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Research Article

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

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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 widescale 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 km² (Omernick 1987). This study is focused on 48 springs that occupy an area of approximately 35 km², 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 onscreen. 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

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 \pm 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),

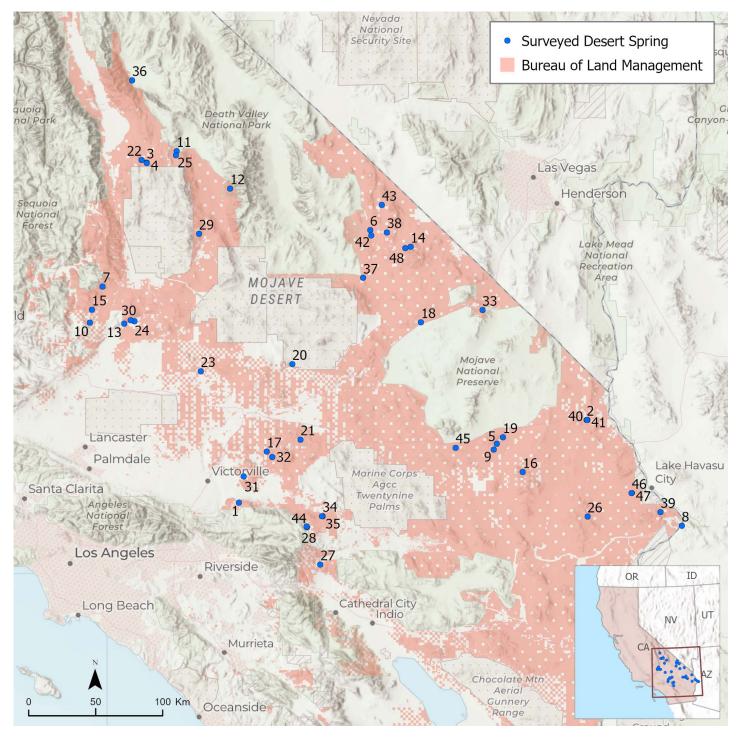


Figure 1.- Location of 48 springs in the Mojave and Sonoran deserts. All springs are on land managed by the Bureau of Land Management (Table 1).

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 \pm 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).



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

| 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,

Count of Wetland Plant Taxa

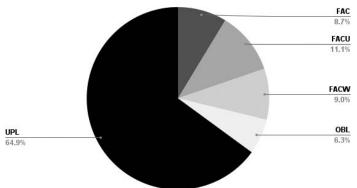


Figure 3.—Relative percentage of upland versus wetland plant taxa. UPL = Upland, FAC = Facultative, FACU = Facultative upland, FACW = Facultative wetland, OBL = Obligate (U.S. Army Corps of Engineers 2022).

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 \sim 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

| 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 julyta (Linder) et Andrey H. Wendi, ex de Dary | 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 psilosiachya DC. 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 |
| | | Artemisia ludoviciana Nutt. | perennial herb | FACU |
| | Asteraceae | Artemisia tudoviciana Nutt. | shrub | FACU |
| | Asteraceae | Artemisia iriaeniaia Nutt. Atrichoseris platyphylla (A. Gray) A. Gray | annual | UPL |
| | Asteraceae | | shrub | UPL |
| | Asteraceae | Baccharis brachyphylla A. Gray Baccharis salicifolia (Ruiz & Pav.) Pers. subsp. salicifolia | shrub | FAC |
| | Asteraceae | | shrub | FAC |
| | Asteraceae | Baccharis salicina Torr. & A. Gray | | |
| | 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 |

| 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 |
| | | | UPL |
| Asteraceae | Psilostrophe cooperi (A. Gray) E. Greene Pulicaria paludosa Link | shrub | |
| Asteraceae | 1 | 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 |
| | Chilopsis linearis (Cav.) Sweet ssp. arcuata (Fosb.) Henrickson | shrub | FAC |
| Bignoniaceae Boraginaceae | · · · · · · · · · · · · · · · · · · · | | |
| погаятнасеае | Amsinckia intermedia Fisch. & C.A. Mey. | annual | UPL |

| Family | Species | Life form | Wetlan |
|----------------|--|----------------|--------|
| 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 |
| 0 | | 1 | |
| 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 |
| 0 | | | UPL |
| Boraginaceae | Phacelia crenulata Torr. var. ambigua (M. E. Jones) J. F. Macbride | annual | |
| 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.) LagrFossat | 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 |
| | | | UPL |
| Cactaceae | Echinocactus polycephalus Engelm. & J. Bigelow | succulent | |
| 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 |
| Campanulacea | Nemacladus rubescens E. Greene | annual | UPL |
| Caryophyllacea | | annual | FAC |
| Caryophynacea | | | |

| ł | 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 attovirens Rydb. | annual | UPL |
| | | Chenopodium unovnens Kydo. Chenopodium berlandieri Moq. | annual | UPL |
| | Chenopodiaceae | | | |
| | 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 |
| | | • | annual | UPL |
| | Convolvulaceae | Cuscuta subinclusa Durand & Hilg. | | |
| | 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 |
| | | Schoenoplectus pungens (Vahl) Palla var. longispicatus (Britton) S.G. Sm. | | |
| | Cyperaceae | | 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 |
| | 1 | $\mathcal{O}^{\prime\prime}$ | | |
| | Euphorbiaceae | Euphorbia albomarginata Torr. & A. Gray | perennial herb | UPL |

| * | 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 tremontii (A. Gray) Barneby | shrub | UPL |
| | Fabaceae | Psorothamnus spinosus (A. Gray) Barneby | | UPL |
| | | | tree | |
| | 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 |
| | | | | UPL |
| | Loasaceae | Mentzelia involucrata S. Watson | annual | |
| | 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 |
| | Managaaa | Morus nigra L. | tree | UPL |
| | Moraceae | | lice | OIL |

| Nyctaginaceae Nyctaginaceae | Boerhavia triquetra S. Wats. | | |
|--------------------------------|---|----------------|------|
| Nyctaginaceae | Deciminar influence of the dot | annual | UPL |
| | 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 |
| | Epilobium canum (Greene) P. H. Raven | perennial herb | UPL |
| Onagraceae | | * | |
| 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 | 1, 1 | | UPL |
| 1 | Argemone munita Durand & Hilg. | perennial herb | |
| 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. | * | FAC |
| | | tree | |
| 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 | <i>Elymus</i> $	imes$ <i>gouldii</i> 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 |
| | Festuca arundinacea Schreb. | graminoid | FACU |

| * | 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 |
| | | Schismus arabicus Nees | | UPL |
| | Poaceae | | annual | |
| | 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 | | | UPL |
| | | Gilia cana subsp. triceps (Brand) A. D. Grant & V. Grant | annual | |
| | 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 |
| | | | | UPL |
| | Polygonaceae | Eriogonum fasciculatum Benth. var. polifolium (Benth. in A. DC.) Torr. & A. Gray | shrub | |
| | 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 |
| | | Rumex nymenosepatus 10fr. Rumex salicifolius Weinm. | * | FACW |
| | Polygonaceae | | perennial herb | |
| | 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 |

| * 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 |
| Scrophulariac | 1 5 | perennial herb | FAC |
| Selaginellacea | | perennial herb | |
| * Simaroubacea | | 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 | |
| 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 | |
| Theophrastace | | perennial herb | OBL |
| Typhaceae | Typha domingensis Pers. | 1 | OBL |
| /1 | <i>/1</i> 0 | perennial herb | |
| 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 | |
| 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 |
| Zannichelliace | 1 | perennial herb | OBL |
| Zygophyllacea | | shrub | UPL |
| * Zygophyllacea | e 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). Winddispersed 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



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

| 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 |

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.

^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, 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 wetlanddependent 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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