

## WEST AFRICA'S SEDGES OVER THE EDGE: FROM REGION TO DOMAIN

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### Abstract

*African sedge phytogeography is explored continent-wide. Ordination is used to clarify relations between regional sedge floras. The Africa-domain has over 1200 sedges, 20% pluricontinental and the rest domain-only. Many pluricontinental sedges occur throughout the tropics, with eastward links also strong. Regionally North Africa's impoverished Carex-rich flora, mainly of pluricontinental species, is very distinct. The Sahara barrier separates the North African region from those further south where most species are strictly African, and Bulbostylis, Cyperus and Scleria prominent. From north to south in Africa endemism increases steadily. A second barrier, the Nile/Congo/Zambesi divide, separates western lowlands from higher eastern lands. In the west Neotropical links are evident. Lowland forest here is notable for Hypolytrum and Mapania. To the east there are more sedges, with species of Ficinia and Isolepis enriching the typical tropical flora. Extratropical Southern Africa's flora is very rich in Ficinia, Isolepis, Schoenus and Tetraria, with seven endemic genera. Long isolated, Madagascar carries a tropical African flora, with some Indian Ocean island sedges. Madagascar's many endemics show the typical island effect of close relation to widespread species. Shared pluricontinental elements and widespread domain-only species link West Africa with other domain regions. Despite being a large area, West Africa is floristically poor and very deficient in endemics. The region is remarkable for the very high proportion (almost half) of pluricontinental sedges in its flora. Wide prevalence of landscapes and conditions favourable to easily dispersed, resilient and versatile pluricontinental species is suggested in explanation.*

**Keywords:** Africa; West Africa; Cyperaceae; sedges; floristics; phytogeography; endemism; ordination

## Introduction

Around 50 years ago, Nigeria's was the most comprehensively known sedge flora in tropical Africa. Given impressive species richness, this was notable. Most other tropical African countries have since developed good knowledge of their sedges, but shared modern names for sedges across Africa only came with Lebrun & Stork (1995). These authors provided the first updated sedge nomenclature for tropical Africa in 90 years. Even so, they acknowledged that more work in sedge taxonomy was still necessary; challenges they highlighted, peculiar to sedges, mainly concern long-standing taxonomic disputes over features important in classification, and recognizing and separating several large and widespread genera.

Lebrun & Stork's welcome publication helped stimulate new sedge work at continental and global level, much tackling the challenges using DNA approaches. A decade or so later a checklist (Govaerts & Simpson, 2007) complemented this activity, at last offering globally the stable classification and consistent naming sedge researchers needed. This progress has been used to advantage for West Africa, with an impressive regional sedge flora (Mesterházy *et al.*, 2022). For tropical Africa overall, significant advance has continued with the successor to Lebrun & Stork (1995). This is the Cyperaceae volume of the major floristic series *Tropical African Flowering Plants* (Lebrun & Stork, 2020), so tropical Africa now has a modern sedge treatment with synonymy, literature, maps and other observations; occurrence beyond tropical Africa is also indicated.

With this improved knowledge of Africa's Cyperaceae, how West Africa fits into a wider picture can be assessed. In this account, the geographic basis of sedge phytogeography previously explored for Nigeria and the West African region (Hall, 2022, 2023) is scaled-up. Consideration extends over an "Africa Domain", explained below, and West Africa is compared with the rest of this domain. Flora and phytogeography are examined for tropical Africa in relation to outlying parts of the domain. Later, sedge floras in continental Africa and Madagascar are analysed and regional differences from West Africa highlighted.

## Methodology

At the core of this study is a dataset of sedge species recorded from African countries. This was assembled using publicly available information - mainly in the form of publications, but with some use of on-line sources. As previously shown for Nigeria (Hall, 2021), many considerations arise during the process of confidently drawing up for a country an authoritative species list using the most recent available nomenclature. Material in the public domain containing indications of sedge species records from African countries is extensive. Well over 200 years separates the earliest sources from the latest. This long

interval introduces complications particularly with nomenclature, and sometimes with assigning reports to the relevant countries of today. On the taxonomic side, as well as simple misidentifications, over time almost every African sedge recognized as a species today has also been known under at least one additional scientific name; in extreme cases over 50 additional names have been used! Related complications arise where in the past what was thought a single species later has become recognized as two or more, or where a species of today was formerly considered as two or more. Many names considered as synonyms today originated in publications appearing over the 1860-1940 period, as numerous collections of African plants received independent attention in different European herbaria. Only after another fifty years, with concerted efforts beginning to refine the copious information that had accumulated, was a global framework of consistent names and taxonomy emerging.

Sooner or later after the early plant collections reached an institution where they were studied, specialists published the first checklist or flora for the country or region. This took account of all material known at the time to be from the same area, beginning the process, still in progress, of rationalising the floristic knowledge. In checklists, earlier nomenclature is updated. Major regional floras complement name updates with more detail, citing specimens, giving (often for a wider area than the one of immediate interest) both updated and previously used names, and overall geographic ranges.

The need for updated historical records arises frequently in taxonomic and phytogeographical work. There are various helpful tools for this. It has long been customary for major herbaria and other centres of botanical study to have a particular interest in developing a rigorous and comprehensive knowledge of certain plant groups and/or the floras of particular areas. Definitive continental or global plant group monographs, and national or regional floras represent the primary results of such efforts. Additional output of historical relevance is sometimes a by-product. One such output is the plant collecting geographical gazetteer; another is a catalogue of plant collectors known to have gathered vascular plant specimens in an area of interest. Chronological accounts of the travels and material obtained by key early collectors active in an area, with whom obscure and doubtful names were often associated, may also have been published removing much of the uncertainty attached to the original naming.

Initially, as information was extracted from a source, database entries were made. Entries, included cited voucher material with collector identified, for the country concerned were made under the plant names the source used. Awareness of collectors and voucher detail allowed listings published later for the same country to be used for updating. In updating country lists, later names replaced those reduced to synonymy, any previous records considered unconfirmed were excluded, and any species more recently confirmed for the country added. Repeating this procedure with later documents concerning the

same area, or other areas which share species with the country under consideration, enables appropriate additional refinements to be made. Extending attention to documents appearing at a later date than the most recent directly addressing the country of interest locates relevant new knowledge. Any necessary adjustments to nomenclature can be made and, especially with monographic revisions of sedges, account taken of previously unlisted occurrences in the country and conversely unjustified list inclusions. As a broad check on the country listings achieved at the end of the record extraction and refinement operation, the database lists were compared with country coverage in the checklist of Govaerts *et al.* (2022). Since the checklist and this database used many sources of information in common, agreement proved very close. However, most taxa entered in the checklist as “unplaced names” were excluded from the database and, there were various other differences reflecting divergence of view on species placement and circumscription.

The data analysis used the FactoMineR library in R where the multivariate procedures were concerned (PCA function - Husson *et al.*, 2017); in this function, species were variables and individuals were geographical units. The two main PCA axes were extracted and geographical units plotted against them, using their axis loadings.

### **The Africa Domain**

The geographic framework (Brummitt, 2001) is that of the International Working Group on Taxonomic Databases for Plant Sciences (TDWG). TDWG's Level-1 Africa unit equates to the Africa Domain understood here: mainland Africa and islands in the surrounding oceans (Fig. 1). Regions are Level-2 units, dividing the domain into areas convenient for floristic and phytogeographical comparison. Level-3 offers finer resolution, most units corresponding to individual countries. In practical terms, Level-3 units (“botanical countries”) are the smallest entities where knowledge enables useful comparisons, and suitable for summarizing species occurrences through extensive areas (Govaerts & Simpson, 2007; Browning & Goetghebeur, 2017; Mesterházy *et al.*, 2022). Two extensions are made to the TDWG Africa unit for present purposes: the Sinai Peninsula (contiguous with Egypt), and the islands of Tristan da Cunha (grouped with Ascension and St Helena, the south-eastern Atlantic islands of TDWG's Africa unit). In all, 74 TDWG Level-3 units form the domain (Appendix). Islands included extend far beyond continental Africa, particularly eastward; the most widely separated parts of the domain are 11 500 km apart!

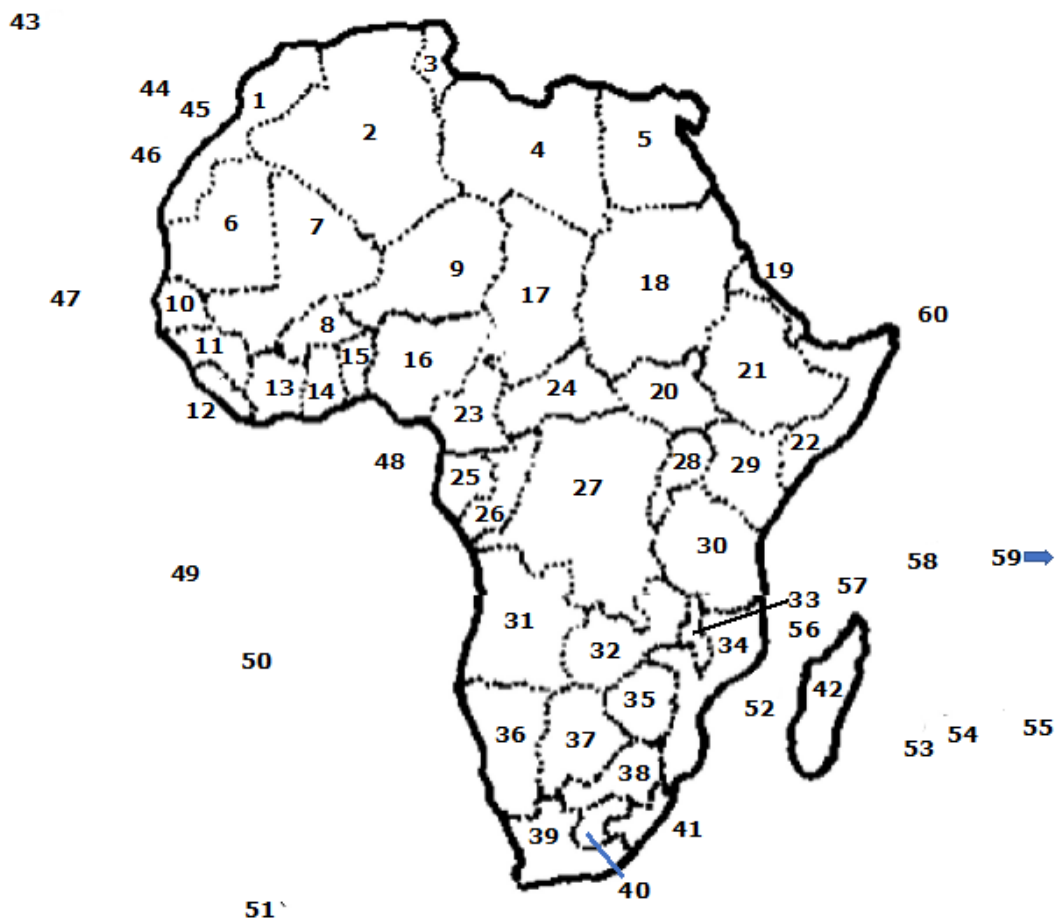


Fig. 1. The Africa domain showing division of continental Africa into Botanical Countries, and Madagascar; islands and island groups are positionally marked by key numbers. Botanical Country names corresponding to key numbers are given in the Appendix.

### The domain's flora

Table 1 shows sedge genera and species numbers for the domain and the five sectors which form it. Tropical Africa, the largest, corresponds to the area covered by Lebrun & Stork (1995, 2020) and is the main sector. The North Africa and Southern Africa sectors cover extratropical continental Africa and there are two offshore sectors – Madagascar and small islands. Most species and genera are represented in tropical Africa but 16 genera are not. Several others, weakly represented at tropical latitudes, are rich in species elsewhere. West Africa's listing is particularly poor in *Carex* but rich in *Eleocharis*, *Fimbristylis* and *Rhynchospora* (genera noted for widespread species); *Ficinia*, *Schoenus* and *Tetraria* are

absent while *Isolepis* is limited to a single species. The last four genera have speciated extensively in Southern Africa, a few of the species ranging to mountainous terrain further north.

The North and Southern Africa sedge floras contrast with that of tropical Africa. Despite the huge area, North Africa's sedge flora is highly impoverished. Numbers for *Carex* and *Cyperus* greatly exceed those in the remaining genera but almost all their species reach tropical Africa (*Cyperus*) and Mediterranean Europe (*Carex*), and often beyond in both genera. The sedge flora of Southern Africa is rich and distinctive - seven endemic genera and very high species numbers in *Ficinia*, *Schoenus* and *Tetraria*. Madagascar's flora shares with tropical continental Africa high species numbers in *Bulbostylis*, *Cyperus* and *Scleria*. Pantropical and cosmopolitan genera are also well represented: *Carex*, *Eleocharis*, *Fimbristylis*, *Rhynchospora*. Distinctive floristic features are the monotypic *Trichoschoenus* and the representation of *Costularia* and *Machaerina*.

The islands category brings together information from widely scattered places. There are some genus links to certain islands/island groups. *Isolepis* is strongly represented in the demanding environment at the southern extreme of the domain (Tristan da Cunha). Closer to the Equator, *Mapania* is recorded from islands in the Gulf of Guinea and the Seychelles.

**Table 1. Sedge floras, by genus, for entire Africa Domain (A) and each of the five sectors which form it (B-F); figures for West Africa (G) are included for comparison.**

Genera	A	B	C	D	E	F	G
<i>Actinoschoenus</i>	2	2	0	0	1	1	0
<i>Afrotrilepis</i>	2	2	0	0	0	0	2
<i>Afroscirpoides</i>	1	0	0	1*	0	0	0
<i>Blysmus</i>	1	0	1	0	0	0	0
<i>Bolboschoenus</i>	3	2	2	2	1	2	1
<i>Bulbostylis</i>	114	94	1	15	22	12	21
<i>Capeobolus</i>	1	0	0	1*	0	0	0
<i>Carex</i>	156	38	49	29	29	46	5
<i>Carpha</i>	10	4	0	5	1	2	0
<i>Chrysitrix</i>	3	0	0	3	0	0	0
<i>Cladium</i>	1	1	1	1	1	1	1
<i>Coleochloa</i>	8	8	0	2	1	2	1
<i>Costularia</i>	15	1	0	1	11	3	0

<i>Cyathocoma</i>	3	0	0	3*	0	0	0
<i>Cyperus</i>	458	384	28	123	131	89	135
<i>Diplacrum</i>	2	2	0	0	1	0	2
<i>Dracoscirpoides</i>	3	0	0	3*	0	0	0
<i>Eleocharis</i>	30	20	6	16	12	12	17
<i>Ficinia</i>	69	4	0	66	1	1	0
<i>Fimbristylis</i>	30	25	5	13	15	10	20
<i>Fuirena</i>	25	22	1	14	7	3	5
<i>Hellmuthia</i>	1	0	0	1*	0	0	0
<i>Hypolytrum</i>	20	18	0	0	2	3	7
<i>Isolepis</i>	45	12	3	35	4	8	1
<i>Lepironia</i>	1	0	0	0	1	0	0
<i>Machaerina</i>	4	1	0	0	3	3	0
<i>Mapania</i>	23	21	0	0	0	6	11
<i>Microdracoides</i>	1	1	0	0	0	0	1
<i>Neesenbeckia</i>	1	0	0	1*	0	0	0
<i>Nelmesia</i>	1	1	0	0	0	0	0
<i>Principina</i>	1	0	0	0	0	1*	0
<i>Pseudoschoenus</i>	1	0	0	1*	0	0	0
<i>Rhynchospora</i>	16	12	1	9	10	4	12
<i>Schoenoplectiella</i>	21	13	6	10	11	5	10
<i>Schoenoplectus</i>	9	3	4	5	2	4	1
<i>Schoenus</i>	41	2	1	41	0	0	0
<i>Scirpoides</i>	3	1	1	3	0	1	0
<i>Scirpus</i>	1	0	0	1	0	0	0
<i>Scleria</i>	98	85	0	24	26	11	34
<i>Tetraria</i>	27	2	0	26	0	0	0
<i>Trianoptiles</i>	3	0	0	3*	0	0	0
<i>Trichophorum</i>	1	0	1	0	0	0	0
<i>Trichoschoenus</i>	1	0	0	0	1*	0	0
<i>Xyroschoenus</i>	1	0	0	0	0	1*	0
<b>GENERA</b>	<b>44</b>	<b>28</b>	<b>16</b>	<b>30</b>	<b>23</b>	<b>23</b>	<b>19</b>
<b>TOTALS</b>	<b>1258</b>	<b>781</b>	<b>111</b>	<b>458</b>	<b>294</b>	<b>228</b>	<b>287</b>

Tabled figures are species numbers. Column codes: A, Whole domain ( $30.3 \times 10^6 \text{ km}^2$ ); B, Domain sector - tropical Africa ( $21.0 \times 10^6 \text{ km}^2$ ); C, Domain sector - North Africa ( $5.7 \times 10^6 \text{ km}^2$ ); D, Domain sector - Southern Africa ( $2.7 \times 10^6 \text{ km}^2$ ); E, Domain sector - Madagascar ( $0.6 \times 10^6 \text{ km}^2$ ); F, Domain sector - small islands ( $29\,843 \text{ km}^2$ ); G, West Africa ( $6.1 \times 10^6 \text{ km}^2$ ). Asterisks signify sector-endemic genera.

Although widely distributed overall, *Bulbostylis* and *Scleria* are particularly prominent in tropical latitudes (Gulf of Guinea and Indian Ocean). *Carex* features very widely through the islands but is much richer in species in Macaronesia, largely because (as in North Africa) many elements of the Mediterranean and southern European flora are present. Smaller Indian Ocean islands share with Madagascar *Carpha*, *Costularia* and *Machaerina*.

### Phytogeography

Globally, sedges are noteworthy for numerous species with pluricontinental ranges (Table 2) but others have limited distributions. Around one in five species recorded from the domain ranges beyond it. This proportion changes if tropical Africa and the parts of its periphery are considered separately.

In Table 2 pluricontinental species are grouped according to links with the north, east, south, or west (trans-Atlantic links), or in more than one of these directions (“widespread”). For the entire domain, the main intercontinental connection is eastward, with northern links and widespread occurrence also prominent. Southward links are few. Strong eastward connections are a constant feature when the parts of the domain are considered - except for North Africa. For North Africa there is, as expected, an extremely strong link to further north. Westward connections are a noteworthy absence from North Africa, while feeble southern connections are almost confined to Atlantic islands and Southern Africa. Widespread species are prominent throughout the domain. Pluricontinental species account for almost half West Africa's sedge flora, mostly showing eastward affinities or being “widespread”; the proportion linking west is relatively high.

**Table 2. Pluricontinental links, in terms of species numbers, in the sedge floras of the Africa Domain and each of the five sectors which form it; percentages of pluricontinental species in the flora are given in parentheses. Numbers for West Africa are included for comparison.**

	All species	All Pluricontinental	To North	To East	To South	To West	Widespread
<b>Africa Domain</b>	1258	255 (20%)	60	107	8	28	52
<b>North Africa</b>	111	100 (90%)	55	22	0	0	23
<b>Southern Africa</b>	458	114 (25%)	3	61	4	11	35
<b>Tropical Africa</b>	781	169 (22%)	6	92	1	25	45
<b>Madagascar</b>	294	113 (38%)	1	60	0	14	38
<b>Small islands</b>	228	137 (60%)	22	56	6	13	40
<b>West Africa</b>	287	135 (47%)	3	65	0	24	43



Species can also be categorized on their distribution within the domain. For Table 3, five patterns have been distinguished. A “Tropical” category mainly contains species reported from only the tropical latitudes of continental Africa. Also included, however, are those present in both tropical islands (some reaching Madagascar) and tropical Africa. Species exclusive to islands form the “Only offshore” category. “Northern” species occur in North Africa – exclusively or extending into tropical Africa. “Southern” species are in Southern Africa – exclusively or extending into tropical Africa. “All” refers to species extending both north and south from tropical Africa. The domain sedge flora varies with latitude and offshore (Table 3).

**Table 3. Species numbers representing distribution patterns in the sedge floras of the Africa Domain and each of the five sectors which form it, by category. Domain-only (top part of table) and pluricontinental (lower part). Categories are separated and their species grouped by distribution pattern. Numbers for West Africa are included for comparison.**

**AFRICA DOMAIN ONLY**

	All	N	Trop	S	Only offshore	Total
<b>Africa Domain</b>	50	9	488	293	163	1003
<b>North Africa</b>	3	8	0	0	0	11
<b>Southern Africa</b>	50	0	0	294	0	344
<b>Tropical Africa</b>	50	5	485	72	0	612
<b>Madagascar</b>	20	0	25	12	124	181
<b>Small islands</b>	10	2	33	1	45	91
<b>West Africa</b>	30	3	110	9	0	152

**PLURICONTINENTAL**

	All	N	Trop	S	Only offshore	Total
<b>Africa Domain</b>	95	69	52	25	14	255
<b>North Africa</b>	37	63	0	0	0	100
<b>Southern Africa</b>	92	0	0	22	0	114
<b>Tropical Africa</b>	93	8	52	16	0	169
<b>Madagascar</b>	72	1	21	8	11	113
<b>Small islands</b>	68	22	24	7	16	137
<b>West Africa</b>	84	4	37	10	0	135

All = found in North, Tropical and South; N = Northern; Trop = Tropical; S = Southern.

A contrast between domain-only and pluricontinental categories is the former's low importance of species found throughout the domain. Suites of species with limited distributions, and not known outside the domain, give different sectors distinctive character. The closest match is between Madagascar and the remaining islands. West Africa's sedge flora is part of the tropical continental sedge flora, and their similarity is evident. Both are distinct from the floras of outlying sectors. For West Africa the contribution of the tropical element is lower than for tropical continental Africa as a whole, while widely spread elements are more important.

A floristic element contributing distinctness to the domain overall, and its sectors, is the endemic species (Fig. 2). For present purposes, "strictly endemic" species are confined to a single "botanical country" (Appendix) of the TDWG scheme. "Near-endemic" species are confined to a botanical country and its immediate neighbours. Here, "endemism" refers to strict- and near-endemic categories combined. At sector level, in North Africa's limited sedge flora under 5% of sedge species are strict endemics. At the other extreme, 35-45% in Southern Africa and Madagascar are strict endemics. In the domain overall, over 500 species are strictly endemic (40%). West Africa has an endemism value far below that for tropical Africa as a whole, showing endemism varies within sectors (and that today's West African flora shows little evidence of localized speciation).

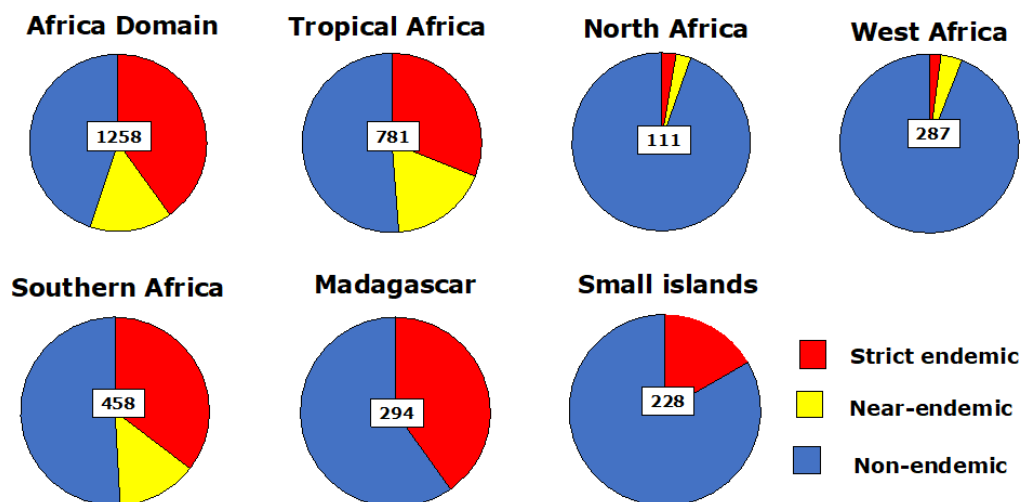


Fig. 2. Sedge endemism in the Africa Domain and each of the five sectors which form it. Entries for West Africa are given for comparison. Pie-slices are percentages of the area's number of species (shown at pie-centre).

## Ordination

Identifying domain sectors with endemism reveals where conditions have favoured speciation. However, many African sedges are neither near- nor strict endemics even though they are not found everywhere. Understanding distribution patterns within the domain requires closer examination of these. Here, floristic lists for TDWG Level-3 units are used to seek patterns through formal analysis by ordination. The ordination tool simultaneously evaluates species lists representing different areas (units – “botanical countries” - for present purposes). Multivariate mathematical procedures reveal the extent of floristic similarities among units. Plottable numerical values are generated and depicted as a scatter of points, each point representing a different unit. Points near each other represent units with similar floras.

Effective application of the technique is achieved when constraints are imposed. Firstly, rare species and extremely common species are excluded; here, no species was included if present in fewer than four, or absent from fewer than four, units. A consequence is the exclusion of all strict endemics and around 80% of near-endemics. The 55 TDWG Level-3 units of continental Africa vary widely in area (Appendix) and the second step is to reduce unit area variation. This is done by combining relatively small units with a contiguous unit, to ensure a minimum area of 100 000 km<sup>2</sup>. The next requirement is for at least 20 species to be represented in every unit entering the analysis: combination of the species-poor Western Sahara with the contiguous Morocco has been necessary. Combining reduced the 55 continental units to 41. Offshore, Madagascar also satisfied requirements, bringing the units total to 42. The remaining 18 Level-3 oceanic island units, creating complications from very small floras and areas (less than 1% of the domain area combined), were excluded.

## Ordination findings

The 42 botanical countries represent eight TDWG regions. Three (North Africa, South Africa, Madagascar) have featured as domain sectors; equivalent information for another, West Africa, has also been given (Tables 2 and 3; Fig. 2). In Tables 4 and 5, and Fig. 3, matching information for the remaining regions is provided.

While Table 4 reveals the lower diversity in the Northeast and West-Central Africa regions, uniformity in the numbers of pluricontinental species across these four regions is also evident.

**Table 4. Pluricontinental links, in terms of species numbers, in the sedge floras of four TDWG\* tropical African regions; percentages of pluricontinental species in the flora are given in parentheses.**

	All species	All Pluricontinental	To North	To East	To South	To West	Widespread
Northeast Africa	325	130 (40%)	4	75	0	13	38
West-Central Africa	400	135 (34%)	1	68	0	23	43
East Africa	470	136 (29%)	1	79	0	15	41
South Tropical Africa	455	136 (30%)	1	74	1	18	42

\*TDWG, International Working Group on Taxonomic Databases for Plant Sciences.

Table 5 highlights the contrasting ways in which the pluricontinental and domain-only categories feature in the regional sedge floras. In every one of the four regions most pluricontinental species extend from the extratropical north to the extratropical south and fewer than 30% are species with strictly tropical African distributions. The corresponding regional values among the more numerous domain-only species always exceed 60%.

**Table 5. Species numbers representing distribution patterns within Africa in the sedge floras of four TDWG\* tropical African regions, in terms of numbers of species by category. Domain-only and pluricontinental categories are separated and their species grouped by distribution pattern.**

	AFRICA DOMAIN ONLY					PLURICONTINENTAL SPECIES				
	All	N	Trop	S	Total	All	N	Trop	S	Total
Northeast Africa	49	4	139	3	195	87	7	34	2	130
West-Central Africa	40	1	209	15	265	84	4	37	10	135
East Africa	50	1	244	39	334	87	7	34	2	136
South Tropical Africa	48	0	203	68	319	87	2	35	12	136

\*TDWG, International Working Group on Taxonomic Databases for Plant Sciences; All = found in North, Tropical and South; N = Northern; Trop = Tropical; S = Southern.

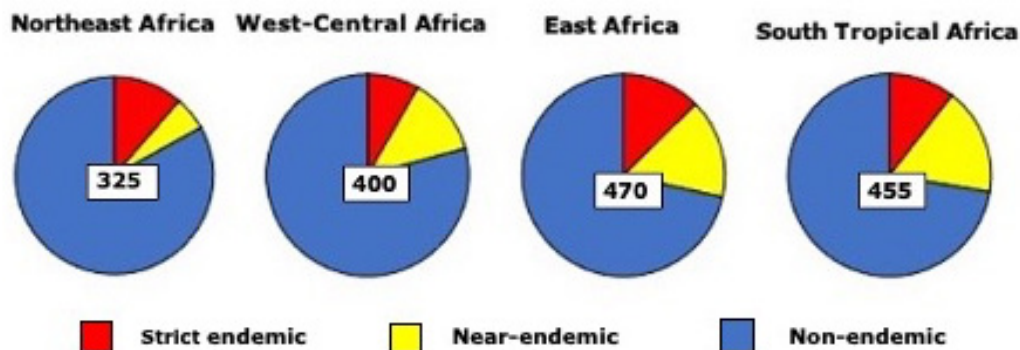


Fig. 3. Sedge endemism in four International Working Group on Taxonomic Databases for Plant Sciences tropical African regions. Pie-slices are percentages of the area's number of species (shown at pie-centre).

Fig. 3 confirms that the relative proportions of endemic categories at regional scale differ markedly from those for mainland tropical Africa as a whole. At regional level non-endemic species far exceed endemic and the proportion of strictly-endemic species is sharply reduced.

Extratropical North Africa and Southern Africa lie at one end of the main (horizontal) ordination axis; countries near the other end are all tropical (Fig. 4). This axis reflects increasing species richness through Africa, coupled with a moisture gradient. North Africa and Northeast Africa are dry regions while West-Central, East and South Tropical Africa are relatively moist. A related axis trend is that proportions of pluricontinental tropical species are high at the drier end and proportions of exclusively African tropical species relatively low.

West and West-Central Africa are at one end of the vertical axis, while Northeast Africa aligns with North Africa in the centre, and the countries of East and South Tropical Africa align with Southern Africa at the other end. Contributing to this axis sequence is the proportion of species with southern distributions – low in North, Northeast, West and West-Central Africa; high in East and South Tropical, and Southern Africa. Madagascar, although centrally set among the tropical regions is well-separated from the main cluster of West African botanical countries. Numbers of both pluricontinental and domain-only species are relatively low in the Madagascar ordination data.

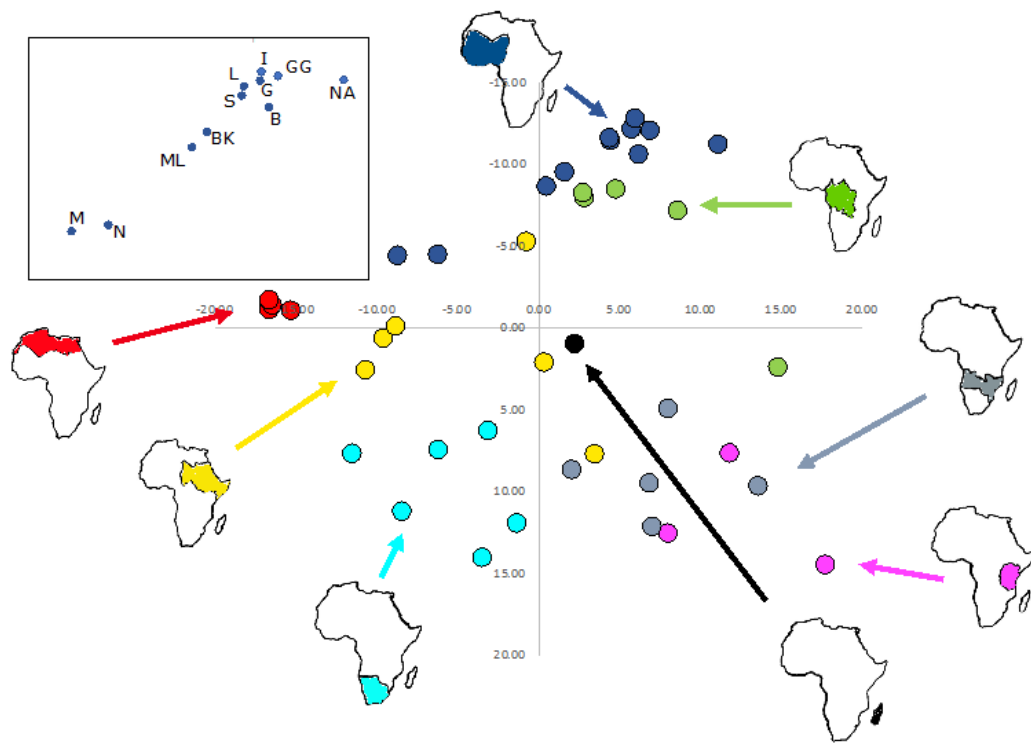


Fig. 3. Ordination based on sedge floras of 42 botanical countries in the Africa Domain, colours indicating botanical regions. Inset (upper left) identifies points for West African countries: B, Benin/Togo; BK, Burkina Faso; G, Ghana; GG, Guinea/Guinea Bissau; I, Ivory Coast; L, Liberia/Sierra Leone; M, Mauretania; ML, Mali; N, Niger Republic; NA, Nigeria; S, Senegal/The Gambia.

### Broader regional consideration

The ordination shows TDWG regions are relevant in the domain, finding relationships between them and identifying phytogeographical gradients. Wider appreciation of the sedge floras comes from regional information additional to the ordination data. Here, emphasis is on regional contrasts with West Africa.

The sedge flora of adjoining North Africa is the most distinct of any region in the domain, and much the poorest in species. The two most similar regions to North Africa are its southern neighbours – Northeast and West Africa. Compared with West Africa, North Africa lacks trans-Atlantic links and is particularly deficient in strictly African species.

Northeast Africa, also adjoining, has a sedge flora like West Africa's. These are the tropical continental regions with fewest species and the lowest endemism. In both, well over half the area is dryland (including tracts of desert and subdesert), a poor environment

for sedge diversity. Northeast Africa's higher endemism is associated with more extensive mountain terrain, to over 4000 m altitude, and rain-shadow isolation of an eastern lowland biodiversity hotspot at the north end of an "arid corridor" (Werger, 1978).

West Africa and the third adjoining region, West-Central Africa, have Africa's strongest trans-Atlantic links; these regions have extensive areas matching the humidity of the east coast of the Neotropics. A low elevation land surface accounts for most of both regions, but natural savanna vegetation covers the majority of West Africa while the natural cover is forest over most of West-Central Africa. The savanna regions are where pluricontinental and widely occurring African elements dominate West Africa's sedge flora. West-Central Africa's extensive lowland forest, however, is rich in domain-only sedge species, particularly from the "tropical" distribution category. Some of these are confined to large lowland forest refuges (Hamilton, 1976) that survived arid Late Quaternary events. Also important in the West-Central region is wider occurrence of land above 1000 m altitude, particularly in the south and east. This higher ground, rising to over 5000 m, offers various upland and montane habitats, also affected by Late Quaternary climate fluctuations (Flenley, 1979). Rises and falls in altitudinal limits of vegetation belts would have resulted in periods of isolation and coalescence of montane plant communities, changing species distributions and persistence, and creating opportunities for endemism. West-Central Africa is floristically much richer than West Africa with much higher endemism.

The remaining continental regions (East, South Tropical and Southern Africa) constitute the core area for Africa's distinctive sedge flora. There is increasing prominence of the southern African distribution pattern and a rise to over 70% in the proportion of domain-only sedges in the flora. Species numbers and endemism increase sharply and, with so much more high ground, the upland/montane effects enhancing endemism and species richness for the West-Central region apply even more strongly. Trans-Atlantic links are noticeably weaker than in West and West-Central Africa.

An interval of 400 km lies between Madagascar and the nearest part of Africa's coast. This isolation has existed since before the Cyperaceae appeared and today's rich sedge flora has arisen from long distance dispersal. Mainland Africa as the nearest land mass of any size can be assumed an important source of colonising species. Over the course of time locally evolved relatives of some colonising species have apparently replaced them, leading to Madagascar's exceptional endemism – a well-known feature of island floras. The island's high endemism is a major difference from West Africa. Further differences arise from terrain contrast and geological history which have enhanced Madagascar's sedge diversity (Muasya *et al.*, 2011). The absence from Madagascar of many tropical species present in West Africa is partly explained by the distance separating them – the island's links with nearer parts of the continent are stronger.

## Discussion

Currently, molecular techniques in sedge study are producing an increasingly reliable phylogeny for the family. At global level, this has become the basis for comprehensive understanding of its evolution and history. Small scale sedge work continues, however, with the production and updating of local and country floras, often with phytogeographical content. Small scale progress is largely achieved through traditional practices, sometimes reflecting molecular work. Other studies relying on traditional practices appear at a regional level. This contribution falls in the gap between regional and global studies, looking at floristic variation among the regions of an entire continent - Africa. The study characterizes Africa's sedge flora as a context for considering West Africa's relationship with other parts of the domain. Simply separating the domain's poleward latitudes and islands from the tropical continent confirms the domain's sedge flora is far from uniform. Differences between regions are shown with the ordination and no single region typifies the domain overall, or its tropical latitudes.

Generally, more than half of the domain's pluricontinental species are represented in every TDWG region in Africa but the similarity this introduces is not reinforced by domain-only elements. In all regions except North Africa domain-only species are in the majority. At the level of the whole domain 80% of sedge species are not known elsewhere, confirming Africa's distinct floristic identity. Assessing domain-only sedge floras region by region reveals more. Unlike pluricontinental species, which are mostly very widespread, domain-only species have narrower ranges - sometimes very limited, suggesting inability to spread widely. Consequently, each region has its own mix of species, a characteristic very forcefully underlined where endemism is highest – as in Madagascar and Southern Africa.

The extensive ranges of typical pluricontinental sedges reflect very effective dispersal processes, resilience to varying environmental conditions, and relatively wide ecological tolerance. Open habitats at low and moderate elevation, often continuous over very large areas, are well-suited to species with these attributes; many sedges in such places are well-known pantropical weeds. Habitats of this kind are so dominant across West Africa that pluricontinental species prevail comprehensively, and domain-only species account for barely half the sedge flora.

For the regions TDWG accepts, national boundaries are used to denote approximately where there are any abrupt and extensive floristic changes. Africa's northern desert belt and the Nile/Congo/Zambesi divide illustrate this situation. The North Africa region is sharply separated from the rest of the continental domain along Africa's greatest biogeographical barrier. This barrier, the Sahara and the drylands of the Libyan and Eastern Deserts further east, separates two floristic kingdoms: the Holarctic represented by a Mediterranean flora, and the Palaeotropical represented by African and Madagascar floras (White, 1983).



The Nile, Congo and Zambesi River divide is between what are often known as the “Low” and “High” parts of Africa (White, 1983), separating the contrasting floras of western (Low) and eastern/southern (High) Africa. The mainly-forested land to the west is Africa’s centre for the ancient and characteristic lowland forest genera *Hypolytrum* and *Mapania*. East and south of the separation land is mostly above 1000 m altitude with grassland or woodland, although scattered mountain ranges with additional ecosystems also occur

Both barriers feature in the ordination scatter: the isolation of the North Africa countries at one end of the horizontal axis (Sahara barrier) and separation of High from Low Africa on the vertical axis (divide barrier). Where there is a barrier, differences are relatively large between sedge floras from the two sides. On the respective sides of the divide, the sedge flora changes more gradually from one region to the next. With Low Africa a moisture gradient is involved; with High Africa there is a strong gradient of rising numbers of species having southern distribution.

Many shared pluricontinental elements, and a suite of widely found species only known from the domain, link other TDWG regions very strongly to West Africa. West Africa’s differences from these involve terrain, biodiversity hotspots and climate refuges, and past geological events and opportunities. Sedge species numbers increase from West Africa towards the southeast as more of these factors are reflected in conditions contrasting with the low and uniform landscapes so favourable to pluricontinental sedges in West Africa. Part of the increase comes from tropical and southern African sedges, including many endemics, in High Africa. West Africa’s sedge flora is not only rather poor for a mainland region south of the Sahara but strongly deficient in endemics and near-endemics, and other species of limited range: the region is far from representative of the Africa Domain.

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**Appendix: A. Units included in ordination**

<b>Area unit names</b>	<b>Numbers (Fig. 1)</b>	<b>Areas (km<sup>2</sup>)</b>	<b>Region</b>
Algeria	2	2 382 000	North Africa
Angola	31	1 246 000	South Tropical Africa
Benin	15*	113 000	West Africa
Botswana	37*	575 000	Southern Africa
Burkina Faso	8	274 000	West Africa
Burundi	28*	28 000	West-Central Africa
Cabinda	26*	7 000	West-Central Africa
Cameroon	23	475 000	West-Central Africa
Caprivi Strip	37*	16 000	Southern Africa
Central African Republic	24	623 000	West-Central Africa
Chad	17	1 284 000	Northeast Africa
Congo Brazzaville	26*	342 000	West-Central Africa
Democratic Republic of Congo	27	2 345 000	West-Central Africa
Djibouti	19*	23 000	Northeast Africa
Egypt	5*	959 000	North Africa
Equatorial Guinea	25*	26 000	West-Central Africa
Eritrea	19*	118 000	Northeast Africa
Eswatini	41*	17 000	Southern Africa
Ethiopia	21	1 104 000	Northeast Africa
Gabon	25*	268 000	West-Central Africa
Ghana	14	239 000	West Africa
Guinea	11*	246 000	West Africa
Guinea-Bissau	11*	36 000	West Africa
Ivory Coast	13	322 000	West Africa
Kenya	29	580 000	East Africa
Lesotho	41*	30 000	Southern Africa
Liberia	12*	96 000	West Africa
Libya	4	1 760 000	North Africa
Malawi	33	119 000	South Tropical Africa
Mali	7	1 240 000	West Africa
Mauritania	6	1 032 000	West Africa
Madagascar	42	594 000	Indian Ocean
Morocco	1*	445 000	North Africa
Mozambique	34	783 000	South Tropical Africa
Namibia	36	808 000	Southern Africa

Niger	9	1 267 000	West Africa
Nigeria	16	924 000	West Africa
Rwanda	28*	26 000	West-Central Africa
Senegal	10*	197 000	West Africa
Sierra Leone	12*	73 000	West Africa
Sinai	5*	61 000	North Africa
Somalia	22	638 000	Northeast Africa
South Africa: Cape Provinces	39	683 000	Southern Africa
South Africa: Free State	40	135 000	Southern Africa
South Africa: KwaZulu-Natal	41*	91 000	Southern Africa
South Africa: Northern Provinces	38	308 000	Southern Africa
South Sudan	20	620 000	Northeast Africa
Sudan	18	1 886 000	Northeast Africa
Tanzania	30	940 000	East Africa
The Gambia	10*	10 000	West Africa
Togo	15*	57 000	West Africa
Tunisia	3	164 000	North Africa
Uganda	28*	238 000	East Africa
Western Sahara	1*	266 000	North Africa
Zambia	32	753 000	South Tropical Africa
Zimbabwe	35	391 000	South Tropical Africa

Key numbers of map applicable to combination units carry asterisks.

## B. Island units excluded from the ordinations

Area unit names	Numbers (Fig. 1)	Areas (km <sup>2</sup> )	Location
Aldabra	57	180	Indian Ocean
Ascension	49	100	Atlantic Ocean
Azores	43	1 800	Macaronesia
Canary Isles	46	7 273	Macaronesia
Cape Verde	47	4 033	Macaronesia
Chagos Archipelago	59	56	Indian Ocean
Comoros	56	2 361	Indian Ocean
Gulf of Guinea Isles	48	3 000	West-Central Africa
Madeira	44	1 279	Macaronesia
Mauritius	54	1 865	Indian Ocean
Mozambique Channel Isles	52	30	Indian Ocean

Réunion	53	2 511	Indian Ocean
Rodrigues	55	709	Indian Ocean
Selvagens	45	15	Macaronesia
Seychelles	58	279	Indian Ocean
Socotra	60	4 000	North-East Africa
St. Helena	50	200	Atlantic Ocean
Tristan da Cunha	51	150	Atlantic Ocean