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

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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

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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. Solo-fondranohatra *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 24302 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, Ecdeiocolea-ceae) 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; Sanbon-matsu & 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* (Rapateaceae) 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 multi-species 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 BIOGEO-BEARS 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).
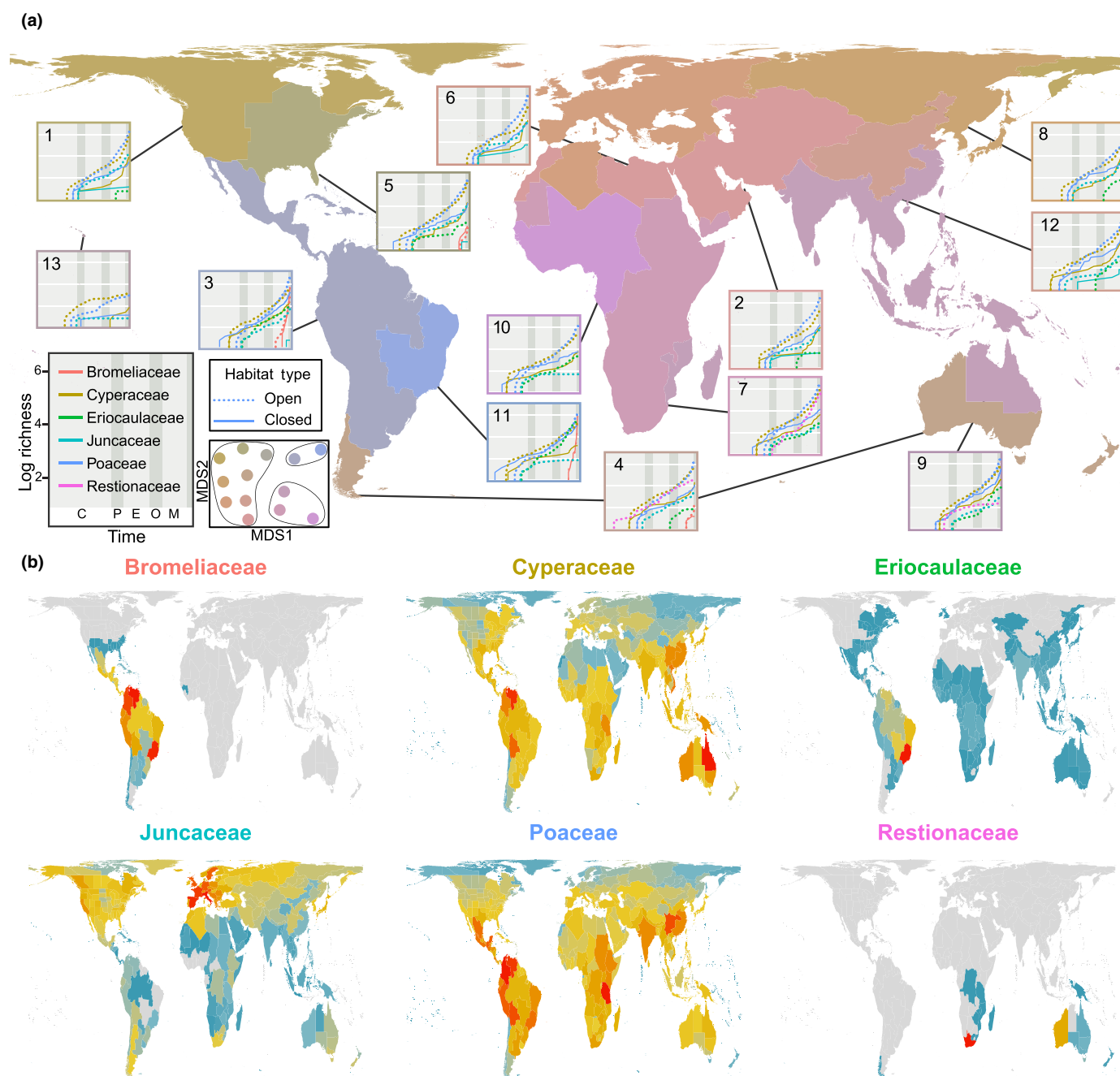
Families differ in their stem age and lineage accumulation over time among the 13 regions (Fig. 2a). Considering the six largest families, Poaceae or Cyperaceae are the oldest in all regions, except for the Restionaceae which are oldest in temperate Australia. Bromeliaceae is the youngest family. Smaller 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):
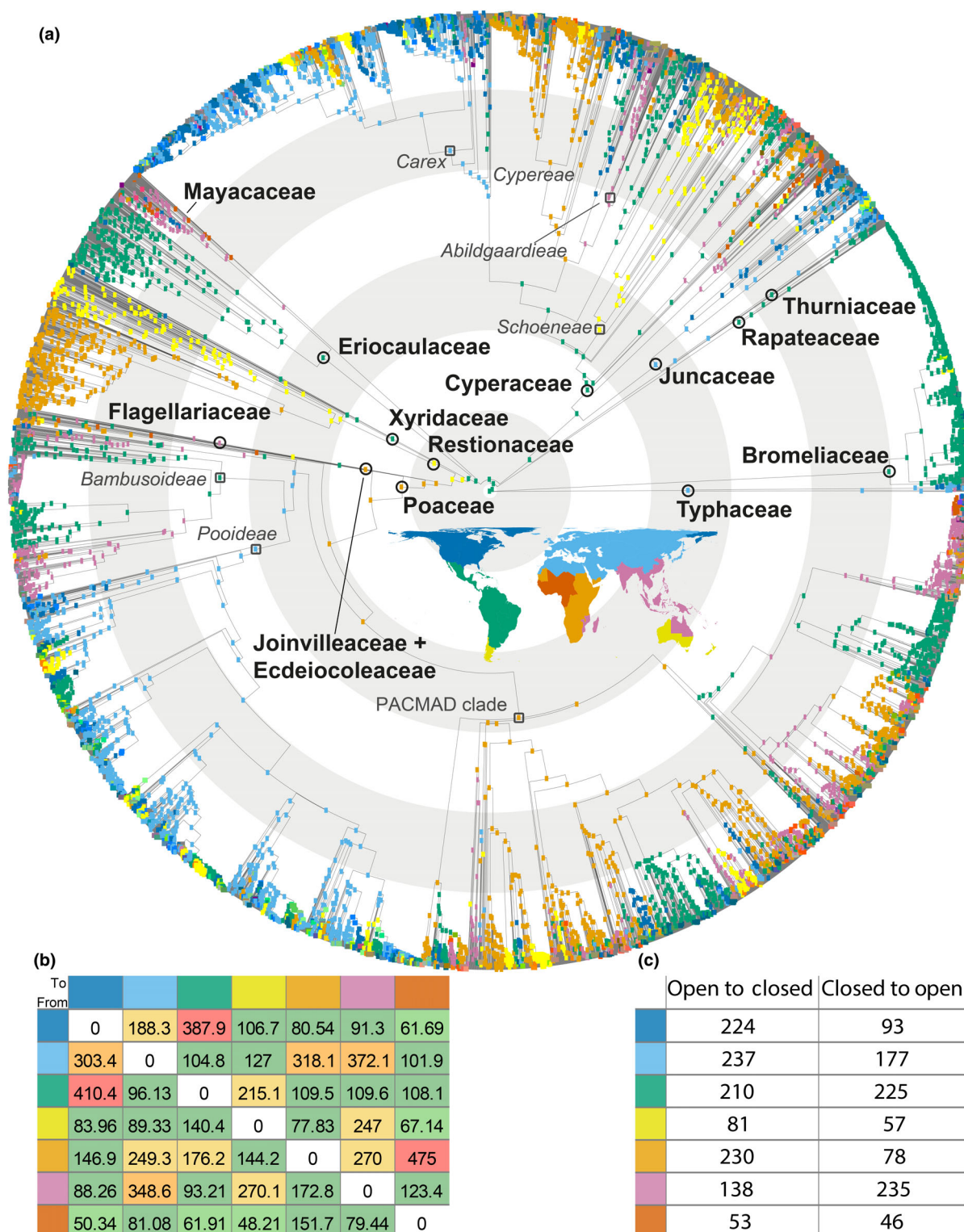
Fig. 2 Global phylogenetic patterns of regionalisation in Poales. (a) Phylogenetic regionalisation of the six largest families of Poales. Graphs represent the logarithmic species richness of the six families through time within each of the 13 phyloregions identified using the elbow and K-means approach, 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).

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.
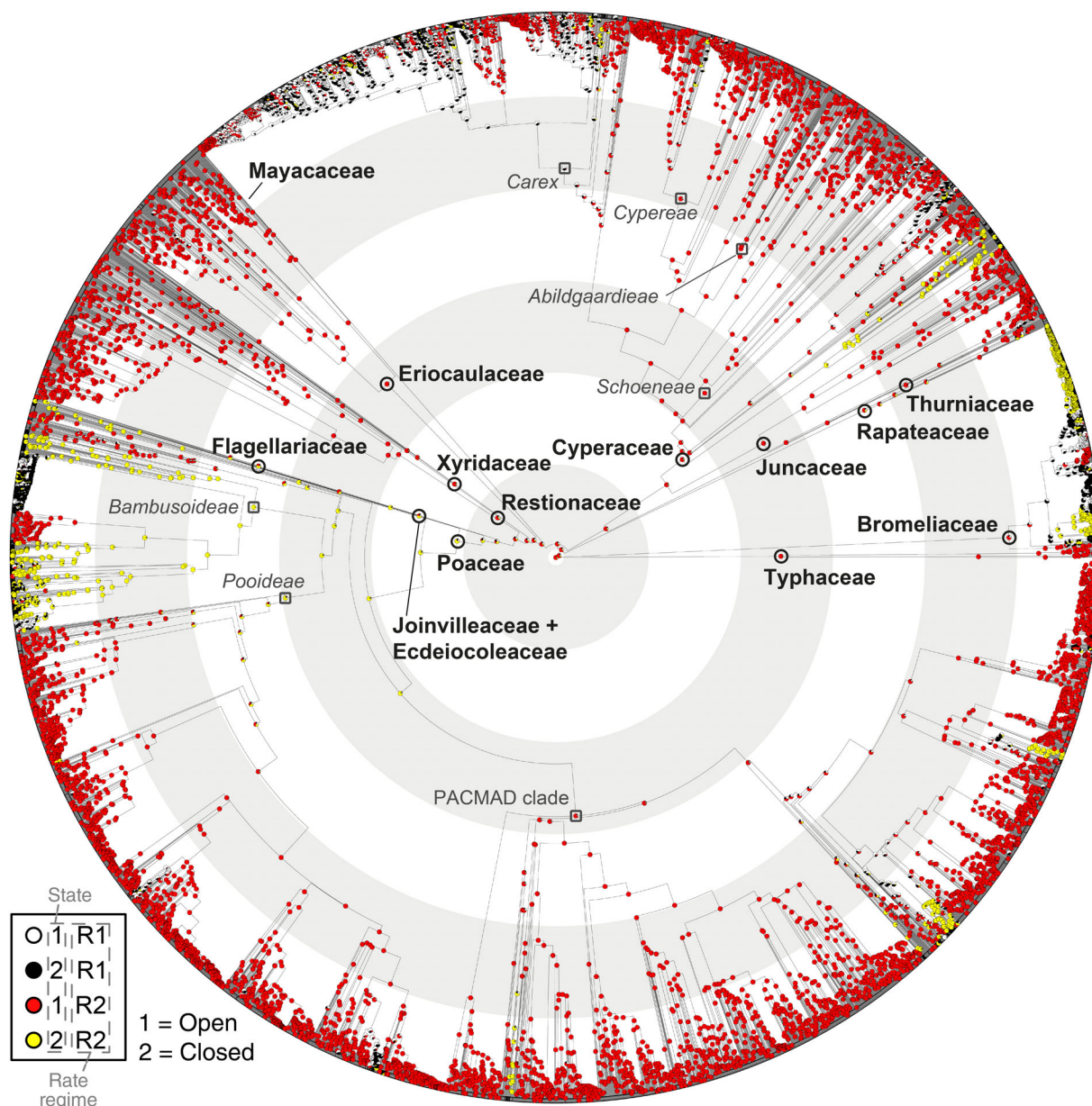
Categorical analysis of endemism (CANAPE; Fig. 5e) shows a general contrasting pattern for Poales between Holarctic (mostly non-significant) and Holotropic + Austral (significant) regions. Palaeo-endemism in Poales was supported in northern South America, southern Africa and Australia – a pattern also 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
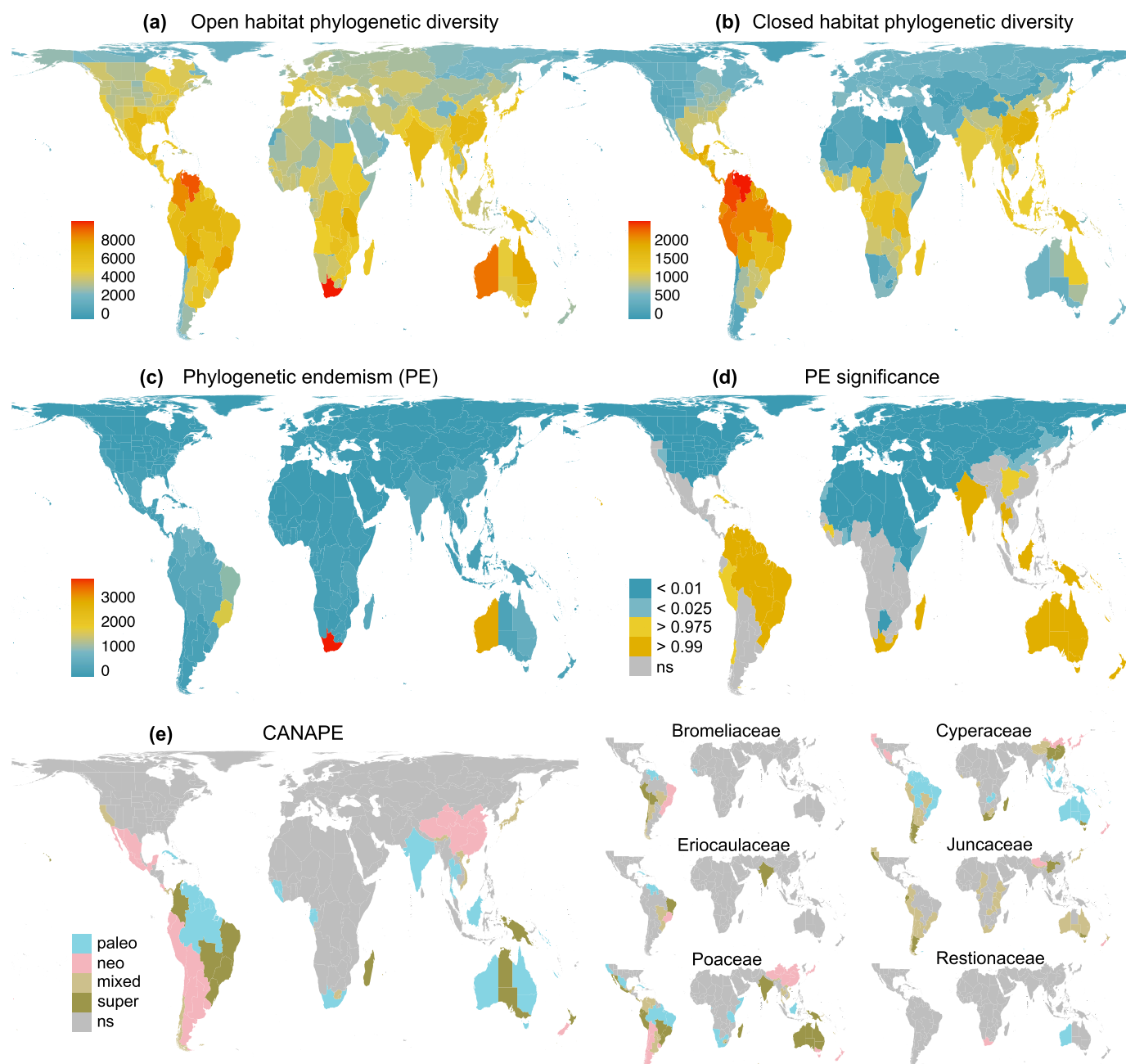
Fig. 4 Ancestral states of open/closed habitats based on Generalized Hidden Markov models, with hidden rates model with two categories and asymmetric rates, implemented with the corHMM package in R. The crown nodes of the families within Poales are shown with black circles, whereas dark grey squares 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 C₃ 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 (holanctarctic, *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 beta-diversity 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.

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.

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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).

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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.

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