

Original Article

New insights into the classification, diversification, and evolutionary dynamics of bromeliads

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ABSTRACT

The Neotropics have been host to a myriad of geological and climatic events that have shaped the biodiversity present in the region. Bromeliaceae forms one of the most prominent components of the Neotropical flora, being considered the largest group nearly exclusive to the Americas, with almost 4000 species divided into eight subfamilies. Here, we utilize a new time-calibrated molecular phylogeny including 1268 bromeliad taxa and integrate habitat and morphological data to answer the following questions: (i) Are bromeliad subfamilies monophyletic, and did Neogene and Quaternary events in South America coincide with their divergence? (ii) Did naked seeds of berry-fruited species, epiphytic growth, and climatic factors increase bromeliad diversification? Our analysis reconstructed a new topology concerning some recently diverged lineages, with the genus *Bromelia* emerging as the sister group of a clade including all remaining Bromelioideae lineages + Puyoideae. Miocene events possibly triggered the diversification of bromeliads after a long period of stasis during the Palaeogene. We hypothesize that the morphological shift between *Bromelia* and Bromelioideae (except *Bromelia*) is related to the colonization of a new high-elevation environment by Puyoideae in the Andes. Additionally, our results show that naked seeds and the epiphytic growth form positively influence diversification rate, while precipitation, temperature, and elevation have a negative influence. We emphasize the importance of considering a variety of morphological and ecological features to enhance our understanding of bromeliad evolution.

Keywords: epiphytes; evolution; monocots; Neotropics; pineapple

INTRODUCTION

Tropical rainforests are characterized by high levels of temperature, precipitation, and species richness, which generally peaks at low latitudes, where forests present the highest canopies (Morley 2000, Zhang *et al.* 2016). Particularly for epiphytes, higher canopies increase niche space because of vertical stratification and microclimatic variation (de la Rosa-Manzano *et al.* 2014, Oliveira and Scheffers 2019). In addition to latitude and

canopy height, elevation also influences biological distribution and diversification, with plant lineages at higher altitudes generally exhibiting elevated rates of speciation (Lagomarsino *et al.* 2016, Testo *et al.* 2019).

The exceptional biodiversity of the Neotropics, marked by high levels of species richness and endemism, is attributed to millions of years of biotic and abiotic interactions (Myers *et al.* 2000, Antonelli and Sanmartín 2011). Factors such as tectonic

activity during the Neogene period, mountain uplift, and the formation of dry forests have spurred species evolution and defined bioregions (Hoorn *et al.* 2010, Smith *et al.* 2014). Additionally, Quaternary glacial cycles, influencing forest expansion and contraction, also significantly shaped species distribution and diversification (Rull 2011).

There are 52 endemic (or nearly so) plant families to the Americas, almost all of which are species-poor (fewer than 100 recognized species; Givnish 2017, Ulloa Ulloa *et al.* 2017). A remarkable exception is the Bromeliaceae (bromeliads), a hyperdiverse family of monocots that includes air plants and pineapples. All but one [*Pitcairnia feliciana* (A.Chev.) Harms & Mildbr.] of the ~3800 recognized species of bromeliads are endemic to the Americas, most of them restricted to the Neotropics (Smith and Downs 1974, Ulloa Ulloa *et al.* 2017, Givnish 2017; Gouda *et al.* [cont. updated]).

Bromeliads were traditionally divided into three subfamilies: Bromelioideae, Pitcairnioideae, and Tillandsioideae (Smith and Downs 1974, 1977, 1979). Molecular phylogenetic studies have since recognized eight subfamilies, of which five were segregated from Pitcairnioideae: Brocchinioideae, Hechtioideae, Lindmanioideae, Navioideae, and Puyoideae (Givnish *et al.* 2007, 2011). Tillandsioideae is the largest and most widespread subfamily in Bromeliaceae, encompassing almost half of the species and occurring from the southern USA to Patagonia (Barfuss *et al.* 2016; Gouda *et al.* [cont. updated]). Bromeliads are ecologically diverse and occur from sea level to ~4000 m in elevation. This ecological diversity is linked to morphological and physiological adaptations, including a tank habit, epiphytic growth form, Crassulacean acid metabolism (CAM) photosynthesis, and a myriad of biotic interactions (Smith and Downs 1974, Benzing 2000, Givnish *et al.* 2014).

There are two means of dispersal in bromeliads: (i) biotic, in berry-fruited species exclusive of Bromelioideae (Givnish *et al.* 2011, 2014, Silva *et al.* 2020) with "naked" seeds, dispersed by vertebrates or insects (Smith and Till 1988); and (ii) abiotic, present in capsule-fruited species (plumose in Tillandsioideae, naked dry in Navioideae, and winged seeds in the remaining subfamilies) dispersed by wind or gravity (Smith and Downs 1974, Benzing 2000). Despite being traditionally associated with naked seeds, studies have shown that some Bromelioideae species develop appendages of different anatomical origins that are often mucilaginous and sticky (Silva *et al.* 2020, Leme *et al.* 2021) and can entangle its seeds (Givnish *et al.* 2014).

Despite the emergence of Bromeliaceae in the early Cretaceous (~120 Mya; Givnish *et al.* 2018), lineage diversification within the family only took place during the early Miocene (~20 Mya; Givnish *et al.* 2011), and the reasons behind this 100-Myr gap in the bromeliad evolutionary history are still unknown (Givnish *et al.* 2014, Kessous *et al.* 2021). In the Neotropics, the end of the Cretaceous was characterized by open-canopied forests and the presence of several vascular plant groups (Carvalho *et al.* 2021). In contrast, the early Palaeocene forests had dense canopies and were species-poor. This difference is probably due to the presence of large herbivores that physically disturbed forests, the infertility of the soils in the Maastrichtian, and the selective extinction of most gymnosperm diversity at the Cretaceous–Palaeogene boundary (Carvalho *et al.* 2021). The slow recovery from the Chicxulub impact 66 Mya and intense

volcanic activity, which suppressed sunlight, changed the atmosphere, and reduced global temperatures, causing a 45% reduction in Palaeocene plant diversity (Alvarez *et al.* 1980, Vajda and Bercovici 2014, Vajda *et al.* 2015, Schulte P. *et al.* 2010b, Hull *et al.* 2020, Carvalho *et al.* 2021).

Changes in water and light availability within closed canopies in more complex Neotropical Palaeocene forests provided opportunities for vertical diversity (Carvalho *et al.* 2021), especially in epiphytes, such as the great part of bromeliads. The earliest bromeliads were terrestrial and thrived in open environments (Bouchenak-Khelladi *et al.* 2014, Givnish *et al.* 2014), in the Guiana Shield (Givnish *et al.* 2011). However, the emergence of the epiphytic growth form during the Mid-Miocene probably acted as a catalyst for rapid and extensive diversification through the whole Neotropics (Givnish *et al.* 2014, Givnish 2017).

The evolution of the epiphytic growth form, CAM metabolism, tank habit, and fleshy fruits (berries) also led to high diversification of subfamily Bromelioideae (Givnish *et al.* 2014, Silvestro *et al.* 2014). This subfamily, encompassing ~1000 species, is traditionally recognized as monophyletic and, together with Puyoideae, was the most recent subfamilial-level group to diverge in Bromeliaceae, ~10 Mya (Terry *et al.* 1997, Horres *et al.* 2000, 2007, Schulte *et al.* 2005, 2009, Givnish *et al.* 2007, 2011, 2014, Sass and Specht 2010, Silvestro *et al.* 2014, Aguirre-Santoro *et al.* 2024; Gouda *et al.* [cont. updated]). Puyoideae is weakly supported as monophyletic and the position of Chilean and non-Chilean clades is unresolved (Givnish *et al.* 2011).

The uniqueness in the distribution, ecology, and endemism of bromeliads provides an excellent opportunity to understand the relationship between dispersal-related traits, diversity patterns, and spatial distribution in the Neotropics. The most recent bromeliad subfamily classification was based on a phylogeny of 90 species, representing 2.5% of the family species diversity (Givnish *et al.* 2011), overlooking a vast majority of biogeographical, morphological, and genetic variation within the family. To advance our understanding, here we aim to test the monophyly of Bromeliaceae subfamilies and assess their temporal divergences, more than 10 years after the last subfamilial classification proposed by Givnish *et al.* (2011). Additionally, we aim to identify how seed morphology and habitat influence diversification in Bromeliaceae. To accomplish this, we compiled Sanger DNA sequence data for 1268 bromeliad taxa to construct a comprehensive phylogeny, assembled morphological, distributional, and ecological datasets, and conducted comparative phylogenetic analyses. Specifically, we addressed the following questions: (i) Are bromeliad subfamilies monophyletic, and did geological events during the Neogene and Quaternary periods in South America temporally coincide with their divergence? (ii) Did naked seeds of berry-fruited species, the epiphytic growth form, and climatic factors such as precipitation, canopy height, temperature, and elevation increase the diversification rate in bromeliads?

MATERIAL AND METHODS

Taxon and sequence sampling

We obtained sequence data for 13 chloroplast (*agt1*, *ycf1*, *rps16-intron*, *rps16-trnK*, *rpl32*, *matK*, *nadH*, *petD*, *trnL-trnF*, *rpoB*, *atpB-rbcL*, *psbA-trnH*, and *trnC-petN*) and three nuclear (*PHYC*,

PRK, and LEAFY) loci from GenBank, for a total of 1268 taxa of Bromeliaceae (~30% of the family) and five outgroups from Typhaceae and Rapateaceae (Supporting Information, S1). We had different sampling fractions for each clade: Bromelioideae + Puyoideae (42%), Tillandsioideae (33%), Navioideae (6%), Brocchinioideae (40%), Lindmanioideae (7%), and Pitcairnioideae (30%).

We aligned each locus with MAFFT using default parameters (Kato and Toh 2007). We removed poorly aligned and divergent regions using Gblocks (Castresana 2000), allowing gap positions in the final blocks and less strict flanking positions, and using Geneious Prime (v.2021.0.1, Biomatters, New Zealand), under the criterion of mean pairwise identity over all pairs in the column of at least 30% (Supporting Information, S2). Alignments were performed in R v.3.5.3 (R Core Team 2019), using the package *ips* 0.0.11 (Heibl 2019). To increase the statistical power and accuracy of the analysis, we concatenated the alignments using Geneious Prime and Mesquite v.3.61 (Maddison and Maddison 2019).

We used the *Encyclopaedia of Bromeliads* (Gouda *et al.* [cont. updated], <https://bromeliad.nl/encyclopedia/>) to standardize the taxonomic classification used in the molecular dataset (Supporting Information, S3). Despite the amount (78%) of missing DNA data in our molecular matrix, recent studies suggest that even matrices with significant amounts of missing data provide essential information for reconstructing phylogenies (Ferreira *et al.* 2022).

Phylogenetic analysis and molecular dating

We have reconstructed a new phylogenetic tree for bromeliads, incorporating 1268 taxa. To address the challenge of converging multiple Markov chain Monte Carlo (MCMC) runs with multilocus and more than 1000 species data, we initially conducted an uncalibrated analysis. This analysis identified parameters with disproportionately high effective sample sizes (ESS) compared with other parameters. Subsequently, we reduced their operator weights under the assumption that the data were informative enough for their estimation, which allowed us to speed up data analysis and optimize the use of computing resources. All XML files generated for these and subsequent runs were generated with BEAUTi v.1.10.4 (Suchard *et al.* 2018).

A large number of terminals required high-performance computing resources. Due to convergence issues, we reduced the model complexity by selecting the HKY substitution model and a strict molecular clock (Yule 1925, Gernhard 2008). This choice facilitates MCMC convergence, essential for analysing a large number of terminals. After adjusting operator weights, we used BEAST v.1.10.4 (Suchard *et al.* 2018) to run three rounds of two independent chains, each with 300 million MCMC generations sampled every 30 000 generations (Supporting Information, S4). After every round, we selected the last tree of the analysis with the best ESS values and used it as the starting tree of a subsequent round in order to reach stationarity in both chains. To obtain the maximum clade credibility (MCC) tree, we summarize the nodes using mean heights and applied a 15% burn-in to the resulting tree distribution such that the remaining ESS values were >600. After all rounds, we reached 549 060 000 sampled generations. We performed all phylogenetic analyses at the Swedish National Infrastructure for Computing

(<https://www.snics.se/>) and in the CIPRES Science Gateway v.3.3 (<https://www.phylo.org/>).

We dated the MCC tree *a posteriori* using penalized likelihood performed in treePL (Smith and O'Meara 2012). Because of the absence of reliable fossils of Bromeliaceae useful for dating (Kessous *et al.* 2021), we performed secondary calibrations based on age constraints from Givnish *et al.* (2018), with minimum and maximum age bounds set at 20% younger and older than the median ages reported for the stem, (96–) 120 (–144) Mya, and crown, (16–) 20 (–24) Mya, of the family. We ran this analysis 100 times and used TreeAnnotator (Bouckaert *et al.* 2014) to generate a consensus tree and calculate the 95% highest posterior density (HPD) for each node age.

Tree topology tests

To assess the fit of the data to the alternative topology, we conducted an additional phylogenetic analysis using maximum likelihood (ML) methods with IQ-TREE 2.2.2.6 (Minh *et al.* 2020). The dataset was divided into partitions for each loci, and model testing was performed using ModelFinder (Kalyaanamoorthy *et al.* 2017) for each partition. The resulting tree (ML tree) using the selected models was then combined with the MCC tree from the BEAST analysis. Subsequently, topology tests were conducted using the Kishino and Hasegawa (p-KH) test (Kishino and Hasegawa 1989) and the approximately unbiased (p-AU) test (Shimodaira 2002) using 10 000 bootstrap replications.

Biotic and abiotic factors

Based on the literature (Smith and Downs 1974, Benzing 2000, Givnish *et al.* 2011; Gouda *et al.* [cont. updated]) we scored each species for seed type: (i) naked (Bromelioideae type); (ii) plumose (Tillandsioideae type); (iii) winged (Pitcairnioideae, Hechtioideae, Brocchinioideae, Lindmanioideae, and Puyoideae type); and (iv) naked dry (Navioideae type). The term naked dry is used to describe species with capsular fruits and seeds without appendages.

In addition to seed morphology, we extracted the growth form of each species using the information *tf_growth_form* from the *bromeliad* R package (Zizka *et al.* 2020) and then simplified the states into two categories: (i) epiphyte and (ii) non-epiphyte. Additionally, we scored four continuous variables related to habitat: mean annual temperature, mean annual precipitation, elevation, and canopy height. We downloaded a canopy height raster with 1-km resolution (<https://landscape.jpl.nasa.gov/>; accessed on 22 March 2021) and an elevation raster with 30-m resolution (https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-shuttle-radar-topography-mission-srtm?qt-science_center_objects=0#qt-science_center_objects; accessed on 22 March 2021). Also, we downloaded the mean annual precipitation and mean annual temperature variables from CHELSA v.1.2 (Karger *et al.* 2017, Karger and Zimmermann 2019; <http://dx.doi.org/doi:10.5061/dryad.kd1d4> accessed; on 22 March 2021).

To obtain the geographical occurrence of species, we downloaded 121 978 records of Bromeliaceae from GBIF (<https://doi.org/10.15468/dl.ny8dnt>). To remove duplicates and erroneous occurrence records, we used the R package CoordinateCleaner 2.0.18 (Zizka *et al.* 2019), flagging "capitals", "centroids", "equal", "institutions", "outliers" and "zeros". In addition, we removed

species with a single occurrence point and deleted duplicates. The final dataset consisted of 68 423 records of 2726 species. We extracted the values of each geographical occurrence point using the R package *raster* 3.4.13 (Hijmans *et al.* 2015) and calculated the mean for each species.

Diversification analyses

We obtained the net diversification tip rates using BAMM v.2.5.0 and analysed the outputs using the R package BAMMTools 2.1.7 (Rabosky *et al.* 2014). To account for incomplete sampling and heterogeneity of the MCC tree (totalling 30% for the whole family), we specified different sampling fractions for each clade, based on the proportion of recognized species present in the phylogeny: Bromelioideae + Puyoideae (0.42), Tillandsioideae (0.33), Navioideae (0.06), Brocchinioideae (0.4), Lindmanioideae (0.07), and Pitcairnioideae (0.3), according to Gouda *et al.* [cont. updated]. We ran four reversible jump MCMC chains, each for 20 million generations, sampling each 20 000 generations. We discarded the first 20% generations as burn-in and checked the convergence in the ESS with a threshold >200.

Generalized linear models

We investigated the effect of biotic and abiotic factors on the diversification rate of each species, resulted from its lineage, using generalized linear models (GLMs) through the *glm* function in R. As BAMM tip rates are not a continuous variable, we treated the diversification response variable as binary (0, low diversification; 1, high diversification), which was separated by its median value. We used seed type, growth form, elevation, canopy height, annual temperature, and annual precipitation as potential predictors.

We automated the testing process by including all 127 possible trait combinations and utilized the Akaike information criterion (AIC) to determine the best-fit model. We also evaluate the influence of the interaction between seed type and canopy height as a potential predictor. Finally, we conducted an ANOVA test using the *Anova* function in the *car* 3.0.13 R package (Fox and Weisberg 2019) to assess the effect of each trait. We assessed the assumptions of all models through visual inspection of the residuals after applying the *qqnorm* function. We checked the contrasts using the *lsmeans* 2.30.0 R package (Lenth 2016) and evaluated the multicollinearity of the analyses through the variance inflation factor (VIF) through the index $G\text{VIF}^{(1/(2^*Df))}$ using the *car* package's *vif* function.

RESULTS

Phylogenetic tree

Our dataset resulted in an alignment of 21 271 bp from 1273 taxa, of which 1268 bromeliads (including 513 Tillandsioideae, 472 Bromelioideae, 196 Pitcairnioideae, 44 Puyoideae, 25 Hechtioidae, 8 Brocchinioideae, 7 Navioideae, and 3 Lindmanioideae) and five outgroups (Supporting Information, S2 and S4). Major clades within the family (subfamilies, tribes, and subtribes) were strongly supported (Figs 1–3; Table 1; Supporting Information, S5). The relationships of lineages within the family correspond to those reported by Givnish *et al.* (2011), except for a new clade of *Bromelia* + (all remaining Bromelioideae + Puyoideae) [posterior probability

(PP) = 0.95]. As expected, some relationships at the generic and infrageneric levels were poorly supported, especially for large and taxonomically problematic genera (such as *Aechmea*, *Billbergia*, *Encholirium*, *Dyckia*, and *Tillandsia*; Supporting Information, S5). The selected model for all partitions in the ML analysis was GTR+F. Both trees included the clade comprising *Bromelia* + (all remaining Bromelioideae + Puyoideae). However, the MCC tree (logL = -172 883.1196, p-KH = 0.964 and p-AU = 0.958) exhibited stronger statistical support and a better fit to the data compared to the ML tree (logL = -173 104.1517, p-KH = 0.0364 and p-AU = 0.0419; Supporting Information, S6 and S7).

Divergence time estimate

The divergence between Bromeliaceae and Typhaceae occurred during the Late Cretaceous (~96 Mya; Fig. 1; Table 1), but the diversification in Bromeliaceae only started at the beginning of the Neogene (~22 Mya). Divergence of the major bromeliad clades occurred during the Miocene (from ~22 Mya), with Brocchinioideae and Lindmanioideae reconstructed as the early divergent subfamilies. Despite the early divergence of these groups, the diversification of all subfamilies only started in the Mid–Late Miocene (between 13.8 and 5.3 Mya), except Lindmanioideae, which diversified during the Pliocene (~4.6 Mya).

Diversification

BAMM diversification analysis identified heterogeneous rates across the tree (Fig. 1; Supporting Information, S8). Higher rates were observed in the clades of *Wittmackia* Mez, *Dyckia* Schult.f., and a group comprising North and Central American *Tillandsia* L. (see Supporting Information, S8). The best-fit model for the diversification among the 127 tested possible trait combinations included growth form, seed type, annual precipitation, annual temperature, and elevation (Tables 2 and 3). However, naked dry and winged seed types were not significant as predictors. Non-epiphytes, plumose seeds, annual precipitation, annual temperature, and elevation negatively influenced the diversification rates (Tables 2 and 3). We found significant differences in the contrast estimates (Table S1) between the naked and plumose seeds ($t = -6.703$, $P < .0001$), plumose and winged seeds ($t = 3.684$, $P = .001$), and epiphyte and non-epiphyte groups ($t = 10.180$, $P < .0001$) groups. The results of the multicollinearity assessment show that all values of VIF are <2, suggesting no multicollinearity in the regression model.

Our analyses show significant P values in the interactions between seed type and canopy height in diversification (Supporting Information, Tables S2 and S3). Canopy height negatively influenced the high diversification in plumose (Est. = -1.09, $P < .0001$) and winged seeds (Est. = -1.23, $P < .0001$). The contrasts were significant in naked-plumose (Est. = 0.546, $P = .0017$), naked-winged (Est. = 1.973, $P < .0001$), and plumose-winged seeds (Est. = 1.427, $P < .0001$). Habitat and morphological information are given in Supporting Information S9.

DISCUSSION

Systematics and taxonomy

Our results reconstruct the subfamily Bromelioideae as non-monophyletic using Bayesian and ML methods. Specifically,

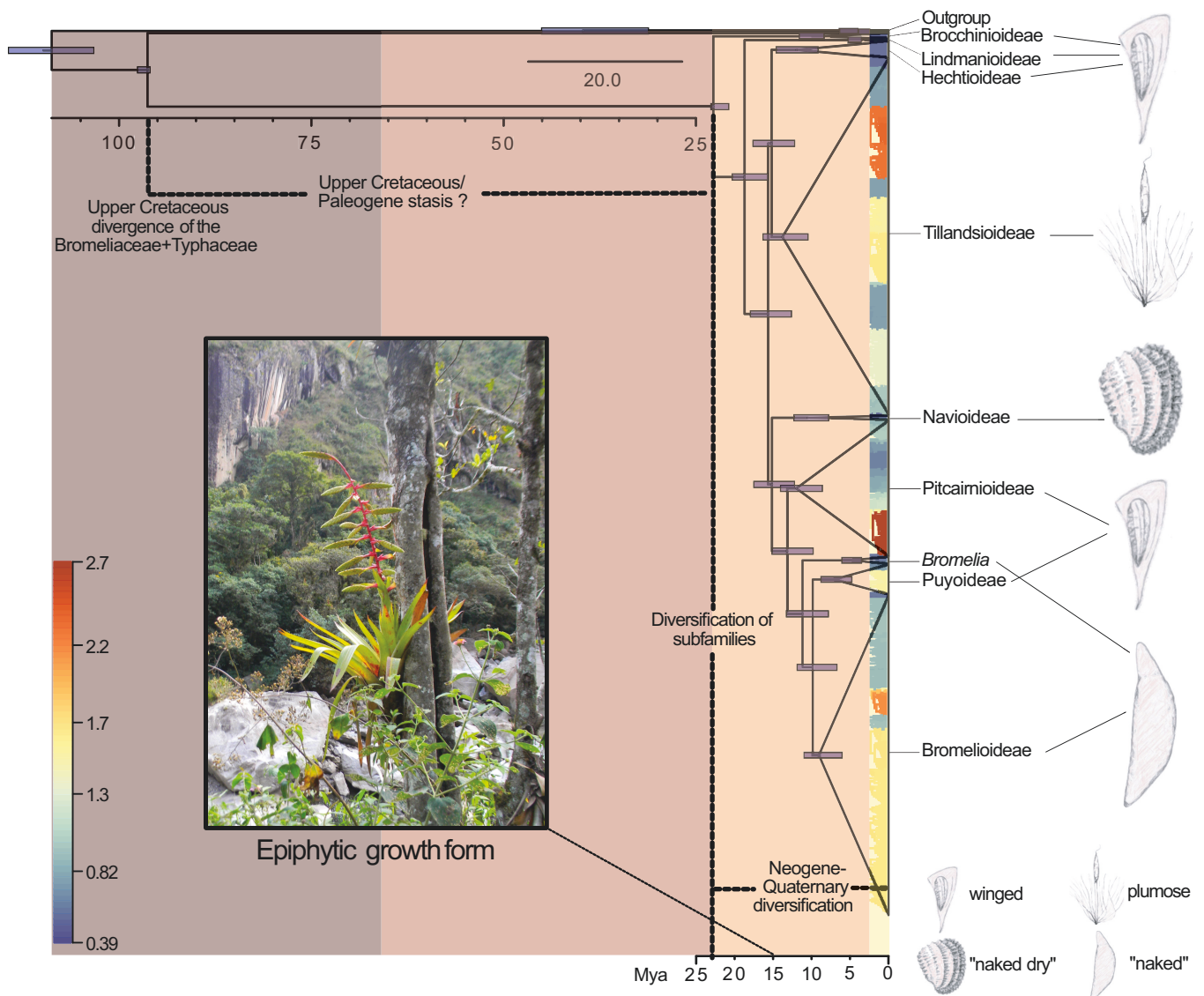


Figure 1. Phylogeny and diversification of bromeliads. Maximum clade credibility (MCC) using the combined sequence data of 1273 taxa. Coloured vertical bars refer to geological periods: Quaternary (light yellow); Neogene (orange); Palaeogene (brownish red); Cretaceous (grey). Horizontal bars on the nodes indicate 95% CI resulting from the treePL analysis (more information of nodes is given in Table 1). The topology of this time-calibrated tree suggests a Cretaceous origin, Late Cretaceous–Palaeogene stasis, and a Neogene–Quaternary diversification of the group. According to Givnish *et al.* (2014), the epiphytic growth form occurred for the first time at 15 Mya. The main type of seed of each clade is represented in the tree and the key colour bar on the left represents lower (blue) to higher (red) diversification. Time axes are in Myr. Seed images modified from Smith and Downs (1974). Photo by Igor M. Kessous.

we report here the clade *Bromelia* strongly supported as a clade separated from the remaining Bromelioideae (Fig. 2). *Bromelia* differs from all other members of Bromelioideae due to the presence of four layers of abaxial sclerenchymatous hypodermis and shares the absence of extra-fascicular fibres with Puyoideae (Monteiro *et al.* 2011, Leme *et al.* 2021). Additionally, the resemblance in scale anatomy (e.g. funnel-shaped scales) and, in certain instances, the presence of an inferior ovary position and CAM metabolism (Varadarajan and Gilmartin 1987, Terry *et al.* 1997) can offer morphological explanations for this newly proposed topology

Previous studies on bromeliad phylogeny have debated the monophyly of Puyoideae, particularly regarding the Chilean

and non-Chilean *Puya* clades (Jabaily and Sytsma 2010, 2013, Givnish *et al.* 2011). Givnish *et al.* (2011) reconstructed a strongly supported Bromelioideae + Puyoideae clade and found both clades to be monophyletic, but weakly supported considering Puyoideae and Bromelioideae separately in the maximum parsimony analysis. In the same study, the authors found Puyoideae to be non-monophyletic in ML and Bayesian analyses. In a supertree approach, Escobedo-Sarti *et al.* (2013) inferred Puyoideae and Bromelioideae as non-monophyletic using the best-fitted method.

In Jabaily and Sytsma's (2010) chloroplast DNA (cpDNA) dataset, a polytomy was formed by the two *Puya* clades and Bromelioideae. The low level of support for *Puya* prompted the

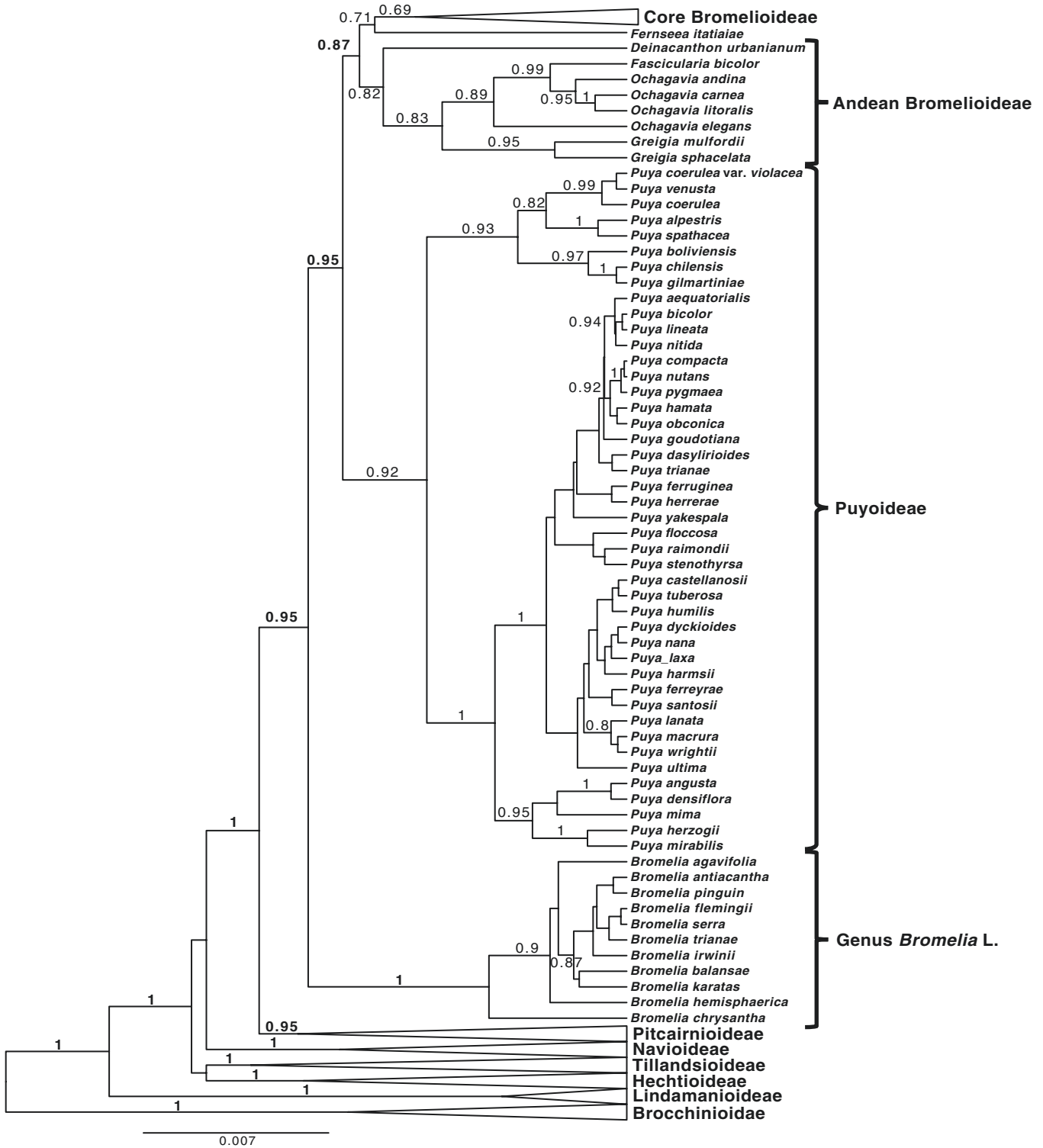


Figure 2. Time-calibrated phylogeny of Bromeliaceae, with a focus on the relationships between subfamilies Bromelioideae and Puyoideae. Maximum clade credibility tree resulting from multilocus analyses of 1273 species performed on BEAST 1.10 software. All clades are collapsed except for *Bromelia*, Puyoideae, and Andean Bromelioideae. Numbers above the branches represent the posterior probability of the clades.

authors to question the monophyly of the group. Their analysis identified Bromelioideae as monophyletic, albeit with low support for the placement of *Bromelia* as the sister group to other Bromelioideae, except for *Ochagavia* (PP = 0.53 and Maximum Likelihood Bootstrap [MLB] = 50). However, the analysis based

solely on nuclear *PHYC* produced different results. In this case, Bromelioideae emerged as non-monophyletic, and the *Bromelia* clade was well supported within this subfamily. However, the early divergent Bromelioideae clade formed by *Greigia*, *Deinacanthon*, and *Ochagavia* was placed as sister to Puyoideae

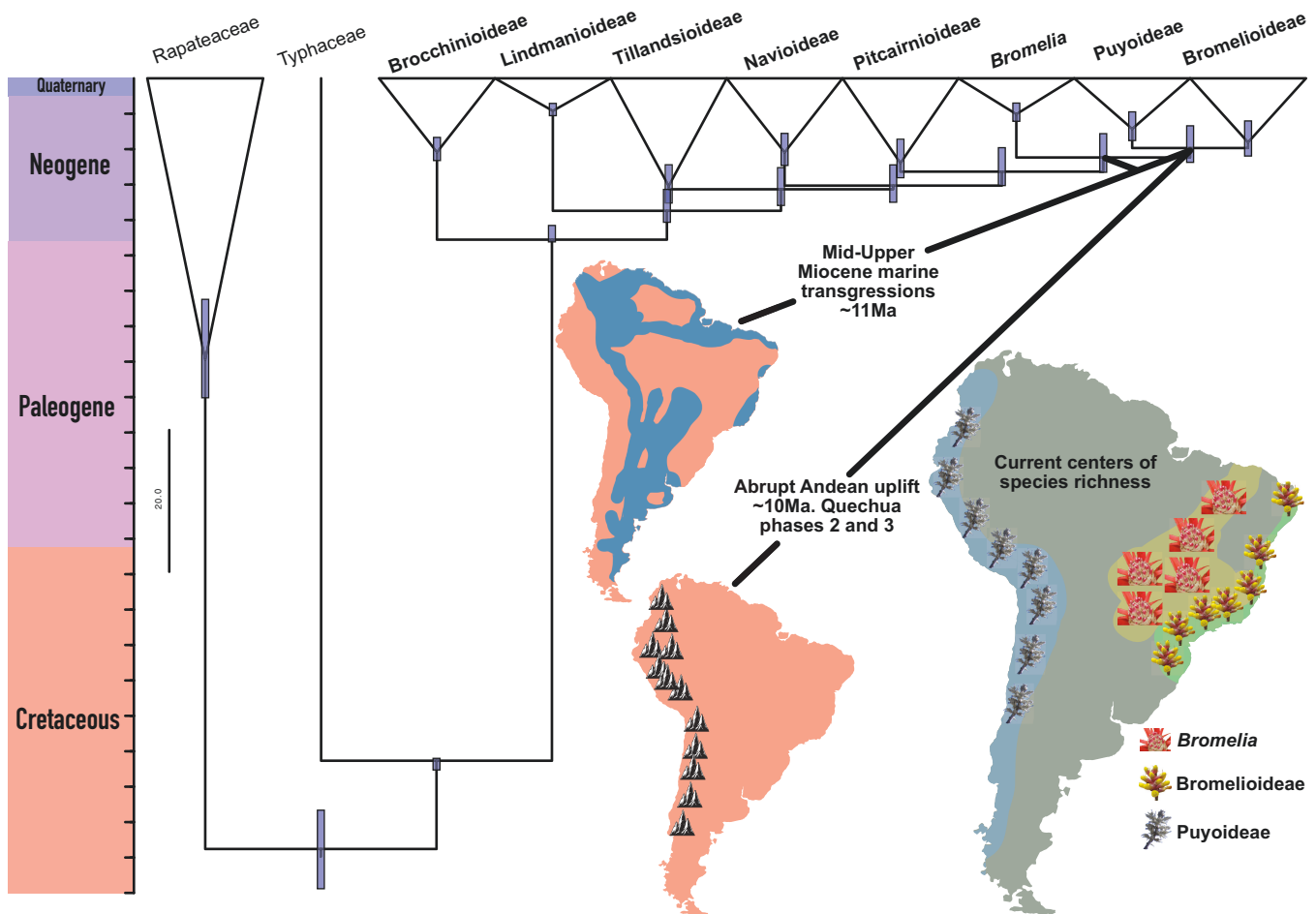


Figure 3. Hypothesis of the origin and spread of Bromeliaceae and its most recent clades (Puyoideae and Bromelioideae). Maximum clade credibility tree obtained by 1273 taxa. Vertical bars on the nodes indicate 95% CI resulted from the treePL analysis (nodes details in Table 1). Maps depict three temporal scenarios. Major geological events of the last 23 Myr coincide with Bromeliaceae diversification. *These distributions represent species richness centers, not the full distribution of the groups (according to [Smith and Downs 1974](#), [Monteiro et al. 2015](#), [Martinelli et al. 2018](#), [Zizka et al. 2020](#)). Scale is represented in 5 Myr.

Table 1. Main clade support and timing of crown and stem ages.

Clade	PP	Mean (Mya), crown	95% CI (Mya), crown	Mean (Mya), stem	95% CI (Mya), stem
Brocchinioidae	1	10.43	8.33–11.60	22.77	20.77–23.09
Bromelioideae (except <i>Bromelia</i>)	0.87	9.03	6.01–10.96	9.84	6.70–11.86
<i>Bromelia</i>	1	5.06	3.5–6.06	11.17	7.81–13.26
Hechtioideae	1	11.95	9.14–14.59	15.19	12.20–17.60
Lindmanioidae	1	4.6	3.54–5.27	18.70	15.67–20.32
Navioideae	1	10.45	7.77–12.29	15.14	12.21–17.49
Pitcairnioidae	0.95	11.97	8.6–14.03	13.17	9.79–15.13
Puyoideae	0.92	7.13	4.72–8.78	9.84	6.70–11.86
Tillandsioidae	1	13.77	12.20–17.60	15.19	12.20–17.60
Bromelioideae + Puyoideae	0.95	11.17	7.81–13.26	11.17	7.81–13.26
Bromeliaceae	1	22.77	20.77–23.09	96.33	96–97.63

Node calibration is based on [Givnish et al. \(2018\)](#); mean and 95% CI resulted from the treePL analysis. PP = posterior probability resulted from the BEAST MCC tree. CI = Confidence Interval. Mya = Million years ago.

(PP = 0.89, MLB = 55), highlighting that this part of the tree remains unresolved and indicating a clear conflict between nuclear and cpDNA data. *Greigia*, *Ochagavia*, and *Fascicularia* share certain traits with *Puya*, such as their distribution range, terrestrial

growth form, and in some cases C3 photosynthesis ([Schulte et al. 2009](#)). A lingering question in this context is whether these traits are present in these two lineages due to a closer common ancestry or as adaptations to a shared environment.

Table 2. Summary of the best-fitting GLM of diversification according to AIC (Akaike information criterion).

Predictor	Estimate	SE	z value	P
(Intercept)	1.63	0.18	9.24	.00
Growth form (non-epiphyte)	-2.59	0.25	-10.18	.00
Seed type (naked dry)	-14.78	538.72	-0.03	.98
Seed type (plumose)	-1.38	0.21	-6.70	.00
Seed type (winged)	-0.24	0.27	-0.90	.37
Annual precipitation	-0.46	0.10	-4.41	.00
Annual temperature	-0.34	0.14	-2.52	.01
Elevation	-0.38	0.13	-3.01	.00

Values are scaled and log-transformed. Net diversification rate on the scale of the high diversified group (see Methods). Predictors with $P < .05$ are highlighted in bold. SE = Standard Error.

Table 3. ANOVA of the best-fitting GLM according to AIC (Akaike information criterion).

Predictor	Sum of squares	d.f.	F value	P
Growth form	132.44	1	123.7192	<2.2e-16
Seed type	53.31	3	16.5982	1.720e-10
Annual precipitation	23.20	1	21.6729	3.743e-06
Annual temperature	6.40	1	5.9830	.014643
Elevation	9.30	1	8.6891	.003288
Residuals	921.71	861		

d.f. = degrees of freedom.

In the combined dataset, Jabaily and Sytsma (2010) proposed Bromelioideae and Puyoideae as strongly supported sister groups (PP = 1, MLB = 98). Our analyses similarly provide robust support for a single monophyletic Puyoideae group (PP = 1), encompassing both the Chilean (PP = 0.93) and non-Chilean *Puya* (PP = 1) clades, with a sister relationship to Bromelioideae, excluding *Bromelia*. The predominance of cpDNA data in our analysis may have influenced the new topology presented here. However, the combination of nuclear and cpDNA data, as we have done, has the potential to enhance the resolution of clades within Bromelioideae and Puyoideae, as suggested by Jabaily and Sytsma (2010).

Monteiro *et al.* (2015), utilizing morphological data, inferred *Bromelia* to be monophyletic and placed it within Bromelioideae. However, they employed only a single terminal of *Puya* to root the tree. More recently, Paule *et al.* (2020) found Bromelioideae to be monophyletic and positioned *Bromelia* within the subfamily. However, their study included only six species of *Puya*. It is important to note that some sampled *Bromelia* species exhibited intraspecific variation in genome size, with the unique case of a clade estimated to have an ancestral chromosome number of $2n = 100$ (Silvestro *et al.* 2014, Paule *et al.* 2020). Two significant aspects warrant discussion with respect to this information. First, the intraspecific differences observed can potentially influence the phylogenetic topology, depending on which terminals are considered. Second, the chromosome number, while not exclusive, distinguishes this clade as the only one reconstructed with this character state as ancestral, serving as an additional

factor explaining the differences in *Bromelia* compared with the majority of the other Bromelioideae.

Fruits and seeds have traditionally been utilized to delimit subfamilies in Bromeliaceae (Smith and Downs 1974, Barfuss *et al.* 2005, Fagundes and Mariath 2010). Puyoideae differs from Bromelioideae in the presence of capsular fruits, presence of rounded and winged seeds, and that it is mostly distributed in the Andes (Smith and Downs 1974, Benzing 2000, Pandey and Ming 2018; Gouda *et al.* [cont. updated]; Fig. 1). *Puya*, characterized by a wide variety of winged seeds, cannot be reliably distinguished by this trait. However, it is characterized by the twisting of its petals into a spiral configuration after anthesis, a characteristic probably lost from Bromelioideae (Jabaily and Sytsma 2010).

The multiple origins of Bromelioideae also imply the potential homoplasy concerning fruits and seeds in bromeliads. However, limited research has been conducted thus far to investigate the homology (e.g. ontogeny) of different fruit and seed types. Silva *et al.* (2020) demonstrated that variations in bromeliad seeds arise from distinct ontogenetic origins. The chalazal appendages observed in naked seeds (mucilaginous) are homologous to those found in plumose seeds, but with distinct anatomical development in response to different dispersal mechanisms (biotic vs. abiotic, respectively; Silva *et al.* 2020). Conversely, there are documented instances of analogous structures present in different bromeliad groups exhibiting the same seed type, such as the appendages in some Tillandsioideae (Palací *et al.* 2004; Magalhães and Mariath 2012).

Homoplasy in fruit morphology is well documented in angiosperms (Knapp *et al.* 2004, Thomas *et al.* 2011, Wang and Shui 2019). However, recent studies investigating the homology of fruit types have refuted homoplastic hypotheses in certain plant groups (Torres-Montúfar *et al.* 2018). Anatomically, capsular fruits in bromeliads show a stronger correlation with the opening mechanism (dehiscent and indehiscent) rather than taxonomic relationships themselves (Fagundes and Mariath 2010).

Other traits, such as floral morphology, photosynthetic metabolism, development, and leaf anatomy, reinforce the affinity between Bromelioideae and Puyoideae. Puyoideae has species with C3 and CAM metabolic pathways, ovaries ranging from superior to partially inferior (inferior in Bromelioideae; Terry *et al.* 1997, Givnish *et al.* 2014), and showy flowers (Smith and Downs 1974, Terry *et al.* 1997, Zizka *et al.* 2013). Additionally, both groups have aerial canals in the ovary mesophyll, but without a homologous hypanthium (Kuhn *et al.* 2020). The origin of Puyoideae is inferred to be in central Chile, where early divergent clades of Bromelioideae (such as *Fascicularia* Mez, *Ochagavia* Phil. and some *Greigia* Regel species; Jabaily and Sytsma 2013; Gouda *et al.* [cont. updated]) occur widely. Some species from these clades share metabolic pathways with Puyoideae, probably due to similar climatic conditions, regardless of their phylogenetic relationship (Quezada *et al.* 2018).

The possibility of including Puyoideae within Bromelioideae was first mentioned by Terry *et al.* (1997) and supported by Givnish *et al.* (2011). Our tree topology could suggest a new infrafamilial classification of bromeliads with three different options: (i) describing a new subfamily that includes all 'Bromelioideae except *Bromelia*' (PP = 0.87; Fig. 2), with Bromelioideae considered monogeneric; (ii) including

'Bromelioideae except *Bromelia*' in Puyoideae (PP = 0.95; Fig. 2), with a monogeneric Bromelioideae; and (iii) synonymizing Puyoideae under Bromelioideae (PP = 0.95; Fig. 2).

The repeated evolution of several traits in bromeliads, such as elevation preferences, CAM metabolism, pollination, and flower and stigma morphology (Jabaily and Sytsma 2013, Silvestro *et al.* 2014, Barfuss *et al.* 2016, Neves *et al.* 2023), suggests that the most parsimonious shifts in character states are not always the best explanations. Rapid diversification in clades makes precise phylogenetic inferences difficult (McLean *et al.* 2019), and nomenclatural modifications in these cases should be made cautiously. As shown here, bromeliads have low genetic variation, probably due to recent diversification (Bratzel *et al.* 2020). Despite the evidence presented here, we find significant differences in reproductive morphology, general habitat, and life forms, in addition to the rapid diversification that occurred in these most recent clades of Bromeliaceae. Additionally, our results were based primarily on plastidial data, and our matrix contains a significant amount of missing data (>70%), which can influence the presented topology.

It is important to highlight that the position of early divergent bromelioids remains speculative in the literature (Schulte *et al.* 2009), especially due to divergent results obtained through different methods employed. It is estimated that the Chilean *Puya* lineages have experienced various levels of hybridization and genetic admixture, suggesting a weak barrier to reproduction within the group, which may have played a role in its evolutionary history (Schulte K. *et al.* 2010a). Therefore, in contrast to the three presented options, we have chosen not to propose nomenclatural modifications since additional data are required to fully understand this evolutionary history.

The topology of the remaining subfamilies followed the previous phylogenetic hypothesis proposed by Givnish *et al.* (2011), except for the weakly supported sister relationship between Tillandsioideae and Hechtioideae.

A hypothesis of the rise and spread of Bromeliaceae and the most recent clades

Bromeliads arose during the Late Cretaceous in the Guyana Shield (Givnish *et al.* 2011, 2014, Bouchenak-Khelladi *et al.* 2014). Despite the rise of several angiosperm lineages during the Palaeocene–Eocene transition (Jaramillo *et al.* 2010, Antonelli and Sanmartín 2011), our analyses corroborate the presence of a complete stasis in bromeliad diversification throughout the Palaeogene. The South American Eocene and Oligocene were characterized by oscillations in temperature and sea level that retracted in the Miocene, reaching the 'Optimum Climaticum' (Ortiz-Jaureguizar and Cladera 2006). Tectonic and climatic events of the Neogene and Quaternary drove the speciation of several groups of organisms in the Neotropics (Rull 2011), possibly also influencing the divergence of Bromeliaceae lineages.

The results on the divergence of the Bromelioideae and Puyoideae clades coincided with significant climatic and orogenic events in South America, as discussed in other bromeliad groups (Givnish *et al.* 2011, Kessous *et al.* 2020). In particular, events occurring during the transition from the Oligocene to Miocene probably influenced the diversification of Bromeliaceae subfamilies (Figs 1, 3). Despite Bromeliaceae having only one reliable fossil from the Pleistocene, molecular clock estimations

consistently suggest a Cretaceous origin, Palaeogene stasis, and Neogene–Quaternary diversification (Givnish *et al.* 2011, 2014, 2018, Kessous *et al.* 2021). Despite using an *a posteriori* dating approach, we obtained similar temporal frames for the divergence of the subfamilies.

Bromelia is widespread in South America, with the current centre of species richness in the savannas of Central Brazil (Cerrado; Smith and Downs 1979, Monteiro *et al.* 2015; Fig. 3). On the other hand, the species richness of Puyoideae peaks in the Andes, and that of remaining Bromelioideae in the Atlantic Forest (Smith and Downs 1979, Martinelli *et al.* 2018, Zizka *et al.* 2020; Fig. 3). The clade Puyoideae + Bromelioideae originated in the Andes at 10 Mya (Givnish *et al.* 2011; ~11 Mya in our analyses) and Central Chile is estimated to be the ancestral area of *Puya* and Bromelioideae (Jabaily and Sytsma 2010). At this time, successive climatic and geological events, such as marine incursions and the abrupt uplift of the Andean Cordillera, shaped the biota of South America (Ortiz-Jaureguizar and Cladera 2006, Hoorn *et al.* 2010) and influenced the divergence of other Bromeliaceae clades (Kessous *et al.* 2020; Fig. 3). According to our results, we hypothesize that the most recent common ancestor of the *Bromelia* + (Bromelioideae + Puyoideae) clade probably split into different lineages in the Andean region because (i) after the regression of the Paranaean Sea (see Ortiz-Jaureguizar and Cladera 2006, Kessous *et al.* 2020), it would have been possible to colonize other regions, and (ii) with the intense Andean uplift, some groups needed to adapt to the high altitudes, as in the case of Puyoideae and the Andean Bromelioideae.

Givnish *et al.* (2011) suggest that *Puya* diverged from Bromelioideae ~10 million years ago, with *Puya* diversifying in the Andes and the core-Bromelioideae in the Brazilian Shield. It is important to note that most genera within Bromelioideae have limited geographical ranges, except for some early divergent clades like *Bromelia* and *Ananas*, which occur in broader ranges encompassing both South and Central America (Givnish *et al.* 2007). The Andes–Atlantic Forest path probably was probably a dispersal corridor for bromeliads (Givnish *et al.* 2011, Zizka *et al.* 2020). The early divergence of *Fernseea* (Bromelioideae), an endemic genus of high-altitude environments in the Atlantic Forest, suggests a past connection between its bromeliad flora and the Andes (Schulte *et al.* 2005, Givnish *et al.* 2011), as found for other plant groups (Safford 1999). After arrival into the Brazilian Shield, a rapid radiation led to the great diversification of Bromelioideae (Schulte *et al.* 2005, Givnish *et al.* 2011, 2014). Subsequently, the formation of the South American Dry Diagonal throughout the Neogene (Ortiz-Jaureguizar and Cladera 2006) triggered the diversification of some groups in this region, such as *Bromelia*.

Taking the pieces of morphological evidence and our results together, we hypothesize that the shift from the berry-fruited group (*Bromelia*/Bromelioideae) to the capsule-fruited group (Puyoideae) is related to the new type of environment colonized by Puyoideae in the Andes. Alternatively, as suggested by Jabaily and Sytsma (2010, 2013), capsules may have appeared before the ascent of Puyoideae to the mountains, thus facilitating their colonization of these environments. High-altitude grasslands and open environments are characterized by a predominance of wind-dispersed groups, such as Asteraceae and Poaceae

(Safford 1999, Kessous and Freitas 2023, Kessous *et al.* 2024). Additionally, the species richness of frugivorous birds tends to diminish at higher elevations (Sam *et al.* 2019). *Bromelia* is distributed largely in open environments, which is also observed for high-altitude bromeliad groups, such as Andean Bromelioideae and *Fernseea*. On the other hand, most of the remaining Bromelioideae are particularly diverse in closed forest environments (Zizka *et al.* 2020).

As shown in our phylogenetic analysis, the Pliocene was an important time in the diversification of most of the Bromeliaceae subfamilies. The final closure of the Panama Isthmus and the resulting 'Great American Biotic Interchange' probably facilitated range expansions towards North America of several groups (Ortiz-Jaureguizar and Cladera 2006, Cody *et al.* 2010, Hoorn *et al.* 2010, Rull 2011). Glaciations and interglaciations during the Pleistocene, which caused cycles of forest expansion and retraction, influenced population dynamics and speciation in bromeliads (Kessous *et al.* 2020), shaping the current distribution of the taxa.

Habitat and seed morphology drive diversification in bromeliads

While the first documented frugivore/plant interactions trace back to the Late Cretaceous, the emergence of fleshy fruits in various plant groups occurred during the Miocene, as evident in bromeliads (Givnish *et al.* 2014, Eriksson 2016). Our results underscore a noteworthy pattern, revealing that species with naked seeds exhibit higher net diversification rates compared to those with plumose seeds (Table 2). The evolution of berry-fruited species with naked seeds, considered a key innovation in Bromelioideae alongside tank-forming rosettes and CAM photosynthetic pathway (Silvestro *et al.* 2014), played a pivotal role in shaping bromeliad diversity.

On the other hand, we highlight the association of plumose seeds with larger ranges, exemplified by the distribution of Tillandsioideae (Barfuss *et al.* 2016, Zizka *et al.* 2020), while the naked seeds of the berries are potentially less dispersed due to the territorial behaviour of understory birds (Givnish 2010). The flight apparatus of plumose seeds appears to be a key innovation facilitating bromeliad dispersal, but it may concurrently limit speciation rates by enhancing gene flow among populations (see Givnish 2010), presenting reduced diversification rates compared to berry-fruited species. These insights deviate from previous research by Kessler (2002a), who proposed a correlation between larger range sizes and berry-fruited species, possibly attributable to variations in study scope, geographical locations, and sampling sizes. It is important to highlight that factors like fertile soils, high precipitation, and windless understoreys can collectively contribute to the evolution of fleshy fruits (Givnish 2010).

Several studies suggest that environmental conditions at high elevations contribute to diversification in mountain ecosystems (Lagomarsino *et al.* 2016, Rahbek *et al.* 2019, Testo *et al.* 2019). In contrast to these findings, we observed a slightly negative influence of elevation in the net diversification of bromeliads (Table 2). This is probably due to the broad elevational range of bromeliads, spanning from coastal *restinga* ecosystems to the highlands of the Andes (Smith and Downs 1974).

Notably, the highest diversity of both shrubs and herbs occurs at midelevations (He *et al.* 2023), as previously noted for bromeliads (Givnish *et al.* 2014). Also, the negative influence of elevation on diversification in our dataset can be attributed to the lower diversity of epiphytes at higher elevations, as this life form emerged as a significant factor for diversification in bromeliads.

Kessler (2002b) demonstrated higher point diversity of bromeliads in dry habitats compared to wet habitats, possibly due to lower competition. Similarly, our findings reveal that diversification is negatively influenced by precipitation. This is probably because highly diverse groups, such as *Dyckia* and some *Tillandsia*, are present in dry habitats. Additionally, dry habitats favoured the development of CAM (Givnish *et al.* 2011), contributing to increased diversification in bromeliads (Silvestro *et al.* 2014).

While canopy height alone is not a predictor of diversification (Table 1), its interaction with naked seeds positively influences diversification compared to the other seed types (Supporting Information, Table S2). These results corroborate the suggestion that the epiphytic growth form favours entangling seeds, supporting the argument for the prevalence of fleshy fruits in forest understoreys due to less effective wind dispersal in these environments (Givnish *et al.* 2014, Givnish 2010). In the Atlantic Forest, one of the three centres of species richness of bromeliads, Orchidaceae and Bromeliaceae rank as the first and fourth most diverse families, comprising ~1300 and 1000 species, respectively. Most of this diversity consists of epiphytes (Stehmann *et al.* 2009). The earliest bromeliads were terrestrial and adapted to open environments (Bouchenak-Khelladi *et al.* 2014, Givnish *et al.* 2014). However, the emergence of the epiphytic growth form during the Mid-Miocene played a pivotal role in triggering rapid and extensive diversification (Fig. 1; Givnish *et al.* 2014). Our study underscores the epiphytic growth form as the most influential predictor of bromeliad diversification. With few exceptions, epiphytic bromeliads are predominantly found in Tillandsioideae and Bromelioideae, constituting almost two-thirds of all bromeliad species (Zotz 2013, Givnish *et al.* 2014).

Givnish *et al.* (2014) suggested a correlation between epiphytic life form and diversification in Bromeliaceae, as we observed here. In addition, the authors highlight significantly higher diversification rates in specific lineages, notably those exhibiting epiphytic habits. The bromelioid tank-epiphytic clade along the coastal regions of Brazil and the core tillandsioids in the Andes and Central America, both characterized by their epiphytic life form, display the highest rates of net diversification. Additionally, the study reveals correlated evolution patterns between epiphytism and other traits, including the tank habit, entangling seeds, and preference for moist and fertile habitats. This implies a coevolution of these traits, potentially contributing to the overall diversification of epiphytic lineages. Furthermore, the identification of six large-scale adaptive radiations in Bromeliaceae, with epiphytic habits associated with some of these radiations, suggests a significant role for epiphytism in driving adaptive events and diversification within the family (Givnish *et al.* 2014). The significance of CAM in facilitating the development of the epiphytic growth form and subsequent diversification cannot be overstated, although other

contributing factors must be considered (according to *Zotz et al. 2023*).

In summary, comparing our results to those presented by *Givnish et al. (2014)* reveals the following: (i) We observed that non-epiphytism negatively influenced diversification rates in bromeliads compared with epiphytism. The authors of the study found that net rates of diversification are closely associated with epiphytism, including a clade of epiphytic and tank-forming Bromelioideae, and core Tillandsioideae from the Andes and Central America, presenting highest rates of diversification. In our study, one of the clades with higher rates of diversification includes *Wittmackia*, a group with broad tanks and usually the epiphytic growth form (*Aguirre-Santoro 2018*), and North and Central American *Tillandsia*. (ii) The entangling seed clades, which include plumose and naked seeds, presented higher net diversification rates compared with the remaining clades in *Givnish et al. (2014)*. We found similar results, as stated in item (i). However, when comparing the diversification of the subtypes of entangling seeds, we observed that plumose seeds of Tillandsioideae negatively influence diversification compared with the naked seeds of Bromelioideae, possibly due to their higher dispersal capacity (see discussion in *Givnish 2010*). (iii) We observed that elevation negatively influenced diversification, while the authors suggested that midelevations have the highest diversity of bromeliad species. This can also be explained by the scarce presence or absence of epiphytes in these environments, as discussed by *Givnish et al. (2014)*. (iv) We found that, for bromeliads in general, precipitation negatively (though weakly) influenced diversification. As diversification in Bromeliaceae is a complex network, not only do moist habitats with epiphytic species favour diversification, but also dry microsites of terrestrial species. Additionally, dry conditions potentially favoured the evolution of CAM, one of the key features that increased diversification in the family (*Givnish et al. 2014, Silvestro et al. 2014*). (v) In our results, we show that canopy height associated with berry-fruited species (those with naked seeds) influenced diversification in bromeliads. This corroborates *Givnish et al. (2014)*, who discussed the origin of fleshy fruits in understoreys, associated with environments with less effective wind dispersal and the lower mobility of understorey birds, which limits dispersal and favours diversification.

CONCLUSION

Using the largest bromeliad phylogenetic tree to date, our results suggest that Bromelioideae is potentially non-monophyletic, contrary to previous findings. Therefore, it is essential to incorporate this question into further analyses using different methods to elucidate the issue. Our results show that the genus *Bromelia* is the sister group of a clade including Puyoideae + Bromelioideae, potentially implying a need for a new classification of the subfamilies. The remaining subfamilies were mostly reconstructed as previous estimates. Furthermore, we have observed that Miocene events in the Neotropics played a significant role in triggering the diversification of bromeliads after a prolonged period of stasis during the Palaeogene, corroborating previous findings. Additionally, considering this new phylogenetic hypothesis, we suggest that the shift from the berry-fruited group to the capsule-fruited group is possibly associated with the colonization of a new environment

by Puyoideae following the abrupt uplift of the Andes and the formation of alpine environments. Furthermore, we hypothesized that the naked seed and the epiphytic growth form positively impact bromeliad diversification, while precipitation, temperature, and elevation negatively influence it. It is crucial for future studies to test hypotheses on fruit homology and explore anatomical and ontogenetic-related characters to investigate synapomorphies in Bromeliaceae. Additionally, incorporating more DNA data and new approaches considering phylogenetic networks will enable us to infer more precise relationships, a stable classification, and better explanations of the spatial and evolutionary dynamics of this megadiverse neotropical family.

SUPPLEMENTARY DATA

Supplementary data are available at *Botanical Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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DATA AVAILABILITY

The data underlying this article are available in the electronic supplement of this paper.

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