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REGULAR PAPER

The Cyperaceae in Madagascar show increased species richness in upland forest and wetland habitats

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Background and aims – Madagascar is a biodiversity hotspot with a high level of plant endemism. However, not all lineages of plants are equally represented and the highest diversity occurs in forest lineages. Cyperaceae frequently occur in grasslands and wetlands in Africa, and the tribe Hypolytreae and *Carex* subgenus *Vigneastra* are among the few predominantly forest lineages. We study the Cyperaceae of Madagascar to discover what lineages are represented (genera/tribes), to determine their unique habitats and key functional traits and to investigate patterns of species richness.
Methods – The World Checklist of Monocotyledons was queried for Cyperaceae occurring in Madagascar. The global distribution of these species was investigated to identify endemic taxa and to evaluate other botanical countries where widespread species occur. Data on life form, habitat and photosynthetic type were scored from literature and personal observations.
Key results – Madagascar has 321 species of Cyperaceae in 33 genera, representing all major clades of the family. The predominantly tropical Cypereae clade composes about half of the sedge flora, of which *Cyperus* represents about a third of the species in Madagascar. The Cariceae, a predominantly northern hemisphere temperate clade, is unusually highly represented and composes 10% of the sedge flora, occurring mostly in the highlands. In Madagascar, 55 species (17% of flora, mainly *Carex* and *Cyperus*) occur in forests and all are C_3 perennials. *Bulbostylis* and *Pycreus*, exclusively C_4 taxa with high proportion of annuals compared to C_3 genera in Madagascar, occur outside forests in seasonal or permanent wetlands. Endemism among the sedge flora is 37% (121 species), a third of which (42 species) occur in forests, mostly in the Central and Eastern highlands.
Conclusion – Cyperaceae are among top ten species richest angiosperm families in Madagascar. When compared with other botanical countries, Madagascar has the second highest endemism level, second to the Cape Provinces. The sedge flora assembly has involved long distance dispersal(s) coupled with Neogene radiation in upland humid forests and open wetland habitats.

Key words – Biogeography, conservation, Cyperaceae, C_4 photosynthesis, functional traits, species richness.

INTRODUCTION

Madagascar is one of the hottest biodiversity hotspots (Myers et al. 2000, Brummitt & Lughadha 2003) with levels of endemism as high as 90% for many groups of plants and animals (Goodman & Benstead 2003, Wilme et al. 2006, Vences et al. 2009). The island, measuring about 594,000 km², has an estimated 14,000 species of higher plants (Goodman & Benstead 2005, Phillipson et al. 2006). Among the larger vascular plant families, the highest species richness and endemism are found in Orchidaceae (871 species/96% endemic, World Checklist of Monocotyledons 2010), Euphorbiaceae (700/mostly endemic, Hoffmann & McPherson 2003), Rubiaceae (650/98% endemic, Davis & Bridson 2003), Leguminosae (573/80% endemic, Labat & Moat 2003) and Melastomataceae (321/99% endemic, Almeda 2003). A number of large angiosperm families such as Asteraceae, Cyperaceae and Poaceae, which are predominantly herbaceous, do not have high levels of endemism, thereby raising questions on what dictates patterns of species richness in Madagascar.

The high level of species richness and endemism is partially due to the geological history of the island. The Malagasy tectonic plate separated from Africa about 165 million years ago (Wells 2003), long before the origin of the extant flora and fauna. The African continent is the closest large land mass, c. 400 km away. Additionally, a number of smaller volcanic islands of varying ages and sizes occur in the surrounding Indian Ocean. The island reached its current latitude only recently and there is overwhelming evidence supporting the Cenozoic origin of Malagasy clades whose sister taxa occur in mainland Africa (Yoder & Nowak 2006). Prior to the Oligocene the southern tip was below 30°S and Madagascar experienced drier conditions (Wells 2003). It is therefore hypothesized that the subarid spiny scrub biome dominated Madagascar and that the other biomes (evergreen and deciduous forests, montane types and grasslands) have evolved subsequently (Wells 2003).

Madagascar's current mostly tropical location accompanied by varied climate, topography and geology, provides a large variety of potential habitats for terrestrial organisms. Elevation and climate (annual rainfall and temperature) determine contemporary boundaries of biomes or bioclimatic regions (Moat & Smith 2007) – the wetter eastern coast has evergreen forests, the central highlands have grasslands and deciduous woodlands, the drier and hotter western slopes and lowlands have deciduous forests, whereas the arid south western areas have spiny scrub (Cornet 1974, Wells 2003). Different functional traits are characteristic of adaption to the various biomes; for example, succulence and specialized photosynthetic systems (C_4 and CAM photosynthesis) are prevalent in the subarid spiny scrub flora.

A large number of the endemic vascular plant lineages (e.g. within the Rubiaceae, and Melastomataceae, Almeda 2003) have diversified in forests located in the evergreen humid and deciduous forests. Diversification in forest habitats involves competition for space, water and light; hence plant lineages with favoured traits (e.g. growing into shrubs/trees, epiphytism, C_3 photosynthesis) dominate, whereas lineages adapted to open canopy habitats would be excluded. Among the graminoids, wetter, forest habitats are dominated by C_3 perennial taxa such as bamboos (Dransfield 2003), whereas drier/arid habitats would be expected to have more C_4, hemicryptophytic and/or annual taxa.

The Cyperaceae is a family of monocotyledons that is most diverse in open habitats. The family comprises c. 5,400 species in 106 genera (Govaerts et al. 2007), classified into sixteen tribes and two subfamilies (Goetghebeur 1998, Muasya et al. 2009). Subfamily Mapanioideae (c. 170 species) comprises tribes Hypolytreae and Chrysitricheae. The former is mostly restricted to tropical forests whereas the latter occurs in southern hemisphere heathlands (Muasya et al. unpubl.). Subfamily Cyperoideae comprises about 97% of the family, with notable diversity in northern temperate (Cariceae, c. 1,900 species), southern temperate (Schoeneae, c. 260 species) and tropical regions (Cypereae, c. 1,100 species; Abildgaardieae, c. 520; Rhynchosporeae, c. 380; Eleocharideae, 260, and Sclerieae, c. 260). In tropical Africa, the family has high species richness among tribes Cypereae and Abildgaardieae in the savannas, exhibiting C_4 photosynthesis, an annual life form, poikilohydry and other adaptations. In Madagascar, the Cyperaceae is the richest wetland plant family, with about 142 wetland species of which 51 are endemic (Andrianasetra Ranarijaona 2003).

Modern lineages of Cyperaceae evolved in the Tertiary (Besnard et al. 2009). Therefore the Cyperaceae in Madagascar have either dispersed into or evolved *in situ* from Gondwanan ancestors or from ancestors that colonized the islands during the Cenozoic. This study explores Cyperaceae diversity: (1) to investigate patterns of species richness and endemism; (2) to identify key functional traits in lineages that have diversified in Madagascar and their corresponding habitats.

MATERIALS AND METHODS

The World Checklist of Monocotyledons (2010) was queried for Cyperaceae growing in Madagascar (electronic appendix 1). This peer-reviewed database of names of accepted taxa provides global distributions of species in botanical countries as recognized by the Taxonomic Databases Working Group (TDWG; Brummitt et al. 2001). Occurrence of Cyperaceae species in Madagascar and other botanical countries, where relevant, was plotted using ArcView GIS Version 3.1. For each species, the habitat (forest/open) and life form (therophyte or not) were scored from literature (e.g. Chermezon, 1937) and supplemented with field observations. The photosynthetic type (C_3/C_4) was based on literature (e.g. Bruhl & Wilson 2007) and supplemented with recent studies (Larridon et al. 2011).

RESULTS

Madagascar has 321 species of Cyperaceae in 33 genera, representing thirteen tribes and all subfamilies (table 1, electronic appendix 1). The largest tribes are Cypereae (49% of the sedge flora), Abildgaardieae (12%) and Cariceae (11%). Four tribes (Bisboeckelereae, Chrysitricheae, Cladieae, Trilepideae) have a single species in Madagascar. *Cyperus* is the largest genus, composing about 31% of the flora, followed by *Carex* (10%). Thirteen genera have a single species (40% of all genera or 4% of all species), one of which (*Trichoschoenus*) is a monotypic endemic genus. A number of the genera with a single species in Madagascar are wetland plants with pantropical (e.g. *Oxycaryum cubense*, *Websteria confervoides*) or cosmopolitan (e.g. *Bolboschoenus maritimus*, *Cladium mariscus*) distribution.

The majority of Cyperaceae (265 species) occur in open habitats and are mostly C_4 taxa in the Cypereae and Abildgaardieae (table 1). A number of C_3 taxa inhabiting open habitats are hemicryptophytes, growing in wetlands, or therophytes growing in seasonally wet habitats. Therophytes comprise about 20% of the sedge flora in Madagascar, with a C_3/ C_4 ratio of 1:2. *Carex* (twenty out of 33 species), *Costularia* (five out of eight), *Hypolytrum* (two out of two), *Schoenoxiphium* (two out of two) and *Trichoschoenus* (one out of one) are

Table 1 – Summary of Cyperaceae diversity in Madagascar showing total species number and proportion (%) of species scored for endemism, C_4 photosynthesis, forest habitat and annual life form.

Tribe	Genus	Species	Endemics	C_4	Forest	Annual
Cypereae	*Cyperus*	100	36	67	19	10
Cariceae	*Carex*	33	88	0	61	0
Sclerieae	*Scleria*	27	22	0	22	26
Cypereae	*Pycreus*	26	38	100	0	38
Abildgaardieae	*Bulbostylis*	21	71	100	0	62
Abildgaardieae	*Fimbristylis*	17	12	100	0	18
Cypereae	*Kyllinga*	13	8	100	0	8
Eleocharideae	*Eleocharis*	11	0	9	0	9
Fuireneae	*Schoenoplectiella*	10	50	0	0	50
Rhynchosporeae	*Rhynchospora*	10	10	10	0	10
Fuireneae	*Fuirena*	8	25	0	0	13
Schoeneae	*Costularia*	8	100	0	63	0
Cypereae	*Lipocarpha*	5	0	100	0	80
Cypereae	*Isolepis*	4	25	0	0	25
Schoeneae	*Machaerina*	4	25	0	0	0
Fuireneae	*Schoenoplectus*	3	0	0	0	0
Cariceae	*Schoenoxiphium*	2	50	0	100	0
Cypereae	*Ascolepis*	2	0	100	0	50
Cypereae	*Courtoisina*	2	0	0	0	100
Hypolytreae	*Hypolytrum*	2	50	0	100	0
Abildgaardieae	*Actinoschoenus*	1	0	0	0	0
Abildgaardieae	*Trichoschoenus*	1	100	0	100	0
Bisboeckelereae	*Diplacrum*	1	0	0	0	100
Chrysitricheae	*Lepironia*	1	0	0	0	0
Cladieae	*Cladium*	1	0	0	0	0
Cypereae	*Alinula*	1	0	100	0	100
Cypereae	*Ficinia*	1	100	0	0	0
Cypereae	*Oxycaryum*	1	0	0	0	0
Cypereae	*Queenslandiella*	1	0	100	0	100
Cypereae	*Remirea*	1	0	100	0	0
Eleocharideae	*Websteria*	1	0	0	0	0
Fuireneae	*Bolboschoenus*	1	0	0	0	0
Trilepideae	*Coleochloa*	1	0	0	0	0

predominantly found in forest habitats. Other genera well represented in forest habitats are *Cyperus* (nineteen out of 98) and *Scleria* (six out of 27 species). All forest Cyperaceae are hemicryptophytes with C_3 photosynthesis.

There are 121 endemic species (37% of the sedge flora), the largest number belonging to *Cyperus* (36% of the species in the genus in Madagascar) and *Carex* (88% of the species in the genus in Madagascar). *Costularia*, a genus also occurring in South Africa and New Caledonia, is notable in having all the eight Madagascan species being endemic. About 35% of the endemics are hemicryptophytes that occur in forests, belonging to *Carex* (seventeen species), *Cyperus* (fifteen species), *Costularia* (five species), and *Scleria* (three species). Of the remaining (non-forest) endemic species, 29% are C_3 hemicryptophytes in open habitats, whereas 36% are C_4 therophytes (fifteen species) or hemicryptophytes (28 species). The C_4 taxa are mostly members of the tribe Cypereae (26 species) and Abildgaardieae (seventeen species).

Among the non-endemic species, Madagascar shares most species with tropical eastern Africa (Tanzania 142 species, Kenya 109 and Uganda 101), as well as tropical West Africa (Nigeria 102 species, Senegal 87), West Central Africa (D.R.Congo 97 species), Southern Africa (KwaZulu-Natal 86 species) and the Indian subcontinent (India 88 species) (fig. 1). Comparison of species shared between Madagascar and other countries – increasing from a single country to 5% of the TDWG countries – shows shared species with adjacent countries in African continent (fig. 2A), increasingly including more countries in sub-Saharan Africa, India and Australia (fig. 2B & C), to pantropical (fig. 2D) distribution pattern.

DISCUSSION

Madagascar is renowned for high species richness and unparalleled levels of endemism. Among the angiosperms, total species richness among the top ten largest families appears to be proportional to global species richness in these families. The total number of Cyperaceae species (321 out of 5,400 species) places the family as the 10th largest in Madagascar, and is comparable in species richness to Melastomataceae, on Madagascar and worldwide (321 and ~ 5,000 species respectively; Almeda 2003). On the other hand, endemism in Cyperaceae (37%) is much lower than endemism in other large families, for example Melastomataceae (99%). The non-endemic Cyperaceae are mostly pantropical (figs 1 & 2) and the family is nearly absent in humid (lowland) forests, habitats that harbour the bulk of endemic species in Melastomataceae and other families with high endemism in Madagascar.

The sedge flora in Madagascar is most similar to tropical Africa and India. This similarity cannot be explained by distance – KwaZulu-Natal has as many shared species as India that is nine times further away. Similarity between the biota in Madagascar region and in Asia (including India), majority of which are too young to be explained by vicariance, has been hypothesized to be due to availability of stepping-stones (Islands in the Indian Ocean over time) and regional processes (wind and current directions) (Warren et al. 2010). In addition, several lineages appear to have dispersed to habitats similar to ancestral areas (niche conservatism; Wiens & Graham 2005), e.g. *Isolepis* and *Ficinia* occurring in alpine habitats similar to the Western Cape of South Africa.

Kenya, a country of comparable size, has 275 Cyperaceae species (World Checklist of Monocotyledons 2010) comprising similar tribes except for Hypolytreae and Schoeneae. The two floras differ in the number of taxa occurring in forest habitats (9% in Kenya vs. 17% in Madagascar), annual life-form (26% vs. 20%) and C_4 photosynthesis (63% vs. 36%). Madagascar has seven times more endemic species than Kenya (37% vs. 6%), with a large number of forest habitat species whereas none of the endemics in Kenya occur in forests. Kenya has predominantly savannah endemics which are mostly C_4 hemicryptophytes in *Kyllinga* and *Cyperus*.

The species endemism of Cyperaceae in Madagascar is notable at the global level (electronic appendix 2). When TDWG level 3 countries are rescaled to eliminate the bias of area, Madagascar is second to Cape Provinces in highest number of endemic species (Muasya et al. unpubl.). Many of the endemic species occur in high altitude forest habitats – richest in *Carex* subgenus *Vigneastra* and C_3 *Cyperus* lineages – than the open (and mostly drier) habitats. The savannah grasslands of Madagascar are particularly species poor and lack endemics among the Cyperaceae, pointing to potential lack of speciation in this habitat. Whereas the antiquity of Madagascar C_4 grasslands and savannah has been demonstrated (e.g. Bond et al. 2008, Willis et al. 2008), it is puzzling that there is no comparable diversification of characteristic lineages (e.g. *Kyllinga*; electronic appendix 3) in this habitat when compared to tropical Africa. This points either to a recent origin of savannah grasslands or to anthropogenic disturbances which may obscure diversity patterns. Widespread conversion of wetlands into paddy fields may lead to extinction of species with narrow ranges and favours widespread taxa thriving in eutrophic conditions.

Part of the sedge endemism in open habitats can be explained by the large geological diversity of Madagascan landscapes. The largest proportion of open wetland endemics belongs to C_4 genera *Bulbostylis* and *Pycreus*. When compared to related C_4 lineages, *Bulbostylis* and *Pycreus* are known to be capable of adapting to habitats with high chemical stress

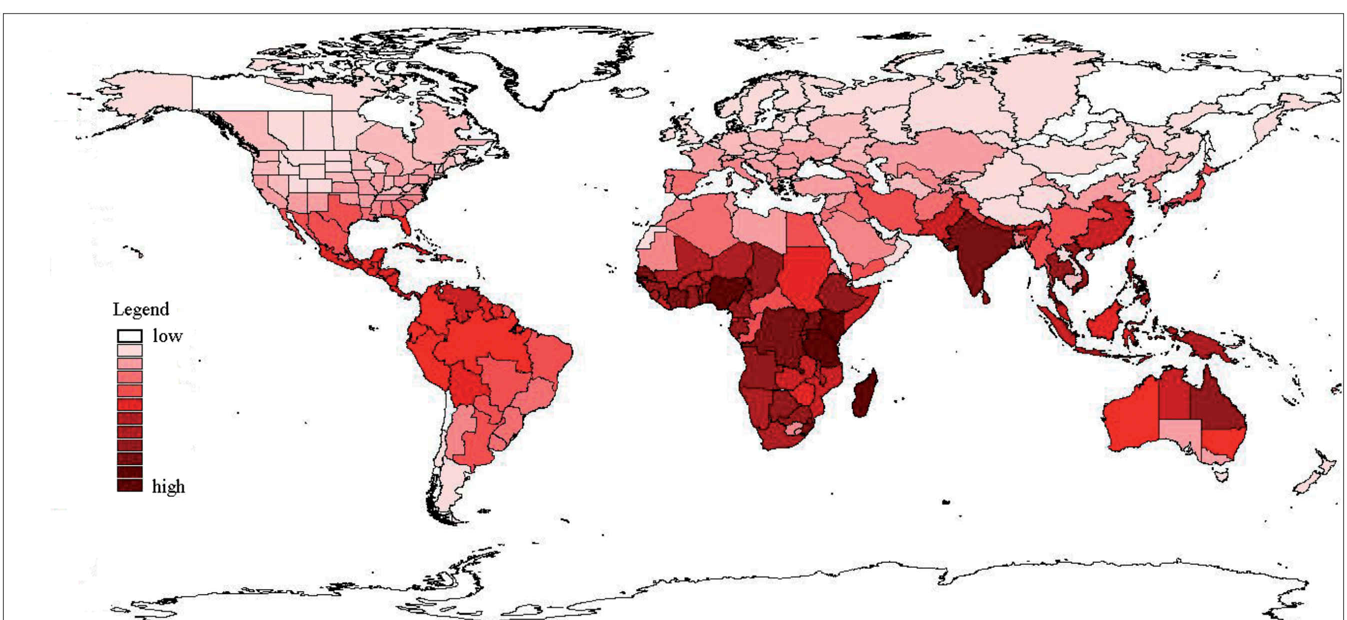

Figure 1 – Cyperaceae species shared by Madagascar and other TDWG level 3 countries using the 314 species recorded in the World Checklist of Monocotyledons (2010). The seven additional taxa, recently recorded, were not plotted (electronic appendix 1). Colour coding range from white (0 species) to dark red (314 species).

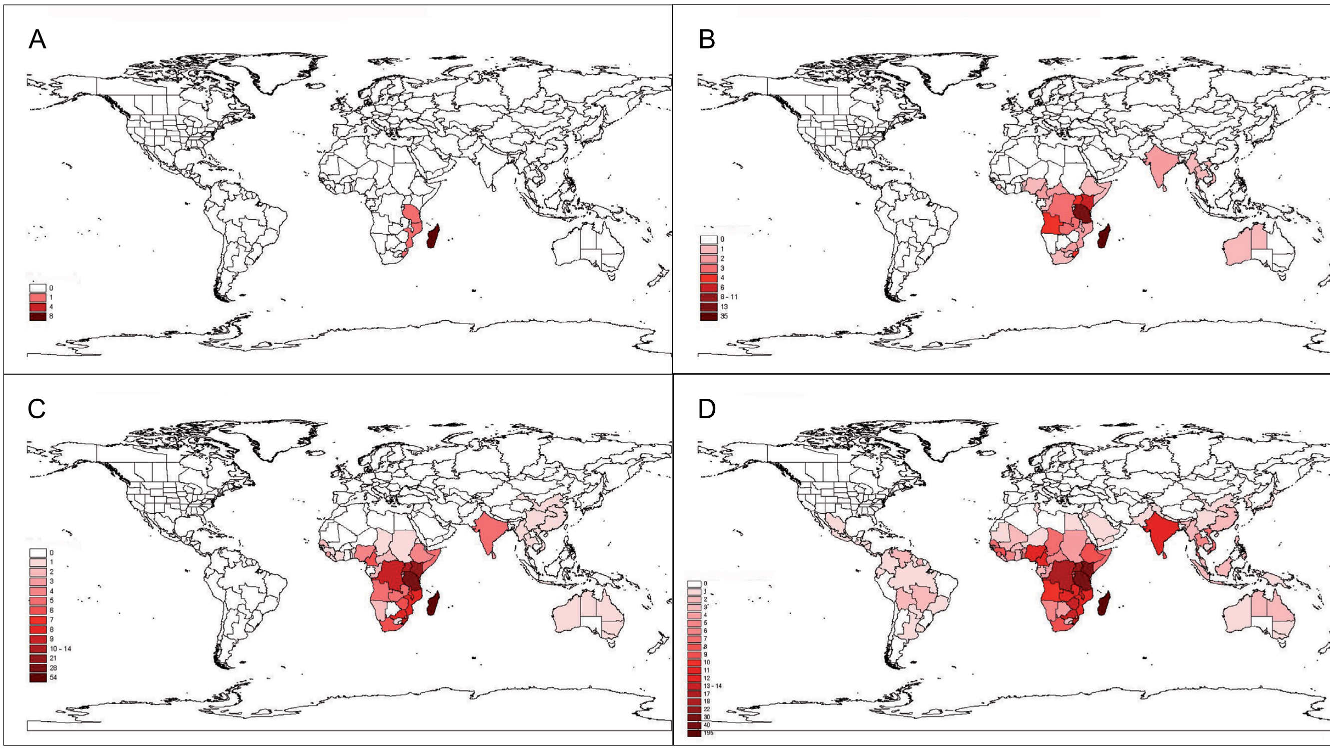

Figure 2 – Comparisons of species occurrence: A, species distributed in Madagascar and 3 other TDWG botanical countries (= 1% of all countries); B, in Madagascar and 5% of all countries; C, in Madagascar and 10% of all countries; D, in Madagascar and 25% of all countries.

(including salinity, heavy metals, acidity; e.g. Leteinturier et al. 1999). In Madagascar, *Pycreus* has three endemics on coastal sand dunes, two on limestone and one on volcanic hot springs and several species in bogs. *Bulbostylis* is also highly diversified on drier, rocky and sandy habitats (Chermezon 1937).

The forest habitats of Madagascar are occupied mainly by lineages that have stem node ages in the Neogene (Besnard et al. 2009, Muasya et al. unpubl.) whereas older forest lineages are absent (*Mapania*) or poorly represented (*Hypolytrum*). Members of *Cyperus* sect. *Incurvi* (Larridon et al. 2011), show several convergent morphologies, and fill the niches which are occupied elsewhere by Mapanioids. This implies that the assembly of the sedge flora in Madagascar has occurred recently, involving the dispersal into and subsequent diversification within the forest habitat. It might also indicate that the formation of the wet forest biome has only occurred in the Tertiary. This is also supported by the view of Wells (2003) that evergreen and deciduous forests, montane types and grasslands have evolved subsequent to the positioning of Madagascar in the tropics.

Biodiversity studies of Madagascar have focussed on charismatic plant families, perhaps skewing the view of species richness and endemism in less conspicuous lineages such as the Cyperaceae. As the family is mostly under-collected and is taxonomically poorly known, the full picture on diversity patterns may change as more focused studies become available. Endemism in open wetland or afro-alpine lineages of *Bulbostylis* and *Pycreus* may be overestimated for Madagascar, with several endemic species likely to be conspecific with taxa in poorly studied areas in mainland Africa (D.R.Congo, Mozambique). However, the evidence for a young wet forest and highland sedge flora is an interesting pattern that is worth investigating in greater detail.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of the following: (1) Full species list for Cyperaceae in Madagascar (pdf); (2) Cyperaceae endemics in to Top 20 TDWG-level 3 botanical countries (pdf); and (3) Comparison of *Kyllinga* species richness in Madagascar and Kenya (pdf).

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REFERENCES

Almeda F. (2003) Melastomataceae, Princes Flowers. In: Goodman S.M., Benstead J.P. (eds) The Natural History of Madagascar: 375–379. Chicago, The University of Chicago Press.

Andrianasetra-Ranarijaona H.L. (2003) Aquatic and Semiaquatic Vascular Plants. Flowers. In: Goodman S.M., Benstead J.P. (eds) The Natural History of Madagascar: 250–256. Chicago, The University of Chicago Press.

Besnard G., Muasya A.M., Russier F., Roalson E.H., Salamin N., Christin P-A. (2009) Phylogenomics of C_4 photosynthesis in sedges (Cyperaceae): Multiple appearances and genetic convergence. Molecular Biology and Evolution 26: 1909–1919. doi:10.1093/molbev/msp103

Bond W.J., Silander Jr J.A., Ranaivonasy J., Ratsirarson J. (2008) The antiquity of Madagascar's grasslands and the rise of C_4 grassy biomes. Journal of Biogeography 35: 1743–1758. doi:10.1111/j.1365-2699.2008.01923.x

Bruhl J.J., Wilson K.L. (2007) Towards a comprehensive survey of C_3 and C_4 photosynthetic pathways in Cyperaceae. Aliso 23: 99–148.

Brummitt N., Lughadha E.N. (2003) Biodiversity: where's hot and where's not. Conservation Biology, 17: 1442–1448. doi:10.1046/j.1523-1739.2003.02344.x

Brummitt R.K., Pando F., Hollis S., Brummitt N.A., and other editors (2001) World Geographical Scheme for Recording Plant Distributions. 2nd Ed. Pittsburgh, Hunt Institute for Botanical Documentation, Carnegie Mellon UniversityChermezon H. (1937) Cypéracées. In: Humbert H. (ed.) Flore de Madagascar: 1–335. Tananarive, Imprimerie Officielle.

Cornet A. (1974) Essai cartographique bioclimatique à Madagascar, carte à 1/2'000'000 et notice explicative N° 55. Paris, ORSTOM.

Davis A., Bridson D. (2003) Introduction to the Rubiaceae. In: Goodman S.M., Benstead J.P. (eds) The Natural History of Madagascar: 431–434. Chicago, The University of Chicago Press.

Dransfield S. (2003) Poaceae, Bambuseae, Bamboos. In: Goodman S.M., Benstead J.P. (eds) The Natural History of Madagascar: 467–471. Chicago, The University of Chicago Press.

Goetghebeur P. (1998) Cyperaceae. In: Kubitzki K., Huber H., Rudall P.J., Stevens P.S., Stutzel T. (eds) The families and genera of vascular plants: 141–190. Berlin, Springer-Verlag.

Goodman S.M., Benstead J.P. (2005) Updated estimates of biotic diversity and endemism for Madagascar. Oryx 39: 73–77. doi:10.1017/S0030605305000128

Goodman S.M., Benstead J.P. (2003) The Natural History of Madagascar. Chicago, University of Chicago Press.

Govaerts R., Simpson D.A., Bruhl J.J., Egorova T., Goetghebeur P., Wilson K.L. (2007) World Checklist of Cyperaceae. Kew, Royal Botanic Gardens.

Hoffmann P., McPherson G. (2003) Euphorbiaceae – Overview. In: Goodman S.M., Benstead J.P. (eds) The Natural History of Madagascar: 379–383. Chicago, The University of Chicago Press.

Labat J.-N., Moat J. (2003) Leguminosae (Fabaceae). In: Goodman S.M., Benstead J.P. (eds) The Natural History of Madagascar: 346–373. Chicago, The University of Chicago Press.

Larridon I., Reynders M., Huygh W. Bauters K., Van de Putte K., Muasya A.M., Boeckx P., Simpson D.A., Vrijdaghs A. Goetghebeur P. (2011) Affinities in C_3 Cyperus lineages (Cyperaceae) revealed using molecular phylogenetic data and carbon isotope analysis. Botanical Journal of the Linnean Society 167: 19–46. doi:10.1111/j.1095-8339.2011.01160.x

Leteinturier B., Baker A.J.M., Malaisse F. (1999) Early stages of natural revegetation of metalliferous mine workings in South Central Africa: a preliminary survey. Biotechnology,Agronomy, Society and Environment 3: 28–41. [available at http://www.bib.fsagx.ac.be/base/text/v3n1/28.pdf]

Moat J., Smith P. (2007) Atlas of the vegetation of Madagascar. Kew, Royal Botanic Gardens.

Muasya A.M., Simpson D.A., Verboom G.A., Goetghebeur P., Naczi R.F.C., Chase M.W., Smets E. (2009) Phylogeny of Cyperaceae based on DNA sequence data: current progress and future prospects. The Botanical Review 75: 2–21. doi:10.1007/s12229-008-9019-3

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B., Kent J. (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. doi:10.1038/35002501

Phillipson P.B., Schatz G.E., Lowry II P.P., Labat J.-N. (2006) A catalogue of the vascular plants of Madagascar. In: Ghazanfar S.A., Beentje H.J. (eds) Taxonomy and ecology of African plants: their conservation and sustainable use: 613–627. Kew, Royal Botanic Gardens.

Vences M., Wollenberg K.C., Vieites D.R., Lees D.C. (2009) Madagascar as a model region of species diversification. Trends in Ecology and Evolution 24: 456–465. doi:10.1016/j.tree.2009.03.011

Warren B.H., Strasberg D., Bruggemann J.H., Prys-Jones R.P., Thébaud C. (2010) Why does the biota of the Madagascar region have such a strong Asiatic flavour? Cladistics 26: 526–538. doi:10.1111/j.1096-0031.2009.00300.x

Wells N.A. (2003) Some hypotheses on the Mesozoic and Cenozoic paleoenvironmental history of Madagascar. In: Goodman S.M., Benstead J.P. (eds) The Natural History of Madagascar: 16–34. Chicago, The University of Chicago Press.

Wiens J.J., Graham C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics 36: 519–539. doi:10.1146/annurev.ecolsys.36.102803.095431

Willis K.J., Gillson L., Virah-Sawmy M. (2008) Nature or nurture: the ambiguity of C_4 grasslands in Madagascar. Journal of Biogeography 35: 1741–1742. doi:10.1111/j.1365-2699.2008.01985.x

Wilme L., Goodman S.M., Ganzhorn J.U. (2006) Biogeographic Evolution of Madagascar's Microendemic Biota. Science 312: 1063–1065. doi:10.1126/science.1122806

World Checklist of Monocotyledons (2010). The Board of Trustees of the Royal Botanic Gardens, Kew. Available at http://www.kew.org/wcsp/ [accessed 1 Apr. 2010]

Yoder A.D., Nowak M.D. (2006) Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. Annual Review of Ecology, Evolution, and Systematics 37: 405–431. doi:10.1146/annurev.ecolsys.37.091305.110239

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