RELICTUAL ORIGINS OF INSULAR ENDEMICS IN QUERCUS

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Although this symposium is primarily intended to treat the California Islands, my subject has rather quickly led me to the mainland of Baja California where equally insular situations center about mountain ranges. Since these have yielded excellent examples of insular effects, I shall draw heavily from them in the development of my theme.

Endemic species can originate either by local speciation through some form of genetic divergence or by attrition of range, creating a relictual population. Occasionally one encounters evidence that both genetic divergence and attrition of range contributed to the making of an insular endemic. If we briefly evaluate a few of the California Island species, the role of these processes will emerge.

Quercus wislizenii A.DC., in a form described by Greene as *Q. parvula,* occurs on Santa Cruz Island as a low, rhizomatous shrub with some of the characters of the mainland population of *Q. wislizenii* var. *frutescens* Jepson in the Santa Ynez Mountain range. Some divergence has occurred in the insular population.

Quercus douglasii H. & A. occurs in a few small groves on Santa Cruz and Santa Catalina islands where it appears to be hybridizing somewhat with *Q. dumosa* Nutt.

Quercus chrysolepis Liebm. is found in very restricted areas on Santa Cruz and Santa Catalina islands. It occurs principally as individuals strongly introgressed by *Q. tomentella* Engelm. although a few show no evidence of hybridization.

Quercus lobata Née occurs on Santa Cruz and Santa Catalina islands and is genetically represented on Santa Rosa, Santa Cruz, and Santa Catalina where it has hybridized freely with *Q. dumosa* to produce a variable population to which Greene applied the name *Q. macdonaldii.*

Within the insular populations of each of these four species *(Quercus wislizenii, Q. douglasii, Q. chrysolepis* and *Q. lobata)* some typical individuals remain, but divergence through hybridization or other cause is strong. The potential exists for the development of an endemic, either through further divergence or through attrition of the mainland range. The likelihood of this

latter occurrence is, of course, extremely low since all four species are very widespread on the mainland.

Quercus tomentella is found on Santa Rosa, Santa Cruz, Anacapa, Santa Catalina, San Clemente, and Guadalupe islands. Although the fossil record of the mainland contains several specimens representative of *Q. tomentella*[1], the species is now totally confined to the islands where it constitutes an endemic of completely relictual origin.

In the Cape Region of Baja California there exists a narrow endemic of relictual origin from a formerly broadly distributed species. *Quercus brandegei* Goldm. occurs only in the foothills of the Sierra de la Victoria. This species is known as a fossil equivalent[2] in Miocene deposits at Tehachapi, almost 1,500 kilometers to the north. In addition, the characters of *Q. brandegei* are very apparent in the derivative species, *Q. fusiformis* Small, which ranges across central Texas from northeastern Mexico (Muller, 1961). These genetically related populations are now separated by 1,000 airline kilometers or 3,000 kilometers by land. The isolated population of the Cape Region shows great uniformity and thus is unlikely to have been modified by any sexually compatible species. Furthermore, its characters agree with those of the Miocene fossils. It is thus evident that its endemism is the consequence of attrition of range. Its mountain situation on a desert peninsula is biologically as insular as an oceanic island.

Quercus cedrosensis Mull. is a recently described species (Muller, 1962) abundant on Cedros Island and scattered widely in small populations on the adjacent mainland of Baja California. Its mainland occurrences include low elevation sites along the Pacific Coast and interior mountain sites to an elevation of 1,400 meters. Several of the mainland populations, including some maritime ones, are in poor condition, exhibiting die-back from desiccation and elimination by heavy browsing. In contrast, the Cedros Island population, centering about Cerro Cedros and ranging down to 1,000 meters, is vigorous and healthy. The maritime influence on the high ocean-facing slopes of Cerro Cedros favors climatic stability in spite of regional deterioration of a formerly mesic climate. The situation, then, is one in which further desiccation could eliminate the mainland populations of *Q. cedrosensis*, leaving the insular population as a relictual endemic. On the other hand, under the present climatic conditions, a subsidence of Baja

1. As *Quercus declinata* Dorf (reviewed by Axelrod, 1944a, p. 134; 1944b, p. 198).
2. As *Quercus mohavensis* Axelrod (Axelrod, 1939, p. 99, pl. 8, fig. 1; MacGinitie, 1953, pp. 101-102, pl. 30, fig. 5-6).

California, leaving islands where the mountain masses now stand, would create an insular endemic population of *Q. cedrosensis* similar in both origin and condition to *Q. tomentella.*

Let us now consider a natural group of species widespread in the northwestern quadrant of the mainland of Mexico (fig. 1). The principal species is *Quercus emoryi* Torr. which ranges from southern Arizona and the Big Bend region of Texas to southern Durango. In some portions of this range *Q. emoryi* is sympatric in the strictest sense with *Q. viminea* Trel. and *Q. eduardii* Trel., both of which are members of the same natural series but seldom if ever hybridize with *Q. emoryi.*

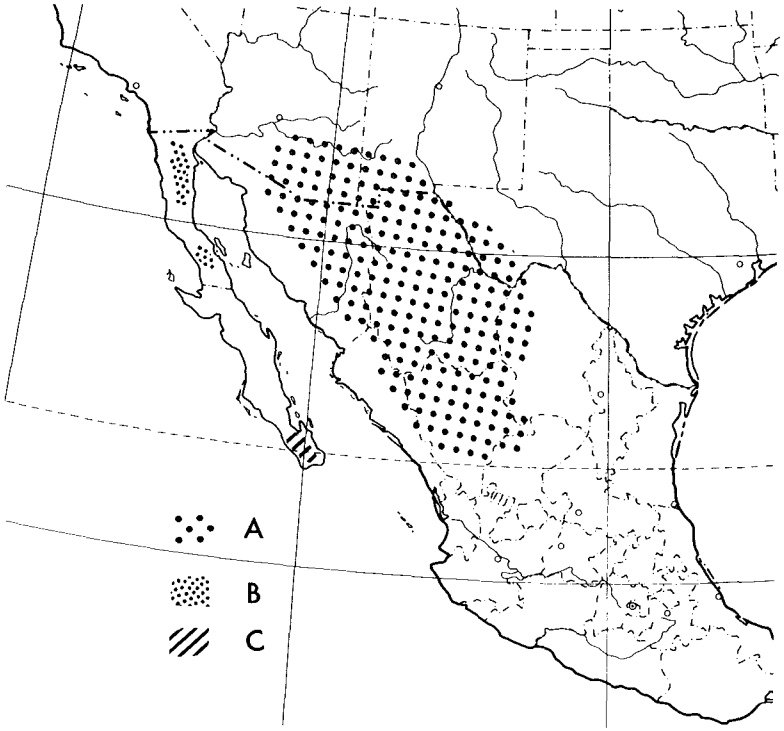

Fig. 1. The distribution of *Quercus emoryi* and derivative species: (A) *Q. emoryi;* (B) *Q. peninsularis;* (C) *Q. devia.*

Two additional species related to *Quercus emoryi* occur in Baja California. These are *Q. peninsularis* Trel. and *Q. devia* Goldm. *Q. peninsularis* is abundant in the Sierra de Juárez and the Sierra de San Pedro Mártir. It has recently been collected by Reid Moran in the Sierra de San Borjas. This northerly species is very similar to *Q. emoryi* in appearance, the principal key

character being a heavy indumentum of the leaves and twigs that is both qualitatively and quantitatively different from that of *Q. emoryi*. The two populations are separated by over 300 kilometers of desert across the delta of the Colorado River.

Quercus devia occurs only in the Sierra de la Victoria of the Cape Region of Baja California. This species, although clearly a derivative of the *Q. emoryi* ancestral plexus, is much more distinct from living *Q. emoryi* than is *Q. peninsularis*. It differs in a number of characters, most of them more fundamental than the indumentum differences exhibited by *Q. peninsularis*. It is separated from *Q. peninsularis* by about 750 kilometers and from *Q. emoryi* by about 1,350 kilometers along the peninsula of Baja California and across southwestern Arizona. Across the Gulf of California the distance from *Q. emoryi* is only about 350 kilometers. This separation of the peninsula from the mainland of Mexico is a relatively ancient one. The consequent biological isolation has effectively restricted several of the species of the Sierra Madre Occidental from reaching the Cape Region while permitting others to arrive. Alternatively, the more mesophytic mainland species may not have survived to the present even after successful early migration to the Cape Region. Thus, there is no evidence of *Q. emoryi* in the Cape Region, but the mainland species, *Q. viminea*, *Q. albocincta* Trel., *Q. rugosa* Née, and *Q. tuberculata* Liebm., are represented by variously vigorous or shrinking populations in the Sierra de la Victoria. One segment of the population of *Q. devia* is introgressed by *Q. viminea* with which it is locally intermixed.

The moist, cool climate of a major mountain range surrounded by rigorous desert is equally as isolated as an island surrounded by a similar expanse of sea. The Sierra de la Victoria is biologically insular in fact, although geomorphologically it may be insular in potential only—that is, it would be an island if subsidence of the peninsula were to flood the desert plains. This biological insularity has isolated the populations of the mesic mountain areas continuously since the development of desert climate on the plains. This period probably began at least as early as late Tertiary. Land connections between the peninsula and the mainland of Mexico occurred as late as the Pliocene in the north but not since early Tertiary in the Cape Region. Thus, the northerly *Quercus peninsularis* might recently have been isolated from *Q. emoryi* while *Q. devia* in the Cape Region has long been isolated by the Gulf of California and by the insular quality of the mountains to which it retreated as desert climate developed. The attrition of range resultant from climatic desiccation, the isolation from genetic contact with *Q. emoryi*, and the divergences that have occurred by whatever means have all combined to produce a narrow endemic strongly divergent from the other species of the series.

The California Islands harbor several unique species similar to *Quercus tomentella* in that their fossils occur on the mainland. It is thus likely that relictual origin can successfully explain a significant proportion of the insular endemics.

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