PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phytogeographical relationships of the northern islands of the New Hebrides

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A brief account is given of the geographical distribution of the major vegetation types in the New Hebrides. Evidence based on computer analysis of field data indicates a disjunction at about 18° S latitude that divides the island chain into 'northern' and 'southern' groups with an attenuation from complex to simple vegetation types as latitude increases. The phytogeography of some of the major vegetation types in the north is discussed within the context of the southwest Pacific region.

Regional phytogeographic analyses usually deal with specific floristic entities, i.e. species or genera rather than associations; comparisons are made between total floristic lists but rarely between defined associations. Although this is often unavoidable due to lack of field data, it is unfortunate, as additional geographic definition is given to a locality by the floristic and structural definition of its plant community. For example, *Kleinhovia hospita* is common to the northern New Hebrides, Papua New Guinea and northeastern Australia but is known to occur with *Castanospermum australe* in sub-littoral cyclone forest situations only in the New Hebrides and Australia. Both species would normally be recorded in a list of species common to both areas, but without community description comparative information would be lost. The implications regarding the dispersal of plant species from distant but physiographically similar loci may become obvious when their community relationships become known.

Where floristic/structural associations are known, the phytogeographer is in a better position to anticipate the potential occurrence or survival of a species in widely separated communities. He is also in a position to examine suggestive negative data, i.e. the absence of a major floristic unit in an otherwise similar floristic/structural type that occurs in two or more geographically distant localities.

A comparative approach of this kind depends on the availability and application of a uniform methodology for identifying plant communities. For this reason alone there is much to be said for the compilation of data acquired in this way at a regional level, e.g. for the southwest Pacific. Beyond a regional level, field logistics become limiting and universal acceptance of uniform field techniques becomes increasingly difficult. The methodology most potentially effective at any level is one which obtains floristic/structural and environmental data by means of a rapid survey technique. The technique and proforma used in the New Hebrides expedition worked very well. The method was a modification of a forest typology proforma developed by L. J. Webb (unpublished). The proforma is in three detailed sections covering structure and physiognomy, floristics and environment, and enables surveys to be conducted rapidly. The data so collected provide a valuable base for the comparison of vegetation types from geographically distant locations, e.g. Papua New Guinea and the New Hebrides. The proforma also provides data in a form suitable for analysis by computer.

This paper deals with some phytogeographical aspects of the northern New Hebridean islands of Espiritu Santo, Malekula and Efate. Phytogeographic relationships within the main island chain of the New Hebrides from Espiritu Santo (15° S lat.) to Aneityum (20° S lat.) are briefly discussed and some comparisons are drawn on a plant community basis, with other island groups within the southwest Pacific region, in particular the continent of Australia and Papua New Guinea where the author has had wider experience in delineating vegetation types. The account has drawn essentially on the as yet unpublished classification by the author of vegetation data collected on proformas from 54 sites in the New Hebrides by Medway and Marshall, Beveridge & Gillison.

The terminology for the forest types of the New Hebrides follows Webb (1968).

Internal relationships

Within the New Hebrides, there is an obvious attenuation of complex vegetation types with increasing latitude. A numerical classification of structural types has shown a marked disjunction at about 18° S lat. – the dividing line between the 'northern' and 'southern' islands. As seen in table 1, all of the complex forest types occur in the northern group while the southern

Table 1. Distribution of major structural vegetation types within the New Hebrides

Structural vegetation type	Southern Islands > 18° S lat	Northern Islands < 18° S lat	Espiritu Santo 15–16° S lat	Malekula 16–17° S lat	Efate 17–18° S lat
complex mesophyll vine forest		×	×	×	×
complex notophyll vine forest		×		×	
notophyll fan palm vine forest (Gillison)		×	×		
mixed notophyll vine forest		×			×
simple mesophyll notophyll vine forest		×			×
semi-deciduous mesophyll vine forest		×		×	
semi-deciduous notophyll vine forest		×		×	
mixed mesophyll vine forest		×		×	
mixed microphyll fern forest		×	×		
mixed microphyll fern thicket		×	×		
mixed mesophyll evergreen vine forest	×				
mixed notophyll evergreen vine forest	×				

group contains structurally more simple and floristically different forest types. The trend appears to be related to a general change towards a cooler drier climatic regime southwards (cf. Brookfield & Hart 1966).

As indicated in table 1, ten of the twelve major (i.e. mostly sub-climax) vegetation types occur in the north. The types recorded for the southern islands are mixed mesophyll and mixed notophyll evergreen vine forests with araucarian emergents (*Agathis*) which are closely related to similar types in Queensland and to some anomalous climatic areas of Papua New Guinea, where both *Agathis* and *Araucaria* occur. From table 1 there appears to be a clear north–south division, but many more samples were taken in the northern group. This gives a better chance of locating different types and the proforma data were collected by people with differing background experience. It is understood there are also some semi-deciduous forest types on some of the southern islands that were not recorded (M. Schmid, personal communication). The

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

extent of these types and their definition must be ascertained before a final statement can be made about the degree of disjunction between the northern and southern groups. In addition, some remote stands of *Agathis* reported to occur in Espiritu Santo were not visited by Expedition members. Nevertheless, relationships between climate and the structural classification as it stands agree broadly with those for Australia and Papua New Guinea.

The distribution of some other biota tends to follow the phytogeographical trends indicated here. A classification of the bird distribution data of Medway and Marshall using a monothetic divisive strategy based on presence/absence data indicates a primary division at 18° S lat. based on the occurrence of the mound building *Megapodius freycinet* only in the northern group.

In the northern group there is an attenuation in both structure and floristics from Espiritu Santo to Efate. Whereas lowland complex mesophyll vine forest occurs in all three islands, the only complex notophyll vine forest variant is found in the drier hill forests of Malekula. Montane vegetation is restricted to the highlands of Espiritu Santo where there is a mixed microphyll fern forest. Also restricted to Espiritu Santo is a lowland notophyll fan palm vine forest. Less complex vegetation on drier sites in Malekula comprises semi-deciduous mesophyll and notophyll vine forest. One of the main floristic components of this type is the deciduous *Garuga* which in Espiritu Santo is most common in drier sites but is found in a wide range of sites. *Garuga* is associated with *Dracontomelon* in both Espiritu Santo and Malekula and with *Gyrocarpus* in both Malekula and Efate. The *Kleinhovia/Dendrocnide* forests that are so widespread on the Espiritu Santo floodplains become increasingly attenuated towards Malekula and Efate. This floristic/structural attenuation is also evidenced in other minor associations such as *Kleinhovia/Castanospermum*. Significantly, *Leucaena* forest is not found in large stands in Espiritu Santo but in Malekula and Efate it occurs in extensive more or less pure communities.

At Efate there is a tendency for forests of a simpler type to predominate. In the hill areas, e.g. Narabut, mixed notophyll vine forest is common and a simple littoral type is also found. Also at Efate there is an increase in trees with smaller leaves (e.g. *Elaeocarpus*) relative to Espiritu Santo or Malekula at similar elevations, and thin plank buttresses and robust woody lianes become less common.

The findings of the Expedition suggest that the overall picture within the New Hebrides is one of attenuation from complex to more simple forest types from Espiritu Santo to Efate with associated floristic changes, and that a greater disjunction occurs again between Efate and the islands to the south. The disjunction may in some way be related to the fact that many of the southern islands are geologically more recent than those in the north (G. Mallick, personal communication). The disjunction at 18° S agrees with a tentative opinion expressed by van Balgooy (1971) on the basis of the then little known floristics of the whole island group, that there is a demarcation somewhere near the middle of the New Hebrides. The implication is that the New Hebrides cannot be compared *in toto* with other geographic areas. Comparisons can be based only on an evaluation of the northern and southern islands as separate phytogeographic entities.

External relationships

The northern islands appear to share vegetation types with adjacent land masses on all points of the compass. It has been suggested by van Balgooy (1971) that the New Hebrides is an overlap area in the Pacific and that least demarcation exists with the flora of Fiji, Tonga and Samoa,

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

although these are more distant than the Solomons. The close proximity of the New Hebrides to the Fijian tectonic plate would tend to enhance this view.

The distribution of *Agathis* communities in the southwest Pacific is confusing. As pointed out by Whitmore (1969) *Agathis* occurs throughout the Melanesian arc with the conspicuous exception of the Solomon Islands. Stands of *Agathis* in Espiritu Santo were not examined by the Expedition but it seems the stand in Aneityum studied by Beveridge with its associated *Syzygium* and *Hernandia* is floristically and structurally similar in many ways to *Araucaria hunsteinii* forests on acid volcanic rocks in Papua New Guinea. In that island there are also dense stands of *Araucaria hunsteinii* and *A. cunninghamii* in anomalous (i.e. dry seasonal) climatic pockets in the Jimi and Bulolo valleys, while *Agathis labillardieri* also occurs as a scattered remnant in the latter. From my own experience in these areas it seems these forests are associated with the sites of former catastrophes. It is possible the gymnosperm forests in the southern islands of the New Hebrides have arisen in a similar way.

Complex mesophyll vine forests and semi-deciduous vine forests in the northern islands possess a strong structural and floristic affinity with some vegetation types in lowland Papua. Whereas the forests of Espiritu Santo and Malekula appear to be floristically attenuated versions of the drier complex mesophyll vine forest (c.m.v.f.) Papuan forests, structurally there are close similarities. The c.m.v.f. *Kleinhovia/Dendrocnide/Dracontomelon/Pterocarpus* associates of the lowlands are also conspicuous in forests along the southeast Papuan coast, and *Licuala* fan palm forests also occur extensively in both areas. The high incidence of deciduous species may be related to the seasonal drought stresses to which both areas are subject.

On the other hand, there are canopy genera in the floristically rich Papuan forest that are conspicuously absent from the forests of the northern New Hebrides islands. These belong to the families Anacardiaceae, Sterculiaceae and Sapotaceae.

There are also structural similarities between Queensland forests (c.m.v.f.) and vegetation of the northern New Hebridean islands, but nowhere in the Queensland forests are there associations of *Kleinhovia* with *Dracontomelon* and *Pterocarpus*. On the other hand there are isolated cyclonic sub-littoral forest communities of *Kleinhovia/Castanospermum* in Queensland just north of 18° S lat. (L. J. Webb, personal communication).

It is the semi-deciduous vine forests that provoke comparison between Malekula (and to a lesser extent Efate), and the forests of dryland Papua, in particular the *Garuga/Gyrocarpus* communities (also mentioned by Whitmore (1969) for Guadalcanal and Western Malaysia). In the low rainfall areas of the Papua central coast, semi-deciduous communities are typified by *Garuga/Gyrocarpus* vine thicket on dry hill slopes which merge into low vine forest on the plains commonly associated with *Intsia*, *Adenanthera* and *Pleiogynium* as prominent canopy genera, as well as the shrubs *Diospyros*, *Psychotria*, *Melicope*, *Murraya* and *Citrus*, the liane *Hoya* and rhamnaceous creepers, and the genus *Cycas* on forest margins. All of these genera diagnostic of disclimax communities are common to both areas. The Sterculiaceae and Combretaceae so evident in the Papuan forests are lacking in the New Hebrides. These community types have been well documented by Heyligers (1965) for dryland Papua, and are similar to many on the west coast of Malekula.

There is a distinct floristic as well as structural similarity between anthropogenous/secondary vegetation types in Espiritu Santo and Malekula with those in Papua New Guinea. The *Themeda/Imperata/Miscanthus* savanna grasslands of the New Hebrides show structural and floristic affinities with both northeastern Australia and Papua New Guinea but more so with

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

the latter, particularly in terms of the vegetation mosaics produced as a result of subsistence gardening. These are recorded in detail for Papua New Guinea by Heyligers (1965) and Paijmans (1967, 1969) and others.

A secondary vegetation type dominated by *Hibiscus tiliaceus* and *Kleinhovia hospita* is recorded by Heyligers (1967) for Bougainville island in Papua New Guinea where it occurs on coastal lowland areas, on plains, slopes and crests. Much the same vegetation type occurs in the New Hebrides in old garden areas and also in localities that suffer frequent cyclone damage.

Marine littoral communities appear to be of little comparative value as many of the genera are fairly cosmopolitan in distribution. However, several brackish swamp communities in Espiritu Santo and Malekula exhibit affinities with those in Papua, particularly the *Hibiscus/Metroxylon* (sago palm) brackish swamp communities recorded at South West Bay on Malekula, and the *Hibiscus/Erythrina* brackish swamp community on the Jordan river floodplains of Espiritu Santo, which has affinities with similar communities in the Northern District of southeast Papua New Guinea.

The disclimax *Leucaena leucocephala* forest so extensive in northern Malekula (approx. 6000 ha) does not occur in similar pure stands in Papua New Guinea but is recorded by Fosberg (1967) for some of the oceanic islands in the Pacific and by Parham (1958) for Fiji.

The dipterocarp and fagaceous forests of southeast Papua New Guinea have no floristic equivalents in the northern islands of the New Hebrides. The occurrence of these forests is attenuated to the southeast through the D'Entrecasteaux Islands to the Louisiade Archipelago. Between the latter and the New Hebrides lie the largely unknown islands of the Santa Cruz group.

In the D'Entrecasteaux islands there are extensive hillside communities in rain shadow situations that are dominated by the deciduous *Pterocarpus*. Pure stands of *Manilkara* are found on the coralline Marshall Bennett group and on the coralline benches of the Duboyne group there are widespread communities dominated by *Myristica*, *Diospyros* and *Intsia* – genera particularly common in the forests of western Malekula.

Montane elements indicate that the mountain vegetation of Mt Tabwemasana in Espiritu Santo is associated with more widespread communities than the lowland types. The *Metrosideros/Weinmannia* forest type apparently is represented in New Zealand (A. E. Beveridge, personal communication) and is represented in montane forest associations of Papua New Guinea and to a limited extent in eastern Australia. Good (1969) has pointed out that *Geissois* (which also occurs in montane forest), is found in New Caledonia, New Hebrides, Fiji and the Santa Cruz Islands. Fagaceae are conspicuously absent in the northern islands of the New Hebrides. Again, 'overlap' indications are shown in the occurrence of *Coriaria* in the summit vegetation, associated with *Balanops* in the *Metrosideros/Weinmannia* forest area. The former is represented in Papua New Guinea and New Zealand (van Balgooy 1971) and the latter in New Caledonia and Australia (Burbidge 1963).

While there appear to be positive associations of vegetation types between the northern islands and Papua New Guinea, relationships with Australia are not clear. The genus *Eucalyptus* common in sclerophyll forests in Australia is absent from the sclerophyll forests of the New Hebrides but is present in Papua New Guinea. Similarly the genus *Acacia* which is associated with vine forests in northeastern Australia and Papua and is widespread over the former continent, is represented by only two species in the northern islands of the New Hebrides. It seems the demarcation between Australia and the northern islands of the New Hebrides is much

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

greater than that of the latter with the Melanesian islands to the north. There is no doubt that the primary influence on vegetation of the northern islands of the New Hebrides is Malaysian in origin.

Conclusions

There are many gaps in our knowledge of the plant communities that lie between the major islands of Papua New Guinea and the New Hebrides, and the distributional relationships of similar plant communities between the latter and the Solomon islands need to be examined more closely. Nonetheless it would seem the area requiring most immediate attention is the Santa Cruz group which lies between the Solomon islands and the New Hebrides. A study of the plant communities of the ultrabasic geological strata in Pentecost Island area may reveal significant relationships with the proteaceous communities that are characteristic of ultrabasic outcrops in some islands off the coast of southeast Papua New Guinea.

It may be seen from the foregoing that apart from an internal division at 18° S lat. within the New Hebrides there appears to be a tenuous link between several isolated plant communities in northeastern Australia, extending northwards through southeast Papua New Guinea and along the archipelagoes formed by the D'Entrecasteaux and Louisiade islands, to the northern islands of the New Hebrides. At present, knowledge of the extent to which plant diaspores may have been distributed by man and other agencies along this 'route' is at best highly speculative. To assume a previous land connection across this arc, which might account for the distribution of some of these plant groups, is contrary to current geological knowledge as there are deep sub-marine trenches between Australia and New Caledonia and the New Hebrides and between the last group and the southeastern islands of Papua New Guinea. No explanation of how these communities came to be distributed in this fashion is immediately apparent – the fact remains that they are there.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES