Diversity and endemism in the flora of Ethiopia and Eritrea – what do the published Flora volumes tell us?

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Data on the distribution of 2959 indigenous taxa dealt with in Flora of Ethiopia and Eritrea, Vol. 2(2), 3, 6 and 7, has been analysed. In this sample Sidamo has the highest diversity of flowering plants, and the total number of endemics or near-endemics to the Flora area (*i.e.* either restricted to the Flora area or also found in an immediately adjacent country) is 827. There is a maximum of both narrow endemics, country endemics and near-endemics in Sidamo. The diversity of the regions follows a pattern with a marked centre in SE Ethiopia (Sidamo, Bale and Harerge), a slightly less marked centre in the highlands from Shewa to Eritrea, and a poorly marked centre in SW & W Ethiopia. A comparison of the floras of the floristic regions by cluster analysis shows two very well defined clusters consisting of (1) a species-poor cluster of lowland of Eritrea and Afar; (2) a species-rich cluster consisting of all the other floristic regions. Within group (2) there are notable clusters of (2.1) Arsi, upland Shewa, Gonder, Gojam, and the upland of Tigray and Eritrea, (2.2) Welega, Kefa and Illubabor, and (2.3) Gamo Gofa, Sidamo, Bale and Harerge. The latter three regional clusters agree largely with the centres of endemism. Diversity gradually increases with altitude from *c.* 350 taxa between 0 and *c.* 300 m to a maximum of *c.* 1600 taxa between *c.* 1200 and 1500 m a.s.l. Then diversity gradually declines again to *c.* 400 taxa between *c.* 2700 and 3000 m, and to well below 100 on the highest mountain peaks. The number of country endemics or near-endemics is relatively high up to *c.* 1500 m, but the highest number is found between 1200 and 1500 m (where the total number of taxa is also highest). The total number of endemics and near-endemics declines with further increase in altitude, while the percentage increases. The flora is most diverse in open habitats, less so in forest, evergreen scrub, lakes, rivers, and in the open sea. The highest numbers of endemic and near-endemic taxa occur in open habitats. – The patterns found in plants agree reasonably well with patterns found in other organisms, *e.g.* birds.

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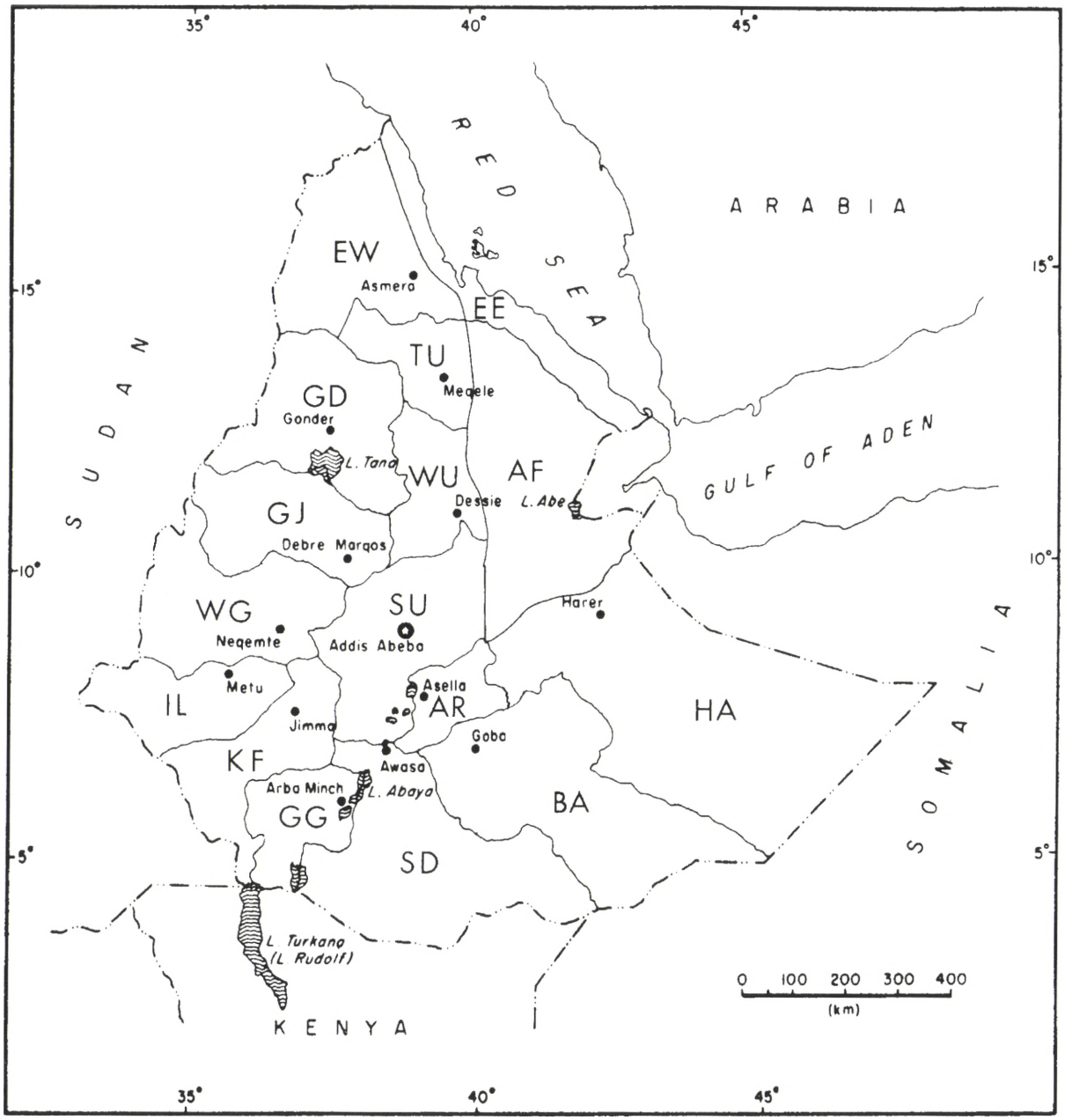

Fig. 1. Floristic regions of Ethiopia and Eritrea used for recording distributions in the Flora and in this study. EW: western Eritrea (above the 1000 m contour). EE: eastern Eritrea, below the 1000 m contour. AF: Afar. TU: upland Tigray; the previous Tigray region above the 1000 m contour. WU: upland Welo, the previous Welo region above the 1000 contour. GD: the previous Gonder region. GJ: the previous Gojam region. SU: upland Shewa, the previous Shewa region above the 1000 m contour. AR: the previous Arsi region. WG: the previous Welega region. IL: the previous Illubabor region. KF: the previous Kefa region. GG: the previous Gamo Gofa region. SD: the previous Sidamo region. BA: the previous Bale region. HA: the previous Harerge region. Reproduced with permission from the *Flora of Ethiopia and Eritrea.*

Introduction

In this paper the distribution- and habitat-data in the four published volumes of the *Flora of Ethiopia and Eritrea* are analysed. The purpose is to ascertain what such analyses can tell us about plant diversity, distribution and endemicity in the Flora area. We also intend to analyse what can be said about the external plant geographical relations of the flora. A detailed analysis of the forests and forest trees of Ethiopia, Eritrea, Djibouti and Somalia was published by Friis (1992). An analysis of certain features of the flora of Ethiopia and Eritrea based on the data available in Vol. 3 of the *Flora of Ethiopia and Eritrea* was presented at the XIIIth Plenary Meeting of AETFAT in Zomba, Malawi (Friis 1994). This was done as part of an overview of some general features of the montane flora of Northeast tropical Africa (Sudan, Eritrea, Ethiopia and Somalia). When the Editorial Board of the FEE met in 1998 in Addis Ababa and discussed the preparations for this symposium it was felt that an updated and, if possible, extended version of some of the analyses of Friis (1992, 1994) would be of interest. It should take into account all information included in the volumes of the Flora published since then, that is Vol. 2(2), Vol. 6 and Vol. 7. The taxa dealt with in the published volumes are expected to be approximately half the total number of taxa in the entire Flora.

An additional reason for redoing the analysis now is the much improved capacity of personal computers and the software they can handle. In Friis (1994) it was sometimes necessary to select subsamples of the material of the 1016 taxa accounted for in Vol. 3, and it was even in some calculations necessary to apply altitudinal zones of 700 m instead of 305 m in order to avoid overflow due to computer limitations. No such limitations have been encountered in the present analyses dealing with almost three times as many taxa. However, other basic limitations in the original data remain, such as the very different size of the floristic regions used for registration of distributions in the *Flora of Ethiopia and Eritrea* (Fig. 1). Also the very different degree of completeness with which the plant distribution in various floristic regions has been recorded is still a serious limitation. The floristic regions are based on the old administrative regions of imperial Ethiopia (incl. Eritrea), as shown in Table 1.

Table 1. Area in square.km. of the old administrative regions of imperial Ethiopia (incl. Eritrea) on which the floristic regions used in the *Flora of Ethiopia and Eritrea* are based. Also indicated are the number of taxa recorded in FEE, Vol. 2(2), 3, 6 & 7 from the floristic regions that more or less match the old administrative regions. The number indicated for Eritrea is the sum of the numbers for EE+EW minus the number of taxa in common. For Tigre, Welo, Shewa and Harerge (indicated with * in the table, the lowland parts of the old administrative regions have been omitted, but the number of taxa omitted by this is probably limited.

Country & Region	Area	Number of taxa		Country & Region	Area	Number of taxa
Eritrea	125750	1062		Welega	77250	561
Tigray	60250	*929		Ilubabor	53500	579
Gonder	80250	863		Kefa	53500	892
Gojam	62250	582		Gamo Gofa	39500	764
Welo	93500	*368		Sidamo	111750	1423
Shewa	82000	*1245		Bale	131250	820
Arsi	21500	523		*Harerge	261250	1113

The Flora area has a number of rather unique geographical features: it is basically a very large dissected, dome-shaped mountain massif consisting of two plateaux which are divided by the Rift Valley. Each plateau has peaks rising from the dome; in the southeastern plateau the highest peak is 4370 m, and in the northwestern plateau the highest peak is 4620 m a.s.l. In the Afar depression, a low-lying and extremely hot and dry northern extension of the Rift Valley, there are extensive salt deposits in exceptionally hot and arid land as low as 126 m below sea level. It is a feature of the *Flora of Ethiopia and Eritrea* that land plants can have an altitudinal range from *c.* 100 m below sea level to *c.* 1000 m above sea level. This is for example the case with the palm *Hyphaene thebaica* (L.) Mart. on p. 522 of FEE, Vol. 6. The Ogaden and Borana regions make up another hot lowland area. The former region is shared between Ethiopia and Somalia. The two regions have altitudes between *c.* 250 and *c.* 1500 m. The western lowlands of Ethiopia and Eritrea have altitudes between 300 and 1000 m above sea level, and have a more humid climate than the eastern lowlands.

Contrasting with these hot and rather inhospitable areas are the extensive highland areas on the plateaux. The areas above 1500 m in the Flora area are the largest in tropical Africa. As mentioned above, due to the separation formed by the Rift Valley they fall in two parts:

1. The North-western Ethiopian Highlands, which are subdivided into a northern and a southern part by the extensive and up to 1000 m deep and 10-50 km wide Blue Nile (Abay) Valley. The northern part is highly dissected, but with altitudes between *c.* 2000 and *c.* 3000 m, they are generally higher than the southern highlands, which are less dissected and have extensive areas between *c.* 1500 m and *c.* 2000 m.
2. The Southeastern highlands are mainly located in Ethiopia, but a narrow mountain chain continues into northern Somalia. Together, these two plateaux measure 1200 to 1500 km across, and span over 16° latitude and 12° longitude. Most of the two highlands consist of Tertiary volcanic rocks, including all the exposed rocks on the plateau and mountain peaks, but not the rocks in the deep river gorges.

The following review of the rainfall regimes is based on Mesfin Wolde Mariam (1970), Daniel Gamachu (1977) and Liljequist (1986). The precipitation on the large, fractured dome is highly dependent on the position in relation to the main rain-bearing winds (Liljequist 1986). The highest rainfall is in the extreme southwestern corner of the North-western Ethiopian Highlands, especially between the towns of Maji, Mezan Tefari and Dembi-Dollo, where there is rain in all months of the year, and the total average annual rainfall ranges between 2200 and 2400 mm (Mesfin Wolde Mariam 1970). Due to the orographic conditions the rainfall is high, locally up to 1500 mm, on the whole western escarpment of the North-western Ethiopian Highlands almost to the border with Eritrea (Liljequist 1986), and generally increasing with increasing altitude up to a certain elevation. The altitude of the rain maximum is variable, but according to the information in the works cited above it is probably in most parts of the Flora area found between 1500 and 2500 m above sea level. The rainfall of the escarpment declines and becomes more and more seasonal, with a more and more marked summer peak, as one moves to the north. The rainfall also declines and becomes more and more seasonal as one moves away from the escarpment and over the Ethiopian Highlands in a north-easterly direction. In the southern and central part there is a marked peak of rainfall in the summer, often with a short dry season separating the "small rains" from the "larger rains". There is a tendency for

rain shadow to develop on the eastern escarpment, except in the northern part of Ethiopia. In Eritrea there is an area with winter rain on the eastern escarpment and on the adjacent parts of the plateau. This pattern is to some degree repeated on the South-eastern Ethiopian Highlands, except that the orographic rain on the western slopes is not so clearly marked. There is more marked tendency to bimodal rainfall in a zone of southern Ethiopia stretching from the southern part of the Gambella lowland through southern Gamo Gofa, Sidamo, Bale and Harerge. This bimodalism is very pronounced in the lowlands, but occurs also in the Bale Highlands, where it, for example, is recorded around the town of Robe.

The vegetation is closely correlated with the rainfall and altitudes, with bushland, thicket, woodland and wooded grassland dominating the lowlands on all sides of the central highland (Friis 1992). The highest concentration of broad-leaved forest is in the high rainfall area in the south-western part of the North-western Ethiopian Highlands. There is a pattern of forest patches, which gradually declines in species richness towards the east, but occurring in a mosaic of forest, evergreen scrub, and montane woodland and wooded grassland on the plateaux. A more detailed, but still brief review of the overall geomorphological structure, climate and vegetation of the Flora area has been summarised in the introduction to Friis (1992).

Material and methods

In order to produce an updated analysis of the available floristic information, all data available on the distribution of 2959 indigenous taxa dealt with in the published volumes of the *Flora of Ethiopia and Eritrea* (Vol. 2(2), 3, 6 and 7) have been entered in a database. The fields in this data base include floristic regions within the Flora area, altitudes, total range of the species, and a crude indication of habitat range within the flora area. The database used was Microsoft Access 97, part of the Microsoft Office 97 packet.

The fields of the database are the following:

1. Taxon names (names of genus, species and infraspecific taxa; text field);
2. There are 16 fields for the distribution on floristic regions in the Flora area (logical fields: yes/no);
3. There are 15 fields for the distribution on the arbitrarily defined altitudinal zones (logical fields: yes/no); one field for endemism in the Flora area (logical field: yes/no), one field for near-endemism in the Flora area, *i.e.* occurring in the Flora area and one neighbouring country only (logical field: yes/no), 12 fields for distributions outside the Flora area, *i.e.* known from the Flora area AND the following geographical areas: "East Africa" (one or more of the following countries: Kenya, Uganda, Tanzania, Rwanda, Burundi; not Kenya only), "South-central Africa" (one or several of the following countries: Angola, Zambia, Zimbabwe, Malawi, Botswana), "tropical South Africa" (Namibia and the tropical part of South Africa, including the previous Transvaal and Natal), "Cape" (the extratropical South Africa), "Mediterranean", "Europe", "Madagascar and the Mascarenes", "West Africa" (the savanna and the sahel parts of western Africa from the Central African Republic to Senegal), "Guineo-Congolian region" (the rain forest region of West Africa, Cameroon, Gabon, Congo-Brazzaville, Congo-Kinshasa), "mainland Asia", "Indonesia, Philippines, New Guinea, Australia, Oceania", and "New World" (all logical fields: yes/no);
4. There are 6 fields for habitats in which the taxa occur in the Flora area: "open habitats", *i.e.* woodland, wooded grassland, grassland, deciduous bushland, "forest", "evergreen scrub", "weedy sites", "fresh water habitats",

"coastal and marine habitats" (all logical fields: yes/no).

The taxa in the analyses are species, subspecies and varieties. The floristic regions used in the *Flora of Ethiopia and Eritrea* appear in Fig. 1, where there is also a list of the abbreviations used. The arbitrarily defined altitudinal zones cover a vertical range of 305 m (*c.* 1000 ft.), which is the definition originally used by Hamilton (1975) in his studies of zonation in Uganda, and later by Friis (1992, 1994) on studies of Ethiopian zonation.

The definition of near-endemic is admittedly problematical, but was the only one feasible with the *Flora of Ethiopia and Eritrea* as the source of the data set. This definition means that species with their main distribution outside the Flora area (but restricted to a single country), and only one record from inside the Flora area, are counted as near-endemics. Such extreme examples are probably rare in reality, but less extreme ones are probably not so rare. It is necessary to keep this problem in mind when interpreting the results. Later, when the distributions of all species in the Flora area are known from reliable distribution maps, or from records in suitably small geographical units, such as squares the size of one degree or less, it may be possible to apply better definitions of endemism.

The analyses consist of enquiries made to this database; subsequent analyses were made with the statistical and graphic programme SigmaPlot Vers. 4.0, and the clustering programme NTSYSpc Vers. 2.02 (Rohlf 1998), a package of programmes designed for numerical classification of taxonomic and plant sociological data. Various modules in the NTSYS package have been used here. They are mentioned below under the section "Floristic similarity between the FEE floristic provinces."

Results

The analyses reported on in this paper include the following:

1. The floristic composition of the 16 floristic provinces used for recording distributions in the Flora was studied; this involved a study of richness of taxa which was done by simple counting of the scores of presence in the fields in question in the database.
2. The floristic similarity between the 16 floristic provinces used for recording distributions in the Flora was analysed by extracting a rectangular presence/absence data matrix from the database, with the columns representing the 16 floristic regions and the rows the 2959 taxa. Subsequently, the floristic similarity of the regions as represented in the matrix was analysed with various similarity indices and clustering methods.
3. The floristic composition of the 15 arbitrarily defined altitudinal zones of 305 m was analysed in the same way as the floristic provinces, that is analyses of species richness, using the same methods.
4. The floristic composition of the 6 major habitat types was analysed in the same way as the floristic provinces, that is analyses of species richness, using the same methods.
5. In all the analyses of floristic composition, studies were also made on the frequency of endemic and near-endemic taxa and, for the regions, also the frequency of single floristic-region endemics.
6. The floristic composition of groups of taxa with identical or similar total range of species (in 12 categories or groups) was analysed in the same way as the floristic provinces. The analyses include number of species in the groups, and floristic similarity between the groups (endemic and near-endemic taxa obviously excepted), using the same methods.
7. Differences in floristic affinities with areas

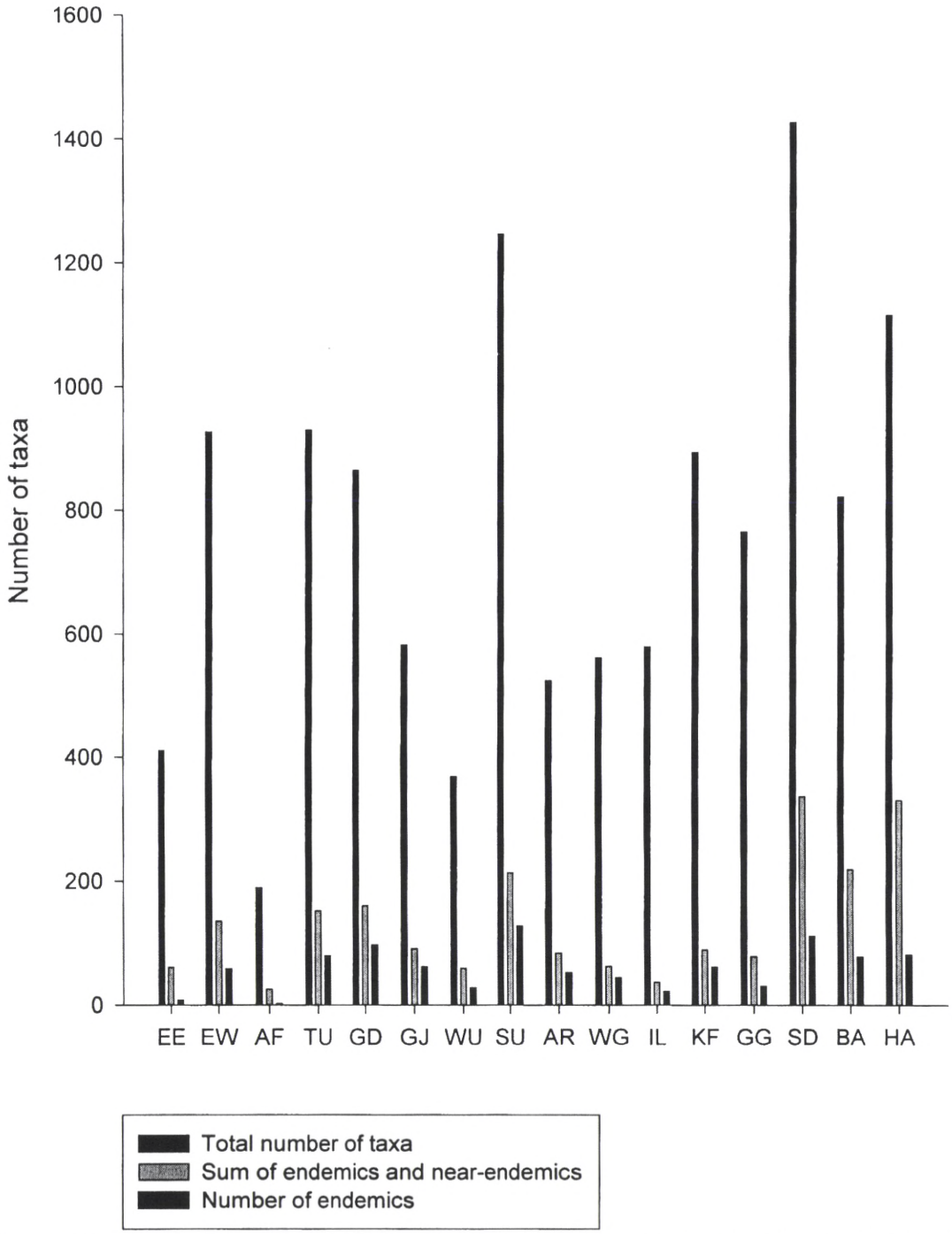

Fig. 2. Bar chart showing the total number of taxa (left bar in each group), sum of endemics and near-endemics (middle bar), and strict Flora area endemics (right bar) in the floristic regions used in the *Flora of Ethiopia and Eritrea*. The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. Abbreviations as in Fig. 1.

outside the flora area were analysed with regard to the northern and the southern parts of the flora area.

Number of taxa and endemism in floristic regions

The term Richness of Taxa was used in Friis (1992) as a simple expression of plant diversity; here we will use Number of taxa. As mentioned, the whole area has a total of 2959 taxa recorded in the sample. The result of our analysis of the total number of taxa in each floristic region is shown as the left hand columns in the bar chart in Fig. 2.

The highest taxonomic diversity, measured as number of taxa, in the floristic regions of Fig. 1 is found in Sidamo (SD), with *c.* 1450 indigenous taxa. This is followed in declining sequence by upland Shewa (SU; *c.* 1300 taxa), Harerge (HA; *c.* 1100 taxa), upland Tigray (TU) and upland (and western) Eritrea (EW; each *c.* 950 taxa), Kefa (KF) and Gonder (GD; each *c.* 850 taxa), Bale (BA) and Gamo Gofa (GG; each *c.* 800 taxa), Illubabor (IL), Arsi (AR), Gojam (GJ) and Welega (WG; each *c.* 600 taxa), the eastern lowland of Eritrea (EE) and the uplands of Welo (WU; each *c.* 350-400 taxa), and Afar (AF; almost 200 taxa). The numbers are illustrated in Fig. 2.

The most prominent feature in the analysis seems to be the centre of diversity in SD. SU is the floristic region where Addis Ababa is located, and therefore the region where the most intensive collecting activity has taken place. It may be premature to indicate SU as a centre of diversity in the highlands. Quite likely, many of the other floristic regions with large highland areas are underrecorded, and future analyses may change the picture in Fig. 2 considerably. It seems, however, that SD, not a particularly central and well-collected floristic province, will maintain its strong position. The rather poorly recorded HA is likely to strengthen its position. The low figure from BA, geographically placed between the two richer provinces of SD and HA, would appear to indicate that that region is strongly underrecorded. The rather well collected KF with good rainfall has a surprisingly low number of taxa; the even lower numbers in WG and IL could be due to underrecording. These areas have good rainfall, as has KF, and IL has in places even higher and more well distributed rainfall than KF. Moreover, the rainfall in the western lowlands of IL (the Gambella region) is high in places (see Jensen & Friis 2001). According to the Flora, GJ has nearly 200 taxa fewer than the fairly well collected GD, which might be due to underrecording in GJ.

The total number of taxa strictly endemic to the Flora area or near-endemic (*i.e.* also found in one or more immediately adjacent countries) is 827 (28%) in the sample. The analysis of the database for endemic and near endemic taxa is shown as the middle columns in the bar chart in Fig 3. Also with regard to the sum of endemic and near-endemic taxa there is a maximum in SD (*c.* 330 taxa). The other regions follow in declining sequence: HA (*c.* 300 taxa), BA (*c.* 210 taxa), SU (*c.* 200 taxa), GD (*c.* 160 taxa), TU (*c.* 150 taxa), EW (*c.* 130 taxa), GJ and KF (each *c.* 90 taxa), and AR, GG, WG, and WU (each with between *c.* 80 and *c.* 60 taxa), IL (*c.* 40 taxa), and AF (*c.* 25 taxa). These figures seem to confirm that there are two main areas with high representation of endemic and near-endemic taxa. These are: (1) the south-eastern part of Ethiopia (SD, BA and HA), and (2) a somewhat less rich area in the highlands from SU to EW; the endemic and near-endemic taxa are less numerous in the south-western and western areas.

The total number of strictly endemic taxa in the sample is 368 (12.5%). The figures from the various floristic regions are indicated as the right-hand column in the bar chart in Fig. 2. It is seen that the distribution of the strict

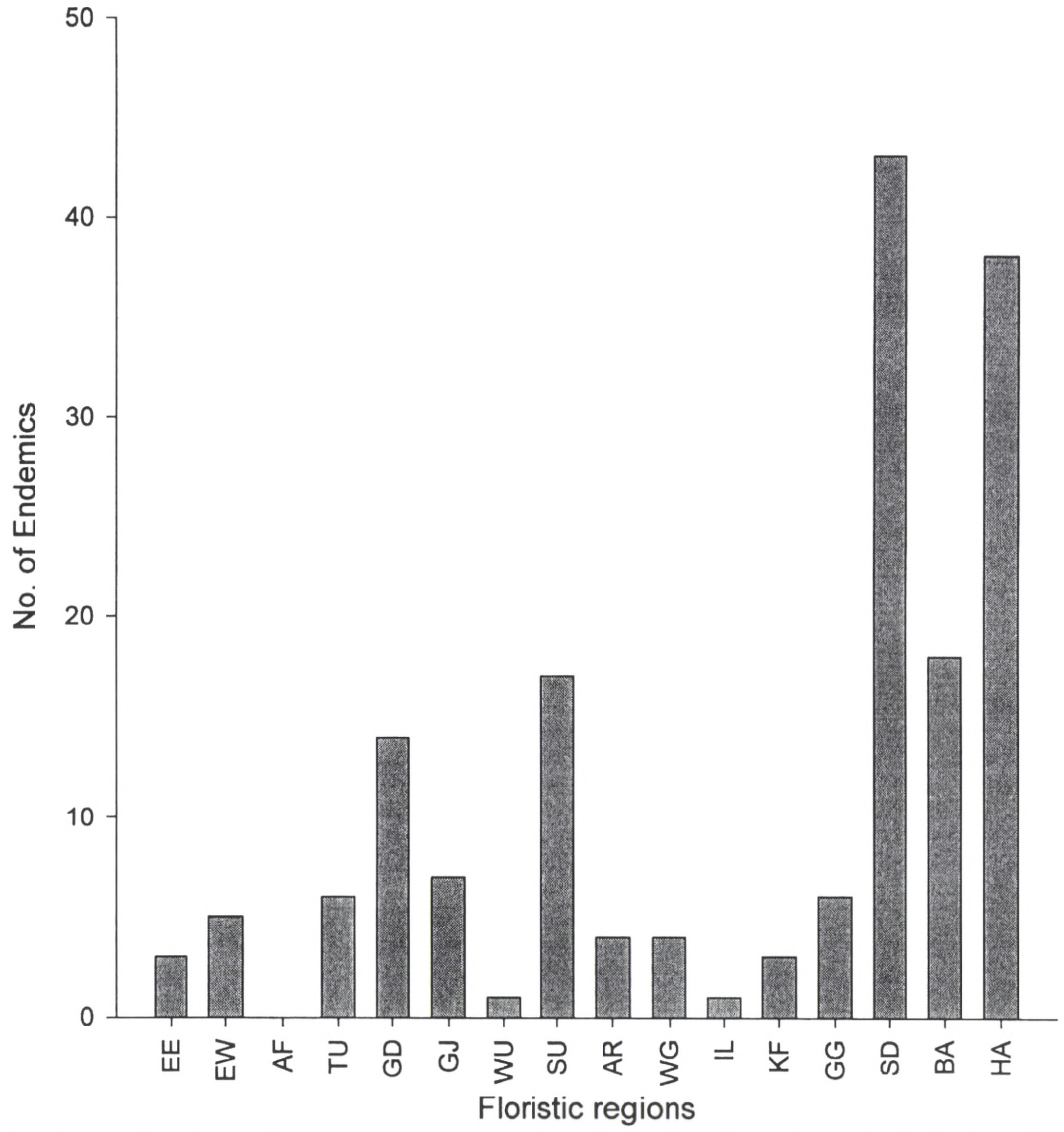

Fig. 3. Bar chart showing the number of narrow endemic taxa in each floristic region. A narrow endemic is here defined as a taxon restricted to a single floristic region. The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. Abbreviations as in Fig. 1.

endemics neither follows the distribution of the total number of taxa nor the number of near-endemics. The latter are very numerous in southern and south-eastern regions of SD, BA and HA, where many taxa just cross the border into Kenya or Somalia. The plateau and highland endemics of upland TU, GD, GJ and upland SU make up a larger fraction of the sum of endemics and near-endemics.

Taxa, which are only known from a single

floristic region, have been recorded as narrow endemics. The distribution of these follows largely the pattern indicated above, and a review of the numbers in each region is given in Fig. 3. The highest number of narrow endemics is found in SD (43), followed by HA (38), BA (18), SU (17), and GD (14). The remaining regions have less than 10 narrow endemics each.

It was tried in the floristic regions to analyse the number of taxa, near-endemics or strict endemics that occurred below or above certain critical altitudes. However, such analyses do not give meaningful results because the altitudinal range for the taxa have been scored for the whole Flora area, not for the individual Floristic regions. This means for example that it is possible from the data base to find taxa that occur in EE above 1000 m (which is the upper altitudinal limit used to define eastern lowland Eritrea). The only condition for this absurdity is that the taxon occurs in EE and above 1000 m in some other places within the Flora area. Such analyses can only be carried out when the altitudinal range of the taxa has been recorded individually for each floristic region.

Floristic zonation: number of taxa and endemism in altitudinal zones

As mentioned in the introduction, analyses of floristic zonation have been carried out, based on arbitrarily defined altitudinal zones with a width of 305 m (1000 ft). The analysis of the database with regard to number of taxa, sum of near-endemics and strict endemics is shown in Fig. 4.

The altitudinal distribution of the taxa shows gradually increasing figures from *c.* 350 taxa in the zone from 0 to *c.* 300 m to a maximum of *c.* 1600 taxa between *c.* 1200 and 1500 m. Then the number is gradually falling off to *c.* 400 taxa between *c.* 2700 and 3000 m. There is a long "tail" of gradually declining figures to the highest mountain peaks at *c.* 4500 m. A similar skew bell-shaped figure was found by Friis (1992) in his analysis of the forest tree data, based on more detailed studies of 260 species of forest trees in Ethiopia, Djibouti and Somalia.

The sum of near-endemic and strict endemic taxa is comparably high in the lowermost altitudinal zone between 0 and 305 m (*c.* 100 taxa, or 20-25% of the total number of taxa in the zone). At gradually higher altitudes this figure does not increase nearly as markedly as the total number of taxa. The highest number of endemic or near-endemic taxa (*c.* 300) is found in the zone between 1200 and 1500 m, where the total number of taxa is also highest, but the endemic and near endemic taxa only make up *c.* 18% of the total number of taxa in the zone. The number of endemic or near endemic taxa keeps declining with increasing altitudes, but the percentage of the total increases again towards the highest values towards the mountain peaks. This agrees with an observation made below that the highest number of widespread Afromontane taxa occurs at the intermediate altitudes. The highest rainfall is almost everywhere in the Flora area between 1500 and 2500 m, which is the zone with the highest number of taxa.

From a comparison between the sum of the near-endemic taxa and the strict endemic taxa it can be seen that the number of strict endemic taxa is small in the lowlands, while the endemic high-altitude taxa are nearly all strict endemics. This is not surprising, because the lowlands mainly occur along the periphery of the Flora area. The locally distributed taxa in the lowlands are therefore very frequently shared with a neighbouring country, while the high altitude taxa of local distribution are only found in the central part of the Flora area. The high rainfall zone between 1500 and 2500 m, which is the zone with the highest number of endemics, is not the zone with the highest percentage of endemism.

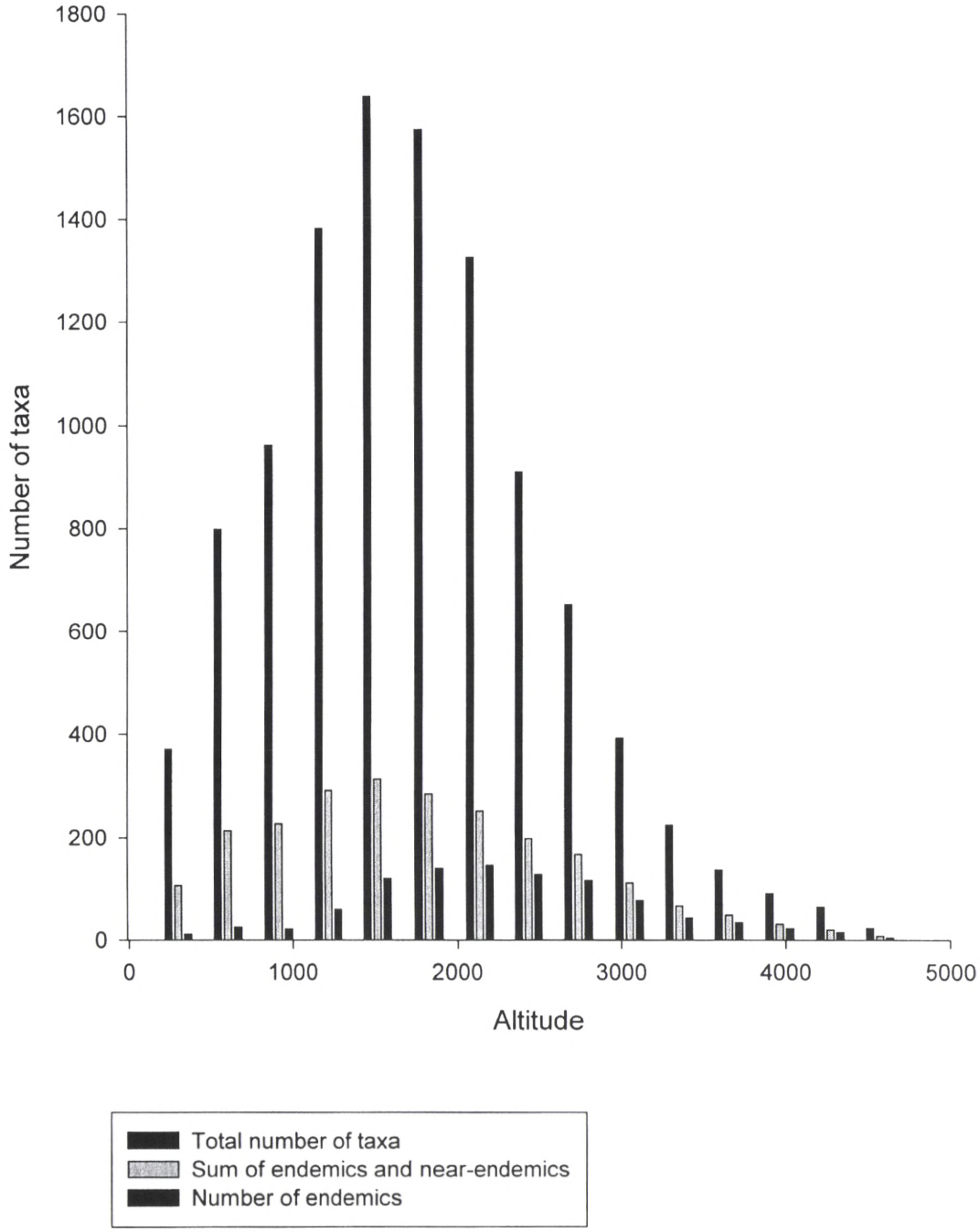

Fig. 4. Bar chart showing the total number of taxa (left bar in each group), the sum of endemics and near-endemics (middle bar), and strict Flora area endemics (right bar) in each of the artificially defined altitudinal zones used in this and a number of previous studies. The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. The altitudinal zones have a range of 305 m, and they are indicated by their upper boundary.

Floristic similarity between the FEE floristic provinces

Lists of taxa recorded from all floristic regions of the Flora area were extracted from the data base. This resulted in a 16 x 2959 matrix with presence and absence data for 2959 taxa in the 16 FEE floristic regions. The matrix was analysed with the NTSYSpc package. All similarity coefficients available for two-state data in the SimQual-module were tried. Very similar results were obtained for most of these coefficients when the resulting similarity-matrices were clustered with the UPGMA (Unweighted Pair-Group Method, Arithmethic average) or the WPGMA (Weighted Pair-Group Method, Arithmethic average) methods in the SAHN module. The major differences between the results with the various coefficients and the UPGMA or the WPGMA methods were the highly changing position of WU on the resulting trees. Rather robust clusters found by this method were (1) the eastern lowlands of EE and AF. This group formed a cluster joining the cluster consisting of all the other floristic regions at a very low level of similarity. Within the larger group there are notable clusters of floristic regions at intermediate levels of similarity. Some of these are (2) WG, KF and IL, (3) GG, SD, BA and HA, and (4) AR, SU, GD, GJ, TU and EW. Within (4) more vaguely marked groups of (5) TU and EW, and (6) GD and GJ were noticed. Particularly the groupings (1), (2), (3) and (4) would seem geographically meaningful. The clusters (3) and (4) agree with the centre of high taxon diversity and endemism pointed out above under the analysis of the bar charts. A typical example of these trees, based on the well-known Jaccard similarity index and UPGMA clustering, both default methods in the NTSYS-package, was very similar to the trees obtained in Friis (1994).

Rohlf recommends in the text of the NTSYS package that the results obtained by UPGMA and WPGMA be tested by the use of the single-link and the complete-link methods in the SAHN module. If the results of these clustering methods are very similar the clusters must be very distinct. The similarity between the results of the single-link and the complete-link methods can be tested by the calculation of a strict consensus tree with the help of the Consen module. For most of the similarity coefficients for two-state data in the NTSYS package there was considerable difference between the results obtained by the single-link and the complete-link methods. Trees obtained with the single-link method showed in these cases a strong tendency to "chaining", *i.e.* one region at the time joining a steadily growing, unresolved cluster. In most of these cases the consensus tree between the single-link and the complete-link trees collapsed to a comb-like structure, and a low consensus index was calculated. However, good consensus trees with rather high consensus indices were obtained from trees calculated with Kulczynski's coefficient no. 2 (K2), the Phi coefficient, the Yule coefficient (Y), the Ochiai coefficient (O), and Rohlf's "unnamed coefficient no 4" (UN4). The highest consensus index between the results of the single-link and the complete-link was obtained with Rohlf's "unnamed coefficient no 5" (UN5), with the highest consensus index (Colless' index. = 0.857) found in the entire analysis. A strict consensus tree based on these calculations is shown in Fig. 5. The clusters mentioned above and obtained with the UPGMA and WPGMA clustering methods reappear in these resolved strict consensus trees. The grouping (1) EE-AF versus the rest of the regions is clearly defined in even the most collapsed strict consensus tree. The groups (2) WG-KF-IL and (3) SD-BA-HA are present (while GG is more loosely associated) in most strict consensus trees, and also the central highland complex, (4) AR-SU-GD-GJ-

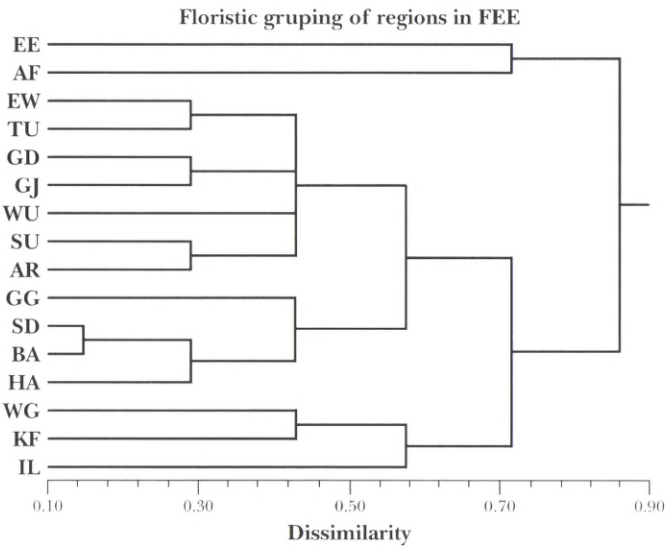

Fig. 5. Cluster diagram showing the floristic grouping of the provinces of Ethiopia and Eritrea used for recording distributions in the Flora and in this study. The diagram is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. This diagram is a strict consensus tree of single- and complete-link trees based on Rohlf's Unnamed Coefficient UN5. Abbreviations as in Fig. 1.

TU-EW, is rather well marked. Within (4) the more vaguely marked groups of (5) TU-EW, and (6) GD-GJ frequently also appear clearly.

Major habitat types: number of taxa and endemism

As mentioned in the introduction, analyses of the flora of the major habitat types have been carried out. The result entailed a certain judgement from the information given in the Flora accounts, and it turned out to be very difficult to distinguish between the open habitats: woodland, wooded grassland, deciduous bushland, *etc.*, for which reason they had to be lumped together. The analysis of the database with regard to number of taxa, sum of near-endemics and strict endemics in these categories is shown in Fig. 6.

The flora of the major habitat/vegetation types shows a strong preponderance of the open habitats from which 2174 taxa are recorded. 534 taxa have been recorded from forest. 350 taxa have been recorded from evergreen scrub. Approximately 140 taxa are from freshwater habitats. Approximately 200 are taxa of weeds of cultivated or fallow land, and *c.* 45 are associated with coastal vegetation or are marine taxa.

By far the highest sum of endemic and near-endemic taxa (*c.* 670; almost 30% of the total number of taxa in these habitats) occur in the open habitats. Only *c.* 90 endemic and near-endemic taxa (less than 20% of the total number of taxa in this habitat) occur in forest habitats. Approximately100 taxa occur in evergreen scrub (nearly 30% of the total number of taxa in this habitat), 9 are coastal plants. 8 taxa are freshwater plants, and *c.* 10 endemic or near endemic taxa are weedy in cultivated or fallow land. The results emphasise the importance of open habitats and evergreen scrub as important habitats for strict or near endemics.

The numbers of strict endemics make up a much greater percentage of the sum of endemic and near-endemic taxa in the forest and evergreen scrub than in the open habitats. The explanation of this is probably the same as mentioned above. The open areas are frequent in the lowlands in the periphery of the Flora area, whereas forests and evergreen scrub occur in the central part of the countries.

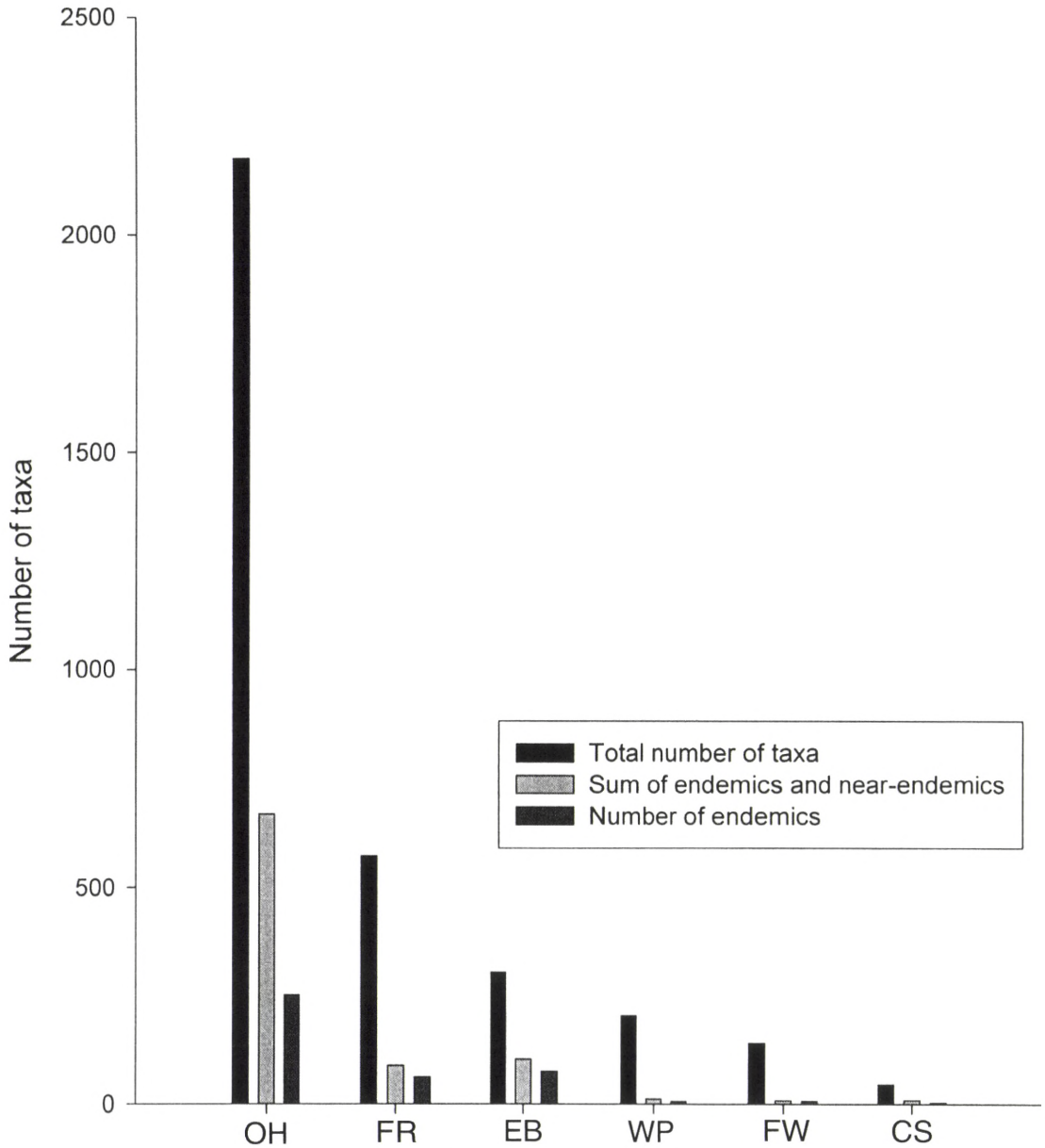

Fig. 6. Bar chart showing the total number of taxa (left bar in each group), the sum of endemics and near-endemics (middle bar), and strict Flora area endemics (right bar) in major habitat types. OH: Open habitats, including woodlands, wooded grasslands, deciduous bushland, grasslands, semi-desert grasslands, etc. FR: Evergreen and semi-evergreen forests. EB: Evergreen bushland, including secondary evergreen bushland. WP: Weedy or ruderal places. FW: Fresh water habitats, incl. permanent swamps, rivers and lakes. CS: Coastal vegetation, incl. marine plants, and saline areas near the sea shores. The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7.

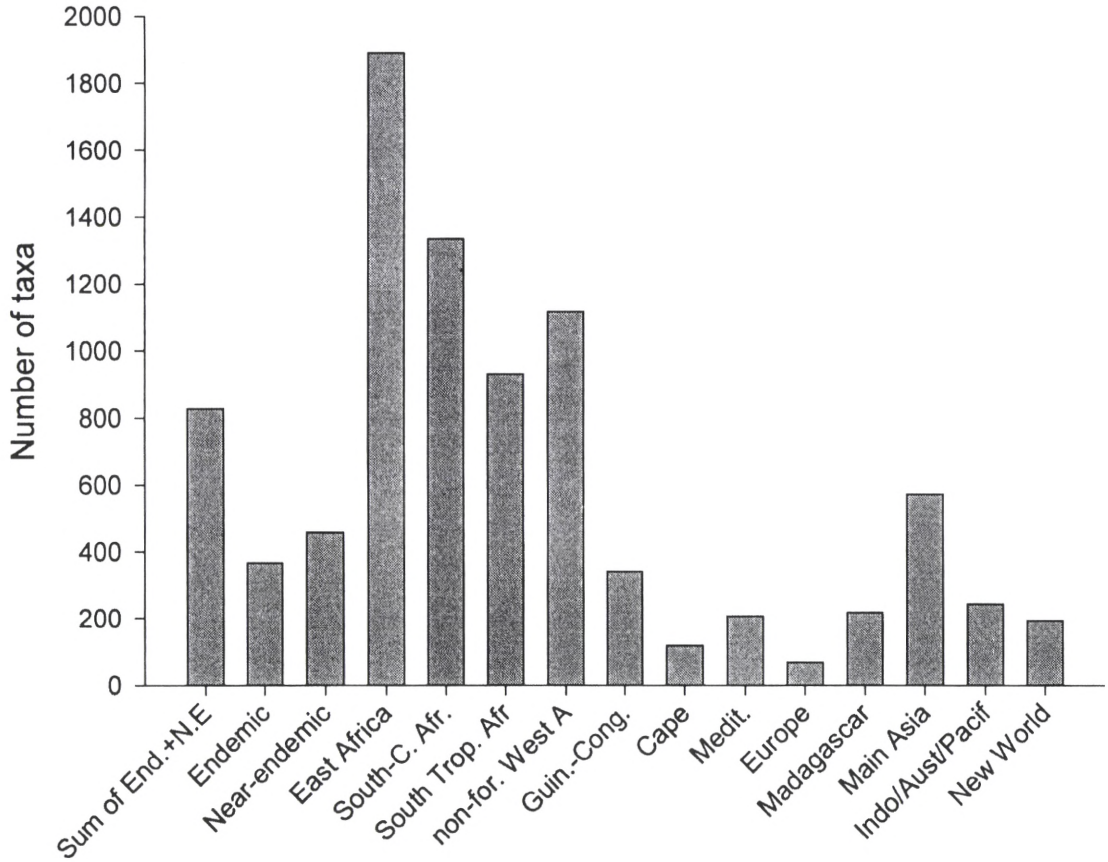

Fig. 7. Bar chart showing the number of taxa in the Flora area which also occur in particular areas outside the Flora area. The left column indicates the sum of endemic and near endemic species. *South-C. Afr.* (south central Africa) includes southern tropical Africa as approximately covered by *Flora Zambesiaca. South Trop. Afr.* (Southern tropical Africa) includes approximately the area covered by *Flora of Southern Africa*, excluding the winter rainfall area, which is indicated as *Cape. Medit* (the Mediterranean) includes approximately the area with cultivation of *Olea europaea. Europe* is excluding the Mediterranean part. *Main Asia* is mainland Asia. *Indo/Aust/Pacif* covers the Indonesian Islands, Australia and Oceania. *New World* covers North and South America. The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7.

Overall range of taxa in the Flora

As mentioned in the introduction, analysis of the general distribution patterns of the taxa outside the Flora area has been carried out, based on the information on the total range of the taxa in the flora accounts. This has, as for the habitat types, entailed a certain judgement when the information was entered in the data base. The analysis of the database with regard to number of taxa in the categories of overall distribution mentioned in the introduction is shown in Fig. 7.

The closest phytogeographical connection for the entire sample is with East Africa (*c.* 1900 taxa). The link with the South-central African region is less pronounced (*c.* 1300 taxa). The links are even less pronounced with the following areas, which have been arranged

in declining order of similarity: non-forested West Africa (*c.* 1100 taxa), South tropical Africa (*c.* 930 taxa), Asian mainland, inc. India, the Himalayas, China and Indochina (*c.* 570 taxa), forest zone of lowland Congo and the Gulf of Guinea (*c.* 340 taxa), Indonesia, the Philippines, New Guinea, Australia and Oceania (*c.* 240 taxa), Madagascar and the Mascarene Islands (*c.* 220 taxa), the New World (*c.* 190 taxa), extratropical South Africa (*c.* 120 taxa), and Europe (*c.* 70 taxa).

Differences between phytogeographical affinities of northern and southern Ethiopia

In a paper presented at the second plenary meeting of AETFAT held in 1953 Gillett (1955: 463) ventured a generalisation. His statement was: "... the flora of southern Ethiopia [south of a line roughly from the Blue Nile to Harerge and Djibouti, roughly the southern limit of FEE regions GJ, WU and AF] is much more like that of Kenya and Uganda than it is like that of northern Ethiopia." Contrarily, Thulin (1986) concluded on the basis of study of the distribution of 151 species of Leguminosae that there is no such "Gillett's line". Thulin provided the explanation of Gillett's result that the flora of the southern highlands of Ethiopia, especially the flora of the high mountains of Arsi and Bale, was very poorly known when Gillett wrote his paper, and that Gillett's sample was therefore biased. What does the much greater data set in FEE Vol. 2(2), Vol. 3, Vol. 6 and Vol. 7 show? Is it possible to say that the flora south of Gillette's line is much more like that of Kenya and Uganda than the flora north of the line, or does an analysis based on the present data set confirm the findings of Thulin (1986)?

We have redone the analysis undertaken for Fig. 7 with the material divided into the 7 floristic regions north of Gillette's line and the 9 Floristic regions south of the line. The phytogeographical spectra of the northern and the southern parts of the Flora area are shown in Fig. 8.

The number of taxa found in the sample from the northern part of the Flora area is only 62% of that from the southern area, and a comparison in absolute numbers is therefore not meaningful. The various elements in the northern and southern profiles are in Fig. 8 shown as a percentage of the total flora in the respective part. It can be seen that the differences between the particular elements in the profiles of the northern and the southern parts of the Flora area are generally only a few percent, indicating that there is very little difference. A difference of more than 5% is seen in the number of near-endemic taxa, where the southern part has the highest values, agreeing with the high number of near-endemic taxa in for example the Ogaden of HA.

It is perhaps surprising that the flora of the northern part of the study area has a higher percentage of species which reach the area of South-central Africa and the South Tropical Africa than has the southern part of the Flora area, which are geographically nearer these areas. The explanation of this must be that the taxa involved are widespread and make up a slightly larger percentage in the north (only just above 5% for the South Tropical African taxa, less than 5% more for the South-central African taxa).

The same can probably be said about the non-Guineo-Congolian species, which reach West Africa. Also in this element the value is about 5% higher in the northern part of the Flora area than in the southern part, indicating that a relatively high proportion of widespread Sudano-Sahelian taxa reach Northern Ethiopia and Eritrea.

Gillett emphasised the species common with the Mediterranean in northern Ethiopia, but such taxa only make up *c.* 4% more of the flora in the northern part of the Flora area than in

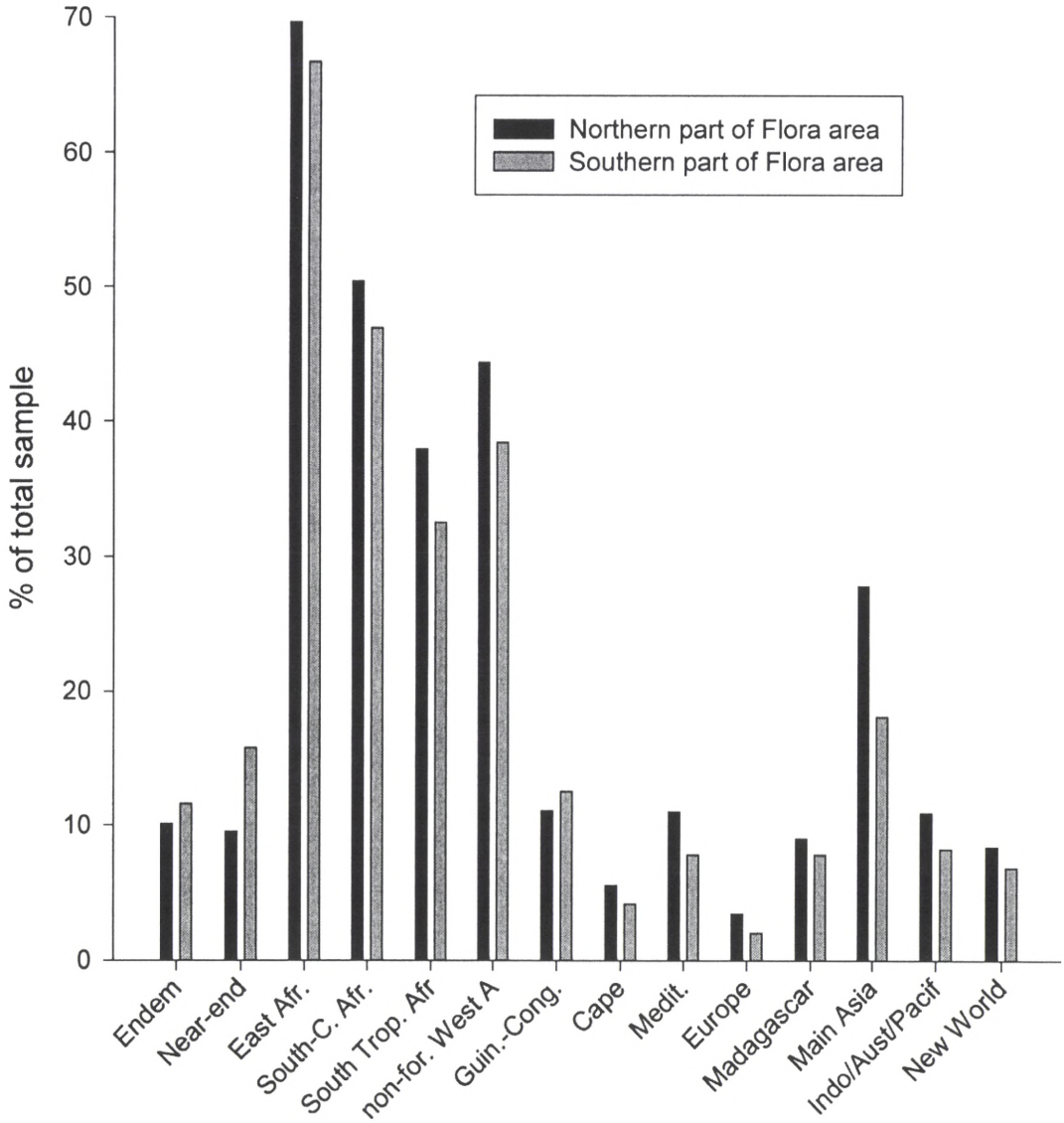

Fig. 8. Bar chart showing percentages of taxa with the same or similar overall range in the northern (left bar in each group) and southern (right bar) part of the Flora area (separated by a line at c. 10° N). The bar chart is based on the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. The phytogeographical groups are the same as those used in Fig. 7.

the southern. The differences with regard to taxa that also occur in Europe are very small.

The most striking difference between the phytogeographical profiles of the two parts of the flora area is found in the elements that also occur in mainland Asia (beyond Yemen). This element is more than 9.5% stronger in northern than in the southern part of the Flora area, an observation which does not seem to have been made before. There are also slightly

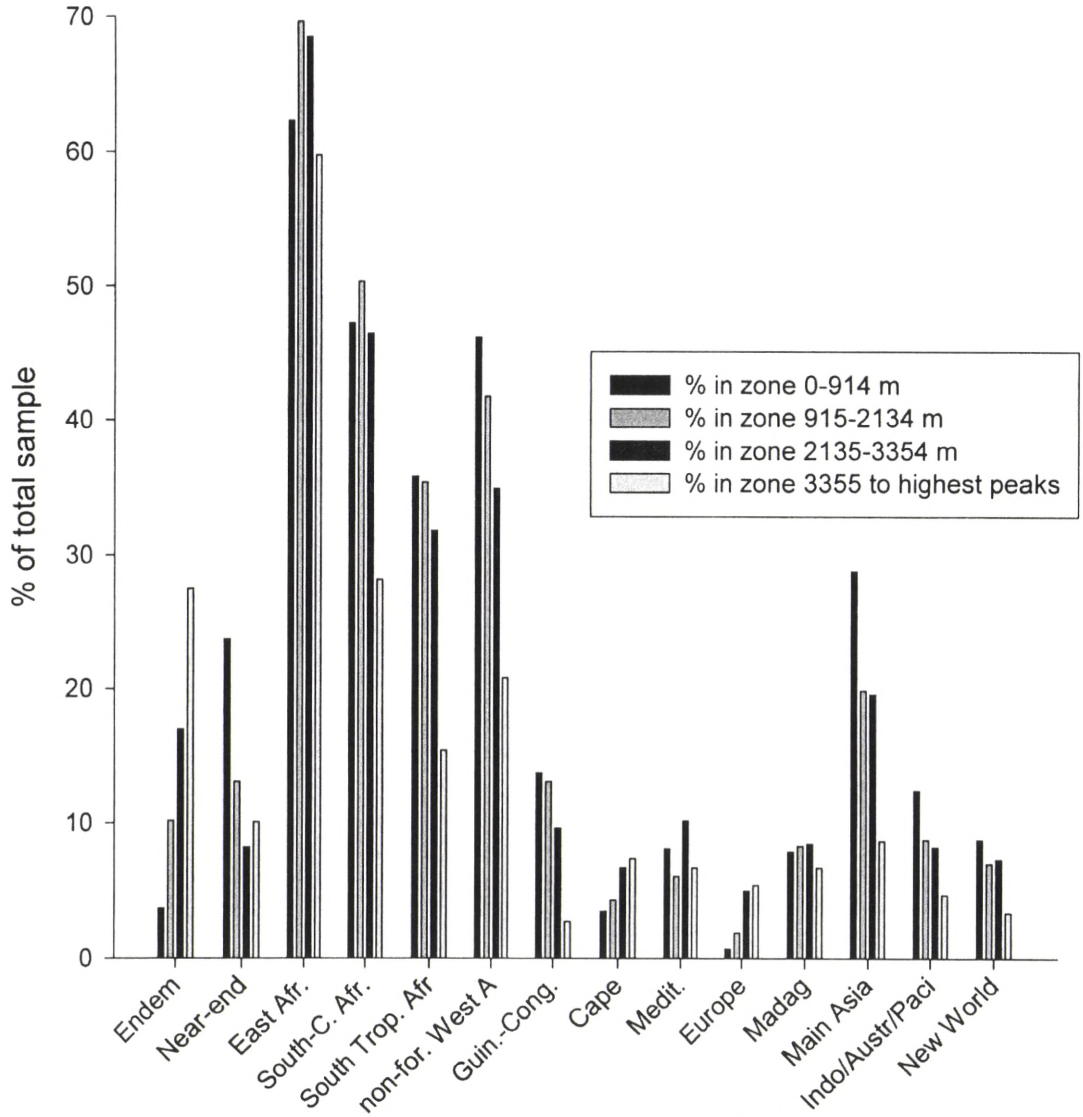

Fig. 9. Bar chart showing percentages of taxa with the same or similar overall range in four arbitrarily defined altitudinal zones (0-914 m a.s.l. (left bar in each group); 915-2134 m a.s.l. (middle left bar); 2135-3354 m a.s.l. (middle right bar); 3355-4500 m a.s.l. (right bar)) in the Flora area. The bar chart is based in the information in the *Flora of Ethiopia and Eritrea*, Vol. 2(2), 3, 6 & 7. The phytogeographical groups are the same as those used in Fig. 7.

stronger elements of Indonesian-Australian-Pacific taxa and New World taxa in the north than in the south. However, these differences are minimal in comparison with the difference with regard to Mainland Asian taxa, of which there are nearly as many in absolute figures in the north as in the south. With the higher absolute number of taxa in the south, this results in a higher percentaged Asian representation in the north.

Differences between phytogeographical affinities at different altitudes

The data from the data base used in Fig. 7 was also reanalysed in order to discover differences in the floristic affinities of the flora in four arbitrarily defined altitudinal zones which cover all altitudes in the Flora area (0-914 m; 915-2134 m; 2135-3354 m; 3355-4500 m). The phytogeographical spectra of the four altitudinal zones are shown in Fig. 9.

There are striking differences between the altitudinal zones with regard to strict country endemics, where the lowest frequency is found at altitudes below 915 m, and the highest at altitudes above 3355 m. Almost a completely opposite trend is shown by the near-endemics. Contrary to these two trends, there are little differences between the altitudinal zones with regard to East African affinities. South-central African, West African and Guineo-Congolian affinities are notably less frequent in the highest altitudinal zone than in the lower zones. The opposite is the case with the Cape-, Mediterranean and European affinities. All this is to be expected. Affinities with Madagascar seem unchanged with altitude. The affinity with mainland Asia is much more pronounced in the lowermost zone than in the upper ones. This trend is less prominent for the affinities with Indonesia, Australia, Oceania and the New World.

Discussion and conclusions

The study shows that results obtained from much smaller data sets are surprisingly robust to the inclusion of additional data and the use of more rigorous methods. The results of this study largely confirm the conclusions of Friis (1992), based on a sample of forest trees from Ethiopia, Eritrea, Djibouti and Somalia, and Friis (1994) which was based on Vol. 3 of the *Flora of Ethiopia and Eritrea* only (1016 taxa). Friis (1994) conclude that the floristic provinces used for indicating the distribution of taxa in the *Flora of Ethiopia and Eritrea* fell into four major groups. The study was based on floristic similarity of a randomly selected sample of 400 taxa of the 1016 recorded in Vol. 3 of the *Flora of Ethiopia and Eritrea*. These four major groups were: (1) a species-poor group of EE and AF, and (2) a species-rich group consisting of all the other floristic regions. Within group (2) notable clusters were (3) AR, SU, GD, GJ, TU and EW, (4) WG, KF and IL, and (4) GG, SD, BA and HA. This result is almost identical with our findings, based on the 2959 indigenous taxa reported in the four volumes that have now been published.

There is a fairly good agreement between areas of high species diversity and a high number of endemics, both the near-endemics, the country-endemics and the single floristic region endemics.

1. The southern regions, with a centre in Sidamo, come out strongly according to both the criteria based on taxa richness and the criteria based on a high number of endemics. SD has the highest number of taxa and the highest number of single floristic-region endemics, whereas it competes with SU for the highest number of country-endemics. This agrees reasonably well with the bird data (Fjeldså & de Klerk 2001), as there is also a well-marked centre of narrow bird endemism in Borana (Sidamo), marking the transition from the Ethiopian highlands to the desert areas east of Lake Turkana. Also in other parts of the Somalia-Masai region of southern Ethiopia and Somalia there are a number of endemic birds which occur singly or in small groups of a few species together in an apparently complex pattern.
2. The south-western regions, centred on Kefa, come out in the floristic survey as a less

important centre according to both the taxon-richness criteria and the total number of Flora endemic and near-endemic taxa, and rather poor with regard to single floristic-region endemics. According to Fjeldså & de Klerk (2001), the south-western region is not a marked centre in birds.

3. The upland/highland regions from Shewa and northwards form a reasonably important centre of diversity and endemism in plants. Among the highland regions, SU, TU and GD have the highest number of taxa. SU has the highest total number of endemics and near endemics and the highest number of single floristic-region endemics. TU has a slightly higher number of taxa than GD, but the situation with regard to all kinds of endemism is the reverse. GJ, and especially WU, seem to be understudied. According to Fjeldså & de Klerk (2001), the Ethiopian highlands form the region's most important and coherent centre of endemism, having a higher number of endemic taxa than any other area, but the endemic birds of the plateaux are widespread in the highlands. This pattern in birds agrees with the comparatively high figures we have found for country-endemic plants in the central part of the Ethiopian highlands, but the data on the distribution in the highlands are as yet not sufficient for a more detailed comparison. It is, however, our impression that there is good agreement between plants and birds in this respect.
4. The zone between *c.* 1200 and 1500 m a.s.l. has both the highest number of species and the highest number of endemics in plants; the zonation in bird endemism is not so easy to analyse, and an analysis has not been presented by Fjeldså & de Klerk, but according to Fjeldså (pers. com.) the highest number of widespread endemic species is probably found above 1500 m a.s.l., while the restricted endemic species are found at lower altitudes.
5. The importance of open habitats as centres of diversity and endemism is prominent in plants, but open habitats seem less important as centres of endemism in birds (Fjeldså & de Klerk 2001).
6. The strong affinity with East Africa is found both in plants and in birds.
7. The observations do not support the suggestion by Gillett that there is much stronger similarity between the floras of southern Ethiopia and East Africa than between northern and southern Ethiopia.
8. However, it seems to be a new observation that the element of species which reach mainland Asia (beyond Yemen) is considerably stronger in northern Ethiopia and Eritrea than in southern Ethiopia. There is a notable change of floristic overall affinity with changing altitude.
9. The flora of Ethiopia and Eritrea seems to have better representation of taxa distributed in the Mediterranean region, Europe and mainland Asia than does the non-migrant bird fauna.

The concentration of fairly widespread highland endemics in the Ethiopian highlands of both plants and birds is perhaps not surprising, considering the large extension and the general isolation of the Ethiopian highlands. But the possible reasons for the concentration in SD, HA and BA of narrow endemics in both plants and birds are not yet clear. Counterparts of this concentration of narrowly endemic species are found in Somalia near the Ceerigaabo (Erigavo) escarpment in northern Somalia, near Hobyo (Obbia) and near Muqdisho (Mogadishu) on the coast, and near Buulobarde (Bulo Burti) between Muqdisho and the Ethiopian border (Thulin 1994). The geological and edaphic explanations for endemism in Somalia, for example the existence of areas or isolated outcrops of limestone and gypsum and very species-rich sand dunes

(Thulin 1986, 1994), do probably not hold for other organisms, including birds. As mentioned in the paper by Fjeldså & de Klerk (2001), the Borana area (SD) has possibly had more stable conditions for a long time (with low interannual variability) than the surrounding area, allowing persistence of relict bird taxa. But that explanation does not explain the very local centres of endemism also found in Somalia. There is certainly scope for further observations on and theories about this subject.

Acknowledgements

Jean Oelkers and Anne-Marie Bürger recorded the data that could be entered unambiguously from the published *Flora of Ethiopia and Eritrea* volumes. Anne-Marie Bürger entered the more complex data, which involved an interpretation of the information provided, such as the total range of the taxa outside the Flora area and the habitat range of the taxa, in collaboration with Ib Friis. We wish to acknowledge the painstaking efforts that Ms. Oeckers and Bürger have made during this lengthy work. We should also like to thank Dr. Mats Thulin for critically reading the manuscript.

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