Extinction and recolonization of local populations on a growing shield volcano

(genetics/evolution/*Drosophila*/Kilauea volcano)

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ABSTRACT   Volcanic action has resulted in the burial of the surfaces of Mauna Loa and Kilauea, Hawaii, by new lava flows at rates as high as 90% per 1000 years. Local populations of organisms on such volcanoes are continually being exterminated; survival of the species requires colonization of younger flows. Certain populations of the endemic Hawaiian species *Drosophila silvestris* exemplify such events in microcosm. Local populations at the base of an altitudinal cline were destroyed by two explosive eruptions within the last 2100 years. Natural recolonization restored the cline except for one young population that is genetically discordant with altitude.

The volcanic islands of the Hawaiian archipelago are believed to have formed above a single fixed melting source in the Earth's mantle. Northwestward movement of the Pacific Plate over this "hotspot" causes volcanism to be restricted to new islands at the southeastern end of the chain (1). The two youngest volcanoes, Mauna Loa and Kilauea of Hawaii Island, are among the most active on Earth; their surfaces are being buried at rates of about 40% (2) and 90% (3) per 1000 years, respectively. The slopes consist of complex lava flow "patchworks" of various ages. These are found at all elevations, so that individual substrates vary not only in age but also according to climate imposed by altitude.

Kilauea is an independent volcano on the southeast flank of the Mauna Loa shield, which rises above it to 4100 m. Near the summit of Kilauea, violently explosive eruptions 2100 years B.P. (about 100 BC) and in AD 1790 produced layered deposits of hot volcanic ash that obliterated all life over areas of several hundred square kilometers (Fig. 1). Deposits from the older, Uwekahuna eruption (4) blanketed an area 11–12 km from the source, and the younger, Keanakakoi eruption (4) extended to 6–7 km. Each of these eruptions produced violent ground-hugging surges that deposited hot ash up to 2 m thick (5). The resulting incinerations left a thin deposit of carbonized material at the bases of the ash deposits (Fig. 2). Ash deposits from the explosive events formed soils, covering the older Mauna Loa flows, that now support rich but very young montane rainforests north of Kilauea Caldera (Fig. 1). To the west and north, the rainforest border is sharply defined both by the western edge of the tradewind rain shadow (marked by the Pu'u O'o Trail, Fig. 1) and by younger lava flows that partly bury the Uwekahuna Ash (6). Eastward, the slope of Mauna Loa descends quickly below 1000 m, where it supports rainforest of a different character (7).

Over the past 25 years, population samples of the ecologically restricted montane rainforest species *Drosophila silvestris* from the island of Hawaii have been studied genetically. Endemic to this island, the species is distributed over five volcanoes; it occurs only in association with certain endemic host plants that have irregular distributions (8). Each population sample has been assayed for the frequencies of 11 polymorphic chromosomal inversions. Three variants (3m, 4k², and 4l²) are widespread on Hawaii Island and display frequencies that show highly significant correlations with altitude (9).

Samples from five sites on Mauna Loa at altitudes between 1200 and 1650 m have been analyzed (Table 1). The sites are between 6 and 13 km from the present Halemaumau Crater of Kilauea, which is believed to be near the center of explosive activity. Except for site 4, the frequency of the 3m⁺ chromosome shows a decline correlated with altitude from site 1 to 2, from site 2 to 3, and from site 3 to 5 ($r = 0.992$; $P < 0.01$). These four sites also display a similar cline involving a chromosome 4 variant (4k²⁺). Although on separate chromosomes, the behavior of these two polymorphisms with altitude is significantly correlated ($r = 0.965$; $P < 0.05$). A third inversion, 4l², is prevalent at site 1 but is infrequent at lower elevations. Although site 4 is discordant (see below), populations at the other four sites behave with altitude as predicted from island-wide data (9) (Fig. 3).

Radiocarbon dating of lava flows near site 1 shows a substrate age of about 8000 years B.P., whereas to the west, the flows are mostly younger, dating from historic times to 1500 years B.P. (6). These latter flows have sparse forest and few host plants; *Drosophila silvestris* has not been collected in these areas. Site 1, protected by the two cinder cones (Pu'u Lalaau and Kulani Cone) and by distance from the crater, was not affected by the Uwekahuna and Keanakakoi devastations.

Following the older event, only site 1 and part of site 2 appear to have been unaffected. In the interval between eruptions, it seems likely that populations at the level of site 3 were established from areas directly to the north having a similar altitude and thus not requiring new selective response. After the Keanakakoi eruption, life was apparently destroyed for a second time at sites 4 and 5. Again, site 5 could have been recolonized from altitudinally concordant local populations from the adjacent area to the northeast, roughly along the 1200 m contour (Fig. 1). Site 4, however, is genetically discordant with altitude (Fig. 3). Its position near the edge of the rain shadow (Pu'u O'o Trail, Fig. 1) puts it in an ecologically marginal position for a rainforest species. We suggest that it was colonized by migration from the nearby high-altitude site 2, from which it does not differ in frequency of any of the three variants (see Table 1). If we allow 150 years for the establishment of suitable host plants, flies may have colonized site 4 only about AD 1940, 25 years before our first collections there. At three generations per year, in 1965 this population would have completed about 75 generations since it was founded. It would follow from these inferences that its genetic adjustment to altitude is not yet complete.

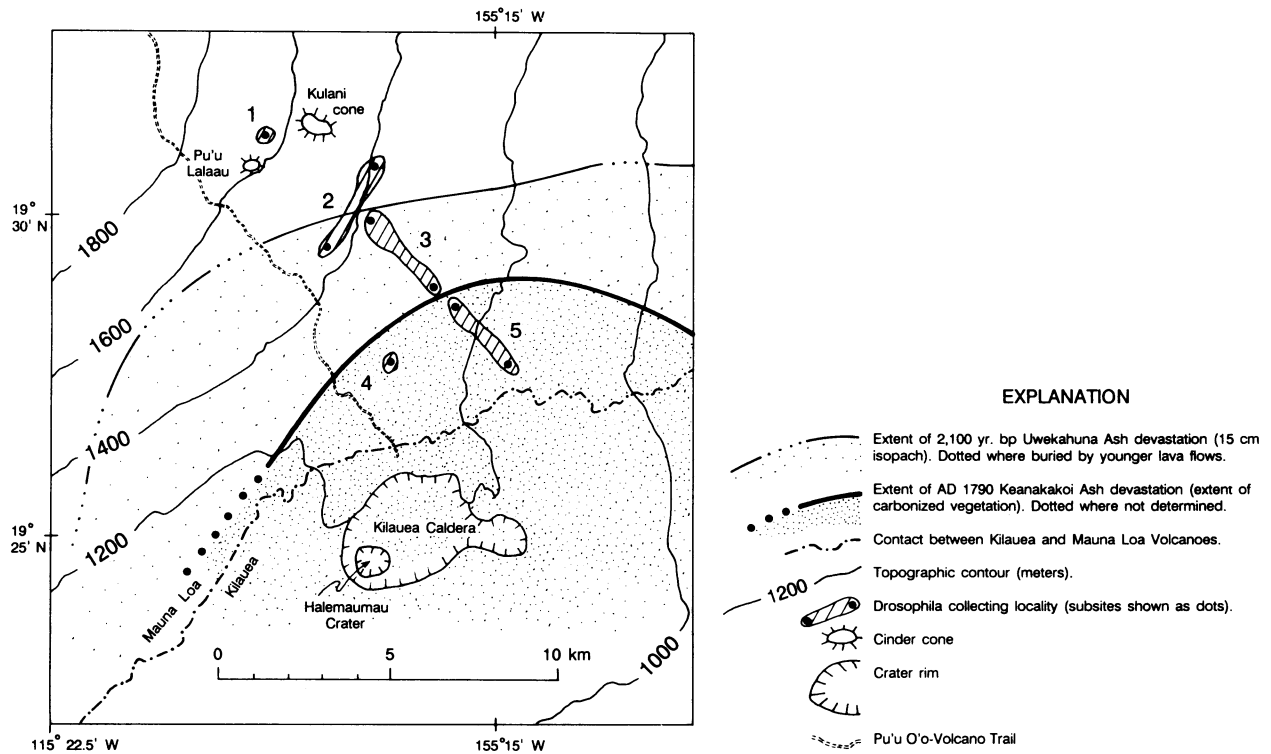[†]To whom reprint requests should be addressed.

FIG. 1.   The southeast flank of Mauna Loa as viewed looking north from Kilauea Crater, Hawaii, showing the five collecting sites and the two cinder cones near site 1. The double dashed line to the left is the Pu'u O'o Trail, which follows the approximate edge of the tradewind shadow.

Geologic mapping and radiocarbon dating of individual Mauna Loa lava flows have permitted reconstruction of the eruptive history of the volcano during Holocene (2). Historical flows cover 14% of the surface. Datings of prehistoric flows show that over one-half of the surface has been buried in the last 1500 years; 90% is covered with rocks less than 4000 years old. Surface turnover is thus characteristic of the whole of Mauna Loa, involving both frequent coverage by its

own lava flows as well as occasional burial of its southeast flank by ash deposits from Kilauea, as described above. Between 1800 and 1000 m altitude, all but the historical and dry north flank flows are presently covered with rich rainforests. Although they give the impression of great age, only small patches are older than 8000 years B.P. (10).

For species populations on such a growing mountain, continual surface turnover means that no nearby ancient
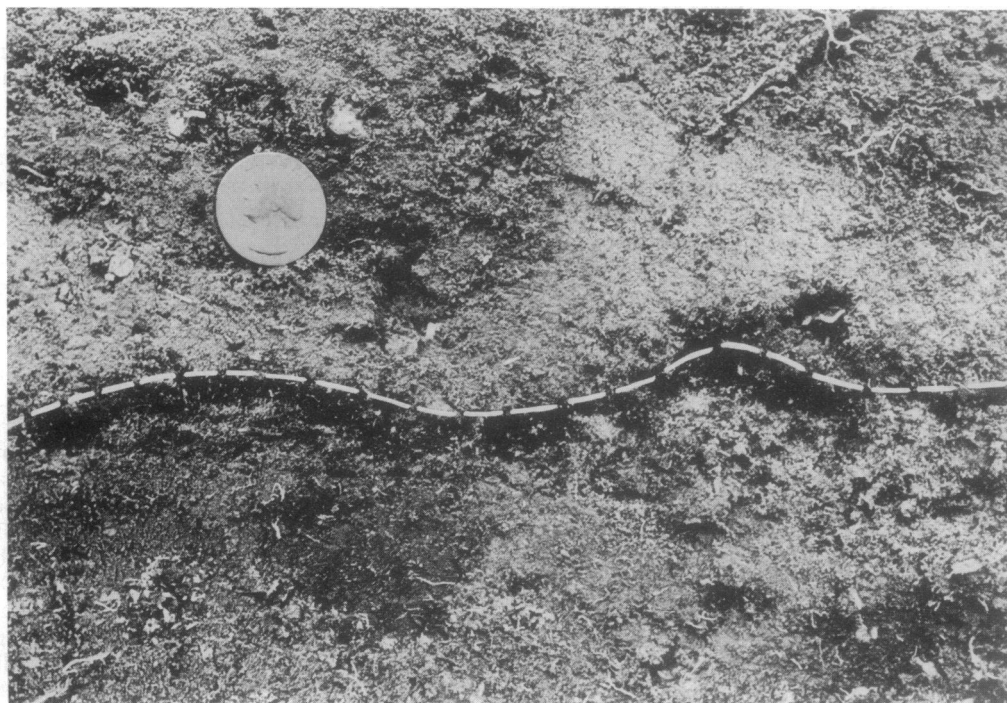

FIG. 2.   Vertical section of the contact between Keanakakoi (above dashed line) and Uwekahuna Ashes (below), showing a layer of carbonized plant material above the Uwekahuna Ash. Locality is near site 4 at 1250 m elevation.

Table 1. Population frequencies of three chromosomal variants of *Drosophila silvestris* at five localities north of Kilauea Crater, Hawaii

No.	Population site	Altitude, m	Distance from crater, km	n	$3m^+$	$4k^{2+}$	$4l^2$
1	Kilauea Forest Reserve	1634	12.5	436	0.677	0.489 ⌉	0.179
2	Trail below Kulani Cone	1448	10.0	159	0.441⌉	⌈0.283⌉	⌈0.013⌉
3	Upper Olaa	1365	8.7	426	0.246⌋	⌊0.218⌋	⌊0.026⌋
4	Keauhou Ranch (rain sheds)	1298	5.8	67	0.493⌋	0.388⌋	⌊0.060⌋
5	Lower Olaa	1192	7.2	300	0.057	0.157	— ⌋

Except for frequencies joined by brackets, all pairwise comparisons between populations are significant ($P < 0.05$).

refugia persist; each species must continually recolonize from nearby areas or become extinct. This imposes a shifting mosaic population structure—i.e., it consists of a metapopulation (11). Some species, like *Drosophila silvestris*, might lose a few rare alleles following a founding event. Nevertheless, since its genetic adjustment depends on balanced, coadaptive polymorphisms (8, 9, 12), abundant polygenic recombinational genetic variability is retained, even if very few individuals are involved in the founder event (13).

Although the idea has been challenged (14), we support a generalized theory that metapopulation structures and founder effects occurring on growing island volcanoes may be crucial factors promoting the evolution of unique species and/or character sets (12). In particular, Hawaiian volcanoes have many examples of such evolutionary diversity (15–17). As volcanism continually requires the founding of new local populations, genetic shifts and/or other episodic evolutionary change would be expected to accelerate during the growth phase of each successive Hawaiian volcano. These influences, however, would decline as each volcano completes its active phase and becomes dormant. Volcanic

activity has always been most vigorous at the youngest, southeasternmost island of the archipelago. We suggest that the youngest island at any one time has always been Hawaii's major evolutionary crucible. The forces that created the Hawaiian islands and their long-ago foundered predecessors not only formed the firmaments upon which life could diversify but also may have played a heretofore unappreciated, direct role in the acceleration of evolutionary processes as they operate in local populations.

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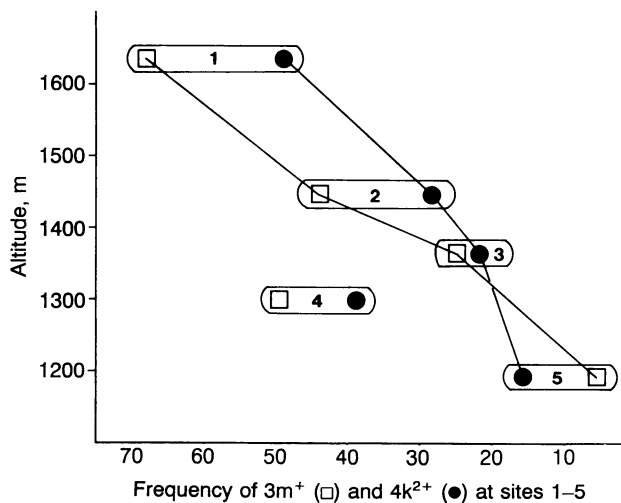
FIG. 3. Frequency of two chromosomal variants plotted against altitude. Sites 1, 2, 3, and 5 show a cline, whereas the frequencies at site 4 are discordant with altitude.