THE FLORISTICS OF THE CALIFORNIA ISLANDS

Peter H. Raven

Stanford University

The Southern California Islands, with their many endemic species of plants and animals, have long attracted the attention of biologists. This archipelago consists of two groups of islands: the Northern Channel Islands and the Southern Channel Islands. The first group is composed of San Miguel, Santa Rosa, Santa Cruz, and Anacapa islands; the greatest water gap between these four is about 6 miles, and the distance of the nearest, Anacapa, from the mainland only about 13 miles. In the southern group there are also four islands: San Clemente, Santa Catalina, Santa Barbara, and San Nicolas. These are much more widely scattered than the islands of the northern group; the shortest distance between them is the 21 miles separating the islands of San Clemente and Santa Catalina, and the nearest island to the mainland is Santa Catalina, some 20 miles off shore.

The purpose of this paper is to analyze the complex floristics of the vascular plants found on this group of islands, and this will be done from three points of view. First will be considered the numbers of species of vascular plants found on each island, then the endemics of these islands, and finally the relationship between the island and mainland localities for these plants. By critically evaluating the accounts of Southern California island plants found in the published works of Eastwood (1941), Millspaugh and Nuttall (1923), Munz (1959), and Raven (1963), one can derive a reasonably accurate account of the plants of the area. Using this as a basis, it is possible to outline the major features of the floristics of the region.

NUMBERS OF SPECIES

In an ecologically uniform region, the number of species s of any group of organisms increases in an approximately logarithmic manner in relation to the area of sampling A (Preston, 1962). This relationship can be expressed as

$$s = bA^z$$

where b and z are constants and $z < 1$. Important deviations from

this relationship occur in islands which are located so far from a source area that the rate of extinction of their species exceeds the rate of immigration (MacArthur & Wilson, 1963). It is therefore of interest to see how closely the relationship between number of species of vascular plants and area holds for the Southern California Islands. In making this analysis, only native plants were considered, as the opportunities for naturalization of introduced species have varied widely from island to island. The pertinent figures are as follows:

Island	Area in square statute miles *(A)*	Number of native species subspecies and varieties *(s)*	Number of endemic species subspecies and varieties Endemics	Distance to mainland in statute miles
Santa Cruz	96	420	7	19 (5 to Anacapa*)
Santa Rosa	84	340	3	27 (3 to San Miguel)
Santa Catalina	75	375	3	20
San Clemente	56	233	11	49 (21 to Santa Catalina)
San Nicolas	22	120	2	61 (28 to Santa Barbara Is.)
San Miguel	14	190	–	26 (3 to Santa Rosa)
Anacapa	1.1	70	–	13
Santa Barbara	1.0	40	1	38 (24 to Santa Catalina)
Santa Monica Mts.	320	640	2	–
Cedros	134	205	16	14 (10 to Natividad)
Guadalupe	98	164	32	157

* Distance to the nearest intervening island in parentheses.

Dr. L. G. Mason has calculated a least-squares fit to the equation relating area and number of species. For the native vascular plants of the Southern California Islands $z = 0.38$, with a correlation of 0.89 between log area and log number of species. A similar relationship between area and numbers of species of reptiles and amphibians and of mammals has been indicated in other papers presented in this symposium. Only San Nicolas Island appears to deviate significantly, with only 120 species of native vascular plants instead of the 175-190 that might be expected in view of its size. This island is the farthest from shore of the group, and its immigration/extinction ratio (MacArthur and Wilson, 1963) might therefore differ appreciably from that of the other islands. In addition it is perhaps among the least diverse ecologically, and this might be an alternative factor limiting the size of its flora. San Nicolas Island was first visited by a botanist in 1897 (Eastwood, 1898). By this time it had been intensively grazed by sheep for 40 years, these reaching a peak of some 30,000 individuals by 1890. In view of this, it is likely that a number of plant species may have been exterminated on the island before they were ever collected. Conversely, the data for the Santa Monica Mountains (Raven and Thompson, unpublished), a mainland area which is geologically a continuation of the axis forming the northern tier of islands, are consistent with the figures for most of the islands. This strongly suggests that all of the islands, with the possible exception of San Nicolas, are approximately "saturated" with species of vascular plants in the sense of MacArthur and Wilson (1963).

No consideration of the Southern California Islands would be complete without mentioning Guadalupe Island. Despite its position some 240 miles south of San Clemente Island, Guadalupe Island has a flora remarkably similar to that of the islands to the north. Dr. Reid Moran has pointed out that 24 of its 164 vascular plants are restricted to Guadalupe Island and to one or more islands of the southern California group. Guadalupe Island is separated from the mainland by a much greater distance (157 miles) than are any of the Southern California Islands. It also has a greater area (98 square miles) than any of these, and were it in the Southern California group, might be expected to have more than 400 species of native vascular plants instead of the 164 that are present. This reduced flora might be a function of the relatively great distance of Guadalupe Island from the mainland. On the other hand, Cedros Island, which is much closer to Guadalupe Island in latitude than are the Southern California Islands but is only 14 miles from the coast of Baja California, has an area of about 134 square miles and a flora of some 205 species (Reid Moran, personal communication). The relationship between area and number of species for these two Baja California

islands is comparable to that prevalent in the southern California group, but with far fewer species involved. This suggests that the two Baja California islands may simply lie in a region with fewer species than do the Southern California Islands, and that ecological factors may predominate in limiting the size of the flora of Guadalupe Island. A more comprehensive analysis of the relationship between area and number of species of the islands and selected mainland areas between approximately 28° and 38°N latitude may shed additional light on this problem (Mason & Raven, in preparation).

ENDEMISM

A second way of analyzing the floristics of the California Islands is in terms of their endemics (Raven, 1963, 1965). There are two genera endemic to Guadalupe Island, *Hesperelaea* (Oleaceae) and *Baeriopsis* (Compositae); one to San Clemente Island, *Munzothamnus* (Compositae); and one to the Southern California Islands as a whole, this being *Lyonothamnus* (Rosaceae). At the level of species, subspecies, and varieties, San Clemente Island, with eleven, has more endemics than any other member of the Southern California group. These endemics are:

Brodiaea kinkiensis
Triteleia clementina
Eriogonum giganteum
subsp. formosum
Lithophragma maxima
Astragalus nevinii
Lotus argophyllus
subsp. adsurgens
Lotus scoparius
subsp. traskiae
Malacothamnus clementinus
Camissonia guadalupensis
subsp. clementina
Castilleja grisea
Munzothamnus blairii

One species, one subspecies, and two varieties are endemic to Santa Catalina Island: *Cercocarpus betuloides* var. *traskiae, Lyonothamnus floribundus* subsp. *floribundus, Solanum wallacei* var. *wallacei, Mimulus traskiae.* The two smaller islands of the southern group have three additional single-island endemics, two *(Phacelia cinerea, Lycium verrucosum)* on San Nicolas Island, and one *(Dudleya traskiae)* on Santa Barbara Island.

There are 21 species, subspecies, and varieties endemic to more than one island in the southern group, as indicated by the following list, in which SCl indicates San Clemente Island, SCa Santa Catalina, SBa Santa Barbara, SN San Nicolas, and G Guadalupe.

Dissanthelium californicum SCl, SCa, G
Eriogonum giganteum subsp. giganteum SCa, SBa

Crossosoma californicum SCl, SCa, G
Astragalus traskiae SBa, SN
Lotus argophyllus subsp. ornithopus SCl, SCa, SBa, SN, G
Lupinus guadalupensis SCl, G
Trifolium palmeri SCl, SCa, SN, G
Gilia nevinii SCl, SCa, G
Lomatium insulare SCl, SN, G
Linanthus pygmaeus subsp. pygmaeus SCl, G
Phacelia floribunda SCl, SBa, G
Phacelia lyonii SCl, SCa
Cryptantha traskiae SCl, SN
Lycium hassei SCl, SCa
Galvezia speciosa SCl, SCa, G
Scrophularia villosa SCl, SCa, G
Galium catalinense var. catalinense SCl, SCa
Artemisia nesiotica SCl, SBa, SN
Eriophyllum nevinii SCl, SCa, SBa
Haplopappus canus SCl, G
Malacothrix foliosa SCl, SBa, Los Coronados

Thus 18 of the 21 species are found on San Clemente Island, 12 on Guadalupe Island, 12 on Santa Catalina Island, 6 on Santa Barbara Island, and 4 on San Nicolas Island. To complete the picture of endemism in the southern group of islands, it should be mentioned that there are 32 species and taxa of subspecific rank endemic on Guadalupe Island. For the Southern California Islands, the importance of San Clemente Island for endemics stands out clearly, with the figures for Santa Catalina Island considerably less impressive and the two smaller islands relatively insignificant.

In the northern group of islands, there are 7 species and varieties *(Arabis hoffmannii, Sibara filifolia, Dudleya nesiotica, Ribes thacherianum, Arctostaphylos subcordata* var. *subcordata, Castilleja affinis* subsp. *insularis, Mimulus brandegei)* endemic to Santa Cruz Island and three *(Dudleya blochmaniae* subsp. *insularis, Arctostaphylos subcordata* var. *confertiflora, Gilia tenuiflora* subsp. *hoffmannii)* on Santa Rosa Island. No taxon is known to be endemic to San Miguel Island or to the three islets making up Anacapa Island. In addition to the 10 endemics on the two major islands, there are 13 species, subspecies, and varieties endemic to more than one island in the northern group. In the following list SMi indicates San Miguel Island, SR Santa Rosa Island, SCr Santa Cruz Island, and A Anacapa Island.

Eriogonum arborescens SR, SCr, A
Berberis pinnata subsp. insularis SR, SCr
Erysimum insulare SMi, SR

Dendromecon rigida subsp. harfordii SR, SCr
Dudleya candelabrum SR, SCr
Heuchera maxima SR, SCr, A
Arctostaphylos insularis SR, SCr
Phacelia divaricata var. insularis SMi, SR
Solanum wallacei var. clokeyi SR, SCr
Castilleja hololeuca SMi, SR, SCr, A
Galium californicum var. miguelense SMi, SR
Galium catalinense var. buxifolium SMi, SCr
Haplopappus detonsus SR, SCr

Twelve of these 13 taxa are found on Santa Rosa Island, only 10 on Santa Cruz Island, 4 on San Miguel Island, and 3 on Anacapa Island. Overall, the representation of endemics on the northern group appears to be roughly proportional to the size of the flora.

Finally, there are 15 species, subspecies, and varieties endemic to at least one island in both the northern and southern groups:

Quercus tomentella SR, SCr, SCl, SCa, G
Eschscholzia ramosa SCr, SCl, SCa, SBa, G
Dudleya greenei SMi, SR, SCr, SCa
Jepsonia malvifolia SR, SCr, SCl, SCa, SN, G
Lyonothamnus floribundus subsp. asplenifolius SR, SCr, SCl, SCa
Astragalus miguelensis SMi, SR, SCr, A, SCl
Ceanothus arboreus SR, SCr, SCa
Ceanothus megacarpus subsp. insularis SR, SCr, ?SCl, ?SCa, ?G
Rhamnus pirifolia SR, SCr, SCl, SCa, G
Lavatera assurgentiflora SMi, SCl, SCa, SBa; doubtfully native on SR, SCr, A
Amsinckia spectabilis var. nicolai SMi, SCl, SN
Mimulus flemingii SR, SCr, A, SCl, ?SCa
Hemizonia clementina A, SCl, SCa, SBa, SN
Malacothrix indecora SMi, SCr, SN
Malacothrix insularis var. squalida SR, SCr, A, SBa

There are, therefore, 13 of these widespread island endemics which occur on Santa Cruz Island, 11 each on Santa Rosa and San Clemente, 10 on Santa Catalina, 5 on San Miguel, Anacapa, and Guadalupe, and 4 on Santa Barbara and San Nicolas. *Eschscholzia ramosa* occurs, in addition to the range given above, on Los Coronados, Todos Santos, San Benitos, and Cedros Islands, and is thus by far the most wide ranging of the island endemics. In considering this list, it is important to remember that a number of species have similar distributions but reach the mainland at some point; among them might be mentioned *Prunus ilicifolia* subsp. *lyonii*, *Calystegia macrostegia* subsp. *macrostegia (Convolvulus macrostegius)*, and *Coreopsis gigantea*. There are also a few cognate taxa that may well have diverged from common ancestors with a similar distribution, such as *Eriogonum arborescens* - *E. giganteum*, *Galium catalinense* var. *buxifolium* - *G. c.* var. *catalinense*, and *Haplopappus detonsus* - *H. canus*.

To summarize these data on endemism in the Southern California Islands, there are 38 species, subspecies, and varieties endemic in the southern group, 23 in the northern group, and 15 common to both groups, for a total of 76 endemics in the Southern California Islands as a whole. Of these endemic taxa, 31 are found on Santa Cruz Island, 26 on Santa Rosa Island, 26 on Santa Catalina Island, 10 on San Nicolas Island, 9 on San Miguel Island, 8 on Anacapa Island, and 11 on Santa Barbara Island. All of these figures agree closely with the sizes of the respective islands and the sizes of their floras. In striking contrast are the 40 island endemics found on San Clemente Island, approximately twice what would be expected on the basis of the size of this island. Even more impressive is the flora of Guadalupe Island, where the flora of some 164 native vascular plant species includes 32 endemic to the island and an additional 24 endemics of the southern California group and Guadalupe Island, the total of 56 island endemics comprising more than a third of the native flora.

MAINLAND LOCALITIES FOR ISLAND PLANTS

At least a tenth of the species of vascular plants of the Southern California Islands have mainland distributions not adjacent to the islands where they occur. A few of these are species generally found in desert areas farther to the south--as *Lycium brevipes* and *Filago arizonica* on San Clemente Island--and some, such as *Achillea lanulosa* on the same island, have generally interior distributions on the mainland. The great majority of the species with non-adjacent mainland distributions, however, are northern species. This is not surprising when we consider that islands, by their very nature, always have more moderate climate than the adjacent continents. In this case, the limiting factor on the adjacent continent is clearly aridity.

Some of the most striking northern species are found on the southernmost island that we have considered, Guadalupe. Among these are *Polypodium scouleri*, *Polystichum munitum*, *Pinus radiata*, *Brodiaea lugens*, *Ribes sanguineum*, *Epilobium minutum* sensu lato, and *Eriophyllum lanatum*. On San Clemente Island are found such northern plants as *Carex tumulicola*, *Juncus patens*, and *Malacothrix incana*, and in the northern group of islands, for example, *Calamagrostis rubescens*, *Elymus triticoides* subsp. *pacificus*, *Carex pansa*, *Lupinus variicolor*, *Trifolium microdon*, *Armeria arctica* subsp. *californica*, *Polygala californica*, *Lomatium caruifolium*, and *Erigeron glaucus*. On the mainland, most of

these species occur no further south than Monterey or northern San Luis Obispo counties, and thus their island stations are from 100 to approximately 300 miles south of their main continuous areas of distribution.

Comparable disjunctions of range are abundant in the flora of California as a whole, and are mainly the result of the persistence of northern species, displaced far southward during Pleistocene pluvial cycles, in locally favorable sites. On Santa Cruz Island itself, a Pleistocene flora with an age estimated by radiocarbon dating as 14,000 B.P. (Orr, this symposium) was described by Chaney and Mason (1930). This flora includes some northern species not now present in the south – *Pseudotsuga menziesii, Cupressus goveniana* – as well as other northern plants which are local in southern California: *Garrya elliptica, Ceanothus thyrsiflorus, Myrica californica.* The assemblage of plants that occurred on Santa Cruz Island at the time this flora was deposited was considered by Chaney and Mason to be most similar to that which occurs at present in the vicinity of Fort Bragg, Mendocino County. This suggests a southward displacement of the flora of some 440 miles during the last pluvial maximum, which ended perhaps 10,500 years ago. It is not strange that some of these migrants have persisted in favorable areas of maritime climate, both on the islands and also on the mainland. Thus we have forests of closed-cone pines in coastal northern Baja California, *Vaccinium ovatum* in coastal San Diego County, and *Myrica californica* in the Santa Monica Mountains, to name just three such Pleistocene relicts.

Particularly instructive are those groups in which a northern form has persisted locally but has been replaced by a more xerophytic relative throughout most of southern California. Thus *Delphinium variegatum* is the only species of its genus on San Clemente Island and also occurs on the mainland from northern San Luis Obispo County northward; on the other islands and the mainland of southern California it has been replaced by the closely related *D. parryi. Camissonia cheiranthifolia* subsp. *cheiranthifolia* and *Ambrosia chamissonis* subsp. *chamissonis* both occur on San Clemente Island and on the northern islands and mainland, but most of southern California's coastline is occupied by *Camissonia cheiranthifolia* subsp. *suffruticosa* and *Ambrosia chamissonis* subsp. *bipinnatisecta.* There is a similar relationship between two subspecies of *Lathyrus laetiflorus*, with *L. l.* subsp. *barbarae* on San Clemente Island and on the northern islands and mainland, while *L. l.* subsp. *alefeldii* is on Santa Catalina Island and on the mainland of southern California.

In one impressive example of this sort, the tetraploid *Clarkia davyi* occurs on Santa Rosa Island and on the coastal bluffs of the mainland from the vicinity of Monterey Bay to the Oregon border, but has been replaced on the mainland of San Luis Obispo and apparently also Santa Barbara counties by its hexaploid derivative, *C. prostrata.* It appears very likely that this hexaploid has originated since the last pluvial maximum, its other parent being the diploid *C. speciosa.*

Many of the island endemics, when their relationships can be traced, are found to exhibit similar patterns. Thus *Eriophyllum nevinii,* found on Santa Catalina, San Clemente, and San Nicolas islands, is closely related to *E. staechadifolium,* which occurs on the Northern Channel Islands and northward. Another island endemic which is a representative of a predominantly northern group of species is *Triteleia clementina,* restricted to San Clemente Island. A final example is *Lomatium insulare,* endemic to San Nicolas, San Clemente, and Guadalupe islands, which is most closely related to, and possibly recently derived from, *L. parvifolium* of coastal Monterey and San Luis Obispo counties.

DISCUSSION AND CONCLUSIONS

In their present form, the California Islands (including Guadalupe) are certainly no older than mid-Pliocene time. During the early Pleistocene, all of the California group with the possible exception of San Clemente Island were broadly joined to the mainland (Clements, 1955). In the late Pleistocene, most of the islands were drastically reduced in size, judging from the wave-cut terraces that reach up to at least 1500 feet elevation on San Clemente Island and 1800 feet on Santa Cruz Island. At this time, San Nicolas and Santa Barbara islands were completely submerged (Clements, op. cit.), and their entire flora and fauna must, therefore, have migrated to them subsequently over the water.

The distinctive flora of the California Islands has accumulated in this region by virtue of the survival of disjunct populations of species in locally favorable sites. For several of the outstanding woody endemics, there is clear paleobotanical evidence (Axelrod, this volume) of progressive restriction in range, sometimes accompanied by the evolution of maritime ecotypes similar to those which are now island endemics *(Lyonothamnus, Quercus tomentella).* Many of the most unusual plants of the region are found not only on the islands but also occur in adjacent mainland areas with similar climate; thus *Pinus torreyana* occurs only on Santa Rosa Island and on a small area of the coast north of San Diego, while *Salvia brandegei* is restricted to the same island and a local colony near Santo Tomas, Baja California.

In general, the representation of endemics in the California Islands is consistent with that in similar, adjacent mainland areas and, as we have seen, roughly proportional to the size of the islands. There are, however, two conspicuous exceptions to

this generalization. Guadalupe Island, with 2 endemic genera, 32 endemic species, subspecies, and varieties, and a total of 56 island endemics, is the most striking; but San Clemente Island, with 1 endemic genus, 11 endemic species, subspecies, and varieties, and a total of 40 island endemics, is likewise very impressive. With respect to Guadalupe Island, it seems clear that a relatively great age together with a high degree of isolation has made possible the accumulation of occasional migrants at different times during the past. On such an isolated island, even if it is "saturated" in terms of numbers of species, establishment must be a relatively rare event and consequently the elimination of persistent relicts less likely than on the mainland or on islands closer to shore. The representation of endemics on San Clemente Island, which is out of proportion to its area or total number of species, suggests that it may likewise have had a relatively high degree of historical permanence and isolation, both of which are compatible with the known geological facts. In comparing the two islands, which are very likely of comparable age, it is tempting to ascribe the higher proportion of endemics on Guadalupe Island mainly to its greater isolation and consequently lower rate of immigration.

There are vast differences between the flora of San Clemente Island and that of Santa Catalina Island, which is considerably closer to the mainland and has certainly been connected to it during parts of the Pleistocene (Raven, 1963). This strongly suggests that the rate of establishment on the islands nearer shore, either overland during the Pleistocene or over the relatively small water gaps that now separate them from the mainland, has been higher than that on San Clemente Island and much higher than that on Guadalupe Island. The floras of Santa Cruz, Santa Rosa, and Santa Catalina islands are relatively similar to those prevalent on the mainland at the present time, whereas those of San Clemente and Guadalupe islands consist of mixtures of various elements present on the mainland in the past, as well as distinctive endemics that may have evolved *in situ*. The floras of the four smaller, recently submerged islands are much poorer in endemics which is consistent with their recent arrival from nearby islands and from the mainland in relatively recent time. The distinctive floras of Guadalupe and San Clemente islands have, not surprisingly, been most susceptible to the activities of European man, his weeds, and grazing animals, and thus provide models for the destruction of island biota which is occurring all too rapidly over the entire surface of the globe.

ACKNOWLEDGMENTS

I am grateful to Dr. L. G. Mason, Department of Biology, State University of New York, Albany, for his calculations based on the data presented in this paper. Mason was supported by Grant 2G-365-R1 from the U.S. Public Health Service-National Institutes of Health. I am also grateful to Dr. Reid Moran for his generous sharing of unpublished data concerning the floras of the islands off the coast of Baja California, and to the National Science Foundation for grants which provided support for my research.

LITERATURE CITED

Chaney, R. W., and H. L. Mason. 1930. A Pleistocene flora from Santa Cruz Island, California. Carnegie Inst. Pub., 415:1-24.

Clements, T. 1955. The Pleistocene history of the Channel Island Region, southern California. *In* Essays in the natural sciences in honor of Captain Allan Hancock, pp. 311-323. Los Angeles.

Eastwood, A. 1898. Notes on the plants of San Nicolas Island. Proc. Calif. Acad. Sci., ser. 3, 1:89-120.

Eastwood, A. 1941. The islands of southern California and a list of the recorded plants. II. Leafl. West. Bot., 3:54-78.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution, 17:373-387.

Millspaugh, C. F., and L. W. Nuttall. 1923. Flora of Santa Catalina Island (California). Field Mus. Nat. Hist. Pub., 212:1-413.

Munz, P. A. 1959. A California flora. Berkeley and Los Angeles. 1681 pp.

Preston, F. W. 1962. The canonical distribution of commonness and rarity. I-II. Ecology, 43:185-215, 410-432.

Raven, P. H. 1963. A flora of San Clemente Island, California. Aliso, 5:289-347.

Raven, P. H. 1965. Notes on the flora of San Clemente Island, California. Aliso, 6:11.