New Phytologist

Research

Global analysis of Poales diversification – parallel evolution in space and time into open and closed habitats

Tammy L. Elliott[1,2]*, Daniel Spalink[3]*, Isabel Larridon[4,5], Alexandre Rizzo Zuntini[4], Marcial Escudero[6], Jan Hackel[4,7], Russell L. Barrett[8], Santiago Martín-Bravo[9], José Ignacio Márquez-Corro[4,9], Carolina Granados Mendoza[10], Aluoneswi C. Mashau[11], Katya J. Romero-Soler[10], Daniel A. Zhigila[12], Berit Gehrke[13], Caroline Oliveira Andrino[14], Darren M. Crayn[15], Maria S. Vorontsova[4], Félix Forest[4], William J. Baker[4], Karen L. Wilson[8], David A. Simpson[4,16] and A. Muthama Muasya[2]

[1]Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlarska 2, Brno, 611 37, Czech Republic; [2]Department of Biological Sciences, University of Cape Town, Cape Town, 7700, South Africa; [3]Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas, TX, 77843-2258, USA; [4]Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK; [5]Systematic and Evolutionary Botany Lab, Department of Biology, Ghent University, K.L. Ledeganckstraat 35, 9000, Gent, Belgium; [6]Department of Plant Biology and Ecology, Faculty of Biology, University of Seville, Reina Mercedes 6, Seville, 41012, Spain; [7]Department of Biology, University of Marburg, Karl-von-Frisch-Str. 8, 35043, Marburg, Germany; [8]National Herbarium of New South Wales, Botanic Gardens of Sydney, Australian Botanic Garden, Locked Bag 6002, Mount Annan, NSW, 2567, Australia; [9]Botany Area, Department of Molecular Biology and Biochemical Engineering, Universidad Pablo de Olavide, ctra. de Utrera km 1, 41013, Seville, Spain; [10]Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, CP 04510, Mexico; [11]Foundational Research and Services, South African National Biodiversity Institute (SANBI), Private Bag X101, Pretoria, 0184, South Africa; [12]Department of Botany, Gombe State University, Tudun Wada, Gombe, 760001, Nigeria; [13]Universitetet i Bergen, Universitetsmuseet, Postboks 7800, NO-5020, Bergen, Norway; [14]Departamento de Botânica, Universidade de Brasília, Brasília, Distrito Federal, CEP 70910-900, Brazil; [15]Sir Robert Norman Building (E2), James Cook University, PO Box 6811, Cairns, QLD, 4870, Australia; [16]Botany Department, School of Natural Sciences, Trinity College, The University of Dublin, Dublin 2, Ireland

Author for correspondence:
A. Muthama Muasya
Email: muthama.muasya@uct.ac.za

Received: *5 July 2023*
Accepted: *3 November 2023*

New Phytologist (2024) **242:** 727–743
doi: 10.1111/nph.19421

Key words: biogeography, evolution, evolutionary transitions, grasslands, grass-like plants, savannas, spatial phylogenetics.

Summary

- Poales are one of the most species-rich, ecologically and economically important orders of plants and often characterise open habitats, enabled by unique suites of traits. We test six hypotheses regarding the evolution and assembly of Poales in open and closed habitats throughout the world, and examine whether diversification patterns demonstrate parallel evolution.
- We sampled 42% of Poales species and obtained taxonomic and biogeographic data from the World Checklist of Vascular Plants database, which was combined with open/closed habitat data scored by taxonomic experts. A dated supertree of Poales was constructed. We integrated spatial phylogenetics with regionalisation analyses, historical biogeography and ancestral state estimations.
- Diversification in Poales and assembly of open and closed habitats result from dynamic evolutionary processes that vary across lineages, time and space, most prominently in tropical and southern latitudes. Our results reveal parallel and recurrent patterns of habitat and trait transitions in the species-rich families Poaceae and Cyperaceae. Smaller families display unique and often divergent evolutionary trajectories.
- The Poales have achieved global dominance via parallel evolution in open habitats, with notable, spatially and phylogenetically restricted divergences into strictly closed habitats.

Introduction

Open and closed habitats are distinct categories of terrestrial environments (Bond, 2019), each with unique ecology and differing in ground layer vegetation strongly constrained by available light (Ratnam *et al.*, 2011; Bond, 2022). Open habitats, comprising nearly 60% of land area (Dinerstein *et al.*, 2017), include treetops that provide suitable habitats for epiphytes, areas too extreme to support trees (e.g. deserts, high altitudes, tundra and rock walls), and grasslands – regions that could potentially support trees but are dominated by grass-like plants because of disturbances (Strömberg, 2011; Buisson *et al.*, 2022). Grasslands occupy a wide biogeographic range and cover nearly 40% of the terrestrial biosphere, including tropical and subtropical savannas, boreal and temperate

---

*These authors contributed equally to this work.

prairies, and Eurasian steppes (Bond, 2019; Buisson *et al.*, 2022). They provide habitat for a wide diversity of animals and plants, and support the livelihood of over 1 billion people worldwide (Buisson *et al.*, 2022). Until now, biogeographical and evolutionary studies of open habitats have focussed on regional scales (e.g. Solofondranohatra *et al.*, 2020) or on the most diverse family occupying these habitats, Poaceae (e.g. Edwards *et al.*, 2010; Linder *et al.*, 2018; Gallaher *et al.*, 2022), although other closely related families can be equally diverse and dominant components of their respective open habitats (Linder & Rudall, 2005; Barrett, 2013).

The ability of plants to occur in either open or closed habitat has evolved repeatedly across the tree of life, in some cases possibly through parallel evolution – the repeated evolution of similar traits in closely related lineages (Bailey *et al.*, 2017; Durán-Castillo *et al.*, 2022) – or through divergent evolution involving large evolutionary distances between populations (or species) in genotypic or phenotypic space (Bolnick *et al.*, 2018). As the morphological and physiological traits of plants are linked to their habitat preferences, the repetitive evolution of traits suggests parallel adaptive evolution (Bolnick *et al.*, 2018). To identify macroevolutionary processes, such as whether evolution is parallel or divergent, it is important to determine the appropriate phylogenetic scope to avoid excluding key lineages that unveil important patterns (Folk *et al.*, 2018). Large comparative studies including comprehensive sampling across a single higher level lineage present opportunity to distinguish which traits might be exceptional at smaller compared with larger phylogenetic scales (e.g. genus vs order; Beaulieu & O'Meara, 2018).

Globally dominant in open habitats, Poales are among the most species-rich orders of angiosperms, comprising 14 families and 24 302 species (APG IV, 2016; Govaerts, 2022; Fig. 1; Table 1). Poales families differ in their species richness and distribution, yet those exhibiting high species richness tend to be cosmopolitan and exhibiting variation in life form and ecological traits (Ricklefs & Renner, 1994). The two largest families, Poaceae and Cyperaceae, are among the three largest monocot families and 10 largest plant families (Govaerts, 2022) and both have a cosmopolitan distribution. Whereas mid-sized families show latitudinal bias (e.g. Restionaceae in austral temperate regions; Bromeliaceae in the American tropics) or are nearly restricted to a single continent (e.g. Rapateaceae in South America). Those that are species-poor (e.g. Typhaceae, Ecdeiocoleaceae) tend to be geographically and/or ecologically restricted. Most families in Poales are largely limited to open habitats or are able to occupy both open and closed habitats. Most are also capable of long-distance dispersal by wind, animals and water (Linder *et al.*, 2018; Martín-Bravo *et al.*, 2019; Vera-Paz *et al.*, 2023). While all Poales families are found in tropical areas, only select clades have diversified extensively in temperate areas (e.g. Poaceae subfamily Pooideae, *Carex*, Juncaceae; Vigeland *et al.*, 2013; Martín-Bravo *et al.*, 2019; Ambroise *et al.*, 2020; Schubert *et al.*, 2020). These lineages tend to be widespread throughout the northern hemisphere, with many genera occupying full Holarctic distributions despite their contingent species displaying strong partitioning of geographic and niche space (Spalink *et al.*, 2016, 2019).

We expect large-scale comparative studies of Poales to reveal that diversification both in and out of open habitats in multiple families occurred repeatedly and in parallel around the world. The ancestor of Poales is hypothesised to have occupied open, and seasonally dry, nutrient-poor, Gondwanan habitats during the Cretaceous (Givnish *et al.*, 2000; Linder & Rudall, 2005; Bouchenak-Khelladi *et al.*, 2014) and would have been herbaceous, with typical monocot features including rhizomes, monocarpic tillers, C_3 photosynthesis and wind pollination (Dahlgren *et al.*, 1985). Several lineages of Poales have entered closed habitats since the Late Cretaceous, but such lineages are predominantly species-poor (e.g. Flagellariaceae), except for Bromeliaceae which has rapidly diversified during the Miocene (Givnish *et al.*, 2011, 2014). Conversely, several species-rich Poales lineages have diversified in open habitats, apparently in conjunction with Crassulacean Acid Metabolism (CAM) and C_4 photosynthetic systems (Bouchenak-Khelladi *et al.*, 2014). This generalisation, however, is based on incomplete sampling (below 2% of species; Bouchenak-Khelladi *et al.*, 2014), which is likely to obscure underlying patterns and processes, and thus remains to be tested with more comprehensive sampling.

Coupling the most inclusive phylogeny of Poales produced to date with comprehensive geographic sampling and habitat scoring, here we integrate historical biogeography, ancestral state estimation and spatial phylogenetics. With this, we test hypotheses regarding the evolution and assembly of Poales in open and closed habitats throughout the world, analyse the impact of evolutionary history on phylogenetic regionalisation and examine whether diversification patterns demonstrate parallel or divergent evolution. Spatial phylogenetic analyses (Mishler *et al.*, 2014) are increasingly used to evaluate the geographic structure of lineage assembly (Holt *et al.*, 2013; Thornhill *et al.*, 2016; Zhang *et al.*, 2022), to link evolutionary processes to the manifestation of biodiversity through time and space (Carter *et al.*, 2022; Nitta *et al.*, 2022; Sanbonmatsu & Spalink, 2022), and for the development of conservation policies (Sechrest *et al.*, 2002; Gonzalez-Orozco *et al.*, 2016; Zhang *et al.*, 2021). While many spatial phylogenetic metrics exist, emerging methods can identify hotspots of remarkable phylogenetic diversity and distinguish between areas of significant palaeo- and neo-endemism (Mishler *et al.*, 2014). Such analyses provide insight into the spatial patterns of evolutionary processes, integrating phylogenetic information (i.e. branch lengths and species relationships) with the geographic ranges of species and clades. When coupled with functional traits, this inclusion of evolutionary information provides a more complete understanding of macroecological processes and phylogenetic patterns of regionalisation (Tucker *et al.*, 2017; Spalink *et al.*, 2018). To our knowledge, this is the first study to incorporate modern spatial phylogenetic approaches with historical biogeographical analyses of a plant order on a global scale. We capitalise on this data set to link our understanding of how lineages evolve with how they assemble at both deep and more shallow phylogenetic scales, avoiding the edge effects of regionally restricted analyses (e.g. Spalink *et al.*, 2018) while minimising bias stemming from incomplete sampling.

We test the following hypotheses: (H1) Phylogenetic regionalisation will reflect a tropical origin and extensive temperate

Fig. 1 Representatives of 12 Poales families. (a) *Tillandsia tovarensis* (Bromeliaceae), epiphytic in cloud forest, Kuelap, N Peru. (b) Insect-pollinated *Rhynchospora colorata* (Cyperaceae), in forest gaps, S Ecuador. (c) *Ecdeiocolea rigens* (Ecdeiocoleaceae), arid heath, SW Australia. (d) *Paepalanthus ensifolius* (Eriocaulaceae), in cloud forest, Podocarpus National Park, S Ecuador. (e) *Flagellaria indica* (Flagellariaceae), rocky savannah, NW Australia. (f) *Mayaca fluviatilis* (Mayacaceae), wetlands, Singapore. (g) *Micraira* sp. Purnululu (Poaceae), a rapid-resurrection species from sandstone pavements in NW Australia. (h) *Guacamaya superba* (Rapataceae) in a sedge and grass swamp in E Colombia. (i) *Lepidobolus preissii* (Restionaceae) from sandy heath, SW Australia. (j) *Prionium serratum* (Thurniaceae) in fynbos, Cape Province, South Africa. (k) *Sparganium japonicum* (Typhaceae) from wetlands in E Russia. (l) *Xyris complanata* (Xyridaceae) from an ephemeral wetland in savannah, NW Australia. Photos by Russell Barrett; except for (f, h, j, k), all posted on iNaturalist as CC-BY-NC; (f) by CheongWeei Gan; (h) by Carlos Eduardo; (j) by Linda Hibbin; (k) by Sergei Prokopenko.

Table 1 Summary of number of species, ancestral habitat and phyloregions corresponding to crown nodes for Poales.

Family	Total	Studied	Studied %	Closed	Phyloregion	Habitat
Poaceae	11 994	5341	45	449	Afrotropical	Closed
Cyperaceae	5870	2690	46	398	Neotropic	Open
Bromeliaceae	3564	1066	30	551	Neotropic	Open
Eriocaulaceae	1206	348	29	6	Neotropic	Open
Restionaceae	552	453	82	3	Austral	Open
Juncaceae	514	209	41	5	Palearctic	Open
Xyridaceae	406	13	3	1	Neotropic	Open
Rapateaceae	97	24	25	2	Neotropic	Open
Typhaceae	74	26	35	0	Palearctic	Open
Thurniaceae	8	4	50	0	Neotropic	Open
Flagellariaceae	5	4	80	2	Indomalayan	Closed
Mayacaceae	5	1	20	0	Neotropic	Open
Joinvilleaceae	4	2	50	2	Indomalayan	Closed
Ecdeiocoleaceae	3	2	67	0	Austral	Open
Total	24 302	10 183		1419		
%		42		14		

Total number of species per family was derived from the 'World Checklist of Vascular Plants' (WCVP; Govaerts, 2022). The number of species found in closed habitats was calculated from Supporting Information Table S3, while Phyloregions corresponding to the crown nodes were inferred from Fig. 3.

diversification only of select clades of Poales. (H2) Given that relatively few clades have diversified in temperate and boreal habitats, and given the propensity of long-distance dispersal in Poales, we expect that north- and south-temperate regions will be more phylogenetically similar to each other than either is to tropical regions. (H3) Evolutionary transitions between open and closed habitats have occurred frequently, rapidly, and in parallel in Poales, as three of the largest families (Poaceae, Cyperaceae, and Bromeliaceae) have diversified in both habitats. (H4) Evolutionary transitions to, and diversification within, open habitats have occurred in synchrony in different parts of the world and across lineages, with the rapid accumulation of species beginning in the Eocene as open habitats became more widespread. We expect our increased sampling over previous studies to reveal that diversification in open habitats did not begin with the now-dominant Poaceae, but rather with multiple families simultaneously around the world. (H5) These historical processes have resulted in high phylogenetic diversity and endemism across the tropics, where most Poalean families have a hypothesised origin, and low endemism in northern temperate habitats, where lineages are widespread even though individual species are spatially restricted. (H6) Across Poales, centres of neo-endemism will occur on young islands and mountainous regions, whereas palaeo-endemism will occur in areas with high bioclimatic stability since the Eocene. We expect no significant neo- or palaeo-endemism in the temperate north, either in Poales as a whole or in individual families, given that these regions are recently assembled and composed of predominantly widespread lineages.

Materials and Methods

Phylogenetic reconstruction

We produced a family-level phylogenomic backbone using 353 nuclear loci (Angiosperms353; Johnson *et al.*, 2019). The sampling for the backbone aimed towards 50% of accepted genera and included newly generated data. Details on data production, sequence assembly and species tree construction are presented in Supporting Information Notes S1 and in Baker *et al.* (2022). Briefly, we inferred the phylogenomic backbone using a multispecies coalescent framework (MSC). Gene trees were inferred using IQ-TREE 2 (Minh *et al.*, 2020). TREESHRINK (Mai & Mirarab, 2018) was used to identify outliers that significantly increased tree space. Alignment and tree building was repeated for those genes with outlier trees. All gene trees were trimmed for poorly supported branches (UFBS < 30%) before use in the MSC analysis in ASTRAL-III (Zhang *et al.*, 2018). To obtain a species tree with branch lengths proportional to the genetic distance, we ranked the genes according to the congruence of their resulting trees to the species tree using SORTADATE (Smith *et al.*, 2018) and then concatenated the alignments of the 25 most congruent genes. Using the MSC species tree as topological constraint and this concatenated alignment, a new phylogram was inferred in IQ-TREE 2. For more details on library preparation and data analyses, please refer to Baker *et al.* (2022).

We inferred separate trees for five groups of families identified with the backbone phylogeny: (1) Bromeliaceae + Typhaceae; (2) Rapateaceae + Thurniaceae + Juncaceae + Cyperaceae + Mayacaceae (the cyperid clade); (3) Xyridaceae + Eriocaulaceae (the xyrid clade); (4) Restionaceae; and (5) Joinvilleaceae + Flagellariaceae + Ecdeiocoleaceae + Poaceae. Available sequences (Table S1) were retrieved from GenBank (Benson *et al.*, 2010). We downloaded all available sequences per marker while disregarding those corresponding to hybrids and not determined to species level, with the exception of the cyperid clade where we preferentially used sequences included in the phylogenetic reconstruction of Elliott *et al.* (2022). Nomenclatural reconciliation was conducted using the R package *TAXIZE* (Chamberlain & Szocs, 2013) and 'World Checklist of Vascular Plants' (WCVP; Govaerts, 2022). We selected one sequence per marker per taxon. Sequence matrices for the five clades were aligned using MAFFT v.7.453 (Katoh & Standley, 2013), edited manually in ALIVIEW v.1.26

(Larsson, 2014) and concatenated. Trees were then inferred under a GTRCAT model in RAxML v.8.2.12 (Stamatakis, 2014), using rapid bootstrapping with 100 replicates followed by a thorough maximum likelihood search on the Czech National Grid Infrastructure. The preliminary phylogenetic trees were manually checked for obviously spurious species placements. Corrected matrices were realigned with outgroup taxa (Table S1). Phylogenetic reconstructions were then conducted using constraint trees derived from the backbone tree.

For time-calibration, we used a mix of primary and secondary calibrations to match dates of major clades to the best-available evidence from previous studies focussing on monocots. The backbone and clade trees were time-calibrated using penalised likelihood as implemented in TREEPL, with the smoothing value identified through cross-validation (Smith & O'Meara, 2012). We used secondary calibration points for the backbone tree, setting fixed ages for the family crown nodes (Table S2) obtained from the plastome tree of Givnish *et al.* (2018). Separate analyses were conducted for Poaceae and Cyperaceae, incorporating additional fossil and secondary priors within the clades using best available information (Spalink *et al.*, 2016; Martín-Bravo *et al.*, 2019; Gallaher *et al.*, 2022; see Table S2). For the remaining clade trees, the root ages were set to one. All subtrees were then grafted into the backbone tree after scaling their age to that of the corresponding nodes in the dated backbone tree.

Species distributions and habitats

We used WCVP to create a species presence/absence matrix in each botanical country (Level 3) as specified by the International Working Group on Taxonomic Databases for Plant Sciences (TDWG; Brummitt *et al.*, 2001). Species missing in the phylogeny were removed from the matrix. Occurrence in open, closed, or both habitats was scored from the literature, especially regional floras, in addition to taxonomic expertise. Habitats noted as 'forests' in floristic treatments, interpreted as closed canopy at least during the active growing season, were scored as 'closed'. We scored species occurring in open and closed habitats as 'both'. For Bromeliaceae, species occurring on sun-exposed rock-walls or treetops were scored as 'open'. A full list of taxa included in the study and their habitat is available in Table S3.

Regionalisation

To determine phylogenetic patterns of regionalisation in Poales, we first calculated phylogenetic beta-diversity across all botanical countries. We then used three metrics to identify the optimal number of phyloregions: K-means and silhouette scores (Hartigan & Wong, 1979; Rousseeuw, 1987), the elbow method (Salvador & Chan, 2004; Zhao *et al.*, 2011) and the gap statistic (Tibshirani *et al.*, 2001). For each analysis, we set the maximum number of phyloregions to 20, allowing for the possibility of high levels of regionalisation. The elbow and K-means approach each identified 13 phyloregions as optimal, whereas the gap statistic identified 20 phyloregions. For simplicity, we used 13 phyloregions for downstream comparative analyses, with regions partitioned to the optimal number identified above using nonmetric multidimensional scaling (NMDS) and hierarchical dendrogram clustering based on a beta-diversity similarity matrix of botanical countries. To determine nestedness of the 13 regions, we completed a final analysis that limited the number of phyloregions to three. Regionalisation analyses were conducted using the R packages PHYLOREGION v.1.0.6 (Daru *et al.*, 2017, 2020a,b), CLUSTER v.2.1.3 (Maechler *et al.*, 2022) and STATS v.4.1.2 (R Core Team, 2021). To summarise the phylogeny and visualise spatial and temporal patterns of lineage assembly in these phyloregions, we used the R package PHYTOOLS v.1.2.0 (Revell, 2012) to construct nonparametric lineage through time plots for the open and closed habitat species of each family. This summary approach does not account for extinction or missing data, but was selected over a model-based estimates of λ (birth rate) and μ (death rate), given that these are difficult to estimate from trees containing only extant species (Louca & Pennell, 2020). We do not use these plots to infer diversification rates, but rather to visualise the approximate timing of assembly of each family in each phyloregion given the phylogeny.

Ancestral state estimations

For ancestral area estimation, we expected that the dispersal–extinction–cladogenesis (DEC) model would have the most appropriate parameters for geographic scale and biology of our study system (Ree *et al.*, 2005; Ree & Smith, 2008; see Notes S2). For comparison to DEC, we also ran the DIVA-like model. While we acknowledge the criticisms of the additional J parameter (Ree & Sanmartín, 2018), we ran DEC and DIVA with and without J given that Poales has a propensity for long-distance dispersal that could lead to speciation. We selected the best model among the four using AICw scores. We used stochastic mapping to estimate the number of dispersal events between phyloregions. Models, model testing and stochastic mapping were implemented using the R package BIOGEOBEARS v1.1.2 (Matzke, 2013, 2014). The geographical unit of comparison was the Poales phyloregions identified above, but simplified to 7 to reduce the state-space explored by the model (see inset map in Fig. 4 later). We did not implement the BAYAREA-like model, which allows 'widespread sympatric speciation', a parameter that is not biologically plausible given the biology of Poales and the geographic scope of our study system. This parameter allows a cosmopolitan species to sympatrically give rise to two other cosmopolitan species, resulting in estimations favouring large ancestral areas and multiple widespread sympatric speciation events.

To estimate ancestral states of open/closed habitat and the transition rates between them, we used Generalised Hidden Markov models, as implemented in the function corHMM in the R package CORHMM v.2.8 (Boyko & Beaulieu, 2021). We ran 'symmetric rates' and 'all rates differ' Markov models separately with a hidden states model with two categories and with a standard model without hidden rates (one category of rates) fitted during the analyses. Akaike information criterion (AIC) was used to select the best fitting model, and ancestral states in the phylogeny were inferred with maximum likelihood and stochastic mapping. We then linked the output of the best-fitting CORHMM models to the DEC analysis to summarise spatial patterns of open/closed habitat transitions, identifying the nodes at which character states shifted, and the geographical areas that those ancestors were inferred to have occupied based on the DEC analysis.

Spatial phylogenetics

We used the R packages PICANTE v.1.8.2 (Kembel *et al*., 2010) and CANAPER v.0.0.2 (Nitta & Iwasaki, 2021) to calculate phylogenetic diversity (PD; Faith, 1992) and phylogenetic endemism (PE; Rosauer *et al*., 2009), as well as to perform categorical analysis of neo- and palaeo-endemism (CANAPE; Mishler *et al*., 2014) across botanical countries. To calculate the standardised effect size of PD and PE, we used two different sequential randomisation algorithms – swap and curveball. The swap algorithm shuffles species presence/absence across the community matrix, while maintaining species ranges sizes and species richness within communities (Gotelli & Entsminger, 2003). The curveball algorithm identifies species occurring in only one of two randomly selected communities, then distributes those species across communities while maintaining richness in communities (Strona *et al*., 2014). For both randomisations, we performed 1000 replications of 100 000 iterations each. These were followed by two-tailed tests to determine whether PD and PE were significantly over-dispersed or clustered. CANAPE methods follow those outlined in Mishler *et al.* (2014) and Nitta & Iwasaki (2021). For PD, PE and CANAPE, analyses were conducted for all Poales combined, as well as separately for the six largest families (Bromeliaceae, Cyperaceae, Eriocaulaceae, Juncaceae, Poaceae and Restionaceae). In addition, PD was calculated for both open and closed habitat species.

Results

Our final phylogeny encompassed 10 100 species (41.6% of Poales; Table 1). All families and 88% of genera in the order were represented. The percentage of species sampled varied from highest in Restionaceae (82%, 453 species), medium for the largest families Poaceae (45%, 5341 species) and Cyperaceae (46%, 2690 species), to lowest in Xyridaceae (3%, 13 species). Habitat scoring was completed for > 80% of species (Table S3). Only 14% of species occur in closed habitats. Ages of major clades were consistent with the previous studies on which the calibrations were based.

Regionalisation

Phylogenetic regionalisation identified 13 regions (Fig. 2a) nested into three major zones (Fig. S1): (I) Temperate (1: temperate North America + Russian far east; 5: central and eastern North America; 2: northern Africa [excluding Algeria] + Arabian peninsula [excluding Yemen] + southwestern Asia; 6: Europe + mediterranean Eurasia + Algeria; 8: northeastern Asia; 12: central and eastern China; 13: north central Pacific); 4: Patagonia + Antarctica + western and southern Australia + New Zealand; (II) American tropics (3: Central- + South America [excluding central and eastern Brazil + Patagonia]; 11: central and eastern Brazil) and (III) Palaeotropics (7: Sub-Saharan Africa [excluding central and western Africa; Madagascar + Mozambique] + Yemen + Mauritania; 9: Indomalayan, comprising India + southeastern Asia + northeastern Australia + Madagascar + Mozambique; 10: central and western tropical Africa [excluding Mauritania]). A NMDS plot shows these 13 regions separated latitudinally, falling into three groups, where northern and southern hemisphere temperate regions form a single cluster separated from the tropics, with the latter separated into Neotropics (excluding Patagonia) and Palaeotropics (Figs 2a, S1).

Families differ in their stem age and lineage accumulation over time among the 13 regions (Fig. 2a). Considering the six largest families, Poaceae or Cyperaceae are the oldest in all regions, except for the Restionaceae which are oldest in temperate Australia. Bromeliaceae is the youngest family. Smaller families (Eriocaulaceae and Juncaceae) are younger than Poaceae and Cyperaceae in regions where they occur. Poaceae and Cyperaceae occur in all regions, Juncaceae is nearly cosmopolitan but is poorly represented in tropical regions, and the other nine families are restricted to one or few regions (Fig. 2a,b).

In all tropical regions, Poales – and specifically Poaceae – diversified first in closed habitats before lineages began accumulating in open habitats (Fig. 2a). By contrast, in northern temperate regions open habitat lineages – specifically, Cyperaceae – diversified first (Fig. 2a). The exception to this latter pattern is in the eastern Nearctic, where closed habitat Poaceae were the first to diversify. However, this exception is likely driven by the inclusion of some subtropical Caribbean islands and southern Florida in this phyloregion. The initial diversification of Poaceae in most temperate regions included both open and closed habitat lineages. Likewise, but in tropical regions only, the initial diversification of open and closed habitat Cyperaceae was concurrent. Open habitat Poaceae displayed the greatest accumulation of lineages (especially during the Oligocene and Miocene) followed by open habitat Cyperaceae in all but the north central Pacific phyloregion, where there was a big lapse in time until Cyperaceae accumulated in closed habitats (Fig. 2a). In all phyloregions, open habitat species richness is higher than closed habitat species richness in all families except Bromeliaceae.

Ancestral state estimations

The BioGeoBEARS model with the highest AICw was the DEC model followed by DEC + J and DIVA models (Table S4; Fig. S1). Subsequent analyses are based on the DEC model (Fig. 3). Poales are inferred to have originated in the Neotropics in Western Gondwana (current South America; Fig. 3a). The crown nodes of most families occur in the Cretaceous (e.g. Cyperaceae, Eriocaulaceae, Juncaceae, Poaceae and Restionaceae) to the Neogene (e.g. Bromeliaceae; Fig. 3a). The family crown nodes are distributed in all major zones (Fig. 3a; Table 1):

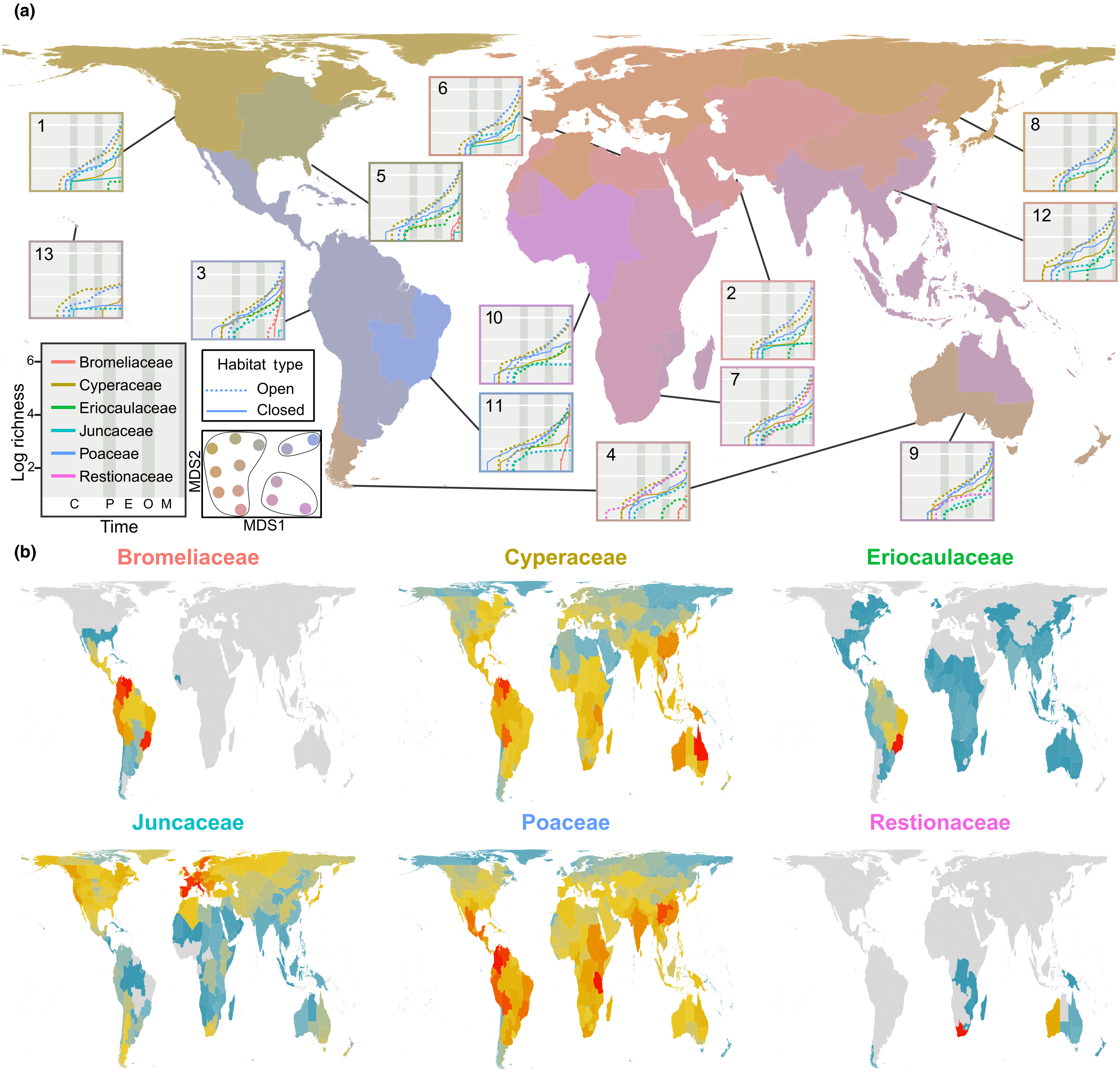
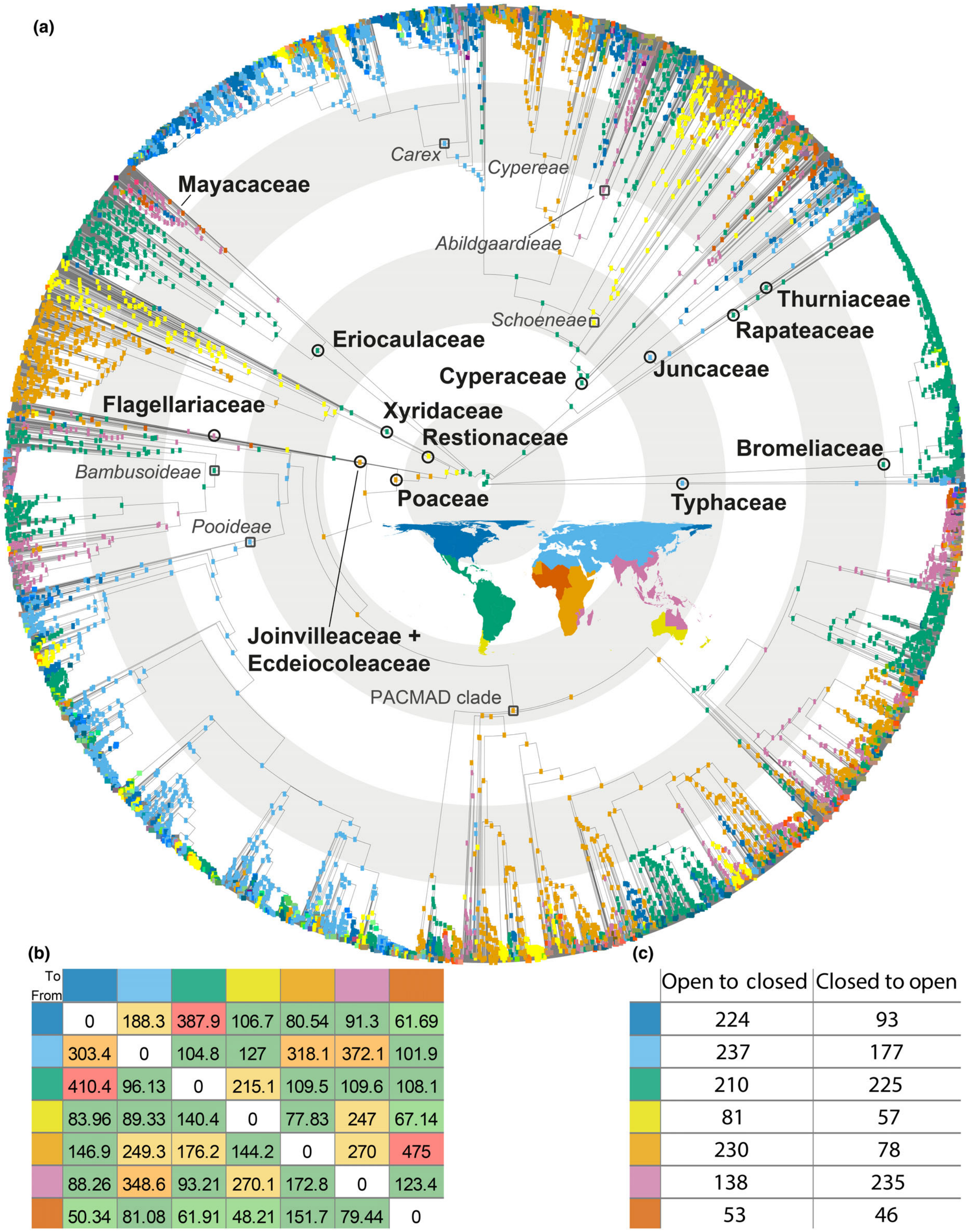


Fig. 2 Global phylogenetic patterns of regionalisation in Poales. (a) Phylogenetic regionalisation of the six largest families of Poales. Graphs represent the logarithmic species richness of the six families through time within each of the 13 phyloregions identified using the elbow and K-means approach, where dotted lines represent open habitat lineages and solid lines indicate closed habitat lineages. A geological timeline is located in the inset in the far left-hand corner, with the following abbreviations: Cretaceous (C: 66–56 Myr); Paleocene (P: 66–56 Myr); Eocene (E: 56–33.9 Myr); Oligocene (O: 33.9–23 Myr) and Miocene (M: 23–5.3 Myr). Inset to the right of the geological timeline shows nestedness of the 13 regions based on non-metric multidimensional scaling (NMDS), where each colour dot represent a phyloregion and the three clusters each with similar colour dots represent the three major botanical kingdoms (Temperate, Neotropics, Palaeotropics). (b) Phylogenetic diversity (PD) of the six most speciose families of Poales, with red and dark blue indicating botanical countries with relatively high and low PD values, respectively. Botanical regions indicated by grey in (b) lack species for the respective family.

Bromeliaceae, Cyperaceae, Eriocaulaceae, Rapataceae and Xyridaceae are assigned a Neotropic origin, while Flagellariaceae and Poaceae are placed in the Palaeotropics. The Holarctic region is ancestral for the Juncaceae and Typhaceae, whereas the Austral region is ancestral for the Restionaceae. Below family rank, Schoeneae originated in the Austral region, *Carex* and Pooideae in Eurasia, Cypereae and the PACMAD clade in Sub-Saharan Africa, Abildgaardieae in Indomalayan region (including NE Australia, Mozambique, and Madagascar) and Bambusoideae in the Neotropics (Fig. 3a).



From \ To	🟦	🩵	🟩	🟨	🟧	🩷	🟥
🟦	0	188.3	387.9	106.7	80.54	91.3	61.69
🩵	303.4	0	104.8	127	318.1	372.1	101.9
🟩	410.4	96.13	0	215.1	109.5	109.6	108.1
🟨	83.96	89.33	140.4	0	77.83	247	67.14
🟧	146.9	249.3	176.2	144.2	0	270	475
🩷	88.26	348.6	93.21	270.1	172.8	0	123.4
🟥	50.34	81.08	61.91	48.21	151.7	79.44	0

	Open to closed	Closed to open
🟦	224	93
🩵	237	177
🟩	210	225
🟨	81	57
🟧	230	78
🩷	138	235
🟥	53	46

Fig. 3 Ancestral area reconstruction within Poales based on seven regions, obtained using the dispersal–extinction–cladogenesis (DEC) model in BioGeoBEARS (a). A global map showing colours corresponding to the seven defined areas for the BioGeoBEARS analysis is in the centre of the phylogenetic reconstruction. The crown nodes of the families within Poales are shown with black circles, whereas dark grey squares are used to depict lineages important for the study's interpretations. Concentric light grey/white rings underlying the phylogeny indicate time slots of 20 Myr intervals. Note that Joinvilleaceae and Ecdeiocoleaceae are depicted together for visual purposes. Number of dispersal events between the seven regions inferred using Biogeographical Stochastic Mapping on the DEC model (b), and (c) number of transitions between open and closed habitats inferred to have occurred within each of the seven areas, calculated through comparison of best fitting corHMM models and historical biogeographical estimates. The colours of row and column labels in (b) and row in (c) correspond to those on inset map in (a).

Poaceae and Cyperaceae experienced a several million-year lag before co-occurring in any phyloregion (Figs 2, 3). This pattern of concurrent but spatially separated diversification is repeated for main lineages within these families as well. In the Paleocene, the grass clades Bambusoideae, PACMAD, and Pooideae originate allopatrically in the Neotropics, Afrotropics, and Eurasia, respectively. In the Eocene, the sedge clades Abildgaardieae, Cypereae, *Carex* and Schoeneae originate in the Indomalayan tropics, Afrotropics, Palearctic, and Austral region, respectively.

Dispersal across all phyloregions has occurred many times throughout the evolution of Poales, most frequently between the Neartic and Neotropics and between the Palearctic and Paleotropics (Fig. 3b). Eurasia is a strong one-way source to North America, tropical Africa and tropical Asia, while equatorial Africa is a notable recipient of lineages from Sub-Saharan Africa (Fig. 3a,b). A relatively high number of transitions between open and closed habitats occurred in the Neotropics and Eurasia compared to equatorial Africa and the Austral region (Fig. 3a,c). Transitions from open to closed are more frequent than the opposite for the Neoarctic and Sub-Saharan Africa, whereas closed to open transitions are more numerous for the Indomalayan region (Fig. 3a,c).

The asymmetrical ("all-rates-different") with hidden states model with two categories is the best fit corHMM model of evolution for open/closed habitats (AIC = 8814.2; Fig. 4; Table S5). An open habitat (Fig. 4) is inferred at the root of Poales and most families, with shift to closed habitat near zero (0.000000001 transitions per million years (Myr) in R2 (Regime rate 2)). However, there are rapid rate transitions between open and closed (0.31 transitions/Myr in R1 [Regime rate 1]) and closed to open (0.51 transitions/Myr in R1) habitats among Bromeliaceae, Cyperaceae (*Carex* clade) and Poaceae (Bambusoideae clade), occurring predominantly during the Miocene.

Spatial phylogenetics

The species in our phylogeny were generally representative of the cosmopolitan distribution of Poales, except for the underrepresentation of tropical areas in South America, India and parts of China (Fig. S2). Across Poales and in all families except Bromeliaceae, phylogenetic diversity is substantially higher in open habitats than closed habitats in all phyloregions (Figs 5a, S3), with the highest values attributed to open habitat species in southern Africa, western Australia and northern South America. High open habitat PD is driven by Cyperaceae, Poaceae and Restionaceae in southern Africa; Cyperaceae, Poaceae and Restionaceae in western Australia; and by Bromeliaceae, Cyperaceae, Eriocaulaceae and Poaceae in northern South America (Figs 3, 5b, S3). Although closed habitat PD is lower overall than open habitat PD, northern South America is a high centre of diversity of these species (Fig. 3b), with high representation of Bromeliaceae, Cyperaceae and Poaceae. Despite the widespread availability of forested habitats throughout the Holarctic, these regions have low PD of closed habitat Poales. Those species that do occur in closed habitats in the Holarctic represent only Cyperaceae, Juncaceae and Poaceae (Fig. S3). With the exception of Juncaceae, closed habitat PD is higher in all major families south of the Tropic of Cancer (Fig. S3).

By far, southern Africa displays the highest PE in Poales (Fig. 5c), driven by high endemism of Cyperaceae, Poaceae and Restionaceae (Fig. S4). Phylogenetic endemicity is also high in Western Australia, again because of restricted lineages from the same three families, and southeastern Brazil, largely due to Bromeliaceae and Eriocaulaceae (Figs 5c, S4). The Neotropical and Paleotropical regions are clearly centres of significant PE, with nearly all Holarctic regions exhibiting significantly low PE and many botanical countries in the tropics and subtropics exhibiting significantly high PE. California is the only north temperate zone with significantly high PE, driven by Poaceae and Juncaceae (Figs 5c, S4). Overall, family-level patterns of significant PE match those of Poales, with low PE in the North and high PE in the South, except for Typhaceae which tends to have low PE in most of its range.

Categorical analysis of endemism (CANAPE; Fig. 5e) shows a general contrasting pattern for Poales between Holarctic (mostly non-significant) and Holotropic + Austral (significant) regions. Palaeo-endemism in Poales was supported in northern South America, southern Africa and Australia – a pattern also shared with Poaceae (including Tanzania, CA) and Cyperaceae, whereas palaeo-endemism is only evident in Australia for the Cyperaceae and Restionaceae. Neo-endemism is observed in western South America (Andean mountains) in the Poales and Poaceae, but in the eastern South American region (Brazil) for Bromeliaceae and Eriocaulaceae; in most of East Asia for the order and families Poaceae and Cyperaceae; and in southern Africa for the Restionaceae. A mixture of both palaeo- and neo-endemism is observed in Australia and South America for both the Poales and Poaceae. Though areas of endemism in Poaceae and Cyperaceae often co-occur, frequently centres of palaeo- or neo-endemism in one family are centres of mixed/super endemism in the other (e.g. Andean Mountains, Australia, southeast Brazil, eastern China, southern Africa).

Discussion

The key outcome of this comprehensive study of Poales is an emerging picture of parallel evolution – in space, through time, across lineages – resulting in the global assembly of open habitats, with notable, spatially and phylogenetically restricted divergence into closed habitats. Our analyses show that each family exhibits a contrasting historical biogeography and pattern of habitat transition, which manifest in unique spatial patterns of assembly. And yet, patterns of evolution and assembly are repeated in most families.

The biogeography and regionalisation of Poales

The Poales represent over 120 Myr of diversification, with an estimated Cretaceous origin in Western Gondwana (Fig. 4a). Consistent with previous phylogenetic studies, our model places the Poaceae origin in the Afrotropics with eventual migration to the Neotropics in the Eocene (Bouchenak-Khelladi *et al*., 2010; Gallaher *et al*., 2022). Meanwhile, Cyperaceae originates in the Neotropics and quickly shifts to Patagonia-Australia before

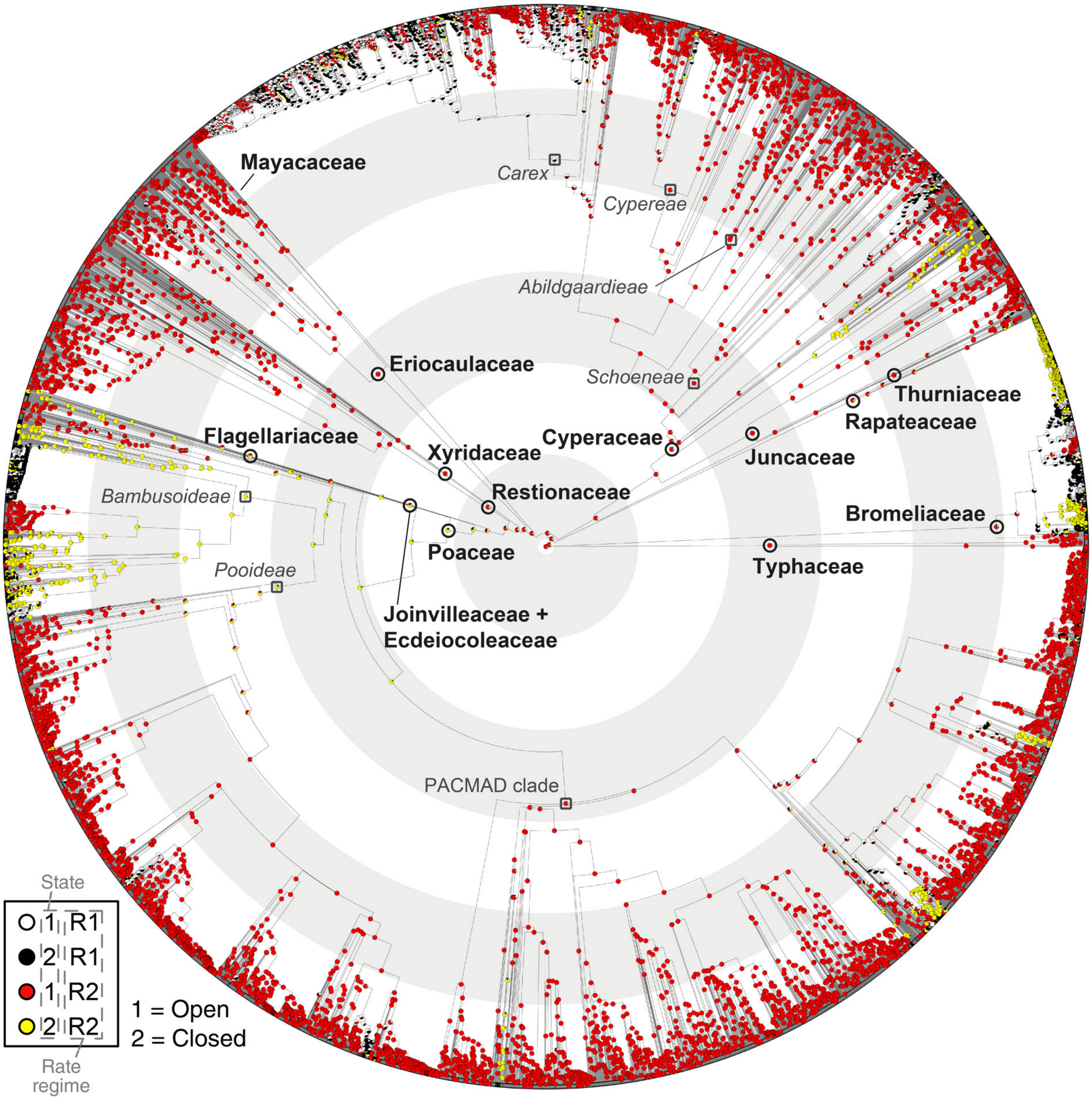


Fig. 4 Ancestral states of open/closed habitats based on Generalized Hidden Markov models, with hidden rates model with two categories and asymmetric rates, implemented with the corHMM package in R. The crown nodes of the families within Poales are shown with black circles, whereas dark grey squares are used to depict lineages important for the study's interpretations. Concentric light grey/white rings underlying the phylogeny indicate time slots of 20 Myr intervals. Detailed transition rates between the states and rate are given in Table S5.

establishing in Africa in the Paleocene (Spalink *et al.*, 2016; Larridon *et al.*, 2021a). The earliest Cyperaceae fossils also place extinct Cyperaceae lineages in Europe by the Paleogene (Smith *et al.*, 2009). Consistent with our hypotheses, the subsequent global dominance of these Poaceae and Cyperaceae clades is a tale of parallel diversification with repeated spatial convergence of distantly related lineages, which is also observed in transitions between open and closed habitats (Fig. 4) and has clear impacts on spatial patterns of phylogenetic endemism.

In contrast to Poaceae and Cyperaceae, the other families have experienced more limited diversification, either spatially or in terms of species richness. The oldest of these is Restionaceae, which originated in Western Australia in the Late Cretaceous and dispersed to southern Africa in the Eocene (Fig. 3a; Linder *et al.*, 2003). This C$_3$ family of predominantly perennials remains restricted to open habitats in these two regions, where they have evolved strategies to withstand frequent fires (reseeder/resprouter; Litsios *et al.*, 2014) and thrive on oligotrophic soils (cluster roots; Lambers *et al.*, 2006), traits only shared by the Abildgaardieae, Rhynchosporeae and Schoeneae (Cyperaceae; Barrett, 2013; Fidelis *et al.*, 2019; Pilon *et al.*, 2023) and lacking in the Poaceae. Typhaceae and Juncaceae, both of Palearctic origin near the KP boundary, are now cosmopolitan but remain species poor. Eriocaulaceae originated in the Neotropics at about the same time,

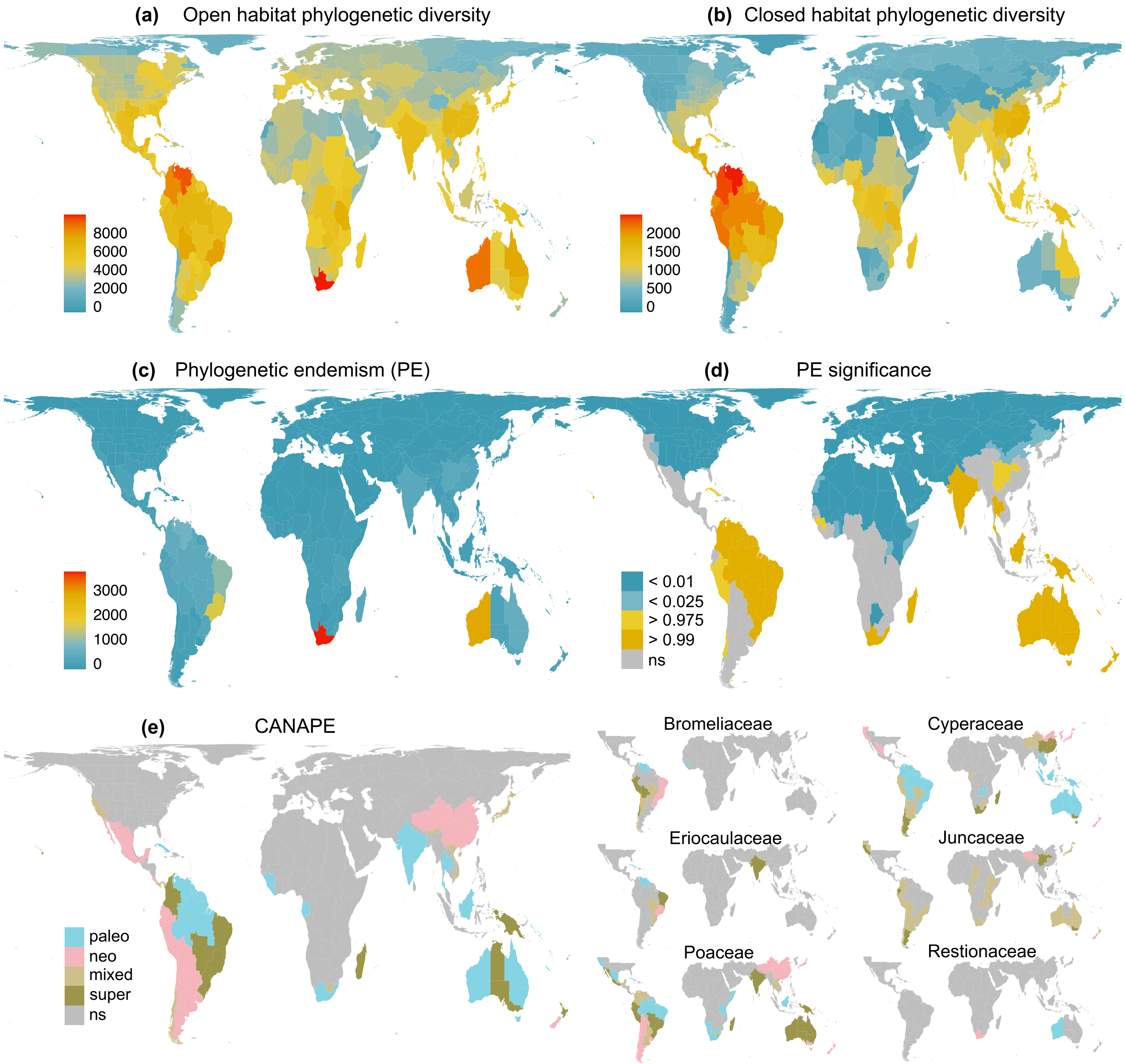


Fig. 5 Biodiversity patterns in Poales represented by Faith's phylogenetic diversity (PD) for open habitat species (a) and PD for closed habitat species (b); (c) Rosauer's phylogenetic endemism (PE) and (d) PE significance; and (e) centres of palaeo- and neo-endemism determined using CANAPE for all Poales (left) and the six most speciose families (right). High PE significance indicates that the region has an overrepresentation of short, rare branches. Low PE significance indicates that short, rare branches are underrepresented. ns, not significant.

and only a few lineages in the family have diversified outside this ancestral zone. Bromeliaceae are perhaps the most unique among the Poales, diversifying nearly exclusively in Central- and South America and with suites of traits not found in other families, such as epiphytism and lithophytism, traits encountered in the Poales outside the Bromeliaceae only among the poikilohydric clade of Cyperaceae (Trilepideae; Muasya *et al.*, 2010; Porembski *et al.*, 2021).

These historical processes have resulted in substantial spatial structure to regionalisation in Poales, with lineages forming 13 distinct phyloregions (Fig. 2a) clustered into three floristic kingdoms (*sensu* Carta *et al.*, 2022; Fig. S5). Despite the propensity for long-distance dispersal in many Poales groups (Linder *et al.*, 2018; Martín-Bravo *et al.*, 2019; Benítez-Benítez *et al.*, 2021; Larridon *et al.*, 2021a; Gallaher *et al.*, 2022), regionalisation in this clade largely mirrors that of all vascular plants, where the tectonic legacy of Gondwana and Laurasia persists in determining, at least in part, the distribution of lineages (Takhtajan, 1986; Carta *et al.*, 2022). In Poales, this is evident in northern temperate regions being distinct from those in the tropical south, and a united Austral-Patagonian (holantarctic, *sensu* Takhtajan, 1986) region reflecting the historical connection of these now-distance land masses. Temperate zones of both hemispheres share more lineages than they do with tropical zones, and the American tropics are phylogenetically distinct from the Paleotropics (Fig. S5). The unified North–South Temperate floristic kingdom may be partly due to bipolar disjunctions within species (at least 14) and genera (at least eight) in Poales (Villaverde *et al.*, 2017). Likely, a more important driver of this pattern is the ecological filtering of lineages with respect to traits that evolved earlier in the diversification of Poales. These would include traits such as frost hardiness and seasonality tolerance in Juncaceae, Typhaceae and select Poaceae and Cyperaceae clades (Vigeland *et al.*, 2013; Martín-Bravo *et al.*, 2019; Ambroise *et al.*, 2020; Schubert *et al.*, 2020), and edaphic specificity coupled with functional traits associated with adaptations to temperature and water extremes, as well as disturbance regimes (e.g. C_4, CAM, silica, tannins, epiphytism; Givnish *et al.*, 2011, 2014; Linder *et al.*, 2018) across Poales. The relatively few lineages that have evolved tolerance to frost and strong climatic seasonality have diversified extensively, virtually in all habitable places where these conditions persist (Fig. 2). The phylogenetic differentiation of the American- and Palaeo- tropical kingdoms has roots deep in the Poales phylogeny. The Neotropical origin of Cyperaceae and Afrotropical origin of Poaceae, the restriction of Eriocaulaceae, Bromeliaceae, and Rapateaceae to the Neotropics, and that of Restionaceae to austral regions (Australia, New Zealand, southern Africa and Patagonia) drive strong phylogenetic betadiversity across the tropics.

Evolutionary parallelism in open and closed habitats

The parallel evolution of open and closed lineages in Poales is most evident in Poaceae and Cyperaceae, which collectively represent *c.* 74% of species richness in the order and the majority of open-habitat PD (Fig. S3). Both families encompass two species-rich lineages (in Cyperaceae: *Carex* and Cypereae; in Poaceae: PACMAD and Pooideae), each of which (except Pooideae) is inferred to have an open-habitat ancestor (Fig. 4). The exclusively C_3 *Carex* and Pooideae are predominately temperate lineages, likely originating in eastern Asia (Fig. 3; Spalink *et al.*, 2016; Martín-Bravo *et al.*, 2019; Gallaher *et al.*, 2022), while tropical Africa is inferred as the origin for the heavily C_4 PACMAD and Cypereae clades (Figs 3a, 4). These species-rich lineages evolved from C_3 ancestors, acquiring cold tolerance (*Carex*, Pooideae; Vigeland *et al.*, 2013; Martín-Bravo *et al.*, 2019; Schubert *et al.*, 2020) and C_4 photosynthesis (Cypereae, Abildgaardieae, PACMAD; Fig. 4) in parallel. The tempo of habitat transition has shifted from slow to fast multiple times (Fig. 4), most notably in *Carex* (> 2000 species; Larridon *et al.*, 2021b), Bambusoideae (*c.* 1700 species; Soreng *et al.*, 2022), and Bromeliaceae (*c.* 3700 species, Gouda & Butcher, 2023). *Carex* is the largest clade in the phylogeny in which fast transitions between open and closed and vice versa are quite frequent (Fig. 4). This may represent the most significant difference with Pooideae. Bambusoideae uniquely grow tall enough to reach the canopy (Soreng *et al.*, 2015; Attigala *et al.*, 2016). Bromeliaceae likely originated in open habitats, but like *Carex*, has rapidly and repeatedly shifted between both habitats (Fig. 4).

Ultimately, our analyses indicate that there was likely a high diversity in all phyloregional species pools from multiple families with beneficial adaptations for survival in open habitats before their expansion in the Miocene (Figs 3, 4; Edwards *et al.*, 2010; Veldman *et al.*, 2015). Consistent with the fossil record (Prasad *et al.*, 2005; Vicentini *et al.*, 2008), the origin of PACMAD (encompassing all known origins of C_4 in Poaceae; Edwards, 2019) and Abildgaardieae and Cypereae (majority of C_4 Cyperaceae) is placed in the Eocene and Palaeocene (Fig. 3; Prasad *et al.*, 2011; Gallaher *et al.*, 2022), but most of the diversification in these clades coincides and is possibly linked with the low CO_2 concentrations, cooler, drier conditions, and increased fire activity and herbivory during the Miocene (Osborne & Freckleton, 2009; Edwards & Smith, 2010; Strömberg, 2011; Maurin *et al.*, 2014; Sage *et al.*, 2018; Peppe *et al.*, 2023). Diversification of most major Poales families occurred in all phyloregions during this time (Fig. 2).

Spatial phylogenetics of Poales

The spatial structure of phylogenetic diversity at the resolution presented here (Figs 5, S4, S5) results from historical biogeographical and ecological processes rather than local contemporary ecological processes (Meynard *et al.*, 2013; Ross *et al.*, 2021). The observed diversity patterns are complex (Fig. 5). Each family exhibits peak PD (Fig. 2) in a different botanical country – usually, but not always in their phyloregion of estimated origin (Fig. 3a). The PD of the order as a whole, and each family independently, defies a traditional latitudinal diversity gradient (Kreft & Jetz, 2007). Though this is the dominant trend in speciose open habitat lineages, the PD of closed habitat lineages peaks in equatorial forests and decreases poleward (Fig. 5a,b). These patterns reflect the tremendous diversification of Poales in open habitats around the world (Figs 2, 3, S4), with much more limited diversification of closed habitat lineages outside ancestral ranges.

Patterns of diversity in Poales generally align with our stated hypotheses. Phylogenetic diversity peaks in the tropics, where most families originated. Hotspots of PE (Fig. 5c–e) are almost strictly a southern hemispheric phenomenon, and apart from California in North America, never occur north of 33°N. This pattern is likely driven both by the presence of spatially restricted families in the Southern Hemisphere (e.g. Bromeliaceae, Restionaceae and Rapateaceae; Fig. 2b) and the propensity of lineages to migrate across the Holarctic (Donoghue & Smith, 2004).

To our knowledge, this is the first study coupling CANAPE with historical biogeographical estimations on a global scale. We find contrasting patterns of palaeo- and neo-endemism clearly reflect historical biogeographical processes at the family level (Fig. 5e). In Bromeliaceae, centres of palaeoendemism occur in the Guayana Shield – the site of putative origin of the family – whereas centres of neoendemism are restricted to the Brazilian Shield, where Bromelioideae subsequently radiated (Givnish *et al.*, 2011). Eriocaulaceae mirror this pattern (Andrino *et al.*, 2023), with the added area of super-endemism in India, where nearly 20% of the family occurs in the Western Ghats region (Sunil *et al.*, 2015). In Restionaceae, Western Australia, the ancestral home of the family, hosts palaeoendemics, while neoendemics are restricted to South Africa (Linder *et al.*, 2003). And finally, Poaceae and Cyperaceae show high levels of both endemism types around the world, reflecting their rapid migration early in their evolutionary history (Fig. 3) and *in situ* diversification across phyloregions (Fig. 2). In both families, tropical savannas and forested regions primarily harbour palaeoendemics, whereas more recent diversification is found frequently on islands – both young and old – and mountains. Significant palaeoendemism is observed within old landscapes with buffered climates (South America, southern Africa, India, and Australia; Hopper *et al.*, 2016), while significant neoendemism is predominantly within regions that have experienced Miocene geomorphological evolution – especially in Andean (Gregory-Wodzicki, 2000) and Himalayan mountains (Wang *et al.*, 2022). Areas containing a mixture of both neo- and palaeoendemism are observed in regions where old and young landscapes are interspersed (Hopper *et al.*, 2016; Vasconcelos *et al.*, 2020; Barros-Souza & Borges, 2023).

Conclusions

The biogeography of individual families in the Poales is distinct from early in their evolution, such that few major clades originating in approximate synchrony do so in the same places. This is particularly evident in Poaceae and Cyperaceae, whose evolution is like two dancers on a global stage – a biogeo(choreo)graphy – characterised by parallel movement through a shared temporality but with varying tempos, spatial staging, and ecological rhythms, ultimately resulting in a final tableau of global dominance. Both families originate in the late Cretaceous, but on either side of the widening Atlantic Ocean, dispersing and evolving in parallel to achieve cosmopolitan distribution. In contrast, the other families have experienced more limited, spatially restricted diversification. We identify latitudinal and longitudinal patterns of diversification, most evident in the phylogenetic distinctiveness of the temperate regions and also in the American tropics separating from the palaeotropics, with highest endemism found in the Neo- and Paleotropics. Parallel evolution is observed in habitat transition, whose tempo has shifted from slow to fast multiple times especially since the Eocene, driven by repeated evolution of traits enabling colonisation of open and closed habitats in different latitudes.

Acknowledgements

The authors acknowledge the team who delivered the WCVP on which many of the analyses performed in this study are based. This work was partly funded by grants from the Calleva Foundation to the Plant and Fungal Trees of Life Project (PAFTOL) at the Royal Botanic Gardens, Kew. The authors are thankful for the Research/Scientific Computing teams at The James Hutton Institute and NIAB for providing computational resources used for the phylogenomic analyses performed in the 'UK's Crop Diversity Bioinformatics HPC' (BBSRC grant BB/S019669/1). Computational resources were also supplied by the project 'e-Infrastruktura CZ' (e-INFRA CZ ID:90140) supported by the Ministry of Education, Youth and Sports of the Czech Republic. Lizzy Wenk extracted data from AusTraits. This work was supported in part by USDA National Institute of Food and Agriculture (McIntire Stennis Project 1018692) and NSF #1902064 to DS; UNAM–DGAPA–PAPIIT (No. IA202319), 'Investigación Científica Básica' CONAHCYT (No. 286249) to CGM; MICINN-AEI to ME (PID2021-122715NB-I00) and SM-B (PID2020-113897GB-I00). KR thanks DGAPA-UNAM for a postdoctoral grant (2022). ARZ and JH were each funded by a 'Future Leader in Plant and Fungal Science' fellowship from the Royal Botanic Gardens, Kew.

Competing interests

None declared.

Author contributions

AMM, TLE, DS and IL conceived the study. AMM, TLE, ME, DS, IL, JH, RLB, SM-B, JIM-C, CGM, ACM, KJR-S, DAZ, COA, DC, MSV, KLW and DAS collected data, while TLE, DS, JH, ARZ and ME conducted the analyses. AMM, TLE and DS wrote the manuscript with input from all co-authors. JIM-C, DS, ME and RLB created the figures. TLE and DS contributed equally to this work.

ORCID

Caroline Oliveira Andrino https://orcid.org/0000-0003-1107-5692
William J. Baker https://orcid.org/0000-0001-6727-1831
Russell L. Barrett https://orcid.org/0000-0003-0360-8321
Darren M. Crayn https://orcid.org/0000-0001-6614-4216
Tammy L. Elliott https://orcid.org/0000-0003-2162-8537
Marcial Escudero https://orcid.org/0000-0002-2541-5427
Félix Forest https://orcid.org/0000-0002-2004-433X
Berit Gehrke https://orcid.org/0000-0001-5866-4430
Carolina Granados Mendoza https://orcid.org/0000-0003-4001-619X
Jan Hackel https://orcid.org/0000-0002-9657-5372
Isabel Larridon https://orcid.org/0000-0003-0285-722X
José Ignacio Márquez-Corro https://orcid.org/0000-0003-4277-2933
Santiago Martín-Bravo https://orcid.org/0000-0003-0626-0770
Aluoneswi C. Mashau https://orcid.org/0000-0001-6028-7064
A. Muthama Muasya https://orcid.org/0000-0002-0763-0780
Katya J. Romero-Soler https://orcid.org/0000-0002-5075-9862

Daniel Spalink https://orcid.org/0000-0003-3250-568X
Karen L. Wilson https://orcid.org/0000-0001-7419-8222
Daniel A. Zhigila https://orcid.org/0000-0002-5529-5964
Alexandre Rizzo Zuntini https://orcid.org/0000-0003-0705-8902

Data availability

The data sets analysed in this study are available as Supporting Information. The new Angiosperms353 raw reads are deposited in the European Nucleotide Archive (PRJEB35285).

References

Ambroise V, Legay S, Guerriero G, Hausman JF, Cuypers A, Sergeant K. 2020. The roots of plant frost hardiness and tolerance. *Plant and Cell Physiology* **61**: 3–20.

Andrino CO, Costa FN, Simon MF, Missagia RV, Sano PT. 2023. Eriocaulaceae: a new classification system based on morphological evolution and molecular evidence. *Taxon* **72**: 515–549.

APG IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* **181**: 1–20.

Attigala L, Wysocki WP, Duvall MR, Clarke LG. 2016. Phylogenetic estimation and morphological evolution of Arundinarieae (Bambusoideae: Poaceae) based on plastome phylogenomic analysis. *Molecular Phylogenetics and Evolution* **101**: 111–121.

Bailey SF, Blanquart F, Bataillon T, Rees K. 2017. What drives parallel evolution? How population size and mutational variation contribute to repeated evolution. *BioEssays* **39**: 1–9.

Baker WJ, Bailey P, Barber V, Barker A, Bellot S, Bishop D, Botigué LR, Brewer G, Carruthers T, Clarkson JJ *et al.* 2022. A comprehensive phylogenomic platform for exploring the Angiosperm tree of life. *Systematic Biology* **71**: 301–319.

Barrett RL. 2013. Ecological importance of sedges: a survey of the Australasian Cyperaceae genus *Lepidosperma*. *Annals of Botany* **111**: 499–529.

Barros-Souza Y, Borges LM. 2023. Spatial-and lineage-dependent processes underpin floristic assembly in the megadiverse Eastern South American mountains. *Journal of Biogeography* **50**: 302–315.

Beaulieu JM, O'Meara BC. 2018. Can we build it? Yes we can, but should we use it? Assessing the quality and value of a very large phylogeny of campanulid angiosperms. *American Journal of Botany* **105**: 417–432.

Benítez-Benítez C, Martín-Bravo S, Bjorå CS, Gebauer S, Hipp AL, Hoffmann MH, Luceño M, Pedersen TM, Reznicek A, Roalson E *et al.* 2021. Geographical vs ecological diversification in *Carex* section *Phacocystis* (Cyperaceae): patterns hidden behind a twisted taxonomy. *Journal of Systematics and Evolution* **59**: 642–667.

Benson DA, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayers EW. 2010. GenBank. *Nucleic Acids Research* **38**: D46–D51.

Bolnick DI, Barrett RDH, Oke KB, Rennison DJ, Stuart YE. 2018. (Non) parallel evolution. *Annual Review of Ecology, Evolution, and Systematics* **49**: 303–330.

Bond WJ. 2019. *Open ecosystems: ecology and evolution beyond the forest edge.* Oxford, UK: Oxford University Press.

Bond WJ. 2022. Out of the shadows: ecology of open ecosystems. *Plant Ecology and Diversity* **14**: 205–222.

Bouchenak-Khelladi Y, Muasya AM, Linder P. 2014. A revised evolutionary history of Poales: origins and diversification. *Botanical Journal of the Linnaean Society* **175**: 4–16.

Bouchenak-Khelladi Y, Verboom GA, Savolainen V, Hodkinson TR. 2010. Biogeography of the grasses (Poaceae): a phylogenetic approach to reveal evolutionary history in geographical space and geological time. *Botanical Journal of the Linnean Society* **162**: 543–557.

Boyko JD, Beaulieu JM. 2021. Generalized hidden Markov models for phylogenetic comparative data sets. *Methods in Ecology and Evolution* **12**: 468–478.

Brummitt RK, Pando F, Hollis S, Brummitt N. 2001. *World geographical scheme for recording plant distributions, 2^{nd} ed.* Pittsburgh, PA, USA: Hunt Institute for Botanical Documentation, Carnegie-Mellon University.

Buisson E, Archibald S, Fidelis A, Suding KN. 2022. Ancient grasslands guide ambitious goals in grassland restoration. *Science* **377**: 594–598.

Carta A, Peruzzi L, Ramírez-Barahona S. 2022. A global phylogenetic regionalization of vascular plants reveals a deep split between Gondwanan and Laurasian biotas. *New Phytologist* **233**: 1494–1504.

Carter BE, Misiewicz TM, Mishler BD. 2022. Spatial phylogenetic patterns in the North American moss flora are shaped by history and climate. *Journal of Biogeography* **49**: 1327–1338.

Chamberlain S, Szocs E. 2013. *taxize – taxonomic search and retrieval in R. F1000Research.* [WWW document] URL https://f1000research.com/articles/2-191/v2 [accessed 11 April 2022].

Dahlgren RM, Clifford HT, Yeo PF. 1985. *The families of the monocotyledons.* Berlin, Germany: Springer-Verlag.

Daru BH, Elliott TL, Park DS, Davies TJ. 2017. Understanding the processes underpinning patterns of phylogenetic regionalization. *Trends in Ecology & Evolution* **32**: 845–860.

Daru BH, Farooq H, Antonelli A, Faurby S. 2020a. Endemism patterns are scale dependent. *Nature Communications* **11**: 2115.

Daru BH, Karunarathne P, Schliep K. 2020b. PHYLOREGION: R package for biogeographic regionalization and macroecology. *Methods in Ecology and Evolution* **11**: 1483–1491.

Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palminteri S, Hedao P, Noss R *et al.* 2017. An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* **67**: 534–545.

Donoghue MJ, Smith SA. 2004. Patterns in the assembly of temperate forests around the Northern Hemisphere. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **359**: 1633–1644.

Durán-Castillo M, Hudson A, Wilson Y, Field DL, Twyford AD. 2022. A phylogeny of *Antirrhinum* reveals parallel evolution of alpine morphology. *New Phytologist* **233**: 1426–1439.

Edwards EJ. 2019. Evolutionary trajectories, accessibility and other metaphors: the case of C_4 and CAM photosynthesis. *New Phytologist* **223**: 1742–1755.

Edwards EJ, Osborne CP, Strömberg CAE, Smith SA, C4 Grasses Consortium, Bond WJ, Christin P-A, Cousins AB, Duvall MR, Fox DL *et al.* 2010. The origins of C_4 grasslands: integrating evolutionary and ecosystem science. *Science* **328**: 587–591.

Edwards EJ, Smith SA. 2010. Phylogenetic analyses reveal the shady history of C_4 grasses. *Proceedings of the National Academy of Sciences, USA* **107**: 2532–2537.

Elliott TL, Zedek F, Barrett RL, Bruhl JJ, Escudero M, Hroudová Z, Joly S, Larridon I, Luceño M, Márquez-Corro JI *et al.* 2022. Chromosome size matters: genome evolution in the cyperid clade. *Annals of Botany* **130**: 999–1013.

Faith DP. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**: 1–10.

Fidelis A, Rosalem P, Zanzarini V, Camargos LS, Martins AR. 2019. From ashes to flowers: a savanna sedge initiates flowers 24 h after fire. *Ecology* **100**: e02648.

Folk RA, Sun M, Soltis PS, Smith SA, Soltis DE, Guralnick RP. 2018. Challenges of comprehensive taxon sampling in comparative biology: wrestling with rosids. *American Journal of Botany* **105**: 433–445.

Gallaher TJ, Peterson PM, Soreng RJ, Zuloaga FO, Li DZ, Clark LG, Tyrrell CD, Welker AD, Kellogg EA, Teisher JK. 2022. Grasses through space and time: an overview of the biogeographical and macroevolutionary history of Poaceae. *Journal of Systematics and Evolution* **60**: 522–569.

Givnish TJ, Barfuss MHJ, van Ee B, Riina R, Schulte K, Horres R, Gonsiska PA, Jabaily R, Crayn DM, Smith JAC *et al.* 2011. Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: insights from an eight-locus plastid phylogeny. *American Journal of Botany* **98**: 872–895.

Givnish TJ, Barfuss MHJ, Van Ee B, Riina R, Schulte K, Horres R, Gonsiska PA, Jabaily RS, Crayn DM, Smith JAC *et al.* 2014. Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. *Molecular Phylogenetics and Evolution* 71: 55–78.

Givnish TJ, Evans TM, Zjhra ML, Patterson TB, Berry PE, Sytsma KJ. 2000. Molecular evolution, adaptive radiation, and geographic diversification in the amphiatlantic family Rapateaceae: evidence from ndhF sequences and morphology. *Evolution* 54: 1915–1937.

Givnish TJ, Zuluaga A, Spalink D, Soto Gomez M, Lam VK, Saarela JM, Sass C, Iles WJ, De Sousa DJ, Leebens-Mack J *et al.* 2018. Monocot plastid phylogenomics, timeline, net rates of species diversification, the power of multi-gene analyses, and a functional model for the origin of monocots. *American Journal of Botany* 105: 1888–1910.

Gonzalez-Orozco CE, Pollock LJ, Thornhill AH, Mishler BD, Knerr N, Laffan SW, Miller JT, Rosauer DF, Faith DP, Nipperess DA *et al.* 2016. Phylogenetic approaches reveal biodiversity threats under climate change. *Nature Climate Change* 6: 1110–1114.

Gotelli NJ, Entsminger NJ. 2003. Swap algorithms in null model analysis. *Ecology* 84: 532–535.

Gouda EJ, Butcher D. 2023. *The new bromeliad taxon list, v.4*. Utrecht, the Netherlands: University Botanic Gardens. [WWW document] URL https://bromeliad.nl/taxonlist/ [accessed 1 February 2023].

Govaerts R, ed. 2022. *WCVP: world checklist of vascular plants*. Kew, UK: Facilitated by the Royal Botanic Gardens. [WWW document] URL http://sftp.kew.org/pub/data-repositories/WCVP/Special_Issue_28_Feb_2022/ [accessed 28 February 2022].

Gregory-Wodzicki KM. 2000. Uplift history of the Central and Northern Andes: a review. *Geological Society of America Bulletin* 112: 1091–1105.

Hartigan JA, Wong MA. 1979. Algorithm AS 136: a K-means clustering algorithm. *Applied Statistics* 28: 100–108.

Holt BG, Lessard JP, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D, Fabre PH, Graham CH, Graves GR, Jønsson KA *et al.* 2013. An update of Wallace's zoogeographic regions of the world. *Science* 339: 74–78.

Hopper SD, Silveira FA, Fiedler PL. 2016. Biodiversity hotspots and Ocbil theory. *Plant and Soil* 403: 167–216.

Johnson MG, Pokorny L, Dodsworth S, Botigue LR, Cowan RS, Devault A, Eiserhardt WL, Epitawalage N, Forest F, Kim JT *et al.* 2019. A universal probe set for targeted sequencing of 353 nuclear genes from any flowering plant designed using k-medoids clustering. *Systematic Biology* 68: 594–606.

Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software v.7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.

Kembel SW, Cowan PD, Helmus MR, Cornwell WL, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010. PICANTE: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.

Kreft H, Jetz W. 2007. Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences, USA* 104: 5925–5930.

Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ. 2006. Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Annals of Botany* 98: 693–713.

Larridon I, Spalink D, Jiménez-Mejías P, Márquez-Corro JI, Martín-Bravo S, Muasya M, Escudero M. 2021a. The evolutionary history of sedges (Cyperaceae) in Madagascar. *Journal of Biogeography* 48: 917–932.

Larridon I, Zuntini AR, Léveillé-Bourret E, Barrett RL, Starr JR, Muasya AM, Villaverde T, Bauters K, Brewer GE, Bruhl JJ *et al.* 2021b. A new classification of Cyperaceae (Poales) supported by phylogenomic data. *Journal of Systematics and Evolution* 59: 852–895.

Larsson A. 2014. ALIVIEW: a fast and lightweight alignment viewer and editor for large data sets. *Bioinformatics* 30: 3276–3278.

Linder HP, Eldenas P, Briggs BG. 2003. Contrasting patterns of radiation in African and Australian Restionaceae. *Evolution* 57: 2688–2702.

Linder HP, Lehmann CER, Archibald S, Osborne CP, Richardson DM. 2018. Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biological Reviews* 93: 1125–1144.

Linder HP, Rudall PJ. 2005. Evolutionary history of Poales. *Annual Review of Ecology, Evolution, and Systematics* 36: 107–124.

Litsios G, Wüest RO, Kostikova A, Forest F, Lexer C, Linder HP, Pearman PB, Zimmermann NE, Salamin N. 2014. Effects of a fire response trait on diversification in replicated radiations. *Evolution* 68: 453–465.

Louca S, Pennell MW. 2020. Extant timetrees are consistent with a myriad of diversification histories. *Nature* 580: 502–505.

Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K. 2022. *cluster: Cluster analysis basics and extensions. R package v.2.1.3*. [WWW document] URL https://CRAN.R-project.org/package=cluster [accessed 1 May 2022].

Mai U, Mirarab S. 2018. TREESHRINK: fast and accurate detection of outlier long branches in collections of phylogenetic trees. *BMC Genomics* 19: 272.

Martín-Bravo S, Jiménez-Mejías P, Villaverde T, Escudero M, Hahn M, Spalink D, Roalson EH, Hipp AL, Global Carex Group. 2019. A tale of worldwide success: behind the scenes of *Carex* (Cyperaceae) biogeography and diversification. *Journal of Systematics and Evolution* 57: 695–718.

Matzke NJ. 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 NJ. 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 TJ, Burrows JE, Daru BH, Yessoufou K, Muasya M, van der Bank M, Bond WJ. 2014. Savanna fire and the origins of the 'underground forests' of Africa. *New Phytologist* 204: 201–214.

Meynard CN, Lavergne S, Boulangeat I, Garraud L, Van Es J, Mouquet N, Thuiller W. 2013. Disentangling the drivers of metacommunity structure across spatial scales. *Journal of Biogeography* 40: 1560–1571.

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Haeseler A, Lanfear R. 2020. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37: 1530–1534.

Mishler BD, Knerr N, González-Orozco CE, Thornhill AH, Laffan SW, Miller JT. 2014. Phylogenetic measures of biodiversity and neo- and paleo-endemism in Australian *Acacia*. *Nature Communications* 5: 4473.

Muasya AM, Harvey Y, Cheek M, Tah K, Simpson DA. 2010. *Coleochloa domensis* (Cyperaceae), a new epiphytic species from Cameroon. *Kew Bulletin* 65: 323–325.

Nitta JH, Iwasaki W. 2021. *CANAPER: categorical analysis of neo- and paleo-endemism in R*. doi: 10.5281/zenodo.5094032.

Nitta JH, Mishler BD, Iwasaki W, Ebihara A. 2022. Spatial phylogenetics of Japanese ferns: patterns, processes, and implications for conservation. *American Journal of Botany* 109: 727–745.

Osborne CP, Freckleton RP. 2009. Ecological selection pressures for C_4 photosynthesis in the grasses. *Proceedings of the Royal Society B: Biological Sciences* 276: 1753–1760.

Peppe DJ, Cote SM, Deino AL, Fox DL, Kingston JD, Kinyanjui RN, Lukens WE, MacLatchy LM, Novello A, Strömberg CA *et al.* 2023. Oldest evidence of abundant C_4 grasses and habitat heterogeneity in eastern Africa. *Science* 380: 173–177.

Pilon NA, Freire CT, Oliveira-Alves MJ, Oliveira RS. 2023. Speedy blooming in Cerrado after fire is not uncommon: new records of Cyperaceae species flowering 24 h after burning. *Austral Ecology* 48: 1042–1045.

Porembski S, Rexroth J, Weising K, Bondi L, Mello-Silva R, Centeno DC, Datar MN, Watve A, Thiombano A, Tindano E *et al.* 2021. An overview on desiccation-tolerant mat-forming monocotyledons on tropical inselbergs. *Flora* 285: 151953.

Prasad V, Stromberg CA, Alimohammadian H, Sahni A. 2005. Dinosaur coprolites and the early evolution of grasses and grazers. *Science* 310: 1177–1180.

Prasad V, Strömberg CAE, Leaché AD, Samant B, Patnaik R, Tang L, Mohabey DM, Ge S, Sahni A. 2011. Late Cretaceous origin of the rice tribe provides evidence for early diversification in Poaceae. *Nature Communications* 2: 480.

R Core Team. 2021. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. [WWW document] URL https://www.R-project.org/ [accessed 1 May 2022].

Ratnam J, Bond WJ, Fensham RJ, Hoffmann WA, Archibald S, Lehmann CER, Anderson MT, Higgins SI, Sankaran M. 2011. When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography* 20: 653–660.

Ree RH, Moore BR, Webb CO, Donoghue MJ. 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* 59: 2299–2311.

Ree RH, 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.

Ree RH, Smith SA. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* **57**: 4–14.

Revell LJ. 2012. PHYTOOLS: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.

Ricklefs RE, Renner SS. 1994. Species richness within families of flowering plants. *Evolution* **48**: 1619–1636.

Rosauer D, Laffan SW, Crisp MD, Donnellan SC, Cook LG. 2009. Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology* **18**: 4061–4072.

Ross S-J, Suzuki Y, Kondoh M, Suzuki K, Villa Martín P, Dornelas M. 2021. Illuminating the intrinsic and extrinsic drivers of ecological stability across scales. *Ecological Research* **36**: 364–378.

Rousseeuw PJ. 1987. Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics* **20**: 53–65.

Sage RF, Monson RK, Ehleringer JR, Adachi S, Pearcy RW. 2018. Some like it hot: the physiological ecology of C_4 plant evolution. *Oecologia* **187**: 941–966.

Salvador S, Chan P. 2004. Determining the number of clusters/segments in hierarchical clustering/segmentation algorithms. In: *Proceedings of the sixteenth IEEE international conference on tools with artificial intelligence.* Piscataway, NS, USA: Institute of Electrical and Electronics Engineers, 576–584.

Sanbonmatsu KK, Spalink D. 2022. A global analysis of mosses reveals low phylogenetic endemism and highlights the importance of long-distance dispersal. *Journal of Biogeography* **49**: 654–667.

Schubert M, Humphreys AM, Lindberg CL, Preston JC, Fjellheim S. 2020. To coldly go where no grass has gone before: a multidisciplinary review of cold adaptation in Poaceae. *Annual Plant Reviews* **3**: 523–562.

Sechrest W, Brooks TM, da Fonseca GAB, Konstant WR, Mittermeier RA, Purvis A, Rylands AB, Gittleman JL. 2002. Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences, USA* **99**: 2067–2071.

Smith SA, Brown JW, Walker JF. 2018. So many genes, so little time: a practical approach to divergence-time estimation in the genomic era. *PLoS ONE* **13**: e0197433.

Smith SA, O'Meara BC. 2012. TREEPL: divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics* **28**: 2689–2690.

Smith SY, Collinson ME, Simpson DA, Rudall PJ, Marone F, Stampanoni 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.

Solofondranohatra CL, Vorontsova MS, Hempson GP, Hackel J, Cable S, Jand V, Lehmann CER. 2020. Fire and grazing determined grasslands of central Madagascar represent ancient assemblages. *Proceedings of the Royal Society B: Biological Sciences* **287**: 20200598.

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Zuloaga FO, Judziewicz EJ, Filgueiras TS, Davis JI, Morrone O. 2015. A worldwide phylogenetic classification of the Poaceae (Gramineae). *Journal of Systematics and Evolution* **53**: 117–137.

Soreng RJ, Peterson PM, Zuloaga RO, Romaschenko K, Clarke LG, Teisher JK, Gillespie LJ, Barberá P, Welker CAD, Kellogg EA. 2022. A worldwide phylogenetic classification of the Poaceae (Gramineae) III: an update. *Journal of Systematics and Evolution* **60**: 476–521.

Spalink D, Drew BT, Pace MC, Zaborsky JG, Starr JR, Cameron KM, Givnish TJ, Sytsma KJ. 2016. Biogeography of the cosmopolitan sedges (Cyperaceae) and the area-richness correlation in plants. *Journal of Biogeography* **43**: 1893–1904.

Spalink D, MacKay R, Sytsma KJ. 2019. Phylogeography, population genetics and distribution modelling reveal vulnerability of *Scirpus longii* (Cyperaceae) and the Atlantic Coastal Plain Flora to climate change. *Molecular Ecology* **28**: 2046–2061.

Spalink D, Pender J, Escudero M, Hipp AL, Roalson EH, Starr JR, Waterway MJ, Bohs L, Sytsma KJ. 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 v.8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1313.

Strömberg CAE. 2011. Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences* **39**: 517–544.

Strona G, Nappo D, Boccacci F, Fattorini S, San-Miguel-Ayanz J. 2014. A fast and unbiased procedure to randomize ecological binary matrices with fixed row and column totals. *Nature Communications* **5**: 4114.

Sunil CN, Ratheesh Narayanan MK, Sivadasan M, Alfarhan AH, Abdul JV. 2015. *Eriocaulon vandaanamense* sp. nov. (Eriocaulaceae) from Kerala, India. *Nordic Journal of Botany* **33**: 155–158.

Takhtajan A. 1986. *Floristic regions of the world.* Berkeley, CA, USA: University of California Press.

Thornhill AH, Mishler BD, Knerr NJ, González-Orozco CE, Costion CM, Crayn DM, Laffan SW, Miller JT. 2016. Continental-scale spatial phylogenetics of Australian angiosperms provides insights into ecology, evolution and conservation. *Journal of Biogeography* **43**: 2085–2098.

Tibshirani R, Walther G, Hastie T. 2001. Estimating the number of data clusters via the Gap statistic. *Journal of the Royal Statistical Society: Series B: Methodological* **63**: 411–423.

Tucker CM, Cadotte MW, Carvalho SB, Davies TJ. 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Review* **92**: 698–715.

Vasconcelos TN, Alcantara S, Andrino CO, Forest F, Reginato M, Simon MF, Pirani JR. 2020. Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient Neotropical mountains. *Proceedings of the Royal Society B: Biological Sciences* **287**: 20192933.

Veldman JW, Buisson E, Durigan G, Fernandes GW, Le Stradic S, Mahy G, Negreiros D, Overbeck GE, Veldman RG, Zaloumis NP. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment* **13**: 154–162.

Vera-Paz S, Granados Mendoza C, Díaz Contreras Díaz DD, Jost M, Salazar GA, Rossado AJ, Montes-Azcué CA, Hernández-Gutiérrez R, Magallón S, Sánchez-González LA *et al.* 2023. Plastome phylogenomics reveals an early Pliocene North- and Central America colonization by long-distance dispersal from South America of a highly diverse bromeliad lineage. *Frontiers in Plant Science* **14**: 1205511.

Vicentini A, Barber JC, Aliscioni SS, Giussani LM, Kellogg EA. 2008. The age of the grasses and clusters of origins of C_4 photosynthesis. *Global Change Biology* **14**: 2963–2977.

Vigeland MD, Spannagl M, Asp T, Paina C, Rudi H, Rognli O-A, Fjellheim S, Sandve SR. 2013. Evidence for adaptive evolution of low-temperature stress response genes in a Pooideae grass ancestor. *New Phytologist* **199**: 1060–1068.

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.

Wang Q, Huang J, Zang R, Li Z, El-Kassaby YA. 2022. Centres of neo-and paleo-endemism for Chinese woody flora and their environmental features. *Biological Conservation* **276**: 109817.

Zhang C, Rabiee M, Sayyari E, Mirarab S. 2018. ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics* **19**: 153.

Zhang XX, Ye JF, Laffan SW, Mishler BD, Thornhill AH, Lu LM, Mao LF, Liu B, Chen YH, Lu AM *et al.* 2022. Spatial phylogenetics of the Chinese angiosperm flora provides insights into endemism and conservation. *Journal of Integrative Plant Biology* **64**: 105–117.

Zhang Y, Qian L, Spalink D, Sun L, Chen J, Sun H. 2021. Spatial phylogenetics of two topographic extremes of the Hengduan Mountains in southwestern China and its implications for biodiversity conservation. *Plant Diversity* **43**: 181–191.

Zhao X, Valen E, Parker BJ, Sandelin A. 2011. Systematic clustering of transcription start site landscapes. *PLoS ONE* **6**: e23409.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Ancestral area reconstruction within Poales based on seven regions, obtained using the DIVA model in BioGeoBEARS.

Fig. S2 Number of species of Poales missing from the phylogenetic data set compared to the number listed in the World Checklist of Vascular Plants as of 28 February 2022, mapped per botanical region.

Fig. S3 Phylogenetic diversity of the six largest Poales families categorised into open and closed habitats.

Fig. S4 Phylogenetic endemicity mapped per botanical region for Poales and eight families with the highest number of species in the data set.

Fig. S5 Poales botanical regions grouped into three 'floristic kingdoms' based on phylogenetic beta-diversity, indicated by different colours and numbers.

Notes S1 Methodological detail on sequence assembly and tree construction.

Notes S2 Justification for selecting dispersal–extinction–cladogeneis model of ancestral estimation.

Table S1 Sequences for the phylogenetic reconstruction.

Table S2 Calibrations used in the TREEPL (Smith & O'Meara, 2012) configuration file.

Table S3 Taxa included in this study, showing habitat scoring across the Poales.

Table S4 Comparison of six ancestral area reconstruction models based on BioGeoBEARS analyses for Poales.

Table S5 Results from CORHMM ancestral state reconstructions.