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Authors: Fraga, Naomi S., Cohen, Brian S., Zdon, Andy, Mejia, Maura Palacios, and Parker, Sophie S.

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Research Article

Floristic Patterns and Conservation Values of Mojave and Sonoran Desert Springs in California

Naomi S. Fraga,[1,6] Brian S. Cohen,[2] Andy Zdon,[3] Maura Palacios Mejia,[4] and Sophie S. Parker[5]

[1]California Botanic Garden, 1500 North College Avenue, Claremont, CA 91711
[2]The Nature Conservancy, 401 W A Street, Suite 1650, San Diego, CA 92101
[3]Roux Associates, 555 12th Street, Suite 250, Oakland, CA 94607
[4]Mount San Antonio College, 1100 North Grand Avenue, Walnut, CA 91789
[5]The Nature Conservancy, 445 S. Figueroa St., Suite 1950, Los Angeles, CA 90071

[6]Corresponding author: nfraga@calbg.org

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ABSTRACT

In the face of a rapidly changing climate, spring-fed habitats are increasingly vulnerable to numerous threats. Botanical inventories provide valuable information to assess the conservation value of desert springs, and can serve as indicators to document changing conditions, including the proportion of native vs. nonnative taxa, diversity of life forms present that influence structure and function of ecosystems, species persistence and longevity, and the proportion of taxa that are rare and sensitive to land use change. Here we evaluate plant species composition and richness within and between springs, and evaluate botanical diversity with respect to physical parameters including hydrology and geography. We find that desert springs collectively support a large proportion of plant diversity, or nearly 22% of the total vascular plant diversity known within the California desert in only 0.000005% of the total land area. The springs we sampled are highly dissimilar in plant species composition, thus, restoration and management activities likely need to be highly individualized and site specific. Monitoring and inventory programs can increase opportunities for restoration and protection by providing information to assess warning signs of habitat degradation, such as changing species composition and local extirpation of wetland-dependent species.

Index terms: botanical inventory; floristics; Mojave Desert; Sonoran Desert; wetland

INTRODUCTION

Desert springs have been identified as high-priority ecosystems and targets to meet conservation goals because of their potential to serve as microrefugia in a changing climate (McLaughlin et al. 2017; Cartwright et al. 2020; Parker et al. 2021). These small and isolated water features often provide perennial water sources in an otherwise arid landscape, supporting the persistence of species under changing conditions (Bogan et al. 2014). Despite their relatively small size (e.g., Jack Spring, San Bernardino County, California, is 0.755 ha), desert springs have wide-ranging ecosystem influence at a landscape scale (Patten et al. 2008; McLaughlin et al. 2017; Cartwright et al. 2020). At a broad scale, desert springs provide respite from harsh conditions for wide-ranging migratory animals (e.g., large mammals and birds), but at a local scale they support narrowly endemic species with limited habitat connectivity and dispersal capacity (Sada et al. 2005).

In the face of a rapidly changing climate, spring-fed habitats of the Mojave and Sonoran deserts, USA, and their associated biota face numerous threats including groundwater extraction, water diversion, introduction of nonnative plant species, impacts from feral animals (e.g., horses and donkeys), cattle grazing, and wide-scale land use change such as habitat alteration and conversion (Sada et al. 2005; Patten et al. 2008; Davis et al. 2017). Land management practices, allocation of resources, and land use changes can significantly alter fragile spring-fed habitats, and substantially impact spring-associated biodiversity and the conservation value of springs (Parker et al. 2021). Specifically, groundwater extraction has the potential to severely impact desert springs that rely on aquifers in regional settings when the extraction rate exceeds the recharge rate, resulting in aquifer drawdown (Zdon et al. 2018), or if pumping is proximal to a spring in a local groundwater system. Furthermore, recharge rates are expected to decline as climate conditions in the American Southwest are expected to become hotter and drier with longer and more frequent drought events (Meixner et al. 2016).

In the Mojave and Sonoran deserts in California (hereinafter referred to as the California desert), springs are largely understudied and biological information, especially with respect to plant diversity, is poorly documented (Zdon et al. 2018; Parker et al. 2021). Yet, plants are foundation species, and especially important in desert environments, because they ameliorate temperature, reduce direct evaporation, and provide food and nesting materials for wildlife (de Grenade 2013; Glenn et al. 2013). Documenting plant diversity is a key component to assessing habitat health and function of fragile wetland ecosystems and can provide essential information on baseline conditions (McLaughlin et al. 2017; Parker et al. 2021). Plant species can serve as bioindicators of spring condition because their distribution is highly influenced by a variety of environmental and anthropogenic factors such as substrate, light, temperature, water availability, pH, and level of disturbance.

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Furthermore, perennial plant species are relatively easy to survey and document, although field-based surveys can be time consuming and require specialized taxonomic expertise (Palacios Mejia et al. 2021). Therefore, increasing the knowledge of plant diversity, combined with an assessment of threats at desert springs, can provide a useful framework to inform restoration and resource management for these critical habitats.

As part of a growing, interdisciplinary body of work that characterizes the conservation values and needs of desert springs, we examined botanical diversity, assessed threats, and characterized hydrological parameters at 48 springs distributed across the California desert (Palacios Mejia et al. 2021; Parker et al. 2021). The goals of this study are to assess plant species composition and richness within and between springs, and to evaluate botanical diversity of wetland plants with respect to physical parameters including hydrology and geography. Specifically, we addressed the following questions: (1) What are the floristic patterns within and between desert springs? (2) Is plant species richness correlated with spring size? (3) How does human use and disturbance influence botanical diversity?

METHODS

Study Area

The California desert is located in the southeastern corner of the state and spans an area of 103,500 km^2 (Omernick 1987). This study is focused on 48 springs that occupy an area of approximately 35 km^2, or less than or 0.000005% of the total landmass of the California desert (Table 1; Figures 1–2). The springs chosen for this study are a subset of 341 springs surveyed by Andy Zdon and Associates (2016) that occur on land managed by the Bureau of Land Management (BLM); we selected these 48 springs because they span a broad geography and capture documented hydrological variation (Figure 1). The springs are well dispersed across the California desert with an average distance of 166 km between springs and only seven pairwise distances between springs that are below 0.5 km (Supplemental Data Table 2).

Field Surveys

Prior to surveys, we examined herbarium specimens, literature, and records from the California Department of Fish and Wildlife Natural Diversity Database (CNDDB 2018) to identify historical records and sensitive plant species previously documented across the survey area. We queried the Consortium of California Herbaria (CCH2 2019) and SEINet (2019) to produce a list of 523 unique historical herbarium specimens and establish baseline documentation of the local vegetation. We collected an additional 524 herbarium specimens in the field and submitted them in the herbarium at California Botanic Garden (formerly Rancho Santa Ana Botanic Garden [acronym RSA]), bringing the total number of herbarium specimens evaluated in this study to 1047 (Supplemental Data Table 1).

We conducted surveys in the fall of 2018 and summer of 2019, when most wetland plant species are reproductive and in the best condition for identification. We identified plants to the minimum rank possible (species, subspecies, or variety), and excluded observations of plants if they could only be identified to genus or family. We collected herbarium specimens to aid in identification of species and provide a verifiable record. We did not collect specimens if plants were not in flower or fruit and could not be confidently identified. We included 222 observations of plant taxa that could be confidently identified in the field, but were not in a suitable condition to collect a voucher specimen (Supplemental Data Table 1). We examined all specimens cited in the study (Supplemental Data Table 1) and identified them using taxonomic keys and descriptions from several references including Baldwin et al. (2012), Jepson Flora Project (2022), and Flora of North America (FNA 2021). We standardized names using the Jepson eFlora revision 9 (2022) and verified all specimen identifications through comparison with annotated specimens in the herbarium at RSA. Plant taxa were categorized by Wetland Indicator Status according to the National List of Plants that Occur in Wetlands developed by the U.S. Army Corps of Engineers (2022). Lifeforms were categorized using Calflora (2022).

Analysis

Plant species occurring at only one spring (singletons) were omitted for Jaccard's similarity index calculation because they contain no shared species and the resulting pairwise calculations would be zero. To analyze the percentage of wetland versus upland taxa at desert springs, we categorized wetland taxa as those occasionally found in wetlands (facultative upland) to taxa that always occur in wetlands (obligate) and all categories in between including facultative and facultative wetland. Upland taxa only consisted of obligate upland taxa (U.S. Army Corps of Engineers 2022). The areal extent of each spring was delineated using "heads-up" digitizing into a polygon feature class within Esri's ArcGIS Desktop 10.8 using the Albers equal-area conic projection. Each spring was located from field documented coordinates (Table 1) and the associated vegetation and footprint visible in NAIP 2018 1 m aerial imagery was traced on-screen. The footprint was determined by consensus of the authors. The CALCULATE AREA tool was used to calculate the hectares of each polygon. The GENERATE NEAR TABLE tool was used to calculate the distances between each of the spring polygons, in meters.

RESULTS

Physical Setting

Sampled springs spanned a wide geography across the California desert and ranged in elevation from 150 m to 1859 m and in size from 0.005 ha to 12.80 ha (Table 1, Figure 1). Underlying bedrock types are variable and include intrusive igneous rocks, extrusive igneous rocks (i.e., volcanic rocks), carbonate rocks (limestone and dolomite), and various metamorphic rocks (Andy Zdon and Associates 2016). The majority of the springs (81%) had water expressed at the surface during our surveys, while nine springs had no detectable water across multiple surveys where hydrological data was gathered (Table 1). The springs we sampled included local springs that are fed primarily by precipitation from their immediate watershed and influenced by local conditions and seasonal patterns, and regional springs that are fed by more extensive groundwater

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Table 1.—Name, location, elevation, and size for 48 sampled springs. Taxa = minimum-rank taxa, *% = the percentage of nonnative taxa, WL% = the percentage of wetland plants present, and W = water present (1) or absent (0).

ID	Spring name	County	Latitude	Longitude	ALT (m)	Size (ha)	Taxa	*%	WL%	W
1	Arrastre Canyon Spring	San Bernardino	34.392	−117.114	1920	0.923	56	14%	58%	1
2	Arrowweed Spring A	San Bernardino	34.848	−114.782	479	0.009	8	0%	50%	1
3	Black Springs - Lower	Inyo	36.251	−117.732	1934	0.037	12	25%	50%	1
4	Black Springs - Upper	Inyo	36.249	−117.732	1859	0.145	21	10%	43%	0
5	Bonanza Spring	San Bernardino	34.685	−115.405	641	1.683	38	12%	56%	1
6	Borehole Spring	Inyo	35.886	−116.234	408	0.757	6	0%	100%	1
7	Boulder Spring	Kern	35.579	−118.028	1234	0.133	26	7%	64%	1
8	Bristol Spring	San Bernardino	34.263	−114.144	150	0.184	9	30%	60%	1
9	Burnt Spring	San Bernardino	34.716	−115.384	742	0.071	10	0%	36%	0
10	Butterbredt Spring	Kern	35.382	−118.113	1186	0.923	64	24%	38%	0
11	China Garden Spring	Inyo	36.314	−117.532	957	0.216	32	24%	61%	1
12	Chris Wicht Camp Spring	Inyo	36.112	−117.173	847	0.122	51	15%	42%	1
13	Coffee Can Spring	Kern	35.377	−117.883	648	0.02	17	32%	32%	1
14	Crystal Spring	San Bernardino	35.795	−115.962	1182	0.213	52	28%	30%	1
15	Dove Spring	Kern	35.453	−118.100	1300	0.256	26	10%	60%	1
16	Dripping Spring	San Bernardino	34.560	−115.210	1100	0.022	20	0%	25%	1
17	Goat Spring	San Bernardino	34.673	−116.927	1323	0.047	22	23%	9%	1
18	Halloran Spring	San Bernardino	35.383	−115.893	909	0.005	22	10%	16%	1
19	Hummingbird Spring	San Bernardino	34.753	−115.344	708	0.291	91	5%	4%	1
20	Jack Spring	San Bernardino	35.155	−116.756	726	0.755	28	14%	59%	1
21	Kane Springs west	San Bernardino	34.740	−116.701	984	0.094	18	17%	35%	1
22	Lower Centennial Spring	Inyo	36.266	−117.766	1714	0.06	16	25%	68%	1
23	McDonald Well	San Bernardino	35.115	−117.370	779	0.006	6	33%	80%	1
24	Mesquite Springs	Kern	35.390	−117.815	640	0.142	13	21%	50%	0
25	Miller's Spring	Inyo	36.292	−117.537	1067	0.071	18	5%	74%	1
26	Mopah Spring	San Bernardino	34.314	−114.776	675	0.08	47	14%	18%	1
27	Morongo Canyon Springs	San Bernardino	34.048	−116.568	765	5.093	171	13%	41%	1
28	Mound Spring	San Bernardino	34.256	−116.657	1656	0.03	36	13%	50%	1
29	Nadeau Spring	Inyo	35.866	−117.382	842	0.253	15	24%	29%	0
30	Poison Spring	Kern	35.394	−117.839	700	0.041	7	0%	57%	1
31	Quail Spring	San Bernardino	34.537	−117.082	1014	0.037	8	36%	64%	1
32	Quill Spring	San Bernardino	34.644	−116.891	1366	0.03	3	25%	25%	1
33	Ricky Spring	San Bernardino	35.450	−115.481	1340	0.018	7	14%	71%	1
34	Rock Corral Spring east	San Bernardino	34.317	−116.553	1216	0.104	26	8%	35%	0
35	Rock Corral Spring west	San Bernardino	34.317	−116.558	1219	0.209	11	18%	36%	0
36	Saline Marsh Spring	Inyo	36.696	−117.830	326	12.792	22	6%	10%	1
37	Salt Spring	San Bernardino	35.626	−116.281	160	8.267	15	6%	44%	1
38	Scofield Spring	Inyo	35.874	−116.121	625	0.136	20	15%	60%	1
39	Scrub Spring	San Bernardino	34.339	−114.286	275	0.009	4	25%	25%	1
40	Tan-Tan Spring	San Bernardino	34.848	−114.778	477	0.024	10	10%	50%	0
41	Tan-Tan Well	San Bernardino	34.848	−114.779	477	0.028	3	67%	10%	1
42	Thom Spring	Inyo	35.857	−116.227	428	0.092	13	7%	29%	1
43	Twelvemile Spring	Inyo	36.022	−116.155	672	0.131	64	14%	34%	1
44	Vaughn Spring	San Bernardino	34.259	−116.659	1646	0.064	43	11%	70%	1
45	Vernandyles Spring	San Bernardino	34.695	−115.661	782	0.014	18	26%	21%	0
46	West Well	San Bernardino	34.444	−114.479	234	0.009	4	0%	29%	1
47	West Well Spring	San Bernardino	34.445	−114.480	232	0.582	17	6%	17%	1
48	Wild Horse Spring	San Bernardino	35.788	−115.998	947	0.159	23	33%	58%	1

aquifers and are susceptible to impacts from regional groundwater pumping (Zdon and Love 2020).

Floristic Summary

Plant species richness ranged from 3 to 171 taxa (mean 16.4 ± 28.7 SD) at each of the 48 springs sampled (Supplemental Data Table 1). We recorded a total of 479 minimum-rank plant taxa, across 78 plant families (Tables 2–3), with individual taxa present at 1–23 springs (Supplemental Data Table 1). Big Morongo Canyon was found to be the most species-rich desert spring site with 171 taxa documented. Six other springs have greater than 50 taxa documented (Table 1). Only 23 taxa (4.2%) were present at 10 springs or more, and 18 of these were native (Supplemental Data Table 1). A total of 185 taxa (38.5%) were individually present only at a single spring (Supplemental Data Table 1). A high proportion of the taxa recorded (87%) are native to the California desert (Table 2). The 10 most common plant taxa occurred at 13 sites or more and had a high proportion of wetland taxa (60%) and nonnative taxa (36%; Supplemental Data Table 1).

The five most common plant families across all springs were Asteraceae (99 taxa), Poaceae (41 taxa), Boraginaceae (34 taxa),

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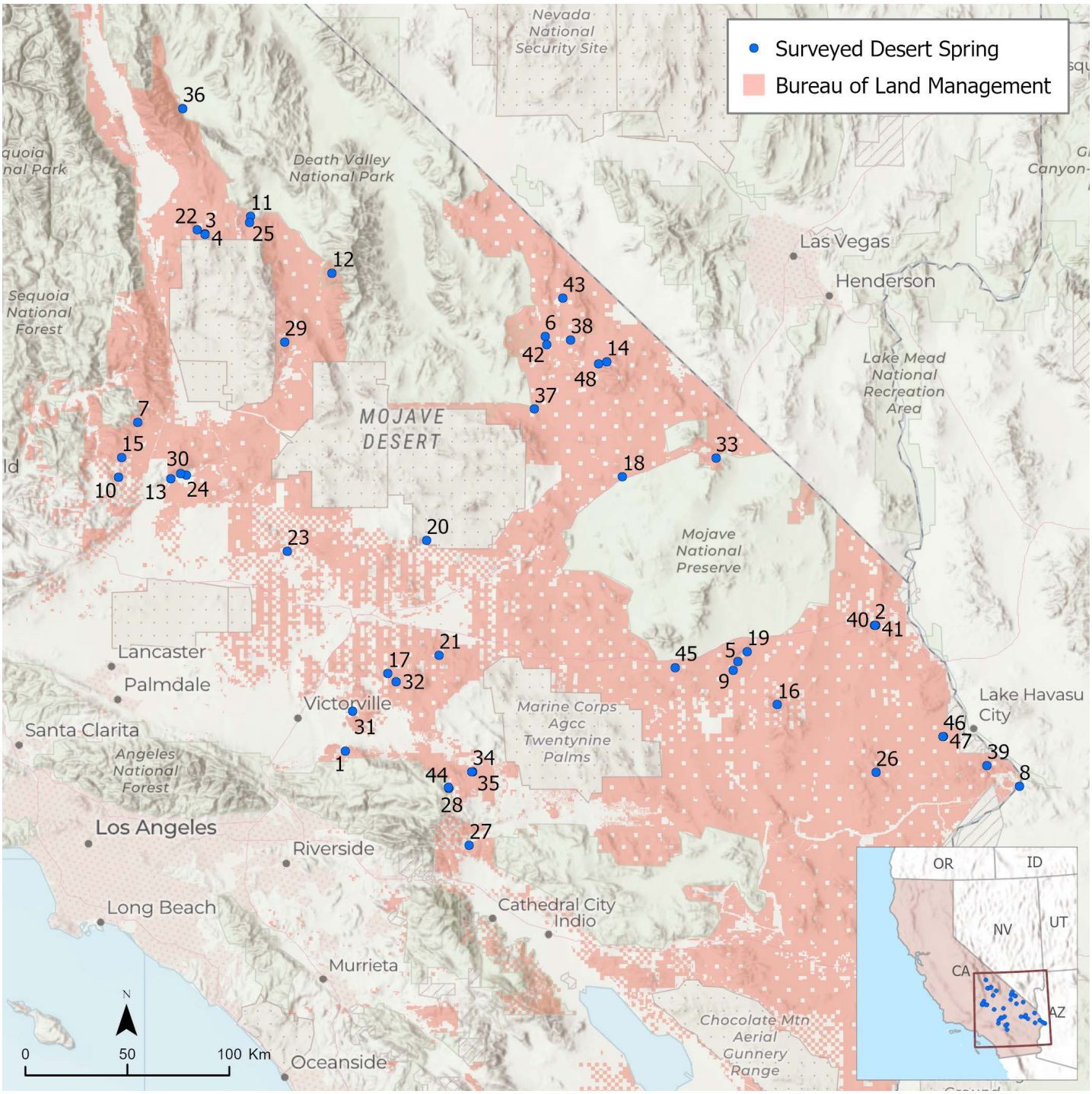

Figure 1.—Location of 48 springs in the Mojave and Sonoran deserts. All springs are on land managed by the Bureau of Land Management (Table 1).

Chenopodiaceae (26 taxa), and Polygonaceae (21 taxa; Tables 2–3). Springs were highly dissimilar based on Jaccard's similarity index with pairwise values ranging from 0 to 0.4 (mean 0.06 ± 0.05 SD). Our results indicated that spring size did not predict species richness when we evaluate all 48 springs together ($R^2 = 0.048$; Table 1). However, if we omit two outlier springs (Saline Marsh Spring and Salt Spring), R^2 increases to 0.611, indicating a positive relationship between spring size and species richness (Pearson's $R = 0.781$, $P < 0.00001$).

Upland taxa are a significant component to the overall plant species composition at the desert springs sampled (Supplemental Data Table 1, Figure 3). Upland taxa comprise 61.7% (295 taxa) of the total species richness while wetland taxa comprise 38.3% (183 taxa) of the total species richness (Figure 3). Of the 33 obligate wetland species documented, four were nonnative (12%) and the majority were perennial herbs (51%) and graminoids (36%). Cyperaceae was the most species-rich family among obligate wetland taxa (27%; Supplemental Data Table 1).

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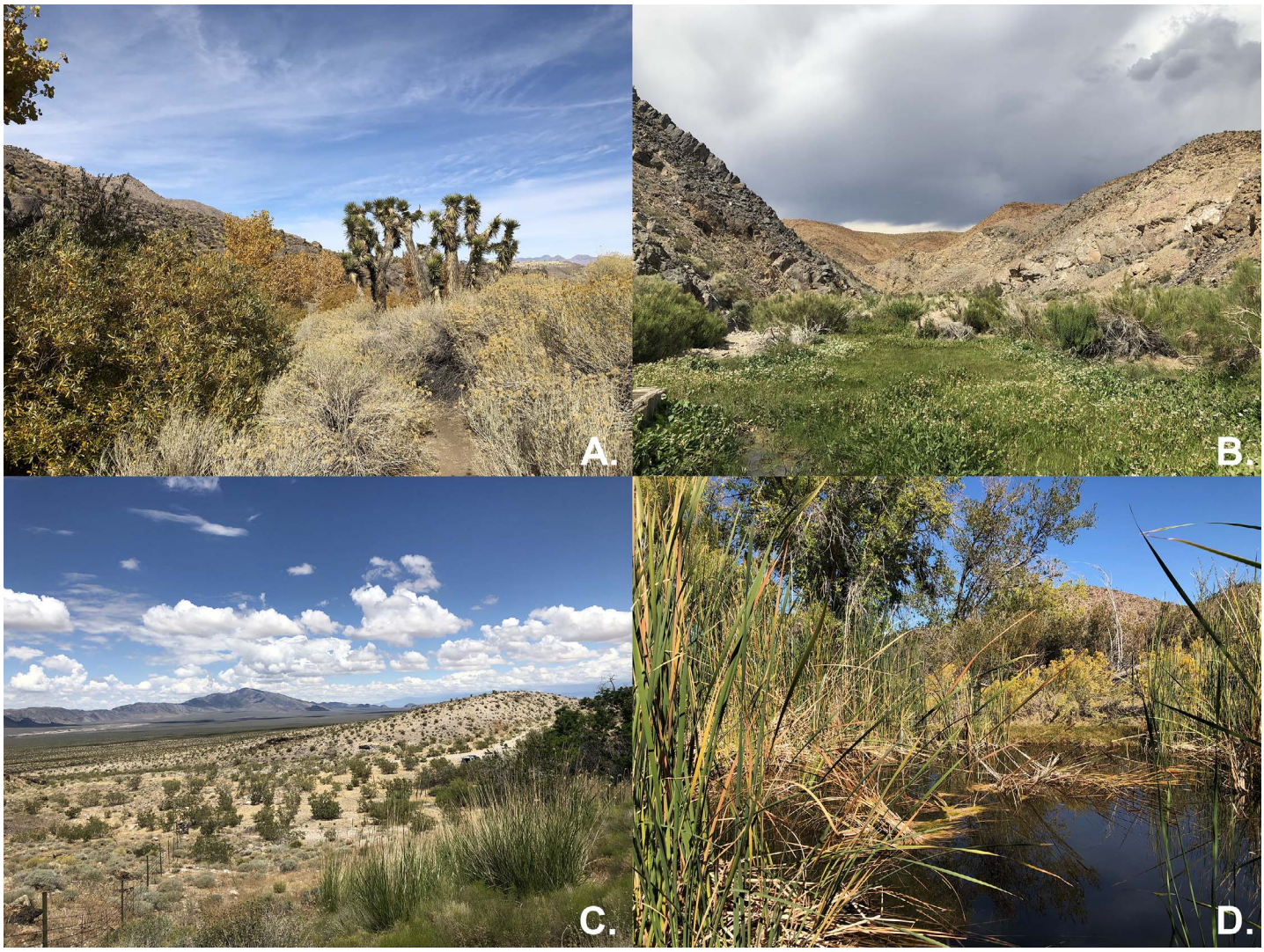

Figure 2.—Photographs of four desert springs sampled. (A) Lower Centennial Spring, Inyo County. (B) Miller Spring, Inyo County. (C) Wildhorse Spring, San Bernardino County. (D) Vaughn Spring, San Bernardino County.

In contrast, of the 296 upland plant taxa we documented, only 6.7% were nonnative taxa, and their life forms primarily consisted of annual herbs (54%), shrubs (19.8%), and perennial herbs (15.8%) (Supplemental Data Table 1). Asteraceae was the most species-rich family among upland taxa (21.6%).

Baseline Botanical Documentation

There are relatively few herbarium records documenting floristic diversity at the 48 desert springs prior to this study. The majority of the historical records (71%) were collected by contemporary botanists or botanists who were active in the last 20 y (e.g., Duncan Bell, Naomi Fraga, Sarah De Groot, George Helmkamp, Andrew Sanders, and Justin Wood). Two prominent botanists made herbarium collections at three springs prior to 1970. Annie Alexander collected at Morongo Canyon Springs and Saline Marsh Spring in 1941 and 1955, respectively. Ernest Twisselman collected plants from Mesquite Spring in the El Paso Mountains in 1964. Plant taxa documented by Annie Alexander at Morongo Canyon Springs and Saline Marsh Spring were observed at both sites during our surveys and are considered extant at these sites. Four native perennial wetland taxa documented by Ernest Twisselman at Mesquite Spring were not relocated: *Baccharis salicifolia* subsp. *salicifolia* (facultative wetland shrub, Asteraceae), *Pluchea sericea* (facultative wetland shrub, Asteraceae), *Eleocharis parishii* (facultative wetland graminoid, Cyperaceae), and *Phragmites australis* (facultative wetland graminoid, Poaceae).

Taxa of Conservation Concern

We documented the occurrence of seven plant taxa of conservation concern; three of these (42.8%) were wetland taxa (Figure 4, Table 4). One species of conservation concern, *Chloropyron tecopense* (Orobanchaceae), was once found at Borehole Spring, Inyo County, California. This is a facultative wetland species that was last documented near Borehole Spring in 2008 (CNDDB 2018). Since 2015, multiple surveys have not relocated this taxon at this specific location, and it is presumed extirpated near Borehole Spring. All other rare plant occurrences

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Table 2.—Floristic numerical summary. Taxa of conservation concern includes plants included in the California Native Plant Society's Inventory of Rare Plants (CNPS 2022). Calflora (2022) was used to categorize life forms.

Flora	Total taxa	% of total flora
Number of families	78	
Minimum-rank taxa	479	
Nonnative	63	13%
Native	416	87%
Taxa of conservation concern	5	1%
Life Forms		
Annual herbs	209	44%
Perennial herbs	105	22%
Shrub	85	18%
Graminoid	47	10%
Tree	26	5%
Succulent	7	1%
Five Largest Families		
Asteraceae	99	21%
Poaceae	41	9%
Boraginaceae	34	7%
Chenopodiaceae	26	5%
Polygonaceae	21	4%

that have been documented within the study area are currently presumed extant.

Nonnative Taxa

We identified 63 nonnative taxa, which constitutes 13% of the total floristic diversity in the study (Table 2). The two most frequently encountered plant taxa across the study were nonnative grasses (Poaceae; *Bromus rubens* and *Polypogon monspeliensis*). These were the only two taxa in the study to occur at 20 springs or more (Supplemental Data Table 1). *Cynodon dactylon* (Poaceae), *Schismus barbatus* (Poaceae), and *Erodium cicutarium* (Geraniaceae) were relatively frequently encountered, occurring at 13, 13, and 12 sites, respectively.

Washingtonia filifera (Arecaceae) is native to the California desert, but is treated as a nonnative species in this study because it is known to be introduced at the specific sites sampled (Jepson eFlora 2022). *Pulicaria paludosa* (Asteraceae) is native to Portugal and Spain and was first recorded as a naturalized nonnative species in California in 1946 (FNA 2021). It primarily occurs in coastal California, but has also spread to the desert, primarily occurring in the low Sonoran Desert from Palm Springs to the Whipple Mountains (CCH2 2019). *Pulicaria paludosa* is common along roadways, streambeds, and seasonal wetland habitats (Jepson eFlora 2022). We documented it for the first time at Halloran Springs in San Bernardino County (Fraga 6440B, UCR), which represents a ~190 km range extension to the north and it is the first record of the species in the central Mojave Desert region.

Nine of the documented nonnative plant taxa are persisting from cultivation. These include *Ailanthus altissima* (Simaroubaceae), *Morus nigra* (Moraceae), *Nelumbo lutea* (Nelumbonaceae), *Nereum oleander* (Apocynaceae), *Parkinsonia aculeata* (Fabaceae), *Robinia pseudoacacia* (Fabaceae), *Tamarix aphylla* (Tamaricaceae), *Ulmus pumila* (Ulmaceae), and *Washingtonia filifera* (Arecaceae) (Table 3). Taxa persisting from cultivation comprise 14% of all nonnative taxa documented in the study,

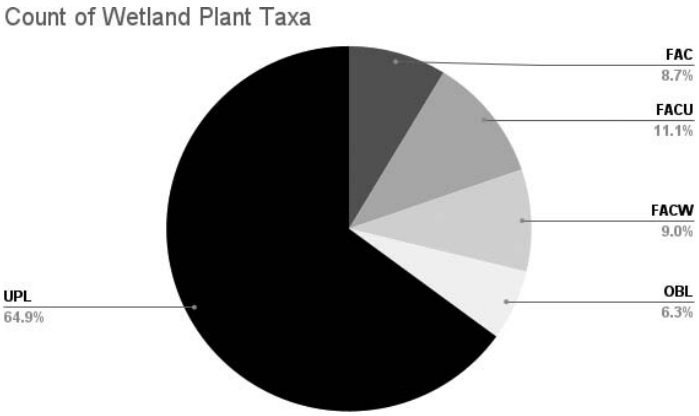

Figure 3.—Relative percentage of upland versus wetland plant taxa. UPL = Upland, FAC = Facultative, FACU = Facultative upland, FACW = Facultative wetland, OBL = Obligate (U.S. Army Corps of Engineers 2022).

67% are categorized as wetland plant taxa, and 89% are trees or large shrubs (Table 3).

DISCUSSION

Species Richness

Botanical diversity documented within the study area accounts for nearly 22% of the total vascular plant diversity known within the California desert, with just 48 springs containing 479 of the ~2200 vascular plant taxa known to occur in the region (André 2014; Jepson eFlora 2021). This level of diversity is extraordinary given that springs sampled make up less than 1% (or 0.000005%) of the total land area for the California desert. One of the largest springs surveyed, Morongo Canyon Springs, was also one of the most species-rich; however, spring size did not predict species richness across all sites. This may be due to two outlier springs that occupy a large area (Saline Marsh Spring at 12.8 ha and Salt Spring 8.3 ha), but have relatively low species richness (22 and 15 plant taxa, respectively; Table 1). These two outlier springs have 1.7 taxa/ha and 1.8 taxa/ha, respectively, while the 48 springs together have a mean of 395 taxa/ha and mode of 444 taxa/ha (Table 1). When we remove Salt Marsh Spring and Salt Spring from our analysis a positive relationship between spring size and species richness is recovered, indicating that springs with larger footprints have the capacity to support increased plant diversity. A physical parameter like high pH or high salinity may be a limiting factor for species richness, as observed at Saline Marsh Spring and Salt Spring, which exhibit high pH (8 and 8.21, respectively) and high salinity (7096 ppm at Salt Spring).

Pattern of Dissimilarity between Springs

The results of the field surveys document a large number of unique plant taxa occurring within desert springs (i.e., singletons), with nearly 40% (185 of 479) of the documented plant taxa recorded at only one site, indicating high beta diversity, and little overlap in plant species composition between sites (Supplemental Data Table 1). This could be influenced by a number of factors including relatively low species richness at a

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Table 3.—A checklist of all vascular taxa documented across 48 desert springs. Nonnative species are denoted with an asterisk (*). Life form (Calflora 2021) and wetland status are provided. UPL = Upland, FAC = Facultative, FACU = Facultative upland, FACW = Facultative wetland, OBL = Obligate (U.S. Army Corps of Engineers 2022).

*	Family	Species	Life form	Wetland
	Adoxaceae	*Sambucus nigra* L. subsp. *caerulea* (Raf.) Bolli	shrub	FACW
	Agavaceae	*Yucca brevifolia* Engelm.	tree	UPL
	Agavaceae	*Yucca schidigera* Roezl ex Ortgies	tree	UPL
*	Amaranthaceae	*Amaranthus albus* L.	annual	FACU
	Amaranthaceae	*Amaranthus fimbriatus* (Torr.) S. Watson	annual	UPL
	Amaranthaceae	*Amaranthus palmeri* S. Watson	annual	FACU
	Amaranthaceae	*Nitrophila occidentalis* (Moq.) S. Watson	perennial herb	FACW
	Amaranthaceae	*Tidestromia suffruticosa* (Torr.) Standl. var. *oblongifolia* (S. Watson) Sánch.Pino & Flores Olv.	annual	UPL
	Anacardiaceae	*Rhus aromatica* Aiton	shrub	FACU
	Anacardiaceae	*Rhus ovata* S. Watson	shrub	UPL
*	Apiaceae	*Apium graveolens* L.	perennial herb	UPL
	Apiaceae	*Berula erecta* (Huds.) Coville	perennial herb	OBL
	Apocynaceae	*Apocynum cannabinum* L.	perennial herb	FAC
	Apocynaceae	*Asclepias erosa* Torr.	perennial herb	UPL
	Apocynaceae	*Asclepias fascicularis* Decne.	perennial herb	FAC
	Apocynaceae	*Asclepias subulata* Decne.	perennial herb	UPL
	Apocynaceae	*Funastrum cynanchoides* (Decne.) Schltr. var. *hartwegii* (Vail) Krings	perennial herb	FACU
	Apocynaceae	*Funastrum hirtellum* (A. Gray) Schltr.	perennial herb	UPL
*	Apocynaceae	*Nerium oleander* L.	tree	UPL
*	Arecaceae	*Washingtonia filifera* (Linden ex André) H. Wendl. ex de Bary	tree	FAC
*	Arecaceae	*Washingtonia robusta* H. Wendl.	tree	FACW
	Asteraceae	*Adenophyllum porophylloides* (A. Gray) Strother	perennial herb	UPL
	Asteraceae	*Ambrosia acanthicarpa* Hook.	annual	UPL
	Asteraceae	*Ambrosia dumosa* (A. Gray) W.W. Payne	shrub	UPL
	Asteraceae	*Ambrosia psilostachya* DC.	perennial herb	FACU
	Asteraceae	*Ambrosia salsola* (Torr. & A. Gray) Strother & B.G. Baldwin	shrub	UPL
	Asteraceae	*Artemisia douglasiana* Besser	perennial herb	FAC
	Asteraceae	*Artemisia dracunculus* L.	perennial herb	FACU
	Asteraceae	*Artemisia ludoviciana* Nutt.	perennial herb	FACU
	Asteraceae	*Artemisia tridentata* Nutt.	shrub	FACU
	Asteraceae	*Atrichoseris platyphylla* (A. Gray) A. Gray	annual	UPL
	Asteraceae	*Baccharis brachyphylla* A. Gray	shrub	UPL
	Asteraceae	*Baccharis salicifolia* (Ruiz & Pav.) Pers. subsp. *salicifolia*	shrub	FAC
	Asteraceae	*Baccharis salicina* Torr. & A. Gray	shrub	FACW
	Asteraceae	*Baccharis sarothroides* A. Gray	shrub	FACU
	Asteraceae	*Baccharis sergiloides* A. Gray	shrub	FACU
	Asteraceae	*Bahiopsis parishii* (Greene) E.E. Schill. & Panero	shrub	UPL
	Asteraceae	*Baileya pleniradiata* Harv. & A. Gray	annual	UPL
	Asteraceae	*Bebbia juncea* (Benth.) Greene var. *aspera* Greene	shrub	UPL
	Asteraceae	*Brickellia californica* (Torr. & A. Gray) A. Gray	perennial herb	FACU
	Asteraceae	*Brickellia desertorum* Coville	shrub	UPL
	Asteraceae	*Brickellia knappiana* E. Drew	shrub	UPL
	Asteraceae	*Brickellia longifolia* S. Watson	shrub	UPL
	Asteraceae	*Brickellia microphylla* (Nutt.) A. Gray	shrub	UPL
	Asteraceae	*Calycoseris parryi* A. Gray	annual	UPL
*	Asteraceae	*Centaurea melitensis* L.	annual	UPL
	Asteraceae	*Chaenactis carphoclinia* A. Gray	annual	UPL
	Asteraceae	*Chaenactis fremontii* A. Gray	annual	UPL
	Asteraceae	*Chaenactis macrantha* D. Eaton	annual	UPL
*	Asteraceae	*Cichorium intybus* L.	perennial herb	FACU
	Asteraceae	*Cirsium mohavense* (E. Greene) Petrak	perennial herb	FACU
	Asteraceae	*Cirsium neomexicanum* A. Gray	perennial herb	UPL
	Asteraceae	*Cirsium occidentale* (Nutt.) Jeps. var. *venustum* (Greene) Jeps.	perennial herb	UPL
*	Asteraceae	*Cirsium vulgare* (Savi) Ten.	perennial herb	FACU
	Asteraceae	*Dieteria canescens* var. *leucanthemifolia* (Greene) D.R. Morgan & R.L. Hartm.	perennial herb	UPL
	Asteraceae	*Encelia actoni* (Elmer) D. D. Keck	shrub	UPL
	Asteraceae	*Encelia farinosa* Torr. & A. Gray	shrub	UPL
	Asteraceae	*Encelia frutescens* (A. Gray) A. Gray	shrub	UPL
	Asteraceae	*Enceliopsis covillei* (A. Nelson) S.F. Blake	perennial herb	UPL
	Asteraceae	*Ericameria cuneata* (A. Gray) McClatchie var. *spathulata* (A. Gray) H. M. Hall	shrub	UPL

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Table 3.—Continued.

*	Family	Species	Life form	Wetland
	Asteraceae	*Ericameria linearifolia* (DC.) Urbatsch & Wussow	shrub	UPL
	Asteraceae	*Ericameria nauseosa* var. *hololeuca* (A. Gray) G.L. Nesom & G.I. Baird	shrub	UPL
	Asteraceae	*Ericameria nauseosa* var. *mohavensis* (Greene) G.L. Nesom & G.I. Baird	shrub	UPL
	Asteraceae	*Ericameria nauseosa* var. *oreophila* (A. Nelson) G.L. Nesom & G.I. Baird	shrub	UPL
	Asteraceae	*Ericameria paniculata* (A. Gray) Rydb.	perennial herb	UPL
	Asteraceae	*Ericameria teretifolia* (Durand & Hilg.) Jeps.	shrub	UPL
	Asteraceae	*Erigeron canadensis* L.	annual	FACU
	Asteraceae	*Erigeron foliosus* Nutt. var. *foliosus*	perennial herb	UPL
	Asteraceae	*Eriophyllum ambiguum* (A. Gray) A. Gray	annual	UPL
	Asteraceae	*Eriophyllum confertiflorum* (DC.) A. Gray	shrub	UPL
	Asteraceae	*Eriophyllum lanosum* (A. Gray) A. Gray	annual	UPL
	Asteraceae	*Eriophyllum pringlei* A. Gray	annual	UPL
	Asteraceae	*Eriophyllum wallacei* (A. Gray) A. Gray	annual	UPL
	Asteraceae	*Euthamia occidentalis* Nutt.	perennial herb	FACW
	Asteraceae	*Gnaphalium palustre* Nutt.	annual	FACW
	Asteraceae	*Gutierrezia microcephala* (DC.) A. Gray	succulent	UPL
	Asteraceae	*Gutierrezia sarothrae* (Pursh) Britton & Rusby	shrub	UPL
	Asteraceae	*Helianthus annuus* L.	annual	FACU
	Asteraceae	*Isocoma acradenia* (E. Greene) E. Greene	shrub	FACU
	Asteraceae	*Iva axillaris* Pursh	perennial herb	FACU
*	Asteraceae	*Lactuca serriola* L.	annual	FACU
	Asteraceae	*Laennecia coulteri* (A. Gray) G.L. Nesom	annual	FAC
	Asteraceae	*Lepidospartum squamatum* (A. Gray) A. Gray	shrub	FACU
	Asteraceae	*Leptosyne bigelovii* (A. Gray) A. Gray	annual	UPL
	Asteraceae	*Leptosyne californica* Nutt.	annual	UPL
	Asteraceae	*Leucosyris carnosa* (A. Gray) Greene	shrub	OBL
	Asteraceae	*Logfia depressa* (A. Gray) Holub	annual	UPL
	Asteraceae	*Logfia filaginoides* (Hook. & Arn.) Morefield	annual	UPL
	Asteraceae	*Malacothrix glabrata* (D. C. Eaton) A. Gray	annual	UPL
	Asteraceae	*Monoptilon bellioides* (A. Gray) H. M. Hall	annual	UPL
	Asteraceae	*Nicolletia occidentalis* A. Gray	perennial herb	UPL
	Asteraceae	*Packera multilobata* (Torr. & A. Gray) W.A. Weber & Á. Löve	perennial herb	UPL
	Asteraceae	*Pectis papposa* Harvey & A. Gray	annual	UPL
	Asteraceae	*Perityle emoryi* Torr.	annual	UPL
	Asteraceae	*Pleurocoronis pluriseta* (A. Gray) R. King & H. Robinson	shrub	UPL
	Asteraceae	*Pluchea odorata* (L.) Cass.	annual	FACW
	Asteraceae	*Pluchea sericea* (Nutt.) Cov.	shrub	FACW
	Asteraceae	*Prenanthella exigua* (A. Gray) Rydb.	annual	UPL
	Asteraceae	*Psathyrotes annua* (Nutt.) A. Gray	annual	FACU
	Asteraceae	*Psathyrotes ramosissima* (Torr.) A. Gray	annual	UPL
*	Asteraceae	*Pseudognaphalium luteo-album* (L.) Hilliard & B.L. Burtt	annual	FAC
	Asteraceae	*Psilostrophe cooperi* (A. Gray) E. Greene	shrub	UPL
*	Asteraceae	*Pulicaria paludosa* Link	annual	FAC
	Asteraceae	*Pyrrocoma racemosa* (Nutt.) Torrey & A. Gray var. *paniculata* (Nutt.) J. Kartez & K. Gandhi	perennial herb	FAC
	Asteraceae	*Rafinesquia californica* Nutt.	annual	UPL
	Asteraceae	*Rafinesquia neomexicana* A. Gray	annual	UPL
	Asteraceae	*Senecio flaccidus* Less.	shrub	UPL
	Asteraceae	*Solidago cofinis* A. Gray	perennial herb	OBL
*	Asteraceae	*Sonchus asper* (L.) Hill	annual	FAC
*	Asteraceae	*Sonchus oleraceus* L.	annual	UPL
	Asteraceae	*Stephanomeria exigua* Nutt.	annual	UPL
	Asteraceae	*Stephanomeria pauciflora* (Nutt.) A. Nelson	perennial herb	UPL
	Asteraceae	*Stylocline micropoides* A. Gray	annual	UPL
	Asteraceae	*Symphyotrichum frondosum* (Nutt.) G.L. Nesom	annual	FACW
	Asteraceae	*Syntrichopappus fremontii* A. Gray	annual	UPL
*	Asteraceae	*Taraxacum officinale* Weber ex G. H. Wiggers	perennial herb	FACU
	Asteraceae	*Uropappus lindleyi* Nutt.	annual	UPL
	Asteraceae	*Xanthisma* (Pursh) D.R. Morgan & R.L. Hartm. var. *gooddingii* (A. Nelson) D.R. Morgan & R.L. Hartm.	perennial herb	UPL
	Asteraceae	*Xanthium strumarium* L.	annual	FAC
	Asteraceae	*Xylorhiza tortifolia* (Torr. & A. Gray) Greene var. *tortifolia*	perennial herb	UPL
	Bignoniaceae	*Chilopsis linearis* (Cav.) Sweet ssp. *arcuata* (Fosb.) Henrickson	shrub	FAC
	Boraginaceae	*Amsinckia intermedia* Fisch. & C.A. Mey.	annual	UPL

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Table 3.—Continued.

*	Family	Species	Life form	Wetland
	Boraginaceae	*Amsinckia menziesii* (Lehm.) A. Nelson & J.F. Macbr.	annual	UPL
	Boraginaceae	*Amsinckia tesselata* A. Gray	annual	UPL
	Boraginaceae	*Cryptantha angustifolia* (Torr.) E. Greene	annual	UPL
	Boraginaceae	*Cryptantha barbigera* (A. Gray) Greene	annual	UPL
	Boraginaceae	*Cryptantha circumscissa* (Hook. & Arn.) I. M. Johnst.	annual	UPL
	Boraginaceae	*Cryptantha decipiens* (M. E. Jones) A. Heller	annual	UPL
	Boraginaceae	*Cryptantha maritima* (E. Greene) E. Greene	annual	UPL
	Boraginaceae	*Cryptantha nevadensis* A. Nelson & Kennedy	annual	UPL
	Boraginaceae	*Cryptantha pterocarya* (Torr.) Greene	annual	UPL
	Boraginaceae	*Cryptantha racemosa* (S. Watson) E. Greene	annual	UPL
	Boraginaceae	*Cryptantha recurvata* Coville	annual	UPL
	Boraginaceae	*Cryptantha utahensis* (A. Gray) E. Greene	annual	UPL
	Boraginaceae	*Emmenanthe penduiflora* Benth. var. *penduiflora*	annual	UPL
	Boraginaceae	*Eriodictyon parryi* (A. Gray) Greene	perennial herb	UPL
	Boraginaceae	*Eriodictyon trichocalyx* A. Heller var. *trichocalyx*	shrub	UPL
	Boraginaceae	*Eucrypta chrysanthemifolia* (Benth.) Greene	annual	UPL
	Boraginaceae	*Eucrypta micrantha* (Torr.) A. A. Heller	annual	UPL
	Boraginaceae	*Heliotropium curassavicum* L. var. *oculatum* (A. Heller) I.M. Johnst. ex Tidestr.	perennial herb	FACU
	Boraginaceae	*Nama demissum* A. Gray var. *demissum*	annual	UPL
	Boraginaceae	*Pectocarya heterocarpa* (I. M. Johnston) I. M. Johnston	annual	UPL
	Boraginaceae	*Pectocarya linearis* (Ruiz & Pav.) DC. subsp. *ferocula* (I. M. Johnst.) Thorne	annual	UPL
	Boraginaceae	*Pectocarya penicillata* (Hook. & Arn.) A. DC.	annual	UPL
	Boraginaceae	*Pectocarya platycarpa* (Munz & I. M. Johnston) Munz & I. M. Johnston	annual	UPL
	Boraginaceae	*Pectocarya recurvata* I. M. Johnst.	annual	UPL
	Boraginaceae	*Pectocarya setosa* A. Gray	annual	UPL
	Boraginaceae	*Phacelia calthifolia* Brand	annual	UPL
	Boraginaceae	*Phacelia campanularia* A. Gray ssp. *vasiformis* G. Gillett	annual	UPL
	Boraginaceae	*Phacelia crenulata* Torr. var. *ambigua* (M. E. Jones) J. F. Macbride	annual	UPL
	Boraginaceae	*Phacelia distans* Benth.	annual	UPL
	Boraginaceae	*Phacelia fremontii* Torr.	annual	UPL
	Boraginaceae	*Phacelia ramosissima* Douglas ex Lehm.	perennial herb	FACU
	Boraginaceae	*Pholisma arenarium* Hook.	perennial herb	UPL
	Boraginaceae	*Pholistoma membranaceum* (Benth.) Constance	annual	UPL
	Brassicaceae	*Caulanthus cooperi* (S. Watson) Payson	annual	UPL
	Brassicaceae	*Caulanthus lasiophyllus* (Hook. & Arn.) Payson	annual	UPL
	Brassicaceae	*Descurainia pinnata* (Walter) Britton	annual	UPL
*	Brassicaceae	*Descurainia sophia* (L.) Webb ex Prantl	annual	UPL
	Brassicaceae	*Draba cuneifolia* Torr. & A. Gray	annual	UPL
*	Brassicaceae	*Hirschfeldia incana* (L.) Lagr.-Fossat	perennial herb	UPL
	Brassicaceae	*Lepidium flavum* Torr.	annual	UPL
	Brassicaceae	*Lepidium fremontii* S. Watson	perennial herb	UPL
	Brassicaceae	*Lepidium lasiocarpum* Torr. & A. Gray var. *lasiocarpum*	annual	UPL
	Brassicaceae	*Lepidium virginicum* L.	annual	FACU
	Brassicaceae	*Nasturtium officinale* R. Br.	perennial herb	OBL
*	Brassicaceae	*Sisymbrium irio* L.	annual	UPL
*	Brassicaceae	*Sisymbrium orientale* L.	annual	UPL
	Brassicaceae	*Stanleya pinnata* (Pursh) Britton var. *pinnata*	perennial herb	UPL
*	Brassicaceae	*Strigosella africana* (L.) Botsch.	annual	UPL
	Brassicaceae	*Thelypodium integrifolium* (Torr. & A. Gray) Endl. ssp. *affine* (E. Greene) Al-Shehbaz	perennial herb	FACW
	Brassicaceae	*Thysanocarpus curvipes* Hook.	annual	UPL
	Brassicaceae	*Thysanocarpus laciniatus* Nutt. ex Torr. & A. Gray	annual	UPL
	Brassicaceae	*Tropidocarpum gracile* Hook.	annual	UPL
	Cactaceae	*Cylindropuntia acanthocarpa* (Engelm. & J.M. Bigelow) F.M. Knuth var. *acanthocarpa*	perennial herb	UPL
	Cactaceae	*Cylindropuntia ramosissima* (Engelm.) F.M. Knuth	succulent	UPL
	Cactaceae	*Echinocactus polycephalus* Engelm. & J. Bigelow	succulent	UPL
	Cactaceae	*Echinocereus engelmannii* (Engelm.) Lamaire	succulent	UPL
	Cactaceae	*Ferocactus cylindraceus* (Engelm.) Orc.	succulent	UPL
	Cactaceae	*Mammillaria tetrancistra* Engelm.	succulent	UPL
	Cactaceae	*Opuntia basilaris* Engelm. & J. Bigel. var. *basilaris*	succulent	UPL
	Campanulaceae	*Nemacladus rubescens* E. Greene	annual	UPL
*	Caryophyllaceae	*Spergularia rubra* (L.) J. S. Presl & C. Presl	annual	FAC
	Chenopodiaceae	*Allenrolfea occidentalis* (S. Watson) Kuntze	shrub	FACW

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Table 3.—Continued.

*	Family	Species	Life form	Wetland
	Chenopodiaceae	*Atriplex canescens* (Pursh) Nutt. var. *canescens*	shrub	UPL
	Chenopodiaceae	*Atriplex canescens* var. *laciniata* Parish	shrub	UPL
	Chenopodiaceae	*Atriplex canescens* var. *linearis* (S. Watson) Munz	shrub	UPL
	Chenopodiaceae	*Atriplex confertifolia* (Torr. & Frém.) S. Watson	shrub	UPL
	Chenopodiaceae	*Atriplex elegans* (Moq.) D. Dietr. var. *fasciculata* (S. Watson) M. E. Jones	annual	UPL
	Chenopodiaceae	*Atriplex hymenelytra* (Torr.) S. Watson	shrub	UPL
	Chenopodiaceae	*Atriplex lentiformis* (Torr.) S. Watson	shrub	FAC
	Chenopodiaceae	*Atriplex parryi* S. Watson	shrub	FAC
	Chenopodiaceae	*Atriplex polycarpa* (Torr.) S. Watson	shrub	FACU
	Chenopodiaceae	*Atriplex rosea* L.	annual	FACU
	Chenopodiaceae	*Atriplex serenana* A. Nelson	annual	FAC
	Chenopodiaceae	*Atriplex torreyi* (S. Watson) S. Watson	annual	FACU
*	Chenopodiaceae	*Bassia hyssopifolia* (Pall.) Kuntze	annual	FACU
	Chenopodiaceae	*Chenopodium album* L.	annual	FACU
	Chenopodiaceae	*Chenopodium atrovirens* Rydb.	annual	UPL
	Chenopodiaceae	*Chenopodium berlandieri* Moq.	annual	UPL
	Chenopodiaceae	*Chenopodium californicum* (S. Watson) S. Watson	perennial herb	UPL
*	Chenopodiaceae	*Chenopodium murale* L.	annual	FACU
	Chenopodiaceae	*Chenopodium pratericola* Rydb.	annual	UPL
	Chenopodiaceae	*Chenopodium rubrum* L.	annual	FACW
	Chenopodiaceae	*Kochia californica* S. Watson	perennial herb	FACW
*	Chenopodiaceae	*Salsola paulsenii* Litv.	annual	UPL
*	Chenopodiaceae	*Salsola tragus* Nelson	annual	FACW
	Chenopodiaceae	*Stutzia covillei* (Standl.) E.H. Zacharias	annual	UPL
	Chenopodiaceae	*Suaeda nigra* (Raf.) J.F. Macbr.	perennial herb	OBL
	Cleomaceae	*Cleomella obtusifolia* Torr. & Frém	annual	UPL
	Cleomaceae	*Peritoma arborea* (Nutt.) H.H. Iltis var. *angustata* (Parish) H.H. Iltis	shrub	UPL
	Cleomaceae	*Wislizenia refracta* Engelm. ssp. *palmeri* (A. Gray) C. S. Keller	annual	FACU
	Convolvulaceae	*Cressa truxillensis* Kunth	perennial herb	FACW
	Convolvulaceae	*Cuscuta californica* Hook. & Arn.	annual	UPL
	Convolvulaceae	*Cuscuta campestris* Yunck.	annual	UPL
	Convolvulaceae	*Cuscuta denticulata* Engelm.	annual	UPL
	Convolvulaceae	*Cuscuta indecora* Choisy	annual	UPL
	Convolvulaceae	*Cuscuta subinclusa* Durand & Hilg.	annual	UPL
	Crassulaceae	*Dudleya arizonica* Rose	perennial herb	*UPL*
	Cucurbitaceae	*Cucurbita palmata* S. Watson	annual	UPL
	Cupressaceae	*Juniperus californica* Carrière	shrub	UPL
	Cupressaceae	*Juniperus osteosperma* (Torr.) Little	shrub	UPL
	Cyperaceae	*Carex alma* L. H. Bailey	graminoid	OBL
	Cyperaceae	*Carex aurea* Nutt.	graminoid	OBL
	Cyperaceae	*Carex praegracilis* W. Boott	graminoid	FACW
	Cyperaceae	*Cyperus involucratus* Rottb.	graminoid	FACW
	Cyperaceae	*Cyperus laevigatus* L.	graminoid	FACW
	Cyperaceae	*Eleocharis montevidensis* Kunth	graminoid	FACW
	Cyperaceae	*Eleocharis parishii* Britton	graminoid	FACW
	Cyperaceae	*Eleocharis rostellata* (Torr.) Torr.	graminoid	OBL
	Cyperaceae	*Fimbristylis thermalis* S. Watson	graminoid	OBL
	Cyperaceae	*Isolepis cernua* (Vahl) Roem. & Schult.	graminoid	OBL
	Cyperaceae	*Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller	graminoid	OBL
	Cyperaceae	*Schoenoplectus californicus* (C.A. Mey.) Soják	graminoid	OBL
	Cyperaceae	*Schoenoplectus pungens* (Vahl) Palla var. *longispicatus* (Britton) S.G. Sm.	graminoid	OBL
*	Elaeagnaceae	*Elaeagnus angustifolia* L.	tree	FAC
	Ephedraceae	*Ephedra californica* S. Watson	shrub	UPL
	Ephedraceae	*Ephedra funerea* Coville & C. Morton	shrub	UPL
	Ephedraceae	*Ephedra nevadensis* S. Watson	shrub	UPL
	Ephedraceae	*Ephedra viridis* Coville	shrub	UPL
	Equisetaceae	*Equisetum hyemale* L. subsp. *affine* (Engelm.) Calder & Roy L. Taylor	perennial herb	FACW
	Equisetaceae	*Equisetum laevigatum* A. Braun	perennial herb	FACW
	Euphorbiaceae	*Croton californicus* Muell. Arg.	perennial herb	UPL
	Euphorbiaceae	*Ditaxis neomexicana* (Muell. Arg.) A. A. Heller	annual	UPL
	Euphorbiaceae	*Euphorbia albomarginata* Torr. & A. Gray	perennial herb	UPL
	Euphorbiaceae	*Euphorbia micromera* Boiss.	annual	UPL

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Table 3.—Continued.

*	Family	Species	Life form	Wetland
	Euphorbiaceae	*Euphorbia polycarpa* Benth.	perennial herb	UPL
	Euphorbiaceae	*Euphorbia revoluta* Engelm.	annual	UPL
	Euphorbiaceae	*Euphorbia setiloba* Engelm.	annual	UPL
	Euphorbiaceae	*Euphorbia vallis-mortae* (Millsp.) J.T. Howell	perennial herb	UPL
	Euphorbiaceae	*Euphorbia serpyllifolia* Pers.	annual	UPL
	Euphorbiaceae	*Stillingia linearifolia* S. Watson	perennial herb	UPL
	Fabaceae	*Acmispon strigosus* (Nutt.) Brouillet	annual	UPL
	Fabaceae	*Glycyrrhiza lepidota* Pursh	perennial herb	FAC
	Fabaceae	*Lupinus concinnus* J. G. Agardh	annual	UPL
	Fabaceae	*Lupinus sparsiflorus* Benth.	annual	UPL
	Fabaceae	*Marina parryi* (Torr. & A. Gray) Barneby	perennial herb	UPL
*	Fabaceae	*Melilotus albus* Medikus	annual	FACU
*	Fabaceae	*Melilotus indicus* (L.) All.	annual	FACU
*	Fabaceae	*Parkinsonia aculeata* L.	tree	FAC
	Fabaceae	*Parkinsonia florida* (A. Gray) S. Watson	tree	UPL
	Fabaceae	*Parkinsonia microphylla* Torr.	tree	UPL
	Fabaceae	*Prosopis glandulosa* Torr. var. *torreyana* (L. Benson) M. Johnston	tree	FACU
	Fabaceae	*Prosopis pubescens* Benth.	tree	FAC
	Fabaceae	*Psorothamnus arborescens* (A. Gray) Barneby var. *minutifolius* (Parish) Barneby	shrub	FACU
	Fabaceae	*Psorothamnus fremontii* (A. Gray) Barneby	shrub	UPL
	Fabaceae	*Psorothamnus spinosus* (A. Gray) Barneby	tree	UPL
*	Fabaceae	*Robinia pseudoacacia* L.	tree	FACU
	Fabaceae	*Senegalia greggii* (A. Gray) Britton & Rose	shrub	FACU
	Fabaceae	*Senna armata* (S. Watson) H. Irwin & Barneby	shrub	UPL
	Gentianaceae	*Zeltnera exaltata* (Griseb.) G. Mans.	annual	FACW
*	Geraniaceae	*Erodium cicutarium* (L.) L'Hér. ex Aiton	annual	UPL
	Grossulariaceae	*Ribes velutinum* Greene	shrub	UPL
	Iridaceae	*Sisyrinchium bellum* S. Watson	perennial herb	FACW
	Juncaceae	*Juncus balticus* Willd. subsp. *ater* (Rydb.) Snogerup	graminoid	FACW
	Juncaceae	*Juncus bufonius* L.	annual	FACW
	Juncaceae	*Juncus cooperi* Engelm.	graminoid	FACW
	Juncaceae	*Juncus dubius* Engelm.	graminoid	FACW
	Juncaceae	*Juncus macrandrus* Coville	graminoid	OBL
	Juncaceae	*Juncus macrophyllus* Coville	graminoid	FACW
	Juncaceae	*Juncus mexicanus* Willd.	graminoid	FACW
	Juncaceae	*Juncus rugulosus* Engelm.	graminoid	OBL
	Juncaceae	*Juncus saximontanus* Nelson	graminoid	FACW
	Juncaceae	*Juncus xiphioides* E. Meyer	graminoid	OBL
	Juncaginaceae	*Triglochin concinna* Burtt Davy var. *debilis* (M.E. Jones) J.T. Howell	perennial herb	OBL
	Juncaginaceae	*Triglochin maritima* L.	perennial herb	OBL
	Krameriaceae	*Krameria bicolor* S. Watson	shrub	UPL
	Lamiaceae	*Condea emoryi* (Torr.) Harley & J.F.B. Pastore	shrub	UPL
*	Lamiaceae	*Marrubium vulgare* L.	perennial herb	FACU
*	Lamiaceae	*Mentha spicata* L.	perennial herb	OBL
	Lamiaceae	*Salvia columbariae* Benth.	annual	UPL
	Lamiaceae	*Scutellaria mexicana* (Torr.) A.J. Paton	shrub	UPL
	Lamiaceae	*Stachys albens* A. Gray	perennial herb	OBL
	Loasaceae	*Eucnide urens* (A. Gray) C. Parry	shrub	UPL
	Loasaceae	*Mentzelia albicaulis* Hook.	annual	UPL
	Loasaceae	*Mentzelia involucrata* S. Watson	annual	UPL
	Loasaceae	*Mentzelia obscura* H. J. Thompson & Joyce Roberts	annual	UPL
	Loasaceae	*Mentzelia reflexa* Coville	annual	UPL
	Lythraceae	*Lythrum californicum* Torr. & A. Gray	perennial herb	OBL
	Malvaceae	*Eremalche rotundifolia* (A. Gray) Greene	annual	UPL
	Malvaceae	*Fremontodendron californicum* (Torr.) Coville	shrub	UPL
	Malvaceae	*Malva parviflora* L.	annual	UPL
	Malvaceae	*Sphaeralcea ambigua* A. Gray var. *ambigua*	perennial herb	UPL
	Molluginaceae	*Mollugo cerviana* (L.) Ser.	annual	FAC
	Montiaceae	*Calyptridium monandrum* Nutt. in Torr. & A. Gray	annual	UPL
	Montiaceae	*Claytonia perfoliata* D. Donn ex Willd.	annual	FAC
*	Moraceae	*Morus nigra* L.	tree	UPL
*	Nelumbonaceae	*Nelumbo lutea* Pers.	perennial herb	OBL

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Table 3.—Continued.

*	Family	Species	Life form	Wetland
	Nyctaginaceae	*Boerhavia triquetra* S. Wats.	annual	UPL
	Nyctaginaceae	*Boerhavia wrightii* A. Gray	annual	UPL
	Nyctaginaceae	*Mirabilis albida* (Walter) Heimerl	perennial herb	UPL
	Nyctaginaceae	*Mirabilis laevis* (Benth.) Curran	perennial herb	UPL
	Oleaceae	*Forestiera pubescens* Nutt.	shrub	FACU
	Oleaceae	*Fraxinus dipetala* Hook. & Arn.	tree	UPL
	Oleaceae	*Fraxinus velutina* Torr.	tree	FAC
	Onagraceae	*Camissonia kernensis* (Munz) P. H. Raven ssp. *kernensis*	annual	UPL
	Onagraceae	*Camissonia strigulosa* (Fisch. & C. A. Mey.) P. H. Raven	annual	UPL
	Onagraceae	*Chylismia brevipes* (A. Gray) Small	annual	UPL
	Onagraceae	*Chylismia cardiophylla* (Torr.) Small	annual	UPL
	Onagraceae	*Chylismia claviformis* (Torr. & Frém.) A. Heller	annual	UPL
	Onagraceae	*Epilobium canum* (Greene) P. H. Raven	perennial herb	UPL
	Onagraceae	*Epilobium ciliatum* Raf. subsp. *ciliatum*	perennial herb	FACW
	Onagraceae	*Eremothera boothii* (Douglas) W.L. Wagner & Hoch ssp. *desertorum* (Munz) W.L. Wagner & Hoch	annual	UPL
	Onagraceae	*Eremothera chamaenerioides* (A. Gray) W.L. Wagner & Hoch	annual	UPL
	Onagraceae	*Eremothera refracta* (S. Watson) W.L. Wagner & Hoch	annual	UPL
	Onagraceae	*Eulobus californicus* Torr. & A. Gray	annual	UPL
	Onagraceae	*Gayophytum decipiens* Harlan Lewis & J. Szweykowski	annual	UPL
	Onagraceae	*Oenothera elata* Kunth ssp. *hookeri* (Torr. & A. Gray) W. Dietr. & W. L. Wagner	perennial herb	FACW
	Orchidaceae	*Epipactis gigantea* Dougles ex Hook.	perennial herb	OBL
	Orobanchaceae	*Castilleja chromosa* A. Nelson	perennial herb	UPL
	Orobanchaceae	*Castilleja foliolosa* Hook. & Arn.	perennial herb	UPL
	Orobanchaceae	*Castilleja linariifolia* Benth.	perennial herb	UPL
	Orobanchaceae	*Castilleja minor* (A. Gray) A. Gray subsp. *spiralis* (Jeps.) T.I. Chuang & Heckard	annual	OBL
	Orobanchaceae	*Chloropyron tecopense* (Munz & J.C. Roos) Tank & J.M. Egger	annual	FACW
	Papaveraceae	*Argemone munita* Durand & Hilg.	perennial herb	UPL
	Papaveraceae	*Eschscholzia minutiflora* S. Watson	annual	UPL
	Phrymaceae	*Diplacus bigelovii* (A. Gray) G.L. Nesom	annual	UPL
	Phrymaceae	*Erythranthe guttata* (Fisch. ex DC.) G.L. Nesom	annual	OBL
	Phrymaceae	*Erythranthe parishii* (Greene) G.L. Nesom & N.S. Fraga	annual	UPL
	Pinaceae	*Pinus monophylla* Torr. & Frém	tree	UPL
	Plantaginaceae	*Antirrhinum filipes* A. Gray	annual	UPL
	Plantaginaceae	*Keckiella antirrhinoides* (Benth.) Straw var. *microphylla* (A. Gray) N. Holmgren	shrub	UPL
	Plantaginaceae	*Penstemon incertus* Brandegee	shrub	UPL
	Plantaginaceae	*Penstemon palmeri* A. Gray	perennial herb	UPL
*	Plantaginaceae	*Plantago lanceolata* L.	perennial herb	FAC
*	Plantaginaceae	*Plantago major* L.	perennial herb	FAC
	Plantaginaceae	*Plantago ovata* Forssk. var. *fastigiata* (Morris) S.C. Meyers & A. Liston	annual	FACU
*	Plantaginaceae	*Veronica anagallis-aquatica* L.	perennial herb	OBL
	Platanaceae	*Platanus racemosa* Nutt.	tree	FAC
	Poaceae	*Andropogon glomeratus* (Walt.) Britton, Sterns, & Pogg. var. *scabriglumis* C. S. Campbell	graminoid	FACW
	Poaceae	*Aristida adscensionis* L.	annual	UPL
	Poaceae	*Aristida purpurea* Nutt.	graminoid	UPL
*	Poaceae	*Arundo donax* L.	graminoid	FACW
	Poaceae	*Bothriochloa barbinodis* (Lagasca) Herter	graminoid	UPL
	Poaceae	*Bouteloua aristidoides* (Kunth.) Griseb.	annual	UPL
	Poaceae	*Bouteloua barbata* Lagasca	annual	UPL
	Poaceae	*Bromus arizonicus* (Shear) Stebbins	annual	UPL
	Poaceae	*Bromus berteroanus* Colla	annual	UPL
*	Poaceae	*Bromus catharticus* Vahl	graminoid	UPL
*	Poaceae	*Bromus diandrus* Roth	annual	UPL
*	Poaceae	*Bromus rubens* L.	annual	UPL
*	Poaceae	*Bromus tectorum* L.	annual	UPL
*	Poaceae	*Cynodon dactylon* (L.) Pers.	graminoid	FACU
	Poaceae	*Dasyochloa pulchella* (Kunth) Willd. ex Rydberg	perennial herb	UPL
	Poaceae	*Distichlis spicata* (L.) Greene	graminoid	FAC
	Poaceae	*Elymus* × *gouldii* J.P. Sm. & Columbus	graminoid	UPL
	Poaceae	*Elymus cinereus* Scribn. & Merr.	graminoid	FAC
	Poaceae	*Elymus elymoides* (Raf.) Swezey	graminoid	FACU
	Poaceae	*Elymus triticoides* Buckley	graminoid	FAC
*	Poaceae	*Festuca arundinacea* Schreb.	graminoid	FACU

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Table 3.—Continued.

*	Family	Species	Life form	Wetland
*	Poaceae	*Festuca bromoides* L.	annual	FACU
	Poaceae	*Hilaria rigida* (Thurb.) Scribn.	graminoid	UPL
*	Poaceae	*Hordeum murinum* L. subsp. *glaucum* (Steud.) Tzvelev	annual	FAC
*	Poaceae	*Hordeum murinum* subsp. *leporinum* (Link) Arcang.	annual	FAC
	Poaceae	*Melica frutescens* Scribn.	graminoid	UPL
	Poaceae	*Melica imperfecta* Trin.	graminoid	UPL
	Poaceae	*Muhlenbergia asperifolia* (Nees & Meyen) Parodi	graminoid	FACW
	Poaceae	*Muhlenbergia rigens* (Benth.) Hitchc.	graminoid	FAC
	Poaceae	*Phragmites australis* (Cav.) Steud.	graminoid	FACW
	Poaceae	*Poa secunda* J. Presl	graminoid	FACU
*	Poaceae	*Polypogon interruptus* Kunth	graminoid	FACW
*	Poaceae	*Polypogon monspeliensis* (L.) Desf.	annual	FACW
*	Poaceae	*Polypogon viridis* (Gouan) Breistr.	graminoid	FACW
*	Poaceae	*Schismus arabicus* Nees	annual	UPL
*	Poaceae	*Schismus barbatus* (L.) Thell.	annual	UPL
*	Poaceae	*Sorghum bicolor* (L.) Moench	annual	FACU
	Poaceae	*Sporobolus airoides* (Torr.) Torr.	graminoid	FAC
	Poaceae	*Sporobolus cryptandrus* (Torr.) A. Gray	graminoid	FACU
	Poaceae	*Stipa hymenoides* Roem. & Schult.	graminoid	UPL
	Poaceae	*Stipa speciosa* Trin. & Rupr.	graminoid	UPL
	Polemoniaceae	*Aliciella latifolia* (S. Watson) J.M. Porter	annual	UPL
	Polemoniaceae	*Eriastrum densifolium* (Benth.) H. Mason	perennial herb	UPL
	Polemoniaceae	*Eriastrum diffusum* (A. Gray) H. Mason	annual	UPL
	Polemoniaceae	*Eriastrum eremicum* (Jeps.) H. Mason	annual	UPL
	Polemoniaceae	*Eriastrum pluriflorum* (A. Heller) H. Mason subsp. *albifaux* S.J. De Groot	annual	UPL
	Polemoniaceae	*Eriastrum sparsiflorum* (Eastw.) H. Mason	annual	UPL
	Polemoniaceae	*Gilia brecciarum* M. E. Jones subsp. *neglecta* A. D. Grant & V. Grant	annual	UPL
	Polemoniaceae	*Gilia cana* (M.E. Jones) A. Heller subsp. *speciformis* A.D. Grant & V.E. Grant	annual	UPL
	Polemoniaceae	*Gilia cana* subsp. *triceps* (Brand) A. D. Grant & V. Grant	annual	UPL
	Polemoniaceae	*Gilia ochroleuca* M. E. Jones subsp. *ochroleuca*	annual	UPL
	Polemoniaceae	*Gilia stellata* A. A. Heller	annual	UPL
	Polemoniaceae	*Gilia transmontana* (H. Mason & A. D. Grant) A. D. Grant & V. Grant	annual	UPL
	Polemoniaceae	*Ipomopsis polycladon* (Tor.) V. Grant	annual	UPL
	Polemoniaceae	*Leptosiphon chrysanthus* J.M. Porter & R. Patt.	annual	UPL
	Polemoniaceae	*Linanthus demissus* (A. Gray) Greene	annual	UPL
	Polemoniaceae	*Linanthus jonesii* (A. Gray) E. Greene	annual	UPL
	Polygonaceae	*Chorizanthe brevicornu* Torr.	annual	UPL
	Polygonaceae	*Chorizanthe staticoides* Benth.	annual	UPL
	Polygonaceae	*Eriogonum brachypodum* Torr. & A. Gray	annual	UPL
	Polygonaceae	*Eriogonum contiguum* (Rev.) Rev.	annual	UPL
	Polygonaceae	*Eriogonum davidsonii* Greene	annual	UPL
	Polygonaceae	*Eriogonum deflexum* Torr.	annual	UPL
	Polygonaceae	*Eriogonum elongatum* Benth.	perennial herb	UPL
	Polygonaceae	*Eriogonum fasciculatum* Benth. var. *polifolium* (Benth. in A. DC.) Torr. & A. Gray	shrub	UPL
	Polygonaceae	*Eriogonum inflatum* Torr. & Frém.	annual	UPL
	Polygonaceae	*Eriogonum maculatum* A. A. Heller	annual	UPL
	Polygonaceae	*Eriogonum nidularium* Coville	annual	UPL
	Polygonaceae	*Eriogonum plumatella* Durand & Hilg.	shrub	UPL
	Polygonaceae	*Eriogonum pusillum* Torr. & A. Gray	annual	UPL
	Polygonaceae	*Eriogonum rixfordii* S. Stokes	annual	UPL
	Polygonaceae	*Eriogonum thomasii* Torr.	annual	UPL
	Polygonaceae	*Oxytheca perfoliata* Torr. & A. Gray	annual	UPL
*	Polygonaceae	*Polygonum argyrocoleon* Kunze	annual	FAC
*	Polygonaceae	*Polygonum aviculare* L.	annual	FAC
*	Polygonaceae	*Polygonum ramosissimum* Michaux	annual	FAC
	Polygonaceae	*Rumex hymenosepalus* Torr.	perennial herb	UPL
	Polygonaceae	*Rumex salicifolius* Weinm.	perennial herb	FACW
	Portulacaceae	*Portulaca oleracea* L.	annual	FAC
	Pteridaceae	*Adiantum capillus-veneris* L.	perennial herb	FACW
	Pteridaceae	*Myriopteris parryi* (D. C. Eaton) Grusz & Windham	perennial herb	UPL
	Ranunculaceae	*Clematis ligusticifolia* Nutt.	perennial herb	FAC
	Ranunculaceae	*Ranunculus cymbalaria* Pursh	perennial herb	OBL

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Table 3.—Continued.

*	Family	Species	Life form	Wetland
	Resedaceae	*Oligomeris linifolia* (M. Vahl) J. F. Macbr.	annual	UPL
	Rhamnaceae	*Ziziphus obtusifolia* (Hook. ex Torr. & A. Gray) A. Gray	shrub	UPL
	Rosaceae	*Coleogyne ramosissima* Torr.	shrub	UPL
	Rosaceae	*Prunus fasciculata* A. Gray	shrub	UPL
	Rosaceae	*Purshia tridentata* (Pursh) DC. var. *glandulosa* (Curran) M. E. Jones	shrub	UPL
	Rosaceae	*Rosa californica* Cham. & Schlecht.	shrub	FAC
	Rosaceae	*Rosa woodsii* Lindl.	shrub	FACU
	Rubiaceae	*Galium angustifolium* Nutt. var. *angustifolium*	perennial herb	UPL
	Rubiaceae	*Galium angustifolium* subsp. *gracillimum* Dempster & Stebbins	perennial herb	UPL
*	Rubiaceae	*Galium aparine* L.	annual	FACU
	Rubiaceae	*Galium stellatum* Kellogg	shrub	UPL
	Ruscaceae	*Nolina bigelovii* (Torr.) S. Watson	perennial herb	UPL
	Salicaceae	*Populus fremontii* S. Watson	tree	FAC
	Salicaceae	*Salix exigua* Nutt.	shrub	FACW
	Salicaceae	*Salix gooddingii* C. Ball	tree	FACW
	Salicaceae	*Salix laevigata* Bebb	tree	FACW
	Salicaceae	*Salix lasiandra* Benth.	tree	FACW
	Salicaceae	*Salix lasiolepis* Benth.	shrub	FACW
	Saururaceae	*Anemopsis californica* (Nutt.) Hook. & Arn.	perennial herb	OBL
	Scrophulariaceae	*Scrophularia californica* Cham. & Schlecht.	perennial herb	FAC
	Selaginellaceae	*Selaginella bigelovii* Underw.	perennial herb	UPL
*	Simaroubaceae	*Ailanthus altissima* (Mill.) Swingle	tree	FACU
	Solanaceae	*Datura wrightii* Regel	perennial herb	UPL
	Solanaceae	*Lycium andersonii* A. Gray	shrub	UPL
	Solanaceae	*Lycium cooperi* A. Gray	shrub	UPL
	Solanaceae	*Nicotiana attenuata* Torr.	annual	FACU
	Solanaceae	*Nicotiana obtusifolia* Martens & Galeotti	perennial herb	FACU
	Solanaceae	*Physalis crassifolia* Benth.	annual	UPL
	Solanaceae	*Solanum americanum* Mill.	annual	FACU
	Solanaceae	*Solanum douglasii* Dunal in DC.	perennial herb	FAC
*	Tamaricaceae	*Tamarix aphylla* (L.) Karsten	shrub	FAC
*	Tamaricaceae	*Tamarix chinensis* Lour.	tree	FAC
*	Tamaricaceae	*Tamarix ramosissima* Ledeb.	tree	OBL
	Themidaceae	*Dipterostemon capitatus* (Benth.) Rydb.	perennial herb	FACU
	Theophrastaceae	*Samolus parviflorus* Raf.	perennial herb	OBL
	Typhaceae	*Typha domingensis* Pers.	perennial herb	OBL
	Typhaceae	*Typha latifolia* L.	perennial herb	OBL
*	Ulmaceae	*Ulmus pumila* L.	tree	UPL
	Urticaceae	*Parietaria hespera* Hinton	annual	FACU
	Urticaceae	*Urtica dioica* L. subsp. *holosericea* (Nutt.) Thorne	perennial herb	FAC
	Viscaceae	*Phoradendron californicum* Nutt.	shrub	UPL
	Viscaceae	*Phoradendron juniperinum* A. Gray	shrub	UPL
	Viscaceae	*Phoradendron leucarpum* (Raf.) Reveal & M.C. Johnst. subsp. *macrophyllum* (Engelm.) J.R. Abbott & R.L. Thomps.	shrub	UPL
	Vitaceae	*Vitis girdiana* Munson	shrub	FAC
	Zannichelliaceae	*Zannichellia palustris* L	perennial herb	OBL
	Zygophyllaceae	*Larrea tridentata* (DC.) Coville	shrub	UPL
*	Zygophyllaceae	*Tribulus terrestris* L.	annual	UPL

large proportion of sites, with nearly 50% of the springs having fewer than 20 taxa present (Table 1). Dissimilarity between springs may also be influenced by the wide dispersion of sampling locations across a broad geographic region, and the relatively high proportion of upland taxa. Upland plant taxa were primarily composed of annual herbs, which are ephemeral by nature, and their occurrence may be more influenced by local conditions (e.g., precipitation and temperature) than wetland taxa.

The most frequently encountered taxa were wetland and nonnative taxa; these are groups that are known to have high dispersal capacity (Soomers et al. 2013; Schöpke et al. 2019). Wetland plant taxa are frequently dispersed by wind and water, and wind dispersal has been shown to be an effective means for relatively long-distance dispersal (Soomers et al. 2013). Wind-dispersed taxa (e.g., *Populus fremontii*, *Salix* sp., and *Typha* sp.) may be especially important contributors to community assembly following significant disturbance (e.g., fire, grazing, or other habitat modification) because these fragmented habitats are not hydrologically connected by surface water (Soomers et al. 2013). Nonnative taxa are frequently readily dispersed and easily established (McKinney and La Sorte 2007). The most common nonnative species we documented were annual grasses that are known for their wide dispersal capacity and potential to invade

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Figure 4.—Selected rare plants documented as a part of this study. (A) *Chloropyron tecopense* (Orobanchaceae). (B) *Enceliopsis covillei* (Asteraceae). (C) *Fimbristylis thermalis* (Cyperaceae). (D) *Juncus cooperi* (Juncaceae).

and dominate habitats (Curtis and Bradley 2015; Brooks et al. 2016).

Taxa of Conservation Concern

Eight taxa of conservation concern were documented within the study area; three of these are wetland plant taxa. There are at least 23 plant taxa of conservation concern known to occur in wetland habitats in the California desert (CNPS 2022). The majority of these were not documented as a part of this study because they may be associated with spring outflow habitats or shallow groundwater (e.g., alkali wetland, marshes, and meadows), and may not be located at spring sources themselves. Rare plant taxa in California also tend to have highly limited and specific distributions (Thorne et al. 2009). Systematic surveys are needed to determine the status of rare plant taxa associated with desert springs in California because rare plants and their habitat

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Table 4.—List of plant taxa of conservation concern, their associated conservation ranks (CNPS 2022), and the number of springs in which they were documented.

Family	Taxon	CNPS Rare Plant Rank[a]	State Rank[b]	Global Rank	# of springs
Orobanchaceae	*Chloropyron tecopense*	1B.2	S1	G2	1
Polygonaceae	*Eriogonum contiguum*	2B.3	S2	G3	1
Euphorbiaceae	*Euphorbia revoluta*	4.3	S4	G5	1
Euphorbiaceae	*Euphorbia vallis-mortae*	4.2	S3	G3	1
Cyperaceae	*Fimbristylis thermalis*	2B.2	S1S2	G4	1
Juncaceae	*Juncus cooperi*	4.3	S3	G4	3
Asteraceae	*Enceliopsis covillei*	1B.2	S2	G2	1

[a] California Native Plant Society (CNPS) Rare Plant Rank:
1B.2: rare, threatened, or endangered in California or elsewhere; moderately threatened.
2B.2: rare, threatened, or endangered in California but more elsewhere; moderately threatened.
2B.3: rare, threatened, or endangered in California but more elsewhere; not very threatened.
4.2: limited distribution watch list; moderately threatened.
4.3: limited distribution watch list; not very threatened.
[b] California State Rank:
S1: critically imperiled because of extreme rarity.
S2: imperiled due to restricted range.
S1S2: rank is between S1 and S2.
S3: vulnerable due to restricted range.
S4: apparently secure; uncommon but not rare.

are highly impacted by the same suite of disturbances that affect desert springs including groundwater pumping, habitat conversion, invasive species, cattle grazing, and feral animals (Fraga et al. 2021; Parker et al. 2021).

Chloropyron tecopense (Tecopa bird's beak) is presumed extirpated at Borehole Spring. Since 2008, discharge at Borehole Spring appears to have slowly decreased, although recreational use of the spring and other human activities have increased substantially during that time frame resulting in channel modifications and vehicle trespass (Partner Engineering and Science, Inc. 2020). This demonstrates the vulnerability of rare plant taxa to local extinction when their habitats are subject to hydrological change and other disturbance.

Species Persisting from Cultivation

We documented nine species persisting from cultivation. These are primarily large shrubs or trees that are known to occur in wetland environments. These taxa can have a disproportionate influence on spring habitats (Sala et al. 1996; Fleishman et al. 2003; Neale et al. 2011). For instance, *Tamarix* can increase water loss from wetland environments due to high rates of evapotranspiration from their high leaf surface area (Sala et al. 1996). Similar mechanisms could be occurring in large trees and shrubs planted at sites that have large water demands. Further, large, woody, nonnative species have a greater community composition effect because they can displace native species and modify the structure and composition of the associated flora via competition for resources such as water, space, and light (Fleishman et al. 2003). However, wildlife (e.g., native birds and mammals) may also utilize these large trees and shrubs persisting from cultivation for shelter, shade, and nesting sites, complicating recommended management actions such as nonnative species removal.

Evidence of Floristic Change

Herbarium specimen records provide valuable baseline data that can be used to evaluate floristic change at sites, especially relating to changing hydrology and water availability at desert springs. We detected floristic change at Mesquite Spring, which currently occupies a relatively small footprint (0.142 ha) and no longer has surface water present (Table 1). Four perennial native wetland taxa no longer occur at the site and are presumed extirpated due to changes in hydrological conditions. Historical records indicate that water flowed at the site and that perhaps wild grapes (*Vitis* sp.) and roses (*Rosa* sp.) once grew there (Parker et al. 2021). Our study documented the loss of four wetland taxa. The floristic data provided here serve as another temporal point to evaluate change in plant species composition through time, which will become increasingly important as the climate is expected to become hotter and drier.

Floristic Diversity as a Metric for Conservation Value

A botanical assessment of the 48 springs in this study is a first step toward evaluating their relative importance for biodiversity conservation in a changing climate. Species richness is frequently used as a metric for assessing conservation value and priorities (Fleishman et al. 2006). However, beyond species richness, a more complete evaluation of the site-level floristic diversity can provide additional criteria to evaluate conservation value. This may include the proportion of native versus nonnative taxa, diversity of life forms that influence structure and function of ecosystems, species persistence and longevity, and the proportion of taxa that are rare and sensitive to land use change.

The results from this floristic inventory have several important implications for assessment of the conservation value of desert springs, and for land management and restoration activities. First, these ecosystems collectively support a large proportion of plant diversity in the California desert. They are a valuable resource for the conservation of landscape-scale plant diversity because they serve as reservoirs and refugia. Second, rare plant taxa are vulnerable to local extirpation, especially due to hydrological change. Third, the high beta diversity and dissimilarity between spring sites indicates that each spring represents a unique assemblage of plant species. Thus,

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restoration and management activities at California desert springs likely need to be highly individualized and site specific. Finally, to maximize the potential for desert springs to serve as refugia under changing climate conditions, inventory and monitoring are essential to recognize warning signs, including changing species composition and local extirpation of wetland-dependent species. Protection from non-climate threats such as water diversion and groundwater pumping, disturbance from feral animals, grazing, and habitat conversion are key to support long-term conservation of these life-sustaining ecosystems.

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Naomi Fraga is Director of Conservation Programs at California Botanic Garden and Research Assistant Professor at Claremont Graduate University in Claremont, California. She received her Ph.D. in Botany from Claremont Graduate University, and she also holds a M.S. in Botany from Claremont Graduate University and a B.S. in Botany and Biology from California Polytechnic University, Pomona. Her research interests include plant geography, conservation biology, rare plants, and taxonomy of monkeyflowers (Phrymaceae). She has been involved in floristics research since 2001.

Brian Cohen is a Spatial Data Scientist for The Nature Conservancy's California Program. During his 17 years at the Conservancy, Brian has interpreted data and developed visual tools to help solve California's most pressing environmental challenges including the impact of development of renewable energy in the Mojave/Sonoran Desert, the potential impact of sea level rise along the coast of California, mountain lion movement analysis in Southern California, and large-scale species recovery efforts on California islands.

Andy Zdon is a hydrogeologist and Technical Director for Roux with more than 33 years of hydrogeological experience in a variety of hydrogeology-related projects. He is a California Professional Geologist, Certified Hydrogeologist and Certified Engineering Geologist, Arizona Professional Geologist, and Utah Professional Geologist.

Maura Palacios Mejia is a professor in the Biology department at Mt. San Antonio College. She received her Ph.D. in Wildlife & Fisheries Sciences from Texas A&M University, M.S. in Biology with an emphasis in Marine Biology from California State University, Los Angeles, and a B.S. in Marine Biology & Zoology from California State University, Long Beach. Her research interests use molecular methods like environmental DNA to assess ecological communities to inform or evaluate conservation and restoration management practices. She also shares a strong passion for broadening access to sustainable organic gardening, particularly in underrepresented communities.

Sophie Parker is a Lead Scientist for the Climate Program in the California chapter of The Nature Conservancy. She has conducted research on a variety of ecology and conservation science topics over the past two decades, including soil and ecosystem ecology, renewable energy siting, ecology of desert springs, and urban biodiversity and nature-based solutions. She holds a B.A. in Biological Sciences from Wellesley College and a Ph.D. in Ecology, Evolution, and Marine Biology from the University of California, Santa Barbara.

LITERATURE CITED

André, J.M. 2014. Floristic diversity and discovery in the California Desert. Fremontia 42:3–8.

Andy Zdon and Associates. 2016. Mojave Desert springs and waterholes: Results of the 2015–2016 Mojave Desert spring survey. Report prepared for Transition Habitat Conservancy, Bureau of Land Management, and The Nature Conservancy.

Baldwin, B.G., D. Goldman, D.J. Keil, R. Patterson, and T.J. Rosatti, eds. 2012. The Jepson Manual: Vascular Plants of California. University of California Press, Berkeley, CA.

Bogan, M.T., N. Noriega-Felix, S.L. Vidal-Aguilar, L.T. Findley, D.A. Lytle, O.G. Gutiérrez-Ruacho, J.A. Alvarado-Castro, and A. Varela-Romero. 2014. Biogeography and conservation of aquatic fauna in spring-fed tropical canyons of the southern Sonoran Desert, Mexico. Biodiversity and Conservation 23:2705–2748.

Brooks, M.L., C.S. Brown, J.C. Chambers, C.M. D'Antonio, J.E. Keeley, and J. Belnap. 2016. Exotic annual *Bromus* invasions: Comparisons among species and ecoregions in the western United States. Pp. 11–60 *in* M. Germino, J. Chambers, and C. Brown, eds., Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US. Springer Series on Environmental Management. Springer, Cham, Switzerland.

Calflora. 2022. Information on California plants for education, research and conservation. The Calflora Database, Berkeley, CA. Accessed 2022 from <https://www.calflora.org/>.

Cartwright, J.M, K.A. Dwire, Z. Freed, S.J. Hammer, B. McLaughlin, L.W. Misztal, E.R. Schenk, J.R. Spence, A.E. Springer, and L.E. Stevens. 2020. Oases of the future? Springs as potential hydrologic refugia in drying climates. Frontiers in Ecology and the Environment 18:245–253.

[CCH2] Consortium of California Herbaria. 2019. Specimen data. Accessed 2019 from <https://www.cch2.org/portal/index.php>.

[CNDDB] California Natural Diversity Database. 2018. RareFind 5. Version 5.2.14. California Department of Fish and Wildlife. Accessed 2018 from <https://map.dfg.ca.gov/rarefind/view/RareFind.aspx>.

[CNPS] California Native Plant Society. 2022. Inventory of rare and endangered plants of California (online edition, v9-01 1.0). Rare Plant Program. Accessed 2022 from <http://www.rareplants.cnps.org>.

Curtis, C.A., and B.A. Bradley. 2015. Climate change may alter both establishment and high abundance of red brome (*Bromus rubens*) and African mustard (*Brassica tournefortii*) in the semiarid southwest United States. Invasive Plant Science and Management 8:341–352.

Davis, J.A., A. Kerezsy, and S. Nicol. 2017. Springs: Conserving perennial water is critical in arid landscapes. Biological Conservation 211:30–35.

de Grenade, R. 2013. Date palm as a keystone species in Baja California peninsula, Mexico oases. Journal of Arid Environments 94:59–67.

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Fleishman, E., N. McDonal, R. MacNally, D.D. Murphy, J. Walters, and T. Floyd. 2003. Effects of floristics, physiognomy and non-native vegetation on riparian bird communities in a Mojave Desert watershed. Journal of Animal Ecology 72:484–490.

Fleishman, E., R. Noss, and B. Noon. 2006. Utility and limitations of species richness metrics for conservation planning. Ecological Indicators 6:543–553.

[FNA] Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico [online]. 22+ vols. New York, NY and Oxford, UK. Accessed 2021 from <http://beta.floranorthamerica.org>.

Fraga, N.S., A.L. Miller, S.J. De Groot, C. Lee, C.L. Lund, and K. Moore-O'Leary. 2021. Status of the Amargosa niterwort (Amaranthaceae) in California and Nevada. California Fish and Wildlife Journal, CESA Special Issue: 78–95.

Glenn, E.P., L. Mexicano, J. Garcia-Hernandez, P.L. Nagler, M.M. Gomez-Sapiens, D. Tang, M.A. Lomeli, J. Ramirez-Hernandez, and F. Zamora-Arroyo. 2013. Evapotranspiration and water balance of an anthropogenic coastal desert wetland: Responses to fire, inflows and salinities. Ecological Engineering 59:176–184.

Jepson Flora Project, eds. 2022. Jepson eFlora. Accessed 6 Jan 2022 from <https://ucjeps.berkeley.edu/eflora/>.

McKinney, M.L., and F.A. La Sorte. 2007. Invasiveness and homogenization: Synergism of wide dispersal and high local abundance. Global Ecology and Biogeography 16:394–400.

McLaughlin, B.C., D.D. Ackerly, P.Z. Klos, J. Natali, T.E. Dawson, and S.E. Thompson. 2017. Hydrologic refugia, plants, and climate change. Global Change Biology 23:2941–2961.

Meixner, T., A.H. Manning, D.A. Stonestrom, D.M. Allen, H. Ajami, K.W. Blasch, A.E. Brookfield, C.L. Castro, J.F. Clark, D.J. Gochis, et al. 2016. Implications of projected climate change for groundwater recharge in the western United States. Journal of Hydrology 534:124–138.

Neale, C.M.U., H. Geli, S. Taghvaeian, A. Masih, R.T. Pack, R.D. Simms, M. Baker, J.A. Milliken, S. O'Meara, and A.J. Witherall. 2011. Estimating evapotranspiration of riparian vegetation using high resolution multispectral, thermal infrared and lidar data. Proceedings of SPIE 8174, Remote Sensing for Agriculture, Ecosystems, and Hydrology XIII, C.M.U. Neale and A. Maltese, eds. Prague, Czech Republic.

Omernik, J.M. 1987. Ecoregions of the conterminous United States. Annals of the Association of American Geographers 77:118–125.

Palacios Mejia, M., E. Curd, K. Edalati, M.A. Renshaw, R. Dunn, D. Potter, N. Fraga, J. Moore, J. Saiz, R. Wayne, and S.S. Parker. 2021. The utility of environmental DNA from sediment and water samples for recovery of observed plant and animal species from four Mojave Desert springs. Environmental DNA 3:214–230.

Parker, S.S., A. Zdon, W.T. Christian, B.S. Cohen, M. Palacios Mejia, N.S. Fraga, E.E. Curd, K. Edalati, and M.A. Renshaw. 2021. Conservation of Mojave Desert springs and associated biota: Status, threats, and policy opportunities. Biodiversity and Conservation 30:311–327.

Partner Engineering and Science, Inc. 2020. 2020 Amargosa state of the basin report, Inyo and San Bernardino counties, California and Nye and Clark counties, Nevada.

Patten, D.T., L. Rouse, and J.C. Stromberg. 2008. Isolated spring wetlands in the Great Basin and Mojave deserts, USA: Potential response of vegetation to groundwater withdrawal. Environmental Management 41:398–413.

Sada, D.W., E. Fleishman, and D.D. Murphy. 2005. Associations among spring-dependent aquatic assemblages and environmental and land use gradients in a Mojave Desert mountain range: Spring-dependent assemblages and disturbance gradients. Diversity and Distributions 11:91–99.

Sala, A., S.D. Smith, and D.A. Devitt. 1996. Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave Desert floodplain. Ecological Applications 6:888–898.

Schöpke, B., J. Heinze, M. Pätzig, and T. Heinken. 2019. Do dispersal traits of wetland plant species explain tolerance against isolation effects in naturally fragmented habitats? Plant Ecology 220:801–815.

SEINet. 2019. SEINet data portal. Accessed 2019 from <https://swbiodiversity.org/seinet/>.

Soomers, H., D. Karssenberg, M.B. Soons, P.A. Verweij, J.T.A. Verhoeven, and M.J. Wassen. 2013. Wind and water dispersal of wetland plants across fragmented landscapes. Ecosystems 16:434–451.

Thorne, J.H., J.H. Viers, J. Price, and D.M. Stoms. 2009. Spatial patterns of endemic plants in California. Natural Areas Journal 29:344–366.

U.S. Army Corps of Engineers. 2022. National Wetland Plant List. Accessed 2022 from <https://wetland-plants.sec.usace.army.mil/nwpl_static/v34/home/home.html>.

Zdon, A., M.L. Davisson, and A.H. Love. 2018. Understanding the source of water for selected springs within Mojave Trails National Monument, California. Environmental Forensics 19:99–111.

Zdon, A., and A.H. Love. 2020. Groundwater forensics approach for differentiating local and regional springs in arid eastern California, USA. Environmental Forensics 22:302–314.

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