VEGETATION OF THE HAWAIIAN ISLANDS

The vegetation of the Hawaiian Islands is relatively complex, often varying greatly over short distances. Recent classification attempts have recognized between 86 (Gagné and Cuddihy, in press) and 152 different plant communities (The Nature Conservancy of Hawaii 1987). This very large number of distinct communities in a small geographic area may be attributed to the great differences in rainfall, substrate, exposure, and topography that occur on each of the main Hawaiian Islands. In some cases, distinctions among communities may be partly an artifact of past disturbance, which has resulted in the disjunction and isolation of relictual stands of native vegetation formerly continuous over large areas.

Vegetation Classification Systems

Existing plant communities may be classified into broader vegetation zones based on one or more factors, such as elevation, moisture regime, substrate, topography, floristics, and plant physiognomy. Many such classification schemes have been developed to explain observed vegetation patterns in the Hawaiian Islands, the first by Gaudichaud-Beaupré in 1819 (St. John and Titcomb 1983; Jacobi, in press a). Since then, many botanists have produced new classification systems for Hawai'i or have refined earlier ones; 20 different Hawaiian vegetation classifications were compared and contrasted by Selling (1948). More recently, major systems were reviewed in depth by Jacobi (in press a).

Two important classification systems of the late 18th and early 19th century were those of Hillebrand (1888) and Rock (1913); both authors used their extensive field experience to classify observed vegetation into elevational zones. Rock also used climate and topography to characterize zones, for which he provided detailed floristic descriptions.

Perhaps the most widely used vegetation classification of the last several decades is that of Ripperton and Hosaka (1942), who produced a map of the main Hawaiian Islands with 10 zones based on elevation, topography, rainfall, and existing vegetation. Their zones were based on field sampling and emphasized differences in moisture regime (Jacobi, in press a). For more than 40 years, this classification of Hawaiian vegetation was generally adopted by most writers and was the basis of many subsequent modifications. A notable refinement of Ripperton and Hosaka's system was the biogeoclimatic zonation scheme developed by Krajina (1963), who incorporated edaphic factors and additional climate variables to distinguish 14 zones, each with a number of native or alien plant indicators.

Single-island classification systems have also been developed. The vegetation of O'ahu and Hawai'i has been the particular focus of several such efforts. Egler (1939) used moisture as a distinguishing environmental factor and recognized six vegetation zones on O'ahu. Egler did not base his classification on elevation or physiognomy, which was considered by Jacobi (in press a) to be a "significant departure from earlier classification systems." Hawai'i Island vegetation zones (or plant formations) were

described and mapped by Robyns and Lamb (1939), who stressed the physiognomy of vegetation in their system (Jacobi, in press a). The zonation pattern of Robyns and Lamb appears very similar in outline to the Hawai'i map of Ripperton and Hosaka, but the former more thoroughly described existing natural vegetation.

Region-specific vegetation classifications were developed for Mauna Kea, Mauna Loa (Mueller-Dombois and Krajina 1968) and Hawaii Volcanoes National Park (Mueller-Dombois 1966). Both studies used extensive ground observations and photo-interpretation to produce profile diagrams detailing actual vegetation types in zones delimited by climate, elevation, and in some cases, substrate.

Most recently, Jacobi (in press b) developed a vegetation classification for the Hawaiian Islands in conjunction with a large-scale bird survey and mapping project (Scott et al. 1986). Emphasizing climate, with elevation secondary, Jacobi recognized 14 major vegetation (or "habitat") zones, each with one or more physiognomic subunits (e.g., grassland, shrubland, forest). The Nature Conservancy of Hawaii (1987) drew heavily on Jacobi's classification system in the organization of its natural community database, as did Gagné and Cuddihy (in press) in their synopsis of Hawaiian vegetation.

The following general discussion of natural vegetation of the Hawaiian Islands follows Jacobi's outline of vegetation zones and physiognomic units as modified by Gagné and Cuddihy and incorporates descriptions and locality information from both The Nature Conservancy of Hawaii (1987) and Gagné and Cuddihy (in press). Five elevational regions are recognized: coastal; lowland, with an upper limit between 500 m (1,640 ft) and 1,000 m (3,280 ft) elevation; montane (500-1,000 m to 2,000 m (6,560 ft) elevation); subalpine (> 2,000 m to 2,800 m (9,180 ft) elevation); and alpine (> 2,800 m). Within these, vegetation is categorized by moisture regime: dry, less than 1,250 mm (50 in.) annual precipitation; moist or mesic, 1,250-2,500 mm (50-100 in.); and wet, > 2,500 mm (100 in.) annual rainfall. Finally, five physiognomic types are used, based on the dominant plant life form: grassland, shrubland, forest, open forest, and parkland. Major vegetation zones of the windward sides of the Islands are presented first, starting at the coast and proceeding upslope to the summits; then lowland and montane zones of the leeward regions are discussed (Cuddihy 1989).

The original vegetation cover of the Hawaiian Islands prior to the arrival of the Polynesians may be inferred from existing vegetation, remnants in disturbed areas, patterns of climate and substrates, and a few fossilized remains. Forests were and are the natural vegetation of most of the main Hawaiian Islands. On the six Hawaiian Islands with elevations exceeding 1,000 m (3,280 ft), the climate "promotes forest development" except in the alpine zone and the driest parts of the leeward lowlands (Mueller-Dombois 1987). Today, wet forests and shrublands still occur on the windward slopes of the two highest main Islands (Hawai'i, Maui) over a large elevational range and at upper elevations of the islands of Kaua'i, O'ahu, Moloka'i, and Lāna'i. Dry grasslands and shrublands are prominent on the leeward sides of all the Hawaiian Islands; without disturbance, many of these would naturally have been forests. Mesic communities occur on leeward slopes transitional between wet and dry areas, in rain shadows caused by orographic interception, or at elevations above a temperature inversion layer on the higher Islands, usually between 1,525 and 2,135 m (5,000-7,000 ft) elevation (Blumenstock and Price 1967). Subalpine and alpine communities are found on the highest islands of Maui and Hawai'i and are basically dry or mesic types of vegetation. Two of the eight main Islands, Ni'ihau and Kaho'olawe, are here considered "low" islands because they contain only coastal and lowland vegetation. (Lāna'i,

lowest of the six main "high" Islands, has a small amount of montane vegetation.) The Northwestern Hawaiian Islands are also low islands; their vegetation is not treated in this volume.

Coastal Vegetation

The coastal zone is a relatively narrow belt encircling each main Island, where vegetation is strongly influenced by the ocean. Coastal communities have been severely altered by humans, and the remaining natural vegetation in this zone is limited in area. Where native plants have not been replaced by alien species, *naupaka-kahakai (Scaevola sericea)* shrubs are often the dominant cover of the strand. Beach morning glory (*Ipomoea pes-caprae*), beach dropseed *(Sporobolus virginicus), pā'ū o Hi'iaka (Jacquemontia ovata)*, and *'ākulikuli* or sea purslane (*Sesuvium portulacastrum*) are also relatively common in remaining strand communities. In some sites, native plants such as *'ilima (Sida fallax), naio (Myoporum sandwicense), hinahina (Heliotropium anomalum)*, and *nehe* (*Lipochaeta* spp.) may be locally abundant and even co-dominant with the naupaka. While many remnant strand communities are species poor, the less disturbed coastal sites such as Mo'omomi Beach on Moloka'i support a rich assemblage of native plants, including very rare species such as *'ohai (Sesbania tomentosa)*. Vegetation of basaltic shores, cliffs, talus slopes, and coral substrates is also frequently dominated by naupaka (Richmond and Mueller-Dombois 1972), often with the addition of *'akoko (Chamaesyce celastroides), maiapilo (Capparis sandwichiana)*, and native sedges and grasses. Many rocky shores have a distinct spray zone community of native sedges and shrubs. On windward Maui and Moloka'i (at least), this spray zone vegetation consists of low-growing *'ākia* (*Wikstroemia* spp.), 'akoko, and *hinahina (Heliotropium curassavicum)* with the sedge *Fimbristylis cymosa.* A species-poor version of this, often supporting only *Fimbristylis*, is common on Hawai'i Island.

Coastal shrub communities dominated by natives other than naupaka may be seen as remnants, particularly in less developed, more remote shores of the Islands. Notable among these are shrublands of Hawaiian cotton or *ma'o (Gossypium tomentosum)*, 'ilima, and naio, all of which extend somewhat upslope away from the coast. Extrapolating from existing native plants, Char and Balakrishnan (1979) proposed that thickets of naio and the endangered *Achyranthes rotundata* were important in the original vegetation of rocky coral substrates of Barbers Point. It is highly likely that other coastal shrublands existed in pre-human Hawai'i, for which remnants no longer exist.

Extant coastal forests occur on some windward shores of Kaua'i, Maui, O'ahu, Moloka'i, and Hawai'i. Most often seen are forests dominated by the indigenous *hala (Pandanus tectorius)*. However, the understory of hala forests is usually dominated by Polynesian introductions and alien plants. Atkinson (1970), in a study of succession on dated substrates in the Puna District, island of Hawai'i, observed that hala forests were the dominant cover only on flows greater than 200 years in age, although young hala trees could be seen in *'ōhi'a* (*Metrosideros polymorpha*)-dominated vegetation of younger flows. Forests and shrublands of the indigenous *hau (Hibiscus tiliaceus)*, generally mixed with some introduced trees, are seen in wet, sheltered, windward sites (Richmond and Mueller-Dombois 1972). In a few sites on the islands of Moloka'i and Hawai'i, forests dominated by 'ōhi'a and *lama (Diospyros sandwicensis)* occur down to the shoreline. Other coastal areas were forested with *loulu* palms (*Pritchardia* spp.). Remnants of such palm forests may still be seen on Huelo Seastack, an islet off the northern coast of Moloka'i, as well as on nearby sea cliffs.

Impressions of loulu trunks may be found in the coastal lavas of the Puna District on Hawai'i Island in areas today devoid of such palms. Evidence for the former widespread occurrence of loulu forests has also been found on O'ahu, where fossil remains of the palm were discovered near Salt Lake (Āliapa'akai) (Lyon 1930). Disjunct stands of loulu still grow in a few upslope localities on both O'ahu and Kaua'i. On uninhabited Nihoa, northwest of Kaua'i, a species of loulu (*P. remota*) is a prominent component of vegetation in two valleys of the small island (Conant 1985).

Windward Zones

Prevailing northeasterly trade winds bring moisture-laden air to the northeast-facing slopes of the main Islands. With increasing elevation, air temperature decreases and water precipitates out on windward slopes and some summit areas, resulting in several zones as follows.

Lowland Wet Forests. Wet forests were undoubtedly the predominant original vegetation of the windward lowlands on the larger main Islands (Zimmerman 1948). However, by the late 18th century when European explorers and botanists began to arrive in Hawai'i, the lowland wet zone was primarily a cultivated region (Menzies 1920; Cook 1967). Where lands cultivated by Hawaiians were not subsequently used for agriculture, grazing, or urban development, they were invaded by species of Polynesian introduction, particularly *kukui (Aleurites moluccana)*, or by later introductions such as common guava (*Psidium guajava*). Therefore, most windward valleys and gently sloping tablelands do not support natural forest vegetation, even though many such areas have not been cleared or developed in the last 150 years. The wet lowland zone characterized by Ripperton and Hosaka (1942) makes up over 10% of the five largest Hawaiian Islands, and wet vegetation of all elevations constitutes about one-third of their area. However, because of long-term anthropogenic disturbance, lowland wet vegetation is particularly difficult to reconstruct and characterize, especially on the older, more dissected Hawaiian Islands like O'ahu (Jacobi, in press b).

Natural lowland rain forests may still be seen in regions with rocky substrates or steep terrain. Examples of these forests occur on peaks and lower summit ridges of O'ahu; ridges and *pali* (cliffs) on Kaua'i, Moloka'i, West Maui, and the Kohala Mountains of Hawai'i Island; and in undeveloped slopes of Puna and Hilo Districts on the island of Hawai'i. The most widespread existing lowland forest type is dominated by *'ōhi'a (Metrosideros polymorpha)*, often with an understory of native trees such as *kōpiko* (*Psychotria* spp.) and *hame (Antidesma platyphyllum)*. The endemic liana *'ie'ie (Freycinetia arborea)* is often abundant in these forests. In the upper reaches of the lowland 'ōhi'a forest on the island of Hawai'i, the understory is dominated by tree ferns or *hāpu'u (Cibotium chamissoi, C. glaucum)*, which form a distinct, closed layer beneath the trees.

A more open 'ōhi'a forest with other scattered native trees and a dense ground cover of the indigenous mat-forming *uluhe (Dicranopteris linearis)* and other related ferns (*Diplopterigium pinnatum, Sticherus owhyensis*) is seen on steep ridges and valley walls of Kaua'i, O'ahu, Moloka'i, Maui, and the Kohala Mountains of Hawai'i Island. This community also covers large expanses of relatively young substrates in the Puna District. Less abundant in Puna is an open 'ōhi'a forest in which *lama (Diospyros sandwicensis)* is a co-dominant. Remnants of this type of forest also occur on steep terrain on windward East Moloka'i, northwestern Kaua'i, and the lower windward slopes of the Kohala Mountains.

In pre-Polynesian times, a lowland wet forest dominated by *koa (Acacia koa)* was probably widespread below 1,000 m (3,280 ft) elevation on the larger Islands in windward areas with deep soils. Such a forest still exists in Kīpahulu Valley of windward East Maui, although it probably extended farther downslope before it was subjected to disturbance. Evidence for a lowland koa forest may also be seen on ridges of Hālawa Valley, Moloka'i (Kirch and Kelly 1975). Skolmen (1986a) speculated that a band of lowland koa forest occurred on the island of Hawai'i all along the Hāmākua coast between 305 and 610 m (1,000-2,000 ft) elevation (above the area used for agriculture by the Hawaiians); remnants of this are visible in a few localities.

Montane Wet Forests and Bogs. The boundary between the lowland and montane wet forests in Hawai'i is not generally agreed upon by all botanists and ecologists, and it may be variable on the different Islands. In any case, a clear picture of prehuman vegetation is complicated by the extreme disturbance the lowlands have suffered. Jacobi (in press b) used 1,000 m (3,280 ft) elevation to divide the two windward zones on Hawai'i Island, but many other classifiers of Hawaiian vegetation place this boundary much lower, generally between 460 m (1,500 ft) and 730 m (2,400 ft) elevation (Hillebrand 1888; Rock 1913; Robyns and Lamb 1939; Ripperton and Hosaka 1942; Krajina 1963).

Wet montane forests still cover relatively large expanses on the islands of Maui and Hawai'i and are also found on the steep windward slopes, ridges, and peaks of Kaua'i, O'ahu, and Moloka'i. In his reconstruction of original vegetation, Jacobi (in press b) mapped more than 150,000 ha (370,500 a) of native wet forests above 500 m (1,640 ft) elevation on Hawai'i Island alone. Extrapolation from Ripperton and Hosaka's (1942) generalized vegetation maps results in about the same amount of montane rain forest (146,000 ha or 360,620 a) for the islands of Maui, Moloka'i, O'ahu, and Kaua'i combined. Most of these forests are dominated by *'ōhi'a* (*Metrosideros polymorpha*) in a closed canopy with a well-developed understory of mixed native tree species, shrubs, and tree ferns (*Cibotium* spp.). Tree ferns often comprise a very dense layer in some montane forests of Hawai'i Island.

'Ōlapa (*Cheirodendron* spp.) is often co-dominant with 'ōhi'a in low-statured, wind-stunted forests of peaks and ridges, areas almost continually brushed by clouds. These cloud forests occur on Kaua'i, O'ahu, Moloka'i, West Maui, and in the Kohala Mountains of Hawai'i. A dense cover of gnarled trees, abundant epiphytes (particularly mosses and liverworts), and a diversity of small native trees, shrubs, and ferns are characteristic of this vegetation (Fosberg 1972). On the older islands such forests may contain several species of *'ōhi'a* (*Metrosideros polymorpha, M. tremuloides, M. rugosa*).

On other steep montane slopes, the 'ōhi'a forest is more open, and *uluhe* (*Dicranopteris linearis*) and related ferns are the ground cover. On the island of Hawai'i, wet montane forests (above 1,000 m) with a significant uluhe component cover only 4,000 ha (9,880 a); this type of vegetation is much more common at lower elevations (Jacobi, in press b).

Less common are wet montane forests with tall *koa* (*Acacia koa*) emergent above a closed canopy of 'ōhi'a. For the island of Hawai'i above 500 m (1,640 ft) elevation, Jacobi (in press b) mapped wet koa/'ōhi'a forests over less than 35,000 ha (86,450 a). This type of forest may once have occurred in a discontinuous band on windward slopes of Mauna Kea, Hualālai, and both windward and leeward slopes of Mauna Loa,

as well as on the windward slopes of Haleakalā, East Maui (Skolmen 1986a). While much reduced through clearing, logging, and ranching activities, a few good examples of this species-rich type of rain forest remain on both Maui and Hawai'i (Smathers 1967; Cooray 1974).

Wet shrublands of the montane zone are found on steep valley walls, cliffs, and ridge crests of all the higher Islands. These may be dominated by stunted 'ōhi'a and other components of nearby forests, or on very steep slopes by native ferns, particularly *'ama'u* (*Sadleria* spp.).

Another type of montane wet community is represented by bogs, which occur on most of the high Hawaiian Islands. Bogs, generally small in area, are found in very wet, poorly drained places near mountain summits on Kaua'i, O'ahu, Moloka'i, and West Maui (Selling 1948; Carlquist 1980); on high-rainfall windward slopes of East Maui (Loope et al., in press a); and on windward slopes of the Kohala Mountains, Mauna Kea, and Mauna Loa on Hawai'i Island (Jacobi, in press b). They are characterized by sedges and grasses (*Oreobolus furcatus, Carex* spp., *Rhynchospora* spp., *Dicanthelium* spp.) and stunted woody plants including 'ōhi'a, *pilo (Coprosma ochracea)*, and *na'ena'e* (*Dubautia* spp.). A diversity of unusual bog-tolerant plants occurs here: greenswords *(Argyroxiphium grayanum), lau-kāhi* (*Plantago* spp.), the diminutive, daisy-like *Lagenophora viridis*, the striking, fleshy-trunked lobelias of Maui and Kaua'i (*Lobelia gloria-montis, L. kauaensis, L. villosa*), the fragile clubmoss *Selaginella deflexa*, and endemic violets (*Viola maviensis, V. robusta*, and others). Each bog, however, is distinct and contains a unique assemblage of native plants. Bogs of the Alaka'i Swamp on Kaua'i were recently studied by Canfield (1986), who recognized three distinct plant communities based on species composition, life form, and structure. A comprehensive and detailed description of the botanically rich bogs of East Maui has been completed by Loope et al. (in press a). One unique high-elevation East Maui bog surrounded by *Deschampsia* grassland was characterized as "alpine" by Vogl and Henrickson (1971) but has much in common with its lower-elevation neighbors.

In addition to small open or raised bogs, the windward slopes of Mauna Kea on the island of Hawai'i contain large expanses of a very wet 'ōhi'a community that has been described as "bog-formation dieback." In very old, water-soaked soils, stands of 'ōhi'a trees undergo dieback and are replaced by low 'ōhi'a shrubs and sedges (Mueller-Dombois 1986).

Based on pollen analysis from upland bogs, Selling (1948) determined that the area covered by rain forest in the montane zone fluctuated with climatic change in the late quarternary period. Selling recognized three periods prior to the present, with the greatest extension of the montane rain forest occurring during the second period. The most important rain forest constituents of this period (based on pollen samples) correspond well with typical dominants found at present in montane wet forests: *Metrosideros*, *Myrsine*, *Cheirodendron*, *Cibotium*, and *Coprosma*. Selling's third period, in which the rain forest retreated and was replaced in some areas by drier vegetation types and plants more typical of subalpine areas, corresponds to the period of Polynesian occupation of the Islands.

Montane Moist Forests and Parkland. Moist or mesic forests occur in the upper montane zone on the islands of Maui and Hawai'i, where they are found on the edges of orographic rain shadows, on windward slopes of mountains near the temperature inversion

layer, and on upper leeward slopes. These forests differ from wet forests in the relative scarcity of tree ferns (*Cibotium* spp.) and epiphytes, the abundance of shrubs such as *pūkiawe* (*Styphelia tameiameiae*) in the understory, and a different complement of native ferns in the ground cover. For most of these forests the dominant trees are either *ʻōhiʻa (Metrosideros polymorpha), koa (Acacia koa),* or a mixture of these two species. In a very few sites, *mānele (Sapindus saponaria)* is a co-dominant species in the koa/ʻōhiʻa canopy. Montane mesic forests have a very restricted distribution and together amount to just slightly more than 50,000 ha (123,500 a) above 1,000 m (3,280 ft) on the island of Hawaiʻi; the koa/ʻōhiʻa mixed forests are important endangered bird habitat and are extremely vulnerable to disturbance (Jacobi, in press b). Maui and Kauaʻi each have only a few thousand hectares of mesic montane forest (Ripperton and Hosaka 1942).

Drier parklands or open woodlands of low, spreading koa and *māmane (Sophora chrysophylla)* trees with native shrubs and grasses were formerly common in the transition area between wet forests and the subalpine zone, at least on the island of Hawaiʻi. Protected examples of such "mountain parklands" have been described in detail by Robyns and Lamb (1939) and Mueller-Dombois (1966, 1967). Jacobi (in press b) has mapped approximately 30,000 ha (74,100 a) of this type of vegetation on the island of Hawaiʻi.

Subalpine Vegetation

The high mountains of East Maui (Haleakalā) and Hawaiʻi (Mauna Kea, Mauna Loa, Hualālai) support extensive native subalpine ecosystems above 2,000 m (6,560 ft) elevation. Most of the plant communities of this zone are dry; grasslands, shrublands, and forests are all represented here. Subalpine grasslands are dominated by the endemic bunchgrass *Deschampsia nubigena.* In cindery substrates such as the upper slopes of Mauna Kea and within Haleakalā Crater, grasslands are relatively dry. More mesic examples of *Deschampsia* grassland occur on the windward slopes of Haleakalā, which are frequently covered by moisture-bearing clouds.

Dry shrublands of the upper mountain slopes are most often dominated by *pūkiawe* (*Styphelia tameiameiae*) and *ʻōhelo (Vaccinium reticulatum),* but *ʻaʻaliʻi (Dodonaea viscosa)* and *naʻenaʻe (Dubautia ciliolata)* may also be important components. Frequently, very scattered *ʻōhiʻa (Metrosideros polymorpha)* trees are found here. A distinctly different dry shrubland composed primarily of *ʻāweoweo (Chenopodium oahuense)* occurs on ashy substrates in the saddle between Mauna Loa and Mauna Kea on Hawaiʻi Island. This shrubland may, at least in some areas, represent former subalpine forest degraded by feral animals, fire, and the activities of humans at a nearby military training camp.

Mesic shrublands dominated by *ʻōhelo* (*Vaccinium* spp.) and *ʻamaʻu* fern (*Sadleria cyatheoides*) are found on the steep upper slopes of East Maui, sandwiched between wet forests and mesic grasslands. The Haleakalā Crater area supports a community of very scattered silversword plants (*Argyroxiphium sandwicense* subsp. *macrocephalum*) and *naʻenaʻe (Dubautia menziesii),* primarily on cinder cones (Loope and Crivellone 1986). A similar community once occurred on Mauna Kea, where silverswords (subsp. *sandwicense*) were so common that the dry leaves and stems were used as fuel for campfires (Douglas 1914). Feral ungulates have nearly exterminated the silversword on Mauna Kea.

Forests of the subalpine zone are relatively dry; two main types of subalpine forest exist. Open forests of low-statured ʻōhiʻa are widespread on less weathered, younger substrates of Hawaiʻi Island, while open to closed forests of *māmane (Sophora chrysophylla)* occur on cinder, ash, and old weathered lavas of both Maui and Hawaiʻi. In some māmane forests of Hawaiʻi Island, especially on Mauna Kea and in the saddle area, *naio (Myoporum sandwicense)* is a co-dominant in a low-statured woodland, called by Robyns and Lamb (1939) "plateau parkland." In some areas, naio grows with māmane all the way to the treeline; the community also extends below the subalpine zone. Subalpine māmane forests have been mapped over nearly 18,000 ha (44,460 a) of Hawaiʻi Island, those with naio cover another 6,000 ha (14,820 a) in the subalpine zone, and an equal area in the montane zone (Jacobi, in press b).

Alpine Vegetation

Vegetation above 2,800 m (9,180 ft) is very sparse and is composed almost entirely of native plant species. Commonly seen shrublands of alpine Maui and Hawaiʻi are composed of very scattered low *pūkiawe (Styphelia tameiameiae)* and *ʻōhelo (Vaccinium reticulatum)*. Very high-elevation areas of Hawaiʻi Island near the summits are essentially devoid of plants and support only a few native lichens, mosses (particularly *Racomitrium lanuginosum*), and grasses (*Trisetum glomeratum, Agrostis sandwicensis*) (Mueller-Dombois and Krajina 1968). Subalpine and alpine communities were probably affected very little by Hawaiians, and even today they remain largely undeveloped, except for buildings such as astronomy observatories and their attendant roads. However, even these high-elevation areas have been impacted by feral and domestic ungulates.

Dry Leeward Zones

The leeward regions of the Hawaiian Islands are much drier than windward-facing slopes, which intercept the moisture-bearing trade winds. Except for parts of the Kona slopes of Hawaiʻi Island, the leeward sides of the Islands typically receive less than 1,250 mm (50 in.) of annual precipitation, and some areas have less than 250 mm (10 in.) per year. Dry and mesic leeward communities begin directly below the subalpine zone on the high islands of Maui and Hawaiʻi, and below the summit rain forests on Kauaʻi, Oʻahu, and Molokaʻi. The lower islands of Niʻihau, Kahoʻolawe, and Lānaʻi are located in rain shadows of larger islands, and their vegetation may be considered to belong almost entirely to the dry leeward zone. Perhaps because of a history of human disturbance, the vegetation of the dry leeward zone is more fragmented and difficult to characterize than that of wet windward zones.

Lowland Grasslands and Shrublands. Grasslands, dominated by alien grass species, are widespread today in the lowlands of all the Hawaiian Islands and in some areas extend above 610 m (2,000 ft) elevation. A few lowland areas on the islands of Hawaiʻi, Maui, Lānaʻi, Kahoʻolawe, and Molokaʻi support grasslands of *pili (Heteropogon contortus)*, a species either indigenous to the Islands or introduced by Polynesians. Extensive lowland grasslands, most likely of pili, were noted by some of the early European travellers to Hawaiʻi (Ellis 1827; Beaglehole 1967; Macrae 1972) but were probably largely the result of the Hawaiian practice of burning. Such grasslands may have been entirely anthropogenic in origin (Kirch 1982). It is likely that endemic annual grasses of the genus *Panicum*, such as *kākonakona* (*P. torridum*), were formerly more important components of dry lowland vegetation, where they probably grew intermixed with native shrubs. Grasslands dominated by the indigenous *ʻemo-loa*

(*Eragrostis variabilis*) were probably more extensive in pre-human Hawai'i; remnants may be seen today on cliffs and steep valley walls on several Islands, most notably Kaua'i, O'ahu, and Moloka'i. On southeastern O'ahu, *Eragrostis* grasslands are found on steep east- or northeast-facing slopes exposed to strong winds, where the grass grows with other natives such as *nehe (Lipochaeta integrifolia)* and the sedge *Fimbristylis cymosa* (Kartawinata and Mueller-Dombois 1972). *Eragrostis* is also an important component of the vegetation of some of the Northwestern Hawaiian Islands (Christophersen and Caum 1931; Conant 1985; Herbst and Wagner, in press).

Native shrublands and forests were undoubtedly much more characteristic of the lowland vegetation before the advent of humans in Hawai'i and probably extended to the coast in many places (Ripperton and Hosaka 1942; Zimmerman 1948). On some leeward slopes of the Islands and on more recent substrates of windward Hawai'i Island, dry and mesic shrublands may still be seen in areas where agriculture and grazing have not been intensive. Native shrubs that are dominants in these communities are *'a'ali'i (Dodonaea viscosa), 'ākia (Wikstroemia* spp.*), 'āweoweo (Chenopodium oahuense); ko'oko'olau (Bidens menziesii), pūkiawe (Styphelia tameiameiae), alahe'e (Canthium odoratum)*, and low-growing *'ōhi'a (Metrosideros polymorpha)*. Such shrubs usually occur in mixed stands with two or more co-dominant shrubs; nonnative grasses are now important components of these shrublands. On steep cliffs, other shrubs such as *'akoko* (*Chamaesyce* spp.), *nehe* (*Lipochaeta* spp.), and *kulu'i (Nototrichium sandwicense)* may represent remnants of formerly more extensive communities. Two very rare shrublands extant in only limited areas give some indication that other shrub communities have disappeared with disturbance; these are a very open community of *'ohai (Sesbania tomentosa* f. *arborea)* and other natives on the leeward slopes of Moloka'i, and a shrubland in the Kōke'e and Nā Pali regions of Kaua'i containing *iliau (Wilkesia gymnoxiphium)* among more common shrubs such as pūkiawe.

Lowland Dry and Mesic Forests. Lowland leeward forests were considered by Rock (1913) to be the richest of all Hawaiian forests in terms of numbers of tree species and unique plants, but today they have been reduced to mere remnants over much of their original range. Most remaining native dry and mesic lowland forests are dominated by *lama (Diospyros sandwicensis)* or *'ōhi'a (Metrosideros polymorpha)*. Either 'ōhi'a or lama may predominate, but often they occur together in mixed stands. Remaining lama/'ōhi'a forests are, for the most part, found on very rocky substrates, steep slopes, or in gulches, areas unsuitable for agricultural development or clearing. In drier, leeward areas of the island of Hawai'i, these forests may contain *alahe'e (Canthium odoratum), kauila (Colubrina oppositifolia), 'aiea (Nothocestrum breviflorum), wiliwili (Erythrina sandwicensis), 'ohe makai (Reynoldsia sandwicensis)*, and endangered tree species such as *uhiuhi (Caesalpinia kavaiense)* and *koki'o (Kokia drynarioides)*. Mesic lama/'ōhi'a forests may still be seen in the Puna and South Kona Districts of the island of Hawai'i. Of all the lowland dry forests surveyed by Jacobi (in press b) on the island of Hawai'i (500-1,000 m or 1,640-3,280 ft), only those dominated by 'ōhi'a had significant cover (> 20,000 ha or 49,400 a).

More rarely-seen lowland forests are those in which the predominant tree is wiliwili, *koa (Acacia koa), koai'a (A. koaia), olopua (Nestegis sandwicensis)*, or *āulu (Sapindus oahuensis)*. The āulu forest type is seen only on O'ahu, where it is restricted to lower slopes and gulch walls of the leeward Wai'anae Mountains. Hatheway (1952) suggested that *Sapindus* and lama forests once covered much of the lower forested region of leeward O'ahu. Wirawan (1974), who two decades later studied the same

forest stands as Hatheway, noted that some native dry forest species were being suppressed by alien grasses and shrubs, but that *Sapindus* was able to maintain dominance and even invade nonnative stands. *Sapindus*-dominated forests may formerly have occurred on Kaua'i, in Waimea Canyon and Makaweli, where Rock (1913) noted that the species was scattered among *kukui (Aleurites moluccana), hōlei* (*Ochrosia* sp.), and *kōpiko* (*Psychotria* spp.).

Open forests or savannas of wiliwili must have been very widespread on lower leeward slopes, where scattered trees and stands are still commonly seen on undeveloped lands or rough substrates. One of the best remaining examples of a wiliwili forest was described by Medeiros et al. (1984) from a site between 200 and 400 m (660-1,310 ft) elevation above Kīhei, Maui. More than a dozen native trees and shrubs were components of this forest, including such rarities as koai'a, *ko'oloa'ula (Abutilon menziesii)*, and the native yellow *Hibiscus* or *ma'o hau hele (H. brackenridgei)*. This exceptional dry forest remnant also contained a rich herbaceous flora including native grasses (*Panicum* spp.), ferns, herbs, and vines (*Sicyos* sp., *Ipomoea* spp., *Bonamia menziesii, Canavalia haleakalensis*).

Based on remnants of native vegetation, Char and Balakrishnan (1979) speculated that the original vegetation of the 'Ewa Plains of O'ahu was an open wiliwili savanna with other trees such as āulu, sandalwood (*Santalum ellipticum* and *S. freycinetianum*), and *naio* (*Myoporum sandwicense*). Native shrubs, including *'akoko* (*Chamaesyce skottsbergii*), *ma'o* (*Gossypium tomentosum*), *Achyranthes rotundata*, *Abutilon incanum*, and *'ilima* (*Sida* spp.), as well as vines, grasses, and a few ferns were also part of this community. Supporting evidence for an open native forest such as this comes from a study of the subfossil land snails of the area (Christensen and Kirch 1981). On Kaho'olawe, extant wiliwili trees on the hill of Moa'ula, evidence from archaeological studies (TenBruggencate 1986a), and 19th century reports of plant cover (Myhre 1970) are indications that the Island probably supported a forest similar to that described for the 'Ewa Plains.

Koai'a forests have been almost entirely converted into pastures. Only in areas fenced to exclude cattle or in inaccessible gulches may remnants of this rare community be seen. In a botanical survey of the Kawaihae-Waimea area on Hawai'i Island, McEldowney (1983) found relict koai'a forests in pastureland ravines between 610 and 1,190 m (2,000-3,900 ft) elevation. Trees associated with koai'a near Kawaihae are naio, olopua, *māmane (Sophora chrysophylla)*, sandalwood (*Santalum* sp.), and wiliwili. Although not strictly a forest type on Maui, koai'a was found to be associated with many native woody species in several stands on the south slope of Haleakalā (Medeiros et al. 1986).

A few forests dominated by olopua or by olopua and lama may still be seen on Lāna'i, Maui, and Hawai'i. The Lāna'i example was described in detail by Spence and Montgomery (1976) and is notable for the number of rare plants it contains. Two federally listed endangered tree species grow there: the Hawaiian gardenia or *nā'ū (G. brighamii)* and the Lāna'i sandalwood (*Santalum freycinetianum* var. *lanaiense*) (U.S. Fish and Wildlife Service 1987). Spence and Montgomery speculated that this type of forest may have once covered much more area on Lāna'i, before the introduction of grazing and browsing animals and subsequent severe wind erosion. Ziegler (1989), who also studied the Kānepu'u forest, estimated that half of Lāna'i could have originally supported a dry forest or woodland.

In a very few sites on leeward slopes of Kaua'i, O'ahu, West Maui, and Lāna'i are remnants of extremely species-rich dry to mesic forests with no clear dominant tree species; these are refugia for nearly extinct trees such as *mēhamehame (Flueggea phyllanthoides)* as well as other rare plants such as *a'e (Zanthoxylum* spp.), *māhoe (Alectryon macrococcum)*, and *halapepe (Pleomele* spp.). Several botanically diverse dry forests of Maui (south slope of Haleakalā) and Hawai'i (Pu'uwa'awa'a and Kapu'a) are described in detail by Rock (1913) and Judd (1932). It was Rock's opinion that a band of this rich dry forest once "encircled the southern slopes of Mauna Loa" but was destroyed by lava flows. Even the relatively young substrates of the East Rift of Kīlauea support dry and mesic forests in areas not overrun by lava for several hundred years (Mueller-Dombois 1966; S.J. Anderson et al., unpubl. data).

Lowland dry and mesic forests dominated by koa, āulu, and olopua, as well as the extremely rich mixed forests, occur as small remnant stands; over most of their original range they have been replaced by alien trees and shrubs. In some leeward lowland areas such as northwestern Kaua'i and Ni'ihau, the only indications of the former native forest cover are the subfossil remains of endemic land snails of the genus *Carelia* (Gage 1988).

Some areas that are quite xeric today may have been more mesic in the past. Fossils of native trees buried in ash near Salt Lake on O'ahu dated from 100,000 years ago indicate that the forest in this leeward area near sea level contained native tree species such as 'ōhi'a, koa, *loulu* palm (*Pritchardia* sp.) (Lyon 1930), and *Pteralyxia* sp. (Selling 1948), species found on O'ahu today only in moister sites at higher elevations.

Montane Grasslands and Shrublands. Grasslands are not an important element in native Hawaiian montane vegetation between approximately 500 and 2,000 m (1,640-6,560 ft). The extensive pasturelands now found in the montane zone of Maui and Hawai'i are not natural but are converted forests and shrublands. In a few dry and mesic areas of Hawai'i Island on the slopes of Mauna Kea, Mauna Loa, and the saddle between them are grasslands dominated by endemics such as *Eragrostis atropioides, Deschampsia nubigena*, and *Panicum tenuifolium*. These grasslands may have covered more area before the advent of alien grasses and introduced ungulates, or they may represent degraded forests.

Shrublands are also not prominent in the leeward montane zone. Dry shrublands containing *'a'ali'i (Dodonaea viscosa), na'ena'e (Dubautia linearis)*, and *ko'oko'olau (Bidens menziesii)* occur on leeward slopes of Mauna Loa and the saddle region among the mountains; elsewhere on Mauna Loa *pūkiawe (Styphelia tameiameiae)* is an important shrubland plant. A dry shrubland composed mainly of low, scattered *'ōhi'a (Metrosideros polymorpha)* and native shrubs is found on leeward slopes of Hawai'i and Maui and may represent an early successional stage of dry 'ōhi'a forest. Jacobi (in press b) mapped this dry shrub community over nearly 20,000 ha (49,400 a) of Hawai'i Island's montane zone.

Montane Dry Forests. Forests are the primary natural vegetation of the leeward montane zone. Dry forests are found on leeward East Maui and Hawai'i and are dominated by one or more of the following tree species: *koa (Acacia koa), māmane (Sophora chrysophylla)*, the ubiquitous *'ōhi'a (Metrosideros polymorpha)*, and much more rarely, *'akoko (Chamaesyce olowaluana, C. celastroides)*. Particularly rich examples of montane dry forests occur at Auwahi on Maui and Pu'uwa'awa'a on the slopes of

Hualālai, Hawai'i; these are described in detail by Rock (1913). More mesic sections of these rare forests have *olopua (Nestegis sandwicensis)* as an important component. While changes (particularly the invasion of alien grasses) have occurred in the 75 years since Rock's work in these areas and may have resulted in drier conditions, both sites remain notable for great tree species diversity and the presence of rare plants (Powell and Warshauer 1985a; Medeiros et al. 1986). Based on the current and historical distribution of tree species characteristic of the Auwahi forest, Medeiros et al. (1986) speculated that a rich dry forest once had a much greater distribution on the south slope of Haleakalā.

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Major activities of humans in modifying Hawai'i's native vegetation will be discussed in the rest of this volume according to time periods, islands, and vegetation zones. A summary of the changes and an indication of what natural areas remain conclude the review.