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SUBSTRATA SPECIFICITY AND EPISODIC CATASTROPHE: CONSTRAINTS ON THE INSULAR PLANT GEOGRAPHY OF SUWARROW ATOLL, NORTHERN COOK ISLANDS

BY

C.D. WOODROFFE AND D.R. STODDART

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SUBSTRATE SPECIFICITY AND EPISODIC CATASTROPHE: CONSTRAINTS ON THE INSULAR PLANT BIOGEOGRAPHY OF SUWARROW ATOLL, NORTHERN COOK ISLANDS

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C. D. WOODROFFE [1] and D. R. STODDART [2]

Coral atolls are natural laboratories within which to examine ecological processes (Sachet, 1967; Lee, 1984). They are often isolated, in some cases little disturbed, and have a geologically recent history of terrestrial plant colonisation. Reef islands around the rim of most atolls are Holocene in age. They are composed of biogenic skeletal sediments and have developed since reef growth caught up with sea level which stabilised after post-glacial sea-level rise. Plant colonisation of most of these islands must have occurred over a period of no more than 6000 years.

Reef islands on coral atoll rims provide an opportunity to test premises and predictions of the MacArthur and Wilson theory of island biogeography (MacArthur and Wilson, 1967). This theory suggested that inter-archipelagic (between-atoll) and intra-archipelagic (within-atoll) variation in plant species richness relate to different processes. Inter-archipelagic trends in diversity reflect regional scale floristic patterns, largely a function of immigration rate which is dependent on distance from 'mainland' source. Intra-archipelagic diversity, on the other hand, reflects local scale differences in plant occurrences, which relate closely to island area, and are a response to area dependent extinction rate. MacArthur and Wilson postulated that the extinction rate would be high on small islands (MacArthur and Wilson, 1967).

Niering (1963), in a study of the vegetation of Kapingamarangi Atoll in the eastern Caroline Islands, demonstrated a relationship between the number of plant species on an island and the logarithm of island area (using 33 islands, 0.01 to 32.0 ha). On islands larger than 1.4 ha, the number of species increased linearly with log area, but on islands smaller than 1.4 ha, the number of species was relatively invariant with area. Niering interpreted this as a result of ecological control, with more mature soils, greater soil moisture and protection from salt spray on islands above this threshold size (Niering, 1963). Similarly Wiens (1962) suggested that the inflection in the species-area relationship resulted from freshwater lens development on islands larger than 1.4 ha.

Ecological control was indicated by Whitehead and Jones (1969) who demonstrated that the Kapingamarangi data could be more closely described by a curvilinear than by a linear correlation, and who divided the flora into strand, non-strand

[1]Department of Geography, University of Wollongong, Wollongong N.S.W. 2500, Australia

[2]Department of Geography, University of California, Berkeley, California 94720, U.S.A.

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and introduced species. Only strand species were found on the smallest island, and as the pool of strand species was restricted the number on an island did not increase markedly as island size increased. The rapid increase in diversity on islands larger than 1.4 ha was attributed primarily to appearance of non-strand species on these islands, with introduced species appearing on the largest of reef islands (Whitehead and Jones, 1969).

MacArthur and Wilson (1967) used the Kapingamarangi data in support of their theory. However, they attributed the poor species-area relationship on small islands to episodic instability of those islands. They implied that catastrophic events, such as tidal waves or tropical cyclones, periodically totally devastate the smallest islands, and thus these are not maintained at equilibrium.

The species-area relationship found on Kapingamarangi is not replicated on other coral atolls for which there is comparable data. There is some evidence for an inflection in the species-area relationship with relatively invariant number of native species on islands smaller than 3 ha (79 islands, 0.04 to 178 ha) on neighbouring Ontong Java Atoll, in the Solomon Islands (Bayliss-Smith, 1973). On Aitutaki, an almost-atoll in the Cook Islands (15 islands, 1.0 to 71.3 ha), the species-area relationship is weaker than on Kapingamarangi, but a linear semi-log relationship does hold for herbs, and to a lesser extent for trees (Stoddart, 1975b). Aitutaki lagoon contains a volcanic island which may be considered a reservoir of potential plant colonists; the fact that these have not established on sandy reef islands demonstrates ecological selection of species which do colonise reef islands (Stoddart, 1975b). A strong linear relationship exists throughout a wide range of island sizes (20 islands, 0.01 to 138 ha) on Nui Atoll in Tuvalu (Woodroffe, 1986).

This paper examines the flora of Suwarrow Atoll, an isolated, uninhabited and largely undisturbed atoll in the northern Cook Islands.

METHODS AND AREA OF STUDY

Suwarrow Atoll (13°14'5, 163°05'W) is an isolated atoll in the northern Cook Islands (Figure 1). It is 272 km from the island of Nassau, 347 km from Manihiki Atoll and 460 km from Palmerston Atoll. The atoll is about 18 km from west to east, and 14 km from north to south. It consists of a lagoon, up to 80 m deep, studded with patch reefs. It is surrounded by a continuous atoll rim, breached only at one place on the northern side where there is an entrance to the lagoon. There are more than 40 reef islands on the atoll rim, the actual number recognised depending upon definition of individual islands. These islands range in area from 0.06 ha (Manu 4) to 41.6 ha (Turtle Island, only 18.3 ha vegetated). The sporadic vegetation cover on several islands has allowed further subdivision such that stands as small as 50 m^2 are considered islands. Whale Island has been subdivided into 15 smaller vegetated islands. New Island contains only 3 coconut trees and has the smallest vegetated area.

The atoll is influenced by southeasterly Trade winds, but lies in the hurricane belt and tropical cyclones come from the north or northwest. Severe storms hit the atoll in

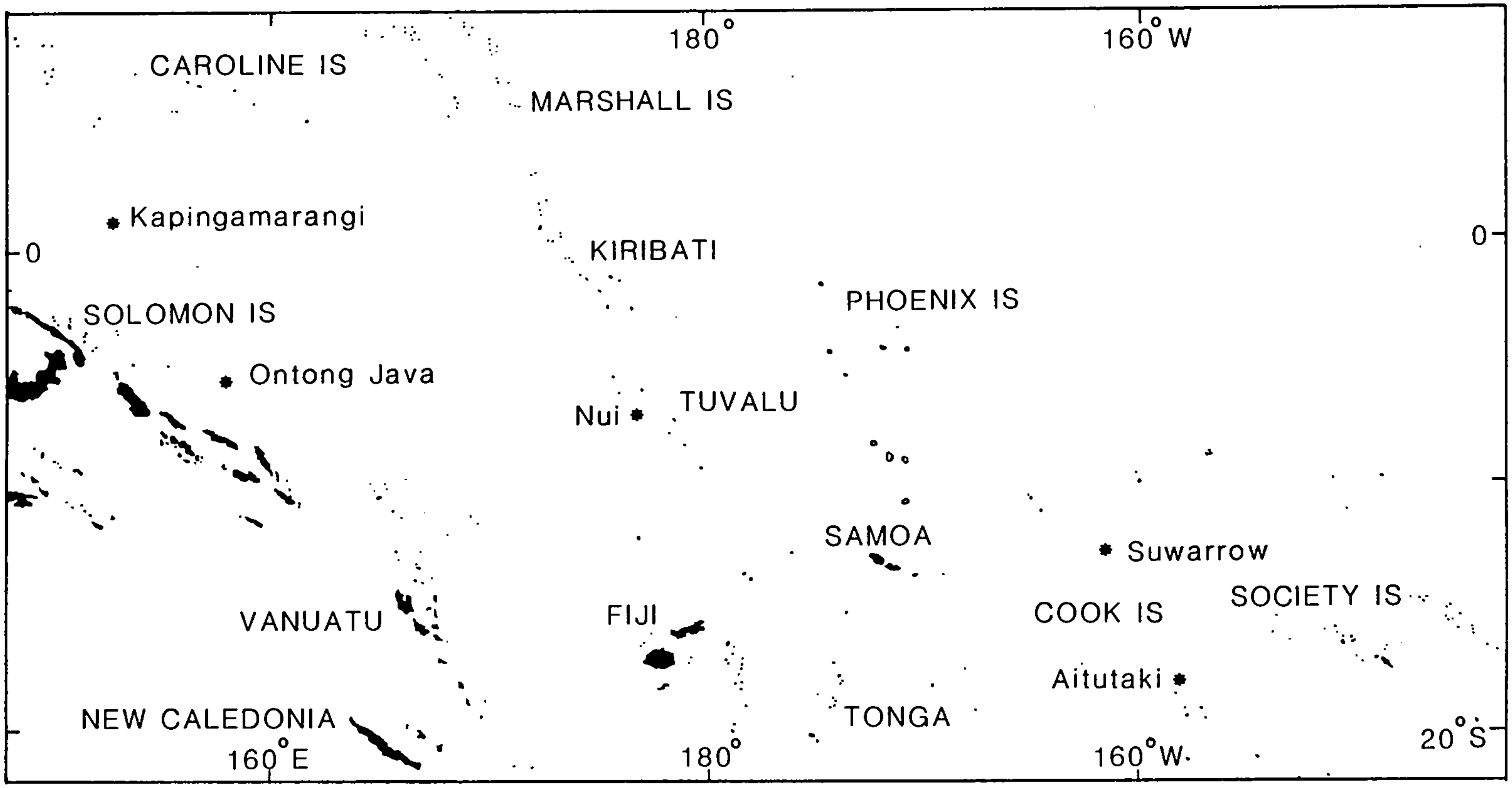

Figure 1. West and Central Pacific showing location of Suwarrow Atoll and other atolls mentioned in text.

1914, 1940, 1942 and 1967. Average annual precipitation is around 2400 mm. Tidal range is slightly less than 1 m.

Suwarrow is uninhabited; however it has had a history of sporadic settlement and some disturbance to vegetation. The atoll was visited by whalers, traders and pearlers. New Zealand coastwatchers lived there during World War II (Helm and Percival, 1973). For many years thereafter it had a lone inhabitant, Tom Neale, a New Zealander (Neale, 1968).

The fieldwork for this study was undertaken in September 1981. Each of the reef islands was visited and was mapped by pace and compass. All species growing on each of the islands were recorded, and an extensive collection was made, which has been deposited at the Smithsonian Institution. Sight and collection records are listed in Fosberg *et al.* (in prep.). The total flora consisted of 45 species of vascular plant, of which 22 species are introduced.

REEF ISLANDS OF SUWARROW ATOLL

The reef islands of Suwarrow Atoll are located at the lagoonward edge of the atoll rim, which varies from 100 to 800 m wide (Figure 2). Many of the islands are composed of a core of reefal limestone, with only a thin veneer of skeletal sands. Some of the larger islands, at the corners of the atoll rim, are unconsolidated boulder, shingle or sand islands.

Wood and Hay (1970) noted emergent reefal deposits at the northern end of Anchorage Island which they suggested might be Pleistocene in age. Radiometric dating implies, however, that all of the islands are mid to late Holocene in age (Kaplin, 1981, Scoffin et al., 1985). The exposed limestones of Suwarrow Atoll are described by Scoffin et al. (1985). There is a widespread *in situ* reef above the present level of coral growth and at about 50 cm above low water level. The reef surface which has been planed off partly by spalling contains numerous faviid corals in growth position, with specimens of *Acropora*, *Pocillopora* and *Millepora* to seaward. The raised reef forms the core of many of the smaller rocky islands. Radiocarbon ages of 4680±50 and 4650±60 years B.P. have been obtained on corals from this reef on Manu Island, an age of 4310±50 years B.P. on Whale Island, and 3670±50 years B.P. on a microatoll (possibly moated) at the northern end of Anchorage Island. It appears that the fossil reef was flourishing 4600-4300 years ago (Scoffin et al., 1985). On the southern rim of the atoll, however, a similar *in situ* reef is about 2000 years younger, radiocarbon-dated 2400±60 years B.P. at Entrance Island and 2400±60 years B.P. at New Island.

The second major limestone unit on the islands is a boulder conglomerate, containing boulders of massive and branching corals, cemented into deposits up to 2 m above the upper limit to coral growth. These boulder conglomerates occur to the oceanward of the *in situ* reef, though degraded remnants of reef do occur still further seaward (Scoffin et al., 1985). Radiocarbon dates on corals within these deposits range from 4460±50 to 2620±50 years B.P. The conglomerate was evidently deposited by storms. It is equivalent to the widespread conglomerate platform described by Stoddart

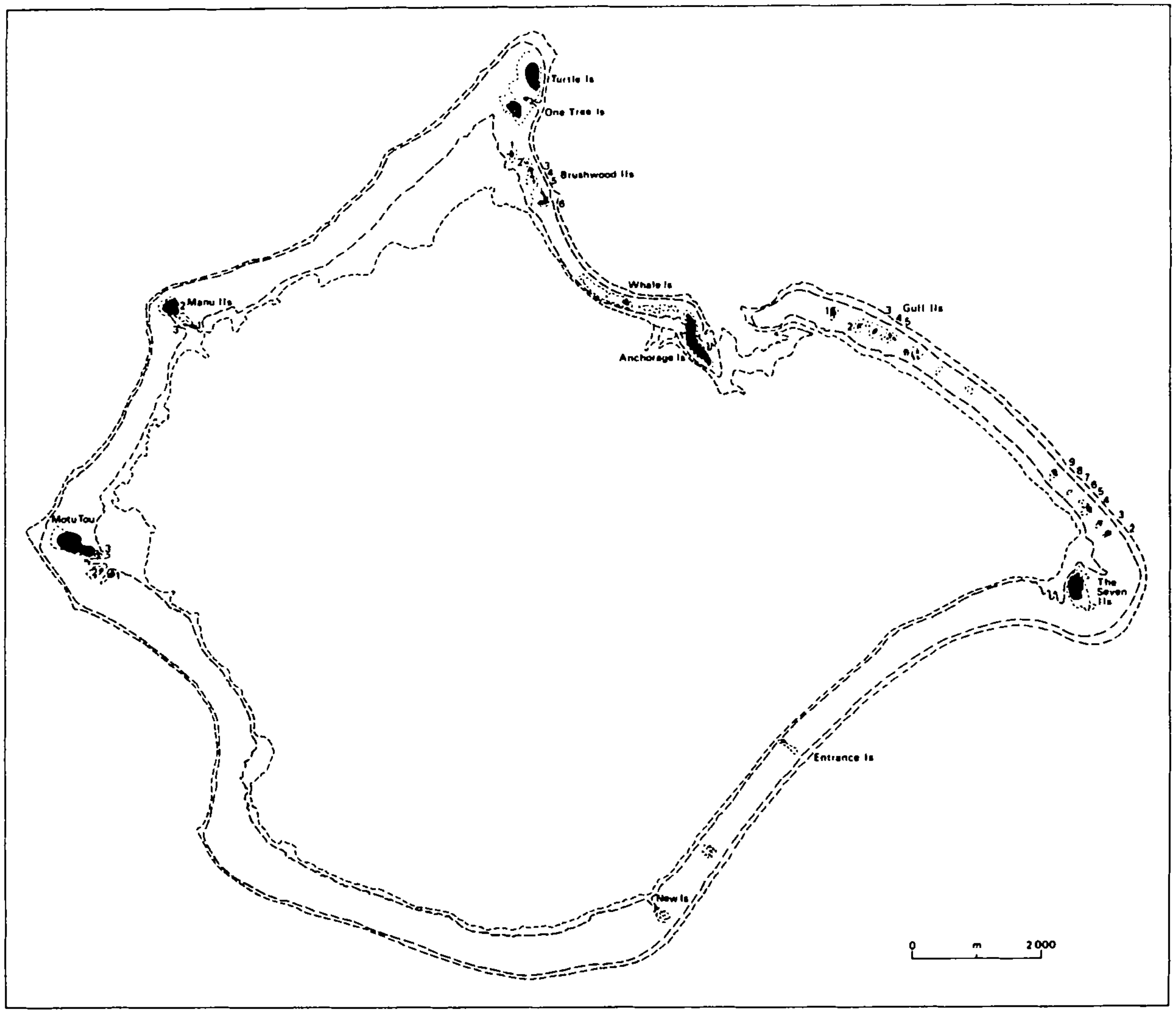

Figure 2. Suwarrow Atoll, and location of reef islands.

(1975a) on Aitutaki, and has been deposited during a series of episodes of storm activity over 2000 years of the late Holocene.

On the northeastern atoll rim, seaward of the Seven Islands there are 3 prominent fossil encrusting coralline algal ridges. The landwardmost ridge, about 1.5 m above low level water, in some places forms a part of the reef islands, and still contains traces of former groove and spur pattern. This ridge has been radiocarbon-dated 4220±60 years B.P. The intermediate ridge is degraded and has been radiocarbon-dated 3420±40 years B.P. The youngest, seawardmost ridge, only 50 cm above low water level and continuous with the present algal ridge, has been radiocarbon dated 1250±35 years B.P. The sequence of 3 ridges indicates periodic horizontal progradation of the reef during the late Holocene, and slight emergence of the mid-Holocene reef.

In addition to the cemented boulder conglomerate there are several unconsolidated boulder deposits. Much of the reef flat, particularly to the northwest of the atoll, is strewn with storm blocks, up to 4 m tall, and coral boulders. Kaplin (1981) reports a radiocarbon age of 3045±116 years B.P. on a boulder from a tract to the west of the westernmost island Motu Tou. Some of the reef islands are composed of unconsolidated boulder deposits, in particular Motu Tou, on which boulders have been radiocarbon-dated to 1225±175 years B.P. (Kaplin, 1981).

Other islands are made of moderately well sorted reef derived sands or coral shingle. The sands are dominated by benthic foraminifera, especially *Amphistegina lobifera* and *Marginopora vertebralis*, but abraded mollusc and coral fragments, *Halimeda* and the foraminiferan *Homotrema* are also prominent (Tudhope et al., 1985). Locally beachrock has formed, particularly on the oceanward beaches.

There is abundant evidence that storms have played a major role in the development and maintenance of the islands. Many of the deposits (ie boulder conglomerate, storm blocks) are storm derived. Wood and Hay (1970) believed that storms were instrumental in keeping the reef islands small. Kaplin (1981) also believed that islands remain small because sediments are washed away, but attributed this to tectonic sinking of the atoll. Tilting, rather than sinking of the atoll, was inferred by Scoffin et al. (1985).

VEGETATION AND FLORA OF SUWARROW ATOLL

The flora of Suwarrow Atoll is impoverished. Forty-five species of plant were collected or observed on the atoll, and 22 of these are considered introduced (Fosberg et al. in prep.). Several species which might be expected do not occur on the atoll, e.g. *Timonius polygama*, *Euphorbia chamissonis*, *Ipomoea pes-caprae*, *Sesuvium portulacastrum*. The native plants and their occurrence are listed in Table 1.

The only extensive vegetation on the rocky island surfaces, over *in situ* reef, or boulder conglomerate is a scrub of *Pemphis acidula* (Plate 3). This often forms a wind-sheared fringe to the north of reef islands, from low divaricating shrubs 1-3 m high on the exposed northern side, to a thicket up to 7 m tall. *Pemphis* scrub is monospecific over

Plate 1. Motu Tou 1, coconut woodland and mixed scrub types. The island has a shingle substrate and is surrounded by boulder tract (foreground).

much of the islands but locally there is a ground cover of *Portulaca johnii*, *Boerhavia tetrandra*, *Lepturus repens* or *Fimbristylis cymosa*.

Where coral shingle or sand has accumulated there is often a scrub of *Tournefortia argentea* (Plate 2). This species commonly forms inliers within *Pemphis* scrub. It forms more extensive stands over some sandy or shingle islands (such as Seven 1 and Manu 1), where it is well-spaced and up to 6 m tall. In addition to the species which form a ground cover beneath *Pemphis*, *Laportea ruderalis* and *Lepidium bidentatum* are also found.

Scrub composed of *Scaevola taccada* var. *tuamotuensis*, which is a dominant vegetation type of Pacific atolls, is relatively restricted on Suwarrow Atoll. It forms a fringe around the outside of the larger sand islands, and on southeastern Anchorage Island forms a scrub 2 m tall, up to 17 m wide. *Suriana maritima* has a very patchy distribution on the reef islands of Suwarrow Atoll, and does not form the marginal scrub that it does on Aitutaki (Stoddart, 1975a).

Plate 2. Pemphis scrub with stands of *Tournefortia argentea* on sandy substrate, overlying *in situ* emergent reef (foreground), one of the Seven Islands.

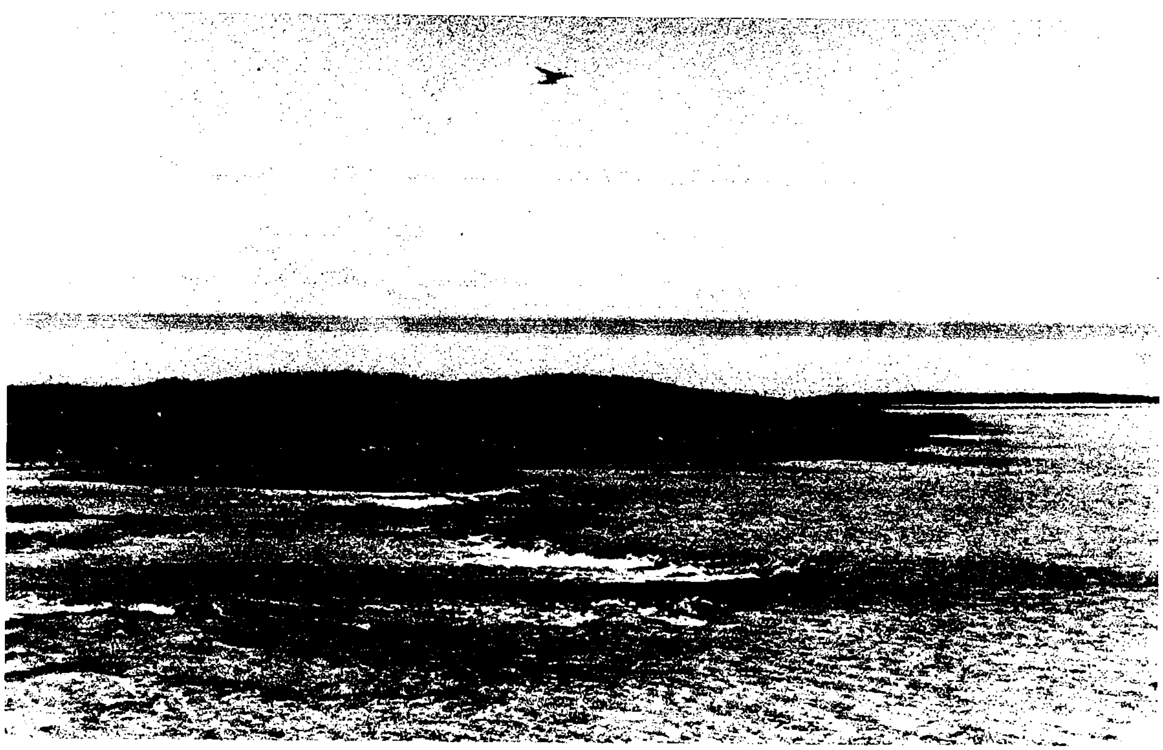

Plate 3. Dense *Pemphis* scrub over rocky substrate, one of the Brushwood Islands.

The interior of three of the four largest islands (Motu Tou, Turtle and Anchorage Islands) is dominated by coconut woodland, up to 20 m tall. Beneath this woodland is undergrowth of *Scaevola* and *Lepturus*, often with *Triumfetta procumbens* and the fern *Polypodium scolopendria*.

Other woodland types are localised in comparison. Woodland of *Pandanus tectorius*, up to 18 m tall, is found on Motu Tou, Turtle and Anchorage Islands, generally with the ferns *Polypodium* and *Asplenium nidus*. Woodland of *Guettarda speciosa*, up to 16 m tall, is associated with *Pandanus* and coconut woodland on Motu Tou. Further open broad-leaved woodland occurs on Turtle, Motu Tou, Motu Tou 1 and Anchorage Islands (Plate l); in some places this is dominated by *Pisonia grandis* and in others by *Cordia subcordata*.

An isolated storm block on the northwestern atoll rim was found to have 4 species on it: *Pemphis acidula*, *Digitaria stenotaphroides*, *Portulaca johnii* and *Laportea ruderalis*.

SPECIES-AREA RELATIONSHIPS

Many of the Suwarrow reef islands have been little disturbed by man. The only island to have been sporadically settled is Anchorage Island and it is on this island that introduced species are widespread. Many of these introduced plants are crop plants (*Musa*, *Carica* etc.) or ornamentals (e.g. *Hibiscus* sp.). Others considered introduced include large trees such as *Barringtonia asiatica* and *Calophyllum inophyllum* native to many Pacific Islands, but only found around a garden area on Anchorage. The polynesian rat occurs on Anchorage Island and does not appear to have spread to other islands. Conversely, four plants were found on other reef islands, but not on Anchorage (*Asplenium nidus*, *Digitaria stenotaphroides*, *Canavalia cathartica* and *Laportea ruderalis*).

In the analyses that follow introduced species have been excluded, and the 23 plant species considered native (including aboriginal introductions) are examined (Table 1). Figure 3 shows the relationship between the number of native species and log total island area, and between the number of native species and log total vegetated area. The relationship between species number and total area is weak ($r^2 = 0.57$); the relationship to total vegetated area is only a little stronger ($r^2 = 0.60$).

Figure 4 demonstrates species-area relationships for trees, shrubs and herbs. There is some ambiguity as to whether to classify individual plants, as a shrub or a tree; *Morinda citrifolia* and *Hibiscus tiliaceus* have been classed as trees and *Tournefortia argentea* as a shrub (Table 1) because that is the form they most frequently adopt on Suwarrow. The relationship between the number of species adopting each life form and log total area of the island is not strong; trees $r^2 = 0.31$, shrubs $r^2 = 0.54$, herbs $r^2 = 0.62$ (Figure 4). The relationship of trees, shrubs and herbs to log vegetated area is only a little stronger; trees $r^2 = 0.32$, shrubs $r^2 = 0.64$ and herbs $r^2 = 0.64$ (Figure 4).

The tree species-area relationship comprises two groups of islands. On the one hand there are the *Pemphis*-dominated islands covering a rocky substrate on which tree diversity is very low or from which trees are absent. On the other hand there are the sand or shingle cays, generally the larger islands on which woodland is established and which are relatively diverse in terms of tree species. Shrub diversity shows some relationship to island area, particularly to vegetated area, but the pool consists of only 4 species all of which are present on the largest islands. The extensive monospecific stands of shrubs that form (except *Suriana* which does not cover a large area on Suwarrow) further compounds the relationship. Herb species show the strongest relationship to island area; in part this may be a derivative of the association of herbs with trees. Locally herb diversity increases where there has been disturbance.

The differentiation between rocky islands dominated by *Pemphis* and sand and shingle cays is an appropriate one not only in terms of the distribution of tree species, but also in relation to the broader distribution of plants on the atoll. The rocky substrate, composed of boulder conglomerate, often with some adjacent *in situ* reef surface, represents an inhospitable environment, lacking soil or water, unfavourable for plant colonisation. There are only few species, principally *Pemphis acidula*, which can overcome these constraints of physiological drought. The area of these islands is determined principally by the topography of the emergent limestones. One Tree and Manu 2 (26.1 and 10.1 ha respectively) are relatively large islands, but because of their domination by rocky substrate, there are few or no additional species which can be expected to colonise and they are scarcely richer than much smaller adjacent islands.

Sand and shingle islands on the other hand are more diverse. However, these represent too small a sample to determine whether or not a species-area relationship exists, particularly in view of the differences in substrate (ie Motu Tou composed mainly of boulders and Seven 1 composed almost entirely of sand) and disturbance (widespread on Anchorage, restricted on Turtle and Motu Tou) between islands.

DISCUSSION

The species-area relationships for Suwarrow Atoll (Figures 3 and 4) are weaker and show more scatter than those for other Pacific atolls for two reasons. Firstly, many of the plants found on Suwarrow are substrate-specific, and there is an extremely limited pool of species which can colonise the rocky limestone surfaces, resulting in extensive monospecific stands of *Pemphis*. Secondly the atoll has been subject to episodic catastrophic hurricanes which devastate the small islands, probably remove much of the accumulated sediment and soil, and help maintain the islands at disequilibrium.

The importance of substrate characteristics has been realised in many island biogeographic studies as a factor influencing the diversity of habitats on islands. Buckley (1982) proposed a habitat unit model in which species-area relationships should be determined for various floristic elements in individual habitats or combinations of habitats, and summed to give a predicted species diversity for particular island areas. Substrate was shown to be a major component of habitat diversity on a group of islands off the coast of Western Australia (Buckley, 1982), but was less important on habitat islands on bare hypersaline mudflats in Queensland (Buckley, 1985).

Table 1: Native species and their occurrence on the reef islands of Suwarrow Atoll

Species	Islands																																																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
TREES																																																									
Pandanus tectorius	X									X										X		X	X	X				X		X																											
Cocos nucifera	X						X	X	X	X	X	X					X			X	X	X	X	X				X		X	X				X											X											
Pisonia grandis	X		X							X										X		X	X					X		X																X											
Hibiscus tiliaceus																								X						X																											
Cordia subcordata										X										X	X	X	X	X						X																											
Guettarda speciosa										X										X		X	X					X		X																											
Morinda citrifolia	X									X										X			X	X				X		X																											
SHRUBS																																																									
Suriana maritima																							X					X	X	X																			X								
Pemphis acidula		X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				X	X	X	X	X	X	X	X
Tournefortia argentea	X	X	X	X	X		X	X	X	X		X	X		X	X		X		X	X	X	X	X	X			X	X	X	X															X	X	X	X	X	X	X			X		X
Scaevola taccada	X	X							X	X										X		X	X					X	X	X																X								X			X
HERBS																																																									
Asplenium nidus																				X			X					X																													
Polypodium scolopendria										X										X	X	X	X					X		X																											
Digitaria stenotaphroides																			X																																						
Lepturus repens	X	X	X	X	X		X	X	X	X		X	X		X	X		X		X	X		X	X	X	X		X	X	X	X															X				X					X		X
Fimbristylis cymosa																X														X																											
Boerhavia tetrandra	X	X	X		X			X	X	X					X	X		X		X	X		X	X				X		X																X						X			X		X
Portulaca johnii	X	X	X	X	X	X	X	X	X			X	X	X	X	X	X	X	X						X	X		X	X	X	X															X				X	X	X			X		X
Lepidium bidentatum	X																			X			X						X	X																											
Canavalia cathartica																						X	X																																		
Laportea ruderalis	X									X									X		X		X					X	X																												
Triumfetta procumbens								X															X							X																											
Ipomoea macrantha																														X																											

Key to Island Numbers: 1 = Seven 1, 2 = Seven 2, 3 = Seven 3, 4 = Seven 4, 5 = Seven 5, 6 = Seven 6, 7 = Seven 7, 8 = Seven 8, 9 = Seven 9, 10 = Entrance, 11 = New, 12 = Gull 1, 13 = Gull 2A, 14 = Gull 2B, 15 = Gull 3, 16 = Gull 4A, 17 = Gull 4B, 18 = Gull 5, 19 = Storm Block, 20 = Motu Tou 1, 21 = Motu Tou 2, 22 = Motu Tou 3, 23 = Motu Tou, 24 = Manu 1, 25 = Manu 2, 26 = Manu 3, 27 = Manu 4, 28 = Turtle, 29 = One Tree, 30 = Anchorage, 31 = Whale 1, 32 = Whale 2, 33 = Whale 3, 34 = Whale 4, 35 = Whale 5, 36 = Whale 6, 37 = Whale 7, 38 = Whale 8, 39 = Whale 9, 40 = Whale 10, 41 = Whale 11, 42 = Whale 12, 43 = Whale 13, 44 = Whale 14, 45 = Whale 15, 46 = Brushwood Main, 47 = Brushwood 1A, 48 = Brushwood 1B, 49 = Brushwood 1C, 50 = Brushwood 1D, 51 = Brushwood 2A, 52 = Brushwood 2B, 53 = Brushwood 3, 54 = Brushwood 4, 55 = Brushwood 5A, 56 = Brushwood 5B, 57 = Brushwood 6

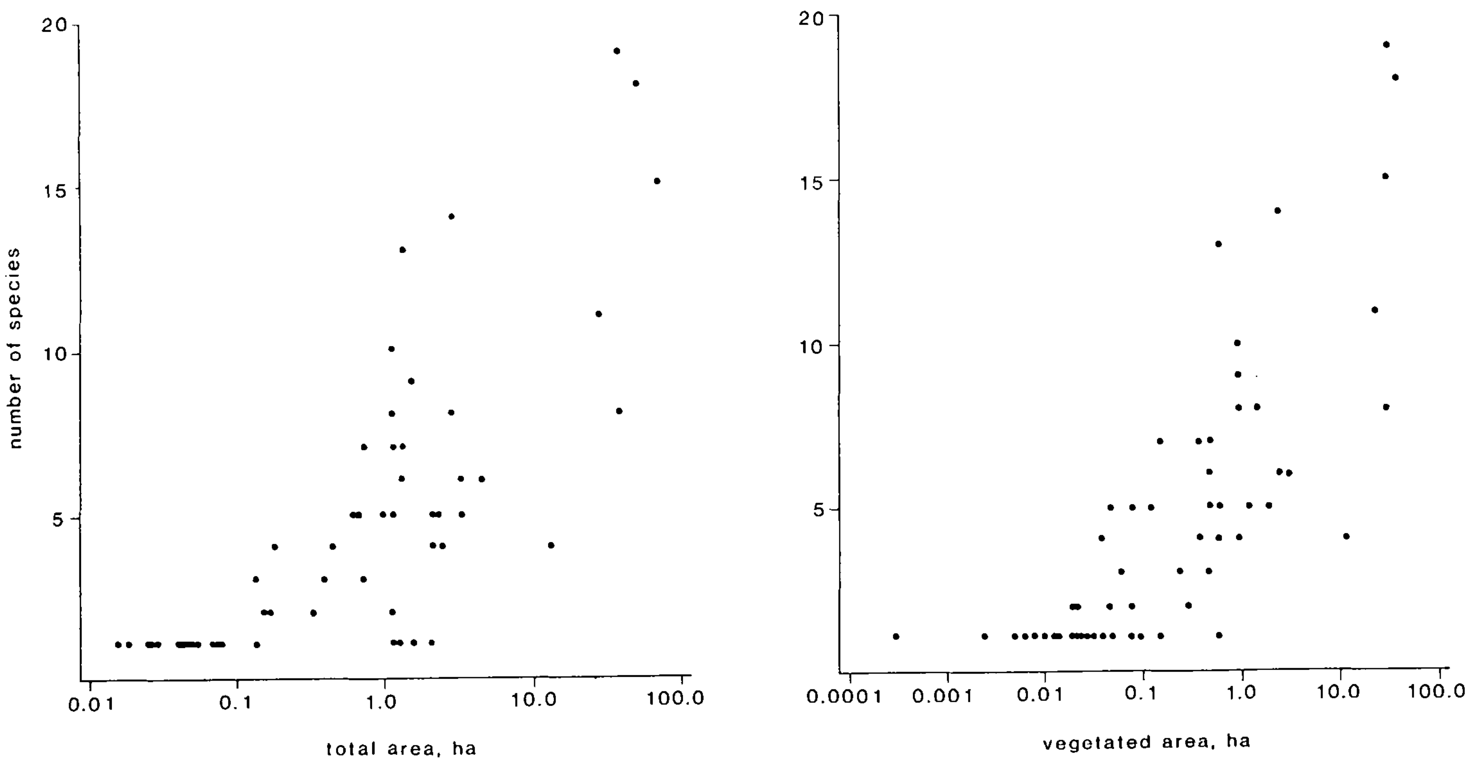

Figure 3. Species-area relationship (native species against total area, and native species against vegetated area).

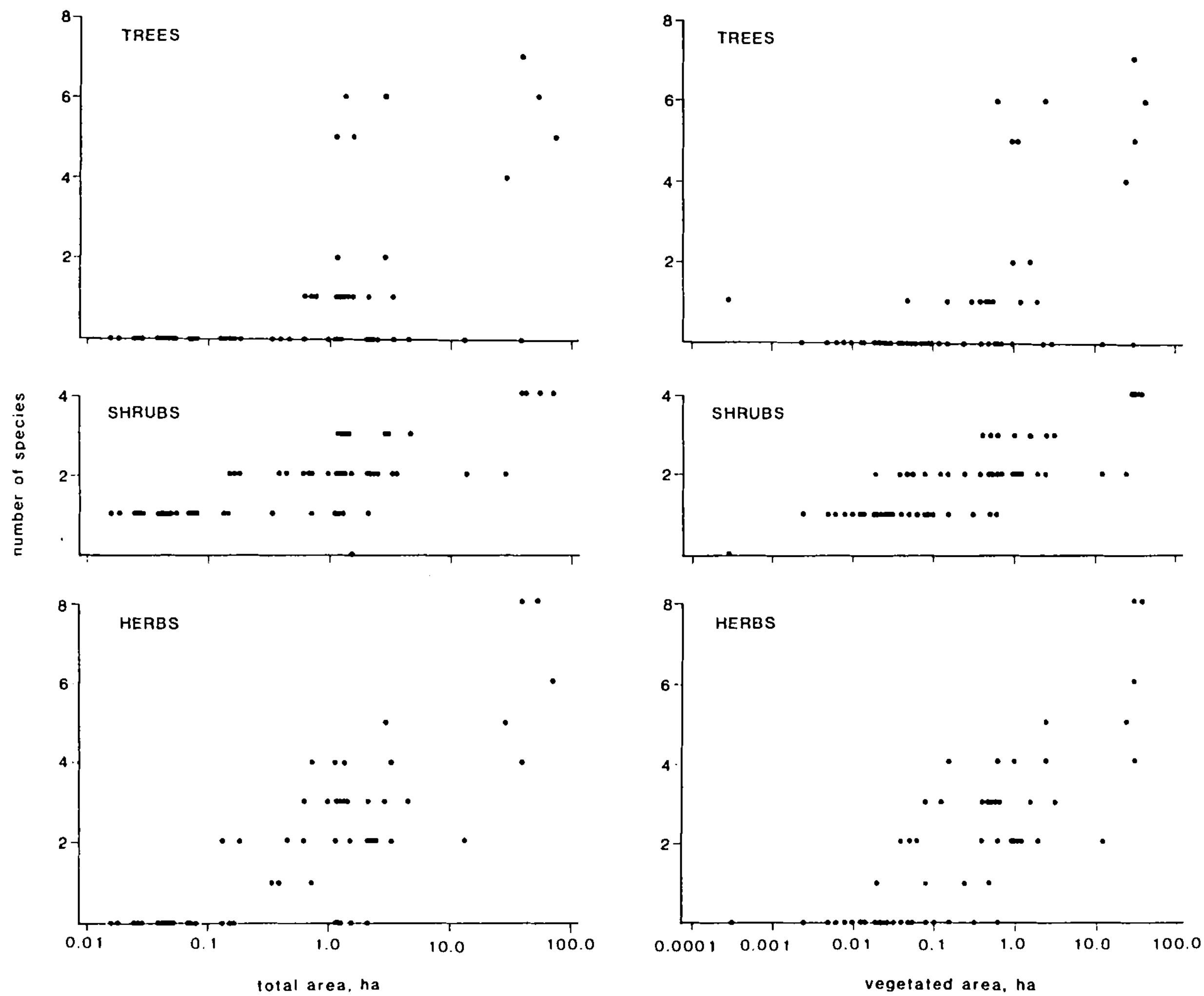

Figure 4. Species-area relationship (native species) for trees, shrubs and herbs against total area and vegetated area.

It is not possible to apply Buckley's habitat unit model to reef islands on Suwarrow Atoll. Firstly despite detailed mapping of vegetation types, the extent of sand or shingle sheets within the interior of *Pemphis* islands cannot be assessed. Secondly the floristic elements for rocky and shingle substrates would be so small as to be invariant with area of habitats.

The significance of catastrophic storms on coral islands has received considerable attention (Stoddart, 1962, 1963; Connell, 1978). On Suwarrow the importance of storms in generating storm blocks and rubble deposits, both with a high preservation potential, has already been noted. In addition, Wood and Hay (1970) have proposed that hurricanes have been instrumental in maintaining the small size of reef islands on the Suwarrow Atoll rim.

The impact of a severe storm on Suwarrow reef islands has been vividly described by Frisbie who, with his children, survived a severe hurricane which passed directly over the atoll in 1942 (Frisbie, 1944). After the storm Frisbie records that Anchorage Island was reduced to 3 barren cays and Whale, Brushwood, One Tree, all of the Gull group and 6 of the 7 Seven Islands had been completely washed off the reef flat (Frisbie, 1944 p. 225-6). Notwithstanding an element of exaggeration this is an impressive account of the destructive potential of catastrophic storms.

The small islands on the atoll rim of Suwarrow are subject to this periodic devastation, which is likely to maintain them at disequilibrium (Bayliss-Smith, 1988). On other reefs, small islands have been shown to have higher extinction rates, and consequently higher turnover rates of species than larger islands (Heatwole and Levins, 1973; Stoddart and Fosberg, 1982; Flood and Heatwole, 1986). The more stable the island the lower the turnover rate (Flood and Heatwole, 1986). Furthermore, on small islands the rate of geomorphological change and change of island area might be of a similar order to the rate of immigration, not permitting the island to attain species equilibrium (Buckley, 1981). These factors, however, are largely inappropriate on Suwarrow Atoll because the pool of species is constrained primarily by ecological potential.

Suwarrow Atoll lies on a steep floristic gradient across the Pacific Ocean. To the west are the floristically relatively diverse coral islands of Tonga, Tuvalu and Kiribati, and to the east the relatively impoverished islands of the Tuamotus and Society Islands. This florisitic gradient partly reflects the rainfall pattern across the Pacific from the wetter islands in the west to the drier ones in the east (Stoddart 1992). Nevertheless Suwarrow Atoll is floristically depauperate, because of its relatively isolated location, with absence of several species which might be expected. In comparing species-area relationships from west to east across the Pacific, this impoverishment to the east corresponds with a decline in the slope of the line of best fit and results in fewer species on islands of any specified size from Kapingamarangi to Aitutaki (Figure 5, Table 2). However, on Suwarrow Atoll the species-area relationship is particularly weak and shows great scatter because of the immaturity and ecological unfavourability of the reef islands (Table 2). By contrast, Nui Atoll, on which hurricanes are particularly rare, shows a strong species-area relationship because reef islands have relatively homogeneous and stable sandy substrates (Woodroffe, 1986). The reef islands of Ontong Java, Kapingamarangi and Aitutaki are more mature and more stable than those of Suwarrow. Of the atolls

Table 2: Details of Pacific atolls and their native plant species-area relationships (see Figure 5)

Atoll	Location	Distance to nearest island (km)	Approx. annual precipitation (mm)	Total land area (ha)	Total plant species	Total [1] native species	Smallest island (ha)	Largest island (ha)	Number of islands	Linear regression native species against log area		
										intercept	slope	r^2
Ontong Java	5°20'S 159°30'E	70	3000	650	146	82	0.04	178	79+	16.44	11.24	0.77
Kapingamarangi	1°05'N 154°45'E	300	2000	112	99	50	0.01	32	33	14.27	10.39	0.76
Nui	7°12'S 177°10'E	130	3000	337	86	44	0.01	138	20	19.90	7.47	0.94
Aitutaki	18°52'S 159°46'W	80	2000	244*	66*	42*	1.0	71.3	15	11.82	7.93	0.51
Suwarrow	13°14'S 163°05'W	270	2400	200	45	23	0.06	41.6	55	5.36	4.20	0.56

[1] including aboriginal introductions
* excludes volcanic islands
+ for which data available (Bayliss-Smith, 1973)

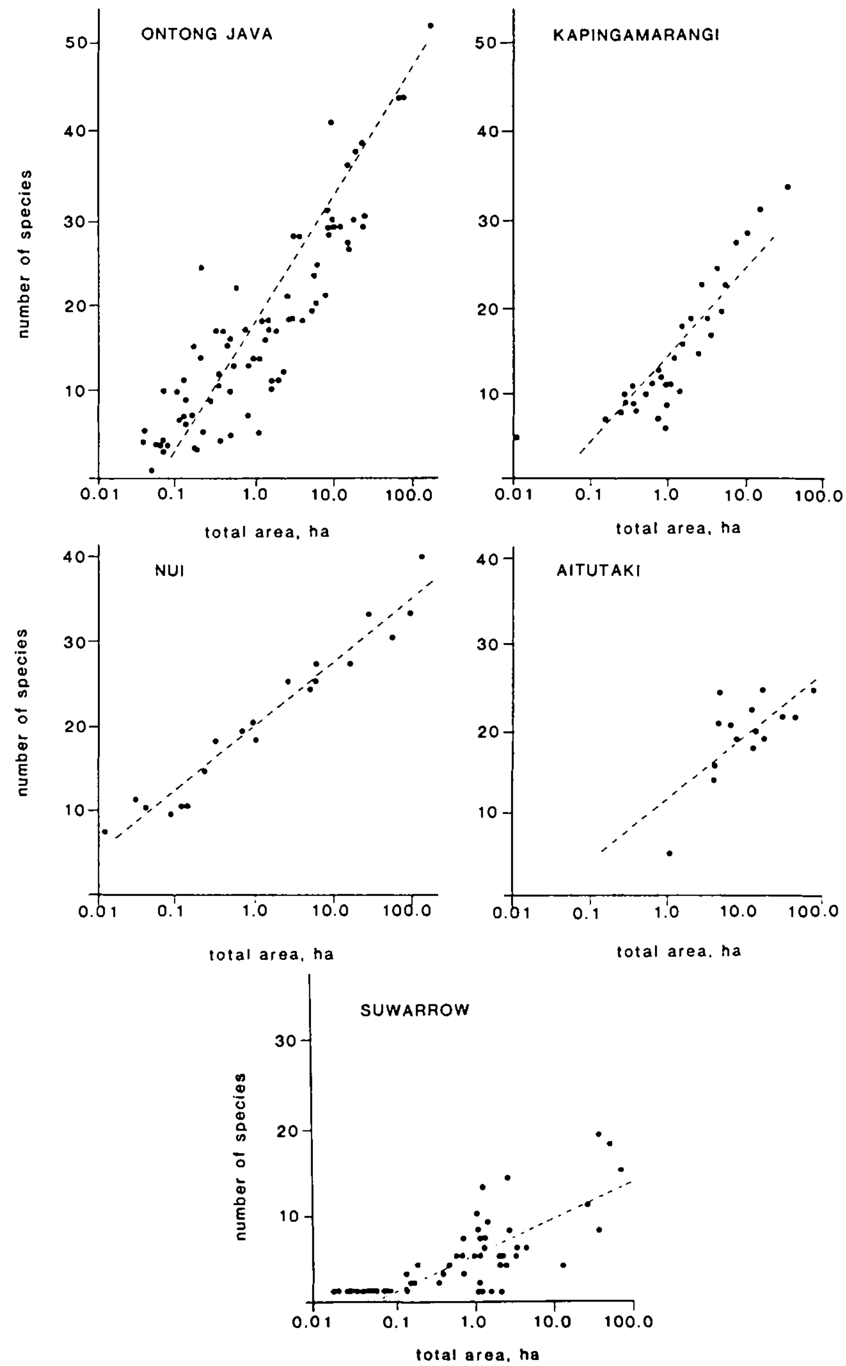

Figure 5. Species-area relationships for native species from Ontong Java Atoll (after Bayliss-Smith, 1973), Kapingamarangi Atoll (after Niering, 1963), Nui Atoll (after Woodroffe, 1986), Aitutaki almost-atoll (after Stoddart, 1975a) and Suwarrow Atoll. Dashed line shows least squares linear regression (details in Table 2).

examined in Table 2 Ontong Java is the closest to a mainland source area; Kapingamarangi and Suwarrow are the most isolated. The small island effect was attributed to ecological control by Niering (1963), Wiens (1962) and Whitehead and Jones (1969), but was attributed to episodic devastation by MacArthur and Wilson (1967), and it was considered that it operated up to a particular threshold size. On Suwarrow Atoll the species-area relationship is very weak, but this relates to a fundamental substrate constraint on many of the islands. The atoll demonstrates both the importance of ecological factors and episodic catastrophic storms in limiting species diversity on reef islands, but not in the way envisaged for atolls in the western Pacific. Catastrophic storms devastate reef islands, stripping many of them bare of vegetation and unconsolidated sediments. This ensures that these islands are composed largely of substrate unfavourable for colonisation by most plant species, and so limits diversity by way of the substrate-specificity of plants. Only on the large shingle and sand motus do woodland types develop and persist through storms, or recover after them, and islands which are more comparable in substrate terms with atolls outside or on the fringe of the hurricane belt develop. On these species-area relationships may be stronger.

CONCLUSIONS

Many of the smaller reef islands on Suwarrow Atoll are located on topographically high points on the atoll rim, which represent remnants of an emergent mid-Holocene reef with a conglomerate of coral boulders deposited between 4400-2600 years B.P. These islands generally contain very localised unconsolidated sediments, they are probably periodically stripped clean by catastrophic storms. The dominant vegetation is a scrub composed of *Pemphis acidula*. The unfavourable substrate, together with episodic devastation by storms means that islands of this type vary considerably in size, but are colonised by only a small pool of species and show a very weak species-area relationship. Larger boulder, shingle and sand islands have developed at the corners of the atoll and support woodland with a more diverse assemblage of species. The woodland has persisted through some storms, and has probably recovered after others. The Suwarrow flora is impoverished, due both to the distance from the Indo-West Pacific source region and to its isolation. Nevertheless it is the substrate specificity of the plants which are found there and the episodic catastrophic storms which account for Suwarrow Atoll having a considerably weaker native plant species-area relationship than other atolls in the Pacific for which comparable data are available.

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