Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Phanerogamic Flora of the New Hebrides and its Relationships

W.-L. Chew

Phil. Trans. R. Soc. Lond. B 1975 **272**, 315-328
doi: 10.1098/rstb.1975.0090

Email alerting service Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: **http://rstb.royalsocietypublishing.org/subscriptions**

This journal is © 1975 The Royal Society

Downloaded from rstb.royalsocietypublishing.org

Phil. Trans. R. Soc. Lond. B. **272**, 315–328 (1975) [315]
Printed in Great Britain

The phanerogamic flora of the New Hebrides and its relationships

By W.-L. Chew
Royal Botanic Gardens, Sydney, Australia

The phanerogamic flora of the New Hebrides is mainly of the Malesian type both in floristic composition and structure of the vegetation. It is however a depauperate sample with fewer families and genera, most of which have a high proportion of elements with very wide geographical ranges of distribution. Most of the species have also been observed to have great ecological amplitude. At the level of family and genus, there is a total absence of endemic and relic elements; and only at the species level is there an appreciable degree of endemism.

Unlike the Solomon Islands, the New Hebrides flora does show some regional differentiation. The northern islands appear to differ from the southern islands not only in frequencies of occurrence of species but also in the actual presence/absence of many significant groups.

The flora of the New Hebrides has been found to have closer affinities with those of Fiji, Samoa and Tonga to the east than to islands to the west and northwest, despite the fact that the New Hebrides are closer geographically to the Solomon Islands and New Caledonia.

It is suggested that the New Hebrides have a very young immigrant flora and that the colonization of the archipelago has taken place very rapidly in very recent times. It is also maintained that plant dispersal to the islands has been trans-marine rather than by migration over land.

1. INTRODUCTION

The phanerogamic flora of the New Hebrides is largely of Malesian derivation. It has all the essential characteristics of the tropical lowland flora of the Palaeo-Oriental realm more particularly of the Indo-Malesian region. Being on a small archipelago, which is also further removed from the main source area than the Solomon Islands, the flora is predictably a greatly attenuated extension of that of Indo-Malesia to the northwest. The rather great latitudinal spread of the archipelago, especially as it lies in higher latitudes, results in the southern islands reaching more seasonal climatic regimes which accounts for the slight differentiation between the floras of the northern and southern islands.

Situated almost in the centre of Melanesia, the New Hebrides have received a somewhat significant number of elements from Australia and New Caledonia in the southwest and from the Pacific probably via Fiji in the east. This island group thus exhibits a much greater intermingling of Paleo-Oriental, Australian and Pacific floristic elements than the Solomons.

In this account, the phanerogamic flora will be examined primarily from a systematic angle; as such, the units of discussion will be mainly taxonomic ones. However, it will be preceded by a very short mention on the general characteristics of the plant community as this will add greatly to a better understanding of the flora as a whole.

This contribution is based on field observations and the preliminary results of the Royal Society Expedition to the New Hebrides supplemented by information gathered from Melanesian collections in the herbaria at Brisbane and Sydney. Among the published data consulted, the most important sources have been the papers on New Hebridean phanerogams by

The Royal Society is collaborating with JSTOR to digitize, preserve, and extend access to *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences.* www.jstor.org

Downloaded from rstb.royalsocietypublishing.org

A. Guillaumin (1931–1933, 1938, 1948) and the mimeographed records of M. Schmid (1970, 1973). Data on the phanerogams, at the generic and species levels, of neighbouring Melanesian archipelagoes for comparison with the New Hebrides have been obtained from the works of A. Guillaumin on New Caledonia, J. W. Parham on Fiji and T. C. Whitmore and D. B. Foreman on the Solomon Islands. The recent very comprehensive account by van Balgooy (1971) on the plant geography of the Pacific has also been consulted. Comparison has also been made with the floras of Samoa and Tonga using the works of Christophersen (1935, 1938), Yuncker (1959) and others; but here, the comparison has been made only at the generic level as the floras of Samoa and Tonga are much too poorly known to permit useful examination at the species level.

2. The phanerogamic community

The flora of the New Hebrides is entirely of the rainforest type characteristic of the Indo-Malesian region. It has all the familiar synusiae such as the independent plants of trees, shrubs and herbs, the dependent synusiae of climbers, stranglers and epiphytes as well as the heterotrophic plants of saprophytes and parasites. These synusiae in the New Hebrides do not differ significantly, in very broad terms, from those of the Indo-Malesian forests in either physiognomic characteristics or general floristic composition.

Thus in the arborescent synusia, the trees have the familiar buttressing, their trunks have the usual ability to produce coppice-shoots, frequency of caulifory etc. In floristic composition, many of the tropical families which contribute significantly to the various independent synusiae in Malesia are present in the New Hebrides in the same manner.

In the epiphytic and strangler synusiae, the major components are, as in Malesia, the Orchidaceae, *Ficus* and araliad genera like *Schefflera* which appear to be similar in all major physiognomic characters to their counter-parts in the source area of the Malay archipelago. So are the synusiae of saprophytes and parasites which in the New Hebrides have essentially the same type of floristic composition as in Indo-Malesia, namely, Burmanniaceae as saprophytes, Loranthaceae and Balanophoraceae, the former occurring abundantly as epi-parasites and the latter frequent as root-parasites.

Because of the overall paucity of the flora in the archipelago however, the entire spectrum of the synusiae is greatly 'thinned' and consequently much less complex in comparison with richer areas like New Guinea or Borneo.

3. Phanerogamic flora

3.1. *The families*

There are 123 families of phanerogams in the New Hebrides. Of these, 3 are gymnosperms and 120 angiosperms. Of the angiosperms, 17 are monocotyledons and the rest, 103 are dicotyledons. Unlike New Caledonia and Fiji, where endemic relic families have been recorded, there is no endemic family in the New Hebrides, relic or modern. In fact the vast majority of them are of very wide distribution, i.e., palaeo-tropical, pan-tropical and cosmopolitan.

Among the cosmopolitan families, the most important in the New Hebrides appear to be Gramineae, Papilionaceae, Compositae and Cyperaceae. Together, these four families are represented by 82 genera and 134 species. Members of these families are particularly prominent in disturbed to very exposed habitats, and many of them no doubt have been brought in by man. Compared with the other three families, the Papilionaceae have relatively more significant

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

representation in undisturbed forested areas where arborescent and scandent members can be locally abundant.

Of the pan-tropical families, the larger ones include Orchidaceae, Rubiaceae, Euphorbiaceae, Moraceae, Urticaceae and Palmae. These six families account for a total of 117 genera and 266 species which amount to 26 % and 30.5 % of the total number of genera and species respectively in the New Hebrides. In habitat spread, the pan-tropical families differ from the cosmopolitan ones in having proportionately more representatives in primary communities. If the two groups of families are taken together, they account for a total of 199 genera and about 400 species which work out to be 44 % and 46 % of the total number of genera and species respectively in the archipelago. In other words, nearly one half of the phanerogamic flora belongs to either cosmopolitan or pan-tropical families, many of which have developed centres of diversity in the Indo-Malesian area (see Table 1).

TABLE 1. REPRESENTATION OF MOST IMPORTANT COSMOPOLITAN AND PAN-TROPICAL FAMILIES IN THE NEW HEBRIDES

	genera	species
cosmopolitan families:		
Compositae Cyperaceae Gramineae Papilionaceae	82	134
pan-tropical families:		
Euphorbiaceae Moraceae Orchidaceae Palmae Rubiaceae Urticaceae	117	266
total	199	400
percentage of New Hebridean phanerogams	44	46

At the other end of the scale, there are a few families of rather restricted distribution which, though not taxonomically diverse in the New Hebrides, nonetheless contribute significantly to ecosystems of the archipelago. The Araucariaceae, for instance, an essentially Melanesian group, are represented in the archipelago by a single species *Agathis obtusa*, which is a co-dominant in the kauri forests of the southern islands. The Cunoniaceae, which are really an Oceania-Australasian group despite the presence of some elements in the New World, are quite prominent in the *Metrosideros-Weinmannia* forests throughout the archipelago. Similarly, the Guttiferae, represented by four species, are also important in the Kauri forest mainly through the species *Calophyllum neo-ebudicum*, another co-dominant.

In terms of taxonomic diversity, the phanerogamic families are poorly developed in the archipelago. There are only 8 families which are represented by more than 10 genera each while the rest, 115 in all, have less than 10 genera. At the top of the list are the Orchidaceae which are represented by 45 genera and a little above 80 species. They are followed, in so far as families with more than 10 genera are concerned, by Gramineae (33 genera, 58 species), Rubiaceae (24 genera, also 58 species), Euphorbiaceae (22 genera, 54 species), Papilionaceae (21 genera, 33 species), Compositae (16 genera, 19 species), Cyperaceae (12 genera, 24 species)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

and Urticaceae (12 genera, 22 species). A frequency distribution of the number of genera per family shows that 59 families (48 %) are represented by one genus each, 16 families (13 %) by 2 genera and 13 (11 %) by 3 genera each. Table 2 shows these proportions clearly: from the cumulative % column, it can be seen that 71.5 % of the families have 3 genera each or less.

Table 2. Frequency table showing number of families with 1, 2, 3, 4, 5, ..., genera each

genera per family	no. of families	%	cumulative %
1	59	47.97	47.97
2	16	13.00	60.97
3	13	10.57	71.54
4	6	4.87	76.41
5	8	6.50	82.91
6	7	5.69	88.60
7	2	1.63	90.23
8	0	—	—
9	4	3.25	93.48
10	0	—	—
11	0	—	—
12	2	1.63	95.11
13	0	—	—
.			
.			
.			
16	1	0.81	95.92
.			
.			
.			
21	1	0.81	96.73
22	1	0.81	97.54
24	1	0.81	98.35
33	1	0.81	99.16
45 (Orchid.)	1	0.81	99.97

When the families are examined with regard to their ecological distribution in the archipelago, it is found that the vast majority of them have representatives in a very wide range of habitats and altitudes. The Euphorbiaceae, for example, have species in the mangroves, in sea-shore strand vegetation, in coral limestone forests, in riverine forests on alluvial soils and in numerous other communities from sea-level to well over 1200 m in altitude. Similarly, families like Papilionaceae, Rubiaceae, etc. are also very widely dispersed. It is noticed, however, that disturbed and other open habitats and vegetation types have a preponderance of families which are cosmopolitan. As one moves from such habitats to more closed communities further inland, families with narrower distributional patterns become more significant both in number and ecological importance.

There does not appear to be any single-family dominance in the arborescent synusiae such as is observed in the dipterocarp forests of Borneo. Only in the epiphytic synusia, is there a single-family dominance. Here, the Orchidaceae form the major components of epiphytes over very large areas throughout the archipelago. There are of course some localities where certain families manage to achieve an appreciable degree of preponderance in number, but these areas are often quite local and somewhat limited in extent.

The low taxonomic diversity observed in the families has naturally an adverse effect on the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

number of endemic elements in each family. A survey of the phanerogamic flora reveals that 63 out of 123 families (which amounts to slightly more than 50 %) have no endemic genera or species, 28 families have only 1 endemic species each, 12 families have 2 endemics and 3 families have 3 endemic species. When summed, 106 families, i.e. a little over 86 %, have 3 endemic species each or less.

As expected, the Orchidaceae with 31 endemic species have the highest number of endemics. This is followed by the Ruciaceae with 15 endemic species, the Euphorbiaceae with 10 and the Araliaceae and the Myrsinaceae which have 9 endemics each.

Lastly, there is the question of relic families in the flora. In this respect the New Hebrides differ greatly from the other archipelagoes in Melanesia in being without relict families. None of the putative primitive families such as the Amborellaceae, the Paracryphiaceae and the Strasburghiaceae of New Caledonia, the Degeneriaceae of Fiji and the Winteraceae of Solomon Islands and other regions is present in the New Hebrides.

In summary, it can be said that the depauperate nature of the phanerogamic flora of the New Hebrides is reflected well at the family level. There is a general lack of taxonomic diversity in the families, most of which have very wide distribution patterns. The absence of relict families is noteworthy especially when such elements are present in the neighbouring areas.

3.2. *The genera*

There are 451 genera of phanerogams in the New Hebrides of which 4 are gymnosperms, 129 monocotyledons and the rest, 318, dicotyledons. The total recorded here is considerably higher than that reported by Balgooy (1971) who credits the archipelago with 396 genera. The increase is due to new findings not only by the Royal Society Expedition, but also by M. Schmid before the 1971 Expedition. Also, many records overlooked by Balgooy have been included.

Compared with neighbouring archipelagoes in Melanesia, the New Hebrides appear to be well endowed with phanerogamic genera. The Solomon Islands, for instance, with an area more than twice that of the New Hebrides, have only 654 genera. The New Hebrides compare favourably with Fiji: both have about the same area, 15000 and 18000 km^2 respectively and have approximately equal number of genera, 451 and 476 respectively.

Just as in the families, the genera have been found to be low in taxonomic diversity. There are only three genera which have more than 8 species per genus; and these are: *Dendrobium*-Orchid. which is represented by 19 species, *Ficus*-Morac. with 17 species and doubtfully *Ipomoea*-Convol. which has 9 species (doubtful because some of the species perhaps do not belong with *Ipomoea* while a couple may not be indigenous to the archipelago). A frequency distribution of the number of genera with different number of species shows that 265 genera (58 % +) are represented by only a single species, 102 (22 % +) by 2 species each and 44 (9 % +) by 3 species (see table 3). As shown in the cumulative percentage column of table 3 more than 90 % of the genera have 3 species each or less.

Of the genera represented by single species notable are *Semecarpus*-Anacard., *Polyalthia*-Annon., *Terminalia*-Combret., *Aleurites*-Euphorb. and other arborescent genera, most of which have large numbers of species in the source area of East Malesia. A large proportion of the single-species genera are, however, actually herbs or small shrubs with wide to very wide geographical distributions. Many of these are prominent elements in open and disturbed habitats or in habitats that are widely found throughout the Palaeo-Tropics.

Genera with two or more species, on the other hand, are mostly found further inland in

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

TABLE 3. FREQUENCY TABLE SHOWING NUMBER OF GENERA WITH 1, 2, 3, 4, 5, ..., ETC. SPECIES EACH

species per genus	no. of genera	%	cumulative %
1	265	58.75	58.75
2	102	22.61	81.36
3	44	9.75	91.11
4	18	3.99	95.10
5	5	1.10	96.20
6	5	1.10	97.30
7	5	1.10	98.40
8	4	0.89	99.29
9	1	0.22	99.51
10	0	—	—
.			
.			
.			
15	1	0.22	99.73
19 (Dendrobium)	1	0.22	99.95

undisturbed high forests such as the kauri forests of the southern islands, coral limestone forests throughout the archipelago and the mixed *Dendrocnide-Kleinhovia* forests in the Apouna valley. The more important genera in this group include large trees such as *Calophyllum*, *Serianthes*, *Myristica*, *Elaeocarpus*, *Ficus*, *Syzygium*, *Hernandia*, etc.; understorey shrubs like *Polycias*, *Schefflera*, *Psychotria*, *Tapeinosperma* and ground herbs exemplified by *Elatostema* and *Peperomia*, the latter existing as epiphytes as well!

There is a putative endemic genus in the New Hebrides, namely *Carpoxylon*, a palm with only one species. Even this is somewhat doubtful as the genus is probably congeneric with some other elsewhere in Melanesia. The genus *Kajewskia*, another palm claimed to be endemic, has been found (Moore 1957) to be none other than *Veitchia*, a Melanesian genus.

An analysis of the genera on the basis of their over-all geographical distribution pattern reveals that they fall primarily into five broad categories of geographical elements. As shown in table 4, column 4, 162 genera, representing 35.9 % of the entire New Hebridean phanerogamic flora, are world wide in range; 218 (48.3 %) are Palaeo-Oriental; 21 (4.6 %) Papuasian; 13 (2.8 %) Australian and 24 (5.3 %) Pacific. If the Papuasian genera are included in the Palaeo-Oriental group, as most biologists would do, then well over 52 % of the phanerogamic genera of the New Hebrides are tropical old world elements. In view of the fact the Australian and Pacific elements add up to a mere 8 % of the entire flora, it can be said that the phanerogamic flora of the archipelago is overwhelmingly Indo-Malesian in the broadest sense of the term. There are no genera of American type native in the New Hebrides. There is another group of 12 genera, not counting the putative endemic mentioned earlier, of such mixed geographical elements as wide temperate, wide subtropical, disjunct southern distribution, etc. as to defy proper categorization. These are not included in the present discussion as they do not contribute significantly to the ecological set-up of the archipelago.

In table 4, the spectrum of geographical elements of the New Hebrides is shown in comparison with those of the six nearest neighbour archipelagoes. (Figures for these archipelagoes other than the New Hebrides are taken from von Balgooy.) A perusal of this table reveals some interesting facts. In comparison with the Solomons and the Bismarcks to the northwest, the

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 4. Spectra of geographical elements of genera in seven Melanesian archipelagoes

	Bis	Sol	N-H	N-C	Fij	Sam	Ton
W-W	196	189	162	186	167	118	118
P-O	379	388	218	206	232	152	115
PAP	35	37	21	36	20	9	12
AUS	4	6	13	51	7	2	3
PAC	3	17	24	31	26	14	9
total	617	637	438	510	452	295	257

Note: Regions: Bis, Bismarck; Sol, Solomons; N-H, New Hebrides; N-C, New Caledonia; Fij, Fiji; Sam, Samoa; Ton, Tonga. Geographical elements: W-W, world wide; P-O, Palaeo-Oriental; PAP, Papuasian; AUS, Australian; PAC, Pacific.

New Hebrides show a significant drop in Palaeo-Oriental and Papuasian elements, but this is compensated for by a very substantial increase in the number of Australian and Pacific elements. When compared with New Caledonia, however, the New Hebrides appear poorer in Australian and Pacific elements but better endowed with Palaeo-Oriental genera. Over-all, the New Hebridean spectrum of geographical elements appears extremely similar to that of Fiji in the east: the only difference being in the Australian elements which are better represented in the former islands than in the latter. As will be discussed in a later section, the Samoan and Tongan spectra of geographical elements are also rather similar to that of the New Hebrides.

The ecological distribution of the geographical elements in the New Hebridean archipelago will now be discussed.

Dealing first with the world wide elements, it is found that the genera of this type fall into three subgroups depending on their habitat preferences. The first subgroup, the largest of the three, includes genera of weedy herbs and climbers frequent in open habitats such as roadsides, deforested hillsides, disturbed high forests and strand vegetation. Most of these genera belong to the families Gramineae, Cyperaceae, Compositae, Malvaceae and Convolvulaceae. Also in this subgroup are ligneous genera such as *Terminalia*, *Cordia*, *Acalypha*, *Croton*, *Thespesia*, *Hibiscus*, *Trema*, *Boehmeria*, and a host of others that often form thickets in secondary communities. The second subgroup, which is smaller in number than the first, comprises those genera which have about as many species in secondary communities as in primary forests. The genera *Hernandia* and *Calophyllum*, for instance, which are usually associated with strand flora, actually have different species which are important components of the *Agathis* forests in the archipelago. In the third subgroup are genera that are found predominantly in primary forests. They are few in number but quite prominent in many forest types. *Schefflera*, *Cryptocarya* and *Litsea*, for example, are important understorey components in the kauri forests of Erromanga. Similarly, the genera *Psychotria*, *Cleidion*, *Rapanea*, *Peperomia*, *Diospyros* and a few others are important understorey shrubs or small trees and herbs in closed primary forests of the northern islands.

The Palaeo-Oriental and Papuasian elements, which form the bulk of the genera in the archipelago, are, on the other hand, mainly found in the interior of forests, with relatively few in secondary vegetation. The more important genera in this category include *Serianthes*, *Elaeocarpus*, *Syzygium*, *Myristica*, *Dendrocnide*, *Dracontomelum*, and *Garuga*, which are important components of kauri forests in the south, coral limestone vegetation throughout the archipelago and the *Dendrocnide-Kleinhovia* forests in the Apuna Valley. So are such herbs and climbers as *Elatostema*, *Procris* and a large number of epiphytic orchids. At higher altitudes *Weinmannia* and

Downloaded from rstb.royalsocietypublishing.org

Metrosideros are the important ones. Those Palaeo-Oriental elements which are largely inhabitants of open habitats and strand vegetation are few in number and they include *Macaranga*, *Aleurites*, *Antiaris*, *Ochrosia* and *Barringtonia*.

The Australian and Pacific elements, though in the minority, do have a few genera that feature quite prominently in the archipelago. *Commersonia*, *Castanospermum*, *Geissois* and *Gahnia* are good examples of Australian elements. The genus *Commersonia* is an important genus in a wide variety of disturbed habitats. *Castanospermum*, the papilionaceous genus found in Queensland and New Caledonia, is very abundant in large areas of coral limestone forests in Malekula, while the genera *Geissois* and *Gahnia* feature quite prominently in disturbed or more open kauri vegetation in Erromanga and Aneityum.

Amongst the Pacific elements, the most important in the New Hebrides is perhaps the palm *Veitchia* which is very abundant in Malekula, particularly in the drier western parts. Other Pacific genera that can be considered to be prominent ecologically are *Tapeinosperma*-Myrsin. and the three araliad genera *Delarbrea*, *Meryta* and *Dizygotheca*. These occur very abundantly as understorey shrubs and treelets in fairly closed forests throughout the archipelago. At higher altitudes, particularly near the summit of Mt Tabwemasana in Espiritu Santo, the genus *Ascarina*-Chloranth. appears to be quite abundant.

This survey of the genera shows that the New Hebridean phanerogamic flora is overwhelmingly made up of world wide and Paleo-Oriental elements and that the latter constitute the bulk of the genera in the forests of the interiors. With only one endemic genus (the status of which is still in doubt), the New Hebridean phanerogamic flora cannot really be considered to have developed an identity of its own, such as is recognizable in New Caledonia and Fiji, and this is further born out by the very great lack of diversification of the genera as a whole.

3.3. *The species*

There are about 870 species of phanerogams in the archipelago. Of these 5 are gymnosperms, 231 monocotyledons and 634 dicotyledons. Compared with the three nearest archipelagoes, the New Hebrides rank with the Solomon Islands (2100 species in area of about 40000 km^2) in paucity of species number. In species density these two island groups are well below Fiji which has about 1600 species in an area of 18000 km^2 and New Caledonia with more than 3100 species in about 24000 km^2.

From the lists of Guillaumin, Schmid and others, I counted a total of about 192 endemic species, which amounts to slightly more than 22%. This figure is probably much higher than the real situation as recent revisions of some groups (e.g. Corner 1965) have revealed that a good proportion are actually conspecific with species in nearby Solomons and/or Fiji. Ames, who described a host of new orchid species in 1932, admitted his intentional greater emphasis on differences than on similarities as he felt that such an action would be less detrimental to biogeographical science! With more revisional studies, particularly if done on a wider regional basis, this high number will probably be reduced; but as further studies are invariably accompanied by the discovery of novelties perhaps one could safely estimate the true species-endemism at about the 15% level. Thus at the species level only, can it be said that the New Hebrides has evolved its own elements.

A cursory examination of the species reveals that a very large proportion of them are of worldwide tropical distribution and a large number of others quite abundant from southeast Asia through Malesia and Melanesia to the south Pacific. Familiar examples include weedy species

Downloaded from rstb.royalsocietypublishing.org

like *Ageratum conyzoides*, *Sida rhombifolia*, *Mikania scandens*, *Ipomoea brasiliensis*, and arborescent species such as *Barringtonia asiatica*, *Calophyllum inophyllum*, *Hibiscus tiliaceus*, and numerous others, much too long a list to cite. As mentioned in connexion with the distribution of families and genera, these wide ranging species are also found mainly in strand vegetation, roadsides, disturbed and otherwise open forests. In such secondary communities, endemic species are practically absent. Indeed, assemblages of closely related sister species are not observable in such situations.

Species with narrower geographical ranges and endemics are found, on the other hand, mainly in inner forest habitats. *Castanospermum australe*, for instance, an Australian species found also in New Caledonia, is mainly on coral limestone forests in Malekula. So are the Melanesian species belonging to the genera *Veitchia*, *Tapeinosperma*, *Psychotria*, *Dendrocnide* and many others. Unlike the world-wide species, there are assemblages of very closely related species of these genera in close proximity, both spatially and ecologically, in the inner forest habitats. Thus, for example, four of the five species of *Veitchia* are found close together especially in the western side of Malekula. The same phenomenon has also been observed in other groups of species, e.g., in the genera *Elatostema*, *Dendrobium*, *Psychotria* etc. Such assemblages, however, are generally very few in number and not a common phenomenon in the archipelago.

Regarding ecological tolerances, most species have been observed to have great ecological amplitude. This increase in ecological tolerances is both altitudinal and spatial. *Myristica fatua*, for instance, though predominating in the alluvial plains of the Apuna Valley, also occurs abundantly in rather dry coral limestone forests in Malekula. The same spread has also been observed in many species of *Ficus*. Species with exceptionally great ecological amplitude include *Antiaris toxicaria*, *Kleinhovia hospita*, *Dendrocnide latifolia* and a few others. These extend in range from very disturbed roadside thickets near the coasts right into the inner forested areas at the foot of Mt Tabwemasana. Sizeable populations of these species have also been observed on coral limestone areas in the northern islands, habitats which are vastly different from those mentioned earlier.

Good examples of species that are spread widely in altitude include *Elatostema macrophyllum*, *Boehmeria platyphylla* and especially *Peperomia pallidinervis* which extends from about sea level to near the summit of Mt Tabwemasana where it reaches its greatest luxuriance at about the 1500 m contour. Partly because of this broadness of ecological amplitude in many species, it is not easy to see any definite and clear-cut altitudinal zonation of vegetation in the New Hebrides as one would see on Mt Kinabalu in Borneo. Whatever altitudinal zones there are in the New Hebrides are greatly telescoped.

Mode of diaspore dispersal has been observed in the field, checked in the herbaria and compared with published information, particularly the very detailed paper on long-distance dispersal by Carlquist (1967). Though not confirmed by experimentation, the information gathered is none the less rather interesting.

There does not appear to be a preponderance of species with diaspores dispersed by the agencies of wind and water. Most of these species are in open secondary communities or in strand vegetation such as the species of Compositae, Asclepiadaceae, Apocynaceae of roadsides etc., and species of *Barringtonia*, *Hernandia*, etc., of sea-shores. The only group of substantial size in the inner forest habitats that have wind-borne diaspores are the species of the Orchidaceae.

The majority of the species in the forest communities both in lowlands and at higher altitudes have diaspores that are animal dispersed, particularly by birds. Fruits of species of *Myristica*,

Downloaded from rstb.royalsocietypublishing.org

Ficus, *Syzygium*, *Elaeocarpus*, for example, are readily fed on by birds. Also a great many species have been observed to have fruits ranging from 0.5 to 20 mm in diameter, often brightly coloured and completely lacking in any devices that might be of aid to dispersal by wind. These are no doubt transported internally by birds. There are also many species which have sticky seeds or fruits such as in the Loranthaceae and many species of the Urticaceae including *Nothocnide* and *Procris*. In these cases the diaspores are often transported externally by birds and bats.

This short survey of the species reveals that only at this taxonomic level do the New Hebrides achieve a certain degree of endemism, despite the fact that a great number of its species are of world-wide distribution. Like the Solomon Islands, great ecological amplitude has also been observed to be a characteristic of the species, the majority of which have diaspores which are obviously suitable for transportation by birds both internally and externally and by bats externally.

3.4. *North/south differentiation of the flora*

The New Hebridean archipelago extends from 15° 30′ to 20° 15′ south, so that the southern islands reach more seasonal climatic regimes. Varying seasonality contributes to a recognizable difference between the floras of the northern and southern parts of the archipelago; and this difference is expressed in many aspects.

The most important of these is the observed relative frequencies of occurrence of populations of the same species in the two portions of the island groups. *Myristica fatua*, *Veitchia joannis*, *Garuga floribunda*, *Dracontomelum vitiense*, *Aleurites moluccana*, species of *Dendrocnide*, to cite only a few examples, are very abundant in the northern islands of Espiritu Santo and Malekula but rather infrequent in Aneityum or Erromanga. Conversely, there are numerous species which are important and frequent elements in the southern islands but occur very infrequently in the northern parts of the archipelago. *Calophyllum neo-ebudicum* and *Serianthes melanesica* are good examples. Relative availability of the right soil type or other substrate was first suspected to be a determinant of this differentiation but field observations do not support the importance of this factor. *Myristica fatua*, for instance, occurs quite abundantly in a great variety of habitats, as pointed out earlier, from the poorly drained alluvial plains of the Apuna Valley in Espiritu Santo to the rather dry coral limestone forests in southwest Malekula. Yet in Aneityum, where such habitats are also available, it is a rarity.

The other difference, and equally important in extent, is the occurrence mainly at higher altitudes in the northern islands of plants which occur abundantly as lowland elements or at lower altitudes in the southern islands. *Metrosideros*, *Weinmannia* and *Geissois*, for instance, quite common on ridges of Aneityum and Erromanga which are not more than 500–700 m in altitude, become abundant and actually dominant in many localities at the 1200–1500 m altitude on Tabwemasana in Espiritu Santo Island. The same phenomenon has also been observed in the epiphytic orchids which, in the southern islands, are abundant at a much lower altitude; but in the northern islands, they do not make any significant presence below the 1000 m contour.

Further, the northern islands are much more diversified and have more Indo-Malesian elements than the southern islands. The Urticaceae and Moraceae, for example, which have large centres of diversity in tropical Indo-Malesia, have more representatives in the islands of Espiritu Santo and Malekula than in Aneityum or Erromanga. This has also been found to apply to other families like Euphorbiaceae, Orchidaceae, Anacardiaceae and many others which are largely Indo-Malesian centred. In this aspect, the determinant of the higher

Downloaded from rstb.royalsocietypublishing.org

diversity in the north is not entirely the climate: area and altitude are no doubt important co-determinants. Espiritu Santo and Malekula are the two largest islands in the archipelago. Besides, Espiritu Santo with mountains rising to 1800 m, is the highest island in the New Hebrides. In effect, the northern New Hebrides have a much larger biota with a greater proportion of Indo-Malesian content than the southern part of the archipelago.

The last aspect of the difference, perhaps the least important one, involves the actual presence/absence of taxa. *Dendrocnide aff. moroides*, for instance, is present from Efate and northward but completely absent in the southern islands. This, however, need not be very significant as it may be due simply to chance.

The New Hebridean archipelago thus differs from the Solomons in having a significant intra-archipelago differentiation in the flora. While most aspects of the differentiation are no doubt influenced by the climatic differences between the islands, others are probably the direct result of differential area and height of the islands.

4. Relationships of the flora

The relationship of the phanerogamic flora of the archipelago has been assessed at both the generic and species levels. At the generic level, the New Hebridean flora has been compared with those of the Bismarck Archipelago, Solomon Islands, New Caledonia, Fiji, Samoa and Tonga. At the species level, however, I have compared it with only the Solomon Islands, New Caledonia and Fiji. This is due simply to the fact that species lists are much too involved both numerically and taxonomically; and unfortunately I have not the time to compare such lists for more than four island groups.

At the level of genera, the affinity has been assessed on two different aspects, namely, (*a*) comparison of the spectrum of geographical elements of the New Hebrides with the other six archipelagoes as shown in table 4, and (*b*) the degree of floristic affinity as computed on the number of genera common between the island groups (table 6).

Table 5. Summary of results of $R \times C$ tests of discrepancy, using the G-statistic, of the New Hebridean spectrum of generic geographical elements with those of the other islands in Melanesia

(Raw data in table 4.)

New Hebrides compared with:	Bis	Sol	N-C	Fij	Sam	Ton
G-values:	43.82†	21.67†	25.53†	2.22‡	7.31	7.94

† Discrepancy statistically significant ($P < 0.001$).
‡ Discrepancy not significant ($0.5 < P < 0.7$).

Regarding the spectra of geographical elements, I have compared them by the $R \times C$ test of discrepancy using the G-statistic (Sokal & Rohlf 1969). As shown in table 5, there are very great discrepancies between the New Hebridean spectrum and those of the Bismarcks, Solomons and New Caledonia to the west and northwest (G greater than 18.465 with 4 d.f.; probability less than 0.001). When compared with the archipelagoes of Fiji, Samoa and Tonga in the east, however, it is found that the discrepancies are not statistically significant. The New Hebridean spectrum is in fact almost identical with that of Fiji (G of 2.2 with 4 d.f.; probability between 0.5 and 0.7), and only slightly different from those of Samoa and Tonga.

Downloaded from rstb.royalsocietypublishing.org

Table 6. Floristic affinities at generic level

(Number of genera in each archipelago shown in brackets. The 3rd row shows the number of genera New Hebrides shares with the other islands. The last row shows the coefficient of dissimilarity of New Hebrides with the others computed by Preston's equation of resemblance (abbreviations as in table 4).)

	Bis	Sol	N-C	Fij	Sam	Ton
	(632)	(654)	(655)	(476)	(302)	(263)
N-H (451)	327	357	340	340	254	227
z values	0.46	0.40	0.44	0.34	0.35	0.36

This largely confirms van Balgooy's findings based on an intuitive assessment of the relationships of the spectra.

With regard to floristic affinity based on the number of common genera, table 6 shows data of the number of genera the New Hebrides have in common with the other archipelagoes mentioned. The degree of affinity was computed by the transcendental resemblance equation $x^{1/z}+y^{1/z}=1$ formulated by Preston (1962), in which x is the fraction in one archipelago obtained by dividing the number of genera in that archipelago by the total number of genera in the two archipelagoes being compared, and y, the corresponding fraction for the second archipelago. Varying from zero to unity, the numerical value of z that satisfies this equation is the coefficient of dissimilarity between the two floras. Thus a low value of z indicates a high degree of affinity, while a high value of z shows a low affinity.

In the last row of table 6, the z values obtained by comparing the New Hebrides with the other six archipelagoes are tabulated. From this it is clear that the highest affinity is the New Hebrides–Fiji pair ($z = 0.34$), followed by New Hebrides–Samoa ($z = 0.35$), New Hebrides–Tonga ($z = 0.36$), etc. Thus this assessment confirms our earlier conclusion that the New Hebridean flora is closest to Fiji, then Samoa and Tonga in the east but less so with the archipelagoes to the west. This agrees closely with the conclusion of Balgooy (1971).

At the species level, table 7 shows in brackets the total number of species in each of the four archipelagoes concerned, and also the number of species the New Hebrides have in common with the other three.

Table 7. Floristic affinities at species level

	Solomon Is. (2069)	New Caledonia (3078)	Fiji (1639)
New Hebrides (870)	260	304	273
z value between New Hebrides and	0.843	0.840	0.818

From the dissimilarity coefficient shown in the bottom row, again Fiji comes up as New Hebrides' closest relative ($z=0.818$). There is a slight discrepancy with regard to the New Hebrides–New Caledonia coefficient, which appears lower than expected. In other words, at the species level, New Caledonia seems closer to New Hebrides than the Solomon Islands. This unexpected finding is no doubt due simply to the fact that the New Hebridean species have been compared more with those of New Caledonia by taxonomists than with the Solomons.

Thus, we can conclude that New Hebridean phanerogams are most closely related with those of the island groups to the east, despite the fact that the latter are further away than the Solomon Islands. This eastward relationship is, I suggest, true; and is to be expected as both

Downloaded from rstb.royalsocietypublishing.org

the New Hebrides and Fiji are at about the same latitude, have very similar climates and have also about the same area and height.

5. Conclusion

This short survey of the nature and relationships of the flora has provided some clues not only on the origin but also on the probable mode of derivation of the flora.

That the flora is largely an immigrant one is beyond doubt. The lack of diversity, the presence of a large percentage of elements of wide geographical ranges and the scarcity of assemblages of closely related taxa are all characteristics of a flora of immigrant origin. In view of the fact that there is also a lack of significant endemism at the generic level, that there is a total absence of relict elements in the flora and that a large number of species have great ecological amplitude, it can be concluded further that the flora of the New Hebrides has been derived very recently and has had insufficient isolation in space and time to permit speciation to develop to any significant degree. Lack of habitat heterogeneity as a consequence of smallness of area, though an important factor, cannot wholly account for the phenomena observed. Fiji, for instance, has about the same area and elevation as the New Hebrides, yet has developed speciation to a remarkable degree. This is because it is not only further removed from the source area of Malesia (which means greater spatial isolation) but also geologically older than the New Hebrides (greater isolation in time).

The overwhelming Indo-Malesian character of the New Hebridean flora indicates clearly that the New Hebrides have derived its flora mainly from Indo-Malesia, like all the other archipelagoes in the southwest Pacific. Because of the close floristic affinity observed between our flora and that of Fiji, it is tempting to conclude that the one has derived its flora from the other, especially if it is borne in mind that Fiji is older than the New Hebrides. As the New Hebrides and Fiji are the youngest archipelagoes in Melanesia, it is highly probable that both have derived their floras from the same sources, and that the similarity of their environmental complexes has resulted in their supporting somewhat similar suites of geographical elements through 'ecological sifting'. This does not imply that there is an absence of floristic interchange between New Hebrides and Fiji. Indeed, this interchange is quite strong in many groups such as the Papilionaceae, Urticaceae etc.; but the greater part of the flora has been derived from the same source in Indo-Malesia, perhaps independently.

Regarding the mode of colonization of the New Hebrides by the phanerogamic flora, there is evidence that plant dispersal to the archipelago has been trans-marine rather than migration over land. Balgooy (1971) has found that a large proportion (of a random sample) of the species have diaspores that are dispersed by birds and bats. Our field observations in the New Hebrides have confirmed this. A great number of species which have brightly coloured fruits have been observed to be fed on by a large number of species of birds. The fruits of *Myristica fatua*, for instance, most of which are about 3 cm × 2 cm overall in size, are readily swallowed by a species of pigeon which is common throughout the southwest Pacific. Other species which have small seeds have devices to attract birds to feed on them, thus aiding dispersal. In *Dendrocnide latifolia*, for example, the small seeds are borne on fleshy pedicels which are fed on by many species of birds which then carry these seeds on their beaks over their range of feeding.

There is now geological evidence in support of the importance of trans-marine dispersal. Mallick (this meeting) indicates that the New Hebrides are oceanic in origin and probably have had no land connection with any of the neighbouring archipelagoes since the origin.

Downloaded from rstb.royalsocietypublishing.org

He further concludes that the archipelago is not only very young but that about 90% of its present area became sub-aerial (and thus available for colonization by land plants) only in the last 1.5 million years. This finding not only confirms that the archipelago has derived its flora largely by trans-marine dispersal, but also shows that the colonization of the islands has been extremely rapid. This latter conclusion provides strong support to one of the current ideas on the phytogeography of the Pacific Islands in general. It is that the present distribution pattern of phanerogams in the Pacific, more particularly in the southwest, could have come about by trans-marine dispersal accomplished in very recent times over an essentially archipelagic region as has been maintained by Carlquist (1967). It is not necessary to invoke plate tectonics to account for this pattern as has been done by Whitmore (1973). Indeed, crustal plates have moved and ocean floors have spread, but these events occurred much too early to have any overall and direct effects on the distribution pattern of the present-day flora of this region.

I am indebted to The Royal Society of London, The Public Service Board of N.S.W., The Director-General of Agriculture of N.S.W. and The Director, Royal Botanic Gardens, Sydney for their support which enabled me to participate in the Royal Society's Expedition to the New Hebrides in 1971 and in this Discussion Meeting.

References (Chew)

Ames, O. 1932 Contributions to the flora of the New Hebrides and Santa Cruz Islands. Orchids collected by S. F. Kajewski in 1928 and 1929. *J. Arnold Arbor.* **13**, 127–141.

Ames, O. 1932 A new genus of the Orchidaceae from the New Hebrides. *J. Arnold Arbor.* **13**, 142–144.

Balgooy, van M. M. J. 1971 Plant geography of the Pacific. *Blumea* (Suppl. 6), 1–222.

Carlquist, S. 1967 The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bull. Torr. Bot. Club*, **94**, 129–162.

Christophersen, E. 1935 Flowering plants of Samoa. *Bull. Bernice P. Bishop Mus.* **128**, 1–221.

Christophersen, E. 1938 Flowering plants of Samoa – II. *Bull. Bernice P. Bishop Mus.* **154**, 1–77.

Corner, E. J. H. 1965 Check-list of *Ficus* in Asia and Australasia with keys to identification. *Gard. Bull. Sing.* **21**, 1–186.

Foreman, D. B. 1971 A check list of the vascular plants of Bougainville, with descriptions of some common forest trees. *Bot. Bull.* no. 5. P.N.G.: Dept. Forests, Lae.

Guillaumin, A. 1931 Contributions to the Flora of the New Hebrides. Plants collected by S. F. Kajewski in 1928 and 1929. *J. Arnold Arbor.* **12**, 221–264.

Guillaumin, A. 1932 Contributions to the Flora of the New Hebrides. Plants collected by S. F. Kajewski in 1928 and 1929. *J. Arnold Arbor.* **13**, 1–29 and 81–126.

Guillaumin, A. 1933 Contributions to the Flora of the New Hebrides. Plants collected by S. F. Kajewski in 1928 and 1929. *J. Arnold Arbor.* **14**, 53–61.

Guillaumin, A. 1938 A florula of the island of Espiritu Santo, one of the New Hebrides. *J. Linn. Soc.* (*Bot.*) **51**, 547–566.

Guillaumin, A. 1948*a* Compendium de la flore phanerogamique des Nouvelles Hebrides. *Annls Mus. colon. Marseille* **6**, 5–6: 5–56.

Guillaumin, A. 1948*b* *Flore analytique et synoptique de la Nouvelle-Caledonie phanerogrames.* Paris: Office de la Recherch Scientifique Coloniale.

Moore, H. E. 1957 Synopses of various genera of Arecoideae. *Gentes Herb.* **8**, 488–536,

Parham, J. W. 1972 *Plants of the Fiji Islands.* Revised ed. Suva: Government Printer.

Preston, F. W. 1962 The canonical distribution of Commoness and rarity. Part I. *Ecology* **43**, 185–215. Part II. *Ecology* **43**, 410–432.

Schmid, M. 1970 *Florule de Tana.* O.R.S.T.O.M. Centre de Noumea. (Mimeographed.)

Schmid, M. 1973 *Flore des Nouvelles Hebrides.* O.R.S.T.O.M. Centre de Noumea. (Mimeographed.)

Sokal, S. S. & Rohlf, R. 1969 *Biometry* U.S.A.: Freeman Publishing Co.

Whitmore, T. C. 1966 *Guide to the forests of the British Solomon Islands.* Oxford University Press.

Whitmore, T. C. 1973 Plate tectonics and some aspects of Pacific plant geography. *New Phytol.* **72**, 1185–1190.

Yuncker, T. G. 1959 Plants of Tonga. *Bull. Bernice P. Bish. Mus.* **220**, 1–283.