

A numerical re-evaluation of the sub-Saharan phytochoria of mainland Africa

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The delimitation of the sub-Saharan mainland African phytochoria was investigated by cluster analysis and non-metric multidimensional scaling of the distributions of 5438 species, recorded from 1918 one-degree grid squares. The clusters obtained were in many instances very similar to the phytochoria delimited by White. The Guineo-Congolian Regional Centre of Endemism (RCE) was retrieved with almost the same borders, including the northern and southern transition zones and the Lake Victoria Regional Mosaic (RM). A larger Zambesian phytochorion was found – this included the Zanzibar-Inhambane Regional Mosaic, as well as part of the Somali-Masai RCE and all of the Ethiopian and Kenyan parts of the Afromontane RCE. In southern Africa the Cape RCE, the Namib-Karoo RCE, as well as an expanded Tongaland – Pondoland RM, which included all the eastern slopes of the subcontinent were located. The central parts of the subcontinent (Kalahari-Highveld Regional Transition Zone (RTZ)) was expanded to include the Drakensberg, but divided into a south-eastern and north-western unit. None of the regional mosaics were retrieved, and the blocks of the Afromontane RCE were included in the various phytochoria in which they are embedded. Cluster analysis retrieved a Sudanian phytochorion, but ordination suggested that the delimitation between the floristic zones in West Africa is complex, and that there may be very broad transitions from one phytochorion to the next.

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Introduction

“If the distributions of all species are used as a basis for the subdivision of a Region, no clear picture will emerge or it will be considerably obscured, since the distinctive patterns of any particular ecological element will be masked by those of other ecological elements or swamped in the mass of statistics produced by such a crude approach.” (White 1965, p. 652).

In a remarkable series of papers from 1965 to 1993 Frank White produced an integrated phytochorological classification of Africa. This classification, which has become very widely used (his “The vegetation of Africa” has been cited at least 600 times to date, according to the Web of Science citation index, February 2003), is remarkable in that it is based on clearly formulated theoretical principles, a broad empirical knowledge of the distribution patterns in the African flora, and access to vast field knowledge. The classification synthesized the knowledge accumulated in the post Second World War botanical exploration of Africa, and exchanged at the regular meetings of AETFAT.

Phytochoria may be defined as large areas (c. 10,000 km² or more) with largely homogeneous plant species composition, which is different from that of other phytochoria. The distribution of species in sub-Saharan Africa is determined by modern climates and soils, as well as past climates. This is manifested by three concepts:

1) The phytochoria should reflect the zonal flora, the flora found in the general area, and the zonal vegetation type.

2) Each phytochorion has many ecological habitats, occupied by an azonal flora (azonal vegetation types).

3) Relicts of previous climates which show disjunct distributions are labelled as tracks.

However, because a rigorous definition of these concepts seems not to be possible, we are left with almost arbitrary decisions as to whether a particular distribution pattern is a phytochorion, vegetation type or historical track. White did not attempt to distinguish between historical and ecological causes of the distribution patterns, and elaborated a set of principles as rules by which to delimit his phytochoria (White 1965, 1971, 1983, 1993). These can be summarized as follows:

1) The classification should not be hierarchical. Instead of Kingdoms, Regions and Provinces, areas are not ranked, but encompass “centres of endemism”. Since they are geographically delimited, he referred to them as “regions”.

2) The delimitation of the choria is based only on species distributions. White often referred to these distributions as the “facts”. Thus neither the vegetation types, nor higher taxonomic groups like genera, were taken into account.

3) Three types of regions are recognised. Regional Centres of Endemism (RCE) contain at least 1000 endemic or near-endemic species, and at least 50% of its phanerogam flora should be endemic. Between centres are broad Regional Transition Zones (RTZ), which always have fewer than 1000 endemic species, and these make up less than 50% of the flora. Regional Mosaics (RM) constitute a mosaic of vegetation types, and an intermingling of otherwise distinct floras. White (1979) discussed the concept of a RCE in detail. Although semantically a centre has no dimensions, he used the concept in a territorial sense, to describe a region with a high concentration of species, which are largely endemic to this region. The other two concepts describe the transitions between these RCE.

4) Although in theory all species should be taken into account, the delimitation is based largely on the dominant species or groups (the

zonal flora), which can be studied in detail (White 1971). In effect this means largely the trees.

The phytogeographical system provides an efficient framework within which to summarize information about the flora and vegetation of Africa. As such it is a ready source of information on species richness, endemism, as well as peculiar features of the flora, vegetation or biota of all the parts of Africa.

White's phytogeographical classification of Africa forms a coherent system, which cannot be evaluated critically in part only. Continuing with his research methodology, mapping species or groups of species over the phytogeography, constitutes no test of the system: at most there will be no support for it. This is illustrated by White's (1990) analysis of a number of disjunct species. A more interesting approach would be to employ precisely the methods White argued against (see the citation above), using a large, *ad hoc* selected set of species, and objective numerical methods, to evaluate the support for African phytogeography. Here we use the largest body of sub-Saharan plant distribution data assembled to date, and subject it to cluster analysis as well as ordination, to establish (1) whether a numerical cluster analysis of the present data delimits phytogeography similar to those of White, (2) whether the transition zones recognised by White can be identified from cluster analysis and ordinations, and (3) whether our dataset and methods of analysis are sufficient to detect "unusual" phytogeography such as archipelago-like regional centres and regional mosaics.

Material and Methods

The plant dataset

The plant dataset analysed in this study comprises 79,648 data points for 5438 taxa, c 13% of the total sub-Saharan African flora (species as well as infra-specific taxa). Distribution data

were obtained from numerous datasources, including the *Distributiones Plantarum Africanarum*, published by Jardin Botanique National de Belgique (Anonymous 1969-), the Flora of Jebel Marra (Wickens 1976), the Protea Atlas Project (Rebello 1991), the arid flora of North Africa (Frankenberg & Klaus 1980), the SIG Ivoire project (Chatelain *et al.* 2001), South African arid plant distribution data (Jürgens 1997), and numerous taxonomic revisions (*e.g.*, Linder 2001a; Linder & Ellis 1990; Linder & Kurzweil 1999; Polhill 1982, pers. com.). Raw data in the form of maps were digitized with a digitizing tableau (see also La Ferla *et al.* 2002 for further method descriptions). Further datasets (Protea Atlas data, distribution data of southern African Orchidaceae, Restionaceae and the grass genus *Pentstemon*) were obtained as one quarter degree resolution presence / absence data for each species. The data were integrated into Microsoft ACCESS databases and analysed with the help of the programmes ArcView GIS 3.2 and WorldMap 4:20:17 (Williams 2002). Based on original data the resolution of which varies between exact coordinates of the plant record localities and nearest one degree square, all data were rescaled to a one degree gridded resolution. This resolution is a compromise between the loss of biogeographical detail on the one hand and the sampling inadequacy of finer resolution as well as the standard software capacities on the other hand. It also guarantees comparability to current zoological analyses (Brooks *et al.* 2001; Burgess *et al.* in prep.) and former studies on African plant diversity (Denys 1980; Linder 1998, 2001c; Lovett *et al.* 2000), as well as animal distribution data (*e.g.*, de Klerk *et al.* 2002). The geographical coverage of the dataset is limited to the African continent south of 20° N and comprises 1918 one-degree grid squares.

Parts of the data are presented at the following addresses:

www.york.ac.uk/res/celp/webpages/projects/
worldmap/worldmap.htm (York)
www.nbi.ac.za/protea (Cape Town)
www.botanik.uni-bonn.de/system/biomaps/biota/
floristicdatabases.html (Bonn)

The current continental database is administered and regularly updated as part of the Biogeographical Information System on African Plant Diversity (URL see above), which is established by the Biomaps Working Group, Bonn, as part of the BIOTA Africa Project (www.biota-africa.de).

Multivariate Analyses

The data were assembled into a square table of grid-cells (1918) and taxa (5438), and the similarity between every pair of grid-cells calculated using the Jaccard Coefficient of similarity (Jaccard 1901). The Jaccard Coefficient is particularly suitable for large phylogeographical analyses because it does not take shared absences into account (Jardine 1972).

The cells were clustered using the UPGMA algorithm. The cluster analysis found at least one tie, consequently a set of 50 dendrograms was calculated. However, it was not possible to build a consensus tree, since there were more items than the consensus-building program could accommodate. Instead several trees were visually inspected to establish whether there were major differences between them. Clusters were not recognised at a consistent level of similarity (the "phenon-line" approach), but we rather searched for large groups of cells that clustered together, and investigated the sub-clustering within these clusters.

Cluster analysis assumes a hierarchical structure in the data, and consequently may "force" clustering, thus distorting the true distances between the cells (Sneath & Sokal 1973). Non-metric multidimensional scaling (NMDS) was used to present these distances, as it maintains the same order of similarity as indicated in the data. It was not technically feasible to ordinate

the entire dataset. Besides, it would be extremely difficult to label the almost 2000 points on one ordination. Consequently, we used NMDS to explore regional patterns: the transition between the rainforest and the desert in West Africa, and the phylogeographical patterns in east Africa and southern Africa.

A Principal Coordinates Analysis (PCOA) was first performed, by extracting the eigenvalues from the double-centered Jaccard similarity matrix. The results from the PCOA were then used as starting configuration for the NMDS, done for three dimensions with the double-centered Jaccard similarity matrix. As a test of fit, the stress was calculated. Each ordination was presented as a three-dimensional plot, and the cells labelled with the phytochoria assigned on the basis of the cluster analysis. All analyses were done using NTSYS-pc (Rohlf 1998).

Calculation of regional richness and endemism

The species richness and endemism for each of the delimited phytochoria were calculated from the underlying dataset in ACCESS. We used both the phytochoria as delimited by White, as well as those determined from the present cluster analysis. For the initial analysis cells, which could not be placed, were ignored (not counted for species richness, nor used in the determination of endemism). Because most phytochoria are not geographically coherent (*e.g.*, include geographically isolated cells), a second analysis with "simplified" phytochoria was performed. Here the phytochorological assignment of the cells was changed according to the following rules. Unassigned cells that had at least seven of the eight neighbouring cells belong to one phytochorion were assigned to that phytochorion. Cells assigned to one phytochorion but embedded within another phytochorion (all eight neighbouring cells belonging to the same, other phyto-

chorion) had their assignation changed. Cells assigned to a phytochorion, but not in contact with any other cells of that phytochorion, but bordering on cells assigned to more than one phytochorion, were changed to “unassigned.” In a small number of cases, almost all involving outliers of the Somalian phytochorion in the Kalahari and the Sahelian phytochoria, the rules were interpreted in a more relaxed fashion to allow clusters of outliers to be transferred to the host phytochorion. This resulted in a geographically more coherent set of phytochoria.

The question whether the level of endemism reported here for the phytochoria is higher than random could not be addressed, since there is a dramatic variation in the proportion of range-restricted species in sub-Saharan Africa (Kier & Barthlott 2001; Linder 1998, 2001c). Consequently the variance around any statistic of the continent-wide average ranges of the species would be enormous and difficult to interpret.

Results

Cluster Analysis

The dendrogram for the whole sub-Saharan Africa shows the major groupings only at a very low level of similarity. At the broadest level, six groups were delimited, as well as a number of cells that were not clustered, but linked more or less directly to the stem of the dendrogram. This lack of clustering may be the result of a low number of species recorded for some cells (236 cells with less than 5 species). Cells with few species are often unplaced, probably due to sensitivity to sampling stochasticity. These unplaced cells were not mapped to any phytochorion, but shown as blank cells (with those cells for which no data were available) on the phytochorological map (Fig. 1). Five of the six groups showed clear internal subgroups (as well as a number of cells that were assigned to

this group, but not resolved to one of the subgroups). Recognising these subgroups, as well as the clusters of unplaced cells, resulted in 19 groups or phytochoria (Fig. 1). These phytochoria were labelled with names somewhat different from the phytochoria names used by White, in order to keep the two sets of concepts distinct. The cells placed to a major group, but not to one of the subgroups, are labelled as “undifferentiated”.

Richness and endemism of phytochoria

The species richness and endemism for the phytochoria as delimited by White (1983), and calculated from our dataset, are presented in Table 1. We sampled an average of 24.3% (between 12% (Guineo-Congolian RCE) and 48% (Sahel RTZ)) of the species richness of each phytochorion. We seemed to have less success in sampling the endemic species, retrieving an average of 18% of the endemic species as predicted by White (between 0.6% (Sudanian RCE) and 68% (Sahara RTZ)).

There is enormous variation in the species richness and endemism of the phytochoria delimited in the present study (Table 2). For the broad phytochoria richness ranges from 410 species (Somalian) to 2612 species (southern Africa), and endemism from 1% (Sudanian) to 85% (Southern African). For the narrow phytochoria (excluding the transitions, which did not form groups) the range is from 168 species in the Sahara, to 1822 species in the Cape. Endemism ranges from 0% for the Sudanian-north to 77% for the Cape. There is no obvious relationship between area and endemism.

The calculated results for the “simplified” phytochoria (Table 3) show clear trends: the species richness of the areas is more or less the same as for the unmodified phytochoria, but the endemism is generally higher. For the Sudanian, Somalian and Angolan phytochoria the richness is substantially reduced, and for

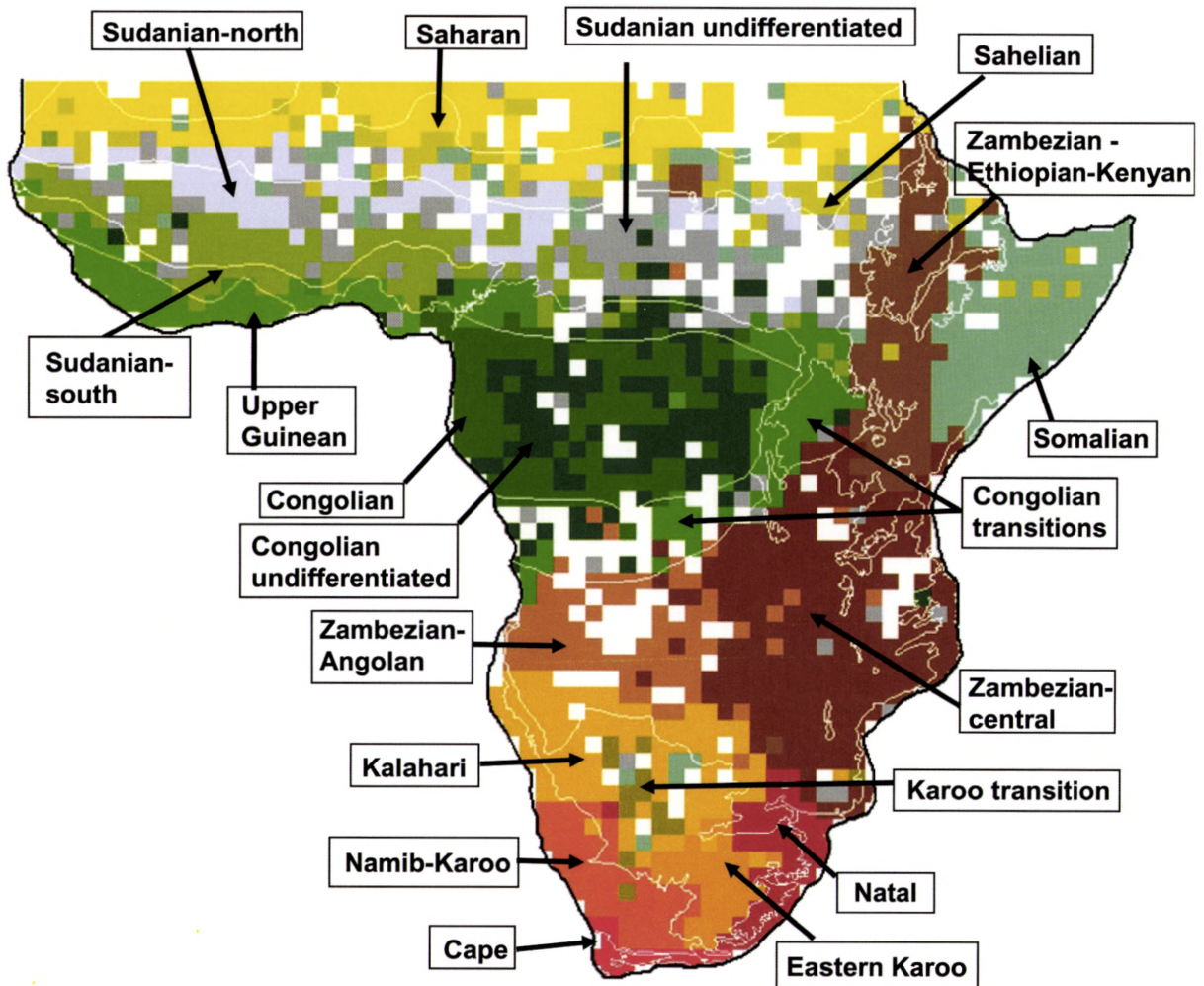


Fig. 1. The mapped results of the cluster analysis. Country boundaries are indicated in black, the boundaries of the White Regions are indicated in white, and the phytochoria retrieved in our analysis are colour coded.

the Ethiopian – Kenyan part of the Zambebian phytochorion the richness increases substantially. The only reduction in endemism is seen for the Congolian part of the Guineo-Congolian phytochorion.

Ordinations

The NMDS ordinations (Fig. 2) show that the clusters overlap to a greater or lesser extent,

but that they are largely recognisable. However, it is evident that the data are not readily shoe-horned into three dimensions, as indicated by the final stress values of 0.64241 for East Africa, 0.57490 for West African and 0.62141 for southern African. Values more than 0.40 are regarded as a poor fit (Rohlf 1998).

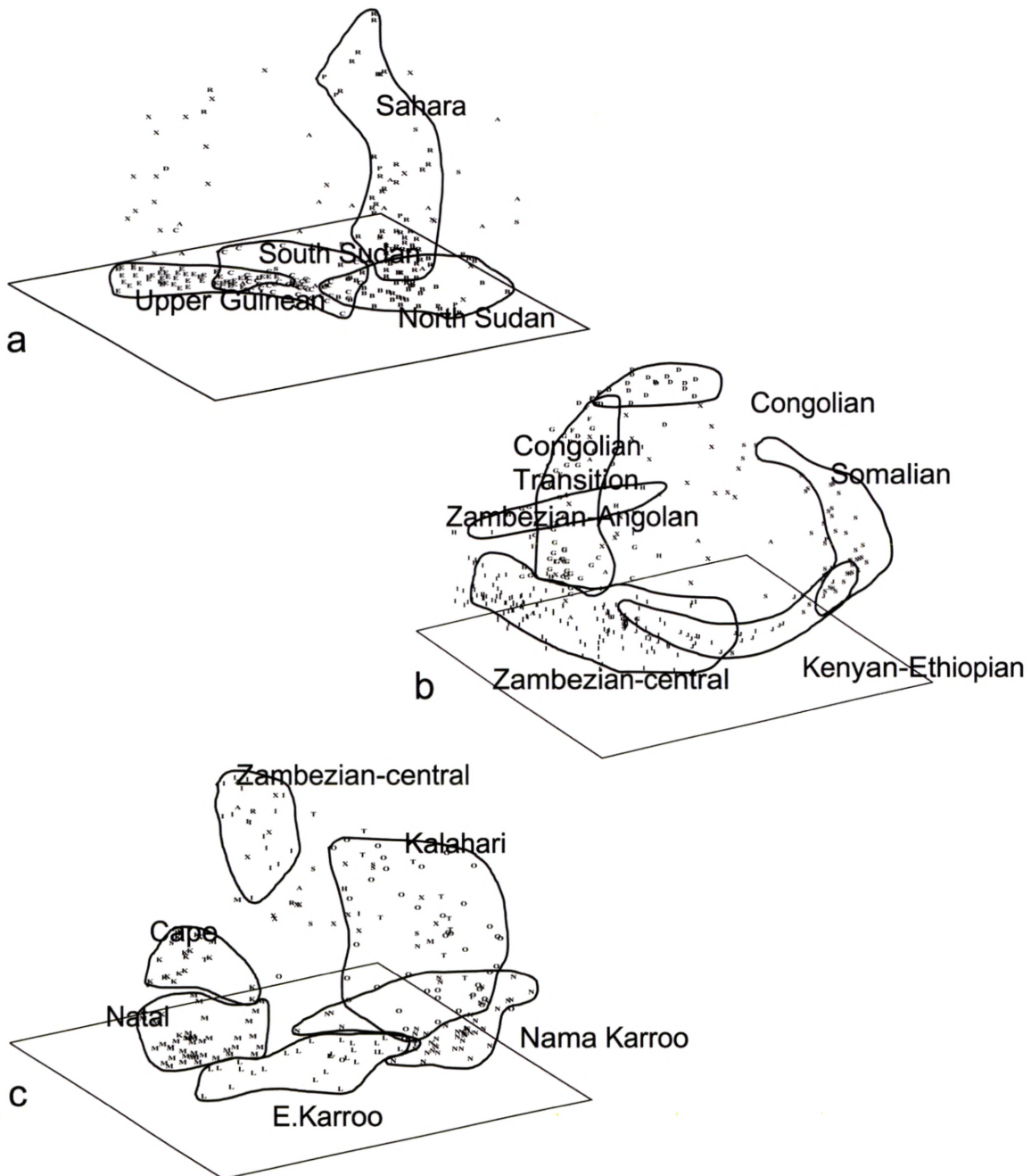


Fig. 2. NMDS ordination of (a) West Africa, (b) East Africa and (c) southern Africa. The circles are labelled with the phytchoria they represent, but not all cells are always included in the circles. The area codes used for all the ordinations are: A = Sudanian undifferentiated; B = Sudanian-north; C = Sudanian-south; D = Congolian undifferentiated; E = Upper Guinean; F = Congolian; G = Congolian transitions; H = Zambebian-Angolan; I = Zambebian-central; J = Zambebian-Ethiopian-Kenyan; K = Cape; L = Eastern Karoo; M = Natal; N = Namib Karoo; O = Kalahari; P = Sahelian; R = Saharan; S = Somalian; T = undifferentiated southern African; X = unplaced.

Table 1. Species richness and endemism of the phytochoria as delimited by White (1983), comparing his estimates of the species richness and endemism with that obtained from our data.

Phytochorion name	White's estimates			Our data			Proportion sampled	
	Species richness	Number endemic species	% endemic species	Species richness	Number endemic species	% endemic species	species	Endemic species
Guineo-Congolian RCE	12000	6400	53	1375	399	29	11.5	6.2
Cape RCE	8600	5870	68	1599	838	52	18.6	14.3
Zambezian RCE	8500	4590	54	1725	377	22	20.3	8.2
Karoo-Namib RCE	7000	3500	50	1036	201	19	14.8	5.7
Afromontane RCE	4000	3000	75	1564	78	5	39.1	2.6
Somali-Masai RCE	4000	1250	31	931	103	11	23.3	8.2
Kalahari/Highveld RTZ	3000	50	2	583	10	2	19.4	20.0
Lake Victoria RM	3000	50	2	504	3	1	16.8	6.0
Tongaland-Pondoland RM	3000	1200	40	813	84	10	27.1	7.0
Zanzibar-Inhambane RM	3000	450	15	576	48	8	19.2	10.7
Sudanian RCE	2750	960	35	684	6	1	24.9	0.6
Guinea-Congolia/Sudania RTZ	2000	50	3	711	5	1	35.6	10.0
Guinea-Congolia/Zambezia RTZ	2000	50	3	571	28	5	28.6	56.0
Sahara RTZ	1620	50	3	289	34	12	17.8	68.0
Sahel RTZ	1200	50	4	579	23	4	48.3	46.0

Discussion

Phytochoria

Guineo-Congolian

The Guineo-Congolian Regional Centre of Endemism (RCE) was retrieved with minor variations in the delimitation from the surrounding phytochoria. These involve the transition zones to the north (Guinea-Congolia/Sudania Regional Transition Zone (RTZ)), the east (Lake Victoria Regional Mosaic (RM)) and the south (Guinea-Congolia/Zambezia RTZ). No East African coastal outliers of the Guineo-Congolian RCE were identified, thus corroborating White's inter-

pretation. While White recorded 53% endemism for his region, our data indicate that only 29% of the species in our sample are restricted (endemic) to this Centre (Table 1).

The Upper Guinean phytochorion is delimited to the east by the Cross River, immediately west of Mt Cameroun, with the lower Niger and its delta clearly included in Upper Guinea. The Cross River boundary was suggested by Léonard (1965) and Clayton and Hepper (1974), but White could not recognize it from his data. The major deviation from White's delimitation is the inclusion of the Fouta Djallon in the Upper Guinean phytochorion, while White placed it in his Guinea-Congolia/Suda-

Table 2. Species richness and endemism in the phytochoria as delimited by our analysis, based on the data used in this paper.

Broad phytochoria	Species richness	Number endemic species	% endemic species	Narrow phytochoria	Species richness	Number endemic species	% endemic species
Sudanian	729	8	1%	Sudanian undifferentiated	452	1	0%
				Sudanian-north	307	0	0%
				Sudanian-south	494	3	1%
Guineo-Congolian	1708	739	43%	Congolian undifferentiated	750	14	2%
				Congolian	1046	200	19%
				Congolian + Congolian undifferentiated	1177	460	39%
				Upper Guinean	578	61	11%
				Congolian transitions	1059	99	9%
Zambeian	1886	766	41%	Zambeian – Ethiopian-Kenyan	506	42	8%
				Zambeian-central	1472	497	34%
				Zambeian-Angolan	810	90	11%
Southern African	2612	2223	85%	Karoo transition	46	0	0%
				Cape	1822	1396	77%
				Eastern Karoo	320	4	1%
				Natal	882	295	33%
				Namib-Karoo	339	65	19%
				Kalahari	294	17	6%
Sahara-Sahelian	474	182	38%	Sahara	168	1	1%
				Sahel	420	173	41%
Somalian	410	47	11%	Somalian	410	47	11%

nia RTZ. The Upper Guinean phytochorion is rather species poor (564 species, compared to the 1137 for the Congolian phytochorion) and with a lower level of endemism (13% compared to 30%; Table 3). Note that the species numbers, and percentages of endemism, referred to here and in the rest of the paper are based on our sample, and are not estimates of the actual species richness of these phytochoria.

The Congolian phytochorion includes both Lower Guinea and the Congo basin. We included in the phytochorion both the “Congolian” and “Congolian-undifferentiated” cells. The cells of the “Congolian undifferentiated” group generally have fewer species than the “Congolian”, and this might reflect collecting intensity (Küper unpublished), rather than actual low species richness. Consequently, in the discussions we combine these two clusters.

Table 3. Species richness and endemism in the simplified phytochoria delimited in this paper, based on the data used in this paper.

Broad phytochoria	Species richness	Number endemic species	% endemic species	Narrow phytochoria	Species richness	Number endemic species	% endemic species
Sudanian	637	53	8%				
Guineo-Congolian	1700	799	47%	Congolian	1137	346	30%
				Upper Guinean	564	71	13%
				Congolian Transition	1060	102	10%
Zambezi	1893	850	45%	Zambezi – Ethiopian-Kenyan	804	104	13%
				Zambezi-central	1477	541	37%
				Zambezi-Angolan	479	55	11%
Southern African	2615	2268	87%	Eastern Karoo	320	1	0%
				Cape	1822	1409	77%
				Kalahari	298	20	7%
				Natal	881	297	34%
				Namib-Karoo	339	69	20%
Sahara	467	199	43%				
Somalian	344	53	15%				

The Congolian phytochorion is both species rich and high in endemism, with the greatest species richness located in Lower Guinea, from Mt Cameroun to the mouth of the Congo River. In tropical Africa, this is the most species-rich area with also the highest concentration of endemics (Barthlott *et al.* 1996; Cheek *et al.* 2001; La Ferla *et al.* 2002; Linder 1998, 2001c; Mutke *et al.* 2001). The distribution of endemics through the region was not investigated, but the cells assigned to “Congolian undifferentiated” have only 2% endemism (restricted to the cells assigned to this cluster) even though 750 species are included in our database for these areas. Adding these to the cluster of species rich cells adds only 131 species to the cluster, but increases the

endemism from 19% to 39% (Table 2). Thus the unplaced cells can have a major impact on the calculation of the endemism levels. However, if outlier cells are “simplified” into the surrounding phytochoria, the endemism is again reduced to 30% (Table 3), but without loss of species richness.

The areas along the borders of the Congolian phytochorion were assigned to the “Congolian transitions”. Three regions can more or less be distinguished in the Jaccard clustering: Bamenda – Adamaoua (part of White’s Guinea-Congolia/Sudania RTZ), Kivu and Uganda (partially the Lake Victoria RM) and the areas around Kananga and Mbuji-Maji (largely the Guinea-Congolia/Zambezia RTZ). It is not clear what combines these three areas,

since they abutt onto different floras. The largest extension beyond White's boundaries is found in the southern Sudan, where the Imatong Mountains are included in our Congolian transition, while White assigned them to the Sudanian RCE. According to Friis (1994) the foothills of these mountains are clothed in Guineo-Congolian forest, and this could contain the species on which the groupings proposed here are based. Surprisingly, this transitional phytochorion has a 10% level of endemism (Table 3).

It is surprising that such consistent groupings were obtained for the Guineo-Congolian RCE, since it is the most poorly sampled phytochorion, with only 12% of the species represented in our analysis (Table 1). However, all previous phytochorological studies have delimited this centre (*e.g.*, Lebrun 1947; Monod 1957; Wickens 1976), indicating that it is distinct from the other phytochoria.

Sudanian

Our data clearly separate the Sudanian RCE and the Zambezi RCE, thus corroborating the results of the careful analysis of White (1965), which upset the previous assumption (Lebrun 1947, Monod 1957) of a horse-shoe shaped phytochorion that partially surrounded the equatorial rainforests of Congo and Guinea with its own flora. The similarity in savanna vegetation structure is not matched by a similarity in floristics. There is as yet no simple explanation for this dissimilarity – whether it is the effect of differences in the modern climates and topography, the consequence of a long period of isolation either side of an Atlantic to Indian Ocean rainforest, or the result of two independent derivations from rainforest.

Our analyses retrieved a Sudanian phytochorion broadly similar to that of White. The cluster analysis retrieves two subgroups. The first (Sudanian-north) contains a mix of cells

attributed to the Sahel RTZ and the Sudanian RCE by White (1983). The second (Sudanian-south) has a mix of Sudanian RCE and the Guinea-Congolia/Sudania RTZ (Fig. 1). The NMDS ordination (Fig. 2a) reveals that there are no distinct clusters of cells in West Africa. This suggests that although there is a large change in the flora from the coastal rainforests to the Sahara, there are no sharp floristic, geographical, boundaries. Thus it appears as if there may be no large set of species in West Africa which have co-incident limits to their distributions. This is consistent with the distribution of forest types (van Rompaey 1996) as well as individual tree species (Bongers *et al.* 1999) in West Africa, which are strongly determined by the steep rainfall gradients from coast to desert.

It may be possible that our results are due to sampling artifacts. Although almost 25% of the Sudanian species have been included in the study (Table 1), more than twice as large a proportion as for the Guineo-Congolian RCE, it is possible that our sampling has missed many of the "typical" Sudanian species. The low level endemism indicated by our data (1%, compared to the 35% suggested by White) suggests such a pattern of undersampling. Furthermore, the large proportion of cells with few species may also indicate undersampling, in addition to distorting the results of the analysis. Simplifying our Sudanian phytochorion by removing the cells that clustered with the Somalian phytochorion, including the cells that were not placed, and removing isolated outlier cells of neighbouring phytochoria resulted in an increase in the endemism levels to 8% (Table 3).

Our data indicate that a geographically coherent, clearly delimited Sudanian phytochorion might not exist. This should be tested in more detail by focussed investigations, particularly using ordinations, of the distribution patterns of a much larger sample of West

African plant species. Indeed, our concerns about the Sudanian phytochorion were already voiced by White in 1993.

Sahara-Sahelian

The Sahara-Sahelian regions continue the pattern implied by the NMDS ordination for the Sudanian phytochorion, and it would have been satisfying if they grouped together. However, on the cluster analyses the two sets of clusters are widely separated. Curiously, the Sahel RTZ is the only region or transition zone for which the endemism suggested by White (4%) is matched by our data. For the Sahara our level of endemism is four times more than suggested by White, which is explained by our only partial inclusion of the Sahara. Thus the Saharo-Sindian elements (Lebrun 1947; White & Léonard 1994) may be represented in our dataset by only a part of their distribution ranges, while the vast majority of the remaining species have their full distribution ranges included. Quézel (1978) demonstrated that the endemism in the Sahara is only 12%, but that a further 23% of the species could be regarded as "Saharo-Arabian", further supporting the substantial contribution of the Saharo-Sindian element. This leads to the spuriously high endemism figure for this small part of the Saharo-Sindian region. In addition, some of our data are artificially truncated at 17.5° N, thus enhancing the floristic dissimilarity between Saharan and Sudanian regions, and increasing the endemism of the Saharan flora.

The Sudanian – Saharan boundary is 1-2 degrees north of the boundary between White's Sudanian RCE and his Sahel RTZ, about halfway across his Sahel RTZ, but aligned more or less parallel to the White boundary.

The distinctiveness of the Saharan flora from that of the Sudanian woodlands is also supported by the ordinations. This suggests that the Saharo-Sindian flora could be distinctive,

much more so than the Sahelian flora. Under these circumstances it might make sense to think in terms of a Saharo-Sindian RCE, albeit with less than 2000 species (Quézel 1978).

Somalian

The Horn of Africa, according to White (1983) forms part of the Somali-Masai RCE, which includes most of Kenya, and reaches south through Tanzania into the valley of the Great Ruaha. However, our analysis, similar to the earlier analysis (Linder 1998), extracts a region limited to Somalia, the Ogaden region of Ethiopia and the North Eastern Province of Kenya.

Mapping the White phytochoria onto our cluster analysis indicates that there are paired clusters assigned to the Somali-Masai RCE and the Afromontane RCE, which in our analysis are embedded in the Zambezan phytochorion. This overlap is also very evident from the ordination (Fig. 2b), which shows a portion of the Somalian centre, while another portion overlaps with the Kenyan-Ethiopian upland part of the Zambezan centre.

Possibly this area was undersampled – our data record 410 taxa and 11% endemism. Simplifying the Somalian phytochorion by removing the outliers in the Sahelian and Kalahari phytochoria results in a reduction in species richness to 344 taxa and an increase in endemism to 15% (Table 3), indicating that the narrower definition makes more phytochorological sense. If all the cells that fall within White's circumscription of the Somali-Masai RCE are included the richness increases to 931 species, but the endemism stays at 11% (Table 1). This sampled figure is slightly over 23% of the flora suggested by White, indicating that the area is actually quite well sampled. However, it is possible that our figures are inflated by the inclusion of Afromontane patches included in the cells assigned to the Somali-Masai RCE. Thulin (1994) estimated

the endemism of the flora of Somalia at 20%, thus substantially more than our figure, which is for a somewhat larger area. The explanation for this could be that in the central portions of Kenya and Tanzania the elements of this flora are found in the rift valley bottoms, while the ridges and mountains which rise to 5000 m contain an Afromontane flora. Consequently many cells contain at least some Afromontane elements, as well as some Somali elements.

There are outliers of the Somalian phytochorion in the central Kalahari of Botswana, as well as along the Sahel to Senegal. These reflect the "arid corridor", a set of disjunct distributions across the arid parts of Africa. Although the arid corridor has been well documented (Balinsky 1962; de Winter 1966, 1971; Ihlenfeldt 1994; Jürgens 1997; Thulin 1994; Thulin & Johansson 1996; Verdcourt 1969), there have been no phylogeographical analyses of any plant species that are part of the corridor, we still lack a reasonable estimation of the date (or dates) of the establishment of this distribution pattern.

Zambeian

The Zambeian phytochorion, as delimited by our analysis, is huge. It covers the whole of south-central Africa, from the Atlantic seaboard of Angola to the whole of Mozambique, Tanzania, and the uplands of Kenya and Ethiopia. As such it includes White's Zambeian RCE, most of the Afromontane RCE, and the Zanzibar-Inhambane RM, as well as the Masai parts of the Somali-Masai RCE. This area includes 1886 species, with 41% endemism (Table 2), or 1700 species and 47% endemism if the phytochorion is simplified (Table 3). It cannot be directly compared with any of Whites centres of endemism, but although the cells falling within the limits of White's Zambeian RCE have 1725 species (thus not much less than our much wider definition), the endemism stands at only 22% (Table 1).

This huge area was not retrieved in an earlier analysis of 794 species (Linder 1998), and instead three separate regions were located: (1) Malawi, Tanzanian, Kenyan and Ethiopia; (2) Mozambique, Zimbabwe and south-eastern Zambia, and (3) the rest of Zambia, Angola and Shaba. Our much larger analysis also located three subdivisions, but they are somewhat different: (1) Angola and Barotseland ("Zambeian-Angolan"), (2) the rest of South-central Africa to Mt Kilimanjaro, inclusive of Shaba and Malawi ("Zambeian-central"), and (3) the Kenyan and Ethiopian uplands ("Zambeian – Ethiopian-Kenyan"). Of these three areas only the Zambeian-central is species-rich, with a high level of endemism. This may not be surprising, since this area includes several local centres of richness and endemism: the Zambezi-Congo watershed (Linder 2001c), Nyika Plateau (Willis *et al.* 2001), the Southern Highlands of Tanzania, and the eastern arc mountains of Tanzania (Lovett 1993). The Angolan area is at least partially undercollected, and includes only one centre of endemism, on the Huilla Plateau (Linder 2001c).

The grouping of the uplands of Ethiopia, Sudan and East Africa into the Zambeian – Ethiopia-Kenya phytochorion is consistent with the distributions of woody and herbaceous Ethiopian Afromontane species, where the most common distribution pattern is of species restricted to Ethiopia and the mountains of East Africa, and the second most common distribution pattern is of species widespread in the Zambeian woodlands (Friis 1994). More curious, though, is the inclusion of those cells with predominantly Somalian species in these clusters. Also puzzling is the low species richness of the uplands (Zambeian – Ethiopian-Kenyan phytochorion), and their low endemism. The low endemism could partially result from the inclusion of species from the Somalian centre that penetrate along the low-

lands and rift valleys of eastern Africa. The low species richness suggests rather that the flora has been undersampled, but many of these cells belong to the Afromontane RCE, which at 39% is the best sampled phytochorion. Thus the results remain somewhat puzzling. The analysis grouped Jebel Marra with the other upland areas, and this might be the result of including the distributions of all species of Jebel Marra, as documented by Wickens (1976) in the dataset.

The east and central African NMDS (Fig. 2b) shows the relationships in this area very clearly. The cells assigned to the Congolian transitions lie between the Congolian and the Zambebian cells. An overlap of a different nature is seen between the Somalian and Zambebian cells, this is made up of the cells assigned to the Kenyan-Ethiopian uplands. Possibly this region, with its complex arrangements of mountains capped with Afromontane flora and valleys with a Somalian flora, should be regarded as a Regional Mosaic.

The remaining two areas are a reasonable match for White's Zambebian RCE. The east coast Zanzibar – Inhambane RM will be discussed below. Again the Afromontane cells are included within their "matrix" flora, this will also be discussed below. The distinction between the Angolan and central portions of the Zambebian phytochorion are more difficult to determine. It could be that the Angolan phytochorion reflects the dominance of miombo woodland species, while the central phytochorion contains a rich mixture of Afromontane species, and few miombo woodland elements.

Southern African

The southern African regions were all retrieved as one group (Fig. 1), with the northern border along the political borders: the Cunene River in the west and the Limpopo in the east. White suggested that the Zambebian

RCE included northern Namibia, northern Botswana and northern South Africa. This shift in the boundary might be the result of orchid distributions being truncated along the political border, but it does seem remarkable that some 50 truncated distribution ranges could have such an effect.

Southern Africa has a high species richness (2615 species) and endemism (87%; Table 3). According to Arnold and de Wet (1993) the region includes c 21,087 species, while sub-Saharan tropical Africa (the rest of Africa excluding the Maghreb, Libya and Egypt) contains 26,274 species (Lebrun & Stork 1997). If we accept 80% endemism to southern Africa (Goldblatt 1978), then 48% of the sub-Saharan flora is found in southern Africa.

Not surprisingly, the Cape Floristic Region, as delimited by Goldblatt (1978), is clearly retrieved (called here "Cape"), both in the cluster analysis and in the ordination. Our analysis included 1822 of the c 9000 species (Goldblatt & Manning 2002) attributed to the flora, and the endemism of 77% (Table 3) is somewhat higher than the just below 70% calculated by Goldblatt and Manning (2002). This higher endemism could be the result of including the Grahamstown fynbos outlier in our Cape phytochorion.

The rest of southern Africa can be summarised as two trends. The first ranges from the wet eastern coastline ("Natal"). West of this zone is the semi-arid "Eastern Karoo", which includes the grassland of the Eastern Cape interior and the plateau of the Free State and the Northern Cape. Along the Atlantic coastline, but also including the drier western margins of the Great Karoo, is the Namib-Karoo phytochorion. The north-south trend is indicated by the distinction of the Kalahari from both the Eastern Karoo and the Namib-Karoo, although it is evident from the NMDS analysis that there is no clear boundary between these three groupings (Figure 2c). These groupings

are unusual, and do not readily fit the previous phytochorological classifications proposed for southern Africa, as summarised by Werger (1978).

The Namib-Karoo phytochorion is similar to that suggested by White, except that the coastal strip following the Namib desert into southern Angola was not detected. This is most likely a sampling artifact, since this coastal strip is species poor and very narrow compared to grid size, and in total only 339 species from the whole phytochorion were included (Table 2, 3). The distinction between the Succulent Karoo and Nama Karoo, described by Rutherford and Westfall (1986) was not detected, which could be due to both undersampling of Succulent Karoo elements and the coarse resolution of our sampling. Although there have been suggestions that the Succulent Karoo region should be included in the Cape flora, and separated from the Nama Karoo region (Bayer 1984; Jürgens 1991), our data show that the Cape and Nama regions are widely separated in the ordination, and that the similarities of the Cape region lie rather with the more mesic Natal region. This could of course be driven by the shared Afromontane elements, as well as the coastal thicket floras, which have more in common between the Cape and the mesic east coast, than the arid west coast. A further element is that the taxa that link the Cape and Succulent Karoo floras (Crassulaceae, Aizoaceae, *Oxalis*, Iridaceae, etc.) were not included in the analysis. The exact delimitation between the western margin of the Cape flora, and the subtropical flora of southern Africa, will need to be investigated in a more detailed study (Linder 2003).

The mesic east coast was included in the Natal phytochorion, which encompasses the whole of the Pondoland-Tongoland RM, as well as the more tropical portions of the northern parts of South Africa. White's Kalahari-Highveld RTZ is divided between the Eastern

Karoo phytochorion in the south, and the Kalahari phytochorion to the north. White estimated his RTZ to include some 3000 species, most marginal transgressors, with a very low level of endemism. Our data support this: while the Namib-Karoo phytochorion has 20% endemism, and the Natal phytochorion 34%, the combined Eastern Karoo and Kalaharia phytochoria muster 7% endemism (Table 3). Curiously, the uplands of Lesotho with their subalpine vegetation are also included in this semi-arid phytochorion.

East Coast phytochoria

White recognised two phytochorological entities along the African east coast (White 1983; White & Moll 1978). North of Inhambane he delimited the Zanzibar-Inhambane RM, whilst south of the Limpopo River, to East London, the Pondoland-Tongoland RM. Neither of these were retrieved as groups equivalent to the other large groups by our analysis. These two phytochoria do not form geographically coherent entities (hence the term "regional mosaics"). The description of the vegetation of these regions (Moll & White 1978) indicates that they are mosaics of very different floristic elements – forests with species with Guineo-Congolian (Faden 1974), or Afromontane affinities (White 1981), elements endemic to the more humid eastern coast (Burgess *et al.* 1998), Zambezian elements in disturbed or somewhat drier areas (Lovett 1993), and Somafrican elements in the rain-shadows behind the coastal mountains (Lovett & Friis 1996). Such a mixture is not likely to be resolved by the analysis of data aggregated into 1° grids, but would need a more flexible matrix.

Nonetheless, the cells ascribed to the Zanzibar-Inhambane RM largely group together (with some additional cells) in a cluster embedded within the Zambezian-central phytochorion. The RM is species-rich (Clarke 1998; Linder 1998, 2001c), and our data set

includes 19% of these species (Table 1). Clarke (1998), in a recent analysis, demonstrated that it includes 1356 endemic species, most of which are found in the northern part of the region (Somalia to the Tanzania-Mozambique border). On these grounds he suggests that this northern region should be separated as a Regional Centre of Endemism, as it includes more than 1000 endemic species. However, it might better be regarded as a local centre of endemism within the Zambezian-central phytochorion.

The cells associated with the Pondoland-Tongaland RM do not aggregate separate from the Natal phytochorion, and the Natal phytochorion could be regarded as an expanded version of the Pondoland-Tongaland RM. The main differences are that some inland areas, attributed to the Afromontane RCE by White, are included.

Afromontane

The recognition, or otherwise, of the Afromontane phytochorion remains contentious. It is, according to White, characterized by a small, but consistent number of tree species (Chapman & White 1970; White 1978, 1981). Because it does not form a geographically contiguous area, White referred to it as an "Archipelago-like Regional Centre of Endemism". From the species richness, endemism, and internal consistency of the flora he found the Afromontane RCE comparable to the other RCE's. The richness of this flora decreases rapidly from East Africa to the Cape.

It is not clear to what extent the Afromontane flora can be distinguished from the surrounding lowland forest flora. Regional East African studies mostly fail to detect a sharp boundary to the Afromontane, and see a gradient going up the mountains (Hamilton 1975; Hamilton & Perrott 1981; Lovett 1993, 1998a). Possibly there is a gradual transition from low-

land to upland forest, but that would be no difference from the transition zones between any other phytochoria. However, Friis (1992) was able to show that at c 1500 m there is a change in forest composition in Ethiopia, and suggested that this represented the transition from lowland to afromontane forest. For the forests of the Eastern Cape of South Africa, Cawe *et al.* (1994) were able to demonstrate a clear distinction between coastal subtropical forests and inland afromontane forests. However, many species transgressed into the "other" forest type, and the frequency of the species in the two different forest types was an important factor to consider. Simple presence – absence data, as used in this study, would not detect the differences between these two types of forests.

The critical issue, though, is whether the affinities of the Afromontane flora on average lies with the lowlands surrounding the mountains, or with other mountains. Continent-wide numerical analyses, including the present one, fail to detect an Afromontane phytochorion. There could be a number of reasons for this. Firstly, the cell size is too large to obtain "pure" Afromontane flora. This could apply to portions of East Africa and South-Central Africa, and might account for the mixture of cells obvious from both the ordinations (Fig. 2b, c) and the cluster analysis. In East Africa, due to the steep topography, transitions between the Somali and Afromontane vegetation can be very abrupt, for example on Mt Kulal and Mt Marsabit. However, this does not apply to Ethiopia or southern Africa. In both these regions there are extensive areas of Afromontane forest and grassland.

Secondly, the most characteristic groups of plants may not have been included in the analysis. However, the Afromontane flora is the best sampled in this study, including 1564 of the estimated 4000 species (Table 1). Of the 12 species listed by White (1983) as defining the

Afromontane region over its whole range, four (*Ilex mitis*, *Nuxia floribunda*, *N. congesta* and *Rapanea melanophloes*) are included in our analysis. In addition, the understory herbs *Impatiens* and *Begonia* were also included. It seems therefore unlikely that our dataset might be especially skewed against the Afromontane flora.

A third factor is the high level of species-level turnover between mountain blocks, especially for herbaceous species. Carbutt and Edwards (2002) estimated that 20% of the species of the southern African Drakensberg are endemic to the region, and Lovett (1993) showed 71% of the Eastern Arc forest species that extend to the south reach the Limpopo, but that only 44% cross the river. Friis (1994) demonstrated that the affinities of the Ethiopian Afromontane species were largely with East Africa, with only 8.3% of the species described as Wide Afromontane taxa (reaching Cameroon and W. Africa), and a mere 3.3% of the taxa reach southern Africa. Similarly, 42% of a sample of 331 vascular plants from the Kitulo Plateau are described as “Eastern Afromontane”, although it is not clear how widespread they are (Lovett *et al.* 1994). It is also evident from White’s (1983) account of the Afromontane phytochorion that there is extensive regionalism. His “Afromontane rainforest” ranges from Ethiopia to Malawi, and he lists a number of undifferentiated forest species found only in southern Africa. Many of the most characteristic species are regionally restricted: *Podocarpus falcatus*, *Widdringtonia whytei*, *Ocotea usambarensis* and *Juniperus procera*. The West African Afromontane flora contains very few species, and is generally nested in extensive disturbed grassland and forests of more Guineo-Congolian affinities (Thomas & Achoundong 1994), so it is not surprising that these were not related to the East African montane floras. Although there might be a small number of species (maybe several hundred) with a wide-

spread Afromontane distribution, most species are endemic to one of three blocks – Kenyan-Ethiopian, Zimbabwean – southern Tanzanian, and southern African. Possibly if genera were used, then the whole track would be retrieved (as has been demonstrated for a number of taxa, such as the Disinae, *Erica*, *Protea* (Linder *et al.* 1992)), but using species only portions of this range appear. Further detailed resolution could be obtained if the Afromontane endemic species are sister taxa (*e.g.*, Griswold 1991). If, however, they are derived independently from the surrounding lowland flora, then the Afromontane is more equivalent to a vegetation type or perhaps as isolated independent phytochoria converging to a common structural flora.

Most likely the combination of undersampling the “typical” widespread Afromontane species, the high degree in species-level local endemism, and the interdigitation between Afromontane and the “matrix” phytochorion might have led to the “loss” of the Afromontane phytochorion in this analysis. Or maybe the Afromontane phytochorion really does not exist.

The Afroalpine Region, proposed by Hauman (1955), was also not retrieved in this analysis. However, this could be expected, since this is a very small flora (Hedberg 1957), restricted to very small areas. It would certainly be interesting to attempt to delimit these areas, and record this flora, to investigate the geographical patterns.

There seem to have been no complete floristic analyses of the phylogeographical affinities of any set of floras of isolated Afromontane areas, possibly because of the incomplete knowledge of these floras (Grimshaw 2001). Clearly, a new Africa-wide analysis of the Afromontane region is needed to determine whether the Afromontane is better regarded as a phytochorion delimited by the common possession of a significant num-

ber of species, or a biogeographical track characterised by a number of closely related but allopatric species.

Phytochoria, tracks and azonal vegetation

In tropical Africa the Guineo-Congolian, Zambezian, Somalian and Saharan phytochoria appear readily distinct. These occupy substantial integral areas, have distinctive genera, have “outliers” in the other areas, and are associated with very different climates. The Guineo-Congolian penetrates into the Zambezian and Sudanian along rivers, and has outliers on the African east coast (White 1979, 1990). The Somalian phytochorion could be seen as the hub of the “arid track” with outliers in the Sahel and Kalahari (Thulin 1994). In historical terms, it suggests that the Horn of Africa would be a refuge area for the arid flora. The Zambezian penetrates into the Congolian along drier ridges, but otherwise seems to lack outliers. Possibly the Saharan flora could also be recognised as a huge, almost empty, phytochorion (White & Léonard 1994).

In southern Africa three centres emerge. The Cape is remarkably species rich (21% of the sub-Saharan African flora!) and has outliers north along the higher mountains (Carbutt & Edwards 2002; Weimarck 1933, 1936, 1941). Along the West Coast is the Namib-Karoo phytochorion, with its unique leaf-succulent flora, and outliers along the east coast, in the Albany Centre (Hartmann 1991), as well as much further north in shallow-soil habitats over bedrock. The Natal phytochorion along the east coast has outliers along the south coast of the Cape phytochorion.

The transition zones are phytochorologically difficult. This applies to the south-north transition from the rainforest on the Gulf of Guinea to the Sahara. A similar transition is found in southern Africa, but this runs in an east-west direction, from the rainforest on the Natal coast to the arid Kalahari. Cluster analysis does

not illustrate these transitions, except as less robust clusters. They show up very clearly on the ordinations. The delimitation of geographically coherent areas for transition zones is largely arbitrary, but field experience indicates that the zonal vegetation is more clearly delimited. Possibly the problem is caused by the zonal flora / vegetation of one region penetrating as an azonal flora / vegetation into the neighbouring region (along rivers, or into well-drained habitats). Presence – absence data, at a 1° grid scale, will simply show a gradual transition.

Similarly, regional mosaics remain difficult to conceptualize. Typical is the African east coast, with its huge vegetational diversity, and high endemism mixed with outliers from diverse other areas. On endemism it would be possible to argue for a Regional Centre of Endemism (Clarke 1998), but there are two arguments against such a classification. The first is lack of geographical coherence (similar to the problem of the Afromontane Centre), the second is the absence of a typical vegetation type associated with a distinct climate. This is similar to large areas of East Africa, with a mixture of Afromontane above 1000 m and Somalian floristic elements below this altitude.

Possibly one of the most difficult phytogeographical elements to integrate into a phytochorological classification is the Afromontane. While almost everywhere distinct from the surrounding floras, it also has a large local endemism component. It seems to be a track without a regional centre on which it could be based.

Most phytochoria contain distinct local centres of species richness (Lovett 1998b). These are separated by extensive areas low in range-restricted species, but where the widespread species are found over the whole area. Thus the Lower Guinea centre of endemism (from Mt Cameroun south to Gabon) has a high concentration of range restricted species. The

remaining area of the Congolian phytochorion largely lacks range-restricted species, and the species found in this area are also found in the Lower Guinean centre. This centre is therefore interpreted as nested within the Congolian phytochorion. Similarly, in the Cape flora a number of species are widespread in the flora, but some parts have a high concentration of range restricted species (Linder 2001b). “Endemism” has become a confusing term: technically it means that the species are restricted to a defined area. Species with restricted ranges should rather be called “range-restricted species”, and centres of range-restricted species should not be confused with phytochoria. The latter are much broader, and include both diverse vegetation types, as one or several centres of range-restricted species.

Implications of data quality for phytochorological analyses

Data representativity

There are 26,274 species in sub-Saharan tropical Africa (Lebrun & Stork 1997) and 21,087 in southern Africa (Arnold & de Wet 1993). With 80% endemism in southern Africa (Goldblatt 1978), it indicates a total flora of 42,700 species, consequently our sample includes some 13% of this flora. In an ideal case, the selected data should representatively reflect the geographical distribution of the entire flora as well as its taxonomic and ecologic composition. However, the availability of distribution data restricted the selection of taxa. At the broadest level, the distribution of taxa seems balanced, with 11% from southern African, and 12% from tropical Africa, but several geographical areas are still comparatively under-represented. This occurs at different spatial scales – be it the areas in intermediate distance to urban centres that are not as well collected as the areas adjacent to the metropol, or entire regions such as Angola or southern

Mosambique, or locally within regions, such as within the Congo basin.

Curiously, the percentages do not simply add up. While some 13% of the flora has been sampled, if we compare our species from each of the White regions, the average sampling is closer to 20%. The simplest explanation for this discrepancy is that our sample was biased towards the more widespread species. The second explanation, that White underestimated the species richness and overestimated the endemism of his centres, seems more likely. This could be the result of his underestimating the distribution ranges of the species, consequently more species occur in neighbouring phytochoria (maybe present as azonal elements), increasing the species richness, and decreasing the endemism.

Theoretically, the actual proportion of the flora included for phytochorological work is not critical, since the delimitation of phytochoria is based on the shared presence of species. However, in practice cells represented by few species tend not to join clusters, possibly because they lack the species that delimit those clusters. Undersampling is therefore not positively misleading, in that it leads to incorrect clustering, but rather in that it leads to a lack of resolution. Undersampling will correctly assign cells for which endemics are present, but not if all species are widespread between clusters. The correct classification of species poor areas (as opposed to undersampled areas) will depend on whether endemics fall out faster than common species as richness declines, and this will usually be the case, except on special substrates. Consequently marginal areas will have a higher incidence of misclassification.

The calculations of species-richness and endemism are strongly affected by undersampling. This could have regional biases. For example, including all the Jebel Marra species in the data set means that all Jebel Marra endemics are included, but from the other

areas only the widespread species (that also occur on Jebel Marra) will be sampled. The data also contain an inherent taxonomic structure, both at the level of their actual distribution (the distribution of one species is most likely not independent of the distribution of its phylogenetic relatives, thus one finds genera of rainforest, savanna or Mediterranean climate species respectively), and at the level of sampling. Only data of taxa that have recently been taxonomically revised can be included, and such studies are mostly organised taxonomically. Since most taxa contain a restricted range of growthforms, this also means that the growthform sampling is biased.

For phytochorological work it may be important to gradually include more taxa “typical” of the different vegetation types, or “ecologically important species”, as suggested by White (1968). Yet such arguments are dangerously circular, or can cryptically lead to the definition of vegetation types, rather than phytochoria. It is obvious that all species are not phytochorologically identical, and this makes the sampling issue difficult.

Spatial resolution

The general implication of working with a one degree gridded dataset is a limitation of analytical detail. Especially in areas with steep environmental gradients and a subsequent high floristic turnover, the one degree grids will pool species with very different biogeographical affinities and therefore blur the analysis. This is a particular problem for the Afromontane region. A related problem may be with long, narrow phytochorological units, which contain a high proportion of cells with admixtures of other phytochoria. This problem might have occurred in and the narrow coastal strip of the Namib desert, the two east coast Regional Mosaics, and the Sudanian and Sahelian phytochoria.

Data structure

Parts of the data are characterized by peculiarities: while the overall majority of the distribution data cover the full continental areas of the species, this is not the case for the data from Frankenberg and Klaus (1980) and many of the exclusively south African plant distributions (*Pentaschistis*, Restionaceae, Orchidaceae). The distribution areas of 80% of the species from Frankenberg and Klaus (1980) are restricted to the area north of 17.5° N, which considerably reduces the floristic overlap and artificially enlarges the “endemism” of the Saharan flora. This effect will be minor in the case of southern Africa case, were about 80% of the species are endemic (including all Restionaceae, and all but one species of *Pentaschistis*), but may still have shifted the boundary of the Zambezian phytochorion to the north.

Almost all of the maps have been established without a direct biogeographical context, *e.g.* by accompanying taxonomic revisions. But 206 species were obtained from the Flora of Jebel Marra (Wickens 1976), so that this certain biogeographical element is disproportionately represented in the dataset. This should not negatively impact on the phytochorological analysis, although it will have dramatic impacts on the patterns of species richness and endemism.

Conclusion

Numerical analysis based on 5438 species distributions (13% of the total flora) was able to retrieve a set of credible phytochoria. These largely match the existing phytochorological classification (for the Guineo-Congolian RCE, Sudanian RCE, Zambezian RCE, Cape RCE, Karoo-Namib RCE, Pondolan-Tongaland RM), and so corroborate the most important elements of the existing phytochorological classification of Africa.

However, there are a number of problems with the existing system. The Sudanian RCE may be arbitrarily delimited, as there seems to be no interval in the change in species composition from the Guinean coast to the Sahara. The Afromontane RCE is not supported. There are a number of possible reasons; the most likely could be that it is not as coherent over the whole of Africa as thought previously. The Regional Mosaics could be dubious phytochorological entities, since it could be difficult to assign a geographically contiguous area to them. Possibly they should be regarded as areas of endemism nested within a broader phytochorion. The southern African phytochorological delimitation should be revisited, possibly a re-interpretation of the limits of the areas would be useful.

However, the danger is still that the dataset is not yet adequate to refute White's negative comments about using large datasets and numerical analyses. But contrary to the situation a few years ago, it is now possible to make a number of concrete suggestions:

1) Afromontane and Afroalpine taxa should be targeted for inclusion in the dataset, to evaluate the coherence of the Afromontane phytochorion. Possibly the most effective approach would be to incorporate as far as possible all species from a number of sample sites, similar to what was done for Jebel Marra. Sites should include the Drakensberg, Malawi or the Southern Highlands of Tanzania, Ethiopia and Mt Cameroun.

2) A number of transects should be analysed for West Africa, to determine whether there are co-ordinated species distribution limits, thus testing for the existence of the Sudanian Phytochorion.

3) The geographical scale of the floristic – vegetational change in West and East Africa should be evaluated, to determine whether geographically coherent phytochoria can be delimited in the region.

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