The origins and diversification of hummingbird pollination in Bromeliaceae

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Abstract

Bromeliaceae are a model group for understanding explosive Neotropical diversification, combining remarkable ecological breadth and high species richness, despite relatively recent evolutionary origins. Several drivers are hypothesised to accelerate bromeliad diversification, and hummingbird pollination is frequently proposed to be among the strongest. However, our understanding has been limited by sparse and uneven pollinator datasets and by the amount of diversification rate variation in bromeliads, much of which can be explained by other drivers. Here we assemble a novel database of published pollinators for 403 bromeliad species spanning 70% of genera across all subfamilies, and analyse these data in a phylogenetic framework. We estimate ancestral states, which indicate widespread lability, including many previously unknown transitions. Many of these occur in recent evolutionary time, indicating ongoing turnover in pollinators. Despite pronounced background diversification rate heterogeneity, hummingbird pollination is confirmed to be a primary driver of diversification, a result that we show is unlikely to change even under unrealistic assumptions of its prevalence in unsampled species. Our findings support hummingbirds as a central organising force in the complex web of bromeliad evolution, and provide a foundation for future data collection and integrative analyses in this charismatic family.

Introduction

The Neotropics are one of the great centres of biodiversity, spanning a vast geographic region and harbouring a large proportion of the planet's vascular plant species, many of which are endemic (Antonelli and Sanmartín 2011; Hughes et al. 2012; Raven et al. 2020). The bromeliads (family Bromeliaceae) capture some of the most remarkable aspects of Neotropical biodiversity and are considered a model system for evolution (Palma-Silva and Fay 2020). With over 3,700 species in eight subfamilies and about 80 genera (Givnish et al. 2011; Kessous et al. 2024), bromeliads are one of the largest flowering plant families in the Neotropics, and occupy an exceptional diversity of ecological niches (Givnish et al. 2011, 2014; Kessous et al. 2024). These range from seasonally dry lowlands and inselbergs to humid mountain forests and cloud forest canopies (Biedinger et al. 2000; Cervantes et al. 2005; Toledo-Aceves et al. 2014). Their ecological breadth is underpinned by remarkable ecomorphological diversity. Within the family, epiphytism has repeatedly evolved (Zotz et al. 2021), along with tank formation which supports numerous animal and microbial species (Males 2016; Ladino et al. 2019; Simão et al. 2020; Barberis et al. 2023), specialised photosynthetic pathways (Crayn et al. 2004, 2015), and a wide range of growth forms and reproductive strategies (Griffiths and Smith 1983; Kessler et al. 2019). What makes bromeliad evolution so remarkable is the evolutionary tempo implied by their estimated age of origin (Palma-Silva and Fay 2020; Kessous et al. 2024). While bromeliads likely originated in the Cretaceous (~100 Mya), molecular evidence suggests that diversification of extant lineages did not begin until the early Miocene (~20 Mya), following a long stem lineage (Givnish et al. 2018; Kessous et al. 2021). This implies that their extant species richness and ecomorphological diversity evolved over a relatively short timescale, meaning that diversification rates exceed those of many large vertebrate groups, which have much older origins (Upham et al. 2019). Bromeliads are therefore an exceptional example of rapid Neotropical diversification, and the forces behind this success remain unresolved (Givnish et al. 2014; Palma-Silva and Fay 2020; Kessous et al. 2024).

Across the angiosperm Tree of Life, research seeks to identify the adaptive traits shaping diversification rates (de Queiroz 2002; Sauquet and Magallón 2018). These are often described as key innovations, readily accessible adaptations that enable species to exploit new resources, reduce competition and expand their ranges, leading to reproductive isolation and speciation (Givnish 2010). The identification of these adaptations, and external forces including climate (Jansson and Davies 2008; Li et al. 2013; Thompson et al. 2023), is therefore central to understanding both the origins of biodiversity and the potential directions it may take in our changing planet (Cahill et al. 2013; Hatfield et al. 2025). When diversification is rapid and occurring alongside repeated ecological divergences, it is often described as an adaptive radiation (Schluter 2000). However, recent work has emphasised that many plant radiations, especially those that are very rich and widespread across heterogeneous environments, may instead indicate explosive diversification (Givnish 2015) driven by interactions between adaptations and environments, rather than any single key innovation acting independently (Givnish et al. 2015; Sauquet and Magallón 2018; Thompson et al. 2024). Within bromeliads, previous phylogenetic studies have implicated several coevolving adaptations in accelerating diversification rate, including avian pollination, epiphytism, the tank-forming habit, CAM photosynthesis, and seed variation (Givnish et al. 2014; Silvestro et al. 2014; Kessous et al. 2024). These traits are thought to have facilitated evolution into new ecological niches, particularly in the mountain environments where bromeliad diversification is known to be faster (Givnish et al. 2014).

The importance of pollinator transitions in driving macroevolution is a large focus of research across angiosperms (van der Niet and Johnson 2012; Van der Niet et al. 2014; Breitkopf et al. 2015; Givnish et al. 2015; Thompson et al. 2024, 2025a). Pollinator transitions play a central role in shaping patterns of pollen transfer, mating systems and reproductive isolation, thereby triggering speciation (Fenster et al. 2004; Schiestl and Schlüter 2009; Rymer et al. 2010; Van der Niet et al. 2014). The importance of this hypothesis in plant evolution stems from Darwin’s early work on orchid variation, which he linked to insect pollinators (Darwin

1889). These effects are often studied in the descriptive framework of pollination syndromes, which characterise the suite of specialised adaptations between plants and pollinators (Fenster et al. 2004). An example is the tubular and red, yellow, or purple diurnal flowers that produce lots of nectar in hummingbird-pollinated plants (Abrahamczyk and Kessler 2014; Kessler et al. 2019; Barreto et al. 2024). However, pollination syndromes are not exclusive categories, and many plants have mixed or flexible pollination systems (Johnson and Steiner 2000), leading macroevolutionary researchers to focus on pollinator identity and transitions among pollinator groups rather than detailed syndrome scoring (Givnish et al. 2014; Hernández-Hernández et al. 2014; Thompson et al. 2024, 2025a). However, macroevolutionary tests of pollinator-driven diversification have produced inconsistent results. Some lineages show strongly positive associations between diversification rate and pollinators (Hernández-Hernández et al. 2014; Serrano-Serrano et al. 2017), whereas others are negative (Wessinger et al. 2019). Within the same group, the relationship can be inconsistent depending on scale and methods (Gravendeel et al. 2004; Givnish et al. 2015). Furthermore, hypothesised macroevolutionary impacts of pollinators can weaken or disappear when taxonomic sampling is improved (Thompson et al. 2024), rate heterogeneity is explicitly accounted for (Thompson et al. 2025a), or additional correlates mediating diversification are considered (Thompson and Venditti 2025).

Hummingbird pollination is particularly important to bromeliad diversification. There are 366 extant species of hummingbird (family Trochilidae), which interact with thousands of plant species across ~100 families (Barreto et al. 2024). However, among these families, bromeliads show an unusually strong association with hummingbirds. Although data is incomplete, hummingbirds are estimated to pollinate approximately half of bromeliad species, and the syndrome is found in the majority of genera, making hummingbirds the dominant pollinator group (Kessler et al. 2019). Additionally, the crown age of hummingbirds is also approximately contemporaneous with that of bromeliads (McGuire et al. 2014), which hints at co-diversification through time. There is reason to suggest hummingbird pollination may act as a key innovation driving adaptive radiation, both through its direct effects on floral specialisation and reproductive isolation (Benzing 2000; Kessler et al. 2019), and through its association with other traits linked to rapid diversification (Givnish et al. 2014). In particular, by driving shifts into montane and epiphytic environments, hummingbird pollination may act as a key organising force within the complex network of ecological and evolutionary factors that shape bromeliad diversification. Furthermore, pollination is evolutionarily labile; previous work has identified at least 12 transitions to hummingbird pollination, as well as a number of transitions to bat pollination (Aguilar-Rodríguez et al. 2019; Kessler et al. 2019), supporting the evolutionary accessibility of this trait. Other pollinators of bromeliads include bats, bees, moths, butterflies and a variety of less frequently reported insect and vertebrate taxa (Frank and Lounibos 2009; Aguilar-Rodríguez et al. 2019; Leal et al. 2020). While these also contribute to bromeliad reproduction, adaptations and ecology, their phylogenetic distributions, evolutionary origins, and role in shaping diversification remain less well documented.

Our current understanding of the origins and diversification of pollination is limited in bromeliads, and largely derives from analyses with highly sparse phylogenetic and pollinator sampling (Givnish et al. 2014; Neves et al. 2023). When sampling is incomplete, which arises from uneven molecular sequencing and limited pollinator data coverage, diversification rate estimates are biased (FitzJohn et al. 2009; Mynard et al. 2023). This affects macroevolutionary inferences because diversification rates vary widely across complex, large groups (Rabosky 2014) and are not necessarily strongly coupled to a single force (Beaulieu and O’Meara 2016; Caetano et al. 2018; Siqueira et al. 2020; Thompson et al. 2024). Across bromeliads, we know that the diversification rate varies strongly (Kessous et al. 2024), and many of the forces hypothesised to shape this variation are correlated across space, through time and between lineages (Givnish et al. 2014; Neves et al. 2023). Even when potential drivers of plant diversification are broadly sampled within an integrative framework, a large portion of the rate heterogeneity remains unexplained (Thompson et al.

2024). Therefore, to characterise the macroevolutionary impact of hummingbird pollination in bromeliads, we need to (1) improve pollinator data sampling, (2) fully characterise rate-heterogeneity in the family, and (3) employ methods designed to accommodate rate-heterogeneity when assessing correlates of diversification explicitly. By doing this, we can identify whether hummingbird pollinators accelerate diversification despite the background rate heterogeneity, much of which is explained by other adaptive traits and forces (Givnish et al. 2014).

If pollinator evolution has played a central role in shaping bromeliad diversification, then understanding its macroevolutionary dynamics is also critical for anticipating how plant diversity will respond to ongoing environmental change. Extinction risk in plants is not randomly distributed across the Tree of Life, and species with ecological specialisation and restricted geographic ranges often have elevated threat levels (Lughadha et al. 2020; Bachman et al. 2024). The bromeliad family is unusual, given the exceptionally high proportion of species that are hummingbird pollinated (Kessler et al. 2019), many of which are restricted to montane regions that are experiencing rapid environmental changes (Zizka et al. 2020; Ramírez-Barahona et al. 2025). A large number of bromeliads in all subfamilies are expected to be threatened (Zizka et al. 2020), due to vulnerability to ongoing threats such as habitat loss, climate change, and disruption of plant-pollinator networks (Siqueira Filho and Tabarelli 2006; Zotz et al. 2010; Wagner and Zotz 2018; Zizka et al. 2020; Leimberger et al. 2022). This is exacerbated by threats to pollinators; 10% of hummingbird species are threatened and 60% are in decline (Zizka et al. 2020; Leimberger et al. 2022), alongside bats and insects which experience similar pressures (Zamora-Gutierrez et al. 2021; Cornelisse et al. 2025). Together, these declines threaten the stability of pollinator-plant networks that have deep coevolutionary roots (Dalsgaard et al. 2018; Sonne et al. 2022).

Here, we investigate the evolution of pollinator variation in Bromeliaceae, and its consequences for diversification rate. We assemble a database of published pollinators, comprising 403 species matched to an extensive recently published phylogenetic framework with extensive taxonomic coverage (Elliott et al. 2024). While this coverage is incomplete, it is comparable to pollinator datasets available for other plant groups (Ackerman et al. 2023,Thompson et al. 2025b), including those that have been used to detect macroevolutionary patterns (Hernández-Hernández et al. 2014), and it represents a broader limitation of pollinator data. We reconstruct ancestral pollinators in a hidden rates framework capturing rate heterogeneity (Boyko and Beaulieu 2020), and characterise the transitions leading to extant pollinator variation across the family. We recover more transitions than previously known, especially in terminal branches, indicating ongoing pollinator turnover. By using a Bayesian method that explicitly accommodates incomplete sampling and diversification rate heterogeneity (Rabosky 2014), we confirm that hummingbird pollination is strongly associated with accelerated diversification. Critically, by exploring a wide range of assumptions about the prevalence of hummingbird pollination in unsampled species (Kessler et al. 2019), we find that this relationship is robust. Even under extreme and biologically implausible assumptions about the true proportion of hummingbird-pollinated species, the positive association between hummingbird pollination and diversification remains unchanged. Our results confirm hummingbird pollination as a strong driver of the origins of Neotropical plant biodiversity, and our dataset provides a strong foundation for future macroevolutionary research and data collection.

Materials and Methods

Phylogenetic framework

We used a recent phylogenetic hypothesis of the family, which we pruned from a larger phylogeny of order Poales (Elliott et al. 2024). This was reconstructed using a phylogenomic backbone, sampling 353 nuclear loci (Johnson et al. 2019), to which published sequences were added from GenBank (Benson et al. 2012). The phylogeny samples 1,065 bromeliads from 77 genera in all subfamilies. It was time-calibrated as part of the larger Poales phylogeny using a mixture of primary and secondary calibrations (Elliott et al. 2024), in the absence of meaningful fossils for Bromeliaceae (Kessous et al. 2021).

Pollinator data collection

We undertook an extensive literature review to gather data on pollinators for as many species in the phylogeny as is possible, to enable analyses in a statistical evolutionary framework. We undertook a literature search between September 2024 and March 2025 in Google Scholar using searches with combinations of [*Genus species*] AND pollina OR pollinated OR pollinator OR pollination, and [*G. species*] AND poll OR pollinated OR pollinator OR pollination, for every species in the phylogeny. Resulting peer-reviewed articles, doctoral theses, and botanical databases were reviewed for information of pollinators. Bromeliad species were scored with the presence of major pollinator groups: hummingbirds, other birds (poorly-sampled groups or unspecified), bats, Hymenoptera, Lepidoptera, other insects (poorly-sampled groups or unspecified), and terrestrial mammals. Where possible, we recorded individual pollinator species. However, macroevolutionary analyses require scoring pollinators at broader functional levels (Hernández-Hernández et al. 2014; Thompson et al. 2024, 2025a), and we grouped pollinator records further in subsequent analyses.

Ancestral pollinator estimation

We estimated ancestral states in a hidden rates framework using the R package corHMM (Boyko and Beaulieu 2020). Three basic models were estimated for comparison, which were replicated with a hidden rate class, totalling six models. These are all-rates-different (ARD), equal rates (ER), and symmetrical (SYM). The model fits were ranked by AIC weight and the best was investigated further by estimating 300 stochastic character maps (Bollback 2006), which were summarised into node support. We combined and excluded some pollinator groups prior to analysis, as poorly-sampled states can lead to spurious transition rates and biased node states (Goldberg and Igić 2008; Sauquet et al. 2017; Reyes et al. 2018). Hummingbirds (n = 298) and other birds (n = 10) were combined as they strongly overlap in our dataset in all but one bromeliad species (*Pitcairnia feliciana* (A.Chev.) Harms & Mildbr.). Furthermore, records of non-hummingbirds may be opportunistic or infrequent visitors instead of primary pollinators. Moths and butterflies were similarly combined into a single Lepidoptera group, due to their shared evolutionary history and similar pollination mechanisms including nectar-based rewards. Other insects and terrestrial (non-bat) mammals were excluded due to their small sample sizes (n = 10, and 2, respectively). Hymenoptera were retained as a separate group, given their distinct pollination biology and sufficient sampling in our dataset. Similarly, bats were retained as a group because they were sufficiently sampled, and have a distinctive pollination syndrome. The four pollinator groups we analysed with corHMM were bats, hummingbirds (containing the nine non-hummingbird birds), Hymenoptera, and Lepidoptera. Species with multiple pollinator groups recorded in our dataset were scored as polymorphic (n = 70). Following analysis, we characterised well-supported internal transitions based on a threshold of support of >0.7 for a given state. We also characterised terminal branch transitions, where the most recent ancestor of a species has >0.7 node support for a given state but there has been a change in pollinator.

Character-independent diversification

The relative paucity of pollinator data, which is observed across families, makes setting state-specific sampling fractions required by -SSE models difficult (Mynard et al. 2023). Following previous work under similar conditions (Thompson et al. 2024, 2025a; Thompson and Venditti 2025), we estimated diversification rate heterogeneity in the character-independent framework Bayesian Analysis of Macroevolutionary Mixtures (BAMM, (Rabosky 2014)). We ran four reversible-jump Monte Carlo Markov chains (rjMCMC) for 50 million generations, sampling every 5,000 and discarding the first 10% as burn-in. We set a conservative prior expectation of one rate shift, and other priors were set in the R package

BAMMtools (Rabosky et al. 2014). We accounted for incomplete taxonomic sampling by providing genus-level sampling fractions. By doing so at genus level, rather than tribe or subfamily, we can capture as much background rate-heterogeneity as possible. Convergence was assessed by ensuring that effective sample sizes for all parameters were>200, using the R package coda (Plummer et al. 2006).

Trait-dependent diversification

Using the BAMM rates, we tested whether hummingbird pollination is associated with higher speciation and net diversification rates, using Structured Rate Permutations on Phylogenies (STRAPP, (Rabosky and Huang 2016)) implemented in the R package BAMMtools (Rabosky et al. 2014). Benefits of STRAPP, beyond the lack of necessity to set state-specific sampling fractions, include that it does not assume all rate variation is either associated with the focal trait or not, and it can account for incomplete sampling at fine scales. This combination of BAMM and STRAPP has been shown to be effective in situations of incomplete trait data, including in pollinator analyses (Thompson and Venditti 2025,Thompson et al. 2025a). Due to the dominance of hummingbird pollinators in gathered observations, we focussed on the impact of hummingbird pollination scored binarily (1 = present, 0 = absent). With STRAPP, we performed 1,000 randomisations and assessed significance with a Mann-Whitney statistical test. Species were coded as 1 if they had evidence of hummingbird pollination, either as the sole pollinator or in combination with observations of other pollinators (n = 298). Species were coded as 0 if they only had records of non-hummingbird pollinators. Species present in the phylogeny but without pollinator records were excluded. We also tested whether diversification rates differed among other pollinator groups. We ran an additional STRAPP analysis in which species were assigned to one of hummingbird, Hymenoptera, Lepidoptera or bat. STRAPP does not allow for polymorphic state scoring, and we excluded polymorphic species from this analysis (n = 70), notably 66 with recorded hummingbird pollination. To assess whether the exclusion of polymorphic species influences our results, we performed a complementary STRAPP analysis in which species were coded by the number of recorded pollinator groups (ranging from one to four). These two multi-group STRAPP analyses used a Kruskal-Wallis test to assess significance.

Sensitivity testing with BiSSE

We performed sensitivity analyses to assess the impacts of uncertainty in state-specific sampling on the estimated relationship between hummingbird pollination and diversification rates. These analyses were not intended to provide biologically meaningful state-specific diversification parameters. They were designed to evaluate whether the direction of the difference between average diversification rate of hummingbird-pollinated species and others is robust across different assumptions of the prevalence of hummingbird pollination. We scored species binarily by the presence of hummingbird pollination, and calculated artificial state sampling fractions assuming our data and phylogeny had sampled from 20% to 80% of species truly pollinated by hummingbirds, in 10% intervals. These span the expert judgment of 50-60% (Kessler et al. 2019) and also explore extreme scenarios. We also tested whether providing state-dependent sampling fractions impacted results, by specifying none in a final analysis. These analyses were implemented with BiSSE (Maddison et al. 2007), using a Bayesian MCMC framework in the R package diversitree (FitzJohn 2012). For each scenario, we fitted a standard BiSSE model under Maximum Likelihood, where state-specific parameters of speciation and extinction rate, and directional transition rate, are estimated freely from the data. These ML estimates were used as starting parameters in the MCMC analyses, and exponential priors were implemented. Each MCMC run was 10,000 generations, sampled every 25 and with the first 2,000 discarded as burn-in. The difference between the average net diversification of hummingbird-pollinated species and other species was calculated, retaining a posterior sample of 320 estimates per scenario.

Results

A dataset of bromeliad pollinators to enable comparative research

Our literature review found pollinator data for 403 species (~39% of species in the phylogeny (Elliott et al. 2024)). This covers ~11% of all bromeliad species in 53 genera (~66% of the total), which is consistent with the sparseness of pollinator data documented in other plant families (Orchidaceae, ~10% species and ~56% genera (Ackerman et al. 2023); Cactaceae, ~18% and ~66% genera (Thompson et al. 2025b)). Hummingbird pollination dominates the dataset, with 298 species recorded (~74%). Hymenoptera was second most common, with 99 species (~25%). Following these are Chiroptera (53 species, ~13%) and Lepidoptera (54 species, ~13%). Small numbers of species are recorded for “other insects” (10 species, ~2%) and terrestrial mammals (3 species, ~0.7%). Pollinator data were available for all eight subfamilies, but coverage was uneven. Sampling coverage varied among subfamilies but reflected their species richness. The two largest subfamilies, Bromelioideae and Tillandsioideae, were the best represented, with pollinator records available for 37 of approximately 40 genera and 20 of approximately 22 genera, respectively. All five genera of Pitcairnioideae were represented in our dataset. Puyoideae, Brocchinioideae, and Hechtioideae are each monogeneric and are fully represented at the genus level. Navioideae and Lindmanioideae, comprising five and two genera, respectively, were partially sampled at three and two genera, respectively. A genus-level summary and the full species-level dataset are available in Supplementary Materials.

The evolution of pollinator diversity in bromeliads

The most recent bromeliad ancestor was most likely pollinated by Hymenoptera (node support 0.75) (Figure 1). This is retained in the earliest-diverging subfamilies, Brocchinioideae, Lindmannioideae, Navioideae and Hechtioideae, with the exception of a shift to bird pollination within *Hechtia* Klotzsch (Ramírez-Morillo et al. 2018). Hummingbird pollination originated independently on two deep branches. One origin is in the branch leading to extant Tillandsioideae (node support 0.75), and a second is in the common ancestor of Pitcairnioideae, Puyoidieae and Bromelioideae (node support 0.80). Following these transitions, pollination systems diversified repeatedly across these four subfamilies. In Tillandsioideae, there are several reversals to Hymenoptera, and transitions to bat and Lepidoptera pollination. There is also one reversal from bat pollination to hummingbird pollination. Pitcairnioideae is similar, with reversals to Hymenoptera and repeated transitions to bat pollination. In contrast, transitions away from hummingbird pollination, either reversals to Hymenoptera or transitions to bats and Lepidoptera, are concentrated in recent branches in Puyoideae and Bromelioideae. In total, there are 14 well-supported shifts in nodes deeper than those preceding terminal branches. Two of these are in nodes descending from a highly uncertain node containing *Werauhia* J.R.Grant and *Alcantarea* (É.Morren ex Mez) Harms, thus the true number may be 13. Beyond these shifts in deeper ancestors, there are many more transitions occurring along terminal branches. 96 species show a change relative to a strongly supported recent ancestral pollinator, of which 63 retain the ancestral pollinator but gain one or more new pollinator groups. Only 31 are complete shifts away from the ancestral pollinator. Gains of each pollinator group were relatively common, especially Hymenoptera and Lepidoptera. It is worth noting that these may not represent true terminal branch transitions, as the taxonomic sampling means shallow internal nodes may not be included. But, the true degree of lability is likely underestimated, as transitions between species within pollinator groups are not modelled.

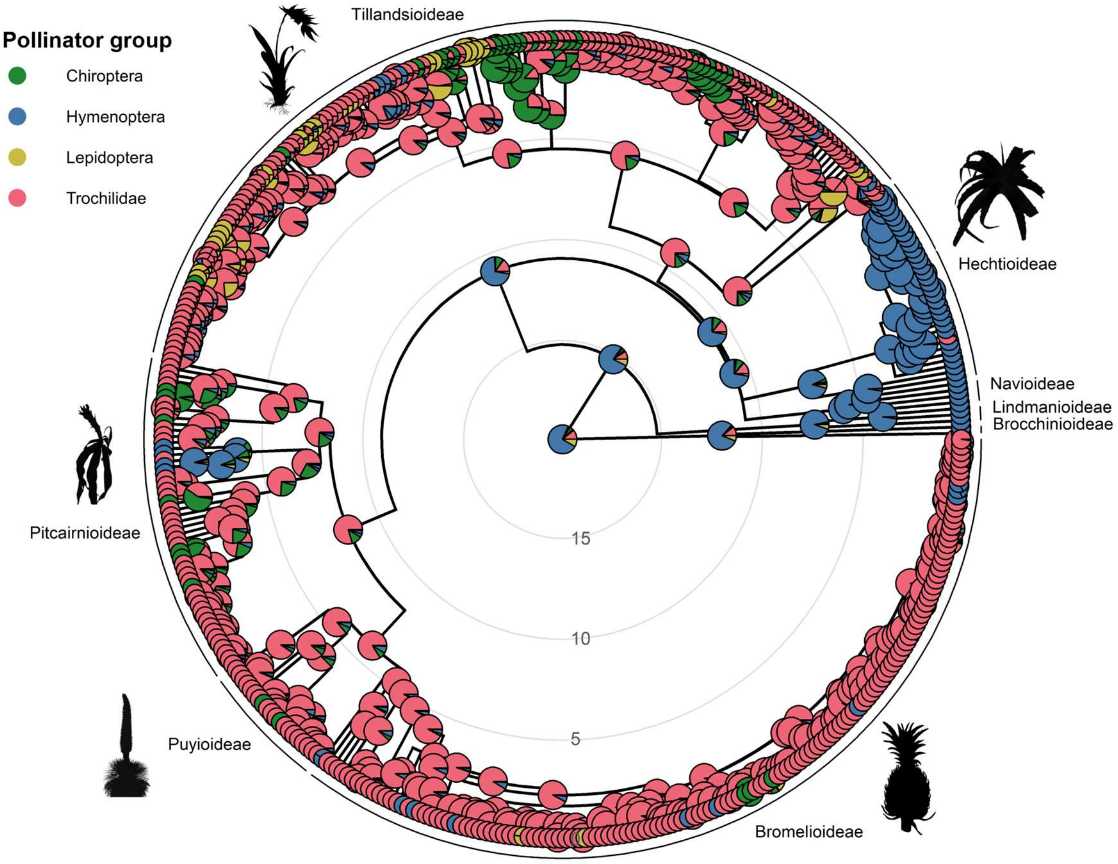

Figure 1: The evolution of pollination across the phylogeny of Bromeliaceae. Tips and ancestors are coloured by pollinator groups: bats (green), hummingbirds (red), Hymenoptera (blue), and Lepidoptera (yellow). Uncertainty of ancestral states was estimated with 300 stochastic character maps, estimated under an all-rates-different model of evolution, with hidden rates. Rate classes were combined for visualisation (i.e. hummingbird fast and slow rate classes were combined). The best supported root state is Hymenoptera, and there are major transitions to hummingbird pollination in the branch leading to the subfamily Tillandsioideae, and the branch leading to Pitcairnioideae, Puyoideae and Bromelioideae. Further transitions to other pollinator groups are nested within these subfamilies, and there is evidence of a loss and regain of hummingbird pollination in Tillandsioideae. Many previously unknown transitions occur in shallower branches, indicating ongoing turnover. The Tillandsioideae and Bromelioideae silhouettes are from Phylopic (https://www.phylopic.org/), and we created the remaining silhouettes using images available under Creative Commons licenses.

Hummingbird pollination accelerates speciation

We tested whether pollination by different animal groups shapes diversification rates in bromeliads using trait-dependent diversification analyses (Figure 2). We performed STRAPP tests using BAMM-estimated rates, in which incomplete sampling was corrected at genus-level and rate-heterogeneity fully characterised. In binary tests of pollinator-dependent diversification for each group, where polymorphic species were not considered, we found that only hummingbird pollination doubles the rate of speciation and net-diversification. Average speciation and net diversification for hummingbird-pollinated bromeliad species are 2.77 and 2.64 (lineages/Ma), respectively. For other species, they are 1.46 and 1.15 (lineages/Ma), respectively. Pollination by bats, Hymenoptera or Lepidoptera scored binarily had insignificant impacts on speciation or net diversification ($p > 0.05$ in all cases). When excluding polymorphic species ($n = 70$), most of which include hummingbird pollination ($n = 66$), and scoring the remaining species into their pollinator group, we found no significant impact of pollinator groups on speciation and net diversification ($p > 0.05$ in both tests). Testing the impact of polymorphically-scored species, which ranged from one to four pollinator groups per species, we also found no significant impact on speciation or net diversification ($p > 0.05$ in both cases).

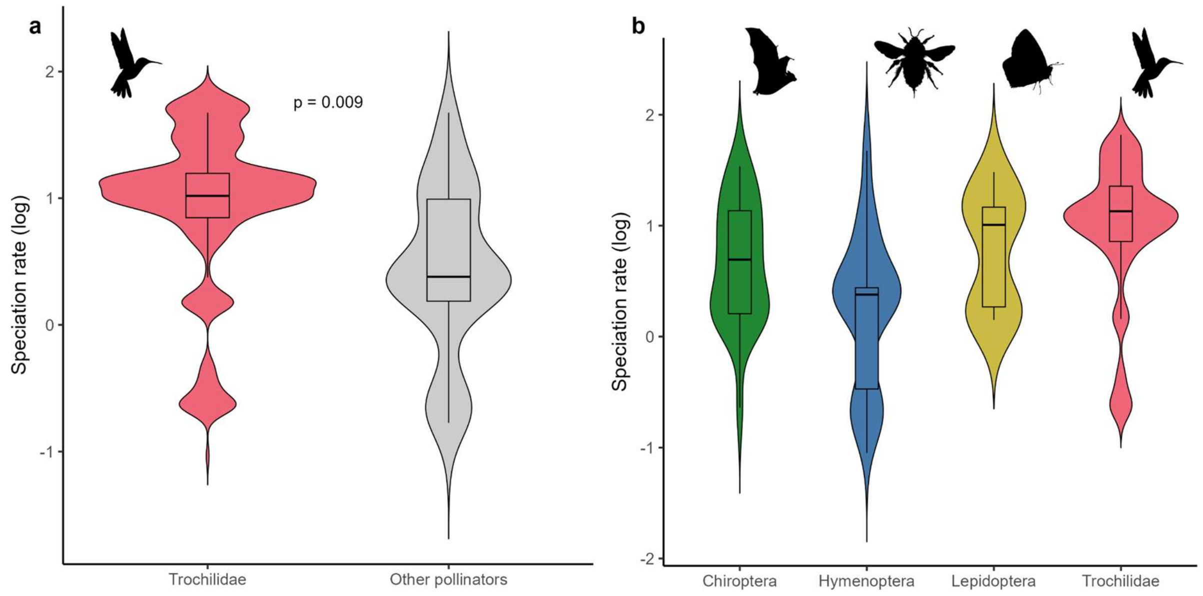

Figure 2: Hummingbird pollination accelerates diversification rate. (a) Mean tip speciation rates, estimated with BAMM, are significantly faster in bromeliads with recorded hummingbird pollination (n = 298) than species pollinated exclusively by other groups (n = 105) ($p < 0.05$). (b) When only species with a single recorded pollinator group are considered simultaneously, speciation rates do not differ significantly among pollinator groups ($p > 0.05$).Violin plots show the distribution of mean tip speciation rates, and boxplots indicate the median and interquartile range. Rates are log-transformed for visualisation. Silhouettes of pollinator groups are from Phylopic (https://www.phylopic.org/).

Unlikely that improving sampling will change the hummingbird-diversification relationship

We tested how sensitive the result that hummingbird pollination accelerates diversification is to incomplete sampling assumptions, which are not known precisely but estimated at 50-60% (Kessler et al. 2019) (Figure 3). To do this, we used simplistic BiSSE tests in which the proportion of sampled hummingbird-pollinated species was altered from extremes of 0.2 to 0.8, assuming a total of 3,700 species. We also tested the impact of making any corrections of state-dependent sampling, enforcing an incorrect total sampling for both states. In every case, the difference between net diversification of hummingbird-pollinated species and others is positive (Figure 3). This is higher when the proportion of unsampled hummingbird-pollinated species is specified as higher.

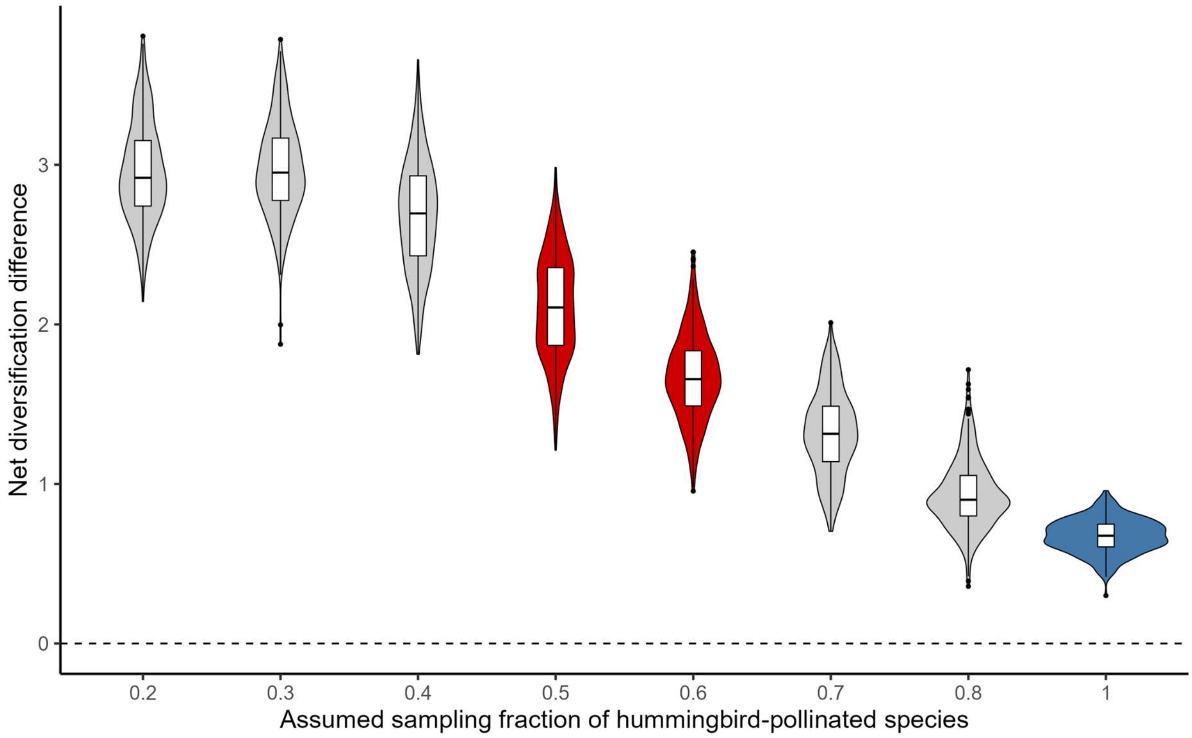

Figure 3: Little sensitivity of the hummingbird-diversification relationship to incomplete sampling. The difference in net diversification between hummingbird-pollinated lineages and other bromeliads under alternative assumptions about the true proportion of hummingbird-pollinated bromeliads. Violins show the posterior distribution of the difference in net diversification estimated from Bayesian BiSSE analyses, assuming we had sampled between 20-80% of all hummingbird-pollinated species, as well as a model without correcting for state-dependent sampling (blue violin). Boxplots indicate the median and interquartile range. Under no sampling scenario is the difference in net diversification negative or zero. The relationship between hummingbird pollination and diversification is therefore robust to uncertainty in sampling.

Discussion

Bromeliaceae have long attracted the attention of evolutionary biologists as a model system for adaptive radiation in the rise of Neotropical biodiversity (Givnish et al. 2014; Palma-Silva and Fay 2020). Their remarkable species richness and variation in ecological strategies has evolved over a remarkably short timescale (Givnish et al. 2011, 2018; Kessous et al. 2024). Why they so rapidly diversified is a major focus of research, and the importance of different forces has been recognised, such as hummingbird pollination, epiphytism, CAM photosynthesis and tank formation (Givnish et al. 2014; Kessous et al. 2024). Among these, pollinator evolution has received particular attention, and is also a major hypothesis beyond bromeliads in other angiosperms groups (van der Niet and Johnson 2012; Van der Niet et al. 2014; Breitkopf et al. 2015; Thompson et al. 2024, 2025a). However, macroevolutionary tests of pollinator-driven diversification have often been limited by sparse and uneven sampling of both pollinator observations and molecular phylogenies (Givnish et al. 2014; Kessler et al. 2019). Recent studies in other plant families demonstrate that increasing phylogenetic and trait sampling can alter long-standing inferences about the macroevolutionary consequences of pollinators (Thompson et al. 2024, 2025a). Here, by assembling a large pollinator dataset, with coverage comparable to recent compilations (Ackerman et al. 2023,Thompson et al. 2025b), we re-evaluated the evolution of pollinator diversity in bromeliads, and its macroevolutionary consequences. By reconstructing ancestral states under a heterogeneous model of evolution, we find there are more transitions than previously thought (Kessler et al. 2019), especially in recent evolutionary time. We confirm there is a strong impact of pollinator evolution on diversification, with hummingbird pollination accelerating rates even after accounting for background rate-heterogeneity. Importantly, we show that this relationship is robust to uncertainty in pollinator sampling. The impact of hummingbird pollination is recovered even under extreme and unrealistic assumptions about future data collection, indicating that this pattern is stable.

New insights from a large dataset of pollinators

We find the dominant pollinator of bromeliads is birds, primarily hummingbirds, as predicted by Kessler et al. (Kessler et al. 2019), although our data may indicate the estimated proportion of 50-60% is slightly conservative. Where possible, we recorded pollinators to species level, although we grouped them into higher taxonomic groups for analysis and description, excluding the rarest groups. Of the 403 species in our dataset, ~74% are bird pollinated, all of which are hummingbird, or hummingbird plus other birds, except one. Hymenoptera was the second most frequent, with ~25% of species, and following this is bats (~13%) and Lepidoptera (~8%). Most bromeliads are pollinated by a single group (~83%), but a substantial minority (~17%) have more than one group recorded.

Pollinator data is difficult to assemble in angiosperms and relatively few family-wide databases exist (although see (Specht et al. 2012; Ackerman et al. 2023,Thompson et al. 2025b)). Although our dataset is incomplete, it facilitates future research in bromeliad evolution, ecology and conservation, and provides a foundation for data collection.

Polymorphic species nearly totally consist of birds in combination with other pollinators. Although a portion of these will be rare or opportunistic visitors, mixed pollination systems are also recognised as common and potentially adaptive in angiosperms (Johnson and Steiner 2000). Mixed pollination can be associated with niche partitioning, including between birds which pollinate during the day and bats at night (Dellinger et al. 2019a,b; Lagomarsino and Muchhala 2019). We note that 26 of the 403 species on our dataset combine bat and hummingbird pollination. Although birds more frequently co-occur with Hymenoptera (38 species) and Lepidoptera (34 species), bats are rarer overall and nearly half of bat pollinated species co-occur with hummingbird pollination. Mixed pollination can also act to reduce effects of extirpation, or temporal changes in pollinator abundances and low pollinator availability (Wilson et al. 2007; Leal et al. 2020). It is also recognised that mixed pollination can be an intermediate evolutionary state (Stebbins 1970). Our data may support this, given that many species are polymorphic, whereas deeper nodes tend to reconstruct as single pollinators. However, this is also somewhat expected from ancestral state reconstructions, as they are informed by extant variation, meaning that transient intermediate states in deep nodes are not recoverable.

The flexible evolution of pollinator diversity in bromeliads

Although hummingbirds are the dominant pollinators across bromeliads, our ancestral reconstructions indicate that the ancestral bromeliad was most likely pollinated by Hymenoptera. This is consistent with previous inferences using much smaller datasets (Givnish et al. 2014; Kessler et al. 2019), and our investigations provide greater resolution by sampling a larger portion of bromeliads and using complex heterogeneous models (Boyko and Beaulieu 2020). We found that evolution from the ancestral pollinator is highly complex, with best support for the model with maximum heterogeneity. Transition rates differ between all pollinator groups, and different lineages evolve at different rates. This suggests that the tempo of pollinator evolution has varied throughout time, between lineages, and across the Neotropics (Graham et al. 2012; Varassin and Sazima 2012; Kriebel et al. 2019). This heterogeneity likely reflects spatiotemporal variation in selective pressures, which arise from distributional and elevational shifts, changes in habitat structure, ecological conditions and pollinator availability. These dynamics are further influenced by interactions and correlated evolution with other adaptations, such as CAM photosynthesis, epiphytism, and tank formation (Givnish et al. 2014; Neves et al. 2023), which are unevenly distributed across the Neotropics and between lineages.

By improving pollinator data coverage, and using a large phylogeny (Elliott et al. 2024), we infer more pollinator transitions have occurred in bromeliad evolution than were previously known. An earlier investigation with a smaller phylogeny inferred two or three deep origins of hummingbird pollination associated with origins of major subfamilies, and 12 reversions to insect pollination in the largest subfamilies (Givnish et al. 2014). Similarly, a synthesis of published findings and floral variation describes 12-14 (Kessler et al. 2019). Our results support these deep transitions, but additionally reveal extensive turnover in pollinators in more recent evolutionary time, in which gains, losses and replacements of pollinators are frequent. These results support that pollinator evolution, including by hummingbirds, remains highly labile and dynamic (Leal et al. 2020; Barreto et al. 2024), and turnover is likely ongoing at a relatively high rate. In total, we infer 110 well-supported pollinator transitions in bromeliad evolution, 96 of which occur along terminal branches. The deeper transitions include three to hummingbirds, ten reversals away from hummingbirds, and four transitions among non-avian pollinators. Transitions away from hummingbird pollination are disproportionately towards bats and Lepidoptera, and include multiple reversals to Hymenoptera, particularly within Tillandsioideae. Transitions along terminal branches are dominated by gains of insect pollinators, and frequently occur in mixed-pollination states rather than replacements of the ancestral pollinator.

Little doubt that hummingbird pollination accelerates diversification

It has long been suggested that hummingbird-pollination accelerates bromeliad diversification (Givnish et al. 2014; Kessler et al. 2019; Barreto et al. 2024). Using pollinator data with over fourfold greater coverage than previous datasets (Givnish et al. 2014), we confirm this. Critically, the effect persists even after accounting for the background rate heterogeneity that shapes bromeliad diversification, a portion of which likely will be driven by factors beyond pollination (Givnish et al. 2014; Kessler et al. 2019; Neves et al. 2023; Thompson et al. 2024). As previously predicted, speciation and net diversification are both doubled on average by the evolution of hummingbird pollination. This pattern is likely to be explained by a combination of forces driving divergences which lead to speciation, including divergences in floral morphology, nectar production and phenology (van der Niet and Johnson 2012; Van der Niet et al. 2014; Kessler et al. 2019; Barreto et al. 2024; Thompson and Venditti 2025). Furthermore, hummingbird pollination is frequently associated with montane and epiphytic ecosystems (Givnish et al. 2014), in which steep ecological gradients and habitat fragmentation can accelerate population divergence (Hughes and Eastwood 2006). Birds are also thought to be able to transfer pollen over greater distances than insects, due to their higher mobility and larger ranges, and higher pollen transfer efficiency (Castellanos et al. 2003; Krauss et al. 2017; Abrahamczyk et al. 2022). These factors increase genetic divergence and adaptive potential, potentially driving diversification. However, the macroevolutionary consequences of long-distance pollen transfer remain debated, as increased gene flow may reduce population structure and the potential for allopatric speciation (Gelmi-Candusso et al. 2017; Gamba and Muchhala 2020; Wessinger 2021). Additionally, not all hummingbirds disperse pollen over greater distances than bees (Schmidt-Lebuhn et al. 2019).

Notably, we find that this pattern is caused by presence of hummingbird pollination, rather than exclusive pollination by hummingbirds. When polymorphic species were excluded to facilitate comparison of rates across four major pollinator groups, the association between pollinators and diversification was no longer significant. This result reflects a methodological limit of the analytical approach that cannot account for polymorphic species (Rabosky and Huang 2016). Indeed, ~94% of polymorphic species in our dataset include hummingbirds among their pollinators, showing that mixed systems are dominated by hummingbirds. The result is not restricted to species relying solely on pollinators, but extends to those that gain or retain hummingbirds alongside others. Although here we describe species with mixed pollination systems as polymorphic, these can be interpreted as a form of ecological generalisation in pollination. Such generalist strategies can confer greater adaptive potential in differing environments (Griffith and Sultan 2012), and that plants can gain additional pollinators without strong trade-offs caused by losing their ancestral pollinator, including documented cases involving hummingbirds (Armbruster 2017). By combining the effects of hummingbird pollination with ecological flexibility, species with multiple pollinator groups may be more likely to proliferate and speciate. Our results therefore support a classic key innovation model, in which the frequent acquisition of hummingbird pollination repeatedly accelerates diversification, even as part of a mixed pollination system and when interacting with other coevolving traits.

Hummingbirds as the organising force in the complex diversification of bromeliads

Our results suggest that hummingbird pollination in bromeliads can be viewed as a key innovation, although we still caution that drivers of diversification are complex and multivariate (Givnish et al. 2014; Silvestro et al. 2014; Sauquet and Magallón 2018; Helmstetter et al. 2023; Thompson et al. 2024). Other factors are still very important, such as epiphytism, CAM photosynthesis, elevation, and tank-formation, but our results suggest they may act additively on hummingbird effects, rather than being equally powerful. This is because hummingbird pollination remains important even after accounting for rate heterogeneity, much of which is explained by other forces (Beaulieu and O'Meara 2016; Rabosky and Huang 2016; Caetano et al. 2018). In other families, such as cacti and orchids, the long presumed effect of pollinator evolution on diversification (Hernández-Hernández et al. 2014; Givnish et al. 2015) disappears once rate heterogeneity is incorporated on an appropriate scale (Thompson et al. 2024, 2025a; Thompson and Venditti 2025). Our finding adds structure and order to what may appear a diffuse network of correlated drivers (Givnish et al. 2014). Although pollinator divergence is not instant, it may act as the key facilitator of this network by promoting access to ecosystem conditions and selective forces under which these correlated traits can evolve. These correlated traits may therefore act additively on diversification once hummingbird pollination facilitates access to high elevation and epiphytic environments, where ecological gradients, habitat structure and resources create conditions under which other traits, such as CAM photosynthesis, tank-formation, and epiphytism further promote diversification (Givnish et al. 2014). With this hypothesised pathway in mind, hummingbird pollination does replace the complex multi-trait view of bromeliad diversification, but provides a primary trait around which the complexity is organised. We hope that our results and interpretation motivate further integrative analyses to explicitly test this hypothesis. Similar hypotheses have been tested recently with structural equation models, which offer some insights into the origins and structure of complex ecological and evolutionary systems (Tietje et al. 2022; Bhadra et al. 2025; Zizka et al. 2025).

A pattern unlikely to change despite incomplete data

It remains unknown exactly how many bromeliad species are pollinated by hummingbird pollinators, and this uncertainty has long constrained trait-dependent diversification analyses. Although our data greatly expands existing pollinator compilations for bromeliads, and is comparable in coverage to those available for other plant families (Specht et al. 2012; Ackerman et al. 2023,Thompson et al. 2025b), incomplete trait sampling remains unavoidable. Although we analysed our dataset within a character independent framework accounting for incomplete sampling (Rabosky 2014), we explicitly explored how different assumptions of the proportion of sampled hummingbird-pollinated species influenced our results. Across a wide range of scenarios, spanning expert judgments (Kessler et al. 2019) as well as deliberately extreme and unrealistic proportions, we find the hummingbird-bromeliad system is a rare case in macroevolution where the pattern is strong enough to overcome incomplete sampling. Diversification rate is consistently higher in hummingbird-pollination species. We found this even under the unrealistically conservative assumption that our dataset sampled 80% of all truly hummingbird-pollinated bromeliads, although the magnitude is reduced. While further pollinator data collection will be invaluable for characterising further evolutionary transitions, and facilitating integrative multivariate analyses across large species sampling, additional data are unlikely to change our findings.

Conclusion

Bromeliaceae is one of the most rapidly evolving and ecologically diverse plant radiations of the Neotropics. The forces driving their success are complex and have been difficult to resolve due to incomplete pollinator data and molecular sequencing. By assembling a family-wide pollinator dataset and analysing it in a large phylogenetic framework, we show that pollinator evolution is highly dynamic and ongoing. Despite this lability, and despite substantial background diversification rate heterogeneity, some of which is associated with other drivers, hummingbird pollination emerges as a powerful driver. Hummingbird pollination is likely to act as an organising factor in bromeliad diversification. Sensitivity analyses show that this pattern is unlikely to change under realistic and unrealistic scenarios of future data collection. Our results and dataset provide a strong foundation for future integrative analyses, to help disentangle the web underlying the origins of Neotropical diversity.

Data Availability

Data and code underlying these results are available in GitHub (https://github.com/elizabethforward03/bromeliad_hummingbird).

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Author Contributions

EAF and JBT designed the study. EAF compiled the data. EAF and JBT analysed the data, interpreted the results, wrote the manuscript, and revised the final version. JBT supervised the research

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