



## Perspective

## Dust storms ahead: Climate change, green energy development and endangered species in the Mojave Desert

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## ARTICLE INFO

## Keywords:

Climate change  
Mojave Desert  
Endangered species  
Yucca  
Solar

## ABSTRACT

The Mojave Desert contains the hottest, driest regions in North America and is also one of the most ecologically intact regions in the contiguous United States. However, a confluence of factors including urbanization, climate change, and energy development are rapidly transforming this ecoregion. As a result of these growing threats, even common, widespread Mojave Desert endemics are at risk of being driven to extinction by the end of the 21st century. Ironically, renewable energy development that could delay or even reverse the effects of climate change in the region is also a potentially significant source of habitat loss for these same organisms. Protecting the Mojave therefore presents difficult choices about how to select among different conservation priorities. We argue that these choices will necessarily involve compromises in which protections for some habitats will have to be prioritized while allowing development in other areas. We review the state of conservation in the Mojave and use the Mojave Desert's iconic Joshua trees (*Yucca brevifolia* and *Y. jaegeriana*) as a case study to describe a framework for identifying habitats that should be given the highest levels of protection to ensure climate change resilience. Finally, using existing spatial data, we evaluate land use and conservation status in the Mojave. The result identifies considerable scope for compromise between conservation and renewable energy development. Although our examples are specific to the Mojave, we argue that these recommendations apply broadly to many biological communities threatened by climate change.

The Mojave Desert is one of the most varied and extreme ecosystems in the world, containing the lowest elevations and the hottest, driest habitats in North America. It also contains large stretches of minimally disturbed habitat for a suite of unique biological communities. Despite being the smallest of the North American deserts, the Mojave hosts >3300 native plant and animal species, including ~700 endemics (Walker and Landau, 2018). The extreme aridity of the region makes it unsuitable for intensive agriculture (Norris, 1982) and its temperature extremes have discouraged extensive human habitation, so the Mojave remains one of the most ecologically intact regions in the contiguous United States (Leu et al., 2008; Parker et al., 2018; Randall et al., 2010). However, expanding urban areas, climate change, and energy

development now threaten to profoundly transform the region. Increasing high temperatures now exceed the physiological limits of many organisms, and even widespread species are threatened with extinction. In addition, the Mojave is second only to the Sahara Desert in levels of incident solar radiation, making it a prime region for renewable energy production. Solar and wind energy development present both a potential solution to the global climate emergency and a significant economic opportunity, but the conversion of wild lands to energy production threatens biodiversity in the Mojave (Parker et al., 2018) and worldwide (Agha et al., 2020; Gibson et al., 2017; Rehbein et al., 2020). In response to these threats, many Mojave Desert species have been listed as endangered at the state and federal levels and more are

**Abbreviations:** USSE, Utility Scale Solar Energy Development; DRECP, Desert Renewable Energy Conservation Plan; TNC, The Nature Conservancy; GAP, US Geological Survey Gap Analysis Project; SDM, Species Distribution Model; SNP, Single Nucleotide Polymorphism.

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<https://doi.org/10.1016/j.biocon.2022.109819>

Received 5 March 2022; Received in revised form 26 September 2022; Accepted 11 November 2022

Available online 1 December 2022

0006-3207/© 2022 Published by Elsevier Ltd.

candidates for future listing (Table 1; Fig. 1). These legal protections have created a growing conflict between conservation concerns and green energy development (Agha et al., 2020; Gibbens, 2022; Roth, 2019, 2022; Sahagún, 2020a, 2020b). Ironically, mitigating the global climate catastrophe could come at the expense of one of the few remaining wild regions in the United States.

Conserving biological diversity amidst these many challenges will require balancing potentially conflicting conservation goals while navigating a stormy political setting. Here we review the status of conservation biology in the Mojave with a focus on conservation plans for Joshua trees (*Yucca brevifolia* and *Y. jaegeriana*) – Mojave Desert endemics that are being considered for protection under both state and federal law. Drawing on biogeography, ecophysiology, landscape genomics, and population ecology we describe a framework for making conservation management decisions to protect widespread species threatened by climate change, both in the Mojave Desert and beyond.

## 1. The changing Mojave

Humans have inhabited the Mojave for millennia, but their impact on the desert was slight until the twentieth century. The many oral traditions of the Cahuilla, Chemehuevi, Kwalisu, Mojave, Serrano, and Southern Paiute record that their ancestors have lived in the region since time immemorial (e.g. Laird, 1974). Similarly, the archaeological record indicates human presence in the Mojave for at least the last 10,000 years (Sutton et al., 2007). Nevertheless, the Mojave remained sparsely inhabited until recently. European explorers did not reach the Mojave until the late 18th Century, and the first large waves of immigrants from the United States did not arrive until after the Fremont expedition in 1844. Homesteading began in the 1870s and continued through the early 1930s, but most settlements were abandoned due to intermittent – sometimes extended – periods of drought (Norris, 1982; Nystrom, 2003). However, the last century has seen dramatic changes in the Mojave. Paved roads were built across the desert in the 1930s, followed by interstate highways in the 1960s and 1970s (Nystrom, 2003). The last 40 years have brought explosive urbanization of the region (Hunter et al., 2003), with 500 % population growth in the cities of Lancaster, Palmdale, and Victorville since 1980. The Las Vegas metropolitan area has ballooned to 2.3 million residents. Together the incorporated regions of these cities now encompass >1000 km<sup>2</sup> (Fig. 2).

The 20th Century also brought conservation efforts to the Mojave Desert. Joshua Tree National Monument (later a National Park) was established early – 1936 – thanks to the tireless leadership of Minerva Hoyt (Sorensen, 1976). A 25-million-acre (10,000 km<sup>2</sup>) Desert Conservation Area was established in 1980 in an expansive “Desert Plan” (Nystrom, 2003). The 1994 Desert Protection Act created the Mojave National Preserve, and designated Death Valley as a National Park. While each of these efforts set aside large areas of the Mojave as wilderness or Areas of Critical Environmental Concern, many endemic species are nevertheless now imperiled. Fifty-eight Mojave Desert species have now been recognized as rare, threatened, or endangered under the United States and California Endangered Species Acts (Table 1) (<https://www.fws.gov/endangered/>, <https://wildlife.ca.gov/Conservation/CESA>). Many of the organisms that were listed during the first decades of the US Endangered Species Act were narrowly distributed endemics, such as Devil's Hole pupfish, which occurs only in a single desert spring. However, because of the rapid development of the desert since 1980 some species that were once widespread and common are now threatened with extinction. These include the Mojave Ground squirrel (*Xerospermophilus mojaviensis*), and the Mojave Desert tortoise (*Gopherus agassizii*; Fig. 1). The desert tortoise management and recovery plan (US Bureau of Land Management, 1988) was once considered an ideal model for conservation biology (Gibbons, 1992), but three decades later, Mojave Desert tortoise populations continue to decline (Allison and McLuckie, 2018).

Other species that are widespread throughout the region are also

now imperiled by global climate change, which is profoundly transforming the Mojave. While all wild places are being impacted by rising global temperatures (Masson-Delmotte et al., 2021), the Mojave Desert is predicted to be one in which the changes will be the most extreme (Diffenbaugh et al., 2008). Monthly surface air temperatures have increased by ~0.39 degrees centigrade per decade from 1979 to 2012 (Zhou et al., 2015), and there has been a roughly 2 degree increase in mean temperatures over the last century (Bai et al., 2011; Iknayan and Beissinger, 2020; Wuebbles et al., 2017). These changes translate into more days of excessive heat. For example, in Barstow, California the number of days with high temperatures above 100 °F (38 °C) increased from 65.3 days per year in the 1950's to 82.3 days per year in the 2010's; the number of days with high temperatures above 110 °F (43 °C) increased from an average of 1.8 days per year to 8.8 days per over the same period (Fig. 3). In addition, increases in the magnitude and frequency of the El Niño Southern Oscillation (ENSO) have led to greater winter rainfall during El Niño periods and more severe drought during the intervening years (Cai et al., 2015; McGregor et al., 2013). Annual precipitation has decreased overall, however (Bai et al., 2011; Seager et al., 2007; Wuebbles et al., 2017); the period from 2000 to 2021 was the driest 19-year period in western North America in >1200 years (Williams et al., 2020, 2022). These changes have been implicated in the collapse of the regional bird communities (Iknayan and Beissinger, 2020) and are among the leading causes of population declines in Mojave Desert tortoises (Allison and McLuckie, 2018).

In addition to the direct impacts of climate change, demand for renewable energy to address the climate crisis has dramatically accelerated the rate at which desert habitats are being converted for human use. Solar energy will likely play a major role in the transition to a renewable energy economy, with some estimates suggesting that solar could provide up to 50 % of global energy while limiting total warming to 2° C (Creutzig et al., 2017). However, this transition will likely bring further development of desert lands on a massive scale. As of July 2022, the US Energy Information Administration identified 234 utility scale solar energy (USSE) installations in the Mojave (Table 2; Supplemental Materials Table S1), including four of the five largest solar energy developments in the world (Gibson et al., 2017) (See Box 1 for a glossary and list of acronyms). Based on their generating capacity, we conservatively estimate that together these facilities cover ~27,000 acres (109 km<sup>2</sup>). The number of renewable energy developments is set to rapidly increase in the very near future. We have identified an additional 67 USSE facilities that are in some stage of development (approved, under construction, or completed but not operational), which together will occupy an additional ~55,000 acres (222 km<sup>2</sup>; Supplemental Materials Table S2).

Recent legislation mandating renewable energy production is set to further increase the rate of development. California Senate Bill 100 (SB 100) requires the state to produce 100 % of retail electricity using renewable energy by 2045, and at the federal level the 2022 Inflation Reduction Act budgets \$60 billion for renewable energy (Paris et al., 2022). The SB 100 California 2045 plan calls for increasing solar power production in California to 70 gigawatts (GW) (Gill et al., 2021) – a more than five-fold increase from the existing 12 GW of solar power production within California. Jacobson et al. (2019) estimate that achieving a carbon-free energy economy in the U.S. as a whole by 2050 will require a total installed capacity of 1580 GW of USSE. Since 2016, energy development on public lands in California has been guided by the Desert Renewable Energy Conservation Plan (DRECP) – an historic agreement between state, federal, and municipal agencies developed in consultation with energy interests and conservation NGOs. The plan set aside 17,000 km<sup>2</sup> for conservation, while designating 1570 km<sup>2</sup> as development zones – an area larger than Las Vegas, Lancaster, Palmdale, and Victorville combined. Although California's goal to produce all retail electricity using renewable sources is potentially achievable within the area designated for energy development under the DRECP, achieving a carbon-free national energy economy would require 4.7

**Table 1**

Rare, threatened, and endangered Mojave Desert species listed under California and US Endangered Species Acts. Species distributions are classified qualitatively: 'Single locality' < ~ 1 km<sup>2</sup>; 'Narrow endemic' = contiguous distribution confined to a single valley or mountain range, typically <20 km<sup>2</sup>; Patchy = multiple sites throughout the Mojave; Widespread = multiple areas of large, contiguous habitat.

| Species  | Common Name                        | Applicable Law | Year Listed | Distribution      | Status                             | Group            |
|--|------------------------------------|----------------|-------------|-------------------|------------------------------------|------------------|
| <i>Cyprinodon diabolis</i>                               | Devil's Hole pupfish               | US Federal ESA | 1967        | Single locality   | Endangered                         | Fishes           |
| <i>Empetrichthys latos</i>                               | Pahrump poolfish                   | US Federal ESA | 1967        | Single locality   | Extinct in the wild                | Fishes           |
| <i>Moapa coriacea</i>                                    | Moapa dace                         | US Federal ESA | 1967        | Single locality   | Endangered                         | Fishes           |
| <i>Gila robusta jordani</i>                              | Pahrnagat roundtail chub           | US Federal ESA | 1970        | Single locality   | Endangered                         | Fishes           |
| <i>Crenichthys baileyi baileyi</i>                       | White River springfish             | US Federal ESA | 1985        | Single locality   | Endangered                         | Fishes           |
| <i>Crenichthys baileyi grandis</i>                       | Hiko White River springfish        | US Federal ESA | 1985        | Single locality   | Endangered                         | Fishes           |
| <i>Ambrysus amargosus</i>                                | Ash Meadows naucorid               | US Federal ESA | 1985        | Single locality   | Threatened                         | Insects          |
| <i>Cyprinodon radiosus</i>                               | Owen's pupfish                     | US Federal ESA | 1967        | Narrow endemic    | Endangered                         | Fishes           |
| <i>Cyprinodon nevadensis pectoralis</i>                  | Warm Springs pupfish               | US Federal ESA | 1970        | Narrow endemic    | Endangered                         | Fishes           |
| <i>Gila bicolor ssp. mohavensis</i>                      | Mohave tui chub                    | US Federal ESA | 1970        | Narrow endemic    | Endangered                         | Fishes           |
| <i>Dedeckera eurekaensis</i>                             | July gold                          | CA State ESA   | 1978        | Narrow Endemic    | Rare                               | Flowering Plants |
| <i>Astragalus lentiginosus</i> var. <i>sesquimetalis</i> | Sodaville milk-vetch               | CA State ESA   | 1979        | Narrow Endemic    | Endangered                         | Flowering Plants |
| <i>Pipilo crissalis eremophilus</i>                      | Inyo California towhee             | US Federal ESA | 1982        | Narrow endemic    | Threatened                         | Birds            |
| <i>Cyprinodon nevadensis mionectes</i>                   | Ash Meadows Amargosa pupfish       | US Federal ESA | 1982        | Narrow endemic    | Endangered                         | Fishes           |
| <i>Rhinichthys osculus nevadensis</i>                    | Ash Meadows speckled dace          | US Federal ESA | 1982        | Narrow endemic    | Endangered                         | Fishes           |
| <i>Microtus mexicanus hualpaiensis</i>                   | Hualapai Mexican Vole              | US Federal ESA | 1982        | Narrow endemic    | Delisted due to taxonomic revision | Mammals          |
| <i>Deinandra arida</i>                                   | Red Rock tarplant                  | CA State ESA   | 1982        | Narrow Endemic    | Rare                               | Flowering Plants |
| <i>Holmgrenanthe petrophila</i>                          | Rocklady                           | CA State ESA   | 1982        | Narrow endemic    | Rare                               | Flowering Plants |
| <i>Microtus californicus scirpensis</i>                  | Amargosa vole                      | US Federal ESA | 1984        | Narrow endemic    | Endangered                         | Mammals          |
| <i>Gila bicolor ssp. snyderi</i>                         | Owens Tui Chub                     | US Federal ESA | 1985        | Narrow endemic    | Endangered                         | Fishes           |
| <i>Astragalus phoenix</i>                                | Ash Meadows milk-vetch             | US Federal ESA | 1985        | Narrow endemic    | Threatened                         | Flowering Plants |
| <i>Enceliopsis nudicaulis</i> var. <i>corrugata</i>      | Ash Meadows sunray                 | US Federal ESA | 1985        | Narrow endemic    | Threatened                         | Flowering Plants |
| <i>Grindelia fraxinipratensis</i>                        | Ash Meadows gumplant               | US Federal ESA | 1985        | Narrow endemic    | Threatened                         | Flowering Plants |
| <i>Ivesia kingii</i> var. <i>eremica</i>                 | Ash Meadows ivesia                 | US Federal ESA | 1985        | Narrow endemic    | Threatened                         | Flowering Plants |
| <i>Mentzelia leucophylla</i>                             | Ash Meadows blazingstar            | US Federal ESA | 1985        | Narrow endemic    | Threatened                         | Flowering Plants |
| <i>Nitrophila mohavensis</i>                             | Amargosa niterwort                 | US Federal ESA | 1985        | Narrow endemic    | Endangered                         | Flowering Plants |
| <i>Crenichthys nevadae</i>                               | Railroad Valley springfish         | US Federal ESA | 1986        | Narrow endemic    | Threatened                         | Fishes           |
| <i>Astragalus albens</i>                                 | Cushenbury milk-vetch              | US Federal ESA | 1993        | Narrow endemic    | Endangered                         | Flowering Plants |
| <i>Empidonax traillii extimus</i>                        | Southwestern willow flycatcher     | US Federal ESA | 1994        | Narrow endemic    | Endangered                         | Birds            |
| <i>Erigeron parishii</i>                                 | Parish's daisy                     | US Federal ESA | 1994        | Narrow endemic    | Threatened                         | Flowering Plants |
| <i>Astragalus lentiginosus</i> var. <i>coachellae</i>    | Coachella Valley milk-vetch        | US Federal ESA | 1998        | Narrow endemic    | Endangered                         | Flowering Plants |
| <i>Astragalus lentiginosus</i> var. <i>piscinensis</i>   | Fish Slough milk-vetch             | US Federal ESA | 1998        | Narrow endemic    | Endangered                         | Flowering Plants |
| <i>Astragalus tricarlinatus</i>                          | Triple-ribbed milk-vetch           | US Federal ESA | 1998        | Narrow endemic    | Threatened                         | Flowering Plants |
| <i>Icaricia (Plebejus) shasta charlestonensis</i>        | Mount Charleston blue butterfly    | US Federal ESA | 1998        | Narrow endemic    | Endangered                         | Flowering Plants |
| <i>Oxytheca parishii</i> var. <i>goodmaniana</i>         | Cushenbury oxytheca                | US Federal ESA | 2013        | Narrow endemic    | Endangered                         | Insects          |
| <i>Eriogonum thornei</i>                                 | Thorne's buckwheat                 | CA State ESA   | 1979        | Patchy            | Endangered                         | Flowering Plants |
| <i>Deinandra mohavensis</i>                              | Mojave tarplant                    | CA State ESA   | 1982        | Patchy            | Endangered                         | Flowering Plants |
| <i>Anaxyrus californicus</i>                             | Arroyo (=arroyo southwestern) toad | US Federal ESA | 1994        | Patchy            | Endangered                         | Amphibians       |
| <i>Xyrauchen texanus</i>                                 | Razorback sucker                   | US Federal ESA | 1991        | Patchy (Riparian) | Endangered                         | Fishes           |

(continued on next page)

Table 1 (continued)

| Species                                 | Common Name                   | Applicable Law           | Year Listed | Distribution      | Status     | Group            |
|---|-------------------------------|--------------------------|-------------|-------------------|------------|------------------|
| <i>Rallus obsoletus</i> [=longirostris] | Yuma Ridgways (clapper) rail  | US Federal ESA           | 1967        | Patchy (Riparian) | Endangered | Birds            |
| <i>Gila cypha</i>                       | Humpback chub                 | US Federal ESA           | 1967        | Patchy (Riparian) | Threatened | Fishes           |
| <i>Plagopterus argentissimus</i>        | Woundfin                      | US Federal ESA           | 1970        | Patchy (Riparian) | Endangered | Fishes           |
| <i>Micrathene whitneyi</i>              | Elf Owl                       | CA State ESA             | 1980        | Patchy (Riparian) | Endangered | Birds            |
| <i>Gila elegans</i>                     | Bonytail                      | US Federal ESA           | 1980        | Patchy (Riparian) | Endangered | Fishes           |
| <i>Centaureum namophilum</i>            | Spring-loving centaury        | US Federal ESA           | 1985        | Patchy (Riparian) | Threatened | Flowering Plants |
| <i>Vireo bellii pusillus</i>            | Least Bell's vireo            | US Federal ESA           | 1986        | Patchy (Riparian) | Endangered | Birds            |
| <i>Cyprinodon macularius</i>            | Desert pupfish                | US Federal ESA           | 1986        | Patchy (Riparian) | Endangered | Fishes           |
| <i>Colaptes chrysoides</i>              | Gilded flicker                | CA State ESA             | 1988        | Patchy (Riparian) | Endangered | Birds            |
| <i>Vireo bellii arizonae</i>            | Arizona Bell's vireo          | CA State ESA             | 1988        | Patchy (Riparian) | Endangered | Birds            |
| <i>Gila seminuda</i> (=robusta)         | Virgin River Chub             | US Federal ESA           | 1989        | Patchy (Riparian) | Endangered | Fishes           |
| <i>Agelaius tricolor</i>                | Tricolored blackbird          | CA State ESA             | 1991        | Patchy (Riparian) | Threatened | Birds            |
| <i>Astragalus jaegerianus</i>           | Lane Mountain milk-vetch      | US Federal ESA           | 1995        | Patchy (Riparian) | Endangered | Flowering Plants |
| <i>Xerospermophilus mojaviensis</i>     | Mojave Desert Ground Squirrel | CA State ESA             | 1971        | Widespread        | Threatened | Mammals          |
| <i>Gopherus agassizii</i>               | Desert tortoise               | US Federal ESA           | 1980        | Widespread        | Threatened | Reptiles         |
| <i>Buteo swainsoni</i>                  | Swainson's hawk               | CA State ESA             | 1983        | Widespread        | Threatened | Birds            |
| <i>Melanerpes uropygialis</i>           | Gila Woodpecker               | CA State ESA             | 1988        | Widespread        | Endangered | Birds            |
| <i>Strix occidentalis lucida</i>        | Mexican spotted owl           | US Federal ESA           | 1993        | Widespread        | Threatened | Birds            |
| <i>Puma concolor</i>                    | Mountain Lion                 | CA State ESA             | 2020        | Widespread        | Concern    | Mammals          |
| <i>Yucca brevifolia</i>                 | Western Joshua Tree           | CA State and Federal ESA | 2021        | Widespread        | Candidate  | Flowering Plants |
| <i>Yucca jaegeriana</i>                 | Eastern Joshua Tree           | Federal ESA              | 2021        | Widespread        | Candidate  | Flowering Plants |

million acres (19,300 km<sup>2</sup>) of USSE production – an area equivalent to 15 % of the entire Mojave Desert Ecoregion (Jacobson pers. comm).

The existing energy developments have already come in conflict with the need to protect biological diversity (Gibson et al., 2017; Lovich and Ennen, 2011; Parker et al., 2018). For example, Inman et al. (2016) estimated that proposed energy developments could lead to the elimination of 10 % of the critical habitat of the Mojave ground squirrel. Similarly, USSE developments frequently result in the destruction of Mojave Desert tortoise habitats. Cameron et al. (2012) estimated that desert tortoises could lose >256,000 acres (1036 km<sup>2</sup>) to solar developments proposed on public land as of 2012, and animals are often relocated to new habitats to make way for developments (Brand et al., 2016; Nussear et al., 2012).

The impacts of new energy development on biodiversity could in principle be reduced by concentrating production in areas that have already been developed for human uses. For example, distributed solar energy production (e.g. “rooftop solar”, and developments in parking lots and landfills), which does not involve disturbing wildlands at great scale, and would maintain the carbon sequestration potential of living soils (Hernandez et al., 2015). However, implementing distributed solar production at the scale necessary to meet current energy needs requires consideration of socioeconomic and environmental justice issues (Lukanov and Krieger, 2019), as well the economic and infrastructure challenges of decentralized power production. It is also unclear whether distributed solar and developments within the built landscape will be sufficient to satisfy the demand for solar development. On the one hand, Hernandez et al. (2015) identified >28,000 km<sup>2</sup> within California's built environment that is compatible with solar energy production, potentially meeting the state's 2015 retail electricity demand at least five times over. On the other hand, Jacobson et al. (2022) estimated that

meeting the projected total energy needs in 2050 for the state of California alone will require 3300 km<sup>2</sup> of new utility-scale renewable energy developments (wind and solar) over and above a ten-fold increase in rooftop solar.

Careful land management planning is therefore needed to resolve potential conflicts between the goals of addressing the climate emergency and protecting both species diversity and functioning ecosystems. The problem is particularly challenging when it comes to species that are currently widespread but that are threatened with extinction in the near future due to climate change. Their broad distributions mean that development will very frequently impact current habitat, and their ubiquity makes it difficult to perceive the extent of the threat. The result is a growing storm playing out in regional politics and the popular press (Gibbens, 2022; Roth, 2022, 2019; Sahagún, 2020a) that promises to renew old battles between economic development and conservation as proponents of green energy find themselves at odds with advocates for open space and biological diversity. This problem is of course not unique to the Mojave (Rehbein et al., 2020), but the lessons learned here may apply to other ecosystems that are imperiled by the twin threats of climate change and development.

## 2. Joshua trees – a case study for conservation in the face of climate change

A harbinger of this approaching storm has been growing concerns about the impacts of climate change on Joshua trees. Joshua trees are nearly synonymous with the Mojave Desert, and the edges of Joshua trees' distribution almost perfectly delimits the extent of the Mojave Desert ecoregion. Spindly, tree-like monocots, their unusual appearance has made them a beloved species of the American West. They are





**Fig. 1.** Imperiled species endemic to the Mojave. Clockwise from top right: the Mojave Desert tortoise (*Gopherus agassizii*, Photo: Todd Esque); the Mojave Desert ground squirrel (Photo: Phil Hedrick); the Tui chub (*Siphatales mohavensis*, photo: Dave Giordanoa © 2022 The Regents of the University of California. All Rights Reserved. Used with permission); the Western Joshua Tree (*Yucca brevifolia*; photo: Christopher Irwin Smith).

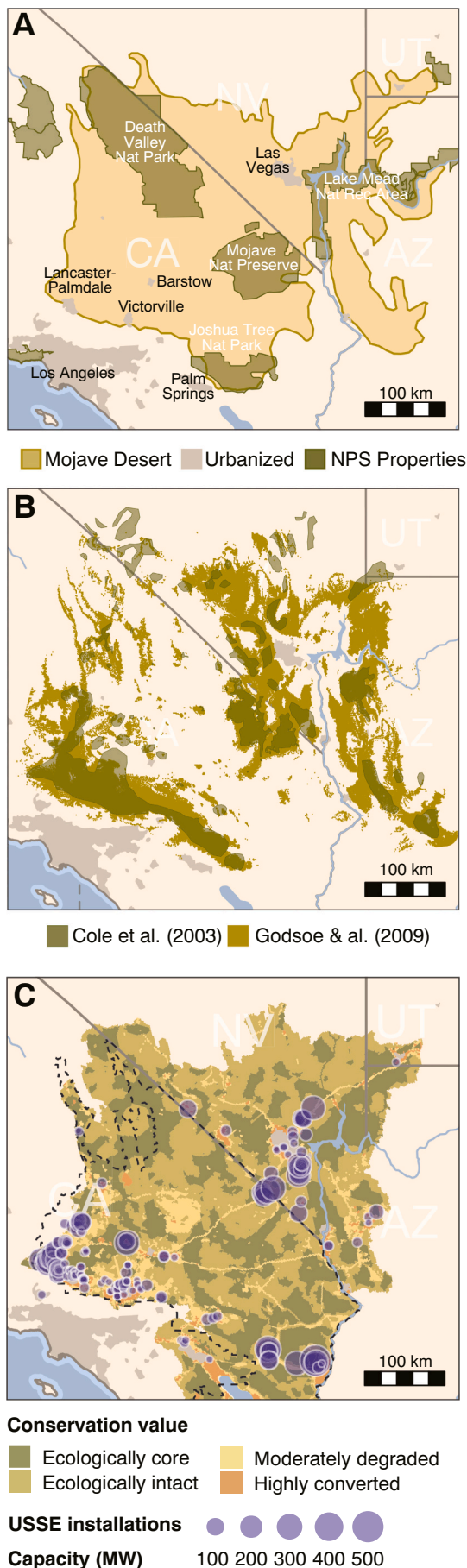
thought to have been named by Mormon settlers for whom the trees' outstretched branches recalled the prophet Joshua pointing the way across the Mojave (McKelvey, 1938). Their association with dramatic desert landscapes motivated the creation of Joshua Tree National Park (JTNP), one of four National Parks and Preserves that now protect Joshua tree woodlands. These parks together received >12 million visitors in 2021, with visitation to JTNP having more than doubled over the past ten years. Lastly, their exclusive reliance on two species of moth for pollination have made Joshua trees a model system for studying coevolution (Godsoe et al., 2008; Smith et al., 2021; Yoder et al., 2013).

This keystone of the Mojave is threatened with extinction due to a host of factors driven by climate change. Multiple species distribution models predict that anthropogenic climate change will make much or all of the Joshua trees' current distribution unsuitable by 2100 (Barrows and Murphy-Mariscal, 2012; Cole et al., 2011; Dole et al., 2003; Shafer et al., 2001; Sweet et al., 2019). Demographic studies show that the predicted impacts are already visible on the landscape; the trees are producing fewer seedlings in many parts of their range, especially hot dry regions in the southern Mojave (Sweet et al., 2019). Joshua tree seedlings are less robust to heat and drought than adults, often requiring shelter from "nurse plants" to reach larger size classes, and juvenile trees (<25 cm) suffer high mortality in droughts due to herbivory by rodents and other small mammals (Esque et al., 2015).

These impacts have been exacerbated by wildfire. Changing rainfall patterns and increasing average temperature have resulted in larger and more frequent wildfires across western North America (Westerling et al., 2006; Williams et al., 2019). Together with increased deposition of anthropogenic nitrogen (Esque et al., 2010; Fenn et al., 2003), the changes in the seasonality and intensity of rainfall promote the

proliferation of annual plants in wet years, building up biomass that fuels catastrophic wildfires during subsequent droughts (Brooks and Matchett, 2006; DeFalco et al., 2010). Joshua trees may be particularly impacted as they are poorly adapted to wildfire, which has been historically absent from the region. Typically <20 % of Joshua trees burned in wildfires survive beyond five years (DeFalco et al., 2010). The 1999 Juniper Fire in Joshua Tree National Park affected >14,000 acres (56 km<sup>2</sup>). In September 2020, the Cima Dome fire destroyed 43,000 acres (174 km<sup>2</sup>), killing an estimated one million Joshua trees, and impacting approximately 18 % of eastern Joshua tree woodlands within the Preserve (Fig. 4. L. Sweet, unpublished data).

The growing threats to Joshua trees, have motivated several efforts to grant them formal legal protections. In 2016 the US Fish and Wildlife Service (USFWS) issued a 90-day finding that there was sufficient evidence that Joshua trees might be endangered to warrant review under the Endangered Species Act (ESA), but in 2019 it declined to enact protections for either species (Paluch and Wilson, 2019). That determination was subsequently challenged, and in September of 2021 the US District Court for the Central District of California ordered USFWS to re-evaluate their decision (Wilson, 2021). In a parallel legal process at the state level, in September of 2020, the California Fish and Game Commission (CFGC) voted to enact temporary protections for the western species of Joshua tree (*Y. brevifolia*) during a one-year status review, while also granting an emergency exemption for 15 solar energy projects already in development (Sahagún, 2020b). A coalition of industry groups including the California Business Properties Association sued to overturn the CFGC decision (Sahagún, 2020a), but this motion was rejected by the California Courts in 2021 (Moore, 2021). Most recently, an advisory technical report recommended against listing the



**Fig. 2.** Geography of the Mojave Desert. A) Regional map showing the extent of the Mojave, urban areas mentioned in the text, and the location of US National Parks. B) Map showing uncertainties in the distribution of Joshua trees (*Y. brevifolia* and *Y. jaegeriana* combined). The Cole et al. (2003) distribution map (dark green) and Godsoe & al (2009) species distribution model (light green) disagree more than they agree. C) Location of USSE facilities in the Mojave Desert and levels of land disturbance based on The Nature Conservancy's ecoregional assessment (Randall et al., 2010). Dotted line shows the extent of the Desert Regional Energy and Conservation Plan. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

trees, but the CGFC has so far not made a determination on whether to extend protections (Sahagún, 2022).

The conservation of Joshua trees therefore presents an important challenge to scientists, conservationists, and policymakers: a widespread tree threatened by climate change over its range, which is also imperiled by the destruction of habitat for renewable energy development that can reduce fossil fuel consumption that drives climate change. How this catch-22 is resolved may set the example going forward for managing species threatened by climate change.

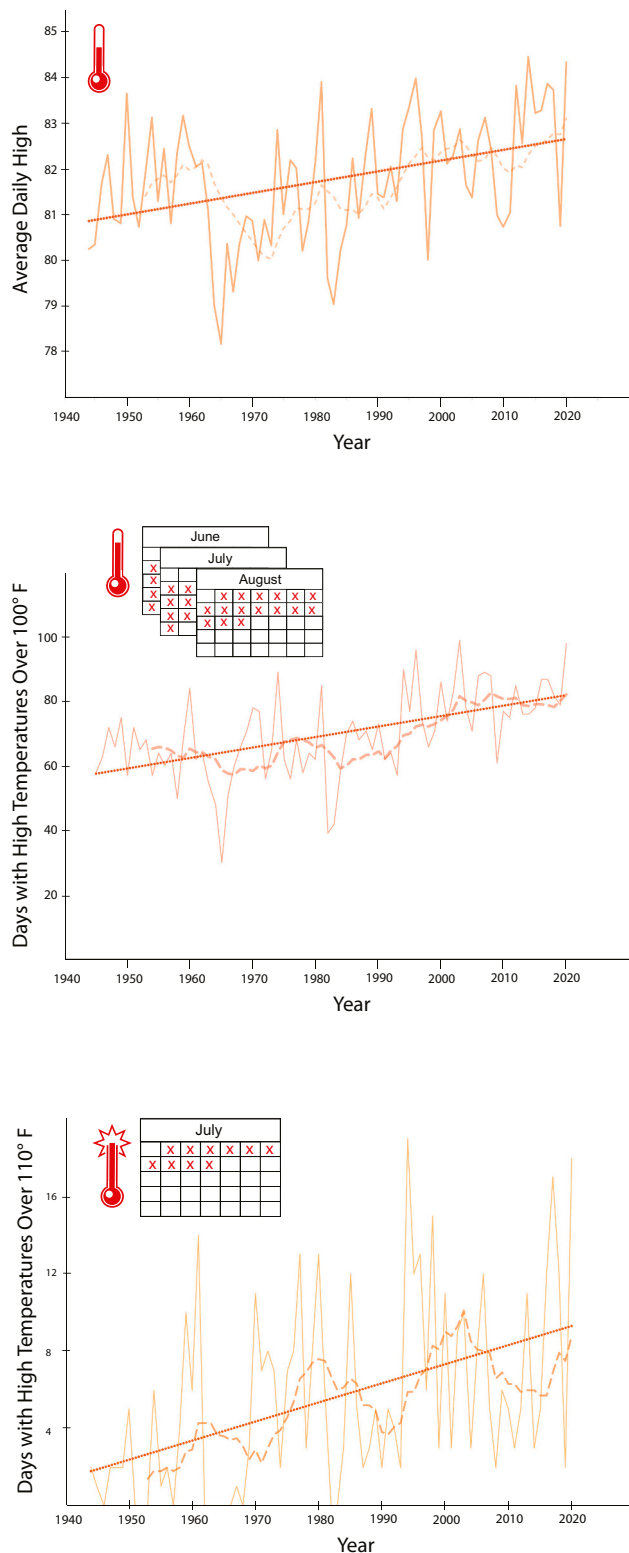
### 3. Assessing the threat of climate change to species persistence

Determining the degree to which climate change poses a threat for any particular species requires the use of explicit species distribution and demographic models (Jones et al., 2016). Distribution models suggest significant range losses for a number of species within the Mojave. For example, Barrows (2011) found that desert tortoises may lose 66 % to 88 % of their suitable habitat in the Joshua Tree National Park region under a moderate climate change scenario. More pessimistically, the Mojave Desert Ground Squirrel (*Xerospermophilus mojavensis*) is predicted to lose 100 % of 'core' habitat (Dilts et al., 2016) and 64 % of its total current habitat by 2080 (Inman et al., 2016). While several studies have evaluated Joshua trees' likely distribution changes under a variety of climate change scenarios, these models make very different predictions about the extent of suitable habitat by the end of this century. Comparing three different models of future climate change, Shafer et al. (2001) found that there was no portion of the current distribution where trees could persist, whereas Dole et al. (2003), using a model that assumed a doubling in atmospheric CO<sub>2</sub> (with no changes in freeze tolerance, see below), predicted a more optimistic future, finding that that the trees could persist in 24 % of their current range. More recent work has also drawn different conclusions about the prospects for Joshua trees. Cole et al. (2011) considered 6 different climate models and predicted up to 90 % decline in distribution (10 % persistence), whereas Barrows and Murphy-Mariscal (2012), considering only the southernmost portion of the range of the western Joshua tree (*Y. brevifolia*), found up to a 98 % reduction in suitable habitat with a 3 °C increase in daily high temperatures in July; this was followed by Sweet et al. (2019) who found declines ranging from 75 to 100 % within the same extent, depending on the Representative Concentration Pathway (RCP) model used. Last, in an analysis that did not use species distribution modeling, a team of researchers from USFWS found that total range size changes might be as small as a 20 % reduction in the southern portion of the range only (Wilkening et al., 2022).

The wide range of results produced by these different analyses in part reflect differences in methodology but are also attributable to differences in the input data. In order for species distribution models to be reliable, they must be based on accurate occurrence data, and need to be validated by independent sources of data (Sweet et al., 2019). In the case of Joshua trees, existing range maps and distribution models (including those presented here) have relied on incomplete presence records and pseudoabsences, or worse, highly inaccurate data compiled from historical records of dubious quality (cf. Cole et al., 2011; Smith et al., 2008). The effect of the differences in the input data is most noticeable

(caption on next column)





**Fig. 3.** Changes in the climate of the Mojave over the past 80 years, based on daily weather data for Barstow, California available from the US National Weather Service (<https://www.weather.gov/wrh/Climate>; Barstow Dagget Airport, CA US; Dec. 1, 1943 - Jul. 21, 2021). A) Average daily high temperatures over the course of a given year; solid line shows yearly average, dashed shows the average over the previous ten years, dotted line shows a least squares regression. B) Number of days with high temperatures over 100 degrees. C) Number of days with high temperatures over 110 degrees. In B and C, solid lines show the number of days in each year, dashed lines show the average over 10-years, dotted lines show least-squares regressions.

when comparing the most widely used maps and distribution models; a species distribution model derived from Godsoe et al.' (2009) study identifies 83,175 km<sup>2</sup> in which Joshua trees are predicted to occur, whereas Cole et al. (2003), using a compilation of historical records, identify only 39,502 km<sup>2</sup> in which Joshua trees were present (Table 3; Fig. 2). The two range maps disagree more than they agree; both indicate Joshua tree presence, in just 28,040 km<sup>2</sup>. Thus, uncertainty about the existing range may severely limit our capacity to make predictions about future distributions.

Fortunately, for Joshua trees, there is high potential to improve the resolution and accuracy of current distribution data. Joshua trees are easily identifiable by amateur naturalists, making crowdsourced data an unusually reliable source for distribution records. Their highly distinctive growth form also makes it possible to recognize Joshua trees and distinguish them from other Mojave Desert plants in satellite imagery. Indeed, a recent study using remote sensing data to identify Joshua trees on the China Lake Naval Air Weapons Station found that existing distribution maps vastly underestimate the true extent of Joshua tree habitat; the remote sensing data, later confirmed by ground truthing, increased the total extent of Joshua tree habitat in the study area by 90 % (Esque et al., 2019). Emerging studies of Joshua tree using remote sensing data promise to produce comprehensive empirical distribution data that is almost perfectly accurate and complete (T. C. Esque, personal communication). A dataset of this quality would be invaluable for identifying 'climate refugia' where local climates will remain favorable into the future. Although it may be difficult to produce comparable distribution data for other species, improvements in monitoring and detection, both by professionals and amateur naturalists, continue to improve datasets describing species' presence.

Species distribution models can also be improved by incorporating physiological data (Buckley et al., 2010; Evans et al., 2015). For example, Loik et al. (2000) used growth chamber experiments to examine the thermal tolerances of three different species of *Yucca* from the Mojave, and found that increasing CO<sub>2</sub> resulted in greater cold tolerance. A follow up study using a species distribution model that incorporated changes in the trees' freezing tolerance predicted that the trees could persist in 29 % of their current range with a doubling in the atmospheric concentrations of CO<sub>2</sub> (Dole et al., 2003). Primary ecophysiological research is therefore critical to understand, model, and mitigate the interactions between climate and threatened species. Current research using Joshua tree seedlings planted in the US Geological Survey's Mojave Desert Common Gardens (MDCG) network and in growth chamber experiments will determine the extent to which different populations are adapted to local climate conditions and reveal the physiological mechanisms by which Joshua trees tolerate heat and drought stress.

Climate change represents a threat for many organisms, including nearly all species listed as "endangered" under the ESA (Delach et al., 2019). Within the Mojave, 11 of 24 plant species listed as threatened or endangered are vulnerable to climate change (Wilkening et al., 2021). However, climate change is often not considered in status assessments and is rarely included in management plans (Delach et al., 2019). For example, the 2019 USFWS decision not to list Joshua trees as endangered species explicitly avoided developing new species distribution models (US Fish and Wildlife Service, 2018). This omission was among the bases for court decision requiring USFWS to revisit its determination (WildEarth Guardians v. Haaland, 2021). It is imperative that management and conservation plans consider not just the current population and available habitat but also their likely futures under realistic climate change scenarios in an explicit, model-based framework. These evaluations must consider a range of climate change scenarios and evaluate sensitivity to model inputs and methodologies. Models should be based on the most accurate distribution data possible and should incorporate available physiological data.

## Box 1

### Glossary

- **Adaptive Genetic Variation:** Genetic differences between individuals that cause differences in fitness and that could increase in frequency through natural selection. Genetic variation that may allow adaptation to environmental change.
- **Amplified Fragment Length Polymorphism (AFLP):** A genotyping technique that relies on restriction enzymes to fragment DNA based on the presence or absence of particular DNA sequences and a selective PCR process to interrogate genetic variation at a random subset of the genome.
- **Annotated Reference Genome:** An individual designated as the standard genome sequence for a particular species to which other individuals can be compared, and in which the location and identity of genes, transposons, regulatory elements, and other features has been identified.
- **Assisted Colonization:** Human-aided movement of individual organisms to areas where a species did not previously occur.
- **Assisted gene flow:** The intentional movement of individuals between populations, within a species' native range in order to increase genetic variation, especially to introduce adaptive genetic variation.
- **Association genetics:** A data analysis approach, such as a genome-wide association study, that identifies loci potentially underlying important phenotypes by comparing phenotypic or environmental variables with genotypes or allele frequencies.
- **Chromatin Structure:** Arrangement of DNA and accessory proteins that influences gene expression and accessibility.
- **Chromatin:** A complex of DNA and protein that constitutes the physical structure of the chromosome.
- **Climate Change Refugia:** Areas where species may survive contemporary climate change; areas where local climate changes may be limited by features of the physical environment. (Morelli et al., 2016).
- **Copy Number Variation:** Differences between individuals in the number of redundant copies of a particular gene contained in the genome.
- **Desert Renewable Energy and Conservation Plan (DRECP):** A policy document developed by the US Department of the Interior, in consultation with conservation organization, energy development interests, and local governments, identifying areas for focused energy development on public lands in the Mojave Desert.
- **Epigenetic Marks:** Minor chemical changes to DNA that affect transcription and gene expression.
- **Gene Regulatory Networks:** A group of genes whose interactions jointly affect a cellular process or organismal phenotype.
- **Genomic Resources:** Data, information, and laboratory techniques that permit the rapid genotyping of many (tens, hundreds, or thousands) of loci from members of a particular species. Genomic resources might include PCR primers and protocols, sequence capture probes, a reference genome, SNP panels, etc.
- **Heterozygosity:** The fraction of the loci at which an individual shows genetic variation.
- **Landscape Genomics:** The study of how genetic variation, across the entire genome, is distributed between populations across a species range.
- **Local adaptation:** Genetic differences between populations due to natural selection mediated by local environmental differences. Individuals have higher fitness in their native environment than elsewhere in a species' range.
- **Microsatellite Markers:** Commonly used in population genetic studies, microsatellite markers are highly variable regions within the genome that contain short, repeated sequences. There may be dozens of alleles at a particular microsatellite locus, and so these markers can be useful for identifying individuals or tracing paternity.
- **Neutral Genetic Variation:** Genetic differences that have little or no effect on individual fitness; genetic variation that is affected more by genetic drift than by natural selection.
- **Protein Coding:** Regions of the genome containing genes that are transcribed to RNA and translated into protein.
- **Species Distribution Models (SDM):** Algorithmic methods to predict the physical environments in which an organism could potentially exist given its physiological requirements.
- **Transcript- or Gene-Based Approaches:** Genotyping strategies that target specific regions of the genomes, such as a specific handful of genes or the many regions that are transcribed into RNA, as opposed to assessing genetic variation across the genome in its entirety.
- **Utility Scale Solar Energy (USSE):** A large scale solar electric plant, typically defined as one with more than one megawatt of capacity.

**Table 2**

The estimated spatial extent of USSE developments within the Mojave, including both currently operational facilities and sites planned for development (approved, under construction, or decommissioned). Numbers are compiled from publicly available data from federal, state, and county governments. For some facilities actual acreages were unavailable, so spatial extents were estimated based on production capacity.

| State      | Status               | Total Area (Acres) | Total Area (km <sup>2</sup> ) |
|------------|----------------------|--------------------|-------------------------------|
| Arizona    | Currently generating | 300                | 1.21                          |
| California | Currently generating | 20,446             | 82.74                         |
| California | Non-operational      | 38,338             | 155                           |
| Nevada     | Currently generating | 6564               | 26.56                         |
| Nevada     | Non-operational      | 16,803             | 67.99                         |
| Utah       | Currently generating | 100                | 0.40                          |

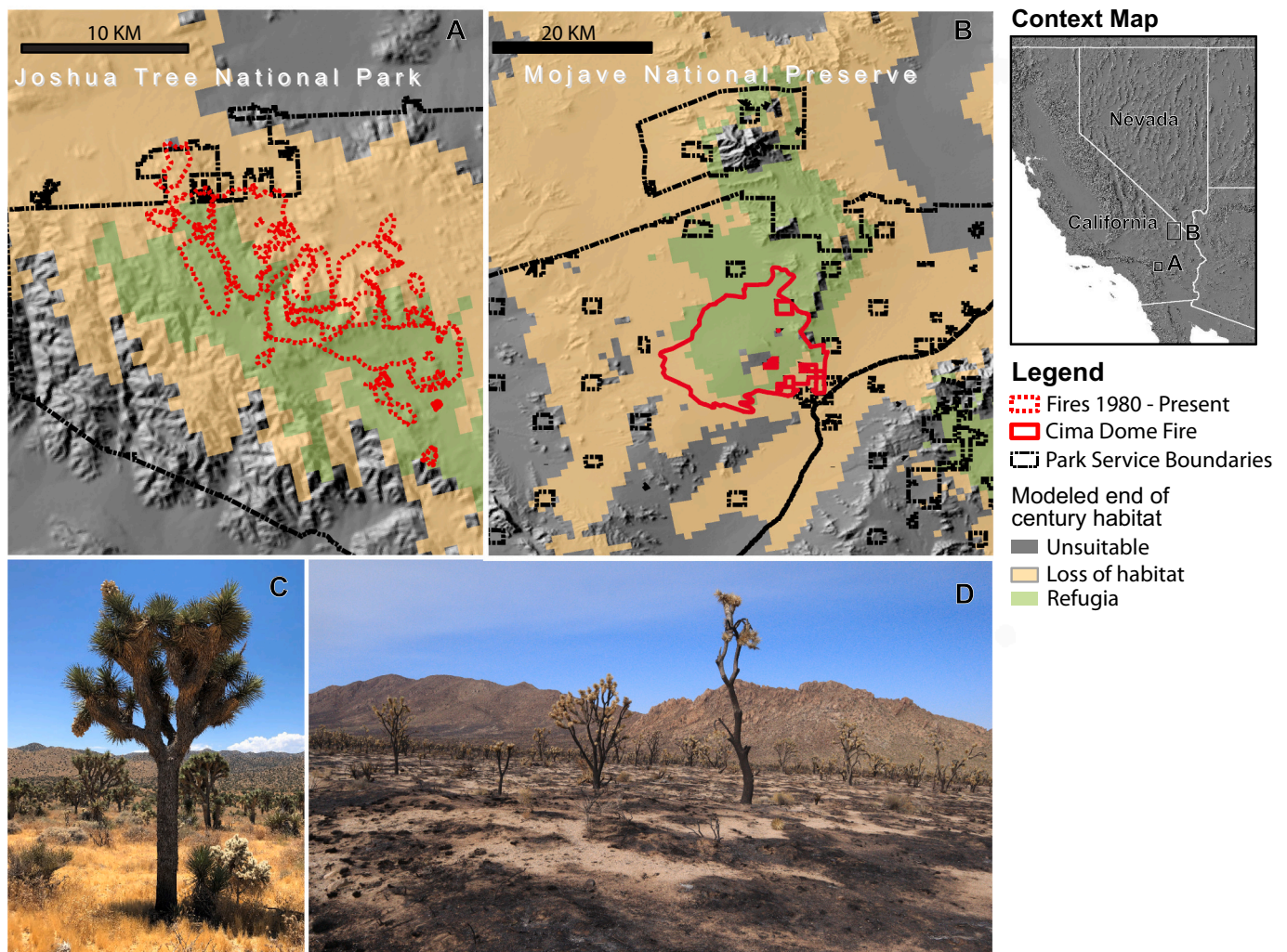
## 4. Climate Refugia

Any successful conservation programs must consider likely future distributions under different climate change scenarios and identify potential climate refugia that should be given high priority for protection (Morelli et al., 2016, 2020). In the case of Joshua trees, climate refugia

identified within JTNP have become the focus of land management interventions such as clearing fuels and making fire breaks to protect them from wildfire (Barrows et al., 2020a, 2020b). However, before these interventions were made, fires had already impacted as much a quarter of the potential refugia within JTNP, and the recent fires in the Mojave National Preserve occurred in areas that our preliminary modeling suggests might also have served as a climate refugium for *Y. jaegeriana* (Fig. 4). Indeed, many potential refugia within existing parks and conservation areas occur in places with high risk for wildfire, so it is vital to identify additional potential refugia and take steps to protect these. The need to expand existing parks and reserves to preserve potential refugia is not unique to Joshua trees. Of the 24 plant species listed as threatened or endangered in the Mojave, 15 occur outside of protected areas, including 4 of the 5 species identified as extremely vulnerable to climate change (Wilkening et al., 2021).

On-the-ground demographic data and other measures of population health are needed to confirm that refugia identified through modeling will be viable in the long term (Sweet et al., 2019). Populations of many long-lived tree species are experiencing long-term population declines (Stanke et al., 2021); incorporating demographic data such as rates of





**Fig. 4.** The combined effects of climate change and wildfire. Modeled distributions for *Yucca brevifolia* in Joshua Tree National Park (A) and *Yucca jaegeriana* in the Mojave National Preserve (B) for the end-of-century assuming the average of all moderately mitigated climate models (RCP 4.5), using the Maxent algorithm. Predicted refugia (green) overlap with areas of recent wildfires (A, B). (C) The proliferation of invasive grasses and annual plants (pictured: Joshua Tree National Park. Photo: Lynn Sweet) fuel catastrophic wildfires (D) (pictured: aftermath of the Cima Dome Fire in Mojave National Preserve. Photo: Lynn Sweet). For full methodology description, see Supplemental Methods text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

population growth or decline has marked impacts on predictions of future distributions (Merow et al., 2014). Fine-scale maps of Joshua tree distributions that include demographic data have been used to predict climate refugia in some select areas, such as Joshua Tree National Park (Barrows and Murphy-Mariscal, 2012; Sweet et al., 2019), but comparable studies at a range-wide scale are needed. Spatial patterns of recruitment alone may help identify potential climate refugia, which could subsequently be compared to predictions based on climate models. For example, Barrows et al. (2020a, 2020b) compared past and current abundance of lizards in Joshua Tree National Park to identify potential refugia for these species.

## 5. Dispersal and assisted migration

The conservation plans for many species often call for the conservation of areas that organisms might colonize in the future. Indeed, species distribution models that account for potential colonization of new areas often predict significantly lower habitat losses (Bateman et al., 2013). For example, distribution modeling for the Mojave Desert Ground Squirrel (*X. mojavensis*) suggests that although climate change may make up to 64 % of the animals' current habitat unsuitable by 2080,

when potential dispersal to new areas is incorporated the total available habitat could increase by up to 50 %. However, predictions about future distributions must also include realistic estimates of an organism's dispersal ability and the accessibility of new habitats (Bateman et al., 2013). For *X. mojavensis*, limited connectivity between current and potential future habitats could limit the animals' capacity to colonize these areas (Dilts et al., 2016). Joshua trees have particularly low potential to colonize new habitats as seeds are typically dispersed only ~100 m from the mother plant (Vander Wall et al., 2006).

The challenges of identifying and protecting extant populations that meet all the necessary criteria have led some to suggest assisted migration for dispersal-limited organisms like Joshua trees (Cole et al., 2011; Williams and Dumroese, 2013), and this approach has been attempted with other long-lived trees threatened by climate change (Torreya Guardians, 2012). However, assisted migration has been strongly criticized by some ecologists for its potential to spread pathogens, promote invasiveness, and disrupt ecosystems (Ricciardi and Simberloff, 2009). Assisted migration may also have a high probability of failure if the organisms are strongly locally adapted to conditions in the source habitat and the conditions in introduction sites are not well matched to the source (Vitt et al., 2010). Assisted migration has been



**Table 3**

Estimated habitat area for Joshua from two published models, and proportions matching conservation value and development planning status under each model.

|   | Joshua tree habitat model |         |  |         |
|---|---------------------------|---------|--|---------|
|   | Cole et al. range         |         | Godsoe et al. Species Distribution Model |         |
|   | Area (ha)                 | Percent | Area (ha)                                | Percent |
| Total area  | 3,950,235                 | 100 %   | 8,317,520                                | 100 %   |
| The Nature Conservancy conservation value                       |                           |         |  |         |
| “Ecologically core”   | 967,252                   | 24 %    | 2,138,093                                | 26 %    |
| “Ecologically intact”   | 1,592,027                 | 40 %    | 3,468,444                                | 42 %    |
| “Moderately degraded”   | 532,248                   | 13 %    | 868,870                                  | 10 %    |
| “Highly converted”  | 269,527                   | 7 %     | 316,403                                  | 4 %     |
| Gap Analysis Project protection status codes                    |                           |         |  |         |
| 1 - Managed for biodiversity, disturbance events proceed        | 243,410                   | 6 %     | 508,722                                  | 6 %     |
| 2 - Managed for biodiversity, disturbance events suppressed     | 708,230                   | 18 %    | 1,666,723                                | 20 %    |
| 3 - Managed for multiple uses, subject to extractive or OHV use | 1,713,542                 | 43 %    | 3,836,699                                | 46 %    |
| Ecologically core or intact with GAP 1 or 2 status code         | 906,026                   | 23 %    | 2,040,421                                | 25 %    |
| Desert Renewable Energy Conservation Plan                       |                           |         |  |         |
| Total area within DRECP   | 2,088,798                 | 53 %    | 3,073,698                                | 37 %    |
| In development focus areas                                      | 19,099                    | <1 %    | 31,176                                   | <1 %    |

suggested for Joshua trees, but we suspect that the cost and logistical planning required for assisted migration to succeed makes this strategy inadvisable.

Likewise, assisted migration wouldn't preserve intact, functional ecosystems, limiting its potential for success. Joshua trees, for example, rely entirely on specialized yucca moths for sexual reproduction, and different populations of pollinators appear to be adapted to the local Joshua tree (Godsoe et al., 2008; Yoder et al., 2013) so they may be ineffective pollinators of trees from other sites (Smith et al., 2009; Starr et al., 2013). Further studies of the pollinators are urgently needed, as recent research completed in Joshua tree National Park suggests that high elevation, cooler climate sites that might serve as climate refugia for the trees may be less suitable for the moths (Harrower and Gilbert, 2018). If this finding holds up across time and space, it may severely limit the number of potential refugia for the species. Current research on patterns of sexual reproduction across the range of the Joshua tree and association genetic studies of their pollinators will be invaluable in this regard.

In addition to pollinators, there may be many organisms that interact with a given species. However, it can be difficult to identify all the organisms that interact with a particular species and the extent to which they are important for the persistence of existing populations or establishing new ones. For example, intriguing new work examining the microbial diversity in desert soils identified 37 different taxa of arbuscular mycorrhizal fungi that form associations with the roots of Joshua trees and contribute to seedling growth (Harrower and Gilbert, 2021). The soil fungal communities varied markedly between different sites in both taxonomic composition and their effects on growth and nutrient uptake, suggesting that the presence of particular species may be important for the establishment of young seedlings. Microbial communities could play a key role in the determining the persistence of populations, but little to nothing is known about the biology of these organisms. Further research in this area is desperately needed.

Thus, any successful strategy for conserving biodiversity in the face of climate change will need to consider the availability of mutualists

such as pollinators and mycorrhizal fungi. Although Joshua trees may seem extraordinarily specific in their ecological requirements, the potential for mismatches between the source and receiving environments to doom assisted migration is by no means unique to them. For example, managed relocation has been used extensively to restore bighorn sheep (*Ovis canadensis*) to areas from which they have been extirpated (Malaney et al., 2015), but ecological mismatches between source populations and receiving environments have reduced the success of some restoration efforts (Wiedmann and Sargeant, 2014). Managed relocation is therefore challenging under the best of circumstances. For Joshua trees and species with similar life histories, focusing conservation efforts on protecting populations that meet multiple criteria for resiliency to climate change – occupying refugia identified with high quality distribution data and mechanistic physiological models, and showing demographic signatures of long-term viability – will give the greatest chances of species persistence.

## 6. Conservation genetics

Studies of genetic variation are of immense value for conservation planning, and a wide range of population genetics, genomics, and experimental methods are available to inform decision making. First, population genetic data can identify distinct populations that require different management strategies and that should be the focus of fine-scale distribution modeling studies (Hohenlohe et al., 2021). For example, population genetic studies indicate that Sonoran and Mojave Desert tortoises are distinct (Avise et al., 1992; Edwards et al., 2015; Murphy et al., 2011), and species distribution modeling indicates that the two occupy substantially different habitats (Inman et al., 2019). Likewise, population genetic work suggests that Joshua trees in the eastern and western Mojave are distinct species that appear to have adapted to different pollinating yucca moths (Royer et al., 2016; Starr et al., 2013; Yoder et al., 2013). Emerging work also suggests that there is significant genetic divergence between populations within species, and that this divergence has been driven by natural selection, perhaps due to differences in climate (Smith et al., 2021). These different populations may respond differently to climate change. Thus, for many species threatened by climate change, it may be necessary to model genetically distinct populations separately when considering potential future distributions and to ensure protection of as many distinct populations as possible to maximize the retention of genetic diversity.

Population genetic data may also help to identify populations with higher genetic diversity and greater potential to adapt to environmental change. For example, Creech et al. (2020) used microsatellite markers to assess genetic variation in isolated populations of bighorn sheep across the Mojave and to evaluate their potential to adapt in response to climate change. Similarly, Vandergast et al. (2013) reviewed existing population genetic studies for Mojave Desert taxa and identified 10 regions where multiple taxa have higher levels of genetic diversity, including six regions within the current range of Joshua trees, and three that coincide with regions of high genetic variation *Y. brevifolia* (cf. Vandergast et al., 2013; Smith et al., 2021).

Like many conservation genetic studies, both the Creech and Vandergast papers examined ‘neutral’ genetic variation that is not affected by natural selection. However, amidst the climate crisis, efforts to conserve genetic variation within species should aim to protect *adaptive* genetic variation (Razgour et al., 2019) that directly affects responses to heat stress, drought, and other environmental factors. Populations that vary at loci underlying climate adaptation have greater potential to adapt to changing climate. Thus, conserving variation at these loci may be more important than conserving overall genetic variation. In addition, incorporating information about the adaptive potential of populations into species distribution models (above) may improve their accuracy in predicting future distributions under climate change (Bush et al., 2016; Razgour et al., 2019).

Understanding the genetic basis of adaptation is challenging, but

emerging technologies and analytical approaches make this practical for most organisms. Landscape genomic methods and association genetics can identify loci that likely underlie local adaptation to climate variation in current populations (Lotterhos and Whitlock, 2015), even in the absence of an annotated reference genome. For example, Shryock et al. (2017) identified amplified fragment length polymorphism (ALFP) loci associated with differences in mean annual temperature and precipitation for two Mojave Desert plants, (*Ephedra nevadensis* and *Sphaeralcea amigua*). Likewise, the Revive and Restore program has supported work to collect whole-genome sequence data from Joshua trees sampled from across the range of climates in which they occur, to identify loci associated with specific climate variables.

Genome-wide association studies of seedling survival, growth, and specific ecophysiological traits also offer significant promise for identifying genes underlying climate adaptation. Studies in common gardens, such as those we have established for Joshua tree in the US Geological Survey's Mojave Desert Common Gardens, are particularly powerful as they can validate the adaptive value of these loci and elucidate the underlying physiological mechanisms (Weigel and Nordborg, 2015). Identification of high-confidence candidate loci for climate-adaptive traits also offers the possibility of predicting those traits in natural populations where direct measurement is impractical (Swarts et al., 2017); this approach will be used to predict Joshua tree populations' likely climatic tolerances and capacities for future adaptation directly from genetic sequence data.

Genome resequencing offers particular promise for conservation genetics (Stillman and Armstrong, 2015). Building genomic resources, especially whole genome sequences, enables researchers to look beyond variation in expression and nucleotide sequences of protein coding genes and into non-coding regions of the genome (Jha et al., 2020), interactive components of gene regulatory networks (Mehta et al., 2021; Wilkins et al., 2016), epigenetic marks (Thiebaut et al., 2019), copy number variation of genes (Bai et al., 2016; Dorant et al., 2020), chromatin structure (Song et al., 2021), and chromosome-level interactions (Probst and Mittelsten Scheid, 2015), all of which have been identified as components of adaptive evolution and climate change response.

Genome sequencing can be expensive and technologically challenging, particularly for the often large and repetitive genomes of plants. However, new long-read technologies can greatly reduce the cost and the time to completion. Recently, we used PacBio Single Molecule, Real-Time (SMRT) Sequencing to generate a chromosome-level assembly for the Joshua tree genome in less than six months from submission of tissue to initial data analysis, at a cost of less than \$19,000 – roughly half the cost of a field vehicle and >100,000 times less expensive than the Human Genome Project. A full genome sequence is already available for desert tortoises (Dolby et al., 2020; Tollis et al., 2017), which Dolby and colleagues used to compare genomes across tortoises. They identified a polymorphism in the TLR83 gene within *G. agassizii* which may be involved in innate immune response (Dolby et al., 2020). More intensive studies at the population scale would likely reveal additional polymorphisms, which may be involved in innate immune response (Dolby et al., 2020). Similarly, recent work examining genome-wide variation in tortoises found that overall heterozygosity predicts long term survival of translocated animals (Scott et al., 2020).

Identifying climate adapted genotypes may also allow for assisted gene flow. Unlike assisted migration, in assisted gene flow individuals or propagules are relocated, not to entirely new habitat, but within the species' existing range to facilitate adaptation to climate change by introducing adaptive genetic variation (Aitken and Whitlock, 2013). Conceptually, assisted gene flow is only a step removed from existing management and restoration plans that identify seed sources based on the environments in which restoration planting will be conducted — but sources are chosen based on predicted future climates rather than current conditions (Aitken and Bemmels, 2016). Assisted gene flow can therefore be integrated into existing management plans as data becomes available for focal species. Assisted gene flow has been most widely

discussed for management and conservation of temperate and boreal tree species (Aitken and Bemmels, 2016; Borrell et al., 2020; Browne et al., 2019; Girardin et al., 2021; Young et al., 2020) but it has also been suggested for herbaceous wildflowers (Prieto-Benítez et al., 2021), amphibians (Rudin-Bitterli et al., 2021), and mammals (Seddon and Schultz, 2020); and it has been successfully put into practice in populations of the endangered coral *Acropora palmata* (Hagedorn et al., 2021).

Conservation genetic work in the Mojave must do more than simply preserve genetic diversity. It is vital to build genomic resources and identify specific genetic variants that may allow for adaptation to climate change. Once climate-associated loci have been identified, wild populations will need to be genotyped to predict their long-term potential to adapt to warming climates. Populations that have the highest probability of adaptation and survival should be prioritized for conservation over those where genetic variation for climate adaptation is low.

## 7. Finding compromise in the Mojave and beyond

Addressing the paired crises of biodiversity loss and climate change present difficult conservation trade-offs both within the Mojave (Conkling et al., 2022) and globally (Gasparatos et al., 2021; Gibson et al., 2017; Grodsky, 2021; Rehbein et al., 2020). At a global scale, the transition to renewable energy is predicted to have significant impacts on biodiversity due to habitat loss (Gibson et al., 2017; McManamay et al., 2021), and renewable energy developments are frequently located within protected areas and regions of high biodiversity (Rehbein et al., 2020). Currently the majority of global renewable energy comes from hydroelectric facilities (Zarfl et al., 2019), which have particularly high impacts on biodiversity (McManamay et al., 2021). Hydroelectric reservoirs are a major source of habitat loss and habitat fragmentation, particularly within New World tropical rainforest where the majority of planned future dams will be constructed (Jones and Bull, 2020; Zarfl et al., 2019), and associated road construction can lead to additional deforestation beyond the construction sites (Jones and Bull, 2020). Other renewable energy development can also have knock-on effects that extend beyond the footprint of the facilities themselves. Mortality for birds, bats, and insects can be significant at both wind and solar facilities (Conkling et al., 2022; Pérez-García et al., 2022), and can impact a species' overall population size and demography both locally and regionally (Conkling et al., 2022). Within the Mojave the largest source of habitat loss to energy infrastructure will be from USSE development. Solar energy has lower overall impacts on biodiversity than other renewables (Jager et al., 2021), but is not without consequences. In addition to direct habitat loss from construction, solar energy developments can also serve as habitat for invasive plant species (Grodsky and Hernandez, 2020) and have been shown to reduce the diversity and abundance and pollinators both within the development and in nearby undisturbed sites (Grodsky et al., 2021).

A number of recent studies suggest that careful siting of wind and solar facilities may be able to reduce the direct impacts of energy development by safeguarding biodiverse and ecologically significant sites (Cameron et al., 2012; Dunnett et al., 2020; Wu et al., 2020). However, the criteria used in siting renewable energy development need to be expanded beyond measures of current biodiversity and habitat quality to include considerations about the impacts of future climate change on imperiled species. Several recent literature reviews have described approaches for incorporating climate change into conservation planning, including strategies for building adaptive capacity, ameliorating the threat posed by climate change (Prober et al., 2019), and accounting for future changes in human land usage (Jones et al., 2016). We argue that an integrative approach, combining all three of these strategies together with genomic and ecological studies of target organisms, will have the greatest success.

The Mojave in particular is facing an onslaught of development at an unprecedented pace. The explosive urban growth and industrialization

of the region is driven by both economic realities and by legal mandates for production of renewable energy. The conversion of even more desert landscapes to USSE productions is therefore likely, if not inevitable. Saving Joshua trees and other Mojave Desert species will require weighing the value of preserving specific sites against the larger benefits of renewable energy production and the reality that further development is inevitable. Balancing this trade-off necessitates identifying areas that have the highest conservation value and sadly agreeing to sacrifice populations where a focal species is doomed to extinction. Some new developments could occur in retired farmlands and industrial sites, but to the extent that new developments must be located in wild lands, these should be concentrated in areas already impacted by human disturbance or likely to be rendered unsuitable by climate change. For example, Cameron et al. (2012) identified areas with 'low conservation value' in the Mojave where the ground is flat enough to allow USSE development. They determined that the available land area was seven times greater than that needed to meet California's renewable energy goals as of 2012 (the newer SB 100 benchmarks are higher than the 2012 standards, however). Similarly, The Nature Conservancy identified 4.6 million acres (19,000 km<sup>2</sup>) that have already seen 'significant levels of disturbance' and 1.2 million acres (4856 km<sup>2</sup>) were classified as 'highly degraded' (Randall et al., 2010). These areas might be candidates for renewable energy development where the impacts on biodiversity may be lower. For example, Wu et al. (2020) identified 31 million acres of 'candidate areas' for USSE development in the Western US, excluding legally protected parks and refuges, critical habitat, ecologically core areas, and areas needed to ensure connectivity between habitats. Though economic and technical constraints reduce the total area available, the area identified by Wu et al. is sufficient to produce 4000 GW of installed capacity — roughly three times the energy requirements for the entire US.

Applying a comparable —if greatly simplified— procedure, we compared the distribution of Joshua trees based on the two best range maps available (above) to three measures of habitat quality and conservation status in the Mojave: The Nature Conservancy's ecoregional assessment (Randall et al., 2010), the USGS Gap Analysis Project Protected Areas Database, and the DRECP development focus zone. We find that roughly 2/3 of the range of the Joshua tree occurs in protected areas (Table 3), and roughly 1/4 is within areas managed for biodiversity (GAP status code 1 or 2). On the other hand, between 8000 and 11,900 km<sup>2</sup> of the current range of Joshua trees (roughly 20 %) were identified as 'moderately degraded' or 'highly degraded' in the Mojave Desert Ecoregional Assessment. <1 % of the trees' range lies within areas identified in the DRECP as energy development zones. These results are

comparable to the Mojave as a whole (Table 4); roughly 3/4 of the total region lies within protected areas, and about 30 % is within areas managed for biodiversity. Although much of the region (~80 %) is of high conservation value, there are very large areas (roughly 16,000 km<sup>2</sup>) that are moderately degraded or highly converted. Last, the development focus areas identified in the DRECP constitute a tiny fraction of the total region.

Given the very large areas of low conservation value available for energy development and other human uses, and the large portion of the Joshua trees' range that exists in protected areas, it should be possible to contain development to areas of lower conservation value while expanding renewable energy production and protecting the most important habitats. A next essential step will be to determine which, if any, areas slated for development contain climate refugia, so that they can be removed from the list of potential development zones; even areas previously identified as being highly degraded may still have conservation value if they contain potential refugia. On the other hand, there may be areas that are ecologically intact, but that will inevitably be so badly damaged by climate change that they have little conservation value in the long term. Fighting to preserve these 'doomed' sites for long-term biodiversity preservation would siphon conservation resources away from more important areas.

Implementing this focused, strategic management strategy will require bringing together a diverse array of public and private stakeholders. The Mojave Desert and the natural distribution of Joshua trees span four states, and include a patchwork of Federal, State, and local land ownerships and jurisdictions, including the US National Park Service, the Bureau of Land Management, the US Forest Service, and numerous state and county reserves. Regulation and policy making at the Federal level is needed to create a coherent management plan across these various agencies. In addition, large portions of the Mojave are made up of private land, especially in Los Angeles and San Bernardino Counties in Southern California. Protecting widespread species threatened by climate change therefore must involve private stakeholders. While limiting development to areas that are already highly converted seems highly achievable given the large amount of space available, landowners in ecologically core areas may feel differently if their financial prospects are limited by conservation needs. A possible solution might be to work with private conservation organizations, such as The Nature Conservancy, The Mojave Desert Land Trust, or the Transition Habitat Conservancy to acquire private land that has been identified as high priority for conservation.

Finally, regulatory and management plans should be focused on interventions that will produce broad public support to maximize conservation value while minimizing political costs. Because the Joshua tree is widespread, stakeholders in any decision to give the species formal protection range from private landowners to local governments, utilities, recreationists, and virtually anyone who perceives that protection will constrain the current panoply of human uses of the Mojave Desert. People are understandably suspicious of changes if they perceive a threat to their livelihoods, and a lack of effective communication between regulatory agencies and local political leaders has derailed past conservation planning in the region (Alagona and Pincetl, 2008). The discussion should not be whether a landowner can make a living off their land, but rather identifying a landscape-scale set of conservation criteria and priorities with landowners included in the discussion. The combination of strategic, focused conservation efforts combined with community engagement will reduce opposition and create broad public support.

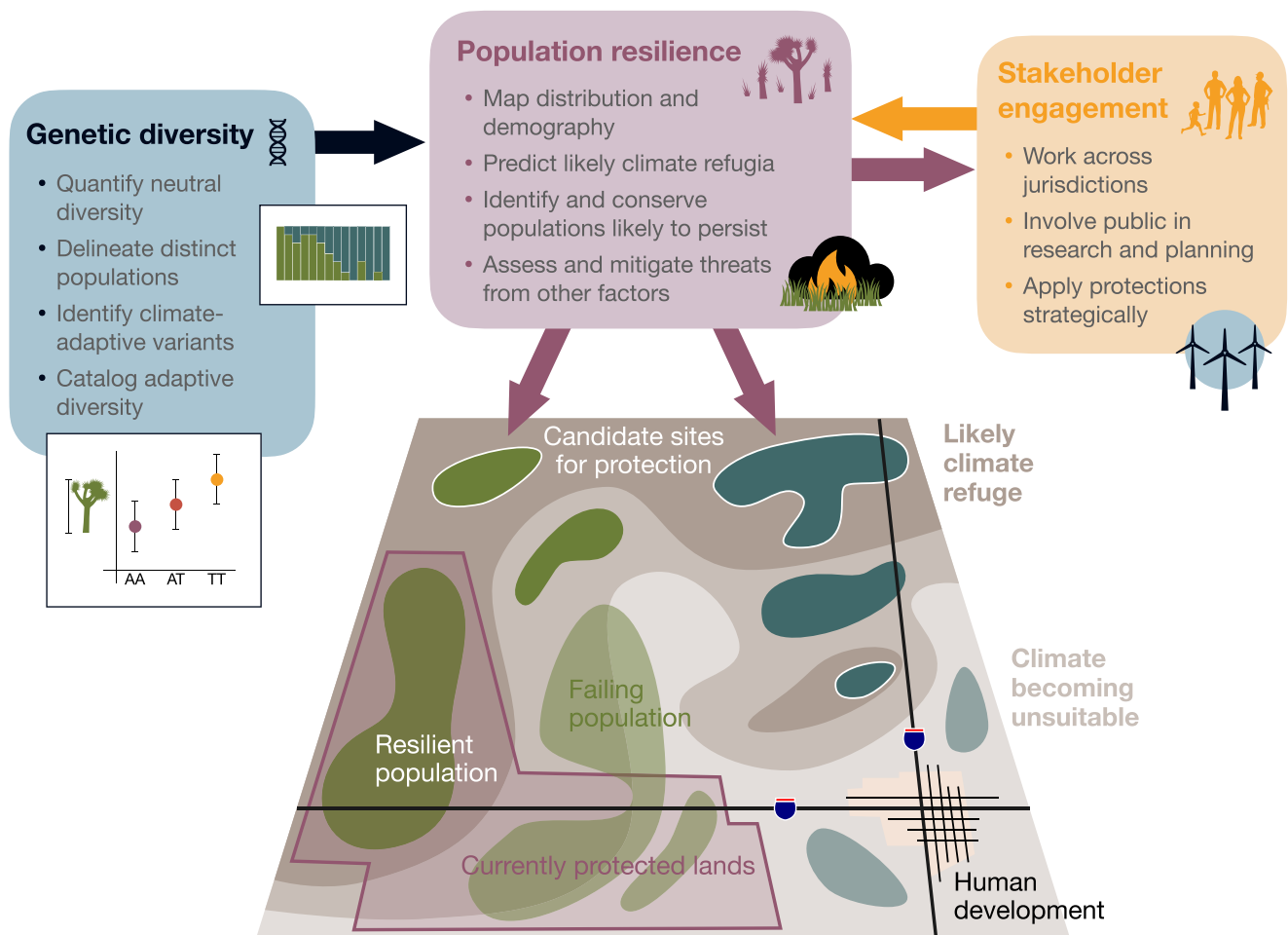
For every species there will be idiosyncratic issues that must be addressed for effective conservation in the face of climate change. Still, what we have outlined here incorporates a set of actions that can be applied in most cases (Fig. 5). These include (in sequential order):

1. Identify genetic structure and distinct populations.

**Table 4**

Area within the Mojave Desert matching conservation value and development planning status.

|   | Mojave Desert |         |
|---|---------------|---------|
|   | Area (ha)     | Percent |
| Total area  | 11,856,953    | 100 %   |
| The Nature Conservancy conservation value                       |               |         |
| "Ecologically core"   | 4,339,059     | 37 %    |
| "Ecologically intact"   | 4,981,347     | 42 %    |
| "Moderately degraded"   | 1,218,906     | 10 %    |
| "Highly converted"  | 389,596       | 3 %     |
| Gap Analysis Project protection status codes                    |               |         |
| 1 - Managed for biodiversity, disturbance events proceed        | 1,679,412     | 14 %    |
| 2 - Managed for biodiversity, disturbance events suppressed     | 1,801,845     | 15 %    |
| 3 - Managed for multiple uses, subject to extractive or OHV use | 5,342,493     | 45 %    |
| Ecologically core or intact with GAP 1 or 2 status code         | 3,311,644     | 28 %    |
| Desert Renewable Energy Conservation Plan                       |               |         |
| Total area within DRECP   | 6,239,613     | 53 %    |
| In development focus areas                                      | 64,709        | <1 %    |



**Fig. 5.** Conceptual map of a species threatened by climate change, and considerations necessary to manage for resilience. Populations are assessed for population genetic structure and adaptive genetic variation (In this example, populations belong to one of two genetic clusters shown as forest green versus blue-green). Distribution data and climate models are used to predict potential refugia. Demographic and genetic data are used to validate refugia and identify populations likely to persist. (Here, the landscape varies in whether it will remain suitable under climate change (darker gray shading) or become unsuitable (lighter gray). Some populations are resilient, recruiting new individuals (dark coloration); others are failing to recruit (lighter coloration). Conservation groups work together with land managers and regulatory bodies to establish conservation priorities, and designate new lands for protection (Here, one resilient population is on currently protected lands; other resilient populations that occupy climate refugia are highlighted with white outlines, and these are candidates for new protections.) Land management strategies are adapted to reduce threats from wildfire and other stressors in refugia. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Develop distribution models for these populations using high-quality occurrence data to identify climate refugia.
3. Validate potential refugia using demographic studies and other independent data sources.
4. Assess adaptive genetic variation within populations, using either association genetics or, ideally, experimental approaches coupled with genomic data.
5. Based on the results of the first four steps, identify locations within each population that should have highest priority for protection (Morelli et al., 2020).
6. Work with local stakeholders to protect these sites while accommodating existing and emerging land uses that are compatible with an overall conservation strategy (Henson et al., 2018)
7. Identify additional factors, beyond climate change alone, that could negatively impact the persistence of a target species (invasive species, incompatible recreation, inappropriate wildfire frequencies) and focus management efforts to mitigate them (Morelli et al., 2020).

These final two steps may be useful in reducing opposition to a conservation program. The concrete outcome of this approach is significant—a stepwise process for selecting specific areas that meet the

above criteria will provide to policymakers the information needed to implement scientifically informed management decisions while minimizing political opposition.

The unfolding climate catastrophe is dramatically reshaping even remote, once pristine wildernesses. The Mojave Desert is no exception in this regard and is already showing the effects of a hotter, more arid climate. The ubiquity of the climate threat means that even widespread, common species may be threatened with extinction. At the same time, the continued growth in human populations and global energy demand mean that wild areas will increasingly be converted for human use. Faced with a potentially bleak future, we need to implement a new conservation paradigm or accept a world where species like Joshua trees are only found in museums and textbooks. This new paradigm may mean making the decision to focus conservation efforts on those organisms and habitats that have a future, while sadly accepting that others will be lost to development, urbanization, and extinction.

Although all wild lands have value—even degraded sites can serve as habitat, open space, or sites for contemplation and spiritual rejuvenation—as a global society we have backed ourselves into a corner with no easy way out. We may have to face the fact that it is no longer possible to “Save All Joshua Trees” as one demonstrator demanded on



the eve of the California Fish and Game Commission's 2020 decision. Rather than asserting that all habitats should be given same level of preservation, protection can and should be strategic (Servheen, 1998), considering the long-term conservation value of sites, available political capital and resources, and the opportunity costs of foregone green energy development and economic growth (Naidoo et al., 2006). Here we identified important ways that interdisciplinary science may inform management decisions about which areas to prioritize for protection in the era of climate change. We argue that an integrative approach, weighing evidence from landscape genomics, ecophysiology, biology, and biogeography, can be used to understand fundamental trade-offs in conservation of habitat. Only by drawing on all available evidence, and fully including all stakeholder perspectives, can we settle the dust around some of the biggest challenges to biodiversity conservation.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109819>.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Christopher Irwin Smith reports financial support was provided by National Science Foundation.

## Data availability

All data have been previously published and are publicly available.

## Acknowledgements

During the development of this paper the authors received support from the National Science Foundation (Award #2001190 to KH, MM, and CIS; and 201180 to JBY) the Fulbright-Garcia-Robles US Scholars Fellowship (to CIS), The Murdock Charitable Trust's Lynwood W Swanson Research Award (to CIS), The Californian Cooperative Ecosystem Studies Unit (Cooperative Agreement P18AC01395 to LCS), and the Joshua Tree National Park Association (to LCS). Patrick Gonzalez provided climate data, and Melanie Davis and Nicolas Graver compiled species point data information. Robert E. Espinoza and two anonymous reviewers provided feedback on earlier drafts of this paper. We gratefully acknowledge this support.

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