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Research Article

Priority Species Lists to Restore Desert Tortoise and Pollinator Habitats in Mojave Desert Shrublands

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ABSTRACT

Mojave Desert shrublands are home to unique plants and wildlife and are experiencing rapid habitat change due to unprecedented large-scale disturbances; yet, established practices to effectively restore disturbed landscapes are not well developed. A priority species list of native plant taxa was developed to guide seed collectors, commercial growers, resource managers, and restoration practitioners in support of the Bureau of Land Management's Mojave Desert Native Plant Program. We identify focal plant taxa that are important for habitats of the threatened Mojave desert tortoise (*Gopherus agassizii*), a widely distributed herbivore in low and middle elevations, and pollinator taxa, including mostly Lepidopterans and Apoidean bees, some of whose populations are in decline. We identified 201 unique plant taxa in the diets of tortoises, and 49 taxa that provide thermal cover for tortoises with some overlapping taxa that provide both diet and cover. We discuss 134 native pollinators associated with plants used for nectaring, larval hosts, or cover and nesting materials. Detailed plant species accounts describing the status-of-knowledge for 57 plant taxonomic groups including detailed information on life history, ecology, and pollinator syndrome relevant to restoration success, methods of seed harvesting, propagation, and historical use in restoration. Our approach for developing a priority plant species list for the Mojave Desert provides a data-guided listing of species for restoration practitioners and identifies knowledge gaps for future investigation.

Index terms: aridland restoration; desert tortoise; Mojave Desert; native species; pollinators

INTRODUCTION

Landscape-scale disturbances in the Mojave Desert are increasing in frequency and extent (Leu et al. 2008; Carter et al. 2020). As fire and other large surface disturbances increase in area and frequency, biotic communities lose native plant diversity and resilience to future perturbations may decline (Allison 2004; Tilman et al. 2006). The footprint of renewable energy development, such as utility-scale solar and wind farms, is rapidly expanding into areas of low and middle elevation desert shrublands, impacting sensitive habitats (BLM and US-DOE 2012; Vandergast et al. 2013).

Natural restoration of disturbed Mojave Desert vegetation is notoriously slow because of harsh climate conditions (Cody 2000; Miller et al. 2009). It is concerning, therefore, that the native seed reserves representing the regeneration potential of Mojave Desert shrublands are vulnerable to disturbances such as wildfires that incinerate seeds and reduce microsite availability (Esque et al. 2010), or are diminished by surface compaction, excavation, or burial (Scoles-Sciulla and DeFalco 2009). Seed dormancy allows them to survive low annual precipitation and high summer temperatures while awaiting favorable germination and growth conditions (Baskin and Baskin 2014) that coincide with adequate precipitation, when it is available, but are often challenged by seasonal to multi-annual drought (Beatley 1974; Turner 1994). Moreover, future climate for the Desert Southwest is expected to be hotter and drier than current conditions with potential shifts in the magnitude, frequency, and timing of precipitation pulses likely altering plant regeneration and persistence (Dai 2013; IPCC 2013). These challenges add to the difficulty of desert restoration and emphasize the importance of genetically diverse plant materials and appropriate guidelines for restoration practitioners to meet future challenges (Bradford et al. 2018).

Historically, conservation strategies strove to minimize new disturbances with designs to reduce the footprint size and minimize edge-to-area ratios. Such strategies are not always feasible due to the configuration of legacy infrastructure. Alternatively, new mitigation lands may be purchased (Spang et al. 1988); however, availability of suitable habitat has dwindled from high demand. One remaining alternative is active restoration of disturbed lands to support diverse, sustainable, resilient, and connected native biotic communities. This can be challenging and costly because native plant materials are not readily available, and consistently successful restoration methods remain poorly developed (Bainbridge 2007; DeFalco and Esque 2014; Olwell and Riibe 2016).

The availability of local plant materials is pivotal for restoring shrubland habitats (Johnson et al. 2010; Olwell and Riibe 2016); however, availability of commercially provided plant materials is limited for the Mojave Desert. Disturbances in low- and mid-elevation Mojave Desert shrublands are a major concern because these shrublands provide habitat for sensitive plants and wildlife including Mojave desert tortoises (*Gopherus agassizii* Cooper), which are protected by the Endangered Species Act (USFWS 2011). Restoration of degraded habitat is the highest research priority for the recovery of the tortoise (USFWS 2011; Drake et al. 2015). As an umbrella species (Tracy and Brussard 1994), the desert tortoise enhances habitat for other species through burrowing activities and indirectly through its legal protection (Nussear and Tuberville 2014). Importantly, desert tortoises depend on herbaceous annuals and grasses for food (Esque et al. 2014; Jennings and Berry 2015) and use shrubs for cover from extreme temperatures and predators (Nussear and Tuberville 2014).

In addition to recovering plant communities for desert tortoises, restoration success in the Mojave Desert includes sustaining habitats for diverse pollinator communities—a goal for many natural resource management agencies (Olwell and Riibe 2016). Plant–pollinator relationships are fundamental to the success of plant communities, and are thus critical to long-term, landscape-scale restoration. Environmental heterogeneity in the Southwest has driven speciation and supports a hotspot of arthropod diversity, particularly for scores of native bee plant specialists (Michener 1979; Minckley et al. 2000; Griswold et al. 2006; Gonzalez and Griswold 2013; Carril et al. 2018). Many plants provide pollinators with nectar or pollen, also providing important structure, cover, and nesting materials (Gonzalez and Griswold 2013). Prioritizing restoration species that benefit pollinators supports the National Strategy to Promote the Health of Honeybees and Other Pollinators (Vilsack and McCarthy 2015) and the National Seed Strategy (Olwell and Riibe 2016).

A focused strategy to understand the genetic variability of native species is paramount to restoring habitats damaged by large disturbances (Shryock et al. 2017). Some native plant species may be suitable for reintroduction across broad environmental gradients; however, others may be at risk of failure under narrower environmental conditions, or their establishment may have negative genetic consequences for local ecotypes (Lesica and Allendorf 1999). In addition, conservation of genetic variation within species is fundamental for adapting to future environmental change. Alternative restoration targets, genetic diversity, genetic structure, and future adaptability need to be considered in restoration programs (Rice and Emery 2003). While there has been progress toward understanding effectiveness of restoration treatments in the Mojave Desert (Bainbridge 2007; Weigand and Rodgers 2009), information is still lacking on appropriate plant materials that are successful in combination with emergent restoration practices. While we emphasize the importance of incorporating native plant species into restoration programs to benefit desert tortoises and native pollinators, the establishment of diverse native plant communities has many important ecosystem consequences (Maron et al. 2014). Diverse plant communities provide energy, essential nutrients, and cover for wildlife while strengthening food chains (Wilson 1987; Tallamy 2004; Burghardt et al. 2009; Burghardt and Tallamy 2013).

Priority species lists have been successfully deployed in other ecoregions to benefit local and regional plant material needs by increasing plant performance and socioeconomic value in Ethiopian drylands (Reubens et al. 2011), identifying phosphorus- and grazing-tolerant species in Australian grasslands (Graff and McIntyre 2014), and evaluating functional diversity of species in Brazilian Amazonian forests (Giannini et al. 2016). Here, our aim is to provide a synthesis of existing information on plants that can be used for restoration of tortoise and pollinator habitats in Mojave Desert shrublands. This priority species list can be used to guide seed collections, seed increase, cultivation of outplantings, and successful deployment of plant materials in disturbed areas in support of Bureau of Land Management's (BLM) Mojave Desert Native Plant Program.

METHODS

Study Area

This study encompasses the Mojave Desert of the western United States including desert shrublands below ~1500 m. The Mojave Desert is intermediate between the cold northerly Great Basin and the warmer Sonoran Desert to the south (MacMahon 1980). Block faulting exposes diverse geological parent materials (Keeler-Wolf 2007; Minnich 2007), resulting in a variety of soil textures, compositions, and depths driving the diversity, structure, and function of vegetation communities. The southern Sierra Nevada, Transverse, and San Bernardino mountains to the west cause a rain shadow of increased aridity across the Mojave Desert (MacMahon and Wagner 1985). Precipitation and temperature vary widely in the Mojave Desert on a daily, seasonal, interannual, and decadal basis (Hereford et al. 2006). Seasonal annual precipitation ranges between 65 and 190 mm for most of the Mojave desert with extremes from 47 mm in Death Valley, California, to as high as 253 mm at Pierce Ferry, Arizona (Turner 1994). Average daily minimum temperatures in January can reach 2.9 °C in Bishop, California, and average maximum monthly temperatures in July can soar to 38.3 °C in Death Valley, California (Minnich 2007). The Mojave Desert is classified as a desert shrubland with many woody shrubs and subshrubs generally less than 2 m tall, various herbaceous perennials, and distinct spring and summer annual floras. A diversity of trees, stem and leaf succulents, geophytes, and parasitic epiphytes (Turner 1994; Keeler-Wolf 2007) add regional distinction to shrubland habitat structure.

Plant Taxa Used in Tortoise Diets

We searched the literature for observations of plant taxa eaten by wild Mojave desert tortoises, particularly empirical studies quantifying diets through bite count studies in which every "bite" (opening and closure of mandibles) was counted (Esque et al. 2014). We supplemented that with qualitatively documented studies of diets through fecal analyses and visual behavioral observations (e.g., Hansen et al. 1976 and annotations in Grover and DeFalco 1995, respectively). The data are reported as the number of bites recorded, number of individual observations, or number of scats (fecal pellets) where species were recorded. The frequency of sites where species occurred in diets illustrates the geographic scope of their use across the Mojave Desert. Plant taxonomy follows the Jepson Flora Project

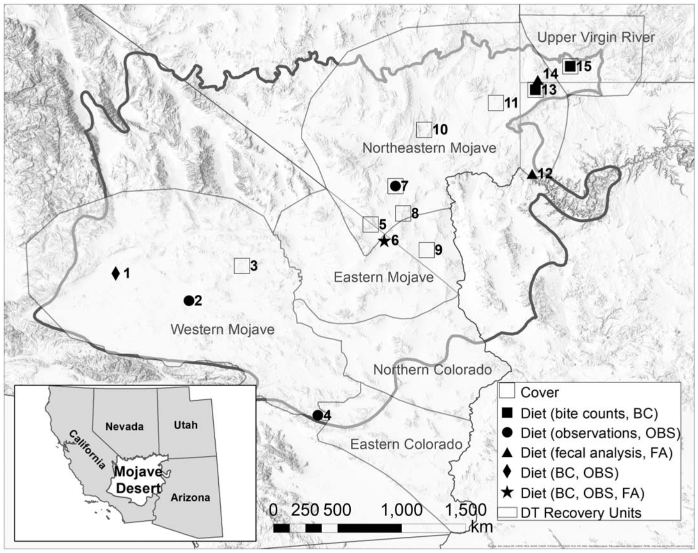

Figure 1.—Map of Mojave Desert (perimeter in dark gray outline) illustrating where shrub cover species and herbaceous diet species were documented within the Mojave desert tortoise recovery units (thin gray outlines). Site names are as follows: Desert Tortoise Natural Area (1), Hinkley (2), Fort Irwin National Training Center (3), Joshua Tree National Park (4), Stateline Pass (5), Ivanpah Valley (6), Arden Study Area (7), McCullough Pass (8), Piute Valley (9), Hidden Valley (10), Halfway (11), Lower Grand Canyon (12), Littlefield Site (13), Beaver Dam Wash (14), City Creek Site (15).

(2018) or the Integrated Taxonomic Information System (ITIS 2021).

Plant Taxa Used as Tortoise Cover

Tortoise cover was monitored at nine sites spanning 37 y to identify shrub species used for cover from thermal extremes and protection from predators from the seven past sampling sites (greater Fort Irwin National Training Center and Stateline Pass in California; McCullough Pass, Piute Valley, Hidden Valley, and Halfway, Nevada; Littlefield Study Site, Arizona; and City Creek Study Site, Utah); and Burge (Arden, Nevada; 1978; Figure 1). Cover taxa were quantified by the frequency and percentage of total observations where each species was used by tortoises on first encounter during field work. In addition to species use, we report the frequency of sites where cover plants were used across the Mojave Desert to indicate the breadth of geographic use.

Plant Taxa Used by Pollinators

First, we identified pollinators that used the plant taxa already identified as diet and cover plants by tortoises. Then, we added common and widespread plant species and their pollinators that we found in the literature. From this list, we researched and highlighted the flower characteristics of the taxa thought to influence visitation by pollinators and known as the pollination syndrome (Baldwin et al. 2002). Pollination syndromes represent "suites of convergent floral traits [e.g., color, shape] hypothesized to adapt distantly related angiosperm species to particular types of pollen vectors" (Ollerton et al. 2009). For example, strongly scented white flowers that are tubular and bloom at night are a pollination syndrome particularly attractive to night-feeding moths. The bloom periods of each taxon are compiled (Jepson Flora Project 2018; SEINet 2020) to ensure diversity of species available, and facilitate planning resources for pollinators throughout the growing season. We documented visitation records, pollinator ecology, and general studies on pollinator communities of the Mojave Desert. Specific citations for all such literature are found in association with the plant taxonomic accounts (Supplement 1, including independent Literature Cited).

Taxonomic Accounts on Life-History Characteristics and Restoration Potential

We summarized supplemental information on key characteristics of selected plant taxa (Supplement 1). Accounts include common names, plant functional groups, flowering times, elevational range, geographic distribution (relative to the Mojave desert tortoise), habitat types, flower form and shape, pollinator use, tortoise use, propagation and production techniques, and documented outcomes when used in restoration. When available, we included technical details on seed biology, seed collection, storage and handling, and establishment. Taxonomic accounts also include information about the recoverability of taxa based on short- and long-term recovery patterns across multiple wildfire studies (Shryock et al. 2014) and some species' affinities to disturbed habitat such as desert washes and roadsides.

RESULTS

Desert Tortoise Diet Taxa

We documented tortoise diets from fifteen studies at nine sites over a 22 y period across the Mojave and Colorado deserts (Table 1, Figure 1, Supplement 2). Bite-count studies were conducted at four sites (five studies) resulting in 210,095 bites by 98 tortoises across California, Arizona, and Utah (Supplement 2A and 2B). Supplementary qualitative observations on foraging tortoises were documented at six sites (seven studies) adding Nevada (Supplement 2C), and two fecal studies added an additional site in Arizona (Supplement 2D).

We found 167 unique native plant taxa in tortoise diets representing bite counts, observational, and fecal studies (Supplement 2). Seventeen diet taxa accounted for greater than 1% of bites at 1 to 6 sites (Table 2). Over 80% of native taxa in bites were annual or perennial forbs, while shrubs, perennial grasses, and succulents each comprised less than 10% of the plant taxa (Supplement 2). Collectively, native taxa comprised over one-half (59%) of the total bites (including exotic species) in tortoise diets and were moderately distributed among sites. The top five native forbs each comprised between $>$2% and 7% of total diets (Supplement 2).

In contrast, each of the top three nonnative species comprised $>$10% of total bites and in combination comprising 42% across geographically diverse sites (Supplement 2, Figure 1): the annual forb *Erodium cicutarium* comprised 14.2% (eight sites), while annual grasses *Bromus madritensis* L., *B. tectorum* L., and *Schismus* P. Beauv spp. collectively comprised 26.9% of bites, and were found in diets at nine, two, and five sites, respectively.

Table 1.—Fifteen studies at nine sites document plant species in the diets of Mojave desert tortoises across the Mojave Desert ecoregion. Methods abbreviated as BC = bite counts, quantified through direct observation, OBS = foraging observations that were not quantified with bites, and FA = fecal analysis of wild tortoises.

Study	Years	Site	Method	Sample
a	1973	Hinkley, San Bernardino Co., CA	OBS	$N = 1$ (+ anecdotal)
b	1973–75	Lower Grand Canyon, Mohave Co., AZ	FA	$N = 66$ fecal pellets
c	1973–75	Beaver Dam Wash, Washington Co., UT	FA	$N = 30$ fecal pellets
d	1975	Arden Study Area, Clark Co., NV	OBS	$N = 100$ observations
e	1976–78	Littlefield Site, Mohave Co., AZ	OBS	$N = 26$ observations
f	1978	Joshua Tree NP, San Bernardino Co., CA	OBS	$N = 15$ observations
g	1979	Desert Tortoise Natural Area, Kern Co., CA	OBS	$N = 39$ observations
h1	1980	Ivanpah Valley, San Bernardino Co., CA	OBS	$N = 3$ observations
h2	1981	Ivanpah Valley, San Bernardino Co., CA	OBS	$N = 59$ observations
h3	1980–81	Ivanpah Valley, San Bernardino Co., CA	FA	$N = 409$ fecal pellets
i	1989–92	City Creek Site, Washington Co., UT	BC	$N = 119{,}198$ bites / 29 tortoises
j	1990–92	Littlefield Site, Mohave Co., AZ	BC	$N = 33{,}805$ bites / 26 tortoises
k	1993, 2015	Desert Tortoise Natural Area, Kern Co., CA	BC	$N = 34{,}243$ bites / 18 tortoises
l	1992–93	Ivanpah Valley, San Bernardino Co., CA	BC*	$N = 27{,}715$ bites / 20 tortoises
m	1994	City Creek Site, Washington Co., UT	BC	$N = 27{,}842$ bites / 5 tortoises

[a] Luckenbach (1982); [b,c]Hansen et al. (1976); [d]Burge & Bradley (1976); [e]Hohman and Ohmart (1980); [f]Barrow 1979; [g]Bickett (1980); [h1,2,3]Medica et al. (1981); [i,j]Esque (1994); [k]Jennings (1993), [k]Jennings and Berry (2015); [l]Avery (1998); [m]DeFalco (1995). *Avery (1998) pooled bite counts by annual and perennial species and could not be separated by species in bite count compilation shown in Table 2.

Although it was not widely abundant in diets, we include *Opuntia basilaris* Englemann and J. Bigelow among the priority species (Supplement 2) because it was consumed abundantly during physiologically stressful years when preferred species were unavailable (Turner et al. 1984; Esque et al. 2014). *Sphaeralcea ambigua* A. Gray was also added to the list because it recovers well after fire, tortoise movements into burned areas were facilitated by *S. ambigua* cover (Drake et al. 2015), the species is readily consumed by captive and wild desert tortoises when available (TCE pers. obs. and Van Devender et al. 2002, respectively), and the nutrition in *Sphaeralcea ambigua* is comparable to other diet species (McArthur et al. 1994). Because tortoise diets are mostly herbaceous annual and perennial species and cover plants are usually woody shrubs, our comparison has only one overlapping taxon among the top 1% of diet and cover plants in either list: *Krameria erecta*.

Desert Tortoise Cover Taxa

Forty-nine unique plant taxa were used for cover by tortoises based on 4187 field observations of radio-telemetered tortoises across nine study sites in Nevada, Utah, and California, and observations at one site in southern Nevada (Burge 1978; Supplement 3). Twelve taxa comprised over 93% of tortoise cover sites and the majority were woody species that typically

Table 2.—Native species that comprise ≥1% of total number of bites.

Habit[a]	Species[b]	# Sites[c]	# Bites	% Use_{all}[d]	% $Use_{natives}$
AF	*Cryptantha micrantha*	4	14,564	6.9	13.3
AF	*Stephanomeria exigua*	3	12,083	5.7	11.0
AF	*Acmispon brachycarpus*	2	10,512	4.9	9.6
AF	*Plantago ovata*	5	7070	3.3	6.4
AF	*Descurainia pinnata*	4	5654	2.7	5.1
AF	*Acmispon oroboides*	2	4316	2.0	3.9
PG	*Stipa hymenoides*	5	3971	1.9	3.6
PF	*Mirabilis laevis*	1	3820	1.8	3.5
PF	*Euphorbia albomarginata*	4	3801	1.8	3.5
AF	*Lepidium lasiocarpum*	3	3241	1.5	2.9
PF	*Astragalus layneae*	2	2902	1.4	2.6
AF	*Cryptantha nevadensis*	3	2568	1.2	2.3
PG	*Hilaria rigida*	6	2515	1.2	2.3
Shr	*Krameria erecta*	3	2371	1.1	2.2
AG	*Festuca octoflora*	5	2226	1.0	2.0
PF	*Androstephium breviflorum*	1	2188	1.0	2.0
PG	*Muhlenbergia porteri*	2	2136	1.0	1.9

[a] Plant growth form abbreviations: annual forb (AF), annual grass (AG), perennial forb (PF), perennial grass (PG), shrub (Shr), sedge (Sedg), yucca (leaf succulent, LS), and cactus (stem succulent, SS).
[b] Species names follow Jepson Flora Project (2018); old nomenclature, as cited by studies, is included in Supplement 1.
[c] The number of sites where species were documented includes those observed during bite counts and other foraging observations, and detected in fecal analysis (see Table 1, Figure 1; $n = 9$).
[d] % Use_{all} refers to the percentage of bites including all plant species observed; % $Use_{natives}$ includes only native species and excludes nonnatives. Unidentified species comprised 1780 bites, or approximately 0.9% Use_{all} and 1.6% $Use_{natives}$.

Table 3.—Plant taxa comprising ≥1% of use for cover by Mojave desert tortoises across eight sites in the Mojave Desert (Figure 1; see Supplement 3 for complete list). Species occurrences include these sites and add Burge (1978) for a total of nine sites for frequency (Figure 1). Plant Functional Type (PFT) is adapted from Shryock et al. (2014) and denotes growth forms that have high ("+") or low ("–") recovery following fire: perennial forbs (PF+) and woody species (W+ or W–) based on life-history traits (i.e., lifespan, seed mass, dispersal, height class, and leaf longevity). Sites refers to the number of the total nine sites where cover was documented based on numeric codes in Figure 1.

PFT	Species	Total	% Use	Freq	Site identifiers
W–	*Larrea tridentata*	1755	41.91	9	3,5,7–11,13,15
W–	*Ambrosia dumosa*	942	22.50	9	3,5,7–11,13,15
W–	*Ephedra* spp.[a]	270	6.45	8	3,5,8–11,13,15
W–	*Yucca schidigera*	185	4.42	6	5,7–11
W–	*Lycium andersonii*	173	4.13	7	3,5,7–11
W+	*Ambrosia salsola*	145	3.46	5	3,8–10,15
PF+ / W+	*Sphaeralcea ambigua*	123	2.94	6	3,5,8–10,11
W–	*Yucca brevifolia*	120	2.87	4	3,9–11
W–	*Krameria* spp.[a]	57	1.36	6	3,5,9–11,15
W–	*Atriplex hymenelytra*	53	1.27	1	3
W–	*Artemisia filifolia*	46	1.10	1	15
W–	*Psorothamnus* spp.[a]	42	1.00	3	3,7,10

[a] *Ephedra* spp. includes *E. nevadensis*, *E. californica*, and *E. viridis*; *Krameria* spp. includes *K. grayi bicolor* and *K. erecta*; *Psorothamnus* spp. includes *P. fremontii* and *Psorothamnus* that was not identified to species. All taxa also include species that were only identified to genus.

recover poorly following wildfire (Table 3). *Larrea tridentata* and *Ambrosia dumosa* alone comprised 64% of use (Table 3). Six taxa had between 100 and 300 observations of use including *Ephedra* spp., *Yucca schidigera*, *Lycium andersonii*, *Ambrosia salsola* Strother and B.G. Baldwin, *Sphaeralcea ambigua*, and *Y. brevifolia* Englemann (Table 3). The genera *Atriplex*, *Encelia*, *Ephedra*, *Eriogonum*, and *Yucca* were each represented by three species used by tortoises.

Pollinator Host Taxa

We compiled 57 plant taxonomic groups including 130 species to identify their use as pollinator hosts (Table 4). Pollinators using these plants include 78.4% of the Apocrita (hereafter bees), 9.7% of Hymenoptera (wasps and others except Apocrita), 5.2% of Diptera (flies), 3.0% of Coleoptera (beetles), 63.4% of Papilionidae (butterflies), 81.3% of Lepidoptera (moths) except Papilionidae, and 5.2% of Apodiformes (hummingbirds) (Table 4). We documented 13 plant taxa used exclusively by moths, 3 only by butterflies, and 1 by bees. Fly, wasp and others, or beetle pollinator groups were not documented using plant taxa exclusively. At least 11 of the 13 plants identified as having exclusive relationships with moths are wind-pollinated, and thus likely function as larval host plants. These included six grasses, three *Ephedra* spp., and two *Ambrosia* spp. The exclusive butterfly relationships also are associated with wind-pollinated plants, including *Plantago* spp. and the perennial grass *Pappostipa* sp. (Table 4).

Fifty-three (93%) of the plant taxa on our list are larval host plants for at least one butterfly or moth taxon. Of these, 37.1% of larval host taxa are herbaceous annuals, 21.4% are herbaceous perennials, and 30.0% are woody shrubs or trees (Table 4). There was only one annual grass, four succulents, and three perennial grasses used by larval pollinators. Nine of 11 moth-pollinated species we listed have white or very light colored corollas (Table 4), and 10 of 11 are tubular (e.g., *Mirabilis* spp.) or have deep hypanthia (e.g., *Chylismia* spp., *Oenothera* spp.); this shape and color combination is the classic syndrome of moth-pollinated plants, particularly hawkmoths (Sphingidae; Raguso and Willis 2003). Eighty-one percent ($N = 76$) of the listed taxa (excluding genera, as well as wind-, self-, and hummingbird-pollinated taxa) have corollas that are blue ($N = 3$), purple ($N = 23$), white ($N = 38$), or yellow ($N = 20$), which are also all attractive to bees (Leleji 1973; Real 1981). Only four plant species (*Echinocereus mojavensis* [= *E. triglochidiatus*] Engelmann and J.M. Bigelow, *Euphorbia micromera* Boissier, *E. parryi* Engelmann, *Penstemon pseudospectabilis* M.E. Jones, and *Sphaeralcea ambigua*) have red to orange corollas, and of these, only the cactus and penstemon have tubular-shaped flowers expected to attract hummingbirds (Table 4, Supplement 1).

There were six plant taxa that are in tortoise diets, but for which no pollinator relationships were found in the literature: *Cryptantha micrantha* (Torr.) I.M. Johnst., *C. nevadensis* A. Nelson & P.B. Kenn., *Eriogonum maculatum* A. Heller, *Malacothrix coulteri* Harv. & A. Gray, *Plantago patagonica* Jacq, and *Stipa hymenoides* Roem. & Shult. While *Plantago* spp. are self-pollinating, *P. ovata* Forsk is a larval host to at least one moth, and many *Eriogonum* spp. are larval hosts to several moths or butterflies. Many *Cryptantha* spp. also have close relationships with native bee pollinators (Supplement 2A), and close relatives of *Malacothrix coulteri* have relationships with several bee species and host moth larvae.

Taxonomic Accounts

The taxonomic accounts provide detailed information in support of key species for 57 taxonomic groups (Supplement 1). Many of the accounts combine several species within a genus because of their morphological and ecological similarities, and rarely some genera were combined into functional groups for similar reasons. We found a wide variety of online resources designed to assist gardeners, restorationists, hobbyists, and professionals on each of the topics in the species accounts, and the availability of these sites is growing rapidly. Their individual development status and usefulness for technical work varies widely.

Table 4.—Mojave Desert priority plant taxa (134 spp. among 57 taxonomic groups) for use in restoration and pollinated by animals, by selfing, or by wind. Higher order pollinator names include Hymenoptera (bees and wasps); Diptera (flies); Coleoptera (beetles); Lepidoptera (butterflies) and (moths). Detailed explanations for codes found in this table are at the bottom of the table. Habit: annual forb (AF), annual grass (AG), biennial (Bien), leaf succulent (LS), perennial forb (PF), perennial grass (PG), shrub (Shr), subshrub (sShr), geophyte (Geo), tree (Tr), stem succulent (SS).

			Pollinators served									
Taxa	Bloom season	Habit	Bee	Wasp	Fly	Beetle	Butterfly	Moth	Bird	Tortoise use	Disturbance recovery	Propagation method
Abronia villosa	Feb-Jul	AF	1					**2, 1,** [(**6**)]		F	Unk	S
Acmispon spp.			2				**6, (7)**	**1**			+w	S
A. brachycarpus	Mar-Jun	AF								**F**		
A. glaber	Jun	sShr								F		
A. oroboides	Mar-Jul	PF								**F**		
A. rigidus	Mar-May	PF								F		
A. strigosus	Mar-Jun	AF								F		
Ambrosia dumosa	Feb-Jun, Sept-Nov	Shr						**5**		**C**, F	−w, −/+ sd	S, stem cuttings, salvage
Ambrosia salsola	Mar-Jun	sShr						**1**		**C**	+w, +sd, +wr	S, stem cuttings, salvage
Amsinckia tessellata	Feb-Jun	AF	(2)		(3)		1	**1**		F	+sd, +wr, +c	S
Androstephium breviflorum	Mar-Jun	Geo	[1]							**F**	+w	Bulb transplant
Aristida purpurea	Feb-Jun	PG						**(2)**		F	Unk	S, tiller plugs
Asclepias erosa	May-Jul	PF	[11, (93)]	(3)	(√)		**2**, (1)			N	+wr, +sd	S; tuber transplant
Astragalus spp.			[(5)]				**3**			**F**	+wr, +w	S
A. acutirostris	Apr-May	AF										
A. didymocarpus	Feb-May	AF										
A. layneae	Mar-Jun	PF										
A. lentiginosus	Mar-Jun	PF										
A. nuttallianus	Mar-May	AF										
Atriplex spp.	Asynch - Jan-Oct			37			**4**	**8, (2)**		**C**	+/−w	S, stem cuttings
A. canescens		Shr										
A. confertifolia		Shr										
A. hymenelytra		Shr										
A. polycarpa		Shr										
Baccharis spp.	Asynch - year-rnd, or spg to fall		15, (1)					**3, (1)**		Unk	+wr?	S, stem cutting
B. glutinosa		Shr										
B. sarothroides		Shr										
B. sergiloides		Shr										
Baileya spp.			2, (4)					**1**		F	+ w, + wr, +sd	S, salvage
B. multiradiata	Apr-Jul	PF										
B. pleniradiata	Mar-Jun	PF										
Bouteloua spp.								**2**		F	Annuals −w; Perennials +w	Annuals – S; Perennials – S
B. aristidoides	Aug-Sept	AG										
B. barbata	Aug-Dec	AG										
B. curtipendula	May-Oct	PG										
B. eriopoda	May-Oct	PG										
B. trifida	Mar-Sep	PG										
Chaenactis fremontii	Feb-May	AF	[2, (29+)]		√					F	+w	S
Chilopsis linearis	May-Sept	Tr	1, (4)					**6**		C	+wr	S, stem cuttings
Chylismia and *Eremothera* spp.			16+					2+		F	+sd	S
C. brevipes	Feb-May	AF										
C. claviformis	Feb-May	AF										
E. boothii	Mar-Jun	AF										
Coreopsis bigelovii	Feb-Jun	AF						**2**		F	−w	S

Table 4.—Continued.

Taxa	Bloom season	Habit	Pollinators served: Bee	Wasp	Fly	Beetle	Butterfly	Moth	Bird	Tortoise use	Disturbance recovery	Propagation method
Cryptantha spp.			[57]				1	**1**, [**1**]		F		S
C. angustifolia	Mar-May	AF									Unk	
C. circumscissa	Jul-Aug	AF									+w	
C. micrantha	Mar-Jun	AF									+w	
C. nevadensis	Mar-May	AF									−w	
C. pterocarya	Mar-Jun	AF									−w	
Dalea spp.			(9)				**1**	**1**		F?	+wr	S
D. mollis	Mar-Jun	AF										
D. mollissima	Mar-May	AF										
Dasyochloa pulchellum	Feb-May	PG					**3**			**F**	+w	S, Stolon cuttings
Descurainia pinnata	Feb-Jun	AF	12					**8**		**F**	Unk	S
Dietaria canescens	May-Jun	AF/ PF	[(41), 1]		[1]		**2**	**5**			+w, +c	S
Echinocereus spp.			3, (1)			2, (1)			√+		−w	S, stem cuttings
E. engelmannii	May-Jun	SS								F		
E. triglochidiatus	Apr-Jun	SS								Unk		
Encelia spp.			(3)					**2**		C	+w, +sd, +wr	S, stem cuttings
E. farinosa	Jan-Jun	Shr										
E. frutescens	Feb-May	Shr										
Ephedra spp.								**2**		**C**, F	−/+w	S, stem cuttings
E. californica	Mar-Jun	Shr										
E. nevadensis	Mar-Jun	Shr										
E. viridis	Feb-Jun	Shr										
Ericameria /			7,				**5**, (**1**)	**7**		C	+w, +sd	S, stem cuttings
Chrysothamnus spp.	Jul-Sep	Shr	(1)									
C. viscidiflorus	Sep-Oct	Shr										
E. laricifolia	Mar-Jun	Shr										
E. linearifolia	Aug-Oct	Shr										
E. nauseosa	Jun-Dec	Shr										
E. paniculata												
Eriogonum spp.			17, (2)	(5)	(6)	(1)	**16**	(**17**, (**2**)				
E. fasciculatum	all year	Shr								F, C	+w	S
E. inflatum	all year	PF								F	Unk	S, salvage
E. maculatum	Apr-Nov	AF								F	Unk	S
E. thomasii	all year	AF								F	Unk	S
Euphorbia spp.			3, [(√)] +		[(√)]+	[(√)]+	1			F	+wr?	S
E. albomarginata	Apr-Nov,	PF										
E. micromera	Apr-Jun, & Sep-Dec	AF										
E. parryi	May-Jun	AF										
Festuca octoflora	Mar-Jun	AG					[√]+	[√]+		**F**	+w, +sd	S
Grayia spinosa	Mar-Jun	Shr						**1**		F, C	+w	S, stem cutting
Gutierrezia spp.			104,				**2**			F, C	+ w, +sd, -c	S, salvage
G. microcephala	July-Nov, May-Oct	sShr	9 (4 unique)									
G. sarothrae		sShr										
Hilaria rigida	Feb-Jun	PG						[**1**]		**F**	Unk	S, salvage
Krameria spp.			[(5)] +				**2**, (**1**)	**1**		**C**, F	−w	S, rhizome
K. bicolor	Apr-May	Shr										
K. erecta	Mar-May	Shr										
Larrea tridentata	Apr-May	Shr	90+	(5) +	(7) +	(6) +		**4**		**C**	−w	S, salvage

Table 4.—Continued.

Taxa	Bloom season	Habit	Pollinators served: Bee	Wasp	Fly	Beetle	Butterfly	Moth	Bird	Tortoise use	Disturbance recovery	Propagation method
Lasthenia spp.			(1) +				[(1)] +	[**1**]		**F**	+w	S
L. californica	Feb-Jun	AF										
L. gracilis		AF										
Lepidium spp.			[70] +, 1				[**2**]			F	Unk	S
L. flavum	Mar-Jun	AF										
L. fremontii	Mar-Jun	PF/sShr										
L. lasiocarpum	Mar-Jun	AF										
Lupinus spp.			(8) +, 3				[(**2**)] +	[4]		F	+wr, +w	S
L. arizonicus	Mar-May	AF										
L. brevicauis	May-Jun,	AF										
L. concinnus	Mar-May	AF										
L. odoratus	Apr-May	AF										
L. shockleyi	Apr-May	AF										
L. sparsiflorus	Mar-May	AF										
Lycium spp.			[(1)]					[**2**]		**C**	/+w	S, stem cuttings
L. andersonii	Mar-May	Shr										
L. cooperi	Mar-May	Shr										
L. pallidum	Mar-May	Shr										
Malacothrix spp.			4, (1), [8]					[**2**]		F	+w, +sd?	S
M. coulteri	Mar-May	AF										
M. glabrata	Mar-Jun	AF										
M. sonchoides	Apr-Jun	AF										
Mentzelia spp.			(6), 8				1	**5**		F	−/+sd	S
M. affinis	Apr-May	AF										
M. albicaulus	Mar-Jul	AF										
M. involucrata	May-Oct	AF										
M. laevicaulis	Mar-Jun	PF										
M. longiloba	Mar-Jun	Bien/PF										
M. tricuspis	Mar-May	AF										
Mirabilis spp.							**1**	**3**, 1, (**1**)		F	+w	S, tuber cuttings
M. laevis	Feb-Jun	PF										
M. multiflora	May-Aug	PF										
Muhlenbergia porteri	Jun-Oct	PG						**1**		**F**	−/+w	S
Nicotiana spp.			[√]+		1+			2+	2	Unk	+w, +sd	S
N. attenuata	May-Oct	AF										
N. obtusifolia	Mar-Jun	PF										
Oenothera spp.			6+					(**2**)		F	+sd	S, root cutting
O. cespitosa	Mar-Aug	PF										
O. deltoides	Feb-Mar	AF										
O. pallida	May-Sep	AF										
O. primiveris	Mar-May	AF										
Opuntia basilaris	Mar-Jun	SS	(7)			1		**1**		F	w	S, cuttings, salvage
Pappostipa speciosa	Apr-Jul	PG					[**3**]				+w	S
Parkinsonia spp.	Apr-May		1, (5)					(√)+		C	/+w	S
P. florida		Tr										
P. microphyllum		Tr										

Table 4.—Continued.

Taxa	Bloom season	Habit	Pollinators served: Bee	Wasp	Fly	Beetle	Butterfly	Moth	Bird	Tortoise use	Disturbance recovery	Propagation method
Penstemon spp.			[51], (4), 9				**5**	**1**		Unk	+w, +sd, −c	S
P. eatoni	Apr-Jun	sShr										
P. palmer	May-Jun	sShr										
P. parryi	Feb-May	sShr										
P. pseudospectabilis	Mar-May	sShr										
Plantago spp.							**1**			**F**	−w	S
P. ovata	Feb-Apr	AF										
P. patagonica	Apr-Aug	AF										
Psorothamnus spp.			3 [35], [(1)]				3	**1**		C,Unk	/+w	S, salvage
P. arborescens	Apr-May	Shr										
P. fremontii	Apr-May	Shr										
P. spinosus	Jun-Jul	Tr										
Salvia spp.			[4]		[(√)]+		**2**	**3, [1]**	1		+sd, +w	S, stem cuttings
S. columbariae	Mar-Jun	AF								C		
S. dorrii	May-Jul	Shr										
S. mohavensis	Mar-Oct	Shr										
Sphaeralcea ambigua	Feb-Jul	PF/sShr	5, (3)		[√?]+	[√?]+	**6**			**C**, F	+w, +wd	S, salvage
Stanleya pinnata	Apr-Sept	PF/sShr	3, (15)				**2**			Unk	Unk	S
Stephanomeria spp.			(3)					**3**		F	+w	S
S. exigua	May-Sep	AF										
S. parryi	May-Jun	PF										
S. pauciflora	Mar-Nov	PF/sShr										
Stipa hymenoides	Apr-Jul	PG								F	+w	S, tillers
Xylorhiza tortifolia	May-May	sSh	[12]				**1**	**2**		C	+sd	S
Yucca spp.							**1**			**C**, F	w	S, salvage
Y. baccata	May-Jun	LS						**1**				
Y. brevifolia	Apr-June	LS						**2?**				
Y. Jaegeriana	April-Jun	LS						**2?**				
Y. schidigera	Apr-May	LS						**1**				
Y. utahensis	Apr-Aug	LS						**1**				

Pollinator use: Pollinators that use the plant taxa are denoted by number of species or genera (without or with parentheses; respectively); e.g., 4, (3) denotes that 4 species are known to use a taxon or group of taxa, and 3 genera or higher taxa are known to use it as well.

Pollinators that use the same genus but are not confirmed to use the ones listed in Supplement 1 are indicated by brackets, e.g., [5] denotes that a similar genus or the same species in another ecoregion is used by 5 species.

For Lepidopterans (moths and butterflies) numbers in bold indicate that the plant is a larval host. A single plant species may be a larval host and also provide nectar, but this is rarely documented in this section; 4, 1 denotes that a plant species or multiple taxa are larval host to 4 lepidopterans and provide nectar to 1 known species.

The check symbol (√) indicates that one to a few species or genera were documented using taxa, an added plus sign (+) indicates several species or genera use the taxon. For example, (√)+ indicates several genera are documented to use a given taxon. Similarly []+ indicates that several species either use a closely related taxon to the focal taxon, or several species use the focal taxon in another region.

Tortoise use: C = cover, F = forage, Unk = Unknown; when in bold they are >1% of diet or cover, excluding exotic plant species.

Plant disturbance recovery:

For annual taxa, "+" or "–" symbolizes an increase or decrease, respectively, in abundance following disturbance types. For perennial taxa, "+" or "–" symbolizes resprouters/reseeders or non-resprouters/non-reseeders, respectively, associated with disturbance types:

"w": does well (+) or poorly (–) after wildfire

"sd": does well (+) or poorly (–) after surface soil disturbance

"c": competes against (+) or outcompeted by (–) nonnative plants

"wr": may recover well after surface disturbance based on affinity to washes or roadsides

Unk: insufficient information about recovery potential

Ratings for perennials are based on Plant Functional Types, either resprouters/reseeders (+), or non-resprouters/reseeders (–) (adapted from Shryock et al. 2014).

DISCUSSION

Priority plant species were identified using multiple selection criteria (Giannini et al. 2016), an approach that in other ecoregions recognizes the benefits of native plants on wildlife and pollinators, local biodiversity, ecosystem services and function, and socioeconomics (Tallis et al. 2008). Because the Mojave desert tortoise is an umbrella species with a broad distribution, the Mojave Desert priority species list includes diverse taxa providing food and cover for this generalist herbivore while recognizing the value of host plants to support an array of native pollinators. By identifying all known plant taxa consumed by tortoises at sites across the Mojave Desert, we present a broad spectrum to guide seed collection and plant propagation to restore diet species in disturbed tortoise habitats.

Diet and cover use vary among individual tortoises, populations, and years (Esque et al. 2014), and the available studies on tortoise diet are limited in duration, location, or seasonality; thus, every project should be tailored to local diversity and conditions whenever possible, and more work on local diets would be useful for restoration. The studies that quantify tortoise plant use in the Mojave Desert are strongly biased toward winter/spring flora. Similarly, most plant taxa we identified as pollinator resources are spring and early-summer flowering, and restoration programs in the Mojave Desert could benefit from more information on the summer flora and their pollinators.

Despite their prevalence in some tortoise diets, nonnative annual species are excluded from our priority list because they reduce native plant diversity (Brown and Minnich 1986; Brooks 1999), cause bodily harm to young tortoises (Medica and Eckert 2007; Drake et al. 2016), and reduce growth and survival of Mojave desert tortoises, possibly influencing negative population growth trends (Drake et al. 2015).

Native forbs and grasses are required in seed mixes to replenish seedbanks that are depleted, such as following wildfire (Esque et al. 2010) and surface compaction or excavation activities (DeFalco et al. 2009). With sufficient winter precipitation, native annuals can be competitively released when perennial species are lost to disturbance. However, recolonization success is hindered by the invasion and rapid dominance by competitive Mediterranean annual grasses like *Bromus* spp. and *Schismus* spp. (Brooks 1999). Wildfires can severely deplete the seed bank, particularly species beneath shrubs (Cave and Patten 1984; Esque et al. 2010), yet annual species with affinities for shrub interspaces may persist following disturbance. Annual species that are known colonizers (*Acmispon*/*Lotus* spp., *Stephanomeria exigua*) may establish well in disturbed areas if seeded in concert with herbicide suppression of invasive annual grasses to reduce competition (DeFalco and Esque 2014), although details of herbicide effects on native communities must be worked out, and potential effects of herbicide treatments on tortoise health have not been documented.

As an alternative to seed dispersal, species that resprout from above- or below-ground structures have the potential to persist after disturbance (Clarke et al. 2013). Resprouting success depends on how and if the regenerating buds are protected from damage, and the location and amount of resources available for resprouting (Clarke et al. 2013). Many of the woody "resprouters" we identified are facultative (e.g., *Lycium* spp.) or obligate inhabitants of riparian areas that experience frequent natural disturbance (e.g., *Chilopsis linearis*, *Prunus* sp.). Long-lived wash species that evolved to resprout after damaging flood events may have an advantage when recovering after other disturbances as well (Bock and Bock 2014). Among perennials we identified as "resprouters," one is a geophyte (*Androstephium breviflorum*), two are perennial grasses with rhizomatous root systems (*Muhlenbergia porteri* and *Hilaria rigida*), and one reproduces from nodal offshoots (*Euphorbia albomarginata* Torr. & A. Gray). Others, like *Mirabilis* sp., *Delphinium* sp., *Allium* sp., and some *Asclepias* sp., also have root systems or tubers capable of resprouting. Although resprouting can be a successful means to persist after damage to aboveground tissues, some desert shrubs and trees resprout poorly after disturbance (Abella 2009) and may only survive low-intensity injury when the root crown remains intact and post-disturbance conditions favor growth (Gibson et al. 2004; DeFalco et al. 2010; Steers and Allen 2011; Esque et al. 2013).

While propagating "colonizers" from seed, and their inclusion in seed mixes may be an economical means to restore large disturbances, poor colonizers such as many native annuals may require nursery propagation from seed or cuttings before outplanting. Fortunately, the cacti included in this group all grow readily from cuttings and may be planted directly into restoration sites without growing to size in a nursery setting. Positioning outplanted seedlings and cuttings in groups to form habitat "islands" may enhance shrubland establishment and eventually restore ecological processes such as facilitation by nurse plants and fertile island development for annual species (Badano et al. 2016) and is being formally tested in the Mojave Desert (LAD, pers. comm.).

We used pollination syndrome as an indicator of pollinator relationships because empirical studies for many of the taxa are lacking. Many of the priority Mojave Desert taxa support classic pollination syndromes found in the literature (Fenster et al. 2004), including a large proportion of the species with purple/blue, yellow, and white corollas, which are bee pollinated (Leleji 1973; Real 1981). Other taxa have shape and color combinations consistent with moth pollination (Raguso and Willis 2003). In contrast, few vertebrate-pollinated floral syndromes were among the taxa we identified: *Echinocereus triglochidiatus* and *Penstemon pseudospectabilis* have red-purple tubular flowers with little or no scent and are considered attractive to hummingbirds. While classical pollination syndromes are useful for indicating visitation by certain groups, they are not always indicative of the whole pollinator guild. We acknowledge that accounts of pollinator visitations must be validated whenever possible because visitation does not always equate to pollination and is a poor proxy for successful plant outcrossing (King et al. 2013).

Insect diversity is high in the southwestern US (Allred 1969; Moldenke and Neff 1974; Michener 1979), and insect pollinators far outnumber vertebrate pollinators (Simpson and Neff 1987). Yet published studies of desert pollinators are biased toward bats, hummingbirds, and specialist relationships. The ubiquity of hymenopteran pollination, particularly the bees (Apoidea), illustrates their importance to desert plants. However, the most comprehensive invertebrate studies are limited to a few plant taxa, including *Larrea tridentata* (Hurd and Linsley 1975a, 1975b; Minckley et al. 2000), *Oenothera* (Raven 1979; Thorp and LaBerge 2005), *Krameria* (Simpson and Neff 1987; Simpson 1989), and *Opuntia* (Grant and Grant 1979), or encompass small geographic areas with high levels of bee endemism (e.g., Griswold et al. 2006). Pollinators may be afforded better protection from predators by woody vegetation, which provides sustainable, reliable nutrition and protection for hosted larvae compared with the short lifespans and the spatiotemporal unpredictability of annuals. Our survey indicates that almost all woody plant taxa are host plants for Lepidopteran larvae, compared to <50% of herbaceous plants. Pollinator studies are needed for the Mojave Desert ecoregion, particularly ecological studies that describe the many oligolectic native bees (i.e., bees that specialize in collecting pollen from a limited number of genera or species of flowering plants), the influences that disturbance has on pollinator diversity and function, how pollinator abundance and diversity respond to restoration of degraded habitats, and how climate change may influence pollinator/host relationships.

While we focused on many generalist species, many native plant species co-evolved with native arthropod consumers such that their life history stages are wholly dependent on plants and can only be replaced by few if any other species (Tallamy 2004; Burghardt and Tallamy 2013). Therefore, the loss of plant species potentially reduces overall species diversity further along the food web. For example, many terrestrial birds are dependent on insect protein, especially for feeding their young during growth periods (Burghardt et al. 2009). While such work has not been quantified for Mojave Desert communities, we predict that failure to restore diverse shrub communities over large areas may have negative consequences for ecoregional biodiversity.

Our priority species list can be used to guide resource managers and practitioners in collecting and storing seeds for landscape-scale restoration projects (e.g., Seeds of Success; Haidet and Olwell 2015), establishing production fields for seed increase (e.g., USDA, Tucson Plant Materials Center, commercial growers), cultivating nursery stock for outplanting (National Park Service, Joshua Tree National Park; Lake Mead National Recreation Area, Mojave Desert Land Trust, Nevada Division of Forestry), and prioritizing research topics. By identifying Mojave Desert priority species for restoration a priori, opportunities may grow for entrepreneurs to develop a diversity of species for socioeconomic benefits, thereby increasing business opportunities while enhancing restoration and conservation. The priority taxa and taxonomic accounts presented here for the Mojave Desert, in combination with seed transfer zones derived from climate and genetic information (Shryock et al. 2017, 2018, 2020), will assist practitioners in creating customized species menus for use on restoration projects across this desert ecoregion. While this priority species listing presents a start, it would be useful to create an online, living repository of Mojave Desert native plant cultivation methods and data that are regularly curated to increase the incentive for community participation.

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