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Woody Vegetation on the Raised Coral Limestone of Mangaia, Southern Cook Islands[1]

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ABSTRACT: Mangaia, the second largest (51.8 km^2) of the Cook Islands, has a central, volcanic region with a maximum elevation of 169 m above sea level. The igneous interior is surrounded by an extensive formation of elevated coral limestone as much as 2 km wide and 70 m above sea level. Although the native vegetation in the volcanic interior has been altered greatly through human interference, a quantitative survey in the raised limestone region indicates that plant life on the elevated reefs is still largely dominated by native species. Seventy percent of the woody species recorded in 20 transects are either indigenous or endemic to the Cook Islands, and native plants accounted for 88% of the total basal area covered by the woody vegetation sampled on the raised coral limestone. Herbaceous ground cover in the study area was almost completely dominated by native species (99%). Four woody plant associations in the limestone areas are recognized by dendrogram analysis: (1) mixed native forest, dominated by *Elaeocarpus tonganus*; (2) disturbed mixed native forest, dominated by *Hernandia moerenhoutiana* or *Cocos nucifera*; (3) *Pandanus* scrub; and (4) *Barringtonia* forest. Some biogeographical aspects of the relatively undisturbed limestone forest region and the ecological implications of human disturbance of the vegetation on Mangaia are also discussed.

SITUATED IN THE REMOTE TROPICAL South Pacific Ocean, between 9° and 23° S latitude and 156° and 167° W longitude, the Cook Islands include 15 small coral and volcanic islands. The total land area of the island group is approximately 240 km^2, spread out over more than 2,170,000 km^2 of ocean (Kennedy 1974).

Ecological disturbance by humans appears to have begun long before European contact, resulting in habitat alteration and displacement of some native biota (W. R. Sykes, 1976, unpublished report on vegetation of Mangaia, Department of Scientific and Industrial Research, Botany Division, Christchurch, New Zealand; Steadman 1985, 1989). The impact of the disturbance has been most intense in the interior volcanic region and has continued during historic and more recent times. The most recent government census for the Cook Islands (1981) recorded 1364 people residing on Mangaia. In addition to subsistence farming, commercial crops of copra and pineapple are cultivated on the island. Some aspects of human impact on the native biota of Mangaia are discussed below.

Although European explorers first located one of the Cook Islands (Manuae) in 1773 during the second voyage of Captain James Cook, neither the flora nor the vegetation of the archipelago has been well documented in the two centuries that have passed since then. The only islands with published floras are Rarotonga, the largest (64 km^2) and highest (652 m) island in the archipelago (Cheeseman 1903, Wilder 1931), and Aitutaki (Stoddart 1975), an "almost-atoll." The two Rarotonga floras are now considered to be dated and harbor many inaccuracies (William Sykes, DSIR, New Zealand, pers. comm., 1987; Whistler 1988). There is also a taxonomic account of the ferns and fern allies found in the

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southern Cook Islands (Brownlie and Philipson 1971).

A brief description of vegetation on the Cook Islands is included in a botanical bibliography prepared by Sykes (1980). In addition, there are two previous studies that describe some qualitative aspects of the vegetation on Rarotonga (Philipson 1971, Fosberg 1972). A quantitative analysis of the upland woody vegetation of Rarotonga (Merlin 1985) described relative dominance and absolute density and revealed that a very large percentage (>90%) of the woody species in the interior montane region is composed of native species.

There is little published information about the flora or vegetation of Mangaia. Buck (1934) and Mark (1976) included some references to the flora of the island that are predominantly ethnobotanical, and Webb (1981) summarized some unpublished qualitative vegetation data collected during a New Zealand government–sponsored soil survey in 1974 (cf. Sykes, unpublished report, 1976). Floras have been published for two raised limestone islands (moderately elevated atolls) in Polynesia: one for Makatea Island, ca. 1400 km northeast of Mangaia, in the Tuamoto Archipelago (Wilder 1934), and another for Henderson Island, more than 3000 km east-southeast of Mangaia (St. John and Philipson 1962). Among the 22 native woody species recorded in the sample transects on Mangaia in the present study, 13 (59%) are also native to Makatea Island, and 9 (41%) are also native to Henderson Island.

According to the descriptions summarized by Webb (1981) and observations I made in 1986, the vegetation of Mangaia can be divided into four general plant associations correlated to three roughly concentric physiographic regions: (1) the interior uplands, (2) the interior lowlands, (3) the raised coral limestone, and (4) the littoral.

The raised limestone region of Mangaia is of special scientific interest for at least two reasons: (1) unlike the interior uplands and lowlands, many parts of the raised limestone still support intact native ecosystems; and (2) there has been no published quantitative vegetation analysis of this type of environment in Polynesia. The major aims of the research reported here were to identify the woody plant associations that occur in the raised reef areas of Mangaia, to measure the relative dominance and frequency of the individual woody species found in those vegetation types, and to quantify the extent to which alien woody species have become naturalized in the elevated limestone on the island.

The island of Mangaia (21° 55′ S latitude and 157° 58′ W longitude) lies at the southeastern end of the archipelago, 204 km east-southeast of Rarotonga. It is the second largest (51.8 km^2) and second highest (169 m) of the Cook Islands, ca. 7.5 km long and 6.5 km wide (see Figure 1). The central region of the island is the subaerial portion of an extinct, basaltic shield volcano typical of those found in the deep Pacific Ocean Basin. It is deeply weathered and extensively dissected, with severe soil erosion in several areas (see Figure 2). The volcanic interior of Mangaia is surrounded by the most extraordinary geomorphological feature of the island—a relatively large area of elevated Oligocene-Miocene coral limestone (Marshall 1927, Stoddart et al. 1985). The raised limestone reaches elevations between 55 m and 70 m above sea level and, in places, is nearly 2 km wide. It is known locally as *makatea* (literally translated: "white rock"). The height of the elevated limestone increases with distance from the coast (see Figure 3) and in most areas ends abruptly as a sheer wall facing the interior (see Figure 4). A narrow, shallow fringing reef surrounds the island.

Although rainfall data collection on Mangaia has been somewhat sporadic (Webb 1981), the mean annual rainfall recorded for the period 1921–1982 was ca. 2 m (Survey Department, Rarotonga 1983). Records indicate extreme variation in both the monthly and annual rainfall, with one month often having "ten times as much rainfall as an adjoining month" (Webb 1981; see also Thompson 1986). Much of the annual rainfall normally falls between December and March, the main summer months of the Southern Hemisphere. It is during this warmer, more humid period that the prevailing southeast trade winds are intermittently interrupted and

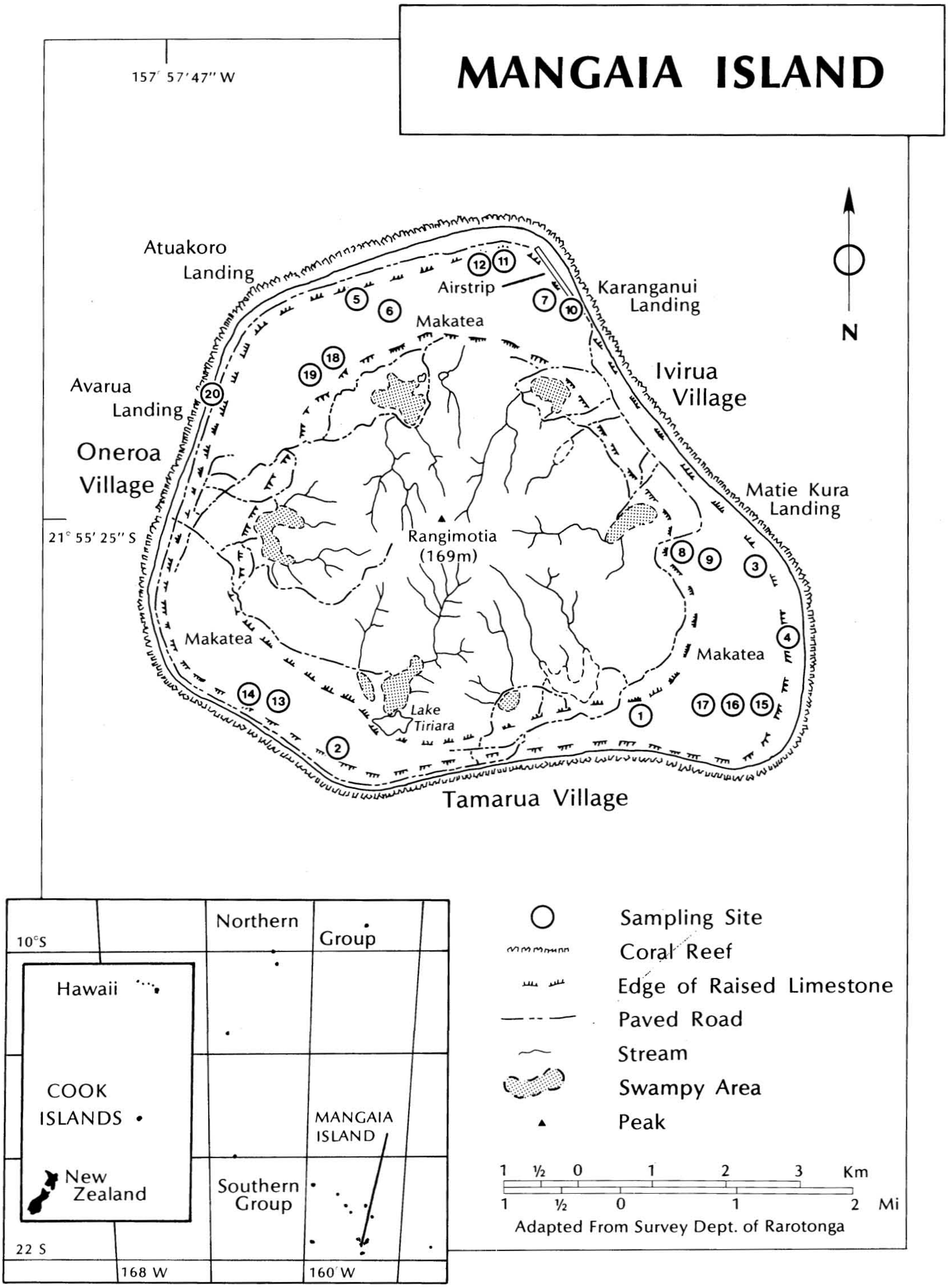

FIGURE 1. Map of the Cook Islands and vegetation sampling sites on Mangaia.

FIGURE 2. The central region of Mangaia is deeply weathered, severely eroded in many areas, and overwhelmingly dominated by alien plant species.

Mangaia, as well as the other southern Cook Islands, is affected by squalls and winds out of the north (cf. Stoddart 1975). Mangaia is also periodically affected by severe tropical storms or cyclone conditions during the hurricane season, which usually lasts from November to April. The most recent hurricane struck the southern Cook Islands in January 1986, causing extensive damage on Rarotonga. Because of the relatively low relief of Mangaia, orographic rainfall probably plays a small or insignificant role in the distribution of moisture on the island, especially within the low-lying *makatea* areas.

Observations of ambient air temperature are not recorded on Mangaia; but because of its tropical location we can expect the mean monthly temperatures in the *makatea* areas on the island to be relatively equable throughout the year and similar to those recorded in the lowlands of Rarotonga, although slightly lower because Mangaia lies at a more southerly position. In the lowlands of Rarotonga, the mean monthly temperature ranges from 22°C in July to 26°C in January (Kennedy 1974). Based on the small size and relatively minor differences in elevation of the *makatea* areas of Mangaia, spatial variation of temperature probably plays a small role in the general patterns of vegetation, especially on the *makatea*.

Aspect to prevailing winds, on the other hand, seems to be an important climatic variable affecting differential distribution of vegetation on the *makatea*, particularly in those areas of Mangaia that are in windward positions near the coast. Salt spray and strong prevailing trade winds in the southeast region of the island produce relatively harsh, windswept conditions near the coast, where the vegetation on rugged raised limestone is stunted or deformed (see Figure 5).

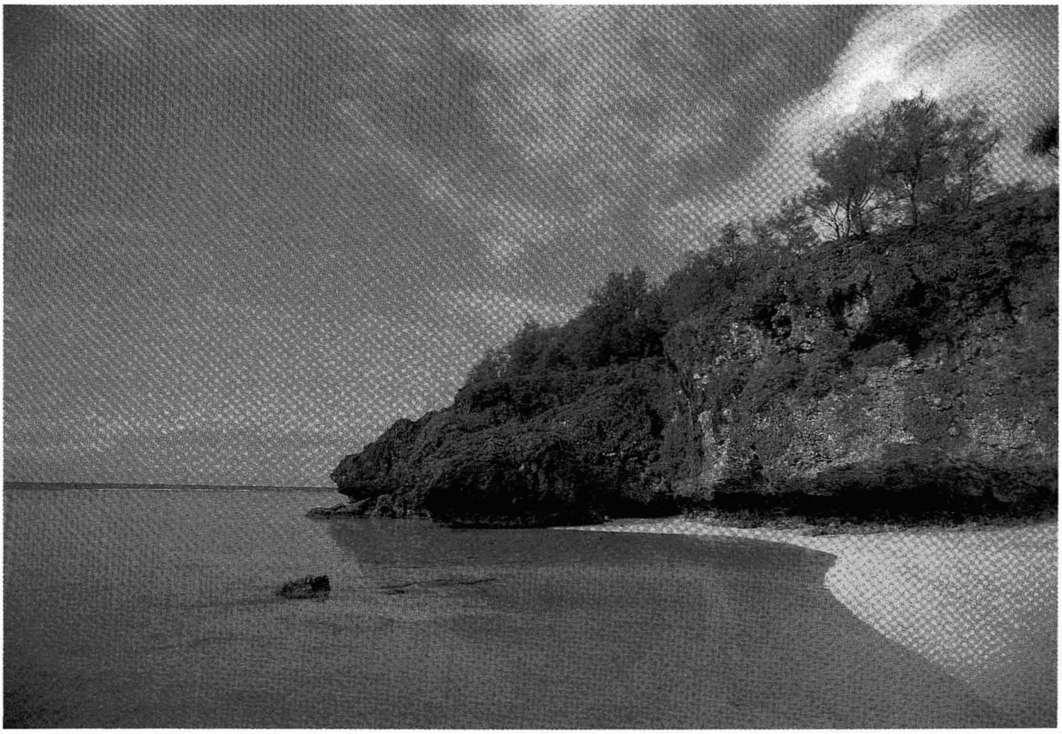

FIGURE 3. Raised limestone (*makatea*) along the western coast of Mangaia.

The characteristics of substrate play a basic role in determining the type of vegetation and species composition on Mangaia. Major differences between the deeply weathered, heavily eroded volcanic soils in the interior parts of the island and the porous, often nutrient-deficient, old calcareous soils of the *makatea* strongly affect the distribution of plants on Mangaia.

Field research in heavily dissected raised limestone areas is often impeded by the rugged, often treacherous terrain. Traversing areas of the elevated limestone surface on Henderson Island was the most difficult walking that St. John experienced in all his years of fieldwork in the Pacific. "The crevasses were often 3 to 7 m deep, with rough and jagged sides. Ground vegetation concealed many of the holes. A slip and a fall into one of these would be a crippling experience" (St. John and Philipson 1962; see also Fosberg et al. 1983). Wilder (1934) referred to the arduous and dangerous task of "botanizing" on the phosphate-exploited, raised limestone plateau of Makatea Island "because of the multitude of deep holes that have, during the passing of years, grown up with all sorts of wayside weeds, ferns, and other plants, so that often what seems to be solid ground turns out to be a pitfall." Sampling the vegetation on the raised limestone of Mangaia proved to be equally difficult.

MATERIALS AND METHODS

A quantitative survey of the woody vegetation in the raised coral limestone region of Mangaia was made during July 1986. The point-centered quarter method of transect sampling (Mueller-Dombois and Ellenberg 1974) was used because of the extremely rugged surface of much of the elevated reef area on the island. Twenty transect sites (see

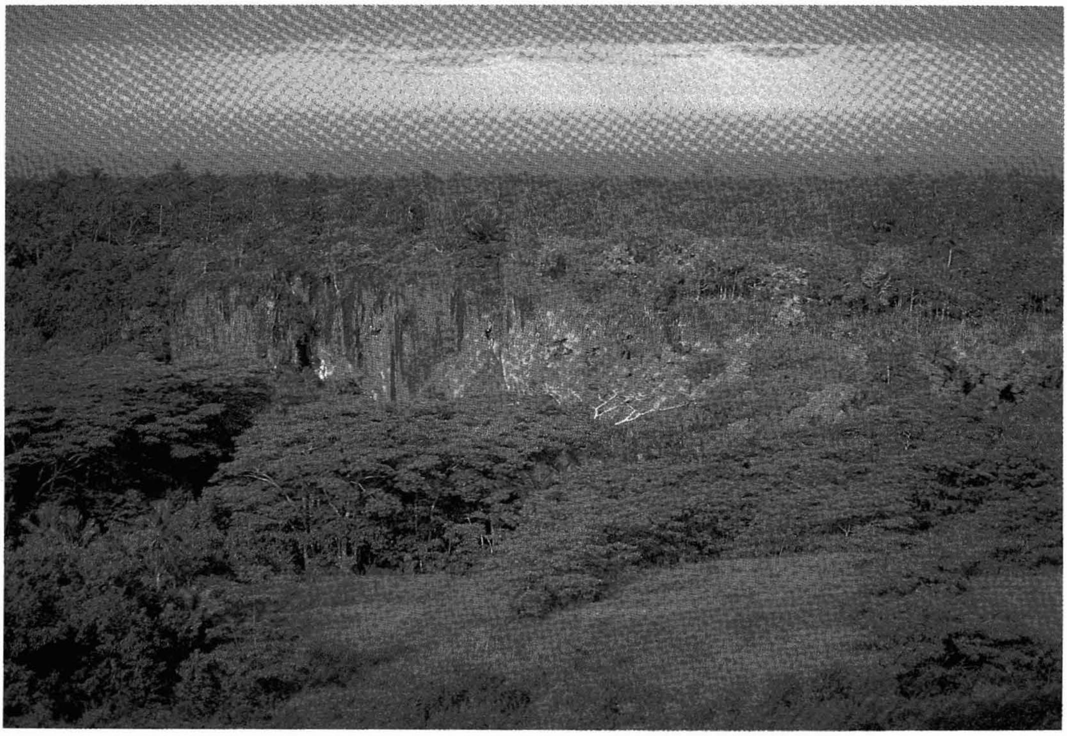

FIGURE 4. Hilly, volcanic interior of Mangaia in the foreground; steep, inner wall and higher area of raised limestone in the background.

Figure 1) were chosen in a stratified random manner to allow for variations in exposure to the prevailing southeast trade winds, the degree of pit and pinnacle development, and the distance from settlements or cultivated plots in the raised coral limestone.

Ten points were established at 10-m intervals along 100-m transect lines. Four quarters were established around each point. In each quarter, the distance to the nearest woody plant with a basal diameter greater than 2.5 cm was measured so that tree and shrub densities could be determined. Plants were then identified to ascertain absolute species frequencies (number of transect points with species recorded), and basal diameters were measured to determine the relative dominance of individual species. The relative dominance of each woody species in a transect was calculated by dividing the total basal area of all individuals of that species recorded in the transect by the total basal area of all woody species recorded in the transect, and then multiplying the quotient by 100. In addition, heights of individual trees were estimated and geographical affinities of the species (native versus alien) were noted. With 10 points in each transect, a sample size of 40 trees per transect and total of 800 trees for all 20 transects combined were observed.

In addition to the observations and measurements of the woody plants, percentage ground cover was estimated for individual herbaceous species in circular sample plots (1.5-m radius) centered at each of the 10 stations in all 20 transects.

A cluster analysis of the woody plant transect data based on species presence/absence and relative dominance was also performed to determine whether plant associations recognized in the field could be supported by objective techniques. The dendrogram technique described by Mueller-Dombois and Bridges (1975) was used to analyze the distribu-

FIGURE 5. Windswept pit and pinnacle region (*raei*) of raised limestone in southeastern Mangaia; vegetation in such areas is severely stunted and overwhelmingly dominated by native plant species.

tion patterns in the study area. The dendrogram computer program applied was COMM (Kent W. Bridges, Botany Department, University of Hawaii at Manoa, pers. comm., 1988).

Plant specimens, including all those recorded in the transects, were collected and deposited in the herbarium of the Bernice P. Bishop Museum, Honolulu, Hawaii (BISH). Additional specimens were deposited in the collection of Dr. Arthur Whistler in the Botany Department of the University of Hawaii at Manoa.

RESULTS AND DISCUSSION

The dendrogram based on the cluster analysis calculations of presence/absence and relative dominance data is shown in Figure 6. The 20 transect study sites are arranged in a linear sequence along the bottom of the figure, and the percentage similarity of the paired plots is indicated on the vertical axis. To identify ecologically meaningful clusters, a single cutoff line was drawn that lumped all but two transects into three similarity clusters. In the computer-derived classification, this condition was satisfied at a within-group similarity of 20% identifying three major clusters: A, B, and C. These three similarity clusters recognize the natural groupings of the vegetation into the categories described below. The relatively special situations of the two transects, nos. 17 and 20, that were not lumped into any of the three clusters at the 20% similarity level are also described in the discussion that follows the presentation of results below.

Mixed and Disturbed Native Forest

The forest on the higher inland *makatea* of Mangaia is largely undisturbed, except in areas near the villages, footpaths, and roads

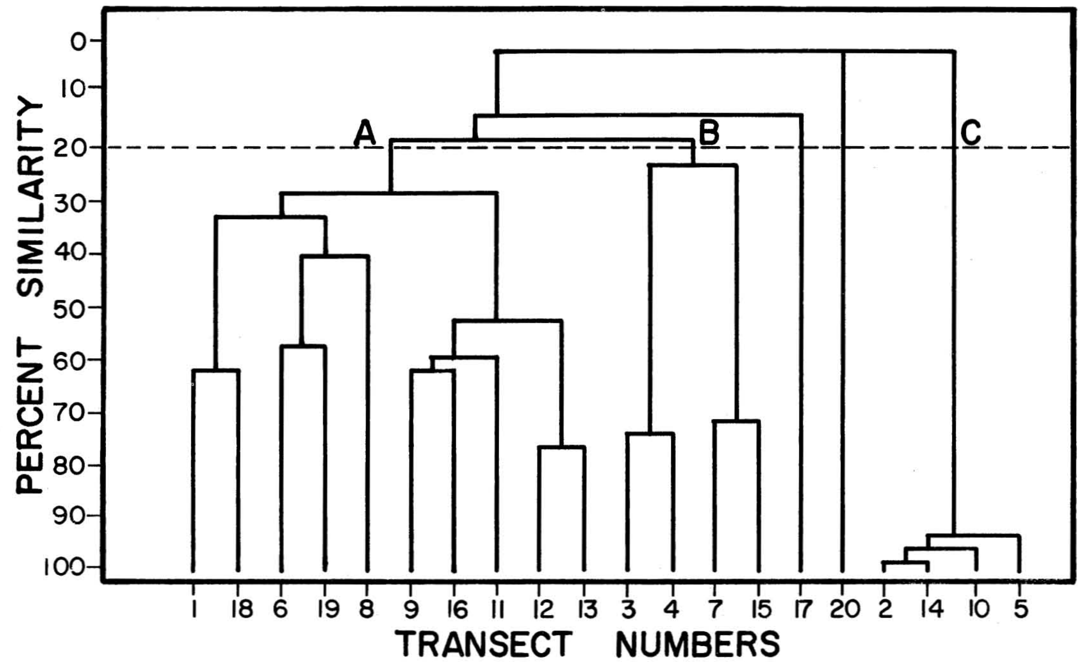

FIGURE 6. Dendrogram based on similarity matrix of species presence/absence and relative dominance for transect data from raised coral limestone region of Mangaia. A 20% cut-off line separates the following clusters: A = mixed forest; B = *Pandanus* scrub; C = *Barringtonia* forest. Cluster A is further divided into two subgroups: the mixed disturbed forest (transect nos. 1, 18, 6, 19, and 8) and the mixed native forest (transect nos. 9, 16, 11, 12, and 13). Transects 17 and 20 were not lumped into any of the three cluster groups at the 20% similarity level. See text for discussion.

(see Figure 7). Cluster A groups 10 transects (nos. 1, 6, 8, 9, 11, 12 ,13, 16, 18, and 19) located on the inland raised coral limestone that are predominately composed of a mixture of native woody species. The limestone has variable pit and pinnacle development with soil occurring in pockets of various horizontal dimensions and differing depths.

Based on the differential presence of alien species as an indicator of the degree of human alteration, cluster A has been divided into two subgroups, one referred to here as the mixed disturbed native forest (transect nos. 1, 18, 6, 19, and 8), and another designated as the mixed native forest (transect nos. 9, 16, 11, 12, and 13; see the computer-derived classification, Figure 6, and Table 1).

Two transects in the mixed disturbed native forest subgrouping (nos. 6 and 19) are dominated by an introduced species, *Cocos nucifera*, which was only recorded in four transects, all in this disturbed forest subgroup. Although the coconut palm is cultivated in a number of areas in the *makatea*, it is also self-sown in these areas and may have become naturalized in other nearby areas through dispersal by hurricane-force winds. In the mixed disturbed forest subgrouping of cluster A, *C. nucifera*, usually the tallest woody species, had mean and maximum heights of 7.1 m and 19.5 m (n = 12), an absolute frequency of 14%, and an average relative dominance of 19%. Alien species were recorded in only two transects of the mixed native forest subgrouping of cluster A: *Aleurites moluccana* in transect no. 9 (relative dominance = 8%) and *Morinda citrifolia* in transect no. 12 (relative dominance = <1%).

The vigor and composition of the inland mixed native *makatea* forests seem to be a function of the degree of soil depth. In areas with relatively large deposits of fertile soil,

FIGURE 7. Native mixed forest on raised limestone above the western coast of Mangaia.

usually deeper than 60 cm, a closed-canopy mixed forest of medium height (ca. 5.5 m) has developed (see Table 2). Small cultivated plots or animal enclosures are found in those areas with deeper soils that occur near settlements or footpaths and roads; disturbance in those areas is usually severe. In inland *makatea* areas where the amount of limestone outcropping is more pronounced, and consequently less soil is available, the forest may not have a closed canopy and normally is lower in height (ca. 1.5 to 2.5 m).

In cluster A (including all 10 transects composing the two subgroups), the more common woody plants included the following species: *Elaeocarpus tonganus*, an indigenous tree with mean and maximum heights of 6.6 m and 12 m ($n = 25$), an average relative dominance of 29%, and an absolute frequency of 23%; *Hernandia moerenhoutiana*, an indigenous tree with mean and maximum heights of 5 m and 7.5 m ($n = 62$), an average relative dominance of 20%, and an absolute frequency of 44%; *Pandanus tectorius*, an indigenous tree with mean and maximum heights of 3.7 m and 7.5 m ($n = 49$), an average relative dominance of 12%, and an absolute frequency of 40%; *Guettarda speciosa*, an indigenous tree with mean and maximum heights of 3.5 m and 7.5 m ($n = 15$), an average relative dominance of 8%, and an absolute frequency of 19%; *Ficus prolixa*, an indigenous tree with mean and maximum heights of 2.8 m and 7.2 m ($n = 67$), an average relative dominance of 5%, and an absolute frequency of 37%; *Aleurites moluccana*, an alien tree with mean and maximum heights of 7 m and 13.5 m ($n = 29$), an average relative dominance of 5%, and an absolute frequency of 15%; and *Pipturus argenteus*, an indigenous shrub or small tree with mean and maximum heights of 1.8 m and 6 m ($n = 44$), an average relative dominance of 3%, and an absolute frequency of 31%.

TABLE 1

Differentiated Table of Relative Dominance (%) of Woody Species Found in the Elevated Coral Limestone Region of Mangaia Island

		MIXED DISTURBED NATIVE FOREST					MIXED NATIVE FOREST					*Pandanus* SCRUB				*Barringtonia* FOREST				NON-CLUSTERED	
ORIGINS*	SPECIES / TRANSECT NOS.	1	18	6	19	8	9	16	11	12	13	3	4	7	15	2	14	10	5	17	20
A	*Cocos nucifera* L.	7	–	37	32	19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	19
A	*Aleurites moluccana* (L.) Willd.	20	5	–	12	2	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
A	*Morinda citrifolia* L.	+	+	1	+	1	–	–	–	+	–	+	+	–	–	–	–	–	–	–	1
A	*Hibiscus tiliaceus* L.	–	–	–	–	16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11
R	*Psidium guajava* L.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
R	*Psidium cattleianum* Sabine	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
I	*Hernandia moerenhoutiana* Guill.	55	70	24	17	2	20	9	2	4	–	–	–	–	–	1	–	1	2	7	–
I	*Elaeocarpus tonganus* Burk.	4	17	22	5	18	31	23	31	78	62	–	–	–	–	+	–	1	2	–	–
I	*Pandanus tectorius* Park.	–	1	10	2	39	10	38	8	3	10	71	96	25	18	+	+	–	+	3	–
I	*Guettarda speciosa* L.	–	+	3	3	–	16	13	31	7	9	22	2	3	–	+	+	–	–	16	+
I	*Pipturus argenteus* (Forst. f.) Seem.	5	1	1	–	–	1	6	7	2	4	–	–	31	35	+	–	+	–	2	–
I	*Ficus prolixa* Forst. f.	1	2	2	–	–	3	6	18	3	13	–	–	41	23	1	–	–	–	1	–
I	*Allophylus timorensis* (DC.) Bl.	8	2	–	–	–	2	–	–	–	1	–	–	–	–	–	–	–	–	2	–
I	*Canthium barbatum* (Forst. f.) Seem.	–	–	1	20	–	+	–	–	–	1	–	–	–	–	–	–	–	–	–	–
I	*Glochidion ramiflorum* Forst. f.	–	–	–	7	3	9	4	2	2	–	–	–	+	20	–	–	–	+	+	–
I	*Ficus tinctoria* Forst. f.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	36	–
A	*Casuarina equisetifolia* L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	32	–
I	*Barringtonia asiatica* (L.) Kurz	–	–	–	–	–	–	–	–	–	–	–	–	–	–	98	99	97	93	–	–
I	*Calophyllum inophyllum* L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
I	*Homalium acuminatum* Cheeseman	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
I	*Caesalpina major* (Medic.) Dandy & Exell	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
I	*Mucuna gigantea* (Willd.) DC.	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
I	*Schleinitzia insularum* (Guill.) Burkhart	–	–	–	–	–	–	–	–	–	–	4	2	–	–	–	–	–	–	–	–
I	*Eugenia reinwardtiana* (Bl.) DC.	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
I	*Xylosma suaveolens* (Forst.) Forst. f.	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
I	*Planchonella grayana* St. John	–	–	–	–	–	–	–	1	–	–	–	–	–	3	–	–	–	–	–	–
I	*Ixora bracteata* Cheesem.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
E	*Geniostoma sykesii* Fosb. & Sachet	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–
I	*Hernandia nymphaeifolia* (Presl) Kubitzki	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	58
A	*Cordia subcordata* Lam.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10

NOTE: + indicates less than 1% relative dominance; – indicates absence. Transects except nos. 17 and 20 are arranged according to the dendrogram classification; see Figure 6.
*I = indigenous; E = endemic to Cook Islands; A = aboriginal introduction; R = recent or historical introduction.

TABLE 2

ABSOLUTE DENSITY, TOTAL BASAL AREA, AND AVERAGE HEIGHT OF WOODY SPECIES IN 20 SAMPLE TRANSECTS ON THE RAISED LIMESTONE OF MANGAIA*

TRANSECT	ABSOLUTE DENSITY OF WOODY PLANTS/100 m^2	TOTAL BASAL AREA/100 m^2	AVERAGE HEIGHT	MAXIMUM HEIGHT (approx.)
Mixed Disturbed Forest (in cluster A)				
1	11.9	2.89 m^2	5.2 m	20 m
18	13.9	2.68 m^2	7.0 m	11 m
6	12.1	2.88 m^2	4.9 m	14 m
19	13.7	2.71 m^2	6.7 m	12 m
8	18.0	2.36 m^2	4.9 m	11 m
Mixed Native Forest (in cluster A)				
9	12.6	2.81 m^2	5.2 m	11 m
16	9.2	3.30 m^2	2.4 m	6 m
11	11.6	2.94 m^2	1.5 m	4 m
12	5.4	4.30 m^2	2.4 m	8 m
13	9.7	3.21 m^2	2.4 m	6 m
Pandanus Scrub (cluster B)				
3	6.8	3.83 m^2	3.3 m	5 m
4	5.8	4.17 m^2	2.7 m	5 m
7	13.5	2.72 m^2	1.8 m	2 m
15	18.6	2.32 m^2	1.2 m	4 m
Barringtonia Forest (cluster C)				
2	5.4	4.32 m^2	5.5 m	9 m
14	5.9	4.11 m^2	6.4 m	9 m
10	2.7	6.04 m^2	8.4 m	15 m
5	2.9	5.92 m^2	9.5 m	18 m
Non-clustered Samples†				
17	17.0	2.42 m^2	4.0 m	8 m
20	22.2	2.13 m^2	8.2 m	15 m

* Absolute density and total basal area/100 m^2 figures were calculated according to the point-centered quarter method described in Mueller-Dombois and Ellenberg (1974).

† See Results and Discussion section for descriptions of these two transects.

The ground cover in the 100 sample plots (10 plots × 10 transects) of cluster A (mixed forest areas) covered an estimated 32% of the surface area (see Table 3). The herbaceous plants in the ground cover included *Nephrolepis* sp. (14%), *Asplenium nidus* (7%), *Davallia solida* (4%), *Peperomia* sp. (2%), *Phymatosorus scolopendria* (1%), *Achyranthes aspera* (1%), *Procris pendunculata* (1%), *Ipomoea macrantha* (1%), *Jasminum didymum* (< 1%), and *Triumfetta procumbens* (< 1%).

Pandanus *Scrub*

Cluster B groups four transects (nos. 3, 4, 7, and 15) located in the windward areas of Mangaia where the *makatea* substrate is extremely dissected and usually windswept (see Figure 8); only nine woody species were found in these transects. In those areas where the transects were placed, soil was shallow and often restricted to small pockets. Substrate limitations in the *Pandanus* scrub are manifest in the relatively short average height of this vegetation association (2.3 m), which is much less that the averages of the other two cluster groups (A = 4.3 m and C = 7.5 m). Windswept areas of extreme pit and pinnacle limestone outcropping with poor soil conditions are known on Mangaia as the *raei.*

All nine woody species recorded in the cluster B transects were indigenous. Similar to the inland mixed *makatea* forest, the dominance of native species in the *Pandanus* scrub can best be explained by the rugged terrain

TABLE 3

WOODY AND HERBACEOUS SPECIES IN CLUSTERS A, B, AND C

CLUSTER	WOODY SPECIES (% average relative dominance for all transects in cluster)		HERBACEOUS SPECIES (% ground cover for all transects in cluster)	
A	*Elaeocarpus tonganus*	(29)	*Nephrolepis* sp.	(14)
Mixed Forest	*Hernandia moerenhoutiana*	(20)	*Asplenium nidus*	(7)
(transects 1, 6, 8, 9, 11,	*Pandanus tectorius*	(12)	*Davaliia solida*	(4)
12, 13, 16, 18, 19)	*Cocos nucifera*	(10)	*Peperomia* sp.	(2)
	Guettarda speciosa	(8)	*Phymatosorus scolopendria*	(1)
	Ficus prolixa	(5)	*Achyranthes aspera*	(1)
	Aleurites moluccana	(5)	*Procris pendunculata*	(1)
	Pipturus argenteus	(3)	*Ipomoea macrantha*	(1)
	Glochidion ramiflorum	(3)	*Jasminum didymum*	(<1)
	Canthium barbatum	(2)	*Triumfetta procumbens*	(<1)
	Allophylus timorensis	(1)	*Psilotum nudum*	(<1)
	Hibiscus tiliaceus	(1)	Bare ground	(68)
	Morinda citrifolia	(<1)		
	Homalium acuminatum	(<1)		
	Caesalpina major	(<1)		
	Mucuna gigantea	(<1)		
	Psidium guajava	(<1)		
	Psidium cattleianum	(<1)		
B	*Pandanus tectorius*	(53)	*Euphorbia chamissonis*	(15)
Pandanus Scrub	*Pipturus argenteus*	(17)	*Nephrolepis* sp.	(9)
(transects 3, 4, 7, 15)	*Ficus prolixa*	(16)	*Asplenium nidus*	(2)
	Guettarda speciosa	(7)	*Phymatosorus scolopendria*	(2)
	Glochidion ramiflorum	(5)	*Davallia solida*	(1)
	Schleinitzia insularum	(1)	*Procris pendunculata*	(1)
	Planchonella grayana	(<1)	*Peperomia* sp.	(1)
	Geniostoma sykesii	(<1)	*Ipomoea macrantha*	(<1)
	Ixora bracteata	(<1)	Bare ground*	(36)
C	*Barringtonia asiatica*	(97)	*Asplenium nidus*	(16)
Barringtonia Forest	*Hernandia moerenhoutiana*	(1)	*Nephrolepis* sp.	(5)
(transects 2, 5, 10, 14)	*Elaeocarpus tonganus*	(1)	*Davallia solida*	(3)
	Calophyllum inophyllum	(<1)	*Phymatosorus scolopendria*	(2)
	Ficus prolixa	(<1)	*Peperomia* sp.	(1)
	Pandanus tectorius	(<1)	*Ipomoea macrantha*	(1)
	Guettarda speciosa	(<1)	*Triumfetta procumbens*	(<1)
	Pipturus argenteus	(<1)	Bare ground	(71)

* Prostrate woody species in the ground cover of the *Pandanus* scrub (cluster B): *Scaevola sericea* (23%); *Eugenia reinwardtiana* (6%); and *Timonius polygamus* (4%).

and absence of alien hoofed mammals. Wind and salt-spray conditions also play a major role in this plant association. As the name implies, this association is dominated by *Pandanus tectorius*, with an average relative dominance of 53%. Although *Pandanus* had by far the highest absolute frequency (66%) in this association, in two of the four transects (nos. 7 and 15) it ranked only third in relative dominance behind *Ficus prolixa* and *Pipturus argenteus*.

The ground cover in the 40 sample plots (10 plots × four transects) of cluster B (*Pandanus* scrub) covered an estimated 64% of the surface area. The herbaceous plants covered ca. 30% of the surface and included *Euphorbia chamissonis* (15%), *Nephrolepis* sp. (9%), *Asplenium nidus* (2%), *Phymatosorus scolopendria* (2%), *Davallia solida* (1%), *Procris pendunculata* (1%), *Peperomia* sp. (1%), and *Ipomoea macrantha* (<1%). Prostrate woody species also covered a significant portion of

FIGURE 8. *Pandanus* scrub vegetation near the coast in the raised limestone region of Mangaia.

the surface area sampled in cluster B, especially in the two windswept transects (nos. 3 and 4) located near the coastal edge of the raised limestone. These woody species included *Scaevola sericea* (23%), *Eugenia reinwardtiana* (6%), and *Timonius polygamus* (4%).

Barringtonia *Forest*

Cluster C groups sample sites nos. 2, 5, 10, and 14, which are all located near the coast. The woody vegetation in these sites is almost completely covered by *Barringtonia asiatica*, with an average relative dominance of 97% (see Figure 9). The overwhelming dominance of *B. asiatica* in cluster group C may be explained by extreme natural disturbance events (e.g., tsunami or hurricanes). Where severe storm conditions produce very strong winds and/or high surf surges that sweep over and destroy the vegetation, cohort colonization by the large-seeded, salt-tolerant *B. asiatica* may occur. Wilder (1934) reported the prevalence of this large tree along the margins of the raised limestone plateau on Makatea Island in the Tuamoto Archipelago, "especially on the northern wind-swept end of the island ... where there is a large forest of them."

In each of the four transects in this cluster, *B. asiatica* had a relative dominance of >92% (*B. asiatica* was not recorded in any of the 16 other transects). The fact that this tree was not recorded in sites far inland or in the upland *makatea* areas lends support to the assumption that extreme disturbance events create the clearance and dispersal conditions appropriate for the establishment of the almost-pure stands of *Barringtonia* in sites near the coast.

The herbaceous ground cover in the 40 sample plots (10 plots × four transects) of cluster C covered an estimated 29% of the surface area. The species included *Asplenium nidus* (16%), *Nephrolepis* sp. (5%), *Davallia solida* (3%), *Phymatosorus scolopendria* (1%),

FIGURE 9. *Barringtonia* forest on the raised limestone of Mangaia.

Peperomia spp. (1%), *Ipomoea macrantha* (< 1%), and *Triumfetta procumbens* (< 1%). *Asplenium nidus* was generally very common in the shaded areas, while *Nephrolepis* sp. was frequently found in the more open environments of the *Barringtonia* forest.

Non-clustered Sites

Two transects (nos. 17 and 20) were not classified in any of the three cluster groups in the dendrogram analysis. *Ficus tinctoria* and *Casuarina equisetifolia*, which had the highest relative dominance figures in transect 17 (36% and 32%, respectively), were only recorded in this transect. The transect was located near the beginning of the rugged, windswept *raei* in the southeastern part of Mangaia, not far from a track leading through somewhat disturbed raised limestone vegetation. All of the woody plants recorded in transect 17 are native to Mangaia, except for *C. equisetifolia* (assumed in this study to be an alien species). Ignoring the question of the origin of *C. equisetifolia*, this transect could be lumped with the mixed native forest association. *Asplenium nidus* was very common in the ground cover (34%) of transect 17. *Euphorbia chamissonis* (13%), *Davallia solida* (9%), *Nephrolepis* sp. (4%), *Procris pendunculata* (3%), *Peperomia* spp. (2%), and *Phymatosorus scolopendria* (1%) were also recorded in the ground cover of this transect.

Transect 20 is the only sample located in the lower *makatea* forest near the coast and, as such, should be seen as belonging to another raised reef association adapted to lower, coastal conditions. Both *Hernandia nymphaeifolia*, and indigenous woody species with the highest relative dominance (58%), and *Cordia subcordata*, a woody aboriginal introduction with a much lower relative dominance (10%), were not found in any other transect.

FIGURE 10. The vegetation of the interior volcanic uplands of Mangaia is almost exclusively composed of alien species, including a successional fern (*Dicranopteris linearis*), guava (*Psidium guajava*, foreground), and ironwood (*Casuarina equisetifolia*, background).

The lower coastal *makatea* is referred to in the discussion below.

Human Impact on the Vegetation of Mangaia

The upland interior of Mangaia contains a deeply weathered and eroded substrate of basaltic soils that support a very open, almost completely anthropogenic vegetation. This predominantly herbaceous vegetation is probably an artifact of cutting and man-made fires that began during the period before European contact (cf. Kirch 1982 for Hawai'i and McGlone 1983 for New Zealand). Sykes (1980), describing the "upper volcanic area" of Mangaia (especially around the summit of Rangimotia), referred to "large areas of grass and fern" that were noted "in Captain Cook's time."

Almost all the plants in the upland interior today are either cultivated or naturalized species. Although some of these alien plants were brought in during the prehistoric Polynesian period, many more were introduced after the initial European contact in 1777.

Alien species, which overwhelmingly dominate the interior of the island, include cultivated plants of pineapple (*Ananas comosus*), cassava (*Manihot esculenta*), and bananas (*Musa* sp.) and widespread weedy species, including a number of grasses such as *Miscanthus japonicus*. Introduced woody species that have become naturalized in the interior uplands include *Casuarina equisetifolia*, *Psidium guajava*, and *Morinda citrifolia* (see Figure 10).

Only a small number of native species are now found in the interior of Mangaia. These include clumps of the early successional fern *Dicranopteris linearis*, within which are found

FIGURE 11. Poorly drained depressions located between the interior upland region and the steep inner wall of the raised limestone contain the most fertile and intensively cultivated soils on Mangaia.

isolated, often stunted, woody individuals of *Glochidion ramiflorum*, *Homalium acuminatum*, *Melastoma denticulatum*, *Dodonea viscosa*, and *Osteomeles anthyllidifolia*.

The lowland interior vegetation zone on Mangaia includes the valley floors, toeslopes, and poorly drained depressions and lake margins that are located between the valley floors or volcanic hills of the interior upland region and the steep, often sheer, inner wall of raised limestone (30–60 m). Although this zone contains the most fertile soils (alluvium and colluvium) on Mangaia (see Figure 11), almost all of the native plant life in the lowlands has been replaced by either cultivated species (especially taro, *Colocasia esculenta*, which is planted in flooded swamps that cover much of the area of this zone) or by a number of alien weeds (see Figure 12). The weeds include sedges and grasses, with *Scirpus subulatus* and *Nymphaea rubra* in the permanently flooded areas and dense broadleaf forest of minimal diversity in the drier areas where fires have had less effect. One of the few native species that can be found occasionally in the lowland interior is *Elaeocarpus tonganus*. The dominant species in this vegetation zone include *Hibiscus tiliaceus* (assumed in this study to be an aboriginal introduction [see Fosberg 1975]) and other alien woody plants such as *Aleurites moluccana*, *Cocos nucifera*, and *Psidium guajava* (Webb 1981).

In addition to the four *makatea* plant associations described above, the limestone vegetation zone can also be divided into the lower coastal *makatea* areas, which are only a few meters above sea level, and the higher inland *makatea* areas, which reach heights of up to 70 m. The lower coastal *makatea* vegetation comprises a thin belt of windswept scrub and small trees that lies near or on the edge of the rocky coast. Species commonly found in the scrub include *Pemphis acidula*, *Scaevola sericea*, *Tournefortia argentea*, *Myoporum*

FIGURE 12. Wetland cultivation of the major staple crop (*Colocasia esculenta*) on Mangaia in foreground; raised coral limestone region in distant background.

sandwicense, *Schleinitzia insularum*, and *Sophora tomentosa*. The area inland from the scrub on the lower coastal *makatea* is covered by a stunted, disturbed broadleaf forest that is normally dominated by *Hernandia nymphaeifolia*, *Pandanus tectorius*, or *Casuarina equisetifolia* and often includes *Hibiscus tiliaceus* and *Cocos nucifera*. In this region, the coconut palms are normally emergent and often self-sown. Only one of the three villages of the island, Oneroa, is located (partially) in the lower coastal *makatea* region. One transect (no. 20) was sampled in this region (north of Oneroa); it was discussed above.

The formidable obstacle of a steep cliff usually presents a clear boundary between the low coastal and higher inland *makatea* regions. Except near villages, roads, and footpaths, the higher *makatea* areas are still largely unaffected by human disturbance. Unlike the vegetation in the interior lowland and interior upland zones on Mangaia, which are predominantly composed of alien species, the woody and herbaceous plants found on much of the rugged higher *makatea* are almost all native to the island. The biomass and height of the woody species in this region are inversely related to the amount of limestone outcropping. In the *raei* areas where the surface contains numerous, closely packed, sharp limestone pinnacles, with limited amounts of soil in the intervening crevices, the vegetation is relatively sparse and usually dominated by stunted *Pandanus tectorius*, and often includes *Guettarda speciosa*, *Ficus prolixa*, and *Pipturus argenteus* (the *Pandanus* scrub association). These *raei* areas (usually quite localized) are difficult and dangerous to traverse, especially when wet. Consequently, they are usually avoided by humans and other large, introduced mammals on the island (Mark 1976). Therefore, the *raei* areas are virtually unchanged by direct or indirect human inter-

FIGURE 13. Disturbed forest on the raised coral limestone of Mangaia with common successional woody component, *Hibiscus tiliaceus*.

ference. A relatively large *raei* area is found in the southwestern part of the island (see Figure 5).

On the more moderately rugged, undisturbed surfaces of the higher, inland *makatea*, a somewhat open-canopied, scrubby forest can be found. This usually includes *Guettarda speciosa*, *Hernandia moerenhoutiana*, *Elaeocarpus tonganus*, *Pandanus tectorius*, *Ficus prolixa*, *Glochidion ramiflorum*, and *Pipturus argenteus*. In some areas of the higher inland *makatea* there are relatively large pockets of fertile soils (up to 60 cm deep) derived from basaltic alluvium deposited in earlier geologic times. These soil pockets, known locally as *kavava*, support well-developed, closed-canopy forest of medium height (the mixed native forest association in undisturbed situations). In a number of places on the inland raised limestone, cultivation does occur, especially in those areas close to two villages (Tamarua and Ivirua) that are located entirely on the higher inland *makatea*, and near footpaths where the surface is less jagged and there are many pockets of deep, rich soil. In those areas the vegetation is in various stages of human alteration (the mixed disturbed forest association), with *Hibiscus tiliaceus* as a common successional woody species that invades abandoned cultivated plots (see Figure 13). Human disturbance in these less rugged, more accessible areas in the upland *makatea* began in the period before Western contact.

Mark (1976) has described an ecologically adapted system of resource utilization that has existed, at least to some extent, on Mangaia since the precontact period. This land use system involved the Mangaian *puna* (equivalent to the *tapere* of Rarotonga and the *ahupua'a* of Hawai'i), which included five major ecological complexes or zones identified and exploited for a variety of organic and inorganic materials. The zones of the Mangaian *puna* include the sea (*tai*), the shoreline (*pae tai*), the raised reef areas (*makatea*), the inland food-producing areas (*kainga*), and the mountain region (*maunga*).

Generally, these ecological zones are arranged concentrically around the fixed central point of Rangimotia peak (169 m), the highest elevation on Mangaia. In precontact times (before 1777), sedentary cultivation of subsistence root and tree crops took place primarily in the uplands and lowlands of the volcanic interior; however, some cultivation as well as hunting and gathering took place on the *makatea*. According to Buck (1934), sweet potatoes (*Ipomoea batatas*) may have been cultivated by members of conquered tribes that had to seek refuge in the rugged *makatea*. On the raised limestone these "defeated peoples" and others collected a variety of edible and other utilitarian materials from wild plants including those from alien species that had become naturalized on the *makatea* such as *Cocos nucifera* (*nu*), *Cordyline fruticosa* (*ti*), *Hibiscus tiliaceus* (*'au*), *Morinda citrifolia* (*nono*), and *Aleurites moluccana* (*tuitui*).

In addition, fruit bats (*Pteropus tonganus*) and rats (*Rattus exulans*) were hunted in the *makatea*; this activity may have had some lasting impact on the vegetation of the raised reef environments. Rats are said to have supplied the human population's "protein requirement" during periods when seas were too rough to carry out successful fishing (Mark 1976). The introduced rats themselves probably had some impact on both plants and animals in the *makatea* before European contact (e.g., extinction of some birds species [see Steadman 1985, 1989]).

Human impact on the vegetation in the raised limestone areas began on a limited scale in precontact times and, as noted above, continues in some areas today. For example, *Calophyllum inophyllum* (*tamanu*) is a traditionally valuable timber tree on Mangaia; it may have been a more common component of the native vegetation before humans colonized the island. Selective cutting of this species over generations probably explains its current rarity on the island. Except for those located in the villages, few large *C. inophyllum* trees are left. Apparently the Mangaian people "know where every one of them is, and keep their eyes on them" (David Steadman, New York State Museum, pers. comm., 1990).

Although the native vegetation of the interior volcanic uplands and much of the coastal margins of Mangaia has been replaced with aboriginally or historically introduced species, the *makatea* vegetation is overwhelmingly dominated by native species, except in raised reef areas close to footpaths, roads, or human habitation. Of the woody species recorded in the sample transects, 73% are native to the island. The average relative dominance of the native woody species in all 20 transects combined on the raised limestone is 88%. There appears to be a direct relationship between the degree of substrate ruggedness and the relative dominance of native woody species on the *makatea*. In both disturbed and undisturbed areas of the raised limestone, the herbaceous vegetation is still almost completely composed of native species. The average relative dominance of native herbaceous plants (percentage ground cover of native versus alien species) for all 20 sample transects is >99%.

From a conservation standpoint, the raised reef environments of Mangaia represent major refugia for native plants. These native plants reveal, to a certain degree, the nature of the original flora and vegetation on Mangaia before humans arrived and began to alter the ecosystems of the island. More ecological research is needed in the interesting and unique *makatea* environments of Mangaia, and elsewhere in the tropical Pacific where raised reef environments are found.

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ADDENDUM

Recent pollen analyses of lake sediment cores from the Cook Islands (e.g., Atiu) indicate that coconut palms (*Cocos nucifera*) "appear to pre-date archaeological settlement records by a considerable amount" (Annette Parks, School of Geography and Earth Resources, University of Hull, pers. comm.). If this interpretation is correct, and the coconut is not alien to Mangaia and other Cook Islands, then the relative dominance of native woody species described here rises significantly in some sample transects (i.e., 1, 6, 19, 8, and 20). It must be kept in mind, however, that the present distribution of coconut palms undoubtedly has been strongly affected by human activity on Mangaia.