

I. SPECIES	<p align="center">The woody <i>Diplacus</i> of southern California (formerly the <i>Mimulus aurantiacus</i> species complex)</p> <p align="center">Family: Phrymaceae; Subclass: Asteridae Order: Scrophulariales; Class: Magnoliopsida</p>			
<p>A. Taxa of <i>Diplacus</i> Primarily sensu Barker et al. (2012)</p> <p>NRCS CODES:</p> <ol style="list-style-type: none"> 1. DIAR6 (MIAR2) 2. DIAU (DIAUA, MIAUA) 3. none (DIAUA2, DIAUA) 4. DICA12 (MILOC) 5. DILO6 (DILOC, MILO) 6. DIPA10 (MIPA11) 7. DIPU4 (MIPU3) 	<p>Taxa that occur in southern California that were within the former <i>M. aurantiacus</i> complex:</p> <ol style="list-style-type: none"> 1. <i>Diplacus aridus</i> Abrams 2. <i>Diplacus aurantiacus</i> (Curtis) Jeps. (included for context owing to complex synonymies) 3. <i>Diplacus x australis</i> (McMinn ex Munz) Tulig 4. <i>Diplacus calycinus</i> Eastw. 5. <i>Diplacus longiflorus</i> Nutt. 6. <i>Diplacus parviflorus</i> Greene 7. <i>Diplacus puniceus</i> Nutt. <p>(note: <i>Diplacus rutilis</i> (A. L. Grant) McMinn, Santa Susanna monkeyflower, recognized by Barton et al. (2012) is included as a form of <i>D. longiflorus</i> in this profile (see I. C. Special Note, below).</p> <p>Other taxa from central to northern California not treated in detail, but listed here for context):</p> <ol style="list-style-type: none"> A. <i>Diplacus grandiflorus</i> Groenland B. <i>Diplacus linearis</i> (Benth.) Greene C. <i>Diplacus x lompocensis</i> McMinn (from hybridization of <i>D. longiflorus</i> and <i>D. aurantiacus</i>.) 			
<p>B. Crosswalk of Intraspecific taxa of <i>Mimulus aurantiacus</i> (<i>sensu</i> Thompson 2012) in relation to above numbered <i>Diplacus</i> taxa (<i>sensu</i> Barker et al. 2012).</p>	<p><i>M. a.</i> var. <i>aridus</i> (Abrams) D. M. Thompson— synonymous with 1. <i>D. aridus</i> <i>M. a.</i> var. <i>aurantiacus</i>— included 2. <i>D. aurantiacus</i> and 3. <i>D. x australis</i> <i>M. a.</i> var. <i>grandiflorus</i> (Lindl. & Paxton) D. M. Thompson— included A. and B, above <i>M. a.</i> var. <i>parviflorus</i> (Greene) D. M. Thompson— synonymous with 6. <i>D. parviflorus</i>. <i>M. a.</i> var. <i>pubescens</i> (Torr.) D. M. Thompson— included 4. <i>D. calycinus</i> and 5. <i>D. longiflorus</i>, and the red form referred to as <i>D. rutilis</i>. <i>M. a.</i> var. <i>puniceus</i> (Nutt.) D. M. Thompson— synonymous with 7. <i>D. puniceus</i>.</p>			
<p>C. Special Note on Nomenclature and why there are so many taxa in this profile.</p> <p>Note, 3/16/2020: The genus <i>Diplacus</i> has been updated in the Flora of North America, Online version (FNA) and in the Jepson eFlora. See URLs at end of this profile. <i>D. rutilis</i> is treated at species level in FNA, but as a color form of <i>D. longiflorus</i> in the Jepson eFlora.</p>	<p>For most profiles, we follow the classification in the printed Jepson Manual (Baldwin et al. 2012). However, a major rearrangement of genera and species within the family Phrymaceae occurred after the 2012 edition went to press. The new classification for the bush monkeyflowers will be updated for the Jepson E-Flora, following Barker et al. (2012) with few exceptions (Naomi Fraga pers. com.). Tulig & Nesom (2012) and Barker et al. (2012) made a strong case for elevating the woody monkeyflowers that were part of <i>Mimulus</i> section <i>Diplacus</i> to the genus <i>Diplacus</i> section <i>Diplacus</i>. They also elevated the six subspecific taxa of <i>Mimulus aurantiacus</i> from the Jepson Manual treatment (Thompson 2012) to the species level and recognized additional taxa similar to McMinn (1951). Forms that Thompson (2012) recognized as part of <i>Mimulus aurantiacus</i> var. <i>pubescens</i> were split out as <i>D. calycinus</i>, <i>D. longiflorus</i>, and the red-flowered <i>D. rutilis</i>. However, the new classification will place <i>D. rutilis</i> as a color variant under <i>D. longiflorus</i> (Naomi Fraga pers. com.), consistent with the findings of Chase et al. (2017). For southern California, one hybrid taxon, <i>D. x australis</i> was also included; however this may change based on evidence that "australis" is more likely an ecotype of <i>D. puniceus</i> rather than a taxon derived from hybridization (Chase et al. 2017). Chase et al. (2017) analyzed the relationships among all the woody monkeyflower taxa recognized by Tulig & Nesom (2012) and Thompson (2012) using floral trait and molecular data (genome-wide single nucleotide polymorphisms, or SNPs).</p> <p>Because of the fluid taxonomy, the close relationships, and the many life-history features shared by the bush monkeyflowers, we include all the currently recognized taxa within southern California within a single plant profile. We also include <i>D. aurantiacus</i> of central and northern California in an attempt to clarify the taxonomy and illustrate differences between that taxon and those that occur in southern California.</p>			
II. ECOLOGICAL & EVOLUTIONARY CONSIDERATIONS FOR RESTORATION				
<p>A. Attribute summary list (based on referenced responses in full table)</p>	<table border="0" style="width: 100%;"> <tr> <td style="vertical-align: top; width: 50%;"> Taxonomic stability - low Longevity - intermediate (5–10+ years) Parity - polycarpic Stress tolerance - moderate Environmental tolerance - narrow to intermediate Reproduction - facultative seeder Fragmentation history - historical and recent Habitat fragmentation - intermediate to high Distribution - restricted to wide (taxa differ) Hybridization potential - high </td> <td style="vertical-align: top; width: 50%;"> Age to first reproduction - 1–2 years Seeds - dormant, intermediate to long-lived Seed dispersal distance - near to intermediate Pollen dispersal - intermediate to far Breeding system - mixed mating system, self-compatible Population structure - clinal Adaptive trait variation - documented, small spatial scale Chromosome number - stable Genetic marker polymorphism - high Average total heterozygosity - unknown </td> </tr> </table> <p>Species distribution models run on lumped <i>Diplacus</i> taxa predict high loss in suitable habitat by midcentury.</p>		Taxonomic stability - low Longevity - intermediate (5–10+ years) Parity - polycarpic Stress tolerance - moderate Environmental tolerance - narrow to intermediate Reproduction - facultative seeder Fragmentation history - historical and recent Habitat fragmentation - intermediate to high Distribution - restricted to wide (taxa differ) Hybridization potential - high	Age to first reproduction - 1–2 years Seeds - dormant, intermediate to long-lived Seed dispersal distance - near to intermediate Pollen dispersal - intermediate to far Breeding system - mixed mating system, self-compatible Population structure - clinal Adaptive trait variation - documented, small spatial scale Chromosome number - stable Genetic marker polymorphism - high Average total heterozygosity - unknown
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B. Implications for seed transfer (summary based on referenced responses in full table)

The bush monkeyflowers have a complex pattern of geographic variation, genetic differentiation of floral form and resin chemistry, local adaptation to moisture environments, and extensive ability to hybridize. Natural, stable hybrid zones are known to occur between geographically distinct populations of the parental taxa. Although gene flow between different recognized taxa may occur when populations come into contact, and intermediates can be found, a combination of selective factors appear to be maintaining the strong geographic patterns noted by early researchers (e.g., McMinn 1939) and which are still evident in the wild. Consequently, to manage the pattern of diversity and success of section *Diplacus*, attention to geographic patterns, flower color and habitat matching when obtaining seeds for planting projects, especially large projects that may increase connectivity among natural populations could help to preserve the observed biodiversity. Use of regionally local seed sources for planting projects can mitigate unknown fitness consequences of out-of-range plantings.

III. Taxonomic Information (Continued from section I)

A. Photos

Images of the bush monkeyflowers



D. aridus, Jacumba, San Diego Co., Cindy Daverin



D. longiflorus, Orange Co., Arlee Montalvo



D. longiflorus, Los Angeles Co., Boneli Park, San Dimas (formerly recognized as *D. rutilis*), Naomi Fraga



D. aurantiacus, Monterey Co., Arlee Montalvo



D. x australis, Santa Ana Mtns., Riverside, Co., RCRC Arlee Montalvo



D. calycinus, San Bernardino Co., Arlee Montalvo



D. longiflorus, Riverside Co., RCRC Arlee Montalvo



D. parviflorus, Keir Morse (cc) Creative Commons



D. puniceus, Riverside Co., Robert Dempster



D. longiflorus, Riverside Co., Arlee Montalvo



Arlee Montalvo

<p>B. Other Major Synonyms:</p> <ol style="list-style-type: none"> 1. <i>D. aridus</i> 2. <i>D. aurantiacus</i> 3. <i>D. x australis</i> 4. <i>D. calycinus</i> 5. <i>D. longiflorus</i> 6. <i>D. parviflorus</i> 7. <i>D. puniceus</i> 	<p>Noted in Grant (1924), Munz & Keck (1968), Tulig & Nesom (2012), USDA Plants (2016)</p> <ol style="list-style-type: none"> 1. <i>Mimulus aridus</i> (Abrams) A. L. Grant 2. <i>Diplacus glutinosus</i> var. <i>aurantiacus</i> (Curtis) Lindl., <i>Mimulus glutinosus</i> J. C. Wendland, <i>Diplacus glutinosus</i> (J.C. Wendland) Nutt., <i>D. leptanthus</i> Nutt., <i>D. latifolius</i> Nutt. 3. <i>Mimulus aurantiacus</i> var. <i>australis</i> (McMinn) Munz; <i>Diplacus aurantiacus</i> (W. Curtis) Jepson. ssp. <i>australis</i> (McMinn) R.M. Beeks; <i>D. australis</i> McMinn 4. <i>M. longiflorus</i> var. <i>calycinus</i> (Eastw.) Munz; <i>M. longiflorus</i> var. <i>calycinus</i> (Eastw.) A. L. Grant; <i>M. longiflorus</i> subsp. <i>calycinus</i> (Eastw.) Jeps. 5. <i>Mimulus longiflorus</i> (Nutt.) A. L. Grant, <i>Mimulus longiflorus</i> var. <i>rutilis</i> (A.L. Grant) McMinn <i>Diplacus glutinosus</i> var. <i>pubescens</i> Torrey, <i>Diplacus longiflorus</i> Nutt., <i>Diplacus rutilus</i> (A. L. Grant) McMinn 6. <i>Mimulus flemingii</i> Munz, <i>Mimulus parviflorus</i> (Greene) A.L. Grant 7. <i>Mimulus puniceus</i> (Nutt.) Steud., <i>Mimulus glutinosus</i> J. C. Wendl. var. <i>puniceus</i>; <i>Diplacus glutinosus</i> (J.C.Wendl.) Nutt. var. <i>puniceus</i> (Nutt.) Benth.
<p>C. Common names of:</p> <ol style="list-style-type: none"> 1. <i>D. aridus</i> 2. <i>D. aurantiacus</i> 3. <i>D. x australis</i> 4. <i>D. calycinus</i> 5. <i>D. longiflorus</i> 6. <i>D. parviflorus</i> 7. <i>D. puniceus</i> 	<ol style="list-style-type: none"> 1. Jacumba bush monkeyflower (Rebman & Simpson 2006), San Diego bush monkeyflower (USDA Plants 2016) 2. orange bush monkeyflower (USDA Plants 2016) 3. southern bush monkeyflower (Allen & Roberts 2013), San Diego bush monkeyflower (Rebman & Simpson 2006) 4. Kaweah bush monkeyflower (USDA Plants 2016), yellow bush monkeyflower 5. hairy bush monkeyflower (Allen & Roberts 2013), southern bush monkeyflower (USDA Plants 2016) 6. island bush monkeyflower (USDA Plants 2016) 7. red bush monkeyflower (USDA Plants 2016), coastal bush monkeyflower (Allen & Roberts 2013)
<p>D. Taxonomic relationships</p>	<p>Until recently, all taxa recognized as species of <i>Diplacus</i> (or as <i>Mimulus</i> section <i>Diplacus</i>) were woody perennials, with the exception of <i>D. clevelandii</i>, a perennial which can be woody at the base. Phylogenetic studies based on chloroplast DNA and two regions of nuclear DNA not only confirmed that all the woody taxa are very closely related, but also found that several annual taxa previously placed in other sections of <i>Mimulus</i> clustered with <i>Diplacus</i> (Beardsley et al. 2004). In their recent taxonomic revision of the family Phrymaceae, Barker et al. (2012) placed many annual species within other sections of <i>Diplacus</i>. This rearrangement recognizes six sections within the genus <i>Diplacus</i> and maintains all woody perennial monkeyflowers in the separate section <i>Diplacus</i>.</p>
<p>E. Related taxa in region</p>	<p>Of the taxa currently recognized as <i>Diplacus</i> section <i>Diplacus</i> (Barker et al. 2012), the most closely related taxon to cluster with the woody monkeyflowers is <i>Diplacus clevelandii</i> (Brandege) E. Greene, a rhizomatous perennial herbaceous plant, weakly woody at the base (Beardsley et al. 2004). The lemon-yellow flowered plant rarely hybridizes with other <i>Diplacus</i> taxa. Cleveland monkeyflower occurs in the Santa Ana Mountains of Riverside and Orange counties and in the Palomar, Cuyamaca, Laguna, Barbour and Otay mountains of San Diego Co., southward into Baja California (Thompson 2005).</p>
<p>F. Taxonomic issues</p>	<p>Although many authors have recognized strong geographic patterns in the distribution of plants with similar floral form (based on flower color, pubescence, size, shape and leaf structure), different approaches have resulted in a fluid taxonomy that changed many times. Furthermore, there is potential for hybridization where more than one taxon or variety (species or floral form) co-occur (see VII. H. Hybridization potential). Since the comprehensive treatments by Grant (1924) and McMinn (1951), taxa have been lumped, separated, and rearranged in different ways. After considerable studies of geographic patterns, pollinator isolating mechanisms, DNA, morphological and phylogenetic analyses, much of McMinn's treatment stands today (Barker et al. 2012, Tulig & Nesom 2012).</p> <p>The numerous changes in nomenclature and taxon concepts, however, make interpreting ecological literature and herbarium records challenging. From 1993 to 2012, many collectors and researchers followed the treatment from the first edition of the Jepson Manual (Thompson 1993) that lumped most of the woody <i>Diplacus</i> of southern California under the name <i>Mimulus aurantiacus</i> with no infraspecific taxa. Many publications during this period used only the name <i>M. aurantiacus</i>, making it difficult, if not impossible, to determine which currently recognized taxonomic unit was studied. Similarly, collections made during that time were deposited into herbaria under the name <i>Mimulus aurantiacus</i> and conflicting annotations followed, impeding modeling and other uses of herbarium data.</p>
<p>G. Other</p>	<p>Bush monkeyflowers occupy coastal hills, interior valleys, and foothills along west to east and north to south gradients in temperature and rainfall. Their correspondingly complex pattern of variation may reflect once isolated and differentiated populations that have come into secondary contact and hybridized. The resulting patterns of genetic diversity and patterns in morphological diversity are complex (Beardsley et al. 2003). Chase et al. (2017) found compelling evidence for rapid evolutionary divergence and convergence, including much shared variation among taxa, and diverse taxa in different stages of divergence.</p>

IV. GENERAL

A. Geographic range

1. *D. aridus*
2. *D. aurantiacus*
3. *D. x australis*
4. *D. calycinus*
5. *D. longiflorus*
6. *D. parviflorus*
7. *D. puniceus*

The pattern of distribution and zones of overlap for all taxa are described by McMinn (1951), Tulig (2000), Tulig & Nesom (2012), Grant (1993b).

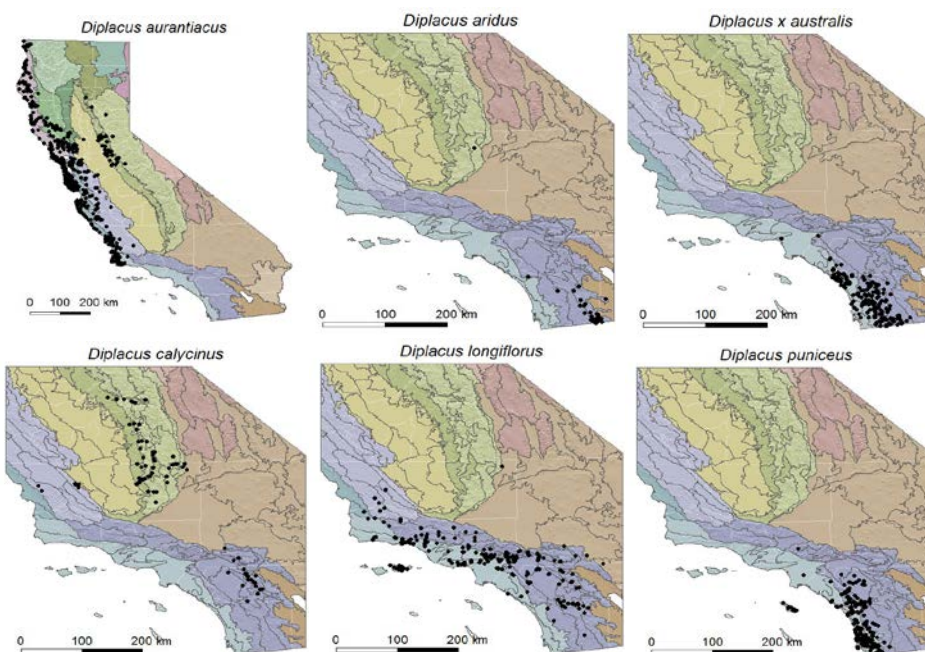
1. Interior mountains of San Diego Co. near Jacumba, California into Baja California
2. Curry Co. in southern Oregon southward through the coast ranges to northern Santa Barbara Co. Also in foothills of Sierra Nevada from Stanislaus Co. to Placer Co.
3. Santa Ana Mountains of Riverside and Orange counties, south to interior San Diego County to Baja California.
4. Middle elevations in mountains from western slopes of southern Sierra Nevada to s. California, Tehachapi Mountains. Also in eastern San Luis Obispo, Los Angeles, San Bernardino, and Riverside counties.
5. Pozo Range in central San Luis Obispo Co., southward into Baja California. Also eastward into Riverside and San Bernardino counties. Red form from Santa Susanna Pass, Ventura Co. to base of San Gabriel Mountains in Los Angeles Co
6. Southern California islands.
7. Coastline and coastal mountains of s. California from Los Angeles Co. south into Baja California. Also eastward into western Riverside Co.

B. Distribution in California; Ecological Section and Subsection (sensu Goudey & Smith 1994, Cleland et al. 2007)

Section Code	
261A	M261G
261B	M262A
262A	M262B
263A	322A
M261A	322B
M261B	322C
M261C	341D
M261D	341F
M261E	342B
M261F	Salton Sea

to see mapped subsection labels see:
http://web.archive.org/web/20070826132132/http://www.fs.fed.us/r5/projects/ecoregions/ca_sections.htm, then click on various map sections.

Data downloaded from the Consortium of California Herbaria (CCH 2016), June 2016. Ecological Sections (colors) and Subsections (black divisions). *D. aurantiacus* provided for comparison.



Diplacus aridus:
 S. Calif. Mtns & Valleys M262B: f,n,o,p
 Sierra Nevada M261E: r? (likely misidentified)

Diplacus x australis:
 S. Calif. Mtns & Valleys M262B: f,n,o
 Southern California Coast 261B: g,i,j

Diplacus calycinus:
 S. Calif. Mtns & Valleys M262B: e, f-g, i-p
 Central California Coast Ranges M262A: e,k
 Sierra Nevada Foothills M261F: c,d
 Sierra Nevada M261E: p,q,r,s,u

Diplacus longiflorus:
 S. Calif. Mtns & Valleys M262B: a-d, e?, f-g, i-p
 Southern California Coast 261B: a-g,i
 Central California Coast 261A: l
 Central California Coast Ranges M262A: e,i
 Sierra Nevada M261E: r? (likely misidentified)


Diplacus puniceus:
 S. Calif. Mtns & Valleys M262B: d?,f,j,k,o,n
 Southern California Coast 261B: g,h,i,j

Diplacus parviflorus (not shown in maps):
 Southern California Coast 261B: c,h (islands)

B. Life history, life form

Fast growing, perennial (iteroparous) subshrubs, especially woody at base. Some taxa are relatively short-lived, lasting only about four years (Thompson 2005), but some are longer-lived. Everett (2012) reports that at RSABG, *D. aurantiacus* has survived over 10 years, *M. bifidus* Pennel, *D. aridus* about 3–4 years, *D. calycinus*, *D. longiflorus*, *D. rutilis* and *D. puniceus* have survived "many" years (10–15 yr). The shorter-lived plants tended to be those sourced from northern California, Channel Islands, or boulder sites near border with Mexico.

C. Distinguishing traits	<p>The 0.5 to 1.5 (rarely to 2.5 m) tall, erect to sprawling subshrubs are often sticky with glandular secretions (McMinn 1951, Thompson 2012, Tulig & Nesom 2012). Leaves are 2–8 cm long, opposite, sessile, glabrous and somewhat resinous above, and narrowly elliptic to narrowly oblong with a strong midrib. Leaf margins are entire to minutely toothed and often rolled under. There are usually clusters of small leaves in the axils of larger leaves. The 3.5–4.5 cm long yellow, orange, red, or salmon flowers, have a long floral tube, spreading limbs, and a large two-lobed stigma. The calyx of fused sepals is pleated and 2–2.5 cm long. Pubescence varies among taxa from glabrous to having unbranched, branched hairs, with or without glands. The main distinguishing traits include:</p> <ol style="list-style-type: none"> 1. <i>D. aridus</i> - Corolla pale yellow, lobes entire, throat broadly campanulate; leaf surfaces uniformly green. 2. <i>D. aurantiacus</i> - Corolla yellowish orange to orange; calyx tube glabrous, glandular; pedicels usually 3–17 mm; lower leaf surface paler than upper. 3. <i>D. x australis</i> - More variable than other taxa. Corolla pale yellow to orange-yellow (apricot) to light orange or salmon colored; calyx glabrous to pubescent. Possibly a form of <i>D. puniceus</i>. 4. <i>D. calycinus</i> - Corolla often pale yellow to cream with darker yellow patches in throat; tube-throat 48–55 mm; calyx tube pubescent (villous to hirsute-villous); lower leaf surface paler than upper. 5. <i>D. longiflorus</i> - Corolla pale yellow to salmon, lobes shallowly notched, tube-throat 40–48 mm; calyx tube pubescent (villous to hirsute-villous); pedicels usually < 17 mm; lower leaf surface paler than upper. In Los Angeles and Ventura counties (in Ecological subsections M262Bd, f, j and 261Be), includes the "rutilis" forms with corolla red to scarlet (and more orange intermediates); calyces villous to hirsute-villous, generally short pedicels < 10 mm. 6. <i>D. parviflorus</i> - Corolla red to scarlet, lobes nearly equal, only slightly notched; calyces glabrous; leaves ovate-oblong, rounded at apex. 7. <i>D. puniceus</i> - Corolla tawny orange to red, lobes unequal and notched; calyces glabrous; leaf surfaces uniformly green; leaves linear-lanceolate, often rolled under; pedicels often longer than in other taxa (9–22 mm).
D. Root system, rhizomes, stolons, etc.	<p>Branched tap root, fibrous (Hellmers et al. 1955), but variable with growing substrate. In granite clefts and rocky bluffs an extensive tap root can develop, in soil filled crevices more extensive lateral branches may develop, and in heavy soils, weak shallow weak roots develop (McMinn 1951).</p>
E. Rooting depth	<p>Literature is sparse but suggests the rooting system in <i>Diplacus</i> is not extensive (Grant 1924, Hellmers et al. 1955). Like other common coastal sage scrub shrubs or subshrubs (e.g., <i>Salvia</i>, <i>Acmispon</i>, <i>Eriogonum</i>), roots of <i>D. longiflorus</i> do not penetrate soil beyond five feet deep and feeder roots are concentrated within the first 3 inches of soil (Hellmers et al. 1955).</p>
V. HABITAT	
A. Vegetation alliances, associations	<p>Coastal sage scrub, lower elevation chaparral, openings of oak woodland, and within rocky outcrops at the edges of shrubland. <i>D. calycinus</i>, the highest elevation taxon in southern California, also grows in rock outcrops in the openings of yellow pine forest. The 2nd edition of the Manual of California Vegetation (Sawyer et al. 2008) used the broad taxonomic definition for the bush monkeyflowers <i>Diplacus aurantiacus</i> (<i>sensu</i> Thompson 1993, see III. F. Taxonomic issues above) and list the species as present within many shrubland alliances at low cover. They report <i>D. aurantiacus</i> as a dominant shrub (having > 50% relative cover in the shrub canopy) in the <i>Diplacus aurantiacus</i> Shrubland Alliance which tends to occur on steep, often unstable slopes (including road cuts) in somewhat mesic settings. Within this alliance in southern California, the bush monkeyflowers co-occur with <i>Artemisia californica</i>, <i>Baccharis pilularis</i>, <i>Ceanothus megacarpus</i>, <i>C. spinosus</i>, <i>Heteromeles arbutifolia</i>, <i>Malosma laurina</i>, <i>Salvia leucophylla</i>, <i>S. mellifera</i>, <i>Sambucus nigra</i>, and/or <i>Toxicodendron diversilobum</i>. There may also be scattered <i>Juglans californica</i>, <i>Platanus racemosa</i>, and <i>Quercus agrifolia</i>.</p> <p>In a survey of coastal sage scrub plant communities in southern California from Santa Barbara across portions of the Santa Ana River and San Jacinto River watersheds, Kirkpatrick & Hutchinson (1977) recognized <i>Mimulus puniceus</i> and <i>M. longiflorus</i> (nomenclature <i>sensu</i> Munz & Keck 1968). They found <i>M. longiflorus</i> to be strongly associated with five communities, including: <i>Artemisia californica</i>–<i>Baccharis pilularis</i>–<i>Elymus condensatus</i> scrub (northerly study area), <i>Salvia mellifera</i>–<i>Rhus laurina</i> scrub, <i>Salvia leucophylla</i>–<i>Rhus laurina</i> scrub (toward coast), <i>Salvia leucophylla</i>–<i>Artemisia</i> scrub (inland between Santa Barbara and Morro Bay), and the <i>Eriogonum fasciculatum</i>–<i>Scophularia californica</i>–<i>Phacelia ramosissima</i> association (within broken granitic rock outcrops in the inland southern areas). <i>M. puniceus</i> was also associated with the later type. (note: <i>Rhus laurina</i> is now recognized as <i>Malosma laurina</i>).</p>
B. Habitat affinity and breadth of habitat	<p>Rocky hillsides, cliffs, slopes, and disturbed areas, usually on the border of chaparral or coastal sage scrub or within open forest, frequently in the crevices of boulders (McMinn 1951, Thompson 2005). Different taxa tend to be favored in different environments; <i>D. longiflorus</i> and <i>D. calycinus</i> tend to occur in more xeric inland areas while <i>D. puniceus</i> tends to be in more mesic coastal areas.</p>

C. Elevation range	Based on Thompson (2005, 2012), Munz & Keck (1968), CCH (2016) 1. <i>D. aridus</i> : 660–1180 m in California populations. 2. <i>D. aurantiacus</i> : below 800 m 3. <i>D. x australis</i> - below 1000 m 4. <i>D. calycinus</i> : 350–2440 m 5. <i>D. longiflorus</i> : 7–2000 m 6. <i>D. parviflorus</i> : below 600 m 7. <i>D. puniceus</i> : below 800 m (occasionally higher)
D. Soil: texture, chemicals, depth	Grows in a variety of well-drained soils derived from sedimentary and granitic rocks. Often on rocky slopes and in the crevices of rock outcrops (Thompson 2005) but also in well-drained soils over bedrock (McMinn 1951).
E. Precipitation	Plants occur in primarily in the Mediterranean climate region of California and Baja California with dry summers and moist to wet winters. The different varieties occur along a gradient of precipitation, from less than 10 inches (25 cm) to over 25 inches (64 cm) of rainfall.
F. Drought tolerance	Drought tolerant. Water availability is the primary limiting factor for both growth and reproduction of <i>D. aurantiacus</i> (Alpert et al. 1985). The spring leaves of woody monkeyflowers are often deciduous under drought stress (Thompson 2005).
G. Flooding or high water tolerance	Not tolerant of wet soils. May tolerate very infrequent, ephemeral flooding in very well-drained, rocky substrate.
H. Wetland indicator status for California	Only <i>Diplacus aurantiacus</i> is listed (USDA Plants 2016) and is FACU for arid west. Section <i>Diplacus</i> taxa are generally upland plants.
I. Shade tolerance	<i>Mimulus aurantiacus</i> / <i>Diplacus longiflorus</i> are tolerant of partial shade and bright shade at inland locations but generally require full sun toward the coast (Newton & Claassen 2003). In horticulture, plants tend to grow best in partial shade (Bornstein et al. 2005). In shade, <i>D. aurantiacus</i> suffers less damage from insect herbivores (Lincoln & Mooney 1984).
VI. CLIMATE CHANGE AND PROJECTED FUTURE SUITABLE HABITAT	
A. Species Distribution Models with climate forecasting	Species distribution models (SDM) of <i>Mimulus aurantiacus</i> (taxonomy sensu Thompson 2012) with climate forecasting predict a 30–44% loss statewide of current climatically suitable habitat by mid-21st century, rising to 39–61% by the end of the century (Riordan & Rundel 2014). In southern California, Riordan & Rundel (2014) predict climate-driven habitat losses in the majority of coastal and low areas by the end of the century, with areas of the Santa Ana, San Gabriel, and Peninsular ranges maintaining or gaining habitat suitability. Similarly, Principe et al. (2013) predict >50% loss of current climatically suitable habitat for <i>M. aurantiacus</i> in southern California by mid-21st century. While both studies model <i>Mimulus aurantiacus</i> sensu Thompson (2012), their results suggest that the southern California <i>Diplacus</i> taxa previously lumped within the species <i>M. aurantiacus</i> may also be vulnerable to climate-driven habitat losses in southern California this century. The modeling effort by Principe et al. (2013) included woody monkey flowers for a geographic extent from Riverside Co., south to the boarder with Mexico which would have included all taxa except for <i>D. aurantiacus</i> (as listed in I A. above). In contrast, the modeling effort of Riordan & Rundel (2014) included a geographic extent from the San Francisco Bay area, southward and would have included all 8 taxa.
VII. GROWTH AND REPRODUCTION	
A. Seedling emergence relevant to general ecology	Seedlings emerge in open areas in late winter following rain. Seeds in section <i>Diplacus</i> germinate after fire, but do not require fire for germination (Thompson 2005).
B. Growth pattern (phenology) common to section <i>Diplacus</i>  <i>D. longiflorus</i> seedlings in early March. A. Montalvo	Both growth and reproduction are primarily water limited. Seedlings emerge after ample winter rainfall events and into the spring after late rains. Plants can reach flowering maturity within a year under good rainfall conditions (e.g. Everett 2012), but many plants flower in their second year. Most growth and leaf flush occurs in late winter to mid spring, after the onset of fall and winter rains. During the summer drought, plants of <i>D. aurantiacus</i> begin to drop larger leaves produced in the rainy season, while retaining smaller leaves produced late in the season under drier, warmer conditions (Gulmon 1983). This pattern was also recorded for <i>D. longiflorus</i> (Westman 1981) and is common to all southern California woody monkeyflowers. Most flowering is between March and June, with sporadic flowering nearly any time of the year under favorable warmth and moisture conditions (Thompson 2005). Flowers of <i>D. aurantiacus</i> and <i>D. longiflorus</i> last up to 10 days (Eckert 1970, Belisle et al. 2012). Within section <i>Diplacus</i> , fruits mature July to August with most fruit dehiscence in the fall and winter (Thompson 2005). A large and relatively constant proportion of carbon and nitrogen are allocated to reproduction in <i>D. aurantiacus</i> , and reproductive structures supply some of their own carbon (Alpert et al. 1985).

C. Vegetative propagation	There are no specialized structures for vegetative spread in the woody monkeyflowers. Plants can be propagated easily from stem cuttings (Everett 2012).
D. Regeneration after fire or other disturbance	After fire, taxa in section <i>Diplacus</i> establish from seeds and sprout vigorously from the base or from underground rhizomes (Thompson 2005). Seed in the soil can survive fire and plants are considered to be facultative seeders, both inland and on the coast (Keeley et al. 2006, studies in southern California citing <i>Mimulus aurantiacus</i> sensu Thompson 1993). Seedling emergence occurred in each of five years following fire, but 60% occurred in the second year (Keeley et al. 2006). Odion (2000) found seedlings emerged from soil cores collected after a fire. Went et al. (1952) found no difference in the emergence of <i>D. longiflorus</i> seedlings from burned and unburned.
E. Pollination	Different species and populations of woody monkeyflowers are known to attract different pollinators depending on their flower color, geographic location, and the relative abundance of pollinating agents (bees, hummingbirds, or hawkmoths). Pollinators of bush monkeyflowers are diverse, with dominant pollinators varying with flower color, flower form, and location (Grant 1993a,b, Streisfeld & Kohn 2005). This reflects a combination of local differentiation, both in the relative abundances of pollinators and pollinator preferences for different floral forms (Streisfeld & Kohn 2007). Fetscher & Kohn (1999) reported Anna's hummingbird as the primary pollinator of a red flower form in San Diego Co. (aka <i>D. puniceus</i>), with black-chinned, Costa's, and rufous hummingbirds as occasional visitors. Bromer et al. (1990) reported that <i>M. longiflorus</i> was generally but not exclusively pollinated by black-chinned and Anna's hummingbirds. In a different population of <i>M. longiflorus</i> , Eckhart (1970) found that almost all pollination was by solitary bees at site in Los Angeles Co., and that Anna's hummingbirds were only occasional visitors. Flowers were visited by many families of bees but most pollination was by leafcutter bees in the genus <i>Osmia</i> and carpenterbees in the genus <i>Ceratina</i> . Others have also observed hummingbird visits to <i>D. puniceus</i> , <i>D. longiflorus</i> , and <i>D. aurantiacus</i> (Grant 1993b, Table 2). Bee species in the following genera were observed visiting <i>D. aurantiacus</i> in NapaCo.: <i>Ceratina</i> , <i>Xylacopa</i> , <i>Bombus</i> , <i>Hyleaus</i> , <i>Dialictus</i> , <i>Lasioglossum</i> , <i>Chelostomopsis</i> , and <i>Osmia</i> but observations of actual pollination were not recorded (Dobson 1993). Finally, Streisfeld & Kohn (2007) documented hawkmoth and hummingbird pollinator visits to yellow versus red-flower forms of the " <i>M. aurantiacus</i> complex" (recognized as <i>D. puniceus</i> and <i>D. longiflorus</i> by Tulig & Nesom 2012). In general, hawkmoths preferred the yellow flowers and hummingbirds preferred the red flowers (see IX. F. Local adaptation/adaptive divergence, below).
F. Seed dispersal	Capsules split open along a single suture allowing the many tiny seeds (~1 mm long, half as wide and nearly flat) to gradually spill out and disperse by gravity and wind. Strong winds are required to shake seeds loose from their fruits (Thompson 2005). While lacking surface area to travel long distances by gentle winds, seeds can likely travel meters during Santa Ana wind conditions and further in gale force winds. Not all populations occur in areas that are affected by such winds so seed dispersal distances are expected to be variable.
G. Breeding system, mating system	Flower morphology of all woody <i>Diplacus</i> favors outcrossing but plants are self-compatible and rates of outcrossing likely vary substantially among species and populations. The morphology of the flowers, type of pollinator and the way they move among flowers and different plants can also have profound effects on outcrossing rates at local scales. <i>D. longiflorus</i> from the Verdugo Hills in Los Angeles Co. was found to be self-compatible, but flowers pollinated by self-pollen produced fewer seeds than flowers pollinated by outcross pollen (Eckert 1970). In addition, stigmas matured one to three days before the anthers released pollen and remained receptive for another one to five days, suggesting plants generally outcross more than they self. Others found evidence for variation in outcrossing rate in <i>D. longiflorus</i> (Bromer et al. 1990). Six populations of <i>D. longiflorus</i> from the Santa Monica Mountains varied in floral morphology, sucrose content of nectar, and anther-stigma separation. Populations with small anther-stigma separation were more likely to be selfing and had less DNA polymorphism. Populations with high pollinator diversity but low visitation rates had shorter corolla tubes and lower sucrose:hexose nectar ratios than populations with less diverse pollinators (Bromer et al. 1990).
H. Hybridization potential	There is a high potential for hybridization where more than one taxon or variety (species or floral form) co-occur (McMinn 1951, Beeks 1962, Wells 1980, Streisfeld & Kohn 2005, Thompson 2005, Everett 2012), but pollinator preference for different floral forms may help to stabilize geographic patterns. Hybridization among taxa in areas of contact appears to be common and backcrossing to parent populations within hybrid zones produces a range of intermediate forms. However, most varieties remain distinct in part from having different habitat preferences which provides some geographic isolation (Thompson 2005, Streisfeld & Kohn 2007, Sobel & Streisfeld 2015), and from strong reproductive isolation owing to pollinator preferences for different floral forms (Streisfeld & Kohn 2005, Streisfeld et al. 2013).

H. Hybridization potential ...continued	<p>Grant (1993a) postulated that populations with different floral forms and affinities for attracting hawkmoths and hummingbirds would be partially reproductively isolated. He hypothesized that <i>Diplacus</i> with red or salmon colored flowers would be primarily hummingbird pollinated and that those with pale yellow flowers and a long corolla tube would be primarily hawkmoth pollinated. Where the habitats of such taxa intermingle there would be hybridization and the hybrids would form a connecting link between the very different forms. Such patterns have been identified empirically.</p> <p>Evidence from recent studies analyzing geographic distribution and floral form, suggest <i>D. x australis</i> is a derivative taxon resulting from the hybridization of <i>D. puniceus</i> and <i>D. longiflorus</i> (Waayers 1996, Thompson 2005, Tulig & Nesom 2012). <i>D. x australis</i> is common in the Santa Ana Mountains and part of San Diego Co. in a zone between areas occupied by <i>D. longiflorus</i> (inland) and <i>D. puniceus</i> (primarily coastal). Tulig & Nesom (2012) recognized the hybrid zone plants studied by Streisfeld & Kohn (2005) as <i>D. x australis</i>.</p> <p>Woody monkeyflowers can hybridize with <i>D. clevelandii</i> (Thompson 2012), but hybrids are rare.</p>
I. Inbreeding and outbreeding effects	<p>Although self-compatible, there is some evidence for inbreeding depression with selfing (e.g., lower production of capsules per plant and higher aborted ovules in self-crosses <i>M. longiflorus</i>) (Eckert 1970).</p>
VIII. BIOLOGICAL INTERACTIONS	
A. Competitiveness	<p>Low. Went et al. (1952) found that germination and survival of <i>Diplacus longiflorus</i> was significantly lower in plots sown with <i>Brassica nigra</i> compared to control plots without the <i>Brassica</i>. In experimental plots seeded with a mix of seven shrub species, "<i>Mimulus aurantiacus</i>" seedlings densities were about 15 times higher in plots that were hand weeded or treated with herbicide prior to seeding compared to controls (Cione et al. 2002). By the second year, <i>M. aurantiacus</i> was absent from the plots whereas <i>Artemisia californica</i>, <i>Eriogonum fasciculatum</i>, <i>Salvia apriana</i>, <i>S. mellifera</i>, and <i>Malacothamnus fasciculatus</i> achieved percent cover ranging from about 3% – 40%.</p>
B. Herbivory, seed predation, disease	<p>Herbivory: Bush monkeyflowers are the larval host of the Chalcedon checkerspot butterfly, <i>Euphydras chalcedona</i> Doubleday and Hewitson, with most reports for <i>D. aurantiacus</i> (Mooney et al. 1981, Lincoln et al. 1982). The timing of the butterfly's emergence and diapause is synchronized with the growth of the plant, but leaves produce a resin that inhibits the growth of larvae. Young leaves produced during the growing season have the highest nitrogen (N) content, carbon gain, and resin content (Lincoln et al. 1982). The growth rate of the <i>Euphydras</i> larvae increases with increasing N but decreases with increasing resin content. After initially feeding on young leaves, the larvae switch to older leaves with lower resin content (Lincoln et al. 1982). During flowering, N is translocated from the leaves, and larvae stop feeding (Mooney et al. 1981). In addition, the larvae of the painted lady butterfly (<i>Vanessa</i>) have been reported to defoliate young plants under cultivation (Bornstein et al. 2005).</p> <p>Disease: Belisle et al. (2012) found many species of nectar-inhabiting fungi in the nectar of <i>M. aurantiacus</i> and that hummingbirds transferred fungi (yeasts) among flowers. The effect of the fungi on reproduction or floral visitors was not mentioned. <i>Diplacus</i> species are susceptible to infection by non-native <i>Phytophthora</i> fungi (see XI. C. Horticulture).</p>
C. Palatability, attractiveness to animals, response to grazing	<p>The plants are avoided by mammals. Bornstein et al. (2005) report that woody <i>Diplacus</i> are ignored by deer and that rabbits and ground squirrels rarely bother with them.</p>
D. Mycorrhizae and nitrogen fixing nodules	<p>We did not find reports of mycorrhizal associations in woody monkeyflowers, and associations are unlikely. The most recent comprehensive reviews of associations (Wang & Qiu 2006, Brundett 2009) do not list any <i>Diplacus</i> species and the only closely related species mentioned as having some arbuscular mycorrhizae were <i>Mimulus ringens</i> and <i>M. guttatus</i> for which reports were mixed.</p>
IX. ECOLOGICAL GENETICS	
A. Ploidy	<p>All <i>Diplacus</i>, section <i>Diplacus</i> studied have n = 10 chromosomes (McMinn 1951, Thompson 2005), but the base number may be x = 9 (Barker et al. 2012). Photo micrographs in McMinn (1951) and Thompson (2005) clearly show that <i>D. clevelandii</i>, <i>D. aridus</i>, <i>D. grandiflorus</i>, and hybrids of <i>D. longiflorus</i> and <i>D. clevelandii</i> have n = 10. McMinn also reported 2n = 20 for work on <i>D. calycinus</i> and <i>D. puniceus</i> by G. Ledyard Stebbins and Leon Snyder.</p>

<p>B. Plasticity</p>	<p>There is high variability in floral, vegetative, chemical, and physiological traits within <i>Diplacus</i> species. The extent to which the variation can be attributed to plasticity vs. genetically determined traits that may be subject to natural selection is an area of ongoing research (see Geographic variation in traits, below). Flower color can vary within plants of <i>D. puniceus</i> from red to orange-red within a single season which indicates some plasticity in flower color. However, most flower color variation is heritable (genetically controlled, Streisfeld & Rausher 2009). There is some evidence for plasticity in seed size. Reciprocal transplant studies with <i>D. longiflorus</i> and <i>D. puniceus</i> showed differences in size and reproduction for seeds grown at inland compared to coastal sites (Streisfeld & Kohn 2007). In <i>D. aurantiacus</i>, Han & Lincoln (1997, 1994) found that total resin production was significantly affected by environment. Leaf resin content and chemistry varied over seasons within individuals and among populations of <i>Diplacus</i> (Hare 2002b; called <i>M. aurantiacus</i> in the publication, but mostly <i>D. puniceus</i>). A common garden study in Riverside suggested that differences among populations across different habitats are more significant than the plastic response observed among seasons (Hare 2002b).</p>
<p>C. Geographic variation in traits (morphological and physiological)</p>	<p>There are geographic patterns in <i>Diplacus</i> traits that vary across the landscape. The patterns relate to topographic barriers to gene flow (mountains), environmental gradients (temperature/aridity), and biotic interactions (pollinators/herbivores). General patterns are described here. The genetic basis of the traits is covered below under “Genetic variation and population structure”.</p> <p>Floral Traits: Geographic variation in floral traits of all section <i>Diplacus</i> taxa has been well documented (Tulig 2000, Tulig & Nesom 2012). Results from a combination of genomic studies, crossing experiments, greenhouse common garden, and field studies support that strong selection for flower traits varies depending on spatial, geographic position. Stankowski et al. (2015) showed sharp clines in six of 10 floral traits measured (including genetic markers for flower color) in <i>D. puniceus</i>, <i>D. longiflorus</i>, and their hybrid taxon <i>D. x australis</i> in San Diego Co., Calif. (identified as red and yellow ecotypes and hybrid form of <i>M. aurantiacus</i>, <i>sensu</i> Thompson 1993). Experimental crosses and backcrosses between the red and yellow forms yielded plants with a gradual and continuous range of flower colors and structures rather than the pattern sharp discontinuity of red, yellow and hybrid forms found in the wild. Their results are consistent with the divergence in floral traits being locally restricted even in the face of gene exchange and that the spatial geographic position of populations can influence the evolution of premating isolation.</p> <p>Ecophysiological Traits: Vegetative and physiological traits also vary geographically among populations of woody monkeyflowers. In a common garden, compared to plants from inland locations, plants from coastal populations of <i>D. puniceus</i> had significantly higher resin concentrations and relative concentrations of the chemicals hypothesized to retard water loss (Hare 2002a, 2008). Coastal plants also had higher concentrations of chemicals known to deter feeding by the larvae of the <i>E. calcedona</i> (see “Phenotypic or genotypic variation in interactions with other organisms”).</p> <p>Michener (1983) showed that differences in wood anatomy among ten <i>Mimulus</i> section <i>Diplacus</i> taxa (<i>sensu</i> Munz & Keck 1968), and among populations of several taxa were correlated with habitat. Plants from relatively mesic habitats had relatively few, large vessel-elements, while plants from xeric habitats had many, small vessel-elements. There was a gradient from coastal (mesic) to inland (xeric), although some of the most xeromorphic plants were found on very sandy soils near the coast.</p> <p>Mooney & Chu (1983) compared water use efficiency in a coastal, mesic-adapted population and an inland, xeric-adapted population of <i>D. aurantiacus</i> and found that under humid, low stress conditions both were highly efficient, maintaining a high rate of photosynthesis relative to transpiration. In a growth chamber study with potted plants, those from an inland site were able to maintain high water-use efficiency under low humidity, while the efficiency of plants from a coastal site diminished rapidly with decreasing atmospheric humidity and increasing evaporative stress.</p>
<p>D. Genetic variation and population structure</p>	<p>Studies in San Diego Co., Calif., show that there is structure within and among populations of <i>Diplacus</i> for various adaptive morphological traits, but not in neutral molecular traits (see Geographic variation in traits, Variation in interactions). For the "<i>Mimulus aurantiacus</i>" complex that includes <i>D. puniceus</i>, <i>D. longiflorus</i>, and their hybrid derivative, <i>D. x australis</i>, Stankowski et al. (2015) found significant spatial variation in a suite of floral traits, including in a marker for a gene that controls the transition from yellow to red flower color. The sigmoid shape of the clines was consistent with their hypothesis that pollinators were responsible for the divergence in the traits. There was evidence for gene flow and a gradual west to east cline in floral traits from coastal populations of the red-flowered <i>D. puniceus</i> toward the far inland, yellow-flowered populations of <i>D. longiflorus</i>, with hybrid intermediates in an intermediate zone between. The clinal patterns were also significantly associated with climatological factors (Sobel & Streisfeld 2015). In contrast, there was no significant structure to molecular variation at restriction site DNA, “neutral” molecular markers used to detect gene flow and patterns consistent with isolation by distance (Sobel & Streisfeld 2015). The lack of structure in neutral markers suggests ample gene flow and complete introgression at the neutral loci across the landscape. When viewed in concert with the strong structure in morphological traits, it is clear that differences in adaptation to climatic conditions and to pollinators must be strong to provide the observed patterns in morphology.</p>

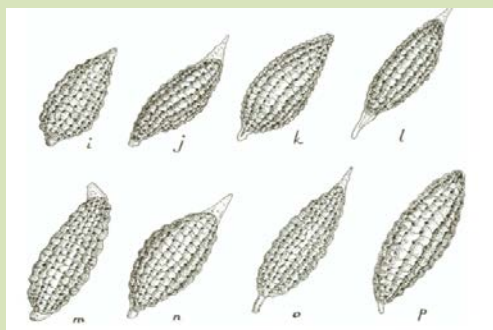
<p>E. Genetic variation in interactions with other organisms</p>	<p>Herbivores: Hare (2002a) examined the chemistry and relative quantities of important resin components for six populations of <i>M. aurantiacus</i> (<i>sensu</i> Thompson 1993) for which nearly 30% of the dry weight of leaves was resin, a family of compounds expected to offer protection from herbivory. The populations were from a range of environments and differed in attack by the larvae of <i>Ephydryas chalcedona</i>. Plants from six populations were grown in a common garden and examined for insect attack and chemistry. The populations differed genetically in chemical components of the resins, but no pattern was found in insect attack.</p> <p>In addition, Hare tested for genetic correlations between defensive chemical compounds and seed production and found leaf resin content was independent of seed production within populations (Hare 2008). Hare concluded that low heritability of defensive chemical production may constrain evolution of chemical defense in response to herbivory in the study populations. Interpretation of the results, however, should consider that Hare followed the nomenclature of Thompson (1993). Based on collection localities of the populations used in the experiments relative to the geographic distributions of taxa and forms described by Munz & Keck (1969), Thompson (2005) and Tulig & Nesom (2012), there may have been more than one species represented in the Hare (2002a, b, 2008) studies. Aliso Canyon plants and Crystal Cove State Park along the Orange Co. coast are home to the typical rusty orange to red-flowered <i>D. puniceus</i>, Hemet and Lake Perris plants have red flowers (also <i>D. puniceus</i>), but most populations from the Box Springs in Riverside have pale yellow flowers and a pubescent calyx (<i>D. longiflorus</i>).</p> <p>Pollinators and Environment: Streisfeld & Kohn (2007) studied pollinator visits (see Pollination above) to yellow-flowered <i>D. longiflorus</i> and red-flowered <i>D. puniceus</i> of the "<i>Mimulus aurantiacus</i>" complex (<i>sensu</i> Thompson 1993) in natural populations and to plants placed in mixed experimental arrays at three locations in southern California. Hummingbirds visited red and yellow flowers at similar rates in natural populations, but in the experimental arrays they showed a more than 95% preference for red flowers. Hawkmoths visited yellow flowers almost exclusively and were only present at inland locations where yellow flowers were native. Stankowski et al. (2015) further studied how geography and different pollinators influence the genetic divergence of flower form in the complex that includes <i>D. puniceus</i>, <i>D. longiflorus</i>, and <i>D. x australis</i> (also see IX. C. Geographic variation in floral traits, above). There is a gradual west to east cline in flower traits from coastal populations of the red-flowered <i>D. puniceus</i> toward the far inland, yellow-flowered populations of <i>D. longiflorus</i>, with hybrid intermediates in an intermediate zone between, and the color traits are associated with patterns in pollinator type.</p>
<p>F. Local adaptation/ adaptive divergence</p>	<p>Some of the observed patterns in morphological and physiological variation have a genetic basis, and a combination of evidence suggests that natural selection has resulted in adaptive differences among populations of some taxa in the divergence of taxa. For example, variation in content and concentration of leaf resin among plants and populations of <i>Diplacus</i> has been hypothesized to evolve in response to herbivores. Leaf resin content varies among plants and populations, and there are physiological trade-offs in resource allocation to growth, reproduction or defense. Han & Lincoln (1994) found significant heritability and maternal effects for resin content within one population of <i>D. aurantiacus</i> originating from Jasper Ridge in Stanford (San Mateo Co.). They also found negative genetic and phenotypic correlations between resin production and growth rate. This indicates there is potential for natural selection and changes in resin content in response to differences in herbivore pressure.</p> <p>Results from a combination of genomic studies, crossing experiments, greenhouse common garden, and field studies support that strong selection for flower traits varies depending on spatial, geographic position. A series of experimental studies involving red, yellow, and hybrid populations of <i>Diplacus</i> from San Diego Co., Calif. have provided evidence for local adaptation between flower form and pollinator type (see Pollination, Geographic variation in traits, Genetic variation in interactions, above). There is also evidence that physical environmental factors have influence the continued geographic separation of the taxa studied (Streisfeld & Kohn 2007, Streisfeld et al. 2013, Sobel & Streisfeld 2015). Seedlings of <i>D. puniceus</i> and <i>D. longiflorus</i> (noted as red and yellow floral races), each raised from seeds from three different populations, were grown together in two common gardens, one at a coastal location (home to <i>D. puniceus</i>) and one at an inland location (home to <i>D. longiflorus</i>). The red-flowered populations survived better than the yellow-flowered ones at both locations and set significantly more fruits at the coastal garden. Plants in the coastal garden generally grew better than at the inland garden. Flower color was correlated with nectar volume, flower size, and shape. Hawkmoths were only at the inland locations, yellow flowers were visited primarily by hawkmoths, and the yellow flowers produced only 13.3% the nectar of red flowers. Hummingbirds strongly preferred red flowers at both inland and coastal locations and were more abundant at coastal sites.</p>
<p>G. Translocation risks</p>	<p>The complex pattern of geographic variation and evidence for local adaptation suggests that local seed sources be used for restoration. Careful attention should be made of flower color and habitat matching when requesting seeds. Hybridization is common in zones of overlap between genetically differentiated populations and when populations are placed together under cultivation.</p>

X. SEEDS

1 mm



D. aridus. Image courtesy of Rancho Santa Ana Botanic Garden Seed Program. <http://www.hazmac.biz/rsabghome.html>



i. *D. grandiflorus*, j. *D. longiflorus*, k. *D. parviflorus*, l. *D. australis*, m. *D. clevelandii*, n. *D. aurantiacus*, o. *D. puniceus*, p. *D. aridus*. McMinn 1951, Fig. 6

A. General

The tiny seeds are enclosed in 1.3–2.5 cm long, narrow, hard, pointed capsules that can contain many seeds (hundreds) in fully, outcross-pollinated flowers. Seeds of *D. aurantiacus* are 0.8–1.00 mm long, oblong-acute (fusiform) and reddish brown (Wall & McDonald 2009, Ransom Seed Lab 2016). All *Diplacus* species have similar seeds generally ≤ 1 mm long (Thompson 2005). The seeds of *D. aurantiacus* have a small, linear embryo with fleshy endosperm; *Diplacus longiflorus* was considered to have an axillary miniature embryo, linear in shape, with a delicate seed coat (Ransom 1980). The seed purity of commercial seed lots is generally low, ranging from 1% –9%, by weight.

B. Seed longevity

Long lived, likely at least 10 years (Thompson 2005). *D. puniceus* seeds stored at room temperature in Riverside, Calif. were still viable seven years after collecting (A. Montalvo, personal obs). Everett (2012) reports seeds of *D. aridus* germinating after 13 years in storage. Seeds are expected to accumulate in soil seed banks.

C. Seed dormancy

Seeds will germinate without pretreatment if exposed to light (Mirov & Kraebel 1939, Schmidt 1980). Exposure to smoke or aqueous extracts of charred wood may improve germination slightly (Keeley 1987) suggesting some dormancy. For *D. aurantiacus*, seed testing is done for 21 days at 15°C for fresh or dormant seed, and GA₃ is recommended (Ransom Seed Lab 2016).

D. Seed maturation

In southern California, seeds mature in summer and are often ready to collect in mid to late summer (A. Montalvo pers. obs). Seeds are available later in the season at the higher elevations and more mesic coastal areas.

E. Seed collecting and harvesting

The dry capsules which are partially enclosed in the dry calyx should be collected just before they dehisce, or at the very beginning of dehiscence, into open containers, paper, or cloth bags. To keep from injuring plants, the capsules need to be plucked by hand from plants.

F. Seed processing

Wall & McDonald (2009) suggest rubbing the fruits (with their floral material) over a small screen to split open capsules and release seeds. Capsules can also be spit open by gently crushing with a rolling pin (A. Montalvo pers. obs.). Avoid over rubbing or crushing the capsules. If broken too much, the chaff is difficult to separate from seeds. After rubbing, sift through #30 and #60 sieves to separate seeds from most of the chaff. Use a blower at low speed to blow off small chaff and empty seeds, and sieve more times depending on how clean the seeds need to be (for planting vs. seed banking).

G. Seed storage

Store dry. Seeds stored under cool, dry conditions can remain viable for many years. Seeds are orthodox seeds for purposes of seed storage. Rancho Santa Ana Botanic Gardens dries *Diplacus* seeds to ~ 15% relative humidity and stores them at - 23°C (Cheryl Birker pers. com.). Seeds have been stored successfully for over five years in a walk-in cold room at about 45% relative humidity and 8°C.

H. Seed germination

Seeds do not require treatment to germinate (Mirov & Kraebel 1939, Emery 1988, Dehart 1994). The average time to germination can vary considerably at different temperatures. For seeds from three populations each of *D. puniceus* and *D. x australis*, time to germination at 5°C averaged from six to seven weeks while at 10°C the time averaged three to four weeks (Waayers 1996). Overall, more seeds germinated at the warmer temperature. Ransom Seed Lab (2016) tests seeds of *D. aurantiacus* at 15°C for 21 days.

I. Seeds/lb

For pure seed of *D. aurantiacus*, the Ransom Seed Lab database (Ransom Seed Lab 2016) reports an average of 27,398 seeds/gram (N = 48) (i.e., over 12 billion seeds/lb). Old estimates of "about 145 million seeds/kg" (Mirov & Kraebel 1939) are grossly under stated. Owing to the low purity of commercial seed lots, S&S Seeds (2016) reports the average number of live seeds per bulk lb to be 180,000 for *D. aurantiacus*, 151,000 for *D. longiflorus*, and 158,400 for *D. puniceus*.

J. Planting	For raising in pots, the tiny seeds should be sown on the surface of the soil and kept moist until seedlings emerge. It is much easier to control the number of seeds sown into flats if the seeds are first mixed with fine sand to dilute the numbers (Arlie Montalvo pers. obs.). Outdoors, they should be planted with shallow broadcasting methods (Montalvo & McMillan 2004).
K. Seed increase activities or potential	Plants produce flowers sequentially over a long season if adequate moisture is available. Fruit ripening also happens sequentially but the capsules with ripe seeds stay on the plants for an extended period and tend to dehisce late in the season. In southern California, it is difficult to obtain adequate quantities of seeds from wild populations for seeding projects. Seed farms do not generally grow <i>Diplacus</i> for sale of seeds, but plugs are sometimes available. As fewer areas become available for seed collection in the fragmented southern California landscape, seed farming may be needed to provide adequate seeds for seeding restoration projects.
XI. USES	
A. Revegetation and erosion control	Bush monkeyflowers have been a component of shrubland and erosion control seeding mixtures and have been planted along highway corridors. Seed mixtures containing various " <i>Mimulus aurantiacus</i> " varieties have been used successfully along roadcuts in southern California.
B. Habitat restoration	<p>Bush monkeyflowers are a component of habitat restoration plant palettes in many locations (A. M. Montalvo pers. obs.) and can be seeded or planted from container stock. Restoration plans have not always included taxa native to the location. For example, Hillyard (1990) reported that seeds of <i>M. aurantiacus</i> and <i>M. longiflorus</i> from unknown source locations were seeded into test plots at Crystal Cove State Park in Orange Co., Calif. (an area that is home to <i>D. puniceus</i>). No cover was recorded for these plants during plot monitoring.</p> <p>Recent studies have found that the plant pathogen, <i>Phytophthora tantaculata</i>, was transferred to restoration sites in northern California from contaminated nursery stock of <i>Diplacus aurantiacus</i> (Rooney-Latham & Blomquist 2014, Rooney-Latham et al. 2015). To prevent such spread of disease, it is critical that all container plants for restoration be grown using practices that prevent infection and spread of pathogens (e.g., http://www.suddenoakdeath.org/pdf/cangc_bpm_FINAL.pdf). In areas where <i>Phytophthora</i> is problematic it may be best to establish plants from seed. (see "Horticulture or agriculture" section below).</p>
C. Horticulture or agriculture	<p>Important plants for water-wise landscaping and pollinator gardens, but care must be taken to avoid problems with pathogens and ornamental cultivars.</p> <p>Pathogens: Care must be taken to follow best-management-practices (BMPs) to grow the plants free of pathogens so that serious plant pathogens are not spread (Rooney-Latham & Blomquist 2014, Rooney-Latham et al. 2015a, b). A serious plant pathogen, <i>Phytophthora tentaculata</i>, was detected in 2012 in nursery container stock of <i>Diplacus aurantiacus</i> in northern California and then in a number of <i>Diplacus</i> cultivars (Rooney-Latham et al. 2015a, b). The pathogen causes root and crown rot in woody and semi-woody plants and has since been found to persist in stock of <i>D. aurantiacus</i> planted into restoration areas. It is likely that all species within section <i>Diplacus</i> can be affected similarly. The spread of this non-native pathogen into the wild is a threat to native plant populations of many species, including a number dominant and co-dominant woody species. Other species of <i>Phytophthora</i> have also been identified within many nurseries, pushing more stringent nursery sanitation procedures. The BMPs to control the spread of <i>Phytophthora ramorum</i> (cause of sudden oak death), can be adopted to help control these other <i>Phytophthora</i> species.</p> <p>Ornamental plants: Many <i>Diplacus</i> species and horticultural selections and hybrids have striking floral displays and flower colors, and are popular ornamental plants (Lenz 1956, Schmidt 1980, Keator 1994, Lutsko 1987, Wasowski and Wasowski 1995, Bornstein et al. 2005). The ornamental selections and cultivars are for gardens and are not appropriate for habitat restoration.</p> <p>Cultivation: Plants can be grown from seeds or cuttings (Everett 2012) but plants grown from seed are more successful (G. Wains and S. Morgan, UCR Botanic Garden, personal communication). Most <i>Diplacus</i> grow best in full sun in coastal areas but do well in light shade inland. Bush monkeyflowers are grown at low elevations. There are potentially important differences among taxa and populations obtained from different elevations in tolerance to cold temperatures. Flowering and leaf production may be extended by summer watering in more arid regions. However, Atkinson et al. (1988) found that watering may increase susceptibility to atmospheric pollution in the dry season.</p> <p>Agriculture: <i>D. aurantiacus</i> have been planted within hedgerow plantings to provide food for native bees and other pollinators, but visitation frequencies were found to be low (Kremen et al 2002).</p>
D. Wildlife value	Bush monkeyflowers provide food for a variety of insects (e.g., larval host for <i>Euphydryas chalcedona</i> , see VIII. B. Herbivory, above), and they provide nectar for hummingbirds, hawkmoths, and a variety of native bees (see VII. E. Pollination, above).

E. Plant material releases by NRCS and cooperators	None. There are numerous horticultural cultivars meant for landscaping.
F. Ethnobotanical	(NAE 2016) Decoctions or infusions of plant parts of <i>D. aurantiacus</i> were used medicinally by the Costanoan as a urinary aid, by the Pomo, Kashaya for an eyewash for sores, and by the Mahuna as an antidiarrheal. Decoctions of leaves and flowers of <i>D. longiflorus</i> or <i>D. aurantiacus</i> were used by the Tubatulabal for stomachaches.
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XIII. CITATION	Montalvo, A. M., E. C. Riordan, and J. L. Beyers. 2017. Plant Profile for The Woody <i>Diplacus</i> of Southern California.. Native Plant Recommendations for Southern California Ecoregions. Riverside-Corona Resource Conservation District and U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Riverside, CA. Online: https://www.rcrcd.org/plant-profiles
XIV. LINKS TO REVIEWED DATABASES & PLANT PROFILES	
Calflora	https://www.calflora.org/
Jepson eFlora (JepsonOnline, 2018 update)	https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=11356
Jepson eFlora (JepsonOnline, 2nd ed.)	http://ucjeps.berkeley.edu/IJM.html
USDA PLANTS	https://plants.usda.gov/java/nameSearch
Native Plant Network Propagation Protocol Database (NPNPP)	https://npn.rngr.net/propagation
Native Seed Network (NSN)	https://www.nativeseednetwork.org/
GRIN (provides links to many resources)	http://www.ars-grin.gov/cgi-bin/npgs/html/paper.pl?language=en&chapter=scient
GRIN as above, second link-	https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearch.aspx
Wildand Shrubs	http://www.fs.fed.us/rm/pubs_other/iitf_qtr026.pdf
Flora of North America (FNA) (online version)	http://beta.floranorthamerica.org/Phrymaceae
Flora of North America (FNA) (online version)	http://beta.floranorthamerica.org/Diplacus
Native American Ethnobotany Database (NAE)	http://naeb.brit.org/uses/search/?string=Diplacus
Rancho Santa Ana Botanic Garden Seed Program, seed photos	http://www.hazmac.biz/rsabghome.html
XV. IMAGES	<p>Image of <i>D. parviflorus</i> by Keir Morse has a Creative Commons Attribution-NonCommercial-ShareAlike 3.0 license (CC BY-NC-SA 3.0, https://creativecommons.org/licenses/by-nc-sa/3.0/) and may be not used for commercial purposes. The image was cropped for use in this profile.</p> <p>Seed images by John Macdonald used with permission from Rancho Santa Ana Botanic Garden Seed Program (RSABG Seed Program); image by Naomi Fraga may be used with permission from RSABG with rights reserved by RSABG. Images may not be used for commercial purposes.</p> <p>All other images by Arlee Montalvo (copyright 2017) unless otherwise indicated with rights reserved by the Riverside-Corona Resource Conservation District (RCRCD). Photos may be used freely for non-commercial and not-for-profit use if credit is provided. All other uses require permission of the authors and the RCRCD.</p>

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