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RESEARCH PAPER

The evolutionary history of sedges (Cyperaceae) in Madagascar

History of sedges in Madagascar

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Abstract

Aim: Madagascar is renowned for its unparalleled biodiversity and endemism. With many ecosystems under threat, research is urgently needed on its unique plant diversity. This applies both to Madagascar's forests and treeless vegetation types. Sedges (Cyperaceae) are among the top ten species-richest angiosperm families in Madagascar (310 native species, 38% endemic), of which two thirds occur in open habitats. We aimed to infer the evolutionary history of sedges in Madagascar, by estimating the number, age and origins of endemic lineages, and how they diversified on the island. We tested contrasting hypotheses of (i) few colonisations but important *in situ* radiations against (ii) a high number of anagenetic colonisations.

Location: Madagascar and the surrounding Indian Ocean islands, integrated within a global dataset.

Taxon: Sedge family Cyperaceae.

Methods: We estimated time-calibrated molecular phylogenies encompassing a large proportion of Madagascar's known sedge flora (incl. 55% of native species), integrating sequence data for 1382 accessions representing almost 25% of the c. 5600 sedge species worldwide, combined with ancestral area reconstruction, diversification analyses and Bayesian stochastic mapping.

Results: Cyperaceae lineages arrived in Madagascar from c. 40 mya with many arriving more recently. About 20 endemic lineages of Cyperaceae occur on the island, of which only six encompass more than five species. All except one of the endemic lineages that diversified in Madagascar use the C_3 photosynthetic pathway. The main biogeographical links of Madagascar's sedge flora are to Southern and Tropical Africa.

Main conclusions: The biogeographical history of Cyperaceae in Madagascar is a chronicle of relatively recent multiple in and out processes of long-distance dispersal colonisations constrained by distance. Also, the Madagascar region is not only a "sink" for immigrant taxa, *in situ* diversification and dispersal to other regions also occurred. Some of the most diverse endemic lineages show clear adaptation to local environments.

INTRODUCTION

As a biodiversity hotspot (Myers, Mittermeier, Mittermeier, da Fonseca & Kent, 2000), Madagascar is renowned for its biodiversity (Ganzhorn, Lowry, Schatz & Sommer, 2001), endemism (Goyder et al., 2017), and role as model system for species diversification (Vences, Wollenberg, Vieites & Lees, 2009). From lemurs and vangas to mayflies and dung beetles, and from tree ferns and olives to orchids and grasses, the exceptional faunistic and floristic diversity and endemism in Madagascar has made the region a natural laboratory for understanding geographical and ecological drivers of diversity (Martin, 1972; Renner, 2004; Janssen et al., 2008; Wirta et al., 2008; Jønsson et al., 2012; Reddy et al., 2012; Strijk et al., 2012; Andriananjamanatsoa et al., 2013; Hong-Wa & Besnard, 2013; Ganzhorn et al., 2014; Herrera, 2017). Dispersal to Madagascar, followed by phenotypic shifts allowing novel ecological invasions (i.e., adaptive radiations) have been invoked in some instances to explain the unique biodiversity of the region. In other cases, Madagascar is described as both a biogeographical sink and source of dispersal, suggesting its importance in the evolution and assembly of biodiversity in the region at large. Though the drivers of diversification vary among lineages, what is clear from the previous body of work is that the long isolation of Madagascar from other land masses (Africa >150 mya–million years ago, India c. 88 mya; Ganzhorn, Wilmé & Mercier, 2014) is fundamental to its biological uniqueness.

Given its richness and uniqueness, continued research on the origin of Madagascar's biodiversity is urgently needed. Approximately 60% of Madagascar's plant species for which the conservation status has been assessed are threatened with extinction, compared to the global average of 24% (IUCN, 2019), and an extraordinary 90% of habitats of been degraded (Myers et al., 2000; Vuataz et al., 2013). Adding the effects of global climate change paints a bleak picture for the future of Madagascar's plant diversity (Brown, Parks, Bethell, Johnson & Mulligan, 2015). Conservation efforts in Madagascar are at cross-roads, particularly pertaining the origin and diversification of biota in open versus forested habitats, with fierce contestations regarding the role of fire and herbivores as tools to maintain these alternative vegetation types especially in the central highlands (e.g. Joseph & Seymour, 2020; Solofondranohatra et al., 2020). Clarifying the evolutionary origin and diversity of Madagascar's fauna and flora is fundamentally important so that we may know what is at stake should ongoing threats be realized.

Nearly 14,000 plant species are native to Madagascar with an average endemicity of >80% (Goyder et al., 2017). When authors discuss Madagascar's exceptional plant diversity and threats to its conservation, they often focus on forests and the species they hold (Allnut et al., 2008; Federman et al., 2015). However, forested habitats make up only a minor portion of Madagascar, whereas savannah and other graminoid-dominated ecosystems account for over 65% of natural areas (Vorontsova et al., 2016). Recent research on grasses has shown that Madagascar's grassy biomes are home to many endemic species (Vorontsova et al., 2016). Some treeless vegetation types, such as the high-elevation ericoid thickets, are particularly

vulnerable to combined effects of climate and land cover change (Brown et al., 2015). Here, we focus on sedges (Cyperaceae), one of the top ten most species-rich plant families in Madagascar with 310 native species (Larridon et al., in press), two thirds of which are found in these open habitats (Muasya et al., 2011). Sedges are phenotypically diverse and are ecologically important in high latitude and elevation ecosystems (Naczi & Ford, 2008), as well as in wetlands where they may constitute the majority of plant biomass (Shaver, Laundre, Giblin & Nadelhoffer, 1996). Madagascar's Cyperaceae display substantial evolutionary diversity (Table 1; Table S1 of the online Supporting Information). The largest tribes are Cypereae, Abildgaardieae and Cariceae, while six tribes are represented by a single species. *Cyperus* is the largest genus, encompassing about 46% of the sedge flora, which agrees with its Afrotropical centre of diversity (Govaerts et al., 2020). Surprisingly, the second richest genus is the mainly Boreo-temperate *Carex* (10%), for which Madagascar is the most species-rich region in sub-Saharan Africa (Gehrke, 2011). The genus with the highest percentage of endemic species is *Costularia* (73%). Ten genera have a single species, including *Trichoschoenus*, a monotypic endemic. The co-occurrence of these distantly related clades suggests that multiple independent dispersal events onto the island were involved in the evolution and assembly of Madagascar's sedge flora.

Muasya et al. (2011) noted that 35% of endemic sedge species (e.g. C_3 species of *Carex, Costularia* and *Cyperus*) occur in forest habitats rather than in open (and mostly drier) habitats. In Madagascar, the level of endemism of C_4 grasses and sedges is similar (28% and 29%), as is the species richness of C_3 lineages in grasses and sedges (175 and 161 species, respectively), however, the diversity of C_4 sedges is much lower (358 C_4 grasses vs. 149 C_4 sedges) (Vorontsova et al., 2016; Table S1). Muasya et al. (2011) had already remarked that Madagascar's grasslands, compared to Africa, lack a comparable species diversification of characteristic C_4 sedge lineages. Since the C_4 grasslands of Madagascar have been dated to the global Miocene grassland expansion (e.g. Bond, Silander, Ranaivonasy & Ratsirarson, 2008; Willis, Gillson & Virah-Sawmy, 2008; Hackel et al., 2018), this is unlikely due to a recent origin of Madagascar's grasslands. Alternatively, higher endemism in C_3 sedges may be caused by increased diversification rates compared with C_4 sedges, or by higher niche conservatism in C_3 compared to C_4 lineages (Wiens & Graham, 2005). Muasya et al. (2011) noted that several lineages appear to have dispersed to habitats similar to ancestral areas, e.g. in Madagascar *Isolepis* and *Ficinia* occur in high-elevation ericoid habitats similar to those found in the Western Cape of South Africa.

In the context of island biogeography, key questions under active research include understanding processes governing species assembly (Liu et al., 2020). Dispersal assemblage implies that multiple independent anagenetic dispersal events without subsequent diversification until all available niches of the island are filled out. *In situ* radiation means that available niches have been filled out from a single colonisation event with subsequent diversification. *In situ* radiation has been considered more plausible when islands are highly

isolated (Valente et al., 2020) or when probability of colonisation is habitat-dependent (some habitats are colonised first, and from there remaining habitats are later colonised; Sukumaran & Knowles, 2018). These two processes are compatible and can act in very closely related lineages. For example, in grasses, C_3 species assemblage in Madagascar was mostly explained by two *in situ* radiations, whereas C_4 species assemblage was related to dispersal assemblage (Hackel et al., 2018).

This study aims to uncover the evolutionary history of sedges in Madagascar by estimating the number and ages of endemic sedge lineages in Madagascar, and by reconstructing ancestral areas. We aim to test the hypotheses of (i) *in situ* radiation against (ii) dispersal assembly bearing in mind the possibility that both processes may be acting in sedges but with similar or dissimilar importance. We also explore and compare biogeographic patterns in Madagascar for species with C_3 and C_4 photosynthetic pathways.

MATERIALS AND METHODS
Taxon sampling
Our total taxon sampling encompasses 1382 accessions, including four species of *Juncus* (Juncaceae) as outgroup (Table S2). We aimed to sample (1) nearly all Cyperaceae genera, (2) species from the global distribution range of each genus, and (3) as many species as possible native to Madagascar and/or the Madagascar region (Madagascar plus islands from the Western Indian Ocean, i.e. Comoros, Mascarenes and Seychelles). The ingroup sampling includes 185 species (represented by 190 accessions) native to the Madagascar region. Of these, 171 species are native to Madagascar (176 accessions), 42 species (43 accessions) are endemic to Madagascar, and a further 14 species are endemic to the Western Indian Ocean Islands but not native to Madagascar. Our sampling includes 55% of sedge species native to Madagascar.

DNA sequence data, phylogenetic analyses and divergence time estimation
A large dataset of two nuclear ribosomal (ETS, ITS) and seven chloroplast markers (*matK, ndhF, rbcL, rpl32-trnL, rps16, trnH-psbA, trnL-F*) was used to estimate a time-calibrated phylogeny. The dataset included (ETS: 848 accessions, ITS: 1008, *matK*: 1586, *ndhF*: 404, *rbcL*: 737, *rpl32-trnL*: 171, rps16: 405, *trnH-psbA*: 156, *trnL-F*: 181). Gene regions were each aligned independently using Muscle v3.8.31 (Edgar, 2004) and then manually assessed to ensure alignment accuracy. The resulting concatenated supermatrix was analysed using maximum likelihood under the GTRCAT model in RAxML v.8.2.12 (Stamatakis, 2014) as implemented on the CIPRES Scientific Gateway (Miller, Pfeiffer & Schwartz, 2010), following similar Cyperaceae-wide analyses (Spalink et al., 2018; Márquez-Corro, Martín-Bravo, Spalink, Luceño & Escudero, 2019).

Dating analyses were carried out using penalized likelihood method as implemented in treePL (Smith & O'Meara, 2012). Multiple calibrations (especially fossil calibrations) are

necessary for an accurate molecular dating estimation (Sauquet, 2013 and references therein). Accordingly, we used eleven calibrations (five secondary calibrations and six fossil calibrations) placed on key nodes throughout the phylogeny a maximum and minimum age were established for each of them (Table S3). The six fossil calibrations were obtained from two recent reviews of fossils focused on Cyperaceae (Smith, Collinson, Rudall & Simpson, 2010) and *Carex* (Jiménez-Mejías et al., 2016), and the five secondary calibrations from two recently published molecular dating studies (Spalink et al., 2016, 2018). We performed cross-validating analyses to evaluate alternative values of smoothing parameters.

Biogeographical analyses
Distribution data was obtained from Govaerts et al. (2020) and recent literature (Larridon et al., 2019; Galán Díaz et al., 2019). Biogeographical analyses were carried out in the R (R Core Team, 2019) package BioGeoBEARS (Matzke, 2013). Coding of the biogeographical regions follows Hackel et al. (2018), see Table S4 (eight areas: the Madagascar region, Southern Africa, Tropical Africa, Eurasia & North Africa, India, Southeast Asia & Australasia, North America, and the Neotropics), and is provided for each accession in Tables S2 and S5. We performed analyses with unconstrained connectivity among the eight areas and also constraining connectivity among areas proportionally to geographic distance following Hackel et al. (2018) adding an additional free parameter (x). BioGeoBEARS implements two main models: DIVA-like (Dispersal–Vicariance Analysis, Ronquist, 1997) and DEC (Dispersal–Extinction–Cladogenesis, Ree, Moore, Webb, & Donoghue, 2005; Ree & Smith, 2008) which have two free anagenetic parameters, dispersal (d) and extinction (e), and different settings of dependent cladogenetic parameters (y = narrow and widespread within-area speciation, s = subset within-area speciation, and v = narrow and widespread vicariance). DEC only allows narrow vicariance: allopatric speciation caused by split of a single geographical range. DIVA-like allows narrow and widespread vicariance. However, DIVA does not include subset within-area speciation (Ronquist & Sanmartín, 2011). Note that we have avoided using the term "sympatric speciation" in favour of "within-area speciation" because speciation within our very widely defined areas does not entail sympatric speciation. DEC and DIVA-like were also combined with the extra free parameter founder (j), which allows for cladogenetic dispersal. Eight models were compared: DEC, DEC+j, DEC+x, DEC+j+x, DIVA-like, DIVA-like+j, DIVA-like+j+x). We compared unconstrained vs. constrained models (with parameter x) and DEC vs. DIVA-like models using AICc. The estimated likelihood (and AICc) of models without cladogenetic dispersal were not compared with estimated likelihood and AIC of models including cladogenetic dispersal (with parameter j), as their likelihoods are not directly comparable based on the way that the cladogenetic dispersal (j) vs. anagenetic dispersal (d) and anagenetic extinction (e) parameters enter into the model (Ree & Sanmartín, 2018). In addition, results from the models considering the parameter j will be interpreted cautiously as they have a greater

tendency toward explaining the data entirely by cladogenetic events and inferring, very frequently, anagenetic parameters equal to 0 (Ree & Sanmartín, 2018).

We performed biogeographical stochastic mapping (BSM) analyses as implemented in Matzke (2014) and Dupin et al. (2017) to estimate the time, number and type of biogeographical events. We conducted BSM using the best-fitting models (DEC+x and DEC+x+j; see results). Event frequencies were estimated by taking the mean and standard deviations of event counts from 50 BSMs.

Diversification pattern analyses

Bayesian Analysis of Macroevolutionary Mixtures (BAMM) v.2.5 (Rabosky, 2014) and the R package BAMMtools (Rabosky et al., 2014) were used to detect and quantify heterogeneity in diversification rates. This approach allows speciation and extinction rates to change over time and among lineages. We ran BAMM for ten million generations. We used the R package coda (Plummer, Best, Cowles & Vines, 2006) to check MCMC convergence. BAMMtools was used to process the results and summarize the parameters of the models with the highest posterior probabilities.

The models implemented in BAMM assess multiple possible diversification rate shift scenarios but assume there are no diversification rate shifts on lineages that go extinct. This assumption causes error in parameter estimates in trees simulated to have rate shifts on extinct lineages, but not for trees simulated to have constant rates (Moore, Höhna, May, Rannala & Huelsenbeck, 2016). The effect of this assumption, common to all diversification rate shift analyses available currently, is suggested to be small in empirical trees (Rabosky, Mitchell, & Chang, 2017). Another concern is that the posterior distribution on the number of rate shifts inferred by BAMM may be overly sensitive to the prior probability on the number of diversification rate shifts. This concern has been addressed in the most recent versions of BAMM (v.2.5) which was used in our analyses (Mitchell & Rabosky, 2017).

Bayesian stochastic mapping analysis of C_3 and C_4 photosynthetic pathway

We fitted ER (equal rates) model and ARD (all-rates-different) model using the R function ace implemented in ape (Paradis & Schliep, 2018) for the binary character C_3 or C_4 photosynthesis. We performed 100 Bayesian stochastic maps based on the best model (ER, see results) using the function simmap.tree implemented in phytools (Revell, 2012).

RESULTS

The obtained dated phylogenetic hypothesis is available in Figure S1. The topology corresponds with previous analyses such as Semmouri et al. (2019) and Márquez-Corro et al. (2019). In the summary tree (Figure 1), we recognise the two subfamilies, Mapanioideae and Cyperoideae. Nearly half of subfamily Cyperoideae corresponds to the Scirpo-Caricoid Clade which encompasses among others the monotypic tribe Cariceae with the megadiverse genus

Carex (c. 2000 species). Nineteen lineages endemic to Madagascar were retrieved (Figure 1), and many more lineages are native to the Madagascar region.

We selected DEC+x and DEC+x+j as the best models for the biogeographical analyses, since the fit (smaller AICc) was significantly better for constrained and DEC models (Table 2). The highest number of dispersal events to Madagascar are from Tropical Africa followed by Southern Africa, while the highest number of dispersal events originating from Madagascar are to Southern Africa (DEC+x; Figure 2, Figure S2, Table 3; DEC+x+j results are provided in the Supporting Information: Figure S3, Table S6).

Resulting from the BSM analyses, the absolute number of biogeographic events has increased in the last 20 million years because of the increase of branches towards the present. At the root of the phylogeny, the four kinds of events are equally frequent (Figure 3a). Anagenetic dispersal is the most frequent biogeographic event 80–60 mya. From 60–1 mya, the most frequent event is within-area speciation followed by anagenetic dispersal. From 1 mya to the present, the frequency of anagenetic dispersal is by far the most frequent (near 95%). Most dispersals to Madagascar are relatively recent (Figure 3b). Between the root of the phylogeny and 60 mya, we can see dispersal to all eight areas except Madagascar. Dispersal destinations to North America, Tropical Africa, Southern Africa, Southeast Asia, Australasia and the Neotropics show peaks of high frequency during this period. From 60–40 mya, all dispersal destinations are approximately equally frequent except Madagascar which is absent until nearly 40 mya. From c. 40 mya to present, all dispersal destinations are approximately equally frequent including Madagascar with exceptional peaks of high frequency for Tropical Africa, the Neotropics and Southeast Asia and Australasia around 37 mya. Madagascar as a dispersal destination is especially frequent around 10 mya.

As recommended when there are many possible scenarios with low PP, we show the maximum shift credibility scenario instead of the scenario with the highest PP. Under this maximum shift credibility scenario, increases in diversification rates are picked up by BAMM analysis in 13 Cyperaceae clades (Table 4, Figure 4, Figures S4–S6), specifically 12 increments and only one decrement in diversification rates: (1) *Scleria* section *Hypoporum*, with an additional increase in its crown clade (2); (3) the crown clade of the genus *Scleria* which consists of seven sections of subgenus *Scleria* (i.e. sections *Foveolidia, Naumannianae, Elatae, Abortivae, Schizolepis, Scleria* and *Ophryoscleria*); (4) the Oreobolus Clade of tribe Schoeneae; (5) a subclade within the crown clade of the genus *Rhynchospora*; (6) a subclade within the crown clade of the genus *Eleocharis*; (7) the Schoenoplectus Clade; (8) the Isolepis+Ficinia Clade; (9) the C_4 Cyperus Clade, with an additional increase in its crown clade (10); (11) the Non-Siderosticta Carex Clade, (12) the crown node of *Carex* subgenera *Psyllophorae+Euthyceras*, which is the only decrement in diversification rates; and (13) *Carex* section *Ovales*. There is a lot of uncertainty in the inferred best scenarios (Figure S5, Table S7). We obtained 3262 distinct shift configurations in the 95% credible set of rate shift configurations sampled with BAMM. The best scenarios

obtained very low posterior probability (PP = c. 0.003–0.001) but they show very similar diversification scenarios with small changes in the number of shifts and in the specific location of some of the less supported shifts.

The BSM analyses reconstructed a very clear history of the evolution of C_4 photosynthetis (Figure S7). All maps are congruent with seven transitions from C_3 to C_4: (1) *Rhynchospora rubra-globosa* clade, (2) *Bulbostylis*, (3) *Fimbristylis*, (4) *Eleocharis retroflexa*, (5) *Eleocharis baldwinii*, (6) *Eleocharis caespitosissima*, and (7) C_4 Cyperus Clade. Note: the exact number of origins of C_4 photosynthesis in *Eleocharis* requires further study because earlier studies reported a complex origin of C_4 photosynthesis in this genus, involving C_4 gene transfers between two lineages (Besnard et al., 2009). No transition from C_4 to C_3 was inferred. Figure S7 shows the shifts between C_3 (red) and C_4 (blue) photosynthesis.

DISCUSSION

Sedge lineages in Madagascar

Of the 310 species of Cyperaceae native to the island, 119 (38%) are endemic (Table 1). This is comparable to grasses, where c. 40% of species are endemic to Madagascar (Vorontsova et al., 2016), but significantly lower than the average of over 80% endemism (Goyder et al., 2017). There are about 20 endemic lineages of Cyperaceae in Madagascar (Figure 1), which is much fewer than grasses with nearly 70 (Hackel et al., 2018). However, many more widely distributed species have reached Madagascar. Cyperaceae lineages present in Madagascar are more or less evenly distributed through the phylogeny, except the Scirpo-Caricoid Clade (Figure 1). This clade, dominated by the megadiverse genus *Carex*, colonised Madagascar very few times in contrast to its high species diversity in temperate regions, especially in the Northern Hemisphere. Cyperaceae lineages appear to have arrived in Madagascar in the last c. 40 my with many lineages arriving more recently (Figures 1–4).

The endemic lineages are often species poor, with only six encompassing more than five species (Figure 1). The largest endemic radiation is represented by species of the Asian-African-American Clade of *Carex* section *Indicae* with 23 out of 26 endemic *Carex* species belonging to this clade. With about 90 species and a circumtropical distribution (Martín-Bravo et al. 2019), this section has colonised the island at least once. Since *Carex* is mostly cold-adapted, its presence in the tropics is limited to higher elevations. Species of section *Indicae* are the only *Carex* group which 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.

Costularia includes 15 species, 11 of which are endemic to Madagascar (Larridon et al., 2018, 2019). Most species grow in high elevation ericoid vegetation. *Cyperus* section *Incurvi* includes 32 species distributed across Africa and Madagascar, the Neotropics, and Australasia (Larridon et al. 2011). Nine species are endemic to Madagascar, mostly restricted

to the tropical montane forests. *Scleria* section *Abortivae* includes five species 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 represent single or multiple arrivals to Madagascar.

Some of the most diverse endemic lineages show clear adaptation to local environments, e.g., *Costularia* radiated in nutrient poor high elevation ericoid vegetation, *Carex* section *Indicae* is confined to tropical montane forests, and *Cyperus* section *Incurvi* adapted to understories of moist evergreen forests. Forest habitats appear to be a hotbed for Cyperaceae radiation in Madagascar similarly to other species-rich plant lineages such as the scaly tree ferns (Janssens et al., 2008). The contemporary biomes are thought to be recent, establishing since the early Eocene after Madagascar shifted north to its current position, with the landmass remaining tectonically and climatically stable during most of Cenozoic (Yoder & Nowak, 2006). Radiations among endemics in this and previous studies (e.g. Janssens et al., 2008; Renner, 2004) indicate a Miocene minimum age of forest lineages. The prevalence of forest radiations among the sedges and grasses, despite the Poales having an ancestral open habitat origin (Bouchenak-Khelladi, Muasya & Linder, 2014), further supports the emerging view that a large proportion of Madagascar's endemic biota have forest origin (Joseph & Seymour, 2020).

Only *Bulbostylis*, *Fimbristylis* and *Cyperus* include a significant number of native and/or endemic species that use the C_4 photosynthetic pathway (Table S1). The other genera with species using the C_4 photosynthetic pathway only have C_3 species in Madagascar (*Eleocharis* and *Rhynchospora*). Most of their C_4 species are found in the Neotropics. Of the six endemic radiations mentioned above, all are found in C_3 groups, except one, i.e. *Bulbostylis*.

Biogeographical history of sedges in Madagascar: repeated in and out long-distance dispersal and colonisation

Colonisation after long-distance dispersal (LDD) has been suggested as a common process to explain the disjunct distribution of many Cyperaceae species and lineages (Viljoen et al., 2013; Spalink et al., 2016; Villaverde et al., 2017; Martín-Bravo et al., 2019; Larridon, Galán Díaz, Bauters & Escudero, 2020). Cyperaceae originated in South America in the late Cretaceous, and subsequently dispersed to reach their current cosmopolitan distribution (Spalink et al., 2016; current results). The existence of sedge lineages of Gondwanan origin has already been dismissed, since the diversification of the main lineages postdates the split of the southern supercontinent 150–180 mya (Spalink et al., 2016). Some lineages originated in the Southern Hemisphere, e.g. tribe Schoeneae originated in Australia during the Paleocene subsequently colonising the rest of the Southern Hemisphere through repeated

LDD (Viljoen et al., 2013). Contrarely *Carex* originated in the Northern Hemisphere (Eastern Palaearctic) in the late Eocene and repeatedly colonised the Southern Hemisphere as well as a number of continental and volcanic islands (Martín-Bravo et al., 2019). In *Scleria,* the rate of dispersal is so high that it is not possible to infer the ancestral range distribution with confidence (Larridon et al., 2020). The current study agrees with previous studies that Cyperaceae have colonised Madagascar repeatedly through LDD from the late Eocene (the timing of the biogeographic events are after the split of Madagascar from Africa) and from all continental land masses (Table 3). Tropical and Southern Africa are the most important contributors (c. 84 out of a total of 154 colonisation events). These findings are consistent with broad studies (e.g. Yoder & Nowak, 2006; Tolley, Townsend & Vences, 2013   ) on the majority of Cenozoic dispersals among plant and animal groups originating from Africa. Three times more dispersal events originate from Tropical Africa than Southern Africa, despite the latter being geographically closer, perhaps indicative of a latitudinal gradient among source vegetation with older lineages near to the equator as observed in savannah lineages (Maurin et al., 2014). We find fewer lineages originating from the Indian subcontinent, in contrast to patterns reported by Warren, Strasberg, Bruggemann, Prys-Jones & Thébaud (2010) who hypothesised the role of the monsoons and existence of oceanic islands acting as stepping-stones in facilitating waif dispersal. Migration from the Americas needs to be taken with caution as it may be due to an effect of sampling gaps of taxa filling intermediate distributions.

The current study also inferred many dispersal events from Madagascar to other continental landmasses (Table 3). Southern and Tropical Africa are also the most important destinations (c. 42 out of 98 dispersal events). Nevertheless, the number of dispersal events is significantly smaller from Madagascar (c. 98 events) than to Madagascar (c. 154 events). Despite the high rate of dispersal among areas, this seems to be constrained by distance (the best models, DEC+x and DEC+x+j, include the parameter x which is a negative distance-scaling parameter). Similar patterns have been found in grasses, (1) negative correlation between dispersal rate and distance (Linder, Antonelli, Humphreys, Pirie & Wüest, 2013; Minaya et al., 2017; Hackel et al., 2018), and (2) Tropical and Southern Africa as the best-connected areas with Madagascar (Hackel et al., 2018). The latter is congruent with previously reported taxonomic similarities among these areas (Buerki, Devey, Callmander, Phillipson & Forest, 2013). In conclusion, the biogeographical history of Cyperaceae in Madagascar is a chronicle of relatively recent multiple in and out processes of LDD colonisations constrained by distance.

What might be the mechanisms that explain LDD colonisation in sedges? Cyperaceae fruits are called nutlets and are often dispersed surrounded by other persistent organs such as a hardened style base, a perianth, one to several bracts–sometimes highly modified, as in *Carex*–, or even the complete spikelet can act as the diaspore (Goetghebeur, 1998). Cyperaceae nutlets can be dispersed by water (sea or freshwater), wind, animals in particular

ants and birds, and humans (Goetghebeur, 1998). Although further research is necessary, the presence or absence of Cyperaceae lineages in Madagascar may reflect their LDD capability. Recent studies have highlighted the importance of "non-classical endozoochory", diaspores that are dispersed through the digestive tracts of vertebrate animals, especially birds and mammals, despite lacking "external flesh" (Costea et al., 2019; Green, Elmberg & Lovas-Kiss, 2019; Lovas-Kiss et al., 2020). This kind of dispersal is performed through granivory (similar to frugivory but the plant pays a cost as a fraction of seeds are ingested instead of the cost of the fleshy-fruit; Costea et al., 2019). Typical plant families that are adapted to granivory like Cyperaceae produce a high number of small diaspores. The silica-rich walls of Cyperaceae nutlets have also been suggested to serve as grinding material in birds' gizzards (Villaverde et al., 2015), adding an additional reason for its active consumption by animals.

Pre-adaptation to Madagascar's environments seems to play an important role in the establishment of different Cyperaceae lineages. While quantitative studies would be desirable, just looking at a broad characterisation of the environments where Madagascar's sedges dwell, the different lineages do not seem to have undergone strong transitions to novel habitats. Indirect evidence of this is the complete absence from Africa and Madagascar of one the few sedge groups displaying unequivocal epizoochorous syndromes (*Carex* section *Uncinia*, former genus *Uncinia* Pers.). That cold-adapted lineage has been able to colonise distant islands from its ancestral area in South America, reaching New Zealand westwards and the subantarctic archipelagos of Tristan da Cunha and Prince Edward eastwards (Martín-Bravo et al., 2019). One may hypothesise that the lack of suitable environments in the southernmost parts of Africa could have prevented section *Uncinia* to colonise Africa and Madagascar.

Diversification patterns
Interestingly most of the shifts in diversification rates occurred from the late Eocene to the middle Oligocene, a period matching a global pattern of decreasing temperatures (Zachos, Pagani, Sloan & Thomas, 2001). In congruence, inferred shifts of diversification rates are C_3 radiations with the exception of the C_4 Cyperus Clade.

A previous comprehensive biogeographical and diversification study of Cyperaceae inferred positive shifts in diversification rates in three species-rich clades: (1) Non-Siderostictae Carex Clade, (2) Cyperus Clade and (3) C_4 Cyperus Clade (Spalink et al., 2016). Escudero et al. (2012), in a study centred on *Carex* and closely related lineages, detected a positive shift in diversification rates in the Non-Siderostictae Carex Clade. Escudero & Hipp's (2013) phylogenetic study of Cyperaceae inferred a positive shift in diversification rates in a temperate and tropical clade (FAEC+SCC Clades) that include the three clades reported by Spalink et al. (2016). In a biogeographical study of *Carex* (Martín-Bravo et al., 2019), c. 17–27 positive shifts in diversification rates were detected, but it did not infer the positive shift in diversification rates in the Non-Siderostictae Carex Clade

detected in our study. The latter shift has repeatedly been detected in other studies too (Escudero et al., 2012; Spalink et al., 2016). This shift has been associated with a shift in the mode of chromosome evolution from low rates of chromosome evolution (including polyploidy –genome duplication– and dysploidy –fission and fusion of chromosomes) to drastically increased rates of fusions and fissions (disploidy; Márquez-Corro et al., 2019). Within *Carex,* we also retrieved a negative shift at the crown node of *Carex* subgenera *Psyllophorae+Euthyceras* which was not retrieved in Martín-Bravo et al (2019). In this study, a positive shift was recovered inside subgenus *Euthyceras*, in core *Kobresia*. The third shift within *Carex* is a positive shift for *Carex* section *Ovales* that matches perfectly with previous results (Martín-Bravo et al., 2019). Partially congruent with previous results (Spalink et al., 2016), we have inferred an increased rate in the C_4 Cyperus Clade, with an additional increase in its crown clade. This has been previously associated with the shift in photosynthetic pathway from C_3 to C_4 (Spalink et al., 2016) and high rates of chromosome evolution (Márquez-Corro et al., 2019). Despite the increased diversification rate in the C_4 Cyperus Clade, Madagascar's sedge flora is species-poor in native and endemic C_4 Cyperus Clade species. While the number of C_4 species of the genus *Cyperus* (108 out c. 760) that occur in Madagascar is three times that of the C_3 ones (33 out of c. 190), the proportion of species native to the island is similar for both (14 vs. 17%, respectively). It can be noted that the endemic C_3 *Cyperus* lineages are markedly older than the endemic C_4 lineages. This means that C_3 sedge lineages had more time for diversification in Madagascar, which could explain their higher endemism compared to C_4 sedges. Also, some C_4 species of the genera *Eleocharis* and *Rhynchospora*, which are mostly found in South America, never made it to the island.

The increase in diversification rates in *Scleria* section *Hypoporum* has been detected in a study focused on this genus (Larridon et al., 2020), but the additional increase in its crown clade was not. An increase in subgenus *Scleria* has also been detected before (Larridon et al., 2020). These shifts in diversification rates were related to climate niche evolution (Larridon et al., 2020). Four further increases in diversification rates were detected: in a subclade within the crown clade of *Rhynchospora*; a subclade within the crown clade of *Eleocharis*; the Isolepis+Ficinia Clade; and the Schoenoplectus Clade. More research is needed to explain these shifts. The Oreobolus Clade of tribe Schoeneae is the only clade with an important *in situ* radiation in Madagascar associated with a positive shift in diversification rates. The Oreobolus Clade includes *Costularia* which is largely endemic to Madagascar (Larridon et al., 2019).

Final remarks
In the broader context of biodiversity in Madagascar, sedges lack apparent signatures of adaptive radiation as seen in other lineages, such as bursts of diversification associated with phenotypic divergence in lemurs (Herrera, 2017) or shifts in diet and habitat associated with

the diversification of dung beetles (Wirta et al., 2008). Rather, sedge diversity in Madagascar is mainly explained by dispersal assemblage: relatively recent multiple long-distance dispersal colonisations from the closest continental land masses. *In situ* diversification, although less important than dispersal assemblage, is the main driver of diversity in some sedge lineages. The evolutionary shifts in important traits, such as photosynthetic pathway and chromosome structure, do not appear to be unequivocal drivers of diversification of the sedges in this region. Finally, Madagascar has been also a source of dispersal to other areas of the world, suggesting an important role of the region in the global diversification and assembly of Cyperaceae.

DATA AVAILABILITY STATEMENT

All sequence data are available from online repositories GenBank and Dryad, see Supporting Information Table S2. The alignments used in this study are equally available from Dryad (see xxx). The geographical information and photosynthesis types are provided in Table S2.

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REFERENCES

Allnut, T. F., Ferrier, S., Manion, G., Powell, G. V. N., Ricketts, T. H., Fisher, B. L., Harper, G. J., Irwin, M. E., Kremen, C., Labat, J.-N., Lees, D. C., Pearce, T. A., & Rakotondrainibe, F. (2008). A method for quantifying biodiversity loss and its application to a 50-year record of deforestation across Madagascar. *Conservation Letters*, 1, 173–181.

Andriananjamanantsoa, H. N., Engberg, S., Louis, E. E., & Brouillet, L. (2016). Diversification of *Angraecum* (Orchidaceae, Vandeae) in Madagascar: revised phylogeny reveals species accumulation through time rather than rapid radiation. *PLOS ONE*, 11, e0163194.

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.

Bond, W. J., Silander, J. A. Jr, Ranaivonasy, J., & Ratsirarson, J. (2008). The antiquity of Madagascar's grasslands and the rise of C4 grassy biomes. *Journal of Biogeography*, 35, 1743–1758.

Bouchenak-Khelladi, Y., Muasya, A.M. & Linder, H.P. (2014) A revised evolutionary history of Poales: origins and diversification. *Botanical Journal of the Linnean Society*, 175, 4–16.

Brown, K. A., Parks, K. E., Bethell, C. A., Johnson, S. E., & Mulligan, M. (2015). Predicting Plant Diversity Patterns in Madagascar: Understanding the Effects of Climate and Land Cover Change in a Biodiversity Hotspot. *PLoS ONE*, 10(4), e0122721.

Buerki, S., Devey, D. S., Callmander, M. W., Phillipson, P. B., & Forest, F. (2013). Spatio-temporal history of the endemic genera of Madagascar. *Botanical Journal of the Linnean Society*, 171, 304–329.

Costea, M., El Miari, H., Laczkó, L., Fekete, R., Molnár, A. V., Lovas-Kiss, Á., & Green, A. J. (2019). The effect of gut passage by waterbirds on the seed coat and pericarp of diaspores lacking "external flesh": Evidence for widespread adaptation to endozoochory in angiosperms. *PLoS ONE*, 14, e0226551.

Dupin, J., Matzke, N. J., Särkinen, T., Knapp, S., Olmstead, R. G., Bohs, L., & Smith, S. D. (2017). Bayesian estimation of the global biogeographical history of the Solanaceae. *Journal of Biogeography*, 44, 887–889.

Edgar, R.C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.

Escudero, M., & Hipp, A. L. (2013). Shifts in diversification rates and clade ages explain species richness in higher-level sedge taxa (Cyperaceae). *American Journal of Botany*, 100, 2403–2411.

Escudero, M., Hipp, A. L., Waterway, M. J., & Valente, L. M. (2012). Diversification rates and chromosome evolution in the most diverse angiosperm genus of the temperate zone (*Carex*, Cyperaceae), *Molecular Phylogenetics and Evolution*, 63, 650–655.

Federman, S., Dornburg, A., Downie, A., Richard, A. F., Daly, D. C., & Donaghue, M. J. (2015). The biogeographic origin of a radiation of trees in Madagascar: implications for the assembly of a tropical forest biome. *BMC Evolutionary Biology*, 15, 2016.

Galán Díaz, J., Bauters, K., Rabarivola, L., Xanthos, M., Goetghebeur, P., & Larridon, I. (2019). A revision of *Scleria* (Cyperaceae) in Madagascar. *Blumea*, 64, 195–213.

Ganzhorn, J. U., Lowry, P. P., Schatz, G. E., & Sommer, S. (2001). The biodiversity of Madagascar: one of the world's hottest hotspots on its way out. *Oryx*, 35, 346–348.

Ganzhorn, J. U, Wilmé, L, & Mercier, J.-L. (2014). Explaining Madagascar's Biodiversity. In: Scales, I. R. (ed.), Conservation and Environmental Management in Madagascar. London: Routledge.

Gehrke, B. (2011). Synopsis of *Carex* (Cyperaceae) from sub-Saharan Africa and Madagascar. *Botanical Journal of the Linnean Society*, 166, 51–99.

Govaerts, R., Jiménez-Mejías, P., Koopman, J., Simpson, D. A., Goetghebeur, P., Wilson, K. L., Egorova, T., & Bruhl J. J. (2020). World checklist of selected plant families.

Cyperaceae. Facilitated by the Royal Botanic Gardens, Kew. Retrieved from http://www.kew.org/wcsp/monocots/.

Goyder, D., Baker, W., Besnard, G., Dransfield, J., Gardiner, L., Moat, J., Rabehevitra, D., Rajaovelona, L., Rakotoarisoa, S., Rakotonasolo, F., Ralimanana, H., Randriamboavonjy, T., Razanatsoa, J., Sarasan, V., Vorontsova, M., Wilkin, P., & Cable, S. (2017). Country focus - status of knowledge of Madagascan plants. In: K. J. Willis (ed.), State of the World's Plants 2017, Chapter 6, pp. 36–41. Richmond: Royal Botanic Gardens, Kew.

Green, A. J., Elmberg, J. & Lovas-Kiss, Á. (2019). Beyond scatter-hoarding and frugivory: European Corvids as overlooked vectors for a broad range of plants. *Frontiers in Ecology and Evolution*, 7, 133.

Hackel, J., Vorontsova, M. S., Nanjarisoa, O. P., Hall, R. C., Razanatsoa, J., Malakasi, P., & Besnard, G. (2018). Grass diversification in Madagascar: In situ radiation of two large C3 shade clades and support for a Miocene to Pliocene origin of C4 grassy biomes. *Journal of Biogeography*, 45, 750–761.

Herrera, J. P. (2017). Testing the adaptive radiation hypothesis for the lemurs of Madagascar. *Royal Society Open Science*, 4, 161014,

Hong-Wa, C., & Besnard, G. (2013). Species limits and diversification in the Madagascar olive (*Noronhia*, Oleaceae). *Botanical Journal of the Linnean Society*, 174, 141–161.

IUCN. (2019). The IUCN Red List of Threatened Species. Version 2019-2. https://www.iucnredlist.org/ Accessed 16 September 2019.

Janssen, T., Bystriakova, N., Rakotondrainibe, F., Coomes, D., Labat J.-N., & Schneider, H. (2008). Neoendemism in Madagascan scaly tree ferns results from recent, coincident diversification bursts. *Evolution*, 62, 1876–1889.

Jiménez-Mejías, P., Martinetto, E., Momohara, A., Popova, S., Smith, S. Y., & Roalson, E. H. (2016). A commented synopsis of the pre-Pleistocene fossil record of *Carex* (Cyperaceae). *The Botanical Review*, 82, 258–345.

Jønsson, K., Fabre, P.-H., Fritz, H., Etienne, R., Ricklefs, R., Jørgensen, T. (2012) Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proceedings of the National Academy of Sciences USA,* 109, 6620–6625.

Joseph, G.S., & Seymour, C.L., (2020) Madagascan highlands: originally woodland and forest containing endemic grasses, not grazing-adapted grassland. *Proceedings of the Royal Society B*, 287: 20201956.

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 C3 *Cyperus* lineages (Cyperaceae) revealed using molecular phylogenetic data and carbon isotope analysis. *Botanical Journal of the Linnean Society,* 167, 19–46.

Larridon, I., Rabarivola, L., Xanthos, M., & Muasya, A. M. (2019). Revision of the Afro-Madagascan genus *Costularia* (Cyperaceae): Infrageneric relationships and species delimitation. *PeerJ*, 7, e6528.

Larridon, I., Spalink, D., Jiménez-Mejías, P., Márquez-Corro, J.I., Martín-Bravo, S., Muasya, A.M., & Escudero, M. (in press). The Cyperaceae of Madagascar. In: Goodman, S. (ed.) The New Natural History of Madagascar. Princeton University Press.

Larridon, I., Galán Díaz, J., Bauters, K., & Escudero, M. (2020). What drives diversification in a pantropical plant lineage with extraordinary capacity for long-distance dispersal and colonization? *Journal of Biogeography*, https://doi.org/10.1111/jbi.13982.

Linder, H. P., Antonelli, A., Humphreys, A. M., Pirie, M. D., & Wüest, R. O. (2013). What determines biogeographical ranges? Historical wanderings and ecological constraints in the danthonioid grasses. *Journal of Biogeography*, 40, 821–834.

Liu, C., Sarnat, E. M., Friedman, N. R., Hita Garcia, F., Darwell, C., Booher, D., ... & Economo, E. P. (2020). Colonize, radiate, decline: Unraveling the dynamics of island community assembly with Fijian trap-jaw ants. *Evolution*, 74, 1082–1097.

Lovas-Kiss, Á., Vincze, O., Kleyheeg, E., Sramkó, G. Laczkó, L., Fekete, R., Molnár V., A., & Green, A. J. (2020). Seed mass, hardness, and phylogeny explain the potential for endozoochory by granivorous waterbirds. *Ecology and Evolution*, 10, 1413–1424.

Márquez-Corro, J. I., Martín-Bravo, S., Spalink, D., Luceño, M., & Escudero, M. (2019). Inferring hypothesis-based transitions in clade-specific models of chromosome number evolution in sedges (Cyperaceae). *Molecular Phylogenetics and Evolution*, 135, 203–209.

Martin, R.D. (1972). Adaptive radiation and behaviour of the Malagasy lemurs. *Philosophical Transacations of the Royal Society of Biology Sciences*, 264, 295–352.

Martín-Bravo, S., Jiménez-Mejías, P., Villaverde, T., Escudero, M., Hahn, M., Spalink, D., Roalson, E. H., Hipp, A. L., and the Global Carex Group: Benítez-Benítez, C., Bruederle, L. P., Fitzek, E., Ford, B. A., Ford, K. A., Garner, M., Gebauer, S., Hoffmann, M. H., Jin, X.-F., Larridon, I., Léveillé-Bourret, É., Lu, Y.-F., Luceño, M., Maguilla, E., Márquez-Corro, J. I., Míguez, M., Naczi, R., Reznicek, A. A., & Starr, J. R. (2019). A tale of worldwide success: behind the scenes of *Carex* (Cyperaceae) biogeography and diversification. *Journal of Systematics and Evolution*, 57, 695–718.

Matzke, N. J. (2013). Probabilistic historical biogeography: New models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers of Biogeography*, 5, 242–248.

Matzke, N. J. (2014). Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology*, 63, 951–970.

Maurin, O., Davies, T. J., Burrows, J. E., Daru, B. H., Yessoufou, K., Muasya, A. M., van der Bank, M., & Bond, W. J. (2014). Savanna fire and the origins of the 'underground forests' of Africa. *New Phytologist*, 204, 201–214.

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES science gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments* (GCE10), 14 November, 2010. New Orleans, LA: IEEE. 1–8.

Minaya, M., Hackel, J., Namaganda, M., Brochmann, C., Vorontsova, M. S., Besnard, G., & Catalán, P. (2017). Contrasting dispersal histories of broad- and fine-leaved temperate Loliinae grasses: Range expansion, founder events, and the roles of distance and barriers. *Journal of Biogeography*, 44, 1980–1993.

Mitchell, J. S., & Rabosky, D. L. (2017). Bayesian model selection with BAMM: effects of the model prior on the inferred number of diversification shifts. *Methods in Ecology and Evolution*, 8, 37–46.

Moore, B. R., Höhna, S., May, M. R., Rannala, B., & Huelsenbeck, J. P. (2016). Critically evaluating the theory and performance of Bayesian analysis of macroevolutionary mixtures. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 9569–9574.

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.

Muasya, A. M., Larridon, I., Reynders, M., Huygh, W., Goetghebeur, P., Cable, S., Simpson, D. A., & Gehrke, B. 2011. The Cyperaceae in Madagascar show high diversification in high altitude forest and wetland habitats. *Plant Ecology and Evolution*, 144, 357–362.

Naczi, R. F. C., & Ford, B. A. (2008). *Sedges: uses, diversity, and systematics of Cyperaceae*. St Louis, MO: Missouri Botanical Garden Press.

Paradis, E., & Schliep, K. (2018). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528.

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, 6, 7–11.

Rabosky, D. L. (2014). Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE*, 9, e89543.

Rabosky, D. L., Grundler, M., Anderson, C., Title, P., Shi, J. J., Brown, J. W., Huang, H., & Larson, J. G. (2014). BAMM tools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution*, 5, 701–707.

Rabosky, D. L., Mitchell, J. S., & Chang, J. (2017). Is BAMM flawed? Theoretical and practical concerns in the analysis of multi-rate diversification models. *Systematic Biology*, 66, 477–498.

R Core Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from http://www.R-project.org/.

Reddy, S., Driskell, A., Rabosky, D. L., Hackett, S.J., & Schulenberg, T.S. (2012). Diversification and the adaptive radiation of the vangas of Madagascar. *Proceedings of the Royal Society B*, 279, 2062–2071.

Ree, R. H., Moore, B. R., Webb, C. O., & Donoghue, M. J. (2005). A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution*, 59, 2299–2311.

Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, 57, 4–14.

Ree, R. H., & Sanmartín, I. (2018). Conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection. *Journal of Biogeography*, 45, 741–749.

Renner, S.S. (2004). Multiple Miocene Melastomataceae dispersal between Madagascar, Africa and India. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359, 1485–1494. https://doi.org/10.1098/rstb.2004.1530

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223.

Ronquist, F. (1997). Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. *Systematic Biology*, 46, 195–203.

Ronquist, F., & Sanmartín, I. (2011). Phylogenetic methods in biogeography. *Annual Review of Ecology, Evolution, and Systematics*, 42, 441–464.

Sauquet, H. (2013). A practical guide to molecular dating. *Comptes Rendus Palevol*, 12, 355–367.

Semmouri, I., Bauters, K., Léveillé-Bourret, É., Starr, J.R., Goetghebeur, P., & Larridon I. (2019). The phylogeny and systematics of Cyperaceae, the evolution and importance of embryo morphology. *Botanical Review*, 85, 1–39.

Shaver, G. R., Laundre, J. A., Giblin, A. E., & Nadelhoffer, K. J. (1996). Changes in Live Plant Biomass, Primary Production, and Species Composition along a Riverside Toposequence in Arctic Alaska, U.S.A. *Arctic and Alpine Research*, 28, 363–379.

Smith, S. A., & O'Meara, B. C. (2012). treePL: divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics*, 28, 2689–2690.

Smith, S. Y., Collinson, M. E., Rudall, P. J., & Simpson, D. A. (2010). The Cretaceous and Paleogene fossil record of Poales: review and current research. Diversity, phylogeny, and evolution in the monocotyledons (ed. by O. Seberg, G. Peterson, A. S. Barford, & J. I. Davis), pp. 333–356. Aarhus University Press.

Solofondranohatra, C.L., Vorontsova, M.S., Hempson, G.P., Hackel, J., Cable, S., Vololoniaina, J., & Lehmann, C.E.R. (2020) Fire and grazing determined grasslands of central Madagascar represent ancient assemblages. *Proceedings of the Royal Society B*, 287, 20200598.

Spalink, D., Drew, B. T., Pace, M. C., Zaborsky, J. G., Starr, J. R., Cameron C., Givnish T. J., & Sytsma, K. J. (2016). Biogeography of the cosmopolitan sedges (Cyperaceae) and the area-richness correlation in plants. *Journal of Biogeography*, 43, 1893–1904.

Spalink, D., Pender, J., Escudero, M., Hipp, A. L., Roalson, E. H., Starr, J. R., Waterway, M., Sytsma, K. J., & Bohs, L. (2018). The spatial structure of phylogenetic and functional diversity in the United States and Canada: an example using the sedge family (Cyperaceae). *Journal of Systematics and Evolution*, 56, 449–465.

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313.

Strijk, J. S., Noyes, R. D., Strasberg, D., Cruaud, C., Gabory, F., Chase, M.W., Abbott, R. J., & Thébaud, C. (2012). In and out of Madagascar: dispersal to peripheral islands, insular speciatioand diversification of Indian Ocean daisy trees (*Psiadia*, Asteraceae). *PLOS ONE*, 7. E42932.

Sukumaran, J., & Knowles L. L. (2018). Trait-dependent biogeography: (re)integrating biology into probabilistic historical biogeographical models. *Trends in Ecology and Evolution*, 33, 390–398.

Valente, L., Phillimore A. B., Melo M., Warren B. H., Clegg S. M., Havenstein K., Tiedemann R., Illera J. C., Thébaud C., Aschenbach T., et al. (2020). A simple dynamic model explains the diversity of island birds worldwide. *Nature*, 579, 92–96.

Vatuaz, L., Sartori, M., Gattolliat, J.-L., & Monaghan, M.T. (2013). Endemism and diversification in freshwater insects of Madagascar revealed by coalescent and phylogenetic analysis of museum and field collections. *Molecular Phylogenetics and Evolution*, 66, 979–991.

Vences, M., Wollenberg, K. C., Vieites, D. R., & Lees, D. C. (2009). Madagascar as a model region of species diversification. *Trends in Ecology & Evolution*, 24, 456–465.

Viljoen, J. A., Muasya, A. M., Barrett, R. L., Bruhl, J. J., Gibbs, A. K., Slingsby, J. A., Wilson, K. L., & Verboom, G. A. (2013). Radiation and repeated transoceanic dispersal of Schoeneae (Cyperaceae) through the southern hemisphere. *American Journal of Botany*, 100, 2494–2508.

Villaverde, T., Escudero, M., Martín-Bravo, S., Bruederle, L. P., Luceño, M., & Starr, J. R. (2015). Direct long-distance dispersal best explains the bipolar distribution of *Carex arctogena* (*Carex* sect. *Capituligerae*, Cyperaceae). *Journal of Biogeography*, 42, 1514–1525.

Villaverde, T., Escudero, M., Martín-Bravo, S., Jiménez-Mejías, P., Sanmartín, I., Vargas, P., & Luceño, M. (2017). Bipolar distributions in vascular plants: A review. *American Journal of Botany*, 104, 1680–1694.

Vorontsova, M. S., Besnard, G., Forest, F., Malakasi, P., Moat, J., Clayton, W. D., Ficinski, P, Savva, G. M., Nanjarisoa, O. P., Razanatsoa, J., Randriantsara, F. O., Kimeu, J. M., Luke, W. R. Q., Kayombo, C., & Linder, P. H. (2016). Madagascar's grasses and grasslands: Anthropogenic or natural? *Proceedings of the Royal Society B*, 283, 20152262.

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.

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.

Willis, K. J., Gillson, L., & Virah-Sawmy, M. (2008). Nature or nurture: the ambiguity of C4 grasslands in Madagascar. *Journal of Biogeography*, 35, 1741–1742.

Wirta, H., Orsini, L., & Hanski, I. (2008). An old adaptive radiation of forest dung beetles in Madagascar. *Molecular Phylogenetics and Evolution*, 47, 1076–1089.

Yoder, A. K., & 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.

Zachos, M., Pagani, L., Sloan, E., & Thomas, K. (2001). Billups Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292, 686–693.

BIOSKETCHES

Isabel Larridon is Research Leader Africa at Royal Botanic Gardens, Kew and visiting professor at Ghent University. She investigates plant evolution, biodiversity and conservation using a multidisciplinary approach, and is a key member of the international Cyperaceae research community. For this study, she collaborated with cyperologists based in South Africa, Spain and the U.S.A., each with a different focus including phylogenetics, biogeography, the megadiverse genus *Carex*, and African Cyperaceae. Authors' contributions: I.L. conceived the idea; I.L., D.S., S.M.-B., J.I.M-C., P.J.-M. compiled the data; D.S. & M.E. analysed the data; I.L. drafted the manuscript; all authors contributed to the writing and preparation of the final version of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

TABLE 1 Overview of Cyperaceae diversity on Madagascar. Classification based on Semmouri et al. (2019); numbers of species globally, native and endemic to Madagascar largely follows Govaerts et al. (2020). An asterisk (*) indicates genera with a single species in Madagascar. The percentages provide a measure of the native species richness and level of endemism.

Subfamily	Tribe	Genus	Number of species				Percentage of species per		
			Global	Madagascar Native	Madagascar Endemic	Per tribe	Tribe	Genus Native	Genus Endemic
Mapanioideae	Chrysitricheae	*Lepironia**	1	1	0	1	0	0	0
	Hypolytreae	*Hypolytrum**	61	1	1	1	0	0	2
Cyperoideae	Abildgaardieae	*Actinoschoenus**	8	1	0	41	13	0	0
		Bulbostylis	227	23	15			7	7
		Fimbristylis	322	17	2			5	1
	Bisboeckelereae	*Diplacrum**	10	1	0	1	0	0	0
	Cariceae	*Carex*	1996	30	26	30	10	10	1
	Carpheae	*Carpha**	15	1	1	1	0	0	7
	Cladieae	*Cladium**	3	1	0	1	0	0	0
	Cypereae	*Cyperus*	955	143	43	148	48	46	5
		*Ficinia**	80	1	1			0	1
		Isolepis	75	4	1			1	1
	Eleocharideae	*Eleocharis*	295	12	0	12	4	4	0
	Fuireneae	*Bolboschoenus**	15	1	0	22	7	0	0
		Fuirena	55	7	2			2	4
		Schoenoplectiella	53	12	5			4	9
		Schoenoplectus	26	2	0			1	0
	Rhynchosporeae	*Rhynchospora*	361	10	1	10	3	3	0
	Schoeneae	*Costularia*	15	11	11	16	5	4	73
		Machaerina	53	4	1			1	2
		*Trichoschoenus**	1	1	1			0	100
	Sclerieae	*Scleria*	258	25	8	25	8	8	3
	Trilepideae	*Coleochloa**	8	1	0	1	0	0	0
Total:	14	23	4893	310	119	310	100	100	

TABLE 2 BioGeoBEARS models comparison. Likelihood, number of parameters, parameters (d, e, x and j) and AICc are shown. The best models are in bold.

Model	LnL	n params	d	e	x	j	AICc
DEC	-4246	2	0.011	0.0018	0	0	8495
DEC+j	-4187	3	0.01	2.20E-09	0	0.007	8380
DIVA-like	-4424	2	0.013	0.0009	0	0	8853
DIVA-like+j	-4368	3	0.012	1.00E-12	0	0.0059	8743
DEC+x	**-4169**	**3**	**0.016**	**0.0021**	**-0.28**	**0**	**8343**
DEC+x+j	**-3971**	**4**	**0.034**	**1.00E-12**	**-1.04**	**0.03**	**7950**
DIVA-like+x	-4372	3	0.016	0.0011	-0.18	0	8751
DIVA-like+x+j	-4142	4	0.046	1.00E-12	-1.21	0.026	8293

TABLE 3. Summary of the number of dispersal events (and standard deviations, sd) between the different considered regions (sources of dispersal in rows and sinks of dispersals in columns) inferred by the BSM analysis under the DEC+x model. Cell colour indicates the range of the number of inferred dispersal events: blue, 0–10; green, 10–20; yellow, 20–30; orange, 30–50; red, >50. For the events inferred under the DEC+x+j model, see Table S6.

From			To Madagascar region	Southern Africa	Tropical Africa	Eurasia & N Africa	India	SE Asia & Australasia	N America	Neotropics
Madagascar region	mean		-	22.62	18.68	12.02	13.62	14.1	6.12	9.9
	sd		-	(4.05)	(3.97)	(2.97)	(3.75)	(3.3)	(2.13)	(2.72)
Southern Africa	mean		23.98	-	25.4	11.56	10.78	14.12	5.3	10.14
	sd		(4.16)	-	(4.38)	(3.09)	(3.23)	(2.52)	(1.69)	(2.95)
Tropical Africa	mean		58.9	65.8	-	33.84	31.26	25.86	18.8	28.2
	sd		(4.57)	(5.42)	-	(4.93)	(5.05)	(4)	(3.62)	(3.35)
Eurasia & N Africa	mean		15.7	17.58	18.08	-	47.58	50.8	73.48	12.98
	sd		(3.39)	(2.91)	(3.16)	-	(5.53)	(7.26)	(6.51)	(2.83)
India	mean		13.66	9.92	10.06	25.38	-	25.86	5.78	5.28
	sd		(3.46)	(2.99)	(2.79)	(4.38)	-	(5.31)	(1.71)	(2.21)
SE Asia & Australasia	mean		16.82	13.62	9.94	34.6	31.84	-	10.7	12.14
	sd		(3.09)	(3.57)	(3.06)	(4.71)	(4.96)	-	(2.51)	(2.7)
N America	mean		8.5	7.7	10.1	77.86	10.52	17.12	-	80.72
	sd		(2.2)	(2.82)	(2.75)	(7.33)	(2.31)	(3.54)	-	(6.11)
Neotropics	mean		13.58	8.78	12.28	10.04	7.7	11.12	47.48	-
	sd		(2.84)	(3.13)	(2.76)	(2.77)	(2.61)	(2.72)	(5.75)	-

TABLE 4. The best diversification scenario inferred by BAMM. Names of the clades (see Figure S4) for which a diversification rate shift was inferred, with their time from the root to crown node (in mya), speciation rate (lam1) and extinction rate (mu1) at the origin of the clade and change of speciation rate within the clade (lam2) are indicated.

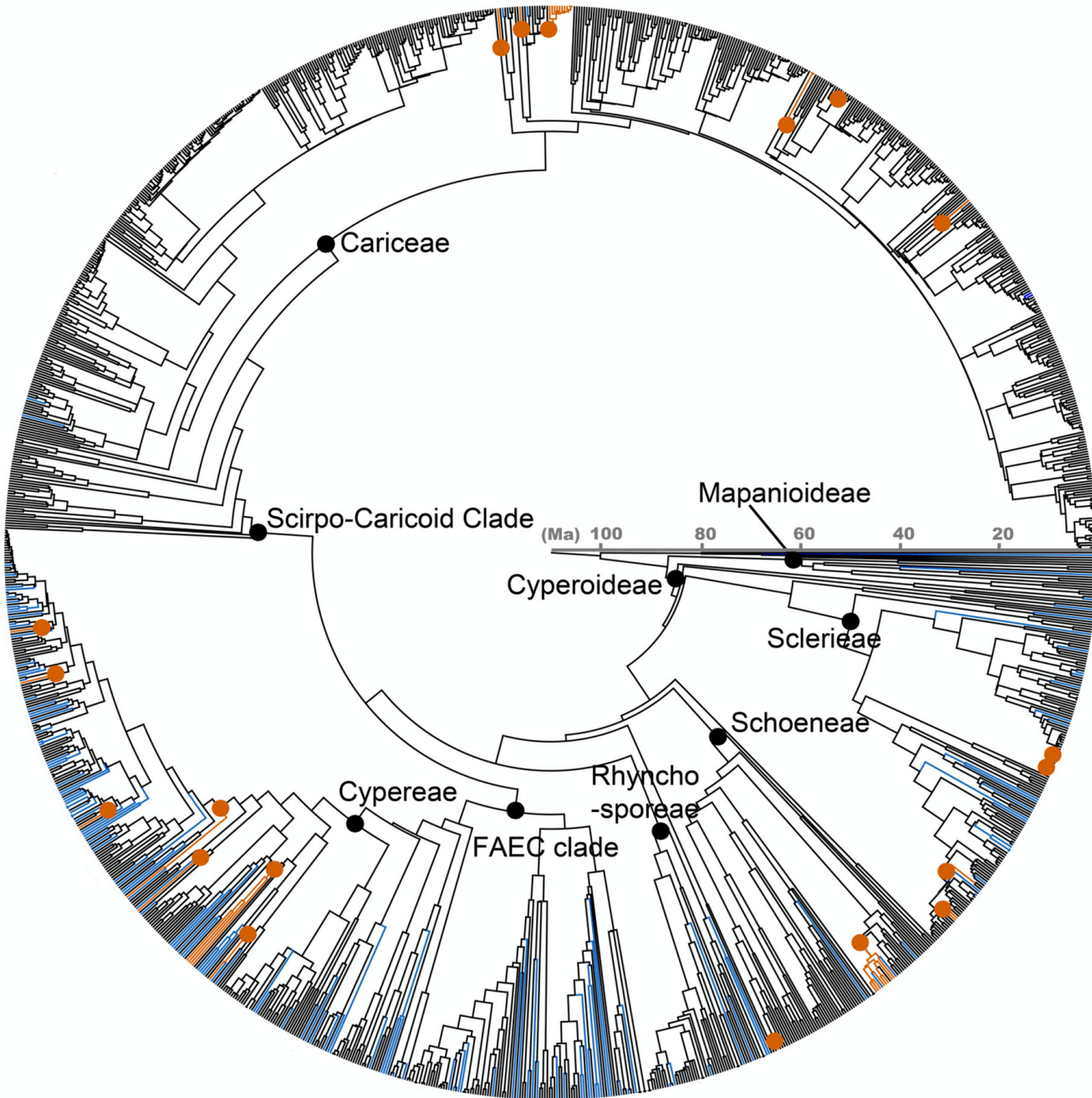| Clade	Time from root	Time to present	lam1	lam2	mu1
Root	0.000	99.570	0.050	0.035	0.001
Non-Siderosticta Carex Clade	50.982	48.588	0.362	0.055	0.433
Carex subgenera					
Psyllophorae+Euthyceras	60.743	38.827	0.404	-0.009	0.196
Schoenoplectus Clade	61.083	38.487	0.318	0.005	0.120
C4 Cyperus Clade	64.344	35.226	0.593	-0.044	0.011
Scleria section *Hypoporum*	64.381	35.189	0.173	0.046	0.023
Isolepis+Ficinia Clade	66.472	33.098	0.141	0.094	0.022
Oreobolus Clade	67.647	31.924	0.370	-0.005	0.063
Eleocharis subclade	67.972	31.598	0.918	-0.027	0.568
Scleria several sections	68.724	30.846	0.562	-0.010	0.083
Rhynchospora subclade	71.676	27.894	0.401	0.018	0.269
Carex section *Ovales*	81.345	18.225	1.417	0.017	0.099
C4 *Cyperus* subclade	83.071	16.499	1.377	0.031	0.624
Scleria section *Hypoporum* subclade	83.777	15.793	1.723	-0.092	0.052

FIGURE 1 Summary phylogeny of the Cyperaceae. Nearly half of the species richness of subfamily Cyperoideae corresponds to the Scirpo-Caricoid Clade (SCC). The most species-rich tribes and clades have also been indicated in the other half of subfamily Cyperoideae, namely the tribes Sclerieae, Schoeneae and Rhynchosporeae, plus the FAEC Clade which includes tribes Fuireneae, Abildgaardieae, Eleocharideae and Cypereae. Lineages native to the Madagascar region are in blue, endemic lineages in dark orange. The 19 lineages with an estimated origin in Madagascar are labelled with dark orange dots.
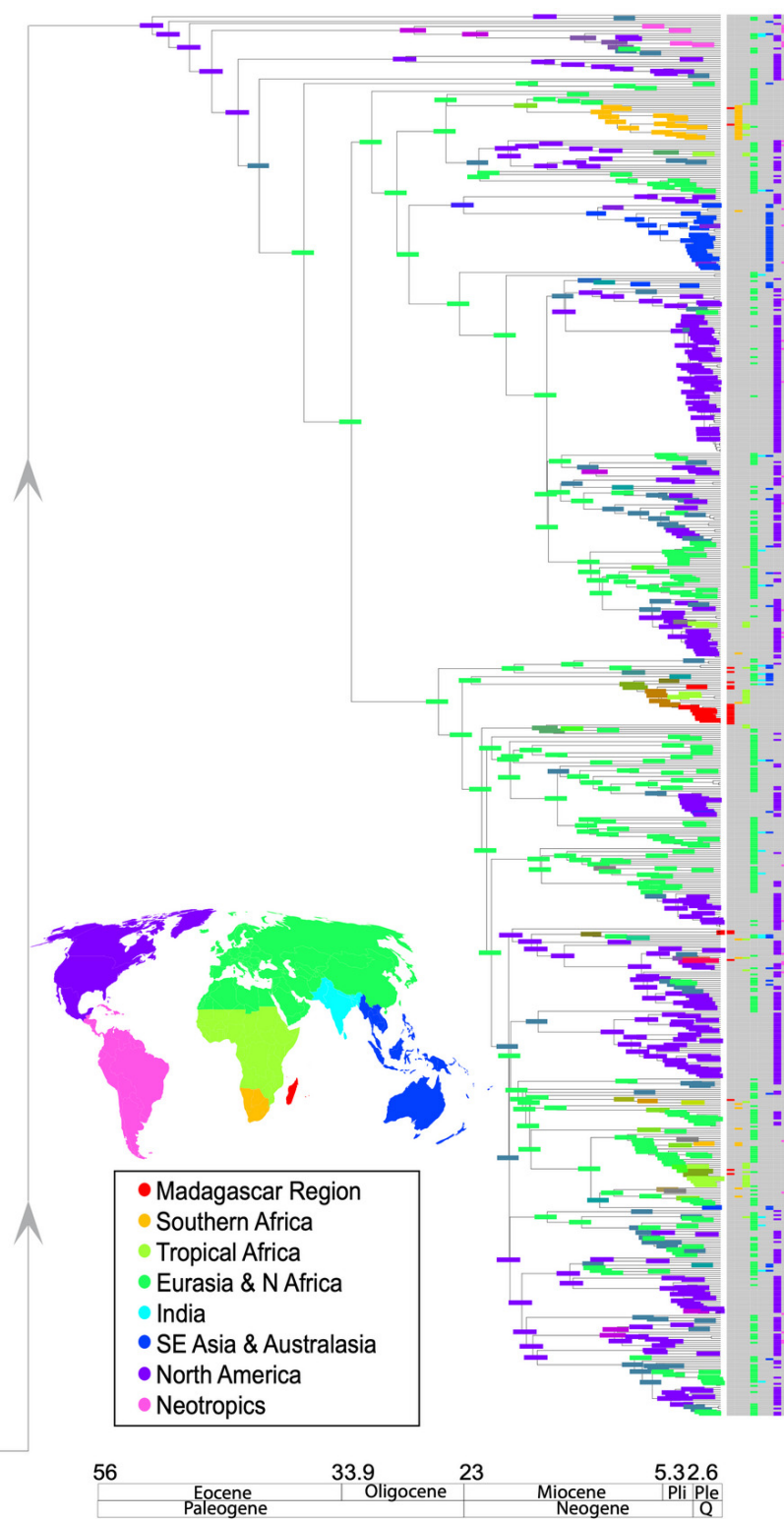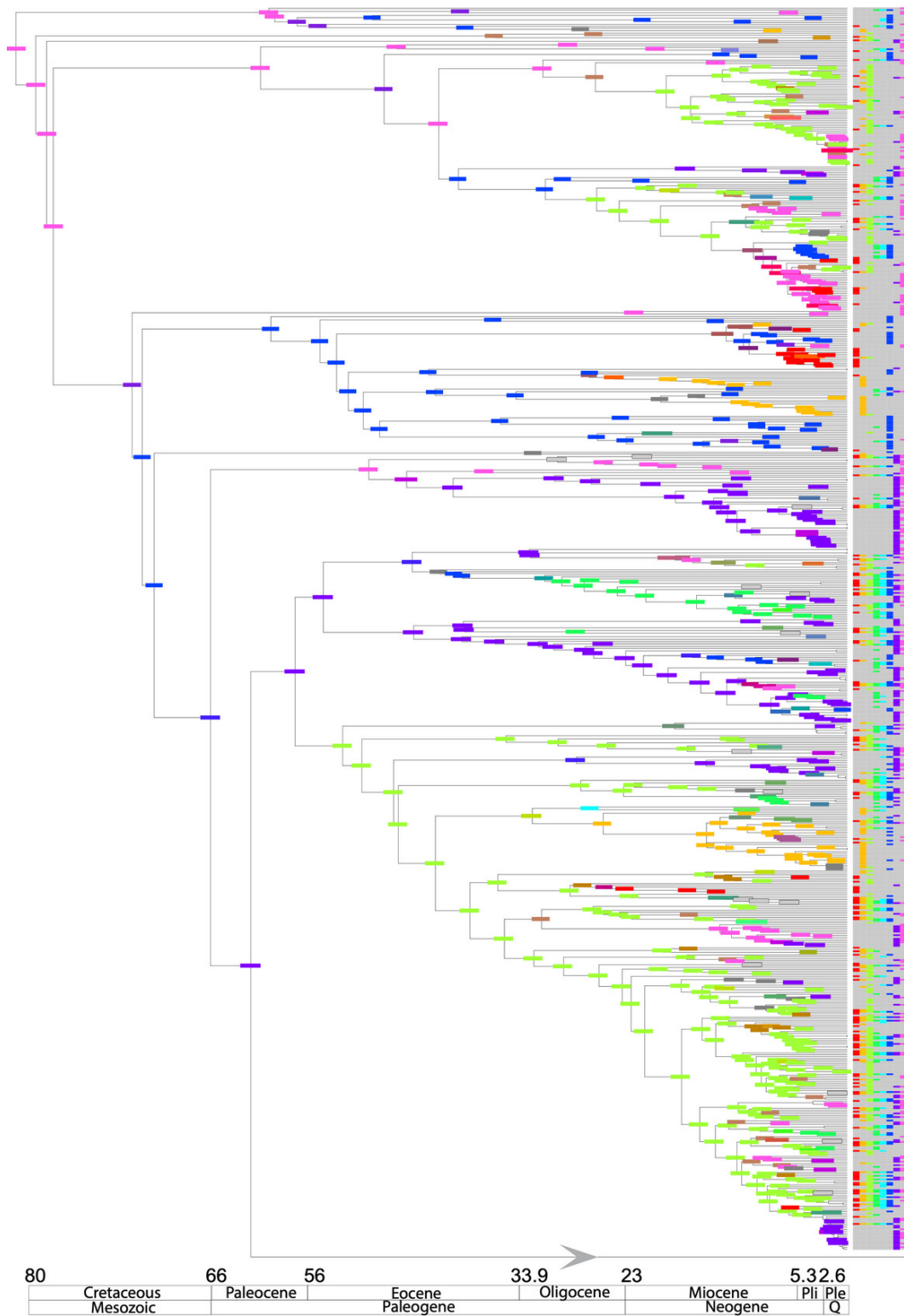
FIGURE 2 Chronogram and ancestral area reconstruction results of the Cyperaceae dataset, constructed in BioGeoBEARS using Biogeographical Stochastic Mapping (DEC+x). Each colour represents one of the eight defined geographic regions, illustrated by the legend at the bottom of the figure. Geological time scale displayed at the bottom.

FIGURE 3 Timing, type, destination and frequency of dispersal events to Madagascar in the ancestral area reconstruction (BSM DEC+x). **(a)** Timing, type and frequency: Within-area (red), Subset within-area (blue), Vicariance (green), and Anagenetic Dispersal (purple). The total number of events is indicated by black dots (•). **(b)** Timing, destination and frequency: Each colour represents one of the eight defined geographic regions, illustrated by the legend at the top of the figure. The total number of events is indicated by black dots (•). For the BSM DEC+x+j summaries see Figure S3.
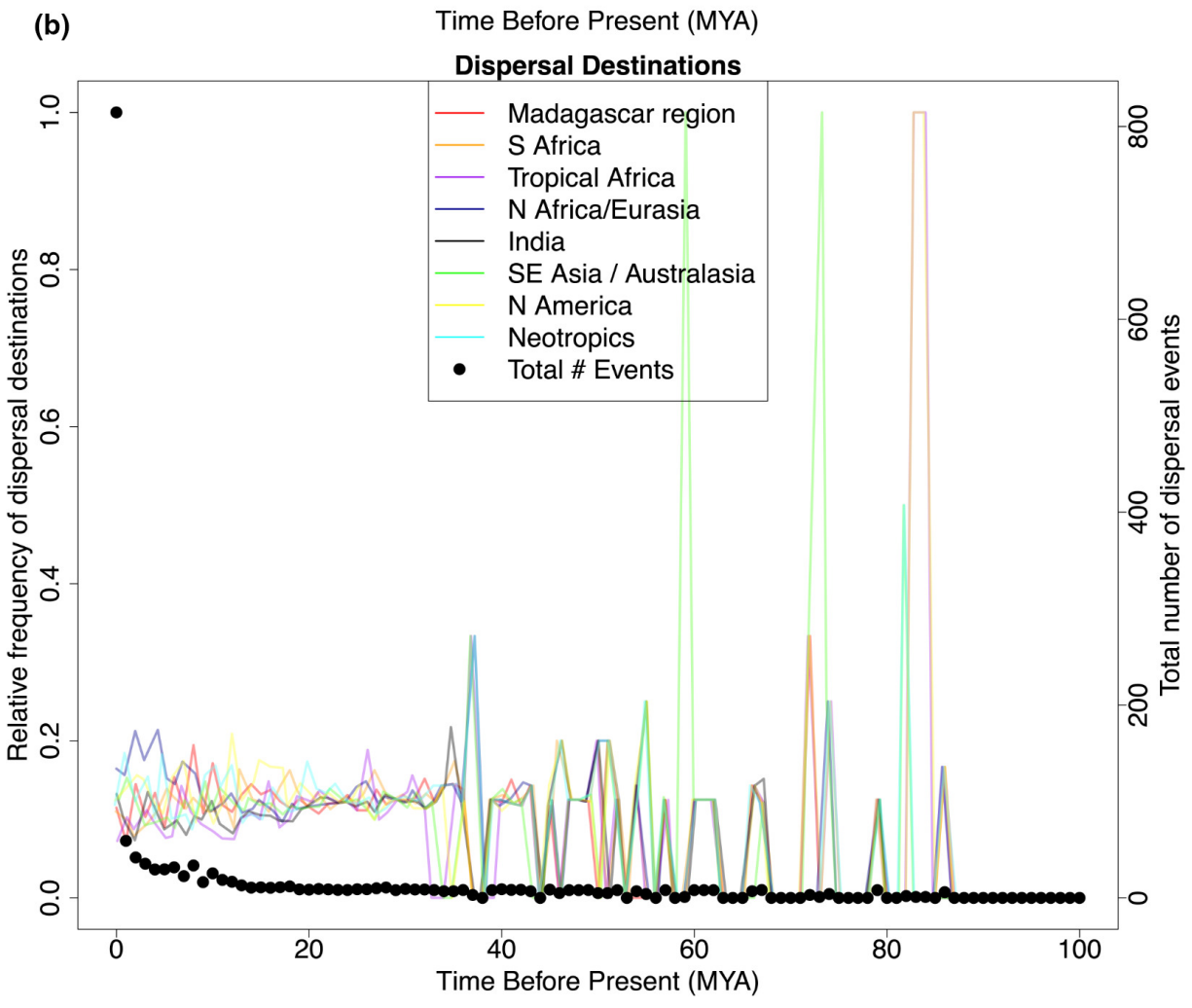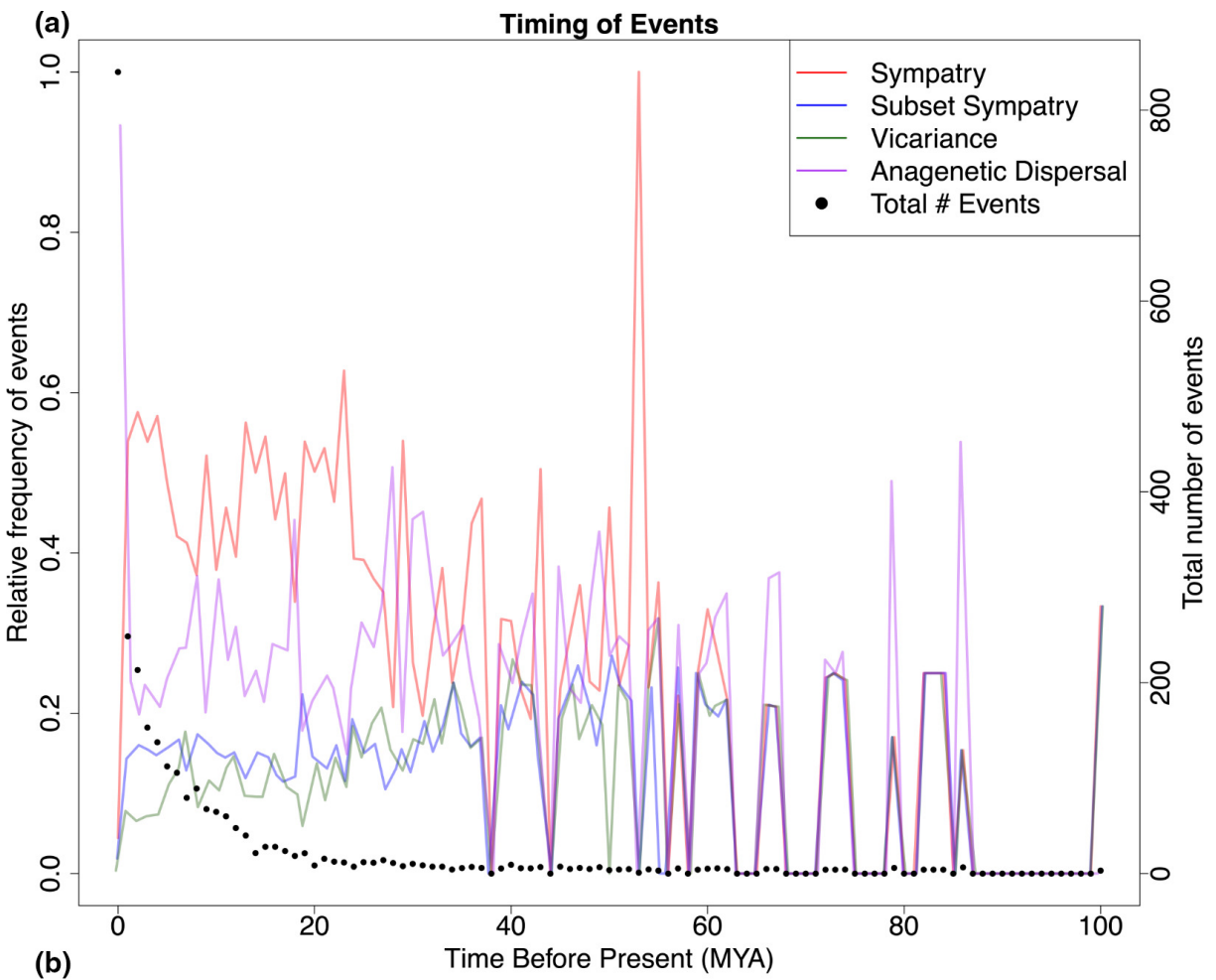
FIGURE 4 BAMM results from the analysis of diversification rate over time in Cyperaceae. **(a)** Phylorate plot. Tree branch colour indicates the model-averaged net diversification rates (species per million year; spp/my) along the branches. Thirteen diversification rate shifts are marked in the figure using red circles. **(b)** The net diversification rate over time. The thick red line marks mean net diversification rate, and the shaded range indicates the confidence interval. **(c)** Histogram.

Native to Madagascar region
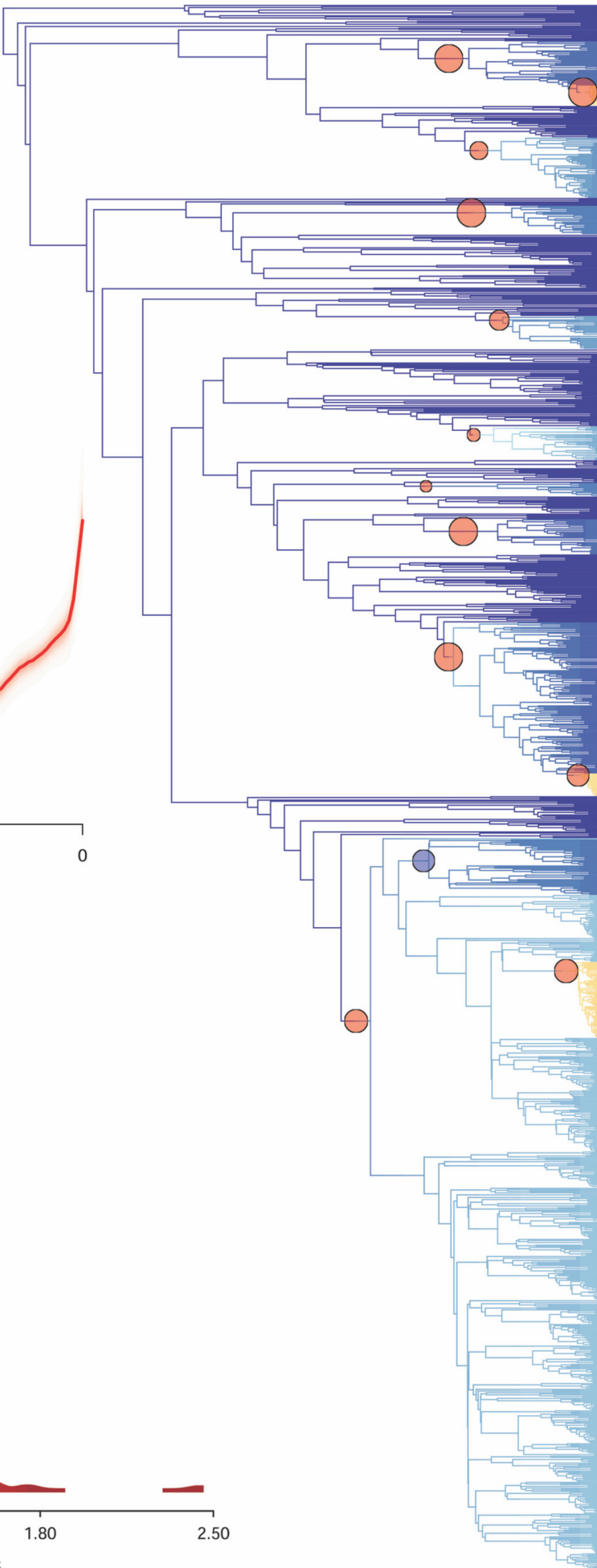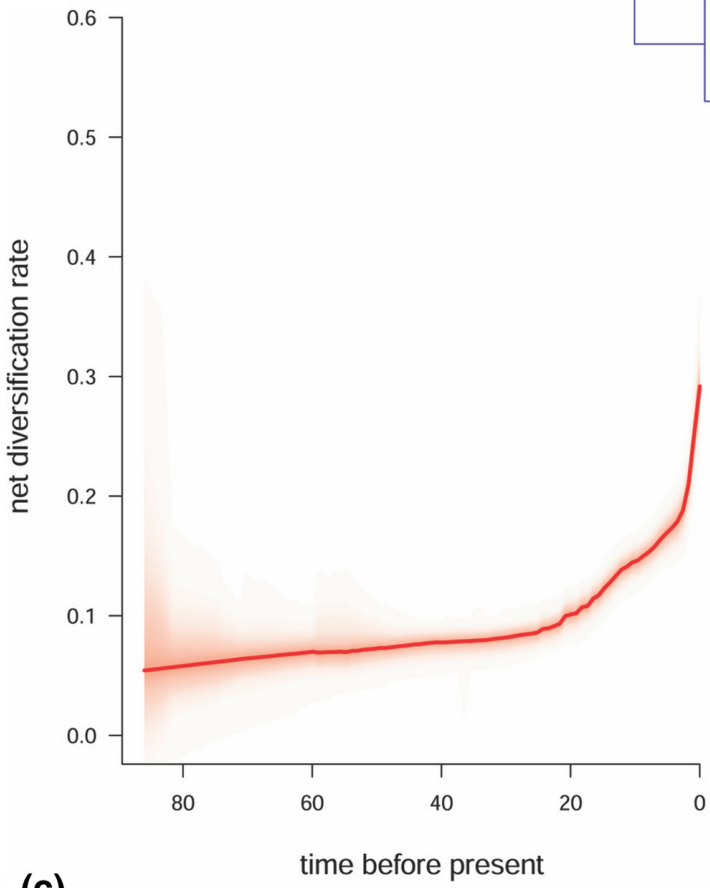Endemic to Madagascar
Estimated origin in Madagascar
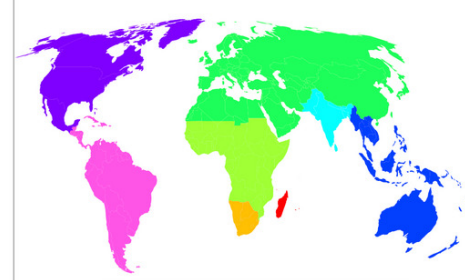
Cariceae

Mapanioideae

(Ma) 100   80   60   40   20

Scirpo-Caricoid Clade

Cyperoideae

Sclerieae

Schoeneae

Cypereae

Rhyncho
-sporeae

FAEC clade

| Madagascar Region
| Southern Africa
| Tropical Africa
| Eurasia & N Africa
| India
| SE Asia & Australasia
| North America
| Neotropics

80   66   56   33.9   23   5.32.6

Cretaceous   Paleocene   Eocene   Oligocene   Miocene   Pli Ple
Mesozoic   Paleogene   Neogene   Q

56   33.9   23   5.32.6

Eocene   Oligocene   Miocene   Pli Ple
Paleogene   Neogene   Q

(a) Timing of Events

(b) Dispersal Destinations

(a)

(b)

(c)

marginal shift probability

1.000

0.875

0.750

0.625

0.500

0.375

0.250

0.125