Hedges, S. B. (2020) Molecular clocks, flotsam, and Caribbean Islands. In…Biogeography: An Ecological and Evolutionary Approach 10th Edition (Cox, Ladle, & Moore; Wiley 2020).

Molecular clocks, flotsam and Caribbean islands

Guest Author

Box 11.4

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The islands of the Caribbean have provided a classic test of the two major mechanisms of historical biogeography: vicariance and dispersal. Formed in the Mid-Cretaceous (about 100 mya), they have had a long and complex geological history that included an early connection between North and South America (proto-Antilles) and a catastrophic asteroid impact (about 66 mya). During the Cenozoic, some large islands (Greater Antilles) broke apart and fused, a stable carbonate platform (Bahamas Bank) kept up with sea-level changes, and a chain of volcanic islands (Lesser Antilles) migrated slowly from west to east [40,41]. Soon after the theory of plate tectonics became accepted, it was recognized that the current biota of the islands may be the fragmented (vicariant) remnant of a once-continuous proto-Antillean biota [42]. Since then, a debate has ensued over the importance of vicariance versus dispersal in the origin of the biota.

The answer has not come easily, nor has it been agreed upon by everyone. Nonetheless, most research suggests that the entire living biota of the Caribbean islands arrived by dispersal and not through the geological breakup of an ancient land mass [43]. Initially, it was thought that the key information to answer the question would come from the phylogenetic relationships of organisms. In part, this thinking emerged from the popularity – in the 1980s – of the fields of cladistics and vicariance biogeography which emphasize relationships of organisms over most other types of data. Undoubtedly, relationships are important, but the problem with this line of thinking is that the branching order of species might match the geological breakup of land areas, but the timing could be very different. So it was soon realized that data on the times of divergence of organisms from their closest relatives on the mainland were critical. The fossil record in this region is poor, but molecular clocks provided those data.

Molecular clocks (see Chapter 9) need calibration against some external events, such as well-dated fossils, or geological events, such as the time of emergence of an island above sea level – for this is the earliest time at which it could be occupied by terrestrial organisms. For the Caribbean islands, it turned out that relationships were not important in answering the basic question of vicariance versus dispersal (Figure 11.13). This is because nearly all of the times of divergence measured by molecular clocks, for many different groups of terrestrial vertebrates, have been too young to have resulted from a Late Cretaceous vicariance event. Instead, the times were scattered throughout the Cenozoic, almost randomly, and in accord with a mechanism that relies on chance events such as dispersal. However, relationships *were* useful in determining the source area of dispersal. For most terrestrial vertebrates that cannot fly or otherwise disperse over water using their own powers, their closest relatives are in South America, while a majority of the birds, bats and freshwater fishes in the Caribbean islands appear to have come from North and Central America. Freshwater fishes are salt-tolerant, so that they could have dispersed to the islands across the sea.

Other diverse evidence, too, supports a dispersal origin for the Caribbean biota. Most important is the taxonomic composition of the endemic groups. There are some enormous adaptive radiations, often with species filling niches different from those for the same genus on the mainland. For example, some of the smallest and largest species of major groups (e.g. cycads, swallowtail butterflies, frogs, lizards, snakes) occur on islands in the Caribbean. Yet at the same time, many major groups, such as caecilian amphibians, marsupials, rabbits, armadillos and carnivorous placental mammals, are absent. The fossil record, including that of the 15–20 million-year-old Dominican amber, which includes the remains of insects, frogs, salamanders, lizards and small mammals, shows a similar taxonomic composition to today's fauna – except for the salamander which no longer lives in the islands [44]. This is best interpreted as a strong filter effect, whereby a few colonists survive long-distance dispersal and then radiate into a diversity of unoccupied ecological niches. This same evidence also argues against an origin for the biota by way of a Mid-Cenozoic (34 mya) land bridge from South America, which has also been suggested, but without firm geological evidence [45]. Such a land bridge would not

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Molecular clocks, flotsam and Caribbean islands (*continued*)

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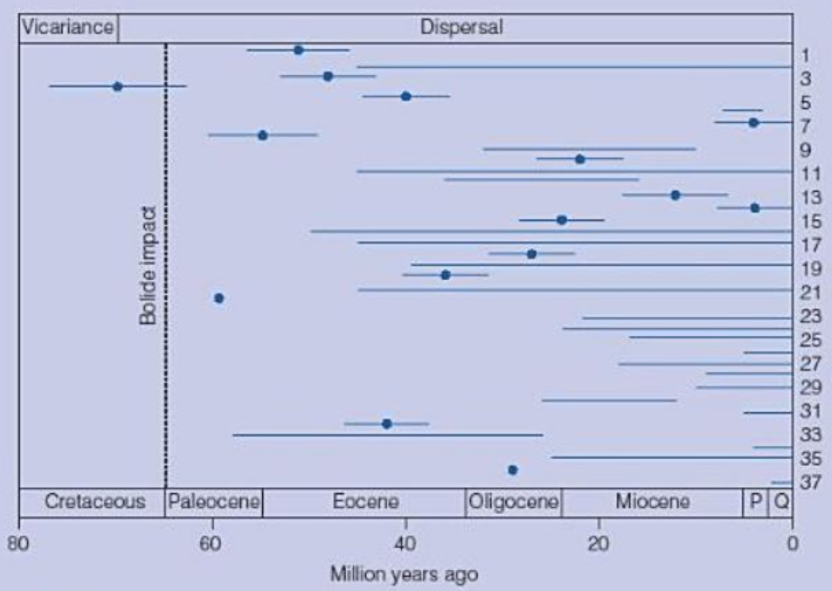

Figure 11.13 Times of origin of 37 independent lineages of endemic West Indian amphibians and reptiles. *Source*: From Hedges [43], reproduced with permission of Missouri Botanical Garden Press, St Louis.

have acted as a strong filter, and would therefore have allowed many other groups, that we do not in fact find there, to enter the archipelago. Because organisms could have arrived in the Caribbean islands by dispersal at any time after the Late Eocene emergence, it is not possible to test the land-bridge hypothesis with molecular clocks, as has been assumed in some studies.

Ocean currents and geographical proximity best explain the source areas of the island colonists identified in molecular phylogenies. Water flows almost unidirectionally from east and southeast to west and northwest in the Caribbean – and this was true even prior to the uplift of the Isthmus of Panama. As a result, flotsam carried down from the rivers in northern and northeastern South America will end up in the Caribbean, if it continues to float. For example, even though Cuba is much closer to North America than to South America, it is much easier for a lizard to arrive in Cuba by floating on vegetation from South America; this is reflected in the composition of the Cuban lizard fauna. But for organisms that can fly or swim, the geographically closer areas are the more likely sources, and the common air current direction in the Caribbean (northeast to southwest) might even assist dispersers flying from North America.

Two lineages of island vertebrates that show old (Cretaceous) times of divergence from their closest relatives on the mainland, using molecular clocks, have been debated as possible examples of proto-Antillean vicariance. These are the giant shrews (solenodons) of Cuba and Hispaniola and the night lizards (xantusiids) of Cuba [43,46]. While an ancient origin cannot be ruled out, both groups are biogeographical relicts as their mainland fossil record demonstrates a wider distribution in the past. This raises the possibility – not normally considered for other groups – that they diverged more recently from close relatives on the mainland that are now extinct and hence inaccessible to molecular clocks. In addition, some geologists are uncertain about whether there was any continuously emergent land in the Caribbean before the Late Eocene (about 34 mya), although this would have been necessary for maintaining such lineages. Moreover, it seems unlikely that these organisms could have survived the end-Cretaceous asteroid impact, which occurred a short distance away. The origin of these two groups will probably continue to be debated.

Now we know that flotsam was critical for the origin of the Caribbean terrestrial biota, but surprisingly little is known about this mode of dispersal across ocean waters. How abundant are floating islands? How long do they stay afloat, and how far do they travel? What organisms do they typically carry? There are many anecdotal accounts of floating islands [43] but almost no scientific studies. Analysis of satellite imagery, GPS tracking and taxonomic surveys of floating islands might answer some of these questions. Whatever the details, we can be certain that long-distance dispersal by flotsam did occur and that fragile animals, such as small frogs, successfully colonized Caribbean islands millions of years ago after riding the ocean waves for weeks on a jumble of logs.