Patterns of plant diversity and endemism in the Horn of Africa

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Data on the distribution of 5518 indigenous taxa of vascular plants in 25 Flora regions on the Horn of Africa have been analysed. The sample is derived from families that are covered in the published parts of all of the following three works, the *Flora of Ethiopia and Eritrea*, the *Flora of Somalia* and *Les plantes Vasculaires de la République de Djibouti*, or from families or smaller groups covered for all parts of the Horn in other works or in unpublished accounts. The sample contains 4247 taxa that occur in Ethiopia, 2520 in Somalia, 1619 in Eritrea and 554 in Djibouti, and it is assumed to cover ca. 80% of the total flora on the Horn. According to the sample, the highest diversity (number of taxa per Flora region) is found in southern, eastern and parts of western and central Ethiopia and western Eritrea. The number of Horn of Africa endemics plus near-endemics in the sample is 1935 (35%), with 1330 endemics (24%) and 605 near-endemics (11%). The endemics make up 29% of the taxa that occur in Somalia, 17% in Ethiopia, 7% in Eritrea and 3% in Djibouti. The near-endemics make up 16% of the taxa that occur in Somalia, 10% in Ethiopia and Djibouti and 8% in Eritrea. The highest number of Horn endemics is found in north-eastern Somalia. The highest number of near-endemics is found in southern Ethiopia, while near-endemics make up the highest proportion of the flora in inland Flora regions of southern Somalia. The highest number of single-region endemics (Horn endemics restricted to one Flora region only) is also found in north-eastern Somalia. On the tip of the Horn there is a high concentration of endemics with their total range restricted to one Flora region or two, while the endemics in other regions of Somalia and even more so in the Ethiopian highlands tend to occur in several Flora regions. A number of ecogeographical parameters (*e.g.* position, distance to the tip of the Horn, altitudinal range, area, perimeter and amount of coastline of the Flora regions) have been analysed and show varying degree of correlation with diversity and endemism. The higher diversity in Ethiopia than in Somalia is correlated with the higher altitudinal range in the former country and agrees also well with the higher climatological diversity in Ethiopia, while the higher endemism in Somalia than in Ethiopia agrees with the observation that the Flora regions in Somalia have higher proportion of their perimeter as coastline and shorter distance to the tip of the Horn, possibly a "peninsular effect." The high number of near-endemics in southern Ethiopia and the high proportion of near-endemics in southern Somalia agree with the observation that many taxa with restricted range that are shared between the Horn and northern Kenya.

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Introduction

The Horn of Africa is in this study defined as the combined area of Ethiopia, Eritrea, Djibouti and Somalia. Thus defined, it includes largely the areas that are found on the eastern side of Africa at the level of the Sudanian and Sahel vegetation zones, which run across Africa as broad bands from the Atlantic Ocean to the Nile Valley. Within the Horn of Africa the arrangement and floristic composition of the vegetation is strongly modified by topography and other parameters. The vegetation of the Horn is therefore not the typical zonal vegetation of these latitudes, as it can be studied in West Africa within the Sudanian and the Sahel zones. The Ethiopian highlands have been placed in the Afromontane region of White (1983, 1993), a phytochorion also found in mountainous areas elsewhere in tropical Africa, while the uniqueness of the vegetation and the flora of the eastern lowlands of the Horn of Africa is the main reason why White (1983, 1993) included this area as a major part of his Somalia-Masai regional centre of endemism, together with some adjacent parts of Kenya, Uganda and Tanzania. Later, White and Léonard (1994) also included Socotra, and the south-western part of the Arabian Peninsula in this phytochorion.

Previous studies of flora and plant diversity

Cufodontis (1953-1972) reviewed the previous literature and produced a carefully prepared check-list of species and infraspecific taxa of the Horn in his *Enumeratio Plantarum Aethiopicae.* Cufodontis' work included 6323 species. This work is now followed up by the production of the *Flora of Ethiopia and Eritrea* and the *Flora of Somalia,* both of which are now approaching completion. A flora for Djibouti, *Les plantes Vasculaires de la République de Djibouti,* has already been finished.

Gillett (1955) was the first to make phytogeographical comparisons between floras in parts of the Horn of Africa and East Africa. He found considerable similarity between the highland regions of Ethiopia, especially the southern part, and East Africa. Brenan (1978) estimated a degree of endemism for Ethiopia (then including Eritrea) of 20.96%, for Djibouti he found only one endemic species, and he estimated the degree of endemism in Somalia to 9.82%. Brenan realised that the flora of the countries of the Horn of Africa was in need of critical revision and that the degree of endemism might be notably changed after such a revision. He pointed out that this might especially be the case for Somalia. Thulin (1986) compared the legume flora in Ethiopia and Somalia and was the first to suggest that the diversity was highest in Ethiopia and the endemism highest in Somalia. Friis (1992) published analyses of the forests and forest trees of Ethiopia, Eritrea, Djibouti and Somalia with phytogeographical and diversity studies. Thulin (1994) produced a review of areas with high endemism in Somalia, together with studies of interesting disjunctions in the Somali flora. Friis (1994) presented an analysis of the diversity of Ethiopia and Eritrea based on the data available in Vol. 3 of the *Flora of Ethiopia.* Friis *et al.* (2001) extended the 1994-analysis to cover information in the four volumes of the *Flora of Ethiopia and Eritrea* produced then. The present paper is an attempt to survey the situation as it appears in 2003, with the sources and methods that are now available for the study of diversity and endemism. The emphasis in this paper is on the horizontal distribution of the flora.

Topography and other ecogeographical parameters

The Horn of Africa has a number of geographical features that sets it apart from the other areas in Africa between the Atlantic Ocean and the Nile Valley. It is divided into a highland and a lowland part. The topography of the Horn is outlined in Fig. 1.

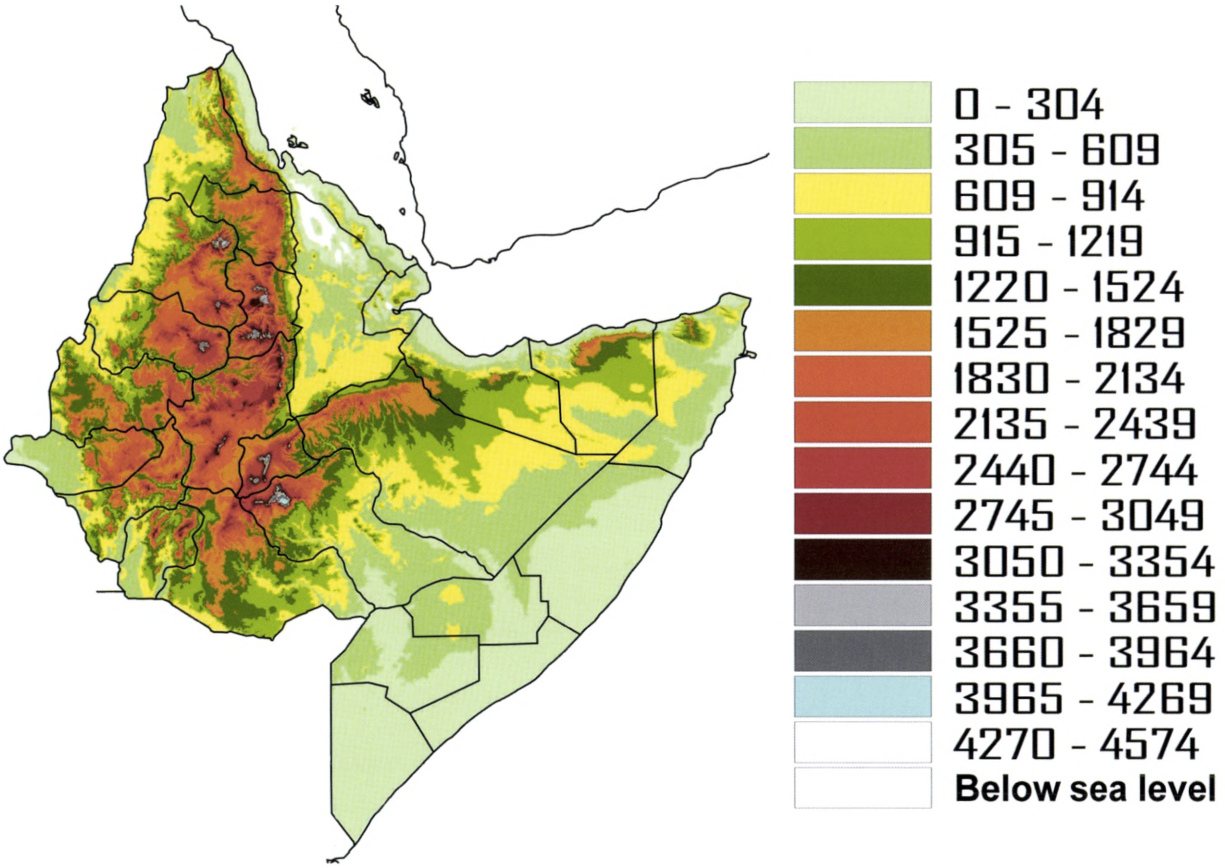

Fig. 1. Map of the Horn of Africa, showing the outline of the Flora regions used in this paper, as well as the altitudinal range (indicated in m) that is found within the regions. The topographical distinction between the north-western Ethiopian and Eritrean highlands and the south-eastern lowlands of Somalia and eastern Ethiopia is clearly notable. The zones 915-11524 m forms the transition between the highlands and the lowlands. The bottom of the Ethiopian part of the Afro-Arabian Rift Valley system is partly above, partly below this altitude; it forms the continuation into the Ethiopian highlands of the Afar depression (the region indicated as AF in Fig. 2) and the Red Sea and the Gulf of Aden (both indicated with name on Fig. 2) and extends to Lake Turkana (Rudolph; south of the region GG on Fig. 2). See also *Introduction: Topography and ecogeographical parameters*.

The topography of the highlands

The broad basal part of the Horn is a large, dome-shaped mountain massif, much dissected and deeply divided into two plateaux by the Ethiopian part of the Afro-Arabian Rift Valley system (from the Afar (Danakil) depression to Lake Turkana (Rudolph)). Together, these two plateaux occupy the major part of Ethiopia, and the western plateau extends into Eritrea. Each plateau has peaks rising from the dome: in the south-eastern plateau the highest peak is 4370 m a.s.l., and in the north-western plateau the highest peak is 4620 m a.s.l. The highlands to the east of the Rift Valley system extend into a mountain chain in the northern part of Somalia, where it reaches almost to the tip of the Horn (Cape Guardafui). The highlands of Ethiopia and parts of the mountains in

northern Somalia are of Tertiary volcanic origin or represent older layers that have been lifted in connection with the formation of the Afro-Arabian Rift Valley system. The areas above 1500 m on the Horn of Africa are the largest montane areas in tropical Africa.

The topography of the lowlands

The Afar (Danakil) depression constitutes a low-lying and extremely hot and dry northern extension of the Afro-Arabian Rift Valley system. It is made up by flat, rock areas and is cut off from the very similar eastern Eritrean lowland by a chain of mountains parallel with the Red Sea. In the Afar depression there are extensive salt deposits in areas as low as 126 m below sea level, but also volcanic mountains rising to over 1000 m. Large areas of the Afar depression are covered by comparatively recent lava flows. Djibouti is basically very similar to the Afar depression and the eastern Eritrea lowlands.

The natural conditions in south-eastern Ethiopia and southern Somalia are very similar and make up another hot lowland area of rocky plains, which has altitudes ranging from sea level to *c.* 1500 m. The western lowlands of Ethiopia and Eritrea have altitudes between 300 and 1000 m above sea level and are made up of low hills and alluvial deposits.

Geology

The geology of the Horn of Africa is complex (Furon 1968; Mohr 1971). The Eritrean and Ethiopian highlands are based on crystalline rocks of Precambrian age. The crystalline basement is in the north covered by 300-500 m thick layers of Adigrat sandstone, of upper Triassic to lower or perhaps even middle Jurassic age. The layer of sandstone gradually becomes thinner towards the south and has disappeared completely to the south of the highlands. The major part of the Eritrean and Ethiopian highlands consists of 1000-3000 m thick strata of volcanic rocks of the Trap Series, and the highlands are geologically very uniform. According to Furon (1968) the oldest basalts of the Trap Series are dated to between 69 and 30 mio. years BP (Eocene), while Mohr (1971) maintains that the palaeontological evidence for the beginning of the Trap Series, at least within Ethiopia, is inadequate for dating. However, the beginning of the formation of the basaltic highland is likely to be contemporary with the uplift of the highlands and formation of the Rift Valley, a process that probably began in the Eocene and has lasted into the Pleistocene. In the Rift Valley, and in the Afar depression there are areas of Pleistocene lava. The very extensive eastern and south eastern lowlands in Ethiopia and Somalia are geologically complex and the surface is formed by a mosaic of Mesozoic sedimentary rocks, mainly Jurassic and Cretaceous limestones, sandstones and gypsum formations. Some of these are visible on the eastern escarpment and in the deep river valleys of the Ethiopian highlands. Near the coast in southern Somalia there are extensive coral rocks and large dune formations rich in coral lime. Together, the geological formations of the lowlands make up a complex mosaic of habitats, much more so than the geologically rather uniform highlands.

Precipitation

The precipitation in the Horn of Africa is highly dependent on the position in relation to the main rain-bearing winds (Liljequist 1986).

The highest rainfall is in the extreme south-western corner of the Ethiopian highlands, where there is rain in all months of the year, and the total average annual rainfall ranges between 2200 and 2400 mm. Due to the orographic conditions the rainfall is high on the whole western escarpment of the Ethiopian highlands and generally the rainfall increases with increasing altitude up to a certain elevation, usually between 1500 and 2000 m.

The rainfall of the western 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 western escarpment and over the central Ethiopian highlands in a north-easterly or easterly direction. In the southern and central part of the highlands 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 on the eastern escarpment. In Eritrea there is an area with winter rain on the eastern escarpment and on the adjacent parts of the plateau.

There is a more marked tendency to bimodal precipitation pattern in the zone stretching from the southern part of the western lowland through southern Ethiopia into Somalia. This bimodalism occurs also in the mountains of northern Somalia, but here local conditions may cause misty conditions and higher humidity than in the surrounding lowlands.

Local rainfall regimes with higher humidity due to mist formation may also be found on isolated mountains in southern Somalia.

Aims of the present investigation

Together, the authors have field experience with the flora of most parts of the Horn of Africa and experience with numerical analyses of biodiversity. In an attempt to combine our experiences, we search for relationships between regional diversity measures and ecogeographical parameters.

The questions that we wish to address are the relations between regional species numbers and species compositions on one side and on the other side geographical parameters like region area, perimeter, altitudinal measures, distance from eastern tip of the Horn of Africa, coast line length, *etc.*

We consider here the following levels of diversity: (i) all Horn of Africa species, (ii) Horn of Africa near endemics (restricted to the Horn of Africa and an adjacent part of a neighbouring country), (iii) Horn of Africa endemics (restricted to the Horn of Africa), and (iv) single Flora region endemics (restricted to one of the floristic regions used for the analyses). In the present context it is not feasible to establish reasonable categories of age and origin of the three categories of endemics.

The numerical methods comprise correlation analyses between species diversity measures and ecogeographical parameters as well as multivariate analysis to establish patterns based on species composition.

More complex measures of altitudinal range and habitat diversity constitute important ecogeographical parameters too. The relations between altitude and diversity have been the subject of much interest in recent literature (*e.g.* Rahbek 1997; Vetaas & Grytnes 2002), and we will investigate the relation between diversity and endemism and altitude in the flora of the Horn of Africa in another treatment.

Materials and methods

Sources and main features of the data set

We have analysed the distributional data for all families treated in the published volumes of the *Flora of Ethiopia and Eritrea* (Edwards *et al.* 1995, 1997, 2000; Hedberg & Edwards 1989, 1995) and the *Flora of Somalia* (Thulin 1993, 1995, 1999). The information about endemicity in the earlier volumes of the *Flora of Somalia* has been updated with observations published in Thulin *et al.* (2001). We have included data concerning some unpublished family accounts of the two floras, mainly Solanaceae, Sapotaceae, Ebenaceae, Asteraceae (including Mesfin Tadesse (in press)), Rubiaceae (including Puff 1989) and Lamiaceae. Data on species in

matching families in the flora of Djibouti have been included in the analysis from Audru *et al.* (1994a, 1994b & 1994c) and Lebrun *et al.* (1989). We have also included data from a number of family- or genera-accounts that are not covered in the above-mentioned flora volumes, and that represent studies of the plant group for the whole of the Horn of Africa (Pichi-Sermolli 1962, 1963a & 1963b, 1965, 1966, 1968, 1969a & 1969b, 1978), Bizzarri (1970, 1975), Gastaldo & Paola (1978), Braggio Morucchio (1970), Friis (1992), Leeuwenberg & van Dilst (2001), Nordal & Sebsebe (2002), Thulin (2002), Vollesen (2000, 2002), Chaerle & Viane (2002), Champluvier (2002), Dioli (2002) and Freitag & Maier-Stolte (2003)).

In order to produce an updated analysis of the available floristic information, all data available on the distribution of the indigenous taxa in the works mentioned above have been entered in a database. The fields in this database include, among others, the scientific names, information about distribution in the Flora regions (areas used for indicating distribution in the Floras) and information on endemism.

For recording of the distributions, a combined system of Flora regions for the *Flora of Ethiopia and Eritrea* and the *Flora of Somalia* has been constructed, attributing the role of a Flora region to the entire Republic of Djibouti. The standard abbreviations for the Flora regions in the *Flora of Ethiopia and Eritrea* and the *Flora of Somalia* have been used and are presented and defined in Fig. 2. These Flora regions are based on the administrative regions as they were when the flora projects were initiated. They therefore lack biological meaning and have no standard size or design as a grid system would have.

Only presence and absence in the regions has been scored. The database software used was Microsoft Access 2000, and occasionally also Excel 2000.

The following rules have been applied during the work with recording data from the various sources:

1. Only families, genera, *etc.*, with information for all geographical parts of the Horn of Africa have been taken into account.
2. Taxa in the source works have, as far as possible, been identified when their identity was not clear. We have used taxonomic levels that can be identified in all the necessary works and left out the details that could not be ascertained for all parts of the Horn.
3. Taxa that are only cultivated or occasionally escaped on the Horn have not been considered. Naturalised taxa have been included where they form part of natural vegetation.
4. Only documented distributions have been taken into consideration (*e.g.* taxa that have been included in the Floras only because they are likely to occur on the Horn, but not yet recorded, are omitted).
5. Undescribed taxa, which according to the conventions of the *Flora of Ethiopia and Eritrea* and the *Flora of Somalia* are referred to as "[generic name] sp. = [collector and number]," have been included where it has seemed reasonable.

The database represents a sample of 5518 taxa indigenous to the Horn of Africa. We do not know exactly how large the total flora of the Horn of Africa is. However, of the 6323 species treated by Cufodontis (1953-1972), 5216 species belong to the families accounted for in our analyses. This means that the taxa in our samples are equivalent to 82% of Cufodontis' total. If we assume that approximately the same relation exists between the number of taxa in Cufodontis' check-list and the actual number of taxa present in the Horn of Africa then it is likely that the total flora of the Horn will con-

tain approximately 6500 indigenous or naturalised taxa. It is therefore quite possible that our sample represents close to 80% of the total number of taxa on the Horn.

The sample contains 4247 taxa that occur in Ethiopia, 1619 that occur in Eritrea, 554 that occur in Djibouti and 2520 that occur in Somalia.

The number of taxa, which were found to be Horn of Africa endemics, Horn of Africa near-endemics, or single-region endemics, has been relativised to the total number of taxa per region. The distribution patterns of Horn of Africa endemics that occur in more than one flora region have been studied. The Flora regions have been ranked according to diversity and various kinds of endemism.

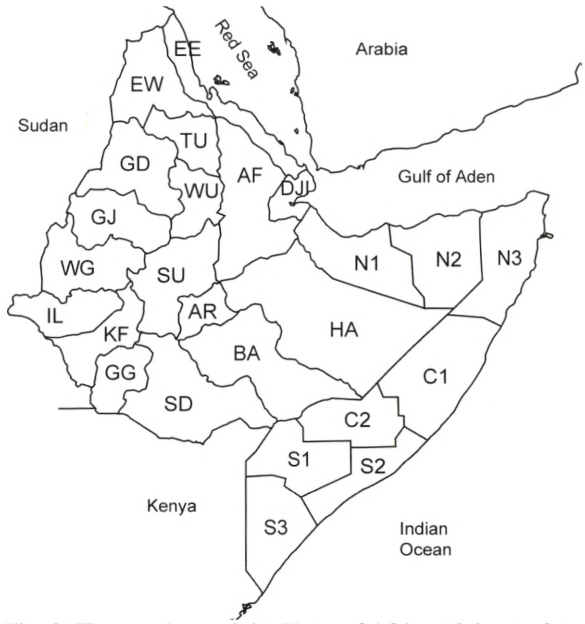

Fig. 2. Flora regions of the Horn of Africa of the modern standard floras of the region. EW: western Eritrea (above the 1000 m contour). EE: eastern Eritrea, below the 1000 m contour. AF: Afar. TU: upland Tigray, the previous Tigray region above the 1000 m contour. WU: upland Welo, the previous Welo region above the 1000 m 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 Gamu-Gofa region. SD: the previous Sidamo region. BA: the previous Bale region. HA: the previous Harerghe region. The floristic regions of Eritrea and Ethiopia are almost all based on the old imperial administrative units. The new administrative and political units of Ethiopia have, with the exception of Afar, which almost equals AF, no relation to the floristic units used here. DJI: The Republic of Djibouti. N1, N2, N3: the three northern Flora regions of the *Flora of Somalia*. C1, C2: the two central Flora regions of the *Flora of Somalia*. S1, S2, S3: the three southern Flora regions of the *Flora of Somalia*.

Analyses, and software used for these

The ecogeographical parameters were assessed by GIS (ArcView 3.2) or directly from maps. The measures comprised (i) region area, (ii) altitude extremes, (iii) perimeter and coastline lengths, and (iv) latitude and longitude of centre (gravity point) of region. From these combined measures were calculated: (v) altitudinal range, (vi) number of altitudinal zones within each region, (vii) altitudinal range/area (a rough measure of the "steepness" of the terrain), (viii) perimeter/area (invert measure of deviation from circular shape), (ix) % perimeter of region that is coastline, and (x) distance from Cape Guardafui.

We also calculated expected species numbers (T_{exp}), based on species-area equations. The equations were established by regressions on data from corresponding species accumulations and area accumulations sequences when a number of regions were selected at random. We let the accumulations go on until we had a total area of 20 square degrees (we consider the latitudinal decline in longitude degree insignificant so close to the Equator). We made 100 random selections of regions. The difference between actual and expected species number is considered a measure of floristic saturation. The calculations were performed in Microsoft Excel 2000 and its random number function was used to perform the permutations of regions.

Figures representing diversity (number of taxa), near-endemism and endemism in the Flora regions were directly compared to each other and to ecogeographical parameters by correlation analysis.

The multivariate analysis (cluster analysis and ordination) were performed with the PC-ORD 4.25 package (McCune & Mefford 1999). The units were the Flora regions, and all analyses are based on presence/absence data.

In the cluster analyses, we ran both nearest neighbour and group average as clustering methods, based on Sørensen's similarity index (Sørensen 1948). The results of these two methods have been compared in order to find the most stable clusters.

In the ordination analysis we ran both Detrended Correspondence Analysis (DCA) and Nonmetric Multidimensional Scaling (NMS), again based on Sørensen's similarity index, in order to test how stable the position of the regions was. The two methods gave consistent ordination diagrams. The ordination procedures presented here are NMS. The autopilot routine in the NMS program of PC-ORD showed that a two-axes NMS was appropriate.

The patterns revealed by ordination and clustering were interpreted according to the parameters that showed significant correlation with the ordination axes.

The graphic presentations were produced using GIS (ArcView 3.2), PC-ORD 4.25, and SigmaPlot 8.01.

Results

Number of taxa in Flora regions

The distribution of taxa in our sample on countries (Eritrea, Ethiopia, Djibouti, Somalia) is shown in Table 1. The result of our analyses of the total number of taxa in each Flora region is shown in Fig. 3. The richness of taxa varies quite considerably from 270 in the Afar depression (AF) to 2152 in southern Ethiopia (SD). See also Table 2 for a ranking of the Flora regions according to taxa richness.

The general trend is that part of the western, the central and southern Flora regions in Ethiopia (plus HA in eastern Ethiopia) have the highest diversity. In some of these regions the richness may partly reflect intensive collecting activity. This is probably the case with SU (where the Addis Ababa University and the National Herbarium of Ethiopia are localised), TU (where most of the collecting activities in the 19th century took place), and EW (where the capital of the Italian colony of Eritrea was placed and formed the centre of studies in the colony from *c.* 1890 and to the Second World War). Among the lower ranking Flora regions is a majority of the Somalia regions. DJI and AF are the absolute lowest ranking Flora regions.

Table 3 shows that there is a significant correlation between the number of taxa per Flora region and the number of endemics, near-endemics and hence endemics plus near-endemics. There is also a significant correlation between number of taxa and, respectively, the number of altitudinal zones that are found within the region and with a number of other ecogeographical parameters related to altitudinal diversity.

Number of taxa in Flora regions compared with expected numbers

There is no strong correlation between taxa numbers and areas of the Flora regions (Table 3).

In the assessment of T_{exp}, the best fit of the species-area regressions turned out to be a linear equation, where T_{exp} is the number of expected taxa in the Flora region and A is the area in square degrees of the region:

$T_{exp} = 587 + 96.57*A \quad (r = 0{,}7398)$.

The results of this analysis are shown in Fig. 4 and the ranking of the Flora regions in Table 2. The richest Flora regions (all with more taxa in the regions than should be expected from their areas, and hence with values above zero in Fig. 4) are located in the western part of Eritrea and the northern, central, western and southern part of Ethiopia. Regions with values below zero are the coastal lowland Flora regions EE, DJI, all the Flora regions in Somalia and the south-eastern lowland regions in Ethiopia (BA, HA). The two quite dissimilar Flora regions IL, partly in the western Ethiopian lowlands, and AR, entirely in the high part of the Ethiopian highlands, have approximately the number of taxa that should be expected from the area of the regions.

Table 3 shows that there is a significant correlation between number of taxa minus expected number on one hand and parameters related to altitudinal diversity, and with distance to the tip of the Horn (and hence a negative correlation with longitude).

Number of Horn of Africa endemics plus near-endemics in Flora regions

The percentages of Horn of Africa endemics plus near-endemics are high, 35% for the flora of the entire Horn, 45% for Somalia, 27% for Ethiopia, and 14% for both Eritrea and Djibouti (Table 1).

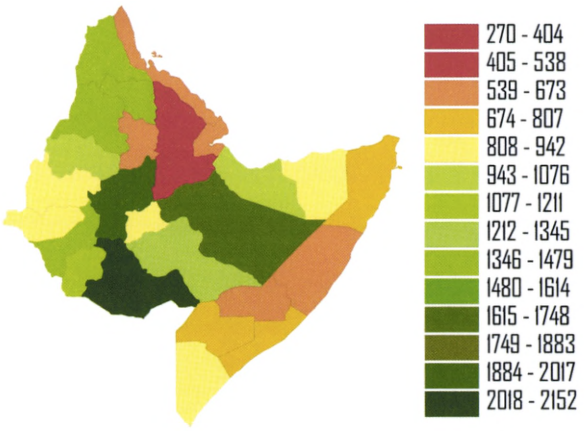

Fig. 3. Number of taxa in each Flora region. See also *Materials and Methods* and *Results: Number of taxa in Flora regions.*

The distribution of the endemics plus near-endemics on Flora regions is shown in Fig. 5 and the ranking of Flora regions in Table 2. As with the total number of taxa, the south Ethiopian Flora region SD is the highest ranking. Among the other high ranking regions are Somali and Ethiopian regions dominated by lowland and a central Ethiopian region dominated by highlands (SU). Throughout the ranking, the trend is rather mixed, with Somalia and Ethiopian regions between each other.

Table 1. Number of taxa, Horn of Africa endemics and near-endemics in the sample (the number of endemics and near-endemics are expressed as a percentage of the number of taxa in each country in the flora of the Horn of Africa as a whole).

	Number of taxa in sample	Number of endemics	Number of near-endemics	Number of near-endemics plus endemics
Ethiopia	4247	709 (17%)	443 (10%)	1152 (27%)
Eritrea	1619	107 (7%)	125 (8%)	232 (14%)
Djibouti	554	19 (3%)	56 (10%)	75 (14%)
Somalia	2520	730 (29%)	400 (16%)	1130 (45%)
Total for the Horn of Africa	5518	1330 (24%)	605 (11%)	1935 (35%)

Table 2. Ranking of Flora regions according to various measurements of diversity and endemism. 1. = Highest ranking. 25. = Lowest ranking.

	Number of taxa	Number of taxa minus expected number	Number of Horn endemics plus near-endemics	Ratio: Number of Horn endemics plus near-endemics to number of taxa	Number of near-endemics	Ratio: Number of near-endemics to number of taxa	Number of Horn endemics	Ratio: Number of Horn endemics to number of taxa	Number of Horn endemics minus expected number	Number of single region endemics	Ratio: Number of single region endemics to number of taxa
1.	SD	SU	SD	C1	SD	C2	N3	C1	N2	N3	N3
2.	SU	SD	HA	N3	HA	S1	N2	N3	N3	N2	N2
3.	HA	TU	N2	C2	S1	C1	HA	N2	SU	SD	C1
4.	EW	KF	N3	N2	N1	N3	SU	C2	GD	C1	C2
5.	TU	EW	SU	S1	N2	N2	C1	N1	AR	HA	S2
6.	GD	GG	BA	N1	BA	N1	SD	S2	TU	N1	S1
7.	KF	GD	C1	S2	C2	S3	GD	HA	C1	S1	N1
8.	BA	AR	N1	HA	N3	S2	BA	GD	C2	S2	HA
9.	GG	IL	C2	BA	S3	SD	N1	BA	SD	BA	SD
10.	N1	GJ	GD	SD	C1	HA	C2	AR	S2	C2	BA
11.	GJ	S3	S1	GD	SU	BA	TU	SU	N1	GD	GD
12.	N2	DJI	TU	AR	S2	DJI	S2	GJ	KF	SU	S3
13.	IL	S2	S2	S3	EW	EE	GJ	S1	GJ	S3	SU
14.	WG	BA	EW	SU	TU	AF	AR	SD	BA	EW	DJI
15.	AR	N1	GJ	GJ	GD	TU	KF	WU	WU	TU	GJ
16.	S3	WG	AR	WU	GG	EW	EW	TU	GG	GG	EW
17.	N3	WU	KF	TU	EE	WU	S1	WG	EW	GJ	WG
18.	S1	N2	S3	WG	DJI	GD	WG	KF	S1	KF	EE
19.	S2	S1	GG	EW	KF	GG	WU	EW	DJI	WG	GG
20.	EE	EE	WG	DJI	GJ	SU	GG	GG	WG	DJI	TU
21.	C2	C2	WU	EE	AR	AR	IL	S3	IL	EE	AR
22.	WU	N3	DJI	AF	WG	WG	S3	IL	HA	AR	KF
23.	C1	HA	EE	KF	WU	GJ	DJI	DJI	EE	WU	AF
24.	DJI	C1	IL	GG	AF	KF	EE	AF	S3	IL	WU
25.	AF	AF	AF	IL	IL	IL	AF	EE	AF	AF	IL

Table 3. Pearson's correlation coefficient (r) between variables. Underlining indicates that r is significant ($P< 0.05$), provided that underlying data are normally distributed and homoschedastic (not tested).

Diversity measures: *Taxnum T*: Diversity (number of taxa). *Endemics E*: Horn of Africa endemics. *Nearend NE*: Horn of Africa near-endemics (see text). *Singlend SE*: Endemics confined to a single Flora region. *T-Texp*: Difference between T and expected T (see text). *E-Eexp*: Equivalent for Horn of Africa endemics.

Ecogeographical measures: *Area A*: Area of Flora region (in square degrees). *Alt. zon.*: Number of altitudinal zones of 305 m in each Flora region. *Min. (m)*: Minimum altitude in each Flora region. *Max. (m).*: Maximum altitude in each Flora region. *Ra.*: Altitudinal range in each Flora region. *Ra./A*: Ratio of altitudinal range to area of each Flora region, a measure of "steepness" of relief. *Perimeter*: Perimeter of each Flora region. *Perim/A*: Ratio perimeter to area in each Flora region, invert measure of "roundness." *Coastline*: Length of coastline (where relevant) of each Flora region. *% to Sea*: Coastline length in pct. of perimeter of each Flora region (where relevant), measurement of "peninsularness." *Lat.* and *Long.*: Latitude and longitude indicated for centre of each Flora region. *Dist to CG*: Distance from centre of each Flora region to the tip of the Horn of Africa (Cape Guardafui).

Mutual correlation between ecogeographical measures was omitted as there was only significant correlation in cases were the relationship was functional or trivial (*e.g.* between *Dist to CG* and *Long*).

	Taxnum T	*Endemics E*	*Nearend NE*	*E+NE*	*Singlend SE*	*E/T*	*NE/T*	*E+NE/T*	*SE/T*	*T- T_{exp}*	*E-E_{exp}*
Endemics E	0.528										
Nearend NE	0.499	0.668									
E+NE	0.563	0.938	0.885								
Singlend SE	0.183	0.810	0.707	0.837							
E/T	-0.092	0.762	0.405	0.666	0.782						
NE/T	-0.260	0.369	0.660	0.539	0.633	0.627					
E+NE/T	-0.173	0.672	0.556	0.680	0.798	0.943	0.851				
SE/T	-0.142	0.661	0.483	0.640	0.920	0.886	0.710	0.901			
T-T_{exp}	0.732	0.098	0.057	0.088	-0.183	-0.324	-0.472	0.901	-0.364		
E-E_{exp}	0.328	0.731	0.295	0.596	0.567	0.673	0.200	0.539	0.554	0.414	
Area A	0.379	0.593	0.608	0.655	0.501	0.314	0.284	0.333	0.300	-0.352	-0.112
Alt. zon.	0.453	0.083	-0.210	-0.046	-0.241	-0.302	-0.703	-0.505	-0.433	0.393	0.058
Min. (m)	0.344	0.077	-0.327	-0.104	-0.327	-0.134	-0.604	-0.349	-0.397	0.504	0.284
Max. (m)	0.514	0.167	-0.182	0.020	-0.205	-0.226	-0.693	-0.450	-0.396	0.468	0.173
Ra.	0.511	0.175	-0.133	0.047	-0.158	-0.229	-0.657	-0.436	-0.363	0.421	0.132
Ra./A	0.025	-0.295	-0.507	-0.421	-0.468	-0.342	-0.627	-0.499	-0.461	0.424	0.116
Perimeter	0.417	0.449	0.489	0.509	0.401	0.104	0.100	0.113	0.171	-0.202	-0.155
Perim/A	-0.268	-0.636	-0.598	-0.677	-0.561	-0.525	-0.464	-0.553	-0.460	0.308	-0.109
Coastline	-0.383	0.134	0.084	0.123	0.498	0.420	0.407	0.457	0.639	-0.360	0.185
% to Sea	-0.423	0.090	0.072	0.090	0.468	0.397	0.426	0.450	0.621	-0.364	0.168
Lat.	-0.017	-0.103	-0.382	-0.242	-0.197	-0.183	-0.440	-0.312	-0.203	0.053	-0.009
Long.	-0.322	0.481	0.497	0.533	0.745	0.748	0.841	0.864	0.842	-0.563	0.308
Dist. to CG	0.286	-0.517	-0.390	-0.506	-0.733	-0.716	-0.666	-0.768	-0.799	0.544	-0.350

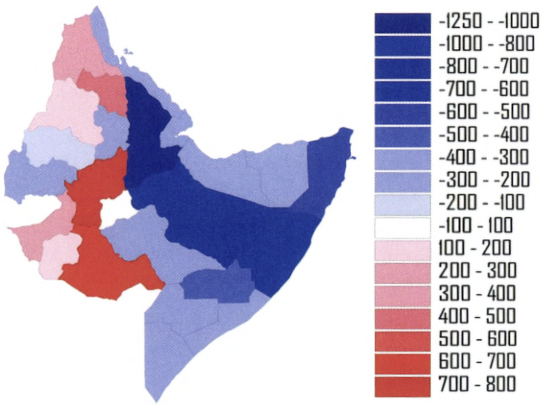

Fig. 4. Observed minus expected number of taxa in each Flora region. See also *Materials and Methods* and *Results: Number of taxa in Flora regions compared with expected numbers.*

The trend towards high ranking for Flora regions in north-eastern Somalia becomes clearer if the ratio is calculated between the number of near-endemics plus endemics and the number of all taxa (Fig. 6, and the ranking of Flora regions in Table 2). The seven highest ranking Flora regions are all located in Somalia, followed by the eastern Ethiopian Flora lowland regions HA, BA and SD. The Ethiopian regions dominated by highland take an intermediate position. The southernmost part of Somalia (S3), which should be expected to have many near-endemics because of its coastal evergreen bushland of the East African type, is in fact the lowest ranking Somali Flora region, probably because the taxa endemic to the East African coastal vegetation are widespread also to the south of Kenya. The lowest values are again found in the taxon- and endemic-poor lowland regions EE and AF and the humid and relatively taxon-rich, but rather endemic-poor south-western Ethiopian regions IL, KF and GG. It seems that this area has a high number of taxa shared with the humid areas to the south-west of the Horn.

Table 3 shows that there is a significant correlation between the number of endemics plus near-endemics and the number of taxa and other categories of endemics. There is also a significant correlation between the number of endemics plus near-endemics and the area of the Flora regions. The significant correlation between the number of endemics plus near-endemics and respectively the measure of "steepness" of relief, the inverted measure of "roundness" of the region and the distance to Cape Guardafui is negative. The ratio endemics plus near-endemics to number of taxa is significantly negatively correlated to parameters relating to altitudinal diversity and significantly positively correlated with parameters related to coastline.

Number of Horn of Africa near-endemics in Flora regions

The distribution of the Horn of Africa near-endemics on Flora regions is shown in Fig. 7 and the ranking of Flora regions in Table 2. The highest number of near-endemics per Flora region is found in southern and south-eastern Ethiopia (SD, HA), followed by southern and northern Somalia (S3, N1). The general trend observed is a concentration of near-

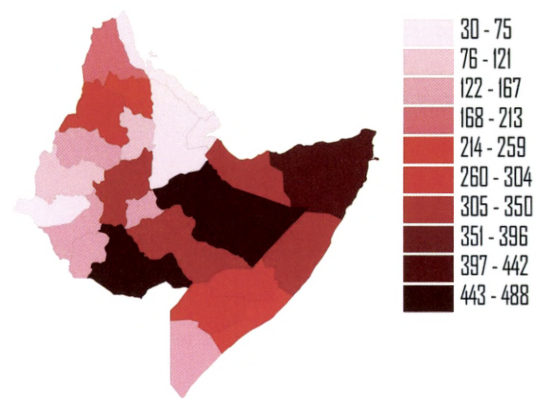

Fig. 5. Number of Horn of Africa endemics plus near-endemics in each Flora region. See also *Materials and Methods* and *Results: Number of Horn of Africa endemics plus near-endemics in Flora regions.*

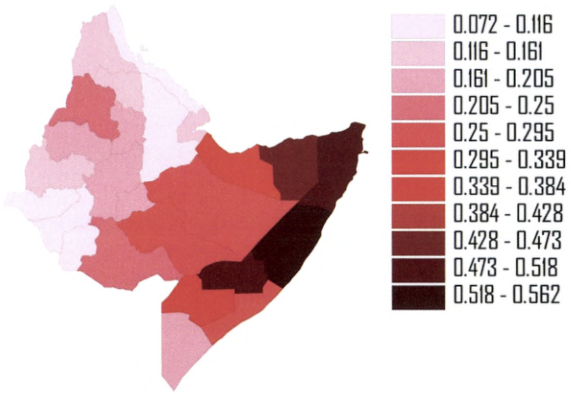

Fig. 6. Number of Horn of Africa endemics plus near-endemics/number of taxa in each Flora region. See also *Materials and Methods* and *Results: Number of Horn of Africa endemics plus near-endemics in Flora regions.*

endemics in the eastern Ethiopian lowlands and Somalia.

This trend is also striking if the ratio is calculated between the number of near-endemics and the number of all taxa (Fig. 8, and the ranking of Flora regions in Table 2), with two inland Flora regions from southern Somalia (C2, S1) as the highest ranking. It is to be expected that the number of near-endemics is high near the border with Kenya, as many taxa with restricted range are known to occur in that area and likely to cross the political boundary that is not a particular natural one with regard to biogeographical significance. More surprising is the relatively high ranking of the Flora regions in north-eastern Somalia, which share near-endemics with southern Arabia and Socotra (see Thulin *et al.* 2001). The low score in western Ethiopia is notable: it is probably explained by a wide distribution to western Africa of many taxa through the Sudanian and Sahel regions of White (1983).

Table 3 shows that there is a significant correlation between the number of near-endemics and the number of taxa and other categories of endemics. The correlation is particularly high with the other categories of endemics. There is also a significant correlation between the number of near-endemics and the area of the Flora regions. The significant correlation between the number of near-endemics and respectively the measure of "steepness" of relief and the inverted measure of "roundness" of the region is negative. The ratio near-endemics to number of taxa is significantly correlated to all parameters studied here, except area and perimeter.

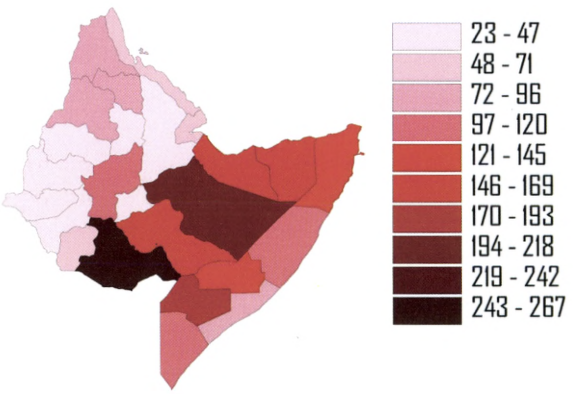

Fig. 7. Number of Horn of Africa near-endemics in each Flora region. See also *Materials and Methods* and *Results: Number of Horn of Africa near-endemics in Flora regions.*

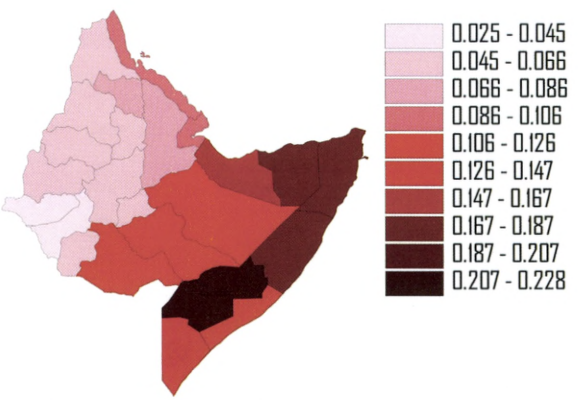

Fig. 8. Number of Horn of Africa near-endemics/number of taxa in each Flora region. See also *Materials and Methods* and *Results: Number of Horn of Africa near-endemics in Flora regions.*

Number of Horn of Africa endemics in Flora regions

The distribution of endemics on Flora regions is shown in Fig. 9, and the ranking of Flora regions in Table 2. The highest numbers of Horn of Africa endemics per Flora region is found in north-eastern Somalia (N3, N2) and in eastern Ethiopia (HA), followed by a mixed sequence of Ethiopian and Somali Flora regions. The most evident general trend is the strong concentration of endemics to the eastern Eathiopian lowlands, but also a relatively notable number of endemics in the regions with high mountains in Ethiopia, such as SU and GD.

If the ratio is calculated between the number of endemics and the number of all taxa, the trend becomes more marked (Fig. 10, and the ranking of Flora regions in Table 2).

Table 3 shows that there is a significant correlation between number of endemics and number of taxa, as well as with the other categories of endemics. The correlation is particularly high with the other categories of endemics. There is also a significant positive correlation between number of endemics and area, perimeter and longitude and a significant negative correlation to the inverted measure of "roundness" of the region and to the distance to the tip of the Horn. The ratio number of endemics to number of taxa is significantly correlated with percent of perimeter that is coastline and longitude (and negatively correlated to distance to the tip of the Horn).

Number of Horn of Africa endemics in Flora regions compared with expected numbers

For this flora element, the best fit of the species-area regressions turned out to be a linear equation, where E_{exp} is the number of expected endemics in the region, and A is the area in square degrees of the region:

$$E_{exp} = 35 + 16.62*A \quad (r = 0.7593).$$

The result of this analysis is shown in Fig. 11, and the ranking of flora regions in Table 2. The Flora regions with the highest number of endemics (all with more endemics in the Flora regions than should be expected from their areas, and hence with values above zero in Fig. 11) are in Somalia and the Ethiopian highlands. Flora regions with values at or below zero are scattered, but most concentrated in the west, the north and the south. The taxon- and endemic-rich region HA in south-eastern

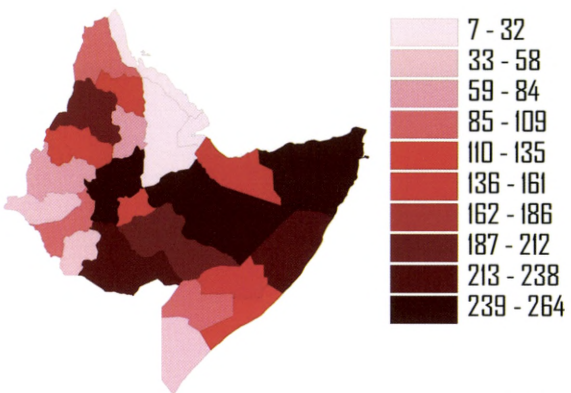

Fig. 9. Number of Horn of Africa endemics in each Flora region. See also *Materials and Methods* and *Results: Number of Horn of Africa endemics in Flora regions.*

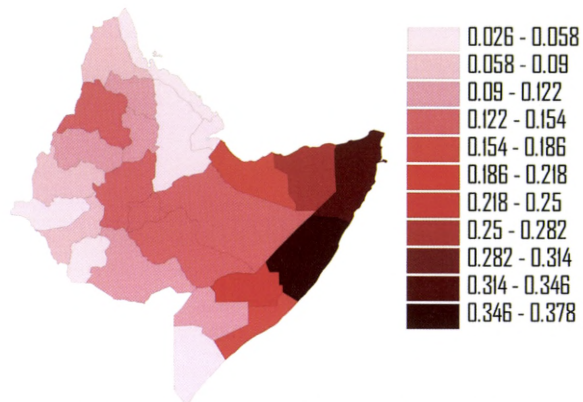

Fig. 10. Number of Horn of Africa endemics/number of taxa in each Flora region. See also *Materials and Methods* and *Results: Number of Horn of Africa endemics in Flora regions.*

Ethiopia is scoring surprisingly low values, as was the case with the observed number of taxa compared with the expected numbers in the same region.

Table 3 shows a significant correlation between the number of endemics minus expected number and other kinds of endemism studied here, but not with any of the ecogeographical parameters studied.

Number of single region endemics in Flora regions

The distribution of narrow endemics has been studied by analysing taxa, which are only known from a single Flora region (Fig. 12, and the ranking of Flora regions in Table 2). This method for identifying restricted range species unfortunately omits such restricted-range species that are located on the border between two regions. As is shown by the analysis of the western Ethiopian escarpment by Sebsebe *et al.* (2005), there may be a significant endemism in long, narrow zones of distinct vegetation that cuts across several Flora regions. This endemism will not be detected as single region endemics in this analysis.

The distribution and ranking of single region endemics follow the trends that have already been described for the endemics. The highest number of narrow endemics is found in Somalia near the tip of the Horn and in the eastern Ethiopian lowlands. The central Ethiopian regions SU and GD occupy an intermediate position.

The same trend towards high values in Somalia and the eastern Ethiopian lowlands, but even more clearly marked, can be seen if the ratio is calculated between the number of single-region endemics and the number of all taxa (Fig. 13, and the ranking of Flora regions in Table 2). Again the highest ranking Flora regions are the seven out of the eight Somali Flora regions, followed by the regions that include eastern Ethiopian lowlands.

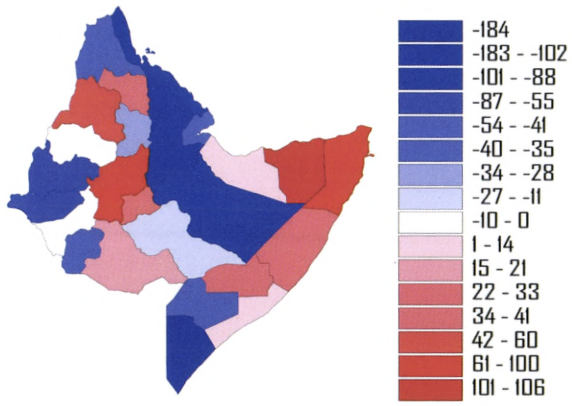

Fig. 11. Observed minus expected number of Horn of Africa endemics in each Flora region. See also *Materials and Methods* and *Results: Number of Horn of Africa endemics in Flora regions compared with expected numbers.*

Table 3 shows a significant correlation between single region endemics and other kinds of endemism studied here. The same applies to the ratio between the number of single-region endemics and the total number of taxa. There is also a significant correlation with area, perimeter of Flora region, percent of perimeter that is coastline and parameters related to longitude. The correlation is particularly high to the latter two parameters.

Ordination and cluster analyses of Flora regions

All taxa

In the NMS analysis, the final configuration was established using the best solution amongst 100 runs (i. e. the solution with least stress) as a seed for the final run. A Monte Carlo test based on 100 runs showed that the stress of the final run occurred in less than 1% of the random runs. The NMS ordination plots are presented in Fig. 14.

The distances between points representing regions in the two-axes projection explained 88.5% of the distances in the original hyperspace. The ordination plot was rotated so that

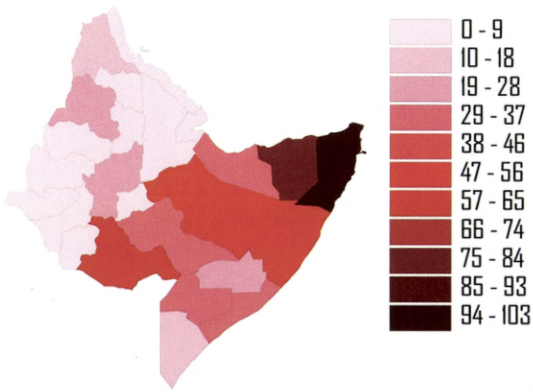

Fig. 12. Number of single-region endemics in each Flora region. See also *Materials and Methods* and *Results: Number of single-region endemics in Flora regions.*

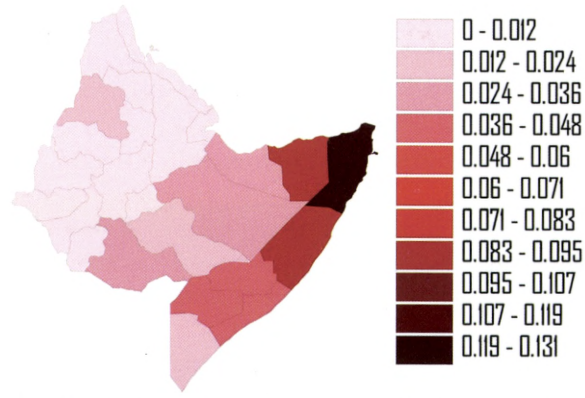

Fig. 13. Number of single-region endemics/number of taxa in each Flora region. See also *Materials and Methods* and *Results: Number of single-region endemics in Flora regions.*

the first axis became parallel to the most important parameter, which showed to be longitude. Latitude then became correlated to the second axis, so there is good similarity between the ordination and a map of the Horn of Africa. The ordination shows a clearly marked gap between on one hand all the eastern lowland regions, including the regions of Somalia, EE, AF and DJI, and on the other hand all the Eritrean and Ethiopian regions of the highlands and western lowlands. The most striking deviations of the ordination from the geographical pattern is that the eastern lowland regions are much more spread out than the rather closely grouped Ethiopian and Eritrean highland regions. BA and HA, that partly belong to the eastern lowland, are in the ordination grouped more with the Ethiopian highlands than with the Somali lowlands, apparently because of a strong component of highland taxa.

The stable clusters from the two different cluster analyses have been marked on the ordination in Fig. 14 in the shape of rings round the regions that appear consistently in clusters. The dark red rings indicate the ultimate clusters, and the salmon pink rings indicate branches that are placed below the ultimate clusters. The regions in the Somali and eastern Ethiopian and Eritrean lowlands show close and consistent clustering: DJI-EE forms a well defined cluster, and the two regions are indeed very similar in topography and geology, dominated by fairly recent lava formations. We would also have expected the topographically and ecologically very similar AF to join, but the total number of taxa in that region is low, and the results therefore unreliable. N1 joins the N2-N3 cluster, forming a northern Somalia group along the northern mountain chain. S1 joins a bigger group consisting of the lowlands in S2-S3 and the C1-C2 clusters in an eastern and southern Somali group. Among the western regions in Ethiopia there are close and consistent clusterings shown by the predominant lowland regions HA-SD. TU-EW seem to form a northern highland core for the other loosely attached regions with a strong component of highland flora, *i.e.* GD, GJ and SU. KF-WG form a south-western cluster with areas of moderate altitude and high humidity.

Horn of Africa endemics that occur in more than one Flora region

This part of the analysis was carried out to study the distribution of the category of the Horn of Africa endemics that were not single-

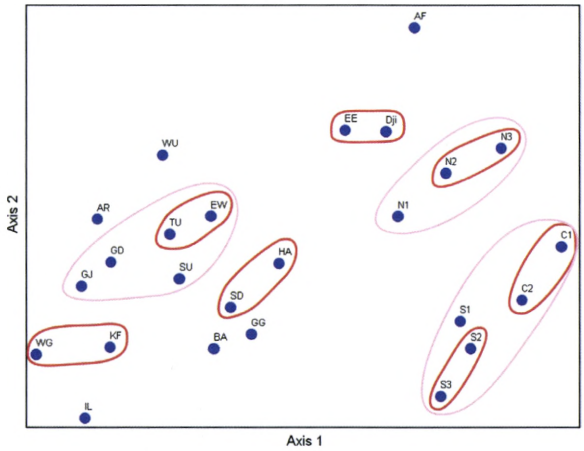

Fig. 14. NMS Ordination of Flora regions based on all taxa, with indication of stable clusters of regions. The dark red rings indicate the ultimate clusters, and the salmon pink rings indicate branches that are placed below the ultimate clusters. The abbreviations are the ones used for the Flora regions (Fig. 2). See also *Materials and Methods* and *Results: Ordination and cluster analyses of the regions – All taxa.*

region endemics. In the NMS analysis, the distances between points representing regions in the two-axes projection explained 77.5% of the distances in the original hyperspace. The stress of the final run occurred in less than 1% of random runs. The NMS ordination plots are presented in Fig. 15.

The overall picture in the ordination of the endemics that occur in more than one region is the same as for all taxa, but the separation between the eastern chiefly Somali lowland regions and the regions in Eritrea and Ethiopia that have a strong component of highland is even more notable here.

The stable clusters from the two different cluster analyses have been marked on the ordination in Fig. 15 in the shape of rings round the regions that appear consistently in clusters. The dark red rings indicate the ultimate clusters, and the salmon pink rings indicate branches that are placed below the ultimate clusters. The cluster analyses show that the endemics that occur in more than one region define clearly marked clusters of regions in northern and central Somalia, where there is also a very high degree of single-region endemism. The clusters involving EE, AF and DJI involve very few taxa, and the results for these regions are not very reliable. The analysis also shows clusters in Ethiopia, with the most marked clusters formed by EW-TU, SU-GD and KF-WG. To the latter two GJ and IL are more loosely attached. The western and central highlands of Ethiopia form clearly defined clusters, and these Flora regions are also from other analyses known to be relatively rich in endemics. The cluster formed by WG and KF is based on relatively few taxa.

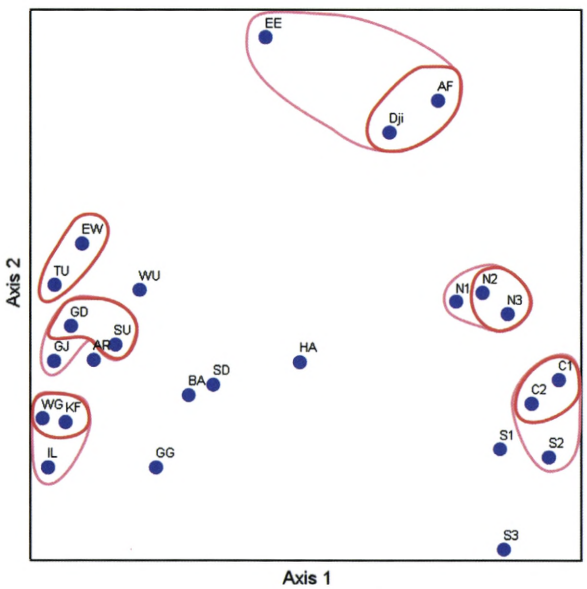

Fig. 15. NMS Ordination of Flora regions based on Horn of Africa endemics that occur in more than one Flora region, with indication of stable clusters of Flora regions. The dark red rings indicate the ultimate clusters, and the salmon pink rings indicate branches that are placed below the ultimate clusters. The abbreviations are the ones used for the Flora regions (Fig. 2). See also *Materials and Methods* and *Results: Ordination and cluster analyses of the regions – Horn of Africa endemics that occur in more than one Flora region.*

Comparison between frequencies of non-endemics and Horn of Africa endemics in western and eastern Flora regions

The few records in the central part of Fig. 15 indicate that the Horn of Africa endemics, which occur in more than one region of the western highland Flora regions of Ethiopia, and the endemics, which occur in more than one region of the eastern lowlands, are more different than should be expected from observations of all taxa (Fig. 14). This was further studied by a comparison between the frequency distribution of non-endemic taxa and endemic taxa that occur in more than one Flora region. Fig. 16 shows the number of non-endemic taxa and the number of endemics in more than one region as the function of the frequency in the western highland regions and in the eastern lowland regions. The taxon-poor lowland regions near the Red Sea (EE, AF) and Djibouti (DJI) have been excluded because of their low number of taxa and endemics and their position in the ordination on Fig. 15, and a Flora region (HA) in eastern Ethiopia has been excluded because it is composite of parts of the Ethiopian highlands and parts of the south-eastern Ethiopian lowlands. The frequency of a taxon is the ratio between the number of regions, in which it occurs, to the total number of regions, expressed as a percentage. The frequencies in the western highlands is plotted along the x-axis, the frequency in the eastern lowlands is plotted along the y-axis and the number along the z-axis. Note that the z-axis is on a logarithmic scale.

Fig. 16 shows that the frequency distribution of non-endemics and endemics in more than one region are even more different than what appears from a comparison between Fig. 14 and 15. The diagram to the left with the non-endemics shows that many taxa have a low frequency in both areas and a low number have a high frequency in both areas. The diagram to the right with the endemics in more than one region shows that there are no endemics that have a frequency of more than 40% in both areas, *i.e.* are frequent in both areas.

However, the frequencies in the two areas are asymmetrically distributed: Many endemics with a frequency of more than 40% in the eastern lowlands occur with low frequencies (between 0 and 40%) in the western highland regions. But most of the endemics that are frequent in the western highland regions do not occur in the eastern lowland regions, in fact only one endemic, which occurs in the western highland regions with a frequency of more than 40%, occurs also in the eastern lowland regions.

This indicates that it is not only the single region endemics that demonstrate the striking separation between the western highland regions and the eastern lowland regions, but also the endemics that occur in more than one region.

Correlation between floristic contents of Flora region and ecogeographical parameters

The correlation analyses presented in Table 3, which are based on the number of taxa and the values for the ecogeographical parameters for each Flora region, has already been commented upon where appropriate. Here we will comment on the correlation between the ecogeographical parameters and the ordination axes scores, which are based on the individual floristic contents of each Flora region. The results are visualised (Fig. 17, 18) in the form of joint plots (McCune & Grace 2002). Only parameters with significant correlation ($r^2 > 0.16$, $p < 0.05$) are depicted.

All taxa

The joint plot with all taxa (Fig. 17) shows that the geographical parameters longitude and latitude are clearly the most important parameters. The percentage of the periphery of each region that borders to the sea ("%to.sea") and

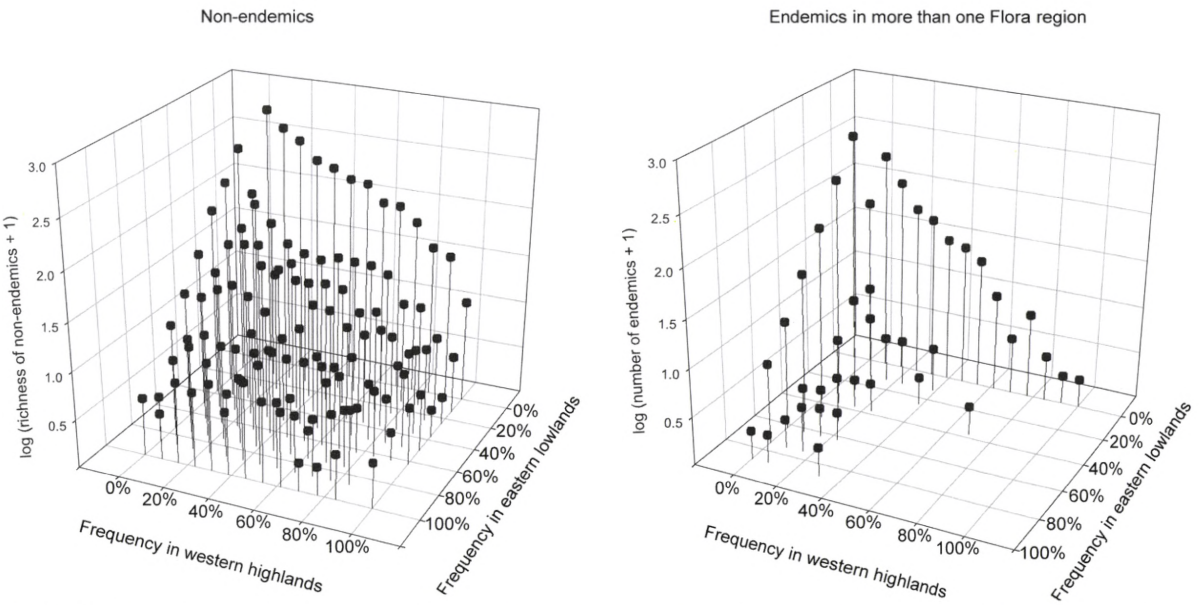

Fig. 16. Number of non-endemic taxa and Horn of Africa endemics as function of taxon frequency in the western highland and the eastern lowland Flora regions (EE, AF, DJI and HA are not considered). Note that the z-axes are on logarithmic scales. See also *Results: Comparisons between frequencies of non-endemics and Horn of Africa endemics in western and eastern Flora regions.*

the distance to the ultimate point of the Horn of Africa, Cape Guardafui, ("D.cape") are other important parameters, together with the number of altitudinal zones per region ("Alt.zon."), the altitudinal range within a region related to area ("Ra./A"), and the maximum altitude within a region ("Max (m)").

Horn of Africa endemics that occur in more than one Flora region

The joint plot with Horn of Africa endemics that occur in more than one Flora region is shown in Fig. 18. The longitude and latitude, percent of perimeter that is coastline, distance to the tip of the Horn and various parameters relating to altitudinal range are parameters that explain the major part of the variation. There is also correlation to single region endemics.

Conclusions and discussion

Diversity

The Flora regions with the highest plant diversity, higher than to be expected from estimates based on the area of the regions, are found in Ethiopia with certain exceptions, particularly the taxon- and endemic-poor lowland regions EE and AF. There is significant correlation between high altitudinal range and a high diversity. There is significant negative correlation with the percentage of the Flora region perimeter that is coastline. The same pattern is seen when the diversity has been adjusted for the effect of area, except that the significant negative correlation with percentage coastline is replaced with the related parameter distance to the tip of the Horn. But both parameters can be considered expressions of the position of the north-eastern Flora regions on a penin-

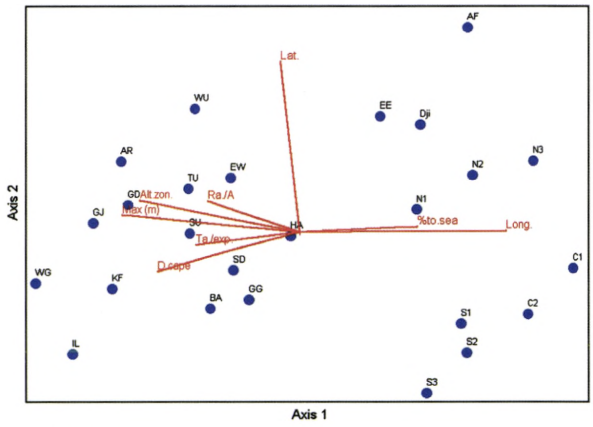

Fig. 17. NMS Ordination of Flora regions based on all taxa, joint plot with analysis of correlated ecogeographical parameters. Ta./exp = Number of taxa in relation to expected number of taxa. A = Area. Alt.zon. = Number of altitudinal zones, each representing an altitudinal range of 305 m, in region. Max (m) = Maximum altitude in the region. Ra. = Altitudinal range (Maximum altitude – minimum altitude). %to.sea = % of perimeter of region that is coastline. Lat. = Latitude. Long. = Longitude. D.cape = Calculated distance to Cape Guardafui (tip of the Horn of Africa). Only ecogeographical parameters that are significantly correlated with the axes are shown. The other abbreviations are the ones used for the Flora regions (Fig. 2). See also *Materials and Methods* and *Results: Correlation between floristic contents of Flora regions and ecogeographical parameters – All taxa.*

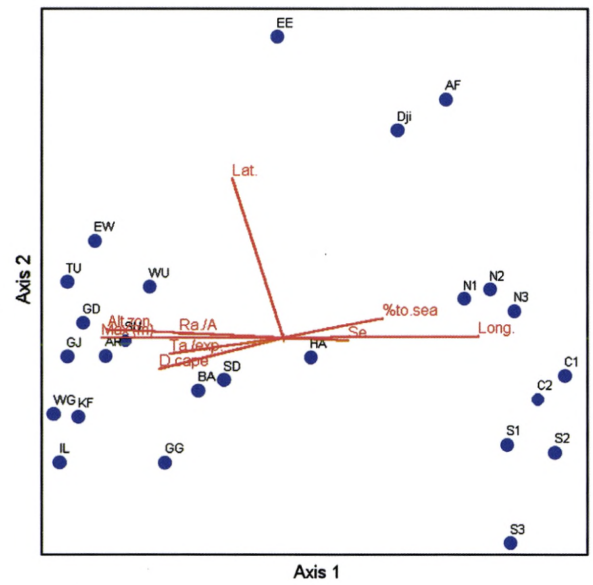

Fig. 18. NMS Ordination of Flora regions based on Horn of Africa endemics that occur in more than one Flora region, joint plot with analysis of correlated ecogeographical parameters. Ta./exp = Number of taxa in relation to expected number of taxa. Se. = Number of single-region endemics. A = Area. Alt.zon. = Number of altitudinal zones, each representing an altitudinal range of 305 m, in region. Max (m) = Maximum altitude in the region. Ra. = Altitudinal range (Maximum altitude – minimum altitude). %to.sea = % of perimeter of region that is coastline. Lat. = Latitude. Long. = Longitude. D.cape = Calculated distance to Cape Guardafui (tip of the Horn of Africa). Only ecogeographical parameters that are significantly correlated with the axes are shown. The other abbreviations are the ones used for the Flora regions (Fig. 2). See also *Materials and Methods* and *Results: Correlation between floristic contents of Flora regions and ecogeographical parameters – Horn of Africa endemics that occur in more than one Flora region.*

sula. The decline in biodiversity towards the tip of a peninsula was first described and analysed in detail from the Baja California peninsula of Mexico (Taylor & Regal 1978; Lawlor 1983; Due & Polis 1986).

Significant correlation was found between the number of taxa and, respectively, the number of altitudinal zones that are found within a region and a number of other ecogeographical parameters. This is hardly surprising because altitudinal diversity is related to climatic and geological diversity, parameters, which have been considered important in the earlier literature on the subject. It is more surprising that there is a significant negative correlation between plant diversity and the percent of the perimeter that is coastline, but that observation agrees well with our finding of relatively low diversity in Somalia.

A number of further observations concerning diversity of specific floristic regions deserve discussion. The low score in the ranking of the two Ethiopian regions WG and WU, surrounded by regions with much higher scores, may be due to undercollecting. The richness of SU in the central Ethiopian highlands may, on

the other hand, be overestimated, and it may be premature to suggest that SU is truly the highest ranking Flora region. It seems, however, that the south Ethiopian Flora region SD, the second highest ranking Flora region and not a particularly central or well-collected area, will maintain its strong position. The reason why the south-eastern Ethiopian Flora region HA has lost the high ranking it had when looking at number of taxa is probably that this very large area is rather poorly recorded, especially the Ogaden area next to Somalia, which has been virtually inaccessible for plant collecting the last *c.* 30 years. Among the other very low ranking Flora regions are a number of Somali regions and the Afar region (AF) while the southernmost part of Somalia (S3), which has a number of taxa in common with the rich East African coastal forests further south, is the highest ranking Somali Flora region.

Near-endemism and endemism

The endemism is notably higher in Somalia than in Ethiopia and the concentrations of both Horn endemics and single region endemics are highest in at the tip of the Horn (N2, N3). It is notable that in Somalia the proximity of the ultimate point of the Horn and the percentage of perimeter of the regions towards the sea are parameters that are significantly positively correlated with endemism. The northern mountains in Somalia (in N2 and N3) are also the part of Somalia with the highest altitudinal range. When the ratios of number of single region endemics to number of taxa or number of Horn endemics plus near-endemics to number of taxa are calculated seven (out of a total of eight) Somali Flora regions are ranked highest. The correlation between longitude and single region endemics is among the highest correlation observed in this study, and the associated negative correlation with the distance to the tip of the Horn is almost equally high.

The concentration of near-endemics in the whole Horn of Africa is highest in southern and south-eastern Ethiopia (SD, HA). The ratio near-endemics to total number of taxa is highest in inland regions of southern Somalia (C2, S1). Both observations can presumably be explained by a high number of taxa with restricted range that are shared between southern Ethiopia, the inland part of southern Somalia and northern Kenya. The political borders between Kenya and southern Ethiopia and south-western Somalia do not follow natural features that are likely to have biogeographical importance, for which reason it is necessary to work with a category of near-endemics. The relatively high score of near-endemics in north-eastern Somalia is probably due to taxa with restricted range shared with southern Arabia and Socotra.

Thulin (1986) documented that based on studies of the legumes there were reasons to believe that the endemicity was considerably higher in Somalia (17-18% of the legume species are endemic) than in Ethiopia (10-11.5% of the legume species are endemic), but that the diversity was higher in Ethiopia, and that there is a high concentration of endemic taxa in certain centres in the northern part of Somalia (the northern mountains and the gypsum areas particularly in the Nugaal Region) and among the fossil sand dunes along the east coast. Later, Thulin (1994) studied the distribution of 204 species that were endemic to Somalia and specified local centres of narrow endemism in Somalia. He pointed out areas near the Ceerigaabo (Erigavo) escarpment in northern Somalia (N2), near Hobyo (Obbia) (C1), near Muqdisho (Mogadishu) on the coast (S2), and near Buulobarde (Bulo Burti) between Muqdisho and the Ethiopian border (C2). In the same work, Thulin suggested that "the northern and north-easternmost part [of Somalia] ranging from 47 degrees in the west to Cape Guardafui in the east" was a "major

zone rich in endemics" and pointed out that the 1 x 1 degree square with Erigavo is the one with the highest number of endemic plants in Somalia. These observations are in agreement with the ones presented here, but Thulin's proposed centres of endemism cannot be directly compared to the results in this paper due to different scales.

Gilbert (1986) pointed out possible centres of high endemicity in the flora of south and south-east Ethiopia, and Friis *et al.* (2001) summarised similar local areas with high endemicity in southern Ethiopia (SD and BA) and south-eastern Ethiopia (HA), although this phenomenon is much less pronounced in Ethiopia.

There is good agreement between these previous and more detailed studies and the more general findings of this paper:

The striking separation between the floras of the western highland regions and the eastern lowland regions, both with regard to single region endemics and endemics that occur in more than one region, agrees with White's placement: the western highland regions in the Afromontane and the eastern lowlands in the Somalia-Masai region (White 1983, 1993).

The presence with low frequency of eastern lowland endemics in the western highlands of Ethiopia agrees well with the penetration of western, southern and south-eastern lowland taxa into the highlands along the deep river gorges, which has been described by several authors (Thulin 1978; Friis 1992).

Agreement between diversity and endemism

It has been shown (Table 3) that there is a significant positive correlation between number of taxa and number of Horn endemics and near-endemics, but it is not strong. Within Ethiopia there is a fairly good agreement between areas of high taxon diversity and a high number of endemics, both the near-endemics, the Horn of Africa endemics and the single Flora region endemics. The highest concentration of the latter are either found in southern Ethiopia (SD) or in central or northern regions with high mountains. But in Somalia there is less agreement between diversity and endemism and areas with a combination of low diversity and high endemism are found. Djibouti is characterised by both low diversity and low endemism. We have also seen that the endemics that occur in more than one region in the eastern lowlands have lower frequency (occur in fewer regions) than the similar category of endemics in the eastern highlands.

Comparison with diversity and endemism in birds

In an analysis of the diversity and endemicity of birds of the Horn of Africa, as defined here, Fjeldså and de Klerk (2001) have found support for a fauna region called "Horn of Africa Province" (approximately equivalent to our northern and north-eastern Flora provinces, N2, N3 and C1), with a high concentration of both widespread and restricted range species at Ceerigabo (Erigavo) and a number of endemics that were more widespread in the "Horn of Africa Province". Another of Fjeldså and de Klerk's fauna regions is the "Somalia Masai District", which extends from northern Somalia (N1) through south-eastern and southern Ethiopia (HA, BA and SD) to southern Somalia, with centres of endemism in N1, SD/BA and along the Somali coast. Fjeldså and de Klerk's Ethiopian highland fauna region, "Ethiopian Highland District", had a range of endemic taxa that were widespread in the highlands. Finally, Fjeldså and de Klerk's region in the southern Ethiopian lowlands was considered a separate fauna region, the "Lake Turkana District", with centres of endemism in southern Ethiopia (SD). Therefore, it seems that there is good agreement between Fjeldså and de Klerk's and our findings with regard to the distribution and frequency of the endemics.

Possible explanations

Among the parameters we have studied here the diversity in the Horn of Africa seems to be correlated with altitudinal range. From the knowledge we have of the topography and the general impression we have of the precipitation pattern it seems also likely that high diversity in Ethiopia is correlated with a combination of a diverse relief and moderate to high precipitation. This agrees with the conclusions of Friis *et al.* (2001).

In several of the papers referred to above, *e.g.* Thulin (1994), geological and edaphic variation for endemism in Somalia and eastern Ethiopian lowlands have been proposed as explanation for the high endemicity. In the major part of the Ethiopian highlands the rocks are either Precambrian crystalline (at low altitudes) or the Tertiary basaltic rocks (above the crystalline rocks) that make up most of the plateaux. In the eastern lowlands the rocks are much more varied, consisting of Mesozoic limestone, sandstone, gypsum, coral limestone, *etc.* This may indeed be an explanation for the higher and more narrowly distributed endemicity in the east, but we cannot demonstrate it with the methods used in this paper.

In the paper mentioned above by Fjeldså and de Klerk (2001) it has been suggested that the eastern lowlands of Ethiopia, especially the Borana area in southern Ethiopia (SD), have had stable local conditions with a low interannual variability over time, and this has been considered essential for the persistence of relict taxa.

These theories may, in combination with the theories about high endemism in areas with special geological conditions, present explanations for the endemism of the Horn.

Based on his study of disjunct species and endemics in the Somali flora, Thulin (1994) suggested that Somalia has served as a refugium for more or less arid relic elements of very different age, which are now either disjunctly distributed, with the current disjunct distribution being part of an old continuous distribution, or endemic in Somalia in areas with special geological conditions. Our findings here suggest that another explanation could be isolation on the peninsula, a "peninsular effect," as is demonstrated by our ordination analysis in this paper. Due to the stabilising influence of the sea on the climatic conditions, the "peninsular effect" may also have caused climatic stability.

Other explanations for the patterns of diversity exist. Colwell and Lees (2000) argue that between "hard boundaries" the highest species richness should be found in the "mid domain", and if the domain between the hard boundaries becomes narrowed, species richness should be expected to decrease. Their models furthermore predict that the closer the location is to a hard boundary, the higher the proportion of narrow-ranged species should be. The endemics of the Somali and the eastern Ethiopian lowlands are actually typically narrow-ranged. Geometrically, the Horn shows a gradual narrowing between the "hard boundaries" of the coastlines towards the tip at Cape Guardafui. Thus, the observed pattern of increasing total species richness and decreasing proportion of endemic species as one moves away from Cape Guardafui is actually in perfect agreement with Colwell and Less' strictly geometrical model.

Consequences; further studies

The clear-cut separation between the Ethiopian and the Somali Flora regions in the ordinations of both all taxa and endemics that occur in several Flora regions, as well as the high number of single-region endemics in north-eastern Somalia and along the coast of the Indian Ocean, support a separation of the (highland) Ethiopia and Somalia into two phytochoria (Afromontane and Somalia-Masai), as it has been suggested by White (1983, 1993). Evi-

dence for a clear-cut separation is also provided by the very little overlap in distribution of western highland and eastern lowland endemics that occur in more than one Flora region.

However, many observations remain unexplained, including the exact status of the western highland phytochorion and the smaller centres of diversity and endemism that various authors have pointed out within the Horn of Africa. There is certainly scope for further observations on and theories about the subject of diversity and endemicity on the Horn of Africa. A study of the altitudinal distribution will obviously be of interest, and is under preparation by the group of authors of this paper. Studies with a finer resolution, perhaps a one degree resolution or studies based on the exact position of the localities, would be even more rewarding than those of this paper, since they would allow pinpointing local centres of endemism, about which there has already been much speculation, and would also allow correlation analyses with more ecogeographical parameters, such as climate, geology and soil, that varies considerably within the Flora regions. Unfortunately, such studies are very labour-intensive and time consuming, and, with our current knowledge of the flora of the Horn of Africa, we may not yet have enough data for a full scale diversity study with such fine resolution. However, a study of the correlation between endemicity and a wide range of ecogeographical parameters seems within reach if only the rather limited resources necessary for travel, data-gathering and analyses of this material could be found.

Unpublished sources

Flora of Ethiopia and Eritrea

M. Thulin, Campanulaceae and Lobeliaceae. I. Friis and F. White, Ebenaceae. I. Friis, Sapotaceae and Solanaceae. O. Ryding *et al.*, Lamiaceae.

Flora of Somalia

M. Thulin, Campanulaceae, Lobeliaceae and Additional records for an Appendix to *Flora of Somalia*, Vol. 3. M. Thulin and I. Friis, Solanaceae. M. Thulin *et al.*, Rubiaceae. H. Beentje *et al.*, Compositae (Asteraceae). I. Friis, Ebenaceae and Sapotaceae. O. Ryding, Lamiaceae.

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