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THE STATUS OF FOREST BIODIVERSITY IN OCEANIA

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WHIFFIN, T. & KIKKAWA, J. 1992. The status of forest biodiversity in Oceania. Within Oceania, a distinction is drawn between the older, continental land masses of Australia, New Guinea, New Caledonia and New Zealand, and the geologically younger islands and island arcs of the Pacific. As a rule, the former show high species richness and high levels of endemism, while the latter show a west to east decline in species richness and endemism, culminating in the impoverished pantropical biota of the oceanic islands. Within continental areas such as Australia, species richness can be related to latitude and altitude (as temperature gradients), rainfall, and soil fertility. Within the Pacific region, differences in species richness between islands or island groups can, in addition, be related to age, isolation, and habitat diversity. The small and often disharmonic biotas of the islands are vulnerable to disturbance and invasion by exotic species, which in places pose severe threats to the native species.

Key words: Biodiversity - species richness - Oceania - flora - fauna

WHIFFIN, T. & KIKKAWA, J. 1992. Status biodiversiti hutan di Oceania. Didalam Oceania terdapat satu garis nyata antara kelompok tanah benua Australia, New Guinea, New Caledonia dan New Zealand, yang lebih tua, dengan pulau-pulau dan rangkaian pulau pasifik yang dari segi geologinya lebih muda. Pada kelazimannya, kelompok tanah benua yang lebih tua ini mempunyai kekayaan spesies dan paras endemik yang tinggi berbanding dengan tanah muda tersebut yang menunjukkan penurunan dari barat ke timur kekayaan spesies dan keendemikannya memuncak kepada flora dan fauna kepulauan tropika yang miskin. Didalam kawasan benua, seperti Australia, kekayaan spesies boleh dikaitkan dengan garislintang dan keluasaan (seperti cerun suhu) hujan dan kesuburan tanah. Didalam kawasan pasifik pula perbezaan kekayaan spesies antara pulau-pulau dan kumpulan-kumpulan pulau boleh juga dikaitkan dengan umur, pengasingan dan kepelbagaian habitat. Biota pulau-pulau ini yang kecil dan tidak harmoni adalah terdedah kepada gangguan dari kemasukan spesies-spesies esotik yang pada satu-satu tempat mungkin mengancam spesies-spesies asli.

Introduction

The concept of Oceania adopted here has a biogeographic rather than a strictly geographic delimitation. Included in the discussion are all areas of the central and western parts of the Pacific, to the east and south of Wallace's Line, showing distinctly Indo-Malesian or Australian relationships in their biota. The area thus delimited contains Australia and New Guinea in the west, New Zealand and offshore islands in the south, and Melanesia, Micronesia and Polynesia in the Pacific as far north and east as Hawaii and Easter Island (Figure 1).

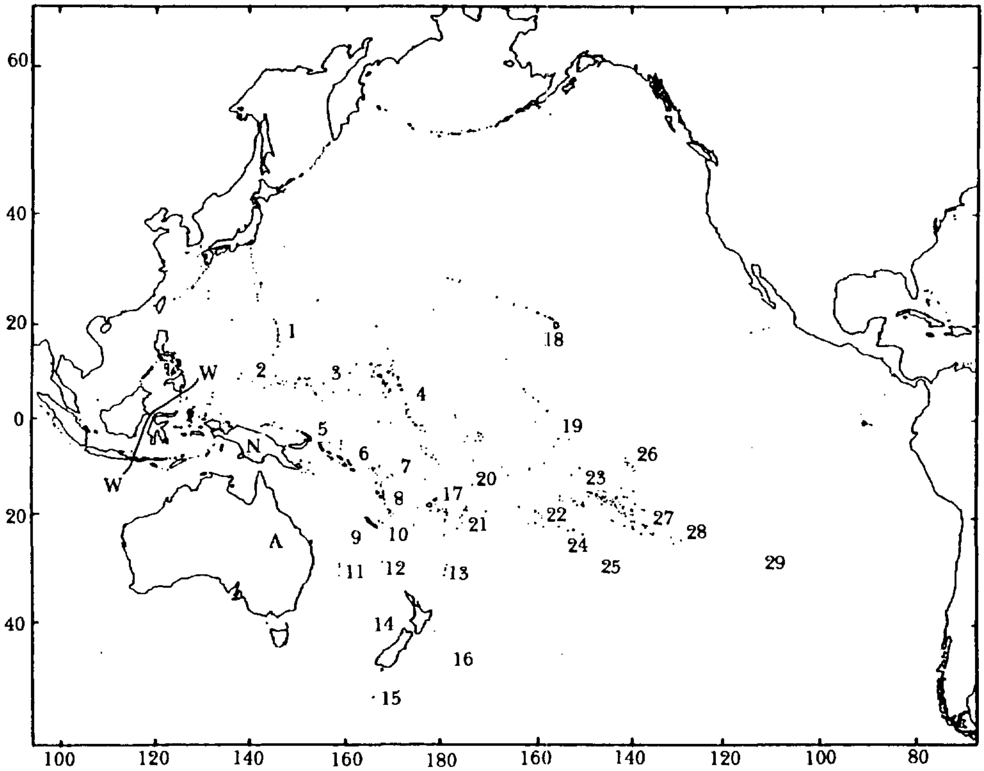

Figure 1. Map of the Pacific region, showing Wallace's Line (W), Australia (A), New Guinea (N), and the Pacific islands forming part of Oceania. 1. Marianas, including Guam; 2. Western Carolines, including Palau and Yap; 3. Eastern Carolines, including Truk, Ponape and Kusaie; 4. Eastern Micronesia, including Marshall Is, Kiribati and Tuvalu; 5. Bismarcks, including New Britain and New Ireland; 6. Solomon Is; 7. St. Cruz; 8. Vanuatu; 9. New Caledonia; 10. Loyalty Is; 11. Lord Howe I; 12. Norfolk I; 13. Kermadec Is; 14. New Zealand; 15. Subantarctic islands; 16. Chatham Is; 17. Fiji Is; 18. Hawaiian Is; 19. East Central Polynesia, including Phoenix, Tokelau and Line Is; 20. Samoa Is; 21. Tonga Is, including Niue; 22. Cook Is; 23. Society Is; 24. Austral or Tubuai Is; 25 Rapa I; 26. Marquesas; 27. Northern Tuamotus; 28. Southern Tuamotus, including Mangareva, Pitcairn and Henderson Is; 29 Easter I

The major division of the land areas recognised is between the distinctly older, continental areas and the geologically more recent islands of various origins and sizes. The former comprise the ancient land masses represented by Australia (including part of New Guinea), New Caledonia and New Zealand. These are fragments of Gondwanaland, and have had some land surface above sea level since at least the Cretaceous. Biogeographically they represent core areas of particular biota, containing a number of old, relictual forms, and having acted as source areas for neighbouring areas. For islands, two distinct types may be recognised, differing in mode of formation, and often in size and elevation. These are the "high islands" and "low islands" long recognised in the Pacific (Fosberg 1984). The low islands may be further subdivided into two forms, firstly the coral cays and atolls and secondly the elevated limestone islands (Fosberg 1984, Stoddart 1992).

This paper will review forest biodiversity in the Oceania region. After a brief account of the geology and biogeography of Oceania, the major trends of biodiversity within the area will be discussed. Forest areas in Australia will be used as examples for intra-area (continental) trends, while the Pacific islands and island-groups will be used for the inter-area trends. Finally, recent evolutionary history, including the impact of people, will be discussed.

Geology and biogeography

The geological and biogeographical history of the area is basically related to the breakup of Gondwanaland, its drift northwards, and the collision with the southeast Asian plate (Raven & Axelrod 1972, Whitmore 1981, Barlow & Hyland 1988). Australia, New Caledonia and New Zealand separated from Antarctica, and from one another, during the late Cretaceous and early Tertiary. These areas carried a basically Gondwanan flora and fauna, which subsequently diversified in isolation as the islands separated.

The Australian plate collided with the southeast Asian (Sunda) plate in the Miocene (Audley-Charles *et al.* 1981), thence gradually forming the configuration of east Malesian island arcs. This contact enabled, from the late Miocene or early Pliocene onwards, a meeting of the Australian and Asian biotas, the effects of which are now seen in Wallace's Line (Audley-Charles 1981, Whitmore 1982, Keast 1983). However, for many groups of plants and animals, there was not a major interchange between the two areas after the collision of the plates (Truswell *et al.* 1987, Truswell 1990). In part at least, this is a reflection of the Tertiary climatic history of the two areas, and the effects of this on the evolution of the constituent biotas. During much of the Tertiary, Australia was more or less covered in rain forest of a predominantly tropical or subtropical nature (Christophel & Greenwood 1988, 1989). From the late Tertiary onwards, however, there was a lowering of the mean annual temperature, and the occurrence of periods of aridity, while the increasingly leached soil became nutrient deficient. This saw the development over much of the continent of a scleromorphic flora and an arid-adapted fauna. Rain forests, of Gondwanan origin, remained only in a few areas along the east and perhaps north coasts (Webb & Tracey 1981).

On the other hand, the newer and often volcanic areas of eastern Malesia, including New Guinea, had nutrient-rich soils and a more equable climate. Here, rain forest remained much more widespread than in Australia, although the New Guinea rain forest was largely separated from the species-rich Asian rain forests by broad waters and arid islands. The collision of the Australian plate and the southeast Asian plate thus brought together a subtropical and arid-adapted biota on the one hand and a tropical, rain forest biota on the other (Hartley 1986, Barlow &

Hyland 1988). The relative scarcity of nutrient-poor soils and arid areas in Malesia reduced the potential of Australian taxa to invade Malesia (van Steenis 1979), while the relative scarcity of nutrient-rich soils and humid climates in Australia prevented movement in the other direction (Mayr 1945).

Wallace's Line, while originally observed as a faunal division, is thus essentially a demarcation between biotas with different ecological adaptations. In plants, these are represented by scleromorphic open forest species on the one hand, and mesomorphic rain forest species on the other. The distinctiveness of Wallace's Line as a biogeographic division is dependent on the ecological attributes and dispersal capabilities of the biota under study (Keast 1983).

There is increasing evidence that the Malesian rain forests may contain a significant Gondwanan component. It has long been recognised that India, splitting off early from Gondwanaland, may have carried a biota that then invaded Malesia from the west (Barlow 1981). It is now also recognised that some parts of Malesia and southeast Asia contain continental fragments rifted from the Australian plate in the late Jurassic (Audley-Charles 1987, Burret *et al.* 1991). While this was too early to explain the distribution patterns of many taxa, these fragments probably provided a series of stepping-stones connecting Australia and southeast Asia during the Tertiary. Thus the Malesian rain forests, like all other rain forests in the world, may be of Gondwanan origin (Barlow & Hyland 1988).

The remaining Pacific islands are carried on the Pacific plate, which underlies the major part of the Pacific Ocean (Briggs 1987). This plate shows a predominantly east to west movement, so that subduction processes at its western boundary have formed a series of island arcs of different ages, as in Melanesia (Holloway 1984, Schmid 1989). These island arcs are thus subcontinental in origin, and will generally show a stepping-stone connection with one or more of the older land masses to their west. Within the Pacific plate, there are sites of intra-plate volcanism, where island chains are formed as the plate moves over hot spots or mantle plumes (Briggs 1987); such a situation is well known in the Hawaiian islands (Walker 1990). These latter islands, such as occur throughout Micronesia and Polynesia, are true oceanic islands, never having been connected to major land masses (Fosberg 1984).

In contrast to the high, volcanic islands, the low islands are either ring-shaped coral atolls with an encircled lagoon, ephemeral coral cays in lagoons, or raised reef limestone islands with a central plateau. They are distributed through much of the area, either more or less scattered as individual islands or island-groups, or forming larger archipelagoes (Fosberg 1984, Stoddart 1992).

Patterns of biodiversity

The species diversity of an area can be shown to be related to a number of different factors, such as temperature, rainfall, soil fertility, age, isolation, and habitat diversity. These factors interact in simple or complex ways to produce the patterns of biodiversity to be seen in Oceania.

Reduction in species diversity along a temperature gradient may be seen latitudinally, from tropical through subtropical to temperate areas, and also altitudinally from sea level to the peaks of mountains in the area. The latitudinal gradient is most pronounced along eastern Australia where it ranges from 12°S to 42°S, while the altitudinal sequence is best developed in New Guinea where forest vegetation is continuous from lowlands to 4000 *m* in several mountains. In some cases there may be other factors such as rainfall or soil fertility associated with this temperature gradient.

Reduction in species diversity along a rainfall gradient, as seen across northern Australia, is accentuated where it is associated with an increase in seasonality of rainfall. Thus there is a lower species diversity under monsoonal climates, with marked wet and dry seasons, than under climates with a comparable annual rainfall distributed more evenly over the year.

Reduction in species diversity is also seen with reduced soil fertility. For example, there is a decrease in both vegetation complexity and species diversity between eutrophic and oligotrophic soils in Australian tropical and subtropical rain forests (Webb & Tracey 1981). There is also generally a lower species diversity associated with the lower soil fertility in sclerophyll vegetation; however, there may be a relatively high species diversity in some forms of sclerophyll vegetation, particularly heathland (Parsons & Cameron 1974).

The relationships between species diversity and age, isolation, and habitat diversity are those encompassed by the theory of island biogeography (MacArthur & Wilson 1967). While the theory was developed for island biota, it has been shown to be applicable to fragmented forest habitats, such as patches of rain forest separated by some form of drier vegetation.

The age of an area will represent the time over which it has been available to receive immigrant biota, while isolation as distance from the source area(s) will reflect the probability of immigration. Habitat diversity is a measure of the availability of different habitats within the area. In general, the greater the habitat diversity, the greater the species diversity, when all other factors are equal. The larger number of niches thus available may, in a direct manner, accommodate more immigrant species or, more indirectly, they may allow diversification and parapatric speciation thus filling these niches.

Species diversity in Australian forests

Within Australia, there is a general vegetation sequence through closed forest (rain forest), tall open eucalypt forest (wet sclerophyll forest), open eucalypt forest (dry sclerophyll forest) and eucalypt woodland (Groves 1981, Ovington & Pryor 1983). This sequence corresponds to a rainfall gradient, from the coast to inland, but may be complicated by soil fertility and other factors (Specht *et al.* 1991). The boundary between rain forest and eucalypt forest may be abrupt (Stocker & Unwin 1989); while it often corresponds to a marked change in soil fertility, the boundary is generally now maintained by fire (Unwin *et al.* 1985, Ash 1988, Unwin 1989).

The species richness of overstorey plants (trees and tall shrubs) decreases along this rainfall-vegetation gradient, in tropical, subtropical and temperate parts of the continent (Table 1). There is also, in general, a latitudinal gradient within each vegetation type, corresponding to a temperature gradient from north to south. The most marked discontinuity is between the tropical and subtropical areas on the one hand and the temperate area on the other; this can be seen in all four vegetation types.

Table 1. Species richness of trees and tall shrubs (per *ha*) in forests and woodlands and of total rain forest birds (in parentheses) in eastern Australia

	Perhumid rain forest	Tall open eucalypt forest	Open eucalypt forest	Eucalypt woodland
Tropical	125 (100)	30+	19	12
Subtropical	98 (80)	38	11	10
Temperate	8 (42)	7	5	4

(data from Specht & Specht 1989a, Specht *et al.* 1991, A.N. Gillison pers. comm. 1992 for plants, and from Kikkawa 1968, 1991 for birds)

These figures relate to overstorey species only, and it has been shown that the species diversity of understorey plants is inversely correlated to the cover of the overstorey (Specht & Specht 1989a, 1989b), which decreases from rain forest through to woodland. However, using data on total vascular plant species diversity (overstorey and understorey) for subtropical vegetation types (Specht *et al.* 1991), it can be seen that the trend apparent in the overstorey species is maintained, though less marked, when all species are considered (Table 2).

Table 2. Species richness of native vascular plants (per *ha*) and of birds (per 8 *ha*) in forests and woodlands of subtropical eastern Australia

	Perhumid rain forest	Tall open eucalypt forest	Open eucalypt forest	Eucalypt woodland
Plants	197	145	88	64
Birds	38	40-44	44-45	21-33

(data from Specht *et al.* 1991 for plants, and Kikkawa 1968, 1991 for birds)

Forest birds in Australia present a somewhat different picture. They show the same decrease in species richness along the latitudinal gradient (Table 1), but their species diversity is greater in semi-arid formations (Table 2) than in rain forest (Kikkawa 1968, 1991). The difference is much greater than indicated if larger areas are compared. The reason for the greater diversity of eucalypt forest birds is that Australia, being primarily a dry continent, has produced more dry-adapted forms than wet-adapted forms through the climatic cycles of the Pleistocene (Brereton & Kikkawa 1963, Keast 1981). This is in contrast to New Guinea where rain forest bird species proliferated, presumably in the same climatic cycles.

Species diversity in Australian rain forests

Rain forests in Australia occupy patches of various sizes along the eastern and northern coasts. There are a series of "core" areas, with tropical rain forest in northeast Queensland, subtropical rain forest in southeast Queensland and adjacent northern New South Wales, cool temperate rain forest in Tasmania, and monsoonal rain forest in Northern Territory (Webb & Tracey 1981, Kershaw & Whiffin 1989). The change from tropical through subtropical to temperate down the east coast may be seen as a temperature gradient, and the change from tropical to monsoonal across the north coast as a rainfall (and its seasonality) gradient.

Within Australia there are approximately 1500 species of rain forest trees (Whiffin & Hyland 1988, 1991). Examining the distribution of these, there is an evident decline in species diversity down the temperature gradient along the east coast, and a perhaps more marked decline down the rainfall gradient along the north coast (Figure 2). However, if the local endemic taxa (*i.e.* those restricted to one region, within Australia at least) are removed, then the patterns of species diversity become less marked (Figure 3). The pattern down the east coast is basically one of a distinction between the species-rich tropical and subtropical rain forests of

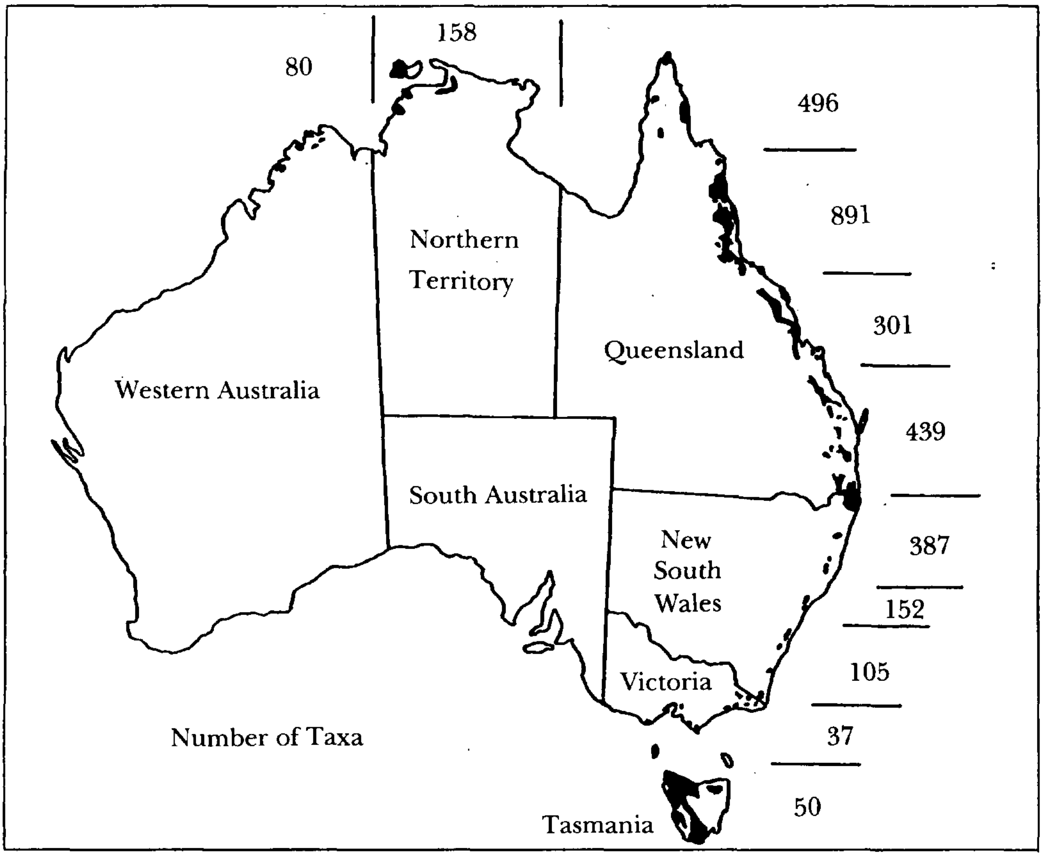

Figure 2. Number of total rain forest tree taxa in northern and eastern Australia; the black patches indicate rain forest areas

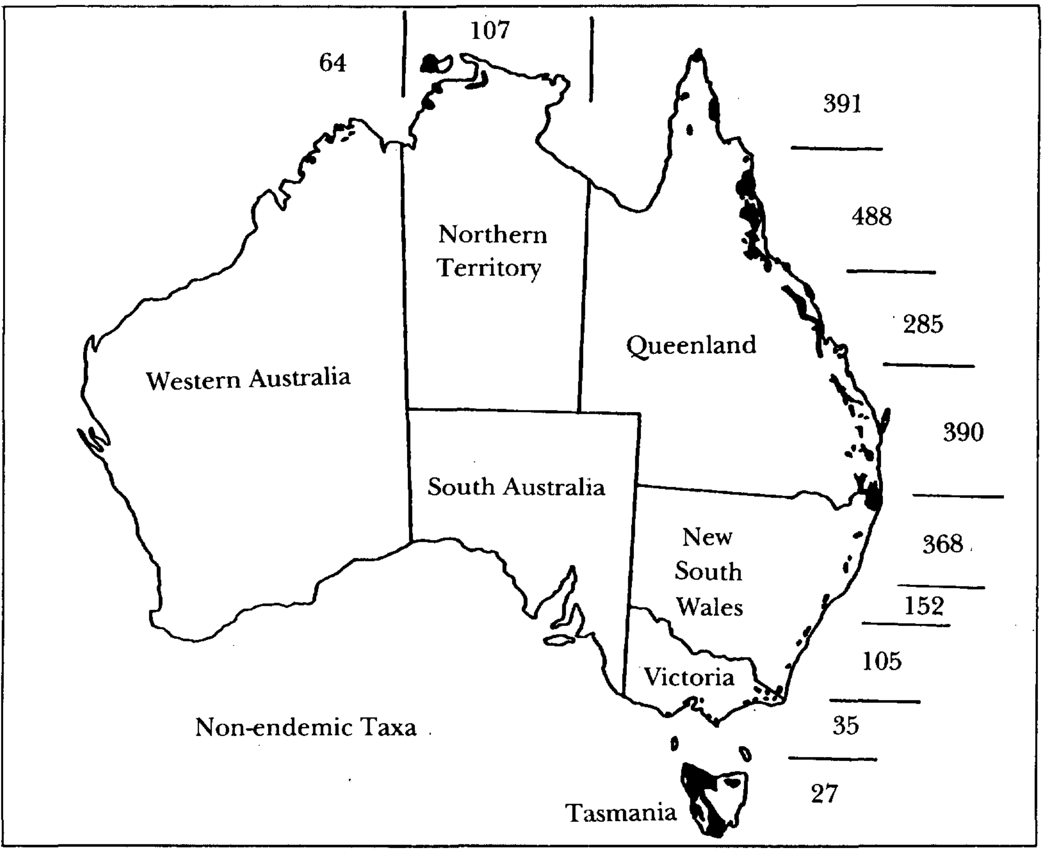

Figure 3. Number of non-endemic rain forest tree taxa in northern and eastern Australia; the black patches indicate rain forest areas

Queensland and New South Wales on the one hand and the species-poor cool temperate rain forests of Tasmania and Victoria on the other. The comparatively great species richness of northeast Queensland is due, in part at least, to a high degree of endemism; this is associated with historical biogeographical events and greater habitat diversity, as the largest area of rain forest refugia and the greatest diversity of rain forest types occur here.

A moderate degree of endemism is also found in forest wildlife of tableland rain forest of northeast Queensland. From here the rain forest fauna as a whole is attenuated to the north (Kikkawa *et al.* 1981a) and west (Kikkawa *et al.* 1981b) along rainfall gradients, and to the south (Kikkawa 1991) along a temperature gradient.

The effect of some of these factors on the patterns of species diversity in Australian rain forests can be seen in a study of the distribution patterns of *Syzygium* and allied genera (Hyland 1983, Whiffin & Hyland 1986), a group of trees or larger shrubs in the Myrtaceae. Numerical analysis of the distribution data led to the recognition of four floristic elements: (1) a northern element centred in Cape York Peninsula, (2) a northeastern element centred in northeast Queensland,

(3) a southern element centred in northern New South Wales, and (4) a northwestern element centred in the Northern Territory. A comparison of the distribution of the taxa and of the floristic elements (Table 3) highlights some aspects of the evolutionary history of this group. There are four centres of species diversity and endemism, a major centre in each of tropical northeast Queensland and subtropical southeast Queensland - northern New South Wales, and a minor centre in each of Cape York Peninsula and Northern Territory. These areas may be seen as representing long-term refugia and epicentres of evolution. All other areas must be seen, for this group of plants at least, as immigrant areas, receiving their flora from one or more of the epicentres. The flora of these immigrant areas tends to reflect the proximity of the various source areas. Thus, for example, the flora in central and southern New South Wales contains only one floristic element, from a single nearby source area, whereas the flora in central Queensland contains two floristic elements, from the north and from the south. In these respects, the rain forest biota within Australia reveal the effects of age, area and isolation caused by ecological factors.

Table 3. Distribution of species and floristic elements in Australian species of *Syzygium* and allied genera

	Number of taxa	Endemic taxa	Floristic element			
			Northern	North eastern	Southern	North western
Western Australia	5			4		1
Northern Territory	12	2		8		4
Cape York Peninsula	25	5	10	15		
Northeast Queensland	46	23	1	41	4	
Central Queensland	10			7	3	
S.E. Qld - northern N.S.W.	14	5		2	12	
Central New South Wales	4				4	
Southern New South Wales	3				3	
Victoria	1				1	

Within Australia the altitudinal change in rain forest vegetation is most marked in northeast Queensland, where there is a sequence from lowland rain forest through submontane rain forest to montane rain forest on a number of the larger mountains (Tracey 1982, Monteith & Davies 1991). A comparison of the species diversity of these rain forest types within the general area of northeast Queensland shows a reduction in species richness with altitude (Table 4), paralleling that found with the latitudinal gradient. This may be counteracted, in small part, by a reverse gradient in rainfall, as the highest rainfalls are recorded from the peaks of some of these mountains (Tracey 1982).

The species diversity of wildlife does not follow the trend seen in tree species diversity, because of the endemism developed in the mid-altitude rain forests of the tablelands. However, a parallel change in the composition of the fauna is evident (Kikkawa 1982). The altitudinal gradient of species diversity is more marked in

New Guinea, where land birds, for example, decrease steadily from 320 species on lowlands to 8 species above 4000 *m* (Kikkawa & Williams 1971).

Table 4. Species richness of trees and tall shrubs (per 0.5 *ha*) in tropical Australian rain forests of different altitudes

Rain forest type		Species richness	
UNESCO (1973)	Webb (1978) and Tracey (1982)	range	mean
Tropical ombrophilous forest			
Lowland forest	Complex mesophyll vine forest	31-117	66.3
	Mesophyll vine forest	17- 95	52.8
Submontane forest	Simple notophyll vine forest	26- 90	53.2
Montane forest	Simple microphyll vine thicket	27- 47	38.7

(data from Tracey 1982)

Species diversity in Pacific islands

The patterns of species diversity in Pacific islands are remarkably consistent in general aspects over different taxonomic groups (Kay 1979), being seen most clearly in plants (van Balgooy 1971) and birds (Diamond 1972, 1984).

Higher levels of species diversity are seen in the older, continental areas of Australia, New Guinea, New Caledonia and, to a lesser extent, New Zealand. These are generally expressed as higher levels of endemism, relatively larger numbers of older, relictual taxa, and a more general distinctiveness of the local flora and fauna. Australia shows a basically Gondwanan biota, both as a relictual component in the rain forests and as a derived component in the sclerophyll vegetation. There is a small Indo-Malesian element, particularly in the tropical and subtropical rain forests. New Guinea is often seen as a mixture, comprising both Gondwanan and Indo-Malesian elements, and both recent and relictual taxa (van Balgooy 1976, Gressit 1982, Diamond 1984). Reflecting its contrasting geographic and climatic positions, its fauna is more predominantly Australian, while its flora is more Indo-Malesian (Diamond 1984). New Caledonia contains both Gondwanan and Indo-Malesian elements, and a high level of endemism, reflecting its geological history and isolation (Morat *et al.* 1984). New Zealand, in contrast to the other land masses, is in temperate latitudes, and shows a lower level of diversity.

The pattern of species diversity on the other Pacific islands can be seen to consist of three parts (Kay 1979, Briggs 1987). The flora and fauna of the Pacific islands show definite western Pacific (i.e. Indo-Malesian) relationships; there is a general west to east decline in species diversity; and there are at points in this decline an abrupt elimination of certain groups, this being related to the dispersal ability of those groups (Diamond 1984). The species diversity of the low islands, particularly of the coral atolls, is much lower than that of the high islands (Fosberg 1984, Stoddart 1992). For example, the Society Islands comprise ten volcanic islands and five coral atolls; the coral atolls show a highly impoverished flora compared with the volcanic islands (Fosberg 1992).

The relationships of the Pacific island biotas are overwhelmingly with the Old World, and in particular with Indo-Malesia. This has been reflected in virtually all biogeographic subdivisions of the Pacific (van Balgooy 1971). The New World element in Oceania is small. The only exception is Hawaii; although predominantly Indo-Malesian, it shows a low but appreciable percentage of an American element in its flora (van Balgooy 1971, Wagner *et al.* 1990), while many or most of its birds are derived from the New World (Diamond 1984).

The pattern of decline in species diversity from west to east in the Pacific has been shown in many plant and animal groups, as recently summarised by Stoddart (1992). For example, the number of genera of vascular plants decreases from 719 in New Caledonia and 654 in the Solomon Islands to 81 in the Pitcairn Islands and 22 on Easter Island (Figure 4). Forest bird species decrease in number from 445 in New Guinea through 184 in Melanesia to 40 in southeastern Polynesia and 38 in New Zealand (Figure 5).

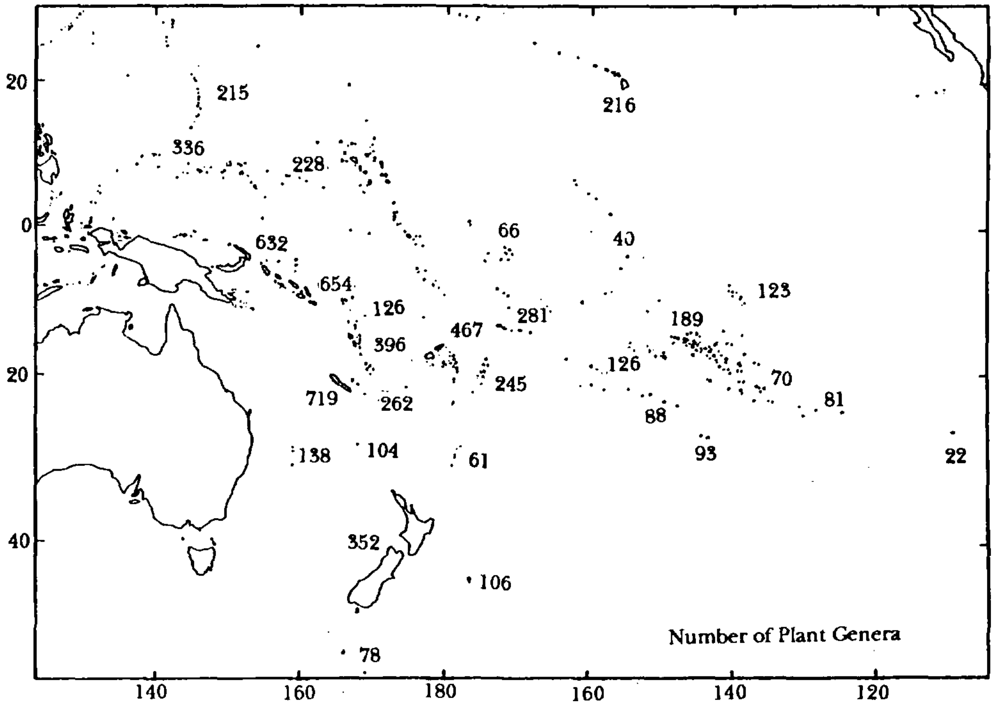

Figure 4. Number of plant genera (angiosperms and gymnosperms) in islands and island groups of Oceania (data from van Balgooy 1971, Schmid 1989, Sohmer 1990)

The nature and causes of this pattern of decline may be seen in the analyses of plant generic distribution by van Balgooy (1971), where he determined the composition of the flora of each island (or island group) in terms of a number of floristic elements. Expressing this composition in percentages allows the underlying causes to be seen within the overall west to east decline in numbers.

MICRONESIA	CENTRAL PACIFIC	CENTRAL POLYNESIA	HAWAII
Marshall Caroline Senyavin Is.	Wake, Marshall Nauru Kiribati, Tuvalu Tokelau Is.	Samoa, Tango Niue Is.	Midway, Laysan Hawaiian Is.
75	12	34	44
(44)	(13)	(17)	(42)

NEW GUINEA	MELANESIA				FIJI	SOUTH-EASTERN POLYNESIA
	Solomon Is.	New Caledonia	Vanuatu	Total		Cook, Society Tuamotu Austral Is.
445	127	52	44	184	50	40
(217)	(63)	(28)	(24)	(97)	(27)	(12)

EASTERN AUSTRALIA	NEW ZEALAND
329	38
(210)	(21)

Figure 5. Number of forest bird species (number of passerine species in parentheses) in Oceania (data from Vuilleumier & Gochfeld 1976, Mayr 1978, Beehler 1985, Pratt *et al.* 1987, Ornithological Society of New Zealand 1990)

Along this diversity gradient, there is a relative decrease in the importance of taxa with Old World affinities (Figure 6) and, more specifically, with Indo-Malesian affinities (Figure 7). Related to this is a relative increase in the importance of taxa with Widespread distributions (Figure 8), so that on the more remote islands this becomes the dominant element. This is generally interpreted as showing that only those genera with the dispersal ability or time necessary to become widespread were able to reach these remoter (eastern) islands. On the other hand, those islands closer to the source of a large biota (primarily New Guinea) were able to receive genera with less dispersal ability or time. The general migration routes for plants implied by these distributions, with New Guinea (and Malesia) as the major source area, parallel the patterns of colonisation determined for land and fresh-water birds (Diamond 1984).

Evolutionary and recent history

Perhaps of greatest significance within the forest biodiversity of the region is the contrast between the rich, endemic continental biota found in the southwest and the impoverished pantropical biota of the oceanic islands, connected by steep diversity gradients through the subcontinental islands. Radiation of the autochthonous flora during the Tertiary was most pronounced on the Gondwanan land masses, where climatic and habitat diversity was greatest. For the fauna this radiation was restricted to Australia and New Guinea, as the subcontinental islands did not receive the founder species (*e.g.*, no marsupials in New Zealand). The relict nature of such fragments, coupled with environmental stresses (such as cold or dry conditions without effective refugia), produced attenuation of the biota on smaller islands. With increasing distance from the source of colonisation, the rate of immigration is reduced and that of extinction increased on remote islands. Chances of colonisation on oceanic islands would be just as small for the island hopping within-region colonisers as for the long distance migrants from other regions. Thus Micronesia received Oriental and Palearctic species of forest birds whereas the Hawaiian islands were colonised by both island hopping western Pacific colonisers and North American vagrants. One from the latter group underwent a spectacular radiation to form most of the endemic avifauna of the Hawaiian islands. These birds happened to be finches (passerines), but in Micronesia a radiation on a much smaller scale occurred among the white-eyes, while in Polynesia and Fiji it was the pigeons and parrots that differentiated. These resulted in different ratios of passerines to non-passerines among the forest birds of different island groups (Figure 5). Such a disharmonic nature is characteristic of the biota of most Pacific islands, and is equally evident in the flora (van Balgooy 1971, Wagner *et al.* 1990).

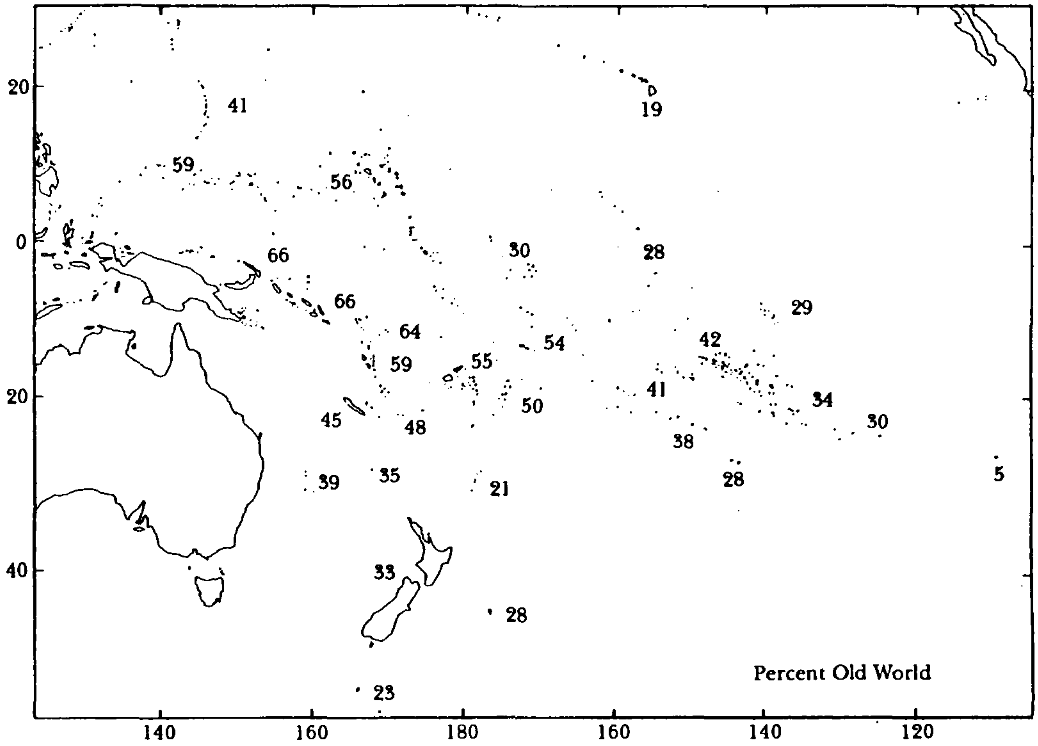

Figure 6. Percentage of plant genera (angiosperms and gymnosperms) with an Old World distribution in islands and island groups of Oceania (data from van Balgooy 1971)

It is interesting to note that the forest communities of islands have been invaded by successful colonisers throughout the long history in which microevolution of older groups has occurred. This mixing of biota and adjusting to one another may still be occurring in many forest habitats, through competition (Mountainspring & Scott 1985) and niche specialisation (Ralph 1990). In fact,

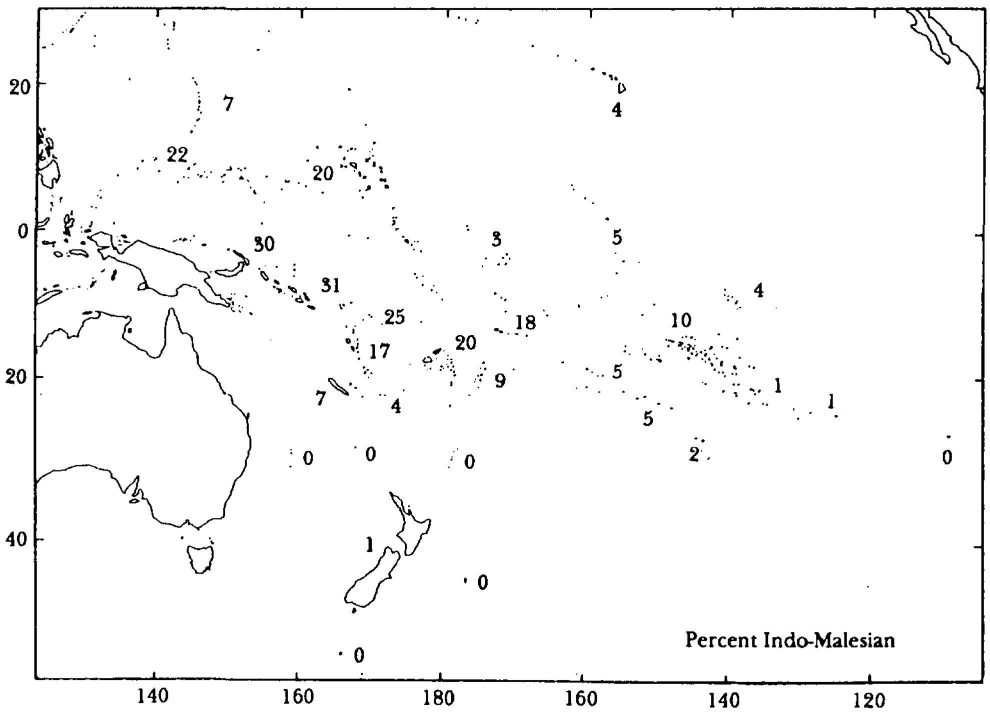

Figure 7. Percentage of plant genera (angiosperms and gymnosperms) with an Indo-Malesian distribution in islands and island groups of Oceania (data from van Balgooy 1971)

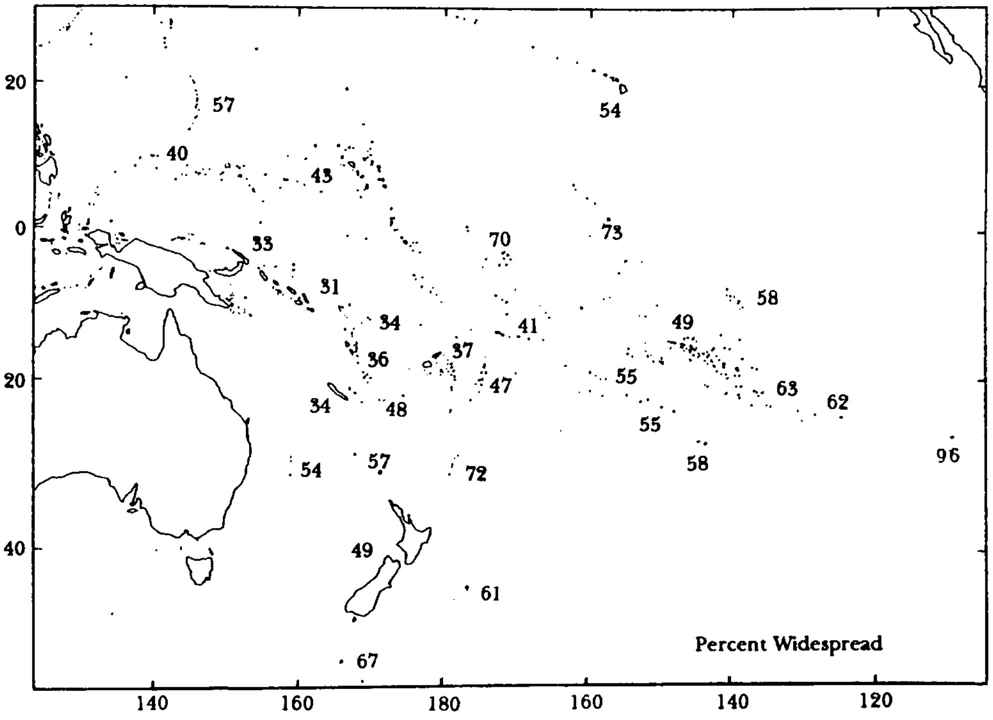

Figure 8. Percentage of plant genera (angiosperms and gymnosperms) with a Widespread distribution (including pantropical genera) in islands and island groups of Oceania (data from van Balgooy 1971)

in spite of the general paucity of forest fauna, specialisation among the forest birds of the region is unexpectedly high. It makes these species, usually with small population sizes, even more vulnerable to introduced influences on the islands. The extinction rate of well-established forest species on islands is notoriously high in historical time. While direct exploitation of species is responsible for many well-known cases, many more suffered extinction through human occupation (*e.g.* Olson & James 1982) and indirect causes.

The accelerated process of extinction of island forest birds through indirect causes is part of the rapid alteration of forest biota caused by the invasion of exotic species. In New Zealand, of 34 introduced species of birds established in the country, 7 passerine species have successfully colonised native forests (Kikkawa 1966) and even reached outlying islands (Williams 1973). The native forest birds have suffered as a consequence of competition from some of these introduced birds, of habitat destruction caused by introduced mammals such as pigs, red deer, wapiti and brush-tailed possums, and of severe predation by introduced predators, particularly black rats, stoats and cats (Gibb & Flux 1973). In the Hawaiian islands, endemic forest birds that survived the onslaughts of the Polynesians and introduced predators have now disappeared from lowland forests as a result of diseases, notably bird malaria, transmitted from exotic species (van Riper *et al.* 1986).

A similar picture is to be found in the flora. While some extinction occurred during the climatic fluctuations of the Pleistocene (Ash 1992), more marked are the direct and indirect influences of people. Clearing, especially of lowland coastal areas, has been widespread throughout the area (Fosberg 1984, 1992, Collins *et al.* 1991, Ash 1992). In the case of some of the low islands, there has been a severe loss of native vegetation (*e.g.* Thaman 1992). Introduced species have become common (Fosberg 1992, Whistler 1992) and may form a numerically important component of the flora. In the Hawaiian islands, for example, naturalised species account for 47% of the total angiosperm flora (Wagner *et al.* 1990). This picture of vegetation alteration or loss is repeated, to varying degrees across Oceania, leading in places to severe threats to the remaining forest biodiversity.

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