

# A floristic analysis of the lowland dipterocarp forests of Borneo

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## Abstract

**Aim** To (1) identify floristic regions in the lowland (below 500 m a.s.l.) tropical dipterocarp rain forest of Borneo based on tree genera, (2) determine the characteristic taxa of these regions, (3) study tree diversity patterns within Borneo, and (4) relate the floristic and diversity patterns to abiotic factors such as mean annual rainfall and geographical distance between plots.

**Location** Lowland tropical dipterocarp rain forest of Borneo.

**Methods** We used tree (diameter at breast height  $\geq 9.8$  cm) inventory data from 28 lowland dipterocarp rain forest locations throughout Borneo. From each location six samples of 640 individuals were drawn randomly. With these data we calculated a Sørensen and Steinhaus similarity matrix for the locations. These matrices were then used in an UPGMA clustering algorithm to determine the floristic relations between the locations (dendrogram). Principal coordinate analysis was used to ordinate the locations. Characteristic taxa for the identified floristic clusters were determined with the use of the INDVAL method of Dufrene & Legendre (1997). Finally, Mantel analysis was applied to determine the influence of mean annual rainfall and geographical distance between plots on floristic composition.

**Results** A total of 77 families and 363 genera were included in the analysis. On average a random sample of 640 trees from a lowland dipterocarp forest in Borneo contains  $41.6 \pm 3.8$  families and  $103.0 \pm 12.7$  genera. Diversity varied strongly on local scales. On a regional scale, diversity was found to be highest in south-east Borneo and central Sarawak. The most common families were Dipterocarpaceae (21.9% of trees) and Euphorbiaceae (12.2% of trees). The most common genera were *Shorea* (12.3% of trees) and *Syzygium* (5.0% of trees). The 28 locations were clustered in geographically distinct floristic regions. This was related to the fact that floristic similarity depended strongly on the geographical distance between plots and similarity in mean annual rainfall.

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**Conclusions** We identified five main floristic regions within the lowland dipterocarp rain forests of Borneo, each of which had its own set of characteristic genera. Mean annual rainfall is an important factor in explaining differences in floristic composition between locations. The influence of geographical distance on floristic similarity between locations is probably related to the fact that abiotic factors change with distance between plots. Borneo's central mountain range generally forms an effective dispersal barrier for the lowland tree flora. Diversity patterns in Borneo are influenced by the mid-domain effect, habitat size and the influence of past climatic changes (ice ages during the Pleistocene).

**Keywords**

Tropical rain forest, Borneo, floristic regions, tree generic composition, diversity patterns, precipitation, geographical distance, dispersal limitation.

## INTRODUCTION

Floristic analyses are very useful for identifying spatial patterns in plant diversity and composition, and when combined with environmental, geological and historical variables, can provide important information on the processes that maintain the high levels of tree species diversity in tropical forests. For that reason floristic analyses have recently received considerable attention in the Neotropics (ter Steege *et al.*, 1993, 2000a,b; Duivenvoorden, 1995; Terborgh & Andresen, 1998; Oliveira-Filho & Fontes, 2000; de Oliveira & Nelson, 2001; Pyke *et al.*, 2001). In Borneo, these kind of studies are still rare, and have been limited to parts of northern Borneo (Ashton, 1976; Proctor *et al.*, 1983; Baille *et al.*, 1987; Newbery, 1991; Potts *et al.*, 2002). However, although still few, the number of reliable tree inventories that is currently available for Borneo now enables us to carry out a first floristic analysis for the lowland tree flora of the whole island.

Borneo is the second largest tropical island in the world after New Guinea and is floristically very rich, possibly harbouring up to 15,000 different plant species including *c.* 3000 species of trees (MacKinnon *et al.*, 1996). The majority of these tree species is found in the lowland rain forests, which in Borneo are usually dominated by species of the Dipterocarpaceae (Whitmore, 1984). Although the geological history of Borneo is rather complicated (Ridder-Numan, 1998; Morley, 2000), it is likely that the recent glacial periods during the Pleistocene have had a profound influence on the present-day tree flora of the island. During these periods Borneo was connected by land bridges to the south-east Asian mainland and present-day islands such as Java and Sumatra (Morley, 2000). Evidence also suggests that during these glacial periods south-western Borneo consisted mainly of savanna vegetation with some scattered rain forest fragments along major rivers and on mountain slopes, while northern and eastern Borneo remained covered with rain forest (Heaney, 1991; Verstappen, 1992; Thomas, 2000; Gathorne-Hardy *et al.*, 2002). This means that the current situation, in which the whole island is covered with rain forest must have developed relatively recently, after the

last glacial period (*c.* 10,000 years ago). If so, this recolonization of south-western Borneo by rain forest trees since the last ice-age might still be visible in the present-day tree flora.

Another factor that can have influenced the floristic composition of the lowland tree flora of different parts of Borneo is the presence of a central mountain range that divides the island in a northern and southern part. Several studies in Borneo have shown that the tree flora changes gradually along altitudinal gradients, and most characteristic lowland tree species become rare above *c.* 800 m altitude (Kitayama, 1992; Pendry & Proctor, 1997; Adam, 2001). As the central mountain range exceeds 800 m altitude along most of its length, it could thus form an effective barrier for the dispersal of the lowland tree floras of northern and southern Borneo.

Next to these historic and geographical factors, environmental variables such as mean annual rainfall probably also influence floristic composition and similarity patterns. Currently there is a lively debate in the literature on the role of these environmental variables relative to chance processes in determining floristic patterns. On the one hand there is a lot of evidence that environmental variables do influence floristic composition (Gentry, 1988; Duivenvoorden & Lips, 1995; Terborgh & Andresen, 1998; ter Steege *et al.*, 2000b; Debski *et al.*, 2002; Potts *et al.*, 2002; Wright, 2002), but on the other hand, these associations are usually weak because the majority of taxa is mostly not associated with any of the studied variables. This has led some researchers to propose that neutral (chance) processes, in the form of dispersal limitation, play a major role in determining floristic composition (Hubbell, 1979, 1997, 2001; Brokaw & Busing, 2000; Chave & Leigh, 2002).

In this paper, we use tree species inventory data from 28 locations of tropical lowland (below 500 m altitude) dipterocarp rain forest from Borneo to investigate the floristic patterns on this island. Our main aims are to: (1) identify floristic regions for Borneo within this forest type, (2) determine the characteristic taxa of these regions, (3) study tree diversity patterns within Borneo and (4) relate the floristic and diversity patterns to abiotic factors such as

mean annual rainfall and geographical distance between plots. Additionally, we want to investigate (a) whether the postulated recent recolonization of south-western Borneo is still visible in the present-day floristic composition of the island and (b) if the central mountain range in Borneo acts as an effective dispersal barrier for the lowland tree flora.

## MATERIALS AND METHODS

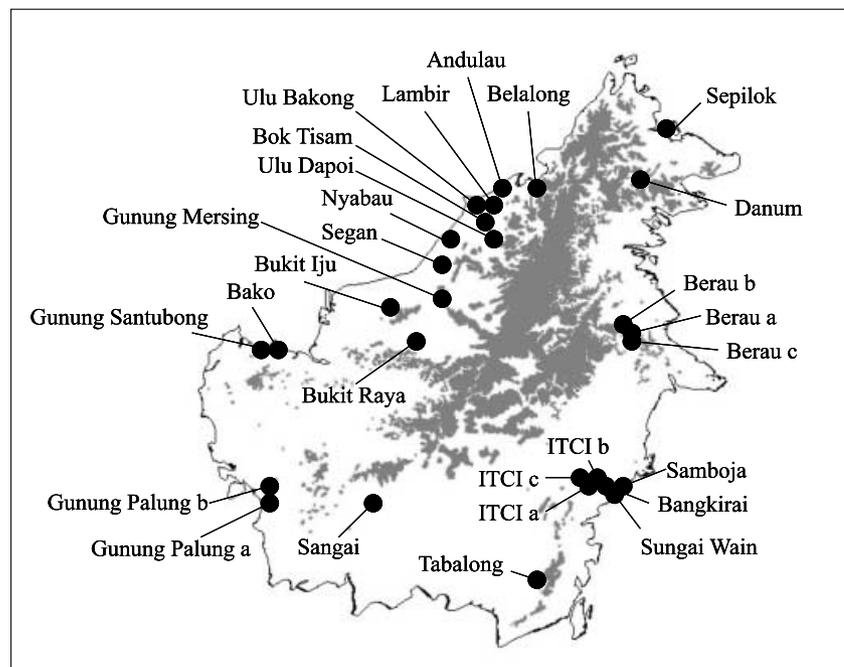
### Data preparation

Inventories of trees (diameter at breast height  $\geq 9.8$  cm) from 28 lowland (below 500 m a.s.l.) dipterocarp rain forest locations throughout Borneo were used for this study (Fig. 1; Table 1). Due to the large number of morpho-species in each inventory we were unable to directly compare the locations based on their species composition. Instead, we used the number of individuals per genus for the floristic analysis because most individuals were identified up to genus level in all inventories (for the nomenclatural authorities of the genera we refer to Steenis, 1987). The disadvantage of this approach is that the precision of the analysis is limited (less detail), but this is compensated for by the higher reliability of the results. Furthermore, Higgins & Ruokolainen (in press) have shown that floristic patterns detected with genera resemble those detected with species very closely.

Plot sizes, shapes, layout, numbers, and the number of trees inventoried differed considerably between locations. Furthermore, most locations consisted of a number of plots located within a radius of several kilometres. To make the locations more comparable, all separate plots within each location were combined. We then randomly drew 640

individuals from each location (this number was based on the location with the smallest number of trees inventoried). To test whether the random draws from locations with small numbers of inventoried trees were not significantly less diverse than those drawn from locations with high numbers of inventoried trees we performed a regression analysis between total number of trees inventoried in a location and the total number of genera in the random samples of 640 trees. This regression analysis showed a small but significant positive linear relation between total number of trees inventoried and the genera diversity of random samples of 640 trees (correlation coefficient = 0.38,  $R^2 = 14.3$ ,  $P = 0.047$ ). However, this relation was strongly influenced by the exceptionally high genera diversity in Lambir (Sarawak), which was identified as an unusual residual in the regression analysis. When Lambir was left out from the regression analysis, no significant relation between number of trees inventoried and genera diversity of the random samples could be detected, e.g. the random samples of 640 trees gave a comparable indication of the genera diversity at the different locations.

To get a better sample of the total genera composition of the locations, the random draws of 640 trees were repeated six times for each location (with replacement of all individuals after each draw of 640 trees). This means that in all further analyses each location was represented by six random samples of 640 trees. A drawback of this method is that six random draws from locations with few trees inventoried will be more similar in generic composition than those of locations with a large number of trees inventoried. However, the floristic similarity between the six draws from each location were, in all cases, much smaller than between locations.



**Figure 1** Map of Borneo with the 28 locations used in this study (see also Table 1). Montane areas (altitude above 500 m) are indicated in grey.

**Table 1** Locations from which tree species inventories were used in this study with their longitude/latitude position, total sampled area, number of trees sampled, diameter at breast height above which trees were included in the inventory, mean annual rainfall of closest weather station, and the source of the inventory data. All forests sampled were old growth, undisturbed forests except the inventory from Tabalong, which had been logged previously

Country/province	Location (longitude/latitude)	Area (ha)	Trees ( <i>n</i> )	Diameter at breast height $\geq$ (cm)	Rainfall (mm year <sup>-1</sup> )	Inventory data from
Brunei						
Andalau	114.32 E 4.38 N	20.0	12,660	9.8	3395	Ashton (1964)
Belalong	115.08 E 4.33 N	20.0	8550	9.8	3756	Ashton (1964), Poulsen <i>et al.</i> (1996)
Kalimantan West						
Gunung Palung a	110.21 E 1.00 S	3.1	968	15.0	4156	Cannon (unpubl. data)
Gunung Palung b	110.10 E 1.15 S	4.5	2797	10.0	4156	Webb (1997)
Kalimantan Central						
Sangai	112.31 E 1.29 S	15.0	7885	10.0	2618	Wilkie (unpubl. data)
Kalimantan South						
Tabalong	115.30 E 3.30 S	2.2	991	10.0	2431	Payne (unpubl. data)
Kalimantan East						
Berau a	117.15 E 1.59 N	3.0	2116	10.0	2329	Slik (unpubl. data)
Berau b	117.08 E 1.54 N	1.0	645	10.0	2329	Slik (unpubl. data)
Berau c	117.14 E 2.02 N	12.0	7195	10.0	2329	Strek (unpubl. data)
Bukit Bankirai	116.52 E 1.02 S	1.4	676	10.0	2695	Slik (unpubl. data)
ITCI a	116.29 E 0.58 S	3.1	1132	10.0	2493	Eyk-Bos (unpubl. data)
ITCI b	116.37 E 0.56 S	3.7	1316	10.0	2493	Eyk-Bos (unpubl. data)
ITCI c	116.23 E 0.49 S	3.9	918	10.0	2493	Slik (unpubl. data)
Samboja	116.57 E 0.59 S	12.5	6404	10.0	2411	Kartawinata, Mathijs & Slik (unpubl. data)
Sungai Wain	116.49 E 1.05 S	5.6	2421	10.0	2472	Eichhorn, Nieuwstadt & Sidiyasa (unpubl. data)
Sabah						
Danum	117.48 E 4.58 N	8.0	3433	10.0	2675	Newbery (unpubl. data)
Sepilok	118.00 E 5.56 N	4.6	2147	10.0	3103	Fox (1973)
Sarawak						
Bako	110.28 E 1.43 N	2.4	1892	9.8	4052	Ashton (unpubl. data)
Bok Tisam	114.06 E 3.38 N	6.0	3533	9.8	2865	Ashton (unpubl. data)
Buki Iju	112.35 E 2.46 N	9.0	9267	9.8	3662	Ashton (unpubl. data)
Bukit Raya	112.57 E 2.01 N	13.2	9580	9.8	3184	Jonkers (1982), Ashton (unpubl. data)
Gunung Santubong	110.20 E 1.44 N	1.2	907	9.8	4052	Ashton (unpubl. data)
Gunung Mersing	113.06 E 2.31 N	9.0	4619	9.8	3184	Ashton (unpubl. data)
Lambir	113.59 E 4.20 N	15.2	11,387	9.8	2993	Ashton & Nagamasu (unpubl. data)
Nyabau	113.06 E 3.14 N	3.0	2848	9.8	3819	Ashton (unpubl. data)
Segan	113.03 E 3.04 N	3.0	2467	9.8	3819	Ashton (unpubl. data)
Ulu Bakong	114.03 E 4.17 N	3.0	1705	9.8	2865	Ashton (unpubl. data)
Ulu Dapoi	114.27 E 3.14 N	1.2	986	9.8	2865	Ashton (unpubl. data)

### Borneo wide diversity patterns

To analyse diversity patterns (both family and genera diversity) in Borneo we used a grid system of 116 cells. For each cell we calculated the expected family and genera diversity based on its relative distance to each of the 28 locations of which we possessed tree inventory data in the following way: (1) we first calculated the distance from the centre of each grid cell to each of the 28 locations; (2) we then took the inverse of these distances so that locations far from the grid cell had lower values than locations that were close to the grid cell; (3) to standardize these values between 0 and 1 we divided the 28 inverse distances by their sum; (4) we then multiplied each standardized distance value with the diversity value (family and genera separate) of the location

where it belonged to; (5) the diversity value for the grid cell was then calculated by summing the 28 values thus obtained. In this way regional differences in family and genera diversity could be visualized on a map of Borneo.

### Cluster analysis

All statistical tests mentioned here and further in this paper were performed with 'Statgraphics for Windows 2.1' (Statistical Graphics Corp., Rockville, USA), 'Multi-Variate Statistical Package 3.01' (Kovach Computing Services, Anglesey, UK), and the 'R-Package' (freely available via P. Legendre's website: <http://www.fas.umontreal.ca/BIOL/legendre/indexEnglish.html>). Locations were grouped using cluster analysis, for which we applied both the Sørensen's

and the Steinhaus indices to calculate the floristic similarity between the locations (Jongman *et al.*, 1987; Legendre & Legendre, 1998). In general, the Steinhaus index partly reflects environmental similarities between locations because it includes abundance data, while Sørensen's index should, in principle, only highlight floristic similarities because it is only based on presence/absence data of taxa (Jongman *et al.*, 1987; Legendre & Legendre, 1998; McGarigal *et al.*, 2000). The locations were clustered using the UPGMA algorithm as the two-dimensional representation of the locations produced by this analysis (dendrogram) retains the true distribution of the locations in multi-dimensional space in an acceptable manner, especially in comparison with other cluster algorithms (McGarigal *et al.*, 2000). The Steinhaus matrix for the locations was based on the  $\ln(1+x)$ -transformed number of individuals per genus to down-rate the influence of dominant genera on the floristic analysis (Jongman *et al.*, 1987). The Sørensen's matrix was based on presence and absence data of genera in each location.

#### Determining characteristic genera for the identified floristic clusters

To determine the characteristic genera for each cluster in the cluster analysis we used the indicator method of Dufrene & Legendre (1997). This method calculates an indicator value (IV) for each genus in predefined clusters (like the clusters identified by a cluster analysis). It is especially suited for identifying indicator taxa independently of the plant (or animal) community as a whole (Dufrene & Legendre, 1997; McGeoch & Chown, 1998). The method gives an integrated measure for the relative mean abundance and the relative frequency of the studied genera in each cluster and is calculated as follows:

$$A_{ij} = N_{\text{individuals},ij} / N_{\text{individuals},i}$$

$$B_{ij} = N_{\text{locations},ij} / N_{\text{locations},j}$$

$$IV_{ij} = A_{ij} \times B_{ij} \times 100\%$$

where  $A_{ij}$  (relative mean abundance) is the mean number of individuals of genus  $i$  in cluster  $j$  divided by the mean number of individuals of genus  $i$  in cluster  $j$  plus the mean number of individuals of genus  $i$  outside cluster  $j$ ;  $B_{ij}$  (relative frequency) is the number of locations in cluster  $j$  where genus  $i$  is present divided by the total number of locations in cluster  $j$ ;  $IV_{ij}$  is the relative mean abundance of genus  $i$  in cluster  $j$  multiplied by the relative frequency of genus  $i$  in cluster  $j$  multiplied by 100%. Genera that are weakly associated with a cluster because they are either not abundant or not present in all the locations within that cluster will score a low IV. Only genera that have both a high mean abundance and are present in the majority of locations of a cluster will score a high IV for that particular cluster. IVs can vary between 0% and 100%, in which 0% indicates no association with a cluster, while 100% indicates that the genus was found in all locations of that particular cluster, and was absent in all other locations outside that cluster.

To test whether the observed IV of a genus in a cluster was significantly higher than could be expected based on a

random distribution of individuals over the locations, the observed IV was compared with 999 randomly generated IVs. These random IVs were generated with a random reallocation procedure in which the number of individuals per genus per location were randomly reshuffled over the locations (see Dufrene & Legendre, 1997). If the observed IV of a genus in a cluster fell within the top 5% of the random IVs (sorted in decreasing order) it was considered to deviate significantly from the expected random mean, i.e. the genus had a significantly higher IV than expected.

#### Ordination of locations

Ordinations of the locations were done using principal coordinate analyses (PCoA) (Legendre & Legendre, 1998) on the floristic similarity matrices (Steinhaus and Sørensen). The similarity matrices were first converted into distance matrices with the formula:  $D = 1 - S$ , where  $D$  is the distance and  $S$  the similarity value, before they were used in the PCoA.

#### Mantel analysis

We used a Mantel analysis (Mantel, 1967; Legendre & Legendre, 1998) to investigate the relative strengths of geographical distance vs. mean annual rainfall as determinants of floristic composition. A complete Mantel analysis entails computing distance matrices and then computing simple and partial Mantel statistics that are identical to those of simple and partial Pearson correlation coefficients, except the Mantel statistics take into account the natural dependence found in the distance matrices. When interpreting the results it is important to keep in mind that the Mantel test gives lower  $r$  values than the corresponding linear Pearson's correlations in univariate cases, but that the two methods generally agree on whether the correlation is statistically significant (Legendre, 2000). The statistical significance of each correlation was determined by a Monte Carlo permutation test to avoid problems related to autocorrelation and non-normal distributions of the measured variables. In all cases, 999 permutations were used, which allows testing of the statistical significance at the  $P < 0.001$  level for each individual correlation.

The spatial distance matrix was prepared by tabulating the pairwise, log-transformed geographical distances between locations. Distances were log-transformed because this has been shown to reflect the rapid decline of similarity between locations at short distances much better than a linear relationship (Condit *et al.*, 2002). The distances between locations were calculated as the shortest distance between them based on their longitude and latitude position, whereby we corrected for the curvature of the globe. The mean annual rainfall distance matrix for the locations was prepared by calculating the (absolute) difference in rainfall between each pair of locations. Mean annual rainfall values for the locations (Table 1) were based on the nearest weather stations. For the floristic distance matrices we used both the Steinhaus and the Sørensen indices.

## RESULTS

### General diversity and composition patterns for Borneo

The data set used for the floristic analysis contained 77 families and 363 genera. On average, a random sample of 640 trees consisted of  $41.6 \pm 3.8$  families and  $103.0 \pm 12.7$  genera. Variation in diversity between locations, even when they were close together, was high (Fig. 2). Lambir (Sarawak) stood out as the most diverse forest in Borneo, with both the highest family (49.0) and genera diversity (139.8). However, on a regional scale, both family and genera diversity were highest in south-east Borneo (Fig. 3a,b), while diversity decreased towards the north-west (West Kalimantan and western Sarawak) and north-east of Borneo (northern East Kalimantan and Sabah). These diversity patterns were more pronounced for genera than for families. No relation was found between mean annual rainfall and family, nor genera diversity.

The Dipterocarpaceae and Euphorbiaceae were by far the most dominant tree families in the lowland dipterocarp forests of Borneo with 21.9% and 12.2% of all trees, respectively (Table 2). *Shorea* (Dipterocarpaceae), *Syzygium* (Myrtaceae), *Diospyros* (Ebenaceae), *Madhuca* (Sapotaceae) and *Dipterocarpus* (Dipterocarpaceae) were the most common tree genera in Borneo with 12.3%, 5.0%, 3.4%, 3.2% and 3.1% of trees, respectively (Table 2).

### Floristic regions in Borneo

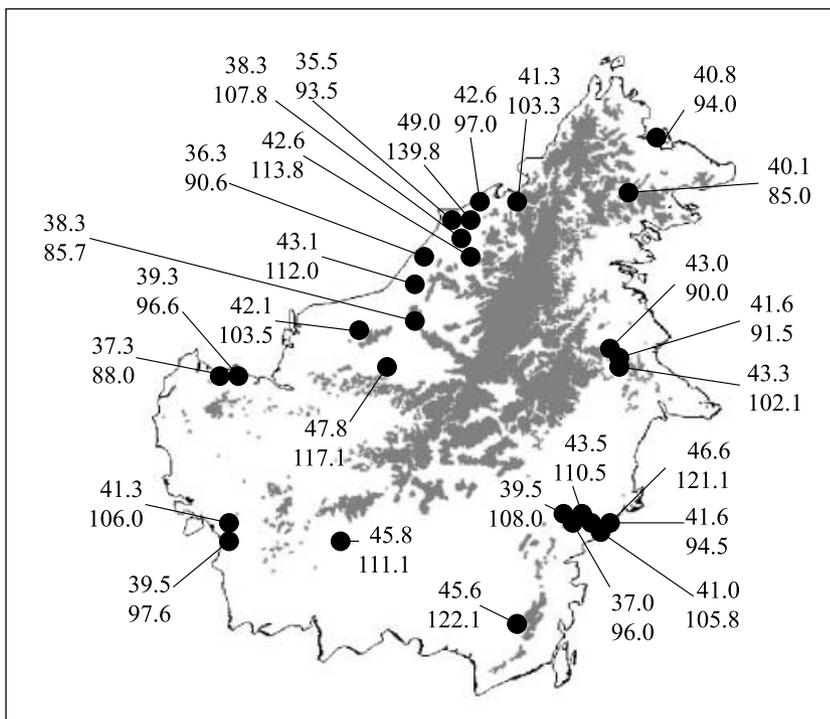
Cluster analysis (based on both Steinhaus and Sørensen's indices) generally clustered locations together that were

spatially close, resulting in geographically recognizable floristic regions (Fig. 4a,b). In both cluster analyses Bako and Gunung Santubong (western Sarawak, cluster A), Danum and Sepilok (eastern Sabah, cluster B), and Ulu Bakong, Bok Tisam, and Gunung Mersing (central Sarawak, cluster C) came out as the floristically most deviating locations in Borneo (Fig. 4a,b). With some minor disagreements between the two cluster analyses, the remaining locations were separated into two main clusters: (1) a northern cluster consisting of locations from Sarawak, Brunei and northern East Kalimantan (cluster E), and (2) a southern cluster consisting of locations from west, central, south and east Kalimantan (cluster D) (Fig. 5a,b). Some disagreement on the position of some of the Berau locations (northern East Kalimantan) existed. Using the Sørensen index, the Berau plots ended up in both cluster D and E, while the Steinhaus index grouped all Berau plots in cluster E. The characteristic genera of all the identified clusters are shown in Appendix 1.

The PCoA shows a clear separation between plots located north and south of Borneo's central Mountain range (Fig. 6a,b). However, the first three axes of the PCoA explained, respectively, 16%, 11% and 8% (Sørensen) and 19%, 12% and 7% (Steinhaus) of data variance only.

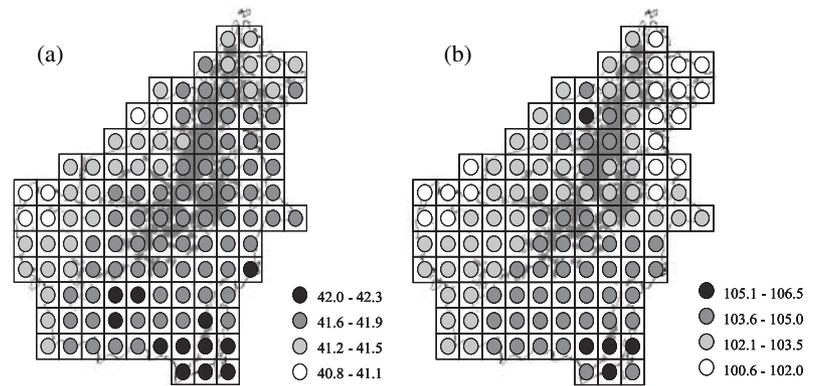
### Influence of geographical distance and rainfall on generic composition

The Mantel analysis showed that similarity in generic composition (based on both the Sørensen and Steinhaus



**Figure 2** Family/genera diversity (based on the average of six random samples of 640 trees at each location) for each of the 28 studied locations.

**Figure 3** Family (a) and genera (b) diversity patterns in Borneo, expressed as number of families (a) and genera (b) in random samples of 640 trees. South-east Borneo and central Sarawak are the most diverse regions, while north-west and north-east Borneo have a relatively low diversity.



**Table 2** The 25 most abundant plant families and genera of Borneo, based on tree inventory data from 28 lowland dipterocarp rain forest locations from Borneo. Abundance indicates the percentage of trees belonging to a particular family or genus in random samples of 640 trees, while frequency indicates the percentage of random samples of 640 trees in which a particular family or genus was present

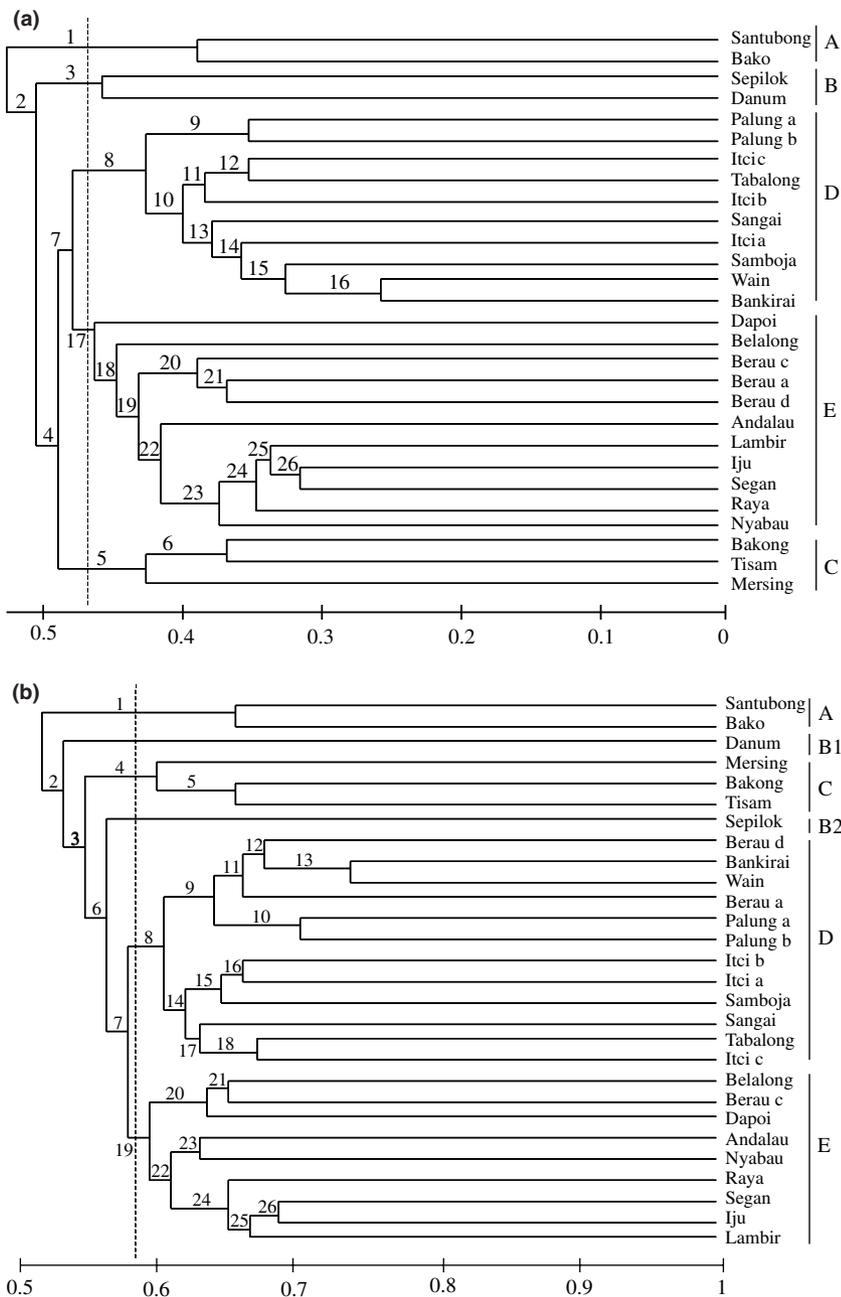
Families	Abundance (%)	Frequency (%)	Genera	Abundance (%)	Frequency (%)
Dipterocarpaceae	21.9	100.0	<i>Shorea</i>	12.3	100.0
Euphorbiaceae	12.2	100.0	<i>Syzygium</i>	5.0	100.0
Myrtaceae	5.2	100.0	<i>Diospyros</i>	3.4	100.0
Sapotaceae	5.0	100.0	<i>Madhuca</i>	3.2	99.4
Lauraceae	4.6	100.0	<i>Dipterocarpus</i>	3.1	100.0
Myristicaceae	4.3	100.0	<i>Hopea</i>	2.4	100.0
Burseraceae	4.0	100.0	<i>Vatica</i>	2.3	96.4
Anacardiaceae	3.6	100.0	<i>Knema</i>	2.2	100.0
Ebenaceae	3.4	100.0	<i>Dacryodes</i>	2.1	100.0
Annonaceae	3.2	100.0	<i>Mallotus</i>	1.6	87.5
Guttiferae	2.6	98.8	<i>Polyalthia</i>	1.5	92.3
Leguminosae	2.5	100.0	<i>Xanthophyllum</i>	1.4	97.0
Meliaceae	1.9	92.9	<i>Gluta</i>	1.4	87.5
Moraceae	1.6	96.4	<i>Artocarpus</i>	1.4	95.2
Flacourtiaceae	1.6	96.4	<i>Palaquium</i>	1.3	94.6
Fagaceae	1.4	97.6	<i>Dryobalanops</i>	1.3	67.3
Rubiaceae	1.4	100.0	<i>Teijsmanniodendron</i>	1.3	73.2
Polygalaceae	1.4	97.0	<i>Hydnocarpus</i>	1.3	83.3
Olacaceae	1.4	87.5	<i>Baccaurea</i>	1.3	99.4
Verbenaceae	1.4	74.4	<i>Aporosa</i>	1.3	93.5
Sterculiaceae	1.1	94.6	<i>Eusideroxylon</i>	1.1	63.1
Tiliaceae	1.1	99.4	<i>Santiria</i>	1.1	89.9
Celastraceae	1.1	97.0	<i>Lithocarpus</i>	1.1	94.6
Melastomataceae	1.0	98.8	<i>Aglaia</i>	1.0	83.9
Sapindaceae	0.9	92.3	<i>Macaranga</i>	1.0	73.8

index) was significantly related to both geographical distance ( $r = 0.40$  and  $0.44$  for Sørensen and Steinhaus, respectively) and mean annual rainfall differences ( $r = 0.31$  and  $0.34$  for Sørensen and Steinhaus, respectively) between locations (Table 3). After correction for dependency between geographical distance and rainfall differences, geographical distance between locations explained floristic similarity better ( $r = 0.31$  and  $0.34$  for Sørensen and Steinhaus, respectively) than mean annual rainfall did ( $r = 0.15$  and  $0.17$  for Sørensen and Steinhaus, respectively).

## DISCUSSION

### General aspects of Borneo's lowland tree flora

As expected the Dipterocarpaceae, which consists mainly of upper canopy and emergent tree species, was the most dominant tree family in Borneo with 21.9% of all trees. The Euphorbiaceae, which mainly consists of understorey and low to upper canopy tree species, ranked second with 12.2% of all trees. This is a pattern typical for most evergreen rain forests in the Sunda region which encompasses the mainland of south-east Asia, Sumatra, Java and Borneo (Ashton, 1964, 1976;



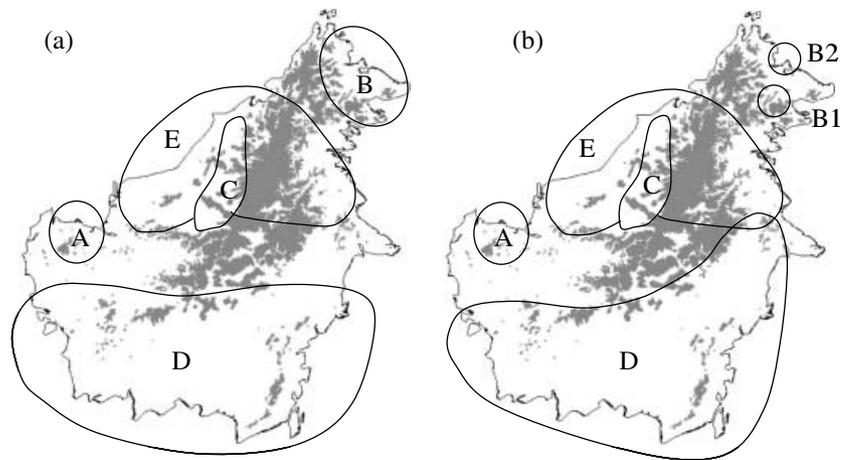
**Figure 4** Results of the UPGMA cluster analyses of the 28 locations from Borneo based on (a) Steinhaus similarity and (b) Sørensen's similarity. Both dendrograms, in general, cluster plots together that are spatially close, resulting in geographically recognizable floristic regions. Numbers along the branches of the dendrograms indicate the cluster numbers used in the indicator taxa analysis (Appendix 1). The dashed line indicates the cut-off level which we used to identify the main floristic regions in Borneo. These regions are indicated with characters (A to E).

Whitmore, 1984; Ho *et al.*, 1987; Gentry, 1988; Kochummen *et al.*, 1990; Kohyama, 1994; MacKinnon *et al.*, 1996; Blanc *et al.*, 2000; Condit *et al.*, 2000). The floristic composition of these forests differs markedly from those of tropical Africa and America where the legume family dominates (Gentry, 1988; Morley, 2000; ter Steege *et al.*, 2000b). Among Borneo's lowland families the legumes only rank 12th, and no legume genus even occurs among the 25 most common genera (Table 2). This difference is probably related to the fact that the flora of the Sunda Region, due to its isolation from other tropical regions since the Middle Cretaceous, followed its own

evolutionary pathway (Morley, 2000). However, it still remains to be explained why the dipterocarps became the dominating tree family in south-east Asia, especially as they only form an inconspicuous element in the tropical tree floras of Africa and America.

### General diversity patterns within Borneo

Highest family and generic diversity was found in south-east Borneo and central Sarawak, which contradicts common opinion that Kalimantan has a relatively low tree



**Figure 5** The main floristic regions identified by the cluster analysis using (a) Steinhaus similarity and (b) Sørensen similarity. Names of the regions correspond to the clusters shown in Fig. 4a,b.

diversity (Wong, 1998, but see Vink, 1981). There are strong indications that these areas have been covered by tropical rain forest for most of their history (Heaney, 1991; Verstappen, 1992; Thomas, 2000; Gathorne-Hardy *et al.*, 2002) and thus formed a very stable habitat for a long period of time. This probably means that extinction levels have been relatively low, which might have resulted in the higher taxa diversity observed for this area. Furthermore, both areas are located in the centre of the lowland habitat type that we studied (central Sarawak is the centre for this habitat type north of Borneo's mountain range, while south-east Borneo is the centre south of this mountain range). This means that the mid-domain effect, which states that highest taxa diversity can be found in the centre of a geographical area in the absence of environmental constraints (Laurie & Solander, 2002) might play a role as well. The mid-domain effect can be explained by the fact that most taxa distributions will overlap in the centre of a geographical region and least along its edges. The mid-domain effect is a qualitative property of all biological models based on range overlap counts and could thus also form an explanation for the diversity pattern that we found in Borneo's lowland forests.

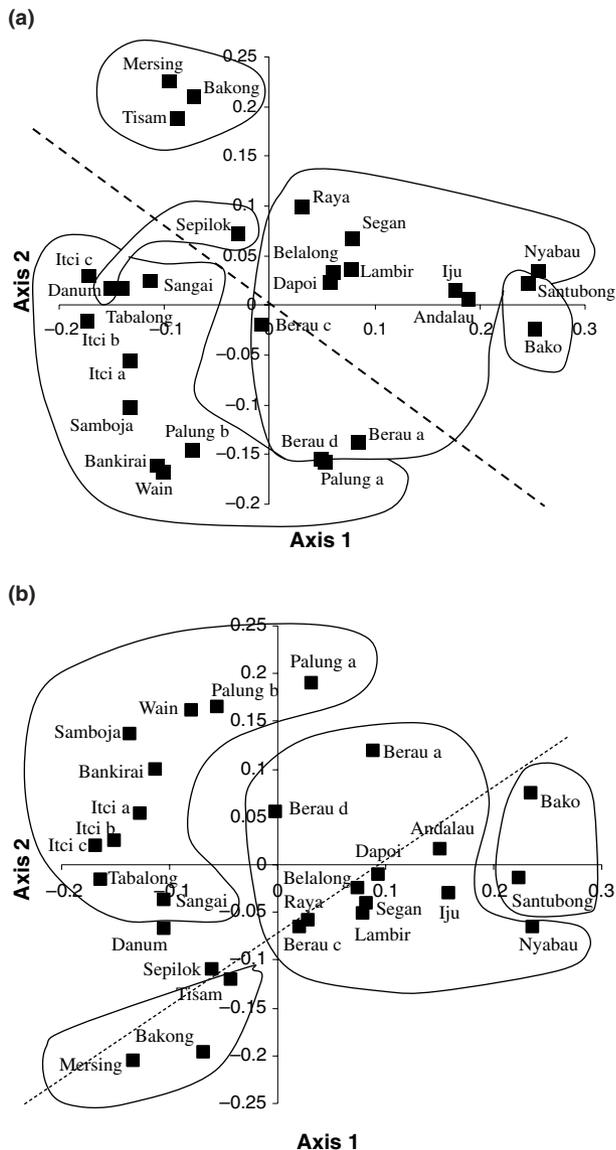
We also identified two major regions in Borneo where both family and genera diversity were considerably lower than in other parts of the island, namely west Borneo (West Kalimantan and western Sarawak) and north-eastern Borneo (Sabah and northern East Kalimantan). Part of the explanation of the low diversity in these areas is probably related to the above-mentioned mid-domain effect. However, for north-eastern Borneo, the low diversity is probably also related to the small size of this area (in fact the area consists of two even smaller lowland areas that are isolated from each other by a mountain range, namely eastern Sabah and northern East Kalimantan), in combination with its relative isolation from other parts in Borneo by mountain ranges. As diversity is negatively related with isolation and habitat size (MacArthur & Wilson, 1963; Schoener, 1976; Rosenzweig, 1995; Lomolino, 2001; Triantis *et al.*, 2003), it is likely that these

two factors have at least contributed to the lower diversity of north-eastern Borneo. For western Borneo, however, which is a large area that is not isolated from other lowland areas, this explanation does not hold. In fact, based on the high annual rainfall in this area (more than 4000 mm year<sup>-1</sup>) one would have expected high diversity in this region as absolute annual rainfall in Neotropical rain forests has been shown to be positively related with diversity (Gentry, 1988, but see ter Steege *et al.*, 2000b). Next to the mid-domain effect, the low diversity in western Borneo is probably also related to the fact that this area only became forested after the last ice-age, *c.* 10,000 years ago (Heaney, 1991; Verstappen, 1992; Thomas, 2000; Gathorne-Hardy *et al.*, 2002). This means that the current flora of western Borneo is of relatively recent origin and possibly has not yet reached an equilibrium between its potential and actual diversity.

#### General floristic patterns within Borneo

We found five major floristic regions within Borneo. The most deviating of these was the Santubong/Bako cluster of western Sarawak (cluster A in Fig. 5a,b). This area is part of the Riau Pocket and has been identified as rather distinct in other studies on the flora (Ashton, 1992; Ridder-Numan, 1998; Wong, 1998; Potts *et al.*, 2002) and fauna (MacKinnon & MacKinnon, 1986) of Borneo as well. The flora of this region has been reported to show relatively strong affinities to both the Malay Peninsula and Sumatra via the Riau Archipelago (Ashton, 1992; Wong, 1998).

Another, quite deviating floristic region in Borneo was identified in Eastern Sabah (cluster B in Fig. 5a,b). This area has also been identified as distinct by other studies on flora (Ashton, 1992; Ridder-Numan, 1998; Wong, 1998) and fauna (MacKinnon & MacKinnon, 1986). According to these studies, this area might extend south into the Tawau-Tarakan lowlands in northern East Kalimantan. This region is reported to show floristic affinities with the Philippines, eastern Malesia and the south-east Asian mainland as a result of a more pronounced seasonal climate (Wong, 1998).



**Figure 6** Position of the 28 locations on the first two axes of the principal coordinate analysis using (a) Steinhaus similarity and (b) Sørensen similarity. Locations from both sides of Borneo's central mountain range can be separated along the indicated dashed line.

Also differing considerably from other forests in Borneo is a small cluster of locations in central Sarawak (cluster C in Fig. 5a,b). This result echoes a similar separation in the species- and plot-based classification of Potts *et al.* (2002) for this region. These authors documented correlation of their classification with soil chemical factors: the Bakong, Mersing and Tisam samples were on adult ultisols whereas other nearby Sarawak locations were on sandy humult ultisols of lower nutrient status. That soils can have considerable influence on tree species composition has also been

**Table 3** Outcomes (*R*-values) of the Mantel analyses performed using both Sørensen and Steinhaus index of floristic similarity. Both rainfall and geographical distance between plots are significantly correlated with floristic similarity independently of each other

Factor	Sørensen (28 locations)	Steinhaus (28 locations)
Geographical distance only	0.40***	0.44***
Rainfall only	0.31***	0.34***
Geographical distance corrected for rainfall	0.31***	0.34***
Rainfall corrected for geographical distance	0.15*	0.17*

\* $P \leq 0.05$  and  $P > 0.01$ , \*\* $P \leq 0.01$  and  $P > 0.001$ , \*\*\* $P \leq 0.001$ .

shown in several other studies (Ashton, 1976; Baillie *et al.*, 1987; Duivenvoorden, 1995; Clark *et al.*, 1999). In central Sarawak these edaphic differences seem to have resulted in floristically distinct forest regions.

Kalimantan (cluster D in Fig. 5a,b) is the largest floristic region identified. Although there is some separation between locations from West Kalimantan and the other Kalimantan sites, this region seems to form a floristically rather homogeneous region, encompassing most of the area south of Borneo's central mountain range. This is in contrast with MacKinnon & MacKinnon (1986) and Ridder-Numan (1998) who subdivide this region into several smaller subunits: (1) west and central Kalimantan, (2) south and southern East Kalimantan (the region around the Meratus Mountain range), and (3) northern East Kalimantan including the Berau region. This difference could be related to the fact that these other studies based their division on a limited number of species distributions while we used the whole tree flora for our study. The fact that we used genera for our floristic analysis might also play a role, although Higgins & Ruokolainen (in press) found that generic floristic patterns correspond very well with species floristic patterns. Although some studies indicate that this large floristic region should be subdivided into smaller subunits, the differences between these subunits are probably small as they cannot be detected based on a generic analysis of the tree flora.

The other large cluster identified by the floristic analysis encompasses most of central Sarawak with an extension across the central Bornean mountain range into northern East Kalimantan (cluster E in Fig. 5a,b). Although this central Sarawak cluster has been recognized in other studies as well (MacKinnon & MacKinnon, 1986; Ridder-Numan, 1998), the connection with northern East Kalimantan has never been found, or even suggested, before. This connection indicates that there is either exchange of lowland floristic elements across the central Bornean mountain range between Sarawak and northern East Kalimantan, or that some shared montane flora elements penetrate into the lowland forests of this region. The fact that some of the Berau plots were placed in the Kalimantan (D) cluster in the Sørensen analysis also indicates that there is floristic exchange between cluster D

and northern East Kalimantan. Northern East Kalimantan thus forms an interesting intermediate area, sharing floristic elements with both Sarawak (from which it is separated by the central Bornean mountain range) as well as the rest of Kalimantan (from which it is separated by the Sangkulirang limestone mountain formation).

### Floristic patterns and neutral theory

Floristic patterns were significantly correlated with geographical distance and differences in mean annual rainfall between locations, a pattern that has also been observed in Neotropical forests (Pyke *et al.*, 2001). Although the Mantel analysis showed that both of these factors had an influence on floristic composition independently, they also showed strong correlation with each other. This means that a large part of the relation between geographical distance and floristic similarity between locations could be explained by a similar pattern in rainfall and vice versa. Potts *et al.* (2002) found a comparable dependency of geographical distance and soil variables on floristic composition between sites in northern Borneo. They showed that the effect of geographical distance on floristic similarity could largely be explained by changes in soil variables with distance. These are important observations in the light of the currently ongoing discussion concerning the influence of chance or neutral processes on floristic composition (Hubbell, 1997, 2001; Chave & Leigh, 2002). These neutral theories state that chance processes in combination with dispersal limitation are sufficient to explain differences in floristic composition between locations. According to this theory, ecological preferences of tree species play no role in their distribution and dominance patterns, and differences in floristic composition between sites should be related to the distance between these sites only. Most studies do indeed show that the floristic similarity between locations is closely related to the geographical distance between them (Terborgh & Andresen, 1998; ter Steege *et al.*, 2000b; Tuomisto & Poulsen, 2000; Pyke *et al.*, 2001; Potts *et al.*, 2002), but these studies also show that geographical distance is usually significantly correlated with environmental gradients. We therefore strongly suspect that the relation between geographical distance and floristic similarity can largely be explained by the fact that environmental variables change with geographical distance between sites as well, i.e., the effect of geographical distance on floristic similarity is non-causal. This would seriously undermine the neutral theory as proposed by Hubbell (1997) and others.

### Floristic patterns and the central Bornean mountain range

Borneo's central mountain range seems to act as an effective dispersal barrier between northern and southern Borneo. Only one floristic region extended consistently (Sørensen and Steinhaus similarity) across this mountain range, namely the central Sarawak/northern East Kali-

mantan region (cluster E in Fig. 5a,b). However, both the principal coordinate and the cluster analyses show that this trans-mountain range connection is rather weak. Our results therefore seem to support that most lowland floristic elements do not disperse across mountain ranges very well, even when such a mountain range is not extremely high (between *c.* 1000 and 2000 m) and dissected by many river valleys. Several studies in Borneo confirm that the tree flora does indeed gradually change along altitudinal gradients, and most characteristic lowland tree species become rare above *c.* 800 m altitude (Kitayama, 1992; Pendry & Proctor, 1997; Adam, 2001).

### Floristic patterns and Pleistocene savanna regions

Evidence suggests that during glacial periods in the Pleistocene, western Borneo consisted mainly of savanna vegetation with some scattered rain forest fragments along major rivers and on mountain slopes, while northern and eastern Borneo remained covered with rain forest (Heaney, 1991; Verstephen, 1992; Thomas, 2000; Gathorne-Hardy *et al.*, 2002). Although western Borneo is currently (potentially) covered by tropical rain forests, the rather drastic difference in vegetation type in the recent past between west and east Borneo might still be visible in the present-day floristic composition. Our results are not unambiguous in this respect. We indeed found that, floristically, north-western Borneo is the most deviating region on the island. However, locations from south-western Borneo were tightly clustered together with locations from south, central and east Kalimantan. Either recolonization of south-western Borneo took place very quickly through a combination of immigration of taxa from south-east Borneo and expansion of remnant forest pockets within the area itself, or south-western Borneo has always retained a considerable forest cover during glacial periods.

North-western Borneo, with its specific flora, seems to have experienced very limited floristic exchange with surrounding regions. This means that hypothesized recolonization of this area mainly took place from remnant forest blocks from within the area itself. The low diversity of this area, which is contrasting to the expected high diversity due to the high mean annual rainfall, could indicate that the forest cover has indeed been significantly reduced and/or fragmented in the recent past.

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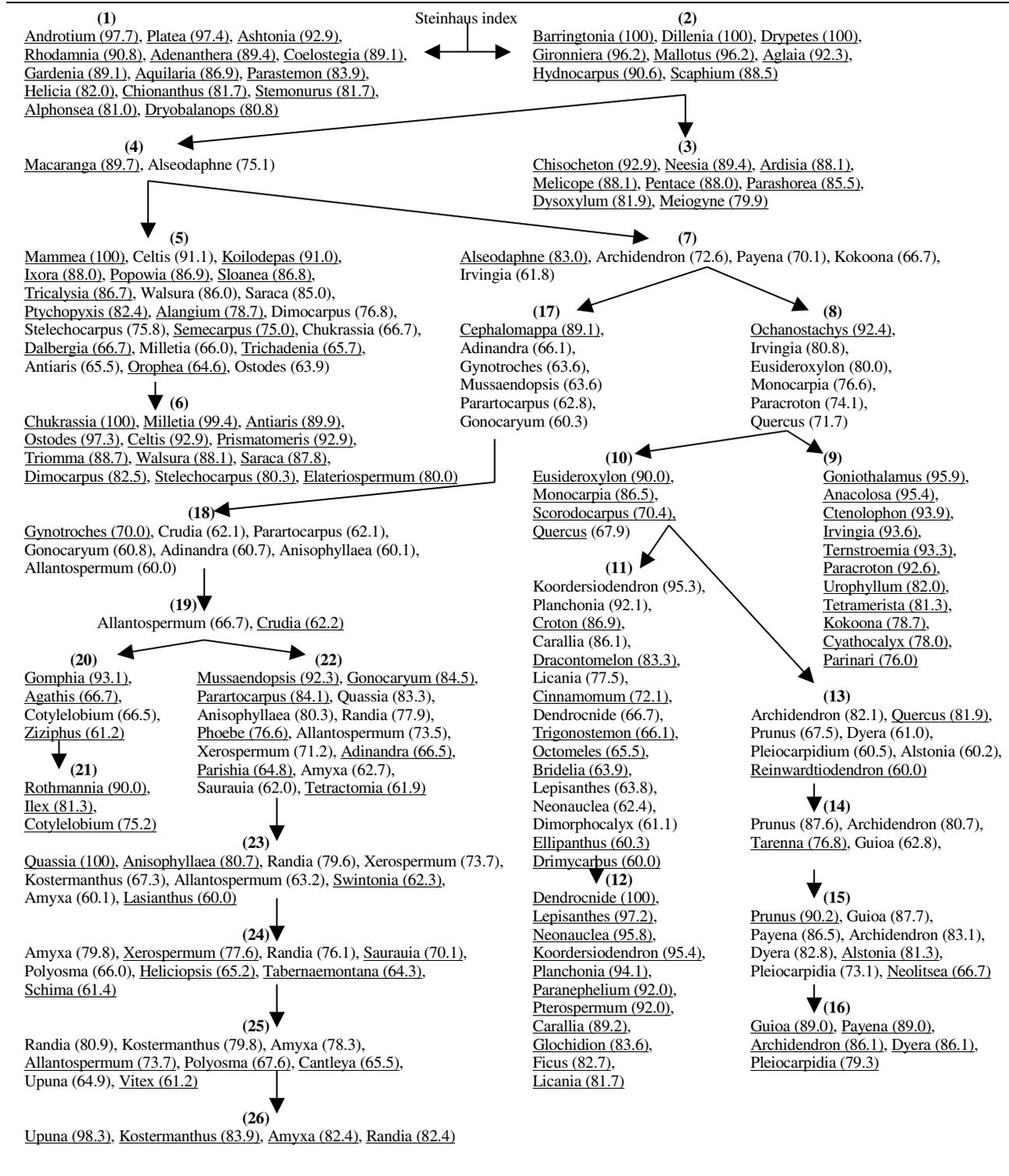
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## BIOSKETCHES

In addition to floristic research, Ferry Slik (Post-doctoral researcher at the Nationaal Herbarium Nederland, Leiden University Branch) is mainly active in developing rapid assessment methods for quantifying forest integrity in south-east Asian tropical forests. This is done with the use of indicator taxa belonging to the genera *Macaranga* and *Mallotus* (Euphorbiaceae). Evolutionary processes in these two genera are studied by comparing phylogenetic hypotheses with ecological, distribution and morphological patterns.

**Appendix I** Indicator taxa for the clusters using (a) Steinhaus similarity and (b) Sørensen similarity. The cluster numbers correspond to the numbers indicated in Fig. 4a,b. The indicator schedules mirror the hierarchical structure of the cluster analyses. Between brackets the indicator values are shown



Appendix I *continued*