6. VEGETATION AND FLORISTICS OF THE AITUTAKI MOTUS

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The vegetation of the Aitutaki reef islands is of interest for several reasons. First, Aitutaki is remotely located in the central Pacific on a diversity gradient extending from the densely vegetated and floristically diverse atolls of the Carolines and southern Marshalls to isolated and depauperate islands such as Clipperton. The gradient effects should be apparent at Aitutaki in the absence of species restricted to the western Pacific (notably the mangroves and the seagrasses, but also many species of broadleaf trees). Second, the comparatively low floristic diversity will mean that certain species will be more important components of the vegetation than they are elsewhere. This is the case with shrubs such as Timonius polygama, abundant at Aitutaki and at Mopelia and throughout the Tuamotus to Henderson Island; and with Euphorbia chamissonis, though this has a wider distribution. Third, the unusual geomorphology of the motus, with stormswept seaward gravel spreads and conglomerate platforms and relatively small sand areas, should influence the type and distribution of the vegetation units present. And fourth, the range of size of the motus should have implications for the MacArthur and Wilson theory of island biogeography; the presence of a high island immediately adjacent to the motus adds a further factor to the analysis of area, distance and ecological diversity.

In this paper, we first consider the floristics of the motus, in terms both of biogeography and of island size and floristic diversity, and then discuss the vegetation units, emphasizing the place of Aitutaki in general Pacific distribution patterns, and noting the absence of certain widespread types which might have been expected in this location. The discussion covers only the vascular plants listed in the accompanying paper by F.R. Fosberg, and does not extend to either marine algae or to terrestrial algae, fungi, lichens, liverworts and mosses.

FLORISTICS OF THE MOTUS

Size of the flora

During the 1969 Expedition 72 numbers of plants (including 3 mosses and lichens) were collected on the Rarotonga reef islands, and 183 (including 14 mosses, liverworts, fungi, lichens and blue-green algae) at Aitutaki. The Rarotonga vascular plants are reported by Fosberg in Stoddart and Fosberg (1972), those from Aitutaki by Fosberg in this Bulletin.

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Of the total of ca 140 species recorded at Aitutaki, 80 or 57 per cent are only found on the main island and not on the motus. 62 species are recorded from the smaller islands, including the Ootu peninsula. Excluding the volcanic islets of Rapota and Moturakau and also the much-disturbed Ootu peninsula, the number of species recorded from the motus is 45 (32 per cent). This compares with 41 species from the three Rarotonga reef islands. Only 26 species are common to the two lists, however: 19 Aitutaki motu species are missing from the Rarotonga islands, and 15 Rarotonga species are not recorded from the Aitutaki islands. Some of the missing species, where they do occur, are extremely common; their absence is further discussed below.

The 45 Aitutaki motu species comprise a flora comparable in size with that of other central and east Pacific atolls (Table 11). At least 50 per cent of the species can be considered indigenous, and this indigenous flora is intermediate in size between those of remote, small or dry islands such as Clipperton, Vostok and Flint, and large, wet or more accessible atolls such as Jaluit, Arno, Kapingamarangi and Onotoa. The number of species is similar to that for atolls in the Society and Tuamotu Islands: the nearest atoll for which a comparable list is available is Mopelia in the Societies (Sachet, in litt.).

Composition of the flora

The Cook Islands, by their remote location in the central Pacific, lack many species common on west Pacific atolls the ranges of which terminate in Tonga, Fiji or Samoa. Van Balgooy (1960, p.410) has clearly shown the magnitude of the floristic demarcation between Tonga and the Cooks when considering the total floras of these groups: in Tonga 104 genera are of 'western' affinity (Palaeotropical, Malaysian-Australian, Australian) compared with 41 such genera in the Cooks. Philipson (1971) has reinforced this conclusion with an analysis of the affinities of the woody species of Rarotonga, though clearly Pacific and pan-tropical components are more important in the strand flora.

15 tree species have been recorded from the Aitutaki islands, 4 of them only from the volcanic islets. Only 8 species are common: Cocos, Guettarda, Pandanus, Morinda, Casuarina, Hernandia, Leucaena and Pisonia. Hibiscus is widely distributed but rare, in sharp contrast to its abundance on the main island. The rarity of three species (Calophyllum inophyllum, Cordia subcordata, Thespesia populnea) is striking when compared with their wide distribution and abundance on other Pacific islands. Thus Thespesia, important on atolls such as Kapingamarangi, forms trees 20 m tall as close to Aitutaki as Penrhyn and Manihiki in the northern Cooks (Linton, 1933). Both Pandanus and Cordia are also absent from the reef islands of Rarotonga. Other common western Pacific atoll

species which are absent from the reef islands are:

Allophylus timorensis	Common on Arno and Kapingamarangi, forms a major woodland type in the southern Marshalls.
Barringtonia asiatica	Present on mainland Rarotonga and Aitutaki, and on the Aitutaki volcanic islets.
Intsia bijuga	Common on Arno and other Marshalls atolls; reaches its eastern limit in Tonga and Samoa (Yuncker, 1959).
Neiosperma oppositifolia	Important woodland type in the Marshalls and extends to the Line Islands; absent in the Tokelaus.
Premna obtusifolia	Common in western Pacific atolls and high islands eastward to Marquesas and Henderson.
Soulamea amara	Common at Kapingamarangi and in most western Pacific atolls.

Of particular significance is the absence of mangroves from the Cook Islands. Six species in the genera Rhizophora, Bruguiera, Lumnitzera and Xylocarpus are recorded from Tonga (Yuncker, 1959) and three from Samoa in the genera Rhizophora, Bruguiera and Xylocarpus (Setchell, 1924). They are also absent from the Society Islands and the Tuamotus and other eastern and northern Pacific atolls, including the Tokelaus (though introduced in Hawaii and Tahiti). Their absence indicates an important vegetational and sedimentary difference between the Cooks and the islands of the west Pacific.

14 species of shrubs are present on the Aitutaki islets, 3 being uncommon recent introductions and the rest widespread and mostly abundant. Some of these shrubs are geographically extensive (Pemphis, Suriana, Tournefortia, Sophora, Scaevola), others are regionally restricted (Timonius polygama). Some are inexplicably absent from the Rarotonga reef islands though present and indeed abundant at Aitutaki: these include Pemphis, Timonius, Pipturus and Corchorus torresianus. Absent from both the Rarotonga and Aitutaki islands are Euphorbia atoto (common on Rangiroa and Raroia in the Tuamotus but here replaced by E. chamissonis) and Pluchea carolinensis (extensive, though recently introduced, in low scrub at Christmas Island).

At least 34 species of herbs are recorded from the Aitutaki motus, with an additional 13 from the Rarotonga reef islands. Of these only 10 are common: Stenotaphrum micranthum (exotic), Fimbristylis cymosa, Heliotropium anomalum, Polypodium scolopendria, Triumfetta procumbens, Cassytha filiformis, Vigna marina and Tacca leontopetaloides (exotic) are found on most motus. There are curious differences between the Rarotonga and Aitutaki lists. Thus Sesuvium portulacastrum, present on Rarotonga, is absent not only from the motus but also from the main island of Aitutaki, in spite of its wide distribution

through the Line Islands and its importance as a vegetation type at Christmas Island (Christophersen, 1927; Jenkin and Foale, 1968). Other species present on Rarotonga but not the Aitutaki islands include Asplenium nidus, Davallia solida, Thuarea involuta, Peperomia species, Portulaca lutea, Canavalia sericea, Stachytarpheta urticifolia (exotic), Vitex trifolia, Sonchus oleraceus (exotic) and Wedelia biflora.

Particularly interesting is the absence, with the mangroves, of the sea grasses. Species of Syringodium, Diplanthera (=Halodule), and Halophila are recorded from Tonga by Yuncker (1959), but there are no records from the Cooks. Halophila is present in Samoa (Setchell, 1924), Tahiti and Hawaii and may be more widely distributed in the central Pacific than the other sea grasses, but it was not seen in the Cooks in 1969. The absence of this group, as with the mangroves, has important sedimentological implications: in consequence Aitutaki and the other Cook atolls more closely resemble the Tuamotus than the reefs of the western Pacific.

Species numbers on the motus

Table 12 gives the area and total numbers of species of vascular plants, classified as trees, shrubs and herbs, for each of the Aitutaki motus, together with the volcanic islets of Moturakau and Rapota and the Ootu peninsula. Data for the three reef islands of Rarotonga which are appended (from Stoddart and Fosberg, 1972) show similar values to those of Aitutaki. The motus have individual floras of 16-25 species each; the largest islands, Tekopua and Akaiami, have 25 and 22 species respectively. The only island to diverge markedly from the general pattern is the small sand cay south of Tapuaeta, with 5 species, while Ootu, a peninsula not a motu, much disturbed by man, has 42 species.

These data are of interest by comparison with those for the islets of Kapingamarangi Atoll, Caroline Islands, determined by Niering (1956). The Kapingamarangi data indicated a constant number of species per island for islands less than 1.4 ha (3.5 acre) in area, with a rapid rise in species numbers with increasing island area above this size. Wiens (1962) suggested that the threshold size is related to the smallest area of land which can support a permanent freshwater lens. The Kapingamarangi data were subsequently used by MacArthur and Wilson (1963; 1967, pp.30-32) in their theory of island biogeography relating the equilibrium level of an island biota to distance from source area (controlling immigration rate) and island size (controlling extinction rate).

The Aitutaki data raise two significant issues concerning the MacArthur and Wilson model and the Kapingamarangi data. First, can a similar control of number of species by island size be demonstrated for Aitutaki, where all except one of the islands lies above the 1.4 ha threshold (Aitutaki and Kapin-

gamarangi have approximately the same annual rainfall of 2000 mm/yr), and where the largest Aitutaki motu is twice as large as Kapingamarangi's? MacArthur and Wilson's theory in fact predicts that the species-area relationship will be more marked in distant islands such as Aitutaki than in near islands such as Kapingamarangi, assuming that the source region in both cases is in the western Pacific. Second, whether or not this relationship exists, what is the effect of the existence of a 'species-reservoir' on the main volcanic island of Aitutaki, with between 4 and 9 times as many species as on individual motus, less than 8 km distant from the farthest of them?

Tables 13-15 document the distribution of trees, shrubs and herbs on the Aitutaki motus, volcanic islets and Ootu peninsula. The tables are based on sight records supplemented by collections made during the surveying of the islands. It is probable that some grasses have been systematically unrecognised in the field, but the other groups are thought to be reasonably complete. It should be noted that these tables are not directly comparable with those of Niering (1956), who classifies Tournefortia and Pemphis as trees and Euphorbia chamissonis as a herb; trees of Tournefortia are found at Aitutaki but this species is usually, and Pemphis is always, a shrub at Aitutaki, and Euphorbia too seems more appropriately termed a dwarf shrub than a herb. Figures 33 and 34, however, show direct comparisons, using Niering's classification, of the Aitutaki and Kapingamarangi data, in terms of numbers of species of trees, shrubs and herbs, and total numbers of species, against island area, and also in terms of the proportion of the number of species in each class for all islands.

It is clear that the close association between species number and island area for the Kapingamarangi islands does not exist on Aitutaki. There is a slight positive relationship between number of species and log area over the size range 4-71 ha but the scatter of points is considerable, and the mean number of species per island (21.1) over this size range is close to that for both small and large islands. There is reasonable agreement between the Kapingamarangi and Aitutaki data for small islands (approximately 27 and 21 species per island at 4 ha) but marked divergence at larger island sizes, with the largest Kapingamarangi islands having 2-3 times as many species as Aitutaki islands of equivalent size. Note that 16 (50 per cent) of the Kapingamarangi islands are smaller than 1 ha in area, compared with 1 at Aitutaki; the species number for this latter (5) is rather low by comparison with Kapingamarangi islands of the same size. It is evident, then, that the influence of island area is masked at Aitutaki when considering total numbers of species.

The influence of size for the two groups of islands can also be compared for the groups of trees, shrubs and herbs. At Kapingamarangi the number of tree species increases over the size range 0.16-32 ha from 5 to 17; while at Aitutaki, ignoring

the smallest islet, the number is relatively invariant at about 7.5 species over the range 3.8-71 ha. At Kapingamarangi the number of shrub species is fairly constant at 1-3 up to 2 ha and then increases slightly to 5 species or more; at Aitutaki the number is variable but averages about 4 species over the size range. The most spectacular increase in species number with area is seen with herbs at Kapingamarangi: from 2.5 on islands of 1 ha to more than 20 (on one island 35) on islands larger than 10 ha. In this case it is clear that the diversity of the herb flora makes a major contribution to the general curve for all species derived by Niering. At Aitutaki, on the other hand, there is only a weak trend, from rather less than 10 to rather more than 10 species per island in the range 3.8-71 ha.

These differences in trend between groups of plants mean that the floras of large islands have a different composition from those of small ones on Kapingamarangi, but this is not the case on Aitutaki. Figure 2, plotting trees, shrubs and herbs as a percentage of the total flora for each island shows that on Kapingamarangi the proportion of trees decreases from about 80 to about 40 per cent with increasing island size; shrubs remain constant at about 20 per cent; and herbs increase from about 10 to about 60 per cent. On Aitutaki trees are fairly constant at 35 per cent, shrubs at 20 per cent, and herbs at 45 per cent.

In interpreting the species-area relationship, therefore, we need to consider not only the total size but also the composition of the island floras. Consider a series of islets on an atoll or almost-atoll such as Kapingamarangi or Aitutaki. The smallest islets will normally support a strand flora of grasses, sedges, vines and other herbs, with beach-crest shrubs and in some cases trees. The plants capable of surviving in such environments are limited in number and many are of pan-tropical or at least Indo-Pacific distribution. On large inhabited islands much of the area will have been cleared during the last few centuries for coconut plantations. This will have had the following effects. (1) The number of tree species will have been reduced on larger islands with the eradication of certain vegetation types. This is illustrated by the disappearance of Barringtonia, Calophyllum, Pisonia and Cordia from many islands. (2) The number of shrub species will probably remain the same, partly because there is probably an upper limit to the number of such species which can be successfully established on such islands, even if artificially introduced, but also because the native shrubs of beach crest, gravel spread and conglomerate platform areas are unlikely to be cleared for economic reasons and survive even on islands severely disturbed by man. (3) With the establishment of plantations and increasing human activity the number of herb species, especially widespread weedy species, will increase, as a result both of deliberate and inadvertent introduction and also because clearing prepares substrates for colonisation and reduces competition from already established species; the effect will be greater on larger islands.

This explanatory scheme is consonant with the Kapingamarangi data, and it perhaps needs to be stressed that on many Pacific atolls we are no longer dealing simply with patterns resulting from natural immigration and extinction, but with vegetation actively managed by man: or, as Hatheway (1953, 6) put it for Arno Atoll, with people and plants rather than flora and habitat.

Does the scheme apply to the Aitutaki motus? Large areas on the bigger motus are covered with coconut woodland, now the most extensive woodland vegetation. There is little doubt that Pisonia - and perhaps other species such as Cordia and Hibiscus - were formerly more extensive. With their removal from some islands a reduction in tree species diversity can be inferred. The number and identity of shrub species is monotonously regular on all the islands: large areas covered with Pemphis and Suriana, and smaller contributions by Tournefortia, Scaevola, Sophora, Euphorbia, Timonius and Corchorus. However, unlike the situation on Kapingamarangi, the herb flora (including weeds) does not markedly increase on the larger islands, in spite of their clearance for coconuts: there is no doubt that a major reason why there is no simple increase in total size of flora with island size on Aitutaki is because the herb component is relatively invariant with size.

Why is this so? If Aitutaki were an atoll, situated in the central Pacific, then it could be argued that immigration was reduced because of the distance from source areas to the west, in Tonga and Fiji. To some extent such an explanation must partially account for the smaller floras of the Cooks, the Tuamotus and other central and east Pacific atolls compared with the Carolines and the Marshalls. But there is at Aitutaki a reservoir of weedy species on the main volcanic island immediately adjacent to the motus. Many species, not only weeds, which are elsewhere common on atoll islands, are widespread on this volcanic island but are absent from the motus. They include ferns (Nephrolepis hirsutula), grasses (Dactyloctenium aegyptium and several others), sedges (several Cyperus species), Portulaca oleracea, Abrus precatorius, Canavalia cathartica, Caesalpinia, Euphorbia hirta, Barringtonia asiatica, Ipomoea littoralis, Stachytarpheta urticifolia, Spermacoce suffrutescens, and Vernonia cinerea. Making allowance for the fact that some motu species may have been overlooked (and this is particularly true of sterile grasses such as Lepturus and Paspalum, it is astonishing that many of these species have not established themselves on the islands. The presence of some of them, such as Calophyllum and Abrus, on the volcanic islets in the south suggests the operation of an ecological control.

The list would be longer if it included certain species recorded from the motus but which cannot be said to have established themselves. Akitua, which can be reached on foot from

the mainland at Ootu, has three herb species (Bidens pilosa, Emilia sonchifolia, Boerhavia repens) not otherwise recorded from the motus, plus, where the path from Ootu reaches the beach, a patch of Cenchrus echinatus. Cenchrus is also recorded at the landing stage on Tekopua, but on no other motu; yet it is common on the mainland and on the Ootu peninsula.

Thus whatever limits the establishment of these species on the motus, it is not lack of colonising material from the Aitutaki "reservoir", and it has nothing to do with isolation in the central Pacific. It seems rather that the present vegetation of the islands has some property or character which inhibits the colonisation, establishment and spread of new species, even of weeds in coconut plantations. This has been noted before, for example in the case of the localisation of weeds such as Mimosa pudica near the landing stage at Diego Garcia Atoll, an intensively managed coconut plantation (Stoddart, 1971, 141), and similar observations have been made by Bayliss Smith (in preparation) at Ontong Java Atoll and by Parham (1971, p.593) in the Tokelau Islands. The processes of colonization by sea- and wind-transported propagules are certainly continuing and important on reef islands, and recent work on the British Honduras cays has shown that extinction and floristic change is more widespread than hitherto suspected, even over short periods of years and in the absence of catastrophic storms, but it nevertheless appears unlikely that these processes account for the present levels of species numbers on the Aitutaki motus, and doubtful that their operation as envisaged by MacArthur and Wilson gives a sufficient explanation of species numbers on the Kapingamarangi islands.

Niering's Kapingamarangi data have recently been re-analysed by Whitehead and Jones (1969). Their analysis, which breaks down the total species numbers into groups of recent introductions, strand species, and non-strand species, is particularly apposite to this discussion. They argue that on small islands, lacking a freshwater lens (i.e. less than 1.5 ha), the flora consists only of salt-tolerant strand species, limited in number by the size of the available "species pool" in this category and hence not greatly affected by island area. They also found that there are no recent introductions on islands of less than 1.6 ha in area. As a result, smaller islands have 7-8 species each and larger islands 12-14. Above the freshwater lens threshold, however, there is a rapid increase in the number of non-strand, salt-intolerant species, with numbers closely related to island area. It is these species, they argue, which control the overall species-area relationship found by Niering. Whitehead and Jones (1969, p.176) suggest that most of the species in both strand and non-strand categories are drift-dispersed. Unfortunately they do not list the species placed by them in each category, apart from the coconut, which they classify (mis-classify?) as a strand species. By implication, however, they regard the dispersal of the non-strand species as a natural phenomenon. They

do not consider the effect of human activities on species numbers, other than in terms of recent introductions. Hence, while clarifying some aspects of the MacArthur and Wilson analysis of the Kapingamarangi data, they do not make it possible to explain in terms of their model the divergent situations at Kapingamarangi and at Aitutaki.

The presence of the volcanic island at Aitutaki affects the floras of the motus other than by serving as a reservoir of weeds and other plants from which they may be colonised. The inhabitants can utilise the fertile volcanic soils rather than cultivate the carbonate sands of the motus. Breadfruit and taro, of common atoll crops, are unknown on the motus; the Polynesian Chestnut Inocarpus fagiferus is only found on the main island, as are Citrus species, Persea americana, Musa species, Sorghum, Capsicum, Solanum species, and other food crops; useful trees such as Ceiba pentandra are similarly distributed, as are decoratives such as Crinum, Canna, Catharanthus, Gloriosa superba, Tagetes, and many others. Carica papaya is found on the motus only on Akitua, although common on the main island. In effect, therefore, although heavily affected by human activities, the motus are islands lacking human populations, settlements and cultivation. Apart from coconuts the only food plant on the motus is the Polynesian Arrowroot Tacca leontopetaloides, which is rather uncommon on the main island. Had there been settlements on the motus, especially on the larger islands of Akaiami and Tekopua, many of these species would have been locally introduced and cultivated and the species numbers would have approached closer to those of Kapingamarangi islands of equivalent size. It would be interesting to test this inference by comparison with inhabited true atolls in the Cook Islands, such as Manihiki, Penrhyn and Palmerston, and with an uninhabited atoll such as Suwarrow. Similarly the Aitutaki patterns should resemble those of other reef-encircled high islands such as Bora-Bora.

VEGETATION OF THE MOTUS

The following accounts of the main vegetation units, arranged by scrub types, woodland types, and herb types, are derived from the surveys and descriptions of the individual islands previously described. The vegetation units recognised follow those of Fosberg (1953, in press). Particular attention is given to the geographical relationships of the units described. This discussion is followed by brief notes on vegetation units absent from the Aitutaki motus though important on other Pacific atolls.

Pemphis Scrub (Plates 28 and 29)

Pemphis acidula commonly forms a narrow zone of scrub on the seaward sides of motus, varying in width from 10 m at Papau, 25-30 m on Ee, Mangere and Tavaerua Iti, 40 m at Motu-

kitiu, to 50 m at Akitua, Angarei, Tavaerua and Muritapua. The scrub consists of shrubs up to 2 m tall, often wind-sheared and aligned in windrows oriented slightly north of west. Pemphis is the characteristic outpost species on the surface of the conglomerate platform. The shrubs are openly branched and lack the height and density of Pemphis scrub on some other atolls such as Aldabra. On islands where the conglomerate platform is much reduced and the seaward coast is formed by a sand and gravel ridge, Pemphis is rare (Tekopua, Akaiami). It is also poorly developed on the seaward side of Papau, possibly because it has been destroyed by rapid beach retreat. On lagoon shores, mainly on sand, Pemphis often forms a narrow belt, often of taller shrubs (e.g. on Ee, Mangere, Angarei, Akitua, Muritapua); in many cases these beaches are slightly retreating and the roots of the Pemphis are exposed to seawater. Wiens (1959) and others have drawn attention to the common association of Pemphis with low rocky substrates, often without soil and subject to salt-water flooding and salt spray.

Pemphis scrub in such situations, on exposed rocky substrates, either of reef-rock (feo) or island conglomerates, is found throughout the Societies and Tuamotus, from Mopelia to Rangiroa, Raroia and Mururoa (Sachet, in litt.; Stoddart and Sachet, 1969; Doty, 1954; Chevalier et al., 1968). In many of the Tuamotu atolls, however, it is more common along channels between islands (hoa) than on seaward coasts, which are generally formed by high sand and gravel ridges rather than by wide horizontal conglomerate platforms. As a result Pemphis is probably less abundant as a vegetation type than on Aitutaki. Pemphis is also found on exposed rocky substrates in the Tokelaus (Parham, 1971) and at Funafuti (Hedley, 1896). In the Gilberts Moul (1957) reports it as a rampart scrub rather than on rocky substrates. In general it appears common in the southern and southeastern Polynesian atolls, though not recorded from some more remote locations such as Oeno (St John and Philipson, 1960). It is widely distributed in the northwest Pacific, but is not recorded from Kapingamarangi. It is widespread and extensive in the central and western Indian Ocean, though absent from Diego Garcia in the Chagos Archipelago. In spite of this wide distribution, it is remarkably absent from the central equatorial and central north Pacific islands: it is not recorded from Hawaii and the other Phoenix Islands*, Caroline, Flint, Vostok, Palmyra, Christmas, Washington, Fanning, Baker and Jarvis islands. Its absence from Christmas is especially noteworthy because of the large areas of terrain covered by similar low scrub communities (Jenkin and Foale, 1968). Pemphis extends through the northern Cooks at least to Penrhyn and Manihiki, where it reaches heights of 6-7 m (Linton, 1933), and the reasons for its absence further north are not known.

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*Since this Bulletin was submitted, F.R. Fosberg and the writer found extensive stands of Pemphis on Hull Atoll, Phoenix Islands and a single individual on Canton. We have since found that Pemphis was collected by J.T. Arundel on Hull and was cited by Hemsley (1884), p.116.

In the Polynesian area Pemphis generally forms shrubs rather than trees, though a large tree is reported from Henderson (St John and Philipson, 1962) and trees are common in the Melanesian area and Marshall Islands.

The occurrence of Pemphis is thus subject to a primary biogeographic control, and to a secondary substrate and exposure control.

Suriana Scrub

Suriana maritima forms a scrub 1-2 m tall, in places reaching 2-3 m and exceptionally 4 m, on the seaward sides of islands, usually inland of the Pemphis zone. The scrub is open, with individual plants 1-2 m apart. It generally covers thin sand and gravel sheets, in contrast to the rocky substrates occupied by Pemphis. The area occupied by Suriana on Aitutaki islands appears to be dependent on the extent of such low-lying sand and gravel sheets. The width of the zone varies from 50-75 m on Akitua, Papau, Tavaerua Iti, Taverua, Muritapua and Tekkopua; 95 m on Motukitiu; 125-130 m on Angarei and Mangere; to a maximum of 50-430 m on Ee. On Tekopua, where Pemphis is weakly developed, Suriana forms a narrow fringe on the seaward beach crest, occupying a very different situation from that on other motus. Similarly on Akaiami, where a seaward gravel spread is also lacking, Suriana forms a narrow fringe on the seaward beach ridge. Ground cover beneath the scrub is sparse. In more exposed areas it is limited to Heliotropium anomalum and Cassytha filiformis with seedling Tournefortia argentea and Suriana. In more inland areas Fimbristylis, Triumfetta procumbens, Ipomoea macrantha and Euphorbia chamissonis are present. Few other shrub species are represented; in inland sites they include Colubrina asiatica and Scaevola taccada (e.g. on Ee and Papau) and to seaward Tournefortia argentea. There is little admixture with Pemphis, though since Suriana stands are often surrounded on their seaward sides by a fringe of Pemphis the area of the latter may appear larger than it actually is. The two species, physiognomically so similar, can be readily distinguished from a distance by the yellow-green colour of Suriana foliage and the blue-grey green of Pemphis.

Suriana scrub occurs in a very different situation on Maina. Here it forms an open scrub 1.5-2 m tall in the interior of a sand cay. The scrub includes Tournefortia shrubs to 2 m tall and some Scaevola taccada, and a patchy ground cover of Cassytha, Triumfetta and Euphorbia chamissonis.

Suriana maritima is pan-tropical in distribution, but usually occupies a rather different situation to that on the Aitutaki motus. It is frequently extensive on lagoonal mudflats, as at Canton and Christmas in the central Pacific (Hatheway, 1955; Jenkin and Foale, 1968), but is rare on the seaward sides of islands. At Canton it is also found "in slab areas and less often in sandy areas swept by waves during violent storms"

(Degener and Gillaspy, 1955), and both here and at Christmas it occupies areas elsewhere characterised by Pemphis acidula. At Raroia, Tuamotus, where it occurs outside the Pemphis zone, Suriana extends out onto the conglomerate platforms and bare beach rock, situations normally occupied by Pemphis (Doty, 1954, p.33; Doty and Morrison, 1954, p.16). Suriana may also form a rampart scrub on seaward beach ridges, as on Akaiami and Tekopua at Aitutaki. Similarly at Rangiroa, Tuamotus, it forms a beach-crest hedge on seaward shores in the absence of Scaevola (Stoddart and Sachet, 1969, p.28), and it is also so distributed on Caroline Atoll (Clapp and Sibley, 1971). Finally it also forms extensive inland stands on sand cays, as at Maina, and is thus described from Alacran, Gulf of Mexico (Fosberg, 1962), and from Christmas Island.

In spite of its wide geographic distribution, Suriana is, like Pemphis, curiously unrecorded from a number of islands, while on others it is rare and fails to form distinctive vegetation units. It is not recorded, for example, from the Tokelaus (Parham, 1971), nor from Fanning, Jarvis, Washington and Baker islands (Christopherson, 1927), nor from Palmyra (Dawson, 1959), though it is common throughout the Australs and the Tuamotus (Brown, 1931). It is present but not common on Onotoa in the Gilberts (Moul, 1957) and present but rare at Jaluit in the Marshalls (Fosberg and Sachet, 1962) though common on other Marshall atolls, e.g. Likiep. Closer to Aitutaki, where it is so extensive, it is almost non-existent on the sand cays and absent from the mainland coast of Rarotonga; one single plant was seen there in 1969 (Stoddart and Fosberg, 1972). These differences suggest that further studies of the ecology of Suriana would be of interest. Fosberg (1974) notes that the species is tolerant of salt spray (though it is often seen dead in very exposed situations, presumably killed by salt-laden wind: Stoddart, 1971, pl. 35 for an example from Diego Garcia); substrate conditions are probably also of importance.

Scaevola scrub (Plate 27)

Scaevola taccada forms three distinct vegetation types at Aitutaki: a narrow beach-crest scrub on exposed shores; an extensive more open scrub on sand flats; and an open scrub under coconut woodland.

At Aitutaki the beach-crest Scaevola hedges are rare, simply because of the absence of seaward beach ridges: such hedges are found on Tekopua and Akaiami, the only islands with well-developed seaward ridges. On nearby Rarotonga, the Scaevola hedge is common and extensive, up to 4 m tall, on seaward beaches of reef islands, both alone and with Tournefortia argentea (Stoddart, 1972). Elsewhere in the Indo-Pacific Scaevola is characteristic of such situations, often forming a scrub 3-5 m tall, as for example at Diego Garcia (Stoddart, 1971); in the Marshalls (Taylor, 1950; Hatheway, 1953; Fosberg and Sachet, 1962); the Gilberts (Moul, 1957); the Ellice Islands

(Hedley, 1896); and the Tokelaus (Parham, 1971). It appears to be less common through the Tuamotus, being not primarily a beach species at Raroia (Doty and Morrison, 1954, p.42), and is absent from Oeno. As a beach-crest scrub it is more common on seaward than on lagoon shores, and is often wind-sheared in consequence; where it does occur on lagoon shores the shrubs are taller and more open with a vertical rather than sloping profile; but unlike Pemphis and Tournefortia, Scaevola rarely becomes a tree. In the northern Cooks, Linton (1933) refers to dominantly lagoon-shore Scaevola at Penrhyn and Manihiki, and low Scaevola occupies lagoon flats at Christmas Island (Jenkin and Foale, 1968).

Inland Scaevola is extensive on several Aitutaki islands, especially Maina and Akitua, where it forms a zone up to 200 m wide between the Suriana scrub and the main woodland area. On Akaiami, Mangere and Angarei it forms a scrub 1-1.5 m tall, with occasional Tournefortia, Pandanus, Guettarda, and Euphorbia chamissonis. Cassytha is locally common, though nowhere reaching the smothering density seen on Scaevola on some Indian Ocean islands (e.g. Assumption: Stoddart et al., 1970, 127). The ground surface is bare with some Fimbristylis. Similar extensive inland scrub is described from Canton (Hatheway, 1955) and Diego Garcia (Stoddart, 1971).

Scaevola under coconuts is less extensively developed on Aitutaki. On Taverua it forms an open scrub up to 1.5 m tall, and similar low open scrub with many other species present has been described from many other Indo-Pacific atolls.

Tournefortia scrub

Tournefortia argentea, though widespread, is a less common component of atoll vegetation than Suriana, Pemphis or Scaevola. It characteristically occurs either as a beach scrub or as an inland scrub-forest. Its Caribbean counterpart, T. gnaphalodes, though smaller, occurs more commonly as a seaward-beach scrub, but never forms trees.

On Aitutaki Tournefortia is not common. It occurs with Scaevola in beach scrub on Mangere and Maina, and probably because of the nature of island topography is more common on channel and lagoon than on seaward shores. In the northern Cooks, on Penrhyn and Manihiki, Tournefortia up to 6 m tall is said to form the main beach scrub (Linton, 1933), and it is characteristic of exposed seaward beaches in the Tokelaus (Parham, 1971) and in the Tuamotus: at Raroia it forms bushes 2-3 m in diameter and height, with a root radius of 40 m (Doty and Morrison, 1953). In the Line Islands, in the absence of Pemphis and Suriana, it is an important beach scrub at Washington, Fanning, Christmas and Palmyra, on lagoon shores as well as seaward shores (Christopherson, 1927; Dawson, 1959).

Inland scrub-forest of Tournefortia is also widespread in

the Pacific, though often now found only as relict patches. It is indeed the main woody vegetation at Pokak, Marshall Islands (Fosberg, 1955), at Gaferut, Caroline Islands (Niering, 1961), at Oeno, Tuamotus (St John and Philipson, 1960) and on Ducie. Groves are also described from Wake, Christmas, Palmyra, Fanning (reaching 12-15 m), Canton and Caroline Atolls. Plants in these groves have well-developed trunks and form gnarled trees rather than shrubs.

Tournefortia seedlings are intolerant of shade, and when mature trees are found under coconut woodland (as on Tekopua), it is presumed that they pre-date the plantation.

Pandanus woodland

At Aitutaki Pandanus forms a narrow zone between Coconut-Guettarda woodland and low scrub to seaward. On Tavaerua Iti it forms a dense exclusive zone, while on Ee it might more properly be termed a Pandanus-Guettarda woodland. In pure stands of Pandanus the ground is covered with dead leaves and no other plants grow. The more mixed type on Aitutaki is equivalent to Parham's (1971) Pandanus-Guettarda facies in the Tokelaus, though in the latter many other species (Cordia, Hernandia, Morinda) are also present.

Pisonia woodland (Plate 33)

Relatively small stands of Pisonia grandis are found on some Aitutaki motus, the largest covering 10 ha on Tekopua and 4.6 ha on Tapuaeta. On Tekopua the trees are 20 m tall and 3-4 m apart; other tree species, including Cocos, Guettarda, Pandanus and Morinda are also present. On Tapuaeta the woodland is more open, with Hernandia and Hibiscus as well as Cocos, Guettarda and Morinda. There is little undergrowth beneath the Pisonia woodland. Pisonia is also found, in a mixed Pisonia-Hernandia woodland, on Papau, and, as scattered trees only, on the Ootu peninsula.

It is possible that Pisonia woodland was more extensive before the spread of coconut woodland at Aitutaki. Certainly the trees do not compare in dimensions with those reported from the northern Cooks: Linton (1933) describes trees 23 m tall and 1 m in diameter at Penrhyn and Manihiki. Pisonia is the sole tree forming woodland on Vostok (Clapp and Sibley, 1971b), and it forms "magnificent stands" at Palmyra (Dawson, 1959, 14) and on atolls westward through the Marshall Islands and in the Indian Ocean. Agassiz reports Pisonia forests from many islands which now have mainly coconut plantations.

Hernandia woodland

Hernandia sonora is a component of woodland on some of the Aitutaki motus, especially those such as Tapuaeta and Papau with stands of Pisonia. It may formerly have been more extensive. Aitutaki is close to the eastern limits of the range of

this pantropical species. It is absent from the Tuamotus (though recorded from Mopelia and Tetiaroa in the Societies) and from Palmyra and Christmas Islands in the Line Islands, but is widespread in the Marshalls and other Micronesian and Melanesian areas, where it often forms very large trees.

Guettarda woodland

With Pandanus, Guettarda frequently forms a transitional zone between seaward scrub and coconut woodland on Aitutaki motus. The trees are up to 7 m tall (exceptionally reaching 10 m on Akaiami) and are located on the fringe of the higher leeward sand area rather than on the low sand and gravel sheets of the seaward sides of the islands. Doty (1954, p.28) has suggested that Guettarda is an indicator of the outer edge of the freshwater lens on islands, and also that since it is tolerant of shade it is widely distributed over the surface of islands beneath coconut woodland.

By comparison with the Tuamotus, where it forms the main native woodland on Raroia and Rangiroa (Doty and Morrison, 1954; Stoddart and Sachet, 1969), often in association with Tournefortia and Pandanus, Guettarda is weakly represented at Aitutaki. At Penrhyn and Manihiki in the northern Cooks there are trees of Guettarda 10 m tall; this is the maximum height of trees on Aitutaki (Linton, 1933). The species is absent from the Line Islands, and an introduction at Palmyra proved unsuccessful (Christophersen, 1927; Dawson, 1959).

Although Guettarda is widespread on the Aitutaki motus it is completely absent from the main volcanic island, with the exception of the Ootu Peninsula, which itself is simply a large motu attached to the main island: the first trees of Guettarda found are those at the northern end of the peninsula, with the transition from volcanic to calcareous soils. Guettarda is present on the two southern volcanic islets of Rapota and Moturakau, but on areas of calcareous sand rather than on volcanic substrates.

Casuarina woodland

Groves of Casuarina equisetifolia, presumably introduced, are found on leeward sandy areas of some motus, notably Ee and Angarei. The stands are not large and there is a ground vegetation of Scaevola taccada and Euphorbia chamissonis. Casuarina is also locally common on the main volcanic island.

Calophyllum woodland

Calophyllum inophyllum is absent from the motus and is found only on the volcanic islets of Moturakau and Rapota. On Moturakau it forms a dense canopy, with Hibiscus, Guettarda, Morinda and Leucaena; on Rapota it is associated with Pandanus. Its absence from the motus is surprising. Linton (1933) records

trees 15 m tall on Manihiki in the northern Cooks but stated that it had been destroyed by man at Penrhyn. In the Tokelaus also it may have been removed by man, primarily for firewood. There are scattered trees on most of the Tuamotu atolls, but the Cook Islands are near the eastern limit of its range and it may have been introduced there. Nowhere on Aitutaki does it form the massive trees overhanging lagoon shores, characteristic of many west Pacific and central Indian Ocean atolls (e.g. Kapingamarangi, Diego Garcia).

Coconut woodland (Plate 31)

Coconut woodland is the dominant woodland vegetation on the motus and has been so for at least a century (Gill, 1876, 1885). Only on Akaiami, where cultivation experiments are in progress (Thomson, 1968), are regular plantations maintained; elsewhere the woodland varies from a relatively clear woodland with little undergrowth, as on parts of Tekopua, to a mixed woodland of crowded coconut palms of different ages intermixed with broadleaf trees. Most of the mature coconuts are 8-10 m tall, though some are higher; the common broadleaf trees include Guettarda (to 10 m), Morinda (to 6 m), Pandanus (to 7 m) Leucaena, Pipturus argenteus, and occasionally Tournefortia and tall Hernandia. There is usually a shrub layer of Timonius polygama (1-2 m), Scaevola (1 m), Corchorus torresianus, Euphorbia chamissonis, and, rather rarely, tall Tacca leontopetaloides. The ground layer is highly variable, with Opomoea, Tournefortia, Boerhavia, Portulaca, grasses, sedges, and ferns; the latter are mainly Polypodium scolopendria. Asplenium nidus, common in the wetter atolls of the Line and Marshall Islands and characteristic of dense woodland in the Tokelaus (Dawson, 1959; Parham, 1971), is absent, as is Psilotum nudum. Perhaps the most striking characteristic of the Aitutaki coconut woodland is the restricted composition of the weedy ground layer: few of the many weeds of the main volcanic island are present on the motus, even though some, such as Stachytarpheta, are elsewhere abundant on such islands even where there is no local reservoir such as the main Aitutaki island provides; while others, such as Cenchrus, are found only on one or two motus near landing stages and have failed to spread and establish themselves.

Cladium marsh

There is one area of Cladium jamaicense marsh on Akitua, forming a dense stand up to 2.5 m tall. This species was not collected on other motus, where there are no similar habitats. It surrounds inland marshes at Avatoru and Tereiao, Rangiroa Atoll, in the Tuamotus (Stoddart and Sachet, 1969, pp.28-29, pl. 13), and may be relatively common in the region. It is common on Tetiaroa in what appear to be ancient abandoned taro marshes.

Pioneer beach communities (Plate 26)

Because of the geomorphology of the motus, pioneer beach communities of herbs, vines and grasses are largely limited to lagoon shores and especially to sandspits on the lagoon sides of islands adjacent to channels. The outpost species are mainly Vigna marina, Triumfetta procumbens and Ipomoea, with Fimbristylis and Heliotropium anomalum. As on other atolls these scattered outpost species can be followed inland through a regular zonation to coconut woodland: on Aitutaki the zonation includes scrub species such as Euphorbia chamissonis, Timonius polygama, juvenile Scaevola, Tournefortia, Suriana and Pemphis, and woodland species such as Guettarda, Pandanus and coconuts. The succession is well seen on the spit at the south end of Tekopua, and on leeward beaches of Ee, Mangere, Papau, Tavaerua and Tavaerua Iti. In many lagoon and channel areas, however, the beaches are narrow and cliffed, and the outpost species are absent. These herbaceous pioneer communities on sandy substrates are of very small extent by comparison with the pioneer scrub species, Pemphis and Suriana, on the seaward conglomerate platforms and gravel sheets of the motus.

ABSENT VEGETATION TYPES

By comparison with other Pacific atolls described in recent years, the Aitutaki motus lack a number of well-marked vegetation units. These fall into two categories: anthropogenic types common elsewhere but absent from the motus because cultivation is concentrated on the main volcanic island, and types absent for biogeographical reasons because of the remote location of the Cook Islands in the central Pacific.

Absent anthropogenic vegetation types

Breadfruit (Artocarpus altilis) groves are completely absent from the motus, though individual trees are common on the main island. On wetter atolls such as Kapingamarangi and Arno the groves reach heights of 20-30 m (Niering, 1956; Hatheway, 1953). Fosberg (1949) has suggested that the location of breadfruit is controlled by groundwater salinity; islands such as Akaiami and Tekopua on Aitutaki would certainly be large enough for this tree to be grown.

Pits for the cultivation of root crops such as Cyrtosperma chamissonis, Colocasia esculenta and Xanthosoma sagittifolia are prominent and in some cases extensive features of atoll islands in the western Pacific, forming the puraka pits of Kapingamarangi, the babai pits of Onotoa, and the yaraj pits of Arno (Niering, 1956; Moul, 1957; Hatheway, 1953). These pits are found on the main island of Aitutaki but on none of the motus. That they would have been dug on the motus had it not been for the existence of alternative food sources is indicated by their presence on Pukapuka and Palmerston Atolls in the northern Cooks (Wood and Hay, 1970, p.65).

Other absent vegetation types

The absence of mangroves and of sea-grasses in the Cooks has already been noted. This is perhaps the most obvious cause of contrast with the reefs and islands of Tonga and islands to the west and of similarity with the Tuamotus and islands to the east. The place of the former is taken on mainland shores of Aitutaki, and on the protected shores of Ngatangiia Harbour on Rarotonga, by dense thickets of *Hibiscus tiliaceus*, and elsewhere by a continuous saturated sward of *Paspalum* and other grasses.

The absence of *Calophyllum* and *Barringtonia* woodland from the motus has also been noted. *Calophyllum* is present on reef islands elsewhere in the Cooks, and *Barringtonia* is common on Aitutaki itself. If either ever existed on the motus they may have been cut for firewood; but the existence of *Calophyllum* woodland on the southern volcanic islets suggests that this is not the true explanation and that the species was never important on the motus.

Cordia subcordata woodland is also absent from the motus, though the species is found on Akitua. It is common in the Tokelaus, forms the main native woodland on Canton and Caroline Atolls (Hatheway, 1953, 3; Clapp and Sibley, 1971b), but is "almost rare" at Raroia in the Tuamotus (Doty, 1954, p.26). Yet in the northern Cooks, at Penrhyn and Manihiki, it is reported to form trees 15-25 m tall and up to 0.6 m in diameter (Linton, 1933).

Certain fleshy herbaceous vegetation types are also absent. *Portulaca* is curiously rare and nowhere on the motus forms a vegetation unit, though at Canton (a much drier atoll), for example, it forms the most extensive vegetation (Hatheway, 1954, p.6). *Sesuvium portulacastrum* is unrecorded from Aitutaki, though present on the reef islands of Rarotonga; Wilder (1931) however noted it as rare at the latter island. At Christmas Island and in the Phoenix Islands *Sesuvium* mats are extensive (Jenkin and Foale, 1968). The species is absent from the Tokelaus and the Marshalls, but present in Phoenix, Wake, and Hawaii, and its distribution might merit further study. Other herbaceous vegetation units unrepresented or weakly represented on the Aitutaki motus include grasses such as *Lepturus* and *Sporobolus* (which also is absent from the Marshall Islands); and the *Ipomoea-Wedelia-Stachytarpheta* type often widespread under coconuts. For further details of these types, see the accounts by Fosberg (1953, 1974).

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Table 11. Size of Pacific atoll floras

Group	Atoll	Number of species (number of indigenous species in brackets)		Source
Marshalls	Ailuk	56	(26)	Fosberg 1955
	Arno	125	(40)	Hatheway 1953
	Bikini	41		Taylor 1950
	Eniwetok	100	(33)	St John 1960
	Jaluit	288	(60)	Fosberg and Sachet 1962
	Jemo	34	(17)	Fosberg 1955
	Kwajalein	89	(25)	Fosberg 1955, 1959
	Lae	61	(35)	Fosberg 1955, 1959
	Likiep	91	(31)	Fosberg 1955, 1959
	Pokak	9		Fosberg 1955
	Rongelap	42		Taylor 1950, Fosberg 1959
	Taka	23	(18)	Fosberg 1955
	Ujae	61	(32)	Fosberg 1955, 1959
	Ujelang	50	(29)	Fosberg 1955, 1959
	Utirik	55	(26)	Fosberg 1955, 1959
	Wotho	40	(28)	Fosberg 1955, 1959
Solomons	Ontong Java	150	(58)	Bayliss-Smith 1973
Carolines	Ant	58		Glassman 1953
	Kapingamarangi	99	(43)	Niering 1962
	Namonuito	94		Stone 1959
	Pingelap	78		St John 1948
	Puluwat	42		Niering 1961
Gilberts	Onotoa	60	(50)	Moul 1957
	Tabiteuea	45		Luomala 1953

Table 11 continued

Group	Atoll	Number of species (number of indigenous species in brackets)	Source
	Tarawa	109 (28)	Catala 1957
Ellice	Funafuti	55	Maiden 1904
Tokelaus	Fakaofo	40	Parham 1971
	Nukunono	55 (35)	Parham 1971
Phoenix	Canton	164 (14)	Degener and Gillaspy 1955
Line	Christmas	41	Chock and Hamilton 1962
	Palmyra	64	Dawson 1959
Cooks	Aitutaki (motus)	45	This paper
	Manihiki	22	Cranwell 1933
	Rarotonga (motus)	41	Stoddart and Fosberg 1972
Societies	Mopelia	78	Sachet in litt.
Tuamotus	Oeno	17 (14)	St John and Philipson 1960
	Mururoa	26	Chevalier et al. 1968
	Rangiroa	121 (39)	Stoddart and Sachet 1969
	Raroia	135 (54)	Doty 1954
Hawaii	Kure	42 (23)	Lamoureux 1961, Clay 1961
	Laysan	38 (27)	Lamoureux 1963, Tsuda 1965
Others	Rose	4	Sachet 1954
	Caroline	35	Clapp and Sibley 1971a
	Flint	36 (13)	St John and Fosberg 1937
	Vostok	2	Clapp and Sibley 1971b
	Clipperton	31 (14)	Sachet 1962
	Wake	94 (20)	Fosberg 1959b, Fosberg and Sachet 1969

Table 12. Numbers of species of vascular plants on Aitutaki and Rarotonga islands

Island	Area ha	Tree species	Shrub species	Herb species	Total number of species
AITUTAKI					
Ootu	ca 175	8	12	22	42
Akitua	14.9	8	9	12	29
Angarei	13.1	6	8	6	20
Ee	29.2	7	7	7	21
Mangere	8.5	5	6	8	19
Papau	5.3	8	7	10	25
Tavaerua Iti	4.1	5	7	10	22
Tavaerua	12.5	4	6	8	18
Akaiami	41.9	5	9	8	22
Muritapua	4.0	3	5	8	16
Tekopua	71.3	7	10	9	26
Tapuaeta	6.0	7	8	6	21
Sand cay	1.0	1	3	1	5
Motukitiu	11.5	5	8	10	23
Moturakau	3.9	7	3	6	16
Rapota	-	11	3	6	20
Maina	17.0	4	5	10	19
RAROTONGA					
Motutapu	11.0	7	3	14	24
Oneroa	10.6	8	6	6	20
Koromiri	3.0	6	3	8	17

Table 13. Distribution of tree species on Aitutaki motus

	Tapueta cay	Muritapua	Tavaerua Iti	Papau	Tapuaeta	Mangere	Motukitiu	Tavaerua	Angarei	Akitua	Maina	Ee	Akaiami	Tekopua	Ootu	Moturakau	Rapota	Total
Cocos nucifera	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	17
Guettarda speciosa		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	16
Pandanus tectorius		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	16
Morinda citrifolia				x	x		x	x	x	x			x	x	x	x	x	11
Casuarina equisetifolia			x	x		x			x	x		x		x	x		x	9
Hibiscus tiliaceus			x		x						x	x	x		x	x	x	8
Hernandia sonora				x	x		x		x					x			x	6
Leucaena insularum				x		x				x		x			x	x		6
Pisonia grandis				x	x							x		x	x			5
Calophyllum inophyllum																x	x	2
Carica papaya										x								1
Cordia subcordata										x								1
Erythrina variegata																	x	1
Mangifera indica																	x	1
Thespesia populnea																	x	1
Total	1	3	5	8	7	5	5	4	6	8	4	7	5	7	8	7	11	

Table 14. Distribution of shrub species on Aitutaki motus

	Tapuaeta cay	Muritapua	Tavaerua Iti	Papau	Tapuaeta	Mangere	Motukitiu	Taverua	Angarei	Akitua	Maina	Ee	Akaiami	Tekopua	Ootu	Moturakau	Rapota	Total
Scaevola taccada	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	17
Pemphis acidula		x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	15
Suriana maritima	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			15
Tournefortia argentea	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	16
Euphorbia chamissonis		x	x	x	x	x	x	x	x	x	x	x	x	x	x			14
Timonius polygama			x	x		x		x	x	x		x	x	x	x			10
Sophora tomentosa				x	x					x		x	x	x	x	x		8
Colubrina asiatica					x		x		x		x		x	x	x			7
Capparis cordifolia							x						x	x	x			4
Pipturus argenteus			x		x		x							x				4
Corchorus torresianus									x	x					x			3
Sida rhombifolia										x								1
Solanum nigrum															x			1
Crotalaria pallida															x			1
Total	3	5	7	7	8	6	8	6	8	9	5	7	9	10	12	3	3	

Table 15. Distribution of herb species on Aitutaki motus

	Tapuaeta cay	Muritapua	Taverua Iti	Papau	Tapuaeta	Mangere	Motukitiu	Tavaerua	Angarei	Akitua	Maina	Ee	Akaiami	Tekopua	Ootu	Moturakau	Rapota	Total
Stenotaphrum micranthum		x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	15
Fimbristylis cymosa		x	x	x	x	x	x	x	x	x	x	x	x	x	x			14
Heliotropium anomalum	x	x	x	x		x	x	x	x		x	x	x	x	x			13
Polypodium scolopendria		x	x	x	x	x	x	x		x	x	x		x		x	x	13
Triumfetta procumbens		x	x	x	x	x	x	x	x	x	x	x			x			12
Cassytha filiformis		x		x			x	x	x	x	x	x	x	x	x			11
Vigna marina			x			x	x	x	x			x	x	x	x	x	x	11
Tacca leontopetaloides		x	x	x	x	x		x			x		x	x			x	10
Ipomoea pes-caprae				x		x				x					x	x	x	6
Ipomoea macrantha		x	x				x			x	x				x			6
Lepidium bidentatum				x							x		x	x				4
Portulaca oleracea				x	x						x				x			4
Cenchrus echinatus										x				x	x			3
Abrus precatorius																x	x	2
Boerhavia tetrandra			x				x											2
Bidens pilosa										x					x			2
Emilia sonchifolia										x					x			2
Digitaria ciliaris			x												x			2

Table 15 continued

	Tapuaeta cay	Muritapua	Taverua Iti	Papau	Tapuaeta	Mangere	Motukitiu	Tavaerua	Angarei	Akitua	Maina	Ee	Akaiami	Tekopua	Ootu	Moturakau	Rapota	Total
Achyranthes velutina							x											1
Boerhavia repens										x								1
Cladium jamaicense										x								1
Sporobolus												x						1
Vernonia cinerea																x		1
Unident. grass													x					1
Total	1	8	10	10	6	8	10	8	6	12	10	7	8	9	22*	6	6	

*includes 10 additional species not listed here

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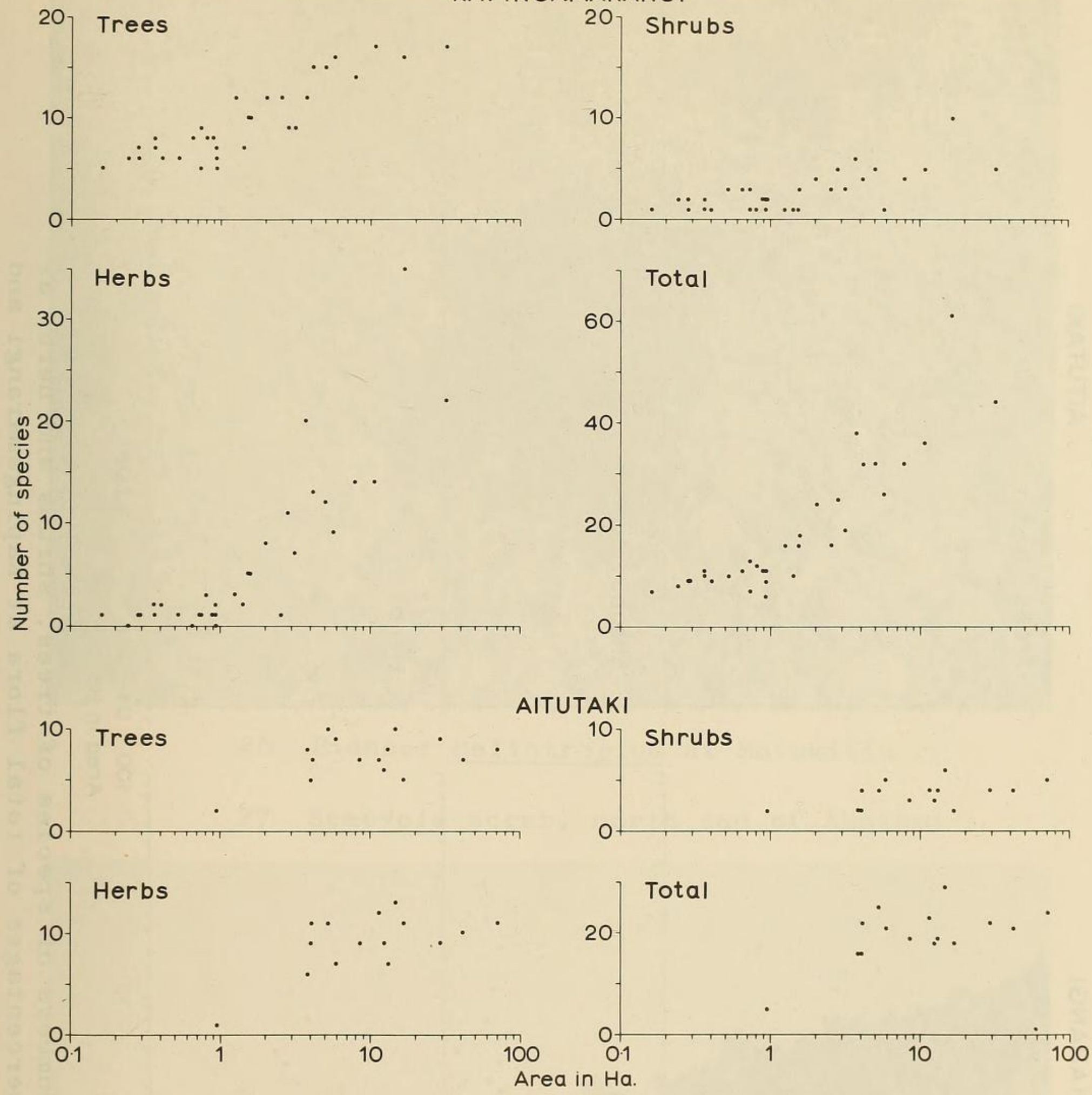


Figure 33. Numbers of species and island area for trees, shrubs and herbs at Kapingamarangi and Aitutaki

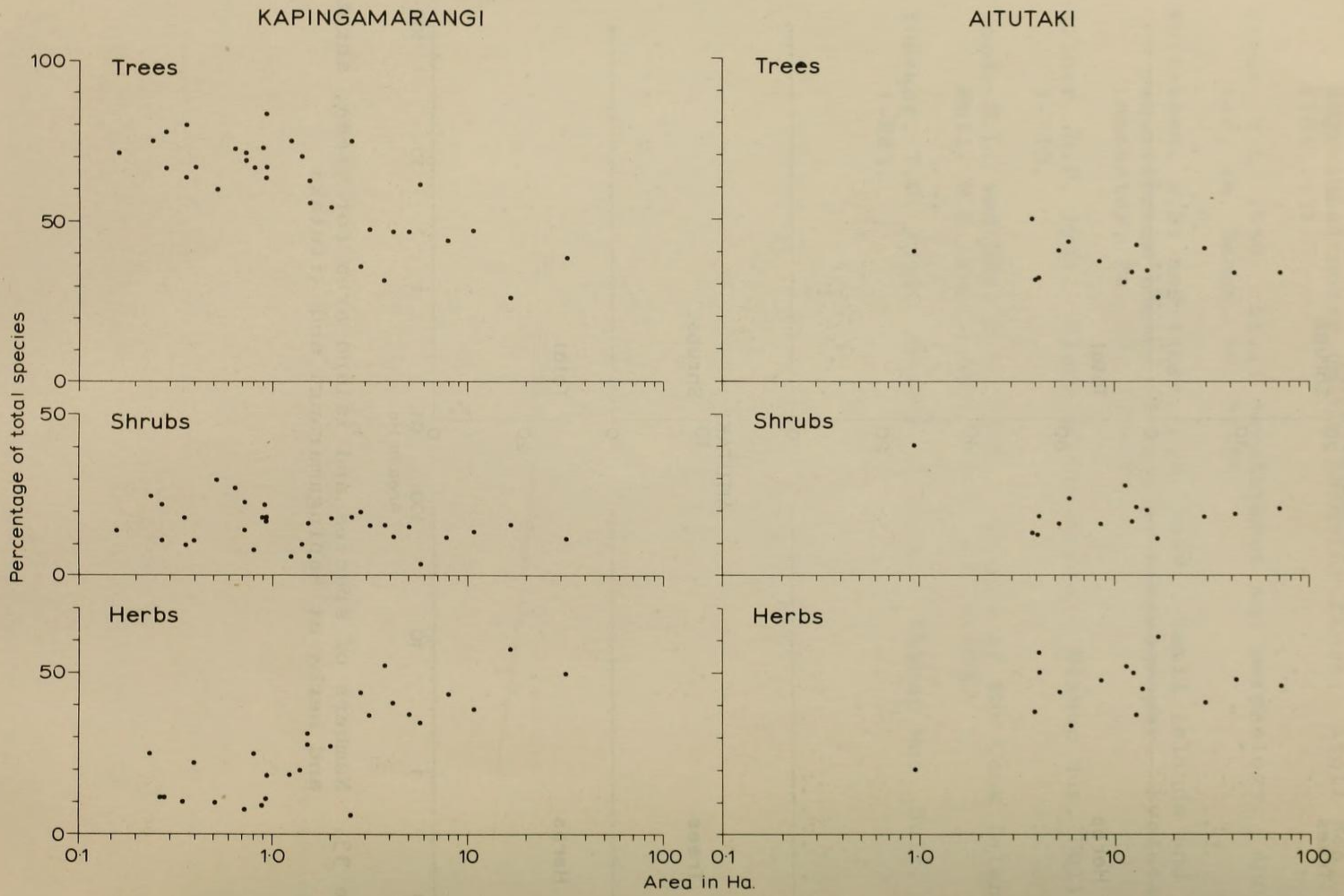
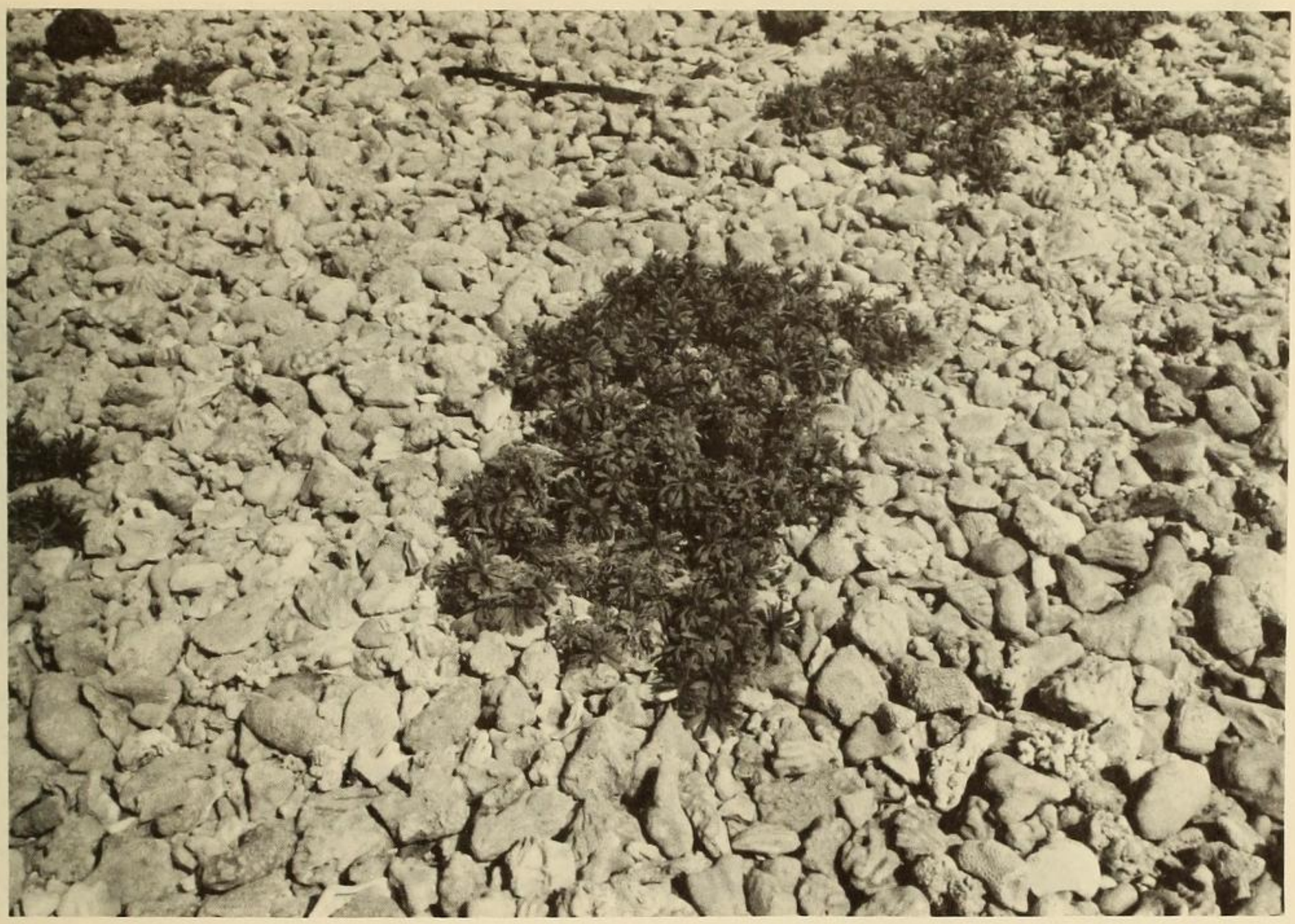
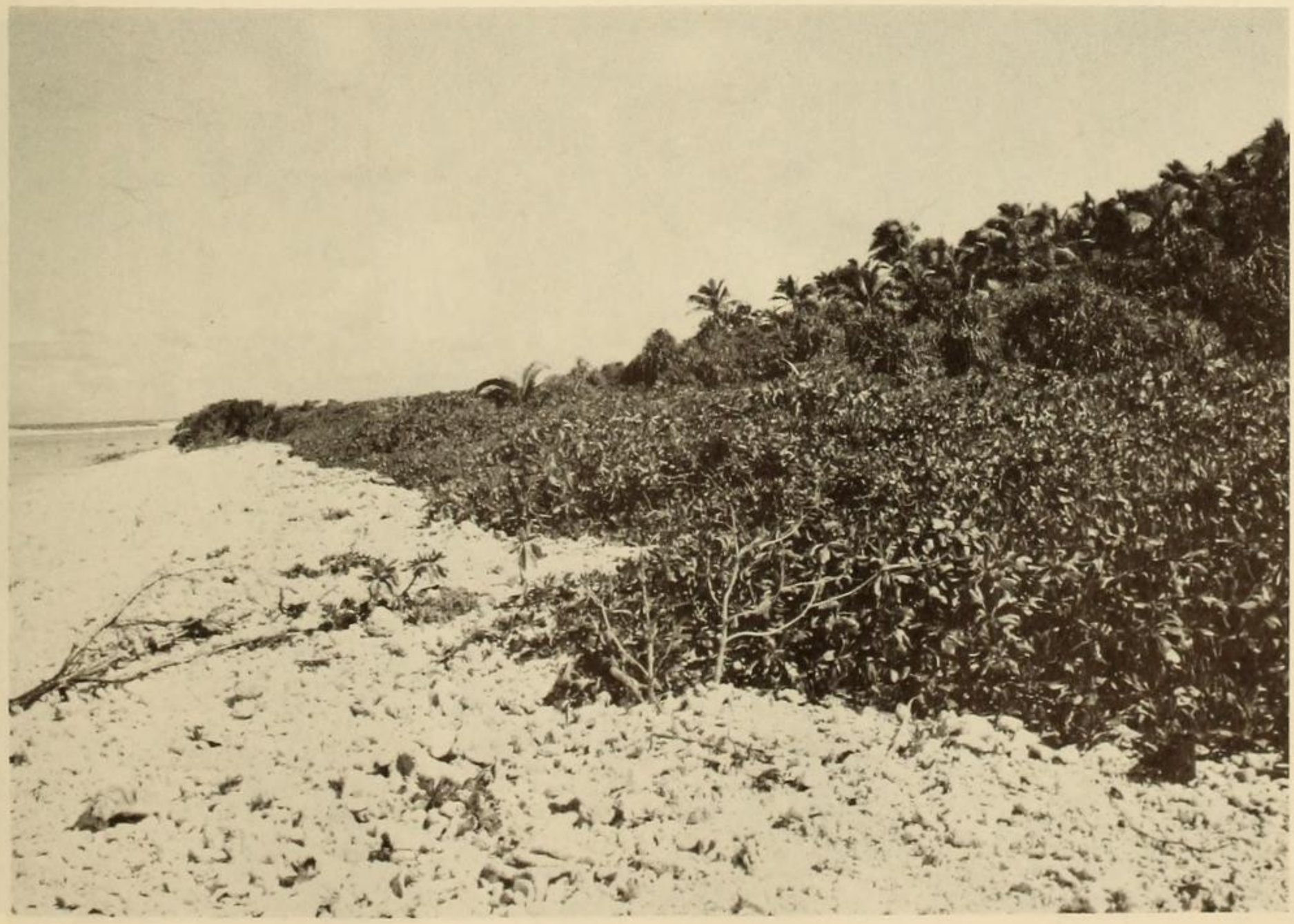


Figure 34. Numbers of species of trees, shrubs and herbs as percentages of total flora at Kapingamarangi and Aitutaki



26 Pioneer Heliotropium at Motukitiu

27 Scaevola scrub, north end of Akaiami



28 Pemphis scrub and leeward woodland at Ee

29 Pemphis scrub and leeward woodland at Muritapua

30 Mixed woodland at the south end of Tekopua

31 Coconut woodland on Motukitiu

32 Tacca on Akaiami in coconut woodland

33 Pisonia woodland on Tapueta