

The mosses of sub-Saharan Africa 2. Endemism and biodiversity

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Abstract: Based on a recent moss checklist of sub-Saharan Africa, an analysis is made of moss diversity and endemism in the area. There are over 3000 taxa, 77% of which are endemic. Figures for diversity and endemism for each country are listed, mapped and graphed, and endemism is also considered at the genus level. As the bryophyte flora of Africa is comparatively poorly known, it is important to be prudent when drawing conclusions about biodiversity and endemism.

Introduction

A checklist of mosses of sub-Saharan Africa (O'Shea, 1995) listed 2939 mosses. The list is being updated as more records are published and it now contains 3048 names. 2348 (77%) are endemic. The number of hepatic names for the same area is estimated by M.J. Wigginton (pers. comm.) as 943, with 698 endemics (74%). The equivalent figure for neotropical mosses is 63%, calculated from the data in Delgadillo, Bello & Cárdenas (1995)¹.

¹ Delgadillo (1994) suggests that the neotropical level of moss endemism is lower than this (48%), by summing the endemics from each country in the LATMOSS database. There are many taxa that are not endemic to any one Latin American country, but are still endemic to Latin America, and if these also are included, the figure increases to 63%. The equivalent figures for sub-Saharan African mosses are even more extreme - summing the individual countries gives only 16.8% endemism, vs. 77% taking the area as

a whole.

This paper uses data derived from O'Shea (1995) to describe and discuss the levels of diversity and endemism for 51 countries in sub-Saharan Africa.

Materials and Methods

The data from which the results are drawn is shown in Table 1, and is based on that collected for a checklist of sub-Saharan African mosses (O'Shea, 1995). It is taken from a database in the TAXA system (O'Shea, 1993) that contains a list of all taxa, including varieties and subspecies, that have appeared in published lists for sub-Saharan Africa, together with their distribution by country. The area covered is *Index Muscorum* divisions Africa-2, Africa-3, and the mainland part of Africa-4; this excludes the northernmost portions of Mali, Niger, and Chad, but includes all other countries and islands south of the Sahara, to as far south as the Cape. A map showing the area is in the checklist. The information in the checklist has

been aggregated to some extent to reduce the number of 'countries' - for instance, the islands of Bioko (Fernando Po) and Pagalu (Annobon) have been included with the mainland Rio Muni as Equatorial Guinea, Senegal and Gambia have been combined as Senegambia, and the four subdivisions of South Africa (Cape, Natal, Orange Free State and Transvaal) have been recombined. This still leaves 51 countries, some of which are quite small islands, such that the largest country (Sudan) is over 100,000 times the size of the smallest (Chagos Is.). The information was converted into map format to demonstrate levels of diversity.

To detect endemism, additional software was developed for TAXA, and moss distribution data from Latin America (Delgadillo, Bello & Cárdenas, 1995), Europe (Corley *et al.*, 1981; Corley & Crundwell 1991) and Indochina (Tan & Iwatsuki, 1993) were added to the database. The resulting list was then checked against Index Muscorum (van der Wijk, Margadant and Florschütz, 1959-1969) to eliminate those taxa which also occur in other parts of the world (mainly Australasia, North America and South America). The list of endemic taxa was summarised in tables, and analysed using Bykov's Index of Endemicity (Bykov, 1979; Major, 1988²) to compare levels of endemism across countries. The method is described in more detail in Appendix A.

Results

Diversity Because of the disparity in size of the units being measured, the diversity of the flora is best pictured using taxa per unit area³. In this case 10,000 km² has been chosen as the unit. This is the same as used by Delgadillo (1994) for neotropical mosses. The data is shown in Table 1, and is shown graphically in Figure 1.

²Bykov's paper is in Russian, so I have depended entirely on Major's description of its contents.

³There are better ways of identifying hotspots or areas of greatest diversity (e.g., Humphries, Williams & Vane-Wright, 1995; Williams *et al.*, 1996), but these are inappropriate for Africa with the quality of data currently available.

Endemism Levels of endemism at specific level

are summarised in the graph at Figure 2 and map at Figure 3. Endemic high taxa are limited to three families and 22 genera (see Table 2). These represent 3.8% of families and 5.9% of genera. Biodiversity within genera is shown in Table 3, which shows the 40 largest genera (those with 20 or more species) and the level of endemism within each genus.

Discussion

Introduction There is an urgent need, particularly for conservation reasons, to be able to provide data on diversity and endemism - however preliminary. The poor state of African taxonomy and collections over much of the continent (O'Shea, 1997) means that any extrapolation from existing knowledge must be made with caution, but it is likely to be many years before better information is available.

Diversity All diversity measures are based on sampling. Our knowledge of some taxonomic groups in Africa, say trees or birds, is quite good, and diversity measures reflect a real understanding of taxonomy and distribution. Our knowledge of the mosses is poor and maps of diversity levels reflect only the level of collecting. To some extent this represents 'target' collecting, where areas of presumed high diversity are visited just because they are thought to be more interesting, but even then the moss collections may have been made incidentally to some other group, such as flowering plants. The very low level of diversity recorded for some countries clearly does not represent a true figure, and the large number of taxa that can be added to a country list by extensive collecting is clear for example from recent activity in Malawi (Longton, 1993). Even taking account of area, reasonably well-collected countries such as Tanzania, with 813 taxa, come out fairly low in comparison with well-collected European countries: the UK with 745 moss taxa comes out higher (42 taxa per 10000 km²) as it is only a quarter of the size of Tanzania. As yet, we have no idea how many taxa an African country such as Tanzania may reasonably be assumed to hold.

In comparison with other African countries, diversity in Eritrea, Somalia and Ethiopia is per-

Table 1. Base data for calculations.

Notes

- 1 The Saharan parts of Chad, Mali, and Niger have been excluded from the country area.
2. 'Tropical Africa' in the table is Sub-Saharan Africa less southern Africa (Botswana, Lesotho, Namibia, South Africa, Swaziland).
3. Africa-4 (N) is the mainland part of 'Africa-4', excluding the islands to the south.
4. The column headings are discussed in Appendix A.
5. * = sub-list : included in previous list total.

Geog.	Geographicunit Taxa/	Total	Endem-	%en-	Normal	Index	Area			
Index	10000	taxa	ics	demics	%	(le)	(sq.km)	(g)		
k m ²				(Ef%)	(En%)					
	U K	1 034	15	1.45	4.7	-3.24	244754	0.61	42.25	
	UK (mosses)	745	12	1.61	4.7	-2.92	244754	0.49	30.44	
	UK (hepatics)	289	3	1.04	4.7	-4.52	244754	0.12	11.81	
	Sub-Saharan Africa	3048	2348	77.03	4.8	1.6	20609815	1.14	1.48	
	Tropical Africa	2788	2156	77.33	3.7	2.09	17935045	1.2	1.55	
	Africa-2	2056	1250	60.8	3.1	1.96	17340812	0.72	1.19	
	Africa-3	1115	641	57.49	2.3	2.5	594233	10.79	18.76	
	Africa-4 (N)	516	124	24.03	1.3	1.85	2674770	0.46	1.93	
1	Angola (Total)	122	25	20.49	1.0	2.05	1246700	0.2	0.98	
	* Angola	122	25	20.49	1.0	2.05	1246700	0.2	0.98	
	* Cabinda	2	0	0	0	1000	0	2.0		
2	Ascension	21	10	47.62	1	47.62	94	1063	2234.04	
3	Benin	8	0	0	0	112622	0	0.71		
4	Botswana	21	0	0	0	581730	0	0.36		
5	Burkina Faso	13	1	7.69	5	1.54	274122	0.04	0.47	
6	Burundi	68		2	2.94	1.6	1.84	278340	0.72	24.43
7	Cameroon	364	60	16.48	6.8	2.42	475500	1.26	7.66	
8	Cape Verde Is.	18	5	27.78	1	27.78	4033	12.4	44.63	
9	Central African Rep.	316	45	14.24	7.4	1.92	624977	0.72	5.06	
10	Chad	9	0	0	0	642000	0	0.14		
11	Chagos Islands	6	0	0	0	0	47	0		
1276.6										
12	Comores	192	40	20.83	1	20.83	2238	178	857.91	
13	Congo	76	7	9.21	5.3	1.74	342000	0.2	2.22	
14	Djibouti	26	0	0	0	0	232000	0	11.21	
15	Equatorial Guinea	73	20	27.4	1.6	17.13	28051	7.13	26.02	
	*Annobon (Pagalu)	18	11	61.11	1	61.11	17	6470	10588.24	
	*Fernando Po (Bioko)	57	8	14.04	1	14.04	2017	39.66	282.6	
	*Rio Muni	0	0	0	0	26017	0	0		
16	Eritrea	73	28	38.36	3	12.79	936802	0.99	7.79	
17	Ethiopia	247	56	22.67	1.0	2.27	1221900	0.46	2.02	
18	Gabon	259	31	11.97	5	2.39	267667	1.16	9.68	
19	Ghana	58	0	0	0	0	238305	0	2.43	
20	Guinea Bissau	1	0	0	0	0	36125	0	0.28	
21	Guinea	204	37	18.14	4.7	3.86	245855	1.5	8.3	
22	Cote d'Ivoire	170	8	4.71	5.3	-1.13	322463	0.25	5.27	
23	Kenya	450	45	10	7	1.43	582644	0.77	7.72	
24	Lesotho	162	2	1.23	1.7	-1.38	30350	0.66	53.38	
25	Liberia	57	6	10.53	3.1	3.4	111370	0.54	5.12	
26	Madagascar	765	328	42.88	7	6.13	587040	5.59	13.03	
27	Malawi	200	2	1	3.1	-3.1	118480	0.17	16.88	
28	Mali	15	0	0	0	620000	0	0.24		
29	Mascarene Is.	450	152	33.78	1	33.78	4481	339.21		
1004.24										
	*Mauritius	236	43	18.22	1	18.22	1865	230.56		
1265.42										
	*Reunion	363	71	19.56	1	19.56	2512	282.64		
1445.06										
	*Rodrigues	34	10	29.41	1	29.41	104	961.54		
3269.23										
30	Mozambique	73	3	4.11	8.2	-2	801590	0.04	0.91	

Geog. Index	Geographicunit Taxa/ 10000	Total taxa	Endem- ics	%en- demics (E%)	Normal % (En%)	Index (le)	Area (sq.km) (lg)
3 1	Namibia	56	3	5.36	8.2	-1.53	824290
3 2	Niger	5	0	0	630000	0	0.08
3 3	Nigeria	149	8	5.37	-1.53	923770	0.09 1.61
3 4	Principe	14	0	0	110	0	1272.73
3 5	Rwanda	278	16	5.76	1.6	3.6	26340 6.07 105.54
3 6	Rep. South Africa	506	129	25.49	10	2.55	1221040 1.06 4.14
	* Cape	387	50	12.92	7.3	1.77	743575 0.67 5.2
	* Natal	339	6	1.77	3	-1.69	91050 0.66 37.23
	* Orange Free State	136	0	0	0	106225	0 12.8
	* Transvaal	297	2	0.67	5	-7.46	242800 0.08 12.23
3 7	Sao Tome	73	15	20.55	1	20.55	854 175.64 854.8
3 8	Senegambia	22	4	18.18	4.1	4.43	208020 0.19 1.06
	* Senegal	22	4	18.18	4.1	4.43	196720 0.20 1.12
	* Gambia	0	0	0	0	11300	0 0
3 9	Seychelles (total)	94	13	13.83	1	13.83	404 321.78
2 3 2 6	* Agalega Is	4	0	0	0	23	0 1739.13
	* Aldabra	1	0	0	0	155	0 64.52
	* Amirante	1	0	0	0	40	0 250
	* Seychelles	93	13	13.98	1	13.98	280 464.29
3 3 2 1	4 0	76	5	6.58	2.5	2.63	71740 0.7 10.59
	4 1	19	6	31.58	1	31.58	3625 16.55 52.41
	4 2	18	9	50	7.4	6.76	637660 0.14 0.28
	4 3	30	10	33.33	1	33.33	121 826.45
2 4 7 9	4 4	29	1	3.45	13	-3.77	1650000 0 0.18
	4 5	89	0	0	0	173600	51.27
	4 6	813	121	14.88	9	1.65	945090 1.28 8.6
	4 7	86	5	5.81	2.2	2.64	567900.88 15.14
	4 8	358	40	11.17	4.1	2.72	235880 1.7 15.18
	4 9	587	75	12.78	12	1.07	2345410 0.32 2.5
	5 0	145	0	0	0	752610	0 1.93
	5 1	264	10	3.79	6	-1.58	390580 0.26 6.76
	Total	8232	1383	16.8	41	-2.44	20609815 0.67 3.99

Table 2. Endemic families and genera of sub-Saharan African mosses. (*Lasiodontium Ochrya* gen. nov. was announced in Miehe & Miehe (1994), but has not yet been formally described.)

Families:

Nanobryaceae
Rutenbergiaceae
Serpotortellaceae (3/78=3.8%)

Genera:

Bryotestua Dicranaceae
Chamaebryum Gigaspermaceae
Cladophascum Dicranaceae
Cygnicollum Funariaceae
Entodontella Entodontaceae
Hypodontium Calymperaceae
Kleioweisiopsis Pottiaceae
Lasiodontium?
Leptoischyrodon Fabroniaceae
Leucoperichaetium Grimmiaceae
Nanobryum Nanobryaceae
Neorutenbergia Rutenbergiaceae
Pocsiella Dicranaceae

<i>Ptychomitriopsis</i>	Ptychomitriaceae	
<i>Pylaisiobryum</i>	Entodontaceae	
<i>Quathlamba</i>	Bartramiaceae	
<i>Rhizofabronia</i>	Fabroniaceae	
<i>Rutenbergia</i>	Rutenbergiaceae	
<i>Schimperella</i>	Brachytheciaceae	
<i>Serpotortella</i>	Serpotortellaceae	(20 / 354 = 5.9%)

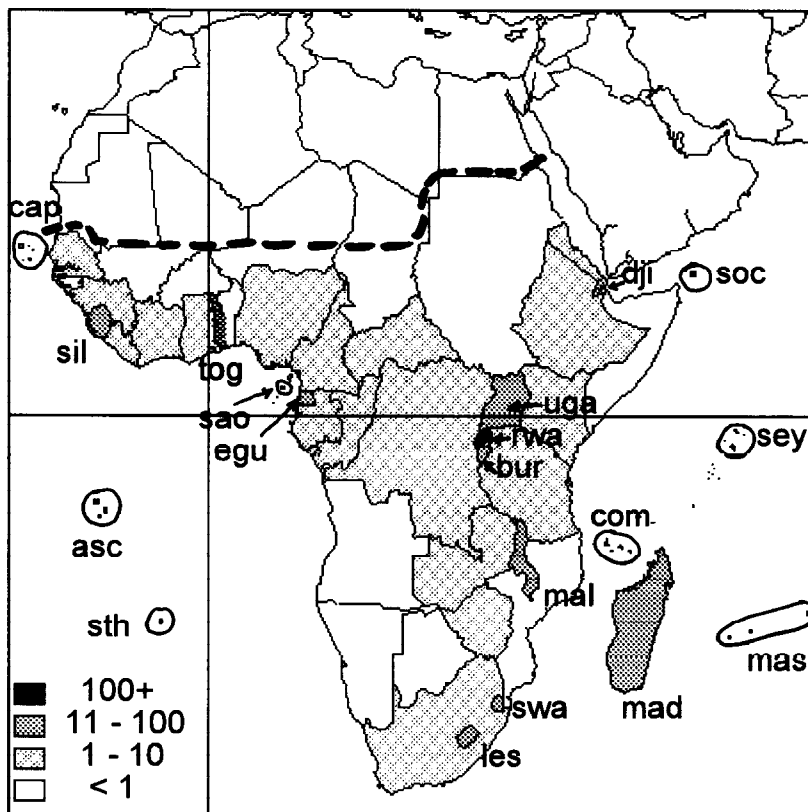
Table 3. Largest moss genera in sub-Saharan Africa, showing percentage of endemic species

	No. of sp.	Endemics	% of total
<i>Fissidens</i>	248	221	89
<i>Leucoloma</i>	105	104	99
<i>Bryum</i>	98	58	59
<i>Philonotis</i>	68	56	82
<i>Isopterygium</i>	67	64	96
<i>Sematophyllum</i>	64	59	92
<i>Macromitrium</i>	56	48	86
<i>Schlotheimia</i>	55	50	95
<i>Ectropothecium</i>	48	46	96
<i>Vesicularia</i>	46	45	98
<i>Campylopus</i>	40	22	55
<i>Trichosteleum</i>	40	38	95
<i>Pilotrichella</i>	37	37	100
<i>Brachythecium</i>	35	29	83
<i>Syrrhopodon</i>	34	26	76
<i>Taxithelium</i>	34	33	97
<i>Fabronia</i>	33	33	100
<i>Leucobryum</i>	33	31	94
<i>Barbula</i>	32	27	84
<i>Brachymenium</i>	32	21	60
<i>Racopilum</i>	30	28	93
<i>Zygodon</i>	30	25	83
<i>Callicostella</i>	29	26	90
<i>Dicranella</i>	29	27	93
<i>Trichostomum</i>	29	24	83
<i>Sphagnum</i>	28	18	64
<i>Hyophila</i>	26	24	92
<i>Trematodon</i>	26	25	96
<i>Cyclodictyon</i>	25	22	88
<i>Tortula</i>	25	17	68
<i>Anoetangium</i>	24	21	88
<i>Rhynchostegium</i>	23	21	91
<i>Entodon</i>	22	21	95
<i>Grimmia</i>	22	12	55
<i>Bartramia</i>	20	15	75
<i>Breutelia</i>	20	18	90
<i>Entosthodon</i>	20	17	85
<i>Mittenothamnium</i>	20	18	90
<i>Pohlia</i>	20	13	65
<i>Weissia</i>	20	17	85

haps artificially high because of the high number of doubtful taxa (mostly *nomina nuda*) in the area, many of which are endemic. I have not excluded these taxa as they are all supported by specimens and it seems unwise to ignore taxa because of nomenclatural mistakes or omissions by authors without examining the specimens. One point to note is that the more diverse mainland floras appear to relate to areas of supposed Pleistocene refugia (O'Shea, unpublished information) although this is less evident when dealing with countries rather than specific geographical areas. Africa covers a wide range of latitudes, and Williamson (1988) demonstrated that the further apart measurements are made, the more different they will be. For many organisms there is an increase in diversity, often significant, from the poles to the equator. This is well known, for instance, in flowering plants, although there are exceptions in many groups. The map (Figure 3) displays no evidence of a latitudinal diversity gradient for mosses.

Endemism Endemism here relates to taxa rather than communities, but the uncertainty about the distinctiveness of many taxa (O'Shea, 1997), and the lack of information about bryophyte communities in the tropics would in any case indicate that work on both taxonomy and bryophyte communities was necessary before consideration of communities was possible. The higher level of endemism in Africa vs. the Neotropics may well be an artefact resulting from the lack of collection data and questionable taxonomy that characterise African bryology. O'Shea (1997) predicts an overall reduction to around 43% of the existing list for Africa if the flora were thoroughly researched, and M.R. Crosby (pers. comm.) expects to find world-wide that most taxa not found or studied since the original description will prove to be synonyms of other taxa; this will make a significant reduction in the African figures for both diversity and endemism. Several recent papers (e.g. Townsend, 1991; O'Shea, Frahm & Porembski, 1996) identify taxa previously considered as endemic to Africa to be synonymous with Asian or pantropical taxa, confirming the trend to more realistic figures for endemism.

In general, the level of endemism increases as the area under consideration increases in size, although this is moderated by ecology and floristic history. Thus Africa-2 would be expected to have more endemics than its component Zaire, but less than Africa as a whole, and Kenya would be expected to have less than its larger neighbour Tanzania. However, the degree of variation between countries is likely to be not only a function of size, but also a function of the relative knowledge of the flora of the two countries, as well as the two factors already mentioned (ecology and floristic history). Bykov (1979) demonstrated that a similar relationship held for endemics as was already known to hold for diversity: the log of the number of species (or the percentage of endemics) occurring in an area increases linearly with the log of the area. 100% endemism occurs in the total land area of the earth (144 million km²), and Bykov estimated that 1% endemism occurred in about 625 km². This area was thought to be the minimum size needed to include all the plants in a region. If these two points (1% and 100%) on a log-log graph are connected, plants above the line will have less than normal endemism, and those below it, more. Bykov's index then measures the degree to which a country differs from the norm, either above or below. Bykov's own information was taken from areas all over the world, and convincingly puts various desert areas above the line and mountainous and tropical areas below it. In an area chosen for the relative uniformity of its phytogeography (such as sub-Saharan Africa or the neotropics) it is not clear that such a positive relationship would hold, particularly when the knowledge of the flora is not good. Nevertheless, this seems the best measure available, and at least provides a means of comparing bryophyte floras of different parts of the world. For this reason I have included the UK in the data table to provide an additional comparison. A possible problem with the 1% - 100% dividing line used by Bykov is that although the number of species increases with greater area, the rate of increase reduces with larger areas (Williamson, 1988), so the line should be curved. This would have the effect of putting more countries below the line (greater endemism), but as there is no equation quoted for the line, its actual shape cannot be quantified.



Key:

100+ asc = Ascension, com = Comores, mas = Mascarenes (Mauritius+Reunion+Rodrigues), rwa = Rwanda, sao = Sao Tomé, sey = Seychelles, sth = St. Helena

11-100 bur = Burundi, cap = Cape Verde, dji = Djibouti, egu = Equatorial Guinea (inc. Bioko & Annobon), les = Lesotho, mad = Madagascar, sil = Sierra Leone, soc = Socotra, swa = Swaziland, tog = Togo, uga = Uganda

Figure 1. Diversity: Taxa per 10,000 km² for each geographic unit

Delgadillo (1994) has already published measures for the neotropics using this index, and so should provide a useful comparison with tropical Africa. Delgadillo found the 1% level to be a rather larger area for bryophytes than for phanerogams, and suggested 5560 km². It appears to be around twice this figure for Africa, but Bykov comments that the slope of the line changes very little for quite large changes in area. Delgadillo chose Puerto Rico (8896 km²) as the nearest entity to 1%, but there were two African countries with around 1% endemism, Malawi and Lesotho. Because of the difference in size of the two countries, the area needed to support 1% endemism in Malawi is 118480 km², and for Lesotho 23332 km² - around 20% of the Malawi figure (and 2.6 times the neotropical figure). Despite Bykov's view about the stability of the graph, using Malawi instead of Puerto Rico as the 1% mark makes a significant difference, and causes around 20% of countries to change from one side of the line to the other. In addition, islands tend to show greater degrees of endemism over equal mainland areas because of their isolation (although this is not taken into account by Bykov's index). Nevertheless, it is probably safer to adopt a standard based on the most reliable (and most conservative) information available until we have a more thorough knowledge, so Puerto Rico has been used here. This allows compatibility to be maintained, but as it is a comparatively small island, it also allows smaller countries not to disappear off the scale. The average size of the countries in tropical Africa is rather smaller than those in the neotropics (500592 km² rather than 725010 km²) and thus we should also expect a lower level of endemism per country (16.8% to 48.2%), although the reverse is true for diversity (3.99 taxa per 10000 km² against 2.36 for the neotropics). The method of constructing the graph and deriving the index is described in Appendix A. Each dot on the graph (Figure 2) represents a country (or island), and the line representing 'normal' endemism is the same norm used by Delgadillo. The 8 dots below right are all islands and effectively go off the scale. The index seems not to be useful in comparing areas of such diverse sizes, but in general it is "unlikely that a transformation better than the log-log fit could be found for the generality of species-area relationships" (Williamson, 1988).

Conservation needs

The use of this data for conservation purposes presents a dilemma. Clearly the paucity of collections and the urgent need for taxonomic review mean that the data does not give an accurate reflection of the actual diversity or endemism of the flora. Nevertheless, despite this difficulty in interpreting the African data, the evidence for both Africa and the neotropics so far shows that there are many more endemic than pantropical bryophytes, and that conservation is needed on all continents to preserve this diversity. Unfortunately we know so little about bryophytes in Africa - their taxonomy, biogeography, habitat requirements, population dynamics, genetics, reproduction and dispersal - that all we can do is to conserve known areas of high diversity and endemism and a variety of habitats, and bear in mind that climate change may make this a continent-wide necessity (O'Shea, unpublished information). We cannot be sure which areas or habitats will be hit by which climatic or biotic factors - but we can have a good guess, and try to conserve the refugia of the future, and the areas that are going to supply them. Diversity in both taxa and habitats is needed.

Acknowledgements

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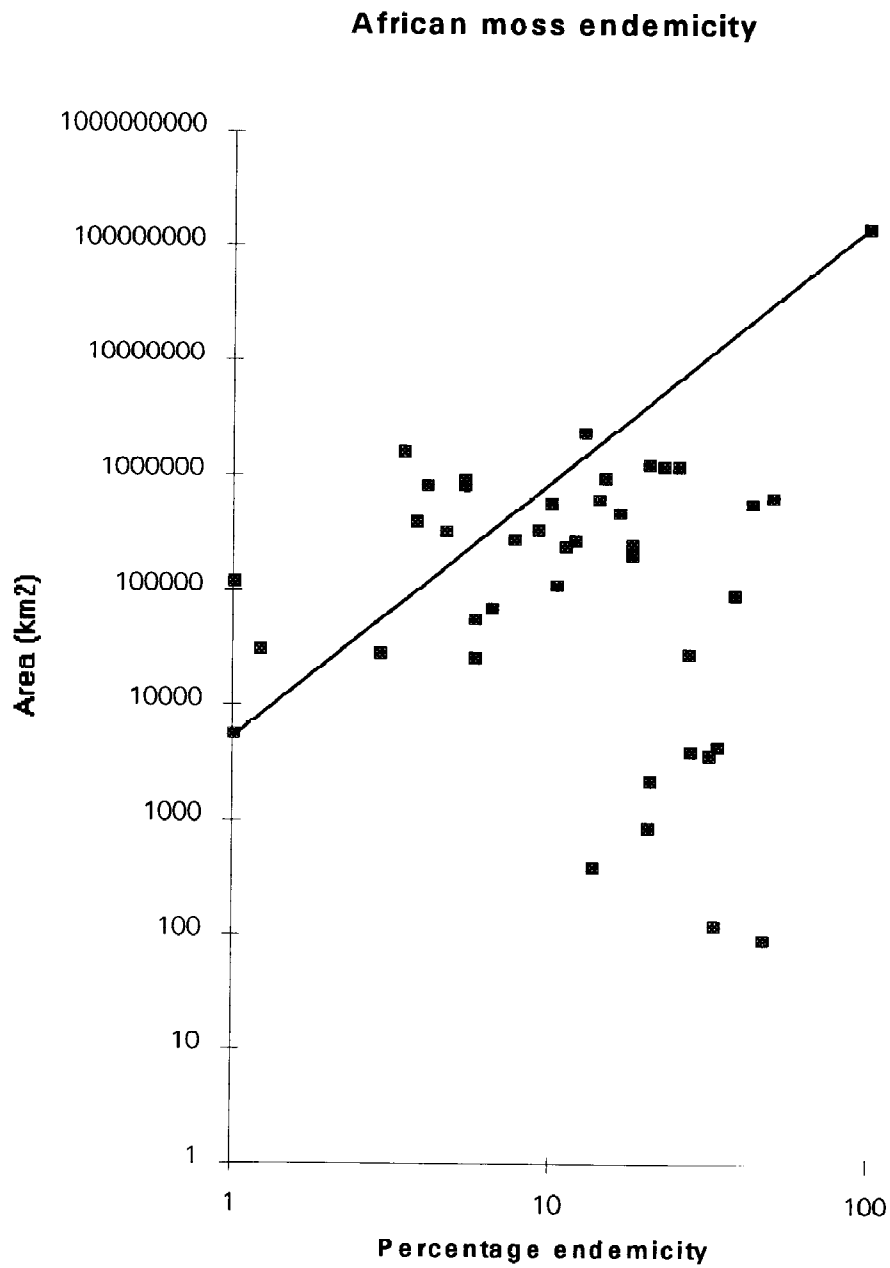
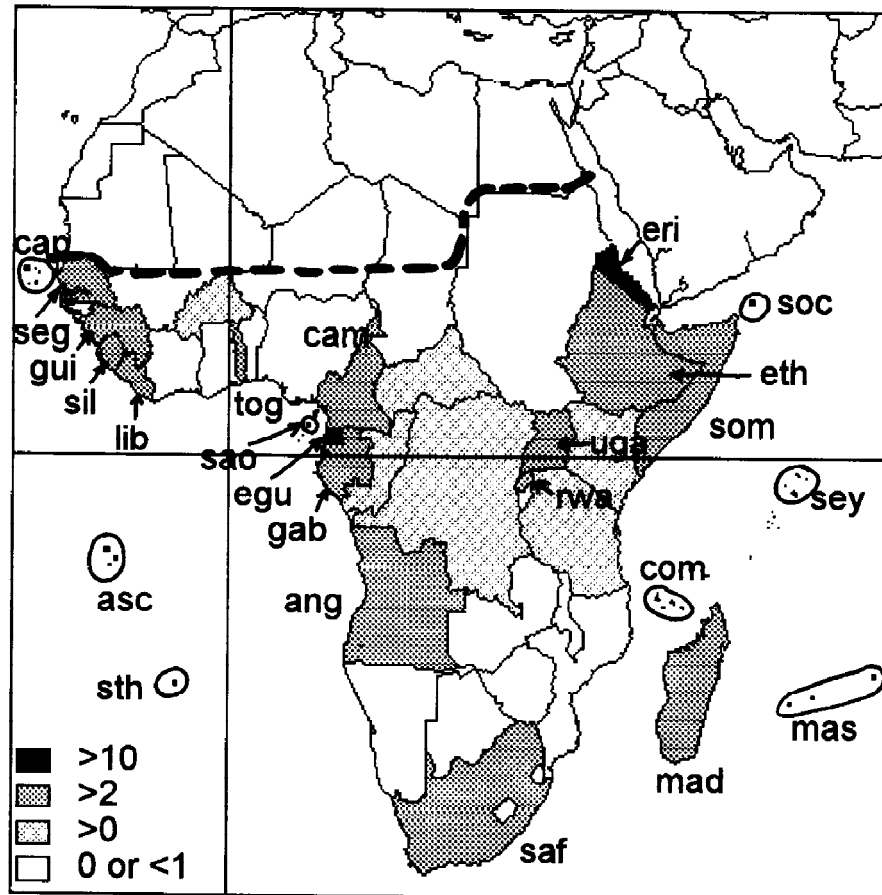


Figure 2. Graph for derivation of Bykov's Index of Endemism



Key:

>10 asc = Ascension, cap = Cape Verde, com = Comores, egu = Equatorial Guinea (inc. Bioko & Annobon), eri = Eritrea, mas = Mascarenes (Mauritius + Reunion + Rodrigues), sey = Seychelles, soc = Socotra, sth = St. Helena

>2 ang = Angola, cam = Cameroon, eth = Ethiopia, gab = Gabon, gui = Guinea, lib = Liberia, mad = Madagascar, rwa = Rwanda, saf = South Africa, seg = Senegambia, sil = Sierra Leone, som = Somalia, tog = Togo, uga = Uganda

Figure 3. Levels of endemism using Bykov's Index of Endemicity

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Appendix A - Calculation of Bykov's Index of Endemicity

The mechanics of deriving Bykov's index was not entirely clear to me after seeing the three references where this technique is discussed (Bykov, 1979; Major, 1988; Delgadillo, 1994), so this Appendix has been added.

Log/log graph paper (i.e., with logarithmic rather than linear scales on each axis) can be used although it is easier to use a computer spreadsheet. Microsoft Excel (version 4) was used for this exercise. In either case, the data should be prepared as a two column table, with an entry for each country, showing area in square kilometres and percentage of endemics (in this case, a subset of Table 1). An extra entry must be made in the table, representing the whole world: 100% endemism, and 144 million square kilometres. The 1% point can either be selected from your own data, or a standard area selected. In this case, Delgadillo's (1994) choice of Puerto Rico was used for the 1% point. When these points are plotted on the graph, a line can then be drawn between the 100% and 1% points representing the norm.

As well as the graph shown at Figure 2, a more detailed graph was maintained which showed the full grid of the graph, with all the dots given a country number. This allows the measurements necessary to measure the index to be made. The horizontal distance from each dot to the 'norm' line is measured using the grid, and entered into the formula as the 'normal %' (En%) to calculate the index (Ie). $Ie = Ef / En$, unless $Ef < En$, when $Ie = -En / Ef$. Those dots above the line are negative (below average), those below the line positive. (Delgadillo also measured a hypothetical index, but this seems unnecessary if a standard 'normal' measure is already being used.)

In Table 1, the column headings indicate the items used in the calculations (Ef%, En%, Ie, Ig) and are as used by Delgadillo (1994).

