

species extinction. Measures to counteract it will come only through ecological research, education, and training for mutual capacity building in cooperation with the Pacific islanders. Mutual capacity building is needed to approach traditional island cultures with respect and for bridging indigenous knowledge together with modern scientific understanding of the dynamics of local ecosystems and landscapes. To be successful, such approaches must also be integrated with conservation management and decision making for environmental policy.

SEE ALSO THE FOLLOWING ARTICLES

Hawaiian Islands, Biology / Island Biogeography, Theory of / Mangrove Islands / Succession / Sustainability

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VICARIANCE

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In plants and animals, closely related species and groups of species often occur in different areas, and this pattern is called vicariance. Its origin can be explained by a pro-

cess, also termed vicariance, in which a widespread common ancestor differentiates and breaks up, more or less in situ, into related descendants. For example, consider a variety of plant or animal that is found only on (i.e., is endemic to) a certain island. It may have its closest relative on a nearby mainland. Isolation and differentiation of the island population from the mainland one could have arisen by vicariance if the island and its life were separated from the mainland by a geological process, such as erosion or subsidence. In an alternative explanation, dispersal theory, the island is colonized after it forms by long distance, overwater dispersal of an individual or seed from the mainland. Colonization then stops, and the new population differentiates to become an island endemic. The well-known "equilibrium theory" of island biogeography is based on dispersal theory and suggests that immigration from a mainland center of origin and extinction together determine biogeography.

DISPERSAL AND VICARIANCE

In dispersal theory, a related group, or taxon, evolves in a restricted area—its "center of origin"—and attains its distribution by dispersing out from there. Each taxon comes into existence on its own, not with others. In contrast, during vicariance of a widespread ancestor, the population of each different sector evolves into a new taxon where it is, often over a wide area. There is no center of origin and no "dispersal," although subsequent range expansion or contraction may take place. In dispersal theory, a "founder" population is established through normal dispersal, but at some point migration stops, and the founder becomes isolated from its parent population. It has never been explained why exactly dispersal would stop, but this is a critical question. In dispersal theory the end of dispersal is attributed to chance rather than to geological or climatic change, as in vicariance.

Normal, "ecological" dispersal, the physical movement of plants and animals, is observed every day. It does not involve the differentiation of new taxa, unlike long-distance, chance dispersal, which is a theory of speciation. All organisms move, and given the amount of geological time available, they should be able to migrate to areas of suitable habitat around the world. However, in fact, most groups show marked local and regional endemism. This creates an apparent paradox: The movement that exists everywhere does not seem related to the most fundamental aspect of distribution. In addition, distribution patterns are usually shared by many taxa with different ecology and means of dispersal. These observations conflict with the dispersal theory of speciation and biogeography and have led to

ongoing debate about biogeographic processes. Normal “ecological” dispersal and vicariance are accepted by all workers. The center of origin/founder dispersal mode of speciation is much more controversial.

DATING TAXA

Attempts have been made to distinguish between origin by vicariance or by dispersal through dating taxa, because dispersal theory generally proposes a geologically younger age for a taxon than does vicariance. There are difficulties with this approach, however. Fossils provide only minimum ages for groups, and most groups are much older than their oldest known fossil. Fossil-based molecular clock calculations also give minimum ages for taxa, but these are often misrepresented as maximum dates and used to rule out earlier vicariance events as irrelevant. Simplistic correlations with paleogeography, such as calibrating all Pacific-Atlantic divergence with the rise of the Isthmus of Panama at 3.5 million years ago, can also give ages for taxa that are much too young.

Dating studies usually assume that evolutionary differentiation is more or less continuous over time and so roughly clock-like. Degree of differentiation would then be more or less proportional to the time since divergence. However, evolution probably proceeds in distinct phases with long periods of stasis, and so taxa may show little or no differentiation despite having been separated for many millions of years.

CENTERS OF ORIGIN

The center of origin for a particular group has often been deduced from the arrangement of taxa in a cladogram or phylogenetic tree. However, the “basal” branch or clade is not a primitive, ancestral group occurring at the center of origin—just a small sister-group, and no more primitive, just less diverse, than the main clade. A series of vicariant taxa that branch off sequentially in a cladogram represents a geographic sequence of differentiation in a widespread ancestor, not a series of chance dispersal events.

VICARIANCE IN THE PACIFIC

The Dispersal Model

Dispersal and vicariance models of Pacific biogeography were vigorously debated by the Victorian naturalists, but after the First World War, dispersal theory became almost universally accepted. According to the theory, all Pacific taxa derive from ancestors that originated in Asia or America and migrated into the Pacific. The dispersalists recognized the existence of prior land in the Pacific, as they knew that many volcanic islands had sunk there,

each leaving only an atoll as a trace. Nevertheless, they interpreted distributions among the islands of the Pacific as the result of dispersal among extant, rather than former, islands. For example, the distinctive Pacific clade of *Cyrtandra* shrubs is endemic to rain forest on islands between the Carolines and southeastern Polynesia. The very wide range has been taken as proof that the plants are highly vagile and have a remarkable capacity for long-distance dispersal. However, this proposal overlooks the many single-island endemic species in the group, the clear-cut vicariance between the group and its relatives (which are absent from the central Pacific), and the volcanism that has been widespread and continuous in the Pacific basin since its formation.

Volcanism and Metapopulations

Dispersal theory for islands involves random volcanism, a center of origin, and long distance dispersal, whereas vicariance emphasizes recurrent volcanism, normal migration among unstable local populations any of which may go extinct, and regional persistence of taxa despite changing geography. The dispersal model assumes that the Pacific region was originally devoid of islands and island life, but this is very unlikely. Volcanism does not occur at random, but takes place around particular sectors over periods that are much longer than the age of the individual volcanoes. Oceanic volcanic islands form at subduction zones, spreading centers, hotspots, and propagated fissures, which have always been active in and around the Pacific. The individual islands are relatively short-lived, but new islands are constantly being formed in the vicinity. These new islands are colonized by “ordinary dispersal” from nearby islands, not by “long-distance dispersal,” and there is no speciation involved. The taxon originates and survives in the region as a population of populations, a metapopulation, and whether or not the current islands have ever been joined to a mainland or not (the distinction between “oceanic” and “continental” islands) is not relevant for their biogeography. Populations on volcanic islands and atolls, and their reefs, survive and evolve in the same way that they do on any other recurring habitat “islands,” such as termite mounds or forest gaps.

Establishing the age of an individual volcanic island is not straightforward and involves more than just dating the exposed strata. An island may be composed of very young volcanics or limestone but could be very old as an island, if new material is added as old material is removed by subsidence, erosion, or burial, which is usually the case. In practice, the age of an island’s rocks is not nearly as important for biogeographic analysis as the age and

history of the associated subduction zone, fissure, or hot-spot that has been generating the volcanism. In Hawaii and the Galápagos, for example, biologists have suggested that endemic taxa are much older than the rocks that currently form the islands. The populations have survived in the region by constantly dispersing from older, now largely eroded islands to nearby younger islands. In one model, island chains form by plate movement over hot-spots, and so archipelagoes may eventually join with others. This process might explain the Hawaii–southeastern Polynesia connections seen in many marine and terrestrial taxa. However, some geologists now suggest that linear island chains are formed not by hotspots but by propagated fissures resulting from plate tectonics processes. The fissures, like subduction zones, may be much older than the individual islands.

Vicariance Model

Recently, several authors have discussed a model for the Pacific which assumes that plants and animals have always occurred there. The fact that the central Pacific is a large, well-marked center of endemism that includes smaller areas of endemism is not well accounted for in traditional biogeographic theory. If the Pacific had been populated by dispersal from a western center of origin, a simple dropping out of individual species across the Pacific from west to east might be predicted. But regional areas of endemism occur throughout the Pacific and often involve parts of one archipelago and parts of another. Across the Pacific, there is a west-to-east drop in total diversity of terrestrial and shallow-water marine species, and this is sometimes cited as evidence for dispersal. However, the decline is simply due to the islands of Indonesia and Melanesia being larger than the islands of Polynesia.

The rain forest trees of *Metrosideros* (Myrtaceae) are a typical example of central Pacific endemism. The distributions of the five main clades are mostly vicariant (Fig. 1), with overlap only in Vanua Levu, Fiji (although clade 3 is only known there from one mountain), and North Island, New Zealand (where clade 1 has a very restricted range). Each of the *Metrosideros* clades occupies an area of endemism also held by many other, very different taxa. Southeastern Polynesia, an important biogeographic sector that is often overlooked, is illustrated here by the land snail *Tubuaia* (Fig. 1). *Metrosideros* has close relatives endemic to New Guinea, the Philippines, South Africa, and Chile, indicating that it originated by vicariance, as the central Pacific representative in a South Africa–Pacific–Chile group. This group, in turn, has vicariant relatives in Australia.

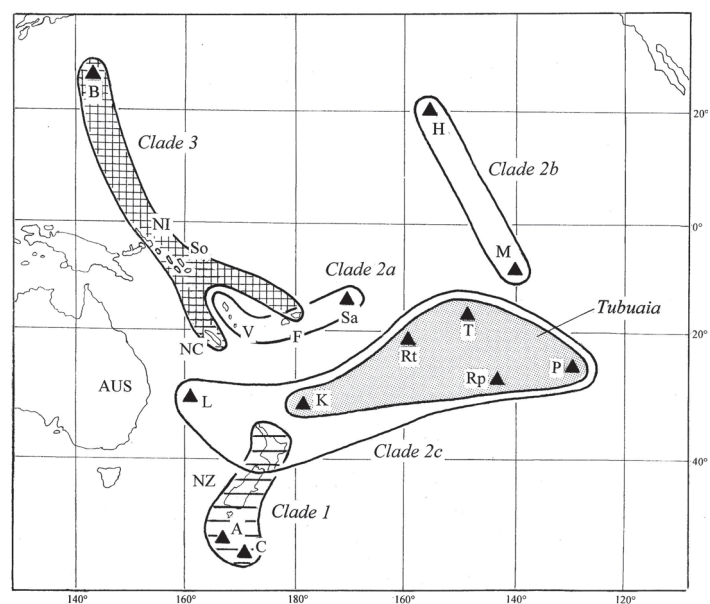


FIGURE 1 Distribution of *Metrosideros* (Myrtaceae), endemic to the central Pacific. The five clades (1, 2a, 2b, 2c, and 3) are mainly vicariant. Distribution of the land snail genus *Tubuaia* (Achatinellidae) is also shown (stippled). A = Auckland Is., AUS = Australia, B = Bonin Is., C = Campbell I., F = Fiji, H = Hawaii, M = Marquesas Is., NZ = New Zealand, Rp = Rapa I. (Austral or Tubuai Is.), Rt = Rarotonga (Cook Is.), Sa = Samoa, K = Kermadec Is., L = Lord Howe I., NI = New Ireland, P = Pitcairn I. (Tuamotu ridge), So = Solomon Is., T = Tahiti (Society Is.), V = Vanuatu.

Atolls, Extinction, and Survival

The atoll zone of the central Pacific comprises a vast area from the Carolines to southeastern Polynesia—an area that has undergone subsidence and massive extinction. Land snails characteristic of high, forested islands occur as fossils on the atolls of the Marshall Islands and Midway Island, west of Hawaii. These atolls are the remains of former high islands, which subsided at least 1500 m over the Cenozoic. As the high islands collapsed, the peaks no longer caught the mists, and this wiped out the moisture-dependent snails and other forest taxa, perhaps including *Metrosideros*. On some Pacific islands, relic species in groups with a high survival coefficient, such as flies and certain birds, still survive on the young limestone covering the sunken volcanics.

PLATE TECTONICS

Rifting of the Earth's crust is a well-known mode of vicariance. Geologists have proposed that the Solomons, Vanuatu, Fiji, and Tonga once formed a continuous island arc, which was rifted apart into separate chains, and zoologists at the Smithsonian Institution have interpreted disjunct distributions in reef fishes and terrestrial lizards as a direct result of this.

A geological terrane is a fault-bounded block of the Earth's crust that has had its own independent history.

Accretion, or the docking and fusion of terranes at convergent plate margins, can also modify and create vicariance patterns. New Guinea, New Caledonia, and New Zealand are larger than the other Pacific islands and include older, continental-type rock. They are often described as “fragments of Gondwana” but are in fact geological and biological composites (like the Greater Antilles in the Caribbean). Each comprises an older, Gondwanic part plus many other terranes, including island arcs, which have accreted to the Gondwana fragments after arriving from the Pacific side with the encroaching Pacific plate. The regions of accreted terranes, like others in Indonesia and the Philippines, show high diversity in many groups and indicate evolution by juxtaposition rather than by radiation from a center of origin. Geological and biological accretion has also occurred in the archipelagoes of Indonesia and the Philippines, and accreted island arc complexes now form vast areas of western North, Central, and South America.

In the central Pacific, very large igneous plateaus formed in the Cretaceous and then moved south, west, and east, colliding with countries like the Solomons, New Zealand, and Colombia. The plateaus are now largely submarine but include many formerly emergent seamounts up to 24-km across, as well as sediment layers with fossil wood.

In summary, the plants and animals of the Pacific islands are probably the result not of Neogene founder dispersal from Asia or America but of long-term survival and evolution in the Pacific basin since its Jurassic origin. Despite enormous extinction, metapopulations in different parts of the Pacific have preserved patterns of endemism and vicariance that reflect plate tectonic rifting and convergence.

OTHER ISLANDS

Outside the Pacific, fossil-calibrated dating studies have inferred dispersal from mainland Africa to Madagascar, but fossils of many groups are scarce there and Mesozoic–Early Cenozoic vicariance better explains the close biogeographic relationship among eastern Africa, the southwestern Indian Ocean islands, and India/Sri Lanka. The Galápagos–West Indies connection was discussed in some early vicariance analyses and illustrates the predictive power of the method. Although molecular dating is generally misleading, molecular cladogram topologies are more reliable and are revealing a vast amount of previously hidden vicariance in all large clades. Recent studies show that Galápagos finches (*Geospiza*, etc.) and Galápagos mockingbirds (*Nesomimus*) each have their sister group in the Caribbean, not

on nearby mainland South America. Some geologists now trace the origin of the Caribbean plate to the Galápagos hotspot, and this would provide an explanation for the distribution pattern.

SEE ALSO THE FOLLOWING ARTICLES

Convergence / Dispersal / Endemism / Island Biogeography, Theory of / Metapopulations / Plate Tectonics

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VOLCANIC ISLANDS

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In the broadest sense, volcanic islands include all islands that form by volcanic processes, even those islands that represent ancient volcanic terranes that have been tectonically exposed, such as Gorgona Island offshore of Colombia or Macquarie Island in the southwestern Pacific. It also should be noted that most atolls represent a calcareous carapace surmounting oceanic volcanoes, the volcanic part of which has subsided below sea level, a concept originally proposed by Charles Darwin and subsequently confirmed by drilling through shallow carbonate atolls into the underlying volcanoes of the Hawaiian and Tuamotu island chains. However, attention here will be restricted to those islands primarily formed by volcanic processes more or less in situ, and where portions of the original volcano are still exposed above sea level. This restriction still leaves a subject that encompasses hundreds of islands and island groups scattered around the world's oceans.

ISLAND ARCS AND OCEANIC ISLANDS

Volcanic islands can be broadly divided into two principal categories, reflecting fundamentally different geo-