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The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2011, **103**, 531–545. With 5 figures

Wallace's Line and plant distributions: two or three phytogeographical areas and where to group Java?

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Received 6 October 2010; revised 14 January 2011; accepted for publication 17 January 2011

Wallace's Line or its variants divide the Malay Archipelago or Malesia into a western and eastern area, but is this suitable for plant distributions? Indeed, all boundaries satisfactorily divide Malesia into two parts, stopping far more species east or west of a line than disperse over the boundary. However, phenetic analyses (principal components analysis, nonmetric multidimensional scaling analysis and the unweighted pair group method with arithmetic mean) of 7340 species distributions revealed a stronger partitioning of Malesia into three instead of two regions: the western Sunda Shelf minus Java (Malay Peninsula, Sumatra, Borneo), central Wallacea (Philippines, Sulawesi, Lesser Sunda Islands, Moluccas, with Java), and the eastern Sahul Shelf (New Guinea). Java always appears to be part of Wallacea, probably because of its mainly dry monsoon climate. The three phytogeographic areas equal the present climatic division of Malesia. An everwet climate exists on the Sunda and Sahul Shelves, whereas most of Wallacea has a yearly dry monsoon. During glacial maxima, the Sunda and Sahul Shelves became land areas connected with Asia and Australia, respectively, whereas sea barriers remained within Wallacea. Consequently, the flora of the two shelves is more homogeneous than the Wallacean flora. Wallacea is a distinct area because it comprises many endemic, drought tolerant floristic elements.

ADDITIONAL KEYWORDS: Kroeber's coefficient – Malay Archipelago – Malesia – NMS – PCA – UPGMA – Zollinger's line.

INTRODUCTION

In the Malay Archipelago (or Malesia; Raes & Van Welzen, 2009) a famous zoological boundary based on the biogeographical work of Wallace is found (i.e. Wallace's Line), with the name being coined by Huxley (1868). The line (Fig. 1) runs east of the Philippines, then depending on the view of Wallace (see below) either west or east of Sulawesi (also known as Celebes), and between Bali and Lombok in the Lesser Sunda Islands. Wallace was uncertain with regards to the position of Sulawesi; placing the line west of Sulawesi in 1859, 1863–1876 and east of Sulawesi in 1860 and 1910. The position of Sulawesi was discussed in his famous book 'Island life' (Wallace, 1880) in which he calls Sulawesi an 'anomalous island' with no continental connections because Sulawesi lacks Sundaic groups and contains (old) endemic and Australasian species. A more complete historical overview is presented in Simpson (1977) and George (1981), who both show that a number of variants of Wallace's Line have been proposed based on study of different groups of organisms (Fig. 1). The area encompassed by these lines includes the Philippines, Sulawesi, the Lesser Sunda Islands, and Moluccas, and is often called Wallacea, a term

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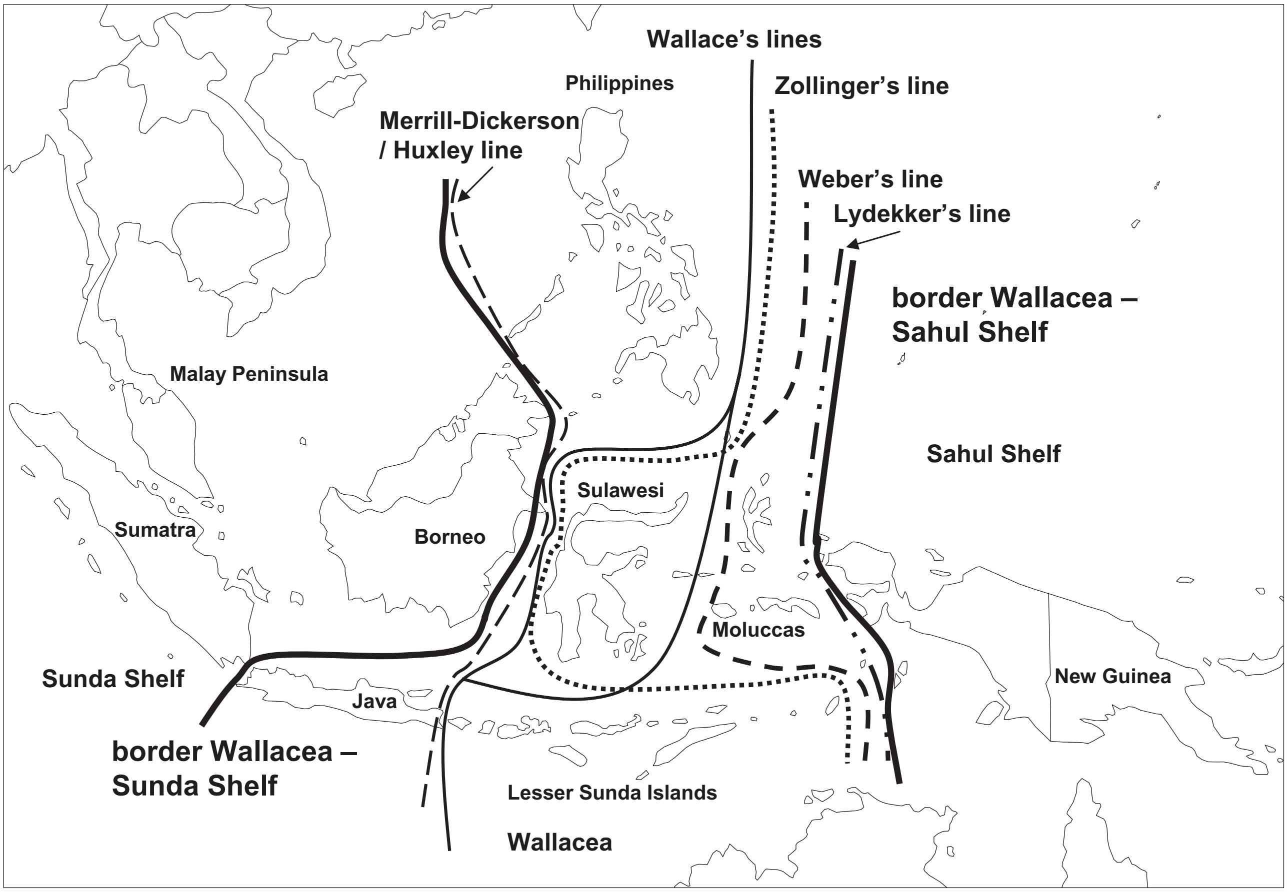

Figure 1. Wallace's Lines (variously around Sulawesi) and variants. In the south the lines have been placed between Java and Bali and between Palawan and Borneo (see Material and methods).

coined by Dickerson (1928), for an area already delimited by Wallace in 1863. The areas to the west (Malay Peninsula, Sumatra, Java, Borneo) and to the east (New Guinea) are referred to the Sunda Shelf and the Sahul Shelf, respectively.

All the boundaries were overwhelmingly based on faunal data and so it is of little surprise that botanists have found none of them very useful (George, 1981). Indeed, Van Steenis (1950a) did not consider Wallace's Line to be a distinct boundary in plant distributions. However, his opinion was based on generic distributions, and not species distributions, which may show a very different result. When Van Welzen, Slik & Alahuhta (2005) reviewed Wallace's Line based on a limited botanical data set on the species level, they concluded that Malesia is not simply split into two halves by this line but that the central part of Malesia deserved the status of a separate phytogeographical area. Recently, Van Welzen & Slik (2009) showed which families in their sample were mainly responsible for the distribution patterns in Malesia. Only twenty, generally species-rich families accounted for most patterns. Three of these families have their centre of diversity on the Sunda Shelf (Dipterocarpaceae, Fagaceae, Nepenthaceae); others are typical for the Sahul Shelf (Ericaceae, Monimiaceae, Sapindaceae), whereas others have no distinct centre (Burseraceae, Caesalpiniaceae, Flacourtiaceae, Meliaceae, Myristicaceae). Families that have their distributional focus in Wallacea (Araliaceae, Boraginaceae, Convolvulaceae, Cyperaceae, Dioscoreaceae, Lamiaceae, Loranthaceae, Mimosaceae, Moraceae) are largely herbaceous and have a high dispersal capacity.

In the present study, we address the following research questions: (1) does Wallace's Line, or perhaps one of its variants, constitute a major phytogeographical boundary; (2) can Malesia be subdivided into phytogeographical areas; and (3) if so, how can we explain the phytogeographic areas?

The results of the present study are of high conservation importance because they can be used to inform current and future efforts that try to preserve the unique flora and fauna of this uniquely diverse tropical region. The study is based on phenetic analyses only. Many authors argue that phylogenies should be used. However, these are still too rare for the Malesian region to be of statistical value, although the first comparisons are appearing (Michaux, 2010). A problem of many phylogenetic analyses is that the circumscription of the units (areas) used in the analysis is often arbitrary or based on the distributions within a single clade only, or based on the geological past of an area in combination with the presence of endemic species (Ridder-Numan, 1996; Michaux, 2010). The use of the geological tectonic past to delimit areas sounds compelling, but specific climate changes, as occurred during glacial/interglacial periods, often largely destroyed those tectonic patterns, especially in groups with a degree of recent speciation. Therefore, a rationale for the present study is that the boundaries found will be less arbitrary ('areas of endemism' as often used in cladistic analyses), and are therefore more suitable for use in historical biogeographic analyses (Alfaro *et al*., 2008), especially for event-based (single taxon) studies.

Brief geological historical overview of Malesia

The geological history of the Malay Archipelago is very complex (Hall, 2009; Michaux, 2010). In the present study, only a short overview is presented. A beautiful animation showing details of the tectonic movements has been created by Hall and colleagues (http://searg.rhul.ac.uk/current_research/plate_tectonics/index.html).

Approximately 50 Mya, the West Malay Archipelago was already in place (with a more north–south orientation). At this time, a series of microplates broke off from Australia to form the eastern half of Malesia. These microplates, together with the northward movement of the New Guinea–Australian plate, caused West Malesia to rotate anticlockwise. Most East Malesian areas are amalgamations of microplates, certainly New Guinea (Pigram & Davies, 1987), Sulawesi, and the Philippines (Hall, 2009). Even when the islands reached their present day locations, most areas were still submerged and it was only approximately 5 Mya that most islands in the central Malesian region started to emerge (Hall, 2009). However, for geologists, it is difficult to find evidence for the exact time of sub/emergence of areas (R. Hall, pers. comm.) and opposed views, allowing for more or earlier emerged areas, certainly exist (Michaux, 2010). Presently, it is very likely that more areas where already above water than described by Hall (2009), although these areas were still isolated (surrounded by water) but could have acted as stepping stones and perhaps as rafts (Michaux, 2010; R. Hall, pers. comm.). This means that the fragments often did not carry terrestrial species and, second, that probably most terrestrial species could only have reached these areas via dispersal from West Malesia, Taiwan (Van Steenis, 1979), and New Guinea. Thus, to use the geological past/origin of the islands directly as criterion for the delimitation of areas in phytogeographic analyses is hazardous.

Sea levels have fluctuated greatly in the region and these fluctuations had considerable impact on the amount and location of exposed land surface. For example, during recent glacial periods (approximately 21 000 BP) sea levels were up to 120 m lower, which exposed currently submerged areas of the sea floor (Emmel & Curray, 1982; Hanebuth, Stattegger & Grootes, 2000) and greatly affected plant distributions. This drop in sea level resulted in dry Sunda and Sahul Shelves (i.e. continuous land masses in the west and east) (Voris, 2000; Bird, Taylor & Hunt, 2005; Sathiamurthy & Voris, 2006). It also resulted in some areas of Wallacea becoming connected (e.g. most of the Lesser Sunda Islands formed a continuous land mass). By contrast to Amazonia and the Congo, Malesian rain forest probably expanded during glacial periods (Cannon, Morley & Bush, 2009). Generally, these changes removed dispersal barriers and allowed for easier terrestrial migration. Nevertheless, sea passages remained between the major island groups in Wallacea (Morley & Flenley, 1987). Conversely, sea levels in the region occasionally did rise above current eustatic levels. They were 5 m higher during the Holocene (5000–7000 years ago; Tjia, 1996; Woodroffe, 2000) and approximately 100 m above present day levels during the middle Miocene (24–13 Mya) and early Pliocene (5–4.5 Mya) (Woodruff, 2003). These latter changes reinforced dispersal barriers.

The climate of the region has also varied significantly over time. When sea levels were low rain forests expanded, although the southern part (Malay Peninsula up to southern Borneo) probably had a drier, savannah-like climate (Morley & Flenley, 1987; Bird *et al*., 2005; Cannon *et al*., 2009; Hall, 2009).

The complex geological processes, their relatively recent time-scale, the changes in climate, and the physical geography of the region resulted in many changes in distributions: dispersal and (partial) extinction of species unable to withdraw to everwet areas (Turner, Hovenkamp & Van Welzen, 2001; Van Welzen, Turner & Hovenkamp, 2003; Muellner *et al*., 2008), vicariance (De Boer, 1995; Ridder-Numan, 1998), and dispersal in conjunction with speciation (secondary vicariance; Van Balgooy, Hovenkamp & Van Welzen, 1996).

MATERIAL AND METHODS

DATA

The basic biogeographical units (BU) that we use are the areas described by Van Steenis (1950b): Malay Peninsula, Sumatra, Borneo, Philippines, Sulawesi, Java, Lesser Sunda Islands, Moluccas, and New Guinea. They are used to indicate distributions in all publications of Flora Malesiana, which forms the basis of our sample (see below). Three additional rationales exist to maintain the apparently outdated floristic regions of Van Steenis, even though they are generally geological composites. All areas form logical units because they are all isolated islands or groups of islands separated from the other islands by water barriers. All nine areas have relatively high amounts of endemic species; they are among the 20 most common distribution patterns (out of 299 realized patterns of the 511 possible ones; Van Welzen *et al.*, 2005). Finally, all areas have a climate that is, for the most part, more or less similar and climate is generally the first regulating factor in species distributions (Elith & Leathwick, 2009).

The structure of the data necessitated a slight change in Wallace's Line. Originally, the southern part of his line passed between Bali and Lombok (Lesser Sunda Islands), although we had to place it between Java and Bali because of our selected operational taxonomic units (OTUs). This is not a new biogeographic proposition because a variant of Wallace's Line running between Java and Bali was first proposed by Murray in 1866 (Simpson, 1977). Similarly, we also had to place the Merrill-Dickerson/Huxley Line between Palawan and Borneo instead of between Palawan and Mindoro.

A database was created containing a large sample of the flora of Malesia. These data were the presence/absence of data per BU of all indigenous species so far published in Flora Malesiana Series 1 (Angiosperms) and Orchid Monographs. These data were selected because:

- Flora Malesiana forms the first thorough inventory of Malesian species. The revisions are made in an almost monographic way, providing the most reliable species delimitations and best estimate of the distributions.
- Because only revised species are used no differential effect is present between better known and less well-known areas (e.g. local floras for Java and the Malay Peninsula exist), these floras are relatively well-known but all other seven areas have checklists at most and are poorly known for the nonrevised families. There still is a difference in collection density between the various areas and as some revisions are half a century old, knowledge of distributions has often increased. Extensions of distributions were published as addenda in Flora Malesiana and these were included in our sampling and analyses.
- The families in Flora Malesiana are published in an arbitrary nonphylogenetic sequence dependent only on their being completed by the relevant expert author. This means that the choice of families is biased towards the small families but, as far as distributions are concerned, the selection is random and the data representative. Species in small families may have different distribution patterns than those in large families but, as already pointed out in the Introduction, only a few large families dominate most patterns (Van Welzen & Slik, 2009); thus, the possible effect of small families can be ignored.

All cultivated and introduced species were ignored. 7340 species, divided over 165 families and 896 genera, were included in the analyses. This represents 25% of the estimated 30 000 species of ferns and Angiosperms in Malesia.

STATISTICAL ANALYSIS

The analyses were performed on both the total (i.e. complete) data-matrix ('all data') and on randomly drawn submatrices of that data-matrix ('100 submatrices', see below). Three different statistical techniques were used to explore possible ambiguity in the results, arising from the differential statistical arithmetic used by the different techniques, and thereby to reveal inherent congruences. A principal components analysis (PCA) and a nonmetric multidimensional scaling analysis (NMS) use, in two very different ways, the variability within the data to cluster the OTUs in groups. On the other hand, the degree of similarity is used to group the OTUs in a cluster analysis. A cluster analysis has two steps, first a pairwise weighted similarity comparison is made between all OTUs after which the OTUs are grouped in a diagram according to their similarities. The latter process involves decisions, that may obscure other, slightly less distinct groupings. To show all weighted similarities, Kroeber's coefficient is used to discuss the position of Java. The similarities are presented in a table but are also visualized in a diagram.

1. The PCA (using Kaiser's rule, centred data; Sneath & Sokal, 1973) was performed with the MultiVariate Statistical Package (MVSP), version 3.13l (Kovach Computing Services). Detrended Correspondence Analysis (DCA) is often recommended for presence/absence data over a long gradient (Malay Peninsula to New Guinea). We performed DCA using MVSP; the results were identical to

those with PCA, and therefore we only present the results of the latter analysis.

2. NMS (Borg & Groenen, 2005), using Lance–Williams distance, two- or three-dimensional solution with stress convergence and minimum stress set to 0.0005, 1000 iterations, and 500 random starts, yielded a normalized raw stress of 0.004 or less. SPSS, version 16.0 (SPSS Inc.) was chosen because it is widely available and can perform NMS on our large data matrix. For technical reasons, the SPSS algorithm is more efficient with dissimilarity/distance measures than with similarity/proximity measures and so requires distance matrices, not similarity matrices (Garson, 2009); Sørensen's coefficient is therefore not available for NMS in the SPSS package. Of the measures available, the most appropriate (and most similar to Sørensen) is Lance–Williams distance, also known as the Bray–Curtis distance, a long-established distance measure (Bray & Curtis, 1957; Legendre & Legendre, 1998).
3. As cluster analysis (using MVSP) unweighted pair group method with arithmetic mean (UPGMA), with Sørensen's coefficient was selected. Sørensen's coefficient (Sørensen, 1948) equals Dice's coefficient (Dice, 1945). Sørensen's coefficient compares the similarity in species present between pairwise areas via $2A/(2A + B + C)$, where A is the number of shared species, B is the number of species only present in one area and C is the number of species only present in the other area.
4. Another measure for similarity coefficients is Kroeber's coefficient, which compares floras between pairs of areas (Kroeber, 1916). The formula used provides a mean similarity percentage (e.g. 50% means that half of the species are the same in both areas). The formula is $50{*}A{*}(X + Y/X{*}Y)$, where A is the number of shared species, X the number of species in one area and Y the number in the other area. This coefficient is comparable to Sørensen's coefficient as used in the cluster analysis but differs in X and Y because $X = A + B$ for Sørensen and $Y = A + C$ for Sørensen. Kroeber's coefficient is applied in the present study because it has been used before in comparable studies of Pacific and Sulawesi botany (Van Balgooy, 1971, 1987; Van Balgooy *et al*., 1996).

Sørensen's and Kroeber's coefficients are sensitive to unequal sample sizes (e.g. differences in sizes of areas and consequently in numbers of species). Because Borneo and New Guinea are much larger than the other areas and contain they far more species of which many are endemic and thus unique (Table 1), this might bias our analyses as well in terms of variability (PCA, NMS) as similarity (UPGMA). To counter the sample size effect, we created a second set of based on hundred submatrices drawn from the main (complete) data-matrix. Each submatrix contained 4500 randomly drawn samples (500 per BU). The size of the random samples (e.g. 100–500 per BU) did not change the results, nor did the sequence of the BUs selected.

Table 1. Number of species, endemic species, and percentage of endemic species per biogeograpical unit (BU) in the Malay Archipelago

BU	Number of species	Endemic species	% Endemic species
Sumatra	2068	215	10.4
Malay Peninsula	2138	276	12.9
Borneo	2714	989	36.4
Java	1347	63	4.7
Philippines	1846	511	27.7
Sulawesi	1215	172	14.2
Lesser Sunda Islands	902	46	5.1
Moluccas	937	83	8.9
New Guinea (Sahul Shelf)	2876	1553	54.0
Malesia	7340	5068	69.0
Sunda Shelf (–Java)	3998	1962	49.1
Sunda Shelf (+Java)	4241	2122	50.0
Wallacea (+Java)	3077	1081	35.0
Wallacea (–Java)	2727	983	36.0

Composite BUs are also shown.

RESULTS

Table 1 shows that there is considerable variation in the number and proportion of endemic species present in each BU. Several of the BUs harbour a large proportion and number of endemic species (particularly New Guinea and, to a lesser extent, Borneo and the Philippines), whereas other BUs have a small proportion and low number of endemic species (particularly Java, the Lesser Sunda Islands, and the Moluccas).

Wallace's Line and several variants are indeed real dispersal barriers at which more species stop than cross. Generally, twice as many are stopped on one side or other of the barrier as pass (Table 2). The filtering power of the variants of Wallace's Line increases from west to east with the most easterly variant, Lydekker's Line, stopping most species, and Huxley's Line, the most westerly line, the fewest. The number of species whose eastward spread is halted increases the more easterly the line under consideration. The reverse argument also applies

Table 2. Numbers of species from the sample stopped east or west by Wallace's Line or other lines, or passing the lines

Line	Stopped west	Passing	Stopped east
Merill–Dickerson or Huxley Line	2742	1499	3099
Wallace Line (Sulawesi with west)	3909	1317	2114
Wallace Line (Sulawesi with east)	3584	1379	2377
Zollinger Line	3810	1274	2256
Weber Line	4223	1099	2018
Lydekker Line	4464	1057	1819

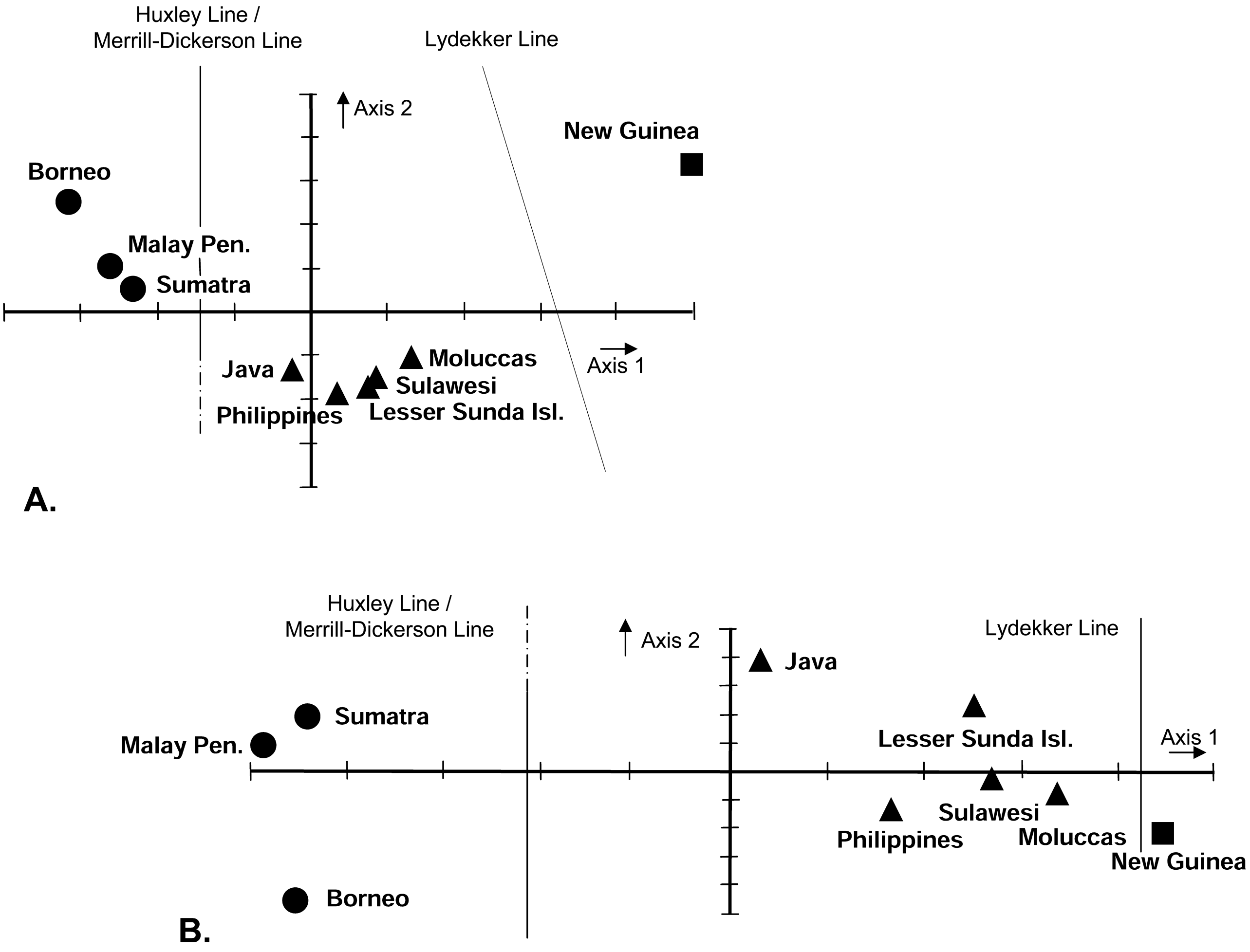

Figure 2. Principal components analysis. A, scatter plot for all data of first two axes (covering 50% of variation). B, scatter plot for 37 of the 100 random submatrices (the others are mirror images or transpositions; for explanation, see text). The Merrill–Dickerson or Huxley Line is dotted near Java to show that the results of the present study place Java at the other side of this line. The different symbols for the islands indicate the different groupings.

(i.e. Huxley's Line represents the strongest westerly boundary and Lydekker's Line represents the weakest).

The PCA (Fig. 2A, all data) shows three groups: the Sunda Shelf BUs are placed together and separate from the Wallacea BUs, which cluster together and both are separate from the Sahul Shelf BU. Thus, the most western and eastern variants of Wallace's Line are shown. However, our analysis shows that Java groups with Wallacea and not, as Wallace's Line and its variants suggest it should, with the Sunda Shelf BUs. All analyses of the 100 submatrices show the

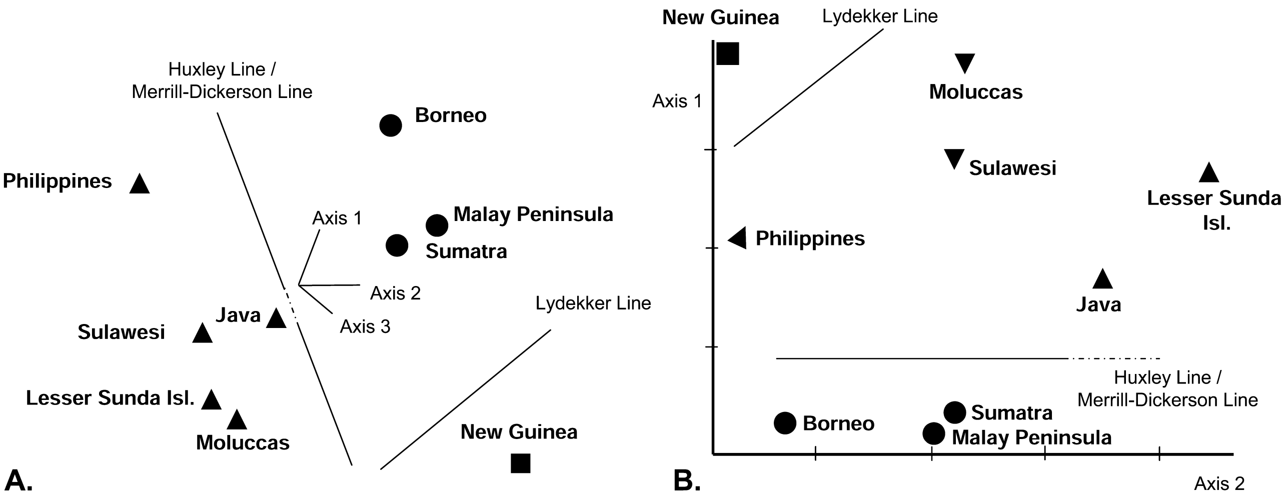

Figure 3. Nonmetric multidimensional scaling ordination. A, scatter plot for all data of the three axes from a three-dimensional solution. B, scatter plot for matrix 100 of the 100 submatrices of the two axes from a two-dimensional solution (the position of the triangles in Wallacea indicate three groupings). The Merrill–Dickerson or Huxley Line is dotted near Java to show that the results of the present study place Java at the other side of this line. The different symbols for the islands indicate the different groupings; in (B), the triangles show three different subgroups.

same groupings of the areas (same relative position) but in four versions that are mirror images of each other. Thirty-seven of the 100 submatrices PCA analyses showed the diagram in Figure 2B, seven cases have a diagram mirrored along axis 1, 40 cases are mirrored along axis 2, and 16 are transposed. The results show a strong grouping of the Malay Peninsula, Sumatra, and Borneo. However, New Guinea does not appear to be too distinct from the Moluccas and Sulawesi. Java is now quite separate from the Wallacea group but always appears on the same side of the axis as the Lesser Sunda Islands.

The NMS analysis of all data (Fig. 3A) also showed that Java is positioned within Wallacea. The analysis of the 100 submatrices provides groupings somewhat similar to those of PCA and cluster analysis with Wallace's Line being interpolatable at 0.0 on the *y* (first) axis. As with PCA, the 100 submatrices result in different scatter diagrams, which are mirror images of each other (one is shown, Fig. 3B): New Guinea is isolated (square); the Sunda Shelf areas group together (dots) with Borneo slightly separate and with Java close to the Lesser Sunda Islands; Wallacea (triangles) is therefore heterogeneous; the Philippines are separate and the Moluccas and Sulawesi group together.

The cluster analysis (Fig. 4A) confirms the results of the PCA for all data with three groups (Malay Peninsula–Sumatra–Borneo: Java–Philippines –Sulawesi–Lesser Sunda Islands–Moluccas: New Guinea), with New Guinea being most different in its floral composition. However, for the 100 random submatrices, the result is different. The Malay Peninsula, Sumatra, and Borneo still form a group but now show the least resemblance to the rest (e.g. basal in the phenogram, Fig. 4B). New Guinea groups with Sulawesi and the Moluccas and the Philippines group with Java and the Lesser Sunda Islands.

Finally, the analyses using Kroeber's coefficient (Fig. 5; see also the Appendix, Table A1) provide a somewhat similar picture to the cluster analysis. In both analyses, Borneo, Sumatra, and the Malay Peninsula show strong ties. New Guinea is separate in the all data analysis (Fig. 5A, all data) but links to the Moluccas and Sulawesi for the 100 submatrices (Fig. 5B). The analysis of all data also shows that the bonds between BUs for Wallacea are not very strong (Fig. 5A) and this is confirmed by the 100 submatrices (Fig. 5B). The position of Java in these latter analyses is ambivalent: Java having strong bonds with the Malay Peninsula and Sumatra (which are two of the BUs of the Sunda Shelf) but somewhat weaker bonds with Borneo, the third BU of the Sunda Shelf. However, Java also has strong bonds not only especially with the Lesser Sunda Islands, but also with Sulawesi and the Philippines, and less with the Moluccas (all of which are Wallacean BUs).

DISCUSSION

PHYTOGEOGRAPHIC AREAS

The proposed boundary lines considered in the present study (Fig. 1) can be effectively used to separate the floras of the BUs. When all data are considered, then Lydekker's Line appears best as the

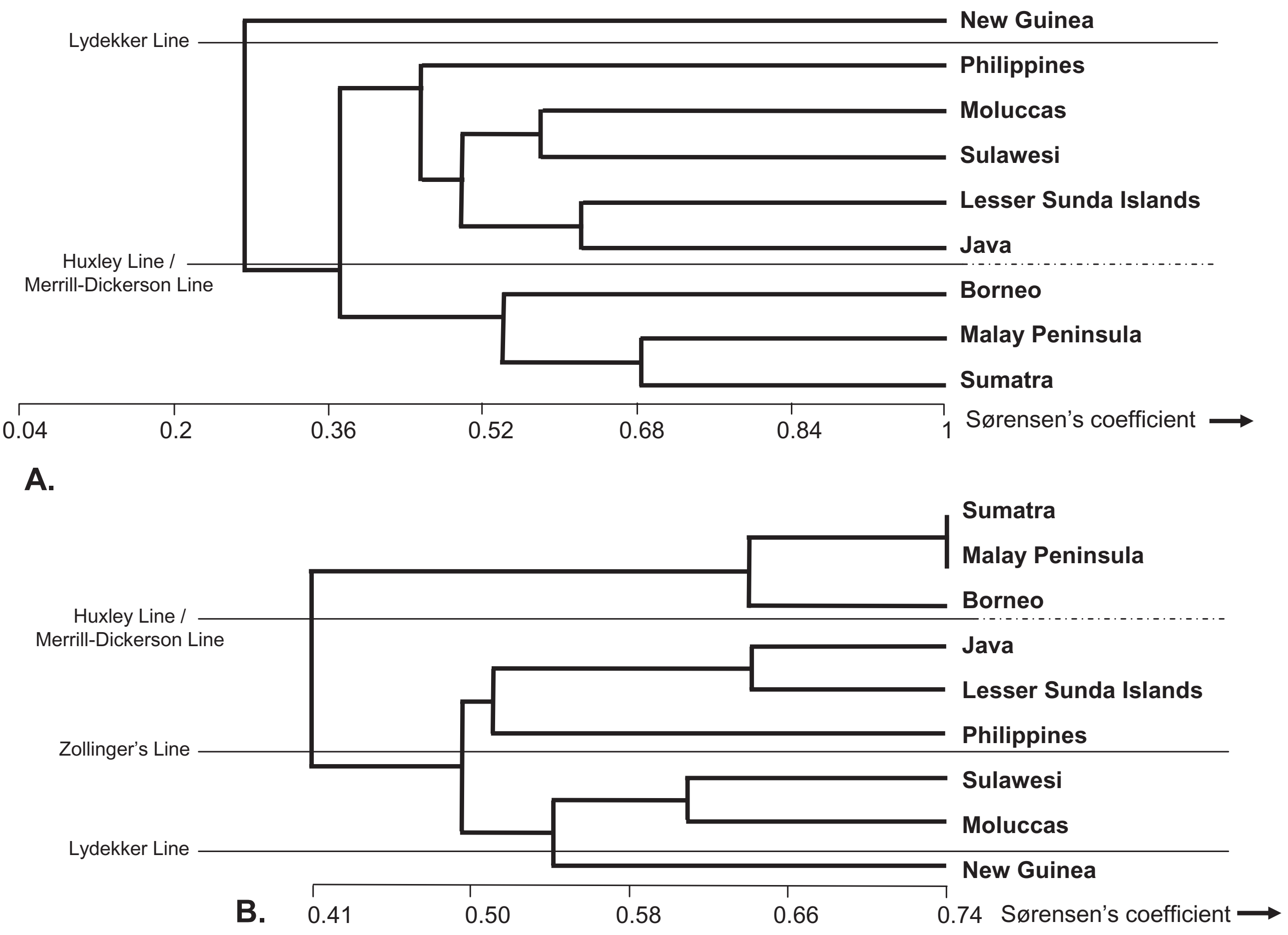

Figure 4. Cluster analysis (UPGMA with Sørensen's coefficient). The Merrill–Dickerson or Huxley Line is dotted near Java to show that the results of the present study place Java at the other side of this line. A, for all data; B, for the 100 submatrices.

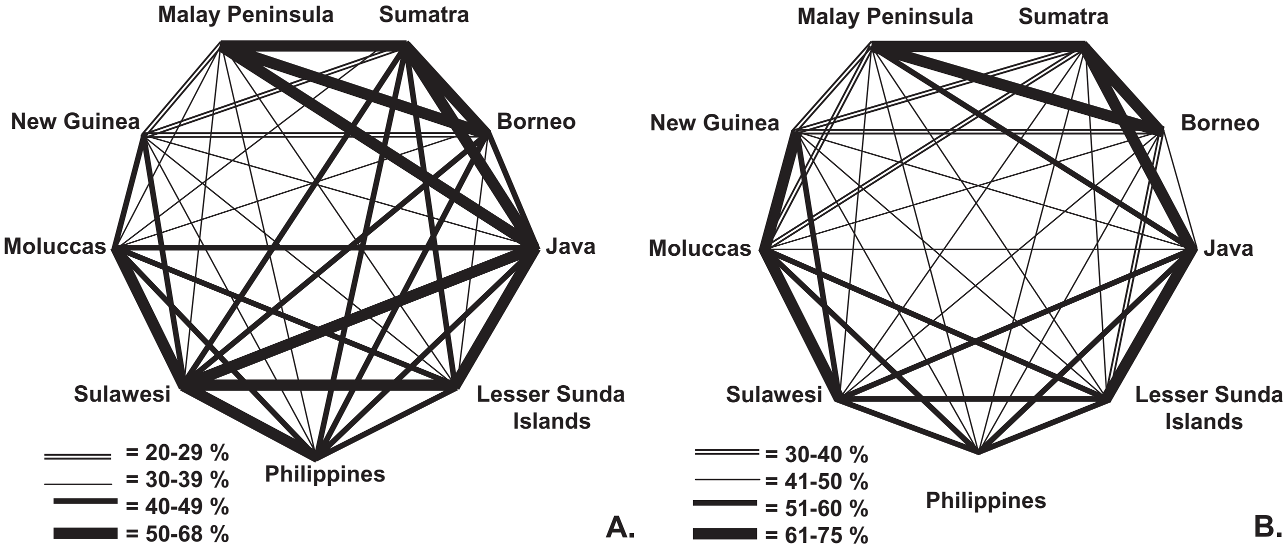

Figure 5. Diagram of Kroeber's coefficient (Appendix, Table A1). The thickness of the lines (four classes) indicates the mean percentages of floral similarity between pairs of areas at the ends of each line, whereby the thickest lines represent the highest similarities. A, for all data; B, for the 100 submatrices.

eastern boundary (Table 2). The western boundary more or less follows the Merrill–Dickerson or Huxley Line (Figs 2A, 3A, 4A) but has to be adjusted for Java, running west of (instead of east of) this island. When the results of the submatrices analysis are considered, then the western boundary follows the adjusted Merrill–Dickerson or Huxley Line but Lydekker's Line no longer forms the eastern boundary because Zollinger's line, which subdivides Wallacea, becomes more important (Figs 1, 4B). The latter line, however, is not distinct in the NMS analysis (Fig. 3B).

All analyses that included the complete data set clearly show that we are not dealing with two areas (east–west) but three areas: the Sunda Shelf, Wallacea, and the Sahul Shelf, and all show that Java forms part of Wallacea. Of these three areas, Wallacea is the weakest phytogeographic area in terms of endemic species and coherence (Kroeber's coefficients, Fig. 5A). This is underpinned by the analyses of the 100 submatrices, which indicate that two lines are valid but limits Wallacea to Java, the Lesser Sunda Islands, and the Philippines (NMS analysis excepted), with Java and the Lesser Sunda Islands showing the highest coherence (Fig. 5B).

In view of the largely unique flora of New Guinea (54% of the species are endemic), we suggest that, based on our phytogeographic results, Malesia should be divided into three geographic areas (Area 1 = Sunda Shelf minus Java; Area 2 = Wallacea with Java, and Area 3 = the Sahul Shelf; Fig. 1, thick lines). Furthermore, we suggest that Wallacea can be subdivided into a western component (Java, Philippines, and the Lesser Sunda Islands) and an eastern component (Sulawesi and the Moluccas). Sulawesi and the Moluccas are more closely linked to the Australian–Papuan phytogeographic region, whereas Java, the Philippines, and the Lesser Sunda Islands are more closely linked to the flora of the Orient. In terms of endemic species, Wallacea as defined here, has fewer endemic species than the Sunda and Sahul Shelves, although, with 35% (Table 1) of the flora endemic, it remains a region worthwhile of recognition and not just a transition zone between the two other areas.

There are two major factors that, most probably, have contributed to the formation of these three areas. First, the areas reflect the present general climatic conditions in Malesia. Currently, the Sunda and Sahul Shelves are everwet throughout the year but most of Wallacea has a yearly dry monsoon (Van Steenis, 1979: fig. 5; Whitmore, 1981: fig. 5.2). Obviously, at the large scale level of our BUs, such large-scale climatic differences will have an obvious direct effect on species composition. Second, during glacial maxima, the Sunda Shelf and the Sahul Shelf formed continuous land masses, whereas most of Wallacea was late to emerge (perhaps even as late as approximately 5 Mya) above sea level and contained sea passages at times when they were absent from the Sunda and Sahul shelves. The presence of dispersal barriers during glacial periods combined with a partly late emergence above the sea explains to a certain extent why the flora of Wallacea is less distinct and less coherent than that of the Sunda and Sahul shelves.

The boundaries between the three areas are clearly important barriers for species dispersal. They show up in historical biogeographic analyses as major vicariance patterns (i.e. dispersal followed by vicariance) (Turner *et al*., 2001; Van Welzen *et al*. 2003).

JAVA'S POSITION

The position of Java is aberrant. The cluster, PCA and NMS analyses of all data and the 100 submatrices all place Java in Wallacea, whereas, normally, Java is considered to be part of the Sunda Shelf area to which it belongs geologically. Apparently, Java is more similar to the Wallacean areas based on overall floral composition (cluster analysis, Kroeber) and variance (PCA, NMS) than to the Sunda Shelf. The placement may, first, be the result of differences in climate between Java and the remainder of the Sunda Shelf BUs. The climate on the greater part of Java varies from slightly seasonal in the West to strongly seasonal in the east; only the south-western tip of Java has an everwet climate resembling that of the Sunda Shelf. Second, most people consider Java to be part of Sunda Shelf area not only as a result of the geological history, but also because they are/were more familiar with the flora of the ever-wet part of the island (i.e. close to Bogor and Jakarta where most plant collecting has occurred) than with the flora of the remaining dryer but much larger (and relatively undercollected) part of Java (preliminary analysis of data in our collection record database). The Kroeber analysis (Fig. 5), which designates (similar to the cluster analysis) resemblance in floral composition, clearly shows the ambivalent character of the flora of Java, indicating that there are strong bonds between its flora and the everwet areas of the Malay Peninsula and Sumatra, as well as with areas in the drier Wallacea (Lesser Sunda Island, Sulawesi). However, the PCA, NMS, and cluster analyses do not show the resemblance of Java with the everwet Sunda land areas. Probably, this reflects the fact that the dry part of Java is much larger than the everwet part and that these analyses necessarily associate BUs on the basis of the stronger overall contribution of the drier elements of the flora of Java, which therefore groups closer with Wallacea. Our analyses necessarily treat Java as a single BU and do not allow for a split into a wetter and drier part. This will be the topic of research that we are presently carrying out, whereby (modelled) distributions of species will be mapped and compared.

The Kroeber analysis (Fig. 5) also shows that, of the BUs on the Sunda Shelf, the flora of Java is most similar to that of Sumatra and the Malay Peninsula and more weakly resembles that of Borneo. This probably reflects the fact that, during glacial maxima, there was a drier savannah corridor running from the South-East Asia main land via the Malay Peninsula, Sumatra, and Java or via the dry sea north of these areas to Wallacea (Morley & Flenley, 1987; Bird *et al*., 2005; Cannon *et al*., 2009; Hall, 2009), probably limiting, or even preventing, species exchange between Java and everwet Borneo. Thus, the resemblance between the three dry corridor areas (Malay Peninsula, Sumatra, and Java) is, to a large extent, based on species that favour a partly dry period. Indeed, differences in climate do not have to be large to create such a distribution boundary. For example, presently, the western boundary of Malesia lies in the most southern provinces of Thailand, just above the Malay border. North of this boundary zone, there is a short annual dry period, south of it an everwet climate is present. This difference is sufficient to prevent 200 genera present north of the boundary zone from crossing to the south and 375 genera present south of the boundary zone from crossing to the north (Van Steenis, 1950a).

PALAWAN'S POSITION

We had to move the Merrill–Dickerson/Huxley Line to lie between North Borneo and Palawan, instead of between Mindoro and Palawan (thus Palawan is now grouped together with the Philippines and not with Borneo). Geologically, north Palawan up to Mindoro is a microplate of Sundaic origin with the southern part of Palawan being formed during the collision with Borneo (Michaux, 2010). Floristically, there is similarity between Palawan and Borneo as a result of either a land connection between North Borneo and Palawan during glacial periods (Morley & Flenley, 1987) or because both areas almost touched in the Pleistocene when the landmasses followed the 120-m bathymetric contour (Heany, Walsh & Townsend Peterson, 2005) and dispersal was facilitated (Smith *et al*., 2000). On the other hand, Palawan harbours many endemic plant species (Madulid, 1987; Esselstyn, Widmann & Heaney, 2004) and shares a large part of its flora with the other Philippine islands. The latter is apparent from Table 2, where the numbers of species being stopped East of our changed Merrill–Dickerson/Huxley Line is 3099, whereas 2742 species are stopped West of the line. Similarly, Tan (1996) has shown that the mosses of Palawan bear little relationship to those of Borneo, being mostly an extension of the moss flora of the Philippines.

FLORISTIC BONDS, KROEBER ANALYSIS, AND GLACIAL MAXIMA

The Kroeber analyses (Fig. 5) show Java and the Lesser Sunda Islands to have strong floristic bonds and, in the cluster analyses (Fig. 4), they also group together. Glacial periods could provide a plausible explanation for this grouping. During glacial maxima, Java and Bali were connected, just as all of the other Lesser Sunda Islands formed a continuous area, with only a narrow sea strait between Bali and Lombok (Morley & Flenley, 1987; this is where Wallace's Line passes). Therefore, easily dispersed species (well represented in Wallacea, see Introduction) could move between Java and the Lesser Sunda Islands connecting to Sulawesi and then to the Philippines and the Moluccas (Van Steenis, 1979; Whitmore, 1981).

The Kroeber coefficients (Fig. 5) also show relatively strong species resemblances between Borneo and the Philippines and between Borneo and Sulawesi. Again, these connections may reflect the effects of glaciation. During glacial periods, land connections (Morley & Flenley, 1987) or only narrow seas (Heany *et al*., 2005) existed between Borneo and the Philippines, thus allowing an exchange of floral elements. The western land connection stretched from North Borneo to Palawan and a few islands north of it; the eastern one linked North-East Borneo and Mindanao up to Luzon and Mindoro (Morley & Flenley, 1987). However, such direct links via land connections did not exist during glacial periods between Borneo and Sulawesi because the deep Makassar Strait was always present (up to 2000 m presently) as a barrier since the Eocene (Hall, 2009).

New Guinea has an isolated position in the Kroeber analysis (Fig. 5) of all data, only showing moderately strong floral affinities with the Moluccas and Sulawesi. The analyses of the 100 submatrices shows that the Moluccas and Sulawesi share large parts of their flora with New Guinea (Appendix, Table A1). This indicates that floral exchange between these three areas must have taken place. Such exchange must have been almost exclusively confined to well-dispersing species as sea barriers were always present between New Guinea and the Moluccas and Sulawesi.

THE DIFFERENT ANALYSES

Our use of two different sets of analyses and a number of different statistical techniques have allowed a full examination of our data. The fact that the analyses produce complimentary results is reassuring and suggests that our conclusions are robust. The PCA, NMS, and UPGMA of the complete dataset all show the same groupings with Java positioned within Wallacea. Kroeber's coefficient clearly adds value to all analyses by demonstrating the equivocal position of Java. Within all analyses, the very strong resemblance in floral composition between the Lesser Sunda Islands and Java overwhelmes the lower resemblance between Java and Sumatra.

The analyses of the 100 submatrices showed that there was an area size (and thus number of species) effect. Borneo remained in more or less the same position in all analyses (Figs 2B, 3B, 4B, 5B), somewhat isolated from the Malay Peninsula and Sumatra. However, there was an effect for New Guinea. In the analyses of all data, New Guinea was clearly isolated from all other areas (Figs 2A, 3A, 4A, 5A) but was much closer to the Moluccas in the PCA, NMS, and Kroeber's coefficient of the 100 submatrices (Figs 2B, 3B, 5B, respectively) and to Sulawesi and the Moluccas in the UPGMA (Fig. 4B). However, based on the unequivocal results of the analyses of all data, the more than 50% endemic species and a wet climea New Guinea should be regarded as a separate floristic area.

CONCLUSIONS AND RECOMMENDATIONS

In conclusion, there is no sharp east–west boundary in plant distributions in Malesia. Indeed, several boundaries apply. We consider that it is better to recognize three areas on the basis of floristic affinities/similarities (not species numbers). All the islands of the Sunda Shelf, except Java, form the everwet Sundaland floristic group. A second floristic group called Wallacea constists of the central islands together with Java. This group can be split into two sub-areas: Java, the Philippines and the Lesser Sunda Islands have a more Oriental flora, whereas Sulawesi and the Moluccas have a more Australian Flora. New Guinea or the Sahul Shelf forms a separate, third entity. Indeed, Java should probably be split into two areas, the everwet part connecting with the Sunda Shelf and the area with a pronounced dry monsoon forming part of Wallacea. We are slowly building a different dataset to address this issue in the future. Despite the complex geological history of Malesia, the species distribution patterns can best be explained by present day climatic differences in Malesia and the long-term effects of land bridges and climatic conditions during glacial maxima. A partial and underlying explanation of these patterns may be that the flora of Wallacea appears less coherent because the areas constituting Wallacea were the last to become united, were late to appear (to a large extent) above the surface of the sea, and comprised the only areas that always had effective dispersal barriers in the form of many sea channels. It is possible, as an analogy, to envisage Wallacea acting as a filter between the everwet floras of the Sunda and Sahul Shelves, although as a filter acting to both retain and subsequently develop its own, unique, contents. Widespread genera ranging from the Sunda Shelf to the Sahul Shelf often show far less and usually endemic species in Wallacea, which is indicative of rare dispersal in combination with isolation and speciation. Perhaps a similar filter-type concept might be usefully applied elsewhere in the South-East Asian region to explain some of the other evident floristic discontinuities such as the Isthmus of Kra, where sea-level changes are also likely to have had significant biogeographic impact (Woodruff, 2003) by differentially cutting-up the landscape spatially and temporally. A future analysis, in which important traits of the life history of plants such as mode of dispersal are compared with distribution, may reveal those ecological groups that cross phytogeographic boundaries, as well as those that do not.

ACKNOWLEDGEMENTS

We thank Bernard Michaux, Ulf Swenson, and the reviewers for very constructive remarks that greatly improved an earlier draft of the manuscript.

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APPENDIX

Table A1. Kroeber's coefficients

	Species	MalPen	Borneo	Java	Philip	Sulawesi	LSI	Moluccas	NG
Results for all data									
Sumatra									
Species	2068	1438	1306	999	809	671	560	470	576
Kc		68	56	61	41	44	45	36	24
%		70/67	63/48	48/74	39/44	32/55	27/62	23/50	28/20
Malpen									
Species	2138		1297	831	744	603	483	443	523
Kc			54	50	38	39	38	34	21
%			61/48	39/62	35/40	28/50	23/54	21/47	24/18
Borneo									
Species	2714			773	892	696	473	508	575
Kc				43	41	41	35	36	21
%				28/57	33/48	26/57	17/52	19/54	21/20
Java									
Species	1347				762	683	702	490	581
Kc					49	53	65	44	32
%					57/41	51/56	52/78	36/52	43/20
Philippines									
Species	1846					784	582	579	696
Kc						53	48	47	31
%						42/65	32/65	31/62	38/24
Sulawesi									
Species	1215						571	624	686
Kc							55	59	40
%							47/63	51/67	56/24
Lesser Sunda Isls									
Species	902							454	515
Kc								49	38
%								50/48	57/18
Moluccas									
Species	937								696
Kc									49
%									74/24
New Guinea									
Species	2876								

Results for the 100 random sub-matrices*									
Sumatra									
Species	1809–1848	1334–1371	1215–1246	980–997	793–807	666–671	555–560	467–470	563–574
Kc		73–75	64–65	64–65	47–48	47–47	47–48	39–40	35–35
Malay Peninsula									
Species	1799–1840		1202–1235	821–830	729–742	599–603	479–483	440–443	514–523
Kc			64–65	54–54	44–45	42–43	41–42	37–38	31–32
Borneo									
Species	1962–2008			762–773	851–874	684–696	468–473	503–508	562–571
Kc				48–49	49–50	47–47	39–40	41–42	33–34
Java									
Species	1309–1329				756–762	679–683	692–702	487–490	576–581
Kc					53–54	55–55	66–68	46–47	41–42
Philippines									
Species	1523–1552					775–784	576–582	569–579	670–688
Kc						58–59	52–53	51–52	45–46
Sulawesi									
Species	1158–1184						566–571	616–624	673–686
Kc							57–58	61–62	52–53
Lesser Sunda Isls									
Species	846–873							447–454	499–513
Kc								51–53	46–47
Moluccas									
Species	867–897								657–678
Kc									60–61
New Guinea									
Species	1474–1491								

The first line per island shows the numbers of species, the second line shows the Kroeber coefficients (*Kc*; mean % of shared species), and the third line (only for all data) shows the percentages of shared flora per BU (the first number for the BU in the first column, the second number for the BU in the top row).

*Ranges indicate the variation among the matrices.