Plant Diversity and Complexity Patterns Local, Regional and Global Dimensions

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Plant Diversity and Complexity Patterns

Local, Regional and Global Dimensions

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Synopsis

This is the proceedings of the symposium *Plant Diversity and Complexity Patterns – Local, Regional and Global Dimensions,* held at the Royal Danish Academy of Sciences and Letters from the 25th to the 28th of May, 2003. The symposium presented an overview of new research on the origins and patterns of vascular plant diversity from a local to a global scale. The symposium covered one geographical scale each day and included a total of 35 lectures and posters. 30 of these presentations have been written up for the present proceedings. These are divided into the following parts: Diversity and complexity patterns at local scales. Diversity and complexity patterns at regional scales. Diversity and complexity patterns in wide-spread genera, families and orders. Diversity and complexity patterns on the global scale. The symposium was planned for 2003 in order to coincide with the opening of the new building for the Global Biodiversity Information Facility (GBIF) in association with the Natural History Museum of Denmark (Zoological Museum) of the University of Copenhagen.

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Plant distribution patterns and plate tectonics in Malesia

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The Malay Archipelago is one of the three areas in the world with a rich tropical rainforest (estimated 42,000 spp.). It is a natural phytogeographic area (70% of the plants endemic), comprising the Sunda Shelf, Wallacea and the Sahul Shelf as subunits, which include nine island groups: Malay Peninsula, Sumatra, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands, Moluccas, and New Guinea. The flora richness of each island group correlates significantly with the size of the areas. The nine areas all possess many endemic species, but the Philippines, Borneo, and especially New Guinea comprise significantly more endemic species than the mean number for every island. Three major distribution patterns in Malesia are treated: Indian-Malesian distributions, circumpacific distributions, and Wallace's line (the division between a west and east Malesian flora). The central part of Malesia, Wallacea, is a transition zone between the Sunda and the Sahul flora. It also forms a barrier (known as Wallace's line) for four reasons: a. The east Malesian elements only rafted during the last 50Ma as plate fragments towards Southeast Asia, where the west Malesian elements were already in place; b. Most stepping stones for dispersal only emerged during the last 10 Ma, especially in Wallacea; c. Wallacea has a dry monsoon climate, while the Sunda and Sahul Shelf have an everwet climate; d. No major land bridges were present in Wallacea during glacial periods. It is shown here that India did not only act as a raft, bringing Gondwanan floral elements to Southeast Asia, but it also received floral elements from mainly Borneo. Most circumpacific distributions can be explained by two land bridge systems due to warm arctic conditions. During the late Cretaceous (Gondwana still breaking up) South America was still connected to Australia via Antarctica (examples: Sapindaceae, *Nothofagus*, Proteaceae). A northern route existed till at least the Eocene between Europe and North America via a continental connection over the arctic (examples: Magnoliaceae, Sabiaceae).

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Introduction

One of the richest tropical rainforests is the Malay Archipelago, also known as Malesia (Fig. 1). It reaches from the southern tip of Thailand, throughout Malaysia and Indonesia to the Philippines and Papua New Guinea. The Malesian flora comprises an estimated 42,000 species (Roos 1993). Most species are still poorly known and only about 15% has been revised during the last 50 years. This hampers the delimitation of distribution patterns seriously, like it was the case with establishing the borders of Malesia.

During his stay in, then still Dutch, Indonesia van Steenis developed the idea to produce a Flora of Indonesia. He did not mean to produce a national flora, but he wanted to describe the flora of a phytogeographical region, an area with many elements of its own (many endemic species). He used genera with a shared geographical boundary, because most plant species were still badly known. Thus he could identify three sharp boundaries (Fig. 1), all of them outside Indonesia. The most western boundary is slightly to the north of the Thai-Malaysian border, where 200 genera reach their southern limit and 375 genera have their northern limit. This border does not coincide with the Isthmus of Kra (the narrowest part of the Thai Peninsula) as is often stated, but occurs more to the south. The most northern border of Malesia is between the Philippines and Taiwan (265 genera to the north and 421 genera to the south of it). The southern boundary is between New Guinea and Australia (644 genera present north of it, 340 genera south of it) (van Steenis 1950a). New Guinea is arbitrarily taken as the eastern border, because in the nineteenforties not enough data were available on the west Pacific Island chains. The natural boundary in the Pacific is in fact to the east of the west Pacific Island chains (van Balgooy *et al.* 1996; Fig. 1).

The genera slowly decrease over these island chains. The whole region is presently known as Malesia and the flora project is Flora Malesiana.

The definition of Malesia was based on distribution patterns. We like to continue this lead and zoom in on the different distribution patterns that exist in Malesia. Likewise, we will only use reliable data and as sample we selected the taxa published in Flora Malesiana so far. These data will first be used to show some of the floristic traits of Malesia and then we will treat three interesting distribution patterns, whereby our sample is mainly used for the first and major question:
– Are there two major provinces in Malesia separated by Wallace's line, like it is shown for zoological data? And if so, how can Wallace's line be explained?

The two other questions are:
– Indian-Malesian distributions, are they all of Indian/Gondwanan origin and brought by India to Southeast Asia?
– What is or are the best explanations for circum-Pacific distributions.

The three research questions will not only be discussed with regards to present day distributions, but also in comparison with recent phylogenetic information and the geological history of the area. The latter is extremely complicated and will be briefly considered first.

Plate tectonics

Malesia, like the Caribbean, is a mosaic of colliding major and smaller plates, with many small tectonic fragments acting as ball-bearings. In Malesia several sea and continental plates meet. The Eurasian plate is slowly moving east (due to the opening of he Atlantic Ocean), the Pacific plate is moving west and disappears below the Eurasian plate and the northward moving New Guinean-Australian plate. The Indian Ocean plate is moving east
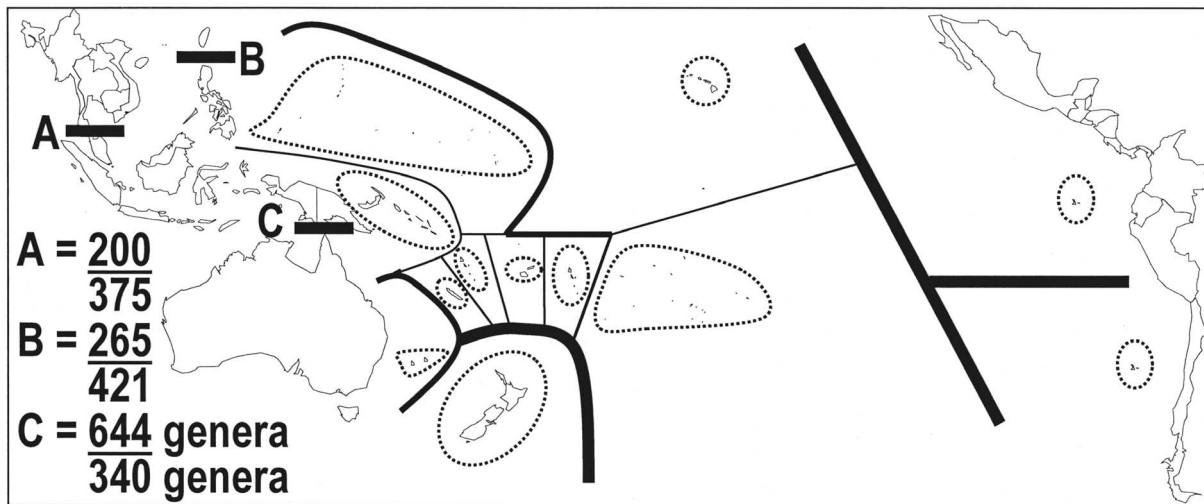
Fig. 1. Demarcation lines of the Flora Malesiana Region. Three borders are defined by numbers of genera that are only present north or south of it (after van Steenis 1950a). The eastern border is placed arbitrarily at New Guinea, but this border is not sharp as indicated by the thin lines between most west Pacific island groups. The thickness of the lines indicates the dissimilarity in floras between the different island groups (thin lines: high similarity in floras, thick lines: high dissimilarity; after van Balgooy *et al.* 1996).

and also subducting below the Malesian island belt (Sumatra up to the Lesser Sunda Islands). The Indian plate is still moving northward and increasing the altitude of the Himalayas. Finally, the Philippine plate has almost disappeared; only some continental debris is left.

During its northward movement many small tectonic slivers broke off from the New Guinean-Australian plate. Audley-Charles (1987) provides a simple overview. The slivers broke off in two waves. The first wave comprised areas, which now form a large part of Southeast Asia mainland (Tibet, Burma, etc.) and which presently constitute west Malesia (Malaysia, Sumatra, Borneo, Java, part of Celebes). This wave broke off at least during the Late Jurassic (c. 160 Ma), but it may have been earlier. Important is that these areas already formed Southeast Asia when the present day flora and fauna developed.

The second wave broke off much later, c. 50 Ma, and now forms east Malesia (part of Celebes, Moluccas, part of Lesser Sunda Islands, New Guinea). Thus, with this second wave the final stepping stones between Southeast Asia mainland and Australia got into position.

The Philippines are a slightly different story. Only parts of Luzon are continental debris left from the original Philippine plate. Palawan and Mintoro are slivers, which broke off from Southeast Asia mainland, and the rest of the Philippines arrived with the second wave of tectonic slivers from the New Guinean-Australian plate. Some parts of Borneo, like Palawan, are possibly also of Southeast Asian origin (Sarawak; Michaux 1991).

New Guinea also has a complicated history (Pigram & Davies 1987). Originally, it only consisted of the southern part (termed Craton). The rest of New Guinea consists of more than 30 tectonic slivers of different origin (island arcs, pieces of sea floor, continental fragments), which collided with New Guinea and now form the Bird's head in the west, the Peninsula in the east and the northern coast.

The collisions of the different fragments resulted in orogenesis and thus the more or less continuous east-west mountain ranges were formed over the whole of New Guinea.

A nicely animated overview of plate tectonic movements during circa the last 50 Ma is shown by Hall: http://www.gl.rhbnc.ac.uk/seasia/Research/Plate_Tect/plate_tect.html.

Material and methods

The sample of plant distributions was taken from all species published in Flora Malesiana series 1 (Angiosperms and Gymnosperms) and the Malesian Orchidaceae as published in Orchid Monographs (formerly the official medium for the Malesian orchids). The distributions were noted per country and per island group (for their definition see under Floristics). Most descriptions of the distributions did not allow for a finer scale. A dBase IV database was built with the various data.

All taxa were noted as either occurring naturally in Malesia, being introduced/cultivated, or being tentatively recorded as expected. All taxa from genus down to infrageneric taxa were recorded. However, only the naturally occurring species were used in the various floristic analyses.

The data are analysed with specially written dBase IV programs for distribution patterns, numbers of species per area, etc. SPSS version 11.5 was used for regression analyses; the Multivariate Statistical Package (Kovach 2003) for the Principle Component Analysis (PCA), and Exel 2000 for figures. The data set proved too large for the PCA (memory limitation), therefore, a representative, random sample of 1000 specimens was selected to perform the analysis. The mean numbers of endemic species per island group are based on the distribution of the total numbers of species per island group. Mean number of endemic species for an island group = number of species on the island group x 3,559 (all endemic species of all islands) / 14,309 (total of all species on all islands) (see table 1 for numbers).

Floristics

In total 175 plant families are treated in Flora Malesiana, 12 of these were introduced. The families comprise 981 genera (142 introduced), and 1418 infraspecific taxa (449 subspecies, 902 varieties, 4 subvarieties and 63 formae). The total number of endigenous species in Malesia is 6616, which includes 8 hybrids (the latter are included because hybridisation is a well-known speciation mechanism in
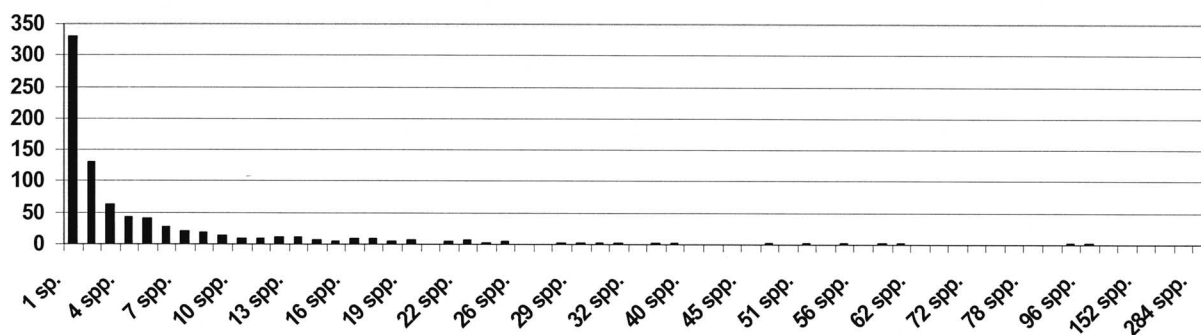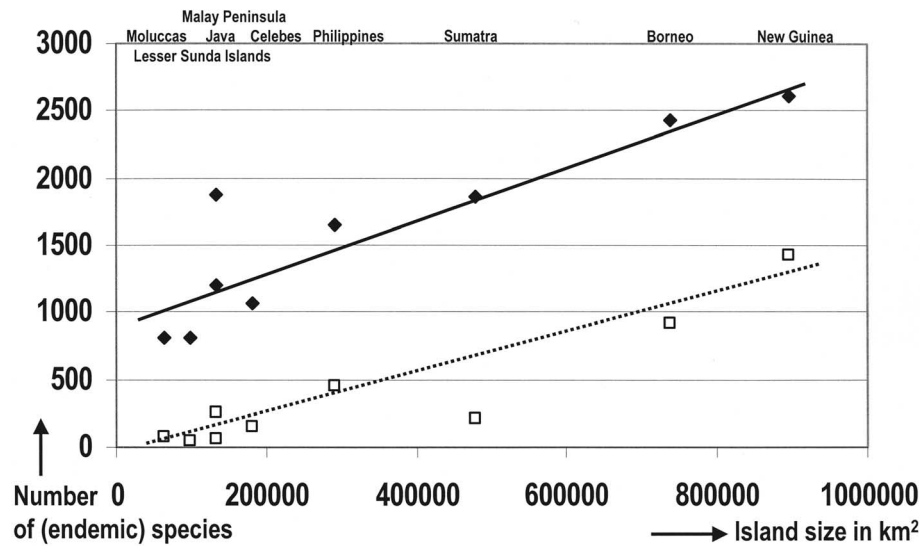

Fig. 2. Numbers of differently sized genera. On the x-axis the size of the genera, varying from 1 to 284 species in Malesia; on the y-axis the numbers of the different size classes.

Fig. 3. The island sizes are significantly correlated with the total numbers of species (black diamonds) and the numbers of endemic species (open squares).

plants). Excluded are 477 introduced/cultivated species and 7 microspecies (though the 3 aggregate species are included).

Out of the 6616 sampled species, 4599 are endemic to Malesia, 70% of the flora. This high percentage confirms the phytogeographi-cal status of Malesia. Fig. 2 shows the frequency of the different genus sizes. About a third of the genera (330 genera) is only represented by a single species in Malesia. All classes above 10 species only comprise 1-3 genera. *Rhododendron* is the most speciose genus revised up to now,

Table 1. The total number of species, the number of endemic species, and the number of non-endemic species per: a. country; b. phytogeographical area (also added, the mean or expected number of endemics: total number of species per island x 3558/14309).

a.

Country	Total	Endemic	Non-end.
Brunei	1234	6	1228
Indonesia	4322	1084	3238
Malaysia	3059	622	2437
Papua New Guinea	2118	661	1457
Philippines	1651	454	1197
Singapore	1066	3	1063

b.

Country	Total	Endemic	Non-end.	Exp. end.
Sumatra	1854	203	1651	461
Malay Peninsula	1895	261	1634	466
Borneo	2436	908	1528	606
Java	1196	56	1140	297
Philippines	1651	454	1197	411
Celebes	1065	144	921	265
Lesser Sunda Islands	815	42	773	203
Moluccas	804	71	733	200
New Guinea	2613	1419	1194	650
Total	14309	3558		

284 species, the majority of which are narrow endemics restricted to a single mountain in Borneo and especially in New Guinea.

Biogeographers are not interested in the numbers of species and endemic species in areas defined by political boundaries. However, politicians might find them interesting. The botanical biodiversity per country is shown in Table 1a. It is surprising that two small countries like Brunei, and especially Singapore, still comprise endemic species (6 and 3 endemics, respectively). A more detailed look at Singapore shows that *Sabia erratica* Water (Sabiaceae) is nowadays also found in Malaysia and *Brackenridgea elegantissima* (Wall.) Kanis (Ochnaceae) is based on a sterile specimen of very doubtful identification. This leaves one real endemic species for Singapore: *Strychnos ridleyi* King & Gamble (Loganiaceae). Of the six endemic species of Brunei one is presently also found in Sarawak (*Vaccinium tenerellum* Sleumer, Ericaceae); all others are still endemic to Brunei: *Bauhinia campanulata* S.S.Larsen (Caesalpiniaceae), *Coelogyne bruneiensis* de Vogel (Orchidaceae), *Xanthophyllum petiolatum* Meijden (Polygalaceae), *Horsfieldia disticha* W.J.de Wilde and *Knema minima* W.J.de Wilde (Myristicaceae).

It is more interesting to look at the numbers of species and endemic species within the phytogeographic subareas of Malesia. These are defined by van Steenis (1950a; see also Fig. 7) and are the major island groups: Malay Peninsula (the only non-island), Sumatra, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands, Moluccas, and New Guinea. Every area has plenty of endemic species, in New Guinea even more than the non-endemic species (Table 1b). The presence of relatively abundant numbers of endemic species is a prerequisite to regard the island groups as phytogeographic units.

The Island theory of MacArthur and Wilson (1967) predicts that there is a positive correlation between the size of the islands and the number of species. They used several islands in the Malay Archipelago to state their case. Therefore, it is not surprising that a re-analysis showed a significantly positive regression between island size and numbers of species and numbers of endemic species (Fig. 3). In fact, the analysis is somewhat flawed, because the island groups had to be taken as single units, as single islands (surfaces according to van Steenis 1950b). Still, the correlation is beautiful. The Malay Peninsula is not a real island, it is connected to Asia main land, and this is perhaps the reason why it possesses relatively more species than the other areas.

With nine phytogeographical areas 511 different distribution patterns are possible, ranging from species present on a single island group to species present in all nine areas. Out of the possible 511 patterns 299 are present. The larger majority is only represented by a few species, 97 patterns are shown by a single species and 157 patterns by 2-10 species. The twenty most common patterns are shown in Fig. 4. It is apparent that the nine island groups are among the most common patterns (marked SI in Fig. 4). This confirms their status as phytogeographical areas (many endemic species). Quite a few species, 244, are widespread and found allover Malesia (AI in Fig. 4). Of the remaining patterns, one pertains to east Malesia (marked EM in Fig. 4), all others are west Malesian patterns (WM in Fig. 4). The west Malesian patterns mainly involve the everwet areas of the Sunda Shelf (see also chapter Wallace's Line), *i.e.,* the Malay Peninsula, Sumatra, and Borneo. Sometimes this extends to Java (WM-J in Fig. 4) or the Philippines (WM-P in Fig. 4). Reasons for this are the presence of an everwet climate in west Java and the flora of Palawan (Philippines), which resembles that of Borneo more closely than that of the other Philippine islands.

If the distributions of the endemic species

are compared with those of all species on the various island groups (Fig. 5), then it is apparent that especially New Guinea, but also Borneo, possess relatively many endemic species (Fig. 5: the pie surface of the endemic species of New Guinea and Borneo, right, is much larger than of the species, left). The expected or mean number of endemic species is shown in Fig. 6. In a G-test and a χ^2-test the mean number of endemic species deviates significantly from the numbers of endemic species. This means that New Guinea, Borneo and the Philippines have significantly more endemic species than the mean number; all other island groups have far less. It was difficult to explain this difference, but it appears that there is a correlation between the geological activities in a region, especially orogenesis, and the number of endemic species. North New Guinea has a rather turbulent geological history and possesses far more endemic species than the southern part (van Welzen 1997). The same holds true for Borneo, here most endemic species are found in the geologically more active areas of Sarawak and North Borneo (especially Mount Kinabalu and the Crocker Range). In the Philippines most endemic species are found on Palawan and especially on Luzon, also areas with more geological activity (van Welzen 1992b, 1997). Other areas in Malesia also have much geological activity, like Celebes, but these areas were often submerged and only emerged during the last few million years (Morley & Flenley 1987). The same applies for Sumatra and Java, in Morley and Flenley's reconstruction only small parts of Sumatra and Java were already emerged, the major part was still under water (see Fig. 13).

Wallace's line

Alfred Russell Wallace was one of the first to draw worldwide attention to the dramatic change in especially the fauna of central Malesia between a Southeast Asian and an New Guinean-Australian fauna. He did so in various letters and publications (George 1981). Wallace, in the tradition of that time, looked for a sharp boundary between the Asian fauna and Australian fauna, this became the famous Wallace's line, running east of the Philippines, between Borneo and Celebes and then finally between Bali and Lombok (between Java and Bali in Fig. 7). Later on he changed the line to the east of Celebes, including Celebes with west Malesia. Later authors moved the line to the east (Weber, Lydekker; Fig. 7) or the west (Huxley, similar to Merrill-Dickerson; Fig. 7) (van Steenis 1950a; George 1981). Van Steenis (1950a) concluded that Wallace's line was not a too sharp demarcation for plants, therefore, it was mainly used to establish faunal provinces. Table 2 shows the numbers of plant species west and east of the various lines and the numbers of species passing a line. It is apparent from Table 2 that whatever line is used, they are all good boundaries, on both sides of the lines usually at least twice as many species stop than cross the line. It is also apparent that moving from west to east, the demarcation line becomes stronger: The lowest amount of species is passing Lydekker's line, which separates New Guinea from the rest. Van Steenis conclusion is definitely not justified, Wallace's line certainly applies to plants as well.

Lydekker's line illustrates the very different nature of the New Guinean flora. This is also nicely shown in the Principle Component Analysis (Fig. 8). New Guinea is completely separated from all areas on Axis 1. Note that the areas that are enclosed by the various demarcation lines (except for Java) are all below Axis 1 and the more western areas above Axis 1. With the exception of Java (should be above the first axis) the Merrill-Dickerson or Huxley line is also present (Fig. 8).

van Balgooy (1987a, b) tried to find a more precise location for Wallace's line with the aid
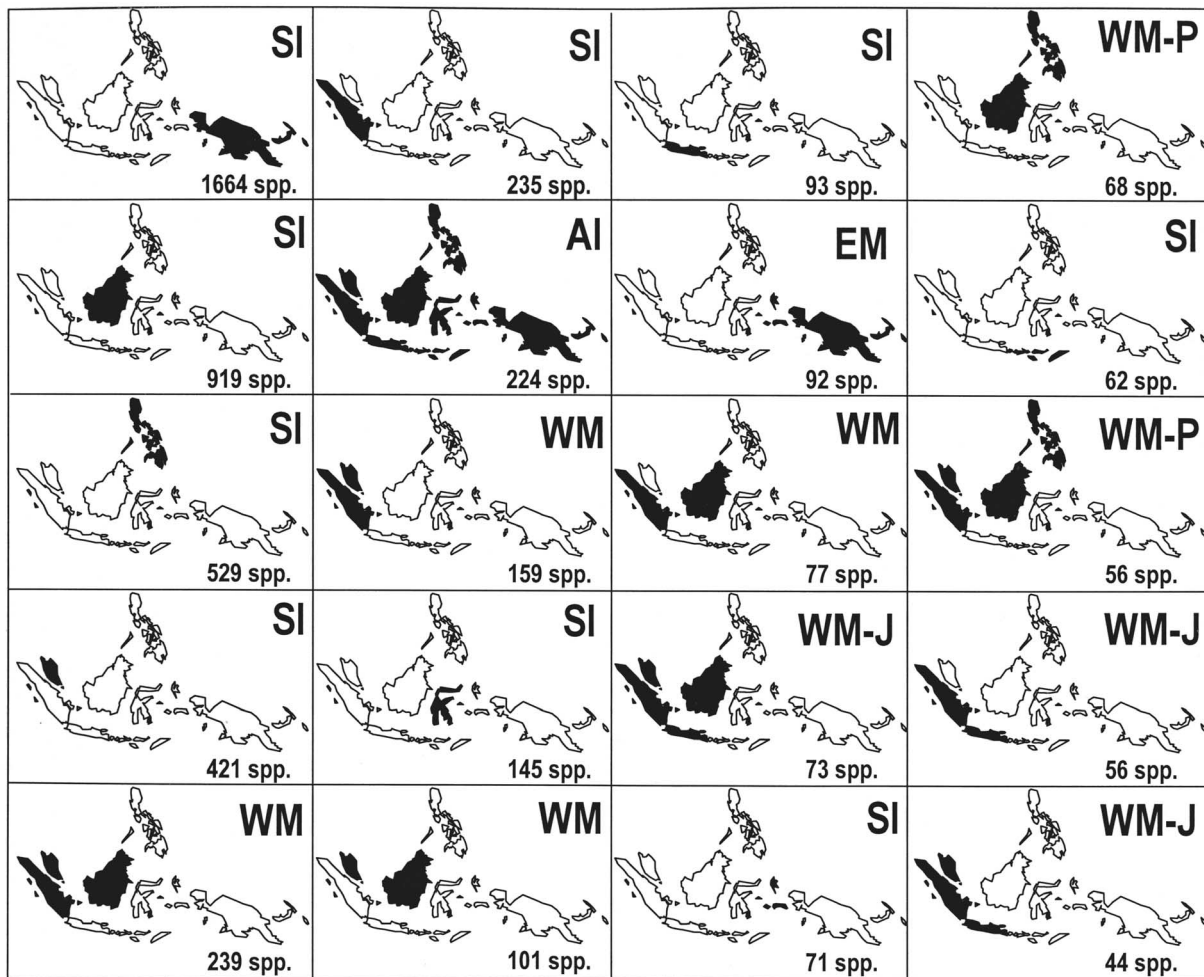
Fig. 4. Twenty most common distribution patterns in Malesia as indicated by the number of species present (bottom right corner of each map). AI = All islands, EM = east Malesia, SI = Single island group, WM = west Malesia, WM-J = west Malesia including Java, WM-P = west Malesia including the Philippines.

of Audley-Charles's reconstruction of the Malay tectonic history (1987). He, with the aid of de Koning and Sosef, tried to see if the line could be drawn through Celebes, because during its geological history Celebes consisted of at least two parts (Audley-Charles 1987), one moving west with the first wave, the other with the second wave. However, their analyses mainly showed the flora of Celebes to be rather homogeneous and (phenetically) most similar

to areas in central Malesia (those encompassed between the Merrill-Dickerson/Huxley line and the Lydekker line), as well on the species as on the generic level. The reason they failed to trace Wallace's line through Celebes is twofold. First of all, Celebes is an amalgamation of more than two areas (see the reconstruction by Hall). And, secondly, most areas, when still microplates, moved submerged, only to emerge after they collided with each other
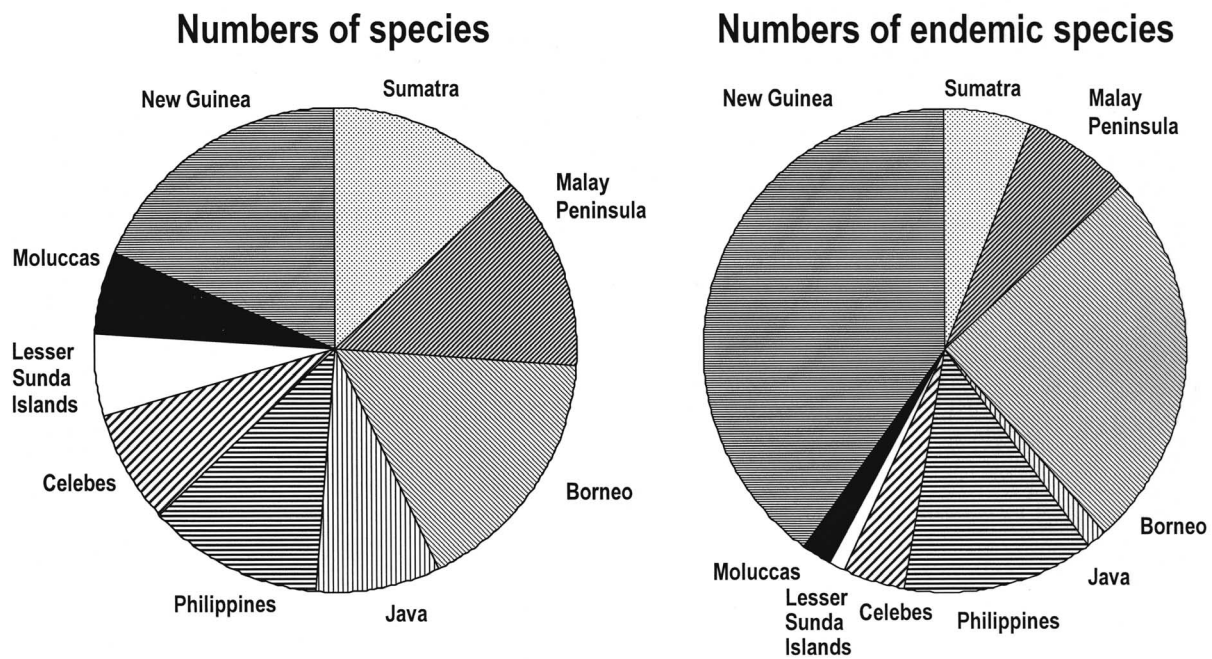
Numbers of species

Numbers of endemic species

Fig. 5. Distribution of numbers of species (left) and endemic species (right) over the island groups (Table 1b).
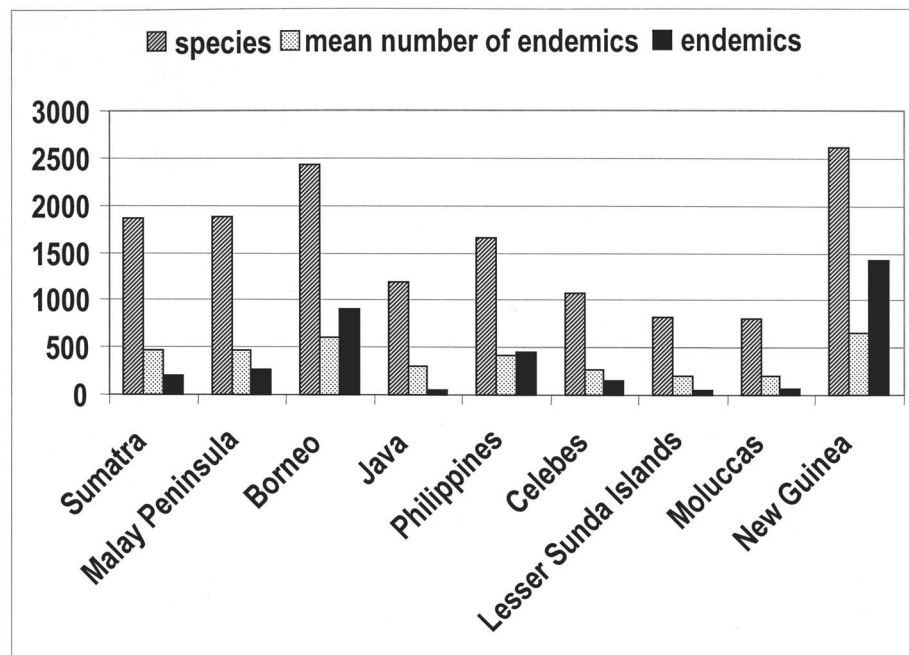

Fig. 6. Numbers of species, expected numbers of endemic species, and endemic species per island group (Table 1b); see formula in paragraph Material and Methods for expected numbers of endemic species.
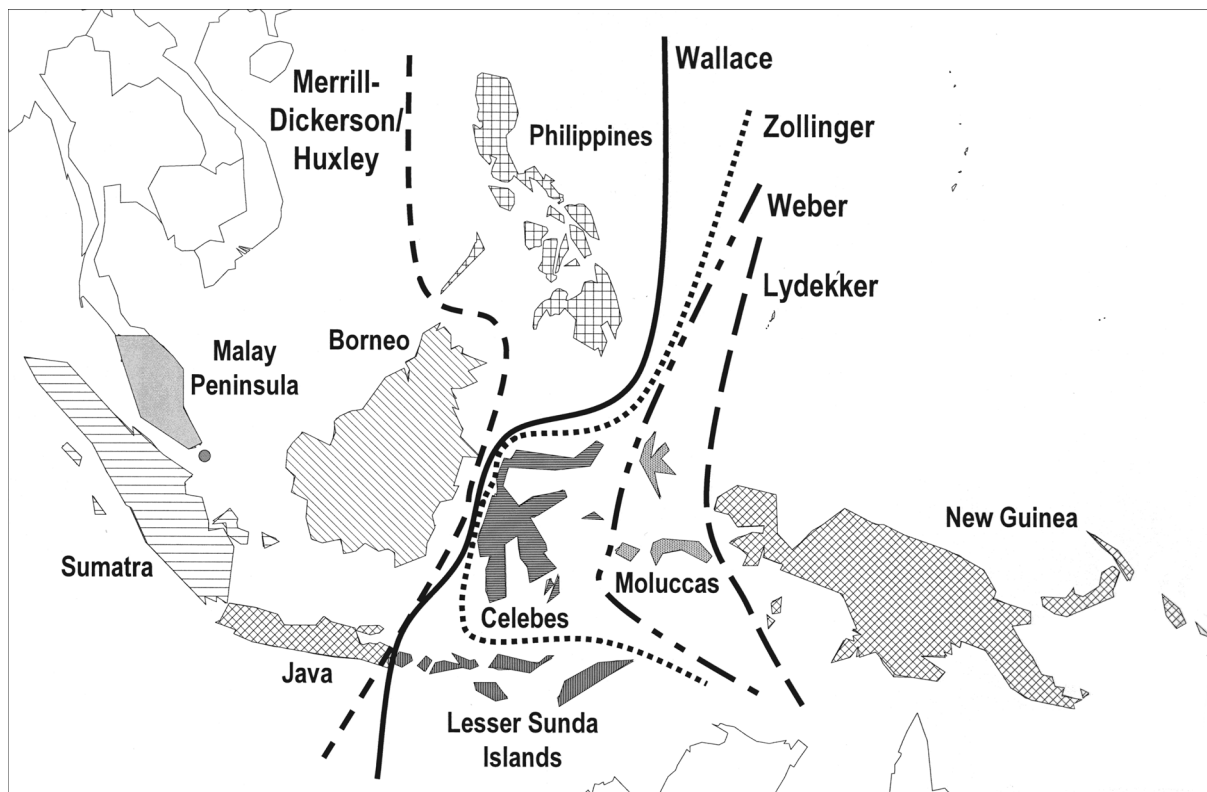
Fig. 7. The phytogeographical subareas (island groups) and Wallace's line and other derived border lines.

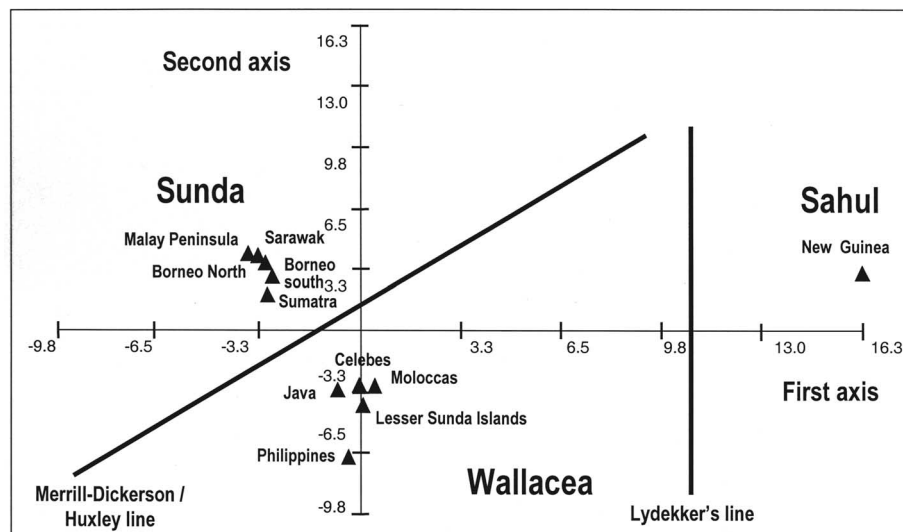**Fig. 8.** Principle Component Analysis of the floras of the island groups. New Guinea is clearly separated from the other island groups (Lydekker's line, Fig. 7). Also, Celebes, Java, Lesser Sunda Islands, and the Philippines form a group, almost equal to the Merrill-Dickerson / Huxley line (Java excepted; Fig. 7). The groups of islands that constitute the Sunda Shelf, Wallacea, and the Sahul Shelf are clearly separated.

Table 2. Numbers of species west and east of various demarcation lines in central Malesia (Fig. 7), and numbers of species crossing a line. The lines are ordered west to east.

Line	West border	East border	Crossing
Merrill-Dickerson / Huxley	2497	2778	1341
Wallace	3247	2132	1237
Zollinger	3451	2020	1145
Weber	3805	1827	984
Lydekker	4003	1664	949

(Morley & Flenley 1987, their plate 5.4). Which means that Celebes only emerged during perhaps the last 10-15 Ma. After that, it could act as stepping stone for dispersing species, but it never acted as a raft for New Guinean/Australian species. In Morley and Flenley's reconstruction (1987) of the Early Miocene (c. 25 Ma) especially all parts in central Malesia were submerged.

van Balgooy's analyses (1987a, b) also show another reason for the existence of Wallace's line. There is also a climatic difference between west Malesia, central Malesia, and east Malesia. West Malesia (also known as the Sunda Shelf) has an everwet climate, it comprises the Malay Peninsula, Sumatra, Borneo, and west Java. During part of the year central Malesia (Wallacea) has a dry monsoon (though there are everwet areas). Wallacea comprises the remaining part of Java, the Philippines, Celebes, the Lesser Sunda Islands, and the Moluccas. East Malesia (Sahul Shelf) is also everwet and only contains New Guinea. In fact, the PCA in Fig. 8 shows the three areas also. [N.B. Due to the way most distributions were noted in Flora Malesiana it was impossible to separate between everwet west Java, and the more drier remaining part. Therefore, in some analyses Java groups with the rest of the Sunda

Shelf (patterns marked WM-J in Fig. 4), while in other analyses it groups with the drier areas in Wallacea (PCA in Fig. 8).] Fig. 9 shows the numbers of species and numbers of endemic species in the three areas: the Sunda Shelf comprises c. 50% endemic species (1813 spp.), Wallacea has 31% endemic species (844 spp.), and the Sahul Shelf contains 54% endemic species (1419 spp.).

Various phylogenetic analyses of Malesian plant taxa show a splitting sequence of often repeating distributions on the Sunda Shelf (two examples in the Papilionoideae, Leguminosae: *Fordia* Hemsl. and *Imbralyx* Geesink, Schot 1991; *Spatholobus* Hassk., Ridder-Numan 1996; one in the Euphorbiaceae: *Baccaurea* Lour., Haegens 2000). This means that species dispersed back and forth over the various island groups on the Sunda Shelf. This is indicative of changes in the size of the island groups and the connections between the island groups. Species could easily disperse at one time and became restricted in their distribution during other times (often became disjunct, which resulted in speciation). At first sight completely unrelated to this is the opposite distribution, species absent from the everwet Sunda Shelf and often having a disjunct distribution between Southeast Asia mainland and the areas in Wallacea (van Steenis 1979). The grass genus *Arthraxon* Beauv. (van Welzen 1981) shows some very nice examples (Fig. 10). *Arthraxon castratus* is disjunct between Southeast Asia mainland and Java (absent in west Java). *Arthraxon lancifolius* is much wider dispersed, ranging from Africa to New Guinea, but absent from the Sunda Shelf. Finally, the most widespread species is *A. hispidus* with a worldwide distribution, but absent from the Sunda Shelf except for some areas on Sumatra. van Steenis (1979) shows these distributions to correlate with the need for a dry climate during part of the year. The occurrence of *Arthraxon* on the everwet Sumatra (*A. hispidus*)

and New Guinea (*A. lancifolius*) coincides with dry pockets on these islands (mainly areas in the rain shade of mountains and, therefore, possessing a much drier climate). The two types of distributions (the everwet Sunda Shelf, or the drier areas around it) are both the result of the alternation between glacial and interglacial periods during the Quaternary. During glacial maxima the Sunda Shelf and Sahul Shelf formed two vast areas of mainland due to sea level drops (Fig. 11; after Morley & Flenley 1987). Thus, everwet species could easily disperse to other areas on the Sunda Shelf, being restricted in their distribution again during interglacial periods, thus becoming disjunct and speciating. During glacial periods the southern part of the Sunda Shelf was much drier, giving opportunity for drought resistant species to disperse. During glacial periods these species had a continuous distribution between Southeast Asia and parts of Malesia, but became disjunct during interglacials like in the present one. Many of the drought-loving species are good dispersers and invaders. They easily dispersed to Wallacea and, because of the drier climate, the flora of Wallacea resembles that of west Malesia and Southeast Asia more than that of Sahul.

Also apparent from Fig. 11 is the absence of extensive land bridges in the Wallacea area. The islands on the Sunda and Sahul Shelves form continuous landmasses with Southeast Asia and Australia, respectively, but not so in Wallacea. There always was a sea strait between Borneo and Celebes and between the Moluccas and New Guinea. This means that many species could disperse over the continuous Sunda or Sahul Shelf, but still met a barrier in Wallacea that they could not bridge. Only the species with longer dispersal ranges could use the different islands in Wallacea as stepping stones to move west or east.

Morley and Flenley (1987) show two land bridge systems over the Philippines (Fig. 11),

one from north Borneo over Palawan, the other from northeast Borneo to Mindanao to Luzon to Mindoro. The two systems provided good opportunities for dispersal. *Guioa pleuropteris* (Blume) Radlk. shows geological clines along both land bridges, the shape, indumentum and domatia of the leaves change (Fig. 11, right part; van Welzen 1989). Two other Sapindaceae also show geological clines along the eastern, longer land bridge system (N.E. Borneo to Mindoro): *Gloeocarpus patentivalvis* (Radlk.) Radlk. (van Welzen 1991) and *Lepidopetalum perrottetii* (Cambess.) Blume (van Welzen 1992a). A possible reason for the change in leaf appearance might be that the Philippines have a different, more drier climate than Borneo.

In conclusion, four reasons are presented why Wallace's line is so distinct:
 – The two waves of microplates, whereby stepping stones between east and west only appeared during the last 10 Ma.
 – The continental parts on most microplates were still submersed during their northward movement, only to appear above water after collisions.
 – Different climatic conditions are present, Wallacea being the drier part between two everwet areas.
 – Glacial periods did not result in extensive land bridges in Wallacea.

Another conclusion can be drawn regarding Wallacea. It is better not to seek for a sharp boundary between west and east Malesia, the line found will always depend on the taxa used for the analysis. It is better to treat Wallacea as a transition zone between the Sunda and Sahul Shelves.

The role of India in taxon distributions

The Indian plate was part of the Gondwanan conglomerate. It detached itself from Africa in the Early Cretaceous (135 Ma), and drifted
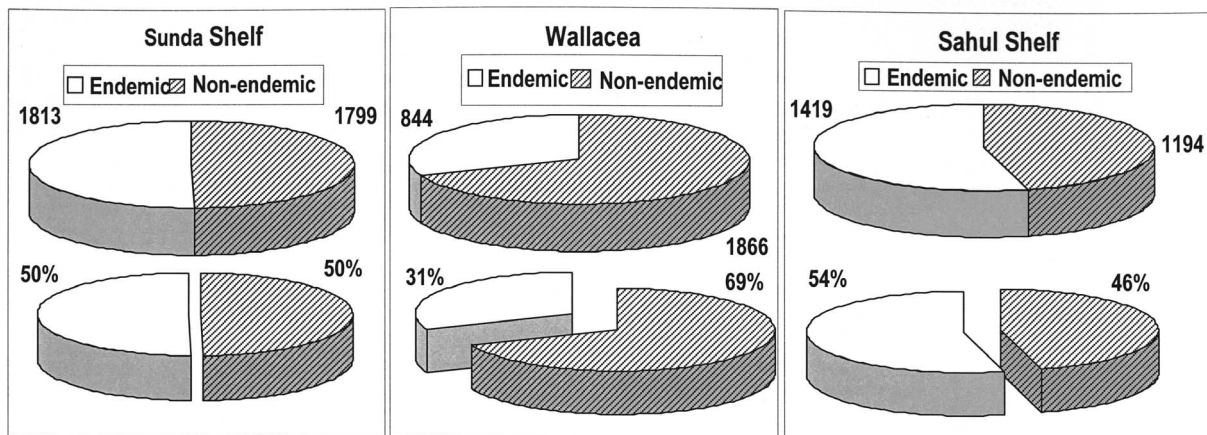
Fig. 9. Total numbers and percentages of endemic and non-endemic species on the Sunda Shelf, Wallacea, and the Sahul Shelf.
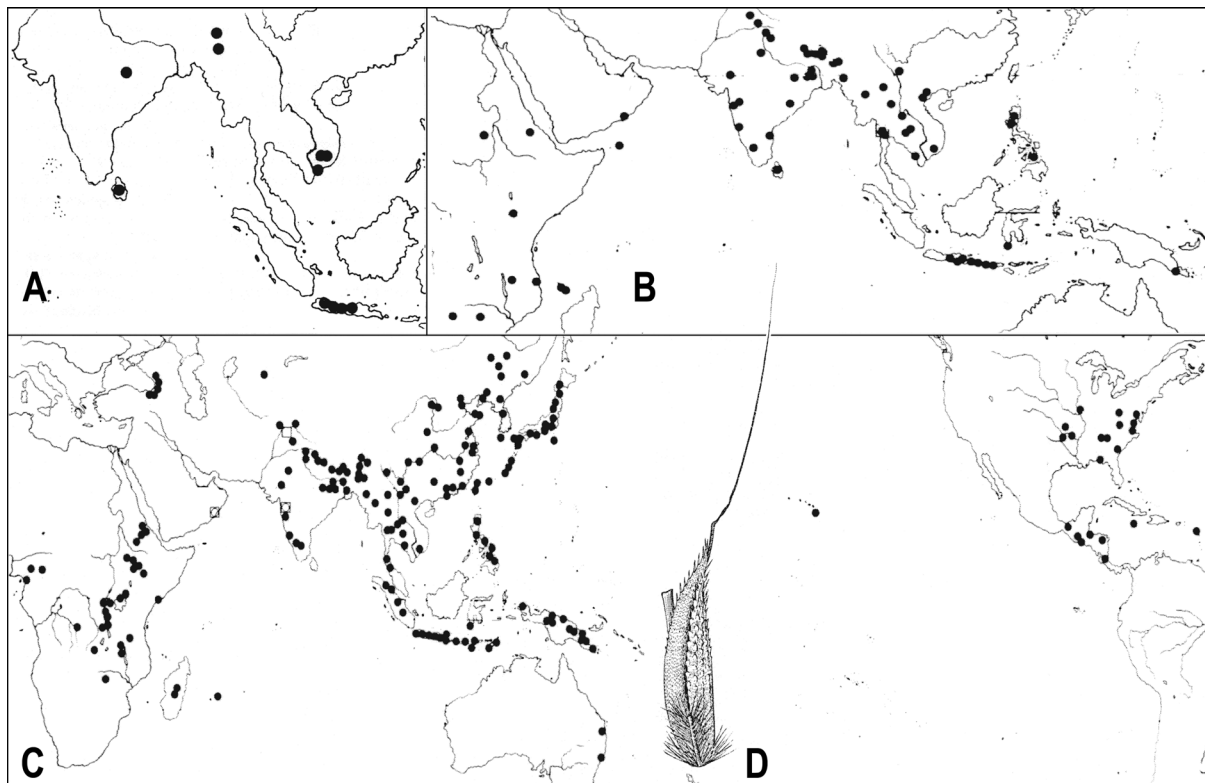
Fig. 10. Distributions of several species of *Arthraxon* (Poaceae – grasses), all evading the everwet Sunda Shelf (Malay Peninsula, Sumatra, Borneo, west Java) except for a few occurrences in drought pockets. A. *A. castratus* (Griff.) Narayanaswami ex Bor (disjunct); B. *A. lancifolius* (Trin.) Hochst.; C. *A. hispidus* (Thunb.) Makino; D. spikelet of *A. castratus*.
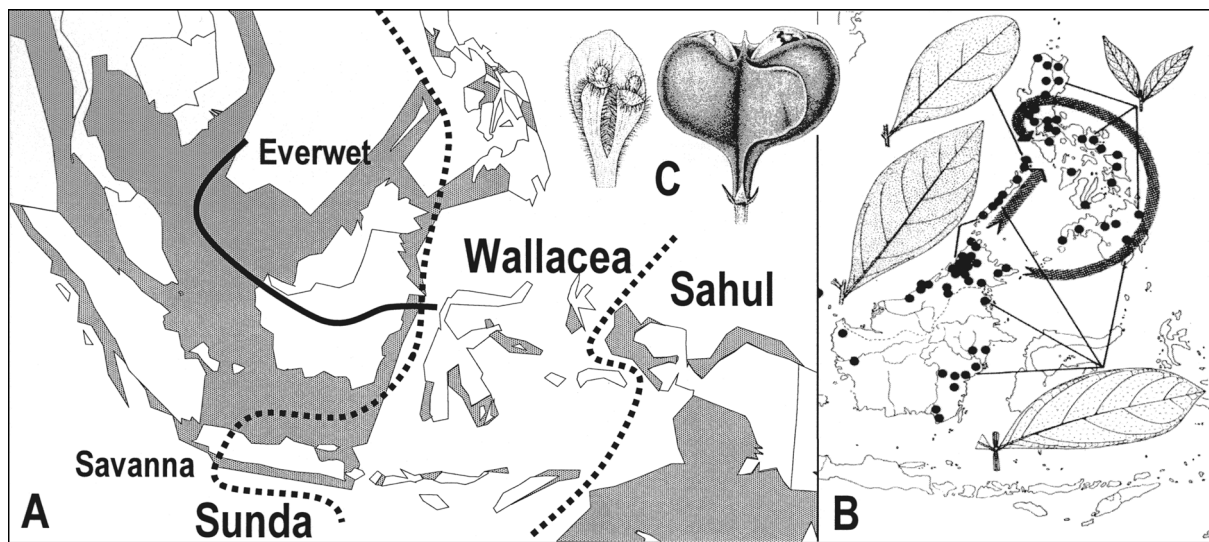
Fig. 11. Glacial periods. A. Maximum land surface (grey) during glacial periods; thick horizontal line indicating possible zone between an everwet core and a savannah corridor; the vertical dotted lines indicating the biogeographic/climatic areas: the everwet Sunda and Sahul Shelfs and Wallacea with its dry monsoon period (after Morley & Flenley 1987); B. Distribution of *Guioa pleuropteris* (Blume) Radlk. (Sapindaceae) with two geographical clines (indicated by the arrows, two distinct changes in leaflet shape, size and indumentum) following the Bornean-Philippine land bridges as shown by Morley and Flenley; C. Petal and fruit of *Guioa pleuropteris* (B & C: van Welzen 1979).

towards Southeast Asia, at first with Madagascar attached to it (*e.g.*, Cox & Moore 1993). After rafting in a rather wide eastern arc India finally collided with Southeast Asia in the Late Oligocene (c. 26 Ma). Doubts about this scenario exist (see already the question marks in Fig. 7.5 of Cox & Moore 1993). Briggs (1989) even suggests a more northern route along the African coast (in fact a more western arc), his argument is mainly the lack of peculiar biota on India that should have developed during the long isolation of India, but which are mainly lacking. Briggs suggests a more or less continuous exchange of floral and faunal elements with Africa. He also suggest that geological traces indicate this more western route of India.

Did India acted as a raft for floral elements, bringing Gondwanan elements to Southeast Asia? According to Cox and Moore (1993) the role of India in this respect was unimportant,

because India became isolated before most of the modern plants and especially animals developed. This is contrary to the view of Briggs (1989, see above) and Morley (2001). Morley sees a very active role for India in the dispersal of Gondwanan plants to Southeast Asia. One of his examples is fossil pollen of *Mischocarpus* Blume (Sapindaceae; this probably corresponds to what van der Ham 1990, calls *Cupanieidites* pollen). Like Morley, van der Ham also shows India as a raft for *Cupanieidites* Cookson & K.M.Pike ex R.Potonié, with a second 'invasion' via Australia (see next chapter). The general view is that India brought new, Gondwanan elements to Lauraceous Southeast Asia.

Spatholobus Hassk. (Ridder-Numan 1996) and its sister taxa (Leguminosae) may be an example of a taxon, which rafted to Southeast Asia on India, and then widely dispersed over west Malesia. The basal lineage (*S. parviflorus*

(Roxb. ex DC.) Kuntze and the outgroups (*Butea* Roxb. ex Willd. and *Meizotropis* Voigt) are present in India (Fig. 12a). However, in the upper part of the cladogram (Fig. 12a) *S. albus* Wiriadinata & Ridder-Numan, *S. crassifolius* Benth., and *S. purpureus* Benth. ex Prain are (mainly) Indian or present close to India (*S. merguensis* Prain in Myanmar). In between, *Spatholobus* only shows taxa present in west Malesia. Similar dispersal patterns can be observed in *Baccaurea* Lour. (Euphorbiaceae; Fig. 12b; Haegens 2000) and *Bromheadia* Lindl. (Orchidaceae; Fig. 12c; Repetur *et al.* 1997). The two latter genera are Malesian, with the basal taxa mainly from Borneo. In both taxa there are two sister(group) species (in an otherwise Malesian clade) of which one is from South India or Sri Lanka (*Baccaurea courtallensis* (Wight) Müll.Arg. and *Bromheadia srilankensis* Kruizinga & de Vogel) and the other from Borneo (*Baccaurea odoratissima* Elmer, and in *Bromheadia* a polytomy with *B. coomansii* J.J.Sm. ex Kruizinga & de Vogel, *B. devogelii* Kruizinga, and *B. gracilis* Kruizinga & de Vogel). Because the origin of the two genera is in Malesia (basal taxa) India could not have acted as a raft for these taxa. How did these two genera reach India?

The Indian plate, before it collided with Southeast Asia, was much larger than present-day India. The northern part was still flat and large before it became part of the Himalayas. This is usually referred to as Larger India (Fig. 13, after Morley 2001). Due to the large northern part it was relatively close to west Malesia. Audley-Charles (1987) even states that India perhaps passed over the place where we find Sumatra nowadays. This means that the distance between Malesia and India could be traversed by plants and that an early exchange of the flora took place. It was probably not necessary that India first collided with Southeast Asia (after which plants could have dispersed to Malesia via Southeast Asia main land). The

cladograms always show sister taxa present in India/Sri Lanka and Borneo. This is logical if one notices that most of Sumatra and Java was submerged in the reconstruction of Morley and Flenley (1987; Fig. 13), only Borneo was above sea level. The general notion that India brought plants to Malesia is not complete, there was an exchange between Malesia and India, and Malesian plants did disperse to India (*e.g.*, later ancestral species in *Spatholobus*, species of *Baccaurea* and *Bromheadia*). After collision with Southeast Asia more taxa could have dispersed from (and to) India and via Southeast Asia mainland to Malesia.

The early exchange of floral elements between India and Malesia cannot be used to decide between the classic theory of India following a more eastern arc and Briggs (1989) with a more western India. In both scenarios India would be in place to exchange floral (and probably faunal) elements with Southeast Asia and Malesia.

Circum-Pacific distributions

Many genera have a circum-Pacific distribution, they are found at both sides of the Pacific in Malesia/Australia and the Americas. van Steenis (1962) provides a nice overview, only a few examples will be mentioned here: Magnoliaceae (Heywood 1978; Azuma *et al.* 1999), Proteaceae (Weston & Crisp 1987, 1994), Fagaceae (van Steenis 1971; Humphries 1981), Sabiaceae (van Beusekom 1971), and Sapindaceae (Adema 1991). The map of the Magnoliaceae (Heywood 1978) shows a distribution in Southeast Asia, Malesia, and India (another of these Malesian-Indian exchanges!) and in the Americas. Azuma *et al.* (1999) show that in the *Magnolia* L. s.l. and the *Liriodendron* L. clade the dispersal/vicariance to/with America/Asia occurred two times, once by a single species, and two times (vicariance?) in parallel by *Magnolia* and *Liriodendron* at the base of their
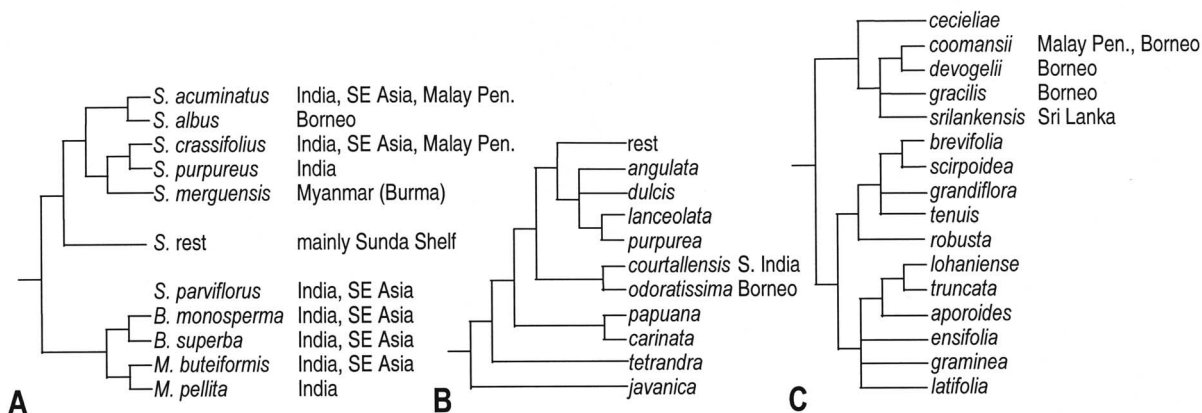
Fig. 12. Partial phylogenies of several taxa and some of the distributions between India and Borneo: A. *Spatholobus* Hassk., *Butea* Roxb. ex Willd., and *Meizotropis* Voigt (Leguminosae; Ridder-Numan 1996); B. *Baccaurea* Lour. (Euphorbiaceae; Haegens 2000); C. *Bromheadia* Lindl. sect. *Aporodes* Schltr. (Repetur *et al.* 1997).

clades. A similar situation is present in the Proteaceae (Weston & Crisp 1987, 1994), the Embothriinae and *Lomatia* R.Br. show a parallel vicariance between the Americas and NewGuinea/Australia at the base of their cladograms. A third similar example is for *Nothofagus* (Humphries 1981), again a basal vicariance between America and Asia/Australia. The situation in the Sapindaceae is slightly different. *Cupaniopsis* Radlk. has been described for Asia, Australia and the Pacific (Adema 1991), while *Cupania* L. occurs in America. However, no real morphological difference between both genera occurs other than a geographic disjunction. In fact, both genera should be united into a circum-Pacific genus. Fossil Sabiaceae are known from Europe and central Asia (van Beusekom 1971), therefore van Beusekom postulated dispersal via the Bering Street to (or from) North America.

Explaining the circum-Pacific distributions was always difficult. Authors always referred to a Gondwanan distribution, but then one would expect the taxa to be present in Africa too, because South America and Australia were at both opposite sides of Gondwana and more or less splitting from it at simultaneous times during the Cretaceous. Presence in Africa is and has certainly never been the case with Magnoliaceae (Heywood 1978) and *Nothofagus* Blume (Fagaceae; van Steenis 1971), of the latter only circum-Pacific fossils are known. Various explanations were given for the circum-Pacific distributions, but only two seem realistic: dispersal over landbridges via Arctica or Antarctica (*e.g.*, Cox & Moore 1993).
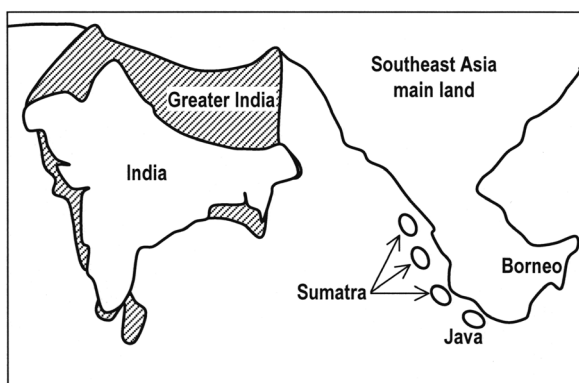
Fig. 13. Greater India reaching Southeast Asia in the Early Miocene (combination of Morley 2001, and Morley & Flenley 1987). Sumatra and Java are mainly submerged with only a few parts above sea level.

Late Cretaceous and early Tertiary (c. 65 Ma) climatic conditions in Arctica and Antarctica were moist, warm and equable (Askin 1989), so that both areas may have played a crucial role in the history of many Gondwanan plant groups (Drinnan & Crane 1989). The major reason for the warm climate is, what is referred to as the earth's belch: due to an increase in global temperatures (massive volcanic eruptions) enormous amounts of methane gas could escape from melting ice crystals in the arctic seas and a rapidly increased hothouse effect was the result (*e.g.*, Kennett & Stott 1991). The present day view (*e.g.*, Barlow 1981) is that South America, Antarctica and Australia formed part of a continuous landmass up until early Tertiary times (*e.g.*, Cox & Moore 1993). Subtropical to temperate forests linked Australia with South America through Antarctica, which at that stage did not possess an ice-cap (Weston & Crisp 1987). A similar situation existed in the Arctic regions (Cox & Moore 1993, their Fig. 8.9), continuous land masses still existed between North America and Europe. Two routes were available via Greenland, the de Geer route (North America – north Greenland-Spitsbergen-Scandinavia) and the Thulean route (North America – south Greenland-England-Europe). It is quite likely that the Sabiaceae and Magnoliaceae used the northern route, because of these groups fossils are found in Europe and Asia (Sabiaceae: van Beusekom 1971; Magnoliaceae: Muller 1981; Mai 1995; Crane 1998). The other groups (*Nothofagus*, Proteaceae, and Sapindaceae) probably used the Antarctic land bridge as their fossils are unknown for Europe. The alternative hypothesis, the Bering Street, as put forward by van Beusekom (1971) for the Sabiaceae, seems quite unlikely. This landbridge appeared in a much later period in glacial times when the climatic conditions were dry and very cold, unsuitable for (sub)tropical taxa.

Conclusions

Malesia is a phytogeographic area except for its eastern boundary, which should have been in the west Pacific. It comprises two levels of phytogeographic subareas, with on the first sublevel the Sunda Shelf, Wallacea, and the Sahul Shelf. The Sunda Shelf comprises the phytogeographical subunits Malay Peninsula, Sumatra, and Borneo; Wallacea comprises Java, the Philippines, Celebes, the Lesser Sunda Islands, and the Moluccas; while the Sahul Shelf only consists of New Guinea. Within Malesia, New Guinea, Borneo, and the Philippines comprise more endemic species than expected, which seems to correlate with their longer record of emergence and the (continuing) geological history.

Wallace's line, which separates a western and eastern Malesian flora, is in fact an area of transition, now better known as Wallacea. Wallacea forms a boundary for four reasons. 1. West and east Malesia consist of small fragments broken off from Australia, but west Malesia was already much longer in its more or less present position than east Malesia. 2. Most fragments were submerged for a long time, even after arrival at their present position, this is especially the case in Wallacea, they did not act as rafts for terrestrial biodiversity. 3. Wallacea has a dry monsoon climate, while the Sunda and Sahul Shelf have an everwet climate. 4. During glacial periods Wallacea did not contain major land bridges, all sea lanes were still present.

India probably acted as a raft, bringing biodiversity to Southeast Asia and Malesia. However, before it collided with Southeast Asia it was already close enough to Malesia (especially the emerged parts of Borneo) for an early exchange of floral elements. Not only did Indian elements disperse to Malesia, but also Malesian taxa moved to India.

The circum-Pacific patterns may be explained by two land bridge systems. A south-

ern Antarctic landbridge existed, linking South America to Ausralia and a northern Arctic landbridge connected North America to Europe. At the end of the Tertiary the climate was warm enough for subtropical taxa to pass these landbridges.

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