



FIGURE 2. Field crew for the Kau forest bird survey of 1976. (Photograph by Miles Nakahara)

THE SURVEY AND ITS OBJECTIVES

By the mid 1970s it was generally acknowledged that any hope for preserving the unique Hawaiian avifauna and associated biota would require obtaining basic information on distribution, abundance, habitat response, and limiting factors. In order to meet these needs, Eugene Kridler, John L. Sincock, and J. Michael Scott conceived the idea of a state-wide forest bird survey in 1975, because such an approach was needed to identify areas requiring protection, research priorities, and management strategies. The Hawaiian Forest Bird Survey (hereafter HFBS), the results of which are detailed herein, began in 1976 (Fig. 2) on the southeast slopes of Mauna Loa, Hawaii, and ended in 1983 in the subalpine woodland of Mauna Kea, Hawaii. About one-third of the area covered by the HFBS had never been explored by ornithologists.

The principal objectives of the Hawaiian Forest Bird Survey were to determine for each bird species in the forests we studied: (1) distribution; (2) population size; (3) density (birds/km²) by vegetation type and elevation; (4) habitat response; and (5) geographical areas where more detailed studies were needed to clarify distributional anomalies and to identify limiting factors of various species. Subsidiary objectives were to (1) develop, improve, and continually evaluate

forest bird survey techniques and their statistical analysis; (2) determine the distribution of native habitat types; and (3) compare land-use patterns and habitat stability in forested areas.

The areas surveyed included all native forests above 1000 m elevation on the islands of Hawaii, Maui, Molokai, and Lanai, and the known distributional area for endangered forest birds on Kauai. We were able to stratify our sampling effort on Kauai because of the pioneering work of John Sincock (unpub. data, Sincock et al. 1984). The islands of Kahoolawe and Niihau were not surveyed because they lack native forest birds. We did not survey Oahu because of the low densities of native birds and the completion of a forest bird survey on military lands (Shallenberger and Vaughn 1978). Sampling efforts 10 times greater than we undertook on the island of Hawaii would have been necessary to make meaningful statements about some nonendangered native birds on Oahu, and it was decided that the money and manpower required would be better spent at that time on other needs.

THE NATURAL ENVIRONMENT

Because the study areas cover a great diversity of habitats and are distributed over a broad area, we include a general account of the major geological, climatic, and vegetation patterns. More

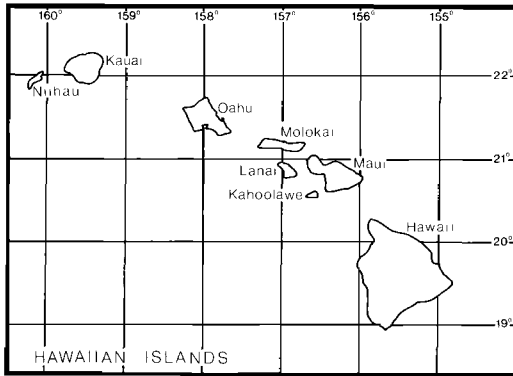


FIGURE 3. The main Hawaiian Islands.

detailed accounts of Hawaiian ecosystems may be found in Rock (1913), Carlquist (1970), Kay (1972), and Mueller-Dombois et al. (1981).

In this monograph we use "Hawaii" to refer only to the big island of Hawaii and "Hawaiian Islands" to refer to all the islands collectively. Names of places, plants, and birds are spelled without the glottal stops and macrons often used in transliterating the Hawaiian language. Scientific names for birds are given in the species account section.

GEOLOGY

The Hawaiian Islands extend for 2650 km across the north Pacific Ocean (Figs. 1, 3). The chain is volcanic in origin, and was formed as the Pacific plate moved over a fixed area of vulcanism currently located under the island of Hawaii (Macdonald et al. 1983). More than 80 shield volcanoes, progressing in age from southeast to northwest, extend northward from the main islands (age 0–6 million years [my] by potassium-argon dating) through the low leeward islands (7–27 my) to the submerged Emperor Seamounts (37–70 my), where additional older volcanoes probably existed to the north but have been subducted into the Kurile-Aleutian trench (Macdonald et al. 1983).

Hawaii, the youngest island, was formed from five independent volcanic systems: Kilauea, Mauna Loa, Hualalai, Mauna Kea, and Kohala. Kilauea on the southeast side of the island is currently active and has erupted over 40 times in the last century (Macdonald et al. 1983). Mauna Loa, the largest mountain on earth, forms the south half of Hawaii, rises to 4169 m, and has erupted 19 times in the last century, most recently in 1975 and 1984. Hualalai, a steep dome studded with cinder cones, forms a portion of west Hawaii, rises to 2522 m, and last erupted in 1800 or 1801. Mauna Kea, the highest insular

mountain on earth, forms most of the north half of Hawaii, reaches 4205 m, and has not erupted for at least 2000 years (Macdonald et al. 1983). Kohala Mountain forms the north end of the island and is aged at approximately 300,000 years (Macdonald et al. 1983).

Maui, Molokai, Lanai, and Kahoolawe are part of a huge massif formed by six volcanic systems. During Pleistocene sea level depressions, these islands were at times joined together as one island called Maui Nui (Stearns 1966); during sea level rises, East and West Maui became separate islands. Haleakala volcano on East Maui, 3055 m elevation, is 800,000 years old and last erupted about 1790; the other volcanic systems of Maui Nui date to 1.3–1.8 my and have not erupted for thousands of years (Macdonald et al. 1983).

Kauai, the oldest main island, has been dated to 5.6 my and has a heavily eroded landscape. The Alakai Swamp occupies the floor of the ancient Olokele caldera (Stearns 1966).

CLIMATE

Interaction between high mountains and prevailing trade winds affects rainfall and produces much of the vegetational zonation in native Hawaiian ecosystems. Prevailing moisture-laden northeast trade winds blow about 90% of the time in summer and 50% in winter (Blumenstock and Price 1967). When these trades encounter highlands, the wind is channelled up and then around or over the upland area, depending on the height. Because of adiabatic cooling, the rising air becomes saturated with water, clouds form, and precipitation occurs. Montane windward slopes of Hawaii, Maui, Molokai, Oahu, and Kauai receive 700–1000 cm of rain annually by this process. At 2000–2300 m elevation, a regional temperature inversion marks the upward limit of the flow of moist air; above this inversion lies a fairly stable mass of dry air (Blumenstock and Price 1967). After passing the crest, shoulder, or ridge of the highland area, the trade air descends, adiabatically warms, and absorbs moisture from substrates. This creates an arid rainshadow on leeward areas exposed to trade flow, where annual precipitation averages 50 cm and may drop below 20 cm (Blumenstock and Price 1967).

Where the trade wind is blocked from areas on the lee side of large mountain masses, convection cells tend to develop in the relatively stationary air, such as along the Kona coast of Hawaii. Strong diurnal sea breezes create an upland precipitation zone similar to that on the windward side, but the lowland areas in a convection cell are arid.

VEGETATION

The indigenous Hawaiian flora, with 1200–1300 species (Wagner et al. 1985), has the highest proportion of endemic species (95%, St. John 1973) of any major flora on earth. The dominant native tree species in a vast breadth of communities is ohia, or ohia-lehua, *Metrosideros polymorpha*. Occurring from sea level to over 2500 m elevation in dry, mesic, wet, and bog habitats, ohia reaches best development in montane rainforests and on recent lava flows and ash deposits. Ohia blooms profusely, and many birds are attracted to its bright red (less frequently yellow or salmon) flowers. Trees on the same landscape show tremendous variation in flowering periods due to differences in elevation, local weather, substrate, tree age, physiological condition, and genotype (Perkins 1903, Baldwin 1953, Porter 1973); ohia forest canopies thus frequently resemble a tapestry of green sprinkled with flowering red patches of many sizes. Particularly in wet areas, ohia exhibits a cohort senescence phenomenon characterized by widespread death or defoliation of canopy trees (Mueller-Dombois and Krajina 1968; Petteys et al. 1975; Mueller-Dombois 1980, 1982, 1983a, 1983b; Jacobi 1983).

Another major tree species is koa, *Acacia koa*. Its range broadly overlaps that of ohia, but it has a narrower elevational range, is absent from very wet rainforests and recent lava flows, and reaches best development on upland mesic sites. It bears small flowers with modest amounts of nectar, produces hard seeds on which several extinct honeycreepers fed, and supports a more diverse and abundant insect fauna than ohia (Swezey 1954). Mamane, *Sophora chrysophylla*, is dominant in dry woodlands at mid to high elevation, but also occurs at low elevations. Its yellow flowers attract several nectarivorous birds, and the Palila is specialized to feed on its seed pods. Naio, *Myoporum sandwicense*, frequently occurs with mamane and may form mixed forests with it and koa. Naio berries provide food for the Palila and several introduced bird species.

The Hawaiian lobeliads (Lobeliaceae) are small understory trees and shrubs that were important nectar and fruit sources for native birds, particularly the Hawaiian Akialoa, Iiwi, Hawaii Mammo, and Black Mammo (Perkins 1903). The seven native genera (*Brighamia*, *Clermontia*, *Cyanea*, *Delissea*, *Lobelia*, *Rollandia*, and *Trematolobelia*) have distinctive growth forms and provide a fascinating example of adaptive radiation (Rock 1919; Carlquist 1970, 1974); most species are in *Clermontia* and *Cyanea*. Many species are now extinct or quite rare, and most populations are

greatly reduced in numbers due to habitat degradation and feral ungulate activity.

Tree ferns (*Cibotium* spp.) are especially characteristic of wet areas on Hawaii, and have monopodial stipes up to 5 m high. Matted ferns, also called uluhe or false staghorn ferns (*Dicranopteris* spp., *Hicriopteris pinnata*, and *Sticherus owhyensis*), are coarse woody-stemmed ferns that often form nearly impenetrable mats 2–3 m thick under open tree canopies, particularly in areas of ohia dieback. The most prominent native vine, ieie (*Freycinetia arborea*), is a stout climber that bears fleshy inflorescence bracts and fruit eaten by the Hawaiian Crow and Ou (Perkins 1903). Typical native ground covers in relatively undisturbed montane areas include the bunchgrass *Deschampsia australis* in dry areas, several sedges (*Carex alligata*, *Uncinia uncinata*, and *Machaerina angustifolia*), several species of *Peperomia*, ground ferns, club mosses, mosses, liverworts, and lichens. Few native ground cover species are not severely impacted by pig activity, and in many rainforest areas the epiphytic flora gives the only indication of the original ground synusium.

Vegetation zonation generally follows precipitation and elevation patterns (Figs. 4–8). Wet forests develop on windward slopes and at the upper portions of convection cells; mesic forests at the margins of wet forest; and dry forests above the inversion layer, on leeward rainshadow slopes, and at the bottom of convection cells.

The vegetation on dry, mesic, and wet montane sites differs strikingly in floristic composition and physiognomy (Table 2). Dry montane areas typically support open woodlands of ohia, mamane, or naio, with substantial cover by small trees and shrubs of *Dodonaea*, *Styphelia*, and *Vaccinium*. Mesic areas tend to have taller, denser forests with ohia, koa, *Coprosma*, *Myrsine*, and a native raspberry (*Rubus hawaiiensis*) frequent. Wet habitats are similar in structure to mesic ones, but have dense epiphytic growth, and subcanopies dominated by small trees of ohia, olapa (*Cheirodendron* spp.), *Broussaisia*, *Coprosma*, *Ilex*, *Myrsine*, *Pelea*, *Psychotria*, and by tree ferns, matted ferns, and vines.

In sharp contrast to dry montane woodlands on recent substrates are the mature dry and mesic forests below 1300 m elevation having a very rich flora (Table 2). These forests are now very localized and most are badly degraded, but they give a glimpse into what was probably an important habitat for many native birds known only from fossils (Olson and James 1982b). Dominant trees in mature dry and mesic woodlands and forests include lama (*Diospyros ferrea*), ohia, kolea (*Myrsine* spp.), sandalwood or iliahi (*Santalum* spp.), olopuu (*Osmanthus sandwicensis*),

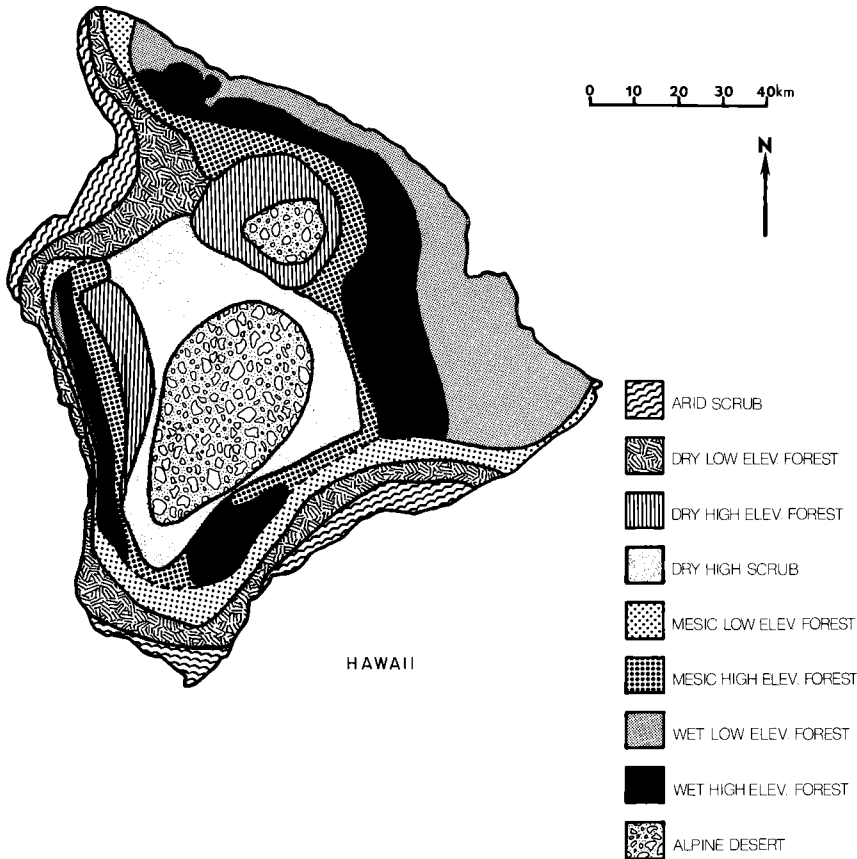


FIGURE 4. Vegetation zones of Hawaii, after Ripperton and Hosaka (1942).

maneie (*Sapindus saponaria*), and halapepe (*Dracaena aurea*) above 500 m elevation, lama, wiliwili (*Erythrina sandwicensis*), ohe (*Reynoldsia sandwicensis*), and alahee (*Canthium odoratum*) below 500 m. Many dry forest species bear flowers or fruits that were probably extensively utilized by birds before Polynesian disturbance.

Substrate and disturbance are major modifiers of vegetation structure and composition. Recent lava flows, for example, have highly porous immature substrates that support early seral vegetation. Because of poor soil development, the vegetation is more xerophytic than on adjacent older substrates. Anthropogenic disturbance encompasses ranching, forestry, agriculture, and urban development. The communities most drastically modified by disturbance include dry lowland (below 700 m elevation) habitats, most mid-elevation dry forests, most lowland wet forests, and virtually all mesic forests and grasslands. Showing less disturbance are montane rainforests, early seral communities, dry subalpine woodland, alpine scrubland, and mid to high

elevation barrens. Feral ungulate disturbance (goats and sheep in dry areas, pigs and deer in wet and mesic areas, cattle formerly in all) is pervasive and quite severe over large areas. Adverse modification of native communities by introduced plants has often accompanied human disturbance, but is less frequent in undisturbed areas.

Introduced plant species dominate disturbed communities and are nearly ubiquitous in occurrence. Strawberry guava (*Psidium cattleianum*) and lemon guava (*P. guajava*) are the most frequently encountered trees and often occur with Christmas-berry (*Schinus terebinthifolius*) in drier areas below 1300 m elevation. Plantations of conifers (especially *Pinus radiata*, *Cryptomeria japonica*, and *Araucaria* spp.) and eucalyptus (*Eucalyptus* spp.) are fairly frequent. Haole koa (*Leucaena leucocephala*) and mesquite or kiawe (*Prosopis pallida*) are common in dry to mesic lowlands. Silky oak (*Grevillea robusta*) occurs on some dry lower elevation sites. Fire tree (*Myrica faya*) is locally common on windward Hawaii on

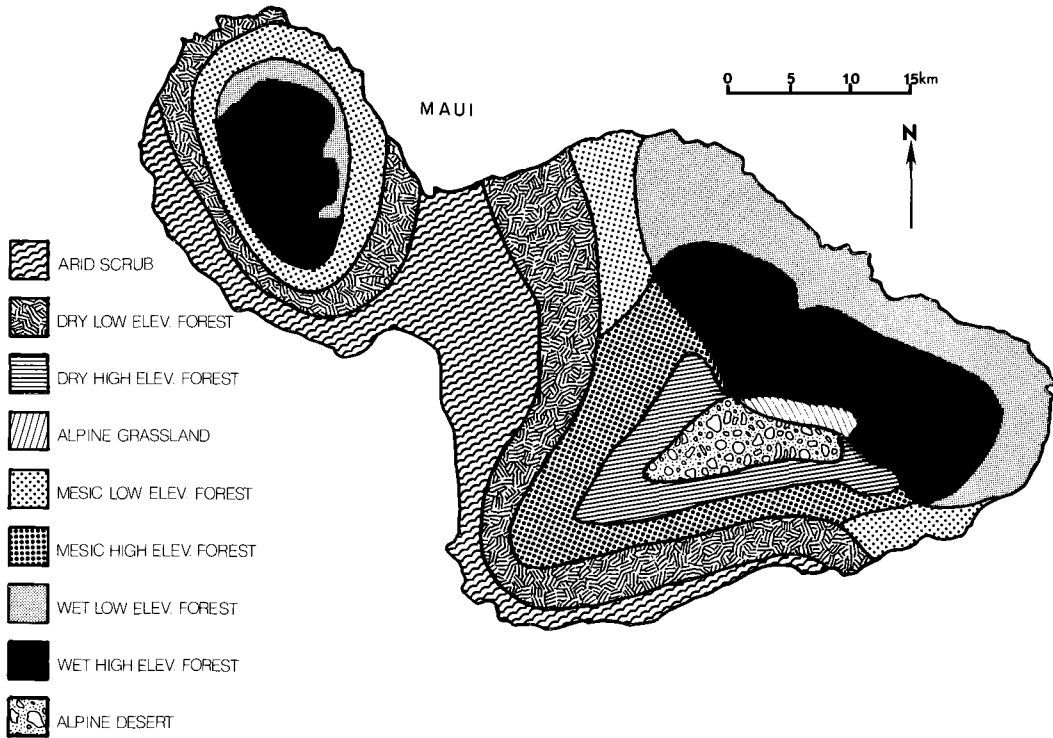


FIGURE 5. Vegetation zones of Maui, after Ripperton and Hosaka (1942).

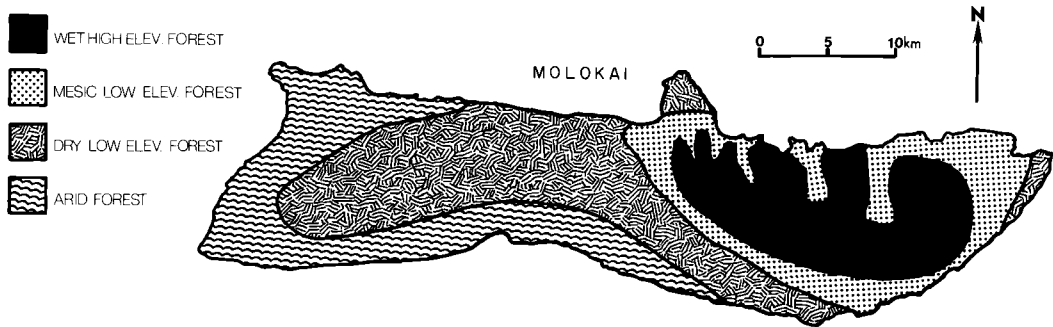


FIGURE 6. Vegetation zones of Molokai, after Ripperton and Hosaka (1942).

dry to wet sites at 500–1300 m elevation. *Passiflora* species (referred to generically in this work as “passiflora”), especially banana poka (*P. mollissima*), have rich nectar and fruit resources that attract many birds. Banana poka is aggressive, forms tree-strangling curtains that extend to the canopy, and inhibits seedling growth in the understory (Warshauer et al. 1983, La Rosa 1984). Other introduced understory plants that invade and disrupt native ecosystems include blackberries (*Rubus* spp., especially *R. penetrans*), gingers

(*Hedychium* spp., especially kahili ginger, *H. gardnerianum*), lantana (*Lantana camara*), Koster’s curse (*Clidemia hirta*), and several aggressive grasses: bush beard grass (*Andropogon glomeratus*), broomsedge (*A. virginicus*), velvet grass (*Holcus lanatus*), molasses grass (*Melinis minutiflora*), meadow ricegrass (*Microlaena stipoides*), kikuyu grass (*Pennisetum clandestinum*), fountain grass (*P. setaceum*), and palm grass (*Setaria palmaefolia*).

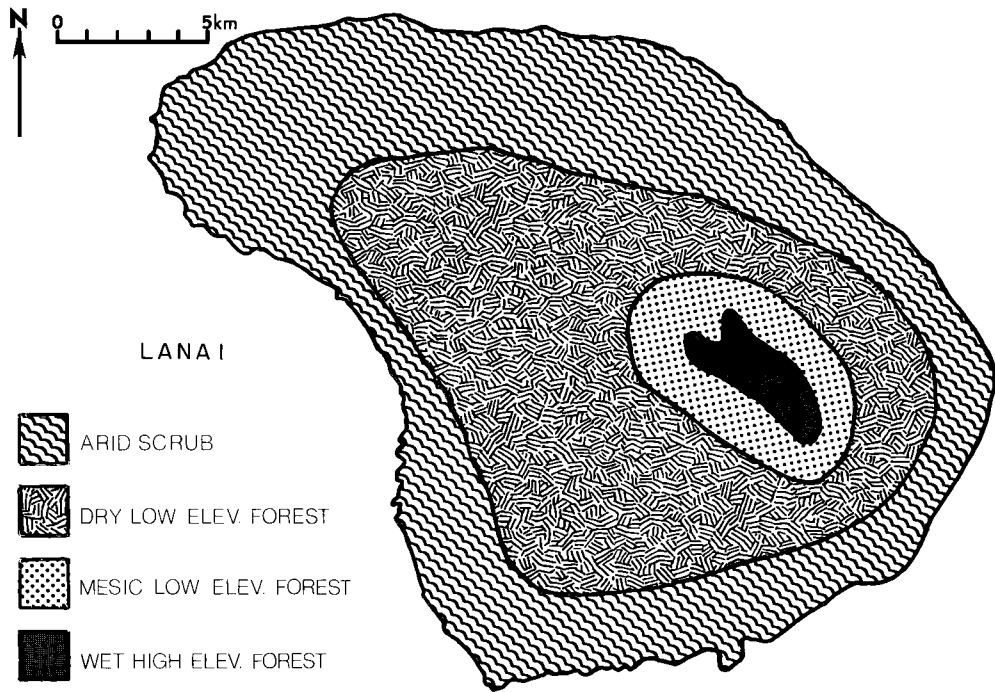


FIGURE 7. Vegetation zones of Lanai, after Ripperton and Hosaka (1942).

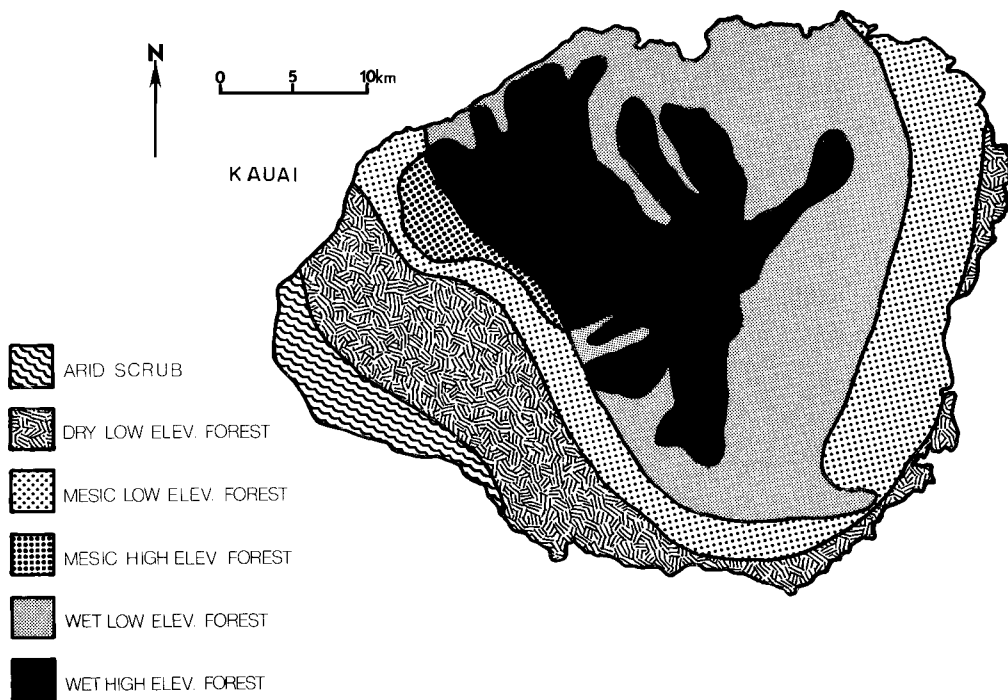


FIGURE 8. Vegetation zones of Kauai, after Ripperton and Hosaka (1942).

TABLE 2
CONTINUED

	Kona ^a				East Maui ^b				Remnant mature dry forests ^c						
	Dry		Wet		Dry		Wet		H1	H2	H3	MA	MO	LA	OA
	Mesic	Mesic	Mesic	Mesic	Mesic	Mesic	Mesic	Mesic							
Araliaceae
<i>Cheirodendron</i>	...	6 (58)	24 (100)	R	R	R	C
<i>Reynoldsia</i>	10 (100)	C	R	A
<i>Tetraplasandra</i>	...	+ (04)	1 (33)	...	C	R	C	C
Celastraceae	R	R
<i>Perrinitia</i>	...	4 (50)	2 (39)
Chenopodiaceae
<i>Chenopodium</i>	R	C	C	C	...	C
Compositae
<i>Dubautia</i>	1 (22)	1 (24)	3 (67)	1 (36)	C	R	R	R	C	C
Ebenaceae	A	A	C	C	C	A	A
<i>Diospyros</i>
Epacridaceae
<i>Styphelia</i>	28 (94)	9 (100)	2 (55)	C	C	C	C	C	C	R	C
Ericaceae	15 (73)
<i>Vaccinium</i>	3 (40)	1 (38)	1 (38)	13 (88)	9 (100)	9 (100)	5 (85)	R	R	R
Euphorbiaceae
<i>Antidesma</i>	...	+ (06)	2 (21)	+ (06)	...	C	R	...	C	X	R	R
<i>Claoxylon</i>	R
<i>Drypetes</i>	R
<i>Euphorbia</i>	R
Flacourtiaceae	C
<i>Xylosma</i>	+ (08)	R	R	C	C	R	C
Geraniaceae
<i>Geranium</i>	+ (11)	+ (03)	...	1 (24)
Goodeniaceae
<i>Scaevola</i>	1 (33)
Hydrangeaceae
<i>Broussaisia</i>	9 (67)	+ (33)	9 (85)
Lauraceae
<i>Cryptocarya</i>	R
Leguminosae
<i>Acacia</i>	2 (14)	16 (72)	8 (33)	2 (06)	10 (33)	10 (33)	5 (21)	A	...	C	X	C
<i>Cassia</i>	R	C	C	C	R	A
<i>Erythrina</i>	R
<i>Mezoneuron</i>	R
<i>Sophora</i>	10 (48)	1 (19)	...	14 (47)	+ (33)	+ (33)	...	C	R	C	C	R	R	R	...

TABLE 2
CONTINUED

	Kona*			East Maui*			Remnant mature dry forests ^{b,c}						
	Dry	Mesic	Wet	Dry	Mesic	Wet	H1	H2	H3	MA	MO	LA	OA
Lobeliaceae													
<i>Clermontia</i>	...	1 (28)	2 (50)	...	+	1 (73)	X
<i>Cyanea</i>	+	X
<i>Delissea</i>	X
<i>Lobelia</i>	+
<i>Trematolobelia</i>	+
Malvaceae													
<i>Hibiscadelphus</i>	R	...	R	X
<i>Hibiscus</i>	X	C
<i>Kokia</i>	R	X	...
Moraceae													
<i>Sireblus</i>	...	+	(03)	R	R	C	R	...	R
Myoporaceae													
<i>Myoporum</i>	8 (48)	3 (47)	+	(04)	C	C	C	C	C	C	C
Myrsinaceae													
<i>Myrsine</i>	2 (22)	6 (56)	6 (62)	+	(06)	3 (70)	C	C	C	C	C	C	C
Myrtaceae													
<i>Eugenia</i>	C
<i>Metrosideros</i>	18 (65)	54 (91)	60 (100)	3 (35)	35 (100)	47 (100)	A	A	A	C	A	...	C
Nyctaginaceae													
<i>Pisonia</i>	...	+	(03)	C	C	R	C	C
Oleaceae													
<i>Osmanthus</i>	...	+	(06)	C	C	C	A	A	A	A
Pittosporaceae													
<i>Pittosporum</i>	...	+	(12)	+	R	C	R	R	...	X	C
Rhamnaceae													
<i>Alphitonia</i>	R	R	C
<i>Colubrina</i>	R	R	C	C
Rosaceae													
<i>Osteomeles</i>	1 (27)	+	(03)	C	R	C	C	R	C
<i>Rubus</i>	+	(06)	5 (47)	3 (42)	1 (06)	5 (67)	C	R
Rubiaceae													
<i>Bobea</i>	R	...	C	C
<i>Canthium</i>	...	+	(06)	C	C	...	C	...	A
<i>Coprosma</i>	2 (43)	3 (66)	4 (63)	6 (82)	10 (100)	5 (82)	C	C	R	C	C
<i>Gardenia</i>	+	R	R	...
<i>Gouldia</i>	...	+	(09)	2 (85)	R	C	R	...	C
<i>Morinda</i>	+	R
<i>Psychotria</i>	...	+	(09)	1 (58)	C	C	R	R	C

TABLE 2
CONTINUED

	Kona ^a			East Maui ^b			Remnant mature dry forests ^{c,c}						
	Dry	Mesic	Wet	Dry	Mesic	Wet	H1	H2	H3	MA	MO	LA	OA
Rutaceae													
<i>Pelea</i>	...	1 (25)	1 (29)	...	3 (33)	4 (97)	R	R	R	C	C
<i>Platydesma</i>	+
<i>Zanthoxylum</i>	R	...	R	R	R
Santalaceae													
<i>Exocarpus</i>	+ (02)	R	X	R
<i>Santalum</i>	3 (37)	+ (06)	...	+ (12)	C	R	C	C	C	R	C
Sapindaceae													
<i>Alectryon</i>	R	R	...	C
<i>Dodonaea</i>	12 (75)	2 (22)	+ (04)	10 (47)	C	C	R	C	C	R	C
<i>Sapindus</i>	A	...	R	A
Sapotaceae													
<i>Nesoluma</i>	R	R	R
<i>Sideroxylon</i>	R	C	C	C	R	C
Solanaceae													
<i>Nothocestrum</i>	+ (04)	...	+ (33)	+ (09)	X	C	R	C	...	R	...
Thymelaceae													
<i>Wikstroemia</i>	+ (06)	...	+ (04)	+ (15)	X	C	R	C	C	...	C
Tiliaceae													
<i>Elaeocarpus</i>	C
Urticaceae													
<i>Neraudia</i>	R	X	C
<i>Pipturus</i>	...	+ (09)	3 (42)	1 (27)	C	C	R	C	R	...	C
<i>Ureia</i>	1 (21)	+ (09)	X	R	R	R	C
Violaceae													
<i>Viola</i>	R	C

^a The first entry for each genus is the average cover in percent, the second entry (in parentheses) is the frequency as percent occurrence on the sites; + indicates mean cover <0.5%.

^b Forest locations: H1 = Kipuka Puuulu, Hawaii; H2 = Kapua Tract, Hawaii; H3 = Puu Waawaa, Hawaii; MA = Auwahi Tract, Maui; MO = central East Molokai; LA = Kanepuu, Lanai; OA = Mokuia, Oahu.

^c Sources: Rook 1913 (all areas); Hatheway 1952 (Mokuia); Mueller-Dombois and Lamoureux 1967 (Kipuka Puuulu), Spence and Kobayashi 1971 (Puu Waawaa); Spence and Montgomery 1976 (Kanepuu); Medeiros et al. 1984 (Auwahi); Hodel 1985 (Kapua); HFBS data (Hawaii and Molokai sites).

^d A = abundant in area; C = common to moderately uncommon; R = very uncommon to quite rare; X = extirpated; ... = not known to have occurred historically.