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Species-environment patterns of forest vegetation on the uplifted reef limestone of Atiu, Mangaia, Ma'uke and Miti'aro, Cook Islands

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Abstract. We examined woody species composition and its relation to environmental variables in native forest growing on four limestone islands in the southern Cook Islands: Atiu, Mangaia, Ma'uke, and Miti'aro. Relative dominance (percent basal area) of woody species in 74 sites was sampled using the point-centered quarter method, and the data were analyzed using clustering and ordination techniques. These tropical forests have a relatively low diversity of native woody species (32 native and 10 introduced species occurred in our sites). Four forest types were recognized: *Pandanus/Guettarda* littoral forest (with several subtypes), *Hernandia nymphaeifolia* littoral forest, *Barringtonia* littoral forest, and *makatea* forest (dominated by *Elaeocarpus tonganus* and *Hernandia moerenhoutiana*). These types were related, using canonical correspondence analysis, to geographical attributes (windwardness, elevation, and proximity to the coast or roads) that served as surrogates for environmental variables (maritime influence, soil variation, and degree of human disturbance). The eigenvalues for this direct ordination were much lower than for indirect ordination (0.32 vs. 0.71 for the first axis), indicating that the measured geographical attributes could explain only a modest portion of the compositional variation.

Keywords: Canonical Correspondence Analysis; Detrended Correspondence Analysis; *Makatea*; Oceania; Ordination; Polynesia; Tropical forest; Two-way indicator species analysis.

Nomenclature: Whistler (1990).

Introduction

Atiu, Mangaia, Ma'uke, and Miti'aro in the southern Cook Islands (Fig. 1) are composed of low central hills of highly weathered volcanic material surrounded by elevated coral limestone formations known locally as *makatea*. This arrangement of geomorphic features is relatively rare among the Pacific islands (Wood & Hay 1970; Stoddart 1975a; Stoddart, Spencer & Scoffin 1985). Alien plant species dominate on the volcanic

areas, the site of agricultural activities; however, native vegetation is largely intact on the rugged *makatea* (Sykes 1976a-d) because the karst topography is unsuitable for most forms of cultivation.

There have been few botanical studies in the southern Cook Islands (Sykes 1980a), and most have been based on collections from Rarotonga, a high island (Cheeseman 1903; Wilder 1931; Philipson 1971; Fosberg & Sachet 1972; Stoddart 1972; see Stoddart 1975a for other references), and Aitutaki, an almost-atoll (Fosberg 1975; Townsend 1975; Stoddart 1975b and c). No flora for the entire Cook Islands has been published. Although there have been some descriptive botanical studies of the *makatea* islands in the Cook Islands (Sykes 1976a-d, 1980b; Whistler 1988, 1990) and elsewhere in the Pacific (Wilder 1934), few quantitative analyses of the species assemblages or species/environment relations of native forest have been carried out in the southern Cook Islands (Merlin 1985, 1991), or anywhere in the tropical Pacific (e.g. Whistler 1983; Sabath 1977; Kirkpatrick & Hassall 1985) other than Hawaii.

Ecological associations on the Pacific islands have been altered by both Polynesian and European introductions of non-native plants and animals (Olson & James 1982, 1984; Kirch 1982; Merlin 1985, 1991; Steadman 1989; Dye & Steadman 1990). An assessment of the extent of human disturbance is critical to conservation of the indigenous biota of the region (Whistler 1980; Sykes 1983; Dahl 1986; Pearsall in press b). For example, many species of landbirds in Polynesia are on the verge of local or complete extinction because of habitat disturbance and destruction by humans (Steadman 1989). A recent study of food resources of native landbirds on Atiu, Ma'uke, and Miti'aro found that they were almost entirely dependent on the fruits and seeds of indigenous forest plants (Franklin & Steadman in press). The objective definition of forest community types and ecoclines (sensu van der Maarel 1990) is a prerequisite to biological conservation in Polynesia (Pearsall in press a; Franklin

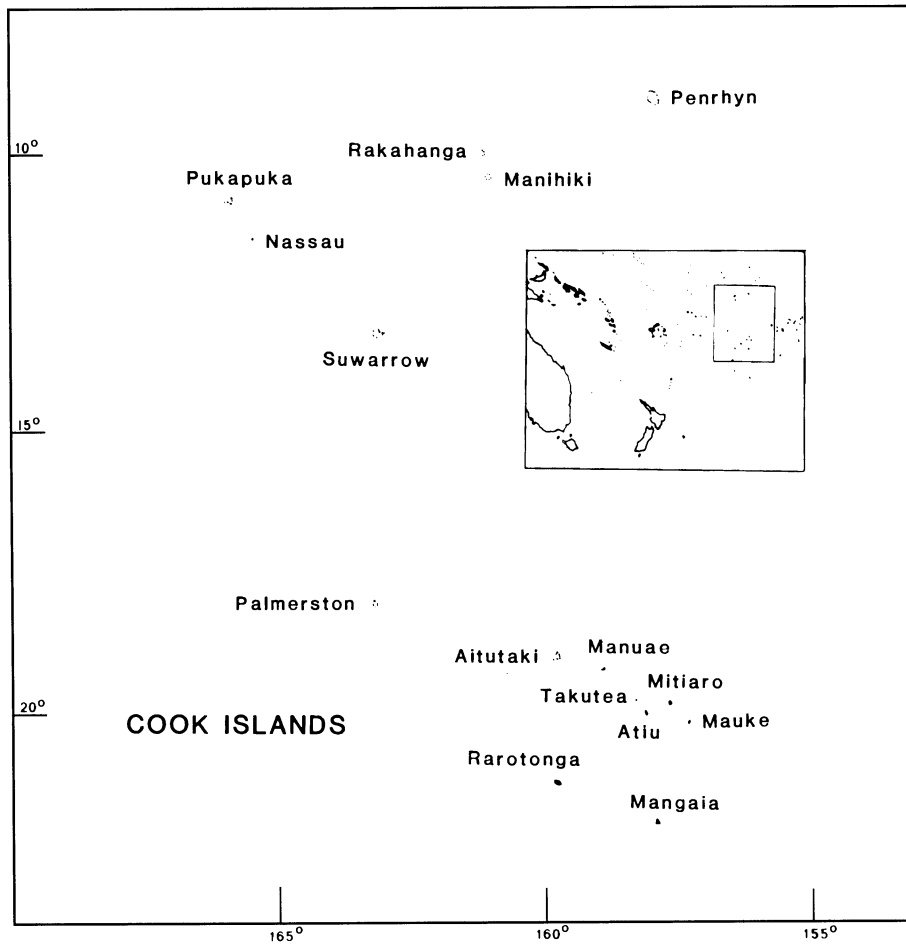


Fig. 1. Map showing location of Atiu, Mangaia, Ma'uke, and Miti'aro in the southern Cook Islands. Inset shows the location of the Cook Islands in the west central Pacific, relative to new Zealand and Australia. Figure reprinted from Franklin & Steadman (in press) by permission of Blackwell Scientific Publishing.

& Steadman in press).

In the present study, our purpose is two-fold: to describe the forest species assemblages on these little-studied *makatea* formations, and to relate species composition gradients to environmental variables. In addition, we wish to answer the following question: given four geomorphologically similar islands, can a general vegetation classification system be defined, or do inter-island floristic differences have an overriding effect on community composition? We addressed these objectives by applying classification and ordination methods to species composition and environmental data from 74 forest sites. Compositional variation was related to environmental variables by calculating correlation coefficients between the environmental variables and ordination axes derived by detrended correspondence analysis (DCA). Finally, canonical correspondence analysis

(CCA) was used to relate the samples directly to the measured environmental variables.

Study area

The southern Cook Islands lie at the southern edge of the persistent trade wind zone of the South Pacific. Winds are most frequently from the east and southeast. Mean annual temperature is 24 to 26 °C, with a greater diurnal than annual range. Rainfall is markedly seasonal with two thirds of the rain falling between November and April. The long-term average annual rainfall is between 1900 and 2050 mm for the southern Cook Islands (Thompson 1986). On Atiu, Mangaia, Ma'uke, and Miti'aro the central hills are separated from the encircling *makatea* by an annular swampy depression.

Just offshore from the *makatea* is a narrow fringing reef. These islands share this raised limestone formation with *makatea* in the Tuamotu Group (Wood & Hay 1970). The *makatea* is an old fringing reef surface that has been exposed through tectonic uplift (Wood & Hay 1970; Stoddart 1975a; Stoddart, Spencer & Scoffin 1985).

The dissected central plateau of Atiu (19° 59' S, 158° 08' W) rises to an elevation of 72 m. The total land area is 2693 ha (Anon. 1983). The *makatea* has a maximum elevation of about 30 m, is almost a km wide in some places, and covers an area of about 1440 ha. The karst surface has sinkholes, caves and pinnacles 1 m or more high (Wood & Hay 1970). The cracks in the *makatea* are filled with lateritic clay soil that supports dense forest cover 10-15 m tall.

Miti'aro is 27 km east-northeast of Atiu (19° 52' S, 157° 43' W) and about the same size (2226 ha), but lower lying with much less arable land. The volcanic center is composed of four small hills (maximum elevation 15 m), extensive swamps, and a large shallow lake. The *makatea* is about 1650 ha and has a maximum elevation of only 10 m. It supports scrub (ca. 3 m high) with taller forest only near the inside edge (toward the swamp) and near the coast on the lee side of the island (Sykes 1976b). The surface of the *makatea* is generally less rugged than on Atiu.

Ma'uke (20° 09' S, 157° 21' W) is 50 km east-southeast of Atiu. It is smaller than the other two islands, covering 1842 ha. The central plateau rises to 29 m, and the *makatea* to about 20 m. Ma'uke supports a forest (8-12 m tall) similar to the one on Atiu except that *Elaeocarpus tonganus* is absent (Sykes 1976c).

Mangaia (21° 55' S 157° 58' W) is 116 km south of Atiu, and is 5180 ha. The volcanic center rises to 169 m elevation and the *makatea* to 50-70 m with a steep cliff face separating it from the interior of the island (Merlin 1991).

In general, the *makatea* vegetation of the southern Cook Islands has been described as grading from littoral strand and coastal scrub communities to the taller forest of the upland *makatea*. The canopy consists mainly of widespread Polynesian littoral species, and a few endemics (Whistler 1988, 1990; Merlin 1991).

Methods

We hypothesized, based on field reconnaissance, that environmental variation on the *makatea* has affected the establishment and survival of forest canopy species in different ways. Although environmental factors could not be sampled exhaustively, we recognized the following gradients: (a) maritime influence (salt spray and wind desiccation) decreased with increasing

distance from the coast and with leewardness (due south-east was considered the extreme windward position in this study); and, (b) soil qualities also vary with distance from the coast. (All sites were located on coralline limestone, but inland sites were located on pit and pinnacle karst with volcanically derived soil in the fissures, while on coastal terraces the limestone was more eroded, and the soil contained more sand.) Depth to and salinity of the water table are probably correlated with distance from the coast and elevation. Also, introduced species tended to be located nearer to cultural features such as roads or tracks. We expected that the species composition of sites would be related to these geographical variables.

Sample site locations were chosen to represent the range of environmental variables analyzed in the study. Stratification was based on field reconnaissance and air photos. Sites were sampled using the point-centered quarter method (Cottam & Curtis 1956) described in Mueller-Dombois & Ellenberg (1974) and used by Merlin (1985, 1991). In brief, every 10 m along a 90 m transect, the distance to and diameter of the nearest tree larger than 2.5 cm diameter at base (DAB) was measured in each quarter, where the quarters are delineated by the sampling transect and a line perpendicular to it. Height of the canopy was also estimated at each point. Relative basal area and density of tree species per site (transect) were calculated from the 40 measured trees. This method was consistent with our goal of sampling within homogeneous areas of the *makatea* forest, which occur in annular rings corresponding to the physiography (Wood & Hay 1970; Franklin & Steadman in press). Species composition tends to remain constant along transects oriented parallel to the coast.

We sampled a total of 74 sites, 29 on Atiu, 7 on Ma'uke, 18 on Miti'aro, and 20 on Mangaia. (Fewer sites were sampled on Ma'uke because MM was only able to arrange to spend a short time there.) Most sampling was done during July 1986 by MM except that eight of the Atiu sites were sampled during October 1987 by JF. Voucher specimens collected by MM were deposited in the Bishop Museum, and duplicates were deposited with A. Whistler, University of Hawaii. Those collected by JF were deposited with M. Simpson, Department of Botany, SDSU. An analysis emphasizing human impact on the vegetation has been published previously for the Mangaia sites (Merlin 1991).

For each site, the following geographic attributes were recorded: (1) distance to the coast, (2) elevation, (3) aspect (direction to the coast) as a measure of leewardness, and (4) distance to the nearest road, track or other cultural feature (e.g. agricultural clearing) as an index of disturbance. These were all measured by pacing the distances, or from a topographic map. An aspect

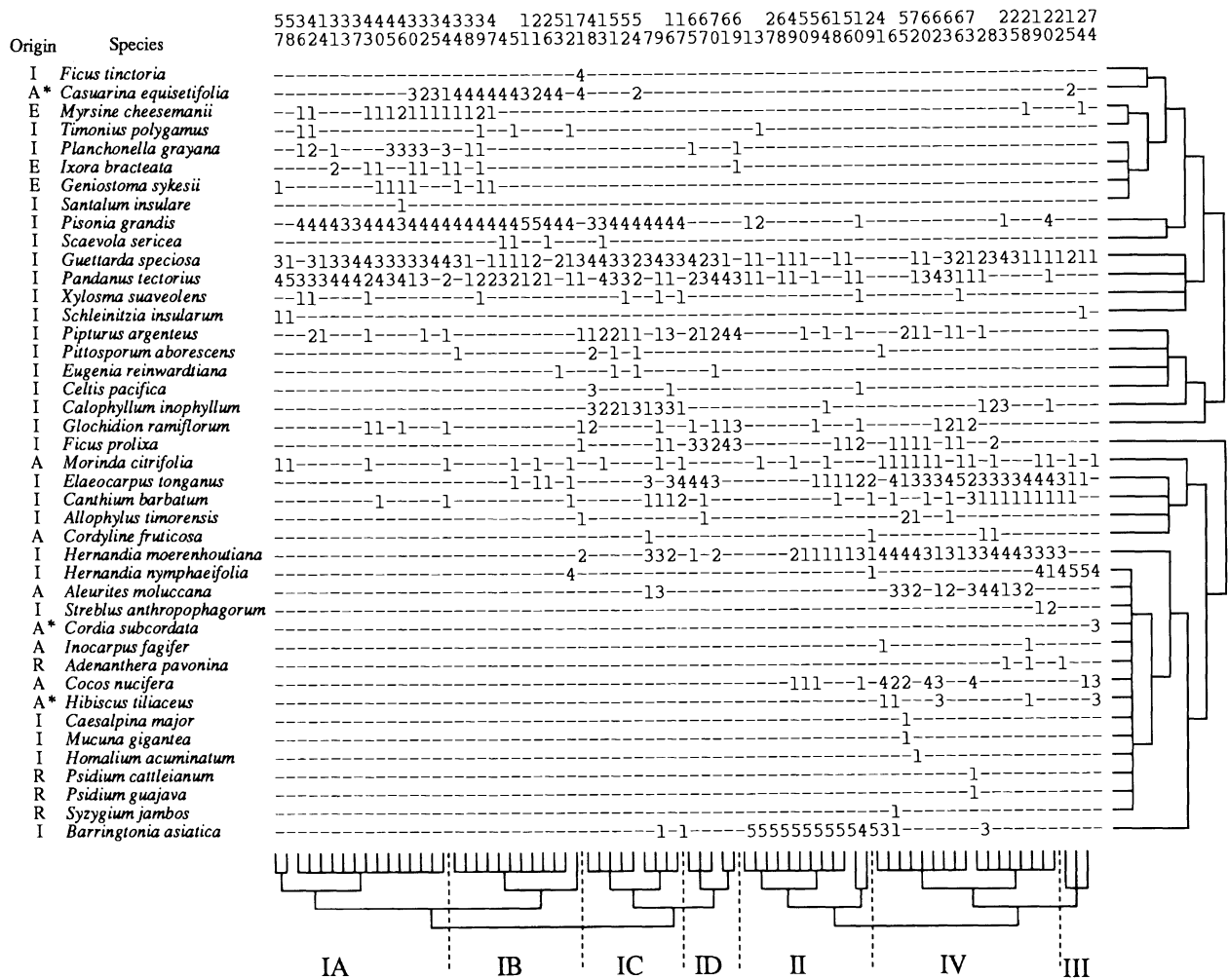


Fig. 2. TWINSpan ordered data table for 74 sites showing linkages based on similarity of site scores (columns) and species scores (rows). Hierarchical linkages of sites are shown in the bottom rows, and of species in the right columns. Symbols for origin of species are: E - endemic; I - indigenous to the Cook Islands; A - aboriginal introduction; R - recent or historical introduction; * - may be indigenous. Numbering of sites (top row) is as follows: 1-29: Atiu sites; 30-47: Miti'aro sites; 48-54: Ma'uake sites and 55-74: Mangaia sites.

of 135° (the prevailing wind direction) was set to zero and all aspects were coded 0-180° symmetrically from southeast (windward) to northwest (leeward). Environmental variables were sorted and plotted against quantiles of the normal distribution to examine for normality. Based on this analysis, aspect was square-root transformed and distance to the coast and distance to disturbance were log transformed. Sampled elevation values were normally distributed and were not transformed. Unfortunately, environmental data were not available for the Mangaia sites because the study was initiated there before direct ordination was considered as a data analysis method.

The clustering technique applied to the species in sites data was Two-Way Indicator Species Analysis

(TWINSpan) (Hill, Bunce & Shaw 1975). In this method site scores and species scores are calculated by reciprocal averaging, as in the ordination techniques described below. The sites are ordered first by divisive, hierarchical clustering, and then the species are clustered based on the classification of the samples. We set the pseudo-species cut levels (equally-weighted classes of relative dominance) to 0-5, 5-10, 10-25, 25-75, and 75-100 percent basal area.

We examined the *makatea* forest community composition using indirect and direct gradient analysis (Noy-Meir & Whittaker 1977; ter Braak 1987a). Ordination assumes that species occurrences are determined by a few environmental variables according to a simple response model. In particular, Correspondence Analysis

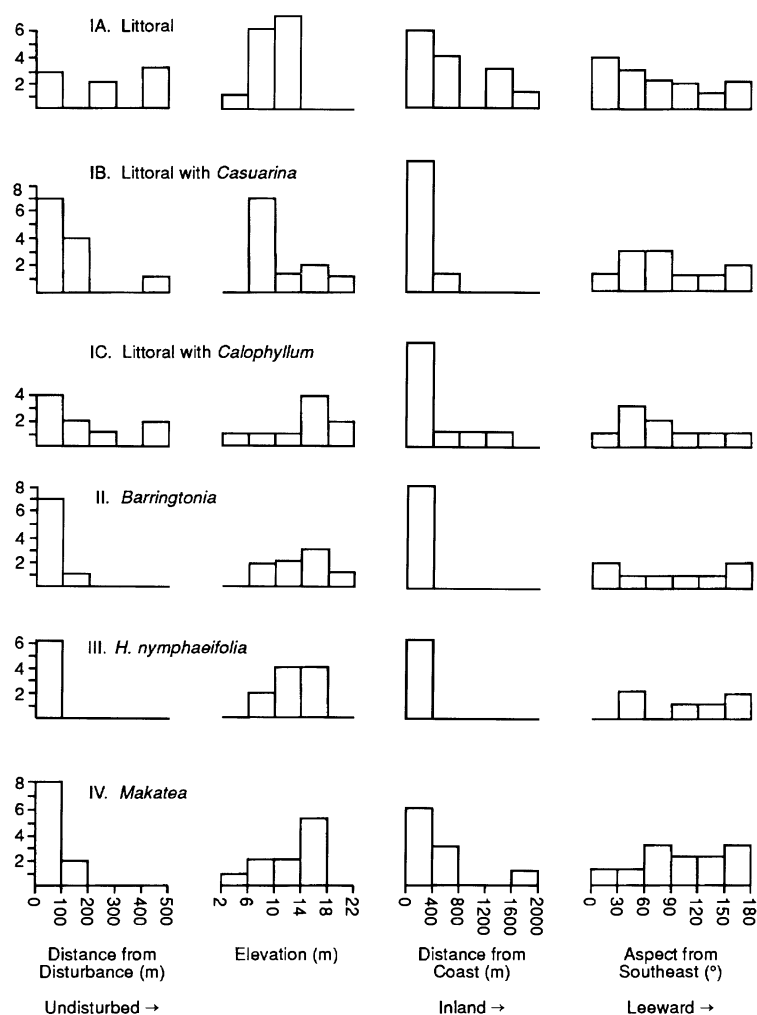


Fig. 3. Histograms showing distribution of environmental variables within the types defined in Fig. 2.

Table 1. Average density, basal area and canopy height for types based on TWINSpan dendrogram (Fig. 2); *n* is the number of sites in the type. Values for Type III included transitional sites 20, 22, 29 and 12 (the latter were also used in the average calculated for their respective types). Standard deviation in parentheses.

Type	<i>n</i>	Density (per 100m ²)	Basal area m ² /100m ²	Height (m)
IA	16	24.5 (16.7)	0.43 (0.50)	4 (2)
IB	12	30.0 (11.4)	0.86 (0.46)	6 (1)
IC	9	16.0 (5.1)	0.41 (0.30)	8 (3)
ID	5	12.5 (3.4)	0.09 (0.01)	4 (1)
II	12	6.8 (3.5)	1.67 (1.11)	11 (3)
III	7	19.8 (10.2)	0.84 (0.54)	11 (4)
IV	17	15.1 (5.3)	0.54 (0.41)	10 (3)

(CA) assumes unimodal species response curves along environmental gradients (ter Braak 1987a). Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980) is a heuristic modification of CA that corrects for the compression of the ordination axes near their ends and the arching of the second axis with respect to the first, and so on (ter Braak 1987a). These ordination techniques do not necessarily yield axes that are stable (Knox & Peet 1989; Knox 1989) or that can be interpreted in terms of underlying environmental variables beyond one or two dimensions (Peet 1980) because the environmental factors may not conform to a consistent, geometric model (Oksanen 1988). However, correspondence analysis is robust with respect to violations of the underlying statistical model (Hill & Gauch 1980).

In the indirect gradient analyses, the relative dominance values were log-transformed in order to decrease the influence of the nearly monospecific stands on the ordination, and rare species were down-weighted. Sites

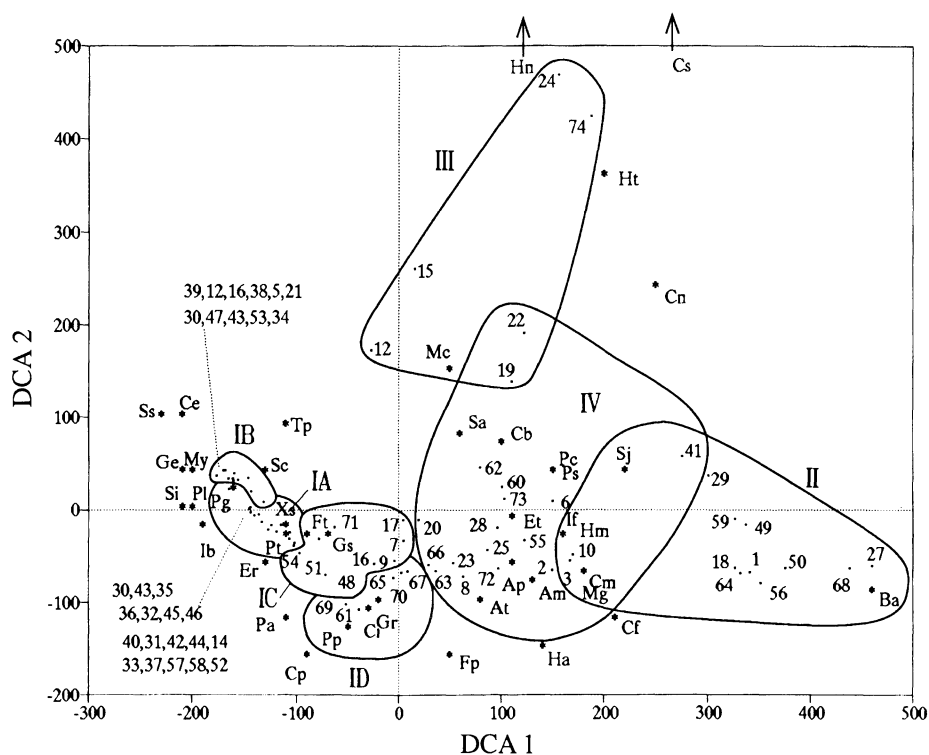


Fig. 4. DCA ordination diagram for 74 sites (•) and 42 species (*) plotted on first (DCA1) and second (DCA2) ordinations axes. Units are average standard deviations of species turnover $\times 100$ (Gauch 1982). Numbering of sites is as in Fig. 2. The types (groups of sites) identified in Fig. 2 are circled. Species are labelled by the first letter of genus and species (refer to Fig. 2) with the following exceptions: Ge = *Geniostoma sykesii*, My = *Myrsine cheesemanii*, Ps = *Psidium guajava*, Sc = *Schleinitzia insularum*.

were analyzed by DCA (detrended by segments) using the computer program CANOCO (ter Braak 1987b). Finally, a direct ordination technique, canonical correspondence analysis (CCA), was performed using CANOCO. CCA constrains the axes to be linear combinations of environmental variables, and maximizes the dispersion of species scores by the method of reciprocal averaging using iterative multiple regression of site scores on environmental variables (ter Braak 1986, 1987b). Ter Braak (1986) suggests using DCA and CCA together to see how much of the variation in the species data is accounted for by the environmental data. The Mangaia sites were included in the CCA as passive samples because environmental data were not available.

Results

Inspection of the dendrogram produced by TWINSPAN (Fig. 2) reveals that sites tend to cluster into four main groups:

I. *Pandanus/Guettarda* littoral forest

The first division in the dendrogram separates the littoral forest sites dominated by *Pandanus tectorius* and *Guettarda speciosa* from all other sites. The majority of the sites on Miti'aro (sites 30-47) and Ma'uke (sites 48-54) fall into this category. This group is further differentiated into (IA) with *Pisonia grandis* as a dominant; (IB) also with *Casuarina equisetifolia*, considered to be an aboriginal introduction in this study; (IC) also with *Calophyllum inophyllum*; and (ID) without *Pisonia grandis* or *C. inophyllum* but with *Ficus prolixa* and *Pipturus argenteus* as codominants (this group composed only of sites from Mangaia). It has been suggested that *C. inophyllum* is rare on Mangaia as a result of human impact (Merlin 1991), but it is not known if the other differences between IC and ID are of ecological or biogeographical significance.

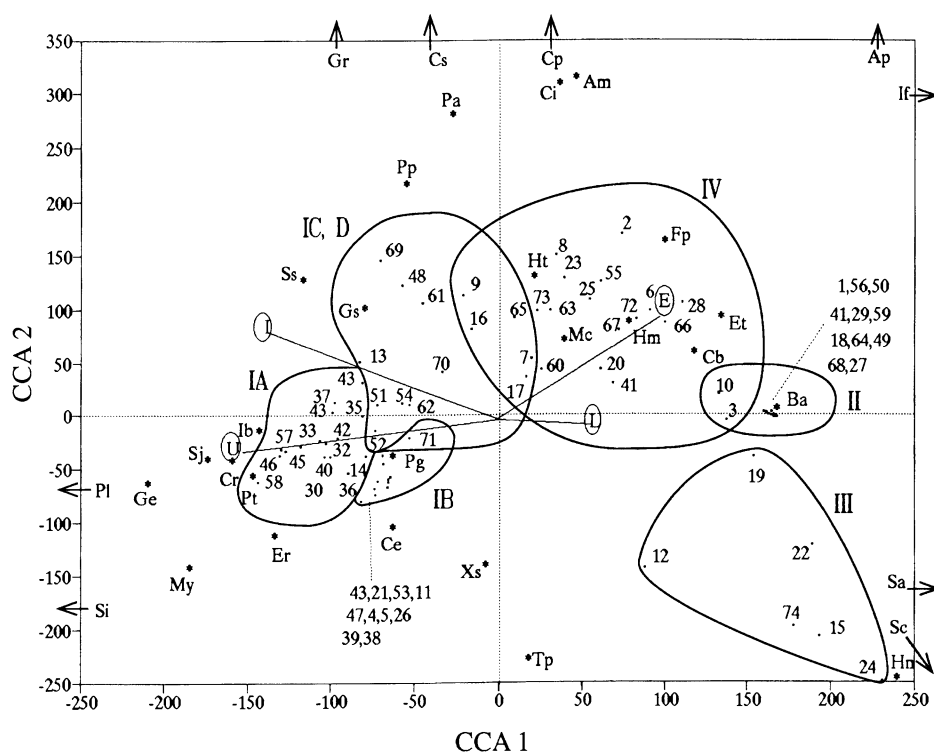


Fig. 5. CCA ordination diagram showing sites (•), species scores (*) and environmental variables (vectors with circled labels), plotted on the on first (CCA1) and second (CCA2) ordinations axes. See caption of Fig. 4 for explanation of species labels. Environmental variables are labeled: U = undisturbed (distance from disturbance); E = elevation; I = inland (distance from coast); L = leewardness (northwest aspect).

II. *Barringtonia* littoral forest

This type consists of almost pure stands of *Barringtonia asiatica* and was sampled on all islands but Miti'aro (although site 41 from Miti'aro is transitional between types II and IV).

III. *Hernandia nymphaeifolia* littoral forest

This type is dominated by *Hernandia nymphaeifolia* and is composed of sites from Atiu and Mangaia, the two larger, higher islands.

IV. *Makatea* forest

This type is dominated by *Hernandia moerenhoutiana* and *Elaeocarpus tonganus*, and is also composed of sites from Atiu and Mangaia (with one site from Miti'aro, 41, mentioned above).

Table 1 shows that these types differ structurally as well, although the sample size is small and variance high. Among the littoral forest type (I), IA is composed of dense stands of small short trees, while IB has higher

basal area and taller trees, and IC is composed of lower density stands. Type ID consists of short, sparse stands with very low basal area. Type II is composed of open stands of *Barringtonia asiatica* with very high basal area. Type III (*Hernandia nymphaeifolia* littoral forest) is similar in structure to IB, and *makatea* forest (Type IV) is similar to IC. It has been suggested that the point-centered quarter (PCQ) sampling method gives higher basal area estimates than fixed-area plot methods because basal area is overestimated in sites with a large range of diameter classes (Mark, Dickinson & Fife 1989 and references therein). PCQ-derived basal area estimates in this study are somewhat higher than those calculated from plot methods for similar forests in Tonga and Hawaii (D. Drake unpubl. data), and one should be cautious when comparing these figures to estimates based on other sampling methods. The basal area for type II is high because individual *Barringtonias* have large basal diameters (one was 244 cm).

The patterns of environmental variables within types (Fig. 3) are ambiguous because of the small variance in the observed values (especially distance to disturbance and to the coast), but some trends are evident. Littoral types IB, II and III only occurred close to the coast and

Table 2. Comparison of the results of Detrended Correspondence Analysis (DCA), Canonical Correspondence Analysis (CCA), and Detrended (by segments) Canonical Correspondence Analysis (DCCA) of *makatea* vegetation data (42 species in 74 sites); eigenvalues and species-environment correlation coefficients for the four species ordination axes.

	Axis			
	1	2	3	4
	Eigenvalues			
DCA	0.71	0.33	0.18	0.10
CCA	0.32	0.15	0.07	0.05
DCCA	0.32	0.14	0.05	0.03
	Species-environment correlation coefficients			
DCA	0.55	0.51	0.41	0.17
CCA	0.65	0.55	0.46	0.42
DCCA	0.67	0.56	0.42	0.42

IB only at the lowest elevations, while types IA and IC (with *Calophyllum inophyllum*) also occur at higher elevations, further inland, and on undisturbed sites. Type IA tends to occur more often on windward aspects and Type II on leeward aspects. *Makatea* forest occurs at higher elevations more frequently than any of the littoral types except IC; but, *makatea* forest occurs more frequently on leeward aspects than IC.

When plotted on the first two DCA ordination axes (Fig. 4), the sites tend to group into the types and subtypes described above. The ordination biplot displays graphically which sites are transitional in their composition between the types differentiated by clustering. The first DCA axis is associated with increasing *Barringtonia* (Ba) and decreasing *Casuarina* (Ce), and the second axis with increasing *Hernandia nymphaeifolia* (Hn) and decreasing *Calophyllum inophyllum* (Ci) and *Ficus prolixa* (Fp). Table 2 shows that eigenvalues, at least for the first DCA axis, were relatively high (this ordination axis captured a large portion of the variation in species composition among sites), but the species-environment correlation coefficients were low for the DCA axes. The species-environment correlation is “the correlation between the site scores which are weighted species scores and the site scores which are linear combinations of environmental variables” (ter Braak 1986 p. 1169). The ordination axes based on the species data alone were not strongly related to the measured environmental variables.

The species-environment correlations are slightly higher for the CCA axes (Table 2). This is expected as the axes in CCA are calculated based on species scores and environmental variables. Correlation coefficients

Table 3. Intraset correlations of environmental data with the first three species axes of Canonical Correspondence Analysis (CCA). The environmental variables were standardized to unit variance after some were transformed (see text).

Axis	Correlation coefficients		
	1	2	3
Environmental variables			
Undisturbed	-0.44	-0.09	0.02
Elevation	0.28	0.34	-0.05
Inland	-0.39	0.27	0.25
Leeward	0.16	-0.02	0.42

indicate that the measured environmental variables do account for some of the species variation. However, the eigenvalues for the CCA axes are substantially lower than for DCA (Table 2) suggesting that important site variables have not been measured.

The correlations of the environmental variables with the CCA axes (Table 3) provide the following interpretation for the CCA ordination diagram shown in Fig. 5: axis 1 is increasingly coastal, disturbed and leeward, and axis 2 shows increasing elevation and distance from the coast. Axis 3 (not shown in Fig. 5) is increasingly leeward. However, intraset correlations are low (Table 3). Some arching is apparent in the CCA biplot (Fig. 5, axis 2 has a quadratic relationship to axis 1), but detrended CCA (detrended by segments) yielded essentially the same results (DCCA, Table 3) and pattern of species and sites distributed on the ordination axes (not shown).

In the CCA ordination (Fig. 5), the position of sites relative to each other is similar to the DCA ordination (Fig. 4), although the dispersion of sites is different. Type I sites occupy more of the ordination space defined by the first two axes, while Type II occupies less. The only major difference in the pattern of sites in the two ordinations was that Types IC and ID did not occur in separate groups in the CCA ordination. This was presumably because the Mangaia sites (comprising ID) were passive and therefore had no influence on the extraction of the ordination axes, but were added afterwards using transition formulae (ter Braak 1987b). The position of the groups of sites relative to the environmental vectors (Fig. 5) provides support for the patterns inferred from Fig. 3. Type IB is more disturbed and coastal than Type IA, and Type IC occurs at higher elevation than IA and B. Type IV occurs on leeward aspects. Note that *Barringtonia asiatica* (Ba) and *Hernandia nymphaeifolia* (Hn) tend to occur in coastal and leeward sites, the introduced species *Aleurites moluccana* (Am), *Adenantha pavonina* (Ap), *Inocarpus fagifer* (If), *Morinda citrifolia* (Mc), and *Hibiscus*

tiliaceus (Ht) in disturbed inland sites, and the indigenous or endemic species *Santalum insulare* (Si), *Geniostoma sykesii* (Ge) and *Myrsine cheesemanii* (My) in undisturbed sites. *Hernandia moerenhoutiana* (Hm) and *Elaeocarpus tonganus* (Et) tend to occur at higher elevation, inland sites.

Discussion

The species groups and the species-environment relationships identified in this study are similar to those described in other studies in the region. Whistler (1980) stated that littoral forest species composition is determined primarily by substratum, and identified four subcommunities in American Samoa dominated by: (a) *Pandanus* (rocky, unprotected shores), (b) *Pisonia* (sandy shores with seabird guano), (c) *Barringtonia* (coral plates and rubble), and (d) mixed (in some areas dominated by *Hernandia nymphaeifolia*). Whistler (1983) and Pearsall (in press a) identified *Barringtonia*, *Pisonia*, *Hernandia* and mixed littoral forest in Western Samoa.

Our *makatea* forest would be a type of coastal forest, defined by Whistler (1980) as lying immediately inland from littoral forest but having different species composition. In the Samoa study, as in ours, there were several 'littoral' species found in this type (e.g. *Calophyllum inophyllum*, *Guettarda speciosa* and *Pandanus tectorius*). The *makatea* forest type, dominated by *Elaeocarpus tonganus* and *Hernandia moerenhoutiana*, has not been described for other areas in Polynesia, however it is composed of species that are widespread in coastal and montane forest in the region.

In a separate cluster analysis of only the Mangaia sites, Merlin (1991) identified (a) *Pandanus* scrub sites (corresponding to Type ID in this study); (b) *Barringtonia asiatica* forest (corresponding to II); and (c) native forest (corresponding to IV). Merlin (1991) differentiated disturbed and undisturbed native forest, the former characterized by the presence of *Cocos nucifera*, *Aleurites moluccana*, and *Morinda citrifolia*. However, there is new palynological evidence that *Cocos nucifera* is native, not an aboriginal introduction, on these islands (Parkes 1990). A disturbed *makatea* forest type was not distinguished in the cluster analysis or ordinations in the present study. Most *makatea* sites sampled contained some *Aleurites moluccana*, and *Morinda citrifolia*, but *M. citrifolia* never accounted for > 5% basal area, and *A. moluccana* made up > 25% basal area in only two sites. One could conclude that all of the *makatea* sites are disturbed to some extent, although introduced species are not dominant at this sampling scale. Alternatively, a larger number of samples might reveal that the distribution of introduced species on the *makatea* is patchy at a

scale that could be detected using this sampling method, and therefore that disturbed and undisturbed classes could be differentiated.

Franklin & Steadman (in press) defined physiognomic vegetation types using aerial photographs based on tone, texture and topographic position for the purpose of mapping bird habitat, and their classification included: (a) littoral forest (within 150 m of coast), (b) *Hernandia nymphaeifolia* leeward littoral forest, (c) coastal forest (50-200 m from coast), (d) *makatea* forest (more than 100 m from the coast and on the *makatea*), (e) disturbed *makatea* forest (indicated by the presence of *Aleurites moluccana* which has a light tone on air photos), and (f) *Barringtonia* forest (which has a dark tone and smooth texture on air photos). The present study revealed no 'coastal forest' of distinct composition on these islands, but only an area transitional between littoral and *makatea* forest (e.g. sites 19, 22, 7, 9, 16, 17, 65, 67 and 70). The quantitative description of the composition of the types derived in the present study will be used to revise the classification by deleting the coastal forest type. The observation that stands of *Aleurites moluccana* were clearly visible on 1:30 000 air photos suggests that more extensive field sampling would result in the identification of a disturbed *makatea* forest type. Certainly it is useful to map identifiable stands of *Aleurites moluccana*, if only because they are not used for food by native landbirds.

Littoral forest species (for example *Barringtonia* and *Hernandia*) tend to be salt water dispersed, or, in the case of *Pisonia*, the sticky seeds are dispersed on the feet of seabirds. In contrast, coastal forest species (such as *Elaeocarpus*) are primarily landbird-dispersed (van der Pijl 1972). A study based on a very limited sample from Atiu, Ma'uke and Miti'aro showed that the two dominant *makatea* forest trees, *Elaeocarpus tonganus* and *Hernandia moerenhoutiana*, are both important in the diet of two native landbirds, Pacific Pigeon (*Ducula pacifica*) and Cook Islands Fruit-Dove (*Ptilinopus rarotongensis*), as are other endemic or indigenous *makatea* forest species such as *Myrsine cheesemanii* (Franklin & Steadman in press). Fruits of a littoral species, *Guettarda speciosa*, are also extremely important in their diet.

Although the objective definition of discrete vegetation types is important for vegetation and habitat mapping, the ordinations show both strong differentiation of the four major types based on species composition, and continuous variation in species abundance among some types (IC, ID and IV, and IA and IB). An understanding of the variations within and transitions between vegetation types is also important for ecosystem inventory (Noss 1987). This variation can be related to plant species turnover along environmental gradients using

environmental data (e.g. the transition from IA to IB may be related to a disturbance gradient, and from IC and D to IV related to increasing distance from the coast and leewardness). However, in our study the relationship between environmental variables and species composition is somewhat weak. There are several possible explanations for this.

The geographical variables that were measured may not have adequately sampled the underlying environmental gradients, either because the spatial sampling scale (100 m transects) was too coarse, or the geographical attributes were not good surrogates for environmental variability (e.g. soil and micrometeorological properties). Many studies have shown soil properties to be heterogeneous over a distance of a few meters (Robertson et al. 1988; Palmer & Dixon 1990) and this would be especially true for the *makatea* where soil collects in pockets on the pit and pinnacle karst (Harvey, Davis & Gale 1988).

Also, the *makatea* is small in extent, the geographical distances are short (although the environmental gradients may be steep), and the canopy includes many cosmopolitan littoral species. Biotic factors (dispersal ability and competition) may have a great influence on species composition at the spatial scale of the sample sites. With their large heavy seeds, *Barringtonia asiatica* and *Aleurites moluccana* tend to cluster among themselves. *Barringtonia* tends to occur in pure stands, presumably because it shades out seedlings of other species (Amerson, Whistler & Schwaner 1982; U. Simpson pers. comm.), and is probably established in cohorts after storm events (Merlin 1991).

Stochastic processes (colonization events and disturbance regimes) may determine the presence or absence of a species on a particular island. However, although only 10 of the 38 indigenous or aboriginally introduced woody species sampled in this study were sampled on all four islands, 28 of them are known to occur on all four islands (A. Whistler unpubl. data; Sykes 1976c). Therefore, it is a sampling artifact that rarer but widespread species were not found in our sites. For example, on Ma'uke, where only seven sites were established, several common species, known to occur there, were not sampled (*Hernandia nymphaeifolia*, *Calophyllum inophyllum*, *Aleurites moluccana*, *Pisonia grandis* and *Canthium barbatum*). While 10 species were only sampled on one of the two larger islands, Atiu or Mangaia, six of those occur on all four islands, and two more on at least two islands. Of the species sampled on only one island, only *Ficus tinctoria* was dominant (>75% basal area) at any sample (site 71 on Mangaia). In summary, the inter-island patterns of composition did not have a primary effect on the ordination or the definition of types.

The inter-island pattern of greatest ecological interest is the absence of the *makatea* dominants *Elaeocarpus tonganus* and *Hernandia moerenhoutiana* from sample sites on the smaller islands, Ma'uke and Miti'aro (although *H. moerenhoutiana* is known to occur on Miti'aro), perhaps indicating the lack of suitable habitat. The remaining mysterious pattern is the absence of *Pisonia grandis* as a littoral dominant on Mangaia (although others have noted that it is locally abundant there; A. Whistler pers. comm.). In spite of the fact that sites from an island tended to cluster together, general patterns of the distribution of species on all four islands were revealed. Most types occurred on at least two islands. In the only case where a type was restricted to one island (due to the presence or absence of a species), it occurred as a subtype (e.g. ID on Mangaia) of a more general category (I, *Pandanus/Guettarda* littoral forest). In other cases where a type was present on only some of the islands, it could be explained in terms of environmental or terrain differences (e.g. types III and IV occur on Mangaia and Atiu which are much larger, higher *makatea* islands than Ma'uke and Miti'aro).

The rugged *makatea* on Atiu, Mangaia, Ma'uke and Miti'aro supports several forest associations that are distinct at our sampling scale where alien species are present but not dominant, as has been found for more continental austral forests in Australia, Madagascar and New Zealand (Holland & Olson 1989). Quantitative descriptions of their composition can be used in mapping and monitoring these vegetation associations and the fauna they support.

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