable was 51% of the size of the area currently observed to be occupied by adult western Joshua trees. Barrows and Murphy-Mariscal (2012) also compared the area modeled for juvenile western Joshua trees under late-20th century suitable climate conditions to the distribution modeled for adult trees under the +1°C warming scenario and suggested that warming that has already taken place may be related to the apparent reduction in area that appears to be suitable for western Joshua tree recruitment. Barrows and Murphy-Mariscal (2012) did not observe any evidence of mortality of western Joshua trees that was not related to fire within Joshua Tree National Park. Barrows and Murphy-Mariscal (2012) did not model suitable climate for juvenile western Joshua trees under future warming scenarios, nor did they report on how well their distribution model for juvenile western Joshua trees accurately predicted actual observations of the distribution of juvenile western Joshua trees in Joshua Tree National Park.

The most recent effort to model how the distribution of western Joshua tree may respond to changes in 20th century suitable climate was conducted by Sweet et al. (2019). Similar to Barrows and Murphy-Mariscal (2012), Sweet et al. (2019) used a finer-scale species distribution modeling approach, focusing only on western Joshua tree within and near Joshua Tree National Park. Sweet et al. (2019) expanded on the western Joshua tree data used by Barrows and Murphy-Mariscal (2012) to generate a Maxent species distribution model. The model developed by Sweet et al. (2019) was developed using climate variables from 1951–1980 and physical environmental variables including soil sand content, slope, and terrain ruggedness. Sweet et al. 2019 identified annual precipitation as being the most important variable for the model, but slope, and annual maximum hot season temperature, minimum cold season temperature, and climatic water deficit were also important predictors of western Joshua tree presence.

Based on the results of this Maxent model, Sweet et al. (2019) projected how much of the area with mid-20th century suitable climate conditions for western Joshua tree would remain within Joshua Tree National Park under the observed climate conditions from 1981–2010 and the climate conditions projected between 2070–2099 under three climate change emissions scenarios: CMIP5 MIROC RCP 4.5, 6.0, and 8.5 (Taylor et al. 2012), representing CO_2 emissions under highly mitigated, moderately mitigated, and unmitigated scenarios, respectively. The model predicted that 13.4% of the area with predicted suitable climate for the species based on climate conditions between 1951 and 1980 remained during the subsequent period between 1981 and 2010. Also compared with the area of 1951–1980 predicted suitable climate conditions, the model predicted that 18.6% of the area would remain at the end of the 21st century under the highly mitigated emissions scenario, 13.9% under the moderately mitigated emissions scenario, and only 0.02% would remain by under the unmitigated emissions scenario. Although the Sweet et al. (2019) model projected substantial loss of the area with mid-20th century suitable climate conditions during the 1981–2010 climate period, western Joshua trees continued to recruit in these climate conditions throughout Joshua Tree National Park during this time period (Frakes 2017a). Continuation of western Joshua tree recruitment in areas of Joshua Tree National Park that Sweet et al. (2019) modeled as no longer containing suitable climate during the 1981–2010 climate period demonstrates that a departure from historical climate conditions does not necessarily mean that the new climate is no longer capable of supporting the species, at least in the short term.

To examine whether recent recruitment of western Joshua trees in Joshua Tree National Park was occurring in areas predicted to be suitable for western Joshua tree between 2070–2099, Sweet et al. (2019) examined demographic information collected from 14 nine-ha macroplots in Joshua Tree National Park in 2016 and 2017. Sweet et al. (2019) considered macroplots that had fewer than 247 western Joshua trees under 60 cm as “low recruiting” and macroplots that had more than 247 western Joshua trees under 60 cm as “high recruiting,” but did not report the number of trees in each macroplot, or use the number of adult trees in these macroplots to put the number of juvenile trees in the macroplots into relative context (areas with low densities of adult western Joshua trees would naturally be expected to have low densities of juvenile western Joshua trees regardless of climate change effects). Sweet et al. (2019) found that “high recruiting” macroplots tended to be geographically closer to areas predicted to be more suitable for western Joshua tree between 2070–2099 under the species distribution model developed for the study, which suggests that climate change could be affecting the demography of populations within Joshua Tree National Park, but there could also be other explanations, which are not contemplated by Sweet et al. (2019).

The Barrows and Murphy-Mariscal (2012) and Sweet et al. (2019) studies provide evidence for the predicted effects of climate change at the southern (trailing) edge of western Joshua tree’s range, and these studies are the first to associate western Joshua tree demographic data with predictions from species distribution models. The climatic conditions and projections for the small geographic area used in these studies (Joshua Tree National Park) does not present a comprehensive representation of future conditions across western Joshua tree’s range. Nevertheless, studies that suggest recruitment of western Joshua tree is decreasing in marginal habitats that have already been subject to the warming effects of climate change can provide field evidence that overall, climatic warming is correlated with lower recruitment (Barrows and Murphy-

Mariscal 2012, Sweet et al. 2019). Species distribution models for western Joshua tree that are validated with random field samples of western Joshua tree demographic data from across the species' range in California would substantially improve the ability to evaluate the predictive capacity of the work initiated by Barrows and Murphy-Mariscal (2012) and Sweet et al. (2019).

Limitations of Models

Species distribution models have substantial inherent limitations and should be credible, transparent, reproducible, and evaluated carefully to be used effectively for decision-making (Sofaer et al. 2019, Lee-Yaw et al. 2021). Natural systems are highly complex, as are the effects of climate change (Pimm 2009), and by necessity predictive species distribution modeling must reduce many complex factors to relatively simple geographic variables that can be used by the relevant software. Limitations in the accuracy and precision of predictive species distribution models arise from the availability of spatially continuous data on biotic and abiotic variables of interest, by the capacity of the scientific community to make accurate measurements or projections of certain variables (e.g., projections of temperature generally are more feasible than projections of wind speed), and by the feasibility and reliability of downscaling or aggregating data to a common spatial and temporal resolution (Pearson and Dawson 2003, Keith et al. 2008). Uncertainty of species distribution model outputs also increases when projected values of predictor variables are outside the range used to build the model and models generally do not account for climate heterogeneity in complex terrain, such as mountains. Species distribution models also often rely on just a few available climate change scenarios that are often selected arbitrarily (Casajus et al. 2016). In addition, species distributions are often dynamic, and not necessarily static on the landscape, and therefore data on the current distribution of species used for models may not accurately represent where species can occur. There are also uncertainties regarding whether species may occupy environments that are not yet present on the landscape, but that are expected to arise in the future (Fitzpatrick and Hargrove 2009). A species may also be adapted to a narrow niche in some areas, and species distribution models that use coarse, homogenized environmental data will not identify small areas of climate change refugia that match the species' niche requirements. Although species distribution models are fundamentally designed to account for variation in the habitat in which a species occurs, they cannot entirely account for resilience to a changing climate that an abundant and widespread species (such as western Joshua tree) may already possess. Species distribution models also do not account for the adaptive potential of a species in the face of a changing climate, but long-lived species and species with limitations to dispersal (such as western Joshua tree) may be unlikely to undergo rapid evolutionary change on the timescale that the climate is projected to change.

A methodology for evaluating the reliability and usefulness of species distribution models is provided by Sofaer et al. (2019), and the Department identified a number of concerns related to the species distribution models that have been prepared for Joshua tree. These include the lack of range-wide validation of results with demographic data, the non-iterative approach of all models evaluated, the relatively short time periods used for describing historically suitable climate data (Roubicek et al. 2010), use of map products with binary instead of continuous data, little discussion of suitability thresholds used, little discussion of data/model assumptions, little discussion of model performance, homogenization of the climate variability that is important for western Joshua tree recruitment, the relatively coarse scale of climate data used, the lumping of western Joshua tree and eastern Joshua tree as one species for modeling despite their differences, and the poor performance of species distribution models to accurately and precisely explain current species distribution patterns using historical climate conditions.

All species distribution models evaluated by the Department used historical climate data from a 30-year period, or in the case of the Cole et al. (2011) study a 40- or 100-year period to define what constitutes suitable climate conditions for the species, and the climate data was averaged over these periods. These time periods are shorter than the maximum lifespan of a western Joshua tree, which can likely live for 150 years or more. As described in the Precipitation and Life History sections of this Status Review, precipitation in western Joshua tree's range oscillates between wetter and drier conditions over multi-year and multi-decade timescales with wet or dry conditions of the Pacific Decadal Oscillation often persisting for two to three decades. These oscillations are likely important for recruitment of western Joshua trees because periods of above average precipitation are important for the episodic recruitment of western Joshua trees and therefore may be more important for characterizing the climate conditions necessary for western Joshua tree to survive and reproduce than averaged climate conditions. There were substantial differences in modeled suitable climate between the base historical 1951–1980 suitable climate conditions and more recent (1981–2010) climate conditions reported by Sweet et al. (2019), demonstrating how sensitive all species distribution models are to the climate data used to construct them. For these reasons, it may not be appropriate to use averages of narrow (30 to 40 year) timeframes to represent the climate conditions and climate variability that western Joshua tree experienced and perhaps developed resiliency to during its evolution in the Mojave Desert and other regions over thousands of years. Climate variability such as the oscillations between wetter and drier conditions over multi-year and multi-decade timescales is excluded from species distribution models that average precipitation data over 30- to 100-year time periods. For this reason, the species distribution models that have been produced so far have, to some extent, mischaracterized the precipitation patterns that western Joshua tree depends on for recruitment. Species distribution models that use average climate conditions over relatively short time periods to characterize the climate tolerances of western Joshua tree produce results that contain substantial uncertainty.

There are substantial limitations in the current understanding of the climate tolerances that the range of western Joshua tree is limited by. The species distribution models that have attempted to model the current distribution of Joshua trees have only produced rough approximations of the current range and distribution of the species. While some of the species distribution modeling efforts for Joshua tree evaluated by the Department provided corresponding information on how well the model predictions matched the current distribution of western Joshua tree (i.e., performance), generally only one performance metric was used, and there was limited discussion of the ecological plausibility of results (Cole et al. 2011, Thomas et al. 2012, Sweet et al. 2019). Because of our limited understanding of the true climate tolerances that the range of western Joshua tree is limited by, the magnitude and timing of effects of the loss of areas with 20th century suitable climate conditions (i.e., sensitivity of the species) is not known. The loss of substantial areas of 20th century suitable climate conditions (i.e., exposure to climate change) that is projected by species distribution models in some areas is expected to have negative effects on populations in the affected areas, but the Department does not have information indicating whether western Joshua trees in the affected areas are likely to die, whether populations are likely to cease reproducing, whether populations will be sustainable, and/or how climate change exposure may affect seedling, juvenile, and adult trees (i.e. the sensitivity of the species to climate change). Loss of areas with 20th century suitable climate conditions may instead result in reductions in population density and distribution that are not likely to result in a serious risk of reduction in a significant portion of the species' range in the foreseeable future.

Due to the inherent limitations in predictions from species distribution models, limitations in the current understanding of the climate conditions that limit western Joshua tree's range (as described in the Climate, Hydrology and Other Factors section of this Status Review), and limited information that relates western Joshua tree demographic and population trends with the predicted effects of climate change (as described in the Population Trends section of this Status Review), the Department does not consider the available data on the potential timing and magnitude of negative effects of climate change on western Joshua tree's range as sufficient to support a conclusion that the species is likely to become endangered in the foreseeable future. The Department does not currently possess information that suggests the effects of climate change on the species in the foreseeable future are likely to place the western Joshua tree in serious danger of becoming extinct throughout all or a significant portion of its range.

Summary of Species Distribution Models

All of the studies assessed by the Department come to similar conclusions that the areas with climate conditions that supported western Joshua tree during the 20th century are expected to contract substantially by the end of the 21st century (2100), especially in the southern and lower elevation portions of the species' range. The information available to the Department indicates that western Joshua tree will have high exposure to the effects of climate change. Areas with historical 20th century suitable climate conditions for the species will also expand to the north and into higher elevation areas in some parts of eastern California, but most substantially in Nevada (outside of the scope of CESA). Western Joshua tree is only likely to colonize areas with newly suitable climate conditions very slowly. Studies assessed by the Department also suggest that areas of 20th century suitable climate conditions for western Joshua tree will remain in some limited areas at the southern and lower elevation portions of its range at the end of the 21st century under some climate scenarios. The results of the species distribution models assessed by the Department provide a useful first approximation of the direction and magnitude of potential impacts of climate change on the species. If western Joshua tree populations are exposed to a severe enough change in climate, a significant loss of range could occur, however, the Department does not have information on how severe this change in climate would need to be to result in a serious risk of significant range loss. The Department has very little information to suggest that loss of 20th century suitable climate conditions for western Joshua tree will result in serious risk of significant range loss. Loss of 20th century suitable climate conditions are nevertheless expected to have negative effects on individuals and populations of western Joshua tree in the affected areas, and those negative effects may result in population declines. But due to the lack of information that correlates climate change with demographic trends over significant portions of the species' range, the Department does not have information indicating that modeled exposure to climate change will mean that there will be a serious risk that western Joshua trees will likely die, or that populations are likely to cease reproducing and no longer be sustainable at the end of the 21st century. Loss of areas with 20th century suitable climate conditions may instead result in reductions in population density and distribution that are not likely to result in a serious risk of reduction in a significant portion of the species' range in the foreseeable future.

Climate Change Vulnerability Assessments

In addition to reviewing the species distribution modeling efforts described above, Department staff assessed the vulnerability of western Joshua tree to climate change using the NatureServe Climate Change Vulnerability Index (CCVI) Version 3.02 (NatureServe 2016, CDFW 2021b). The CCVI is a rapid means of estimating a plant or animal species' relative vulnerability to climate change. The CCVI analyzes exposure to local climate change within a species' range and assesses indirect climate change effects and the species sensitivity and adaptive capacity to provide a qualitative assessment of how the abundance and/or range extent of the species may change due to climate change. The results of the CCVI indicated that western Joshua tree has a climate change vulnerability index value of moderately vulnerable (MV), indicating that "abundance and/or range extent within geographical area assessed likely to decrease by 2050;" however, the confidence in this vulnerability index score is low, indicating that a higher vulnerability score is also a possible result. Factors contributing to these vulnerability assessments include barriers to western Joshua tree dispersal and limited dispersal capability, the species physiological thermal niche, the historical hydrological niche of the species, increasing wildfire activity, dependence on an obligate pollinating moth, and existing documented or modeled response to climate change (i.e., the species distribution models described above).

In 2016, Thorne et al. conducted a CCVI assessment that evaluated the sensitivity and adaptive capacity of five major plant species of the Mojavean–Sonoran Desert Scrub vegetation macrogroup, including Joshua tree (Thorne et al. 2016). Joshua tree was assessed individually as highly vulnerable to climate change. Thorne et al. (2016) ranked the adaptive capacity of Joshua tree to be low due to its low adaptivity to fire and its slow and limited recruitment abilities. Thorne et al. (2016) also identified fire sensitivity, requirements for germination, and limited dispersal capacity as primary reasons for the high sensitivity of Joshua tree to climate change. Thorne et al. (2016) concluded that the Mojavean–Sonoran Desert Scrub vegetation macrogroup was moderately vulnerable to climate change in California.

Indirect and Cumulative Effects

Changes to precipitation due to climate change could have cascading effects on western Joshua tree. Climate change within the range of western Joshua tree will affect the abundance and distribution of plant species, sometimes with unexpected results (Kimball et al. 2010), and may increase suitability for presence and high abundance of some invasive plant species (Curtis and Bradley 2015). Climate variability could result in more extreme wet periods that result in extensive growth and spread of invasive annual plant species, which would have implications for wildfire frequency and intensity that would affect western Joshua tree. These negative effects on western Joshua tree are discussed in more detail in the Wildfire section of this Status Review. Climate change could also contribute to more severe drought events, which would reduce the amount of resources available for animals, potentially increasing herbivory and damage to western Joshua tree as described in more detail in the Herbivory and Predation section of this Status Review.

Climate change may also indirectly impact western Joshua tree habitat via an increase in renewable energy development in areas occupied by the species. Impacts of development are discussed in the Development and Other Human Activities section of this Status Review.

Climate change could also indirectly impact western Joshua tree through effects on western Joshua tree's specialized obligate pollinator, the yucca moth *T. synthetica*, because the two species are dependent upon one another for sexual reproduction. In general, species of butterflies and moths are predicted to experience changes in abundance, distribution, and timing of life history events as a result of climate change, and examples of such changes have been observed in different parts of the world (Kocsis 2011). The extent to which climate change may affect *T. synthetica* is not currently known, but climate change could affect the mutualism with western Joshua tree in various ways that either increase the number of viable seeds produced (benefitting western Joshua tree), increase the number of seeds eaten by moth larvae (benefitting *T. synthetica*), or disrupting the mutualism in a way that harms both western Joshua tree and *T. synthetica*. Harrower and Gilbert (2018) examined various aspects of the mutualism between western Joshua tree and *T. synthetica* along an elevation gradient within Joshua Tree National Park, which provides some context for how climate change may affect this mutualistic relationship. Harrower and Gilbert (2018) collected western Joshua tree demographic data and data on the abundance of *T. synthetica* and bogus yucca moths (*Prodoxus* sp.) at 11 sampling sites along a 1,200 m (3,900 ft) elevational gradient from 1,004 to 2,212 m (3,294 to 7,257 ft). *Prodoxus* sp. moths parasitize western Joshua trees and do not pollinate them. Harrower and Gilbert (2018) found that near 1,250 m (4,100 ft) in elevation western Joshua trees were numerous and large and produced many flowers, pods, seeds, fertile seeds, and seedlings that grew from seeds; this site also had a high abundance of both *T. synthetica* and *Prodoxus* sp. moths. *T. synthetica* was not observed, and sexual reproduction was not found to occur at the highest elevation sampling site at 2,212 m (7,257 ft) or at the lowest elevation sampling site at 1,004 m (3,294 ft). Harrower and Gilbert (2018) found that at an elevation of approximately 1,500 to 1,600 m (4,900 to 5,250 ft) where western Joshua trees were at their highest density, *T. synthetica* abundance was relatively low, and there were fewer viable seeds produced at that sampling site. Harrower and Gilbert (2018) speculated that the range of environmental conditions that support *T. synthetica* may be narrower than those for western Joshua tree. The Department has very little information on the range of *T. synthetica*, but it is possible that climate change may make some low-elevation areas unsuitable for the species. In areas outside of the distribution of *T. synthetica*, sexual reproduction is not possible and asexual reproduction is the only viable reproductive strategy for western Joshua tree. Sexual reproduction promotes genetically diverse offspring through recombination, mutation, and gene flow from immigrants thereby allowing for evolutionary adaptation (Hoffmann and Sgro 2011, Yang and Kim 2016). Sexual reproduction also allows for increased dispersal ability (Winkler and Fischer 2002). Therefore, if *T. synthetica* were lost from western Joshua tree populations the loss of sexual reproduction would present serious additional challenges for the long-term persistence of affected populations.

Considered collectively, the direct and indirect effects of climate change, the direct and indirect effects of development and other human activities, and the direct and indirect effects of wildfire are interconnected and will affect different portions of western Joshua tree's range in different ways, sometimes cumulatively. Climate change may reduce recruitment and abundance in southern and lower elevation portions of western Joshua tree's range, with higher elevation areas perhaps remaining more suitable for the species. These higher elevation areas are also at higher risk of wildfire, as described in the Wildfire section of this Status Review, and fire is expected to kill a proportion of trees in burned areas and temporarily reduce recruitment in those areas. Sweet et al. (2019) calculated the area where the refugia for western Joshua tree modeled within Joshua Tree National Park at the end of the 21st century under climate change emissions scenario CMIP5 MIROC RCP 4.5 (representing CO_2 emissions under a highly mitigated scenario) (Taylor et al. 2012) would overlap with the approximate area of historic fires, circa 1890s to 2018. The area of overlap of the refugia under CMIP5 MIROC RCP 4.5 and historic fires was over 6000 ha or approximately 49.9%, demonstrating that wildfire may disproportionately affect areas most likely to support western Joshua tree in the future. If the amount of habitat for western Joshua tree does become severely limited in the future, wildfire has a greater potential to result in impacts that will affect the species' range.

Development and Other Human Activities

Habitat loss is considered the primary cause for species extinctions at all scales: local, regional, and global (Dirzo and Raven 2003). Habitat loss is caused by a variety of human activities including cultivation of land for agriculture; development of land for residential, commercial, or industrial use; development of utilities, roads, and other infrastructure; resource harvest and extraction; use of land for livestock; and recreational use of land including off-highway vehicle use. These activities often involve removing native vegetation, disturbing soil and the biological communities therein, and installing structures, impermeable surfaces, and other features that render areas incapable of supporting native species assemblages (habitat destruction). Even if human activities do not result in the complete elimination of habitat in an area, the indirect effects from such activities can cause substantial changes to the environment (habitat modification), which can affect the abundance of native species. Indirect effects from development and other human activities include soil disturbance and compaction; introduction and spread of exotic species and pathogens; increased dust, pollution, runoff, and trash; artificial noise, light, and vibration; and use of herbicides, pesticides, and other chemicals. The contribution of development and other human activities to the introduction and spread of invasive plants is discussed in the Wildfire and Invasive Plants sections of the Status Review. While development and other human activities often result in habitat loss and largely negative impacts to native species, some native species could benefit from certain human activities, for example irrigation near populated areas could increase survival of perennial plants during drought.

Development and other human activities reduce the amount of contiguous habitat, resulting in habitat fragmentation. Habitat fragmentation may have several repercussions for individual species or entire ecosystems, including increased edge effects, reduced ability of species to migrate or colonize, and reductions in species richness (i.e., number of total species), although fragmentation, in and of itself, may not necessarily be bad for biodiversity (Haddad et al. 2015, Evans et al. 2017, Fletcher et al. 2018, Fahrig et al. 2019). The Department does not have information on the effects of habitat fragmentation on western Joshua tree or on the yucca moth *T. synthetica* specifically, however western Joshua tree is a poor disperser and habitat fragmentation could disrupt plant and pollinator population dynamics by altering pollinator densities and behavior (Xiao et al. 2016).

Western Joshua tree habitat has been subject to a history of habitat modification and destruction in California (see the Inferred Long-term Trends section of this Status Review), and this habitat modification and destruction is expected to continue. Much of the recent western Joshua tree habitat modification and destruction has been the result of ongoing urban development, typically on private property within the general vicinity of existing developed areas. The USFWS (2019) reported that approximately 50% of the southern part of western Joshua tree’s range is on private property, 2% of the northern part of western Joshua tree’s range is on private property, with the remainder predominately on federal land. WEST Inc. (2021b) found a higher percentage of western Joshua tree’s range on private property than the USFWS did, with approximately 65% of the southern range on private property, and approximately 13% of the northern range on private property. Due to very limited regulation prior to CESA candidacy, as described in the Regulatory Status and Legal Protections section of this Status Review, western Joshua trees and habitats on private property have been very vulnerable to habitat modification and destruction. Local land use planning and state legal protections such as the 1970 California Environmental Quality Act may have led to the avoidance of some impacts to western Joshua tree. However, development has continued, and cities within the range of the species have expanded substantially into previously undeveloped areas contributing to the loss of many western Joshua trees and habitat. During the candidacy period for western Joshua tree, the Department received numerous reports of the unpermitted killing of western Joshua trees on private property and related habitat modification and destruction.

Renewable energy development has been increasing rapidly in recent decades with development primarily occurring on private lands and lands managed by the U.S. Bureau of Land Management (BLM) in less-developed portions of the Mojave Desert. Under the Desert Renewable Energy Conservation Plan which was finalized in 2016, 157,000 ha (388,000 ac) of BLM lands in the plan area were identified for solar, wind, and geothermal development, with more than 162,000 additional ha (400,000 ac) that could be considered for renewable energy development in the future (BLM 2016). Under the Desert Renewable Energy Conservation Plan, substantial areas of habitat were also identified for conservation. During the candidacy period for western Joshua tree, land with western Joshua trees has been approved to be cleared for renewable energy development following a Special Order approved by the Commission pursuant to Fish and Game Code section 2084. Authorizations under this Special Order required that take of western Joshua tree is mitigated.

Private property that has not been protected from development is at a high risk of habitat modification and destruction in the foreseeable future, and this threat is highest in the southern and western part of western Joshua tree's range, where most of the western Joshua trees on private property occur. Private property within incorporated city limits of Palmdale, Lancaster, Yucca Valley, Joshua Tree, Twentynine Palms, Victorville, Hesperia, and Apple Valley may be at greatest risk of habitat modification and destruction in the foreseeable future, although expansive development of rural "ranchettes" and related infrastructure are likely to continue in unincorporated communities (Figure in Krantz comments, Appendix B). To a lesser extent, western Joshua tree habitat modification and destruction is likely to occur on federal lands due to renewable energy development, off-highway vehicle use, resource extraction activities, livestock grazing activities on BLM lands, and military activities on U.S. Department of Defense lands. While habitat is likely to be modified or destroyed on BLM lands and U.S. Department of Defense lands in the foreseeable future from ongoing activities or facility expansions, habitat destruction from activities on these lands may be limited, as much of these areas are expected to be maintained in an undeveloped state. Lands close to existing base infrastructure may be developed and used for military purposes, however, U.S. Department of Defense has historically maintained large buffers of natural habitat around many of its military bases, including lands maintained to "enable realistic, mission essential testing, training, and operations" (Department of Defense 2021).

Habitat modification from development and other human activities may also impact the ability of western Joshua tree to recruit new individuals from seed in ways that are not fully understood. As described in the Demographic Information section of this Status Review, information submitted to the Department suggests that relatively few western Joshua trees established from seed in recent decades at six proposed development project sites near the cities of Palmdale and Lancaster. This decreasing recruitment may have been due, in part, to mid-20th century dry conditions illustrated in Figure 5, combined with environmental degradation related to urban and agricultural use and development. Habitat modification and destruction from development and other human activities in these areas may have impacted the ability of western Joshua tree to sexually recruit new individuals by disrupting the fulfillment of one or more of western Joshua tree's critical life history needs. Western Joshua tree's obligate pollinating moth *T. synthetica* could be disrupted while dormant in the soil or as adults. The seed dispersal behavior of rodents could be disrupted, which is the primary way that western Joshua tree seeds are buried at a soil depth suitable for germination. Nurse plants that are critical for western Joshua tree seedling survival could also be eliminated. Any one or a combination of these disturbances may have contributed to the observed population declines.

There is much uncertainty in predicting the extent of future development within the range of western Joshua tree. The magnitude of this habitat modification and destruction will be related to the economic values of development and other human activities in the Mojave Desert and surrounding areas, and the effectiveness of local, state, and federal regulatory and legal mechanisms for protecting western Joshua tree individuals and habitat. During the candidacy period for western Joshua tree, the Department received at least 36 applications for incidental take permits to remove western Joshua trees for development projects. Regional general plans, landscape planning efforts, and specific development plans may influence where development of private property occurs in the future, but the Department considers any private property that is not protected to be at substantial ongoing risk of habitat modification and destruction from development and other human activities.

The economic value of western Joshua tree habitat for energy generation may also continue to increase. According to an analysis done by the USFWS using U.S. Environmental Protection Agency Integrated Climate and Land Use Scenarios projections, between 22% and 42% of the habitat within the southern part of western Joshua tree's range may be lost by the year 2095 due to urban growth and renewable energy development; however, less than one percent of the habitat within the northern part of western Joshua tree's range is expected to be lost during this time period (EPA 2009, 2016, USFWS 2018). Irrespective of the ultimate amount of habitat that will be lost, habitat modification and destruction of western Joshua tree habitat from development and other human activities is certain to continue.

Some areas within western Joshua tree habitat were subject to temporary disturbances or land clearing in the past but have since been left fallow. Joshua tree reestablishment in areas after disturbance from plowing and other land use such as homestead sites appears to occur very slowly if at all (Carpenter et al. 1986, Abella 2010). As described in the Establishment and Early Survival section of this Status Review, nurse plants appear to be critical habitat components for Joshua tree establishment. Regeneration of western Joshua tree to pre-disturbance levels may require the reestablishment of nurse plants before western Joshua tree seedlings are able to reestablish. The rate that Mojave Desert vegetation recovers from human-related degradation depends on the nature and severity of impacts, but recovery generally happens very slowly (Lovich 1999). Based on a review of 47 studies, Abella (2010) reported that cover of perennial vegetation in the Mojave Desert generally rebounds faster after fire compared with other disturbances such as land clearing, and this is likely due to the roots and seeds that survive wildfire. In this way modification or destruction of habitat from land clearing and other human activities is more destructive to western Joshua tree habitat than the impacts from wildfire. Development and other human activities are also a source of ignition that likely contributes to wildfire risk, as discussed in the Wildfire section of this Status Review.

As described under the Climate Change section of this Status Review, there may be a time delay between when an area becomes no longer suitable for sustaining a species, and when that species becomes locally extinct. Delayed local extinction could be occurring in areas where western Joshua tree adults remain relatively abundant, but juvenile western Joshua trees are rare, such as at the six development project sites near the cities of Palmdale and Lancaster for which the Department received western Joshua tree height data in 2021 (see Figure 8).

Present or threatened modification or destruction of habitat is a substantial threat to western Joshua tree in California, particularly at renewable energy development sites, on private property, and within the vicinity of existing urban areas in the southern part of western Joshua tree's range.

Wildfire

Fire is a defining component in many of California's ecosystems, as it is in most of the world's Mediterranean-climate regions (Keeley et al. 2011, Sugihara et al. 2018); however, the frequency and severity of fire is generally lower in California deserts than it is in other California ecosystems. Fire occurrence in the southeastern deserts of California is primarily limited by the availability of fuels, and fire return intervals in California deserts tend to be relatively long (Brooks et al. 2018, CNPS 2021a). Fire is unevenly distributed in the Mojave Desert, and fire occurrence tends to align with distinct precipitation regime boundaries, with most large and recurring fires occurring in areas that have a relatively high amount of precipitation in summer (Tagestad et al. 2016). Fuels tend to be more available, and fires tend to be more frequent at higher-elevation areas of the Mojave Desert, and the availability of fuels and frequency of fires is somewhat lower at middle elevation areas, and still lower at the low elevation areas of the Mojave Desert (Brooks et al. 2018). The abundance and distribution of invasive grasses in California deserts fluctuates with precipitation patterns. Periods of relatively high and low fire activity have been associated with periods of relatively wet and dry conditions in the Mojave Desert Region, respectively, and can be influenced by global-scale climate fluctuations including the El Ninõ-Southern Oscillation and the Pacific Decadal Oscillation, as described in the Precipitation section of this Status Review (see Figure 5). During multi-decadal periods of relatively wet conditions, cover of perennial vegetation may expand, increasing the amount of fuel on the landscape. High precipitation in one or more years may also result in a high biomass of annual plant species in those years, particularly in the spaces between perennial and woody vegetation (Brooks and Matchett 2006, Van Linn et al. 2013, Gray et al. 2014, Hegeman et al. 2014, Rao et al. 2015, Tagestad et al. 2016). Fire potential may, then, be greatest when one or more high precipitation years occurs near the end of a multi-decadal period of relatively wet conditions (Brooks et al. 2018).

Wildfire ignitions in the southeastern deserts of California were prehistorically caused by lightning, which occurs at a higher frequency in the southeastern deserts region of California than in other parts of the state (van Wagtendonk and Cayan 2008). Native Americans also ignited fires in the southeastern deserts when they arrived in California approximately 12,000 years ago (Anderson 2018). Fire regimes and related ecosystem processes were profoundly altered by land use practices associated with Euro-American settlement beginning in the mid-1800s, and these changes have in turn led to major modifications in vegetation distribution, structure, and composition (Skinner and Chang 1996, Barbour et al. 2007, Safford and Van de Water 2014, van Wagtendonk et al. 2018). When Euro-Americans began occupying lands in the Mojave Deserts region in the mid-1800s, ignitions from traditional Native American practices were curtailed, invasive plant species were widely introduced and spread, and livestock grazing became a widely implemented land use practice (Brooks et al. 2018). Livestock grazing and use of off-road vehicles, which can be extensive in the Mojave Desert, are generally associated with expansion of non-native invasive grasses. As the human population and associated electrical and transportation infrastructure rapidly increased from the early 1900s to present, sources of human-caused wildfire ignitions in the Mojave Desert also increased.

Syphard et al. (2017) examined the variety of factors contributing to wildfire in the Mojave Desert and nearby areas for a 40-year timespan. While the variables contributing to wildfires in the region are complex, Syphard et al. (2017) found that the spatial and temporal distribution of most fires (including many small fires) in the Mojave Desert from 1970 to 2010 was correlated with human disturbance, with ignitions concentrated near roads and areas of nitrogen deposition. The relationship between nitrogen deposition and fire is discussed in the Invasive Plants section of this Status Review. Syphard et al. (2017) also looked at the variables contributing to the spatial and temporal distribution of large (> 20 ha) fires, which can affect much larger areas of western Joshua tree habitat during one event. Most large fires in the Mojave Desert from 1970 to 2010 were correlated with a number of variables, but the most important variables identified were measures of the current year's and the previous year's vegetation cover, followed by nitrogen deposition and elevation. The human-caused variables contributing most to the spatial and temporal distribution of large fires was the location of power lines, oil and gas wells, wind turbines, and power plants.

There was less summer precipitation and fewer fires during the mid-20th century period of dry conditions in the Mojave Desert that took place from approximately 1947–1975 (Tagestad et al. 2016), but since that time, particularly since the beginning of the 2000s, desert ecosystems in California have become increasingly susceptible to wildfire (Syphard et al. 2017, Brooks et al. 2018). One reason for this increasing susceptibility to wildfire is the presence of exotic annual plant species (D'Antonio and Vitousek 1992, Brooks et al. 2004, Brooks and Matchett 2006, Brooks and Chambers 2011, Fuentes-Ramirez et al. 2015, 2016). Invasive plant species were likely first introduced to the Mojave Desert by the Spanish during the late 1500s, and current human activities, such as livestock grazing, water diversion, mineral and gas extraction, military training, and recreational activities have likely continued the introduction and spread of invasive plants species in the region (Brooks 1999, Brooks and Pyke 2001). Annual plants in the spaces between shrubs provide a more continuous fuel source that allows fire to spread more easily, increasing wildfire risk (Brooks et al. 2016, Klinger et al. 2018). While native annual plants contribute to wildfire risk in the Mojave Desert, exotic annual plant species have a greater impact on wildfire risk as these species are more likely to occur in areas between shrubs and other vegetation, helping perpetuate the wildfire (Moloney et al. 2019).

There is some evidence that invasive plant species in the Mojave Desert are contributing to a grass/fire cycle (D'Antonio and Vitousek 1992), particularly in the middle-elevation areas, which is where western Joshua tree is most frequently found (Brooks and Matchett 2006, Brooks et al. 2018). The grass/fire cycle occurs when an invasive annual grass colonizes an area and provides the fine fuel necessary for the initiation and propagation of fire, leading to an increase in frequency, area, and perhaps intensity of wildfires. Following these grass-fueled fires, invasive species can increase more rapidly than native species, creating a positive feedback loop that further increases susceptibility to wildfire, and areas that previously burned may burn again

(Zouhar et al. 2008, Klinger and Brooks 2017). Red brome (*Bromus madritensis* ssp. *rubens*) can dominate middle-elevations of the Mojave Desert where western Joshua tree is frequently found, and contributes to the grass/fire cycle in these areas. Cheatgrass (*Bromus tectorum*) has dramatically shortened fire return intervals in the Great Basin, which is a cold desert province (Whisenant 1992, Balch et al. 2013), and the grass/fire cycle has caused substantial ecological impacts in the region (Brooks and Pyke 2001, Brooks et al. 2018). Cheatgrass also occurs in higher elevation areas of the Mojave Desert, a warm desert province, which receives less consistent precipitation from year to year than the Great Basin. The wildfire behavior in the middle elevation areas of the Mojave Desert is influenced by the grass/fire cycle after years of high precipitation, but less so during relatively dry periods (Brooks et al. 2016). Over the short-term, fire may have a positive effect on soil nutrients in the immediate vicinity of burned shrubs, but this effect fades in the long term (Fuentes-Ramirez et al. 2015). Wildfires can increase nitrogen availability, making soils more suitable for invasive annual species like cheatgrass, which in turn can create a feedback loop by increasing the area affected by fire (Kerns and Day 2017). There is also evidence that cheatgrass itself can increase soil nitrogen availability (Stark and Norton 2015).

Western Joshua trees tend to be found at highest densities in the middle-elevation areas of the Mojave Desert. Brooks et al. (2018) reported that the middle elevation areas of the Mojave Desert had a fire return interval of approximately 687 years based on data from 1984–2013, which is equivalent to approximately 3.0% of these middle elevation areas burning every 20 years. Brooks et al. (2018) also reported an increase in annual fire area in middle elevation areas during this 1984–2013 period (Brooks et al. 2018). Fire probability is also related to elevation, as the proportion of area burned was largest at higher elevations and lowest at lower elevations (Brooks and Matchett 2006, Brooks et al. 2018). As discussed in the Species Distribution Models section of the Status Review, high-elevation areas of the Mojave Desert likely have the highest probability of retaining 20th century suitable climate conditions for western Joshua tree, however, these areas also have a high probability of wildfire, which means that wildfire may disproportionately affect areas of climate refugia for the species.

The Department evaluated California Department of Forestry and Fire Protection (CALFIRE 2021) records of areas burned by wildfire from 1900 to present within western Joshua tree's California range, as shown on Figure 9. Wildfire primarily affects the southern and western edges of western Joshua tree's range. Based on California Department of Forestry and Fire Protection records, the area burned within western Joshua tree's California range has increased over the period of 1900–2020 (Figure 10).

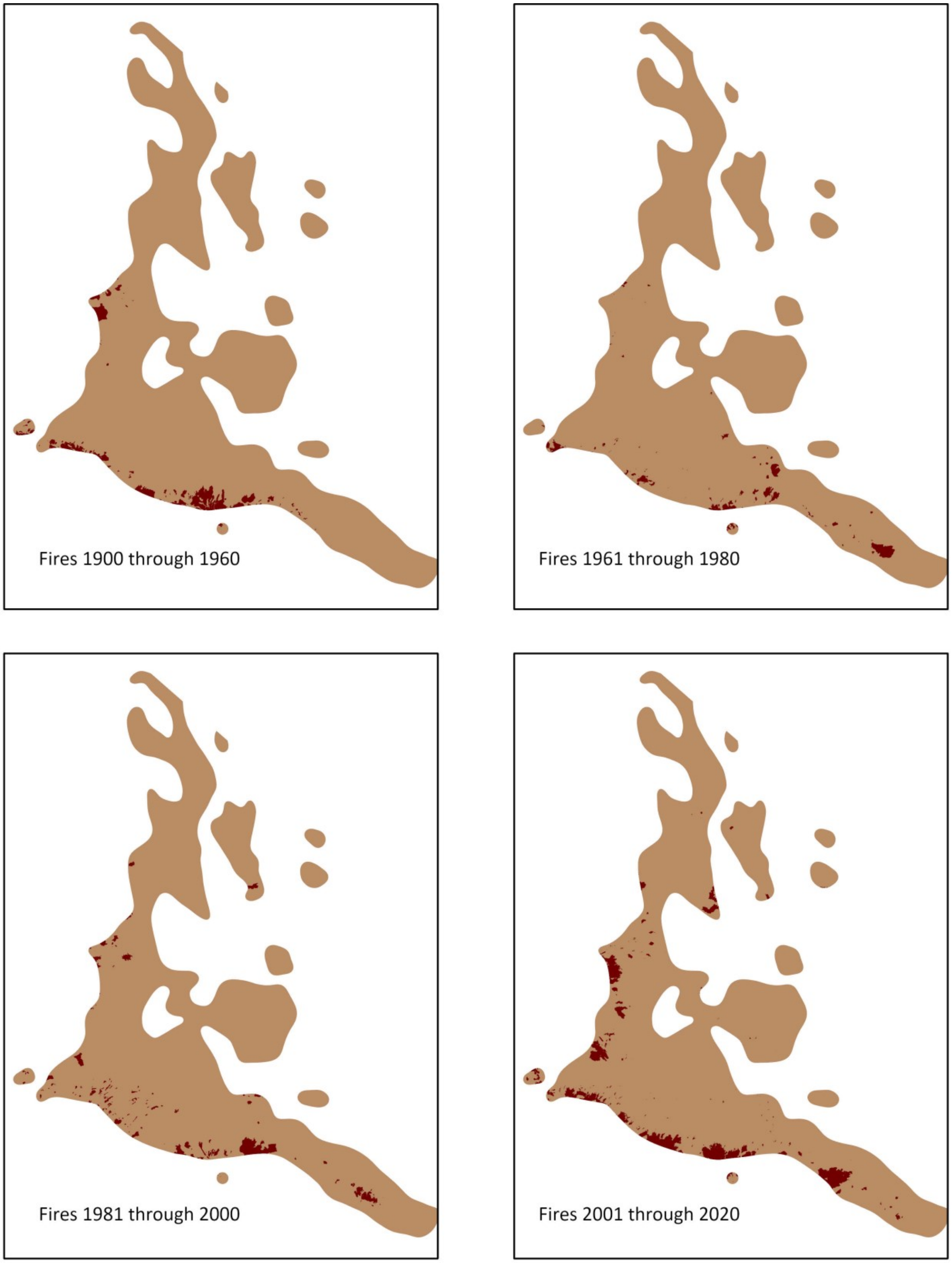

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Figure 9: Fires within the California Range of Western Joshua Tree, 1900–2020 (CALFIRE 2021)

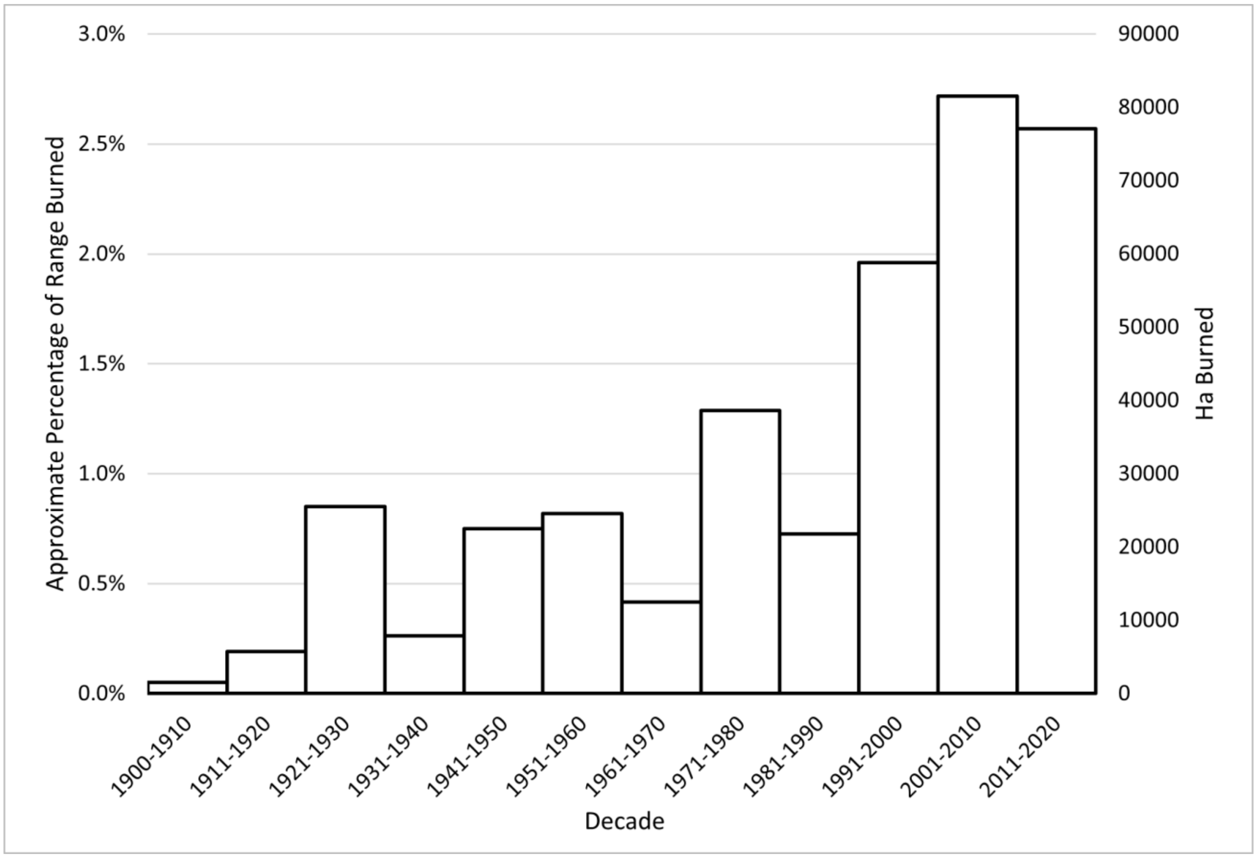

Figure 10: Area Burned Within Western Joshua Tree Range, 1900–2020 (CALFIRE 2021)

Wildfire has increased from burning less than 0.5% of western Joshua tree's California range each decade in the early 1900s, to burning approximately 2.5% of the species' range per decade between 2001–2020, though some of the increase in burned area shown in Figure 10 may be attributable to increasingly accurate and complete records in the second half of the 20th century and into the 2000s. Some areas of western Joshua tree habitat may have burned more than once over short time periods, so the areas burned within western Joshua tree's range are not necessarily cumulative. Many of the fire areas shown in Figure 9 roughly overlap with areas that have higher cover of western Joshua tree, as shown in Figure 4. In a separate analysis of California Department of Forestry and Fire Protection (CALFIRE 2021) records, Thompson (2021) calculated that 6.62% of the southern portion of western Joshua tree's range was affected by one or more wildfires between 1980–2019, however, Krantz (Appendix B) later reported that approximately 8% of total western Joshua range, and as much as 12.9% of the southern portion of western Joshua tree's range, was affected by one or more wildfires during this time period. There have been many fires in Joshua tree habitat, and the recent 2020 Dome Fire burned over 17,000 hectares (43,000 acres), and was estimated by the National Park Service (2020) to have killed 1.3 million eastern

Joshua trees, demonstrating how rapidly a wildfire can impact a dense Joshua tree population.

Fire has been recognized as a threat to Joshua tree for many decades (Webber 1953), and Joshua trees are negatively impacted or killed by wildfire and slow to recover from impacts (Minnich 1995, Loik et al. 2000b, DeFalco et al. 2010, Vamstad and Rotenberry 2010, Cornett 2012, Abella et al. 2020). Taller western Joshua trees may escape mortality from fire and heat due to their tall stature (Minnich 1995); however shorter trees are more severely affected by surface fires, with DeFalco et al. (2010) finding only approximately 20 percent of trees less than 1 m (3.2 ft) in height surviving five years after fire. The severe effect of wildfire on shorter trees causes long-lasting negative effects on the demographic health of affected populations. Persistent dead leaves along western Joshua tree trunks sometimes carry fire to the canopies of taller trees (Minnich 1995). As discussed in the Growth and Longevity section of this Status Review, post-fire recruitment from seeds appears to be rare (Borchert 2021), so Joshua tree may primarily recover from wildfire via resprouting. The new sprouts are prone to herbivory, and herbivory of western Joshua tree rhizome sprouts has been observed to be very high in the first year after a fire; however, sprouts continue to be produced in the second year after fire (Borchert pers. Comm. 2021). Western Joshua tree populations are very slow to recover from fire. Minnich (1995) found that 64% to 95% of western Joshua tree stems were fatally damaged by wildfire in all but one of 13 study sites in Joshua Tree National Park, and western Joshua tree cover and density remained low in burned sites compared with unburned sites, even 47 years after burning. DeFalco et al. (2010) found that plants in burned plots declined by 80% between 1999–2004 in Joshua Tree National Park, and plants in unburned plots declined by 26%, with drought likely contributing to the decline in both burned and unburned plots during the monitoring period. Barrios et al. (2017) compared aerial photography from 1992 with field survey results from 2017 to examine western Joshua tree survivorship and regeneration in two areas affected by a fire on Edwards Air Force Base in 1999. Barrios et al. (2017) found that the number of western Joshua trees in study areas increased from 108 in 1992 to 127 in 2017, but acknowledged that smaller western Joshua trees may not have been discernable via aerial imagery in 1992, and therefore may have been underreported. Barrios et al. (2017) reported that 73 of the 127 trees present in 2017 (57%) had been burned by the 1999 fire but resprouted and were alive.

Heat from wildfire may also kill western Joshua tree seeds on or in the soil. Keeley and Meyers (1985) found that Joshua tree seeds could not germinate after heat treatments of two hours at 90°C (194°F) or five minutes at 120°C (248°F). Peak fire temperatures reported by Brooks (2002) under and near shrubs in the Mojave Desert suggests that temperatures hot enough to kill Joshua tree seeds sometimes occur during wildfire, particularly if Joshua tree seeds are near burning shrubs and are not buried under soil.

Negative effects of wildfire on western Joshua tree could also affect *T. synthetica* populations because of the mutualistic relationship between the species, and these effects could therefore create a negative feedback loop. Lybbert and St. Clair (2016) examined the possible extended effects of wildfire on flower production, fruit production, yucca moth visitation, and cattle herbivory of eastern Joshua tree approximately eight to nine years after fire but did not find significant differences between burned and unburned populations of eastern Joshua tree. The study only examined areas where some eastern Joshua trees survived, because areas without surviving trees could not be assessed. These results suggest that the fire did not present a significant long-term impact to the population of its specialized pollinating yucca moth, or a long-term disruption to sexual reproduction, but Lybbert and St. Clair (2016) did note that the selection of eastern Joshua tree study locations in burned areas was limited due to low post-fire survival of the species.

In addition to directly killing adult and juvenile western Joshua trees, wildfire may eliminate important nurse plants (Loik et al. 2000b, Abella 2010, Brooks et al. 2018, Abella et al. 2020), increase herbivory and predation due to lowered resource availability (see Herbivory and Predation section of this Status Review), and create conditions that are more favorable for the establishment and spread of invasive species. Vamstad and Rotenberry (2010) examined how vegetation in a western Joshua tree woodland recovers after fire by examining a chronological sequence of historic burns in Joshua Tree National Park. Vamstad and Rotenberry (2010) found that while plant cover values returned to pre-fire levels between 19 and 65 years after wildfire, the reestablished vegetation assemblages in burned areas did not converge to the assumed pre-burn composition, even after 65 years. The authors suggest that the slow recovery is likely due to slow rates of reestablishment for some species. There is evidence that native annual plants in the Mojave Desert may reestablish more quickly than the Mojave Desert invasive plant species *Bromus madritensis* ssp. *rubens* (red brome) in the years immediately after fire, but red brome populations can reestablish to pre-fire conditions within two to nine years (Abella et al. 2009, Vamstad and Rotenberry 2010, Jurand and Abella 2013). Blackbrush vegetation communities appear to be particularly affected by wildfire in the Mojave Desert, and are very slow to recover from wildfire (Tagestad et al. 2016).

The amount and seasonality of precipitation in the Mojave Desert will affect fire potential in the future, but climate change effects on precipitation patterns in the Mojave Desert are still uncertain. Although many factors could be contributing to increasing wildfire risk and the spread of the invasive species that contribute to this risk in the western U.S., climate change could add to these effects via increases in the length of the growing seasons of invasive species and decreases in episodic cold mortality events, changes in the frequency of extreme precipitation events, and increases in the frequency of conditions that are conducive to increased fire potential (Abatzoglou and Kolden 2011, Hopkins 2018). Smith et al. (2000) found that elevated CO_2 increased the productivity and success of invasive species in an arid ecosystem, which suggests that climate change might enhance the long-term success of invasive species in the Mojave Desert, further increasing wildfire risk. Regardless of the extent to which climate change is contributing to wildfire risk in the Mojave Desert, if the wildfire trends reported by Brooks et al. (2018) and shown in Figure 10 continue, the threat of wildfire to western Joshua tree will increase.

Summary of Wildfire Threat

Wildfire is a substantial threat to western Joshua tree and invasive plants contribute to that threat, but wildfire does not affect the entire range of the species evenly, does not necessarily burn through areas in a uniform, high-intensity way, and does not typically result in the complete elimination of western Joshua tree from burned areas. For these reasons, wildfire is likely to reduce the abundance of the species, and may negatively impact the species distribution, however, it is unlikely to result in a serious danger of elimination of the species throughout a significant portion of its range. Nevertheless, because western Joshua tree recruitment from seed is rare, and because the species takes a long time to reestablish in burned areas, wildfire causes long-lasting negative effects in burned areas. The Department expects that the impacts from continuing and increasing wildfire activity in the Mojave Desert and surrounding areas will cause ongoing gradual reductions in the size of at-risk populations of western Joshua tree within California, but the range of the species is unlikely to be affected by wildfire in the foreseeable future, because western Joshua tree is unlikely to be completely eliminated from affected areas due to its high abundance and widespread distribution.

Invasive Plants

Non-native species are those that did not naturally occur in an area but that have become established and continue to reproduce in the wild. Invasive species are non-native species that have been determined to cause negative impacts to the environment or economy. Invasive species are often cited as the second greatest threat to biodiversity behind habitat loss (Wilcove et al. 1998, Mack et al. 2000, Levine et al. 2003, Pimentel et al. 2004) and North America has accumulated the largest number of naturalized, non-native plants in the world (van Kleunen et al. 2015). Many studies hypothesize or suggest that competition is the process responsible for observed invasive species impacts to biodiversity; however, invasive species may impact native species in a variety of ways (Levine et al. 2003). Invasive species may threaten native populations through competition for light, water, or nutrients; deposition of harmful biochemicals to soil; alteration of soil chemistry (e.g., pH, salinity); thatch accumulation that inhibits seed germination and seedling recruitment; changes in fire frequency; disruptions to pollination or seed-dispersal mutualisms; changes in soil microorganisms; diseases; or other mechanisms. The magnitude of invasive species impacts depends on the characteristics of the invading species and the characteristics of the location being invaded (Gaertner et al. 2009, Fried et al. 2014). Invasive species may also influence native species' colonization rates, leading to declines in local diversity over longer timescales (Yurkonis and Meiners 2004).

Invasive plant species are widespread in the Mojave Desert and throughout California, and in many cases, they compose large proportions of overall plant biomass (Brooks and Berry 2006). Invasive plant species that have reached "infested" to "spreading" status by the California Invasive Plant Council and that are causing severe ecological impacts within the Mojave Desert region of California include Saharan mustard (*Brassica tournefortii*), red brome, and cheatgrass (California Invasive Plant Council 2021). Russian-thistle (*Salsola tragus*), Arabian schismus (*Schismus arabicus*), and common Mediterranean grass (*Schismus barbatus*) are also reported by the California Invasive Plant Council to have reached "infested" to "spreading" status within the Mojave Desert region of California, but are not currently causing as severe of ecological impacts as Saharan mustard, red brome, and cheatgrass (California Invasive Plant Council 2021). There are many other species of plants that are not native to the Mojave Desert region of California but that have become established, and are continuing to reproduce and persist in the region (Weatherwax et al. 2002). The best predictors for the abundance and diversity of non-native and invasive plant species in the Mojave Desert may be proximity to human disturbance and development, including roads, off-highway vehicle use, livestock grazing and agriculture (Brooks and Berry 2006). Even within the protected lands of Joshua Tree National Park, there are few, if any, areas that have not been invaded by non-native and invasive grasses (Frakes pers. comm. 2021).

Increased nutrient availability through anthropogenic nitrogen deposition from air pollution has been shown to be a contributor to the abundance and spread of invasive plant species, including within the Mojave Desert (Allen et al. 2009, Allen and Geiser 2011, Pardo et al. 2011, Bytnerowicz et al. 2015, Rao et al. 2015). While precipitation is the primary driver influencing the biomass of invasive species in the Mojave Desert, nitrogen deposition has a smaller contributing effect (Rao et al. 2015), and this nitrogen deposition is already making an indirect, but substantial contribution to the spatial and temporal patterns of wildfire in the Mojave Desert (Syphard et al. 2017). Nitrogen deposition from anthropogenic sources is expected to increase in some parts of the world with increasing global emissions in the coming decades, particularly in areas that are still developing, but the depositions may show decreases in the 2100s even under different emissions scenarios (Zhang et al. 2019).

The primary way in which non-native and invasive plant species currently affect western Joshua tree is indirectly by fueling wildfire, as discussed in the Wildfire section of this Status Review. The contribution of invasive plant species to wildfire is expected to continue in the future, as human activities continue to promote the spread of non-native and invasive species within the range of western Joshua tree.

The Department is not aware of any studies examining the competitive effects of other plant species on western Joshua tree specifically, but invasive plant species, especially annual grasses, can rapidly invade Mojave Desert habitats and can compete with other plants for light, water, space, and nutrients (Brooks 2000, DeFalco et al. 2003, 2007, Blank 2010, Perkins and Hatfield 2014). Western Joshua tree is likely the most vulnerable to competitive effects from invasive plant species in the years immediately following germination, and plants likely become less vulnerable as they get larger. The Department currently considers competition with invasive plant species to be a minor threat to western Joshua tree.

Herbivory and Predation

Consumption of western Joshua tree seeds by both *T. synthetica* larvae, and seed-caching rodents is a natural component of the western Joshua tree life cycle. While there is a cost of these ecological relationships for western Joshua tree, the species also receives benefits in the form of sexual reproduction and seed dispersal. Physical damage to ovules of another species, Adam's needle (*Yucca filamentosa*), can trigger affected flowers to selectively abort and drop (Pellmyr and Huth 1994, Huth and Pellmyr 2000, Marr and Pellmyr 2003), which suggests that western Joshua tree may also be able to limit excessive negative effects from moth larvae eating seeds by dropping flowers that may have too many moth eggs. The relative costs and benefits of the ecological relationships between western Joshua tree, *T. synthetica*, and seed-caching rodents likely fluctuates based on environmental conditions and other factors, and the costs might outweigh the benefits when other stressors are acting upon the system, such as the factors that are discussed in this Status Review.

Other moth species may also oviposit on Joshua tree flowers so that their larvae may hatch inside and feed on seeds, but this relationship is strictly parasitic, because these moth species do not also pollinate western Joshua tree (Althoff et al. 2004). Along an elevational gradient within Joshua Tree National Park, Harrower and Gilbert (2018) found bogus yucca moth (*Prodoxus* sp.) that parasitizes western Joshua tree to be the most abundant in areas with the highest density of western Joshua tree, except at the highest elevation sampling site at 2,212 m (7,257 ft) where no sexual reproduction of western Joshua tree was observed, and asexual reproduction was abundant. Western Joshua tree may be able to limit impacts of seed predation from these moth larvae by dropping fruit before maturity, and infertile seeds could also help limit predation because moth larvae sometimes exit the fruit after encountering infertile seeds (Ziv and Bronstein 1996). There has been some investigation into how strongly the bogus yucca moths negatively impact the reproductive success of *Yucca* spp., but a strong effect has not been found (Althoff et al. 2004).

Other insect species feed on western Joshua tree as well. Yucca weevil (*Scyphophorus yuccae*) is a native insect species that feeds on *Yucca* spp. and related plants in the southwestern region of the United States, and has been found on Joshua tree (Vaurie 1971, Huxman et al. 1997). Yucca weevil larvae build protective cases near the ends of Joshua tree branches, and resulting damage to the meristem has been noted to cause branching in affected plants (Jaeger 1965). The Navaho yucca borer butterfly (*Megathymus yuccae navaho*) is reported to ignore young Joshua tree plants growing from seeds, and instead lays eggs only in Joshua trees that arise from asexual growth, with the resulting larvae boring into the underground rhizomes, where they feed and later pupate (Jaeger 1965). Lastly, a small contained outbreak of the yucca plant bug (*Halticoma valida*) was reported as impacting several planted Joshua trees at a demonstration garden in the town of Joshua Tree (JTNP 2017).

Domestic grazing animals can modify and degrade western Joshua tree habitat, and cattle may also eat portions of western Joshua tree plants. Cattle have been reported to graze on Joshua tree flowers when they can be reached (Wallace and Romney 1972, Lybbert and St. Clair 2017), and seeds and fruits are reported to be “fairly good feed materials” (Webber 1953). Cornett (2013) observed conspicuous cattle browsing on shrubs and other plants at one monitoring plot in Death Valley National Park but did not observe any evidence that cattle browsed western Joshua trees within the plot. Lybbert and St. Clair (2017) found that cattle removed 40% of eastern Joshua tree flower inflorescences that were lower than 2 m (6.6 ft) in one study area in Nevada but found that flower inflorescences above this height were not removed. Conversely, Cornett (1995) speculated that grazing by cattle can benefit Joshua tree by reducing bunch grass, favoring the presence of shrubs (nurse plants) that aid in Joshua tree seedling survival.

Small mammals, including antelope ground squirrels (*Ammospermophilus leucurus*), Botta’s pocket gophers (*Thomomys bottae*), black-tailed jackrabbits (*Lepus californicus*), and woodrat (*Neotoma* spp.) sometimes strip the periderm (bark) from Joshua trees, exposing large light-colored patches of underlying tissue and hollowing out stems, and this occurs more frequently during periods of drought (Esque et al. 2003, 2015, DeFalco et al. 2010). Following observations of damage to the trunks of western Joshua trees within Joshua Tree National Park in October of 2001, Esque et al. (2003) measured the survivorship of damaged trees in the summers of 2002 and 2003 and found that 95% of undamaged trees survived, but only 42% of trees with bark damage survived. The more damaged the western Joshua trees were, the less likely they were to be alive in 2003. No trees with more than 25% of their bark removed survived, but 60% of the trees with <5% of their bark removed survived. Five years after a wildfire and after a period of drought in Joshua Tree National Park, DeFalco et al. (2010) found that 14% of western Joshua trees in unburned areas and 28% of western Joshua trees in burned areas had bark damage from small mammals and this bark damage was correlated with reduced survival of plants, particularly at lower elevation areas where the most bark damage occurred.

Mammals can also eat other parts of western Joshua tree. Black-tailed jackrabbits can consume young western Joshua tree rhizome sprouts (Cornett 1995) and seedlings. Over half of a cohort of 53 five to seven year-old western Joshua tree plants were killed from black-tailed jackrabbit herbivory during a drought in 1989 and 1990 (Esque et al. 2015). Herbivory on basal sprouts may also be particularly high in the first year after a fire (Borchert pers. comm. 2021). Sanford and Huntly (2009) found that desert woodrats (*Neotoma lepida*) primarily fed on the tips of eastern Joshua tree leaves, tending to leave the leaf bases intact, and that they prefer leaves with higher nitrogen content, which tends to occur on the south side of plants.

Herbivory and predation result in relatively minor negative impacts overall to western Joshua tree. Impacts from small mammals are likely highest in non-masting years, when they consume nearly all of the western Joshua tree seeds that are produced, and during periods of drought, when they can damage the bark of trees, potentially causing mortality in affected trees. Cattle may also consume quantities of flowers in grazed areas. Herbivory during early seedling stages may negatively impact recruitment because the species may be particularly vulnerable at this life stage. Herbivory of western Joshua tree may also increase if droughts become more frequent and longer due to climate change (Esque et al. 2015). Nevertheless, because western Joshua tree is currently abundant and widespread, the Department considers the overall threat to the species from herbivory and predation to be relatively small.

Use and Vandalism

Western Joshua tree has long been available and used in the horticultural trade, with seeds and plants collected from the wild, and individuals planted within and outside of the species' native range. Joshua tree was briefly but unsuccessfully used for paper pulp and surgical splints in the late 1800s and early 1900s (McKelvey 1938). Concern about impacts from commercial collecting and overutilization of Joshua trees and other desert plants was raised as early as 1930 (Carr 1930, Griffin 1930, Runyon 1930), and shortly afterwards some areas of the Mojave Desert were protected. Desert vegetation also received protection from commercial collection with the passage of the California

Desert Native Plants Act (DNPA) in the early 1980s. Collection of western Joshua tree seeds and plants from the wild for horticultural reasons likely continues to occur to some extent near roads, but the impact to the species from these activities is considered relatively minor. Western Joshua tree may also continue to be used traditionally by Native Americans (Coville 1892, Stoffle et al. 1990, Fowler 1995, Small 2013, Gaughen pers. comm. 2020), but impact to the species from these activities is also considered relatively minor. Vandalism of western Joshua trees occasionally occurs in some areas (Airhart 2019), and one of the largest known western Joshua trees was maliciously burned to the ground (McKelvey 1938, Cummings 2019). Western Joshua tree is currently abundant and widespread, and the threat to the species from use and vandalism is currently considered relatively minor.

EXISTING MANAGEMENT

Regulatory Status and Legal Protections

Some local, state, and federal laws apply to activities undertaken in California that may provide western Joshua tree and its habitat some level of protection from development and other human activities. A discussion of some of the local, state, and federal laws that are applicable to western Joshua tree is provided below; however, the following is not an exhaustive list.

In general, the highest level of regulatory protection that western Joshua tree has received so far has been the result of the species being designated a candidate under CESA on October 9, 2020, which prohibits take of the species during the candidacy period and typically requires take to be minimized and fully mitigated to Department standards. Absent the protections of CESA, other federal, state, and local laws and regulations may provide limited avoidance, minimization, and mitigation of impacts for the species, with protection or mitigation of impacts often only required when a controlling agency or project proponent determines it is feasible to do so. In many cases, removal of western Joshua trees and related habitat destruction may proceed with a permit from a local agency that does not require mitigation for habitat loss. Permits may also be issued that only require moving individual western Joshua trees out of the habitat that is to be destroyed, but the habitat destruction is not mitigated. Absent the protections of CESA, trends of western Joshua tree habitat loss and degradation from development and other human activities will likely continue.

During the candidacy period for western Joshua tree, the Department has also received numerous reports of the unpermitted killing of western Joshua trees on private property, and related habitat modification and destruction. Impacts from unpermitted or illegal activities do take place, and laws and regulatory mechanisms are only effective if they are followed and enforced.

Federal

Federal Endangered Species Act

Western Joshua tree has no regulatory protection under the federal ESA. Both western Joshua tree and eastern Joshua tree were petitioned to be listed as threatened under the federal ESA (16 U.S.C. §§ 1531-1544) in 2015 (Jones and Goldrick 2015). After conducting an assessment of the two species, the USFWS issued a decision (12 Month Finding) that listing Joshua tree as an endangered or threatened species was not warranted (USFWS 2018, 2019). In *WildEarth Guardians v. Haaland*, 2021 U.S. Dist. LEXIS 179024, the United States District Court for the Central District of Columbia set aside the USFWS' 12 Month Finding as arbitrary, capricious, and contrary to the federal ESA and remanded the 12 Month Finding to the USFWS for reconsideration consistent with the court's findings.

National Environmental Policy Act

The National Environmental Policy Act (NEPA) requires federal agencies to assess the environmental effects of their proposed actions prior to making certain decisions. Using the NEPA process, agencies evaluate the environmental and related social and economic effects of their proposed actions. Agencies also provide opportunities for public review and comment on those evaluations. Title I of NEPA contains a Declaration of National Environmental Policy. This policy requires the federal government to use all practicable means to create and maintain conditions under which man and nature can exist in productive harmony. Section 102 in Title I of the Act requires federal agencies to incorporate environmental considerations in their planning and decision-making through a systematic interdisciplinary approach. Specifically, all federal agencies are to prepare detailed statements assessing the environmental impact of and alternatives to major federal actions significantly affecting the environment. These statements are commonly referred to as Environmental Impact Statements and Environmental Assessments.

State

California Endangered Species Act

Western Joshua tree was designated a candidate species under CESA on October 9, 2020. During candidacy, CESA prohibits the import, export, take, possession, purchase, or sale of western Joshua tree, or any part or product of western Joshua tree, except as otherwise provided by the Native Plant Protection Act (NPPA), the DNPA, or Fish and Game Code, such as through a permit or agreement issued by the Department under the authority of the Fish and Game Code (Fish & G. Code, § 2080 et seq.). For example, the Department may issue permits that allow the incidental take of listed and candidate species if the take is minimized and fully mitigated, the activity will not jeopardize the continued existence of the species, and other conditions are met (*Id*. at § 2081, subd. (b)). The Department may also authorize the take and possession of listed and candidate species for scientific, educational, or management purposes (*Id*. at § 2081, subd. (a)). Furthermore, the Department may issue a Safe Harbor Agreement to authorize incidental take of listed or candidate species if a landowner provides a net conservation benefit to the species, implements practices to avoid or minimize incidental take, establishes a monitoring program, and meets other program conditions (*Id*. at § 2089.2 et seq.). Finally, the Department may authorize take associated with routine and ongoing agricultural activities through Voluntary Local Programs if management practices avoid and minimize take to the maximum extent practicable, as supported by the best scientific information for both agricultural and conservation practices, among other conditions (*Id*. at § 2086).

Native Plant Protection Act

The NPPA (Fish and G. Code, §§ 1900-1913) was enacted to preserve, protect, and enhance endangered or rare native plants in the state. (*Id*. at § 1900). The NPPA allows the Fish and Game Commission (Commission) to designate plants as rare or endangered. (*Id*. at § 1904). Section 1908 of the NPPA prohibits the take, possession, or sale of any endangered or rare native plant or part or product thereof except as otherwise provided by the NPPA. Provisions in the NPPA allow for the take of rare and endangered plants under limited circumstances, including clearing of land for agricultural practices or fire control measures as authorized by a public agency; timber operations conducted in accordance with a timber harvesting plan submitted pursuant to the Z'berg-Nejedly Forest Practice Act of 1973; required mining assessment work pursuant to federal or state mining laws; removal of endangered or rare native plants from a canal, lateral ditch, building site, or road, or other right-of-way by the landowner or his agent; or performance by a public agency or public utility of its obligation to provide service to the public (*Id*. at § 1913, subd. (a) and (b)). A landowner who has been notified by the Department pursuant to NPPA section 1903.5 that a rare or endangered native plant is growing on their land must notify the Department at least 10 days before changing the land use to allow for salvage of such plants (*Id*. at § 1913, subd. (c)). If the Department fails to salvage plants within 10 days of notification, the landowner shall be entitled to proceed without regard to the NPAA. (*Id*.) The NPPA does not apply to western Joshua tree because it is a candidate for listing as a threatened species, and the NPPA only applies to endangered and rare species.

California Desert Native Plants Act

The DNPA (Food and Ag. Code, § 80001 et seq.) generally allows for take of specified desert native plants (including yuccas, such as western Joshua tree) upon issuance of a permit from the county commissioner or sheriff. The DNPA allows for harvest or possession of five or fewer plants without a permit (*Id.* at § 80118). The DNPA also provides exemptions from permitting for a variety of activities, including land clearing for agricultural purposes, fire control, and required mining assessment work pursuant to federal or state mining laws; recreational events sanctioned by BLM; clearing or removal of native plants from a canal, lateral ditch, survey line, building site, or road, or other right-of-way by a landowner or his agent; and actions taken by a public agency or public utility in the performance of its obligation to provide service to the public (*Id*. at § 80117). The DNPA states that rare, endangered, and threatened native plants are exempt from its requirements (*Id*. at § 80075). Pursuant to this provision, the DNPA does not apply to western Joshua tree because it is a candidate for listing as a threatened species.

California Environmental Quality Act

State and local agencies must conduct environmental review under the California Environmental Quality Act (CEQA) for discretionary projects proposed to be carried out or approved by the public agency unless the agency properly determines the project is exempt from CEQA (Pub. Resources Code, § 21080). If a project has the potential to substantially reduce the habitat, decrease the number, or restrict the range of any rare, threatened, or endangered species, the lead agency must make a finding that the project will have a significant effect on the environment and prepare an environmental impact report (EIR) or mitigated negative declaration as appropriate before proceeding with or approving the project (Cal. Code Regs., tit. 14, §§ 15065(a)(1), 15070, and 15380). An agency cannot approve or carry out any project for which the EIR identifies one or more significant effects on the environment unless it makes one or more of the following findings: (1) changes have been required in or incorporated into the project that avoid the significant environmental effects or mitigate them to a less than significant level; (2) those changes are in the responsibility and jurisdiction of another agency and have been, or can and should be, adopted by that other agency; or (3) specific economic, legal, social, technological, or other considerations make infeasible the mitigation measures or alternatives identified in the environmental impact report (Pub. Resources Code, § 21081; Cal. Code Regs., tit. 14, §§ 15091 and 15093). For (3), the agency must make a statement of overriding considerations finding that the overriding benefits of the project outweigh the significant effects on the environment. CEQA establishes a duty for public agencies to avoid or minimize such significant negative effects where feasible (Cal. Code regs., tit. 14, § 15021). Impacts to western Joshua tree, as a CESA-candidate species, should be identified, evaluated, disclosed, and mitigated or justified under the Biological Resources section of an environmental document prepared pursuant to CEQA.

Local

Many local city and county ordinances regulate tree removal, some with specific regulations potentially applicable to western Joshua trees. As applied to western Joshua tree, most of these local ordinances are currently preempted by CESA given the species' candidacy status and will continue to be preempted if the species is listed. The only two exceptions are the newer ordinances adopted by the City of Palmdale and Town of Yucca Valley to implement the Fish and Game Code section 2084 regulation adopted by the Commission. However, the City of Palmdale and Town of Yucca Valley ordinances will only be valid during western Joshua tree's candidacy since section 2084 regulations cannot apply to western Joshua tree after candidacy. If western Joshua tree is not listed as a threatened or endangered species under CESA or the federal ESA after candidacy, certain local ordinances would allow for removal of western Joshua tree without required mitigation under specified circumstances. Therefore, these local regulations may not adequately protect western Joshua trees from direct removal or loss of habitat, and the species may remain threatened by human development absent protections under CESA.

Inyo County

Property owners are responsible for maintenance of trees on private property and no permit is required for private property owners to trim or remove trees in the streetside apron or on private property (Inyo County Code, tit. 12, §§ 12.20.030, 12.20.040). In districts zoned for wireless communications or solar facilities, the planning commission may consider the nature, type, and extent of tree coverage when reviewing and issuing a conditional use permit (*Id*. at tit. 18, §§ 18.76.080, 18.79.080). Grading, filling, or stripping vegetation during subdivision development must be performed concurrently with the final map or parcel map improvement and required bonds, or must be authorized pursuant to a grading permit issued by the advisory agency with appropriate erosion control conditions to protect adjoining properties and the general welfare (*Id*. at tit. 16, § 16.040.030).

City of Bishop

The location and type of all trees greater than four inches in diameter must be shown on final maps and parcel maps, including parcels proposed for subdivision (City of Bishop Code, tit. 16, §§ 16.20.320, 16.16.100). The city may require removal of trees on right-of-way easements (*Id*. at § 16.28.170). Grading restrictions defer to the subdivision map or parcel map improvement and bonds requirements, or to authority given by the planning commission (*Id*. at § 16.28.170). Applications for conditional use permits for conversion of residential units to condominiums must include development plans specifying the location of and provisions for any unique natural and/or vegetative site features (*Id*. at tit. 17, § 17.84.030).

Kern County

The Kern County Code of Ordinances does not provide any protection for western Joshua trees. In general, tree removal is not prohibited. Development permits may require a landscaping plan or assessment of native vegetation to be removed but do not restrict removal nor encourage retention.

California City

The California City code of ordinances provides regulations for maintenance and removal of trees in public places and prohibits persons operating off-road vehicles from malicious or unnecessary damage to vegetative resources (California City Code, tit. 4, § 4-2.606 and tit. 7, § 7-8.104). No regulations for trees on private property are included in this code of ordinances.

Ridgecrest

The Ridgecrest City Planning Commission may require development plan standards related to planting and maintenance of trees (City of Ridgecrest Code, § 106-347). Development projects and rezoning proposals must undergo site review; applications must describe the location of existing and proposed trees (*Id*. at § 106-172). Grading permits are reviewed by the city engineer and applicants must present detailed written plans for the site (*Id*. at § 104-4).

Tehachapi

In public spaces in Tehachapi, the removal, maintenance, and replacement of trees is overseen by the street superintendent (Tehachapi Code, tit. 12, § 12.08.080). In the area zoned for the airport, regulations limit tree height and provide for removal of nonconforming or deteriorated/decaying trees (*Id*. at tit. 11, § 11.12.150). Removal of trees on utility easements may be required by the city (*Id*. at tit. 17, § 17.28.140).

Los Angeles County

Within Significant Ecological Areas designated in the Los Angeles General Plan, protections for western Joshua tree are thorough and detailed (Los Angeles County Code of Ordinances, tit.22, § 22.102). In these areas, Los Angeles County issues

Protected Tree Permits and Conditional Use Permits requiring mitigation for removal of any single heritage tree, removal of two or more non-heritage trees, or encroachment into more than 10% of the buffer zone around any western Joshua tree. Exceptions include removal related to construction or improvement of single-family residences, accessory structures, and animal keeping facilities, fuel reduction around existing buildings (no buffer limit stated), and maintenance related to public utility lines.

City of Lancaster

The City of Lancaster incentivizes the retention of Joshua trees by allowing commercial and industrial zoning parcel adjustments by up to 10% if the changes will result in the retention or preservation of Joshua trees (City of Lancaster Code of Ordinances, tit. 17, §§ 17.12.100, 17.12.780, and 17.16.090).

City of Palmdale

Pursuant to the Special Order approved by the Commission on December 10, 2020, pursuant to Fish and Game Code section 2084, the City of Palmdale amended Chapter 14.04 of the Palmdale Municipal Code to authorize removal of western Joshua trees only as consistent and compliant with the Special Order. With limited exceptions, Chapter 14.04 generally prohibits the removal of western Joshua trees and other specified native desert vegetation without approval by permit from the City's Landscape Architect, or in lieu thereof, the Director of Public Works' designee (Palmdale Municipal Code, § 14.04.040). All development proposals for sites containing native desert vegetation must contain a written report and site plan with specified information on each western Joshua tree located on-site, a site landscaping plan, and a long-term maintenance program for any western Joshua trees preserved on-site (*Id*. at § 14.04.050). These development proposals must also meet minimum preservation criteria, including preservation of at least two western Joshua trees per gross ac on average unless specified conditions are met that allow for use of a different standard determined by a desert native plant specialist (*Id*. at § 14.04.060). In specified circumstances, western Joshua trees may be transplanted (*Id*.). If western Joshua trees will be removed and not replanted on-site, they can be made available to the City of Palmdale or the public to plant elsewhere (*Id*.) If none of those options are feasible, the proponent may pay an in-lieu fee to the City of Palmdale (*Id*.). After construction of the development proposal and final inspection, project proponents must meet ongoing maintenance requirements, including maintaining western Joshua trees and other native desert vegetation in healthy condition for at least two growing seasons (*Id*. at § 14.04.070). Except in limited circumstances, a violation of Chapter 14.04 is a misdemeanor punishable by a fine of up to $1,000, imprisonment for up to six months, or both such fine and imprisonment (*Id*. at §§ 14.04.110, 1.12.010, and 1.12.020). In addition to these penalties, Chapter 14.04 requires the responsible party to replace any damaged, illegally cut, destroyed, killed, removed, mutilated or harvested western Joshua trees pursuant to the recommendation of an authorized desert native plant specialist retained at the responsible party's expense (*Id*. at § 14.04.100).

<u>County of Riverside</u>

A permit is required for the removal of living native trees located above 5,000 ft in elevation in the unincorporated areas of the county, unless an exemption for timber operations, federal or state government actions, or public utility actions applies; unless the removal is authorized under an approved conditional use or public use permit; or unless the tree constitutes an immediate threat to public health, safety, or general welfare. Trees can also be removed if they are located within 20 ft of an existing permitted structure; the tree is diseased, dead, or dying and removal is recommended by the California Department of Forestry and Fire Protection to protect forest health; or the fire protection agency with jurisdiction requires removal pursuant to a fire hazard reduction program. (Riverside County Code of Ordinances, tit. 12, § 12.24). Trees located below 5,000 ft in elevation receive no protection. All known western Joshua trees within Riverside County that are above 5,000 ft are within Joshua Tree National Park.

<u>County of San Bernardino</u>

Preconstruction inspections shall be required before approval of development permits to determine the presence of regulated trees and plants (County of San Bernardino Code, tit. 8, § 83.10.050). All Joshua trees are designated as Regulated Desert Native Plants; thus, a Tree or Plant Removal Permit is required for removal of any western Joshua tree or any part thereof (*Id*. at tit. 8, § 83.10.060). These permits may be issued by the County Director of Land Use Services in conjunction with or not in conjunction with a land use application or development permit. The permit review authority may require certification from an appropriate arborist, registered professional forester, or desert native plant expert that the proposed removal activities are appropriate, supportive of a healthy environment, and in compliance with both the County of San Bernardino Municipal Code and the California Department of Fish and Wildlife's procedures. The permit conditions of approval may specify criteria, methods, and persons authorized to conduct the tree removal and may require the trees to be transplanted and/or stockpiled for future transplanting.

In order to authorize the removal of a western Joshua tree, the applicable review authority must find that removal is justified for one of the following reasons: the location of the tree or its dripline interferes with an allowed structure, street, or other planned improvement and there is no other feasible location for the improvement; the tree is hazardous to pedestrian or vehicular travel or safety, or is causing extensive damage to public structures, or the tree is in such close proximity to an existing or proposed structure that the tree will sustain significant damage. If the tree is located in the desert region of San Bernardino County, additional findings must be made including that western Joshua trees will be transplanted or stockpiled for future transplanting wherever possible and that for removal of specimen-sized western Joshua trees (circumference equal to or greater than 50 in, total height of 15 ft or greater, possessing a bark-like trunk, or in a cluster of ten or more individual tress of any size), no other reasonable alternative exists for the development of the land.

For each removal of a separate tree, penalties for illegal removal can include misdemeanor charges, fines of $500-$1000 and/or six months in jail, and other requirements to correct the conditions resulting from the violation.

The 2020 San Bernardino Countywide Plan includes the County Policy Plan, which encourages retention of western Joshua trees but does not provide regulations nor clarify a permit review process. Community plans nested within this plan describe values and characteristics of planned communities but do not regulate removal or retention of western Joshua trees. While much of San Bernardino County is federal property, these community plans cover most of the remaining private land within county boundaries.

<u>City of Adelanto</u>

Any application for a new development or for proposal to increase existing land use or outdoor recreational or other use by 25% must provide a biological resources report including mitigating measures to reduce or eliminate impacts to biological resources (City of Adelanto Code, tit. 17, § 17.57.030). Development projects must abide by County of San Bernardino requirements for relocation of Joshua trees (*Id*. at tit. 17, § 17.57.040). Only the City Engineer may be authorized to trim, prune, cut, or deface trees on City property, roads, or streets (*Id*. at tit. 13, § 13.50.050).

<u>Town of Apple Valley</u>

Town of Apple Valley must review and approve any removal of a Joshua tree on any property within any zoning district (Apple Valley Code of Ordinances, tit. 9, § 9.76.040). The code includes detailed requirements for documented removal justification, provides guidance for relocation/transplanting, and establishes a Joshua Tree Preservation and Adoption program. Development permits must find that all Joshua trees are adequately protected and preserved where feasible (*Id*. at tit. 9, § 9.17.080).

City of Barstow

City of Barstow Code of Ordinances suggests retention of native vegetation where possible but does not prohibit removal or require a survey or review process (Barstow Code of Ordinances, tit. 19, § 19.08.050). The code does not specifically reference western Joshua trees.

Hesperia

Removal of any western Joshua tree requires a permit issued by the agricultural commissioner or other applicable review authority (Hesperia Code of Ordinances, tit. 16, §16.24.150). However, the Hesperia Code does not provide specific information about the review process. Penalties for violation of the code include revocation of the permit, prohibition on issuance of new permits for one year (first offence) or life (second offense), and requirements to turn over any unused tags and seals or wood receipts (*Id*. at tit. 16, § 16.24.170). Lot design standards encourage retention of dense stands of Joshua trees to the maximum extent possible (*Id*. at tit. 17, § 17.48.070).

City of San Bernardino

There is a small population of western Joshua trees in Cajon Wash in the City of San Bernardino. A permit is required for removal of more than five trees within any 36-month period from a development site or parcel of property (City of San Bernardino Code of Ordinances, tit. 15, § 15.34.020). Permits are issued by the Development Services Department of the City of San Bernardino, wherein the Planning Official determines whether the trees can be removed without detriment to the environment and welfare of the community and thereby issues or denies the permit (*Id*. at tit. 15, § 15.34.040). Penalties for noncompliance include infraction or misdemeanor, fine, and restitution to the City of San Bernardino for the amount not to exceed the replacement value (*Id*. at tit. 15, § 15.34.060). Development standards encourage retention of natural vegetation where possible and Conditional Use Permits require a landscaping plan showing disposition of existing trees (*Id*. at tit. 19, §§ 19.17.070, 19.17.080).

Twentynine Palms

To reduce disturbances to fragile desert soils and reduce the amount of fugitive dust, removal of natural vegetation on parcels one ac or greater in size for construction of building pads, driveways, landscaping, agriculture, or other allowed uses in the underlying zone requires a Building Permit or Grading Permit issued by the City's Building Official (Twentynine Palms Code of Ordinances, tit. 19, § 19.64.030). In areas zoned for scenic vistas or scenic highways and geologic hazards, retention of native vegetation is encouraged but not required (*Id*. at tit. 19, §§ 19.26.030, 19.26.040). The code does not specifically reference western Joshua trees.

<u>Victorville</u>

Written approval from the director of parks and recreation or his designee is required to cut, damage, destroy, dig up, or harvest a western Joshua tree (Victorville Code of Ordinances, tit. 13, §13.33.040). The code does not include details about the approval process. Penalties include misdemeanor charge and up to six months in jail and/or $500 fine (*Id*. at tit. 13, §13.33.040).

<u>Town of Yucca Valley</u>

Pursuant to the Special Order approved by the Commission on December 10, 2020, pursuant to Fish and Game Code section 2084, the Town of Yucca Valley adopted Chapter 9.56 of its Code of Ordinances authorizing removal of western Joshua trees only as consistent and compliant with the Special Order. The Town of Yucca Valley Planning Commission may authorize the take of western Joshua tree associated with developing single-family residences, accessory structures, and public works projects concurrent with its approval of the project subject to specified census, application, and submittal conditions (Yucca Valley Code of Ordinances, § 9.56.060). No project will be eligible to receive take authorization pursuant to Chapter 9.56 if it will result in the take of more than 10 western Joshua trees from the project site (*Id*. at § 9.56.060(A)(1)). Projects authorized under Chapter 9.56 must avoid take of western Joshua trees to the extent practicable and avoid ground-disturbing activities within 10 ft of any western Joshua tree except under limited specified circumstances (*Id*. at §§ 9.56.070 and 9.56.080). To the maximum extent feasible, the project proponent must relocate all western Joshua trees that cannot be avoided to another location to the project site in accordance with specified conditions (*Id*. at § 9.56.090). Western Joshua trees may only be removed subject to Chapter 9.56 requirements if they cannot feasibly be avoided or relocated pursuant to Chapter 9.56 (*Id*. at § 9.56.100). Before presenting an application to the Planning Commission, project proponents must pay specified mitigation fees to the Town of Yucca Valley's Western Joshua Tree Mitigation fund (*Id*. at § 9.56.110). The Planning Commission may issue permits to authorize the removal of a dead western Joshua tree or the trimming of a western Joshua tree (*Id*. at § 9.56.120). Permits for removal of a dead western Joshua tree or the trimming of a western Joshua tree may be issued without payment of mitigation fees if the tree or limb has fallen over and is within 30 ft of a structure, is leaning against an existing structure, or creates an imminent threat to health or safety (*Id*. at § 9.56.120). Any violation of Chapter 9.56 shall constitute a misdemeanor and may be punishable by an administrative citation of $1,000 per western Joshua tree taken or trimmed without a permit (*Id*. at § 9.56.130). In addition, any person or entity that takes or trims a western Joshua tree without a permit required under Chapter 9.56 must subsequently obtain a permit under this Chapter (*Id*. at § 9.56.130). Failure to submit a permit application within 30 days of service of a notice of violation of Chapter 9.56 shall constitute a separate violation of Chapter 9.56 for which a separate administrative citation, fine, or other penalty may be imposed (*Id*. at § 9.56.130).

Nonregulatory Status

Species that are not listed under CESA or the federal ESA may nevertheless be rare or at risk of extinction and nonprofit organizations often assign such species a nonregulatory status, sometimes in collaboration with a government agency. Impacts to species that have a nonregulatory status may sometimes be analyzed and mitigated under CEQA and NEPA, even if the species are not listed under CESA or the federal ESA.

Natural Heritage Program Ranking and IUCN Red List

All natural heritage programs, such as the CNDDB, use the same ranking methodology originally developed by The Nature Conservancy and now maintained by NatureServe. This ranking methodology consists of a global rank describing the rank for a given taxon over its entire distribution, and a state rank describing the rank for the taxon over its state distribution. Both global and state ranks reflect a combination of rarity, threat, and trend factors. The ranking methodology uses a standardized calculator that uses available information to assign a numeric score or range of scores to the taxon, with lower scores indicating that a taxon is more vulnerable to extinction, and higher scores indicating that a taxon is more stable (Faber-Langendoen et al. 2012). The rank calculation process begins with an initial rank score based on rarity and threats, with rarity (multiplied by 0.7) factored more heavily into the calculator than threats (multiplied by 0.3). The combined rarity and threat rank is then either raised or lowered based on trends. When there is a negative trend, the rank score is lowered, and when there is a positive trend the rank score is raised. Short-term trends are factored more heavily into the calculator than long-term trends.

Western Joshua tree has been assigned a global rank of G3G4 indicating that there is uncertainty regarding the rank of the species, and it is either "G3 vulnerable and at moderate risk of extinction or collapse due to a fairly restricted range, relatively few populations or occurrences, recent and widespread declines, threats, or other factors" or "G4 apparently secure and at fairly low risk of extinction or collapse due to an extensive range and/or many populations or occurrences, but with possible cause for some concern as a result of local recent declines, threats, or other factors." The factors cited for this rank include fire, drought, climate change, and numerous threats related to habitat loss including off road vehicle use (Master et al. 2012, NatureServe 2021). Western Joshua tree's conservation status in California under this ranking system has not yet been assessed. Natural heritage ranking does not provide any regulatory protections but is often considered during the CEQA process (Hammerson et al. 2008).

The International Union for Conservation of Nature (IUCN) Red List provided a global scope assessment of western Joshua tree in October 2020 (Esque et al. 2020b) resulting in a designation of Least Concern, which is the Red List category representing the lowest risk of extinction, and is assigned when a taxon has been evaluated against the ranking criteria and does not qualify for Critically Endangered, Endangered, Vulnerable, or Near Threatened (IUCN 2012). In the IUCN assessment of western Joshua tree, the reviewers noted a decreasing population trend due to the severely fragmented population as well as the reduced number of and continuing decline of mature individuals (Esque et al. 2020b). Noted threats include renewable energy development, gathering terrestrial plants, fire and fire suppression, invasive non-native species and diseases, and drought. IUCN's assessment also states that no international legislation, management, or trade controls exist for western Joshua tree.

IUCN and NatureServe assess extinction risk for species using a time period of 10 years or 3 generations, whichever is longer, up to a maximum of 100 years (Faber-Langendoen et al. 2012, IUCN 2012).

<u>California Rare Plant Rank</u>

The Department works in collaboration with the California Native Plant Society and botanical experts throughout the state to assign rare and endangered plants a California Rare Plant Rank reflective of their status. Joshua tree was considered for a California Rare Plant Rank in 2011 but a rank was not assigned due to the species being too common (CNPS 2021b).

Management Efforts

There are currently no federal or state range-wide management efforts or recovery plans for western Joshua tree; however, because most of the known range of the species is under federal jurisdiction the species receives some special protection and management by federal agencies. Natural resources within designated wilderness areas receive a very high level of protection from human impacts. There are also various ongoing efforts to study Joshua tree biology, ecology, threats, conservation, genetics, and other topics related to the species.

National Park Service

Lands administered by the National Park Service within California that have western Joshua tree include Death Valley National Park, Joshua Tree National Park, and Manzanar National Historic Site (horticultural plantings). Natural resources on lands managed by the National Park Service generally receive a high level of protection, including some active management for the benefit of natural resources, although they may also be subject to impacts from recreational use and development and maintenance of related infrastructure.

Western Joshua tree does not occur in the Mojave National Preserve, but the preserve does support a large population of eastern Joshua tree. Mojave National Preserve is currently undergoing a large restoration effort in response to the 2020 Dome Fire with a primary focus on returning Joshua trees to an area that was predicted to be a climate refugium for the species (Kaiser 2021).

Joshua Tree National Park

The Joshua Tree Wilderness was designated in 1976 and includes 1,890 km^2 (730 mi^2) protected by The Wilderness Act (Public Law 94-567 [H.R. 13160]). The Superintendent's Compendium applies to all persons within the boundaries of federally owned or designated public use lands within Joshua Tree National Park and prohibits possessing, destroying, injuring, defacing, removing, digging, or disturbing Joshua trees, including climbing, sitting, or standing on live Joshua trees or using them as anchors for hammocks or slacklines (36 CFR § 2.1 (a)(1)(ii)).

Joshua Tree National Park established a Foundation Statement which states that adult populations of Joshua trees are stable, but knowledge of community structure and distribution is incomplete, and trends are unknown (Rogers pers. comm. 2021). It further designates Joshua trees as a fundamental resource and value, warranting primary consideration during park planning and management activities. In addition, Joshua Tree National Park is actively engaged in conservation efforts to protect areas identified as potential climate change refugia for Joshua trees. This includes fuel breaks, defensible space, removing nonnative grasses around mature reproductive trees (Frakes 2017b), and extensive long term demographic monitoring across the population. In the early 2000's, Joshua Tree National Park shifted fire management philosophies from considering the use of fire on the landscape (controlled burns and allowing fires to burn) to full suppression, acknowledging the unacceptable risks to Joshua tree woodlands, and Joshua Tree National Park continues to manage fires aggressively to protect native vegetation (Frakes 2017a).

Joshua Tree National Park has also implemented restoration activities involving western Joshua trees and other native plants within Joshua Tree National Park, typically for revegetation purposes associated with road realignment projects, social trails restoration, and burned area rehabilitation (Frakes 2017a). Joshua trees have also been salvaged and subsequently transplanted by Joshua Tree National Park following planned disturbances such as road realignments. These activities are labor intensive and expensive, and generally require prolonged follow-up care in the form of protective caging and two years of bi-weekly irrigation. (Frakes 2017a)

A number of monitoring efforts by Joshua Tree National Park are underway (Frakes pers. comm. 2021). Joshua Tree National Park established three 500 x 500 m (1,640 x 1,640 ft) "range edge plots" in 2016 and 2017 at lower elevation areas of Joshua Tree National Park that support western Joshua trees. In-depth tree-by-tree demographic data were collected within these plots, and these plots will likely be very important in the future for direct observations of possible western Joshua tree range reductions. Joshua Tree National Park also established 100 50 x 50 m (164 x 164 ft) plots that were randomly placed within vegetation communities in Joshua Tree National Park where western Joshua tree is currently relatively abundant to monitor changes that take place in these areas. Joshua Tree National Park staff also revisited and collected data from 55 western Joshua tree monitoring plots in 2021 that were established by Todd Esque in 2008.

Death Valley National Park

The Death Valley Wilderness was designated in 1994 and includes 12,911 km^2 (4,985 mi^2) protected by The Wilderness Act (Public Law 94-567 [H.R. 13160]), making it the largest wilderness in the U.S. The Superintendent's Compendium applies to all persons within the boundaries of federally owned or designated public use lands within Death Valley National Park and prohibits taking biological specimens (plants, fish, and wildlife) rocks or minerals except in accordance with other regulations or pursuant to the terms and conditions of a specimen collection permit (36 CFR § 2.5 (a)). Death Valley National Park contains roughly 209 km^2 (81 mi^2) of western Joshua tree habitat and supports scientific research through a permitting system (Reynolds pers. comm. 2021).

United States Department of Defense

The Department of Defense manages natural resources on military lands via development and implementation of integrated natural resources management plans (INRMPs). INRMPs use an ecosystem based approach, and balance conservation and mission activities to provide "no net loss" to testing, training, and operational activities (Department of Defense 2021). Military installations coordinate their INRMPs with the USFWS and the appropriate state fish and wildlife agency pursuant to the Sikes Act.

The INRMP for Edwards Air Force Base incorporates avoidance and minimization measures that could reduce individual fatalities of western Joshua tree and disturbance of its habitat. (U.S. Air Force 2020). The INRMP for National Training Center and Fort Irwin requires that if removal is necessary, trees must be re-located to sites with the same orientation and similar characteristics as their original sites to reduce the risk of tree mortality (U.S. Army 2006). The INRMP for Naval Air Weapons Station China Lake does not list western Joshua tree as a sensitive species, but discusses the sensitivity of the species to fire, and mentions transplantation of western Joshua tree as a component of revegetation or landscaping (U.S. Navy n.d.).

Bureau of Land Management

Several wilderness areas managed by the BLM in California support populations of western Joshua tree. Wilderness areas managed by the BLM in California that may support populations of western Joshua tree and provide them with a high level of protection from human impacts include Black Mountain Wilderness, Bright Star Wilderness, Chimney Peak Wilderness, Coso Range Wilderness, Darwin Falls Wilderness, Domeland Wilderness, El Paso Mountains Wilderness, Grass Valley Wilderness, Inyo Mountains Wilderness, Kiavah Wilderness, Owens Peak Wilderness, Piper Mountain Wilderness, Rodman Mountains Wilderness, Sacatar Trail Wilderness, Surprise Canyon Wilderness, and White Mountains Wilderness.

Outside of wilderness areas, populations of western Joshua tree on BLM lands may receive various levels of protection from human impacts, but lands supporting western Joshua tree may also be utilized for destructive non-conservation purposes. A number of plans have been adopted regarding management of BLM lands within the range of western Joshua tree including the California Desert Conservation Area Plan, Desert Renewable Energy Conservation Plan, West Mojave Plan, and West Mojave Route Network Project Land Use Plan Amendment (BLM 1980, 2005, 2016, 2019). The Desert Renewable Energy Conservation Plan identified large areas of western Joshua tree habitat for conservation.

United States Forest Service

There are several wilderness areas managed by the United States Forest Service in California that may support populations of western Joshua tree and provide them with a high level of protection from human impacts, including Bighorn Mountain Wilderness, Golden Trout Wilderness, Kiavah Wilderness, Pleasant View Ridge Wilderness, and Sheep Mountain Wilderness. Western Joshua tree may occur to some extent within Angeles National Forest, Inyo National Forest, San Bernardino National Forest, and Sequoia National Forest. Forest Service lands are generally at a low risk of habitat destruction due to forest management policies, but habitat modification from land use may still occur.

State of California

Some areas of western Joshua tree habitat occur on lands managed by the California Department of Parks and Recreation. Natural resources on lands managed by the California Department of Parks and Recreation generally receive a high level of protection, including some active management for the benefit of natural resources, although they may also be subject to impacts from recreational use and development and maintenance of related infrastructure. Natural resources on vehicular recreation areas are subject to many impacts from off highway vehicle use. The following lands managed by the California Department of Parks and Recreation may support western Joshua tree: Antelope Valley California Poppy Preserve State Natural Reserve, Antelope Valley Indian Museum State Historic Park, Arthur B. Ripley Desert Woodland State Park, Eastern Kern County Onyx Ranch State Vehicular Recreation Area, Hungry Valley State Vehicular Recreation Area, Red Rock Canyon State Park, and Saddleback Butte State Park. California Department of Parks and Recreation is planning to gather baseline information on western Joshua trees within the Great Basin District (Tejada pers. comm. 2020).

Some western Joshua tree habitat is within lands managed by the Department. Natural resources on lands managed by the Department generally receive a high level of protection, including some active management for the benefit of natural resources, although they may also be subject to impacts from recreational use and development and maintenance of related infrastructure. The following lands managed by the Department may support western Joshua tree: Canebrake Ecological Reserve, Fremont Valley Ecological Reserve, King Clone Ecological Reserve, Mojave River Public Access, West Mojave Desert Ecological Reserve, and several undesignated lands.

The California Desert Conservation Act (Fish & G. Code, § 1450 et seq.) became effective on January 1, 2022, and establishes a California Desert Conservation Program within the Wildlife Conservation Board with the goals of protecting habitat in California's Mojave and Colorado deserts by planning and implementing land acquisition and restoration projects. The California Desert Conservation Program could result in conservation or restoration of western Joshua tree habitat in California.

Western Joshua tree may benefit from land use planning and conservation planning efforts in the Mojave Desert. The Natural Community Conservation Planning Program is a program by the State of California to promote collaborative planning efforts designed to provide for region-wide conservation of plants, animals, and their habitats, while allowing for compatible and appropriate economic activity. There is currently a Natural

Community Conservation Plan in development for the Town of Apple Valley that intends to include Joshua tree as a covered species. However, it is not yet known when this plan will be finalized, or the extent to which this plan may help conserve western Joshua tree habitat. Regional Conservation Investment Strategies is a program by the State of California to encourage voluntary, non-regulatory regional planning intended to result in high-quality conservation outcomes. There is currently one Regional Conservation Investment Strategy in development for the Antelope Valley area that is near completion, and another for western San Bernardino County that is still in development. Both Regional Conservation Investment Strategies include Joshua tree as a focal species, but it is not yet known the extent to which these strategies will help conserve western Joshua tree habitat.

Other

Some nonprofit organizations work to acquire, restore, and protect areas supporting western Joshua tree within the Mojave Desert for conservation and preservation purposes (MDLT 2021).

Desert revegetation may be an important component of western Joshua tree management in the future and there have been some scientific investigations into the effectiveness of desert revegetation activities. Abella and Newton (2009) reviewed 15 planting and 8 seeding studies conducted in the Mojave Desert and found that treatments of irrigation (3 studies), caging (3 studies), and shelter (2 studies) generally resulted in increases in plant survival. Only two of the studies reviewed by Abella and Newton (2009) included Joshua tree. Hunter et al. (1980) examined how fencing affected survival of 14 species of desert plants in Nevada and found that wire fencing generally marginally improved survival of plants, including western Joshua tree and *Yucca schidigera*, but only six western Joshua trees were used in the study. Krantz (Appendix B) reports that western Joshua trees as tall as 3-3.7 m (10-12 ft) with moderate branching can be transplanted using a 36-inch hydraulic tree spade, and that after transplanting larger trees must be tethered to stabilize the weight of the tree and receive additional irrigation. Wallace et al. (1980) reported the results of a study in Nevada where 16 western Joshua trees were transplanted in 1971 and watered as needed for the first six months, with seven of them surrounded by wire cages and nine of them left uncaged. Five years later in 1976, two of the seven caged western Joshua trees had survived (28%) and four of the nine uncaged western Joshua trees had survived (44%). Franson (1995) reported the health and survival of 1,447 eastern Joshua trees that were salvaged and transplanted in rows to two different nurseries. Two years after transplanting 36% of the eastern Joshua trees were rated as being in excellent health, 56% of the trees were rated as being in poor health, and 8% of the trees had died.

The Joshua Tree Genome Project (2020) is an ongoing effort to assemble a Joshua tree reference genome and conduct other investigations such as a large common garden experiment. The Department is also aware of various ongoing western Joshua tree research and monitoring efforts that will continue to improve the scientific understanding of the status of western Joshua tree in California.

SUMMARY OF LISTING FACTORS

CESA directs the Department to prepare this report regarding the status of western Joshua tree based upon the best scientific information available to the Department (Fish & G. Code, § 2074.6). CESA's implementing regulations identify key factors that are relevant to the Department's analyses. Specifically, a "species shall be listed as endangered or threatened ... if the Commission determines that its continued existence is in serious danger or is threatened by any one or any combination of the following factors: 1. Present or threatened modification or destruction of its habitat; 2. Overexploitation; 3. Predation; 4. Competition; 5. Disease; or 6. Other natural occurrences or human-related activities" (Cal. Code Regs., tit. 14, § 670.1, subd. (i)(1)(A)).

The definitions of endangered and threatened species in the Fish and Game Code provide key guidance to the Department's scientific analyses. An endangered species under CESA is one "which 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" (Fish & G. Code, § 2062). A threatened species under CESA is one "that, although not presently threatened with extinction, is likely to become an endangered species in the foreseeable future in the absence of special protection and management efforts required by [CESA]" (*Id.*, § 2067). A species' range for CESA purposes is the species' California range (*Cal. Forestry Assn. v. Cal. Fish and Game Com*. (2007) 156 Cal.App.4th 1535, 1551).

The preceding sections of this Status Review describe the best scientific information available to the Department, with respect to the key factors identified in the regulations. The section below considers the significance of any threat to the continued existence of western Joshua tree for each or a combination of the factors. The best available science focuses on projecting conditions near the end of the 21st century. There is much uncertainty in predicting future outcomes in complicated systems, and there is an even greater uncertainty in projecting outcomes further into the future. Therefore, the Department's determinations for this Status Review focus only on end of the 21st century projected conditions.

The physical and biological systems and relationships that affect the future of western Joshua tree are complicated, and despite the body of scientific information that is currently available, uncertainty remains. Additionally, the future of western Joshua tree not only depends on predictions that are based on the physical and biological sciences, but factors related to national and international laws, politics, and economics; the value that humanity places on conserving biodiversity; and the global human responses to climate change.

The Department is required to make a recommendation on whether the petitioned action is warranted. The Department acknowledges that the combined and cumulative effects of the listing factors discussed in this Status Review can be interpreted in different ways (see independent peer review in Appendix B). The Department also acknowledges the possibility that the combined and cumulative effects of the factors discussed in this Status Review could be severe enough to result in a serious risk of loss of a significant portion of western Joshua tree's range in the foreseeable future. However, given the uncertainties and limitations of the information currently available to the Department, this Status Review presents the outcome that the Department considers to be the most likely.

Present or Threatened Modification or Destruction of Habitat

Western Joshua tree habitat could be modified in a negative way or destroyed by several factors discussed under the Factors Affecting the Ability to Survive and Reproduce section of this Status Review. These factors include the direct and indirect effects of climate change; the direct and indirect effects of development and other human activities; and the direct and indirect effects of wildfire. Some of these factors are interconnected and cumulative, and the southern portion of the species' range faces greater threats than the northern portion of the species' range.

Based on the best available science, available information suggests that the direct and indirect effects of climate change will cause a reduction in the areas with 20th century suitable climate conditions for western Joshua tree by the end of the 21st century (2100), especially in the southern and lower elevation portions of its range. Areas with 20th century suitable climate conditions for the species will also expand to the north and into higher elevation areas, though the species is unlikely to naturally colonize these areas in the foreseeable future. While 20th century suitable climate conditions for the species are predicted to expand into areas of eastern California, it will primarily expand into Nevada where it is not considered under CESA. Studies assessed by the Department suggest that at the end of the 21st century, some areas of climate refugia for western Joshua tree will remain at the southern and lower elevation portions of its range.

While the available evidence suggests that the area with 20th century suitable climate conditions for western Joshua tree within California will decline substantially through the end of the 21st century (2100) due to climate change, the Department does not have any data on the extent to which these climate changes will likely affect the demographics of the species (such as recruitment and mortality) in the foreseeable future. Based on fossil records following climate changes approximately 11,700 years ago, the Department expects that any changes in the range of western Joshua tree that are ultimately caused by climate change will likely occur very slowly, perhaps over thousands of years. Because adult western Joshua trees are relatively resilient to harsh climate conditions, the Department expects that the effects of the reduction of areas with 20th century suitable climate conditions within the species' range in the foreseeable future will likely have a greater negative effect on seedling recruitment than on adult tree mortality, although both may occur. Additionally, because western Joshua tree is currently abundant and widespread, it likely has a high capacity to withstand or recover from stochastic (random) disturbance events. Therefore, it may already have capacity to withstand changing conditions, and the species may be able to withstand changes to 20th century suitable climate conditions in the foreseeable future without becoming in serious danger of extinction throughout all or a significant portion of its range within California.

Due to western Joshua tree's ability to survive harsh conditions and reproduce asexually, there may be a long time delay between when an area becomes no longer suitable for sustaining western Joshua tree populations and when the species is no longer present in that area, and it may not be possible to easily recognize whether populations in an area are ultimately sustainable. Based on the current best available science, the Department expects that the effects of climate change will cause the abundance of western Joshua tree to decline in the southern part of its range by the end of the 21st century, but because the Department does not have demographic data showing that departures from 20th century suitable climate conditions will mean that the species will not be able to persist in significant portions of its range, the Department does not foresee that western Joshua tree is likely to be in serious danger of becoming extinct throughout all or a significant portion of its range by the end of the 21st century (2100) due to climate change. The Department does not expect that the special protection and management efforts required by CESA would ameliorate the direct and indirect effects of climate change on western Joshua tree.

Based on the best available science, the Department expects that the direct and indirect effects of development and other human activities will cause negative modification and destruction of habitat for western Joshua tree in some areas by the end of the 21st century, particularly in the southern part of the species' range. The Department expects that habitat modification and destruction will primarily be limited to private property, lands within the vicinity of roads and existing development, and lands chosen for renewable energy development. The magnitude of this habitat modification and destruction will likely be related to the economic values of development and other human activities in the Mojave Desert and surrounding areas, and the effectiveness of state and federal regulatory and legal protections that are enforced through the end of the 21st century.

The USFWS predicted that between 22% and 42% of the habitat within the southern part of western Joshua tree's range may be lost by the year 2095 due to urban growth and renewable energy development. The extent to which development and other human activities will cause habitat for western Joshua tree to be negatively modified and destroyed by the end of the 21st century is uncertain. The Department does expect that habitat modification and destruction will continue on lands that remain unprotected from development, but that undeveloped, protected lands supporting western Joshua tree habitat will also remain throughout the range of the species, though they may be fragmented. Additionally, because western Joshua tree is currently abundant and widespread, scattered habitat loss is unlikely to result in a change in the overall range of the species, particularly when lost habitat continues to be surrounded by occupied habitat on protected lands and on occupied undeveloped lands that may be protected in the future. While habitat loss continues to be a substantial, ongoing threat, it does not necessarily mean that the species is likely to be at serious risk of extinction throughout all or a significant portion of its range. The Department does not foresee that western Joshua tree will be in serious danger of becoming extinct in a significant portion of its range by the end of the 21st century due to habitat modification and destruction caused by development and other human activities. The Department does expect that the special protection and management efforts required by CESA would ameliorate some of the direct and indirect effects of development and other human activities on western Joshua tree in the southern portion of its range, because a large proportion of western Joshua tree's habitat in this area occurs on private land that is vulnerable to continuing modification and destruction.

Based on the best available science, available information suggests that when a wildfire burns through an area, the immediate and delayed effects of wildfire may kill a majority (greater than 50%) of western Joshua trees in burned areas. Some western Joshua trees and their seeds are likely to survive burning, providing the opportunity for the species to repopulate burned areas, which may take one or more centuries. The direct and indirect effects of wildfire are also likely to temporarily modify western Joshua tree habitat by eliminating important nurse plants and by potentially increasing the suitability of burned areas for further invasion by invasive plant species. The average area burned by wildfire each decade since the early 1900s appears to have generally increased, and approximately 2.5% of western Joshua tree's range burned each decade from 2001–2010 and from 2011–2020, and some areas may have burned more than once. The wildfire activity in western Joshua tree habitat has likely increased in recent decades due to the effects of invasive species with nitrogen deposition contributing to invasive species abundance. Large fires can be triggered after one or more years of relatively high precipitation, favoring vegetation growth leading to higher fuel loads. Invasive plant species are expected to continue their spread across the Mojave Desert, and nitrogen deposition is not expected to cease in the near future. It is unknown if wildfire activity will continue to increase at the same rate observed in recent decades. Based on the current best available science, the Department expects that wildfire will continue to cause reductions in the population of western Joshua trees and will cause temporary modifications to habitat in burned areas that will reduce the ability of the species to recruit new individuals. However, because western Joshua tree is currently abundant and widespread, it is inherently less vulnerable to extinction from the effects of stochastic and localized events such as wildfire. Furthermore, losses in abundance due to wildfire are not expected to change the species’ range in the foreseeable future because some trees within burned areas survive, and occupied habitat remains outside of burned areas. The Department does not foresee that western Joshua tree is in serious danger of becoming extinct in a significant portion of its range by the end of the 21st century due to wildfire. The Department does not expect that the special protection and management efforts required by CESA would ameliorate the direct and indirect effects of wildfire on western Joshua tree.

Considered collectively, the direct and indirect effects of climate change, the direct and indirect effects of development and other human activities, and the direct and indirect effects of wildfire are interconnected and will affect different portions of western Joshua tree’s range in different ways, sometimes cumulatively. Climate change may reduce recruitment and abundance in southern and lower elevation portions of western Joshua tree’s range, development and other human activities are expected to destroy and modify habitat on unprotected private property, and fire is expected to kill a proportion of trees in burned areas and temporarily reduce recruitment in those areas. Climate change and wildfire will have interconnected and cumulative negative effects on western Joshua tree populations in some areas, and the effects of climate change and the direct and indirect effects of development and other human activities will also have interconnected and cumulative negative effects on western Joshua tree populations in some areas. Development and other human activities may also contribute to wildfire risk. The cumulative impacts of climate change, wildfire, and development and other human activities may also affect populations of *T. synthetica*, reducing western Joshua tree’s ability to sexually reproduce.

In summary, the Department expects that western Joshua tree will be subject to ongoing habit modification and destruction through the end of the 21st century due to substantial threats from climate change, wildfire, development and other human activities, and the interconnected cumulative effects of some of these threats, particularly in the southern portion of its range, but western Joshua tree is also currently abundant and widespread, which lessens the overall relative impact of these threats to the species.

Overexploitation

Based on the best available science, the Department does not believe that overexploitation is a threat to western Joshua tree, primarily because western Joshua tree is currently abundant and widespread, and the impacts to the species from overexploitation are relatively small.

Predation

Based on the best available science, the Department believes that predation and herbivory is a minor threat to western Joshua tree, and the threat should be considered in the context of the threats from climate change and wildfire. Impacts from small mammals are likely most severe in non-masting years, when they consume nearly all of the western Joshua tree seeds that are produced, and during periods of drought, when they can damage the bark of trees, potentially causing mortality in affected trees. Cattle may also consume quantities of flowers in grazed areas. Nevertheless, because western Joshua tree is currently abundant and widespread, the Department considers the threat to the species from herbivory and predation to be relatively small.

Competition

Based on the best available science, the Department believes that competition is a minor threat to western Joshua tree. Although invasive plant species are prevalent throughout the range of the species, the primary way in which invasive plant species currently affect western Joshua tree is indirectly by fueling wildfires. Invasive plant species may also directly compete with western Joshua tree seedlings for light, water, space, or nutrients, but the Department does not currently have enough information to consider this interaction a major threat to the species.

Disease

The Department does not have any information on diseases or parasites affecting western Joshua tree. The Department does not consider disease or parasites to be a significant threat to the continued existence of western Joshua tree.

Other Natural Occurrences or Human-related Activities

The primary threats to western Joshua tree are from climate change, wildfire, and development and other human activities, and are discussed in the Present or

Threatened Modification or Destruction of Habitat section above. While these primary threats may most often manifest themselves in the form of habitat modification and destruction, they could result in direct mortality of western Joshua trees or have other direct or indirect effects to western Joshua trees that are not necessarily related to a modification or destruction of habitat. It could therefore be appropriate to also categorize them here under Other Natural Occurrences and Human-related Activities. The Department's determinations under the Present or Threatened Modification or Destruction of Habitat section above take into account all of the effects of climate change, wildfire, and development and other human activities on western Joshua tree based on a broad interpretation of what constitutes habitat modification and destruction under the appropriate regulation (Cal. Code Regs., tit. 14, § 670.1, subd. (i)(1)(A)). Under this interpretation, there are no other natural occurrences or human-related activities that the Department considers to be significant threats to the continued existence of western Joshua tree.

Summary of Key Findings

Western Joshua tree is a widespread and abundant species that is found in the Mojave Desert and Great Basin. Climate in the desert regions where western Joshua tree occurs consists of long, hot summers, mild winters, and low overall precipitation. Precipitation across the Mojave Desert region is highly variable from year to year and oscillates between periods of wetter and drier conditions over multi-year and multi-decade timescales.

Joshua tree has received a large amount of attention from the scientific community, and its life history has been studied for over 150 years. Sexual reproduction requires the presence of western Joshua tree's obligate pollinating moth *T. synthetica*. After a mast seeding event, seed dispersal is facilitated by the scatter hoarding behavior of rodents, which results in burial of some western Joshua tree seeds at a soil depth suitable for germination. Western Joshua tree seedlings most successfully establish after large mast seeding events, which perhaps only occur once or twice per decade. Seedlings that emerge from under nurse plants are more likely to survive. Several successive years of sufficiently wet and/or cool conditions are likely required to ensure that seeds germinate and that seedlings can reach a sufficiently large size before the arrival of a period of drier and/or hotter conditions. A western Joshua tree may require 30 to 50 or more years to reach reproductive maturity and begin producing seeds. Individual western Joshua trees can survive for very long periods of time, perhaps over 150 years, and the species is also capable of asexual growth which may allow individuals to survive indefinitely under appropriate conditions.

The population size and area occupied by western Joshua tree has declined since European settlement of the Mojave Desert due to habitat modification and destruction, a trend that has continued to the present. Despite the declines since European settlement, the range of the species has remained largely unchanged, with the species continuing to occupy the same general geographical area within California. The primary threats to the species are the direct and indirect effects of climate change, development and other human activities, and wildfire. Available species distribution models suggest that areas with 20th century suitable climate conditions for western Joshua tree will be reduced substantially through the end of the 21st century (2100) as a result of climate change, especially in southern and lower elevation portions of its range. Areas with 20th century suitable climate conditions for western Joshua tree may also expand to the north and into higher elevation areas, though the species is unlikely to colonize these areas quickly, and climate refugia for western Joshua tree will likely remain at the southern and lower elevation portions of its range at the end of the 21st century.

Species distribution models of future conditions have substantial limitations, and there is much uncertainty of what the predicted effects of climate change will be on western Joshua tree individuals, populations, distribution, abundance, and ultimately range. The Department does not have scientific information on how changes from the 20th century suitable climate conditions within Joshua tree’s range will affect the demographics of western Joshua tree populations in California, which limits the extent to which the effects of climate change on populations of western Joshua tree in the foreseeable future can be reasonably predicted. The future of the species will largely depend on its existing ability to withstand change and the magnitude of the global human response to climate change. The effects of development and other human activities will also cause habitat for western Joshua tree to decline and become more fragmented by the end of the 21st century, particularly in the southern part of the species’ range, however, western Joshua tree populations on protected and undeveloped lands are expected to remain, and therefore the continuing habitat loss will not necessarily result in an overall change in the range of the species. Western Joshua trees on private property, on lands within the vicinity of roads and existing development, and lands chosen for renewable energy development may be at the highest risk of being lost. Wildfire poses a substantial threat and may kill over half of western Joshua trees in burned areas. In each of the last two decades, approximately 2.5% of western Joshua tree’s range burned. Additionally, western Joshua tree is susceptible to herbivory by large and small mammals, especially during periods of drought, although this is considered a minor threat to the species. Competition from invasive plant species is a minor threat to western Joshua tree, and some of the threats to western Joshua tree are interconnected and may affect the species cumulatively.

The combined threats to western Joshua tree are cause for substantial concern. Nevertheless, western Joshua tree is currently abundant and widespread, which lessens the overall relative impact of the threats to the species. The Department anticipates that the threats acting upon western Joshua tree will result in a reduction in the abundance of the species by the end of the 21st century, and that the abundance may continue to decline after that time. However, due to the high uncertainty in projecting the pace and magnitude of climate change and other threats into the 22nd century (after 2100), and the lack of scientific information in the Department's possession that contemplates such timeframes for the species, the Department does not yet consider the range of the species in the 22nd century to be foreseeable. The Department anticipates that the scientific information on the status of western Joshua tree will continue to improve in the coming years and decades, with demographic data and species distribution modeling eventually allowing for an analysis of the viability of western Joshua tree populations across their entire California range.

PROTECTION AFFORDED BY LISTING

It is the policy of the state to conserve, protect, restore and enhance any endangered or any threatened species and its habitat (Fish & G. Code, § 2052). If western Joshua tree is listed under CESA, unauthorized "take" of western Joshua tree would be prohibited, and the conservation, protection, and enhancement of the species and its habitat would be an issue of statewide concern. Under CESA, "take" is defined as hunt, pursue, catch, capture, or kill, or attempt to hunt, pursue, catch, capture, or kill (*Id.*, § 86). Any person violating the take prohibition would be punishable under state law. The Fish and Game Code provides the Department with related authority to authorize "take" under certain circumstances (*Id.*, §§ 2081, 2081.1, 2086, 2087, 2089.6, 2089.10 and 2835). As authorized through an incidental take permit, however, impacts of the take of an endangered or threatened species caused by the activity must be minimized and fully mitigated according to state standards.

Protection of western Joshua tree could also occur with required public agency environmental review under CEQA, and its federal counterpart NEPA. CEQA and NEPA both require affected public agencies to analyze and disclose project-related environmental effects, including potentially significant impacts on endangered, threatened, and rare special status species. Under CEQA's "substantive mandate," for example, state and local agencies in California must avoid or substantially lessen significant environmental effects to the extent feasible. Impacts to species that are of conservation concern may be analyzed and mitigated under CEQA and NEPA even if the species are not listed; however, in common practice, potential impacts to listed species are examined more closely in CEQA and NEPA documents than potential impacts to unlisted species. State listing, in this respect, and required consultation with the Department during state and local agency environmental review under CEQA, may benefit western Joshua tree.

If western Joshua tree is listed under CESA, it may also increase the likelihood that state and federal land and resource management agencies will allocate funds towards protection and recovery actions. CESA listing of western Joshua tree could also increase public awareness of the conservation needs of the species and California desert ecosystems, and could lead to an increased interest in scientific research on the species.

RECOMMENDATION FOR PETITIONED ACTION

CESA directs the Department to prepare this report regarding the status of western Joshua tree in California based upon the best scientific information available to the Department (Fish & G. Code, § 2074.6). CESA also directs the Department to indicate in this Status Review whether the petitioned action is warranted (Fish & G. Code, § 2074.6; Cal. Code Regs., tit. 14, § 670.1, subd. (f)). Based on the criteria described above, the best scientific information available to the Department at this time indicates that western Joshua tree is not 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, and is not likely to become an endangered species in the foreseeable future in the absence of special protection and management efforts required by CESA.

The Department recommends that the Commission find the petitioned action to list western Joshua tree as a threatened species to be not warranted.

MANAGEMENT RECOMMENDATIONS AND RECOVERY MEASURES

CESA directs the Department to include in its Status Review recommended management activities and other recommendations for recovery of western Joshua tree (Fish & G. Code, § 2074.6; Cal. Code Regs., tit. 14, § 670.1, subd. (f)). Department staff generated the following list of recommended management actions and recovery measures based on considerations from federal agencies, researchers, non-profit organizations, and other interested parties. The following list is not a detailed conservation strategy for western Joshua tree; however, it outlines possible components of a preliminary strategy to conserve the species. Although the Department's recommendation in this Status Review is to find the petitioned action to be not warranted, the Department does recognize that the combined threats to western Joshua tree are a substantial cause for concern. Western Joshua tree faces serious challenges, and long-term conservation of the species is likely beyond the scope of any one government, agency, or organization, and could require new funding and legislation. The Department therefore recommends that the following actions be conducted in coordination with a broad group of stakeholders including private citizens, scientists, and other local, state, and federal governments and organizations, consistent with California’s goals of conserving biodiversity and preventing the extinction of rare, threatened, and endangered species.

- Continue efforts to drastically reduce greenhouse gas emissions.
- Complete a western Joshua tree conservation plan in partnership with a broad group of stakeholders.
- Identify, preserve, and manage western Joshua tree habitat in areas with high recruitment and areas projected to be climate refugia.
- Minimize wildfire risk to western Joshua tree woodlands via vegetation management or other means, particularly following one or more years of high precipitation, and particularly in areas with high recruitment and areas projected to be climate refugia.
- Manage active fires aggressively to protect Joshua tree woodlands, particularly in areas with high recruitment and areas projected to be climate refugia.
- Implement disincentives to destruction of western Joshua tree habitat and individuals via legislation, regulatory change, or other means, particularly in areas with high recruitment and areas projected to be climate refugia.
- Implement and ensure proper enforcement of state and/or local laws and regulations that limit unmitigated impacts to high quality western Joshua tree habitat.
- Develop standards and protocols for environmental assessment and mitigation of impacts to western Joshua tree habitat and individuals.
- Continue scientific investigations into the biology, ecology and genetics of western Joshua tree and the species and habitats upon which it depends, and integrate results of scientific research into management and conservation actions:
    - Collect and analyze range-wide demographic information to detect baseline population trends and identify populations that do not appear to be recruiting new individuals at sustainable levels.
    - Implement long-term range-wide direct population monitoring and vegetation monitoring with emphasis on leading and trailing edges and highest and lowest elevations of the species’ range.
    - Produce and improve upon range-wide species distribution models for western Joshua tree.
    - Investigate the significance of multi-year and multi-decade climate variability patterns for western Joshua tree recruitment.

- Investigate the life history, environmental tolerances, and distribution of western Joshua tree's obligate pollinating moth *T. synthetica*.
- Produce range-wide species distribution models for *T. synthetica*.
- Investigate ways to control the spread and abundance of invasive plant species to reduce wildfire risk.
- Investigate the feasibility, practicality, and risks of implementing assisted migration and translocation.

PUBLIC RESPONSE

Comments on the petitioned action were invited via a general notification dated October 21, 2020, and a tribal notification dated November 12, 2020. These notifications were distributed to tribes; industry organizations; nonprofit organizations; media outlets; scientists familiar with western Joshua tree and related topics; universities; federal, state, and local agencies; and other interested individuals and organizations. Responses to the notifications are included in Appendix A.

PEER REVIEW

Independent experts familiar with western Joshua tree and the subjects discussed in this Status Review were invited to review the Status Review report before submission to the Commission. All comments received are included in Appendix B. The Department's response to the independent peer review is included in Appendix B. Independent experts that reviewed the Status Review are listed in Table 2, below.

Table 2: Status Review Peer Reviewers

Name	Affiliation
Dr. Cameron Barrows	University of California Riverside
Dr. Erica Fleishman	Oregon Climate Change Research Institute
Dr. Timothy Krantz	University of Redlands
Dr. Lynn Sweet	University of California, Riverside
Dr. Jeremy B. Yoder	California State University Northridge

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APPENDIX A: COMMENTS FROM AFFECTED AND INTERESTED PARTIES ON THE PETITIONED ACTION

APPENDIX B: COMMENTS FROM PEER REVIEWERS ON THE WESTERN JOSHUA TREE STATUS REVIEW REPORT