

## Biogeography of the Tropical Pacific<sup>1</sup>

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**ABSTRACT:** Many previous biogeographic regionalizations of the islands and reefs of the tropical Pacific are unsatisfactory: the regions as defined are heterogeneous, localities with unlike biotas are grouped together, and those with similar characteristics are placed in separate categories. Often distinctions appear to be based on cultural or political rather than biogeographic considerations. Criteria are defined for the establishment of biogeographic boundaries. Instead of the hierarchical schemes often utilized, it is proposed that the basis of biogeographic regionalization be typological. A distinction is made between the biogeographic characteristics of atolls and other reef islands, elevated limestone (*makatea*) islands, and high (often volcanic) islands. It is concluded that if the first two categories are filtered out, the treatment of the biogeography of the third group and hence the regionalization of the Pacific becomes relatively unproblematical.

BIOGEOGRAPHERS HAVE BEEN CONCERNED with the distribution of plants and animals in the tropical Pacific for over a century (Sclater 1858, Wallace 1876, 1882), and the differences between Pacific insular biotas and those of East and Southeast Asia and Australia have long been recognized. Hedley (1899) was among the first to describe the profound differences within the Pacific basin, especially between the islands of the western Pacific and those of the north, central, and eastern Pacific. Indeed he located a profound discontinuity in diversity, moving eastward across the ocean, between Tonga and Samoa. In more recent years, in addition to the accumulation of many new data, biogeographic problems have been discussed in the symposia edited by Gressitt (1963) and Radovsky et al. (1984), and notably in a masterly review by Kay (1979).

In spite of this, the biogeographic regionalization of the tropical Pacific remains in a most unsatisfactory state: it is perhaps indicative that although Kay (1979) discussed a number of regional schemes she herself refrained from adding to them. In this paper I

discuss the difficulties associated with existing schemes and suggest solutions for them.

### BIOGEOGRAPHIC REGIONAL SCHEMES

The problems may be illustrated by reference to regional schemes proposed by the zoologist Gressitt (1961, 1963) and the botanist Thorne (1963).

Gressitt's scheme involves a hierarchy of regions, subregions, divisions, and subdivisions, though how these are related is not immediately apparent from his map (Figure 1). Papua, the Philippines, and the Ryukyus are each separated at the subregional level from "Polynesia." This unit includes most of the tropical Pacific islands; it includes the divisions of New Caledonia and Hawaii, and the subdivisions of Micronesia, central Polynesia and Southeast Polynesia. Leaving to one side the problem of nomenclature, this regionalization has problems that are also frequently characteristic of other such schemes.

The "Micronesian" subdivision is heterogeneous: it extends from the Marianas and Palau to Kiribati and includes the Carolines and the Marshalls. There is little in common between Wake Island and Palau, for example,

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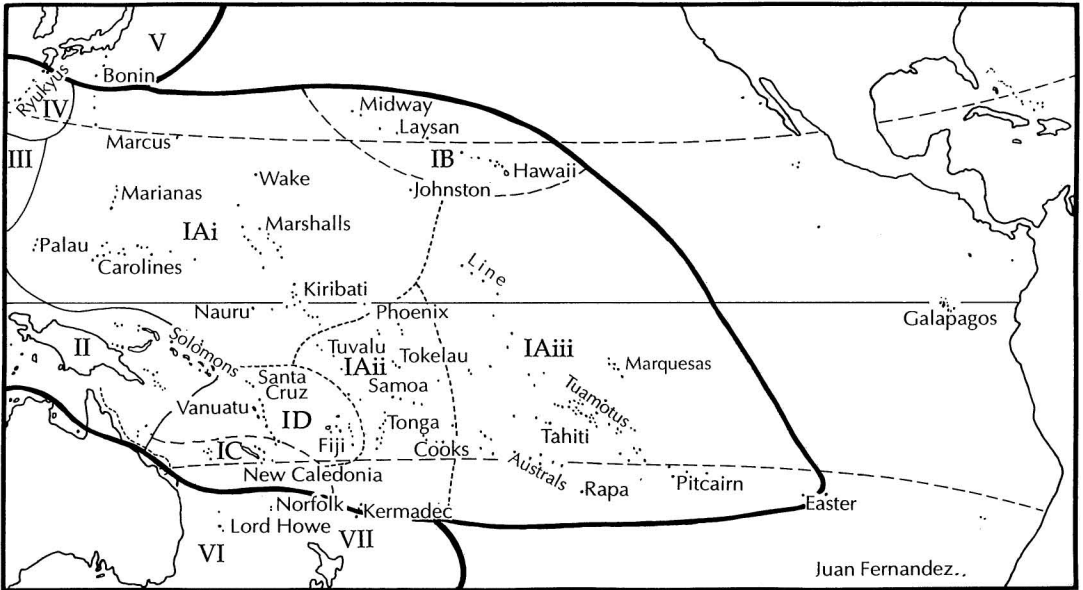


FIGURE 1. Biogeographic regionalization of the Pacific (after Gressitt 1956, 1961).

even though they are included in this subdivision. More surprisingly, Kiribati is included in the Micronesian subdivision whereas adjacent Tuvalu is placed in central Polynesia: there is a persistent and indeed illogical tradition in Pacific insular biogeography that places weight on the comparatively recent human settlement of the area and the cultural differences between island groups that have resulted. As Hedley (1899:395) long ago remarked: "The use of political boundaries has much confused the lines of zoogeographical demarcation." Gressitt's central Polynesian subdivision extends from the Phoenix Islands in latitude  $3^{\circ}$  S to the Kermadecs in latitude  $30^{\circ}$  S: these islands have virtually nothing in common. The Kermadecs themselves straddle the regional boundary between Polynesia and New Zealand. Norfolk Island is placed in the latter, but Lord Howe in the Australian region. The Southeast Polynesia subdivision extends from the northern Line Islands to Easter Island; it includes both the high islands of the Societies, Gambiers, Cooks, and Marquesas, and the atolls of the northern Cooks and the Tuamotus. The Hawaii division includes all the islands of the archipelago

from Kure to Hawaii, even though the low coral islands in the west have little in common with the high volcanic islands in the east.

Thorne (1963) proposed a more detailed regionalization organized hierarchically by region, subregion, province, and district. His scheme is set out in Table 1, to which I have added enumeration codes to facilitate cross-reference to the map (Figure 2), which has been extended on the basis of Table 1 from that originally published by Thorne. The majority of the tropical Pacific islands are placed in the Polynesian subregion, composing the Fijian and Polynesian provinces, and the latter the Micronesian, Polynesian, and Hawaiian districts: nomenclature of the units again becomes confusing. The units are necessarily both vast and heterogeneous. The Micronesian district extends from Palau and the Bonin Islands to Tokelau and the Phoenix group: the former cannot usefully be compared with the latter. The Polynesian district extends from the Lines and the Cooks to Ducie Atoll, a longitudinal span of  $70^{\circ}$ . It includes the southern Cooks, Societies, Australs, Marquesas, and Gambiers; Pitcairn, Easter, and Sala-y-Gomez; Niue and Hender-

TABLE 1  
BIOGEOGRAPHIC REGIONS OF THE PACIFIC  
(AFTER THORNE 1963)

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I.	Oriental Region
IA.	Papuan Subregion
IAi.	Papuan province
IAii.	Torresian province
IAiii.	Bismarckian province
	Bismarckian district
	Solomonian district
IB.	Polynesian Subregion
IBi.	Fijian province
IBia.	New Hebridean district [includes Santa Cruz]
IBib.	Fijian district [includes Tonga and Samoa]
IBii.	Polynesian province
IBiia.	Micronesian district
IBiib.	Polynesian district
IBiic.	Hawaiian district
IC.	Neocaledonian Subregion
ICi.	Neocaledonian province [includes Loyalties]
II.	Australian Region
IIA.	Australian Subregion
IIB.	Neozeylandic Subregion
IIBi.	Kermadecian province
IIBia.	Lord Howean district
IIBib.	Norfolkian district
IIBic.	Kermadecian district
IIBii.	Neozeylandic province
III.	Neotropical Region
IIIA.	Chilean Subregion
IIIAi.	Fernandezian province
IIIB.	Peruvian Subregion
IIIBi.	Galapagean province
IV.	Holarctic Region
IVA.	Nearctic Subregion
IVAi.	Caribbean province
IVAia.	Mexican district [includes Clipperton]
IVAii.	Sonoran province
IVAiii.	California province

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son; and the atolls of the Line Islands, the northern Cooks, and the Tuamotus. Such a unit has no biogeographical coherence except at the most superficial level. The Hawaiian district includes both the high islands, the leeward reef islands, and Johnston Atoll. The Neocaledonian Province includes the uplifted atolls of the Loyalties. Lord Howe is placed in the Neozeylandic rather than the Austra-

lian subregion. The difficulties of Thorne's scheme reach their maximum when Clipperton Atoll (10° N, 109° W), 1000 km west from the coast of Mexico, is placed in the Mexican district of the Caribbean province. It may be noted that Thorne's biogeographical mosaic is much finer in the Southwest Pacific, where he placed boundaries of varying level between New Guinea, New Britain, the Solomon Islands, the Santa Cruz Islands, and Vanuatu; and Fiji, Tonga, and Samoa.

Kay (1979) also drew attention to Schilder's scheme, based on the distribution of the gastropod family Cypraeidae (Figure 3, Table 2). This regionalization places boundaries between the Carolines and the Marshalls, the Phoenix and the Lines, and Rarotonga and Samoa; the Lines are grouped with Easter Island and Samoa and Fiji with the Kermadecs. The Samoan region extends latitudinally from Pukapuka in the northern Cooks to the Kermadecs. Similar reservations arise with Udvardy's (1975) classification (Figure 4, Table 3). His Micronesian, Southeast Polynesian and central Polynesian regions are highly heterogeneous (the latter again extends from the Phoenix to the Kermadecs); his New Caledonian region includes both Lord Howe and Norfolk islands.

Finally, Dahl's (1979, 1980) biogeographic provinces, although confined to the area covered by the South Pacific Commission, provide an illuminating conspectus of information and a useful bibliography. He distinguished 20 provinces of reasonably comparable magnitude (Figure 5, Table 4). These are, however, based on political units, doubtless because of data availability, and this means that quite dissimilar islands are frequently placed in the same "province" (e.g., Tongatapu and Niue; Palmyra and Canton; Tarawa and Nauru; Palau and Ulithi; Rapa and Ducie). On the other hand Dahl does group Lord Howe, Norfolk, and the Kermadecs together.

A number of these schemes was available at the time of Kay's (1979) review, and not surprisingly she also found them unsatisfactory. "Many of the subdivisions recognized [in the tropical Pacific] seem more reminiscent of geographical boundaries than representa-

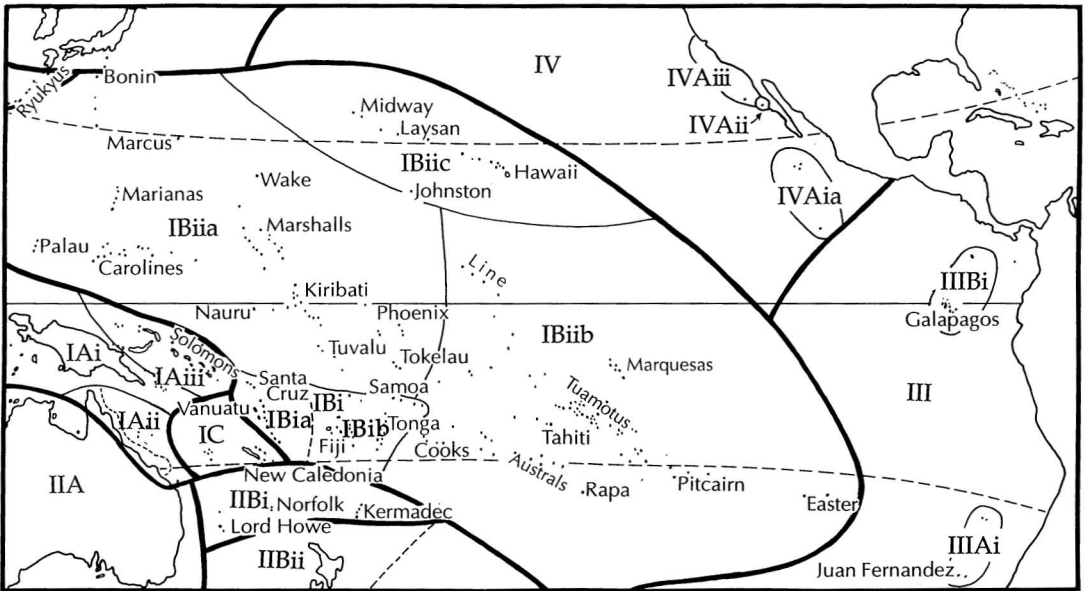


FIGURE 2. Biogeographic regionalization of the Pacific (after Thorne 1963). For explanation see Table 1.

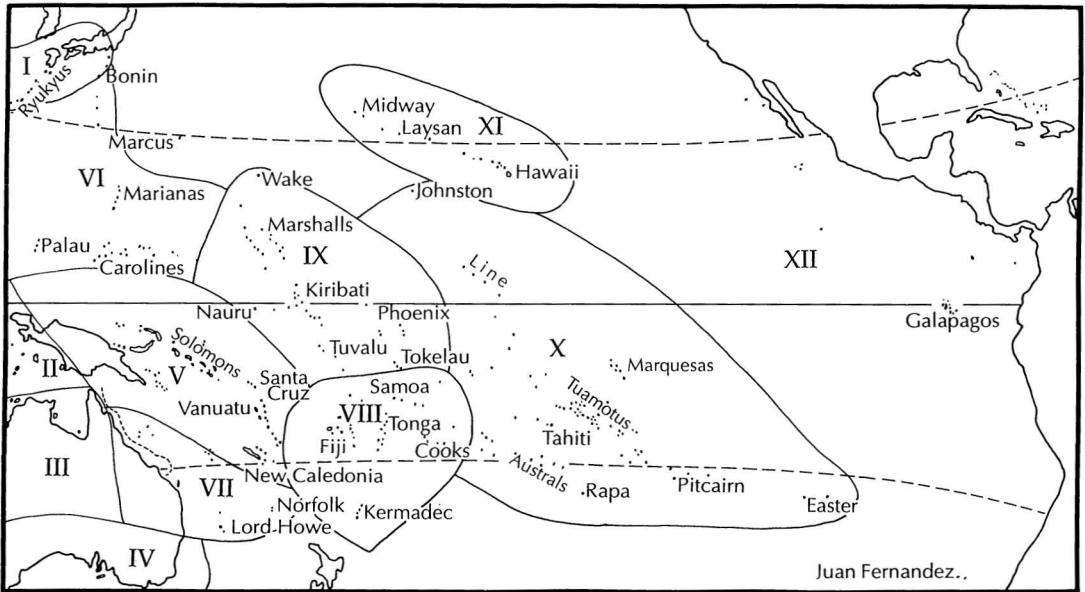


FIGURE 3. Biogeographic regionalization of the Pacific based on the distribution of the Cypraeidae (Mollusca) (after Schilder 1961). For explanation see Table 2.



TABLE 2

BIOGEOGRAPHIC REGIONALIZATION OF THE TROPICAL PACIFIC BASED ON CYPRAEIDAE (AFTER SCHILDER 1961)

I	Japanese
II	Moluccan
III	Dampierian
IV	South Australian
V	Melanesian
VI	Micronesian
VII	Queensland
VIII	Samoan
IX	Oceanic
X	Polynesian
XI	Hawaiian
XII	Rest of the Pacific

tive of areas with a characteristic biota" (Kay 1979: 7). In seeking a solution she avoided the distinction between continental and oceanic islands made long ago by Wallace, "because it is more usefully construed as an explanation for observed distribution patterns than as a generalization of observations" (Kay 1979: 16). Nevertheless, she made two important points. First, "in both the marine and terrestrial biota differences in development

[of the distribution patterns of organisms in the Pacific] are associated with island types, that is high islands and low islands" (Kay 1979: 18). And second, "the terrestrial biota is discrete and disjunct, the populations separated by the very nature of the islands themselves" (Kay 1979: 25). These observations go far to explain the defective nature of the regionalizations previously discussed.

#### CRITERIA FOR BIOGEOGRAPHIC REGIONALIZATION

I take it as axiomatic that there are two criteria fundamental to biogeographic regionalization. First, any boundary between units at whatever level should maximize both the homogeneity of the individual islands and reefs within the boundary and also the differences between these islands and reefs and those of adjacent areas. The differences within areas cannot be greater than the differences between them. Most existing schemes fail to meet this criterion, which should apply at all levels if the scheme is hierarchical. Second, there must be a fundamental congruity in the

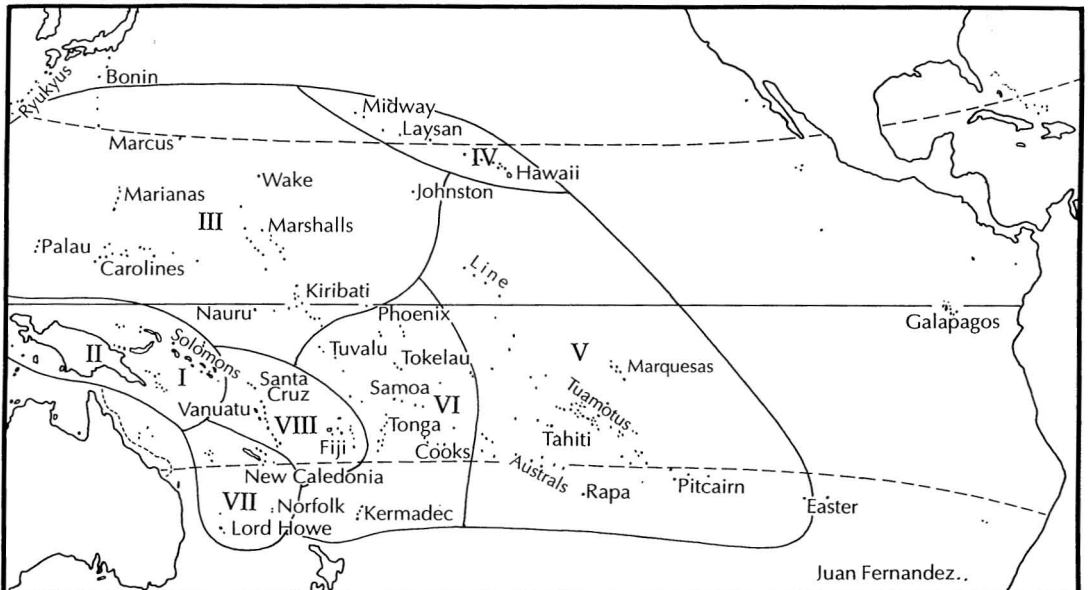


FIGURE 4. Biogeographic regionalization of the Pacific based on Udvardy (1975). For explanation see Table 3.

TABLE 3  
 BIOGEOGRAPHIC REGIONALIZATION OF THE TROPICAL  
 PACIFIC (AFTER UDVARDY 1975)

Oceanian Realm	
I	Papuan rainforest
II	Papuan savanna
III	Micronesian
IV	Hawaiian
V	Southeast Polynesian
VI	Central Polynesian
VII	New Caledonian
VIII	East Melanesian

items being grouped: a scheme that ignores the evident differences between islands such as Hawaii (elevation 4164 m), Makatea (114 m), and atolls less than 5 m in land elevation cannot have meaning.

Two further problems may also be identified. The first is the apparent concern of previous workers that the areal units identified be spatially contiguous when mapped. This concern is clearly antithetic to the insular and scattered character of the islands and reefs being grouped. A regionalization

scheme should comprehend the discontinuous nature of biogeographic insular distributions. Second, the use of hierarchical schemes has introduced confusion: different workers have used undefined areal terms ranked in unspecified ways. The use of terms such as province, region, subregion, realm, division, and district may each connote a variety of scales and ranks. For simplicity, therefore, biogeographical schemes should group like reefs and islands, and optimally in a non-hierarchical manner. Such schemes should not be constrained by present cultural distributions or political boundaries.

I propose therefore to resolve the problem of the insular biogeography of the tropical Pacific by disaggregating it into component parts. The approach is thus typological rather than hierarchical. It is based on the habitats and biotas of islands and reefs and not on inferred histories or processes. The logic of classification of areal units has been discussed by Grigg (1965, 1967).

It is generally agreed that the islands of the tropical Pacific fall into three main classes: (a) atolls and other low coral islands; (b) raised

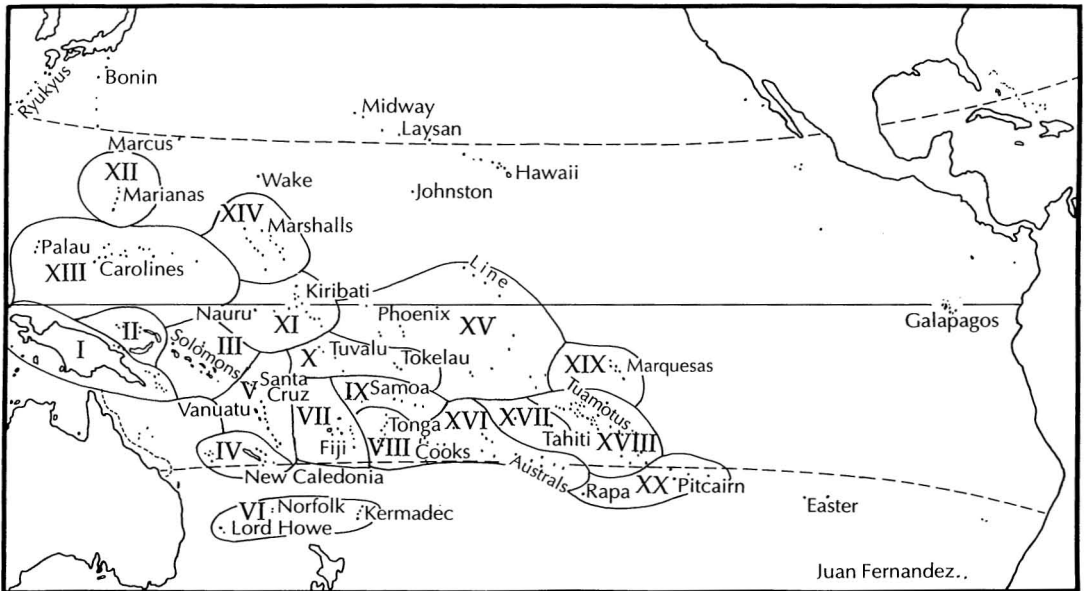


FIGURE 5. Biogeographic provinces of the area covered by the South Pacific Commission (after Dahl 1979, 1980). For explanation see Table 4.

TABLE 4

BIOGEOGRAPHIC PROVINCES OF THE SOUTH PACIFIC COMMISSION AREA (AFTER DAHL 1979, 1980)

I	New Guinea
II	Bismarck Archipelago
III	Solomon Islands
IV	New Caledonia and Loyalty Islands
V	New Hebrides and Santa Cruz Islands
VI	Norfolk, Lord Howe, and Kermadec Islands
VII	Fiji
VIII	Tonga and Niue
IX	Samoa, Wallis, Futuna
X	Tuvalu and Tokelau
XI	Kiribati and Nauru
XII	Marinas
XIII	Caroline Islands
XIV	Marshall Islands
XV	Phoenix, Line, and northern Cook Islands
XVI	Lower Cook Islands and Austral Islands
XVII	Society Islands
XVIII	Tuamotu Archipelago
XIX	Marquesas
XX	Pitcairn, Rapa, Gambier Islands

ATOLLS

Pacific atolls and reef islands are remarkably coherently distributed (Figure 6), from Kure and Ngaruagl (Palau) in the northwest to Ducie in the southeast. There are two outliers: Clipperton (technically an almost-atoll) in the eastern Pacific, and the reefs and islands of the Coral Sea about which remarkably little is known. It has to be stated at the outset that there has been grave misunderstanding of the biogeography of atolls as a result of the uncritical acceptance of MacArthur and Wilson's (1967) "theory of island biogeography." This was supported by a data set from the individual motus of Kapingamarangi Atoll, Caroline Islands (Niering 1963), which MacArthur and Wilson misunderstood, and a flawed data set from the Dry Tortugas, Florida, on which they placed too much reliance (Stoddart and Fosberg 1981). MacArthur and Wilson's major controls on biotic diversity were distance from the source of propagules and island area (as a surrogate for environmental diversity). In the case of atolls, there is a strictly limited assemblage of plants and animals with the capacity

limestone islands (*makatea*); (c) high islands composed of either volcanic or continental rocks, or admixtures of both. We will examine the biogeography of each of these in turn.

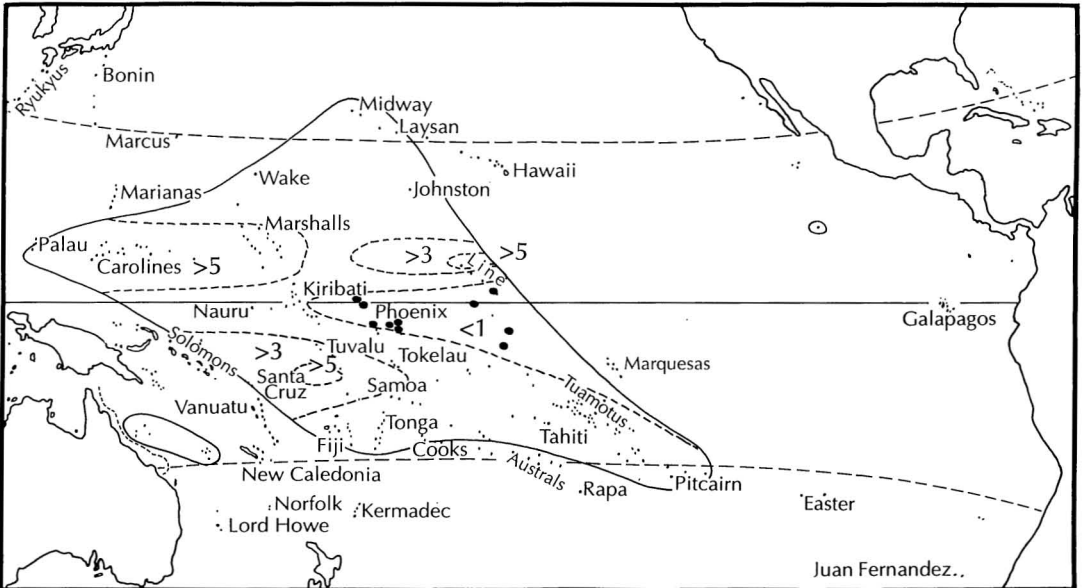


FIGURE 6. Distribution of atolls and reef islands in the tropical Pacific. Numbers refer to mean annual rainfall distribution in meters (dashed lines). Black circles are treeless dry islands.

for over-water dispersal and for survival in atoll habitats. Although it is true that atoll biotas become depleted across the Pacific from west to east, it is also true that they remain quite remarkably homogeneous. Indeed atoll floras are recognizable as such from the westernmost Indian Ocean to the easternmost Pacific (Fosberg 1974, 1984). There is simply a limited pool of trees, shrubs, and herbs that can colonize and survive in such habitats: however extensive an atoll island perimeter, for example, it will only be colonized by *Scaevola*, *Tournefortia*, *Suriana*, and a handful of other species. In the case of plants, high species numbers on atoll islands simply denote the replacement of native vegetation by cultigens and weeds (Stoddart 1975).

The main controls on atoll biota in the Pacific are ecological. Atoll vegetation responds asymmetrically to rainfall extremes: it is more sensitive to drought than to wetness. The world's wettest atoll, Palmyra in the Line Islands, is not recognized for an unusual biota, though its mean annual rainfall is 4.2 m (Funafuti in Tuvalu, with an annual mean of 3.6 m, received 6.7 m in 1940). Conversely, coconuts cannot remain viable with a mean annual rainfall of less than 1 m, and islands thus situated have a highly distinctive aspect. Note also that as annual means decrease inter-annual variability increases and this exacerbates the asymmetry of the biotic response: thus wet Palmyra (mean of 4.2 m) has a range in annual rainfall of 3.1–5.1 m, whereas dry Kiritimati (Christmas) Atoll with a mean of 0.77 m has a range of 0.18–2.6 m.

The implications of this were clearly recognized in the Marshall Islands by Fosberg in what came to be termed the "Fosberg zones" (Fosberg 1956). These were originally described from the northern Marshall Islands and subsequently extended from Wake Island in the north to Tuvalu in the south. Figure 7 shows rainfall gradients on this longitudinal transect: the profile is yet more dramatic 20° farther east. In Fosberg's zone 1 (Wake and Taongi) no coconuts grow. In zone 2 at Bikar there is *Pisonia* forest. In zone 3 there is *Cordia*, *Pemphis*, mixed forest, and coconuts. In zone 4 there is *Neisosperma* forest and

breadfruit; in zone 5 coconuts and breadfruit; and in zone 6 dense forest. Zones 7, 8, and 9 mirror zones 5, 4, and 3 to the south. Note that if these zones are defined simply in terms of mean annual rainfall, then inter-annual fluctuations of  $\pm 25\%$  are sufficient to move an island from the center of one zone to the center of another, and smaller fluctuations can take an island across a zonal boundary: variability at the 10–25% level is common.

The argument is well illustrated by Figure 8. This shows indigenous plant species richness plotted in terms of atoll land area and mean annual rainfall for the Marshall Islands. This clearly shows that atoll floras are unresponsive to land area (and indeed distance from presumed source area) but instead reflect rainfall: only Onotoa is anomalous with a rainfall of 1210 mm and 50 native species of vascular plants. In considering atoll phytogeography it is essential to discuss only presumed indigenous species; the total flora of most atolls is now dominated by introductions (Table 5).

The driest reef islands are unmistakable. Figure 6 shows not only those atoll areas with mean annual rainfalls greater than 3 and 5 m, but also those with less than 1 m. These include the world's driest reef islands: Malden (mean annual rainfall 689 mm), Canton (696 mm), and Johnston (710 mm). Figure 6 shows these dry islands (which include Jarvis, Starbuck, Baker, Howland, Phoenix, Birnie, Enderbury, McKean, and Christmas), all of which bear a striking similarity to similar dry islands in other oceans. All of these islands lie in the equatorial dry zone. The only exception is Laysan in the leeward Hawaiian Islands. I would group Laysan with the above-mentioned islands, except that it formerly had *Pritchardia* and other upland plants and also land snails and birds indicative of a complex history (Schlanger and Gillett 1976, Rotondo et al. 1981). In aspect and other respects, however, it belongs, in spite of distance, with the class of low dry coral islands.

#### ELEVATED LIMESTONE (*makatea*) ISLANDS

The second class of island here considered is that of raised reef limestone islands. In the

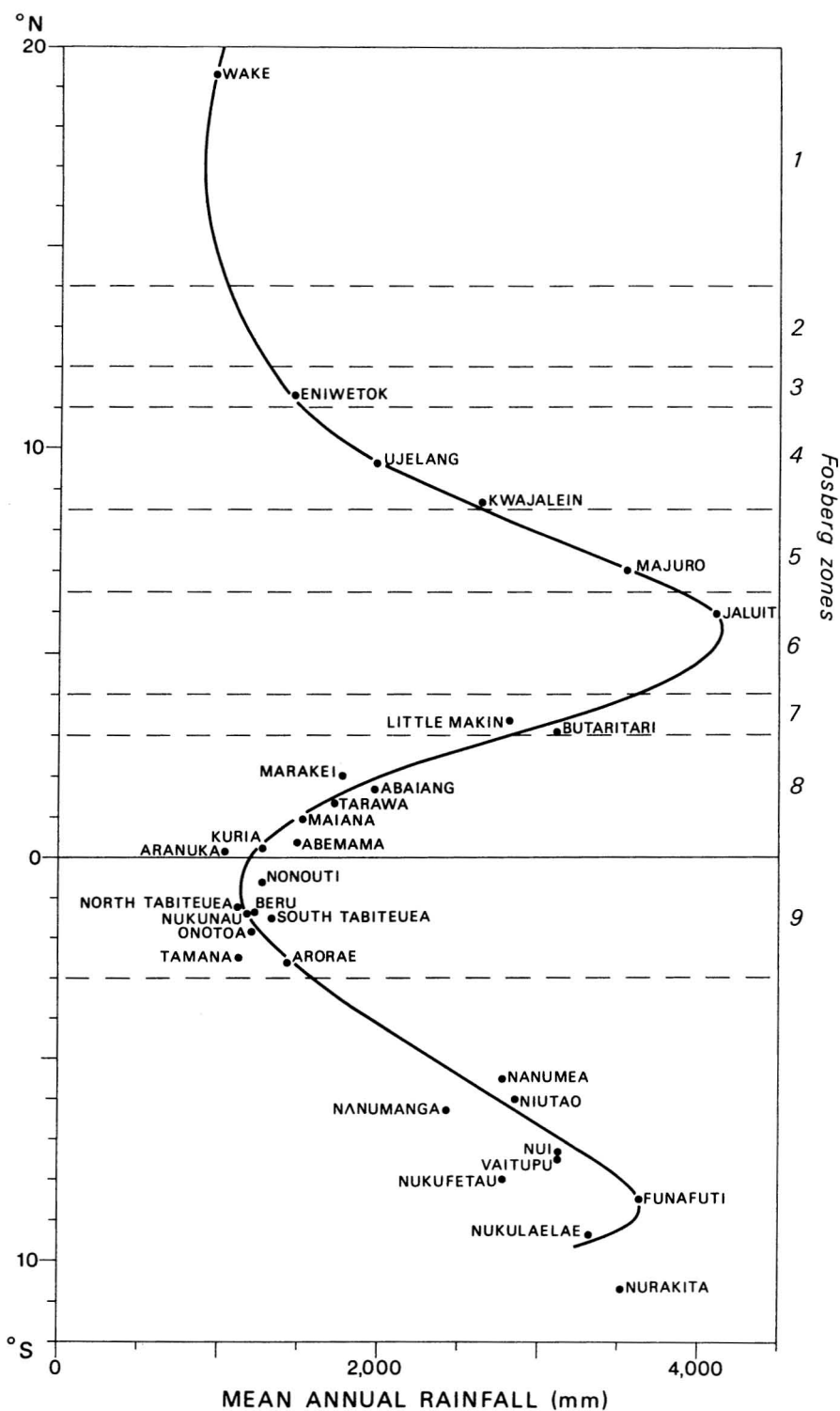


FIGURE 7. Mean annual rainfall and Fosberg zones in the west-central Pacific (Marshalls, Kiribati, and Tuvalu). Rainfall data from Taylor (1973).

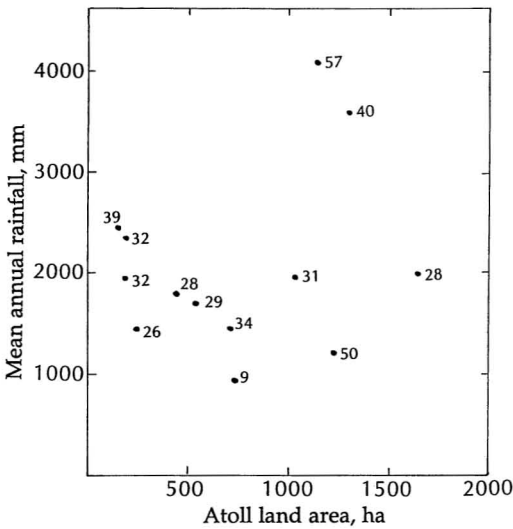


FIGURE 8. Number of native species of vascular plants on Marshall Islands atolls in terms of mean annual rainfall and land area.

TABLE 5  
INDIGENOUS SPECIES IN THE TOTAL FLORA OF  
PACIFIC ATOLLS

Canton	24	[97]
Fanning	22	[102]
Kapingamarangi	43	[99]
Laysan	27	[44]
Midway	19	[38]
Namouito	41	[91]
Ontong Java	64	[150]
Rangiroa	41	[121]
Raroia	41	[135]
Satawal	50	[103]
Wake	20	[94]

NOTE: The first figure is the number of indigenous species of vascular plants; the figure in brackets is the total flora.

open Pacific these reach a maximum elevation of 329 m at Eua. Makatea reaches 113 m and Mangaia 70 m; others are lower. They are few in number in the open Pacific, but scattered between Henderson in the east and Rennell and Bellona in the west; the solid line in Figure 9 delimits an area within which elevated limestone islands are common (e.g., in New Guinea and the Solomons). It is interesting that within the open Pacific

*makatea* islands have a relatively uniform environment. Mean annual rainfall ranges from 1.5 to 2.6 m, though some equatorial islands (such as Nauru and Banaba) have highly variable regimes (0.28–4.6 and 0.36–4.5 m per annum, respectively). The higher rainfalls are confined to the western Pacific: 3.1 m at Angaur, Palau, and 4 m at Rennell and Bellona.

Fosberg (1976) remarked on the dramatic increase in biotic diversity associated with even small increases in elevation of reef islands. Many raised reef islands in the Pacific have unfortunately been devastated by phosphate mining (e.g., Nauru, Banaba, Marcus, Angaur), and it is thus difficult to reconstruct their native biota. In the easternmost Pacific, however, the raised *makatea* island of Henderson has 67 species of vascular plants, including four introductions, whereas the neighboring atolls of Oeno and Ducie have a total recorded flora, including introductions, of 15 and four species, respectively (Fosberg et al. 1983, Fosberg et al. 1989). Not only is diversity higher on *makatea* islands but so is endemism, reaching 10% of the flora at Henderson. It is, however, proper to state that no comparative analysis of the biotas of Pacific *makatea* islands has yet been carried out, and indeed it may now in most cases be too late to do so.

#### HIGH ISLANDS

Having considered atolls and elevated limestone islands, we are left with the high islands of the Pacific basin, which must indeed be the focus of biogeographic explanation. These comprise (a) the spatially and geologically related islands of the western Pacific, mainly within the “andesite line”; (b) the relict island of New Caledonia (but not the adjacent Loyalties, which belong as uplifted atolls with the *makatea* islands); and (c) the isolated basaltic volcanoes of the open Pacific.

Figure 10 distinguishes these entities. It is noteworthy that the West Pacific islands are wet (many with annual rainfall means of 3–5 m; Kosrae in the Carolines has a mean of 5.3 m and an extreme of 7.7 m), and Vanikoro

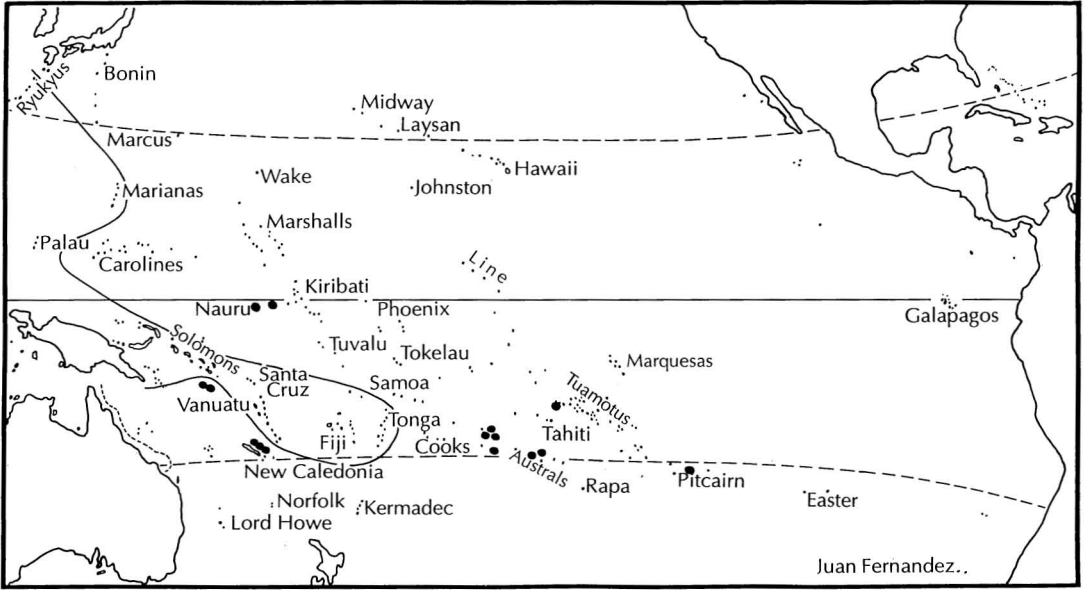


FIGURE 9. Raised *makatea* islands in the tropical Pacific. These islands are abundant west of the solid line (i.e., in the Solomons, New Guinea, Palau, Marianas, Fiji, and Tonga); black circles show *makatea* islands or volcanic islands with substantial raised limestone in the open Pacific.

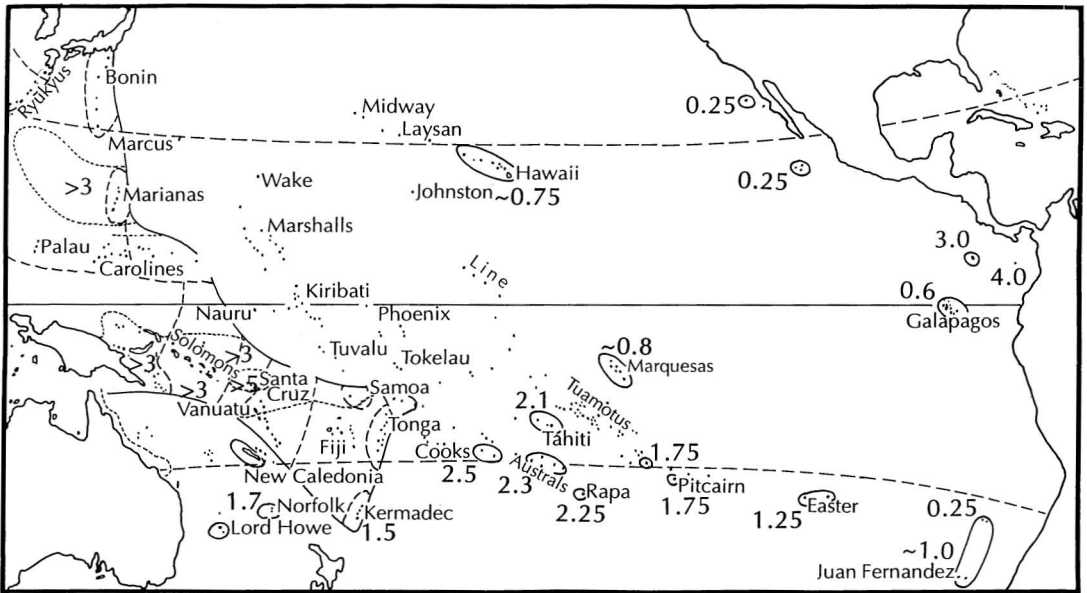


FIGURE 10. High islands in the tropical Pacific. These islands are frequent west of the continuous line; possible biogeographic boundaries within this area are indicated. East of the line individual islands or clusters of high islands are indicated. Numbers refer to mean annual sea-level rainfall in meters, though this may vary widely according to topographic situation (rainfall data from Brookfield and Hart 1966 and Taylor 1973).



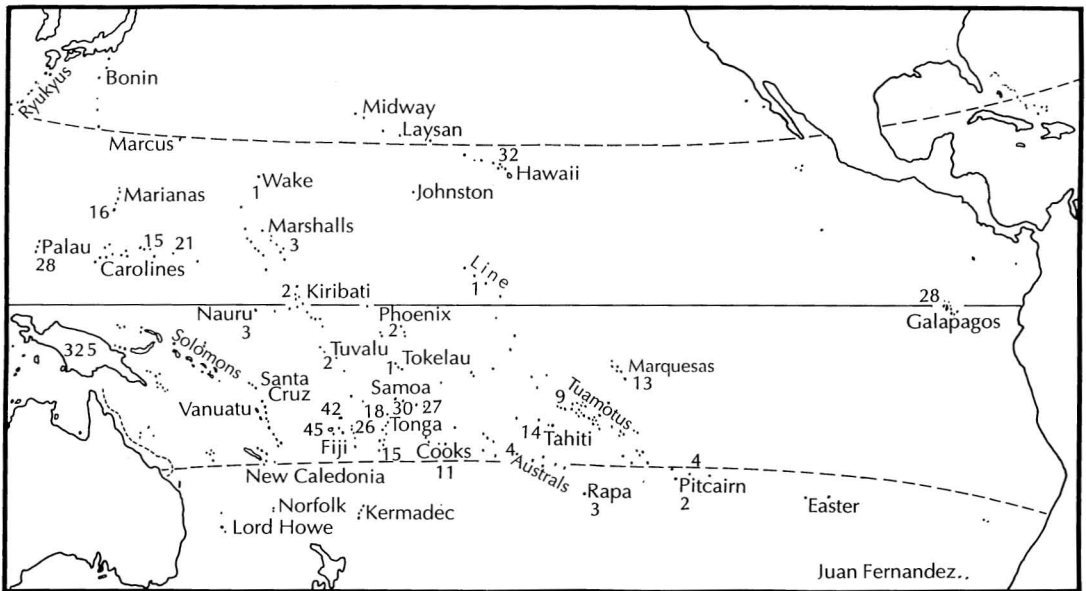


FIGURE 11. Distribution of native land bird species in the tropical Pacific (excluding the easternmost Pacific). Data from Pratt et al. (1987) and other sources.

in the Santa Cruz Islands has a mean of 5.6 m and an extreme of 7.9 m). By comparison, most of the Polynesian volcanoes have sea-level rainfalls of 1.5–2.5 m, and those in the North and Northwest Pacific less than 1 m. Close to the coast of central America rainfalls rise to 3–4 m.

With the exception of the easternmost Pacific islands, which show marked American influence (the Galápagos have many reptiles, bats, and rodents, for example), the Pacific high islands have two main characteristics: in terms of distance from source areas of propagules they show marked diminution in species diversity from west to east, and in terms of area and elevation they exhibit considerable ecological diversity. It is in this group that MacArthur and Wilson's (1967) principles of island biogeography have greatest relevance. This has been demonstrated in the western Pacific for terrestrial mollusca, arthropods, and birds (Wilson and Taylor 1967, Greenslade 1968, 1969, Peake 1969), as well as for many other groups (cf. Darlington 1965).

Land birds are particularly instructive (Fig-

ure 11), although Steadman (1989) cautioned against too ready inference from present species distributions, given the now-demonstrated scale of historical and prehistorical extinctions. The total resident land and freshwater avifauna of New Guinea is over 500 species, with 325 species present on the main island (Diamond 1973). On Bougainville and in the Solomons the number of species falls below 100 (Diamond and Mayr 1976). In Fiji it is less than 50 (Viti Levu 45, Vanua Levu 42, Taveuni 41, Kadavu 35, Lau 26), and in the high Carolines and Marianas less than 30 (Palau 28, Pohnpei 21, Guam 16, Truk 15). Northern Tonga and Ha'apai have 18, southern Tonga 15. In Samoa Savai'i has 30, Upolu 27, and Tutuila and Manoa also 27. Outside these limits diversity decreases drastically. Of the high volcanic islands, Wallis and Futuna have 11, the southern Cooks 11, the Marquesas 13, Tahiti and Moorea 14, the Australs 4, Rapa 3, and Pitcairn 2. Of the *makatea* islands Niue has 11, Nauru 3, and Henderson 4. Of the atolls the Tuamotus have 9, Marshalls 3, Kiribati, the Phoenix, and Tuvalu 2 each, Wake, the Line Islands, and

Tokelau 1 each. (These numbers, which refer to residents, migratory breeders, visitors, winter residents, and historically extinct species, are derived from Pratt et al. 1987.) Only where there has been extensive local speciation, as in Hawaii (32 species of passerines: Juvik and Austring 1979) and the Galápagos (28 species of land birds: Grant 1983), are such numbers for oceanic islands substantially exceeded.

Within the distribution of Pacific high islands, west to east, the most basic divide is at the Tonga Trench: there is no more dramatic biogeographic boundary in the Pacific than that between the southern Cooks and the southern Tonga islands. The latter have mangroves and seagrasses, and a distinctly West Pacific aspect; the former lack them. Figure 12 shows the eastern limits of the seagrass genera *Thalassia*, *Enhalus*, *Halophila*, and *Syringodium*, all of which are confined to the western-most Pacific (Den Hartog 1970 and other sources). Figure 13 shows the eastern limits of the mangrove genera *Rhizophora*, *Avicennia*, and *Excoecaria*, which are similarly delimited (Woodroffe 1987 and other

sources). Figure 14 shows the rapid decline of scleractinian coral genera east of Fiji, Tonga, and Samoa. Figure 15 shows the distribution of the gastropod genus *Strombus* in the Pacific, together with the western Pacific distribution of one species, *Strombus labiatus* (Abbott 1960, Springer 1982). Figure 16 shows the distribution of warm-water marine shorefishes in the tropical Pacific (Springer 1982) and Figure 17 that of the family Pomacentridae, together with the similar distribution of *Amphiprion clarkii* (Allen 1975 in Briggs 1984, Springer 1982). Springer (1982) gave a multitude of comparable distributional examples for Pacific inshore fishes: the patterns of elasmobranchs are particularly instructive. Cephalopods including *Sepia* and *Nautilus* (Saunders 1981) also show a marked western Pacific limitation. Similar distribution patterns can readily be replicated from many other groups, including the terrestrial insular biota. These include mammals, notably bats, fruitbats, and rodents; reptiles (particularly iguanids and crocodylians) (Brown 1956); amphibians (Myers 1953a); insects

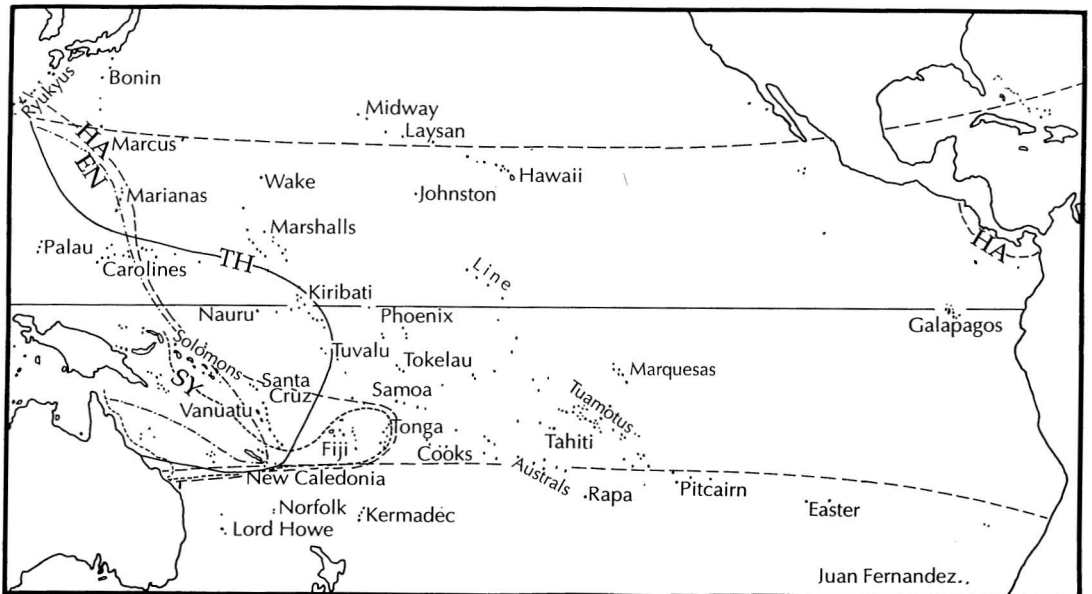


FIGURE 12. Pacific limits of the seagrass genera *Thalassia* (TH), *Enhalus* (EN), *Halophila* (HA), and *Syringodium* (SY). Data from Den Hartog (1970), with additions.

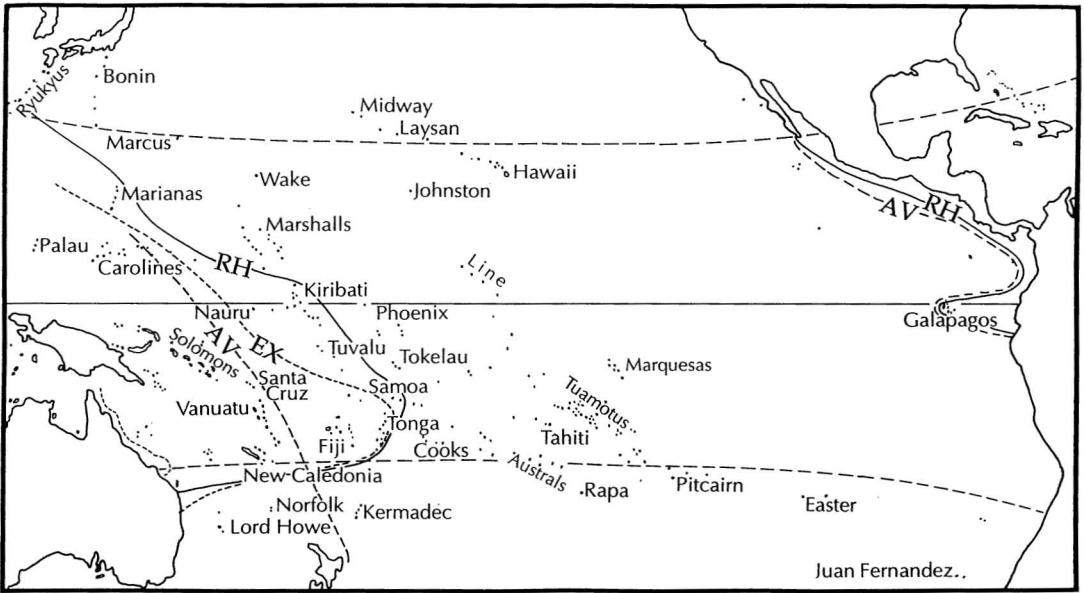


FIGURE 13. Pacific limits of the mangrove genera *Rhizophora* (RH), *Avicennia* (AV), and *Excoecaria* (EX). Data from various sources.

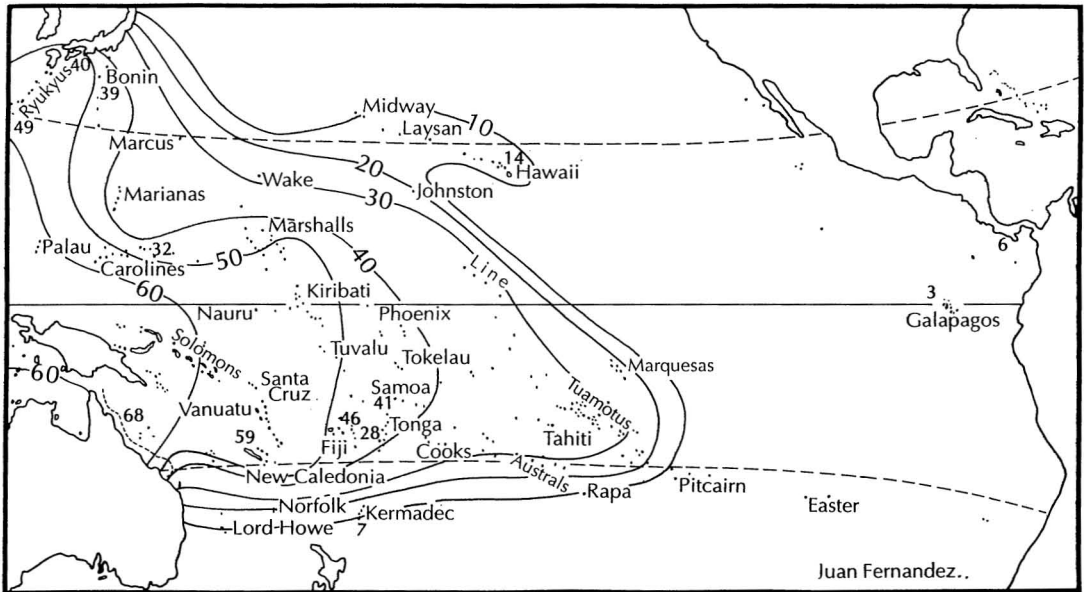


FIGURE 14. Generic diversity of scleractinian corals in the tropical Pacific (after Coudray and Montaggioni 1983).

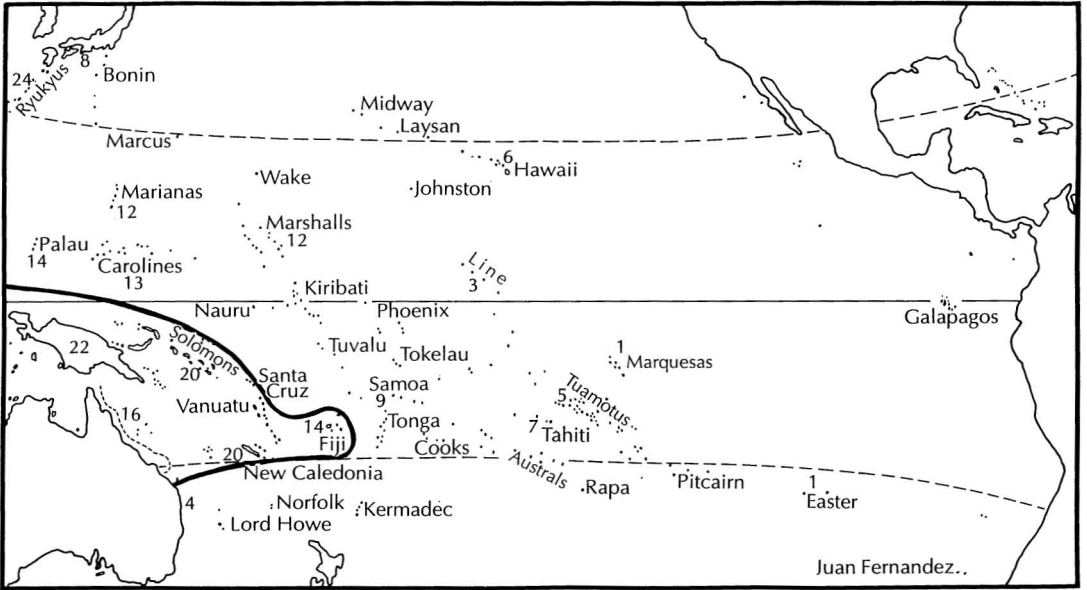


FIGURE 15. Distribution of numbers of taxa in the genus *Strombus* (Mollusca, Gastropoda); the solid line shows the eastern limits of *Strombus labiatus* (after Abbott 1960).

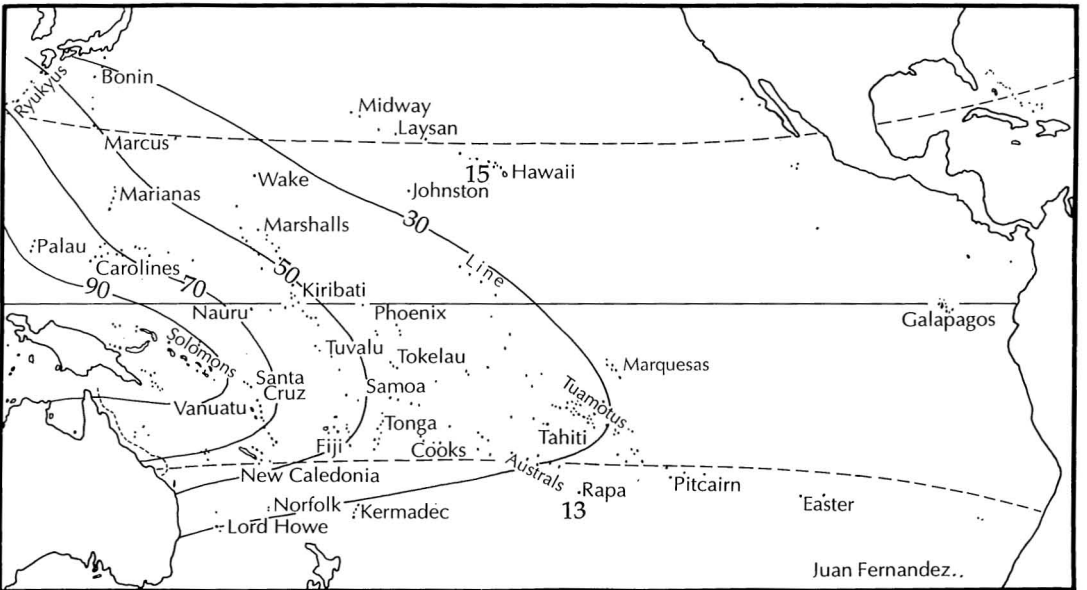


FIGURE 16. Distribution of families of warm-water marine shorefishes in the tropical Pacific (after Springer 1982). [The figures are derived from Springer's table 1 and differ slightly from those in his figure 58 and table 2.]

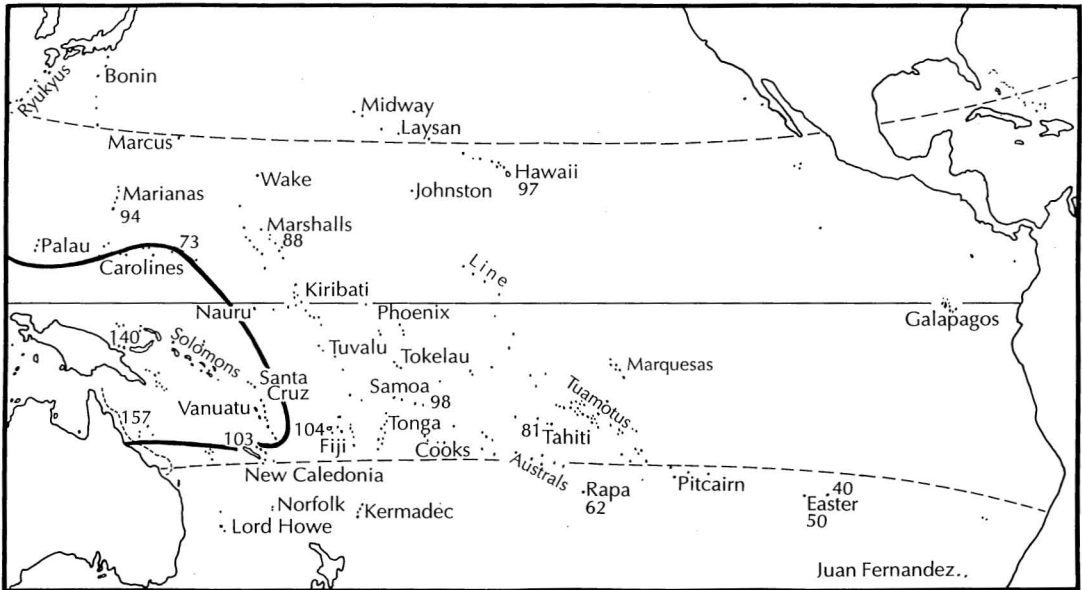


FIGURE 17. Distribution of species of damselfish (Pomacentridae) in the tropical Pacific; the solid line shows the eastern limits of *Amphiprion clarkii* (after Allen 1975 in Briggs 1984 and Springer 1982).

(notably Carabidae); true freshwater fishes (Myers 1953b); and many vascular plants (Smith 1955, Van Balgooy 1971). Springer (1982) argued that the margins of the Pacific Plate constitute a primary biogeographic boundary in the Pacific. There is much support for this in the distributions of both marine and terrestrial biota, though one need not necessarily accept in toto Springer's explanation for it.

#### CONCLUSIONS

It is not the purpose of this paper to give a systematic review of the distribution of marine and terrestrial biota on tropical Pacific islands. I wish rather to show that, by defining types of islands and their environments, it is possible to simplify the apparent problems of biogeographic regionalization. Atolls have a comparatively unproblematic (though highly interesting) biota, and do not enter the regionalization problem. *Makatea* islands have

more diverse and characteristic biotas, but are few in number and often no longer undisturbed. The problem of tropical Pacific insular biogeography thus resolves itself into the consideration of the biotas of high islands. Hedley in 1899 argued for a distinct decline in diversity east of Fiji. On the basis of both terrestrial and marine biota there is evidence that the main discontinuity lies at the Tonga Trench. By analogy with the well-known biogeographic discontinuity named after Alfred Russel Wallace (Wallace 1876) it would be appropriate to define this boundary as "Hedley's line." Eastward of that boundary the high islands of the tropical Pacific are widely scattered, and it becomes meaningless to attempt to encompass them in contiguous regions. Such biogeographic regions as can be defined exist not simply in terms of latitude and longitude (i.e., space-filling entities) but rather in a multidimensional space encompassing area, altitude, climate, and other environmental constraints. The problems associated with previous biogeographic regionalizations are thus resolved.

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