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SPECIAL PAPER

Biogeography of the cosmopolitan sedges (Cyperaceae) and the area-richness correlation in plants

Daniel Spalink[1]*, Bryan T. Drew[2], Matthew C. Pace[2,3], John G. Zaborsky[1], Julian R. Starr[4], Kenneth M. Cameron[1], Thomas J. Givnish[1] and Kenneth J. Sytsma[1]

[1]Department of Botany, University of Wisconsin-Madison, Madison, WI 53706, USA, [2]Department of Biology, University of Nebraska at Kearny, Kearny, NE 68849, USA, [3]The New York Botanical Garden, Bronx, NY 10458, USA, [4]Department of Biology, University of Ottawa, ON K1N 6N5, Canada

*Correspondence: Daniel Spalink, Department of Botany, University of Wisconsin-Madison, WI 53706, USA.
E-mail: dspalink@wisc.edu

ABSTRACT

Aim Across angiosperm families, the area occupied by a family is strongly correlated with its richness. We explore the causes of this area-richness correlation using the cosmopolitan family, Cyperaceae Juss., as a model. We test the hypothesis that, despite a proposed tropical origin, temperate lineages in the family diversified at elevated rates. We test the hypothesis that the area-richness correlation is maintained within intrafamilial clades, and that this relationship could be described as a function of niche space. We also test the hypothesis that the partitioning of geographical and ecological space, not the extent of this space, is the factor most closely associated with clade richness.

Location Cosmopolitan.

Methods We use molecular data from four genes sequenced in 384 taxa to develop a chronogram of Cyperaceae. We then develop a model of ancestral ranges and measure rates of diversification throughout the history of the family. Integrating data from over 4,800,000 digitized herbarium records, we characterize the range and niche of more than 4500 species and test for correlations of the species richness maintained within clades with range size, range partitioning, range overlap, niche, clade age and rate of diversification.

Results Cyperaceae originated in South America in the late Cretaceous and subsequently dispersed throughout the globe. Of three increases in diversification rate, two occurred in the temperate Northern Hemisphere. The variable most closely associated with clade richness is the partitioning of geographical space by species within each clade.

Main conclusions We show that species-rich clades in Cyperaceae are not only more widespread, occupy more niche space, and diversify more quickly, but also exhibit patterns that are consistent with the partitioning of geographical and ecological space as a major correlate to diversification.

Keywords

area-richness correlation, BAMM, beast, BioGeoBEARS, Cyperaceae, herbarium specimens, historical biogeography, Poales

INTRODUCTION

Explaining why some clades are species rich and others are species poor, and how these patterns of diversity are distributed throughout the globe, remain central tasks in biology and require the multiple perspectives afforded by evolution, geography, and ecology. From an evolutionary perspective, in its simplest form species richness is a function of net diversification rate and clade age. In integrating geography and ecology, however, both the physical location and extent of clade ranges are also related to species richness. For example, the tropics are the location of origination (i.e. 'museum') and subsequent diversification (i.e. 'cradle') in many clades owing to the climatic stability, high productivity and large geographical extent of the tropics over geological time-scales (Pianka, 1966; Chown & Gaston, 2000;

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Jablonski *et al.*, 2006; Mittelbach *et al.*, 2007). Some lineages are actually more diverse in temperate than tropical regions (Kindlmann *et al.*, 2007; Sánchez-Ramírez *et al.*, 2015), however, despite the propensity of these temperate lineages to be nested within tropical clades (i.e. tropical museum and temperate cradle of diversification; Mittelbach *et al.*, 2007). Furthermore, clades that occupy both tropical and extratropical regions are more than five times more species rich than strictly tropical clades (Ricklefs & Renner, 1994), and across angiosperm families, the total area occupied by a family is strongly correlated with its richness (Vamosi & Vamosi, 2011).

Although widespread families are generally species rich, the causes of this area-richness correlation remain untested. Speciation resulting from geographical barriers to gene flow should be dominant in families lacking obvious mechanisms for long-distance dispersal (Chown & Gaston, 2000; Givnish, 2010), which we argue should lead to a positive relationship between clade range and species richness and would be manifest in the partitioning of total clade range by relatively narrowly distributed and largely allopatric species. The diversification of widespread lineages could also be ecologically driven, however, as differences in distributions among species within a clade might represent a form of resource partitioning at regional scales, with greater diversity expected the greater the overall range of geographically structured conditions being partitioned by a clade. Given that environmental differences tend to increase with geographical distance (e.g. Lichstein *et al.*, 2002), and that the rate of niche evolution is positively correlated with the rate of diversification and overall richness (Kozak & Wiens, 2010; Gómez-Rodríguez *et al.*, 2015; Spalink *et al.*, 2016), the area-richness correlation might just as rightly be called the niche space-richness correlation. Were this moniker justified, we would expect to see that species-rich clades occupy a broader niche space, and that this niche space was more finely partitioned by the species it contains, than species-poor clades.

The sedge family (Cyperaceae Juss.) presents an ideal opportunity to explore the processes contributing to the diversification and maintenance of biodiversity in relation to clade age, diversification rate, area and niche space. Cyperaceae is cosmopolitan in distribution, composed of roughly 5500 species in *c.* 98 genera and 15 tribes, and the 10th most species-rich family among the angiosperms (Govaerts *et al.*, 2015). The family is hyperdiverse in temperate regions despite a proposed tropical origin for the clade (Givnish *et al.*, 1999; Bremer, 2002). Although the subsequent geographical diversification of Cyperaceae on a family-wide, global scale remains unexplored, this suggests that the species rich, temperate clades are derived from a tropical origin. Thus, in a departure from the pattern observed among many angiosperm lineages, the tropics may be the museum of Cyperaceae origination while subsequent radiations occurred in temperate cradles. Were this true, we would expect to see ancestral area estimates place the Cyperaceae stem lineage in the tropics and significant increases in diversification rate occurring in temperate regions.

Sedge genera vary considerably in richness and geographical extent, ranging from monotypic to containing over 2000 species, and from narrowly restricted to essentially cosmopolitan. Some genera (e.g. *Eriophorum* L.) are adapted to long-distance wind dispersal, but the majority lack obvious dispersal adaptations and are carried short distances by gravity, wind, water or animals (Kern, 1974). As might be expected in a lineage with poor dispersibility, diversification rates are tightly correlated with rates of range and niche evolution among the North American sedges (Spalink *et al.*, 2016). Given this pattern, the lack of dispersal mechanisms in most clades, and the disparity in clade range and species richness within the family, we expect that geographical divergence and physiological adaptation at relatively small spatial scales are key processes in the diversification within Cyperaceae on a global scale. If this is the case, diverse clades should be more widespread and occupy a broader niche space than species-poor clades, geographical and ecological space should be more finely partitioned by species within diverse clades, and net diversification rates should be greater in clades where this partitioning occurs.

In this article, we explore the evolutionary, geographical and ecological patterns that are manifest in the distribution of sedge richness throughout the globe. We construct a fossil-calibrated chronogram of Poales, estimate the historical biogeographical divergence of Cyperaceae, and measure net rates of diversification to test the tropical museum-temperate cradle hypothesis for the family. We then integrate this framework with millions of georeferenced herbarium records to test the hypothesis that clades occurring over large geographical and ecological extents are more diverse than spatially and ecologically restricted clades; that clade richness and diversification rate increase with the ratio of the average species range within a clade to the clade's overall range; that clade richness and diversification rate similarly increase with the ratio of the average species niche space within a clade to the clade's overall niche space; and that clade richness is more tightly correlated with these ratios than to clade age or speciation rate.

MATERIALS AND METHODS

Molecular dating analysis

The fossil record is poor within Cyperaceae (Smith *et al.*, 2010), so we designed our sampling to accommodate as many fossils as possible from Poales rather than relying entirely on a secondary Cyperaceae crown prior and the few sedge fossils. Through *de novo* sequencing of the chloroplast DNA genes *matK*, *ndhF*, *rbcL* and *trnL-F*, and downloading supplemental data from GenBank, we included a total of 384 taxa, of which 295 taxa represent all tribes and 80 out of 98 genera in Cyperaceae (Govaerts *et al.*, 2015). We utilized placeholders for the orders Zingiberales, Commelinales and

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Arecales as outgroups. The remaining taxa were selected to optimize the placement of fossil priors. Details regarding sampling and laboratory procedures are provided in Appendix S1.

Phylogenetic inference and divergence-time estimation were conducted using a lognormal clock and Yule speciation process in BEAST 1.8.0 (Drummond *et al.*, 2012). We offset the ages of 20 nodes throughout Poales and the stem nodes of the four commelinid orders. The placement, offsets and priors for all age constraints are listed in Table 1 and discussed in detail in Appendix S1. We conducted a second BEAST analysis, sampling only from the priors, to assess whether any priors were being overridden by the data. We also tested an exponential clock and a birth-death process to determine if these resulted in a reconstruction different than that obtained using a lognormal clock and Yule process.

Ancestral area estimation

We estimated ancestral areas using the program BioGeoBEARS (Matzke, 2014), which incorporates a 'jump dispersal' (J) parameter that treats dispersal as a cladogenetic process and has been shown through simulation and empirical studies to significantly improve model likelihoods (Matzke, 2014). Given the cosmopolitan distribution of Cyperaceae and the disparate range sizes of individual clades and species within the family, we chose the DEC (dispersal-extinction-cladogenesis; Ree & Smith, 2008) and DEC+J models for ancestral area estimations for their inclusion of parameters allowing both sympatric and vicariant events that involve descendants inheriting only a portion of their ancestral range. We built these models using the maximum clade credibility tree from BEAST after pruning it to include only cyperids (Cyperaceae, Juncaceae Juss., Thurniaceae Engl.), and accounted for phylogenetic uncertainty by analysing an additional 100 pruned trees selected at random from the BEAST posterior. We then compared the likelihoods of our data given the nested DEC and DEC+J models using likelihood ratio tests. To measure the probability of dispersal given the biogeographical models, distribution data and phylogeny, we conducted 100 stochastic mapping replicates on the maximum clade credibility tree and averaged the occurrences of

Table 1 List of fossil and secondary priors utilized in BEAST analysis. The systematic placement, crown and stem positions, prior distributions and offsets (Ma = millions of years ago) are provided for each prior. Sources provide fossil descriptions and justifications for prior distributions and offsets. PACMAD = Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, Danthonioideae. BEP = Bambusoideae, Ehrhartoideae, Pooideae.

Systematic affinity	Position	Prior distribution	Offset (Ma)	Source
Cyperaceae				
Cariceae	Crown	Lognormal	33.9	Smith *et al.* (2010)
Scleria	Crown	Lognormal	33.9	Smith *et al.* (2010)
Scirpus	Crown	Lognormal	28.4	Smith *et al.* (2010)
Cladium	Crown	Lognormal	25.7	Smith *et al.* (2010)
Fimbristylis, excluding *F. variegata*	Crown	Lognormal	25.7	Smith *et al.* (2010)
Mapanioideae	Crown	Lognormal	48	Smith *et al.* (2009)
Poacae				
Setaria	Crown	Lognormal	7	Elias (1942)
Distichlis	Stem	Lognormal	14	Dugas & Retallack (1993)
Chloridoideae	Crown	Lognormal	19	Strömburg (2005)
Bambusoideae	Crown	Lognormal	35	Strömburg (2005)
PACMAD clade	Crown	Lognormal	40	Zucol *et al.* (2010)
Pooideae	Crown	Lognormal	40	Zucol *et al.* (2010)
BEP clade	Crown	Lognormal	67	Prasad *et al.* (2010)
Other Poales				
Juncus, Distichia, Oxychloe, Patosia, Marsippospermum, and *Rostkovia,* but excluding *J. capitatus* and *J. trifidus*	Crown	Lognormal	33.9	Collinson (1983); Collinson & Cleal (2001)
Restionaceae	Crown	Lognormal	70	Knoblock & Mai (1986)
Typhaceae	Crown	Lognormal	70	Knoblock & Mai (1986)
Secondary Calibrations				
Poales	Crown	Uniform	83–116	Janssen & Bremer (2004); Merckx *et al.* (2008)
Commelinales+Zingiberales	Crown	Uniform	81–122	Wilkström *et al.* (2001); Kress & Specht (2006)
Poales+Commelinales+Zingiberales	Crown	Uniform	84–123	Mennes *et al.* (2013); Magallón & Castillo (2009)
Commelinidae	Crown	Uniform	93–128	Mennes *et al.* (2013); Magallón & Castillo (2009)

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vicariance, sympatry and jump dispersal. To ensure the robustness of the patterns observed in these models to the assumptions inherent to DEC, we also estimated ancestral areas using the DIVA (dispersal–vicariance analysis; Yu *et al.*, 2010) and BayArea (Landis *et al.*, 2013) models as implemented in BioGeoBEARS. Additional details regarding model development, including the geographical regions involved, species coding, temporal stratification, and dispersal probabilities among the geographical regions through time are provided in Appendix S1.

Correlates of diversity

We estimated diversification rates using BAMM 2.0 (Rabosky *et al.*, 2014). To account for incomplete taxonomic sampling, we assigned tips to the smallest clades for which species richness could confidently be calculated based on phylogenetic, morphological and taxonomic data, and specified the proportion of the total clade diversity sampled in the phylogeny (Govaerts *et al.*, 2015; see Table S3 in Appendix S2). We initiated two independent chains of 25,000,000 generations, assessed convergence and effective sample sizes using CODA (Plummer *et al.*, 2006), and identified the model with the highest Bayes factor score as the overall best model (Rabosky *et al.*, 2014). We then calculated the average net diversification rate for each clade originally used to assign species richness. We repeated this analysis seven times by increasing the Poisson rate prior from 0.7 to 1.3 by 0.1 increments to determine the robustness of the results.

To identify correlations between clade richness, age, diversification rate, area and niche, we characterized the distributions of every sedge species for which specimen data were available. We mined the Global Biodiversity Information Facility (GBIF; www.gbif.org) and downloaded all georeferenced samples recorded as having no known coordinate ambiguities (accessed 3 November 2015). We supplemented this data set using the online databases of herbaria that have not contributed their data to GBIF, and also contacted curators directly from herbaria that have been digitized but whose data are not publically available. As public databases are useful but prone to error (Maldonado *et al.*, 2015; Spalink *et al.*, 2016), we subjected our waypoint data set to a series of rigorous filtering steps. First, to ensure that each record matched a correct taxon name, we used Taxonstand (Cayuela & Oksanen, 2014) to validate and update names as necessary. We eliminated all records with ambiguous names. We then plotted the specimen records for each species individually, eliminated records that were clearly outside of their species' ranges, and ensured that the remaining waypoints captured the species ranges as characterized in the eMonocot portal (www.emonocot.org; accessed 10 November 2015). Finally, we eliminated all duplicate records. After filtering the waypoint data, we assigned each species to one of the clades identified in the BAMM analysis using *Sedges of the World* (eMonocot Team Cyperaceae, 2015; see Table S3) as a guide.

To measure the range sizes of species and clades, we developed a world-wide 7 arc-degree grid map under the WGS84 coordinate system. These cell dimensions were selected after a series of trials to determine the optimum size that sufficiently captured species' ranges based on available data without unnecessarily sacrificing resolution. We then calculated the total area of each grid cell, overlaid the waypoint data onto the map, and summed the total area of the cells in which the waypoints occurred for each species. To measure the degree to which geographical space is partitioned among species within a clade, we calculated the range size of each species relative to the total range of the clade in which it is contained. We also measured the average range overlap among species within each clade by dividing the number of cells shared by any two species by their total collective range. To calculate the niche space occupied by each species and clade, we overlaid the waypoint data on 18 bioclimatic raster layers downloaded from WorldClim (Hijmans *et al.*, 2005) at 5 arc-minutes resolution. We calculated the total range of values for every variable and clade, and the average of the range of values of the species within the clades. We then calculated the size of the climatic niche space for every clade and the relative sizes of the species within the clades.

Using these data (see Appendix S2, Table S4), we tested a series of hypotheses to identify which factors are most significantly associated with clade richness using phylogenetic generalized least squares (PGLS) regressions. We used a skeleton tree derived from the beast maximum clade credibility tree, with clades reduced to single tips as identified in the BAMM analysis ($n = 36$), and repeated the analyses using 100 trees randomly selected from the beast posterior. We regressed clade richness against crown and stem ages, net rate of diversification, clade range, mean latitude, relative range of species within the clades, average range overlap of species within the clades, clade niche breadth, and the relative niche breadth of species within the clades. We similarly regressed average clade range and diversification rate against these variables. We log-transformed all variables prior to regression, and conducted PGLS analyses using *caper* (Orme *et al.*, 2013).

RESULTS

Phylogenetic analysis and divergence-time estimates

The final data set consisted of *matK* data for 232 taxa, *ndhF* data for 265 taxa, *rbcL* data for 359 taxa, and *trnL-F* data for 303 taxa and in total was comprised of 384 taxa and 4953 aligned base pairs (see Table S5 in Appendix S2). Our chronogram provides moderate to strong support for most familial relationships in Poales and is consistent with previous analyses (Fig. 1; see Figure S1 in Appendix S3). A comparison of posterior marginal probability distributions between the analyses with and without nucleotide sequence data indicates that the *Juncus vectensis* Collinson prior is overridden when molecular data are included, suggesting that

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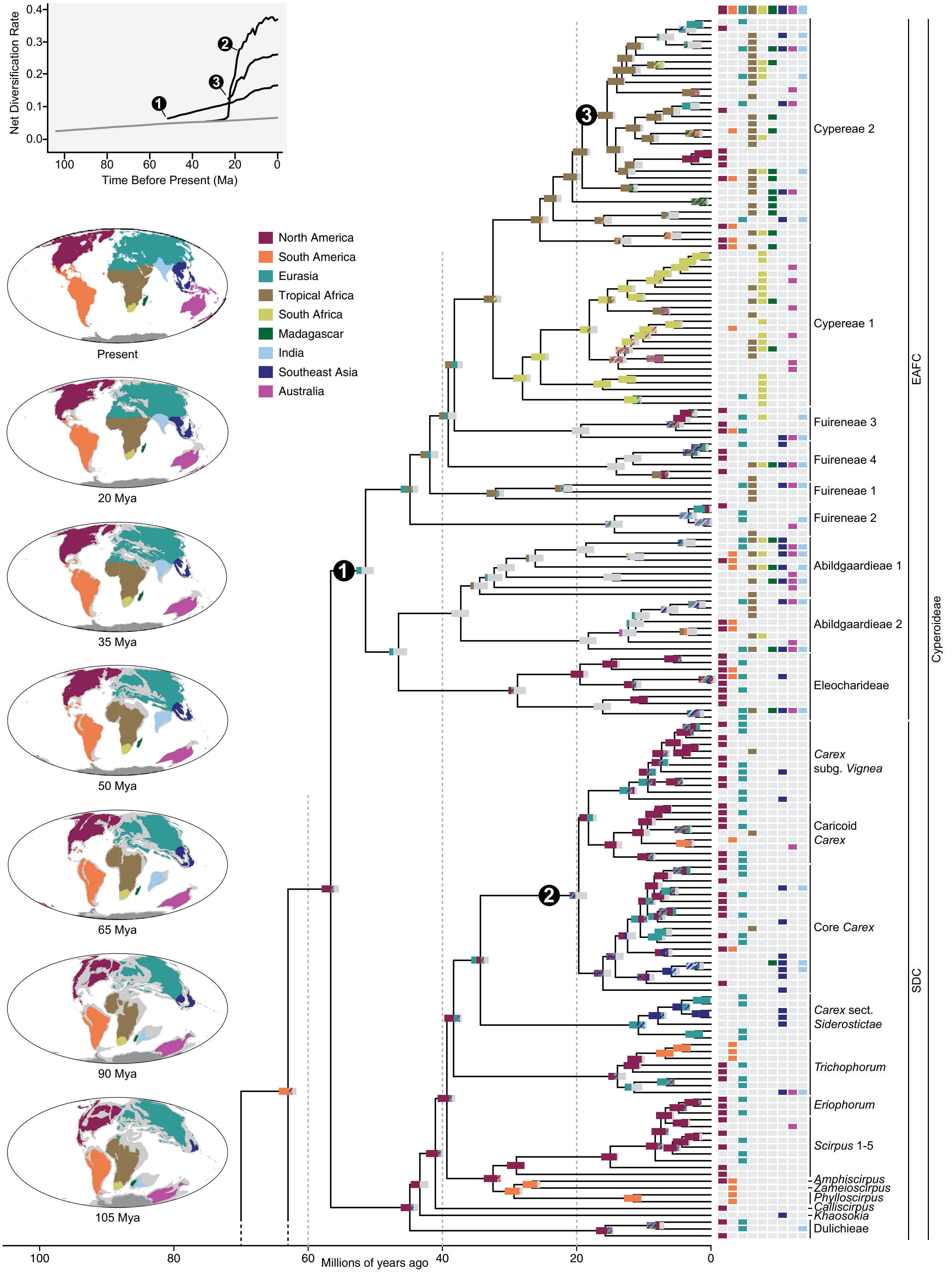
Net Diversification Rate
0.4
0.3
0.2
0.1
0.0
100
80
60
40
20
0
Time Before Present (Ma)
1
2
3
Present
20 Mya
35 Mya
50 Mya
65 Mya
90 Mya
105 Mya
North America
South America
Eurasia
Tropical Africa
South Africa
Madagascar
India
Southeast Asia
Australia
Cypereae 2
Cypereae 1
Fuireneae 3
Fuireneae 4
Fuireneae 1
Fuireneae 2
Abildgaardieae 1
Abildgaardieae 2
Eleocharideae
Carex subg. *Vignea*
Caricoid *Carex*
Core *Carex*
Carex sect. *Siderostictae*
Trichophorum
Eriophorum
Scirpus 1-5
Amphiscirpus
Zameioscirpus
Phylloscirpus
Calliscirpus
Khaosokia
Dulichieae
EAFC
SDC
Cyperoideae
100
80
60
Millions of years ago
40
20
0

Figure 1

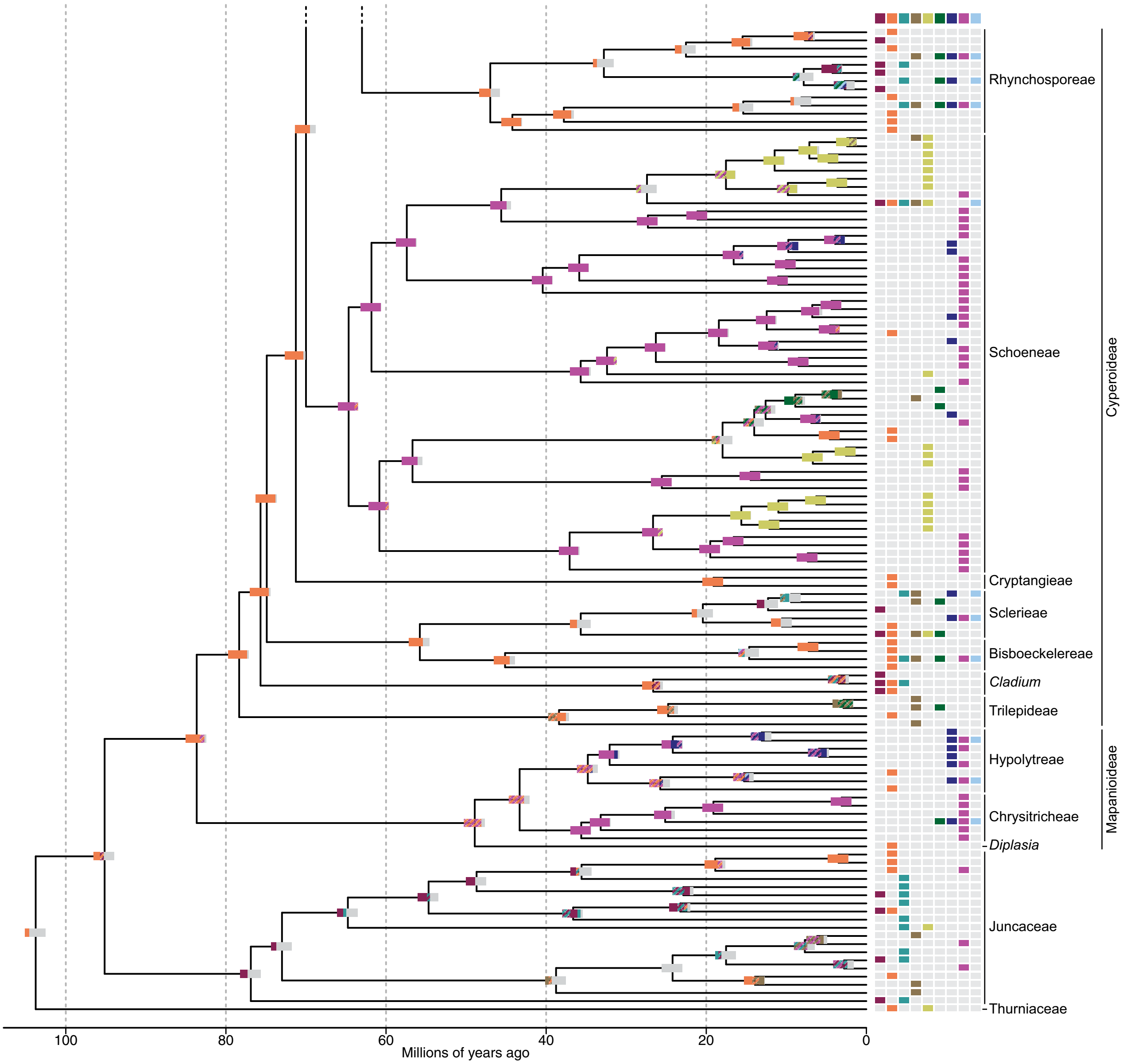

Figure 1 BEAST chronogram, DEC+J model for the estimated historical biogeographical areas occupied, and BAMM rates of diversification of the cyperids. Node labels represent the relative probabilities of the ancestral area occupied by each inferred ancestor based on the DEC+J model. All possible ancestral areas with at least 15% likelihood are represented, with grey bars representing the sum of all estimated areas with lower than 15% likelihood. Node colours correspond to the areas on the maps, with diagonals representing widespread ancestral areas that include more than a single region. The ranges of extant taxa are indicated by tip labels. World maps show geographical areas defined for ancestral area estimation and their estimated locations throughout geological time. In these maps, grey areas represent uncertainty regarding the extent of exposed continental shelf and are based on the reconstructions of Blakely (© Ron Blakey, Colorado Plateau Geosystems). Inset diversification-through-time plot shows the background net diversification rate of the cyperids as a grey line, while the three black lines represent the three numbered clades involved in diversification rate shifts. Numerical labels correspond to numerical node labels on the chronogram, which indicate the location of the rate shifts. Diversification rate units are in species species^{-1} million years^{-1}.

its use as an offset on the crown of *Juncus s.l.* is inappropriate and it should be placed on a more internal node. Subsequent results are based on analyses conducted with this prior omitted. Differences between the analyses with the lognormal and exponential clock prior and between the Yule and birth-death processes were trivial, and all node ages were within each other's 95% confidence intervals. Within Cyperaceae, subfamilies Mapanioideae and Cyperoideae are both supported as monophyletic and relationships within subfamilies are in agreement with previous analyses. Our analysis dates the Poales crown to 116 Ma [95% confidence interval (CI) = 112–127 Ma], the divergence of Cyperaceae and

Juncaceae to 96 Ma (95% CI = 88–100 Ma), and the Cyperaceae crown to 85 Ma (95% CI = 77–89 Ma).

Ancestral area estimations

The inclusion of the 'J' parameter in the DEC+J model produced significantly more likely ancestral estimations than the DEC model alone as indicated by likelihood ratio tests (DEC LnL = −1095; DEC+J LnL = −1048, *P*-value = 1.61×10^{-22}). We found no instances where the most likely area estimated for nodes of interest in the maximum clade credibility tree differed from the most commonly estimated area among the 100 trees from the BEAST posterior. We therefore base all subsequent discussions on the DEC+J model constructed on the maximum clade credibility tree. Given the parameters of this model, 63% of cladogenetic events involve sympatry, 14% involve vicariance and 23% involve jump dispersals.

Our estimations place the crown of the cyperids, the most recent common ancestor (MRCA) of Cyperaceae and Juncaceae, and the Cyperaceae crown in South America in the Late Cretaceous (Fig. 1). Within Cyperaceae, our model suggests two independent Cretaceous migrations to Australia from South America, first along the stem of subfamily Mapanioideae and second along the stem of tribe Schoeneae. Most diversification within subfamily Mapanioideae occurred within Australia and South America, while migrations to India, Southeast Asia and Africa occurred from an Australian source in tribe Schoeneae. Tribes Trilepideae, Bisboeckelereae, Sclerieae, Rhynchosporeae, and the genus *Cladium* P.Browne originated within South America and migrated throughout the Southern Hemisphere with only occasional introductions to the Northern Hemisphere.

Our model places the first arrival of Cyperaceae in the Northern Hemisphere in the beginning of the Palaeocene (*c.* 63 Ma) following a dispersal event from South America to North America along the stem of the MRCA of the Dulicheae-Scirpeae-Cariceae (DSC) and Eleocharideae-Abildgaardieae-Fuireneae-Cypereae (EAFC) clades. All DSC backbone cladogenetic events are estimated to have occurred in North America, from which migrations to Eurasia and the Southern Hemisphere are suggested. Tribe Cariceae originated in eastern Eurasia, with migration to North America occurring along the stem of the hyperdiverse, non-*Siderostictae* clade of *Carex*. Within the EAFC clade, the Northern Hemisphere remained the primary site of cladogenesis in Eleocharideae. A return to tropical Africa from a Eurasian source coincided with the diversification of tribes Fuireneae, Abildgaardieae and Cypereae. While the Cypereae 1 clade diversified in South Africa, tropical Africa hosted the radiation of the Cypereae 2 clade.

These patterns were all recovered in the DIVA and BayArea models when the J parameter was included, which also resulted in significantly better models than when this parameter was omitted (*P*-value $< 1 \times 10^{-15}$; see Appendix S3, Figures S2 and S3). All analyses placed the origin of Cyperaceae within South America, the diversification of the EAFC clade within the Northern Hemisphere (with the inclusion of Australia in the BayArea model), the DSC clade within North America and Eurasia, and the Cypereae 2 clade within tropical Africa.

Dynamics of diversification

BAMM analyses converged and achieved sufficient effective samples sizes after 25,000,000 generations. The best fitting model favoured three shifts in speciation rate to explain levels of diversity in Cyperaceae (Fig. 1), and these shifts were robust to changes to the priors. The earliest shift in net diversification rate occurred *c.* 52 Ma on the stem leading to the EAFC clade, increasing net diversification rates to 0.075 sp sp^{-1} myr^{-1}. The second shift occurred *c.* 20 Ma on the stem leading to the non-*Siderostictae Carex*, increasing net diversification rates to 0.4 sp sp^{-1} myr^{-1}. The final shift occurred *c.* 15 Ma within the Cypereae 2 clade, increasing net diversification rates to 0.29 sp sp^{-1} myr^{-1}.

We obtained a total of 4,834,838 specimen records representing 4511 taxa from GBIF, the Consortium of Northeastern Herbaria (neherbaria.org), the Intermountain Regional Herbarium Network (intermountainbiota.org), AAU, ALA, AVH, HUH, IFP, JAQC, KSC, NHN, RM, SASK, USCH and WIS. Following our filtering steps, our final data set consisted of 2,678,553 records for 4290 species.

Based on phylogenetic generalized least squares regressions (Table 2), clade species richness increased with net diversification rate ($r^2 = 0.41$), clade range ($r^2 = 0.56$) and niche space as measured by all bioclimatic variables (average $r^2 = 0.31$), and increased as the relative species ranges ($r^2 = 0.81$), the proportion of sympatric species ($r^2 = 0.47$), and the relative size of species niche space ($r^2 = 0.66$) decreased. Clade range increased with diversification rate ($r^2 = 0.34$), average clade niche space ($r^2 = 0.62$), and the average range of individual species ($r^2 = 0.32$), and increased as clade age ($r^2 = 0.21$ for crown ages and $r^2 = 0.16$ for stem ages), the relative species ranges ($r^2 = 0.61$), and the proportion of sympatric species ($r^2 = 0.47$) decreased. Net diversification rate increased with clade range ($r^2 = 0.34$) and clade niche space ($r^2 = 0.14$), and increased as the relative species range ($r^2 = 0.40$), proportion of sympatric species ($r^2 = 0.23$), and relative species niche space ($r^2 = 0.23$) decreased. All significant regressions in the maximum clade credibility tree were robust to topological uncertainty as assessed using 100 trees from the BEAST posterior (Table 2).

DISCUSSION

Divergence-time estimations are improved with additional fossils

Our data set, which includes the largest BEAST chronogram of Cyperaceae in terms of number of taxa, loci and fossil calibrations included, corroborates recent hypotheses regarding the timing of Cyperaceae diversification (Escudero *et al.*, 2012;

Table 2 Phylogenetic generalized least squares (PGLS) regressions. Values in parentheses represent the average and standard deviation of the values obtained from analyses conducted on 100 trees randomly selected from the BEAST posterior. Only significant relationships are shown. (a) PGLS regressions with clade richness as the response variable. (b) PGLS regressions with clade range as the response variable. (c) PGLS regressions with diversification rate as the response variable.

Predictor variable	R^2	Slope	*P*-value
(a) Response variable: clade richness			
Diversification rate	0.41 (0.43, 0.02)	2.66 (2.56, 0.11)	2.42E-5 (1.45E-5, 8.49E-6)
Clade range	0.56 (0.57, 0.02)	1.08 (1.11, 0.02)	1.74E-7 (1.18E-7, 9.8E-8)
Relative species range	0.82 (0.82, 0.01)	−1.78 (−1.61, 0.02)	8.37E-14 (6.7E-14, 1.84E-13)
Species range overlap	0.47 (0.49, 0.02)	−1.04 (−1.07, 0.03)	4.56E-6 (2.14E-6, 1.56E-6)
Average clade niche space	0.31 (0.32, 0.02)	1.19 (1.26, 0.05)	2.50E-3 (1.09E-3, 4.10E-4)
Relative species niche space	0.66 (0.65, 0.02)	−2.91 (−2.93, 0.08)	1.13E-5 (1.89E-6, 3.98E-6)
(b) Response variable: clade range			
Crown age	0.21 (0.21, 0.03)	−1.08 (−1.09, 0.05)	4.7E-3 (6.52E-3, 4.39E-3)
Stem age	0.16 (0.19, 0.03)	−1.22 (−1.35, 0.11)	1.50E-2 (9.09E-3, 6.58E-3)
Diversification rate	0.34 (0.38, 0.03)	1.62 (1.63, 0.03)	1.89E-4 (8.79E-5, 7.52E-5)
Clade richness	0.56 (0.57, 0.02)	0.50 (0.52, 0.01)	1.74E-7 (1.18E-7, 9.8E-8)
Average species range	0.32 (0.32, 0.02)	0.93 (0.97, 0.01)	5.78E-5 (3.53E-4, 2.07E-4)
Relative species range	0.61 (0.64, 0.02)	−1.03 (−0.97, 0.02)	1.72E-8 (8.59E-9, 9.88E-9)
Species range overlap	0.51 (0.54, 0.03)	−0.74 (−0.77, 0.03)	8.84E-7 (5.45E-7, 6.39E-7)
Average clade niche space	0.62 (0.62, 0.01)	1.13 (1.16, 0.03)	1.45E-6 (2.04E-6, 7.49E-7)
Relative species niche space	0.47 (0.47, 0.03)	−1.64 (−1.69, 0.06)	1.13E-5 (1.69E-5, 1.55E-5)
(c) Response variable: diversification rate			
Clade range	0.34 (0.38, 0.03)	0.21 (0.23, 0.02)	1.89E-4 (8.79E-5, 7.52E-5)
Relative species range	0.40 (0.43, 0.02)	−0.27 (−0.30, 0.03)	3.56E-5 (1.75E-5, 1.51E-5)
Species range overlap	0.23 (0.25, 0.02)	−0.29 (−0.20, 0.02)	3.13E-3 (2.04E-3, 1.07E-3)
Average clade niche space	0.14 (0.16, 0.01)	0.19 (0.23, 0.02)	2.80E-2 (1.76E-2, 4.53E-3)
Relative species niche space	0.23 (0.22, 0.02)	−0.41 (−0.44, 0.03)	4.39E-3 (5.71E-3, 2.11E-3)

Escudero & Hipp, 2013; Bouchenak-Khelladi *et al.*, 2014). We see three benefits of placing Cyperaceae within a broad Poales framework. First, increasing outgroup sampling allowed us to avoid depending on secondary priors on key nodes of interest – in this instance, the crown and stem nodes of Cyperaceae. While we acknowledge the importance of secondary priors (Magallón *et al.*, 2013; Sytsma *et al.*, 2014), placing key nodes of interest in a more fossil-rich context lowers the probability of introducing bias in divergence-time estimates by constraining these nodes themselves. Second, by increasing sampling of both taxa and fossils we were able to demonstrate that the use of *Juncus vectensis* as a *Juncus* crown fossil prior is not appropriate. Although this is the oldest known *Juncus* fossil, dated to the Eocene-Oligocene boundary (33.9 Ma), our results indicate that the *Juncus s.l.* crown is much older. Third, despite placing priors under lognormal distributions with larger standard deviations than previous analyses (e.g. Escudero & Hipp, 2013), the 95% confidence intervals surrounding node ages are smaller in our analysis. This relationship between the number of fossil priors and the precision of divergence-time estimates has been demonstrated with both empirical and simulated data sets (Battistuzzi *et al.*, 2010; Bibi, 2013; Magallón *et al.*, 2013).

Ancestral area estimations suggest a tropical museum but multiple cradles

Our ancestral area estimation is the first to examine the global geographical diversification of Cyperaceae. The model we present is consistent with trends emerging from studies of similarly distributed clades that postdate the initial breakup of Gondwana (180–150 Ma; White *et al.*, 2013), and we highlight three major patterns here. First, we find that an interplay of migration and extinction events between South America and Australia in the Cretaceous, at the exclusion of Africa, account for geographical divergence of early sedge lineages in the Southern Hemisphere. Most recent models suggest that Patagonia and the Antarctic Peninsula were connected until *c.* 57 Ma (Reguero *et al.*, 2014) and that Australia and Eastern Antarctica separated only *c.* 45 Ma (White *et al.*, 2013). South America and Australia were therefore a nearly continuous landmass until at least the Palaeocene. While we lack the fossil evidence to confirm that Antarctica facilitated the Southern Hemispheric patterns observed during the Cretaceous, our model serves as one more example of a vicariant pattern between South America and Australia following the breakup of Gondwana (e.g. Nothofagaceae Kuprian, Swenson *et al.*, 2001; *Fuchsia* L., Berry *et al.*, 2004; Proteaceae Juss., Milner *et al.*, 2015; Brassicales Brom., Cardinal-McTeague *et al.*, 2016).

Second, our model suggests that dispersal between South America and Africa and between Africa and Australia, patterns observed in several other Southern Hemispheric lineages (e.g. Givnish & Renner, 2004; Sytsma *et al.*, 2004; Viljoen *et al.*, 2013; Berger *et al.*, 2015), coincided with the diversification of tribes Schoeneae, Bisboechelereae, Trilepideae, Rhynchosporeae, Fuireneae and Abildgaardieae. Interestingly, our model indicates that all direct dispersal events

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between Australia and Africa occurred prior to the end of the Eocene (*c.* 34 Ma). We propose that the Indian subcontinent, which commenced its rapid journey from the southern Indian Ocean in the Palaeocene and began to collide with Asia by the middle Eocene (DeCelles *et al.*, 2014), may have facilitated these early dispersals between Australia and Africa at the exclusion of Asia (Conti *et al.*, 2002; Cardinal-McTeague *et al.*, 2016). This was a unique moment in history, where the Indian Ocean contained a large landmass that could have served as an intermediary dispersal point. As a point of contrast, all instances in our model of Southern Hemispheric migrations involving both Africa and Australia since the Eocene also involve distributions that include Southeast Asia and/or Eurasia. These results are consistent with the independent analysis of tribe Schoeneae as presented by Viljoen *et al.* (2013), and are not biased by our temporal partitioning of the model, which maintains constant dispersal probabilities between Australia and Africa since the end of the Cretaceous.

Third, while the South American tropics appear to have been the site of origin for the family, the temperate Northern Hemisphere is the primary cradle of diversification. The migration of the sedges into the Northern Hemisphere in the Eocene appears to be an important event for the diversification of Cyperaceae, as the descendants of this ancestor account for over 76% of the total diversity in the family. This migration was followed almost immediately by the first increase in diversification rate that we observe in our data along the stem of the EAFC clade (Fig. 1, #1). The second increase in diversification rate, which occurred along the stem of the non-*Siderostictae Carex* (Fig. 1, #2), was also a Northern Hemispheric event occurring in the more temperate Miocene. Tropical Africa, however, hosted the third major increase in diversification rate and is the cradle for the genus *Cyperus* L. (Fig. 1, #3).

Range and niche partitioning are strongly associated with sedge diversity

The results from our biogeographical stochastic mapping indicate that 23% of the cladogenetic events in our model involved dispersal. To our knowledge, this is the highest rate of cladogenetic dispersal observed in any study of this kind to date (e.g. Matzke, 2014; Berger *et al.*, 2015; T. Givnish, unpublished data). Clearly, reproductive isolation resulting from long-distance dispersal has contributed to the diversification of the sedges. And yet, 63% of cladogenetic events in our model were characterized as sympatric given our discretization of space in this model. In reality, any discretization of geographical space is a subjective imposition on the continuous dynamics of species' ranges. By increasing the resolution of this discretization in our grid analyses, we uncovered several patterns suggesting that sympatric speciation in the strict sense is likely not a common event in Cyperaceae.

First, our analyses confirm that the total range of a clade is correlated with its richness ($r^2 = 0.56$, Table 2A). This pattern has been uncovered many times, but almost always as an interfamilial phenomenon (Vamosi & Vamosi, 2011), and very rarely as an intrafamilial pattern (Ricklefs & Renner, 1994). Second, we find that the ratio of average species range to clade range is the trait most strongly correlated with clade richness ($r^2 = 0.82$). Furthermore, although clade range increases with average species range within that clade ($r^2 = 0.32$), it also increases with allopatry among those species ($r^2 = 0.61$) and decreases as species occupy a larger proportion of the total clade range ($r^2 = 0.51$). Thus, the partitioning of geographical space – as would be expected under a model of geographical speciation involving limited dispersal, and possible specialization on local conditions and partitioning of environmental resources at regional scales – is reflected in the diversification of the species-rich clades in Cyperaceae.

Third, our results suggest that the niche space occupied by a clade ($r^2 = 0.31$) is a good predictor of clade richness, and the partitioning of this niche space ($r^2 = 0.66$) is the second best predictor of richness following the partitioning of geographical space (Table 2B). It remains challenging to determine whether niche occupancy is an artefact of range exploration or a causative agent in diversification. We suggest, however, that the area-richness correlation observed among angiosperm families (Vamosi & Vamosi, 2011) should be revisited from this ecological perspective. Fourth, consistent with our expectations under a model of geographical speciation, we find that clades that are more widespread, occupy more niche space, and exhibit more finely partitioned geographical and ecological space have diversified more quickly than more geographically and ecologically restricted clades (Table 2C). While these results would be strengthened by sister-species comparisons of range and niche on a global scale, they corroborate a recent analysis of the North American sedge flora, which had over 75% complete sampling and found very close correlations of speciation rate with the rates of range and climatic niche evolution (Spalink *et al.*, 2016). Fifth, we find that clade range, range partitioning, species allopatry, and niche partitioning are all better predictors of clade richness than net diversification rates, highlighting the importance of geography in the diversification of Cyperaceae. Lastly, we found no correlation between clade richness and age, a relationship that was supported in previous studies when the operational taxonomic unit was restricted to the sedge tribes ($n = 28$, compared to our $n = 36$; Escudero & Hipp, 2013).

Our integration of fossil, molecular, climatic, biogeographical and herbarium data allowed us to tackle two of the most persistent questions in biogeography: Why are some clades more diverse in temperate regions than the tropics, and what are the underlying patterns explaining the area-richness correlation across angiosperms? We established South America as the museum of sedge diversification, present an ancestral area estimation that invokes dispersal as the mechanism by which the sedges have covered the globe, and demonstrate that high temperate diversity is explained by two non-

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tropical cradles. Lastly, we show that species-rich clades are not only more widespread, occupy more niche space, and diversify more quickly, but also exhibit patterns that are consistent with the partitioning of geographical and ecological space as a major contributor to diversification. However, diversification of any lineage is a complex and non-linear process. While we have focused on the extrinsic variables associated with the diversification of Cyperaceae, and the key role of resource partitioning and clade range versus individual species range, we recognize that they form only a part of the story. The chromosomal lability of *Carex,* the multiple origins of C_4 photosynthesis in tribes Abildgaardieae and Cypereae, and the invasion of high latitudes by the DSC clades are also surely involved (Escudero *et al.*, 2012; Bouchenak-Khelladi *et al.*, 2014; Spalink *et al.*, 2016).

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REFERENCES

Battistuzzi, F.U., Filipski, A., Hedges, S.B. & Kumar, S. (2010) Performance of relaxed-clock methods in estimating evolutionary divergence times and their credibility intervals. *Molecular Biology and Evolution*, **27**, 1289–1300.

Berger, B.A., Kriebel, R., Spalink, D. & Sytsma, K.J. (2015) Divergence times, historical biogeography, and shifts in speciation rates of Myrtales. *Molecular Phylogenetics and Evolution*, **95**, 116–136.

Berry, P.E., Hahn, W.J., Systma, K.J., Hall, J.C. & Mast, A. (2004) Phylogenetic relationships of Fuchsia (Onagraceae) based on noncoding nuclear and chloroplast DNA data. *American Journal of Botany*, **91**, 601–614.

Bibi, F. (2013) A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla, Ruminantia) and the importance of the fossil record to systematics. *BMC Evolutionary Biology*, **13**, 166.

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.

Bremer, K. (2002) Gondwanan evolution of the grass alliance of families (Poales). *Evolution*, **56**, 1374–1387.

Cardinal-McTeague, W.M., Sytsma, K.J. & Hall, J.C. (2016) Biogeography and diversification of Brassicales: a 103 million year chronicle. *Molecular Phylogenetics and Evolution*, **99**, 204–224.

Cayuela, L. & Oksanen, J. (2014) *Taxonstand: taxonomic standardization of plant species names*. R package version 1.7. http://CRAN.R-project.org/package=Taxonstand.

Chown, S.L. & Gaston, K.J. (2000) Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology and Evolution*, **15**, 311–315.

Collinson, M.E. (1983) Palaeofloristic assemblages and palaeoecology of the Lower Oligocene Bembridge Marls, Hamstead Ledge, Isle of Wight. *Botanical Journal of the Linnean Society*, **86**, 177–225.

Collinson, M.E. & Cleal, C.J. (2001) Late middle Eocene-early Oligocene (Bartonian-Rupelian) and Miocene palaeobotany of Great Britain. *Mesozoic and Tertiary palaeobotany of Great Britain* (ed. by C.J. Cleal, B.A. Thomas, D.J. Batten and M.E. Collinson), pp. 227–274. Geological Conservation Review Series No. 22, Join Nature Conservation Committee, Peterborough, UK.

Conti, E., Eriksson, T., Schönenberger, J., Sytsma, K.J. & Baum, D.A. (2002) Early Tertiary out-of-India dispersal of Crypteroniaceae: evidence from phylogeny and molecular dating. *Evolution*, **56**, 1931–1942.

DeCelles, P.G., Kapp, P., Gehrels, G.E. & Ding, L. (2014) Paleocene-Eocene foreland basin evolution in the Himalaya of southern Tibet and Nepal: implications for the age of initial India-Asia collision. *Tectonics*, **33**, 824–849.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**, 1969–1973.

Dugas, D.P. & Retallack, G.J. (1993) Middle Miocene fossil grasses from Fort Ternan, Kenya. *Journal of Paleontology*, **67**, 113–128.

Elias, M.K. (1942) Tertiary prairie grasses and other herbs from the high plains. *Geological Society of America Special Papers*, **41**, 7–171.

Escudero, M. & Hipp, A. (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.

Givnish, T.J. (2010) Ecology of plant speciation. *Taxon*, **59**, 1326–1366.

Givnish, T.J. & Renner, S. (2004) Tropical intercontinental disjunctions: Gondwana breakup, immigration from the boreotropics, and transoceanic dispersal. *International Journal of Plant Sciences*, **165**, 1–6.

Givnish, T.J., Evans, T.M., Pires, J.C. & Sytsma, K.J. (1999) Polyphyly and convergent morphological evolution in

© 2016 John Wiley & Sons Ltd

Commelinales and Commelinidae: evidence from *rbcL* sequence data. *Molecular Phylogenetics and Evolution*, **12**, 360–385.

Gómez-Rodríguez, C., Baselga, A. & Wiens, J.J. (2015) Is diversification rate related to climatic niche width? *Global Ecology and Biogeography*, **24**, 383–395.

Govaerts, R., Koopman, J., Simpson, D.A., Goetghebeur, P., Wilson, K., Egorova, T. & Bruhl, J.J. (2015) *World checklist of Cyperaceae*. The Board of Trustees of the Royal Botanic Gardens, Kew.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the Tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102–106.

Janssen, T. & Bremer, K. (2004) The age of major monocot groups inferred from 800+ *rbcL* sequences. *Botanical Journal of the Linnean Society*, **146**, 385–398.

Kern, J.H. (1974) Cyperaceae. *Flora Malesiana*, **7**, 435–753.

Kindlmann, P., Schödelbauerová, I. & Dixon, A. (2007) Inverse latitudinal gradients in species diversity. *Scaling biodiversity* (ed. by D. Storch, P.A. Marquet and J.H. Brown), pp. 246–257. Cambridge University Press, Cambridge.

Knoblock, E. & Mai, D.H. (1986) Monographie der Früchte und Samen in der Kreide von Mitteleuropa. *Rozpravy Ústředního Ústavu Geologického*, **47**, 1–219.

Kozak, K.H. & Wiens, J.J. (2010) Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, **13**, 1378–1389.

Kress, W.J. & Specht, C.D. (2006) The evolutionary and biogeographic origin and diversification of the tropical monocot order Zingiberales. *Aliso*, **22**, 621–632.

Landis, M.J., Matzke, N.J., Moore, B.R. & Huelsenbeck, J.P. (2013) Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology*, **62**, 789–804.

Lichstein, J.W., Simons, T.R., Shriner, S.A. & Franzreb, K.E. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs*, **73**, 445–463.

Magallón, S. & Castillo, A. (2009) Angiosperm diversification through time. *American Journal of Botany*, **96**, 349–365.

Magallón, S., Hilu, K.W. & Quandt, D. (2013) Land Plant Evolutionary Timeline: gene effects are secondary to fossil constraints in relaxed clock estimation of age and substitution rates. *American Journal of Botany*, **100**, 556–573.

Maldonado, C., Molina, C.I., Zizka, A., Persson, C., Taylor, C.M., Albán, J., Chilquillo, E., Rønsted, N. & Antonelli, A. (2015) Estimating species diversity and distribution in the era of Big Data: to what extent can we trust public databases? *Global Ecology and Biogeography*, **24**, 973–984. doi:10.1111/geb.12326.

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. doi:10.1093/sysbio/syu056.

Mennes, C.B., Smets, E.F., Moses, S.N. & Merckx, V.S.F.T. (2013) New insights in the long-debated evolutionary history of Triuridaceae (Pandanales). *Molecular Phylogenetics and Evolution*, **69**, 994–1004.

Merckx, V., Chatrou, L.W., Lemaire, B., Sainge, M.N., Huysmans, S. & Smets, E.F. (2008) Diversification of mycoheterotrophic angiosperms: evidence from Burmanniaceae. *BMC Evolutionary Biology*, **8**, 178.

Milner, M.L., Weston, P.H., Rossetto, M. & Crisp, M.D. (2015) Biogeography of the Gondwanan genus Lomatia (Proteaceae): vicariance at continental and intercontinental scales. *Journal of Biogeography*, **42**, 2440–2451. doi:10.1111/jbi.12588.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.

eMonocot Team Cyperaceae (2015) *eMonocot Cyperaceae*. Available at: http://cyperaceae.e-monocot.org (accessed 10 November 2015).

Orme, D., Freckleton, R., Thomas, G., Petzoltd, T., Fritz, S., Isaac, N & Pearce, W. (2013) *caper: comparative analysis of phylogenetics and evolution in R*. R package version 0.5.2. http://CRAN.R-project.org/package=caper

Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, **100**, 33.

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

Prasad, V., Strömberg, C.A.E., Leaché, A.D., Samant, B., Patnaik, R., Tang, L., Mohabey, D.M., Ge, S. & Sahni, A. (2010) Late Cretaceous origin of the rice tribe provide evidence for early diversification in Poaceae. *Nature Communications*, **2**, 480.

Rabosky, D.L., Donnellan, S.C., Grundler, M. & Lovette, I.J. (2014) Analysis and visualization of complex macroevolutionary dynamics: an example from Australian scincid lizards. *Systematic Biology*, **63**, 610–627.

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.

Reguero, M.A., Gelfo, J.N., López, G.M., Bond, M., Abello, A., Santillana, S.N. & Marenssi, S.A. (2014) Final Gondwana breakup: the Paleogene South American native ungulates and the demise of the South America-Antarctica land connection. *Global and Planetary Change*, **123**, 400–413. doi:10.1016/j.gloplacha.2014.07.016.

Ricklefs, R.E. & Renner, S.S. (1994) Species richness within families of flowering plants. *Evolution*, **48**, 1–18.

Sánchez-Ramírez, S., Etienne, R.S. & Moncalvo, J.-M. (2015) High speciation rate at temperate latitudes explains unusual diversity gradients in a clade of ectomycorrhizal fungi. *Evolution*, **69**, 2196–2209.

Smith, S.Y., Collinson, M.E., Simpson, D.A., Rudall, P.J., Marone, F. & Stampononi, M. (2009) Elucidating the affinities and habitat of ancient, widespread Cyperaceae: *Volkeria messelensis* Gen. Et Sp. Nov., a fossil mapanioid sedge from the Eocene of Europe. *American Journal of Botany*, **96**, 1506–1518.

Smith, S.Y., Collinson, M.E., Rudall, P.J. & Simpson, D.A. (2010) 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 and J.I. Davis), pp. 333–356. Aarhus University Press, Lancaster.

Spalink, D., Drew, B.T., Pace, M.C., Zaborsky, J.G., Li, P., Cameron, K.M., Givnish, T.J. & Sytsma, K.J. (2016) Evolution of geographical place and niche space: patterns of diversification in the North American sedge (Cyperaceae) flora. *Molecular Phylogenetics and Evolution*, **95**, 183–195.

Strömberg, C.A.E. (2005) Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proceedings of the National Academy of Sciences*, **102**, 11980–11984.

Swenson, U., Hill, R.S. & McLoughlin, S. (2001) Biogeography of Nothofagus supports the sequence of Gondwana break-up. *Taxon*, **50**, 1025–1041.

Sytsma, K.J., Litt, A., Zjhra, M.L., Pires, J.C., Nepokroeff, M., Conti, E., Walker, J. & Wilson, P.G. (2004) Clades, clocks, and continents: historical and biogeographical analysis of Myrtaceae, Vochysiaceae, and relatives in the southern hemisphere. *International Journal of Plant Sciences*, **165**, S85–S105.

Sytsma, K.J., Spalink, D. & Berger, B. (2014) Calibrated chronograms, fossils, outgroup relationships, and root priors: re-examining the historical biogeography of Geraniales. *Biological Journal of the Linnean Society*, **113**, 29–49.

Vamosi, J.C. & Vamosi, S.M. (2011) Factors influencing diversification in angiosperms: at the crossroads of intrinsic and extrinsic traits. *American Journal of Botany*, **98**, 460–471.

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

White, L.T., Gibson, G.M. & Lister, G.S. (2013) A reassessment of paleogeographic reconstructions of eastern Gondwana: bringing geology back into the equation. *Gondwana Research*, **24**, 984–998.

Wilkström, N., Savolainen, V. & Chase, M.W. (2001) Evolution of the angiosperms: calibrating the tree of life. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 2211–2220.

Yu, Y., Harris, A.J. & He, X. (2010) S-DIVA (Statistical Dispersal-Vicariance Analysis): a tool for inferring biogeographical histories. *Molecular Phylogenetics and Evolution*, **56**, 848–850.

Zucol, A.F., Brea, M. & Bellosi, E. (2010) Phytolith studies in Gran Barranca (central Patagonia, Argentina): the middle-late Eocene. *The Paleontology of Gran Barranca* (ed. by R.H. Madden, A.A. Carlini, M.G. Vucetich and R.F. Kay), pp. 317–340. Cambridge University Press, Cambridge.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary Materials and Methods.
Appendix S2 Supplementary Tables.
Appendix S3 Supplementary Figures.

BIOSKETCH

Daniel Spalink investigates the diversification of Cyperaceae on a global scale, with particular interest in the North American sedge flora and the genus *Scirpus*. Collectively, our group studies the systematics, phylogenetics, biogeography and evolution of a wide range of angiosperms, including the Asparagales, Asterales, Brassicales, Ericales, Lamiales, Liliales, Myrtales, Poales and Rosales. We are particularly interested in correlates of diversification in these lineages, linking topics such as biogeography, morphology, and ecology with phylogenetics.

Author contributions: D.S. and K.J.S. conceived and undertook the project; K.M.C., B.T.D, T.J.G., M.C.P., J.R.S., D.S. and J.G.Z. collected the data; D.S. analysed the data and led the writing with contributions from all authors.

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