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REGULAR PAPER

Richness, similarity and specificity of Madagascar flora compared with Sub-Saharan Africa

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Background and aims – Based on presence/absence information for all angiosperms in Tropical Africa, Southern Africa and Madagascar, we review the similarities and differences between these floras. We compare specific and generic richness for the three areas, and examine their degree of overlap. Madagascar and Sub-Saharan Africa are compared in terms of: the specific and generic richness of their angiosperm families, and specific richness of their genera.
Methods – Using the *African Plant Database*, global figures of specific and generic richness for Tropical Africa, Southern Africa and Madagascar have been calculated and illustrated by Venn diagrams. For each family or genus similarity between Sub-Saharan Africa and Madagascar has been calculated using the Jaccard Index. Madagascar specificity has been defined as the ratio of Madagascar-exclusive species richness to total richness.
Key results – The study confirms the general trends of richness and endemism in the Malagasy flora, but provides accurate figures based on the current state of angiosperm taxonomy. Overlap between the floras of Southern African, Tropical African and Madagascar flora is provided with precise figures. Similarity between Madagascar and Sub-Saharan Africa is very low at species level (0.029) and eight times higher at generic level (0.246). Madagascar specificity reaches 0.165 at specific level and 0.105 at generic level. Calculation of these two indexes for families and genera, based for the first time on APG III, confirms general trends observed so far, and the richest families of the Malagasy flora are listed according to major patterns of their diversity and distribution.

Key words – Madagascar, Africa, African Plant Database, biogeography, diversity, specific and generic richness, similarity, specificity.

INTRODUCTION

Intuitively, it has always been assumed that the biogeographic connections of the living organisms of Madagascar are primarily with Africa – the Mozambique Channel being no more than 400 km broad at its narrowest point. In Engler's (1882) classical phytogeographic system, Madagascar is considered to be part of the Paleotropical Floristic Kingdom, included within its African Territory. Although, as Engler pointed out, some elements are shared with tropical Asia (his "Monsoon Territory"). Following this early work, these main trends have been confirmed by numerous botanists in works focusing on the Malagasy flora (Baron 1889, Hochreutiner 1907, Perrier de la Bâthie 1936, Humbert 1959, Leroy 1978), while the Asian connections were specifically reviewed more recently by Schatz (1996).

Recent developments in continental checklists have allowed the compilation of a database that includes all angiosperm species in Africa and Madagascar. Analysis of this unique data set provides accurate figures for the first time on the richness and degree of overlap of these floras based on the entire angiosperm flora. In a separate contribution, the authors have proved statistics for the endemism of the Malagasy flora based on a revised dataset for Madagascar (Callmander et al. 2011). Here, however, we concentrate on the richness, similarity and specificity of the Malagasy flora, as compared to the continental Sub-Saharan Africa.

METHODS

The *African Plant Database* (http://www.ville-ge.ch/cjb/bd/africa/) has developed since 2002 through the collaboration between the South African National Botanical Institute and the Conservatoire et Jardin botaniques de la Ville de Genève (Gautier et al. 2006). The merging of checklists for Tropical Africa (Lebrun & Stork 1991–1997) and Southern Africa (Germishuisen & Meyer 2003) has resulted in the first consolidated checklist of all angiosperm species for Sub-Saharan Africa (Klopper et al. 2006). The database developed further in 2007 with the incorporation of a set of North African data provided by Alain Dobignard (Dobignard & Chatelain 2010–2011) and subsequently floristic information for Madagascar have been integrated through collaboration with Missouri Botanical Garden, and the *Catalogue of the Vascular Plants of Madagascar Project* (http://www.efloras.org/madagascar). In its current state, the *African Plant Database* (APD) represents a unique source of information on angiosperms for the continental Africa and Madagascar, providing a synonymy index and nomenclatural information for more than 187,500 names, as well as information on the ecology and geographic distribution of the c. 63,500 accepted species of the area. However, data on the other Indian Ocean Islands (Mascarenes, Comoros and Seychelles) have not yet been included. The systematic screening of published botanical literature enables the incorporation of new information and we envisage this to continue for the foreseeable future thus providing a permanently updated database.

APD will continue to evolve as new information becomes available and taxonomic changes are incorporated from different sources, and it is important to mention that the data analyzed for this present article were extracted from the database in April 2011. This accounts for small discrepancies in some of the statistics on endemism provided here for Madagascar as compared with our analysis of updated information from the Madagascar Catalogue in our related article (Callmander et al. 2011). For analyses, a taxon is considered present in an area if it is native to the area.

Our preliminary analysis of the data in the APD indicated that there were only 371 species shared between North Africa and Madagascar, representing less than 0.6% of total, and being generally widely dispersed cosmopolitan species, like *Amaranthus viridis* L., *Waltheria indica* L. or *Corchorus tridens* L. (nomenclature follows APD). Only eighteen species (mainly naturalized cultivated temperate plants) were shared between Madagascar and North Africa only. As a consequence, data from APD have first been filtered to eliminate all records of taxa occurring North of the Sahara for the analyses presented here.

Based on species distribution information in the APD, we classified each species and genus according to their presence in:
Madagascar (MA)
Southern Africa (SA) (including RSA, Namibia, Botswana, Lesotho, and Swaziland)
Tropical Africa (TA) (i.e. Sub-Saharan Africa, but excluding the preceding)

Venn diagrams were then drawn to illustrate the extent of overlap imbrications of the floras at specific and generic levels.

In a second analysis, data from SA and TA were grouped as Sub-Saharan Africa (SSA). Each species was assigned to one of the following categories:
MA endemic
MA non-endemic, but absent from SSA
present both in MA and in SSA (and possibly elsewhere)
absent from MA, present in SSA (and possibly elsewhere)

These data were then grouped as follows to allow analyses at three different levels: specific richness per family, generic richness per family, and specific richness per genus. Attribution of genera to families follows APG III (APG 2009). At each level of analysis, similarity and specificity of Madagascar relative to SSA was calculated. For similarity we used the Jaccard Index, i.e. the ratio of the number of shared species (or genera) to total richness (Jaccard 1901). Madagascar specificity is defined here as the ratio of the number of Madagascar species (or genera) absent from SSA to total richness. For each of these analyses, a global value (i.e. for the whole angiosperm flora) was calculated, as well as value for each taxon considered. The value is considered as high if it is more than 3/2 times the global value. It is considered as low if it is less than 2/3 the global value.

RESULTS

Comparison of the specific and generic richness between Tropical Africa (TA), Southern Africa (SA) and Madagascar (MA)

Total specific richness for the area comprises 55,099 species. A Venn diagram of specific richness for the three areas is shown in fig. 1. With 29,833 species (54.1% of total) TA is the richest, followed by SA: 20,617 (37.4%) and MA: 10,657 (19.3%). Only 817 species (1.5%) are shared among all three areas. The overlap between TA and SA (but excluding MA) is high, with 3,613 species. It is c. five times greater

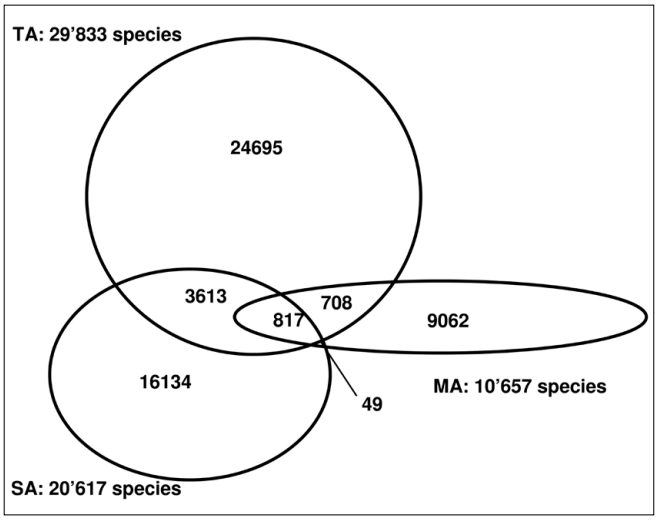

Figure 1 – Venn diagram of specific richness in Tropical Africa (TA), Southern Africa (SA) and Madagascar (MA).

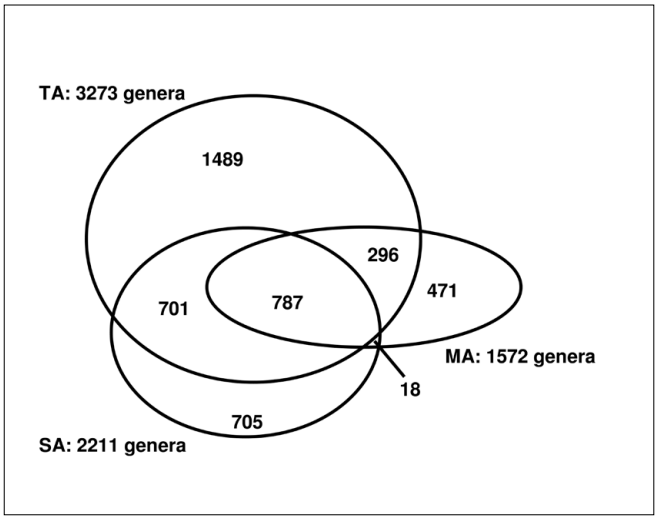

Figure 2 – Venn diagram of generic richness in Tropical Africa (TA), Southern Africa (SA) and Madagascar (MA).

than the overlap between TA and MA (excluding SA), which totals only 708. Only 49 species are shared uniquely between SA and MA.

At generic level (fig. 2), total richness is 4467 genera, with the same ranking of the 3 areas: TA: 3273 genera (73.3% of total), SA: 2211 (49.5%); MA: 1572 (35.2%). Overlap of generic richness is of course higher than at specific level: 787 genera (17.6%) are shared amongst all three regions, which represents a 12-fold percentage increase compared to specific level. The proportion of genera which occur in two regions only is also higher than at species level. Compared with species level it increases by 2.4-fold between TA and SA only, but by more than 4.5-fold for both TA-MA and SA-MA. Consequently, the percentage of genera limited to one of the three regions decreases compared with specific level, especially for SA and MA.

Comparison of the specific richness of families between Madagascar (MA) and Sub Saharan Africa (SSA)

Table 1 presents specific richness, MA–SSA similarity and MA specificity for the thirty most species-rich families in Madagascar.

The five richest families in Madagascar are the same as for the whole area, but in a different sequence. Orchidaceae rank first in MA, but are only fourth for the whole area, for which Fabaceae, Asteraceae and Rubiaceae are first, second and third respectively. Other families which increase significantly their richness ranking in MA compared to total area include: Melastomataceae; Arecaceae; Balsaminaceae; Lauraceae; Primulaceae; Sapindaceae, Salicaceae, Pandanaceae and Ebenaceae. Conversely: Aizoaceae, Iridaceae, Asparagaceae, Proteaceae and Geraniaceae (all families highly represented in the Cape Floristic Region) have a significantly lower rank for MA than for total area.

The global value for similarity between MA and SSA, based on the Jaccard index is very low (0.029). Notable exceptions (> 1.5 × global value) include Poaceae, Cyperaceae and Convolvulaceae. On the contrary, low values (< 2/3 × global value) occur in many of these top 30 families in Madagascar: notably in Pandanaceae, Bignoniaceae and Malpighiaceae, which have no species in common between the two areas, but also in Annonaceae, Xanthorrhoeaceae, Sapotaceae, Balsaminaceae, Lauraceae, Ebenaceae, Euphorbiaceae, etc.

Madagascar specificity (see also fig. 3A & B) has a global value of 0.165. It is especially high (> 1.5 × global value) in eighteen of these thirty families notably in Arecaceae, Pandanaceae, Malpighiaceae, Balsaminaceae, Lauraceae, Bi-

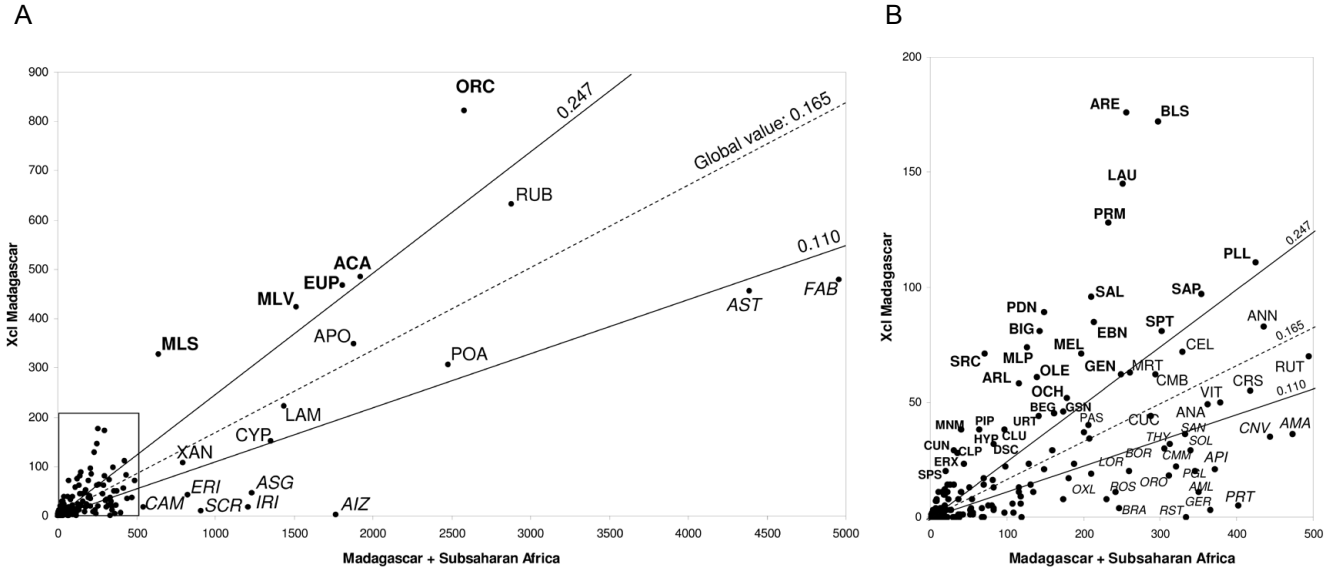

Figure 3 – Specific richness of families. X-axis: number of species in the whole area (Sub Saharan Africa and Madagascar); Y-axis: number of species occurring only in Madagascar (and possibly elsewhere, but not in SSA). Dotted line: global value for all angiosperms. Solid lines: 0.110 (2/3 × global value) and 0.247 (1.5 × global value) ratios. Acronyms of families according to Weber (1982) Italics and bold: Families with low (resp. high) Madagascar specificity. A, whole graph; B, detail of bottom-left corner.

Table 1 – Species richness, similarity and Madagascar specificity of the top 30 species-rich families in Madagascar.
Xcl: exclusively; end: endemics; MA: Madagascar; SAA: Sub Saharan Africa; high values (> 1.5 × global value) of affinity and specificity in bold, low values (< 2/3 × global value) in italics.

Family	Total MA	Xcl MA (end MA)	Total SSA	Xcl SSA	Shared MA / SSA	Total	Similarity	Specificity
Orchidaceae	869	821 (734)	1761	1713	48	2582	*0.019*	**0.318**
Rubiaceae	675	631 (612)	2247	2203	44	2878	*0.015*	0.219
Fabaceae	640	478 (449)	4479	4317	162	4957	0.033	*0.096*
Poaceae	566	306 (272)	2176	1916	260	2482	**0.105**	0.123
Asteraceae	541	455 (441)	3935	3849	86	4390	0.020	*0.104*
Acanthaceae	512	484 (476)	1437	1409	28	1921	*0.015*	**0.252**
Malvaceae	486	424 (402)	1090	1028	62	1514	0.041	**0.280**
Euphorbiaceae	484	467 (448)	1339	1322	17	1806	*0.009*	**0.259**
Apocynaceae	376	349 (336)	1532	1505	27	1881	*0.014*	0.186
Melastomataceae	335	328 (325)	313	306	7	641	*0.011*	**0.512**
Cyperaceae	287	152 (120)	1203	1068	135	1355	**0.100**	0.112
Lamiaceae	249	222 (218)	1214	1187	27	1436	*0.019*	0.155
Arecaceae	181	176 (175)	80	75	5	256	0.020	**0.688**
Balsaminaceae	173	172 (172)	125	124	1	297	*0.003*	**0.579**
Lauraceae	146	145 (142)	106	105	1	251	*0.004*	**0.578**
Primulaceae	133	128 (122)	104	99	5	232	0.022	**0.552**
Phyllanthaceae	122	111 (100)	313	302	11	424	0.026	**0.262**
Xanthorrhoeaceae	110	108 (108)	690	688	2	798	*0.003*	0.135
Sapindaceae	106	97 (93)	257	248	9	354	0.025	**0.274**
Salicaceae	99	96 (96)	114	111	3	210	*0.014*	**0.457**
Convolvulaceae	90	35 (30)	408	353	55	443	**0.124**	*0.079*
Pandanaceae	89	89 (89)	60	60	0	149	*0.000*	**0.597**
Ebenaceae	86	85 (84)	129	128	1	214	*0.005*	**0.397**
Celastraceae	84	72 (71)	257	245	12	329	0.036	0.219
Annonaceae	84	83 (80)	352	351	1	435	*0.002*	0.191
Sapotaceae	82	81 (79)	221	220	1	302	*0.003*	**0.268**
Bignoniaceae	81	81 (79)	62	62	0	143	*0.000*	**0.566**
Rutaceae	75	70 (65)	424	419	5	494	*0.010*	0.142
Malpighiaceae	74	74 (74)	52	52	0	126	*0.000*	**0.587**
Meliaceae	74	71 (68)	126	123	3	197	*0.015*	**0.360**
...	**...**		**...**	**...**	**...**	**...**	**...**	**...**
Total	**10657**	**9083 (8583)**	**46016**	**44442**	**1574**	**55099**		
Global value							**0.029**	**0.165**

gnoniaceae, Primulaceae and Melastomataceae. Low values (< 2/3 × global value) were obtained for Convolvulaceae, Fabaceae, and Asteraceae. Others major families (> 400 species in total area) with a low MA specificity include Aizoaceae, Asparagaceae, Iridaceae, Scrophulariaceae, Ericaceae, Campanulaceae, Amaranthaceae and Proteaceae, which are relatively poor in species richness in MA.

Comparison of the generic richness of families between Madagascar (MA) and Sub Saharan Africa (SSA)

Table 2 presents generic richness, MA–SAA similarity and MA specificity of the 38 families with ten or more genera in Madagascar.

The nine richest families for genera are the same as for species, although their sequence differs slightly. Compared with total area, Poaceae rank first in MA, but third globally, these ranks being inverted for Asteraceae. As a whole, there is much less difference in generic richness ranking between MA and the total area than for specific richness ranking. However some families display a higher rank of generic richness for the whole area. These include predominantly subtropical-temperate families like Brassicaceae, Aizoaceae, Iridaceae, Scrophulariaceae, Caryophyllaceae and Apiaceae, but also some predominantly tropical families like Annonaceae, Sapotaceae and Rutaceae. On contrary some families have a higher rank in MA like Sarcolaenaceae (MA endemic

Table 2 – Generic richness, similarity and Madagascar specificity of the top 38 genus-rich families in Madagascar.
Xcl: exclusively; end: endemics; MA: Madagascar; SAA: Sub Saharan Africa; high values (> 1.5 × global value) of affinity and specificity in bold, low values (< 2/3 × global value) in italics.

Family	Total MA	Xcl MA	Total SSA	Xcl SSA	Shared MA / SSA	Total	Similarity	Specificity
Poaceae	143	25	305	187	118	330	0.358	0.076
Fabaceae	112	27	316	231	85	343	0.248	0.079
Asteraceae	100	26	355	281	74	381	0.194	*0.068*
Rubiaceae	88	38	197	147	50	235	0.213	**0.162**
Acanthaceae	66	30	86	50	36	116	0.310	**0.259**
Orchidaceae	58	24	106	72	34	130	0.262	**0.185**
Apocynaceae	48	13	185	150	35	198	0.177	*0.066*
Malvaceae	45	14	72	41	31	86	0.360	**0.163**
Euphorbiaceae	41	17	85	61	24	102	0.235	**0.167**
Cyperaceae	33	3	58	28	30	61	**0.492**	*0.049*
Lamiaceae	31	4	77	50	27	81	0.333	*0.049*
Sapindaceae	26	12	44	30	14	56	0.250	**0.214**
Cucurbitaceae	23	9	36	22	14	45	0.311	**0.200**
Convolvulaceae	21	4	31	14	17	35	**0.486**	0.114
Amaranthaceae	20	3	67	50	17	70	0.243	*0.043*
Celastraceae	18	8	37	27	10	45	0.222	**0.178**
Arecaceae	16	11	23	18	5	34	*0.147*	**0.324**
Phyllanthaceae	16	4	25	13	12	29	**0.414**	0.138
Plantaginaceae	15	5	25	15	10	30	0.333	**0.167**
Urticaceae	15	1	21	7	14	22	**0.636**	*0.045*
Meliaceae	14	7	26	19	7	33	0.212	**0.212**
Orobanchaceae	13	5	25	17	8	30	0.267	**0.167**
Apiaceae	13	8	76	71	5	84	*0.060*	0.095
Melastomataceae	12	3	30	21	9	33	0.273	0.091
Anacardiaceae	11	8	22	19	3	30	*0.100*	**0.267**
Primulaceae	11	3	12	4	8	15	**0.533**	**0.200**
Gentianaceae	11	3	22	14	8	25	0.320	0.120
Asparagaceae	11	2	42	33	9	44	0.205	*0.045*
Sarcolaenaceae	10	10	0	0	0	10	*0.000*	**1.000**
Moraceae	10	4	15	9	6	19	0.316	**0.211**
Menispermaceae	10	6	26	22	4	32	*0.125*	**0.188**
Salicaceae	10	3	17	10	7	20	0.350	0.150
Commelinaceae	10	3	18	11	7	21	0.333	0.143
Araceae	10	5	32	27	5	37	*0.135*	0.135
Rhamnaceae	10	1	17	8	9	18	**0.500**	*0.056*
Solanaceae	10	1	18	9	9	19	**0.474**	*0.053*
Annonaceae	10	2	43	35	8	45	0.178	*0.044*
Connaraceae	10	0	11	1	10	11	**0.909**	*0.000*
...	**...**	**...**	**...**	**...**	**...**	**...**	**...**	**...**
Total	**1572**	**471**	**3996**	**2895**	**1101**	**4467**		
Global value							**0.246**	**0.105**

family) Primulaceae and Connaraceae (not all shown on table 2).

The global value of similarity between MA and SSA based on the Jaccard index (0.246) is eight times higher than at specific level. High values are found in Connaraceae, Urticaceae, Primulaceae, Rhamnaceae, Cyperaceae, Convolvulaceae, Solanaceae and Phyllanthaceae. In contrast, low similarity at generic level occurs in Sarcolaenaceae, Apiaceae, Anacardiaceae, Menispermaceae, Araceae, Arecaceae. Among families with lower generic richness in Madagascar

(not shown on table 2), low similarity values are also found in Bignoniaceae, Sapotaceae and Rutaceae.

Madagascar specificity at generic level (see also fig. 4A & B) has a global value of 0.105, which is of course lower than at species level. High values are observed in seventeen of these 38 families, and especially in Sarcolaenaceae, Arecaceae, Anacardiaceae, Acanthaceae, Sapindaceae, Meliaceae, Moraceae and Primulaceae. In contrast, low values (< 0.07) are observed in Connaraceae, Amaranthaceae, Annonaceae, Asparagaceae, Urticaceae, Annonaceae, Asparagaceae, Cyperaceae, Lamiaceae, Solanaceae, Rhamnaceae, Apocynaceae and Asteraceae.

Comparison of the specific richness of genera between Madagascar (MA) and Sub Saharan Africa (SSA)

Table 3 presents specific richness, MA–SAA similarity and MA specificity for the 31 most species-rich genera in Madagascar.

The richest genus in MA is *Bulbophyllum* with 193 species, followed by *Impatiens*, *Dombeya*, *Croton*, *Dypsis*, *Angraecum* and *Euphorbia*. Eleven genera in the top 31 richest in MA also belong to the top 31 of the whole area. They are (listed by decreasing richness for total area): *Euphorbia*, *Senecio*, *Helichrysum*, *Aloe*, *Vernonia*, *Psychotria*, *Impatiens*, *Cyperus*, *Bulbophyllum*, *Plectranthus* and *Justicia*. Other genera with very high diversity in MA + SSA, but with low richness in MA include typically highly diversified SA genera like *Erica* L., *Thesium* L. and *Pelargonium* L'Hér. ex Aiton (with a few representatives in MA) *Aspalathus* L., *Ruschia* Schwantes or *Lampranthus* N.E.Br. (completely absent from MA). They also include genera whose diversity is mainly in TA like *Crotalaria* L., *Indigofera* L. or *Habenaria* Willd.

Global similarity has of course the same value as presented above (0.029). Twenty-three out of these 31 genera have a much lower value. Among them, a similarity value of zero is found in eleven genera. Three of them have only endemic species in MA (*Dypsis*, *Pandanus*, *Gravesia*) and one is not represented in SSA: *Anisostachya*. The endemic genera of MA are not represented in this list, the most diverse (*Aspidostemon* Rohwer & H.G.Richt. and *Microsteira* Baker) comprising only 28 species each (Callmander et al. 2011). High values are found in *Kalanchoe*, *Hibiscus*, *Cyperus* and *Panicum* L.

Regarding MA specificity (global value of 0.165, fig. 5), 22 out of the 31 richest genera have significantly higher values and none of them has a low value (< 0.10). Genera for which this MA specificity is maximal include *Bulbophyllum*, *Impatiens*, *Dombeya*, *Dypsis*, *Croton* and *Angraecum* for the most diverse, but also *Gravesia*, *Cynorkis*, *Oncostemum*, *Hypoestes*, *Memecylon*, *Pandanus*, *Cynanchum*, *Medinilla*, *Secamone* and *Anisostachya*. It is noteworthy that among this list, three genera belong to Orchidaceae.

DISCUSSION

Comparing the angiosperm richness of the three areas

At specific level, MA flora is highly distinct from both TA and SA. In contrast, overlap between TA and SA is high, which is not surprising considering that boundaries between them are political: Southern Africa as circumscribed here contains not only the areas experiencing winter rainfall regime of the Cape Floristic Region (Goldblatt & Manning 2000), but also all the subtropical regions of Southern Africa (notably the Kalahari, the northern provinces of RSA and KwaZulu-Natal) which intergrade with the tropical African flora. Species shared between the three areas are mainly pantropical species (e.g. *Abrus precatorius* L.) or species widely distributed

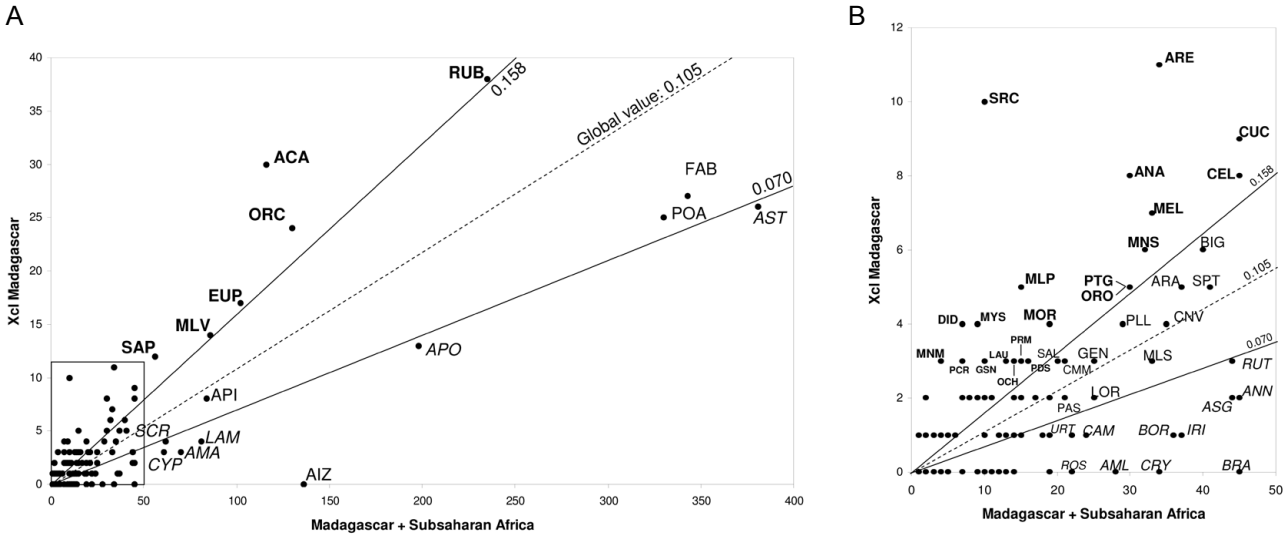

Figure 4 – Generic richness of families. X-axis: number of genera in the whole area (Sub Saharan Africa and Madagascar); Y-axis: number of genera occurring only in Madagascar (and possibly elsewhere, but not in SSA). Dotted line: global value for all angiosperms. Solid lines 0.070 (2/3 × global value) and 0.158 (1.5 × global value) ratios. Acronyms of families according to Weber (1982). Italics and bold: Families with low (resp. high) Madagascar specificity. A, whole graph; B, detail of bottom-left corner.

Table 3 – Species richness, affinities and Madagascar specificity of the top 31 species-rich genera in Madagascar.
Xcl: exclusively; end: endemics; MA: Madagascar; SAA: Sub Saharan Africa; high values (> 1.5 × global value) of affinity and specificity in bold, low values (< 2/3 × global value) in italics.

Genus	Family	Total MA	Xcl MA (end MA)	Total SSA	Xcl SSA	Shared MA / SSA	Total	Similarity	Specificity
Bulbophyllum Thouars	Orchidaceae	193	188 (179)	95	90	5	283	*0.018*	**0.664**
Dombeya Lam.	Malvaceae	182	181 (173)	21	20	1	202	*0.005*	**0.896**
Impatiens L.	Balsaminaceae	172	171 (171)	125	124	1	296	*0.003*	**0.578**
Croton L.	Euphorbiaceae	150	148 (143)	62	60	2	210	*0.010*	**0.705**
Dypsis Noronha ex. Mart.	Arecaceae	145	145 (145)	0	0	0	145	*0.000*	**1.000**
Angraecum Bory	Orchidaceae	135	133 (120)	54	52	2	187	*0.011*	**0,711**
Euphorbia L.	Euphorbiaceae	129	126 (120)	779	776	3	905	*0.003*	0.139
Helichrysum Mill.	Asteraceae	112	111 (110)	350	349	1	461	*0.002*	0.241
Gravesia Naudin	Melastomataceae	108	108 (108)	5	5	0	113	*0.000*	**0.956**
Psychotria L.	Rubiaceae	103	103 (102)	234	234	0	337	*0.000*	**0.306**
*Cynorkis*Thouars	Orchidaceae	102	102 (91)	18	18	0	120	*0.000*	**0.850**
Oncostemum A.Juss.	Primulaceae	100	100 (99)	0	0	0	100	*0.000*	**1.000**
Hypoestes Sol. ex R.Br.	Acanthaceae	93	93 (90)	18	18	0	111	*0.000*	**0.838**
Aloe L.	Xanthorrhoeaceae	91	90 (90)	320	319	1	410	*0.002*	0.220
Justicia L.	Acanthaceae	87	83 (83)	161	157	4	244	*0.016*	**0.340**
Memecylon L.	Melastomataceae	86	85 (85)	55	54	1	140	*0.007*	**0.607**
Diospyros L.	Ebenaceae	86	85 (84)	112	111	1	197	*0.005*	**0.431**
Pandanus Parkinson	Pandanaceae	84	84 (84)	60	60	0	144	*0.000*	**0.583**
Cyperus L.	Cyperaceae	82	49 (35)	238	205	33	287	**0.115**	0.171
Cynanchum L.	Apocynaceae	80	77 (77)	35	32	3	112	0.027	**0.688**
Vernonia Schreb.	Asteraceae	76	71 (70)	310	305	5	381	*0.013*	0.186
Medinilla Gaudich.	Melastomataceae	70	70 (68)	4	4	0	74	*0.000*	**0.946**
Secamone R.Br.	Apocynaceae	70	70 (68)	20	20	0	90	*0.000*	**0.778**
Grewia L.	Malvaceae	65	57 (55)	124	116	8	181	**0.044**	**0.315**
Kalanchoe Adans.	Crassulaceae	63	50 (48)	72	59	13	122	**0,107**	**0.410**
Senecio L.	Asteraceae	63	57 (56)	423	417	6	480	*0.013*	0.119
Anisostachya Nees	Acanthaceae	60	60 (59)	0	0	0	60	*0.000*	**1.000**
Clerodendrum L.	Lamiaceae	60	60 (57)	90	90	0	150	*0.000*	**0.400**
Plectranthus L'Hér.	Lamiaceae	53	47 (46)	213	207	6	260	0.023	0.181
Coffea L.	Rubiaceae	52	51 (49)	44	43	1	95	*0.011*	**0.537**
Hibiscus L.	Malvaceae	52	35 (32)	173	156	17	208	**0.082**	0.168
...	**...**	**...**	**...**	**...**	**...**	**...**	**...**	**...**	**...**
Total		**10657**	**9083 (8583)**	**46016**	**44442**	**1574**	**55099**		
Global value								**0.029**	**0.165**

in the African region (e.g. *Urera trinervis* (Hochst.) Friis & Immelman or *Ficus lutea* Vahl). Their distribution in Southern Africa is generally limited to the eastern subtropical humid coast of KwaZulu-Natal. With respect to MA however, there are many more species shared with TA than with SA. The number of 49 species shared with SA would probably be reduced to almost zero, if only the overlap with the Cape Floristic Region had been considered.

At generic level, richness ranking of the three areas is the same as for species and the topology of the Venn diagram is similar. However, as expected, the intersections of the Venn diagram are larger. Comparing raw data between specific and generic level is of little interest, the comparison in relative terms is more informative. Taxa that occur in all three areas demonstrate a relative increase of × 12 when the generic level is compared with the specific level. Consequently, number

of taxa restricted to one of the three areas under study is lower: × 0.5 for SA, × 0.6 for MA and × 0.7 for TA. Taxa shared between two areas only have a relative increase of × 5.2 for the TA-MA intersection, of × 4.5 for the SA-MA, but this increase is only of × 2.4 for the TA-SA intersection. Two different characteristics of the floras concerned serve to explain this difference. First the SA flora contains a strong endemic element at the generic level, represented by the numerous endemic genera of the Cape Floristic Region. Second, while the endemicity of MA is exceptionally high at specific level, many genera are shared with TA.

Comparing the richness of families and genera between Sub Saharan Africa (SSA) and Madagascar (MA)

Poaceae, Asteraceae, Fabaceae and Rubiaceae are clearly the richest families of the total area under study, both in terms of species and genus richness. Poaceae shows the highest generic and specific similarities between MA and SSA. In contrast, Rubiaceae has a lower similarity between MA and SSA, especially at the specific level, but higher MA specificity, as exemplified by the genus *Psychotria*. The large genera of Fabaceae in Africa are much less well represented in MA (*Crotalaria* and *Indigofera*) or even absent (*Aspalathus*). In Asteraceae however, the large African genera (*Senecio*, *Helichrysum*, *Vernonia*) are generally also well represented in MA.

Orchidaceae is the family with highest specific richness in Madagascar, but ranks only 6th in number of genera. It has a high MA specificity in species, mainly caused by very large genera, three of which are amongst the most diverse in MA and which each possesses high MA specificity (*Bulbophyllum*, *Angraecum* and *Cynorkis*).

Acanthaceae, Apocynaceae, Euphorbiaceae, Malvaceae and Lamiaceae are next in specific and generic richness in the whole area and in Madagascar. In this group of families, specific similarity is low, except for Malvaceae. Generic similarity is generally above average, with the exception of Euphorbiaceae and Apocynaceae. MA specificity at generic level is high in Acanthaceae, and low in Apocynaceae. In Euphorbiaceae, *Euphorbia* is the largest genus in Africa and is also very diverse in MA, whereas *Croton* has achieved a spectacular richness in MA. Other important genera with high MA specificity in this group of families include *Dombeya* in Malvaceae; *Hypoestes*, *Justicia* and *Anisostachya* in Acanthaceae; *Secamone* and *Cynanchum* in Apocynaceae.

Cyperaceae and Convolvulaceae share a high specific MA/SSA similarity, although Cyperaceae is richer at specific and generic level, while Convolvulaceae displays low MA specificity at species level. The genus *Cyperus* has an average MA specificity, but many species in MA are shared either with SSA or with other areas.

In contrast, some families such as Melastomataceae, Arecaceae, Balsaminaceae, Lauraceae, Primulaceae (incl. Myrsinaceae), Salicaceae (incl. Flacourtiaceae p.p.), Pandanaceae, Ebenaceae, Bignoniaceae and Malpighiaceae are very rich in species in MA compared with SSA; their MA specificity is often in excess of 0.5 which means that they have more species in MA than in the whole of SSA. In general, they display low to very low similarity at specific level and an average to high similarity at generic level (but low in Arecaceae). These families often have several MA endemic gen-

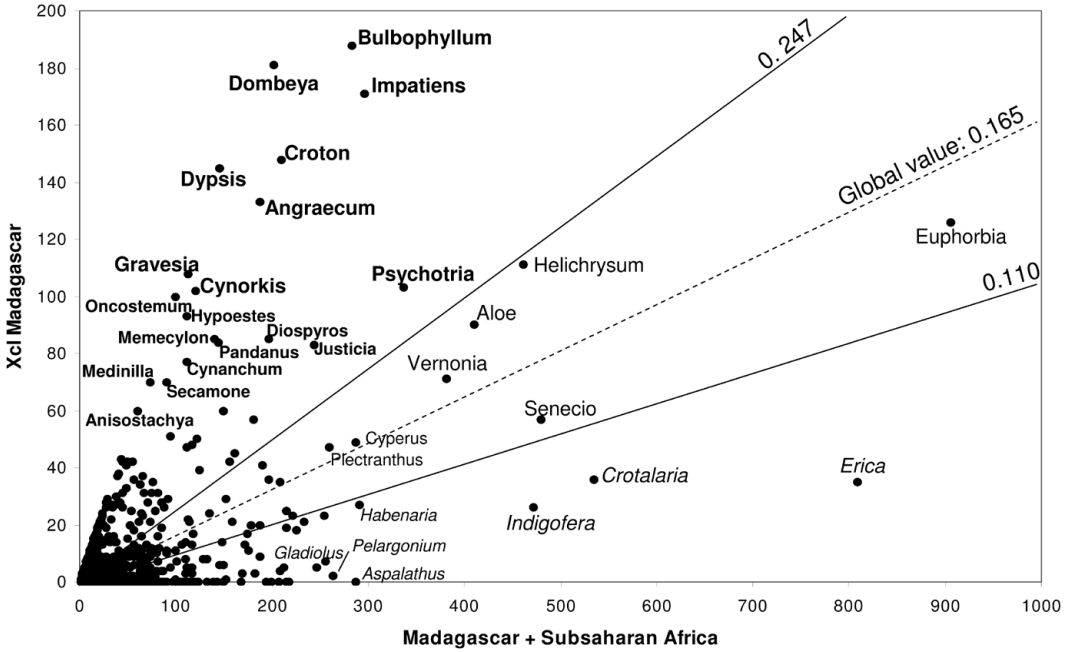

Figure 5 – Specific richness of genera. X-axis: number of species in the whole area (Sub Saharan Africa and Madagascar); Y-axis: number of species occurring only in Madagascar (and possibly elsewhere, but not in SSA). Dotted line: global value for all angiosperms. Solid lines 0.110 (2/3 × global value) and 0.247 (1.5 × global value) ratios. Italics and bold: Families with low (resp. high) Madagascar specificity.

era (or absent from SSA), some of them being particularly rich: *Oncostemum* in Primulaceae, *Dypsis* in Arecaceae, and *Gravesia* in Melastomataceae. Their high MA specificity is also the consequence of important non-endemic genera with numerous endemic species like *Memecylon* and *Medinilla* in Melastomataceae, *Ocotea* and *Cryptocarya* in Lauraceae and *Homalium* in Salicaceae. Certain families are exceptions in this group because they consist of a single genus (Balsaminaceae: *Impatiens* and Ebenaceae: *Diospyros*) or almost (Pandanaceae: *Pandanus*).

A further group of families that should be mentioned comprises medium-sized tropical families such as Phyllanthaceae (formerly included in Euphorbiaceae), Sapindaceae, Annonaceae, Celastraceae, Rutaceae, Sapotaceae and Meliaceae. At specific level, these families generally have a low similarity (except Celastraceae) and a relatively rich MA component (except Rutaceae, because of a very high specific richness in SA). At generic level, similarity generally has average values (but high in Phyllanthaceae and low in Rutaceae and Sapotaceae), and relatively high MA specificity (except Rutaceae and Annonaceae).

A set of families with high specific richness in the entire area, but which are species-poor in Madagascar comprises Aizoaceae, Asparagaceae, Iridaceae, Scrophulariaceae, Proteaceae, and Geraniaceae. These families mostly include very large SA genera like *Ruschia* or *Lampranthus* in Aizoaceae, *Gladiolus* in Iridaceae, and *Pelargonium* in Geraniaceae. They consequently have very low similarity values.

The same kind of pattern appears in Xanthorrhoeaceae and Ericaceae, except that these two families are dominated by single genera (*Aloe* and *Erica* respectively) that are also well represented in Madagascar by endemic species.

Among families with less than seventy species in MA, some reach exceptionally high values of MA specificity at specific level (> 0.8). These include MA endemic families (Sarcolaenaceae, Sphaerosepalaceae, Asteropeiaceae, etc.); families that are very poorly represented in SSA like Monimiaceae, Cunoniaceae and Calophyllaceae (formerly included in Clusiaceae), and Elaeocarpaceae. Further families with a very high MA specificity (between 0.5 and 0.8) include Araliaceae, Piperaceae, Erythroxylaceae, Myristicaceae, Talinaceae, Hydrostachyaceae, Didiereaceae and Picrodendraceae.

CONCLUSION

The study confirms the general trends of richness and endemism of the Madagascar flora published so far and provides precise figures based on the current knowledge of taxonomy, representing a valuable up-to-date contribution to the understanding of the relationships between the floras of Africa. Further collaborations will aim at the integration of additional distribution data in the *African Plant Database*, especially for the western Indian Ocean Islands. In addition to the growing body of phylogenetic work, it will contribute to a more in-depth understanding of the fascinating biogeography of Madagascar.

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