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Molecular Evolution in Hawaiian Drosophilids

Rob DeSalle and John A. Hunt

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The evolutionary relationships of the Hawaiian drosophilids have been studied by several molecular techniques. Immunological measurements have determined some of the distances between the major groups. More detailed studies have used protein polymorphism, DNA *hybridization,* DNA *restriction enzyme analysis and* DNA *sequence studies of both nuclear and mitochondrial genomes. These studies indicate both the strengths and the weaknesses of the various methods and suggest new ways to examine phylogenetic relationships and question some of the accepted phylogenies.*

The Hawaiian Drosophilidae comprise two genera, *Drosophila* and *Scaptomyza* (see Kaneshiro and Boake, Box I, this issue, for a detailed description). Within the genus *Drosophila* there are four major groups – the picture-wings, modified mouthparts, leaf feeders and *engioscaptomyza* – which are found on all of the major high islands of the archipelago. Several studies have demonstrated that the evolution of these flies could have occurred by the introduction of one or a few gravid females to the island chain[1,2]. 'Founder events' predominate in the inter-island colonization by the flies, leading to the evolution of new populations and species.

The development of genetic and molecular techniques has added greatly to our understanding of evolutionary pattern and process in the Hawaiian drosophilids. One of the earliest studies involved the chromosomal inversions of the picture-wing group (see Carson in this issue). Because this group has been the best studied chromosomally[2,3] and many of the species can be reared in the laboratory, other measurements of divergence have been made, either directly or indirectly related to nuclear or mitochondrial DNA changes which have occurred over the course of evolution of the group. Prior to the development of DNA sequencing techniques, soluble cell proteins were used to study molecular evolution; these techniques include classical isozyme surveys[4–7], studies of gene regulation and differential gene expression[8] and the use of microcomplement fixation techniques[9] to examine phylogeny.

Recent advances in molecular biology have enhanced our ability to examine molecular evolution at the DNA sequence level in these flies. In this review we illustrate the use of DNA sequence analysis to study a wide range of phylogenetic and genetic questions in the Hawaiian drosophilids. The evolutionary dynamics of the molecules and DNA sequences are also of great interest. For instance, the Hawaiian drosophilids have undergone rapid morphological and behavioral evolution compared to the continental drosophilids. A question of great importance, therefore, is whether the Hawaiian species are evolving differently at the molecular level than the continental species. We include in this review an examination of the tempo and mode of evolution of nuclear and mitochondrial DNA sequences in the Hawaiian drosophilids.

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Protein studies of evolution

Protein polymorphism studies[4–6] were made with a large number of the species of the *planitibia* subgroup from all of the islands (Fig. 1a). However, this work suffered from the small number of loci studied and in some cases the small number of flies examined. By contrast, Ayala[7] studied flies from only one island but with many more loci and individuals, allowing comparisons of picture-wing, *engioscaptomyza* and fungus feeder groups but only limited comparisons within a subgroup[10] (Fig. 1b).

Microcomplement fixation is another technique for examining evolutionary divergence among proteins. This technique, when applied to one larval haemolymph protein, suggested that the Hawaiian drosophilids are an evolutionary old group – much older than the age of the present oldest high island capable of sustaining these flies (Kauai, 5 million years) – implying that the Hawaiian drosophilids occurred on one of the now eroded islands in the northwest part of the Hawaiian island chain[9]. This idea is intriguing but the larval haemolymph data, which was claimed to be useful for determining distances between the *Scaptomyza*, picture-wing and modified mouthparts groups, leaves much to be desired. For instance, it could not distinguish species within the picture-wing group except for one species group, D. *adiastola* (Fig. 1c)*, and when applied to distances

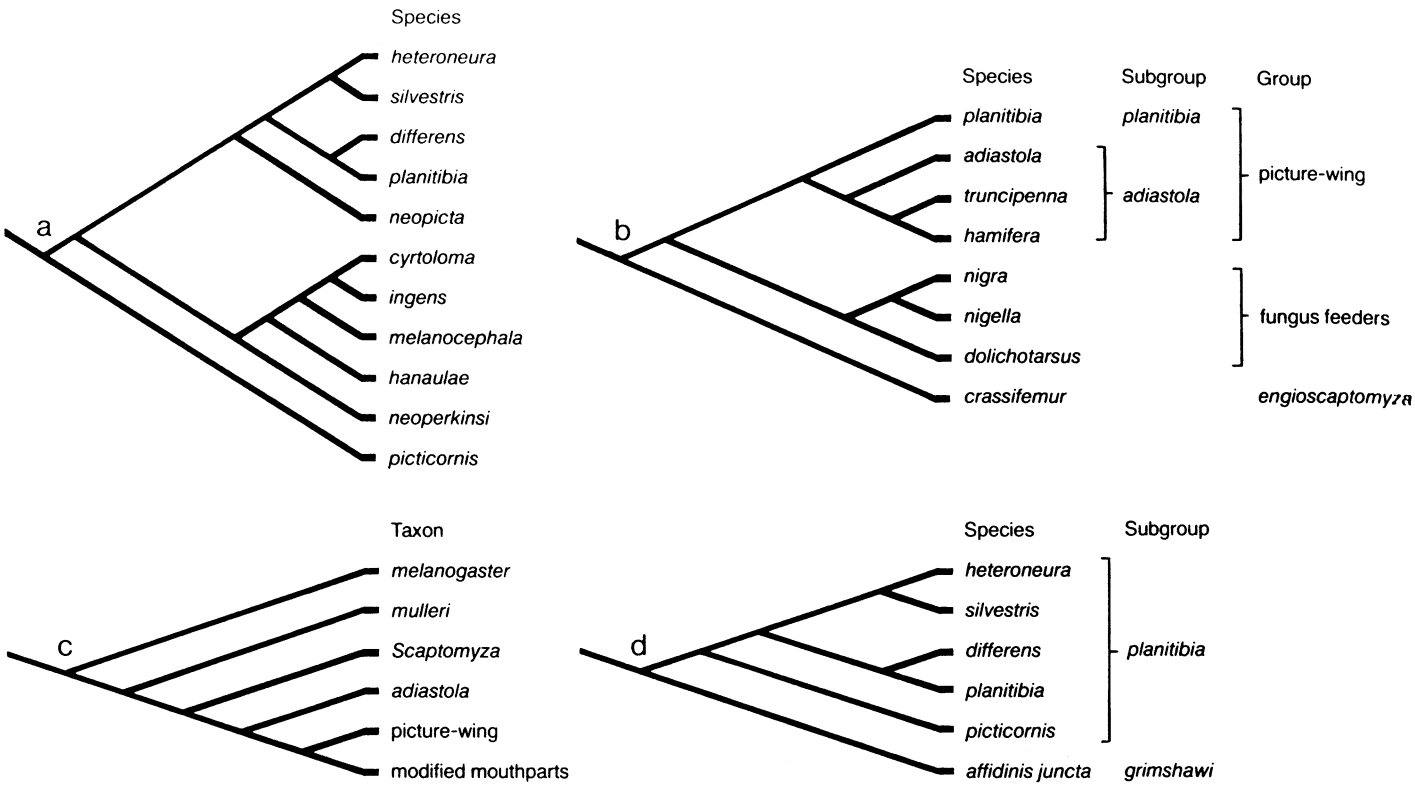

Fig. 1. Dendograms derived from distance measures of: (a) protein polymorphism from the *planitibia* subgroup of the picture-wing *Drosophila*[4,10]; (b) protein polymorphism of several species from the island of Maui[7,10]; (c) larval hemolymph protein microcomplement fixation[9]; (d) DNA sequences of the *planitibia* subgroup from DNA hybridization[17,18] and restriction enzyme mapping[12].

among groups the estimates of divergence had considerable variability. The estimated distance between the picture-wing D. *crucigera* and the modified mouthparts group was 29 ± 10 (range 17–39); the distance between D. *adiastola* and the modified mouthparts group was 51 (range 49–53); and the distance between D. *adiastola* and the rest of the picture-wings was 37 (range 34–40). From these non-metric data, with their large partially overlapping ranges, it is difficult to say whether the *adiastola* group is closer to the 'other' picture-wings or the modified mouthparts group. It may therefore be premature to claim ancient origin for the Hawaiian drosophilids or the rearrangement of phylogenies on the basis of distance measurements from this single protein. Furthermore, the calibration of times of divergence for the molecular clock was based on uncertain paleontological evidence (times of divergence for higher dipteran taxa were based on approximate biogeographic and evolutionary scenarios and on very few available fossils[11]).

Nuclear DNA as a tracer of evolution

Restriction site mapping and DNA sequence analysis has so far been confined to the alcohol dehydrogenase gene region[12] (Fig. 1d). This gene has been sequenced for many other species of *Drosophila*[13–15], facilitating comparison among a wide range of species. The sequence of chorion and vitellogenin genes are also being studied in five species of the *planitibia* subgroup, D. *heteroneura*, D. *silvestris*, D. *planitibia*, D. *differens* and D. *picticornis*. The comparison of restriction site maps from both genomic DNA and comparison of cloned DNA sequences has given essentially the same relationships as found by DNA–DNA hybridization[16–17], except that the rate of change is double that for the rate detected by DNA–DNA hybridization. This higher rate (5×10^{-9} per year) is very close to the maximal rate of nucleotide substitution found for synonymous substitutions in the protein coding regions in mammals[18].

One feature revealed by the DNA sequence analysis is that the non-coding regions change very rapidly in comparison with the coding regions, not because of single nucleotide substitutions, but by small deletions and insertions in the sequences. In general, the insertions are not related to adjacent sequences, and by their nature they generate more highly significant character state changes since they are not subject to the same types of convergence that are observed for single nucleotide changes. All of the character state changes so far agree with the trees constructed by DNA hybridization or restriction enzyme analysis in the *planitibia* group species.

The distribution of a transposable element in the same five species of the *planitibia* subgroup shows an increasing number of sites from D. *picticornis* through D. *differens*, D. *planitibia* and D. *heteroneura* and D. *silvestris*[19]. While the distribution of the element varies between individuals of the same species, the overall distribution tends to group D. *heteroneura* and D. *silvestris* as one pair and D. *differens* and D. *planitibia* as another.

Mitochondrial DNA as a tracer of evolution

Some of the more interesting questions about evolution of the Hawaiian drosophilids have concentrated on the morphologically distinct but sympatric species pair from the island of Hawaii, D. *silvestris* and D. *heteroneura*[20]. *Drosophila heteroneura* is morphologically distinct from D. *silvestris* in many aspects (see Kaneshiro and Boake, this issue). Within D. *silvestris* two morphologically distinct lineages exist; on the west side of the island of Hawaii, D. *silvestris* populations consist of individuals with two rows of cilia on the tibia of the foreleg; east

*Kaneshiro places the *adiastola* group outside of picture-wings on the basis of morphological characters.

Box 1. Molecular glossary

Single-copy DNA *hybridization*. DNA is sheared to 800 base pair lengths and denatured to separate the complementary strands. This DNA is allowed to renature in the presence of a small amount of radioactively labelled denatured DNA which has been fractionated to remove the repetitive DNA. The radioactive 'tracer' DNA may be from the same species or another species. The hybrid DNA is then 'melted' by increasing the temperature and the amount of denatured DNA is monitored. The temperature at which 50% melting occurs (T_m) is used to assess the degree of mismatch of the 'tracer' DNA. A lowering of the T_m by 1°C is equivalent to a 1% mismatch of DNA sequence.

Restriction mapping. There are many different enzymes which cleave DNA at specific base sequences (usually six- or four-base sequences). DNA is digested with a restriction enzyme and the fragments generated are fractionated according to their size by agarose or acrylamide gel electrophoresis. A 'blot' is made by transferring the fragments to nitrocellulose paper. A radioactive probe made from the DNA which is of interest (i.e. a gene such as alcohol dehydrogenase, or mitochondrial DNA) is then used to hybridize with the transferred fragments on the nitrocellulose paper, and the bands of hybridization are visualized by exposure to X-ray film. The size of the various restriction fragments can be calculated and restriction maps constructed using different restriction enzymes which will show the distance between the different enzyme sites on the DNA. Comparison of the restriction maps from different individuals within or between species will show the loss or gain of sites and allows an estimate of the number of nucleotide changes to be made.

Synonymous changes. Due to the degeneracy of the genetic code (64 codons are used for the 20 amino acids found in proteins), there are sites which can change their nucleotide sequence without changing the amino acid sequence. Since there is no apparent constraint on the changes which can occur in these regions as far as amino acid sequence is concerned, it is expected that the rate of change of nucleotides at these positions will be maximal and the same in different proteins, while the non-synonymous changes which affect protein sequences may vary in the rate of change for various proteins.

side populations have individuals with three rows. *Drosophila heteroneura* has two rows of cilia on the foreleg, as have the putative ancestors of the two species on the island of Hawaii, from Maui (D. *planitibia*) and Molokai (D. *differens*)[20,21].

Chromosomal, isozyme[5,6] and DNA–DNA hybridization[15,16] analyses have been used to examine the genetic relationships of these flies: little genetic differentiation has been demonstrated. Mitochondrial DNA genealogies of the two species were examined using restriction site analysis[22,23], revealing that the two bristle row D. *silvestris* was more closely related to D. *heteroneura* than it was to its three bristle row conspecific from the east side of the island of Hawaii. This rather surprising result suggests that bristle row number may be the more important morphological character indicating speciation in this trio of morphological types than the extreme head shape differences.

Mitochondrial DNA restriction site analysis has also been used to examine the phylogeny of several closely related species of the *planitibia* subgroup. In particular, DeSalle and Giddings[24] examined the genealogical relationships of D. *heteroneura*, D. *silvestris*, D. *planitibia* and D. *differens*, using D. *neopicta* as an outgroup. When the phylogeny obtained by analysing mitochondrial DNA for these species is compared to the nuclear DNA phylogeny (Fig. 2) a discrepancy in branching order is observed. The mitochondrial DNA data imply that the four species diverged from a common ancestor in a sequential fashion that correlates with the geological formation of the Hawaiian islands. That is, the first species that diverged from the common ancestor inhabits the oldest of the islands in the chain, while the second species to diverge inhabits the second oldest, and so on. Analysis of nuclear DNA, as explained above, implies that D. *differens* and D. *planitibia* should cluster together and that D. *heteroneura* and D. *silvestris* should cluster together. Restriction site analysis of the mitochondrial DNA of several other species of *planitibia* subgroup flies[25,26], on the other hand, was in good agreement with previous nuclear studies using isozymes[4].

Convergence of restriction site patterns[27] and the general inability to align restriction site maps of distantly related taxa[28] make the examination of phylogenetic relationships of more distantly related taxa difficult by this technique. A more precise method for this purpose is direct DNA sequence analysis of particular regions of the mitochondrial DNA. For example, mitochondrial DNA sequence data of the ribosomal RNA gene and the ND-1 gene (NADH dehydrogenase subunit 1) have shown that D. *clavisetae* from the *adiastola* subgroup is as distant from other members of the picture-wing group as it is from the modified mouthparts and *antopocerus* groups[29]. These data are consistent with those of Beverly and Wilson[9] (Fig. 3), and also support the idea that the Hawaiian drosophilids may be older than the oldest island in the chain presently capable of sustaining drosophilids (Kauai)[9].

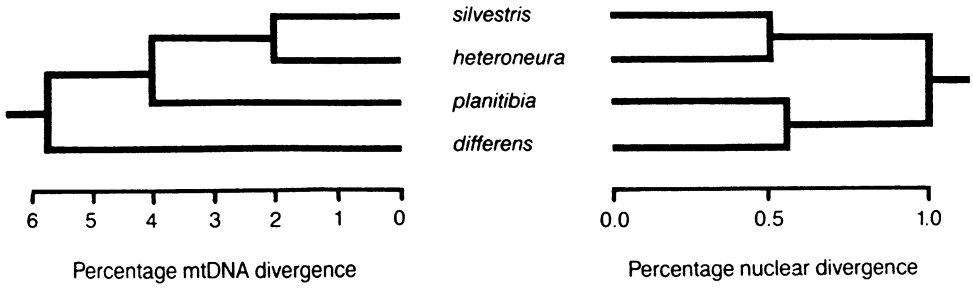

Fig. 2. Dendograms showing the discrepancy between the mitochondrial DNA data[24] and the nuclear DNA data[12,17,18]. For possible explanations of this discrepancy see the text and Ref. 24.

The evolutionary dynamics of mitochondrial DNA sequence change

There are several peculiarities of the tempo and mode of sequence change in drosophilid mitochondrial DNA that can be examined using sequence comparisons in the Hawaiian species. First, direct comparison of mitochondrial DNA sequences in the *melanogaster* subgroup species[30] suggested that transitional changes (purine [A,G] to purine, or pyrimidine [T,C] to pyrimidine) occurred with the same frequency as tranversional changes (purine to pyrimidine change or vice versa). This observation is in direct contrast with the pattern for vertebrates, where an extreme transition bias occurs[31].

Using biogeographical calibrations of divergence times, DeSalle *et al.*[29] examined the tempo and mode of sequence change in mitochondrial DNA of Hawaiian drosophilids (Fig. 4). An extreme transition to transversion bias exists for early stages of divergence, but the bias appears to erode with larger divergence times, as mutable nucleotide positions appear to be saturated. Furthermore, this saturation effect appears to occur at a lower percentage nucleotide change (15%) in Hawaiian drosophilids than in vertebrates (30%). The AT richness of the *Drosophila* mitochondrial genome[32,33] may constrain the number of nucleotide positions that can accept

substitutions and hence lower the maximum percentage divergence that *Drosophila* mitochondrial DNAs can have. The original discrepancy in transition to transversion bias observed for the *melanogaster* group may therefore be the result of comparing taxa (D. *melanogaster* and D. *yakuba*) that are too distantly related and lie in this zone of saturation.

Second, the rate of sequence change in the mitochondrial DNA of *Drosophila* has been reported to be slow relative to the rate observed for the nuclear DNA and to the rate observed for other taxa[33–35]. In contrast to the continental *Drosophila*, it appears that the mitochondrial DNA of some species of Hawaiian *Drosophila* is evolving at a faster rate than the nuclear DNA. A comparison of sequence change in the mitochondrial DNA of four species of picture-wing flies[24] with the amount of sequence change in the nuclear genome of these same four species[17] indicates that mitochondrial DNA is evolving four to five times faster than the nuclear component (Fig. 2). However, the rates of nucleotide change are calculated by different methods and the DNA hybridization rate may be an underestimate.

A possible explanation for this faster rate of mitochondrial DNA evolution in Hawaiian *Drosophila* is that the high probability of founder events in this group, and the reported small population sizes of some of the species, could create a situation where fixation of rare variants would be enhanced by drift[20,30]. DeSalle and Templeton[25] have tested this hypothesis by comparing the rates of mitochondrial DNA evolution in closely related species of Hawaiian *Drosophila* with different evolutionary histories. In particular, they found that the mitochondrial DNA rate of change in a group of flies that have undergone repeated bottlenecks due to inter-island colonization is three times faster than in a group of flies that have had contact during speciation on the same island complex.

Future molecular analysis

The use of molecular analysis for phylogenetic and genetic purposes in the Hawaiian drosophilids has very great potential. Evolutionary questions at several taxonomic levels can now be approached using sequence analysis of nuclear and mitochondrial DNA. For instance, fine scale population genetic questions, such as levels of genetic contact and maternal contribution to population structure, can be examined using mitochondrial DNA[37]. On a wider level, three specific taxonomic questions are currently being examined using both nuclear and mitochondrial DNA sequencing. First, how are the major groups of Hawaiian *Drosophila* (picture-wings, modified mouthparts, fungus feeders and *engioscaptomyza*) related to each other? Second, how is the genus *Scaptomyza* related to the Hawaiian *Drosophila* and the continental *Drosophila*? Finally, which continental *Drosophila* group or groups gave rise to the Hawaiian *Drosophila*, and when did the species colonize the Hawaiian islands?

Essential to all of the studies is the accumulation of information from many unlinked loci to construct as many independent gene trees as possible. In many cases it is possible to find important character state changes, such as deletions and insertions, which give more phylogenetic information than single nucleotide substitutions alone. The continued examination of the tempo and mode of evolution of these DNA sequences, and an examination of the types of sequence changes that occur in these flies, also promises to expand our overall knowledge of evolutionary processes.

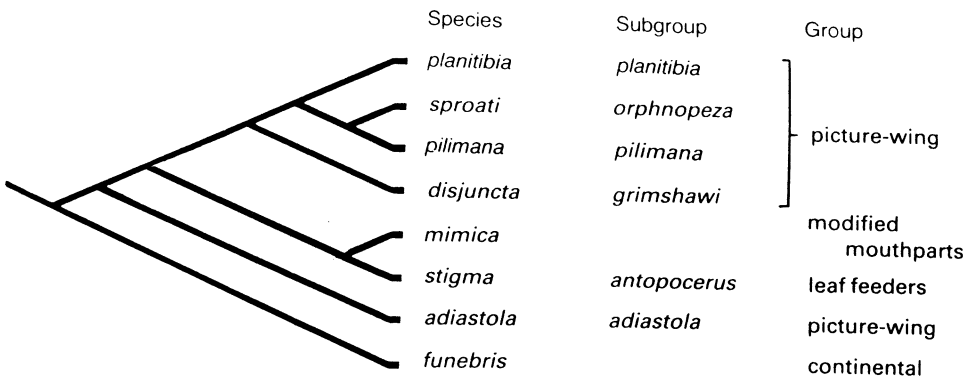

Fig. 3. Mitochondrial DNA cladogram showing the branching relationships of several Hawaiian *Drosophila* and a continental *Drosophila* (*funebris*). The tree was constructed by Phylogenetic Analysis Using Parsimony (PAUP) from DNA sequence data of the large rRNA gene and the ND-1 gene of the mitochondrial genome[29].

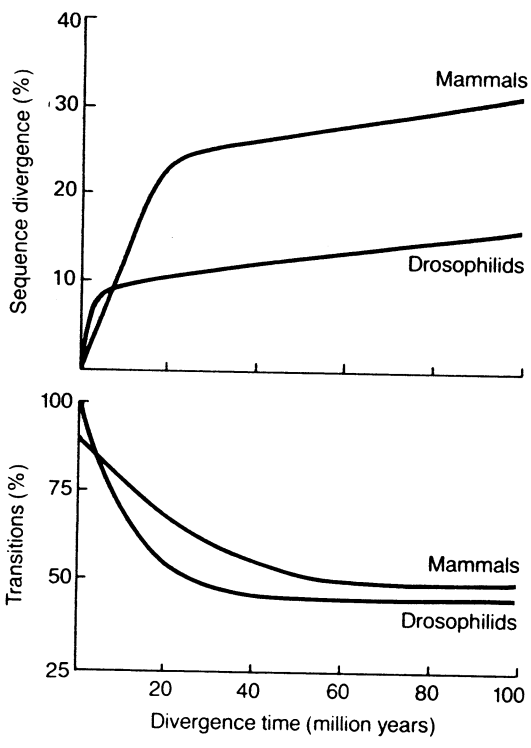

Fig. 4. Plots of divergence time versus total percentage sequence divergence (top) and percentage of total changes that were transitions (bottom). For *Drosophila*, transitions were in a 900 bp segment of mt DNA[29]. Divergence times for mammals were based on the fossil record[32] and for drosophilids on biogeographical considerations and immunological calibrations[29].

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Forest Dynamics in Hawaii

Dieter Mueller-Dombois

The land surfaces of the Hawaiian islands represent an age sequence from very recent on the island of Hawaii to over 5 million years old on the island of Kauai. Development of indigenous forest on the new basaltic lava flows of Hawaii begins with Metrosideros polymorpha *forming mono-dominant canopy stands within 400 years in lowland rain forest environments. In seasonal environments,* M. polymorpha *is displaced during succession by species such as* Acacia koa *and* Sophora chrysophylla. *In the montane rain forest,* M. polymorpha *has persisted as the dominant canopy species over millions of years. The mechanism of long-term persistence in the latter biome is explained as resulting from two processes: periodic canopy breakdown or stand-level dieback and the appearance or evolution of successional varieties in* M. polymorpha.

Dynamic processes initiated by human agency in Hawaii concern in particular the ecological consequences of introduced alien biota, which is the specific subject of another article in this issue. This review will concentrate on the natural dynamic processes, which are those time-related changes or variations in forests that occur independently of anthropogenic influences. Although the two kinds are often intermixed, it is of importance in a causative analysis of long-term ecosystem processes to keep the two apart and to understand the relative significance of each.

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In view of the geographically extreme and historically permanent isolation of the Hawaiian islands, it is perhaps surprising that forests developed there naturally at all. Yet a very limited forest flora of trees and associated life forms has become established[1] over several millions of years, and apparently self-maintaining forests covered the mountain slopes when the first Polynesian settlers arrived, some 1500 years ago. Subsequently, much of the indigenous forest area has been converted to other uses, but sizeable remnants are still present in the Hawaiian mountains. Their natural maintenance dynamics, although threatened by further fragmentation and the invasion of exotic species, is still well displayed in some areas, particularly in the montane rain forest.

An understanding of forest dynamics is complicated by the fact that trees, as a rule, have much longer life spans than humans. Conclusions must necessarily be based on inferences drawn from patterns that occur side-by-side in space, and on others that occur at different scales in space and time. Moreover, forest dynamics is a broad subject. Here, I will restrict myself to a brief overview relating to forest distribution, volcanic succession, canopy dieback and evolutionary implications.

Forest distribution

The climate (see centrepage diagram in this issue) of the six higher Hawaiian islands generally promotes forest development. Exceptions are the nocturnally frosty alpine environments above 2500 m on the three high mountains, Haleakala (3055 m, Maui), Mauna Kea (4205 m, Hawaii) and Mauna Loa (4169 m, Hawaii), and the driest areas in the leeward lowlands. Other naturally non-forested habitats include the almost vertical escarpments on the windward mountain ranges of the older high islands, certain extreme mountain bogs, the beach areas in the surf range, the coastal marshes and the new volcanic surfaces on the island of Hawaii.

Descriptions of the vegetation zones[2–6] have emphasized plant formations arranged in altitudinal belts with only a few (4–5) native dominant canopy species. The low number of canopy species is an important characteristic differentiating the Hawaiian mountains from other tropical mountains[5]. In addition there are many other native tree species, about 250 in all*, but most are of rather local distribution. In the rain forest they belong to such families as Rubiaceae, Rutaceae, Araliaceae, Aquifoliaceae, Euphorbiaceae, among others, and they usually occur as subordinate members under the canopy of the endemic *Metrosideros polymorpha* (Myrtaceae). Although there are a few, small-area remnants of native dry zone forest left, most of the leeward and seasonally dry habitats are now occupied by replacement communities consisting mostly of alien species. They are dominated by canopy species such as *Leucaena leucocephala*,

* W. L. Wagner and D. R. Herbst, pers. commun. These authors are working on the new flora of the Hawaiian islands.