

## INVITED REVIEW

# The role of hummingbirds in the evolution and diversification of Bromeliaceae: unsupported claims and untested hypotheses

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At least half of the 3600 species of Bromeliaceae are pollinated by hummingbirds. There is little doubt that the four to 12 evolutionary shifts towards and c. 32 shifts away from hummingbird pollination opened new evolutionary spaces for bromeliad diversification, and that hummingbird pollination has led to increased bromeliad diversification rates. However, the mechanisms leading to these increased rates remain unclear. We here propose that there are four main types of mechanisms that may increase diversification rates of hummingbird-pollinated bromeliad clades: (1) bromeliad speciation through adaptation to different hummingbird species; (2) increased allopatric speciation in hummingbird-pollinated clades due to lower pollen transfer efficiency compared with other pollinators; (3) differential speciation rates in hummingbird-pollinated clades dependent on of flowering phenology and hummingbird behaviour; and (4) higher speciation rates of bromeliads in montane environments (where hummingbird pollination predominates) due to topographic population fragmentation. To date, none of these hypotheses has been appropriately tested, partly due to a lack of data, but also because research so far has focused on documenting the pattern of increased diversification in hummingbird-pollinated clades, implicitly assuming that this pattern supports an underlying mechanism while ignoring the fact that several competing mechanisms may be considered. The aim of the present review is to increase awareness of these mechanisms and to trigger research aimed at specifically testing them. We conclude that much additional research on the roles of hummingbird behaviour and gene flow between bromeliad species is needed to elucidate their contribution to the evolution of diversity in bromeliads and other plant families.

**ADDITIONAL KEYWORDS:** flowering phenology – evolutionary loss – speciation mechanism – pollination syndrome – reproductive system – territorial birds – trapliner – *Vriesea*.

With c. 3600 species (Gouda, Butcher & Gouda, 2019), Bromeliaceae are among the most species-rich non-woody plant families in the Neotropics and have undergone one of the most remarkable adaptive radiations in angiosperms (Benzing, 2000;

Givnish *et al.*, 2014). More than half of the genera include epiphytic species (Zotz, 2013; Givnish *et al.*, 2014). Among bromeliads, pollination by vertebrates predominates over that by insects, and many species are pollinated by hummingbirds (Kessler & Krömer, 2000; Canela & Sazima, 2005; Krömer, Kessler & Herzog, 2006; Fig. 1). In some bromeliad genera (e.g. *Guzmania* Ruiz & Pav., *Pitcairnia* L'Hér., *Tillandsia* L. and *Vriesea* Lindl.), pollination by insects, birds and bats has repeatedly evolved independently

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**Figure 1.** Examples of some hummingbird species visiting bromeliads. A, *Coeligena torquata* visiting *Puya pearcei*; B, *Phaetornis ruber* visiting *Aechmea* sp.; C, *Pterophanes cyanopterus* visiting *Puya atra*; D, *Oreotrochilus adela* visiting *Puya humilis*. Photographs: A: B. Téllez-Baños. B: T. Pinto. C: E. Cuba. D: T. Calahuma.

(Benzing, 2000; Givnish *et al.*, 2014; Aguilar-Rodríguez *et al.*, 2019). However, for many species pollinator observations and the differentiation between flower

visitors and pollinators are lacking and pollinators can only be inferred by pollination syndromes (Krömer *et al.*, 2008).

Hummingbird pollination occurs in at least 45 of the 75 genera of Bromeliaceae (Givnish *et al.*, 2014; Abrahamczyk & Kessler, 2015; M. Kessler *et al.*, unpubl. data). There are no published family-wide accounts of the number of bromeliads with hummingbird pollination, but we estimate that the proportion of bromeliad species with hummingbird-pollination syndromes (red flowers or bracts, narrow flowers, exerted stamens, etc.) is 50–60% (M. Kessler *et al.*, unpubl. data). In mountain ranges, such as the Andes or the Atlantic Rainforest of Brazil, 40–85% of the local bromeliad species are primarily or exclusively pollinated by hummingbirds or at least have an ornithophilous pollination syndrome (Fig. 2; Kessler & Krömer, 2000; Krömer *et al.*, 2006; de Queiroz Piacentini & Varassin, 2007). Hummingbird-pollinated bromeliad clades have diversified roughly twice as fast as clades pollinated by other animals, such as insects (Schmidt-Lebuhn, Kessler & Hensen, 2007; Givnish *et al.*, 2014). From this pattern, it has been suggested that the shift to hummingbird pollination has been one of the key evolutionary innovations influencing bromeliad diversification, mainly through co-evolution by specialization to morphologically different hummingbird species as pollinators (Gentry, 1982; Benzing, 2000; Givnish *et al.*, 2014). However, empirical evidence for specific adaptations of closely related bromeliad species to morphologically different hummingbird species is scarce, and hummingbird pollination co-varies with numerous other factors that may also drive bromeliad diversification (Givnish *et al.*, 2014). Thus, there are various potential mechanisms that may lead to the observed pattern of high diversification in hummingbird-pollinated bromeliad clades. Such mechanisms may be pollinator switches or different flowering strategies in combination with diverging feeding strategies of hummingbirds or geographical isolation induced by mountain uplift (Castellanos *et al.*, 2003; Schmidt-Lebuhn *et al.*, 2007). In the present review, we evaluate the evidence for various mechanistic links between hummingbird pollination and bromeliad diversification.

#### BROMELIAD DIVERSIFICATION THROUGH GAIN AND LOSS OF HUMMINGBIRD POLLINATION

A common reason for plant speciation is the adaptation of a population to a new group of pollinators (Rieseberg & Willis, 2007; Givnish, 2010), and bromeliads are no exception, with hummingbird pollination being gained and lost repeatedly. Nevertheless, the exact numbers of gains and losses of hummingbird pollination remain unclear. Hummingbird pollination evolved at least two to ten times from insect pollination and once from

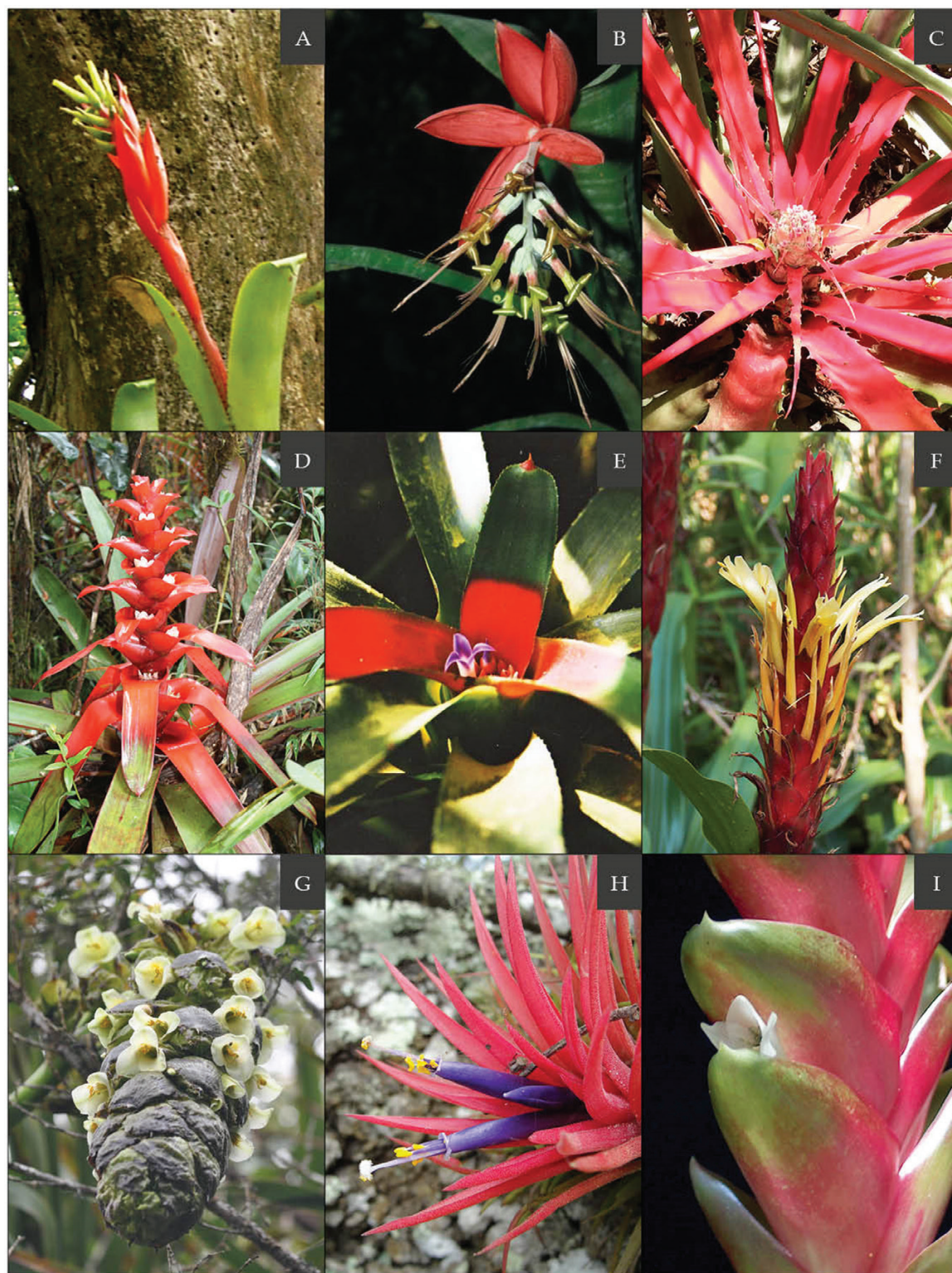
bat pollination, the results depending on sample size and methodology of the ancestral state reconstruction (Givnish *et al.*, 2014; Aguilar-Rodríguez *et al.*, 2019). By plotting pollinator information on the phylogenetic tree for *Vriesea* of Gomes-da-Silva & Souza-Chies (2018), we here document one additional shift from bat to hummingbird pollination in *V. thyrsoides* Mez (for details see legend to Fig. 3 and Supporting Information, Table S1). There are probably a number of additional, still undetected gains of hummingbird pollination, although most of these will involve only a few species. An example of a species not yet included in a phylogenetic analysis is *Fosterella spectabilis* H.Luther, the only species with a bird pollination syndrome in the otherwise insect-pollinated genus *Fosterella* L.B.Sm. (Kessler & Krömer, 2000).

Concerning losses of hummingbird pollination, Givnish *et al.* (2014) reported 12 shifts from hummingbird to insect pollination and four shifts from hummingbird to bat pollination based on a phylogenetic tree including 90 species from 45 genera of Bromeliaceae. However, a closer look at some of the larger genera of Bromeliaceae reveals that in fact there were many more switches from hummingbird to insect or bat pollination. For instance, by plotting pollinator information on the above-mentioned phylogenetic tree for *Vriesea* (containing 69 out of 214 species), we here document three additional shifts from hummingbird to bat pollination (Fig. 3). Furthermore, studies on the reproductive ecology of *Pitcairnia* (Wendt *et al.*, 2001, 2002) in combination with the phylogenetic analysis of Saraiva, Mantovani & Forzza (2015) indicate that at least one switch from hummingbird to insect pollination and one switch to bat pollination has occurred in *Pitcairnia*. Additionally, independent switches to bat pollination have been reported in the *Billbergia* Thunb. clade (seven switches), in *Bromelia* L. (two switches) and in *Deuterocohnia* Mez (one switch) (Aguilar-Rodríguez *et al.*, 2019). Finally, in *Puya* Molina, bat pollination is reported for four species (Vogel, 1969; Varadarajan & Brown, 1988; Aguilar-Rodríguez *et al.*, 2019), and generalist songbird pollination is reported for at least five species (Johow, 1898; Scogin & Freeman, 1984; González-Gómez *et al.*, 2004; Hornung-Leoni, González-Gómez & Troncoso, 2013), whereas Givnish *et al.* (2014) reconstructed the genus as being purely hummingbird-pollinated based on eight out of 214 species.

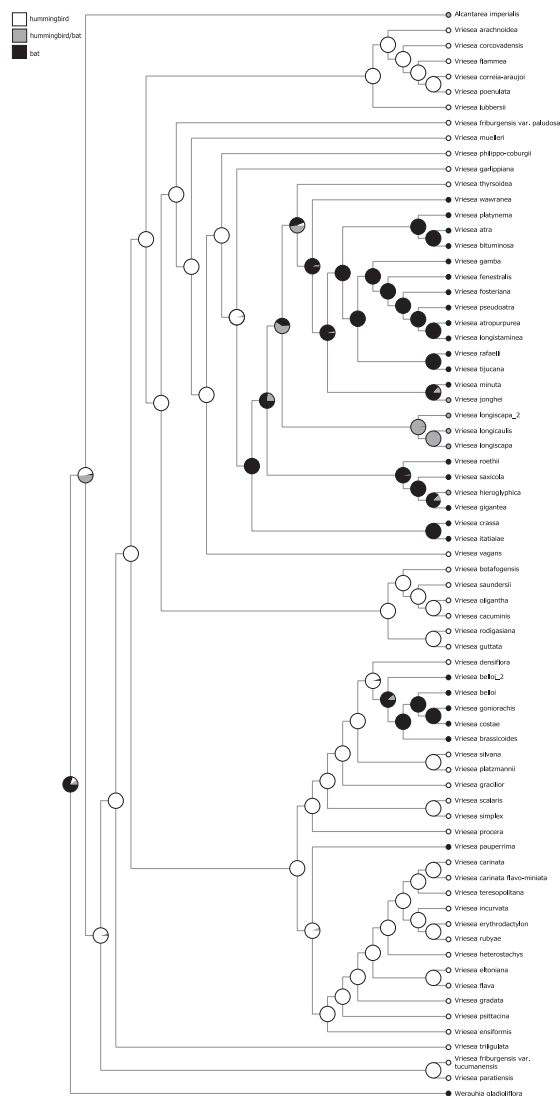
In conclusion, it is evident that gains and losses of hummingbird pollination are common in Bromeliaceae, with at least four to 12 gains and 32 switches away from hummingbird pollination. These observations lead to two questions. (1) How have these shifts happened? (2) What are the implications for bromeliad diversification?

The distribution patterns of pollination syndromes in the Neotropics are shaped by abiotic and geographical





**Figure 2.** Examples of some bromeliad species with an ornithophilous pollination syndrome. A, *Aechmea nudicaulis*; B, *Billbergia issingiana*; C, *Bromelia* sp.; D, *Guzmania* sp.; E, *Neoregelia* sp.; F, *Pitcairnia imbricata*; G, *Puya ctenorhyncha*; H, *Tillandsia ionantha*; I, *Vriesea heliconioides*. Photographs: A, B, E, F, I: T. Krömer. C, D: M. Kessler. G: P. Velásquez-Noriega. H: C. I. Carvajal-Hernández.



**Figure 3.** Ancestral pollinator state reconstruction for the *Vriesea* radiation from the Atlantic Rainforests of eastern Brazil showing repeated shifts between bat and hummingbird pollination. For this analysis, we used the phylogenetic tree of [Gomes-da-Silva & Souza-Chies \(2018\)](#) and collected information of pollinator groups from the literature for >50% of the species (for references see Supporting Information, [Table S1](#)). For species lacking pollinator information, we applied the concept of pollination syndromes based on floral morphology ([Fægri & van der Pijl 1979](#)). We categorized groups either as hummingbird-, hummingbird-/bat- or bat-pollinated and reconstructed ancestral pollinator states applying a Bayesian Markov chain Monte Carlo (MCMC) analysis in RASP version 2.1 beta ([Yu, Harris & He, 2012](#)). Using the Jukes–Cantor + G model, sampling each of 100 generations, we ran the MCMC analysis for 50 000 generations and allowed all character combinations. We chose the MCMC approach because it offers the opportunity to code hummingbird/bat pollination as an intermediate stage.

factors: bee-pollinated species are most diverse in arid lowland forests, whereas bat-pollinated species are most diverse in humid lowland to mid-elevation forests and hummingbird-pollinated species are most diverse in mid- to high-elevation areas ([Kessler & Krömer, 2000](#); [Krömer \*et al.\*, 2006](#); [Varassin & Sazima, 2012](#)). These diversity patterns are in line with the physiological preferences of the individual pollinator groups: hummingbirds are best adapted to deal with cool and wet conditions in montane forests; insects use stored food or hibernate in pupal stages to survive arid periods in seasonally dry climates; and bats exploit the warm nocturnal airspace of humid lowland forests ([Cruden, 1972](#); [Kessler & Krömer, 2000](#); [Krömer \*et al.\*, 2006](#); [Givnish \*et al.\*, 2014](#); [Abrahamczyk & Kessler, 2015](#); [Aguilar-Rodríguez \*et al.\*, 2019](#)). The distribution pattern of shifts of pollination syndromes also seems to follow the pattern described above: bromeliad species with mixed hummingbird/bat or hummingbird/bee syndromes are often found at the transition zones where evergreen and deciduous forests meet and at mid-elevations where the dominances of syndromes change ([Krömer \*et al.\*, 2006](#); [Aguilar-Rodríguez \*et al.\*, 2014](#); [Bastos \*et al.\*, 2017](#)). This suggests that transitions between syndromes may evolve predominantly in these transition zones, although an explicit test of this hypothesis is lacking. As a potential example of this, one might consider the bat-pollinated species *Tillandsia macropetala* Wawra [= *Pseudalcantarea macropetala* (Wawra) Pinzón & Barfuss] that is also visited by hummingbirds. [Aguilar-Rodríguez \*et al.\* \(2014\)](#) reported that in the morning, when flowers are still open and hummingbirds start visiting them, pollen is no longer available, precluding hummingbird pollination. However, if such a species were to colonize higher elevations with a decreased bat abundance, pollen might still be available in the morning, and hummingbirds may become pollinators. In a second step, the population would then adapt to the new pollinator assemblage and the evolution of a new species with another syndrome may begin. An alternative hypothesis would be that if in the original habitat bat densities were to decline temporarily, hummingbird pollination might become more important. In this case, the evolution towards hummingbird pollination would start and enable the species to later increase its range to higher elevations. Shifts in pollination probably evolve in both ways, but they are impossible to tease apart after the shift has evolved.

Focusing on the consequences for bromeliad diversification, there is little doubt that shifts between pollinator groups opened new adaptive niche spaces for bromeliads ([Benzing, 2000](#); [Givnish \*et al.\*, 2014](#)). These authors suggest that potentially this can happen in two ways: (1) as detailed above, by allowing bromeliad clades to adapt to new climatic conditions where



these would not otherwise find suitable pollinators; or (2) by adapting to a new pollinator group induced by a reduction in the visitation frequency of the original pollinator group. After establishment, both closely related species can coexist by using different pollinators and thus by being reproductively isolated. It is difficult to quantify the contributions of these two processes in increasing bromeliad diversity. However, considering the large proportion of hummingbird-pollinated bromeliad species, one might argue that if bromeliads had been unable to evolve this pollination syndrome, the overall diversity would be considerably lower because the adaptation to hummingbird pollination enabled bromeliads to colonize and speciate in the montane rainforests much more intensively than possible when relying only on the less reliable insect pollinators.

#### BROMELIAD DIVERSIFICATION THROUGH SPECIALIZATION TO DIFFERENT HUMMINGBIRD SPECIES

The standard interpretation of the high diversification of hummingbird-pollinated bromeliad clades is that the different bromeliad species have adapted to different hummingbird species with different bill morphologies, leading to pre-mating reproductive isolation (Gentry, 1982; Benzing, 2000; Givnish *et al.*, 2014). However, as we show below, there is little actual evidence for this hypothesis.

To show that bromeliad diversification is driven by the adaptation to different hummingbird species as pollinators, it would be necessary to show that bromeliad speciation events are linked to shifts in hummingbird pollinators. To our knowledge, no study has yet shown this. This is largely a result of incomplete data, ranging from under-sampled bromeliad phylogenetic trees that do not allow identification of sister species to insufficient data on the pollinators. Clearly, much remains to be learnt in this context, and at present we need to accept that there is no direct support in favour or against this hypothesis.

There may, however, be some indirect evidence available. Overall, there are several times more species of hummingbird-pollinated bromeliads than of hummingbirds, and many hummingbird species are morphologically similar. This is also reflected at more local scales where up to 42 hummingbird-pollinated bromeliad species have been found to co-occur sympatrically at single sites, but where the numbers of visiting hummingbird species are generally much lower (e.g. Martinelli, 1994; Varassin & Sazima, 2000; Dzedzioch, Stevens & Gottsberger, 2003; Wendt *et al.*, 2008). For instance, the 12 closely related, small-ranging *Vriesea* spp. occurring in the Brazilian

Atlantic Rainforest of Santa Teresa, Espírito Santo, are visited by only four species of hummingbirds, and ten of the species share *Ramphodon naevius* as a pollinator (Wendt *et al.*, 2008). Furthermore, during the flowering time of each individual species three to nine other *Vriesea* spp. are co-flowering. This example reflects the general pattern that many hummingbird-pollinated bromeliad species have highly overlapping pollinator communities.

Many bromeliad species have small ranges (Kessler, 2002), and it is conceivable that species today occurring in sympatry may have originated at different locations, interacted with different hummingbird species and have only secondarily attained sympatry. Nevertheless, even if this were the case, their current floral morphology and overlapping pollinator guilds still lead to the conclusion that there is little evidence for specialization by adaptation to morphologically different hummingbird species.

The strong overlap of hummingbird visitors to different bromeliad species raises the question of how these plants avoid hybridization and introgression, effectively resulting in a reduction of species numbers. Although bromeliads hybridize easily in cultivation, relatively few hybrids are known to occur in the wild (Wendt *et al.*, 2008). This is probably a result of a combination of: pre- and post-zygotic reproductive barriers, including morphometrical differences in stigma and stamen length leading to the deposition of pollen at different parts of the bodies of the birds (Christianini, Forzza & Buzato, 2013; Neri *et al.*, 2017); partly overlapping flowering time or anthesis during different times of the day (Kaehler, Varassin & Goldenberg, 2005; Wendt *et al.*, 2008; Zanella *et al.*, 2016); differences in reproductive strategy with closely related species producing seeds either mainly by selfing or by outcrossing (e.g. Wendt *et al.*, 2002; Matallana *et al.*, 2010; Wagner *et al.*, 2015; Neri *et al.*, 2017); inhibition of pollen tube growth at interspecific crosses (Matallana *et al.*, 2016; de Souza *et al.*, 2017); low germination rates of hybrid seeds (Neri *et al.*, 2017); and the difficulty in recognizing hybrid individuals in the wild (A. Hernández, pers. comm.). An increase in seed production by selfing is often related to a reduction of corolla length and nectar production (Matallana *et al.*, 2010), which also reduces the overall attractiveness of the flowers to hummingbirds. Clearly, much more needs to be known about levels of gene flow between co-occurring bromeliad species pollinated by the same hummingbird species to understand how species identities are maintained and potentially how speciation may be linked to pollinator shifts.

Viewed from the hummingbird perspective, single species of hummingbirds often visit large numbers of plant species. For example, even the highly specialized sword-billed hummingbird (*Ensifera ensifera*) visits

37 species of long-tubed passionflowers [*Passiflora* L. section *Tacsonia* (Juss.) Harms] (Abrahamczyk, Souto-Vilarós, & Renner, 2014). Clearly, although evolution of this plant group appears to have been triggered by the adaptation to its specialized pollinator, diversification among the sword-billed hummingbird-pollinated species cannot be explained by further pollinator specialization. However, in the sword-billed hummingbird-pollinated clade reversions to short-billed hummingbird pollination and thus further diversification occurred (Abrahamczyk *et al.*, 2014).

To complicate matters even further, the same bromeliad species is often pollinated by different hummingbird species in different parts of its range. For example, the widespread *Aechmea nudicaulis* (L.) Griseb. was studied by Buzato, Sazima & Sazima (2000) at two different sites in the Atlantic Rainforest of Sao Paulo state, south-eastern Brazil, where three hummingbird species were its pollinators at the lowland site (*Hylocharis cyanus*, *Ramphodon naevius*, *Thalurania glaucopis*) and four species were its pollinators at the highland site (*Phaethornis eurynome*, *Clytolaema rubricauda*, *Leucochloris albicollis*, *Stephanoxis lalandi*). For the same bromeliad species, Fonseca *et al.* (2015) recorded *Amazilia fimbriata* as the main floral visitor at a coastal restinga ecosystem in the state of Rio de Janeiro, whereas Machado & Semir (2006) and Schmid *et al.* (2011a) at montane and coastal dune vegetation sites in Atlantic Rainforest, respectively, also observed *T. glaucopis* as being the most frequent visitor of *A. nudicaulis* (Table 1). Other bromeliad species with multiple hummingbird visitors or pollinators at different sites in the Atlantic Rainforest are *Tillandsia stricta* Sol. ex Sims (Martinelli, 1994; Buzato *et al.*, 2000; Machado & Semir, 2006; Fonseca *et al.*, 2015) and *Vriesea altodaserrae* L.B.Sm. (Kaehler *et al.*, 2005; Machado & Semir, 2006; Nunes *et al.*, 2018). Neither *A. nudicaulis* nor *T. stricta* shows significant variation in corolla lengths between populations. However, corolla lengths differ significantly between different populations of *V. altodaserrae*, with values ranging from  $22.8 \pm 2.3$  mm (Kaehler *et al.*, 2005) to  $31.5 \pm 0.5$  mm (Machado & Semir, 2006) and  $34.5 \pm 5.0$  mm (Nunes *et al.*, 2018). These differences might suggest regional adaptations to different pollinator guilds, but we did not find a relationship between corolla length and mean bill length of the pollinating hummingbird species per site calculated based on mean culmen length of males (based on measurements from Wolf, 1970; Grantsau, 1988; Colwell, 2000; Williamson, 2001; Graham *et al.*, 2012; and our own measurements, S. Abrahamczyk, unpubl. data), with values of  $20.6 \pm 7.1$  mm (Kaehler *et al.*, 2005),  $20.9 \pm 5.9$  mm (Machado & Semir, 2006) and  $19.9 \pm 2.9$  mm (Nunes *et al.*, 2018). The published data are, however, not detailed enough to weigh visiting

hummingbird species by their visitation frequency, but at present there appears to be no evidence that variation in corolla length of *V. altodaserrae* can be explained by differences in pollinators.

In conclusion, with the data available at present, the interpretation that the increased diversification rate of hummingbird-pollinated clades in Bromeliaceae and other plant families is driven by adaptation to morphologically different hummingbird species as pollinators in closely related species (Givnish *et al.*, 2014; Lagomarsino *et al.*, 2016; Serrano-Serrano *et al.*, 2017; Kriebel *et al.*, 2019) is unsupported. In contrast, there is indirect evidence that such specialization may not be common, although we cannot exclude the possibility of diffuse co-evolution. In short, we simply do not currently have the necessary data to test this hypothesis, demonstrating the need for careful future research.

#### BROMELIAD DIVERSIFICATION THROUGH LIMITED POLLEN TRANSFER BY HUMMINGBIRDS

Reduced gene flow between plant populations can lead to speciation (Rieseberg & Willis, 2007). Hummingbirds have been considered to be more efficient long-distance pollen dispersers than insects, specifically bees (Schmidt-Lebuhn *et al.*, 2007; Serrano-Serrano *et al.*, 2017). This conception might be based on the larger size of hummingbirds and their ability to cover large distances, whereas bees mostly forage within a few hundred metres of their nests (Krauss *et al.*, 2017). However, little is known about actual pollen transfer distances by hummingbirds and co-occurring insects. A North American study of three insect- and hummingbird-pollinated plant species did not find significant differences in flight distance between these groups (Waser, 1982). In contrast, a recent study using coloured pollen analogues showed that in the tropical shrub genus *Justicia* L. (Acanthaceae), species pollinated by mostly territorial hummingbirds had significantly shorter pollen dispersal distances than bee-pollinated species (Schmidt-Lebuhn *et al.*, 2019). Furthermore, pollination by long-billed, traplining hummingbirds, which have movement distances of c. 1 km per day, may result in stronger pollen tube growth, higher paternity and thus increased seed set than pollination by territorial hummingbirds (Betts, Hadley & Kress, 2015; Krauss *et al.*, 2017). These studies suggest that the diversification rates of hummingbird-pollinated clades of bromeliads and other plant groups may be influenced by pollen transfer distances (Schmidt-Lebuhn *et al.*, 2007). Pollination mainly by territorial hummingbirds would thus lead to reduced gene flow between populations, and ultimately to allopatric speciation. A similar case

**Table 1.** List of species of Bromeliaceae with information on life form, habit, flower visitors/pollinators, phenology type and references

Species	Life form	Habit	Flower visitors/pollinators	Phenology type	Reference
<i>Aechmea bracteata</i> (Sw.) Griseb.	ep (sa)	ta		ss	22
<i>Aechmea distichantha</i> Lem.	ep, sa, te	ta	Leual, Pheu, Rana, Stla	ss	3, 19
<i>Aechmea lindenii</i> (É.Morren) Baker	sa, te	ta	Amfi, Thgl, Thsp	ss	17
<i>Aechmea magdalenae</i> (André) André ex Baker	te	no	Phsu	ss	20
<i>Aechmea nudicaulis</i> (L.) Griseb.	ep, te	ta	Amfi, Clru, Hycy, Leal, Pheu, Phid, Rana, Stla, Thgl	ss	3, 10, 18, 27
<i>Aechmea organensis</i> Wawra	ep, te	ta	Clru, Thgl	ss*	18
<i>Aechmea ornata</i> (Gaudich.) Baker	ep, te	ta	Pheu, Thgl	ss*	18
<i>Aechmea pectinata</i> Baker	ep, sa, te	ta	Amfi, Rana, Thgl	ss	3, 5
<i>Alcantarea nahoumii</i> (Leme) J.R.Grant	sa	ta	Anni, Chmo, Euma, Flfu, Thgl	ss	31
<i>Ananas ananassoides</i> (Baker) L.B.Sm.	te	no	Amfi, Hych, Thgl	ss*	9, 30
<i>Billbergia amoena</i> (Lodd.) Lindl.	ep, te	ta	Clru, Heau, Pheu	co	18, 19
<i>Billbergia distachia</i> (Vell.) Mez	ep, te	ta	Leal, Pheu	co*	3
<i>Billbergia pyramidalis</i> (Sims) Lindl.	ep, te	ta	Mefu, Pheu, Rana	co	3, 19
<i>Bromelia antiacantha</i> Bertol.	te	no	Amfi, Rana, Thgl	bb	5
<i>Bromelia balansae</i> Mez	te	no	Hych, Pheu	co*	1
<i>Canistropsis seidelii</i> (L.B.Sm.) Leme	ep, te	ta	Rana	ss*	3
<i>Canistrum aurantiacum</i> É.Morren	ep, te	ta	Chau, Glhi, Phpr, Phru, Thwa	ss	29
<i>Canistrum cyathiforme</i> (Vell.) Mez	ep	ta	Amve, Leal, Pheu, Thgl	ss*	15
<i>Deuterocohnia longipetala</i> (Baker) Mez	sa, te	no	Clau	co*	2
<i>Dyckia brevifolia</i> Baker	sa	no	Amve	co	25
<i>Dyckia floribunda</i> Griseb.	sa, te	no	Chau, Sasp	co*	2
<i>Dyckia pseudococcinea</i> L.B.Sm.	sa, te	no	Amfi	ss	19
<i>Dyckia velascana</i> Mez	sa, te	no	Sasp, Clau	co*	2
<i>Edmundoa ambigua</i> (Wand. & Leme) Leme	ep, te	ta	Pheu	ss*	3
<i>Encholirium heloisae</i> (L.B.Sm.) Forzza & Wand.	sa, te	no	Ausc, Chlu, Cose, Euma, Phpr	co	6
<i>Encholirium spectabile</i> Mart. ex Schult. & Schult.f.	te	no	Chlu, Euma, Hesa	co*	16
<i>Encholirium vogelii</i> Rauh	sa, te	no	Ausc, Cose, Euma, Phpr	co	6
<i>Guzmania</i> aff. <i>killipiana</i> L.B.Sm.	ep	ta	Myfa	ss	7
<i>Guzmania besseae</i> H.Luther	ep	ta	Cocoe	ss	7
<i>Guzmania confusa</i> L.B.Sm. var. <i>foetida</i> Rauh	ep	ta	Adme	ss	7
<i>Guzmania coriostachya</i> (Griseb.) Mez	ep	ta	Coth, Coto, Heas, Ocu, Chmu	ss	7
<i>Guzmania gloriosa</i> (André) André ex Mez	ep	ta	Cocoe	ss	7
<i>Guzmania paniculata</i> Mez	ep	ta	Boma	ss	7
<i>Hohenbergia</i> cf. <i>catingae</i> Ule	te	ta	Chlu	ss*	16
<i>Neoregelia compacta</i> (Mez) L.B.Sm.	ep, sa, te	ta	Amfi, Chau	ss*	19
<i>Neoregelia cruenta</i> (Graham) L.B.Sm.	ep, te	ta	Amfi	ss*	10
<i>Neoregelia johannis</i> (Carrière) L.B.Sm.	ep, te	ta	Rana	ss*	3
<i>Neoregelia marmorata</i> (Baker) L.B.Sm.	sa, te	ta	Chau	ss*	19
<i>Nidularium angustibracteatum</i> Leme	ep	ta	Pheu	ss*	3
<i>Nidularium billbergioides</i> (Schult.f.) L.B.Sm.	ep, te	ta	Chau	ss*	19
<i>Nidularium campo-alegrensis</i> Leme	te	ta	Pheu	ss*	15
<i>Nidularium innocentii</i> Lem.	ep, te	ta	Pheu, Rana	ss*	3, 18
<i>Nidularium marigoii</i> Leme	ep, te	ta	Rana	ss*	3
<i>Nidularium procerum</i> Lindm.	ep, te	ta	Rana, Thgl	ss*	3



Table 1. Continued

Species	Life form	Habit	Flower visitors/pollinators	Phenology type	Reference
<i>Nidularium rubens</i> Mez	ep, te	ta	Pheu	ss*	18
<i>Nidularium scheremetiewii</i> Regel	ep, te	ta	Heau	ss*	19
<i>Pitcairnia angustifolia</i> Aiton	te	no	Chma	ss*	11
<i>Pitcairnia corcovadensis</i> Wawra	sa	no		ss	32
<i>Pitcairnia flammea</i> Lindl.	sa	no	Amfl, Mefu, Pheu, Phpr, Thgl	co	19, 32
<i>Pitcairnia riparia</i> Mez	ep	no	Adme, Heam	ss	7
<i>Pitcairnia</i> sp.	ep	no	Adme, Heam	ss	7
<i>Puya alpestris</i> (Poepp.) Gay	te	no	Anpa, Cucu, Didi, Elal, Mith, Pagi, Zoca	co*	14
<i>Puya chilensis</i> Molina	te	no	Agli, Mith, Stlo, Tufa, Zoca	co*	14
<i>Puya coerulea</i> Lindl.	te	no	Cucu, Orle, Pagi	co*	14
<i>Puya hamata</i> L.B.Sm.	te	no	Agcu, Chher, Ores, Ptcy	co*	12
<i>Puya nitida</i> Mez	te	no	Chhet, Dihu, Erve, Ptcy	co*	23
<i>Puya raimondii</i> Harms	te	no	Cocor, Ores, Pagi, Phpu	bb*	14
<i>Puya spathacea</i> (Griseb.) Mez	sa, te	no	Clau, Sasp	co*	2
<i>Puya trianae</i> Baker	te	no	Chhe, Levi, Ptcy	co*	23
<i>Puya venusta</i> (Baker) Phil.	te	no	Orle, Pagi, Phga	co*	14
<i>Quesnelia arvensis</i> (Vell.) Mez	sa, te	ta	Amfi, Chau, Rana, Thgl	ss	3, 19, 26
<i>Quesnelia augusto-coburgii</i> Wawra	ep, sa	ta	Leal, Phpe	co	19
<i>Quesnelia humilis</i> Mez	ep, te	ta	Hycy, Rana, Thgl	co*	3
<i>Quesnelia lateralis</i> Wawra	(ep) sa, te	ta		co	19
<i>Quesnelia liboniana</i> (De Jonghe) Mez	ep	ta	Clru, Phsp	ss*	19
<i>Quesnelia marmorata</i> (Lem.) Read	ep	ta	Phru	co	3, 19
<i>Quesnelia quesneliana</i> (Brongn.) L.B.Sm.	ep	ta	Amfi, Phid	co*	10
<i>Racinaea seemannii</i> (Baker) M.A.Spencer & L.B.Sm.	ep	ta	Myfa	ss	7
<i>Racinaea tetrantha</i> (Ruiz & Pav.) M.A.Spencer & L.B.Sm.	ep	ta	Adme, Coto, Heam	ss	7
<i>Racinaea undulifolia</i> (Mez) H.Luther	ep	ta	Adme, Ocun	ss	7
<i>Tillandsia barbeyana</i> Wittm.	ep	ta	Coto, Heam, Ocun	ss	7
<i>Tillandsia complanata</i> Benth.	ep	ta	Adme, Heam, Ocun	ss	7
<i>Tillandsia confinis</i> L.B.Sm.	ep	ta	Cocoe, Coto, Heam, Phsy	ss	7
<i>Tillandsia gardneri</i> Lindl.	ep	ta	Pheu, Phru, Phid	ss*	3, 10
<i>Tillandsia geminiflora</i> Brongn.	ep	ta	Amve, Chau, Clru, Leal, Stla, Pheu, Thgl	ss*	3, 18
<i>Tillandsia lorentziana</i> Griseb.	ep, sa	no	Clau	ss*	2
<i>Tillandsia prodigiosa</i> (Lem.) Baker	ep	ta		co	8
<i>Tillandsia stricta</i> Sol. ex Sims	ep, sa	no	Pheu, Clru, Leal, Stla, Thgl, Chau, Amve	co	3, 10, 18, 19
<i>Tillandsia tenuifolia</i> L.	ep	no	Leal	co*	3, 18
<i>Tillandsia truncata</i> L.B.Sm.	ep	ta	Chmu	ss	7
<i>Vriesea altodaserrae</i> L.B.Sm.	ep	ta	Amfi, Amve, Anni, Chau, Clru, Leal, Mefu, Pheu, Rana, Thgl	ss	3, 15, 18, 21
<i>Vriesea altomacaensis</i> Costa	te	ta	Clru, Leal, Stla	ss	19
<i>Vriesea appendiculata</i> (L.B.Sm.) L.B.Sm.	ep	ta	Agki, Coth, Coto, Heam, Phsy	ss	7
<i>Vriesea carinata</i> Wawra	ep, te	ta	Pheu	ss*	18
<i>Vriesea ensiformis</i> (Vell.) Beer	ep	ta	Rana, Mefu, Leal, Amfi	ss	3, 19
<i>Vriesea flammea</i> L.B.Sm.	ep, sa	ta	Clru, Leal, Pheu, Rana	ss	3, 18
<i>Vriesea friburgensis</i> Mez	ep, te	ta	Amfl, Cocoe, Thgl	ss	2, 28
<i>Vriesea guttata</i> Linden & André	ep	ta	Pheu	ss*	15
<i>Vriesea haematina</i> L.B.Sm.	ep	ta	Clru, Leal, Stla	ss	18
<i>Vriesea heterostachys</i> (Baker) L.B. Sm.	ep	ta	Leal, Pheu	ss	15, 19

Table 1. Continued

Species	Life form	Habit	Flower visitors/pollinators	Phenology type	Reference
<i>Vriesea incurva</i> (Griseb.) Read	ep	ta	Haau, Heam	ss	7
<i>Vriesea incurvata</i> Gaudich.	ep	ta	Amfi, Mefu, Pheu	ss	3, 18, 19
<i>Vriesea morreniana</i> É.Morren	ep	ta	Rana	ss*	3
<i>Vriesea neoglutinosa</i> Mez	ep, sa	ta	Amfi, Chau	ss	9, 19
<i>Vriesea paraibica</i> Wawra	ep	ta		ss	19
<i>Vriesea philippocoburgii</i> Wawra	ep, te	ta	Amfi, Thgl	ss*	3, 18
<i>Vriesea procera</i> Mez	ep (te)	ta	Phru, Thgl	ss*	3
<i>Vriesea psittacina</i> (Hooker) Lindl.	ep	ta	Mefu, Phpe	ss	19
<i>Vriesea rodigasiana</i> É.Morren	ep	ta	Amve, Rana, Thgl	ss	3, 24
<i>Vriesea rubrobracteata</i> Rauh	ep	ta	Coto	ss	7
<i>Vriesea scalaris</i> É.Morren	ep	ta	Rana	ss*	3
<i>Vriesea sceptrum</i> Mez	ep, te	ta	Leal, Pheu	ss*	3
<i>Vriesea sparsiflora</i> L.B.Sm.	ep (te)	ta	Clru, Leal, Stla	ss	19
<i>Vriesea vagans</i> (L.B.Sm) L.B.Sm	ep	ta		ss*	19
<i>Wittrockia cyathiformis</i> (Vell.) Leme	ep, te	ta	Leal, Pheu	ss*	3

Life form [ep: epiphytic; sa: saxicolous; te: terrestrial (life form occurring occasionally)], habit (ta: water-impounding tank; no: tank-less rosette), flower visitors/pollinators (Adme: *Adelomyia melanogenys*; Agcu: *Aglaeactis cupripennis*; Agki: *Agelaiocercus kingi*; Agli: *Agriornis livida*; Amfi: *Amazilia fimbriata*; Amve: *Amazilia versicolor*; Anpa: *Anairetes parulus*; Anni: *Anthracothonax nigricollis*; Ausc: *Augastes scutatus*; Boma: *Boissonneaua matthewsii*; Chmu: *Chaetocercus mulsant*; Chher: *Chalcostigma herrani*; Chhet: *Chalcostigma heteropogon*; Chau: *Chlorostilbon aureiventris*; Chlu: *Chlorostilbon lucidus*; Chma: *Chlorostilbon maugaeus*; Chmo: *Chrysolampis mosquitus*; Clru: *Clytolaema rubricauda*; Cocoe: *Coeligena coeligena*; Coto: *Coeligena torquata*; Cocor: *Colibri coruscans*; Cose: *Colibri serrirostris*; Coth: *Colibri thalassinus*; Cucu: *Curaeus curaeus*; Dihu: *Diglossa humeralis*; Didi: *Diuca diuca*; Elal: *Elaenia albiceps*; Erve: *Eriocnemis vestita*; Euma: *Eupetomena macroura*; Flfu: *Florisuga fusca*; Glhi: *Glaucis hirsuta*; Haau: *Haplophadia aureliae*; Heam: *Helianthus amethysticollis*; Hesq: *Heliothryx squamosus*; Heau: *Heliothryx aurita*; Hych: *Hylocharis chrysura*; Hycy: *Hylocharis cyanus*; Levi: *Lesbia victoriae*; Leal: *Leucochloris albicollis*; Mefu: *Melanotrochilus fuscus*; Mith: *Mimus thenca*; Myfa: *Myrtis fanny*; Ocu: *Ocreatus underwoodii*; Ores: *Oreotrochilus estella*; Orle: *Oreotrochilus leucopleurus*; Pagi: *Patagona gigas*; Phid: *Phaethon idaliae*; Pheu: *Phaethornis eurynome*; Phpr: *Phaethornis pretrei*; Phru: *Phaethornis ruber*; Phsy: *Phaethornis symatophorus*; Phsp: *Phaethornis sp.*; Phsu: *Phaethornis superciliosus*; Phga: *Phrygilus gagi*; Phpu: *Phrygilus punensis*; Ptey: *Pterophanes cyanocephalus*; Rana: *Ramphodon naevius*; Sasp: *Sappho sparganura*; Stla: *Stephanoxis lalandi*; Stlo: *Sturnella loyca*; Thgl: *Thalurania glaucopis*; Thsp: *Thalurania sp.*; Thwa: *Thalurania watertonii*; Tufa: *Turdus falcklandii*; Zoca: *Zonotrichia capensis*), phenology type (ss: steady state; co: cornucopia; bb: big bang; \*deduced), references (1: Araujo & Sazima, 2003; 2: Bernardello, Galetto & Juliani, 1991; 3: Buzato *et al.*, 2000; 4: Canela & Sazima, 2003; 5: Canela & Sazima, 2005; 6: Christiani *et al.*, 2013; 7: Dziedziuch *et al.*, 2003; 8: Escobedo-Sarti, 2007; 9: Ferreira, Maruyama & Oliveira, 2016; 10: Fonseca *et al.*, 2015; 11: Fumero-Caba & Melendez-Ackerman, 2007; 12: García-Meneses & Ramsay, 2012; 13: García-Meneses & Ramsay, 2012; 14: Hornung *et al.*, 2013; 15: Kaehler *et al.*, 2005; 16: Las Casas, Azevedo-Júnior & Dias-Filho, 2012; 17: Lenzi, Zarur de Matos & Orth, 2006; 18: Machado & Semir, 2006; 19: Martinelli, 1994; 20: Murawski & Hamrick, 1990; 21: Nunes *et al.*, 2018; 22: Pool-Chalée *et al.*, 2018; 23: Restrepo-Chica & Bonilla-Gómez, 2017; 24: Rocca & Sazima, 2013; 25: Rogalski *et al.*, 2009; 26: Sazima *et al.*, 1995; 27: Schmid *et al.*, 2011a; 28: Schmid *et al.*, 2011b; 29: Siqueira Filho & Machado, 2001; 30: Stahl *et al.*, 2017; 31: Souza *et al.*, 2017; 32: Wendt *et al.*, 2002)

for speciation via limited gene flow has been made for limited fruit dispersal by territorial birds in the understorey of tropical forests (Givnish, 2010; Theim, Shirk & Givnish, 2014). In contrast, speciation in bromeliads pollinated by traplining hummingbirds may be mostly induced by other factors, such as geographical isolation, or changes in flower phenology or in reproductive system. Again, these hypotheses remain to be tested.

#### BROMELIAD DIVERSIFICATION AS A RESULT OF DIFFERENT FLOWERING PHENOLOGY TYPES

In general, Bromeliaceae include examples of three different flowering phenology types (Gentry, 1974): 'steady state', with plants producing relatively few flowers per day over extended periods of several

months or more; 'cornucopia', with the plants producing a large number of flowers daily over a time span of several weeks; and 'big-bang', in which the plants in an area have a precise synchronization so that they come into flower for a relatively brief spell of a few days (Martinelli, 1994). The steady state flowering strategy has been found to be the most common in ornithophilous (but also chiropterophilous) species of bromeliads (e.g. Martinelli, 1994; Sazima, Buzato & Sazima, 1995; Buzato *et al.*, 2000; Dziedziuch *et al.*, 2003; Aguilar-Rodríguez *et al.*, 2019), whereas the cornucopia pattern has been reported in a lower number of species (Martinelli, 1994; Wendt *et al.*, 2002; Rogalski *et al.*, 2009); 'big-bang' seems to be rare and to our knowledge is restricted to species of *Bromelia* and *Puya* (Canela & Sazima, 2005).

To gather information about ornithophilous bromeliads, we conducted an extensive literature review utilizing common scientific databases including

ISI Web of Science and the Scientific Electronic Library Online (SciELO) and internet search engines such as Google Scholar, using operators such as 'Bromeliaceae', 'bromeliads', 'hummingbird', 'pollination' and/or 'ornithophily' in the title, keywords or abstract. In addition, we searched the grey literature (e.g. theses) and cross-checked references between studies. We found 32 relevant publications including data on life form, habit and/or flowering phenology types for mainly hummingbird-visited or hummingbird-pollinated bromeliads together with a classification based on deductions from floral information and images of flowering inflorescences (e.g. Smith & Downs, 1974, 1977, 1979; Rauh, 1990; Florida Council of Bromeliad Societies Bromeliad Photo Index, 2018; Flora do Brasil, 2020) of species for which no such information was available (Table 1). This review revealed that from a total of 105 bromeliad species in 22 genera, 75 show steady state flowering, whereas 28 have a cornucopia and only two a big-bang pattern. Considering the three main bromeliad life forms (epiphytic, saxicolous and terrestrial; in many cases, a species belongs to two or all of these) in relation to the flowering phenology types (Fig. 4A), most species with steady state flowering are epiphytic (57%), whereas only 11% are saxicolous and 32% are terrestrial. In contrast, only a minority of the species with cornucopia flowering are epiphytic (26%) or saxicolous (26%), whereas the majority (48%) are terrestrial. Regarding the habit associated with water availability, i.e. open water-impounding tank rosettes of mainly epiphytic or saxicolous plants vs. often xeromorphic tank-less rosettes of ground-rooting plants (Fig. 4B), 88% of the tank bromeliads showed steady state flowering, whereas in tank-less plants only 29% of the species had this pattern, but 71% showed cornucopia flowering.

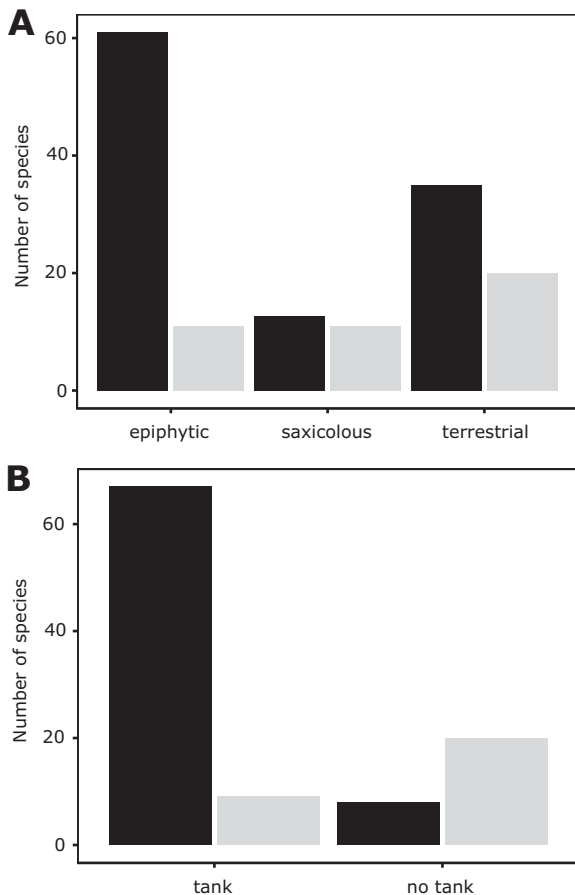
The steady state flowering strategy has been associated with so-called traplining hummingbirds, which forage along a sequence of plants over tracks c. 1 km in length (Martinelli, 1994). Traplining hummingbirds prefer plants that offer regular and constant resources (Wolf, Stiles & Hainsworth, 1976), favouring long flowering periods among the visited plants (Stiles, 1978; Canela & Sazima, 2003). Such steady state-flowering bromeliads generally have a flowering period of several weeks and on average open one to few flowers per day, such as observed in various *Vriesea* spp. of the Atlantic Rainforest (Martinelli, 1994; Schmid *et al.*, 2011b; Rocca & Sazima, 2013). Single individuals of large saxicolous *Tillandsia* spp. may even flower for over a year in cultivation (M. Kessler, pers. obs.). Such visiting behaviour favours fruit set through xenogamy (Feinsinger 1978). Overall, this phenological type leads to a situation in which pollen is likely to be transported over fairly large distances over extended periods of time.

Opposed to this, the cornucopia and big-bang strategies are adapted to mobile hummingbird species that move around searching for abundant nectar sources and often become territorial at highly productive sources. There are large differences in the distance of pollen transfer or pollination efficiency depending whether a plant species is mostly pollinated by territorial or traplining hummingbird species (Linhart, 1973; Murawski & Gilbert, 1986; Maruyama, Justino & Oliveira, 2016). For instance, we conducted opportunistic observations in the Bolivian Andes at a patch of flowering *Puya herzogii* Wittm., which has large inflorescences with dozens of flowers open at the same time and producing large amounts of nectar. Over several days, we saw the presumably same individual hummingbirds foraging and perching in an area of <100 m<sup>2</sup> (M. Kessler, pers. obs.), thus resulting mostly in self-pollination. Also, some hummingbird species behave as intruders on plants defended by the territorial individuals, which may alter pollen dispersal distances of species pollinated by territorial hummingbirds. However, we are not aware of any study documenting the movement patterns of such intruders.

To complicate matters, the hummingbird behaviour (trapliner vs. territorial) may change within the same species depending on factors such as the spatial distribution and population density of the bromeliad species, which, moreover, can be visited by several hummingbird species with different foraging strategies. For example, Araujo & Sazima (2003) observed that *Hylocharis chrysura* is territorial when visiting clumps of the terrestrial species *Bromelia balansae* Mez with cornucopia flowering, whereas in plant species with a low density of flowers, it might show a low-reward trapliner or generalist behaviour. Similarly, the study by Canela & Sazima (2005) of the terrestrial *Bromelia antiacantha* Bertol. with big-bang flowering showed that three hummingbird species (*T. glaucopsis*, *A. fimbriata* and *R. naevius*) acted as 'low-reward trapliners', although *T. glaucopsis* and *A. fimbriata* are typically territorial (Feinsinger & Colwell, 1978). This suggests that *B. antiacantha* was not a sufficiently stable food source over time and/or space to provide advantages to establish territories because their individuals occurred in small distributed groups and its flowering period is short (4–5 days), contributing to the predominance of the traplining behaviour. Other studies showing such shifts in pollinator behaviour include Miller (1988), Buzato *et al.* (2000), Woods & Ramsay (2001), García-Meneses & Ramsay (2012), Rocca & Sazima (2013) and Restrepo-Chica & Bonilla-Gómez (2017).

Analogous to the situation with the hummingbird and bee pollen transfer distances, based on these





**Figure 4.** A, number of bromeliad species with epiphytic, saxicolous or terrestrial growth and steady state (black) or cornucopia flowering (grey). If a species grows, for example, as terrestrial and saxicolous we counted it for both categories. B, number of bromeliad species with water-impounding tank or tank-less rosettes showing steady state (black) or cornucopia flowering (grey).

observations, we propose that steady state-flowering bromeliads may have longer pollen dispersal distances than those with cornucopia and big-bang syndromes. In cornucopia and big-bang bromeliads, this would lead to stronger genetic differentiation between populations and accordingly higher rates of allopatric speciation. The steady state syndrome is commonly found in epiphytes (Fig. 4A). This may be because epiphytic plants are generally water-limited (Givnish *et al.*, 2014), so that they are also limited in the amount of nectar production. Epiphytic bromeliads have larger distributional ranges than terrestrial and saxicolous species (Kessler, 2002), which may be partly a result of this increased gene flow, although many other factors are certainly involved as well.

#### THE BROMELIAD DIVERSIFICATION – HUMMINGBIRD POLLINATION RELATIONSHIP AS AN INDIRECT EFFECT

So far, we have considered that the observed increased diversification rate of hummingbird-pollinated bromeliad clades is the result of a direct causal relationship. However, the causality may be more indirect. As discussed above, hummingbird pollination is most common in high-elevation ecosystems, where insects and bats are physiologically limited (Kessler & Krömer, 2000; Krömer *et al.*, 2006; Abrahamczyk & Kessler, 2015). Mountains such as the Andes are well known to have exceptional rates of plant diversification even in spore-dispersed plants that are completely independent of pollinators (Testo, Sessa & Barrington, 2019). Such radiations may partly have been driven by adaptive evolution, but they are also largely due to the topographic complexity of the terrain, leading to patchy habitats, isolated plant populations and allopatric speciation (Hughes & Eastwood, 2006; Hoorn *et al.*, 2013; Antonelli, 2015; Quintero & Jetz, 2018). This process has also been suggested for hummingbird-pollinated plants (Givnish *et al.*, 2014; Abrahamczyk & Renner, 2015). Thus, speciation in Bromeliaceae and other plant families may be triggered more by geographical isolation and site adaptations than by hummingbird pollination as such (Jabaily & Sytsma, 2012; Givnish *et al.*, 2014; Krapp *et al.*, 2014). In this situation, hummingbird pollination, as an effective means of pollination in montane habitats, could therefore be interpreted as a promoter of speciation, but not as a mechanism inducing speciation.

#### CONCLUSIONS

Our exploration of the mechanisms leading to hummingbird-pollinated radiations in Bromeliaceae has revealed that the situation is much more complex than commonly depicted. Rather than bromeliad diversification simply being the result of an adaptation to morphologically different hummingbird species, there are several, non-exclusive mechanisms that may increase bromeliad diversification in hummingbird-pollinated clades.

We have differentiated four main types of mechanisms that may lead to high diversification rates of hummingbird-pollinated bromeliad clades: (1) bromeliad speciation through adaptation to different hummingbird species; (2) increased allopatric speciation in hummingbird-pollinated clades due to lower pollen transfer efficiency compared with other pollinators; (3) differential speciation rates

in hummingbird-pollinated clades in dependence of flowering phenology and hummingbird behaviour; and (4) higher speciation rates of bromeliads in montane environments (where hummingbird pollination predominates) due to topographic population fragmentation. To date, none of these hypotheses has been appropriately tested, partly due to a lack of data, but also because research has been focused on documenting the pattern of increased diversification in hummingbird-pollinated clades, implicitly assuming that this supports an underlying mechanism and ignoring the fact that several competing mechanisms might be considered. Also, the covariance of some of these factors, such as bromeliad pollination and high elevation, makes it difficult to separate the effects of these factors (Givnish *et al.*, 2014). Despite these challenges, we hope that the present review increases awareness of the different mechanisms and triggers research aimed at specifically testing and teasing them apart.

Perhaps the main conclusion we can draw from this review is how little we know about the relevant parameters to truly understand how bromeliad diversification is causally linked to hummingbird pollination. Particularly important questions that merit future studies include the following. What is the quantitative contribution of shifts between major pollinator groups (hummingbirds, insects, bats) in driving bromeliad diversification? Can we find any cases where a bromeliad speciation event can be linked to a shift between two hummingbird species with different morphology? What are the levels of gene flow between co-occurring bromeliad species that share the same hummingbird pollinator species and how does this affect the evolution of bromeliad species? Do bromeliad species with different pollinator groups (insects, territorial or traplining hummingbirds) differ in pollen-dispersal distances and how does this affect genetic population differentiation? Are different flowering strategies of bromeliads (steady state, cornucopia, big-bang) correlated with different foraging behaviours of hummingbirds and accordingly with gene flow and genetic population differentiation? Are there different influences of pollen dispersal rates and distances at the level of bromeliad individuals (fitness) as opposed to populations (speciation)? How are all of the above related to a range of environmental factors that may also influence bromeliad diversification rates, such as topography or climate?

Although our review has focused specifically on bromeliads, many of the ideas related to the role of hummingbird pollination and plant diversification are also relevant for other groups of hummingbird-pollinated plants.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

**Table S1.** Pollinator groups of the *Vriesea* radiation from the Atlantic Rainforests of eastern Brazil. The pollination syndrome concept is applied for species without pollinator information from the literature.