Hawaii and the Pacific Islands

Overview of the Pacific

The Pacific is the world's largest ocean--20,000 kilometers across from Singapore to Panama. The Pacific Islands are commonly divided into the three geographic areas of Polynesia, Micronesia, and Melanesia (Fig. 1). These areas together contain 789 habitable islands (Douglas 1969) ranging in size from New Guinea at 800,000 square kilometers to the tiniest coral atolls. Although these geographic divisions were originally based on the appearance and culture of the peoples who lived within their boundaries (Oliver 1989), they are also somewhat meaningful from geological and biogeographical standpoints.

The Melanesian islands (Melanesia), which are close to the Asian and Australian continents, are composed of rock that originated from volcanoes or sediments similar to those found on the continents. These relatively large islands usually have many kinds of animals and plants, but few species are limited to single islands or island groups. Within Melanesia, as one travels greater distances from the Asian mainland and the distance between islands becomes greater, the total number of animal and plant species found on each island decreases, but the number of species found only on each island (endemic species) increases.

Courtesy B. Gagné, Hawaii Department of Land and Natural Resources

Micronesia has a large number of very small islands and a total land area of less than 3,000 square kilometers. Micronesia has two main cultural and environmental divisions, with the volcanic Palau and Mariana islands of western Micronesia differing markedly from the atolls (low-lying, ringlike coral islands) of the Caroline, Marshall, and Gilbert island groups.

Polynesia includes 287 islands and is the largest of the Pacific geographic areas, although its land area of approximately 300,000 square kilometers is much less than that of Melanesia (Bellwood 1979). Polynesia is triangular, with Hawaii, New Zealand, and Easter Island at the apexes. New Zealand (268,570 square kilometers) and the Hawaiian Islands (16,558 square kilometers) are the largest island groups, respectively accounting for 89.5% and 5.5% of the land area of Polynesia. Polynesian islands generally lack sedimentary rocks other than recent alluvial deposits, and they are much smaller and more widely separated than the islands of Melanesia. The islands of Polynesia (except Tonga and New Zealand) are formed of basaltic rocks extruded from ancient volcanoes. The only active volcanoes in Polynesia are in Hawaii and New Zealand. Although the best-known Polynesian islands are high volcanic islands with jagged profiles, deep gorgelike valleys, and cascading waterfalls (for example, Society, Hawaiian, and Samoa islands), Polynesia has many atolls. Animals and plants of Polynesian high islands originated from ancestors that came across thousands of kilometers of empty ocean; the islands generally have few animal and plant species, many of which are found nowhere else.

Many kinds of political systems exist on the Pacific islands. Those islands associated with the U.S. government, in Polynesia and Micronesia, are listed in the Table. We have focused this discussion of the status and trends of nonmarine animals and plants and their ecosystems in the Pacific on the state of Hawaii, which includes all the Hawaiian Islands. To a certain extent, status and trends of Hawaii's biological resources and habitats are similar to those throughout the Pacific region, although important differences do exist. The Hawaiian Islands are larger, have more topographic diversity, and have higher biological uniqueness than most other Pacific islands. Although invasive nonindigenous species are problematic throughout the Pacific, Hawaii is more in the mainstream of commerce, thus more nonindigenous animals and plants are accidentally carried there by planes and ships.

Finally, the Hawaiian Islands have been studied more intensively and received more conservation management attention than most other Pacific islands (except New Zealand), primarily because Hawaii is a U.S. state and because the Hawaiian Islands have a set of unique animals and plants that are renowned for their evolution in geographic isolation.

Overview of the Hawaiian Islands

The Hawaiian archipelago, the most isolated island group of comparable size and topographic diversity on Earth, is about 4,000 kilometers from the nearest continent and 3,200 kilometers from the nearest high-island group (the Marquesas Islands of French Polynesia). The state of Hawaii consists of 132 islands, reefs, and shoals stretching 2,400 kilometers in a northwest-southeast direction between latitudes 28°N and 19°N (Price 1983). The eight major high islands, located at the southeast end of the chain (Fig. 2), make up more than 99% of the total land area. The youngest island, Hawaii, has an area of more than 10,000 square kilometers (63% of the total area of the state) and has elevations of more than 4,000 meters. The island of Hawaii has five volcanoes, two of which are highly active. These islands are part of a longer chain that was produced during at least a 70-million-year period by the northwestward movement of the ocean floor over a hot spot below the Earth's crust (Fig. 3). The oldest rocks of the eight high islands range from 420,000 years old (the island of Hawaii) to about 5 million years old (Kauai). The relatively tiny eroded and submerged islands and reefs extending to the northwest are remnants of high islands that existed millions of years ago (Macdonald et al. 1983).

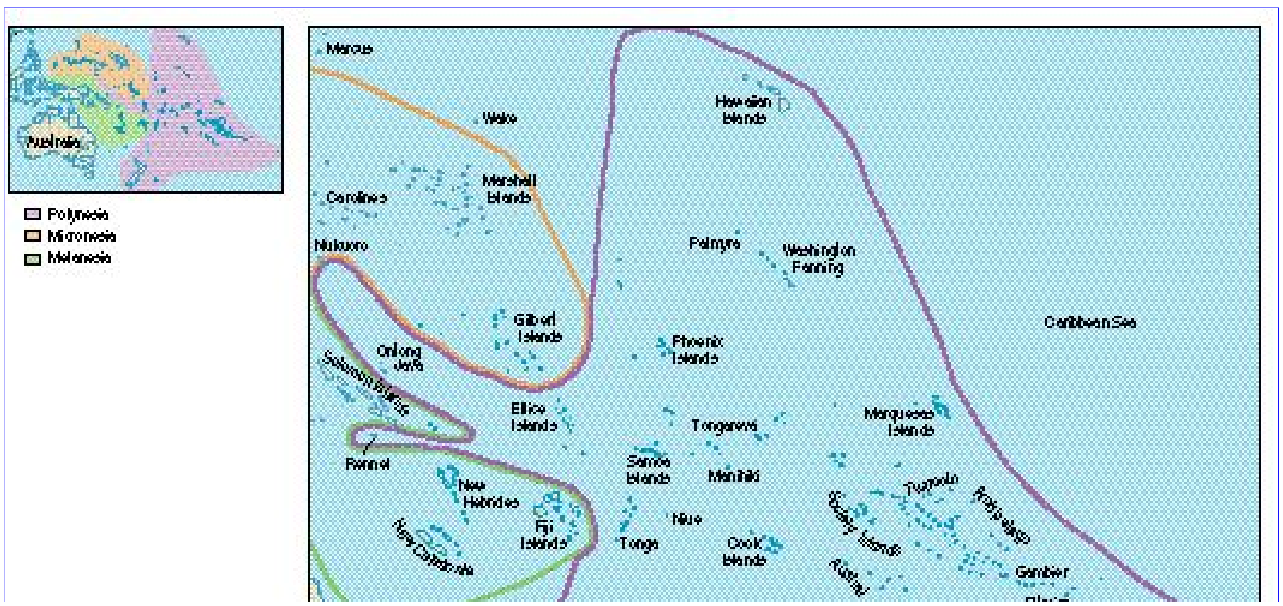
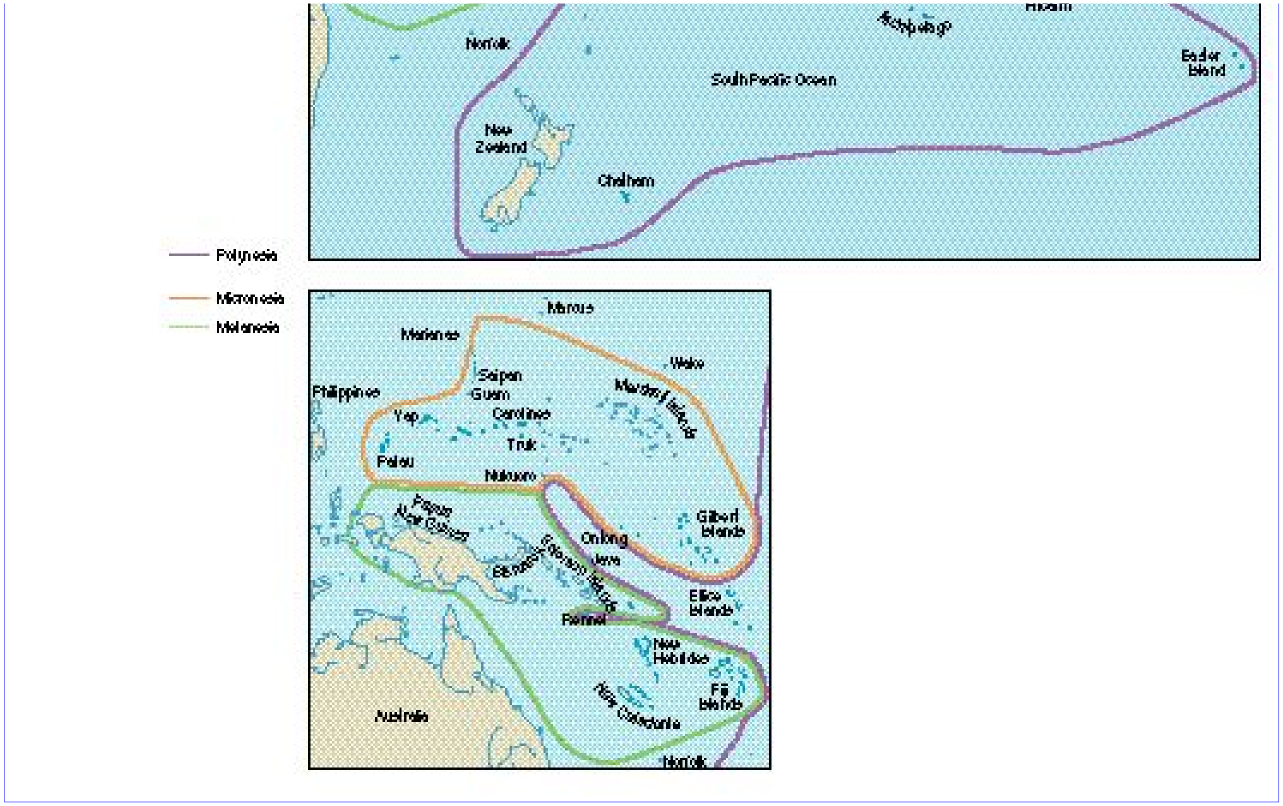
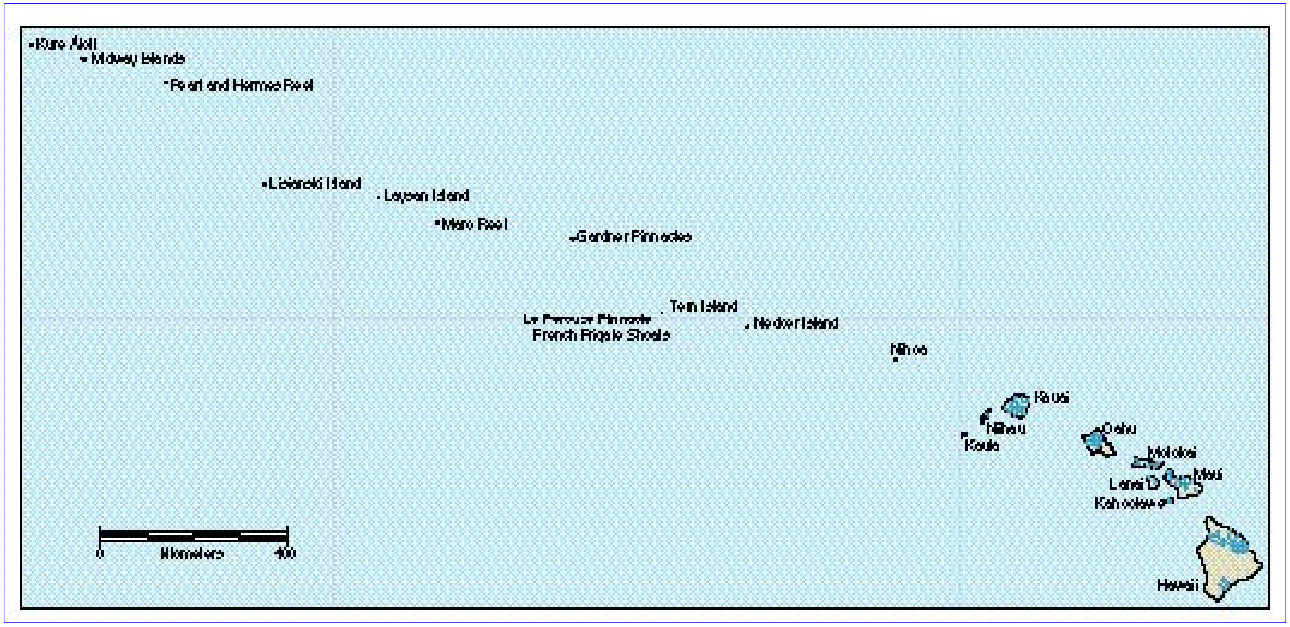


Fig. 1. The three geographic areas of the Pacific, based on ethnicity of the human inhabitants, but also somewhat relevant geologically and biologically (after Oliver 1989).



Rainfall averages from 63 to 75 centimeters per year over the open ocean near Hawaii, yet the islands themselves receive up to 15 times as much rain in some places and less than one-third as much rain in other places. These great differences in rainfall are the result of the moisture-laden trade winds flowing from the northeast over the steep, complicated terrain of the islands (Price 1983). The resulting combinations of temperature and rainfall (and some snow at the highest elevations) account for nearly 95% of the climatic variation in the Earth's tropics (George et al. 1987).

Fig. 2. The Hawaiian Islands.



The Hawaiian animals and plants began to evolve as much as 70 million years ago in nearly complete isolation; successful colonization through long-distance transport of species from elsewhere was infrequent. Many groups of organisms common on continents were never able to successfully make the journey to Hawaii. Hawaii lacks any native examples of ants, conifers, or most bird families, for example, and has only one native land-dwelling mammal (a bat). The low number of colonizers has been partially offset by enrichment of

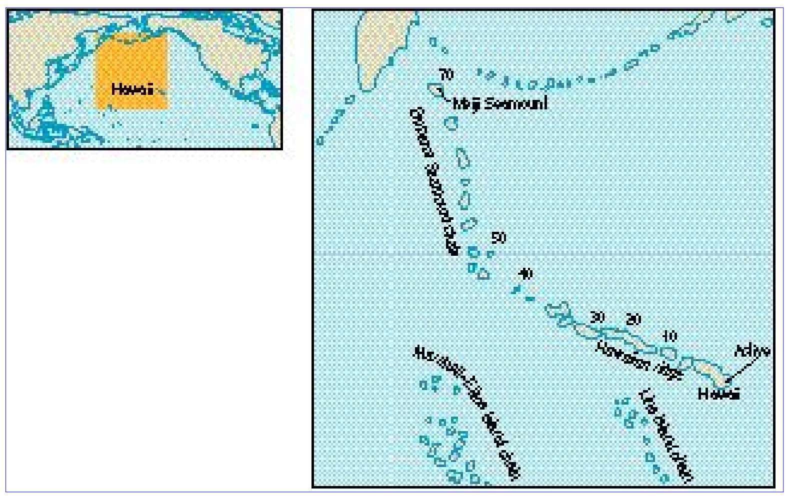


Fig. 3. Map showing islands produced by a hot spot below the Earth's crust, beginning with the Emperor Seamounts 70 million years ago and actively extending the Hawaiian chain at present. The numbers alongside the islands

biological diversity through evolution after establishment of these species. The few animals and plants that reached Hawaii over thousands of kilometers of open ocean--on the winds, by floating, or attached to storm-driven birds--arrived in a remarkably diverse potential habitat (Carlquist 1974).

are ages in millions of years (© University of Hawaii Press).

The percentage of endemic species (species found nowhere in the world except Hawaii) is very high. The land-dwelling animals and plants of Hawaii (including liverworts, mosses, fungi, and lichens, in addition to the groups listed in this section) are believed to have evolved from roughly 2,000 ancestors that arrived on the islands by chance. Based on the age of the islands, an average of only one successful immigrant arrived every 35,000 years. Researchers believe that a flora of about 960 species of flowering plants (Wagner et al. 1990) has evolved from about 270 colonizing ancestors (Fosberg 1948); 168 species of ferns and fern allies evolved from about 135 original immigrants (Fosberg 1948). The 6,000-10,000 insects and allied forms native to Hawaii evolved from about 300 to 400 ancestral immigrant species (Hardy 1983; Gagné and Christensen 1985); about 1,200 native land snails evolved from as few as 22-24 long-distance immigrants, probably carried by birds (Zimmerman 1948); and about 115 endemic land birds (including some species only known as fossils) evolved from as few as 20 ancestral immigrants (Olson and James 1982; James 1995).

Some animal and plant groups reached the geologically developing Hawaiian Islands more slowly than others, leaving much opportunity for the early immigrants to evolve into new roles and habitats. Beginning with only a single colonizing species, certain animal or plant groups underwent a sequence of speciation events that produced large numbers of related species that live in a wide range of habitats and play a variety of ecological roles. Only a few of the successful colonizing species are the sources of spectacular evolutionary adaptive radiation. Only about 1 in 10 successful flowering plant colonists was the source of a radiation (Wagner et al. 1990). Examples include the silversword-tarweed group in the sunflower family (comprised of three unique genera for debautia, silversword, and wilkesia; Robichaux et al. 1990; Baldwin et al. 1991) and the lobelias in the family Campanulaceae (including the endemic genera for brighamia, clermontia, cyanea, rollandia, and false lobelia; Wagner et al. 1990).

Table. Pacific islands associated with the government of the United States[a] (H. Smith and others, U.S. Fish and Wildlife Service, personal communication).

Island(s)	Area (square kilometers)	Number of islands	1990-1991 population
Polynesia			
Hawaiian Islands			
State of Hawaii	16,558	132	1,108,229
Midway Atoll	5.2	2	453
Samoa Islands, including U.S. Territory of American Samoa	199	7	43,052
Central Pacific islands, including:			
Johnston Atoll	2.8	1	1,325
Palmyra Atoll	10	1	-
Kingman Atoll	1.0	1	-
Howland Island	about 2	1	0[b]
Baker Island	about 2	1	0[b]

Jarvis Island	4.5	1	-
Micronesia			
Mariana Islands			
Commonwealth of the Northern Mariana Islands	759	9	23,494
Territory of Guam	541	1	144,928
Caroline Islands, including Republic of Palau	458	200+	107,662
Federated States of Micronesia, Marshall Islands (the Republic of the Marshall Islands)	180	31	48,091
Wake Atoll	6.5	3	195

[a] Subunits of Pacific Islands Ecoregion of the U.S. Fish and Wildlife Service.

[b] Island uninhabited.

- Data not available

Among birds, the Hawaiian honeycreepers (Fig. 4), and among insects, the vinegar flies (Kaneshiro 1988), are the best-known examples of adaptive radiation in Hawaiian animals.

Fig. 4. The impressive adaptive radiation in Hawaiian honeycreepers. Original art © H. D. Pratt, Louisiana State University Museum of Zoology

The Galapagos Islands have gained considerable fame from Charles Darwin's 1832 visit there and his observations of classic radiations among the island group's animals. These observations led to the birth of Darwin's theory of evolution. The Hawaiian Islands, however, have become an even more important site for modern evolutionary studies because their native animals and plants have evolved much longer in isolation and have a much greater variety of habitats to occupy.

Prehistoric Human Impacts in Polynesia

Until about 15 years ago, most biologists mistakenly believed that the native Pacific peoples had only a small effect on island habitats and their native animals and plants and that drastic modification of island environments is almost entirely due to more recent effects brought on by European and American cultures. This misinterpretation was partly a result of the cultural influence of the "noble savage" view championed by Rousseau in the eighteenth century, but was even more attributable to a lack of interdisciplinary research. In fact, Polynesians were changing their environments in a major way for thousands of years before their first contacts with Europeans. Polynesians changed native habitats through cutting, burning, and the introduction of nonindigenous plants for agriculture (Kirch 1997). The most convincing evidence for environmental change is from bird bones of species forced to extinction, found in archaeological sites, lava tubes, and sand deposits (Kirch 1982; Olson and James 1982; Steadman

1995).

Prehistoric extinctions of animals and plants that resulted from human activity have been documented throughout the world (Martin 1984). Effects of prehistoric humans in altering island environments may have been more consistently severe because islands are smaller than continents and lack alternative space for species survival. Virtually all habitable islands in the tropical Pacific, except for the Galapagos archipelago, were inhabited at some time in prehistory by humans (Steadman 1995). Although the postglacial fauna of the Galapagos was unaffected until its discovery by Europeans in 1535, major human-caused loss of biodiversity had occurred before European contact almost everywhere else, based on studies by Olson and James in the Hawaiian Islands and by Steadman and his colleagues in the Marquesas Islands, Society Islands, and Cook Islands, and on Henderson Island, Easter Island, Samoa, Tonga, and Polynesian outliers in Melanesia (summarized by Steadman 1995, 1997).

Numbers of bird extinctions caused by humans in Polynesia before European discovery of the islands are far greater than those since then. More than 2,000 bird species, mostly flightless rails (small chickenlike birds), may have been eliminated by prehistoric humans in Polynesia (Steadman 1995).

Seabird populations supplied a major food source for early Polynesians, and their exploitation by native peoples led to significant decreases in the number of seabird species and the size of remaining populations. An analysis of 11,000 bird bones from an archaeological site on Ua Huka, Marquesas Islands, shows that seven species of shearwaters and petrels were abundant and easily obtained from their nesting burrows. Six of the 20 seabird species from the site are no longer found near the island. Today, most of the other 14 seabird species are found only on tiny offshore islets (Steadman 1997).

Humans have caused an estimated 100- 1,000-fold loss of nesting seabirds in the Pacific during the past 3,000 years (Steadman 1997). Direct removal of birds and eggs by humans was likely the major factor in this reduction. A second important factor is likely to have been the Polynesian rat, which was introduced throughout Polynesia prehistorically, either intentionally or as a stowaway in voyaging canoes (Steadman 1997). The extremely conservative breeding strategy of seabirds, who normally produce no more than a single young bird per breeding pair per year, makes them quite vulnerable to predation by rats or humans (Atkinson 1985).

The Hawaiian Islands were reached by colonizing Polynesians, probably from the Marquesas Islands, in about the fourth century A.D., somewhat later than most other Polynesian islands. The human population reached 200,000 before contact with Europeans in 1778. Landscapes were modified through the use of shifting cultivation and fire and through the creation of sizeable wetlands for aquaculture. Throughout the Hawaiian Islands, most land below 600 meters elevation with even moderately good soils was cultivated by the Hawaiians in the thirteenth to eighteenth centuries (Kirch 1982). Polynesians introduced pigs, jungle fowl, dogs, Polynesian rats, and various stowaway geckos, skinks, and snails (Kirch 1982), as well as at least 32 plant species, including major food plants and species providing source materials for the manufacture of cloth, rope, and musical instruments (Nagata 1985).

About half of Hawaii's native land birds were extinct before European scientists could observe them. As more extinct birds are discovered in lava tubes and sand dune deposits, the proportion may have to be revised upward (James 1995).

If the known pollen record is a good indicator, plant species may have been more resistant to prehistoric extinction than animals (James 1995). One instance of plant loss was recently shown by a lost pollen type, which was once abundant in Oahu's lowland pollen record but did not match the pollen of any known living plant (Athens et al. 1992). Meanwhile, two plants whose pollen matched the once-abundant type were found on a cliff on the island of Kahoolawe and were described as a new genus and species (Lorence and Wood 1994). The best guess for the unusual match is that the disappearance of the plant from Oahu was due to habitat modification by the early Hawaiians and predation by the introduced Polynesian rat (L. Mehrhoff, U.S. Fish and Wildlife Service, personal communication).

Human Effects on Hawaii after Western Contact

Destruction of native ecosystems and losses of native plants and animals accelerated after the arrival of Captain James Cook's ships in the Hawaiian Islands in 1778. The greatest early effects were from grazing and browsing animals--especially feral cattle, goats, and sheep. These animals continue to affect their surroundings, but feral pigs are now causing the most destruction to remaining native ecosystems. Commercial exploitation of sandalwood and firewood for whaling ships, sugar and pineapple production, logging of koa and ohia, ranching, and real estate development have also progressively destroyed native habitats over the past two centuries (Cuddihy and Stone 1990). Although quite significant direct conflicts exist in Hawaii between proponents of economic development and those supporting preservation of native biota and natural resources, the greater conflicts are indirect, through continued introduction of aggressive animals and plants from elsewhere in the world, both intentionally and inadvertently, by modern transportation and commerce.

Effects of Invasive Animals and Plants

Oceanic islands throughout the world are notoriously vulnerable to biological invasions. Islands experience long periods of evolution in isolation from those forces faced routinely by plants and animals on continents (such as browsing and trampling by herbivorous mammals, predation by ants, virulent disease, and frequent and intense fires). This isolation contributes to the vulnerability of islands to biological invasion (Loope and Mueller-Dombois 1989). Smaller numbers of native species on isolated islands and the intensity of human impacts on small land areas of islands have clearly made the situation worse by increasing most islands' susceptibility to invasion.

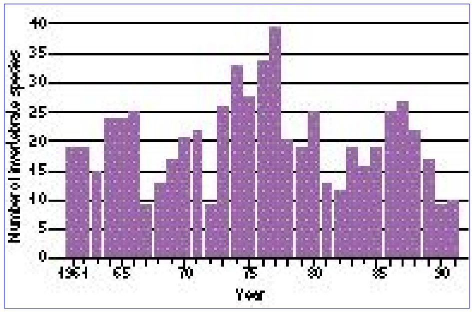


Fig. 5. Number of immigrant invertebrates reported in Hawaii, 1961-1991. Adapted from graphic by The Nature Conservancy of Hawaii and the Natural Resources Defense Council (1992); data were extracted from the Proceedings of the Hawaiian Entomological Society.

Upon the arrival of the Polynesians in the fourth century A.D., the rate of species immigration began to accelerate from 1 every 35,000 years over a 70-million-year period to about 3-4 per century over about 1,400 years (Kirch 1982; Nagata 1985). In modern times, Beardsley (1979) found that on the average, 15-20 species of immigrant insects alone become established in Hawaii each year (Fig. 5). The Hawaiian archipelago has more than 8,000 introduced plant species or cultivars (Yee and Gagné 1992), an average of 40 introductions per year over the past two centuries; 861 (11%) of these are now established and have reproducing populations (Wagner et al. 1990). Smith (1985) listed 86 invasive nonindigenous plant species present in Hawaii that pose threats to native Hawaiian ecosystems, but this number needs to be revised upward, because new invaders and changing trends of known invaders have become apparent during the past decade.

The following accounts provide sketches of the biology and effects of some of the most destructive invading species in Hawaii. Efforts to control these species for conservation purposes have achieved varying levels of success. In addition, species already present may increase their destructiveness in the future, and new species will invade. Efforts to prevent new invasive species from establishing in Hawaii are extremely important (The Nature Conservancy of Hawaii and the Natural Resources Defense Council 1992; U.S. Congress, Office of Technology Assessment 1993). Active management is needed to protect native Hawaiian ecosystems from being eventually overwhelmed by forces that began to act 1,500 years ago when the Polynesians arrived on Hawaiian shores.

Feral Pigs

Feral pigs are currently the primary modifiers of remaining Hawaiian rain forest and have substantial effects on other ecosystems. Although pigs were brought to the Hawaiian Islands by Polynesians as early as the fourth century A.D., the current severe environmental damage inflicted by pigs apparently began much more recently and seems to have resulted entirely from release of domestic, non-Polynesian genotypes (Diong 1982). Polynesian pigs were much smaller, more docile, and less prone to taking up a feral existence than those introduced in historical times (Tomich 1986). In the early 1900's, the damage caused by feral European pigs in native rain forests was recognized; the Hawaii Territorial Board of Agriculture and Forestry subsequently started a feral pig eradication project that lasted until 1958 and removed 170,000 pigs from forests statewide (Diong 1982).

Perhaps the best example of how recently pigs have damaged native ecosystems comes from the island of Maui. Although goats, cattle, and wild dogs were reported by nineteenth- century explorers of the island, they made no mention of pigs (Diong 1982). Feral pigs were absent in West Maui until someone introduced them in the 1960's; although they have since spread throughout the northeastern portion of the West Maui Mountains, the remainder of high-elevation West Maui has never been degraded by pigs (R. W. Hobdy, Hawaii Department of Land and Natural Resources, personal communication). Feral pigs were first seen in high-elevation East Maui (Haleakala Crater) in the 1930's at Paliku (elevation 1,920 meters). These pigs were probably descended from runaway domestic breeds in lowland areas. Perhaps aided by a seasonally abundant and expanding carbohydrate source--the invading nonindigenous strawberry guava--and by an enhanced protein source from abundant nonindigenous earthworms, truly feral pig populations developed and spread into adjacent pristine forest. By 1945 pigs had moved into the upper Kipahulu Valley of East Maui, though an expedition in that year found no pigs in the valley between 610 and 1,375 meters elevation. By 1967 pig damage could be found for the first time throughout Kipahulu Valley, although damage at that time was still moderate. After 1967 pig densities greatly increased. By 1979-1981, pig densities in Kipahulu Valley ranged from 5 to 31 per square kilometer (Diong 1982). Similar trends in feral pig populations have unfolded across the entire north and northeastern slopes of East Maui during the past 30 years (Hobdy, personal communication).

In addition to eating the foods more common in their diets (starch from tree-fern trunks, strawberry guava fruits, earthworms), pigs selectively seek out certain currently rare plant species for food. Plants with particularly fragile stems and leaves have drastically declined because of such predation by pigs. The ground cover of mosses and small ferns has probably been altered most, based on observations made in the few remaining pig-free areas of the Hawaiian Islands--areas protected by surrounding cliffs such as Lihau on West Maui, Olokui on Molokai, and a few kipukas (areas with soil and vegetation surrounded by recent lava flows) on Hawaii. These mosses and ferns have, for the most part, not been totally eliminated because they survive as epiphytes (plants physically growing on other plants) on tree trunks (especially trunks of native tree-ferns) and on downed logs. In rain forests of East Maui, native tree-ferns--originally the dominant subcanopy species at elevations up to 1,500 meters--are rapidly being depleted by pig predation. As mature tree-ferns become further reduced in abundance, fewer individuals of rare species will be able to survive as epiphytes.

Opportunistic plant species, often nonindigenous, occupy the habitats remaining after feral pigs have eliminated native species. Seeds of nonindigenous plants are carried on pigs' coats or in their digestive tracts, and they thrive upon germination on the forest floor where pigs have exposed mineral soil. Once these aggressive plant invaders have obtained a new foothold in the forest, they spread opportunistically, aided by pigs and nonindigenous birds. The spread of nonindigenous plants has been better documented for Maui's Kipahulu Valley than for most remote areas in Hawaii (Yoshinaga 1980; Anderson et al. 1992). Removal of feral pigs from the valley in the late 1980's by the National Park Service (Anderson and Stone 1993) has substantially slowed the rate of nonindigenous plant invasion and has already resulted in substantial recovery of the forest understory.

Feral Goats

The negative effect of goats on vegetation is well known worldwide. Damage caused by goats in Hawaii is worse than in other places because Hawaiian plant species evolved in the absence of mammalian grazing and browsing pressure. Goats were introduced to the eight major Hawaiian islands before 1800 and within a few decades had reached remote areas (Cuddihy and Stone 1990). Goats have reduced or eliminated whole populations of native plants, have aided in nonindigenous plant invasion, and have hastened soil erosion (Yocum 1967; Baker and Reeser 1972; Spatz and Mueller-Dombois 1973; Mueller-Dombois and Spatz 1975). Sustained, locally high populations of goats have obliterated even the most unpalatable native plant species. Indeed, some plant species survive only on ledges (Fig. 6) and other sites that are inaccessible to goats, or they are older trees that had reached a size that made them less vulnerable when goats occupied their habitats (Stone and Loope 1987).

Fig. 6. *Haleakala schiedia*, endemic to Haleakala Crater, survives only on ledge or cliff faces out of the reach of feral goats.
Courtesy A. Medeiros, USGS

Fig. 7. Feral goats in Hawaii Volcanoes National Park before boundary fencing and control implemented in the 1970's.
Courtesy B. Harry, National Park Service

Goats were eradicated on Niihau, Lanai (1981), and Kahoolawe (1990). Eradication of feral goats on uninhabited Kahoolawe (a former bombing range, 115 square kilometers) was conducted by the U.S. Navy before the island was returned to the state of Hawaii; unfortunately, most native vegetation had already been destroyed. Feral goats, once abundant in Hawaii's two largest national parks--Hawaii Volcanoes (Fig. 7) and Haleakala--were virtually eliminated there in the 1970's and 1980's with the aid of fencing (Fig. 8), resulting in marked changes in vegetation dynamics (Mueller-Dombois 1981a; Stone et al. 1992; Tunison et al. 1995) and at least partial recovery of rare plant populations (Fig. 9; Loope and Medeiros 1994a).

Cattle

Fig. 8. Fencing constructed in the 1980's has eliminated goats within Haleakala National Park and allowed partial recovery of native vegetation.
Courtesy A. Medeiros, USGS

Feral cattle were abundant in the Hawaiian Islands in the 1800's and early 1900's (Tomich 1986). Cattle have contributed substantially to the decline of many plant species (compare Rock 1913). Most cattle grazing is now on private, managed lands, but wild cattle persist locally, numbering in the thousands in the forested areas on the island of Hawaii (P. M. Vitousek, Stanford University, personal communication). Relatively small numbers of feral or domestic cattle can do appreciable damage to native vegetation. Cattle are a continuing significant threat to the Hawaiian flora, especially in certain coastal and lowland leeward habitats.

Rats and Mice

Of four rodent species introduced to the Hawaiian Islands, the arboreal black rat probably has the greatest effect on native fauna and flora (Stone and Loope 1987). Rodents feed on the fleshy fruits and flowers of Hawaiian plants or they girdle and strip tender branches (Cuddihy and Stone 1990). Past and continuing effects of black rats on birds, snails, and insects of Hawaiian rain forests have been enormous (Atkinson 1977; Hadfield 1986; Stone and Loope 1987).

Mosquitoes and Avian Malaria

Fig. 9. Reproduction of *Lysimachia kipahuluensis*, an East Maui endemic, in western Kaupo Gap, an area of Haleakala National Park where it was once eliminated (except on ledges and cliff

faces) by feral goats.
Courtesy A. Medeiros, USGS

Avian malaria is believed to be one of the most important factors limiting Hawaiian forest bird populations. The southern house mosquito, a vector of malaria, arrived in Hawaii before the protozoan parasite was established. The parasite was originally carried by nonindigenous game birds brought to the islands in the early 1900's for recreational hunting (van Riper et al. 1986). Van Riper et al. (1986) demonstrated that the highest incidence of malaria is in wet midelevation forests between 900 and 1,500 meters, where vector mosquito populations overlap the ranges of highly susceptible native birds. Current investigations support those observations (Jacobi and Atkinson 1995).

Invasive Plants

Approximately 90 of the roughly 900 naturalized nonindigenous plant species in Hawaii pose significant threats to native ecosystems. Among the most destructive invading plants are various grasses, banana poka (Jacobi and Warshauer 1992; La Rosa 1992), strawberry guava (Jacobi and Warshauer 1992; Loope et al. 1992), firetree (Vitousek and Walker 1989; Whiteaker and Gardner 1992), kahili ginger (Smith 1985; Fig. 10), Australian tree-fern (Medeiros et al. 1992, 1993), and clidemia.

Fig. 10. Dense growth of kahili ginger in Kipahulu Valley, Haleakala National Park, Maui.
Courtesy A. Medeiros, USGS

The spread of the invasive plant clidemia represents the worst of plant invaders in Hawaii and the Pacific. This densely branching shrub (to 4 meters tall) is native to the New World tropics (southern Mexico and West Indies to Argentina). Clidemia has become an aggressive invader in parts of India, Southeast Asia, and the Pacific Islands, including the Hawaiian Islands, where it was introduced about 1940. In Hawaii, clidemia forms dense stands in moist to wet environments. The invasion of this plant is particularly severe on Oahu, where it expanded its distribution, mainly by bird dispersal, from less than 100 hectares in 1952 to an estimated 31,000-38,000 hectares in the late 1970's. More recently, the area occupied by clidemia approaches the total habitat available and is estimated at 100,000 hectares (Smith 1992). It has now spread to Hawaii (1972), Molokai (1973), Maui (1976), Kauai (1982), and Lanai (1988). Its elevational range is from just above sea level to about 1,220 meters. The primary mode of inter-island dispersal of clidemia is believed to be as seeds in mud on people's shoes. Because of its status as one of the most ecologically disruptive plant invaders in Hawaii and the Pacific, clidemia has been a focus of biological control efforts, which involve the import of natural enemies (usually insects or diseases) from the native range of the plant. Several insects that eat the leaves of this plant show promise of limiting the further invasion of clidemia on islands other than Oahu (Nakahara et al. 1992; Smith 1992).

Some of the most disruptive weeds are such formidable competitors that they can gradually convert native forest to single-species stands, particularly when invasion is accompanied by disturbances such as a hurricane (Fig. 11) or ohia dieback. Others can alter ecosystem-level processes such as nutrient cycling, sometimes aiding the invasion of other nonindigenous species (Vitousek 1986; Vitousek and

Fig. 11. Downed trunks of ohia, Alakai Swamp, Kauai, September 1983. Severe hurricanes have affected Hawaiian Island forests in recent years only on the island of Kauai. Forest openings caused by the 1982 and 1992 hurricanes on Kauai have greatly accelerated invasion by nonindigenous plant species. Courtesy A. Medeiros, USGS

Walker 1989; Aplet 1990). Managers of natural areas in Hawaii are actively combating plant invasions (Holt 1992; Tunison 1992a,b). These efforts should be accompanied by a reduction of entry and establishment of weeds and by developing regional approaches to control (Tunison et al. 1992).

The Special Case of Invasive Nonindigenous Grasses

Alteration of the fire cycle in Hawaii by nonindigenous grasses merits special mention. In contrast to the influence of fire in many terrestrial environments of the world, it does not seem to have played an important evolutionary role in most native ecosystems of the Hawaiian Islands, and relatively few Hawaiian endemic plant species possess adaptations to fire (Mueller-Dombois 1981b). Lightning is uncommon on oceanic islands because small island land mass is not conducive to convective buildup of thunderheads. Many native Hawaiian ecosystems may have lacked adequate fuel to carry fires ignited by lightning or vulcanism (Mueller-Dombois 1981b). Fires in modern Hawaii are mostly human-caused, fueled primarily by nonindigenous grasses, and generally highly destructive to native plant species.

The major grasses fueling fires in Hawaii are beardgrass, broomsedge, buffel grass, fountain grass, and molassesgrass. Invasion by these grasses in otherwise undisturbed native ecosystems adds enough fine fuel to previously fire-free sites to carry fire. Most native species are eventually eliminated by fire (if not by the first fire, then by later ones), whereas invasive grasses recover rapidly after fire, increase flammability of the site, and become increasingly dominant after repeated fires (Hughes et al. 1991; D'Antonio and Vitousek 1992).

Incipient or Recent Invaders: Brown Tree Snake, Miconia, and Two-spotted Leafhopper

The following accounts provide sketches of some recent invaders and potential invaders of some areas of the Pacific Islands and the potentially catastrophic consequences they may have. The brown tree snake is native to the Solomon Islands, Papua New Guinea, and northern Australia. This species became established on Guam about the time of World War II and eventually attained population densities of 4,000-12,000 snakes per square kilometer, feeding on birds, rats, shrews, and lizards. Nine of the 11 native bird species present on Guam in 1945 have been eliminated by the snake (Savidge 1987). The high densities of snakes in general on Guam and brown tree snakes' nocturnal habits make them more likely to be undetected stowaways in air and ship cargo.

The brown tree snake is not known to be established in the Hawaiian Islands, but it has been singled out as a serious and imminent potential invader there (U.S. Congress, Office of Technology Assessment 1993). Seven brown tree snakes were found in Hawaii between 1981 and 1994, the most recent in December 1994 in an Oahu military warehouse containing cargo recently arrived from Guam (*Honolulu Advertiser*, 22 December 1994). The snakes would be virtually impossible to eradicate once escaped in Hawaii. They would be able to spread throughout native bird habitat, almost certainly eliminating most bird species, and would cause a host of problems to society through damaging power lines, biting and poisoning small children, and entering homes.

Miconia, a tree native to New World tropical forests at 300-1,800 meters elevation, is now known to be an unusually aggressive invader of moist island habitats. Introduced to Tahiti in 1937, miconia formed dense thickets that by the 1980's had replaced the native forest over most of the island (Fig. 12), with substantial losses of native animal and plant species (Meyer 1996). Because of its attractive purple and green foliage, miconia was introduced as an ornamental species to the Hawaiian Islands in the 1960's. In 1990 its detection on Maui by conservation agencies raised an alarm (Fig. 13). Nearly 20,000 individual miconia trees were removed from private lands by agency staff and volunteers in 1991-1993, and control seemed feasible. In September 1993, however, an aerial survey revealed a previously undetected miconia population on state land. This population, which occurred on more than 100 hectares, covered an area far larger than all previously known populations on Maui. In January 1994 an interagency working group developed and implemented a containment strategy of spraying from a helicopter individual emergent miconia trees with the herbicide Garlon 4. Efforts to mobilize a successful long-term control effort are gaining momentum (Loope and Medeiros 1994b).

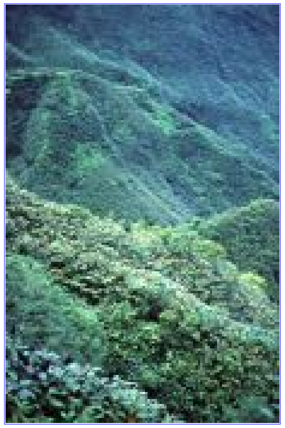


Fig. 12. Nearly monospecific cover of the Neotropical tree miconia on slopes of Vaihiria Valley, Tahiti, French Polynesia, in June 1994. Invasion of this species has eliminated much of the biodiversity on that island.
Courtesy A. Medeiros, USGS

Fig. 13. Dense patch of miconia seedlings near Hana, Maui, Hawaii.
Courtesy A. Medeiros, USGS

The two-spotted leafhopper was first noted in Hawaii on a farm on Oahu in 1987. Since then, this insect has been found in association with many plant species that exhibit such symptoms as chlorosis, leaf distortion, stunting, and death. The most conspicuous effect of this invader has been the phenomenon of uluhe dieback, where single-species stands of the fern uluhe (Fig. 14) have died; this phenomenon was first observed on Kauai and in the Manoa and Palolo valleys of Oahu. Preliminary results showed the leafhopper widely distributed on all islands surveyed

(Hawaii, Maui, Oahu, and Kauai) and on a range of hosts including 268 plant species (53 natives) representing 78 plant families (Fukada 1994). Uluhe dieback has not been observed on the island of Hawaii. By early 1995 the tree species ohia was also exhibiting severe leafhopper damage on Oahu, especially in mesic habitats (J. Lau, The Nature Conservancy of Hawaii, personal communication). Severe effects are not confined to native species; nonindigenous species, such as Brazilian pepper, firetree, and strawberry guava are also heavily damaged in some localities. Thus far, no damage to native communities has occurred at high elevations or in extremely wet areas.

The mechanism of the leafhopper's damage to plant tissue is not completely understood. However, preliminary studies lead investigators to suspect that the insect injects a protein-degrading enzyme to aid its feeding on leaf tissue, and female leafhoppers damage leaf veins (vascular bundles) when they deposit eggs (V. Jones, University of Hawaii, personal communication).

Fig. 14. Extensive monospecific stands of uluhe exist in the montane wet zones of all islands. Extensive uluhe dieback caused by the two-spotted leafhopper has occurred since 1990 on Oahu and Kauai and is also present on Maui. Courtesy A. Medeiros, USGS

No other invading insect has been documented in the worldwide literature as causing as much damage across as broad a range of vascular plant families as the two-spotted leafhopper. As of early 1995, this invader from China seems to pose a severe and perhaps unmanageable threat to Hawaiian biota. Biological control may hold much promise, however.

Some Factors Influencing Native Ecosystem Development in Hawaii

Ecologists are beginning to understand the long-term changes that occur in Hawaiian forests from the colonization of bare lava or volcanic cinder to the persistence of plants on soils that are millions of years old. This growing understanding is made possible by recent precise dating of lava flows (Lockwood et al. 1988) and research on such areas conducted by an interdisciplinary team.

Changes in Forest Composition and Structure in Relation to Soil Age and Soil Nutrients

Kitayama and Mueller-Dombois (1995) studied plots at 1,200 meters elevation from Hawaii (Big Island) to Kauai with a range in age of 300 years to 4.1 million years. The eight mesic forest sites studied had an annual rainfall of 2,500 millimeters and soil ages of 300, 2,100, 5,000, 20,000, 150,000 years (all Hawaii Island), 410,000 years (East Maui), 1.4 million years (Molokai), and 4.1 million years (Kauai). In addition, the investigators studied eight wet forest sites with annual rainfall of 4,000 millimeters and substrate ages of 400, 1,400, 5,000, 9,000 years (all Hawaii Island), 410,000 years (East Maui), 1.3 million years (West Maui), 1.4 million years (Molokai), and 4.1 million years (Kauai). A single tree species, ohia, dominates the forest canopies at all these sites. The mean height and diameter at breast height of canopy ohia trees increased from lowest values at the youngest site to maximum values at the 2,100-, 5,000-, and 9,000-year-old sites, and successively declined at older sites. The maximum standing biomass (the weight of all plant material in a plot) was found on young soils. The younger soils consistently had a high availability of phosphorus (Crews et al. 1995), and the leaves of trees growing there exhibited high concentrations of phosphorus and nitrogen (Vitousek et al. 1995). Phosphorus, a crucial element, apparently becomes less available to plant roots as Hawaiian soils age and available phosphorus is leached from the soil or is tied up in insoluble forms.

The pattern of replacement of pioneer species by species that thrive in mature forests was similar in both the wet and mesic sites, although replacement occurred more rapidly at the wetter sites, a situation consistent with the concept that soils of wetter forests lose nutrients more rapidly. The greatest numbers of plant species in plots of both mesic and wet sites were at East Maui sites (with a 410,000-year-old substrate, well past maximum phosphorus availability), indicating that species numbers are not determined by soil fertility alone.

Ohia Dieback

An understanding of nutrient availability in soils of different ages is important to our understanding the phenomenon known as ohia dieback. Because ohia dominates 80% of the relatively intact remaining forest in the Hawaiian Islands, ohia dieback is an extremely important phenomenon. Of added significance is that aggressive nonindigenous plants can establish on a large scale during dieback if seed sources are present in the area, so that native forests are eventually replaced by nonindigenous forests.

Extensive stands of ohia died on Hawaii Island in the 1970's. The death of virtually all canopy trees in entire stands affected about half of a 80,000-hectare area of rain forest on the eastern slopes of Mauna Loa and Mauna Kea from the 1950's through the 1970's (Hodges et al. 1986). The phenomenon was initially thought to be caused by a pathogen, but a decade of research led to the conclusion that the trees were dying from some other cause (Mueller-Dombois 1985; Hodges et al. 1986).

Many stands of ohia undergoing dieback are composed of older, perhaps senescent, trees (Mueller-Dombois 1983). Climatic changes that are difficult to notice may have triggered dieback over the large area. Another possibility is that this dominant species faces reduced competition in its island environment and thus invades sites over an extremely broad ecological spectrum. Ohia is not well adapted for some of these sites, such as those having soils with high (toxic) aluminum levels or waterlogged soils. As a consequence, ohia dies periodically over part of its range in response to environmental changes (Mueller-Dombois 1986). No native species is capable of replacing it as a dominant, however, and ohia seedlings usually reinvade vigorously (Jacobi et al. 1983). The cause for stand-level dieback seems to be the even-aged nature of most ohia forest stands. After canopy closure of the first-generation forest, ohia regeneration is confined to small seedlings only, which remain small and are replaced under the canopy without graduating to the sapling life stage. Seedlings and saplings of ohia grow tall and enter the canopy only after the canopy of older ohia trees collapses. Such synchronous stand dieback is to be expected only in forests with a canopy composed of a single species and thus only (at least in the tropics or subtropics) on islands or mountains where biogeographic isolation has strongly limited colonization by other canopy species (Mueller-Dombois 1987).

Loss of Seabirds and Their Guano

Olson and James 199173;1,000-fold human-caused loss of nesting seabirds in the Pacific also applies to the main Hawaiian Islands (Steadman 1997) and is consistent with the findings of Olson and James in Hawaii (for example, Olson and James 1991). Seabird guano deposits, rich in nitrogen and phosphorus, represent a large amount of potential natural fertilizer transported from sea to land. Seabirds were probably once abundant throughout the slopes of the major Hawaiian islands before predation by humans and introduced predator species, because the few islands in the world that lack rats and other predators have extensive seabird colonies. The guano deposits of seabirds would have enriched soils and likely affected vegetation growing on the soils.

We have good reason to suspect that seabirds nested in large numbers on the forest floor in the pre-Polynesian Hawaiian Islands, based on observations of expeditions to remote forested islands where predators have not been introduced (A. Medeiros, U.S. Geological Survey, personal communication). The Newell's Townsend's shearwater currently nests in wet forests of Kauai. The endangered Hawaiian dark-rumped petrel survives today primarily on the extreme upper cliffs in Haleakala Crater at elevations of 2,500-3,000 meters (Figs. 15 and 16). This bird was once the most abundant seabird in the Hawaiian Islands, present in

Fig. 15. Inner cliffs of Haleakala Crater provide a relatively secure habitat for the endangered Hawaiian dark-rumped petrel or uau. Once common throughout the Hawaiian Islands, this seabird now nests primarily in deep burrows dug in cinder along cliffs on the upper slopes of Haleakala

coastal areas and uplands as documented by bones found in a lava tube in the rain forest of Kipahulu Valley, Maui, at 1,860 meters elevation (James 1995; H. F. James, Smithsonian Institution, personal communication). If seabirds nested throughout Hawaii's forests in pre-Polynesian times, nutrient cycling was markedly altered by their disappearance, possibly influencing ohia dieback and changes in tree species composition of Hawaii's forests.

volcano. Courtesy A. Medeiros, USGS

Status of Hawaiian Ecosystems

Subalpine-Alpine Ecosystems

Fig. 16. The chick of the rarely seen endangered Hawaiian dark-rumped petrel.
Courtesy J. W. Larson, National Park Service

In the Hawaiian Islands, the mean temperature decreases about half a degree centigrade for every 100-meter increase in elevation. For example, at sea level the mean annual temperature is about 25°C, but it is only 10°C at 3,000 meters. Closed forest extends to only about 2,000 meters. The subalpine and alpine ecosystems--shrublands and open parkland with small trees (mamane parkland on Mauna Kea)--exist above this elevation (the approximate level of the trade-wind inversion, an atmospheric layer that often restricts upward movement of clouds) on volcanoes of Maui and Hawaii islands. Weather becomes increasingly severe at higher elevations and near mountain summits; vegetation there becomes sparser and plants grow lower to the ground. Near-barren eolian habitats on these mountaintops are notable for endemic predator-scavenger insects and spiders that seem to subsist on insects that are blown by wind up to the summits from below (Howarth and Montgomery 1980; Ashlock and Gagné 1983). Many other insects in these eolian habitats--carabid beetles, lacewings (Fig. 17), moths, and true bugs--are flightless, localized, and found only on these summits (Loope and Medeiros 1994c).

Fig. 17. This strange-looking flightless lacewing had not been collected since 1945, until rediscovered by Steve Montgomery in October 1994. This remarkable species is known from only a small area near the summit of Haleakala volcano at 2,900 meters elevation.

Subalpine and alpine communities were probably little affected by the early Hawaiians and even today remain largely undeveloped, except for the presence of astronomical observatories with their associated buildings and roads. Animal species have altered these communities. Goats, sheep, and cattle have damaged the vegetation through grazing. One of the greatest threats to eolian habitats is the Argentine ant, which seems capable of invading areas in which ants were previously absent, even throughout the evolutionary history of flightless species (Cole et al. 1992; Loope and Medeiros 1995).

Rain Forests

Although most Hawaiian rain forests at low elevations were destroyed long ago, rain forests still cover relatively large expanses on the islands of Maui and Hawaii and are also found on the steep windward slopes, ridges, and peaks of Kauai, Oahu, and Molokai (Cuddihy and Stone 1990). Jacobi and Scott (1985) reported the presence of about 140,000 hectares of wet forest dominated by native species on the island of Hawaii. Cuddihy and Stone (1990) estimate a similar area of wet forest for the other four largest islands combined. Most of these forests are dominated by ohia with a closed canopy and a well-developed subcanopy layer of mixed native tree species, shrubs, and tree-ferns. Koa is locally dominant or codominant with ohia.

The long-term prognosis for ecological integrity of these forests is not good, given the recent invasion of feral pigs. Effects of feral pigs on rain forests range from the slow and long-term (gradual loss of native understory species and gradual invasion by aggressive weeds) to the acute and drastic (aggressive tilling of the forest floor, massive erosion of soil and organic matter, or trunks of tree-ferns broken and the starch consumed).

In the past 30 years, gradual, continuous degradation of Hawaii's rain forests by pigs has come to be expected. The best-documented example (but one where the trend toward degradation has been reversed) is Maui's Kipahulu Valley. The National Park Service initially intended to maintain this rain forest ecosystem in a natural, undisturbed state by keeping people out. Addition of the area to the national park system in 1969 coincided with a rapid invasion and expansion of pig populations and weed invasion (Lamoureux and Stemmermann 1976; Anderson et al. 1992). Removal of pigs in the late 1980's (Anderson and Stone 1993), together with fencing, led to partial recovery of forest understory and a noticeable slowing of invasions by weedy aggressive plants. New invasions, formerly occurring throughout extensive pig-disturbed areas, are now largely confined to areas of frequent natural disturbance such as trailsides, stream courses, and landslides. Removal of invasive plants by park managers holds promise for the nearly full restoration of the ecosystem.

Similarly well-documented rain forest degradation by pigs and invasive plants has occurred in the Olao Rain Forest of Hawaii Volcanoes National Park on Hawaii Island. In 1975 this rain forest was virtually free of invasive weeds, although some feral pig activity was detected (J. D. Jacobi and F. R. Warshauer, Hawaii Volcanoes National Park, unpublished report). Two decades later, much of the area had been fenced and feral pigs removed. In places where the pigs had been removed before extensive weed invasion, excellent forest restoration was achieved. However, where nonindigenous plants (kahili ginger, banana poka, strawberry guava, Himalayan raspberry, palmgrass) had already obtained a foothold before pig exclusion, these weedy plants continue to spread (J. T. Tunison, Hawaii Volcanoes National Park, personal communication).

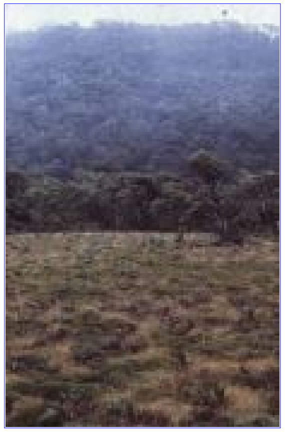


Fig. 18. Pristine bog vegetation, windward East Maui, at 1,860 meters elevation, before feral pig impacts. Dominant species are Hawaii Island sedge and prickly sedge. Broad-leaved Maui plantain is conspicuous. By 1981, when this bog was fenced, digging by feral pigs had removed 95% of the vegetation cover. By 1984, the dominants had recovered, but plantain was nearly eliminated and remains rare today.
Courtesy J. Jacobi, USGS

Only about 10% of Hawaii's remaining rain forest presently receives protection from feral pigs. As a result, although high-elevation Hawaiian rain forests are the most unaltered plant and animal communities remaining in Hawaii, their ecological integrity is being gradually eroded. This process is difficult to reverse after degradation reaches a certain stage. In contrast, in areas where managers of state, federal, and private conservation lands have removed pigs from rain forests before pigs had excessively degraded the area, excellent ecosystem recovery is under way.

Montane Bogs

Hawaiian bogs exist, mostly at higher elevations, as openings in cloud forest on the islands of Hawaii, Maui, Molokai, Oahu, and Kauai. The largest wetland complex in the Hawaiian Islands is on the Alakai Plateau of Kauai, where rainfall amounts are among the highest recorded on Earth. Numerous bogs also exist on Maui at elevations as high as 2,270 meters. Although most Hawaiian bogs are not large, many endemic plant species are largely confined to bog habitats.

Because of their remote locations and extremely wet climates, most Hawaiian montane bogs have until recently been little disturbed. However, feral pigs had finally reached bogs on all islands by the 1980's (Figs. 18 and 19). An example of recent and major progressive pig damage to a formerly pristine area is the montane bogs of East Maui. Feral pigs arrived in undisturbed sedge-dominated bogs in the upper Hana rain forest of Haleakala National Park in the early 1970's. The pigs were apparently attracted to bog habitats by the availability of nonindigenous earthworms, which are probably an important protein source (Loope et al. 1991a). In extreme situations, removal of plant cover in these bogs by pigs can approach 100% (Loope et al. 1991b). In the early 1980's, digging by pigs increased in bogs at 1,650 to 1,660 meters elevation, and nonindigenous plant invasion was under way. A series of sampling plots was established to determine the trends of damage by pigs. In sites dominated by prickly sedge, cover of nonindigenous species increased from 6% in 1982 to 30% in 1988 (Fig. 20), at which time the habitat was fenced for protection from pigs.

Fig. 19. Feral pig, Hawaii Volcanoes National Park. © J. Jeffrey

Cover of native plant species was simultaneously reduced because of digging by pigs and by invasion of nonindigenous plants; nonindigenous plant species inhibited reproduction of rare endemic plants such as the Maui greensword (Fig. 21; Medeiros et al. 1991).

Dryland and Mesic Forests

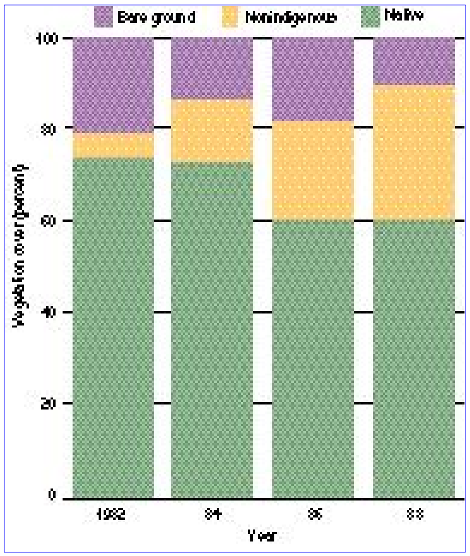


Fig. 20. Graph showing invasion of nonindigenous plants resulting from pig damage to montane bog sites on East Maui, 1982-1988 (from Medeiros et al. 1991).

Lowland dry forests were once considered the richest of all Hawaiian forests in numbers of tree species (Rock 1913), but by the early 1900's they had been largely reduced to small remnants. Direct habitat destruction by humans was the most important factor in the forest's reduction; most leeward forest sites with soil were converted to agriculture by the Hawaiians. In modern times, the effects of browsing animals, invading nonindigenous grasses, and fire have been pervasive. Spectacular undisturbed forests remain in sites such as Auwahi, Maui, and Puuwaawaa, Hawaii, where rich assemblages of tree species persist, but they include only very old individuals, have had no reproduction for many years, and exhibit conditions that seem to make reproduction impossible without heroic restoration efforts. The understory of the remnant native forest at Auwahi, Maui, is covered by a dense mat (about 30-40 centimeters thick) of kikuyu grass, introduced as a pasture grass from East Africa, which smothers any reproduction by native plants (Fig. 22). Dryland forests of Puuwaawaa and other sites on Hawaii Island are being rapidly (over one to two decades) degraded by fires carried by nonindigenous fountain grass from North Africa. The successful perpetuation of dryland forest sites poses one of the greatest challenges to conservation managers (Fig. 23).

Intact mesic (moist) forest remnants at higher elevations are commonly dominated by koa. These forests have generally been degraded by browsing goats or cattle, as have forests in Kahikinui, Maui, although excellent potential for recovery exists if these animals are removed. After 20 years of protection, koa parkland in Hawaii Volcanoes National Park has recovered to a great extent from damage by browsing cattle (Tunison et al. 1995).

Fig. 21. Maui greensword in a montane bog at 1,890 meters elevation, windward East Maui. Feral pigs directly damage greensword plants and their habitat by promoting dispersal and establishment of nonindigenous plant species. Courtesy B. Gagné, Hawaii Department of Land and Natural Resources

Subterranean Ecosystems

Fig. 22. Undisturbed forest in Auwahi, with an understory of kikuyu grass, a nonindigenous species.
Courtesy A. Medeiros, USGS

Unique, interesting, and scientifically important assemblages of endemic, cave-adapted invertebrates (insects and spiders) exist in young lava tubes on at least five of the Hawaiian Islands; about 45 species of obligate cave-dwellers, evolved in most instances from known surface relatives, are now documented (Howarth 1983, 1987). Essential components of the cave ecosystems that are home to these invertebrates include extremely constant conditions of temperature and humidity and the roots of surface plants, which provide a food supply. The primary threats to native cave invertebrates include direct effects of humans (garbage dumping, physical and chemical damage caused by exploring, and root breakage), and destruction of native surface vegetation above the caves by humans, hooved mammals, nonindigenous plants, and fire.

Fig. 23. Relatively intact dryland forest of Kanaio Natural Area Reserve, East Maui, elevation 800 meters. Dominant trees are lama and Maui hale pepe.
Courtesy A. Medeiros, USGS

Cave ecosystems are destroyed when the overlying forest that provides the caves their life-giving roots is lost (Howarth 1987); this has happened in several known instances during the past decade (F. G. Howarth, B. P. Bishop Museum, personal communication). On the other hand, many intact cave ecosystems receive protection within national parks.

Freshwater Ecosystems

Except for streams, bodies of fresh water in Hawaii are few and small. Hawaiian streams, islands of freshwater habitat within highly isolated oceanic islands (Fig. 24), are not rich in biological diversity but possess a unique and extremely interesting biota. These streams provide examples of how vacant island habitats are colonized from afar. Many members of the stream biota--including all five species of fish (four gobies and an eleotrid), shrimp, and snails--are descendants of marine forms that colonized stream habitats (Ford and Kinzie 1982). In contrast, insects (most notably damselflies, which have undergone spectacular adaptive radiation involving 17 or more endemic species) reached Hawaiian fresh waters from continental freshwater habitats.

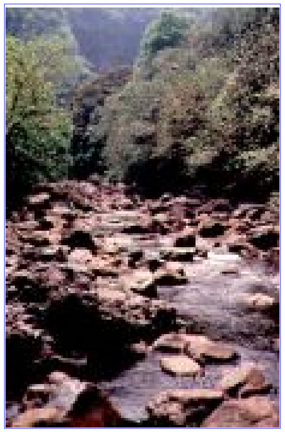


Fig. 24. Hawaiian stream habitat.
Courtesy A. Medeiros, USGS

The Hawaiian stream macrofauna is still largely intact but is seriously imperiled by habitat destruction (for example, channel alteration), pollution, rampant introduction of nonindigenous species, and withdrawal of water from streams for human use (Maciolek 1977, 1979; Parrish et al. 1978; Devick 1991). The conflict between extensive use of water resources and conservation of Hawaiian freshwater habitats has been severe. In many streams in developed areas, especially on Oahu and Maui, some native species have been extirpated or their populations have been greatly reduced. Careful preservation of relatively few intact stream ecosystems may provide for persistence of most native species, because most freshwater species in Hawaii have naturally extensive distributions within the islands. The recent major reduction in plantation agriculture of sugar and pineapple in much of the state, together with new legislative and administrative mandates for water management, offers opportunities to protect and even restore many damaged or threatened stream habitats. Immediate and vigorous action is required to curtail the alarming increase in accidental, unauthorized introductions of invasive nonindigenous species and to develop control measures for harmful nonindigenous populations.

Only a few Hawaiian streams have protected status. Among the best examples are Pelekunu Stream (within a Nature Conservancy preserve) on Molokai and Palikea Stream in Kipahulu Valley of Haleakala National Park.

Coastal Ecosystems and the Northwestern Hawaiian (Leeward) Islands

A narrow belt of strand vegetation exists around each island. On the main Hawaiian Islands, these communities have been severely damaged, especially by development and grazing mammals. Some largely intact coastal habitats persist, however, the most notable of which is at Moomomi on the north coast of Molokai. Many native coastal plant species generally persist in rocky shoreline habitats. Relatively few coastal species have been lost to extinction, largely because of steep or rugged coastal habitats that are not easily developed. Restoration of coastal habitats has much potential. Excellent small-scale restoration examples exist at Wailea Point on Maui, Kilauea Point on Kauai, and Kaena Point on Oahu.

The northwestern Hawaiian Islands (politically part of the state of Hawaii except for Midway, which belongs to the U.S. Navy) extend northwest of Kauai for 1,210 kilometers from Nihoa to Kure Atoll. About 40 emergent islands make up a total of about 10.1 square kilometers of dry land. They vary in maximum elevation from 3 to 277 meters. The strand vegetation that covers most of these islands is more intact than the strand of the main islands because these islands receive less disturbance, although past disturbance to individual islands (for example, Laysan and Lisianski, where rabbits were introduced) has been great. Although the islands have only 8 endemic and 42 indigenous plant species, 114 nonindigenous species are naturalized; the nonindigenous species seem largely in balance with the rest of the flora, although close monitoring is warranted (Herbst and Wagner 1992).

Selected Biological Resource Issues of Other Pacific Islands

Pacific islands other than Hawaii are extremely varied and can only be discussed superficially here. The land area of most of these islands is small in relation to Hawaii, but biological diversity is in many instances quite significant. For example, the Republic of Palau has a land area of 458 square kilometers and has approximately 839 species and varieties of higher plants, of which 9% are endemic (Canfield 1981). Tutuila Island (142 square kilometers) of American Samoa supports 308 native flowering plants and 115 native fern species--over half the flora of the Samoan archipelago--and about 30% of its native flowering plants are endemic (Whistler 1993).

Nonindigenous Species

We have already discussed in some detail the effects of invasive nonindigenous plants and animals in Hawaii. Other islands in the Pacific have, in extreme instances, been subjected to even more drastic impacts. The brown tree snake in Guam (Savidge 1987) and miconia in Tahiti (Meyer 1996) should serve as important lessons for Hawaii and other islands. A third example, the effect of the purposely introduced snail *Euglandina* on endemic snails of Moorea, French Polynesia (see box) illustrates even more clearly the urgent need for educating government officials to safeguard the biological diversity of the Pacific.

Although these specific examples of nonindigenous species introductions have had extreme effects, many Pacific island ecosystems have suffered significantly less than Hawaii from inadvertent and intentional introductions. Islands not heavily damaged by direct human habitat modification and without introduced hooved mammals such as goats and pigs have been found to be relatively resistant to plant invasion (Merlin and Juvik 1993). In the proposed national park of American Samoa and other cloud forest areas of Samoa, for example, Whistler (1993, 1994) found that feral pigs are largely kept at low numbers by local villagers and thus have not yet caused extensive damage to the forests and, with one exception (clidemia), invasive plants are not a serious problem.

Disruption of Mangrove Communities

Mangroves are tropical trees, classified in several plant families, that can tolerate flooding and high salinity and that usually have aerial roots. Mangrove forests occur in shallow coastal waters in sheltered conditions. No mangrove species are native to the Hawaiian Islands, whereas about 25 species exist elsewhere in the Pacific, and substantial areas of mangrove forest occur in the Mariana Islands and Micronesia (J. C. Ellison, East-West Center, Honolulu, Hawaii, unpublished report). Nine mangrove species exist on Guam, 12 on Palau, and 12 in the Federated States of Micronesia. The 355-square-kilometer island of Pohnpei (Federated States of Micronesia) has 55 square kilometers of mangrove forest.

Mangrove communities are widely recognized as an important biological resource and are traditionally used in the Pacific for fishing and gathering of clams and crabs, as a source of wood for construction, handicrafts, and fuel, and for many other specialized uses (Ellison, unpublished report).

Mangrove communities of small islands throughout the Pacific are rapidly disappearing or undergoing degradation. Creation of the large naval installations around Apra Harbor has destroyed the most extensive mangrove areas formerly existing on Guam; other areas have been lost to urban and aquaculture developments. Mangroves on Guam also suffer from pollutants such as oil spillage and heavy metals. In Palau, mangrove areas have been subjected to extensive clearing for development. Heavy harvesting has removed a large portion of the mangroves on Kosrae (Federated States of Micronesia). Mangroves on Yap (Federated States of Micronesia) were damaged by sedimentation caused by road construction. Degradation of mangroves also occurs from natural causes, especially cyclones. In February 1990, for example, 6 hectares of 16-meter-tall mangrove forest were destroyed by Cyclone Ofa in Tutuila, American Samoa (Ellison, unpublished report).

Destruction of Montane Cloud Forests

Pacific island cloud forests must be considered a high conservation priority because of their importance as traditional sources of food, building materials, medicines, and various other material products for indigenous peoples, as well as for their highly endemic biological diversity (Raynor 1993; Hamilton et al. 1995). Samoa has a large area and rugged topography; it retains more intact native forest than many other Polynesian islands, yet its cloud forests are subjected to increasing inroads by forest industry to support a growing population (Whistler 1993). Montane cloud forest is found on only two high islands in Micronesia, Pohnpei, and Kosrae, where the high-elevation ecosystem has remained largely intact for 2,500 years of human habitation. Population pressure and increasing cultivation of the narcotic crop *sakau* now pose a severe threat to the cloud forests (Raynor 1993).

Subsistence Harvest of Wildlife

The effects of prehistoric human harvest of island birds were enormous (Steadman 1995). Hunting on a small land area continues to threaten the surviving wildlife of many Pacific islands. On the island of Tutuila in American Samoa, an estimated 2,100-4,200 Pacific pigeons, 500-1,000 purple-capped fruit-doves, and 500-1,600 fruit bats were killed by hunters in recent years (Craig et al. 1994a). These removal rates are extremely high in comparison with current population levels of these animals. After a hurricane in 1990, when bats were particularly vulnerable to hunting because of food limitations, more bats were killed (about 3,100) than survived in 1992. In 1987-1992, populations of the two fruit bat species on American Samoa were reduced in size by 80% to 90% (Craig et al. 1994b).

Global Climate Change and Sea-Level Rise

The Intergovernmental Panel on Climate Change estimates that a worldwide sea-level rise of 30-100 centimeters will take place over the next century as a result of melting of glaciers and ice sheets and thermal expansion of ocean water (Markham et al. 1993). Mangrove swamps, particularly those of low islands, are likely to be sensitive to a rise in sea level (Ellison, unpublished report). A sea-level rise poses an obviously severe threat to low-lying Pacific islands. The Republic of the Marshall Islands, for example, has a human population of 48,000 living on a land area of 110 square kilometers and a mean height above sea level of 2.0 meters.

Other Issues

Pacific island ecosystems, because of their very small land size, are highly vulnerable to numerous human activities such as road construction, tourism development, military use, mining, hydropower development, forest fires, and pollution. The rapidly growing human populations of some island nations make such problems more severe. In the Republic of the Marshall Islands, for example, the population growth rate is approximately 4% annually (Thistlethwait and Votaw 1992). The human population of Tutuila of American Samoa, which is only 142 square kilometers in area, has grown 44% in the past 10 years, a rate that, if continued, will result in 100,000 people by the year 2010 (Whistler 1994). Increased tourism and internationalization of trade generate growing transportation to Pacific islands, a trend that poses a severe threat to areas not yet hit by major nonindigenous species invasion (R. A. Holt, The Nature Conservancy, personal communication).

Status and Trends of Animal and Plant Species of Hawaii and Other Pacific Islands

The native Hawaiian biota has suffered substantial extinction and endangerment. This is not surprising in view of the vulnerability of island biota and the drastic changes brought about by humans through habitat modification and species introductions. Much has been lost, with land snails and birds more decimated than other groups, but the Hawaiian Islands still have a rich native biological diversity. Relatively intact ecosystems exist at upper elevations and in the coastal strand ecosystems of the northwest Hawaiian Islands. Biological invasions, both from organisms already present and those that may arrive in the next decades, present the greatest threat to sustained survival of diverse native ecosystems. Active management of biological invasions is essential if most of the remaining diversity is to be saved over the next century.

Birds

The most spectacular land bird assemblage ever found on any remote oceanic archipelago evolved in the Hawaiian Islands (Freed et al. 1987). This status remains arguably true today for the surviving land birds, even though an extremely high percentage of them became extinct through the actions of humans. The precise percentage of this loss is not easy to determine for several reasons: methods differ for delineating the Hawaiian bird fauna (for example, residents versus visitors [Pyle 1995]); numbers depend on whether numbers of species or of subspecies are used; and the recent fossil record is continually expanding and is certainly incomplete. Numbers given here are based on species, include only Hawaiian endemics (based on taxonomy used by Olson and James 1991), and include fossil data (including 22 undescribed species) from Olson and James (1991) and James and Olson (1991).

Of the 76 species of endemic Hawaiian perching birds and songbirds, 31 are known only as fossils. Of the 45 species known historically, 19 are now extinct, 18 are federally listed as endangered (including 9 that have not been seen for several years and are possibly extinct), and only 8 species are not classified as endangered. Of the 39 species of endemic Hawaiian nonpasserine species (including geese, ducks, rails, ibises, and raptors), 31 are known only as fossils. Of the eight species known historically, two are now extinct and six are federally listed as endangered. Surviving endemic Hawaiian land bird species not listed as endangered, all passerines, include six Hawaiian honeycreepers (apapane, anianiau, common amakihi, Kauai creeper, Maui creeper, and iiwi); a thrush (omao); and a monarch (elepaio).

The Hawaiian honeycreepers, with a minimum of 57 species derived from a single finchlike ancestral species (James and Olson 1991), make up by far the largest bird family in Hawaii; their fame in evolutionary biology rivals that of Darwin's finches, a group in the Galapagos archipelago where 14 fairly similar but distinct species are derived from a common ancestor. Whereas all species and most island populations of the Galapagos finches survive today and are subject to little immediate endangerment, the story is quite different for the Hawaiian honeycreepers. At least 29 species of Hawaiian honeycreepers were eliminated prehistorically, and another 8 have been eliminated since Europeans first arrived in 1778.

Nevertheless, the 20 living species (14 of which are federally listed as endangered) still provide the most impressive example of adaptive radiation among birds. Their bills range from stout seed crushers (palila) through parrot shapes (Maui parrotbill), crossed (akepa), and warblerlike forceps (Maui creeper), to decurved probes (iiwi) that in the Hawaiian akialoa span one-third of the bird's overall length (Scott et al. 1988; Fig. 4).

The threats that have reduced the honeycreepers to a fraction of their original diversity and abundance continue largely unabated. Most surviving honeycreeper species inhabit ohia or ohia-koa forests. The factors believed to be most responsible for the continuing decline of honeycreepers and other Hawaiian birds are habitat loss, susceptibility to introduced bird diseases, predation by introduced mammals, competition from introduced birds, and reduction in abundance of arthropod food items (Scott et al. 1986; Jacobi and Atkinson 1995).

Fig. 25. Iiwi.
Courtesy J. Jeffrey, U.S. Fish and Wildlife Service

The three most common honeycreeper species (apapane, amakihi, and iiwi), which account for 95% of the honeycreeper individuals (Scott et al. 1986), show signs of vulnerability. Even the apapane, with more than 1 million individuals on Hawaii Island alone and densities of more than 1,600 birds per square kilometer, has very marginal populations on Lanai (fewer than 1,000 individuals) and Oahu. The amakihi disappeared from Lanai in the 1970's. The iiwi (Fig. 25), with more than 400,000 individuals in the 1970's (Scott et al. 1986), has disappeared from many midelevation sites over the past 20 years where it was previously common, presumably because of high susceptibility to mosquito-borne malaria (Jacobi and Atkinson 1995).

Fig. 26. Poo-uli.
Courtesy P. Baker, USGS

The poo-uli (Fig. 26) illustrates well the decline toward extinction of the rarest honeycreepers. This bird was not discovered until 1973, by which time it was present within a range of 13 square kilometers on the wet northeast slope of Haleakala volcano (elevation 1,500-1,800 meters) on Maui Island (Mountainspring et al. 1990). More recently, poo-uli have been found in the fossil record at 600 meters elevation on the dry, southwestern slope of Haleakala volcano (James et al. 1987). In a 50-hectare study area on upper Haleakala, numbers of poo-uli declined by 90% from 1975 to 1985. During this period, feral pig activity (based on ground disturbance) increased 473% (Mountainspring et al. 1990). Ground disturbance by pigs was found to be 9 to 24 times greater in nearby areas outside poo-uli range than within the range. Disturbance by feral pigs is apparently particularly disruptive to the poo-uli, a species that feeds on invertebrates found in the forest understory (Scott et al. 1988). No poo-uli were detected, in spite of sporadic efforts at locating them, between 1988 and 1993. In surveys throughout the range in 1994-1996, birds have been difficult to locate. As of 1996, the poo-uli population was estimated at 10 birds or less (T. Pratt, U.S. Geological Survey, personal communication).

Of 12 Mariana Islands bird species federally listed as endangered, 10 are endemic to those islands; on Guam, those 10 have been nearly or completely wiped out by the brown tree snake. The other two listed bird species are the Ponape mountain starling and the Ponape greater whiteye (U.S. Fish and Wildlife Service 1994).

The northwestern Hawaiian Islands are renowned for their seabird colonies. Whereas 86% of the seabird species in Hawaii and 48% of the populations exist on main islands, 95% of the breeding pairs nest in the northwestern Hawaiian Islands (Scott et al. 1988). Pyle (1995) states that seabird population estimates made in the 1960's and 1970's are not comparable for trends analysis because of the varying techniques used. Harrison (1990) discussed the difficulties involved in making representative counts and finds no evidence of long-term trends in species numbers, although some wide fluctuations occurred earlier in this century.

Important seabird populations survive in other areas of the American Pacific, including the Northern Mariana Islands; Howland, Baker, and Jarvis islands; Wake Atoll; Palau; and the Marshall Islands. Johnston Atoll provides the only roosting and breeding habitat for seabirds in 2.1 million square kilometers of ocean (R. Smith and others, U.S. Fish and Wildlife Service, personal communication).

Mammals

As a result of its extreme isolation from other land masses, Hawaii has only one native land mammal, the Hawaiian hoary bat, and one amphibious mammal, the Hawaiian monk seal. Both species are federally listed as endangered.

Two fruit bat species from Guam are federally listed as endangered as a result of habitat destruction and overharvesting by humans for food. Two fruit bat species from American Samoa are in rapid decline (see the section on subsistence harvest of wildlife, this chapter).

Reptiles and Amphibians

Hawaii has no native reptiles or amphibians that spend most of their lives on land. However, five sea turtle species come ashore in the Hawaiian Islands to deposit eggs; none are local endemics but are widespread in the Pacific (see chapter on Marine Resources). Two species, the leatherback and the hawksbill, are federally listed as endangered. The three other species--the loggerhead (see chapter on Caribbean), the green turtle, and the olive ridley--are listed as threatened. A saltwater crocodile found on Palau is federally listed as endangered (U.S. Fish and Wildlife Service 1994).

Fishes

Fig. 27. Oopu alamoo.
Courtesy M. Yamamoto, Hawaii Department of Land and Natural Resources

None of the five species of native freshwater fishes (four gobies and an eleotrid), descendants of marine forms that colonized Hawaiian stream habitats, has been federally listed, even though many stream habitats have been drastically altered. The oopu alamoo (Fig. 27) is considered a potential candidate for listing as endangered or threatened, based on its reduced distribution.

Only a few other native fish species occupy freshwater habitat in the American Pacific; none have been federally listed as endangered.

Land Snails

Fig. 28. *Achatinella* tree snail, Oahu.
© W.P. Mull, Volcano, Hawaii

Approximately 900 species (71%) of about 1,263 historically described species of Hawaiian land snails are extinct (S. Miller, U.S. Fish and Wildlife Service, personal communication). Additional extinct species are abundant in archaeological sites and sediments in limestone sinkholes (Gagné and Christensen 1985). The entire genus *Achatinella* (Fig. 28), with 41 species, was federally listed as endangered in the 1970's; all but 2 species are either extinct or near extinction. The endemic Hawaiian family Amastridae, with more than 330 species, has been virtually eliminated from Hawaii.

Fig. 29. *Euglandina rosea* (top image is printed actual size).

a.
Courtesy R. Hue, Hawaii Department of Agriculture

No endemic Hawaiian land snail species can be regarded as secure, as a result of predation by rats and by the nonindigenous snail *Euglandina rosea* (Fig. 29), which was introduced in 1958 as a biological control agent to control (unsuccessfully) another introduced snail. Vulnerability of Hawaiian land snails to predation is to a large extent a result of life-history patterns. Hadfield (1986) and coworkers have found that the Hawaiian snails in the genera *Achatinella* and *Partulina* mature slowly (after about 6-7 years) and live to a maximum age of roughly 20 years. All those studied have low reproductive rates (as few as one offspring each year and no more than about seven per year). When a comparison is made with the life-history characteristics of the predatory snail Euglandina--which takes less than a year to mature, produces more than 600 eggs per individual per year, and has a life span of up to 5 years--it is easy to see why the native snails are being driven to extinction by predation (Simon 1987). American Samoa, the Mariana Islands, and Palau have endemic tree snails that are subjected to similar threats as Hawaiian snails but are not yet federally listed.

Arthropods

b.

The number of native Hawaiian arthropods is probably near 10,000, but only about 5,500 of these have been described (including about 5,100 insect species and 150 spiders; Howarth and Mull 1992). The conservation status of these organisms is poorly known compared with that of most other groups, as intensive surveys are almost completely lacking. Only 36 species of arthropods have been recognized as extinct by the U.S. Fish and Wildlife Service; although this is probably a gross underestimate, several of those believed extinct have been rediscovered (Howarth et al. 1995). Because many Hawaiian insects are highly host-specific, many species have likely been and will continue to be lost as their host plants become rare and are destroyed.

The primary threats to the arthropod fauna are habitat and host-plant destruction and introduction of nonindigenous arthropods. About 2,600 insect species have been established in Hawaii through human activities (Howarth et al. 1995). In places where land has been converted to agriculture, few native arthropod species survive; for example, Asquith and Messing (1993) found that less than 10% of the insect fauna of a lowland agricultural area on Kauai consists of native species. Of nonindigenous insects, certain predators, especially ants (Cole et al. 1992; Gillespie and Reimer 1993; Loope and Medeiros 1995) and yellowjackets (Gambino et al. 1987, 1990; Foote and Carson 1995) may have devastating effects on native species. Nonindigenous parasites, especially ones that have broad host ranges, are also believed responsible for many instances of rarity and extinction of arthropods. Such instances are not easy to document, but abundant circumstantial evidence implicates even some insect parasites introduced for biological control (Howarth et al. 1995).

Probably the best quantitative information on decline of an insect group in Hawaii comes from the relatively well-studied endemic picture-wing vinegar flies of the Olao Rain Forest of Hawaii Island (Foote and Carson 1995; Figs. 30 and 31). Declines of these flies were attributed in part to declines in host-plant populations, and predation by yellowjackets.

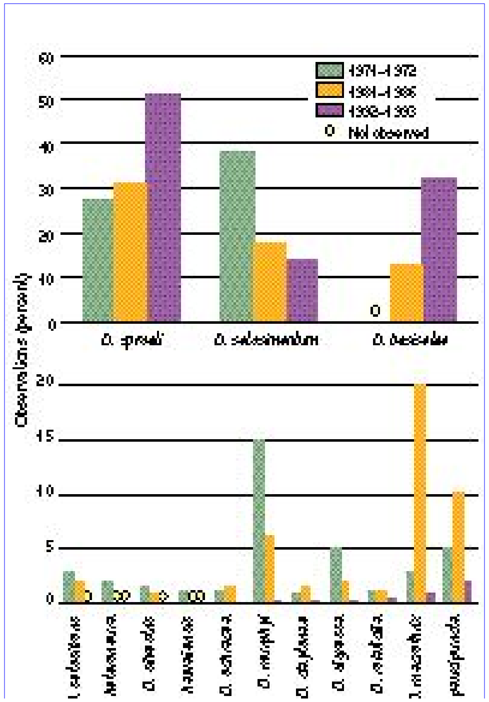


Fig. 30. A comparison of the relative frequencies of 14 endemic species of picture-wing vinegar flies *(Drosophila* species) over three periods of observation from 1971 to 1993 in Olao Rain Forest in Hawaii Volcanoes National Park. The data are expressed as a percentage of total observations within a survey period (Foote and Carson 1995).

The poorly known conservation status of Hawaiian arthropods (Howarth et al. 1995) and the few detailed studies that show unidirectional declines (Foote and Carson 1995) should not create the assumption that most highly radiated arthropod groups may be doomed to extinction in the near future. Neither can one assume that all highly radiated arthropod groups have already been discovered. One newly explored group exhibiting remarkable adaptive radiation as well as resilience in the face of disturbance and biological invasions is the ecologically important but inconspicuous (nocturnal) long-jawed spiders. Before the 1990's, only nine species of long-jawed spiders had been described in the Hawaiian Islands, based on collections made before 1900. Gillespie and colleagues (1994) recently described 19 new species in this group and collected some 50 additional new types that apparently merit species status. The Hawaiian long-jawed spiders seem to have radiated from two ancestral species (Gillespie et al. 1994). The Hawaiian tetragnathids span a huge spectrum of colors, shapes, sizes, habitats, and behaviors, far exceeding the limits to form and behavior of this group outside Hawaii. Few of the known Hawaiian species, all of which occupy wet or mesic forest habitats, seem imperiled, and some survive in highly modified habitats (R. G. Gillespie, University of Hawaii, personal communication). These spiders are, however, extremely vulnerable to ant predation (Gillespie and Reimer 1993).

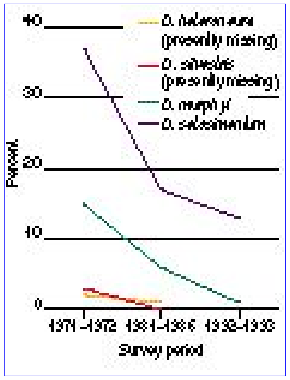


Fig. 31. Long-term trends within one host-specific guild of picture-wing vinegar flies (*Drosophila* species) that breed in rotting bark of native lobelioids (Foote and Carson 1995).

The state of knowledge of Pacific arthropods outside Hawaii is notably inadequate, making even a preliminary assessment of their status very difficult (A. Asquith, U.S. Fish and Wildlife Service, personal communication).

Flowering Plants, Ferns, and Fern Allies

The known Hawaiian vascular flora includes about 1,302 taxa (including species, subspecies, and varieties), of which 1,158 are endemic to Hawaii. About 106 (8%) of these taxa are extinct. An additional 373 taxa (29%) are considered at some risk of becoming extinct in the near future. As of March 1995, Hawaii had 199 plant taxa federally listed as endangered or threatened; this is 38% of the total listed plants nationwide. The Endangered Species Act mandates the U.S. Fish and Wildlife Service to provide for recovery of all listed species, an extremely difficult task because 104 taxa in Hawaii have fewer than 20 known individuals remaining in the wild (Mehrhoff, personal communication).

Some success stories exist for the Hawaiian flora. The most notable may be that of the Haleakala silversword in the Mt. Haleakala crater. Reduced to no more than 4,000 plants in the 1920's and 1930's through human vandalism and goat and cattle browsing, this local endemic has thrived under National Park Service protection and now numbers more than 60,000 (Loope and Medeiros 1995).

Plant endangerment and extinction are also problems throughout the Pacific, but not at the extreme levels found in Hawaii (Mehrhoff, personal communication). Only one plant species, a tree of the Mariana Islands, has been listed as endangered.

Conclusions

"This extraordinary Hawaiian biota would have continued its remarkable adaptive radiation at a rapid rate had man not caused its recent decimation," observes E. C. Zimmerman.

Now a drastic new set of unfavorable conditions faces the delicately adapted biota, and a large fraction of it is doomed to extermination. What the future holds for it we cannot predict, and we shall not know anything like it again. Many of its glorious products, the fruit of ages, have already vanished, and its very mountains are being washed back into the sea from whence they came. (1970)

Fig. 32. Kipahulu Valley, in Haleakala National Park, supports extensive, relatively pristine rain forest vegetation.
Courtesy A. Medeiros, USGS

Much has been written about the tragic destruction and fragmentation of the Hawaiian biota. The extent of the losses (for example, over 70% of endemic land birds and land snail species) is unequaled in any other region of the United States. Hawaii is well known as the extinction capital of the United States, possessing one-third of the species federally listed as endangered. What is not generally appreciated is that much of Hawaii's unique biological heritage remains and can be protected with careful management. Large tracts of near-pristine ecosystems remain at high elevations (Figs. 32 and 33). Even with the high incidence of extinction and endangerment in the Hawaiian Islands, Hawaii has more nonendangered endemic species of vascular plants, birds, and insects than any other state except California. Equally good opportunities exist elsewhere in the Pacific for long-term conservation.

Fig. 33. Cloud forest, East Maui.
Courtesy A. Medeiros, USGS

Degradation of Hawaii's ecosystems has been going on for more than 1,500 years, since the first arrival of Polynesians in the fourth century A.D. Nevertheless, prevention of further invasions and management of existing ones require urgent attention. The movement, establishment, and spread of species to new geographic areas have created enough worldwide havoc to support the emerging view of biological invasions as a major component of global environmental change (D'Antonio and Vitousek 1992). Few areas in the world have suffered such negative effects of biological invasions as Hawaii, yet much remains to be lost. The specter of the establishment of some new devastating nonindigenous species such as the brown tree snake is always on the immediate horizon in the Hawaiian and other Pacific islands. Careful management of the flow of species from the continental United States and from foreign countries is crucial to long-term protection of the natural heritage of all Pacific islands.

More than any other invader, the feral pig is ideally suited to degrade the remaining pristine high-elevation rain forest environments. Feral pigs have spread into formerly pristine areas in recent decades, where they have aided in the establishment of invasive plants and invertebrates. How effectively feral pigs are managed in the coming decades will probably be the major determinant of how much more of Hawaii's near-pristine environments will be irreparably degraded.

Although the Hawaiian biota is relatively well known compared with biota of other Pacific islands, huge gaps in biological information exist throughout the region. For example, many endemic Hawaiian insect and spider species have yet to be discovered and described, as illustrated by Gillespie's recent work with spiders. Almost nothing is known of the ecology and status of most invertebrate species (Howarth and Ramsey 1991). We also need to better understand the implications of the human-caused massive reduction of seabirds and the associated reduction in nutrient cycling from sea to land. Our lack of biological information is not limited to animals. We have only superficial knowledge of factors limiting recovery of the 300 or more endangered, proposed, and candidate plant species of Hawaii. In spite of these knowledge gaps, lack of research is not the major factor limiting management.

Some conservation biologists argue that too much emphasis in the total conservation effort is placed upon research and management of individual rare species. Ultimately, they argue, almost nothing will be safe without active management, given the progressive pervasiveness of feral pigs into Hawaiian forest and the continuing associated onslaught of nonindigenous plants. A more accurate assessment is that the work with rare species is crucial, but much more must be done to protect additional large ecosystem tracts from pigs and weeds if a substantial part of Hawaii's biological diversity is to be preserved. The efforts under way in Hawaii to protect parks and reserves from invasive species, to prevent new invasive species from establishing, and to develop regional (island-by-island) approaches to invasive species management should be strengthened. Continuing research is needed to understand the biology and effects of invasive species, to provide the tools needed to manage the most destructive invasive species and ensure ecological restoration, and to develop and refine conservation strategies.

The surviving natural heritage of Pacific island ecosystems is a unique biological treasure. Because humans introduced invasive nonindigenous species into these ecosystems, this natural heritage is in serious jeopardy. Continuing ecological research and refinement of management strategies have important roles. However, conservation biologists know enough at present to confidently predict that much can be saved in the long run if the political will exists to implement the needed management. The crucial factor limiting conservation of biological diversity in the Pacific seems not to be a dearth of research but the lack of an adequate base of public understanding and support, at both the state and national levels. Ironically, protection of terrestrial biodiversity in Hawaii and the Pacific may be threatened less by economic conflicts than by apathy of a large segment of the public.

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Fig. 1. The three geographic areas of the Pacific, based on ethnicity of the human inhabitants, but also somewhat relevant geologically and biologically (after Oliver 1989).

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Fig. 2. The Hawaiian Islands.

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Fig. 3. Map showing islands produced by a hot spot below the Earth's crust, beginning with the Emperor Seamounts 70 million years ago and actively extending the Hawaiian chain at present. The numbers alongside the islands are ages in millions of years (© University of Hawaii Press).

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Fig. 4. The impressive adaptive radiation in Hawaiian honeycreepers.

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Fig. 5. Number of immigrant invertebrates reported in Hawaii, 1961-1991. Adapted from graphic by The Nature Conservancy of Hawaii and the Natural Resources Defense Council (1992); data were extracted from the Proceedings of the Hawaiian Entomological Society.

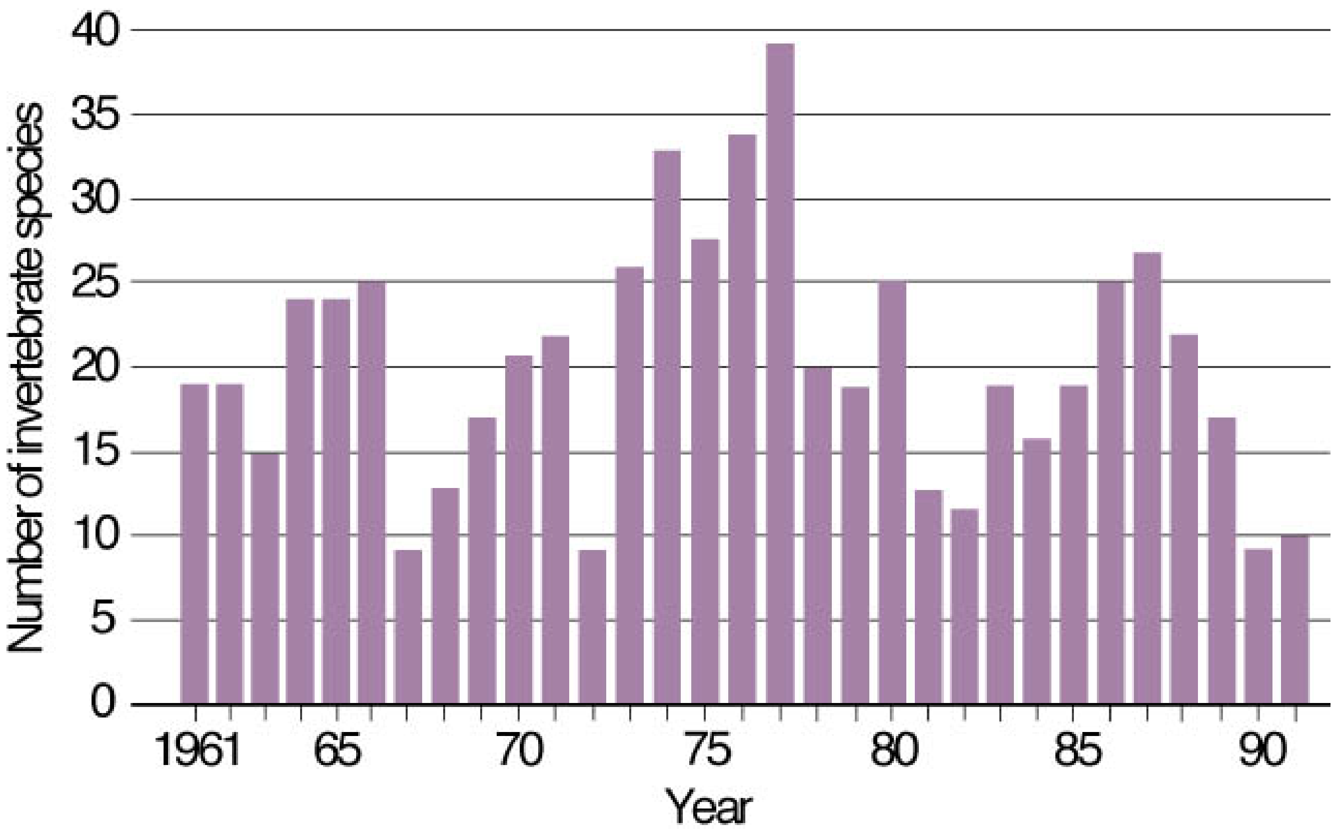

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Fig. 6. *Haleakala schiedia*, endemic to Haleakala Crater, survives only on ledge or cliff faces out of the reach of feral goats.

Courtesy A. Medeiros, USGS

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Fig. 7. Feral goats in Hawaii Volcanoes National Park before boundary fencing and control implemented in the 1970's.

Courtesy B. Harry, National Park Service

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Fig. 8. Fencing constructed in the 1980's has eliminated goats within Haleakala National Park and allowed partial recovery of native vegetation.

Courtesy A. Medeiros, USGS

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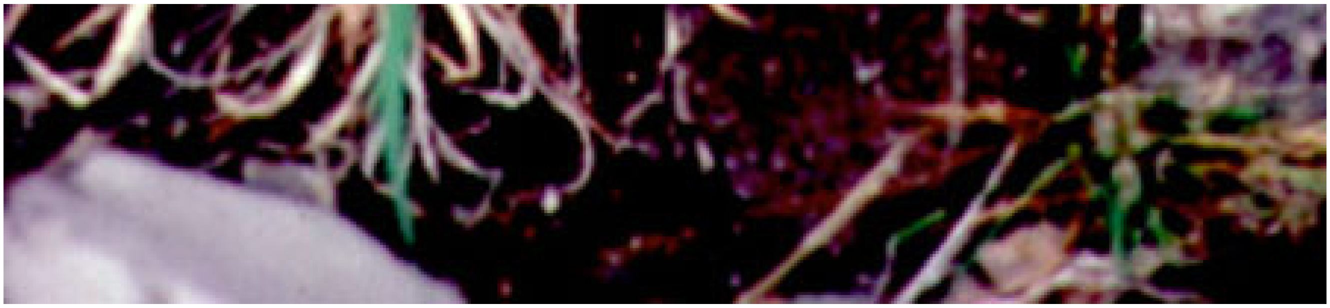
Fig. 9. Reproduction of *Lysimachia kipahuluensis,* an East Maui endemic, in western Kaupo Gap, an area of Haleakala National Park where it was once eliminated (except on ledges and cliff faces) by feral goats.



Courtesy A. Medeiros, USGS

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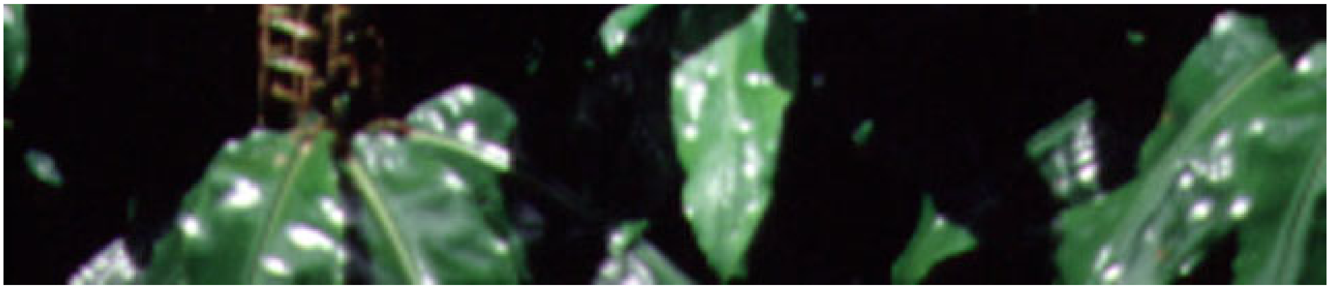
Fig. 10. Dense growth of kahili ginger in Kipahulu Valley, Haleakala National Park, Maui.



Courtesy A. Medeiros, USGS

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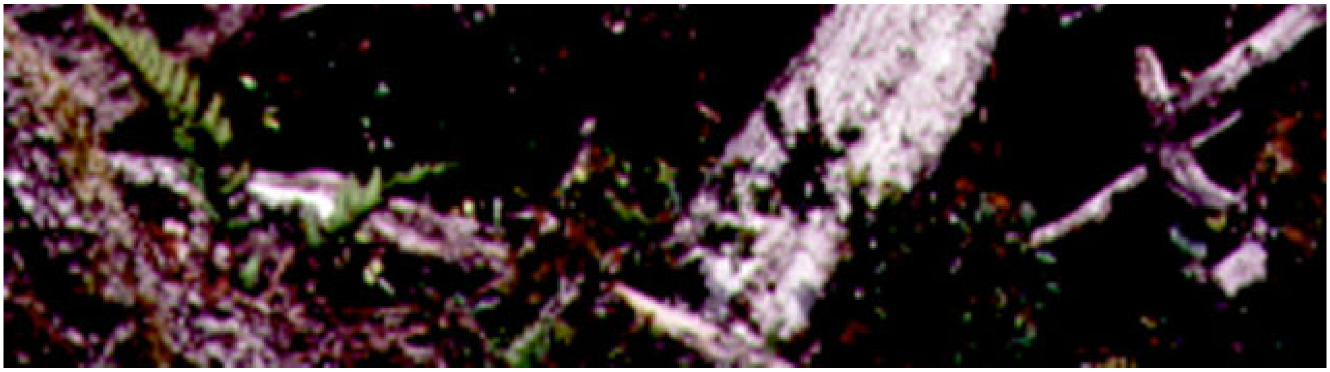
Fig. 11. Downed trunks of ohia, Alakai Swamp, Kauai, September 1983. Severe hurricanes have affected Hawaiian Island forests in recent years only on the island of Kauai. Forest openings caused by the 1982 and 1992 hurricanes on Kauai have greatly accelerated invasion by nonindigenous plant species.



Courtesy A. Medeiros, USGS

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Fig. 12. Nearly monospecific cover of the Neotropical tree miconia on slopes of Vaihiria Valley, Tahiti, French Polynesia, in June 1994. Invasion of this species has eliminated much of the biodiversity on that island.

Courtesy A. Medeiros, USGS

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Fig. 13. Dense patch of miconia seedlings near Hana, Maui, Hawaii.

Courtesy A. Medeiros, USGS

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Fig. 14. Extensive monospecific stands of uluhe exist in the montane wet zones of all islands. Extensive uluhe dieback caused by the two-spotted leafhopper has occurred since 1990 on Oahu and Kauai and is also present on Maui.

Courtesy A. Medeiros, USGS

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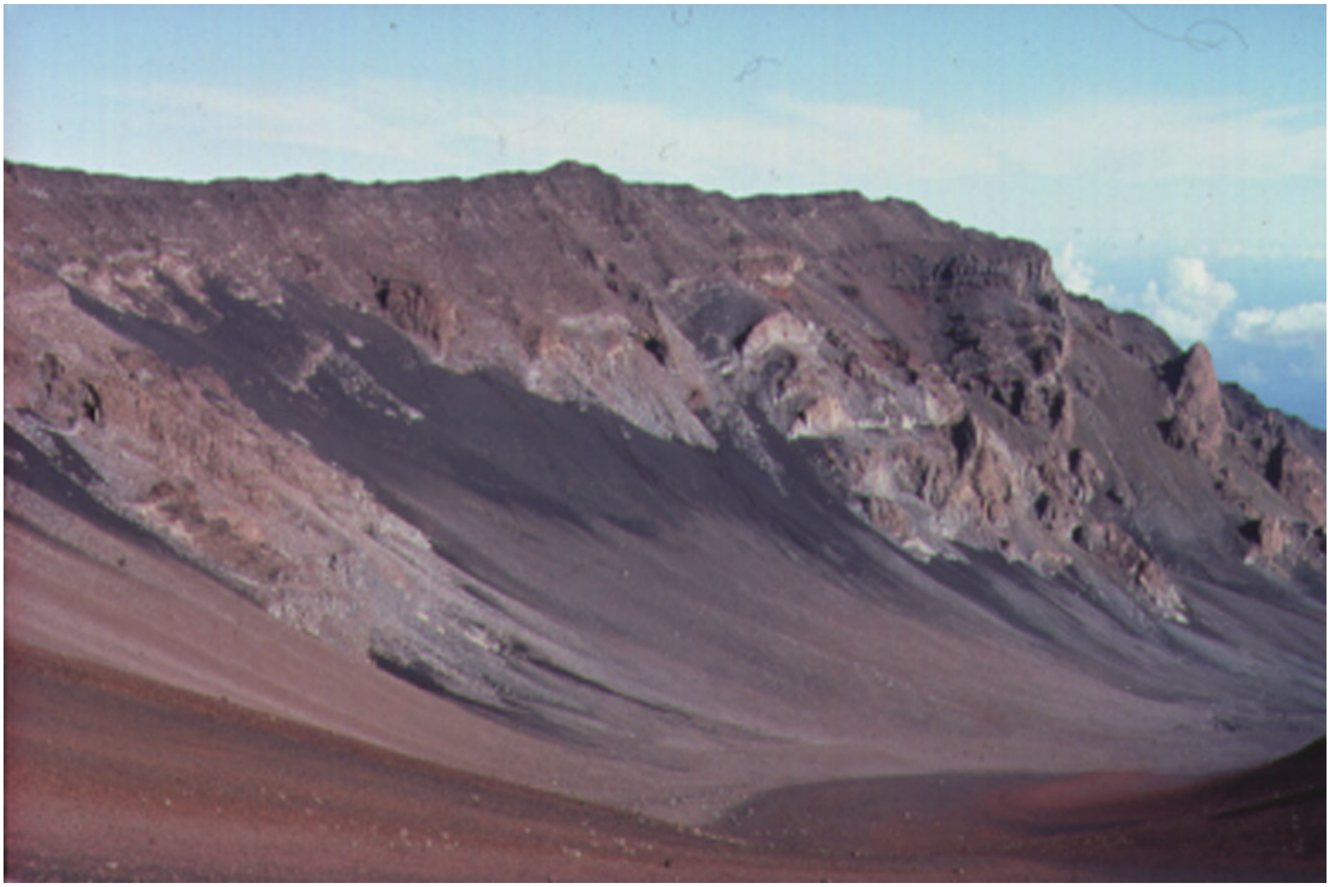
Fig. 15. Inner cliffs of Haleakala Crater provide a relatively secure habitat for the endangered Hawaiian dark-rumped petrel or uau. Once common throughout the Hawaiian Islands, this seabird now nests primarily in deep burrows dug in cinder along cliffs on the upper slopes of Haleakala volcano.



Courtesy A. Medeiros, USGS

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Fig. 16. The chick of the rarely seen endangered Hawaiian dark-rumped petrel.

Courtesy J. W. Larson, National Park Service

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Fig. 17. This strange-looking flightless lacewing had not been collected since 1945, until rediscovered by Steve Montgomery in October 1994. This remarkable species is known from only a small area near the summit of Haleakala volcano at 2,900 meters elevation.

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Fig. 18. Pristine bog vegetation, windward East Maui, at 1,860 meters elevation, before feral pig impacts. Dominant species are Hawaii Island sedge and prickly sedge. Broad-leaved Maui plantain is conspicuous. By 1981, when this bog was fenced, digging by feral pigs had removed 95% of the vegetation cover. By 1984, the dominants had recovered, but plantain was nearly eliminated and remains rare today.

Courtesy J. Jacobi, USGS

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Fig. 19. Feral pig, Hawaii Volcanoes National Park.

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Fig. 20. Graph showing invasion of nonindigenous plants resulting from pig damage to montane bog sites on East Maui, 1982-1988 (from Medeiros et al. 1991).

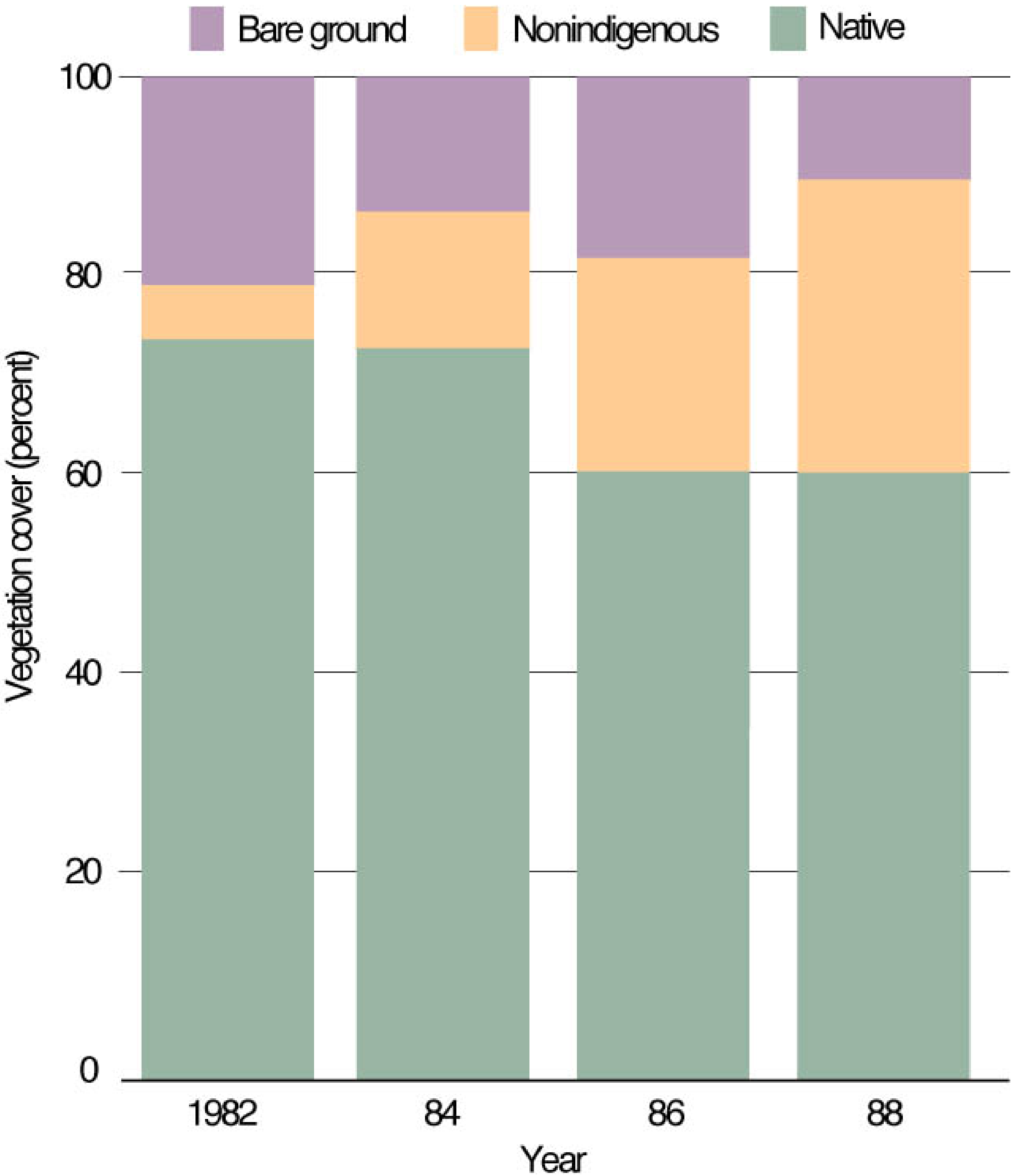

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Fig. 21. Maui greensword in a montane bog at 1,890 meters elevation, windward East Maui. Feral pigs directly damage greensword plants and their habitat by promoting dispersal and establishment of nonindigenous plant species.

Courtesy B. Gagné, Hawaii Department of Land and Natural Resources

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Fig. 22. Undisturbed forest in Auwahi, with an understory of kikuyu grass, a nonindigenous species.

Courtesy A. Medeiros, USGS

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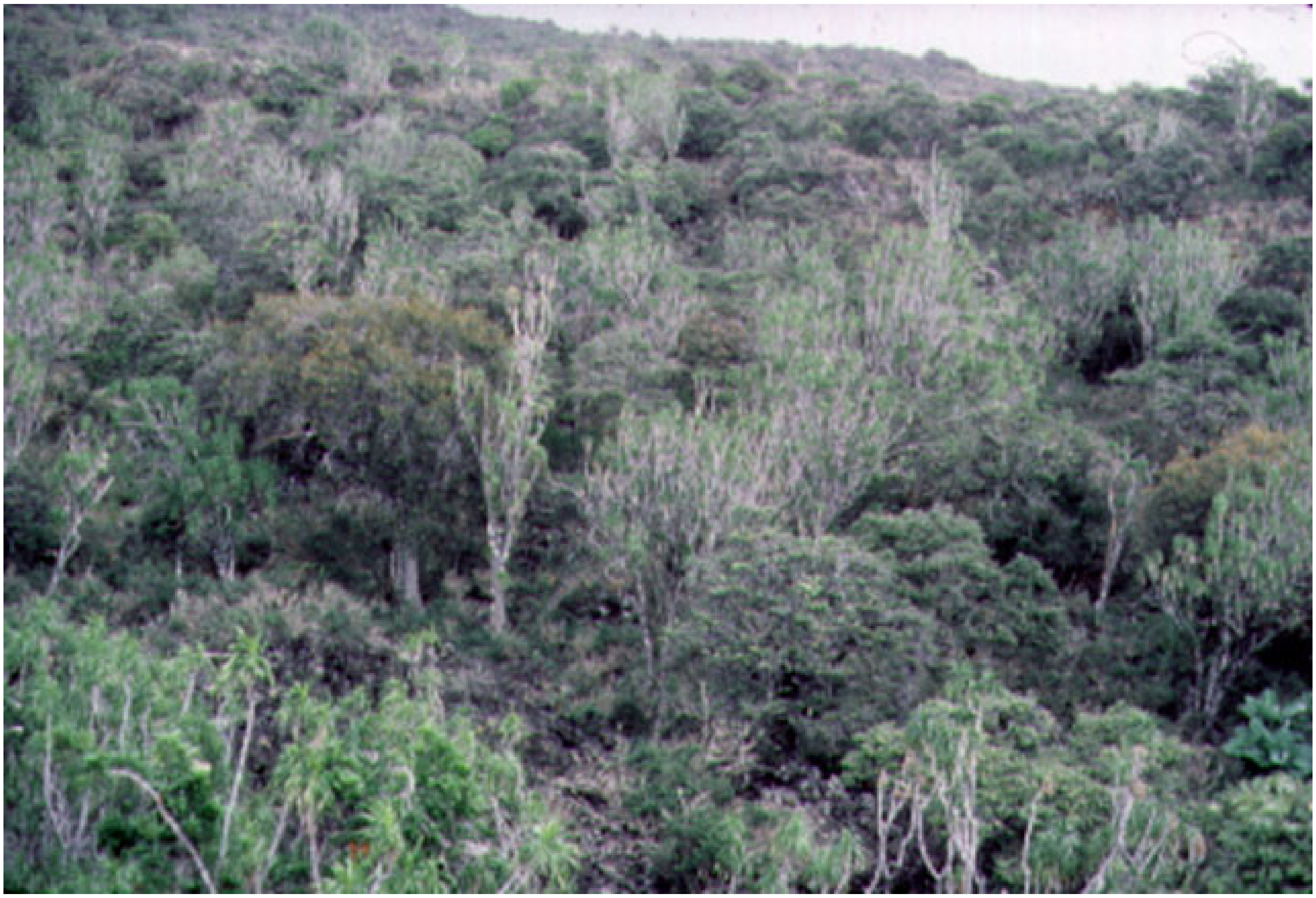
Fig. 23. Relatively intact dryland forest of Kanaio Natural Area Reserve, East Maui, elevation 800 meters. Dominant trees are lama and Maui hale pepe.



Courtesy A. Medeiros, USGS

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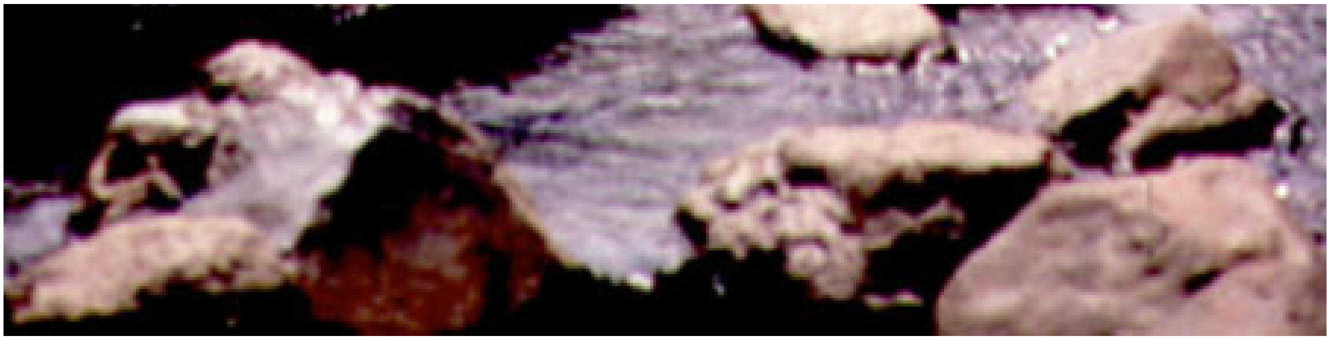
Fig. 24. Hawaiian stream habitat.



Courtesy A. Medeiros, USGS

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Fig. 25. Iiwi.

Courtesy J. Jeffrey, U.S. Fish and Wildlife Service

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Fig. 26. Poo-uli.

Courtesy P. Baker, USGS

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Fig. 27. Oopu alamoo.

Courtesy M. Yamamoto, Hawaii Department of Land and Natural Resources

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Fig. 28. *Achatinella* tree snail, Oahu.

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Fig. 29. *Euglandina rosea* (top image is printed actual size).

a.

Courtesy R. Hue, Hawaii Department of Agriculture

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b.

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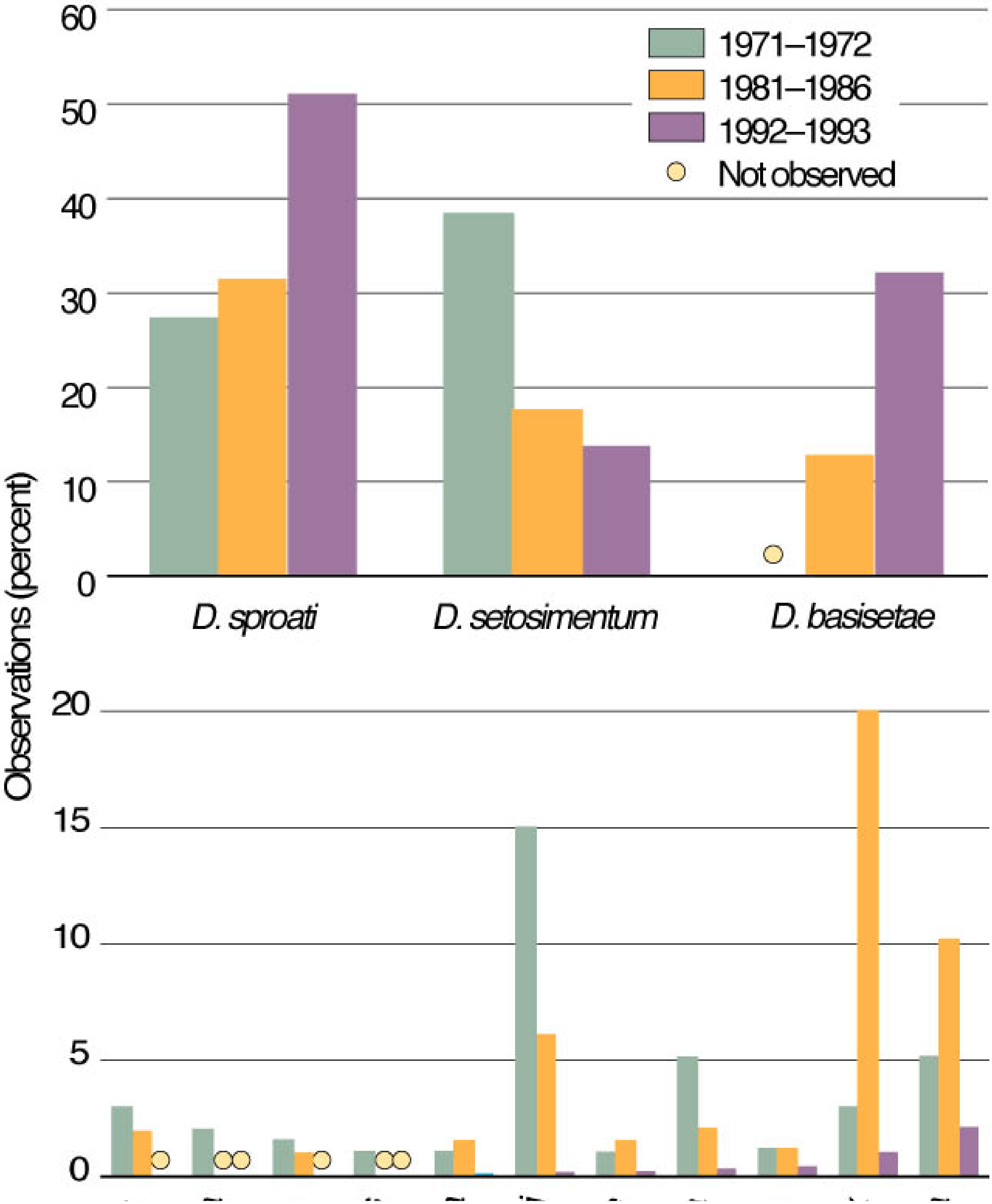
Fig. 30. A comparison of the relative frequencies of 14 endemic species of picture-wing vinegar flies *(Drosophila* species) over three periods of observation from 1971 to 1993 in Olao Rain Forest in Hawaii Volcanoes National Park. The data are expressed as a percentage of total observations within a survey period (Foote and Carson 1995).



D. setosifrons

D. heteroneura

D. silvestris

D. hawaiiensis

D. ochracea

D. murphyi

D. daytonae

D. digressa

D. rolaticilia

D. macrothrix

D. paucipuncta

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Fig. 31. Long-term trends within one host-specific guild of picture-wing vinegar flies (*Drosophila* species) that breed in rotting bark of native lobelioids (Foote and Carson 1995).

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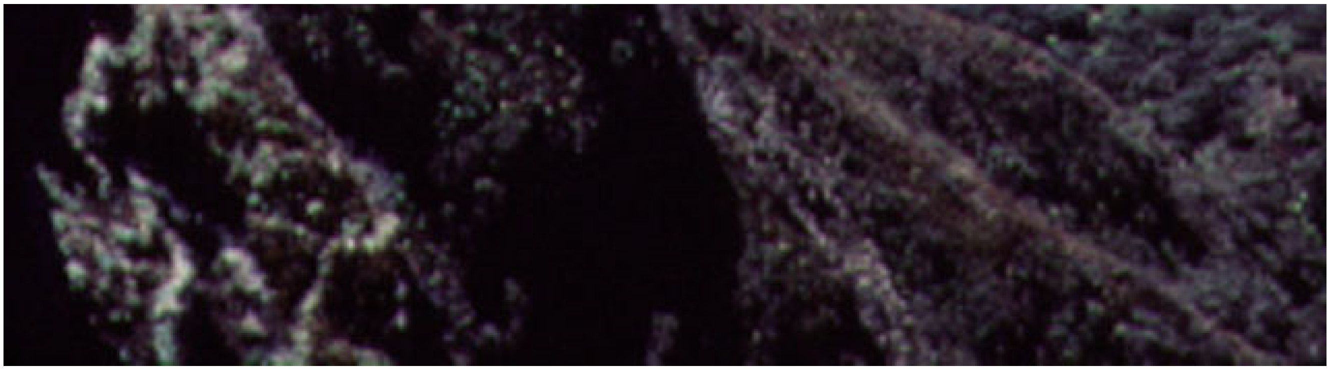
Fig. 32. Kipahulu Valley, in Haleakala National Park, supports extensive, relatively pristine rain forest vegetation.



Courtesy A. Medeiros, USGS

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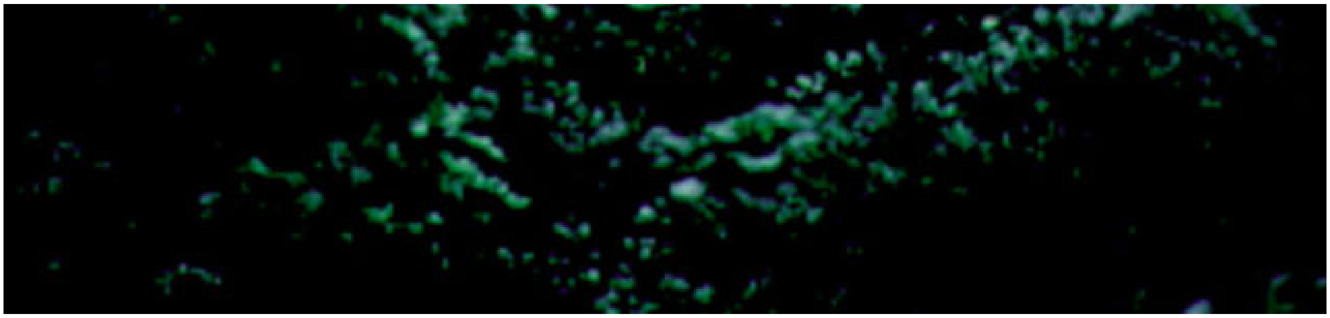
Fig. 33. Cloud forest, East Maui.



Courtesy A. Medeiros, USGS