

Distribution and Evolution of Endemic Plants of the California Islands

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INTRODUCTION

How different are the plants of the California Islands from those of the mainland? In a plant found only on these islands, how much variation is there from island to island? To investigate these questions, I have gathered information on the endemic plants of the California Islands; pertinent information on a few nonendemic island plants is also included. This information is taken from the literature, from personal communication with other botanists, and from work in the field, in the herbarium, and with cultivated island plants by myself and others at the Santa Barbara Botanic Garden.

I have used such phrases as "island plant" to include any plant growing naturally on the California Islands. An "endemic plant" or "island endemic," on the other hand, denotes here a plant that does not occur naturally on the mainland and for which the entire known distribution is confined to one or more of these islands.

The organization of this paper is as follows: (1) plants with slight differences between island and mainland populations; (2) plants with slight differences from island to island; (3) subspecific taxa on different islands, with a special discussion of the Island Mallow, *Lavatera assurgentiflora*; (4) island endemics at the species level; (5) island endemics at the genus level; and (6) morphological and evolutionary tendencies and some of the processes resulting in hybridization, extinction, abundance, and widespread distribution among island plants.

Before proceeding, I wish to point out some distinctively different plants that were thought to be restricted to the islands and have been recently reported, or obscurely reported, from the mainland. These include the shrubby *Crossosoma californicum* from Palos Verdes in coastal Los Angeles County (J. Henrickson, pers. comm.); a Live-forever, *Dudleya virens*, from Palos Verdes (R. Moran, pers. comm.); a Buckwheat, *Eriogonum grande grande*, from Punta Banda, Baja California (M. Benedict, pers. comm.; T. Mulroy, pers. comm.); Island Wallflower, *Erysimum insulare*, from San Luis Obispo County (Cockerell 1937, Hoover 1970); a Tar Weed, *Hemizonia greeneana peninsularis* (Carlquist 1965, Moran 1969); *Orobanche parishii brachyloba* (Heckard 1973); Catalina Cherry, *Prunus ilicifolia lyonii* (Brandege 1889); Island Black Sage, *Salvia brandegei* (Raven 1965); and *Senecio lyonii* (Munz 1935). Furthermore, Giant Coreopsis, *Coreopsis gigantea*, and Santa Cruz Island Pine, *Pinus remorata*, which are often thought of as island endemic plants, are well known from several scattered mainland locations along the California coast. Thus, none of the above are truly insular endemics, although their major concentrations are confined to the California Islands, and relatively minor environmental changes on the mainland could limit any of these to an island distribution.

A few insular endemics are known also from the fossil record of the mainland. Fossils of a Manzanita, *Arctostaphylos insularis*, are reported from La Brea Tar Pits in Los Angeles (J. Warter, pers. comm.). Fossils of Island Ironwood, *Lyonothamnus floribundus*, are known from various sites in California and Nevada. It is of special interest that the fossils of the Santa Catalina Island subspecies are found in coastal southern California while those of the equally insular subspecies *asplenifolius* occur in more interior locations (Raven and Axelrod 1978). Fossils of Island Oak, *Quercus tomentella*, are also known from the mainland of the western

United States. I am not aware of detailed morphological studies that contrast any present-day island plants with their mainland fossil counterparts. Presumably, the island and mainland populations once formed parts of widespread, more or less coherent taxa.

SLIGHT DIFFERENCES BETWEEN ISLAND AND MAINLAND POPULATIONS

Several species exhibit slight morphological differences between island and mainland populations. Within the widespread species *Arbutus menziesii*, the mainland plants usually have mature inflorescences of 9 to 14 cm. From the collections of Ralph Hoffmann (herbarium specimens at SBM)¹ and of Michael Benedict (SBBG), about five Madrone plants are known from Santa Cruz Island. Although other small samples of isolated individuals might show similar distinctions, it is interesting that the island Madrones, otherwise quite like those of the California mainland, are somewhat smaller and have consistently longer inflorescences of 17 to 24 cm.

In a similar way, the small population of the grass *Elymus condensatus* on Prince Island off San Miguel Island differs from those on the mainland and on other islands by its low habit of growth, conspicuously glaucous leaves, long glumes (20 mm), and long pubescence at the rachis nodes (1 mm for the island plants vs. a maximum of 0.7 for those from the mainland); these differences persist under cultivation on the mainland. Although the few *Elymus* plants on Prince Island are extreme for the morphological characters under discussion, individual clones at Gaviota on the mainland and at Cuyler Harbor on San Miguel do have glaucous leaves.

SLIGHT DIFFERENCES AMONG POPULATIONS FROM ISLAND TO ISLAND

Some plants, including four island endemics of the genera *Ceanothus*, *Eriophyllum*, *Lavatera*, and *Lotus*, differ slightly from island to island. The large shrub *Ceanothus arboreus* occurs only on Santa Rosa, Santa Cruz, and Santa Catalina Islands. The plants are quite similar, but those from the northern islands have small, dark, ellipsoidal seeds and small, relatively smooth fruit, while those on Santa Catalina have larger, olive-green, spherical seeds and large, warty fruit. Further study of the leaf pubescence and fruit surface will probably document slight differences between even the Santa Cruz and Santa Rosa populations.

The Silver-lace, *Eriophyllum nevinii*, is an island endemic of the floristically related Santa Barbara, Santa Catalina, and San Clemente Islands. The plants on each of these three islands have modally distinct leaf shapes.

The Santa Rosa Island *Lavatera assurgentiflora* is very similar to that on San Miguel, but when representatives of the two island populations are grown together under cultivation, the petals of the Santa Rosa plants are longer (5 mm or greater vs. less than 5 mm). In a similar manner, the sepals, floral bracts, and pedicels are also longer for the Santa Rosa material.

Three subspecies of low-growing *Lotus argophyllus* are restricted to the California Islands, and the subspecies *L. a. ornithopus* occurs on five islands (the four southern islands from Santa Barbara to San Clemente plus Guadalupe). The Santa Barbara Island populations differ from all others by having distinctly shorter peduncles.

SUBSPECIFIC DIFFERENCES

In contrast to these slight differences, about 30 subspecies (or varieties) are endemic to one or more of the California Islands and are thus different from all known mainland populations.

Eriogonum giganteum compactum is restricted to Santa Barbara Island (Philbrick 1972), *E.*

¹Full names and addresses for standard herbarium abbreviations are given in Index Herbariorum (Regnum Vegetabile 92:303-354, 1974). Most of the specimens without herbarium citations are deposited at the Santa Barbara Botanic Garden (SBBG).

g. giganteum to Santa Catalina Island, and *E. g. formosum* to San Clemente Island. This level of taxonomic distinction among these Buckwheats is based on significant morphological differences including habit, leaf shape, and inflorescence.

Equally as distinct, but not yet recognized by a subspecific name, are the two taxa of Island Snapdragon, *Galvezia speciosa*. The well-known collections from Santa Catalina and San Clemente Islands contrast with those from Guadalupe Island, the latter being more subject to frost damage and having a different leaf shape, flower, and fruit, and a different habit of growth.

The wide-ranging subspecies *Lotus argophyllus ornithopus* is mentioned above as occurring on five islands. Two additional insular endemic subspecies are *L. a. nivus* on Santa Cruz and the strikingly beautiful *L. a. adsurgens* on San Clemente.

One of the best known examples of different subspecies occurring on different islands is offered by the two taxa of Island Ironwood, *Lyonothamnus floribundus*. The subspecies *L. f. asplenifolius*, with palmately divided leaves and incised leaflets, is found only on Santa Rosa, Santa Cruz, and San Clemente; the entire-leaved *L. f. floribundus* is only on Santa Catalina. Some confusion has persisted in the literature on this distribution pattern, perhaps in part because very young seedlings of both taxa have divided leaves and also because the shape of occasional leaves of either subspecies may approach those of the other [Blakley 5401; Brandege 1890a, pl. 5, figs. 1-7; Moran 652 (LAM, SBBG); Piehl 62-422&62-512; Philbrick s.n., in 1969; Philbrick s.n., in 1970].

Lavatera assurgentiflora

Special emphasis is given here to a particularly interesting island plant, the Island Mallow, *Lavatera assurgentiflora*. This plant has been known botanically and horticulturally for over 125 years [Parry s.n., March 1850 (NY)], and by 1918 was cultivated as far south as Ecuador [Pachano 68 (US)]. It has been documented for several of the California Islands and is extensively grown in mainland California and Mexico.

San Miguel Island *Lavatera* was described in 1874 as "a small grove of malva-trees, whose green leaves and penciled blossoms refresh the eyes" (Dall 1874:524). Then E. L. Greene collected *Lavatera* on this island in September 1886 (A, GH, JEPS, NDG, NY, UC), and reported (Greene 1887:77-78) these plants as being restricted to two separate colonies, as follows:

[N]ear the western extremity, in an open grassy valley looking southward there is a group of some thirty small trees of . . . *Lavatera assurgentiflora*. . . . The other specimens seen by me were three or four depressed and straggling bushes growing on an open slope fully exposed to the winds, at the very western end of San Miguel; and these although stunted by exposure were flowering and fruiting.

Not until E. R. Blakley's collection of 1961 (SBBG) were any Island Mallows again reported for San Miguel. He found about 20 shrubs, some up to 1.2 m tall, that formed a colony 6 m in diameter. These plants were located in a flat sandy area adjacent to a blowout in the dunes north of Adams Cove, near the western end of the island. This is probably fairly close to the location of Greene's larger population, with some modification of the habitat by subsequent wind erosion and grazing. Greene's "open grassy valley" also may have been a result of the heavy erosion of 1886 (Johnson 1972:278).

Subsequent observations in 1966 and 1978 show this population to be basically unchanged since 1961, although there are presently more than 20 mature plants.

From 1969 through 1974, Richard S. Peterson, Robert L. DeLong, and George A. Antonelis, Jr., all biologists studying San Miguel Island marine mammals, transplanted seedling Island Mallows from the only known remaining natural population, north of Adams Cove, to two other higher locations in this same general part of the island (R. DeLong, pers. comm.; G. Antonelis, pers. comm.).

Then in 1978, one mature *Lavatera* shrub (2 m tall, 3 m across, and with a basal diameter of 13 cm) was found at the opposite end of the island at an elevation of about 6 m, roughly 1 km southeast of the mouth of Willow Canyon, between Bay Point and Triangulation Point Fish (Philbrick *et al.* B78-376). Under the canopy of this shrub were about two dozen thin seedlings up to 15 cm tall. It is presumed that this shrub, which was not known to have been there in the 1960s, was intentionally or unintentionally established, perhaps from the Adams Cove population.

Brandegee (1890b) lists *Lavatera assurgentiflora* for four islands, including Santa Rosa; however, this does not agree with his more detailed discussion of the same year (1890a). Parish (1890) notes the same four islands, yet I know of no specimens of *Lavatera* for Santa Rosa prior to F. H. Elmore's collection in August of 1938 at "Becher's Bay" (AHFH). M. B. Dunkle made a similar collection one year later that he labeled as coming from "Streambank, Ranch Canyon" (AHFH, LAM). I suspect that both of these collections were from the same general area in the gully at the Vail Ranch headquarters where J. R. Haller and I collected two Island Mallows in 1965. Plants persist in this location to the present, where they are suspiciously near the ranch buildings and have the appearance of having been introduced there. According to C. F. Smith (1976:191) they were "planted at the main ranch on Santa Rosa Island, the source from (?) a native stand on the island." Smith's insertion of a question mark in this quotation indicates his uncertainty; no such native stand, or substantive clue thereof, is known.

According to Brandegee (1890a:109-110) *Lavatera* "has been found on . . . various islets and rocks about Santa Catalina and Santa Cruz"; however, we have searched extensively on Santa Cruz Island and adjacent islets and have found no Island Mallows in the wild, although they are presently cultivated at the Stanton Ranch and at the University of California Field Station. Evidence of *Lavatera* on Anacapa Island begins with Kellogg's type description of *L. assurgentiflora* "from the island of Anacapa off the coast of Santa Barbara and now to some extent cultivated. . ." (Kellogg 1854). It was reported by Brandegee (1890a:109) that "the species was described from a cultivated specimen obtained by Dr. Trask from a garden in Santa Barbara." He further states, "The seed he [she] was told came from the island of Anacapa. . ." According to Lyon (1886:204) "sealers reported that once abundant upon Anacapa and San Nicolas, it is now scarce. . ." Then in 1930 Ralph Hoffmann collected "4 or 5 plants on steep hillside above old sheep landing . . . Anacapa Island" (SBM). None were found on this island by M. B. Dunkle in the late 1930s or early 1940s, nor by subsequent collectors, until in 1978 two live and four dead Island Mallows were found at the top of a 100-m sea bluff on West Anacapa near Portuguese Rock (Timbrook & Philbrick 652 & 653). Then in 1979 one small young plant was found near the top of a similar sea bluff on Middle Anacapa (Junak & Amick MA-36).

Early mention of *Lavatera* on San Nicolas Island is sketchy. In 1853 Nidever "found some high bushes, called by the natives *malva real* . . ." (Ellison 1937:79), and 33 years later Lyon mentioned the sealers' report as given above. No further San Nicolas record is known until 1978, when both Marla Daily (Daily 86) and R. M. Beauchamp collected cultivated specimens from that island.

For Santa Catalina Island *Lavatera*, the known history begins with Lyon's (1886:204) report for "Bird Island [probably Bird Rock, off Fisherman's Cove]." By 1890 Brandegee (1890a:109) had seen this Island Mallow on "a small rock . . . near the isthmus" and reported that it was also known from a second islet to the northwest. It is likely that the second islet was Indian Rock, off Emerald Bay, where *Lavatera* was collected by Moran (LAM, SBBG) in 1941. However, in contrast to this restricted distribution, Parish (1890:301) wrote that *Lavatera* "occupied within the memory of living men, a large part of the island, only yielding to the overstocking of it with sheep and goats." Island Mallow was cultivated in the Avalon area at least as early as 1908 when Jepson collected a San Clemente Island plant grown by Blanche Trask, and, at present, northern

island *Lavatera* is naturalized in this same part of the island (Thorne 1967).

On San Clemente Island, *Lavatera* has been documented from three general areas. At the northwest end of the island, natural and transplanted populations have been found near West Cove (Blakley 6414, in 1963; Boutin 1623, in 1967; Murbarger 208, in 1936, cultivated; Raven 1963:330) and near Wilson Cove (Benedict *s.n.*, in 1971, cultivated; Raven 1963:330). Trask also collected "one tree near sea edge . . . West End" (Trask 282, in 1903); this collection was reported the next year as follows: "in a region of Pot's Valley . . . it was a foot in diameter and twelve feet high; low and bent and splitting at base" (Trask 1904:94).

The second *Lavatera* area on San Clemente is Seal Cove, near the middle of the outer coast of the island. The label of the Nell Murbarger specimen mentioned above states that her West Cove collection was from a tree moved from Seal Cove by a fisherman; this would date a Seal Cove location prior to 1936.

Lavatera was documented for the southeast portion of the island by a second Trask collection (Trask 283, in 1903). The following year this collection was described as "one tree eight inches in diameter—looking into the sea from a cliff near Mosquito Harbor. . ." (Trask 1904:94).

Lyon (1886:204) reported that about 1874, *Lavatera* "constituted unbroken forest, extending for miles upon the high plateaus." And Trask (1904:94-95) wrote that "Johnny [Robearts, a 20-year resident of the island] tells me that formerly there were many 'Malva Rosas' as he calls them; some even on the south coast; mostly eaten by cattle in years when feed was scarce. He recalls these forming groves." Therefore, the historic record for San Clemente Island makes it clear that we can now study only a fragment of a once very extensive population of *Lavatera*.

A single *Lavatera* shrub was found on Todos Santos del Sur in 1965 (Philbrick & Benedict B65-1554) at the base of an inland cliff in the northeastern portion of the island. This plant was estimated to be 1.5 m tall, and in 1968 a basal diameter of 20 cm was recorded. Ten years later a basal diameter of 25 cm was noted for the largest of nine plants that ranged from 0.5 to over 2 m high.

The Todos Santos Island population was most likely planted in recent decades. This hypothesis is supported by three facts: (1) no *Lavatera* was noted for the Anthony, Brandegee, and Stockton collections of 1897 (Brandegee 1900) or for the Moran, Lindsay, Thomas, and Wiggins collections of 1948 and 1949 (Moran 1950); (2) the number of individual Island Mallows has increased markedly since these plants were first collected in 1965; and (3) this population is morphologically very similar to mainland cultivated material.

From the above information it can be assumed that *Lavatera assurgentiflora* is native to at least San Miguel, Anacapa, Santa Catalina, and San Clemente Islands. It was possibly also native to Santa Rosa and San Nicolas Islands. Of these six islands, sufficient study material is available for all except San Nicolas. The *Lavatera* from San Miguel, Santa Rosa, and Anacapa Islands, and nearly all the cultivated populations (including those on Todos Santos), differ from the native populations of Santa Catalina and San Clemente Islands by consistently having a pubescent upper leaf surface, a subentire petal apex, and a pubescent staminal tube. The Santa Catalina and San Clemente taxon is characterized by a glabrous or subglabrous upper surface of the leaf and usually by an erose petal apex and a glabrous or subglabrous staminal tube.

Lavatera assurgentiflora is thus divided here into two subspecies, *L. assurgentiflora* Kell. subsp. *glabra* subsp. nov., and *L. assurgentiflora* Kell. subsp. *assurgentiflora*. A formal description of the new subspecies follows.

Lavatera assurgentiflora Kell. subsp. *glabra* subsp. nov., including *Saviniona clementina* Greene (Leaf. Bot. Observ. Crit. 2:160-161, 1911) and *S. reticulata* Greene (Leaf. Bot. Observ. Crit. 2:161, 1911). Superficies folii glabra usque subglabra, viridis vivide; apex petali plerumque erosus; tubus staminalis glaber usque subglaber.

Upper surface of leaf glabrous to subglabrous, bright green; petal apex usually erose;

staminal tube glabrous to subglabrous.

Type.—Bird Rock, Santa Catalina Island, Los Angeles County, California, U.S.A., 23 September 1961, *E. R. Blakley 4739* (SBBG).

Known distribution.—Santa Catalina and San Clemente Islands, California.

Specimens examined.—United States: California, Los Angeles County, Santa Catalina Island: one locality, flowers pale rose color, May 1896, *Blanche Trask s.n.* (US); one tree, buds and flowers snow white, February 1898, *Blanche Trask s.n.* (isotype of *S. reticulata*, US); two localities, March 1898, *Blanche Trask s.n.* (NY); on islets off north coast, March 1898, *Blanche Trask s.n.* (US); on two islets, March 1899, *Blanche Trask s.n.* (A); Indian Rock, 26 February 1941, *Reid Moran 625* (SBBG); Indian Rock, 4 October 1962, *E. R. Blakley 5415* (SBBG); preceding collection in cultivation, 20 April 1966, *R. N. Philbrick s.n.* (SBBG); Bird Rock, 22 May 1931, *F. R. Fosberg 7167* (UC, US); Bird Rock, 23 September 1961, *E. R. Blakley 4739* (type, SBBG); in cultivation from Bird Rock, 20 April 1966, *R. N. Philbrick s.n.* (SBBG); San Clemente Island; no definite locality, April 1885, *Nevin & Lyon s.n.* (GH); in cultivation, July 1908, *W. L. Jepson 14050* (JEPS); no definite locality, no date, received October 1911, *Blanche Trask s.n.* (A); one tree near sea edge, West End [northwest portion of island], June 1903, *Blanche Trask 282* (isotypes of *S. clementina*, A, NY, US); between Driggs and West Rock, 11 April 1962, *P. H. Raven 17303* (SBBG); SW of airstrip runway, 23 April 1967, *F. C. Boutin 1623* (SBBG); West Cove in cultivation, May 1936, *Nell Murbarger 208* (UC); West Cove, 8 December 1963, *E. R. Blakley 6414* (SBBG); preceding collection in cultivation, 20 April 1966, *R. N. Philbrick s.n.* (SBBG); Wilson Cove in cultivation, 27 June 1971, *M. R. Benedict s.n.* (SBBG); one tree, East End [southeast portion of island], June 1903, *Blanche Trask 283* (A, NY, US).

Therefore, *Lavatera assurgentiflora* becomes another example of an endemic plant with different subspecies on different islands.

DIFFERENCES AT THE SPECIES LEVEL

About 100 species are restricted to the California Islands, and a few such endemic plants are present as different species on different islands. These include species of *Arctostaphylos*, *Astragalus*, *Castilleja*, *Dudleya*, *Eriogonum*, *Eschscholzia*, *Haplopappus*, *Hemizonia*, *Lavatera*, *Lotus*, *Malacothrix*, and *Senecio*.

The tomentose maritime Locoweeds, *Astragalus miguelensis*, *A. nevinii*, and *A. traskiae*, are good examples of such a pattern of distribution. *A. miguelensis* occurs on the four northern islands from San Miguel to Anacapa, plus San Clemente Island, where it grows sympatrically with the San Clemente endemic *A. nevinii*. This latter *Astragalus* is very closely related to *A. traskiae*, which is restricted to Santa Barbara and San Nicolas Islands.

The genus *Dudleya* probably contains more island endemic taxa than any other. These include about nine published and unpublished island species, illustrated by *D. candelabrum* of Santa Rosa and Santa Cruz Islands, *D. traskiae* of Santa Barbara Island, and *D. greenii* (*sensu lato*) of San Miguel, Santa Rosa, and Santa Cruz Islands, and perhaps once from Santa Catalina Island.

Buckwheats of the genus *Eriogonum* have also evolved into a number of different island species, including the northern island *E. arborescens* and the southern island *E. giganteum*. The narrow-leaved *E. arborescens* occurs on Santa Rosa, Santa Cruz, and Anacapa, while the broad-leaved *E. giganteum* (*sensu lato*) is on Santa Barbara, Santa Catalina, and San Clemente.

The insular *Haplopappus* shrubs have also evolved into northern and southern island species (Raven 1963). *Haplopappus detonsus* occurs on Santa Rosa, Santa Cruz, and Anacapa; it has thick, coarsely serrate, pubescent leaves and densely white-woolly phyllaries. *Haplopappus canus*, on the other hand, has nearly glabrous phyllaries and relatively thin, finely serrate leaves

that are glabrate on the upper surface. The known distribution of the latter species is restricted to San Clemente and Guadalupe Islands.

DIFFERENCES AT THE GENERIC LEVEL

Although no plant family is restricted to the California Islands, four genera, *Baeriopsis*, *Hesperelaea*, *Lyonothamnus*, and *Munzothamnus*, occur only on these islands. Three are known from only a single island. The same three are each considered to consist of a single species. Two are members of the family Compositae. Two are woody trees. Two are known only from Guadalupe Island, and two occur on San Clemente Island.

One of these four insular endemic genera, *Hesperelaea*, is a member of the Olive family, found only on Guadalupe Island, and now thought to be extinct; this extinction is not surprising in view of the devastation by goats on that island and in view of Watson's 1876 (p. 118) description and comment:

A rather compact tree, twenty to twenty-five feet high, flowers lemon-color. Only three living trees were found in a canyon on the east side, no young trees seen, but many dead ones.

Baeriopsis, the other Guadalupe Island endemic, is reported to be quite rare (R. Moran, pers. comm.), and this herbaceous member of the Compositae is in danger of being further reduced by goats. In spite of the implication of its name, *Baeriopsis* is morphologically very different from *Baeria* (now included within the genus *Lasthenia*).

Munzothamnus is a larger, semi-woody endemic of San Clemente Island where it, too, is in danger of reduction by goats. It is generally recognized as a distinct genus, but is a close relative of *Malacothrix*.

The only wide-ranging endemic genus on the California Islands is *Lyonothamnus* of the Rosaceae. As discussed above under subspecific differences, this tree occurs on Santa Rosa, Santa Cruz, Santa Catalina, and San Clemente Islands. It differs from many of its woody relatives by having opposite leaves.

EVOLUTIONARY TENDENCIES AMONG ISLAND PLANTS

Ten evolutionary trends and processes that are particularly conspicuous among island plants are discussed here.

Pink flower color.—A striking trend among both the endemic and nonendemic plants of the California Islands is the occurrence of pink-flowered forms in plants that usually have other flower colors throughout most of their range. Although frequencies need to be calculated and compared for island and mainland locations and the genetics and pollination biology must be worked out, preliminary information is given here for several interesting examples.

The island endemic Morning Glory, *Calystegia macrostegia macrostegia* (see Philbrick 1972), usually has white flowers; however, a few plants on Anacapa and Santa Cruz have a light pink cast to their flowers (*Blakley 3951 & 4407*).

The shrubby Paintbrush, *Castilleja hololeuca*, is also endemic to the islands. Nearly all San Miguel and Santa Rosa populations have yellow flowers. Yellow, red, and pink flowers occur on Santa Cruz, and red and pink predominate on Anacapa.

The island populations of several nonendemic species are of equal interest. The Yarrow, *Achillea borealis*, usually has white ray petals; however, both pink- and white-flowered forms are abundant on San Miguel. A few pink forms also appear on Santa Rosa, for example in Cow Canyon (*Philbrick & Broder B65-1036*), and in scattered locations on Santa Cruz, such as Saucos Canyon, Lower Embudo, and above China Harbor (*Philbrick B66-187, Philbrick et al. B68-269, Philbrick & Benedict B65-1390*). In all of these pink-flowered populations the color is variable, but the original color persists under cultivation on the mainland.

The Santa Cruz Island Buckwheat, *Eriogonum grande grande*, occurs on the northern islands, plus Santa Catalina, San Clemente, and Todos Santos, and in a very limited way on mainland Baja California. All of the San Miguel Island plants, some of those on Santa Rosa, and a few of those on Santa Cruz are short in stature and have gray foliage and intense rose pink to light pink flower clusters. These have been treated by some as a distinct species, *E. rubescens*; however, they intergrade in all these characters with the taller, green-leaved, whitish-flowered taxon.

A few plants of Indian Pink, *Silene laciniata*, found near Ragged Mountain and East Twin Harbor on Santa Cruz Island, have pink flowers (*Benedict s.n.*, in 1967, *Philbrick & Benedict B65-1307, B65-1309, & B65-1329*). These are in sharp contrast to the usual intensely red flowers seen in this species on the mainland and in numerous other island populations.

The prevalence of such evolutionary experimentation among island populations of predominantly mainland plants suggests incipient speciation in these groups leading possibly to further adaptive radiation on the islands.

Variability in leaf shape.—Variation in vegetative structures, such as leaves, is usually more extreme than variation in reproductive structures. Nevertheless, it is of interest to note that the leaf shape of such island endemics as *Eriophyllum nevinii* and *Lyonothamnus floribundus asplenifolius* differs markedly from island to island.

The leaf shape of island populations of the widespread Toyon, *Heteromeles arbutifolia*, varies in a different way. This Toyon undoubtedly exhibits a certain amount of variability in nearly all of its populations, mainland and island; however, the amount of variation within and between various populations on the same and on different islands is remarkable even when these variants are grown together in cultivation. Leaf characters that vary include: the length/width ratio, the angle of folding along the midrib, the shape of the base and apex, and the amount of serration along the margin.

Gray foliage.—A third trend noted particularly among island plants is the predominance of gray foliage, especially among insular endemics in strictly maritime habitats.

This tendency is exemplified by a Pine, *Pinus torreyana*; a Century Plant, *Agave sebastiana*; a grass, the *Elymus condensatus* from Prince Island; several Buckweats, including *Eriogonum giganteum*; various Poppies, including *Eschscholzia ramosa* and insular races of *E. californica*; the related Bush Poppy, *Dendromecon*; a number of *Dudleya* endemics; legumes such as *Lotus cedrosensis*, insular subspecies of *L. argophyllum*, and *Astragalus miguelsenis* and its relatives; *Ceanothus arboreus*; *Lavatera assurgentiflora assurgentiflora*; the Santa Cruz Island *Garrya*; members of the Snapdragon family, *Castilleja hololeuca* and *Galvezia speciosa*; and several Compositae including *Artemisia californica insularis*, *Eriophyllum nevinii*, and *Haplopappus detonsus*.

Thomas Mulroy (1976, 1979) has made an extensive study of the glaucous gray foliage in *Dudleya*. His work establishes a genetic basis for this glaucousness and correlates the waxy surface with reduced herbivore damage, increased leaf longevity, and probably with reduced nutrient loss due to leaching.

Nancy Vivrette (pers. comm.) has been particularly interested in a number of maritime plants with pubescent gray leaves. In these cases the gray coloration is correlated with a slower rate of growth; it is speculated that selective advantages may involve increased water collection and protection from predation, fungus, and salt spray, especially by the pubescent underside of developing leaves in the bud stage.

Gray and green foliage races.—If the assumptions regarding the selective advantages of gray-leaved insular plants are valid, it is somewhat surprising that races with both gray and green leaves occur within several island species. This is true, for example, with nearly sympatric races of both the succulent *Dudleya* and the shrubby *Galvezia*. Several different

island *Dudleya*s exhibit this phenomenon, for example *D. albiflora* as it occurs on Cedros, the *D. candida* of Los Coronados, *D. greenei* on the three most westerly islands, and *D. traskiae* on Santa Barbara. Mulroy (1976) has carefully studied the habitat preferences of the gray and green races of *D. brittonii*, a primarily mainland relative of *D. candida*; although these taxa are superficially sympatric, he has established subtle differences in their microhabitats. Perhaps, then, this type of evolutionary divergence allows for the exploitation of different microhabitats by very closely related taxa.

Insular plants with relatively large habit, leaves, or fruit.—Carlquist (1966) nicely documented the occurrence on islands of large plants with relatively large plant parts. This phenomenon has been studied in detail by Hochberg (1980) for the leaves of three California Island plants.

The following partial list suggests the prevalence of such gigantism among woody and semi-woody island endemics of the flora under consideration: a Buckwheat, *Eriogonum giganteum*; Bush Poppy, *Dendromecon*; *Ceanothus arboreus* and *C. megacarpus insularis*; *Lomatium insulare*; Island Morning Glory, *Calystegia macrostegia macrostegia*; a Paintbrush, *Castilleja hololeuca*; Island Coastal Sage, *Artemisia californica insularis*; *Eriophyllum nevinii*; and *Haplopappus detonsus*.

Prostrate races of nonendemic island plant species.—Again, as with flower color variants, the prostrate races of California Island plants seem to be mostly among widespread nonendemic species that usually occur as nonprostrate plants on both the mainland and the islands. Transplant culture at the Santa Barbara Botanic Garden has demonstrated a genetic dwarfing for the following perennials, all originally collected in windy island habitats: Blue-eyed Grass, *Sisyrinchium bellum*; California Buckwheat, *Eriogonum fasciculatum*; Chamise, *Adenostoma fasciculatum*; and Coastal Sagebrush, *Artemisia californica*. It will also be important to compare genetic and environmental factors for mainland dwarfs. However, it seems possible that the insular or maritime habitat may be conducive to such incipient speciation through the selective advantage of dwarfing mutations.

Hybridization.—Open habitats and nonrigorous selection probably play a major part in increasing the frequency of apparent hybridization on these islands.

On Santa Catalina Island a few relictual plants of the Island Mountain Mahogany, *Cercocarpus betuloides traskiae*, persist in a depauperate hybrid swarm with *C. betuloides blanchea* (Thorne 1969a).

A surprising intersectional *Opuntia* hybrid was found on San Clemente Island by Nell Murbarger (UC). Morphologically this plant is an *F1* hybrid between two nonendemic cacti, a Cholla, *O. prolifera*, and a Prickly-pear, either *O. littoralis* or *O. oricola*. This plant represents the only known evidence for such a wide cross (either natural or artificial) in the genus *Opuntia*.

Another remarkable hybrid swarm occurs among the Cuyler Harbor Chicories on San Miguel Island (*Philbrick B74-157, Philbrick & Benedict B68-316 through B68-322, Philbrick & Ricker B73-301 & B73-302*). Here the caespitose Beach Chicories, *Malacothrix incana (sensu stricto)* and *M. succulenta*, hybridize freely with *Malacothrix implicata*. These particular crosses are so remarkable to those familiar with *Malacothrix* that W. S. Davis, biosystematic specialist in this genus, at first rejected our report as impossible. Subsequent examination of the specimens, however, offers at least preliminary supporting evidence (W. S. Davis, pers. comm.). Two other similar hybridizing populations have recently been found on San Miguel.

One of the most fascinating island hybrids is a single arborescent shrub of *Ceanothus* found by Michael Benedict on Santa Cruz (*Benedict s.n.*, in 1969; *Philbrick et al. B78-2; Philbrick & Benedict, B69-114*). It shares many characteristics with the Santa Cruz Island *C. arboreus* but differs in a number of ways (Tables 1 and 2). Regardless of its precise parentage, this unusual shrub is most probably of hybrid origin. With sample sizes of 500 to 1,000 pollen grains from

TABLE 1. A comparison of the Santa Cruz Island hybrid *Ceanothus* with *Ceanothus arboreus* and *Ceanothus spinosus*.

	<i>Ceanothus arboreus</i>	<i>Ceanothus hybrid</i>	<i>Ceanothus spinosus</i>
Burl	absent	present	present
Color of new bark	gray	gray with green cast	bright yellow-green
Petiole length	7 to 15 mm	6 to 11 mm	2 to 9 mm
Leaf blade shape	broadly ovate to elliptic	ovate to elliptic	elliptic to oblong
Maximum leaf blade length	8 cm	6 cm	4 cm
Leaf margin	serrulate to serrate	serrulate, lower 1/3 subentire	mostly entire, sometimes toothed near apex
Leaf apex	acute to obtuse	acute to obtuse	obtuse to emarginate
Leaf venation	3-veined	3-veined	3-veined only on burl sprouts
Upper leaf surface	puberulent	glabrous to subglabrous	glabrous
Lower leaf surface	canescent	strigose along veins	glabrous or somewhat strigose on midrib
Fruit shape	3-sided	globose	globose
Fruit width	5.5 to 6.5 mm	4.5 to 5.5 mm	4.0 to 6.0 mm

single plants, the Santa Cruz Island *C. arboreus* has 96 per cent stainable pollen, mainland *C. spinosus* has 98 per cent, and mainland *C. thyrsiflorus* has 99 per cent, yet the Santa Cruz Island shrub has only 40 per cent stainable pollen.

The hybrid shrub grows adjacent to *C. arboreus* in a mesic phase of island chaparral. A few feet away a 1-m seedling, which looks very much like the original hybrid, has become established. In addition to this natural seedling, about 200 seedlings have been grown in cultivation from open-pollinated seed collected in the wild from the original shrub. These progeny range from some approaching *C. arboreus* to some with the bark, leaf, and fruit characteristics of the Greenbark *Ceanothus*, *C. spinosus*, a species which is not known from the fossil or current record of any of the California Islands. It is of interest to note, however, that Axelrod (1967:290) lists a "species similar to" *C. spinosus* among the mainland fossil associates of the now insular *Lyonothamnus* and *Quercus tomentella*.

Chaney and Mason (1930) reported fossil seed of *C. thyrsiflorus* from Santa Cruz Island, and it is tempting to consider the possibility that the hybrid shrub is a cross between *C. arboreus* and a now extinct island population of *C. thyrsiflorus*. However, we have studied the size and shape of seeds of *C. arboreus*, *C. thyrsiflorus*, and *C. spinosus*, as well as the actual Chaney and Mason fossils; we find no evidence to support the hypothesis. Furthermore, one cannot argue that the fossil seeds are actually representative of *C. spinosus* or the Santa Cruz Island hybrid, for the fossil seeds match rather closely those of contemporary *C. thyrsiflorus*. The average fossil seed length \times width is 1.18×1.07 mm. Adding 25 per cent to restore live dimensions (15 to 25 per cent proposed by Chaney and Mason), these fossil seeds would reflect a live seed size

TABLE 2. Simplified comparison of the Santa Cruz Island hybrid with *Ceanothus arboreus* and *Ceanothus spinosus*.

	Like <i>C. arboreus</i>	Intermediate	Like <i>C. spinosus</i>
Burl	—	—	X
Bark color	—	X	—
Petiole length	—	X	—
Leaf blade shape	X	—	—
Leaf blade length	—	X	—
Leaf margin	—	X	—
Leaf apex	X	—	—
Leaf venation	X	—	—
Upper leaf surface	—	X	—
Lower leaf surface	—	X	—
Fruit shape	—	—	X
Fruit width	—	X	—

of about 1.5×1.3 mm, which compares favorably with 1.8×1.5 mm for contemporary *C. thyrsiflorus* but definitely not with the 2.4×2.4 mm of the Santa Cruz Island hybrid or the even larger-seeded *C. spinosus*.

All available morphological data considered, it seems to us that *C. spinosus* is the more probable absent parent, especially because of the *C. spinosus*-like progeny and the intermediate nature of so many salient characteristics of the Santa Cruz Island shrub (Tables 1 and 2).

In addition to hybridization in the wild, island taxa also have a propensity to hybridize when brought into cultivation. *Eriogonum giganteum giganteum* from Santa Catalina Island and the native *E. arborescens* have been grown together for several years at the Stanton Ranch on Santa Cruz. In 1971 apparent *F₁* hybrids were noted at this same location and have since been found elsewhere on the island. These hybrids appear to be morphologically intermediate between the two rather different looking Buckwheats (*Philbrick B71-46* through *B71-48*). Similar hybridization has also been found in cultivation on the mainland (*Philbrick s.n.*, in 1979).

Mahonia pinnata insularis from Santa Cruz Island has been grown in cultivation with the mainland subspecies *M. p. pinnata*, and the two collections remain morphologically distinct. However, volunteer seedlings growing under a plant of the smooth leaflet insular subspecies produced the spiny leaflets characteristic of mainland populations. Apparently cross-pollination occurred in cultivation, and the spiny leaflet margin is genetically dominant.

Island species of the genus *Lavatera* offer another example of interspecific hybridization in cultivation. Volunteer seedlings have resulted from uncontrolled cross-pollination between *L. venosa* and both *L. assurgentiflora* and *L. occidentalis* [*Hall s.n.*, in 1903 (UC), *Philbrick s.n.*, in 1971].

Such hybridization in cultivation suggests that these island endemics have resulted from morphological evolution that has not been accompanied by the evolution of intrinsic reproductive barriers.

Reduction and extinction.—For 16 relatively small islands we can easily list 21 insular endemic plants that have been eliminated or drastically reduced on at least some of these islands. This is a result of both the fragility of these plants and the vulnerability of their habitats. It is an especially discouraging trend for those who are interested in the study of island endemic plants. There is, however, always the possibility that some of these plants may again be found

where they are now thought to have been eliminated.

The grass *Dissanthelium californicum* has yielded to grazing pressures and is extinct throughout its known range which once included at least three of the larger southern islands.

Mahonia pinnata insularis was probably never abundant anywhere during the past century and has not been collected again on Santa Rosa or Anacapa Island in recent decades. This leaves only a few small populations on Santa Cruz to perpetuate this ornamental island shrub.

Three insular members of the Mustard family have been reduced or eliminated. *Arabis hoffmannii* can no longer be found on Santa Cruz, nor *Sibara filifolia* on Santa Cruz or Santa Catalina. The Santa Cruz Island endemic *Thysanocarpus conchuliferus* is reduced to a small fraction of its original distribution on this island; now it is usually found only on relatively inaccessible rocky ledges.

Succulent *Dudleyas* are especially vulnerable. *Dudleya candelabrum* is rare on Santa Rosa Island and presently even harder to find on Santa Cruz. The Santa Barbara Island *Dudleya traskiae* was thought to be extinct as of 1969 (Philbrick 1972). Since 1974, however, reduction in the feral rabbits on Santa Barbara Island has allowed a few scattered plants to become re-established in areas in and around Cave, Middle, and Cat Canyons. There is also a thriving colony, probably of several hundred plants, recently discovered by Molly Hunt on the nearly vertical westerly face of Signal Peak (Philbrick & Cummings B76-1). This population has apparently been inaccessible to the rabbits, but could be eliminated by landsliding.

The herbaceous Saxifrage, *Lithophragma maximum*, has been collected only on San Clemente Island, and there only once, in 1936 (Bacigalupi 1963).

Only a very few individual plants of the endemic Mountain Mahogany, *Cercocarpus betuloides traskiae*, now occur on Santa Catalina Island.

Two subspecies of *Lotus argophyllus*, *L. a. adsurgens* of San Clemente Island and *L. a. niveus* of Santa Cruz Island, are extremely rare and apparently vulnerable to grazing. A third legume, *Trifolium palmeri*, is reported as extinct for Santa Catalina Island (Thorne 1967); it is known otherwise only from four other southern islands.

Lomatium insulare cannot now be found on San Clemente Island, where it is known only from a 1918 collection (Raven 1967, Thorne 1969b). Apparently this plant has been extinct on San Clemente for several decades.

The extinction of *Hesperelaea*, the endemic tree from Guadalupe Island, is discussed above under generic endemics and again emphasizes the irreversible destruction of uncontrolled grazing on islands.

One endemic species of *Phacelia* and two of *Lycium* have not been collected since the 1930s or earlier. *Phacelia cinerea* is known only from San Nicolas Island, where it was collected only once or twice [Trask s.n. (GH), in 1901, not seen; Trask s.n. (UC), no date]. *Lycium hassei* is known only from one plant each on Santa Catalina and San Clemente Islands. The San Clemente plant was reported as dead in 1936 and that on Santa Catalina was intentionally removed by 1908 (Raven 1963). *L. verrucosum* is known only from San Nicolas Island and is another of those plants collected only by Blanche Trask [Trask s.n. (CAS), in 1897; Trask s.n. (LAM), in 1901]. It has not been seen since.

The genus *Mimulus* contains three small, fragile island Monkey Flowers that have not been found by any contemporary botanist and must be assumed to be extinct. These three are *M. brandegei* from Santa Cruz Island, *M. latifolius* from Guadalupe Island, and *M. traskiae* from Santa Catalina Island. The most recent collection of these annual Monkey Flowers was in 1932.

Abundance.—Diametrically opposed to extinction is a trend among some island endemic plants to be extremely abundant where they do occur. This may result from the presence of favorable habitats within a nonsaturated flora and from appropriate plant adaptations.

Examples of such abundant endemics are: Buckwheats, including *Eriogonum arborescens*

and *E. grande*; *Dudleya*, such as *D. greenei* on San Miguel Island; a Locoweed, *Astragalus miguelensis*; a White Popcorn Flower, *Cryptantha maritima cedrosensis*; Paintbrushes, such as *Castilleja hololeuca* on Anacapa Island; *Haplopappus detonsus* on West Anacapa; a Tar Weed, *Hemizonia clementina*; and *Malacothrix foliosa (sensu lato)* on Santa Barbara Island.

Widespread distribution.—A few plants that are known only from the California Islands have a remarkably wide distribution within that limit. An annual, *Gilia nevinii*; an herbaceous perennial, *Jepsonia malvifolia*; and a tree, *Quercus tomentella*, each occur on six of these islands. All three occur on Santa Cruz, Santa Catalina, San Clemente, and Guadalupe. In addition, the *Gilia* is known from Anacapa and Santa Barbara Islands; the *Jepsonia*, from Santa Rosa and San Nicolas Islands; and the oak, from Santa Rosa and Anacapa Islands.

The Island Morning Glory, *Calystegia macrostegia macrostegia*, has an even wider distribution; it occurs on 10 islands from San Miguel to Guadalupe.

The Island Poppy, *Eschscholzia ramosa*, has recently been collected on San Nicolas Island by Mitchel Beauchamp (pers. comm.). This collection, plus previously overlooked reports for Natividad Island (Brandege 1900) and for Anacapa Island (Dunkle 1942:131 as "*Eschscholtzia elegans* Greene"), extends the reported distribution for this delicate annual endemic to all of the California Islands except San Miguel.

Such extensive distributions for strictly insular plants may be related to a relatively uniform climate over broad distances and to successful plant adaptations.

SUMMARY

Among the plants discussed in this paper are a new subspecies of *Lavatera assurgentiflora* and a hybrid related to *Ceanothus arboreus*.

Many plants are restricted to the California Islands and differ from their mainland relatives and those on other islands. Some of these plants have minor differences of a few trivial characters; at the opposite extreme, others differ by the aggregation of numerous characters, resulting in generic endemics.

Of particular interest are the morphological and physiological experimentations, which play a part in allowing endemic island organisms to exploit the favorable, open habitats of these islands.

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The plants of the California Islands are available for field study to all qualified botanists with sufficient patience, hardiness, and flexibility who obtain the necessary private and governmental permission. Some of the most interesting island plants have been well documented in herbarium collections such as those of the University of California, California Academy of Sciences, Santa Barbara Botanic Garden, Santa Barbara Museum of Natural History, Los Angeles County Museum of Natural History, Rancho Santa Ana Botanic Garden, San Diego Museum of Natural History, University of Notre Dame, and the Smithsonian Institution.

Our island plant research at the Santa Barbara Botanic Garden has resulted from the field and herbarium work of several botanists, but special credit is due Michael R. Benedict, Botanic Garden Research Associate, for extensive collecting, especially on Santa Cruz Island, and for discovering, rediscovering, or making repeated field observations on the island *Arbutus* and the *Ceanothus* hybrid discussed here. Steven A. Junak, Botanic Garden Botanist, has contributed careful herbarium study of *Lavatera assurgentiflora*, the Prince Island *Elymus*, and the hybrid *Ceanothus* and its presumed parents. The Latin translation was provided by Robert W. Patterson.

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