

extinction risk as the majority of species that occur at such sites are often still assessed as threatened, indicating that important pressures persist in these areas.

Ex situ conservation is for the time being the mainstay of conservation efforts for some of the rarest species. For instance, the Parc Botanique et Zoologique de Tsimbazaza in Antananarivo and the Arboretum de Ranomafana, Ifanadiana, have some of the rarest species in their living collections; for example, the only known individual of *D. robusta* on Madagascar is at the Ranomafana site (J. Dransfield et al. 2012). Since its discovery in 1994, this single tree has continued providing seeds for horticulture. A conservation project is being undertaken in these two botanic gardens, which produces seedlings of rare and threatened species in nurseries for planting in public places across Madagascar in the near future in order to raise awareness of the importance of conserving palms.

At the moment, it is difficult to predict how many more palm taxa on Madagascar will be discovered and described. There remain significant areas of the island, such as the Tsaratanàna Massif, that are still underrepresented by palm specimens in herbaria. Fieldwork since 1995 shows clearly that small forest fragments in the east coast lowlands, or even unexpected dry habitat as where *Tabina*

was found, are likely to yield further novelties. Species turnover seems to happen over very short distances. In some sites in the eastern region, such as Makira, Masoala, Andilamena, and Vondrozo, adjacent hills may possess quite different palm floras, and most of the new species recently described have been discovered from particular habitats. Most of the remaining humid evergreen lowland forests should be prioritized for further palms surveys, not only for completing the catalog of the flora of Madagascar, but also for documenting new population occurrences, which is important for defining the extinction risk for each species.

Unfortunately, threats to biodiversity continue to increase every year; many rare species might even become extinct before they are known to science. To prevent such biodiversity loss for Madagascar palms, a critical conservation strategy is required to focus attention on conservation priorities, to stimulate necessary action, and to raise public awareness. With the biodiversity crisis in Madagascar ongoing, the current phylogenetic studies of all Madagascar palms being conducted at Kew and Aarhus University will provide a framework for managing species information in the future.

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## CYPERACEAE, SEDGES

I. Larridon, D. Spalink, P. Jiménez-Mejías, J. I. Márquez-Corro, S. Martín-Bravo, A. M. Muasya, and M. Escudero

### DIVERSITY AND PHYLOGENY

Cyperaceae (sedges) is among the 10 largest families of angiosperms and is the third largest monocot family in the world. The main diagnostic characteristics of the Cyperaceae relate to their highly reduced flowers, often composed of three stamens and a single ovary placed on the axil of a glume or scale and arranged in the form of spikelets (Goetghebeur 1998). The perianth is missing or reduced to bristles or scales. The leaves are linear, with parallel nerves, much like in grasses (see Vorontsova et al., pp. 585–98). Sedges are often seen as a rather uniform group of plants from wetland environments, but like grasses they are phenotypically and ecologically very diverse (Naczi and Ford 2008). They are of great ecological importance in high-latitude and high-elevation ecosystems, as well as in wetland habitats where they may constitute the majority of the plant biomass. Although not to the level of the Poaceae, Cyperaceae also have an economic significance with about 10% of species used by humans (Simpson and Inglis 2001), several species being notorious weeds in agriculture, and a remarkable—and often overlooked—importance in human history (e.g., totora, papyrus) and evolution (Sponheimer et al. 2013; Dominy 2012). Despite their importance, many questions concerning their evolutionary history remain, and much work is needed to fully understand this interesting group of plants. For example, dozens of species continue to be described every year (e.g.,

Bauters et al. 2018; Larridon et al. 2019a), including from areas assumed to be well explored, such as Europe and North America (e.g., Derieg et al. 2013; Maguilla and Escudero 2016).

With 310 species, the Cyperaceae is among the top 10 most species-rich angiosperm families on Madagascar, and the island is among the four countries that are most species rich for sedges in the African-Malagasy region.

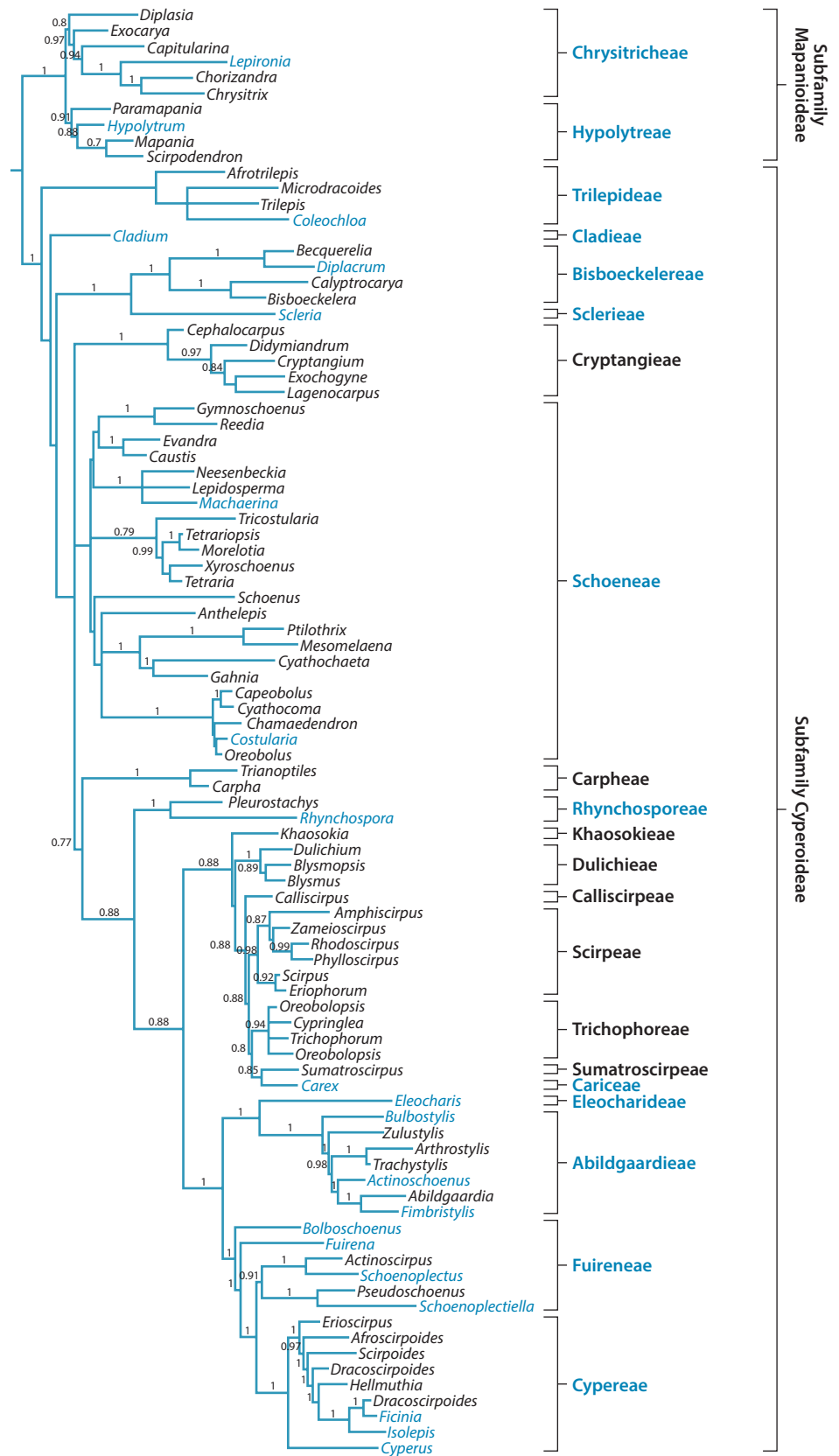
Madagascar is home to both subfamilies of Cyperaceae, the Mapanioideae and Cyperoideae (Figure 8.25). The latter is by far

TABLE 8.19. The four most species-rich African-Malagasy countries for Cyperaceae

COUNTRY	NUMBER OF SPECIES	AREA (km <sup>2</sup> )
South Africa	452	1,221,037
Tanzania	450	947,303
Democratic Republic of Congo	318	2,345,409
Madagascar	310	587,041

Sources: Area figures from Wikipedia. Number of species follows Govaerts et al. (2020d).

FIGURE 8.25 Summary phylogeny of the Cyperaceae family based on Semmouri et al. (2019), indicating the tribes and genera with species native to Madagascar (in blue). Tribal classification follows Semmouri et al. (2019) and L evell-Bourret and Starr (2019).



the more diverse, encompassing 99% of the species, and includes 12 tribes, 21 genera, and 308 species on the island (Govaerts et al. 2020d; Semmouri et al. 2019). The subfamily Mapanioideae, on the other hand, is limited to two species in two genera (*Lepironia*

and *Hypolytrum*) (Govaerts et al. 2020d). This is not surprising as the subfamily encompasses ~3% of global Cyperaceae species diversity and is largely restricted to the tropics. Table 8.20 provides an overview of the Cyperaceae of Madagascar.

TABLE 8.20. Overview of Cyperaceae diversity on Madagascar

SUBFAMILY	TRIBE	GENUS	NUMBER OF SPECIES GLOBALLY	NUMBER OF SPECIES MADAGASCAR	NUMBER OF ENDEMIC SPECIES
Mapanioideae	Chrysitricheae	<i>Lepironia</i>	1	1	0
	Hypolytreae	<i>Hypolytrum</i>	61	1	1
Cyperoideae	Abildgaardieae	<i>Actinoschoenus</i>	8	1	0
		<i>Bulbostylis</i>	227	23	15
		<i>Fimbristylis</i>	322	17	2
	Bisboeckelereae	<i>Diplacrum</i>	10	1	0
	Cariceae	<i>Carex</i>	1996	30	26
	Cladieae	<i>Cladium</i>	3	1	0
	Carpheae	<i>Carpha</i>	15	1	1
	Cypereae	<i>Cyperus</i>	955	143	43
		<i>Ficinia</i>	80	1	1
		<i>Isolepis</i>	75	4	1
	Eleocharideae	<i>Eleocharis</i>	295	12	0
	Fuireneae	<i>Bolboschoenus</i>	15	1	0
		<i>Fuirena</i>	55	7	2
		<i>Schoenoplectiella</i>	53	12	5
		<i>Schoenoplectus</i>	26	2	0
	Rhynchosporeae	<i>Rhynchospora</i>	361	10	1
	Schoeneae	<i>Costularia</i>	15	11	11
		<i>Machaerina</i>	53	4	1
		<i>Trichoschoenus</i>	1	1	1
	Sclerieae	<i>Scleria</i>	258	25	8
Trilepideae	<i>Coleochloa</i>	8	1	0	

Sources: Classification based on Semmouri et al. (2019). Species numbers and distribution follow Govaerts et al. (2020d).

The largest tribes are Cypereae (48% of the sedge flora), Abildgaardieae (13%), and Cariceae (10%). Six tribes (Bisboeckelereae, Chrysitricheae, Carpheae, Cladieae, Hypolytreae, and Trilepideae) have only a single species on Madagascar. *Cyperus* is the most species-rich genus, encompassing about 46% of the flora, which makes sense given the Afrotropical center of diversity of this genus (Larridon et al. 2014a; Govaerts et al. 2020d). The second-richest genus is the mainly boreo-temperate *Carex* (10%). The genus with the highest proportion of endemic species is *Costularia* with 73% of the genus's global diversity endemic to the island. Ten genera have a single species (43% of all genera and representing ~3% of all species), one of which (*Trichoschoenus*) is a monotypic endemic genus only known from its type collection, made by Henri Humbert in 1955. Two species (*Bolboschoenus glaucus* and *Cladium mariscus*) that occur on Madagascar, but with cosmopolitan distribution, are wetland plants.

## RECENT DEVELOPMENTS IN SYSTEMATICS

Since the review by Muasya et al. (2011) of the diversity and ecology of Malagasy Cyperaceae, which largely followed the classification of Goetghebeur (1998), the circumscriptions of several genera native to Madagascar have been altered. In the tribe Abildgaardieae, the circumscriptions of *Bulbostylis* and *Fimbristylis* have changed, although these changes do not concern species native to Madagascar. Recently, the small mainland African genus *Nemum* was synonymized with *Bulbostylis* (Roalson et al. 2019a; Larridon et al. 2019b). Also, the Australian monotypic genus *Crosslandia* was assimilated into *Fimbristylis* (Roalson et al. 2019b). More relevant to the knowledge of the systematics of Malagasy Cyperaceae are the taxonomic changes that occurred in the tribes Cariceae, Eleocharideae, and Cypereae.

Recently, the Global Carex Group (2015) recircumscribed the megadiverse genus *Carex* (~2000 species) as a monophyletic group. To do so, they synonymized the genera *Cymophyllus* (monotypic), *Kobresia* (~60 species), *Schoenoxiphium* (~15 species), and *Uncinia* (~70 species) with *Carex*. Two *Carex* species from Madagascar belong to the *Schoenoxiphium* group: *C. chermesonii*, previously known as *S. gracile*, and *C. multispiculata*, previously known as *S. madagascariense*. Most of the other *Carex* species on Madagascar belong to a single clade (the Asian-African-American clade of *Carex* section *Indicae*) (Martin-Bravo et al. 2019). An almost complete revision of the genus (excluding the species formerly placed in *Schoenoxiphium*) was recently carried out for the African-Malagasy region, including an exhaustive account of the Malagasy species and their subgeneric and section placement (Gehrke 2011). In the tribe Eleocharideae, the monotypic genus *Websteria* (with the aquatic species *W. confervoides*) was assimilated into the large and widely distributed wetland genus *Eleocharis* (Hinchcliff et al. 2010).

The biggest taxonomic changes have occurred in the tribe Cyperaceae. After the now monotypic tribe Cariceae, the second most species-rich tribe in Cyperaceae is Cyperaceae with well over 1000 species (Govaerts et al. 2020d). Before the molecular era, the tribe Cyperaceae was circumscribed based on embryo morphology; all species included in this tribe have either a *Cyperus*-type embryo or similar *Ficinia*-type embryo (Goetghebeur 1998; Semmouri et al. 2019). Studies have shown that embryos provide some of the best morphological characters to delimit Cyperaceae groups in accordance with molecular phylogenetic results (Semmouri et al. 2019). Two clades are distinguished in tribe Cyperaceae, the *Ficinia* clade and the *Cyperus* clade. *Ficinia* clade species are predominantly characterized by having spikelets with spirally arranged glumes. In Madagascar, this clade includes the genera *Ficinia* and *Isolepis*. In contrast, species of the *Cyperus* clade usually have spikelets with distichous or two-ranked glumes. Besides *Cyperus sensu stricto*, a

range of segregate genera as circumscribed by the classification of Goetghebeur (1998) are included in the *Cyperus* clade. Nine of these genera (*Alinula*, *Ascolepis*, *Courtoisina*, *Kyllinga*, *Lipocarpha*, *Oxycaryum*, *Pycurus*, *Queenslandiella*, and *Remirea*) occur on Madagascar (Muasya et al. 2011), and most were originally described based on their derived spikelet morphologies (e.g., Larridon et al. 2013). Molecular phylogenetic studies revealed that these segregate genera of the *Cyperus* clade are all nested in *Cyperus sensu stricto* and that several of them do not form natural groups (Larridon et al. 2011a, 2013; Bauters et al. 2014). As a result, their species were recently transferred to *Cyperus* (Larridon et al. 2011b, 2014b; Bauters et al. 2014; Govaerts et al. 2020d). To summarize, while Muasya et al. (2011) recognized 33 genera on Madagascar, following the taxonomy presented herein, just 22 genera occur on the island; and the genus *Cyperus* went from encompassing 31% of the sedge flora to 46%.

ENDEMISM

In total, 5.5% of Cyperaceae species worldwide are native to Madagascar (or ~6% of the species richness of the native genera). Of the 310 species of Cyperaceae native to the island, 119 (38%) are endemic (Figure 8.26, Table 8.20). Although Madagascar has the second-highest level of endemism for Cyperaceae after the Cape Provinces (Muasya et al. 2011), compared with similar sized plant families such as Melastomataceae, its level of endemism is much lower (321 species, 99% endemic; Almeda 2003). Among large plant families, the level of endemism of the sedge family is only comparable to that in grasses, where ~40% of species are endemic to Madagascar (Vorontsova et al. 2016).

Nineteen lineages of endemic species were retrieved in a recent molecular phylogenetic reconstruction that included ~50% of

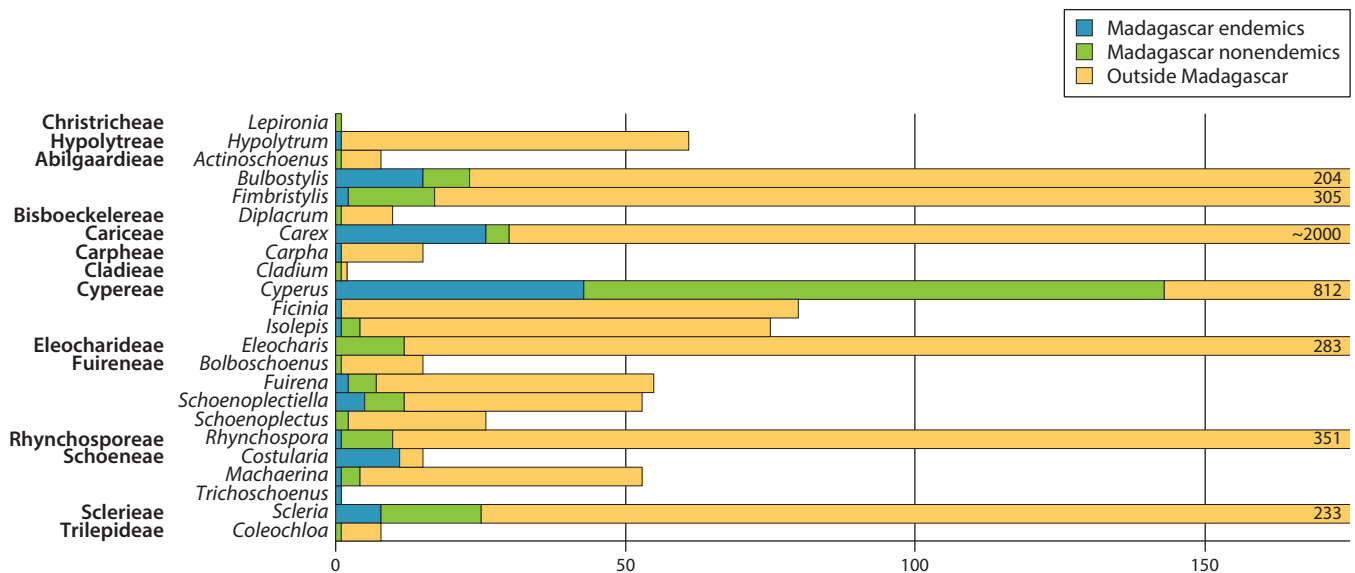


FIGURE 8.26 Diversity and endemism diagram of Malagasy Cyperaceae at the level of genera, showing three different species counts: 1) endemic to Madagascar, 2) nonendemic but native to Madagascar, and 3) those occurring elsewhere in the world (for further information see text). In cases when species diversity exceeds or does not conform to that presented on the horizontal graph scale, the figures are written along the respective horizontal line of a given genus.

## PLANTS

Cyperaceae species native to Madagascar (Larridon et al. 2019c). The taxonomic groups of Cyperaceae present on the island are more or less evenly distributed through the Cyperaceae phylogeny, with the exception of the Scirpo-Caricoid clade. This clade, dominated by the megadiverse, mostly temperate genus *Carex*, has limited presence on Madagascar in contrast to its high species diversity in temperate regions, especially in the Northern Hemisphere. The endemic lineages appear to have arrived on Madagascar in the last ~20 million years (Larridon et al. 2019c), and these are often species poor. Only a few lineages appear to have radiated within Madagascar.

Cyperaceae fruits are called nutlets and are often dispersed within persistent organs such as a hardened stylebase, a perianth, one to several glumes, or even the complete spikelet (Goetghebeur 1998). Although little data is available on dispersal of Cyperaceae, nutlets can be dispersed by water (sea or freshwater), wind, animals—particular ants and birds—and humans (Goetghebeur 1998).

Although further research is necessary, the presence or absence of Cyperaceae lineages on Madagascar may reflect their long-distance dispersal capability.

The largest endemic radiation is represented by the Asian-African-American clade of *Carex* section *Indicae* (Martín-Bravo et al. 2019) with 23 out of 26 endemic *Carex* species belonging to this clade (Figure 8.27a). With about 90 species and a circumtropical distribution (Martín-Bravo et al. 2019), this section has apparently colonized the island at least once. Since *Carex* is mostly a cold-adapted genus, its presence in the tropics is limited to higher elevations. Species of section *Indicae* are the only group of *Carex* species that is almost entirely confined to tropical montane forests. The orography of eastern Madagascar seems to have enabled the establishment and diversification of this group in suitable habitats.

The genus *Costularia*, which was recently recircumscribed (Larridon et al. 2018), includes 15 species (Larridon et al. 2019a), 11 of



**FIGURE 8.27 Diversity of Malagasy endemic Cyperaceae species.** A) *Carex haematosaccus*, B) *Costularia purpurea*, C) *Cyperus chamaecephalus*, and D) *C. sciaphilus*. All photographed in Mantadia National Park (PHOTOS A–C by I. Larridon, and D by M. Vorontsova.)

which are endemic to Madagascar. Most species of this genus grow in high-elevation ericoid vegetation (Figure 8.27b). *Cyperus* section *Incurvi* is a group of 32 *Cyperus* species distributed across Africa, Latin America, and Australasia (Larridon et al. 2011a). Nine species in this group are endemic to Madagascar; these are found mainly in the understory of moist evergreen forests and show clear adaptations to this habitat (e.g., broad and/or purplish leaves) (Figures 8.27c and d) (Gautier et al. 2010).

*Scleria* section *Abortivae* includes five species that are endemic to Madagascar and the western Indian Ocean islands (Galán Díaz et al. 2019). Two other genera include a significant number of endemic species: *Bulbostylis* and *Schoenoplectiella*. However, we lack sufficient sequence data and recent taxonomic treatments for these genera. Further study is required to assess whether these endemic species represent one or multiple arrivals to Madagascar.

## CONSERVATION

The conservation status of 136 out of 310 species (~44%) have been assessed using the IUCN (International Union for the Conservation of Nature) Red List guidelines (IUCN 2019). Out of these 136 assessed species, five have been classified as Critically Endangered, 14 are Endangered, eight are Vulnerable, one Near Threatened, and two Data Deficient. The others, which are largely widely distributed species, were classified as of Least Concern. This means that ~20% of Cyperaceae species native to Madagascar are threatened, which is in line with the estimation that one in five plant species globally is threatened with extinction (RBG Kew 2016). When we look at the endemic Cyperaceae species, just 33 of the 119 species were assessed (~28%), with 75% of these species given a threatened category. This low percentage of species

that have been assessed and high level of threat among those that have been highlights the need for more conservation studies to understand the future of the endemic Malagasy sedge flora.

## WORK IN PROGRESS

Efforts are underway to study the Cyperaceae of Madagascar. This has already resulted in taxonomic revisions of the genera *Costularia* (Larridon et al. 2019a) and *Scleria* (Galán Díaz et al. 2019). Further research is ongoing to study the endemic species *Cyperus* section *Incurvi* (I. Larridon et al., unpublished data), and work is underway to generate a checklist of Cyperaceae for the Itremo Massif protected area (F. Rasaminirina et al., unpublished data). Furthermore, we aim to estimate the number, age, and origins of endemic sedge lineages in the Malagasy Region, and to compare the diversification of C<sub>3</sub> and C<sub>4</sub> taxa (see Lehmann et al., pp. 152–68, for further details). This may contribute to the growing literature on whether or not certain grassland ecosystems in Madagascar are natural or derive from human activities (Vorontsova et al. 2016). Revisionary work on *Carex* is also in preparation, and the vast majority of species will be reassigned to sections or informal groups. Other avenues for future research may include investigating key traits that have allowed some lineages to diversify successfully on Madagascar and the local and traditional uses of sedge species. In their revision of *Economic, Ethnobotanical and Horticultural Importance of Cyperaceae*, Simpson and Inglis (2001) only list uses for five species specifically on Madagascar. However, undoubtedly many more species are used, for example, as packing, matting, and basketwork material.

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## POACEAE, GRASSES (INCLUDING BAMBOOS)

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The Poaceae (grasses), including bamboos, is one of the largest plant families both worldwide and on Madagascar, providing the majority of human food and driving ecosystem dynamics where they are abundant. They are found in all of the island's terrestrial habitats except the darkest moist evergreen forest understory. Most prominently, they dominate the vast open areas. Here we use the word “grassland” to denote both natural and secondary grass-dominated ecosystems, with or without trees. This contribution attempts to give an overview of Malagasy grass diversity as currently understood.

A full Poaceae species checklist of 541 species including 217 endemics (40% endemism) was published by Vorontsova et al. (2016), building on Bosser (1969), who documented around half of the

known species, as well as unpublished manuscripts by Emmet J. Judziewicz and Bryan K. Simon. As of March 2019, there were 14,670 Poaceae occurrence records from Madagascar available via the Global Biodiversity Information Facility or GBIF (Rabarivola et al. 2019a, 2019b, 2019c), including all herbaria holdings of the Muséum National d'Histoire Naturelle in Paris and Parc Botanique et Zoologique de Tsimbazaza in Antananarivo, the two herbaria together holding about 75% of these collections. The GBIF records include the 488 wild species listed in Table 8.21. Occurrence maps of every species are available in the *Madagascar Grass Atlas* (Rabarivola et al. 2019d). An identification guide (Vorontsova et al. 2018) presents a description and a color scan for each of the 144 genera in 10 subfamilies.