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Long-distance dispersal of organisms, widely accepted as a major cause of distribution patterns, poses challenging problems of analysis

Instances of chance dispersal have been observed and reported from time to time, and many biogeographers believe that this phenomenon has played an important role in the natural distribution of plants and animals. Yet other scientists doubt that such occurrences as seeds or snails clinging to birds' feathers can account for the development of the floras and faunas of entire islands, viewing these events as freak happenings of no significance. This paper will discuss examples of chance dispersal, and will outline another prominent theory for the spread of organisms.

Charles Darwin was interested in the phenomenon of dispersal to islands because his theory of evolution dictated that a given species originated only once, and then spread thereafter. The alternate idea that a species could originate independently in various places throughout the world required an essentially Lamarckian explanation. Thus in Darwin's 1859 correspondence with Sir Joseph Hooker, for example, he mentions with delight Milner's discovery that nestling petrels on the Scottish island

of St. Kilda had West Indian seeds in their crops.

In this case it seems unlikely that the petrels themselves carried the seeds from the West Indies to St. Kilda. Rather, the adult petrels may have picked up the seeds along Scottish beaches and fed them to juveniles; the Gulf Stream deposits seeds from the West Indies on the shores of the British Isles. However, this example does show the tendency of marine birds to ingest seeds, and could also explain how seeds deposited on a beach by ocean currents could reach an upland locality more suitable for their growth. Other examples of marine birds consuming seeds and fruits appear in Ridley's wonderful compendium of instances of seed dispersal (1930), which lists so many observed occasions of dispersal of all kinds that the chance events seem to add up to a genuine phenomenon, that of long-distance dispersal.

Guppy (1906) devoted most of a volume to his observations on plant dispersal in the Pacific. He noted distributions of plants in the region and attempted to find a correlation with means of dispersal. The easiest method of dispersal to test is that of flotation in seawater, and Guppy's book contains an overwhelming amount of data showing which seeds and fruits float, and for how long. One can only imagine that Guppy lived for years surrounded by jars of floating seeds. His experiments predictably showed that most beach plants are dispersed by seawater, and revealed similar dispersal possibilities for some inland plants, such as the vines *Entada* and *Mucuna*, which must drop seeds into rivers or in some places overhang the seacoast. However,

Guppy's studies focus mainly on the dispersal of beach plants, and we must therefore look elsewhere for examples of other kinds of chance dispersal.

Other documented instances of dispersal show the surprising range and variety of the phenomenon. Small snails have been found adhering to bird feathers in a number of cases (Vagvolgyi 1975), and seeds discovered in bird feathers and in the mud on birds' feet have been successfully germinated (Wallace 1895). Rand (1955) noted that the purple gallinule, known as a chance visitor to Tristan de Cunha for many years, has finally formed breeding colonies there, and similar instances of dispersal of bird species followed by establishment have been recorded by MacDowall (1978). Wheeler (1916) reported that ants survived a journey of about 5 km in a floating log from the Brazilian coast to São Sebastião Island. Monarch butterflies, which occasionally migrate over the Pacific, were observed to establish colonies on Canton Island by Zwaluwenberg (1942), who also noted the simultaneous establishment of the food plants they needed. When I visited Pearl and Hermes Reef in Hawaii, I noticed that numerous *Mucuna* seeds had floated ashore. A few were germinating, but these soon withered in the hot sun, since *Mucuna* grows successfully only in wet forest. This example, like many of the preceding ones, indicates that, rare as events of chance dispersal are, adverse ecological conditions may be a greater obstacle to the establishment of a species in a new location than transport itself.

The ideal site for the study of chance

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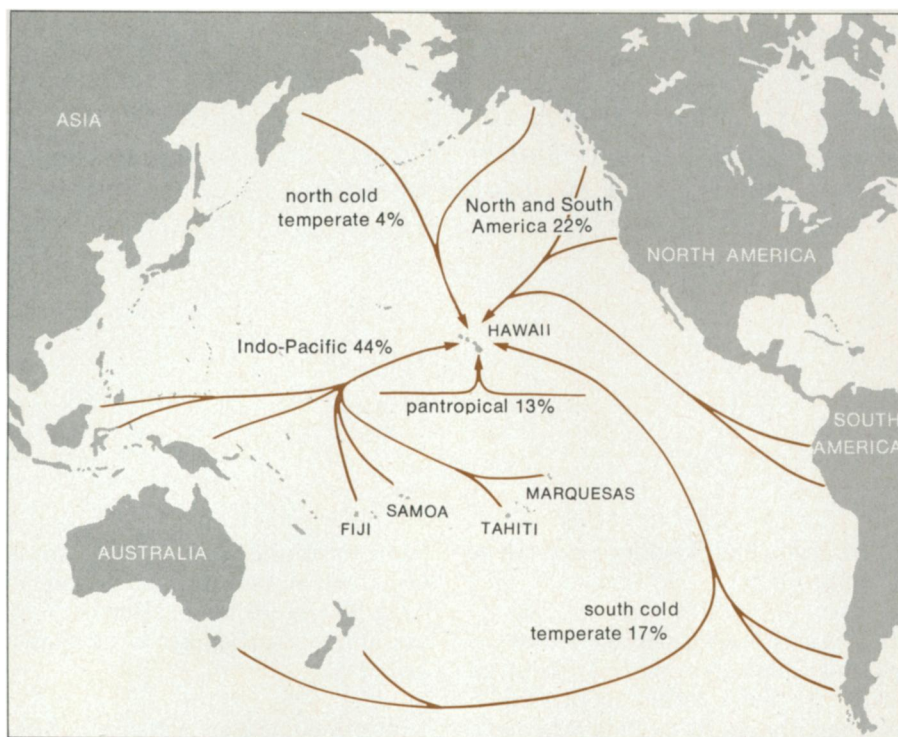


Figure 1. Evidence suggests that there were 272 hypothetical ancestors of Hawaii's flowering plants, arriving from various regions. Biologists agree that both the patterns of distribution and

the relationship of Hawaiian angiosperms to other angiosperm species point to long-distance dispersal as the source of the island's flora. (Data from Zimmerman 1948.)

dispersal is an island, because an island represents the ultimate test of long-distance transport. If a seed transported by wind falls to the ground, it can be picked up again, but if it falls into the sea, the dispersal event usually ends. An ideal island would be one newly emerged from the sea, not previously in contact with any land mass, and completely devoid of any life at its time of origin. It should be large enough and high enough to support various types of life, and should be in a climatically favorable part of an ocean. The island should be well removed from continents and other islands: if dispersal is too easy, one learns little.

Though no such ideal site is now available for study, the island of Surtsey, near Iceland—too close to Iceland and in too unfavorable a climate to have shown a great deal since its emergence in 1963—has nevertheless illustrated some dispersal phenomena well (Einarsson 1967). Beach plants dispersed by drift, such as sea rocket (*Cakile*), were the first to arrive.

The island closest to the ideal in the

past was Krakatau, in the strait between Java and Sumatra. In 1883 Krakatau erupted with extraordinary violence. Very few species, if any, survived. Fortunately, the significance of the island was appreciated, and studies were begun soon after the eruption. Reports covering fifty years of recovery of life on the island have been prepared, for animals by Dammernann (1948) and for plants by Docters van Leeuwen (1936).

These studies show that both plant and animal species appeared slowly in the years following the eruption; then, as soils and plant cover formed, the rate of immigration accelerated. Later, when the number of species began to approach what might be expected on a small island in this region, there were fewer new colonizations. Although the distances traversed were small—Krakatau is only 45 km from Java, and an even shorter distance from other islands—the organisms that appeared could all be said to have good dispersal mechanisms. The studies of Krakatau firmly support the idea that chance dispersal over long distances occurs, but since the island is not on the scale of, say,

the Hawaiian Islands, some scientists have been reluctant to concede that this phenomenon is capable of explaining the colonization of larger areas.

Experiments with chance dispersal

Neither random observations nor data on the forms, attachment devices, and viability of seeds, fruits, and eggs offer as broad a picture as one could wish. Hence some biologists have attempted to test possibilities of dispersal in such a way that quantifiable and repeatable data can be obtained. For example, experiments have been carried out on the dispersal of seeds by shorebirds. Vlaming and Proctor (1968) have shown that shorebirds confined in pens will eat seeds, retaining them in the case of the killdeer for as long as 120 hours. Killdeer fly at speeds of 80 to 100 kph, and could thus disperse seeds over a range of more than 8,000 km in non-stop flight. Shorebirds retain large seeds longer than small seeds, so that long-distance dispersal of seeds the size of olive pits is not at all in conflict with the observed biology of these birds.

Although the transport of seeds over distances as great as 8,000 km is rare, we should remember that the rare does occur. If such events were common, the flora and fauna of each climatic zone would long since have been homogenized the world over—which is not the case. The fact that so many Hawaiian plant and animal species have evolved new characteristics distinguishing them from species in the source areas indicates that most of them were introduced in Hawaii only once, then never reintroduced by a second natural event of long-distance dispersal.

Williams and Williams (1978) have used sources of evidence such as radar to document the large numbers of individuals that participate in bird migrations. At Palo Alto Marsh in California as many as 11,700 migrating shorebirds have been counted on a peak day; 4,000 to 5,000 individuals is not an unusual number (Jurek and Leach 1971, 1972). Given these large numbers, transportation of seeds on bird feathers is easily believable. It is not even necessary, at this rate, to invoke numerous species of birds as agents; only a few species of birds and

many years would be sufficient to effect dispersal.

Another type of experimental evidence has been supplied by the entomologist J. Linsey Gressitt and his co-workers (1958, 1961). Using nets attached to ships and airplanes, they recovered airborne insects in areas far from land. The insects they collected belonged to the same families as those native to islands, suggesting that insular insects represent groups especially well adapted to flotation in air. The insects caught were also small in body size—as are, in general, the insects of oceanic islands. Interestingly, snails on Pacific islands also have small body sizes or are derived from types with small body sizes (Vagvolgyi 1975), making them more likely candidates for dispersal by birds now or at some earlier point in their evolution.

The Hawaiian criterion

An insular biota is itself a collection of evidence in support of long-distance dispersal of plants and animals, offering a living archive of dispersal events. The flora and fauna of the Hawaiian Islands are an interesting case in point. Darwin and Wallace considered the Hawaiian chain to be oceanic islands, never connected to other land masses, an opinion reinforced by the added evidence of sea-floor spreading (Menard 1956; Menard and Hamilton 1963; Dalrymple et al. 1973). The Leeward Hawaiian Chain, extending westward from Kauai and Niihau to Midway, is a remnant of the older Hawaiian Islands. Further to the west, Midway is an atoll marking a still earlier series of islands, while the Emperor Seamounts, stretching toward Siberia, may be the most ancient portions, the beginning of these arcs of islands.

No one has claimed that any of these islands were ever connected to a continent, and biologists who have studied the flora and fauna of the Hawaiian Islands universally agree that the biota is the result of chance immigrations. Both the distribution patterns shown by Hawaiian species and their relationships to other species are compatible with the hypothesis that they reached the island by long-distance dispersal. “Stepping-stone” islands may have helped, but the intervening distances were still undoubtedly long ones. Certainly



Figure 2. Biologists believe that Hawaii's flowering plants were introduced by a number of modes of chance dispersal. Some of the seeds and fruits characteristically transported in these various ways are pictured here. Fleshy fruits such as *Vaccinium dentatum* (top) are often consumed by birds, which retain and later disperse the seeds, accounting for 38.9% of the 272 arrivals hypothesized. *Bidens pilosa* is typical of a number of barbed or bristly seeds or fruits that become attached to birds' feathers (12.8%), whereas *Lobelia cardinalis* is representative of various small seeds that readily adhere to the mud on birds' feet or lodge in crevices in their feathers' (12.8%). Viscid seeds or fruits such as *Pisonia umbellifera* also frequently adhere to birds (10.3%). Other methods of dispersal by which Hawaiian flora arrived are flotation in ocean currents (14.3%), rare forms of ocean flotation such as rafting, or attachment to floating logs or vegetation (8.5%), and flotation in upper air currents (1.4%). Less important methods account for the remaining 1%. The seeds and fruits shown are respectively about 10 mm in diameter, 15 mm long, 1.5 mm in diameter, and 3 cm long. (Percentages are from Carlquist 1974.)

the plethora of animals and weedy plants that have been introduced by humans and gone wild in the Hawaiian chain shows that ecological conditions there are suitable for many more kinds of organisms than arrived in prehuman times.

By grouping species probably evolved from a common ancestor since that ancestor arrived on the Islands, biologists have arrived at the minimum number of hypothetical immigrants needed to account for the Hawaiian flora and fauna: 272 flowering plants, 37 ferns, 233 insects, 22 land molluscs, and 7 land birds (Zimmerman 1948). Experts on various taxonomic groups have compared the Hawaiian species with their probable mainland relatives, thereby obtaining a picture of the geographical affinities of Hawaiian plants and animals (see Zimmerman 1948). Figure 1 shows the results for flowering plants. Although other plant and animal groups probably have similar geographical sources, flowering plants, having the greatest number of hypothetical immigrants, demonstrate the contributions of the various source areas most clearly.

The sources of Hawaiian flowering plants are highly diverse, and each probable dispersal event has its own logic. That logic is dictated by two things: a method of transport, and an equivalence between the ecology of the source area and that of the recip-

ient area. Plants of wet Hawaiian forests are related to plants of the southwestern Pacific, where similar wet forests occur. Plants of dry alpine Hawaii show a kinship mostly with plants of the dry southwestern United States and adjacent Mexico, whereas Hawaiian beach plants are related to beach plants of other tropical Pacific islands and tropical continental shores. The evolution of Hawaiian plants after their arrival has included gigantism of fruits and loss of dis-

currents too cold to favor successful transport of seeds. Judging from the appearance and size of the seeds of Hawaiian plants (Fig. 2), only a few arrived this way.

The numerous beaches and atolls of the Pacific have contributed some floatable seeds and fruits to Hawaiian shores, but the quantity is by no means generous. The currents running east and west across the equatorial Pacific effectively bar the rich

land birds are good dispersers there. Shorebirds, which are known to include a certain proportion of seeds and fruits in their diet, are capable of traversing oceanic distances and can thereby serve to transport these plants from one land mass to another.

Guppy (1906) envisioned a now-vanished race of migratory pigeons that once crossed the Pacific carrying seeds. While the existence of such pigeons seems unlikely, the Torres Strait pigeon does migrate from southeastern Australia to New Guinea each year—a very great distance. Moreover, five kinds of shorebirds known to eat seeds and fruits migrate annually from North America to Hawaii or further south. Some, such as the Pacific golden plover, go as far south as the Marquesas, Tahiti, or Tuamotu islands. Contrary to what their name suggests, shorebirds may visit inland areas with some regularity. Marine birds also occasionally eat seeds, but certainly fewer than shorebirds do.

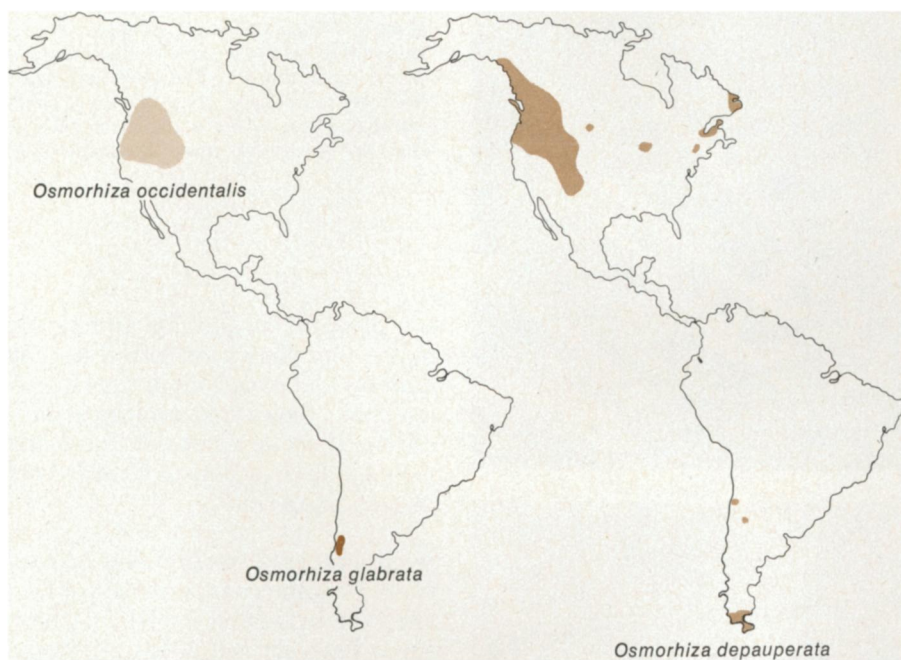


Figure 3. Two closely related herb species of the same genus—*Osmorhiza occidentalis* and *O. glabrata*—are found in widely separated areas of North and South America (left). A single species of this same genus, *O. depauperata*,

also occurs in two widely separated localities on the two continents (right). These and similar disjunctions in the locations of flowering plants can be explained by the migratory routes of birds. (From Constance 1963.)

persibility, and thus the seeds and fruits of species alive today are not necessarily exactly like those of the hypothetical immigrants (Carlquist 1974).

The popular impression that wind or ocean currents provide the most effective means of transport does not seem to be justified, if one considers how the genera that comprise the Hawaiian flora behave in flotation experiments, or what is known of their dispersal elsewhere. Although air flotation accounts for the arrival of insects and plant spores in Hawaii, the distance is apparently too great and the temperature of the upper air

South Pacific beach flora from reaching the Hawaiian chain. Moreover, beaches comprise only a small proportion of the Hawaiian Islands, so that plants drifting into the region have only limited habitat niches available.

Far more of the volcanic island is upland forest with moderate to heavy rainfall, and even though dispersal of fleshy fruits by birds seems a relatively unreliable method of transportation, it has succeeded to a remarkable extent with the help of these favorable ecological conditions (Fig. 2). Plants with fleshy fruits are abundant in tropical forests because

External attachment of seeds and fruits to birds has also played an appreciable role in the dispersal of flora to Hawaii (Fig. 2). Seeds or fruits become attached to birds by bristles or barbs, by viscid coverings, or by virtue of being so small that they catch in the crevices of feathers or in mud or other substances adhering to birds. Fewer plants have reached Hawaii in this fashion than have traveled there as fleshy fruits inside birds, but relatively few seeds and fruits are adapted to such transport. However, the proportion of seeds and fruits that have arrived externally on birds is higher than the incidence of adaptations favoring transport in continental floras, suggesting that the adaptations have operated very well indeed where the distance to be traversed is great, as here. An advantage of external transportation is the fact that once a seed or fruit is attached to the bird, the time involved in migration is immaterial: the only requirement is that the bird must remain long enough in the new location to preen its feathers, thereby inadvertently dislodging the seed.

In the world flora at large, there are numerous seeds or fruits that have hooks or barbs, sticky coverings, or minute size. On continents, these adaptations serve to hitch seeds to

terrestrial mammals that live at ground level near the seeds. However, mammals obviously cannot traverse long oceanic distances, so the feathers of migratory birds provide a substitute animal surface where dispersal to islands is involved. Any plant with these adaptations that grows near the nesting or foraging grounds of shorebirds or marine birds is a likely candidate for dispersal in this fashion. Since most of these nesting or foraging areas tend to be located in lowlands rather than in wet upland forest, externally transported seeds and fruits in the Hawaiian flora are mainly found at lower elevations.

Herbs of North and South America

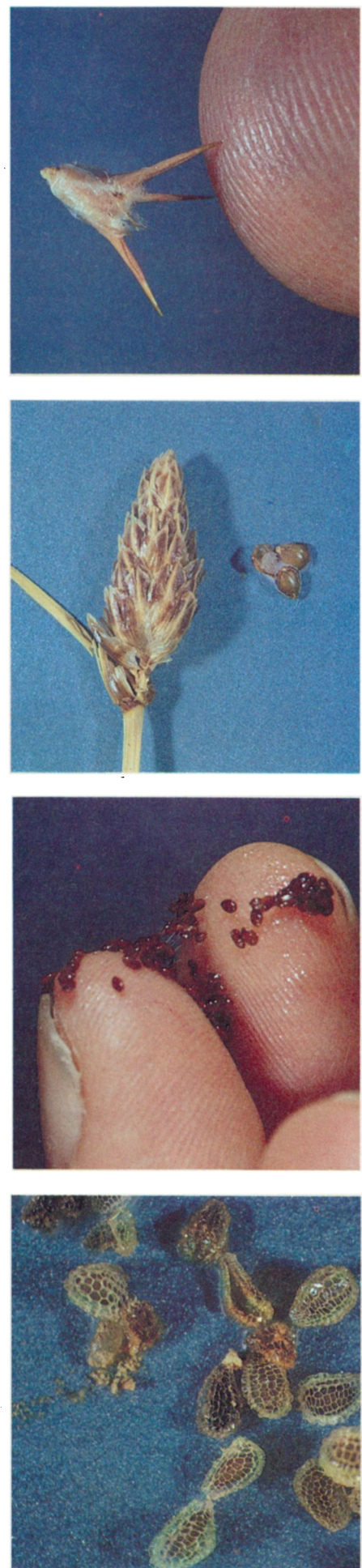
Long-distance dispersal must also have operated in the case of a series of herbs—mostly annuals—found in Chile and California or nearby regions (Fig. 3). Constance (1963) and others have documented this series of plants (more than 100 species are involved), in which closely related species—or in a few instances the same species—occur in small pockets of Chile and North America, with enormous distances in between. The great similarity of the species in the two regions can only mean that they have been distributed recently—probably less than 5 million years ago at most—since as time elapses the herbs will naturally evolve into quite different species or genera.

Not only must this disjunction be the result of a rather recent dispersal; the dispersal agent must be a good one. Humans, who are notoriously good dispersal agents, can be ruled out here, because the species involved do not follow the patterns of weeds or other plants known to be carried around the world by humans. Nor does tectonic plate movement seem to be a possible explanation: the pattern is too recent, the distances too great, and the crustal movements of the earth have, in fact, worked contrary to this distribution. North and South America have been moving slowly toward each other, not diverging. The connection of South America to North America via Panama has come into existence only recently, and the gap of ocean between the two continents in the Pliocene and earlier would have made migration more difficult.

However, at least seventeen species of shorebirds and marine birds are known to migrate over this route every year. Of these, ten shorebird species have been seen to feed on seeds, berries, or other plant material (Collins 1974). Two of the shorebird species are often seen well inland, so that distribution of inland as well as coastal plants can be attributed to birds. Moreover, during wetter periods of the Pleistocene, swampy, low-lying areas attractive to shorebirds were widespread in both Chile and California. Plants now more restricted in distribution probably grew along the muddy shores of ponds, swamps, or even inland seas such as the one then occupying the San Joaquin Valley in California.

Transport of seeds and fruits on or in birds can account for virtually all of the disjunctions of the Chile-California herbs (Fig. 4). Only a single instance, the morning glory *Calystegia soldanella*, requires another explanation. Although the seeds of this plant float in seawater, it would have been virtually impossible for them to have floated from North to South America or vice versa, because the currents in the intervening area would have swept floating seeds westward into the equatorial Pacific. However, the seeds could have drifted from a Pacific locality to both North and South America; *Calystegia soldanella* also occurs in Australia, New Zealand, and Japan, as well as in the Atlantic.

Figure 4. The presence in temperate South America of 106 herb species either identical with or closely related to North American species has been attributed to the migratory patterns of birds. Herb seeds or fruits with various adaptations that enhance the possibility of transport by birds are shown here. Species with barbed or bristly seeds or fruits, such as *Cardionema ramosissima* (top), account for 42.4% of the 106 cases of dispersal. *Scirpus nevadensis* is a member of a group of seeds or fruits consumed by birds as fodder and later excreted in new locations; of the 106 species, 19.9% are believed to have traveled in this fashion. Viscid seeds or fruits that become attached to birds' feathers, here represented by *Carpobrotus inequilateralis*, account for an additional 18.9%, while small seeds like *Orthocarpus attenuatus*, easily carried in mud or sticky substances on birds' feet or on their feathers, account for 15.1%. Less important methods of transport account for the remaining 3.7%. The fruits and seeds shown are respectively about 4, 2, 1.4, and 1.6 mm in size. (Percentages are from Carlquist, unpubl.)



Vicariance biogeography

The nonreproducible nature of chance dispersal events makes their analysis by use of statistical methods difficult, if not impossible. However, some biogeographers who have felt the need for rigorous precision have invented a methodology known as vicariance biogeography. Does this method indeed solve problems of distribution, or is it merely applicable to cases where organisms move only short distances over long periods of time?

Vicariance biogeography assumes that patterns of distribution follow geographical and climatic events such as the breaking apart of land masses—continental drift—and major shifts of wet and dry, cold and warm. If several groups of plants or animals independently show the same distribution patterns, the proposed explanation is seen as more likely. Replicate patterns have been appreciated since the time of Hooker (1860), who thought that the southern continents must have once been interconnected because of the many organisms they share. However, vicariance biogeography as a methodology may be said to have begun with the writings of Croizat (1958, 1962). A lucid account of the methods of vicariance biogeography has been offered by Wiley (1980), on whose account the following summary of procedure is based.

The biogeographer first collects data on the distribution of particular plant and animal groups, and these data are then plotted on maps to produce patterns of distribution called “tracks.” Tracks that simulate or replicate each other are now sought. A common pattern of distribution for several different groups would be called a “generalized track.” This type of activity, known as “track synthesis,” is considered a reduction of basic data.

Next, the biogeographer identifies areas of endemism, or the restriction of species to particular areas. By grouping species restricted to these areas, it is possible to analyze the phylogenetic relationships of the various species in an attempt to form probable evolutionary trees for the organisms. The investigator asks two questions: What is the scheme of relationships among species of the or-

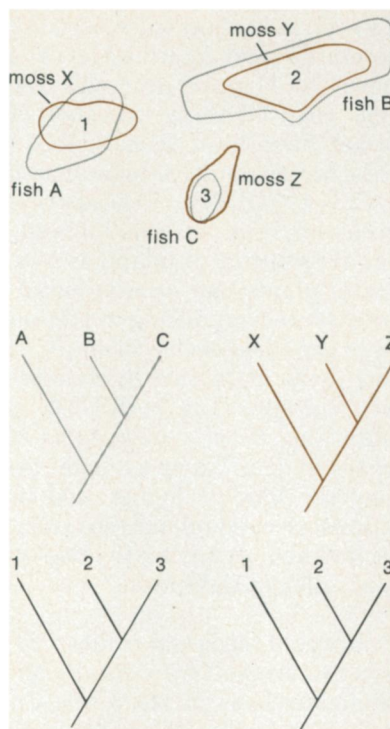


Figure 5. In this area cladogram, the phylogenetic relationships of two groups, fish and moss, confined to three areas of endemism are analyzed. After the ranges of the two groups have been determined (*top*), possible evolutionary trees are formulated and compared (*middle*). The area occupied by each species is then substituted for the species name (*bottom*). In this imaginary example, there is a complete match between the phylogenetic tree of each group and that for the areas in which they occur, suggesting that common factors affected the evolution and distribution of the two groups. (From Wiley 1980.)

ganisms occupying the endemic areas? Do the interrelationships of the organisms reflect the geologic histories of the areas?

The biogeographer then formulates various possible evolutionary trees, trying to find a match with the pattern of areas inhabited. To do this, the area in which a species is found is substituted for the species name in the evolutionary hypothesis. Such a hypothesis is called an “area cladogram.” Figure 5 analyzes the phylogenetic relationships of two groups, fish and moss, confined to three areas of endemism. Patterns will be similar to the extent that common or general factors affected the evolution and distribution of two or more groups of organisms. In order to find such similarity, the biogeographer must be able to separate unique factors found

in a single group from the common factors present in the evolution of all the groups considered.

Does this scheme work in practice? Separating “unique” from “common” factors might be a troubling task, possibly involving arbitrary or intuitive assessments. However, proponents of vicariance biogeography point to the compelling nature of replicated patterns, once these have been located.

Even supposing that an objective or less subjective method is used to locate unifying patterns, does this work for all situations? Chance dispersal over time, widening the area occupied by a species or suddenly causing a species to skip to new areas, would destroy identity of patterns. If one of the species of moss in Figure 5 begins to colonize new areas by dispersal, whereas the fish do not, the generalized track would at first be altered, and eventually might be obscured to the point where an original pattern could no longer be discerned. A weedy species would, in fact, be expected to spread in just such an irregular fashion.

The majority of vicariance biogeographers concede that long-distance dispersal exists, but they feel that it creates at most a minor “noise level” superimposed on the basic patterns dictated by geological history, such as tectonic plate movements or the rising of a mountain chain. They believe that most species respond to geological and climatic changes similarly, and that species leave traces of their responses in their distribution patterns. The sum of similar responses, in the opinion of these scientists, amounts to statements of statistical likelihood and attendant verification or falsification. But is dispersal by plants or animals to new areas so slow or infrequent that basic patterns are not obscured? Can this “noise level” become so loud that no basic pattern other than long-distance dispersal itself is evident?

Vicariance biogeography seems to come closest to explaining the situation when an organism is capable of dispersing only over very short distances, and therefore shifts to new ecological zones very rarely or extremely slowly. Freshwater fish not adaptable to brackish water or seawater are such organisms. It is no ac-

cident that the most vocal proponent of vicariance biogeography, Rosen (1975), studies such fish. Those who investigate organisms capable of long-distance dispersal and those who study islands or other areas that were probably populated by long-distance dispersal have not adopted the methods of vicariance biogeography.

Oceanic islands and areas such as those colonized by the disjunctive herbs we have described above are not the only places where long-distance dispersal may prevail. Many groups of organisms characteristically excel at dispersal and are found in multiple environments. Algae, fungi, and protozoa are among groups with little endemism: a species found in Europe is often also found in Australia or South Africa and at any suitable location in between. Can these organisms, or relatively dispersible groups such as flowering plants, ferns, insects, and land snails, illustrate the movement of tectonic plates? Only a few families of flowering plants have distributions that suggest continental drift (Thorne 1972); indeed, only older groups of flowering plants, because of their time of origin, could be expected to show such distributions.

It is also apparent that we may find clues to the reason for a particular distribution pattern by taking into account factors other than phylogenetic trees and endemic areas. A good example of this is seen in the plants of the African volcanoes, which are mainly related to European plants, and those of the Andean volcanoes, which show a strong affinity with plants of temperate North America. Both of these high-altitude environments require plants adapted to cold. Tropical plants are apparently unable to make this adaptation readily because of the long period of time necessary for the numerous changes required, whereas Europe and temperate North America are rich in plants adapted to cold. The plants of these two areas, moreover, tend to have evolved good dispersal mechanisms because of the mountainous, discontinuous terrain in which they live. The appearance of these plants in the new African and Andean locations suggests that these mechanisms are capable of operating over very long distances as well as over fairly short ones.

A new synthesis?

Most modern investigators combine tectonic plate movement with chance dispersal in some fashion to explain present-day distributions (e.g., Raven and Axelrod 1974). The problem is not whether chance dispersal occurs, but the extent to which the patterns we see have been caused by it, and how, if such patterns occur frequently, we may analyze them.

One possibility involving both tectonic plate movement and long-distance dispersal should be mentioned: Was there interchange among continents *while* they were moving apart? Too often, it seems to have been assumed that interchange essentially ceased when the rifts were initiated. However, suitable habitats for a given organism are often distributed in a scattered fashion, and there is not much difference between habitats scattered on a single continent and those scattered on two continents still close to each other. Most families of flowering plants have patterns in which dispersal among continents after the split has been a major factor. If such a small target area as the Hawaiian Islands has received so many successful colonists in such a short time, could not a continent receive many more? Unfortunately, the tools available to analyze and identify this phenomenon are poor, and the results are not in any range of statistical significance.

The desire of vicariance biogeographers for methods that can operate with precision is understandable, since biogeography is a field with little unanimity in interpretations. The refinements of geology are now making interpretations a little more certain: the hypothetical land bridges once erected or obliterated with abandon by some biogeographers cannot be entertained in the hard light of newer geological evidence. However, our knowledge of any unique event in the history of life is still limited, especially if subsequent complexities destroy the pattern created by the original event.

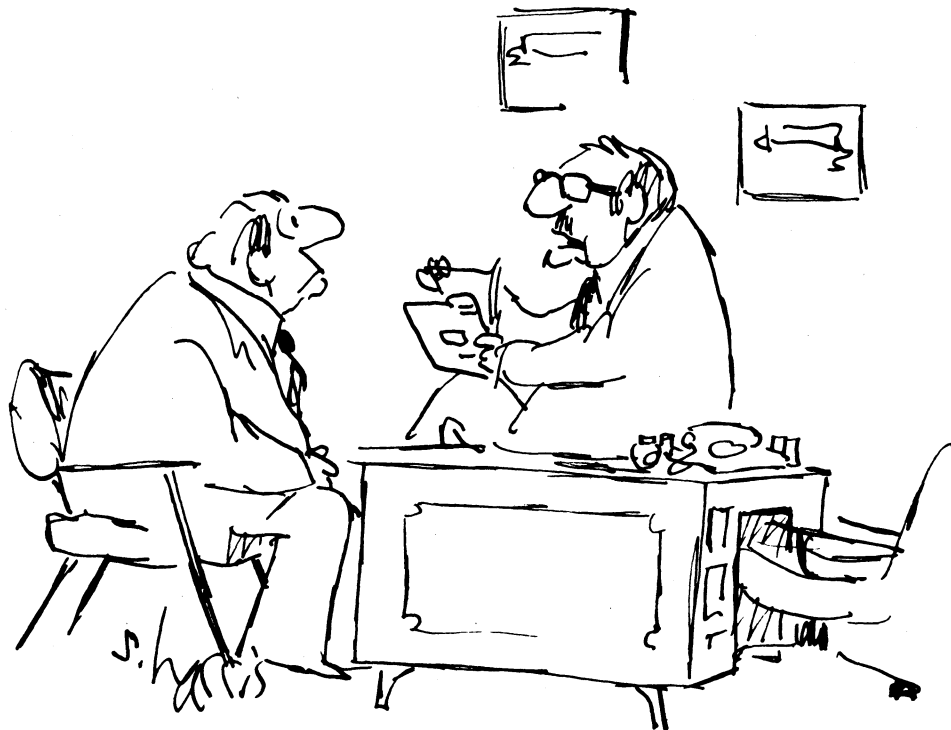
For groups like the primary-division freshwater fish, the use of the methods of vicariance biogeography seems defensible, since—at least in the clearest cases—patterns are not erased or destroyed. On the other hand, patterns which circumstances

tell us have probably resulted from long-distance dispersal, such as the distributions of Hawaiian organisms and of the herbs in disjunctive locations, seem unlikely to yield to the methods of the vicariance biogeographers—who indeed have not entered those areas. The biogeographer who deals with patterns probably created by long-distance dispersal must use evidence that is circumstantial, indirect, and subjective, and therefore vulnerable. However, if that kind of evidence leads to plausible answers, we cannot afford to rule it out of court. Long-distance dispersal, although annoyingly difficult to study or take into account, appears to be a persistent theme which will not go away, and it is to be hoped that future biogeographers will find a way to incorporate it with skill.

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