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Bat pollination in Bromeliaceae

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ABSTRACT

Background: Chiropterophily encompasses the floral traits by which bats are attracted as the main pollinators. Among the chiropterophilous flowering plants of the New World, Bromeliaceae is one of the most ecologically important families; however, information about the chiropterophilous interaction in this family is still scarce.

Aims: We present a comprehensive review of bat pollination in bromeliads, covering floral traits, rewards offered to pollinators, floral attractants and the identity of visiting bat species.

Methods: We discuss traits shared among chiropterophilous bromeliads and present general trends in an evolutionary context. We constructed a phylogenetic tree to elucidate the ancestral pollination syndromes of the 42 extant bromeliad species (ca. 1% of total) known to be bat-pollinated.

Results: Most of the species within the ten genera reported belong to the Tillandsioideae subfamily, with three genera appearing to be exclusively bat-pollinated. Floral visitors include 19 bat species of 11 genera from the Phyllostomidae.

Conclusions: Our analysis indicated that chiropterophilous floral features originated multiple times in bromeliad evolution, most probably from ornithophilous. The evidence for floral traits associated with bat pollination and the chiropterophilous syndrome presented by certain Bromeliaceae indicate the important role played by bats in the evolution of this plant family.

Introduction

The floral syndrome concept has been criticised for failing to consider the complete diversity of floral traits, as well as the entire spectrum of floral visitors (Ollerton et al. 2009). Nevertheless, it remains a useful tool for predicting the main pollinators of plants, especially in tropical regions (Rosas-Guerrero et al. 2014; Ashworth et al. 2015 and references therein). This seems to be the case for bat-pollinated plant species, which tend to possess flowers that are morphologically distinct from those of other pollination guilds (von Helversen 1993; Fleming and Muchhala 2008).

Chiropterophily, or the syndrome of pollination via interaction with bats, encompasses the floral traits (e.g. size, shape, colour, nectar characteristics and scent) shared by many angiosperms in order to attract bats (Mammalia: Chiroptera) as their main pollinators (Tschapka and Dressler 2002; von Helversen and Winter 2003; Fleming et al. 2009). Bat pollination occurs in the tropical and subtropical regions of both the Old and New World and is found in more than

500 plant species (Dobat and Peikert-Holle 1985; Fleming et al. 2009). The chiropterophily syndrome may encompass the following characteristics (van der Pijl 1961; von Helversen 1993; von Helversen et al. 2000; Tschapka and Dressler 2002; von Helversen and Winter 2003; Krömer et al. 2008; Rosas-Guerrero et al. 2014): (1) nocturnal or crepuscular anthesis; (2) pale or dullish colours in the perianth (predominantly white, pale green, yellow) without nectar lines; (3) flagelliflory (flowers suspended on long stalks, situated at a distance from the branches and leaves) and/or cauliflory (flowers emerging directly from the tree trunk or from larger branches); (4) tubular, zygomorphic or radially symmetrical flowers that fit the snout of the bat like a 'mask', and also 'brush-type' flowers/inflorescences with protruding stamens; (5) large and sturdy flowers; (6) musty or unpleasant odour, described as garlic- or onion-like; (7) relatively large amounts of dilute nectar with an average sugar concentration of *ca.* 17%, and a predominantly hexose-rich composition (e.g. low sucrose content, high levels of glucose and fructose); (8) large quantities of

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pollen and, in some cases, (9) edible plant tissues as rewards (see Cox 1984; Cunningham 1995). However, these characteristics are highly variable among plant families and some of the allegedly chiropterophilous traits (such as nocturnal anthesis) are not exclusive to plants pollinated by bats. A possible explanation for this is that bats present relatively low floral constancy, so a bat can visit flowers of many species in a single night and will thus frequently deliver mixed pollen loads to receptive stigmas (Fleming et al. 2005; Muchhala et al. 2008; but see evidence for differential pollen placement by bats in Muchhala and Thomson 2012; Stewart and Dudash 2016). In this sense, most bat-pollinated plants have evolved as a pollination-guild, comprising non-related species that share a pollinator with similar behaviour and morphology (Muchhala and Jarrín-V 2002) rather than being specialised to one bat species pollinating only one plant species (but see *Centropogon nigricans* and the bat *Anoura fistulata*; Muchhala et al. 2005; Muchhala and Thomson 2009).

The study of bat-pollination has developed considerably since the early observations of Moseley (1870) and Burck (1892). The beginning of formal studies dates back to the 1930s and 1960s (e.g. Porsch 1932 or Vogel 1958, 1969; see also van del Pijl 1961). Classic studies by Faegri and van der Pijl (1979) and Dobat and Peikert-Holle (1985) then provided detailed information about the chiropterophilous syndrome and confirmed a number of bat-pollinated plants, to which other examples have since been added (e.g. Fleming et al. 2009; Geiselman and Defex 2015).

The Bromeliaceae is one of the most frequently reported bat-pollinated plant families (von Helversen 1993; Fleming et al. 2009). It includes more than 3500 herbaceous species from 70 genera (Barfuss et al. 2016; Gouda et al. 2017). The specialised nectarivorous bats responsible for most reports of bat-pollination in the Neotropics are found within the subfamilies Glossophaginae and Lonchophyllinae, among the highly diverse leaf-nosed bats (Phyllostomidae). These bats comprise 20 genera and more than 50 species (Simmons 2005; Mantilla-Meluk and Baker 2010; Bolzan et al. 2015; Moratelli and Dias 2015; Cirranello et al. 2016).

Pollination by vertebrates occurs within the Bromeliaceae more frequently than insect pollination (Benzing 2000; Kessler and Krömer 2000; Canela and Sazima 2005; Krömer et al. 2006) and some species, especially among the Tillandsioideae and Bromelioideae subfamilies, present a mixed pollination system (Benzing 2000; Givnish et al. 2014). Bats

are the second most common vertebrate pollinators of the Bromeliaceae, more frequently reported than passerine birds or opossums, and surpassed only by hummingbirds (Trochilidae) (Martinelli 1994, 1997; Kessler and Krömer 2000; Araujo et al. 2004; Canela and Sazima 2005; Hornung-Leoni and Sosa 2006; Krömer et al. 2006; Queiroz et al. 2016). Most of our current knowledge of bat-pollinated bromeliads, defined as species in which bats perform most of the legitimate visits to the flowers, comes from opportunistic observations. Comprehensive and quantitative information remains scarce, and a detailed understanding of the reproductive biology exists for only a few species (e.g. *Pitcairnia albiflos, Pseudalcantarea macropetala, Werauhia gladioliflora*; Aguilar-Rodríguez et al. 2014; Wendt et al. 2001; Cascante-Marín et al. 2005; Tschapka and von Helversen 2007). Variation in floral adaptations exhibited by Bromeliaceae probably accounts for their adaptability in terms of changing traits associated with different pollinators and reproductive systems, even between closely related species (Gardner 1986; Varadarajan and Brown 1988; Benzing 2000; Givnish et al. 2014).

To consolidate the rather scattered information currently available, we present a comprehensive review based on all available reports of bat pollination in the Bromeliaceae, including the identity of bat species involved where available. We obtained information about chiropterophilous bromeliads from an extensive review of the available literature, as well as common scientific databases including ISI Web of Science, SciELO and Redalyc and internet search engines such as Google Scholar, using operators such as 'chiropterophily' and 'bromeliads' or 'Bromeliaceae'; 'bat-pollination' and 'Anoura', 'Glossophaga' and 'Lonchophylla'; 'Alcantarea', 'Encholirium', 'Pitcairnia', 'Puya', 'Vriesea' and 'Werauhia'', either in the title, keywords or abstract. In addition, we searched the grey literature (e.g. theses) and cross-checked references between studies, including those provided in Fleming et al. (2009) and Geiselman and Defex (2015), as well as asking certain authors to suggest publications related to the topic (see Acknowledgements). Furthermore, in order to improve our understanding of the evolution of chiropterophily in the Bromeliaceae, we constructed a phylogenetic tree for the family, based on chloroplast (cp) DNA sequence variation, and used this tree as a means to examine the origin of chiropterophily in different clades of the family and to determine which pollination systems might be ancestral across these clades.

We summarise and discuss some of the traits that characterise chiropterophily within bromeliads, presenting an overview of documented bat-pollinated species and their geographic distributions. Finally, we highlight some additional bromeliad species that appear to exhibit the chiropterophilous syndrome and which may also therefore be pollinated by bats.

Studies of bat-pollinated bromeliads

Following early comments about chiropterophilous floral traits in the bromeliad family by Müller (1897) and Porsch (1932, 1934)), initial field observations were reported by Vogel (1969), with more detailed studies conducted in the 1990s (*e.g.* Martinelli 1994, 1997; Sazima et al. 1999). Bromeliads with apparently chiropterophilous flowers are most commonly found in wet lowland forests (Kessler and Krömer 2000; Fleming et al. 2005, 2009), where the diversity of flower-visiting bats is also highest. However, this contrasts with the diversity of confirmed bat-pollinated bromeliads, which peaks at high elevations such as in the humid montane forests of the Andean region (Benzing 2000; Givnish et al. 2011). This apparent contradiction might be due to sampling bias, with researchers focusing on few and frequently (or recurrently) studied regions. Only a handful of studies cover large study areas or a broad altitudinal range (*e.g.* Martinelli 1994, 1997; Sazima et al. 1999; Kessler and Krömer 2000; Krömer et al. 2006). Lowland records come from Brazilian *Vriesea* (5–500 m asl; Martinelli 1994; 1997; Sazima et al. 1995, 1999) and Costa Rican *Werauhia* (40 m; Tschapka and von Helversen 2007), while records from high altitude have been obtained from the Bolivian Andes (over 2000 m asl; Kessler and Krömer 2000) and Costa

Rica (3000 m a.s.l.; Salas 1973). Most studies, however, have been conducted at elevations between 1000 and 1600 m a.s.l. (e.g. Sazima et al. 1989; Vogel 1969; Martinelli 1997; Kaehler et al. 2005; Fabián et al. 2008; Aguilar-Rodríguez et al. 2014; Aguilar-Rodríguez et al. 2016; see Tables S2, S3).

Most reports regarding bromeliads with chiropterophilous traits are from species of the subfamily Tillandsioideae in humid montane forests (*i.e.* Aguilar-Rodríguez et al. 2014; Salas 1973; Ramírez and Seres 1994; Sazima et al. 1995; Seres and Ramírez 1995; Martinelli 1997; Muchhala and Jarrín-V 2002; Krömer 2003; Cascante-Marín et al. 2005; Kaehler et al. 2005; Krömer et al. 2005, 2007). Other studies have been conducted in tropical rainforest habitats (*e.g.* von Helversen 1993; Martinelli 1994, 1997; Sazima et al. 1995, 1999; Tschapka and von Helversen 2007), while some have taken place on granitic/rocky outcrops, especially for species of the subfamily Pitcairnioideae (Fischer 1994; Martinelli 1994; Wendt et al. 2001; Christianini et al. 2013), in deserts (Kessler and Krömer 2000), the Brazilian 'cerrado' (Sazima et al. 1989) and in tropical coastal 'restinga' and 'caatinga' (e.g. Fischer 1994; Queiroz et al. 2016) habitats.

According to our literature review, bats have been confirmed as floral visitors for 42 bromeliad species belonging to four of the eight Bromeliaceae subfamilies (Table 1). Most reports suggest that bats are the only probable pollinator of these bromeliads (Table S2). Bat pollination is also suggested for a number of additional species (based on their floral characteristics) and, thus, a total of more than 100 species of bromeliads from 13 genera and five subfamilies (Tables S2, S3) are thought to be bat-pollinated. Most of these bromeliads belong to the genera *Vriesea* and *Werauhia* of the subfamily Tillandsioideae (see

Table 1. The number of bromelia species confirmed or suggested to be bat-pollinated (i.e. with chiropterophilous floral traits) in the literature.

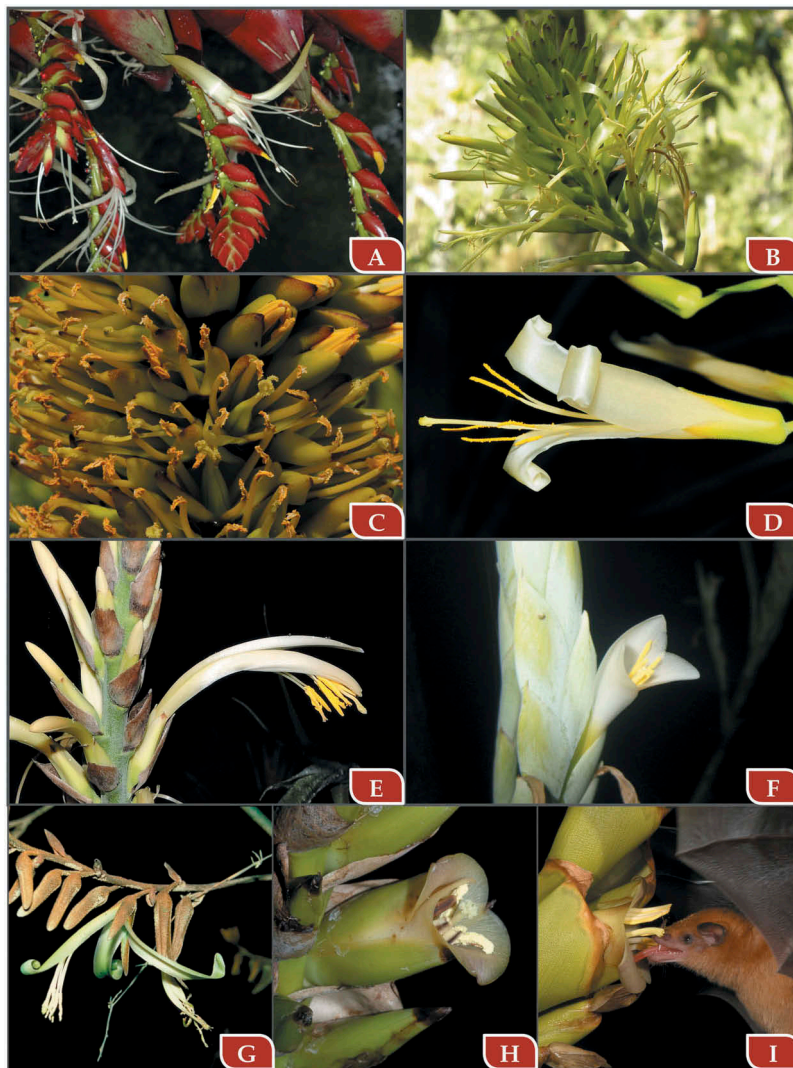| Subfamily	Genus	Confirmed	Putative	Total
Bromelioideae	*Billbergia*	1	1	2
Brocchinioideae	*Brocchinia*	0	1	1
Pitcairnioidea	*Encholirium*	5	0	5
	Pitcairnia	6	10	16
Puyoideae	*Puya*	2	2	4
Tillandsioideae	*Alcantarea*	2	7	9
	Guzmania	0	13	13
	Lutheria	1	0	1
	Pseudalcantarea	3	0	3
	Stigmatodon	0	1	1
	Tillandsia	2	0	2
	Vriesea	13	18	31
	Werauhia	7	28	35
Total		**42**	**81**	**123**

Figure 1. Examples of some bat-pollinated bromeliads: (a) *Alcantarea imperialis*, (b) *Billbergia horrida*, (c) *Encholirium spectabile*, (d) *Pitcairnia albiflos*, (e) *Pitcairnia recurvata*, (f) *Tillandsia heterophylla*, (g) *Puya ferruginea*, (h) *Vriesea longiscapa*, (i), *Werauhia* cf. *sanguinolenta* visited by *Lonchophylla robusta*. Note the pale-colored corolla in all species, and the predominance of the cup-like floral morphology in the members of the Tillandsioideae subfamily (e, f, h, i). Photos: **A, C, D, H**: Elton M. C. Leme. **B**: Ana Paula G. Faria. **E, F, I, J**: Pedro A. Aguilar-Rodríguez. **G**: Thorsten Krömer. **I**: Marco Tschapka.

Figure 1), and most (Table S2) are reported to possess a 'typical' chiropterophilous flower (short, wide and large flowers with pale petals; Figure 1) and are visited mainly by bats of the genus *Anoura*, especially at elevations of 1000 m a.s.l. or higher in tropical montane forests. However, *Alcantarea* and *Encholirium* species possess less restrictive floral morphologies that may also allow visits by non-specialised nectarivorous bats. The dry and hot environment and the reduced presence of bats in habitats where these *Alcantarea* and *Encholirium* species occur might act to promote these more generalist floral features. In addition, these species are frequently locally abundant and may thus serve as an important resource for many different flower-visiting animals, a role analogous to that of the columnar cacti and *Agave* in North America (Fleming 2004), and may therefore receive many secondary pollinators or opportunistic floral visitors.

Even if many bromeliad species have the potential for self-pollination (Matallana et al. 2010: but see *Encholirium* spp.; Christianini et al. 2013; Hmeljevski et al. 2017), pollinators such as far-ranging bats are valuable in terms of promoting gene flow among plant populations (see *Vriesea gigantea* in Palma-Silva et al. 2009). Such occasional cross-pollination by animal pollen vectors, including bats, could be important in terms of mitigating the potential disadvantages of a reproductive system that is based mainly on self-pollination (Shivanna and Tandon 2014), as well as maintaining the boundaries between species (see *Pitcairnia* spp. in Palma-Silva et al. 2011). Nevertheless, Barbará et al. (2007) suggested that

pollinators of *Alcantarea imperialis* (which probably include *Anoura caudifer* and *Artibeus lituratus*; Martinelli 1994) are likely to be insufficient in number to maintain connectivity among populations of this species in the Brazilian 'inselbergs', having found that such populations were highly differentiated genetically. However, further studies are required to confirm this hypothesis. In species that produce many flowers per day, for example *Alcantarea* spp., foraging bats might promote geitonogamy over allogamy. This, in addition to short pollen movement distances between individuals within populations (see discussion in Hmeljevski et al. 2017) could lead to a certain level of inbreeding.

Evolution of bat-pollinated bromeliads

The Bromeliaceae originated in South America in the Guiana shield region over 70–100 million years ago (mya) (Givnish et al. 2007, 2011), but extant lineages did not appear until 15–19 mya. This coincides with the origin of epiphytism in the family and the rise of the Andean mountain chain (Barfuss et al. 2005; Givnish et al. 2007) in the so-called 'bromeliad revolution' (*ca.* 15 mya), when the family spread to other parts of tropical and subtropical America, such as the Northern Andes and Central America (Givnish et al. 2014).

Our understanding of the phylogeny of the Bromeliaceae has changed repeatedly over the last two decades, revealing that some groups formerly defined by floral morphology and habit are in fact paraphyletic (*e.g.* Terry et al. 1997; ; Barfuss et al. 2005; Givnish et al. 2007, 2011, 2014; Escobedo-Sarti et al. 2013; see the revision in Palma-Silva et al. 2016). However, the monophyly of Bromeliaceae has been commonly accepted on the basis of morphological, anatomical and molecular characters (Gilmartin and Brown 1987; Crayn et al. 2004; Givnish et al. 2004, 2007).

The ancestral pollination mode of bromeliads seems to be entomophily, but ornithophilous flowers evolved independently on two occasions: first in the ancestral Tillandsioideae (*ca.* 15.4 mya) and secondly, in the common ancestor of Bromelioideae/Pitcairnioideae/Puyoideae (*ca.* 14.4 mya; Givnish et al. 2007, 2014).

Within the family, there are more bromeliads with ornithophilous than with chiropterophilous characters (60–80% *vs.* 10–20%; see Martinelli 1994, 1997; Sazima et al. 1999; Kessler and Krömer 2000; Araujo et al. 2004). The characters of bird pollination include red floral bracts, showy but small flowers and anthers,

a tube-like purple or yellow corolla and diurnal anthesis. Ornithophily seems to be the main pollination mode within all genera, including the allegedly chiropterophilous bromeliads (Givnish et al. 2014; Figure 2), except for the genera *Encholirium* (Givnish et al. 2007; but see *Encholirium heloisae*; Christianini et al. 2013) and *Werauhia* (Grant 1995). The clades comprising the hummingbird-pollinated species are three to five times richer in species.

Ornithophilous bromeliad lineages have higher rates of diversification than species that possess floral traits associated with other syndromes, as demonstrated by Givnish et al. (2014). This might be a result of the synergy between 1) the occurrence in humid montane habitats, which 2) favours epiphytism, and 3) having a water-holding 'tank-like' body (phytotelma), all three of which promoted the development of avian pollination (Givnish et al. 2014).

It is noteworthy that the putative pollination syndromes of bromeliad species included in phylogenetic analyses are not always mentioned (see Givnish et al. 2014 as an exception), and where they are, most species are reported as bird-pollinated, leading to a deficit of species with other pollination syndromes.

To examine the evolution of chiropterophylous bromeliad species in more detail, we generated a phylogenetic tree of bromeliads and mapped the pollination syndromes of these species on to the tree. For this purpose, we modified the cpDNA sequence super-matrix used in Escobedo-Sarti et al. (2013) with additional sequences downloaded from GenBank and selected a wide spectrum of bromeliad species with different pollination syndromes, including more chiropterophilous species (totalling 41) than in previous phylogenetic studies of the family. All eight subfamilies of Bromeliaceae (Tillandsioideae, Bromelioideae, Brocchinioideae, Lindmanioideae, Hechtioideae, Puyoideae, Navioideae and Pitcairnioidea s.str.) proposed by Givnish et al. (2007), and which are mainly characterised by molecular data and the morphology of flowers, fruits and seeds (Givnish et al. 2007, 2011), were represented in the analysis. The final matrix included 136 taxa and 9049 characters (*ca.* 6.13% of gaps, with most taxa having complete sequences for all cpDNA regions), based on the regions: *atpB-rbcL, ndhF, psbA-trnH, rpl32-trnL, rps16, trnK-matK* and *trnL-F* (see Table S1 for vouchers of all sequences). In this matrix, 135 species belong to the Bromeliaceae, while *Rapatea paludosa* (Rapateaceae) was selected as an outgroup (see Givnish et al. 2007, 2011, 2014).
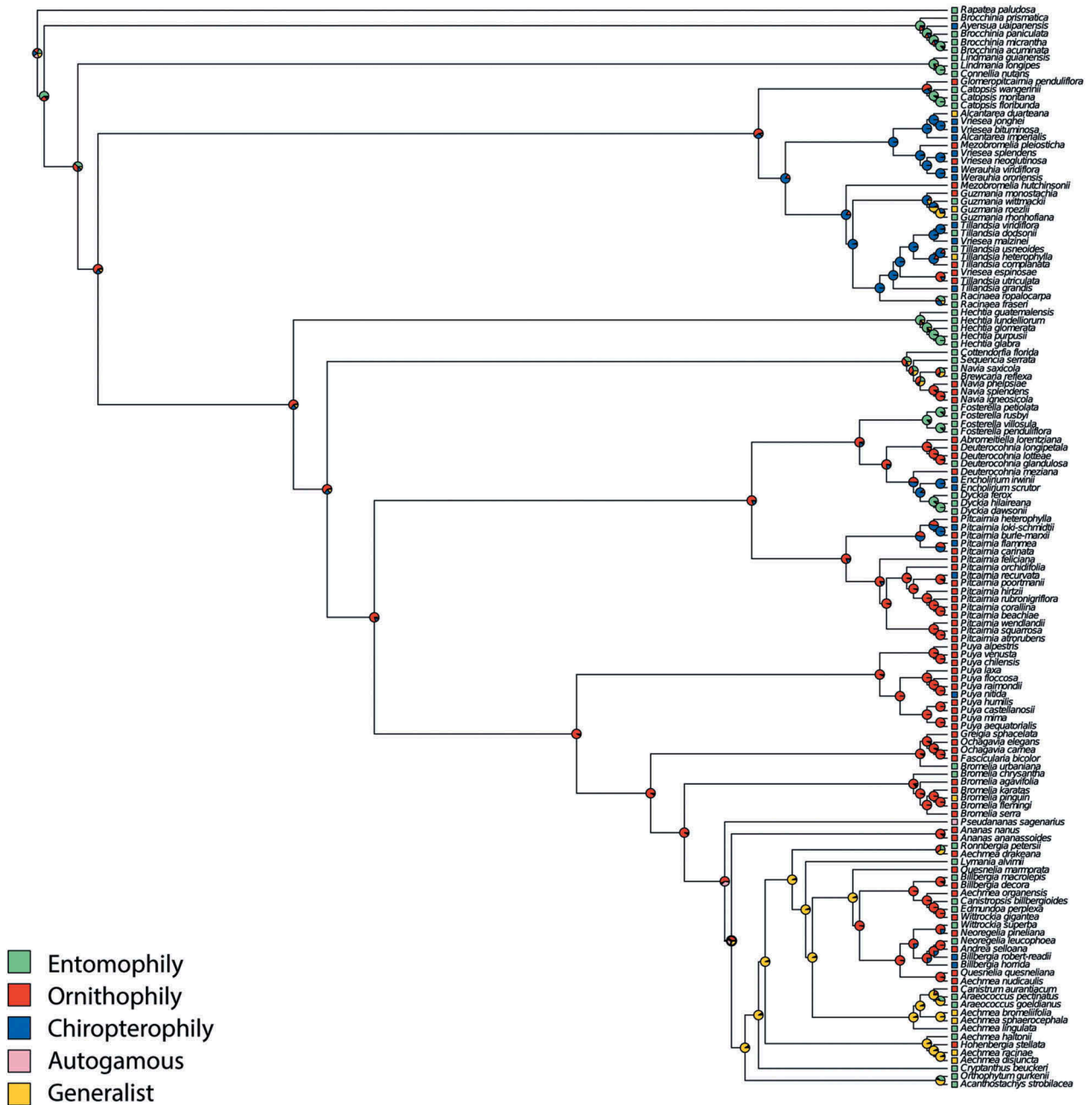
Figure 2. Phylogenetic tree of bromeliads and their pollination syndromes. Different colours on the nodes indicate different pollination syndromes (green: entomophily, red: ornithophily, blue: chiropterophily, pink autogamous, yellow: generalist pollination). Notes: Alcantarea duarteana is not mentioned in the literature as bat-pollinated, but we consider that it possible is; however, since Siqueira Filho (2003) suggested also moth-pollination within the genus, we provisionally refer to it as bimodal. Tillandsia malzinei is referred as a species with chiropterophilous flowers; it was considered a member of the former Vriesea subg. Xiphion (currently, the accepted name would be sect. Synandra; see Barfuss et al. 2016). We describe Tillandsia heterophylla with a bimodal pollination syndrome since diurnal floral visitors could serve as pollinators, even if most of the visits are by bats (Aguilar-Rodríguez et al. 2016). The form of Pitcairnia flammea represented in this figure with chiropter-ophilous floral traits refers only to P. flammea var. pallida.

We aligned sequences of the regions using Muscle (Edgar 2004) and analysed the data with JModelTest 2.7.1 in order to estimate the evolutionary model (Darriba et al. 2012). The best-fitting model for the regions was GTR+I + G. We concatenated the data in a supermatrix that was analysed in GARLI (Zwickl 2006) on the CIPRES Science Gateway platform (Miller et al. 2010). We used independent models among regions, and additionally used the phylogenetic tree of Escobedo-Sarti et al. (2013) to define topological constraints, assuming an accurate topology that would reflect the phylogeny of bromeliads.

Pollination syndromes of bromeliad species according to the literature, and our field observations, were coded as follows: 0, entomophily; 1, ornithophily; 2, chiropterophily; 3, autogamous; 4, generalist
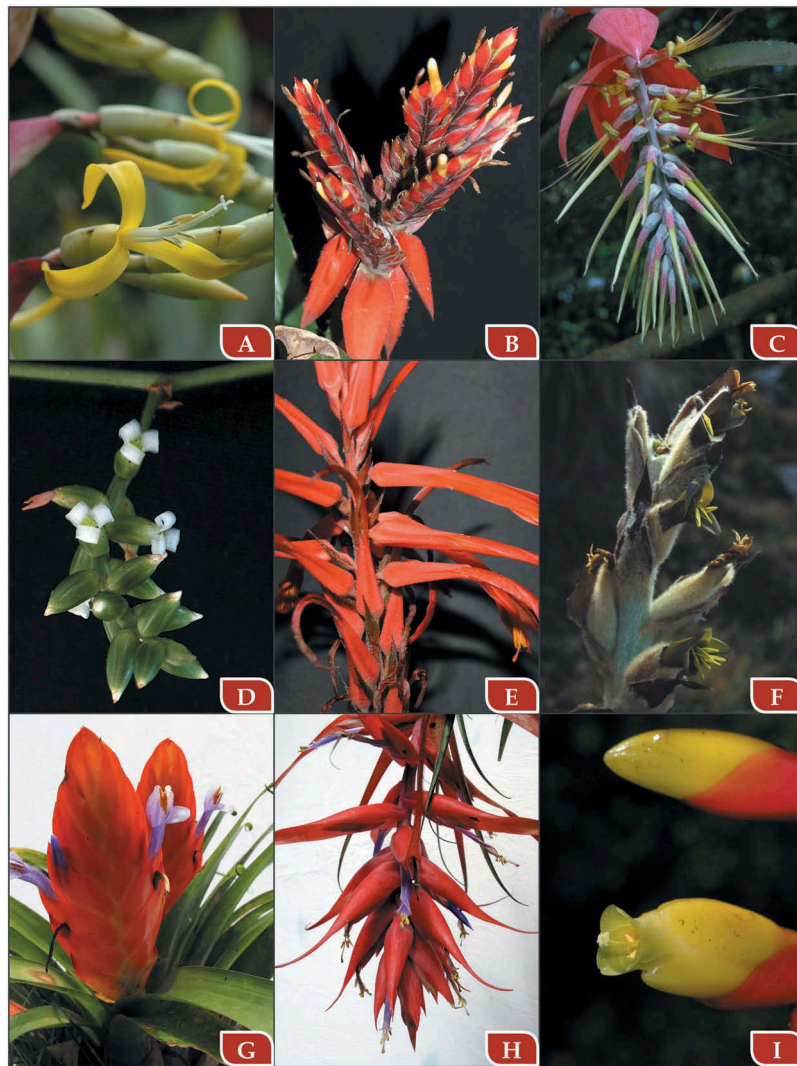
Figure 3. Examples of some bromeliads with diurnal anthesis: A) Alcantarea geniculata, bird-pollinated, B) Aechmea tillandsioides, bimodal pollination by birds and insects, probably bees, C) Billbergia issingiana, bird-pollinated, D) Catopsis sessiliflora, probably entomophilic, E) Pitcairnia ringens, bird-pollinated, F) Puya riparia, probably bird-pollinated, G) Tillandsia multicaulis, bird-pollinated, H) Tillandsia violacea, bird-pollinated, I) Vriesea platynema, probably bird-pollinated. Note the bright-coloration, principally red, of the bird-pollinated species, and the tubular shape of the corolla. Photos: A, I: Elton M. C. Leme. B, C, D, F, G, H: Thorsten Krömer. E: Pedro A. Aguilar-Rodríguez. This image was elaborated by J. Escobedo Sarti, one of the coauthors.

pollination (species with two or more complementary pollinators from different functional groups; see Schmid et al. 2011; Aguilar-Rodríguez et al. 2016). We used this information to assemble a character matrix and selected the most appropriate evolutionary model for pollination syndrome, based on this matrix and the ML tree obtained with GARLI, as well as the Geiger package and APE (Paradis et al. 2004; Harmon et al. 2008), implemented in R (R Core Team 2016). The test consisted of calculating the plausibility of all of the evolutionary models available in Geiger. Based on the Akaike Information Criterion (AIC), we then identified the Automatic Relevance Determination regression (ARD) model to present the best fit, before reconstructing ancestral characters with more plausibility and the ARD model.

Our phylogenetic tree (Figure 2) strongly suggests that chiropterophilous floral features have appeared multiple times from ornithophilous ancestors in the Bromeliaceae, especially within Tillandsioideae. Thus, all clades of the bromeliads with chiropterophilous traits are embedded within groups of ornithophilous species, and in general, chiropterophilous floral traits appear derived from ornithophilous or sphingophilous floral traits (Tschapka and Dressler 2002; von Helversen and Winter 2003; Fleming et al. 2009).The transition within plant families from ornithophilous to chiropterophilous traits seems to be more common than in the opposite direction, and also more common than transitions from other syndromes (*e.g.* melittophily or sphingophily) to chiropterophily (van der Niet and

Johnson 2012; Rosas-Guerrero et al. 2014), suggesting that it may constitute an evolutionary 'dead-end' (Tripp and Manos 2008). Within the Bromeliaceae, this transition seems to have occurred independently in different genera, particularly within the Tillandsioideae subfamily (Versieux et al. 2012; Givnish et al. 2014). As a whole, chiropterophilous flowers have appeared independently many times in clades with different evolutionary histories; in different genera among the 'core' members of the Tillandsioideae subfamily, once in the *Encholirium* clade, independently in *Pitcairnia* within the Pitcairnioideae, and separately in *Puya* and *Billbergia*, each within its own subfamily. However, it is important to acknowledge that the taxonomy of this family has proved difficult to resolve (Givnish et al. 2007; Barfuss et al. 2016).

Some bat-pollinated bromeliads may use diurnal visitors as secondary pollinators (see examples in *Billbergia*, *Encholirium*, *Guzmania*, *Pitcairnia* and *Tillandsia*; Krömer 2003; Christianini et al. 2013; Marques et al. 2015; Aguilar-Rodríguez et al. 2016; Queiroz et al. 2016; Silva Jorge et al. 2018), with hummingbirds being the most frequently reported floral visitors/secondary pollinators (Table S1). In many angiosperms, secondary pollinators frequently coincide with the probable ancestral pollinator group (Rosas-Guerrero et al. 2014), and this is reflected in our inference that chiropterophilous features in bat-pollinated bromeliads are derived from ornithophilous traits present in hummingbird-pollinated species. Changes in the corolla, as well as the time of anthesis/flower duration, might be important modifications to restrict hummingbird visits. However, there is evidence of 'intermediate' floral traits in some species, suggesting either that this transition is ongoing or that this is a steady state in which different functional groups of pollinators complement each other in contributing to the reproductive success of the bromeliad (*e.g. Billbergia horrida*, *Tillandsia heterophylla*; Marques et al. 2015; Aguilar-Rodríguez et al. 2016).

The chiropterophilous syndrome within Bromeliaceae

The comparably recent origin of both Neotropical nectarivorous bats and bromeliads (Givnish et al. 2007, 2011; Baker et al. 2012) indicates that there has been only a relatively short time span in which to develop similar, highly specific adaptations to bat-pollination as in other, much older plant families such as the Asparagaceae (*Agave*) and Cactaceae (Fleming et al. 2009; Rosas-Guerrero et al. 2014). In this section, we examine the chiropterophilous floral traits present in bromeliads.

Phenology related to bat visitation

Anthesis in the bat-pollinated bromeliads mainly starts at dusk, although some species open their flowers during mid-afternoon (i.e. *Encholirium spectabile*, *E. vogelii*, *Tillandsia heterophylla*, *Vriesea bituminosa* var. *bituminosa*, *V. hydrophora*, *V. longicaulis*, *V. longiscapa* and *Werauhia ororiensis*; Salas 1973; Martinelli 1994, 1997; Seres and Ramírez 1995; Christianini et al. 2013; Aguilar-Rodríguez et al. 2016). Duration of anthesis varies considerably between species; from the shortest in *Pitcairnia* (5 to 10 h in *P. albiflos* and *P. flammea*; Martinelli 1994; Wendt et al. 2001) to the longest in *Billbergia horrida* Regel (24 h; Marques et al. 2015) and *Encholirium subsecundum* (3 d; Sazima et al. 1989).

The crepuscular anthesis of these species might be a remnant of ornithophilous ancestors with diurnal anthesis (except in *Pitcairnia recurvata*, which opens flowers late at night, P. A. Aguilar-Rodríguez et al., unpublished data). In addition, an extended anthesis could increase the probability of pollination by other animals, such as hummingbirds, although these might not be as effective pollinators as bats (Christianini et al. 2013; Marques et al. 2015; Aguilar-Rodríguez et al. 2016; Queiroz et al. 2016; Silva Jorge et al. 2018; but see Tschapka and von Helversen 2007). Hummingbirds, moths and, to a lesser extent, various species of bees, are often frequent alternative visitors of bat-pollinated bromeliads (Table S1); however, the timing of visits in relation to stigma receptivity, and floral morphology may preclude pollination by bees (Aguilar-Rodríguez et al. 2014; Christianini et al. 2013; Marques et al. 2015; Aguilar-Rodríguez et al. 2016).

Nearly all bat-pollinated bromeliad species studied present a 'steady-state' flowering pattern (i.e. each individual in the population produces one or two flowers per night, over many days or weeks; *sensu* Gentry 1974), with an annual or biannual flowering period (Martinelli 1997). Two exceptions are *Alcantarea imperialis* and *Vriesea gigantea* with large inflorescences that open up to 18 and 10 flowers per day, respectively (Martinelli 1994; Araujo et al. 2004). Another exception, *Pitcairnia flammea*, exhibits a

'cornucopia' pattern (i.e. various individuals in the population present many flowers simultaneously, over a short period of time; Martinelli 1994), while individuals of *E. spectabile* may flower over 30 days with an entire population of *E. subsecundum* sometimes flowering for three to four months (Sazima et al. 1989).

Sympatric bromeliad species that share pollinators may present staggered flowering seasons to avoid competition for pollinators (Fischer 1994; Araujo et al. 2004), while simultaneously preventing hybridisation. However, this staggered flowering pattern is not present in all bromeliad communities (see Martinelli 1997; García-Franco et al. 2001; Versieux et al. 2012).

Floral morphology

While the flower buds of many Tillandsioideae are initiated in two opposite rows along the inflorescence, they undergo reorientation during ontogeny to face the same direction at anthesis (*e.g. Werauhia* spp.), thus allowing a bat to visit the inflorescence over several days always from the same direction. Most bat-pollinated bromeliads have pale yellow, green, creamy or white petals, occasionally with a reddish tint on the calyx, for example some species of *Alcantarea* and *Vriesea* (Martinelli 1994, 1997; Sazima et al. 1999; Moura and Costa 2014; Versieux and Wanderley 2015). At least four distinct flower shapes can be distinguished among such bromeliads: i) the zygomorphic tube-type of some *Billbergia*, *Vriesea*, *Pitcairnia* and *Puya* species (Sazima et al. 1999; Kessler and Krömer 2000; Schmid H 2000; Kowalski and Tardivo 2015; Macías-Rodríguez et al. 2007; Scultori Da Silva 2009; Figure 1(b,c,g)); ii) the zygomorphic bell-shape type present in *Vriesea* and *Werauhia* and even *Tillandsia* (Utley 1983; Grant 1995; Leme 1995; Tschapka and von Helversen 2007; Figure 1(f,h,i)); iii) the heliciform actinomorphic flower with strap-like petals and protruding stamens in *Alcantarea* and *Pseudalcantarea* (Martinelli 1994; Krömer et al. 2012; Versieux et al. 2012; Aguilar-Rodríguez et al. 2014; Figure 1(a)); and iv) the brush-type flower of *Encholirium* (Sazima et al. 1989; Christianini et al. 2013; Queiroz et al. 2016; Gomes et al. 2018; Figure 1(c); but see *Encholirium horridum* in Hmeljevski et al. 2017).

These distinct flower shapes could be related to intrinsic differences in the floral morphology between subfamilies and genera (but see the similarities between flowers in *Alcantarea*, *Pseudalcantarea*, *Tillandsia baliophylla* and *T.*

paniculata; Beaman and Judd 1996; Barfuss et al. 2016). Ornithophilous bromeliads share several floral features with chiropterophilous species, and the latter pollination syndrome may have evolved quite easily from the former, as indicated by several evolutionary shifts observed among other species (van der Niet and Johnson 2012) (see also examples among the genus *Alcantarea*; Versieux et al. 2012).

Floral morphology plays an important role in pollen placement on the body of the bat, and in reducing the amount of pollen wasted on heterospecific stigmas (Stewart and Dudash 2017). In most species of *Vriesea* and *Werauhia*, the anthers are positioned on the dorsal or ventral side of the corolla, but in some species, such as *Vriesea gigantea* and *V. limae*, or in *Stigmatodon* spp., the anthers are radially or laterally oriented (von Helversen 1993; Sazima et al. 1995; Siqueira Filho 2003). One important difference between diurnal and chiropterophilous bromeliad species is that the former present tubular corollas with stamens arranged in a bundle around the centre of the flower such that pollen is deposited on the beak of perching and hovering birds; in contrast, chiropterophilous species have larger, broader, cup-like and generally quite open flowers with stamens spreading from the centre. Stamen position during anthesis is an important floral trait that separates chiropterophilous from ornithophilous *Alcantarea* species (spreading *vs.* bundle forming; Versieux et al. 2012). The model of Muchhala (2007) suggests that wider corollas would be selected in flowering species where bats conduct more than 44% of all visits, in order to match the bat morphology and reduce pollen waste by hummingbirds. This might apply to flowers of *Werauhia* (Tschapka and von Helversen 2007) and even to the spirally twisted petals of *P. macropetala*. In the latter species, the petals form an open corolla, in which only a bat can contact both the exerted anthers and the stigma simultaneously during a visit to the flower, while hummingbirds fail to do this due to their visitation behaviour and because of changes to floral parts following anthesis, for example the stigma pointing downwards due to turgor loss in the style, so the hummingbird does not come into direct contact with it (Aguilar-Rodríguez et al. 2014). Pollen of bell-shaped chiropterophilous bromeliad flowers, for example in *Werauhia* and *Vriesea*, is placed on the head of the bat (Figure 1(k)), while in actinomorphic heliciform flowers, such as in *Pseudalcantarea macropetala*, it is deposited on the ventral side of the wings (Aguilar-Rodríguez et al. 2014).

The position of the stigma below the anthers and facing downwards in some *Vriesea* and *Werauhia* species might allow the stigma to make contact with the bat fur before it reaches the anthers, thus favouring outcrossing when the flower is fully opened, in spite of self-compatibility (Salas 1973).

Nectar characteristics

Nectar is one of the main rewards offered to flower-visiting bats in the Neotropics, with the nectar of bat-pollinated species possessing characteristics that distinguish it from that provided by plant species to other floral visitors ((von Helversen and Winter 2003), see also Mosti et al. 2013 for information about nectar secretion in bromeliads). In fact, some of the most robust evidence for bat-pollination in bromeliads is based on the particular characteristics of nectar. The sucrose/hexose ratio of various bromeliad species studied by Krömer et al. (2008) indicated that the nectar of chiropterophilous species is hexose-rich, leading them to suggest that some Bolivian *Guzmania* species which produce hexose-rich nectar are bat-pollinated, even though they present brightly-coloured floral bracts more often associated with bird-pollinated species. Many bromeliads with chiropterophilous floral traits within Tillandsioideae show tank-forming rosettes, in which water and detritus are collected. Givnish et al. (2014) suggested that the tank-habit might originally have favoured ornithophily, since the water-filled tanks may facilitate the production of relatively large amounts of nectar. However, the same reasoning holds true for chiropterophilous species since nectarivorous bats require an even higher amount of nectar than hummingbirds (Tschapka and Dressler 2002). Nectar volume varies widely among chiropterophilous bromeliads species (Table S1, Table S2), ranging from 4 μl in *Encholirium vogelli* (Christianini et al. 2013) to 1129 μl in *W. gladioliflora* (Tschapka and von Helversen 2007). Moreover, sugar concentration ranges from 4% in *Encholirium subsecundum* (Sazima et al. 1989) to 21% in *Vriesea atra* var. *atra* (Fischer 1994). This high variability in nectar volume and constituency could, at least partly, be attributed to the different methodologies used in different studies. For example, measurement of accumulated nectar over the entire life of the flower *vs.* standing crop measurements (Corbet 2003). Furthermore, there is interplant variation of nectar traits (*e.g.* Hodges 1993) and environmental factors may also affect nectar measurements (Jakobsen and Kritjánsson 1994; Willmer 2011). Another explanation could be that the rather short evolutionary time span of the mutualism between bats and bromeliads may not yet have allowed the development of a clear nectar production pattern (Rodríguez-Peña et al. 2016).

In general, bat-pollinated bromeliads present lower nectar volumes and sugar concentrations than other bat-pollinated plants (Tschapka and Dressler 2002; Fleming et al. 2009). The study of Krömer et al. (2008) showed that chiropterophilous species had the lowest sugar concentration of all bromeliads studied (11.5 ± 4.0%; but see *W. gladioliflora*; Tschapka and von Helversen 2007). The low nectar sugar concentration in bat-pollinated bromeliads (Table S1) might require visitors to consume rather high quantities of nectar to meet their energetic needs (von Helversen and Reyer 1984), thus necessitating an increased number of flower visits. More dilute nectar may evolve when competition for food among bats is higher (Nachev et al. 2017), but we still lack sufficient information to confirm this hypothesis.

Floral scent

Floral scent probably serves as a long-distance attractant for bats, but will also aid close-range location of flowers (von Helversen et al. 2000; Gonzalez-Terrazas et al. 2016). Many authors report that chiropterophilous bromeliads present a characteristic floral scent described as 'musky' or garlic-like (Table S1, Table S2). However, to date, the scent volatiles of only two species of bat-pollinated bromeliads have been identified: in *Werauhia gladioliflora* (Bestmann et al. 1997) and *Pseudalcantarea macropetala* (Aguilar-Rodríguez et al. 2014). In the former, dimethyl disulphide was present, a volatile that is innately attractive to New World nectarivorous bats (von Helversen et al. 2000). Sulphur-containing compounds are common in the scent of chiropterophilous plants, but not omnipresent (Knudsen and Tollsten 1995). Thus, in the case of *P. macropetala*, no sulphur-containing volatiles were found. It is possible that this specific attractant has evolved in *Werauhia*, a genus highly specialised in bat-pollination, but not yet in *P. macropetala*. The volatiles identified from 13 species of different Bromeliaceae genera of all pollination syndromes are highly variable, even within the same genus (Hilo de Souza et al. 2016), and some of the volatile compounds detected in these diurnally flowering species are

shared with those identified for *W. gladioliflora* by Bestmann et al. (1997) and *P. macropetala* in Aguilar-Rodríguez et al. (2014).

Acoustic signals

A study by von Helversen et al. (2003) has suggested that *W. gladioliflora* might have flowers with special echo-reflecting properties. Unlike other bromeliads, *W. gladioliflora* presents flowers that are largely embedded within the stalk of the inflorescence, covered by bracts, and only exposed when fully opened. The only section protruding from the stalk is the distal portion of the corolla, as well as the stamens and stigma. The cup-like corolla of *Werauhia* could produce a distinctive echo that might help a bat investigate the inflorescence and locate the flower entrance (von Helversen et al. 2003).

Characteristics of bats visiting bromeliads

The bat family Phyllostomidae of New World Leaf-nosed bats originated about 30.3 mya (Rojas et al. 2016). Nectarivorous feeding habits evolved twice within the family (Baker et al. 2012; Tschapka et al. 2015); firstly, around 21.55 mya (23.4–19.7; subfamily Glossophaginae) and secondly around 11.13 mya (11.4–10.9; subfamily Lonchophyllinae) in South America, with the exception of some genera (*Brachyphylla, Erophylla, Phyllonycteris, Monophyllus, Leptonycteris* and *Glossophaga*; Rojas et al. 2016) that originated in the Antilles. The oldest fossil of a Neotropical nectarivorous bat is from *Palynephyllum antimaster* (about 12–13 mya; Morgan and Czaplewki 2012) and the majority of extant nectarivorous bat genera originated around 10–5 mya (Rojas et al. 2016). There is evidence of the presence of *Anoura* in the Peruvian Andes dating from the Pleistocene (at least 2.5 mya; Shockey et al. 2009). Thus, specialised nectarivorous bats occurred at the same time and location as the 'bromeliad revolution', with most of the extant nectarivorous genera already present by the time of the origin of some bromeliad genera such as *Encholirium, Pseudalcantarea* and *Werauhia* (Givnish et al. 2014).

The Andean region is particularly important for species diversity of genera comprising bat-pollinated bromeliads, as well as for the bat genus *Anoura* (Patterson et al. 1996; Muchhala et al. 2008; Mantilla-Meluk et al. 2009; Shockey et al. 2009; Mantilla-Meluk and Baker 2010). This bat genus diversified over the last 10 mya or less (Rojas et al.

2011) and comprises the 'core' species of the nectar-ivorous bat guild at higher elevations (Fleming et al. 2005; Moras et al. 2013), as well as being the bat genus most frequently reported to visit bromeliads (Table S1). In addition to other characteristics (i.e. long dense fur, reduced uropatagium, hairy feet and toes, small ears and a higher body mass than the lowland nectarivorous bats; Soriano et al. 2002), the basal metabolic rate of most *Anoura* species (Figure 4(a,b)) reflects their tolerance to lower environmental temperatures (Ortega-García et al. 2017; but see *Anoura caudifer* in the lowland of the Amazonian region) and allows them to remain active during cold nights at high elevations. This might be the reason for the frequent reports of members of this bat genus as floral visitors of bromeliads at high elevations. In contrast, at low elevations in Mexico and Central America, the 'core' nectarivorous bat-fauna is formed by the genus *Glossophaga* (Fleming et al. 2005, 2009), as shown by studies carried out in Costa Rica on *W. gladioliflora* (Tschapka 2004; Tschapka and von Helversen 2007).

To date, a total of 19 species from ten phyllostomid genera have been recorded visiting bromeliad flowers (Table S1), 15 of which belong to the specialised nectarivorous subfamilies Glossophaginae and Lonchophyllinae: *Anoura* (4 spp.), *Glossophaga* (2 spp.), *Hylonycteris* (1 sp.), *Lichonycteris* (1 sp.), *Lonchophylla* (5 spp.), *Platalina* (1 sp.) and *Xeronycteris* (1 sp.) (Figure 4). Furthermore, three frugivorous species from the subfamily Stenodermatinae are reported: *Artibeus lituratus* and *Pygoderma bilabiatum*, visiting bromeliads with open or brush-like corollas (*Alcantarea imperialis, A. regina, Vriesea bituminosa* var. *bituminosa* and *V. hoehneana*; Martinelli 1994; Kaehler et al. 2005); and *Carollia perspicillata* visiting the 'tube-like' flower of *Pitcairnia paniculata* (Maguiña et al. 2012). In addition, *Phyllostomus discolor* from the Phyllostominae subfamily visits and pollinates flowers of *Encholirium spectabile* (Queiroz et al. 2016).

It has been proposed that bats re-visit flowers over the course of the night in a behaviour known as 'traplining' (*sensu* Janzen 1971; von Helversen 1993; Fleming et al. 2009). Almost all authors who observed bat visits to bromeliads have suggested the occurrence of such a foraging mode; however, no study to date has experimentally confirmed this behaviour. The duration of the actual flower visit is extremely short (less than one second; Aguilar-Rodríguez et al. 2014; Sazima et al. 1995; Wendt et al. 2001; Tschapka and von Helversen 2007) and the bats usually insert their head into the corolla or lap the nectar directly from the inflorescence (as in *Encholirium*; Sazima et al. 1989).
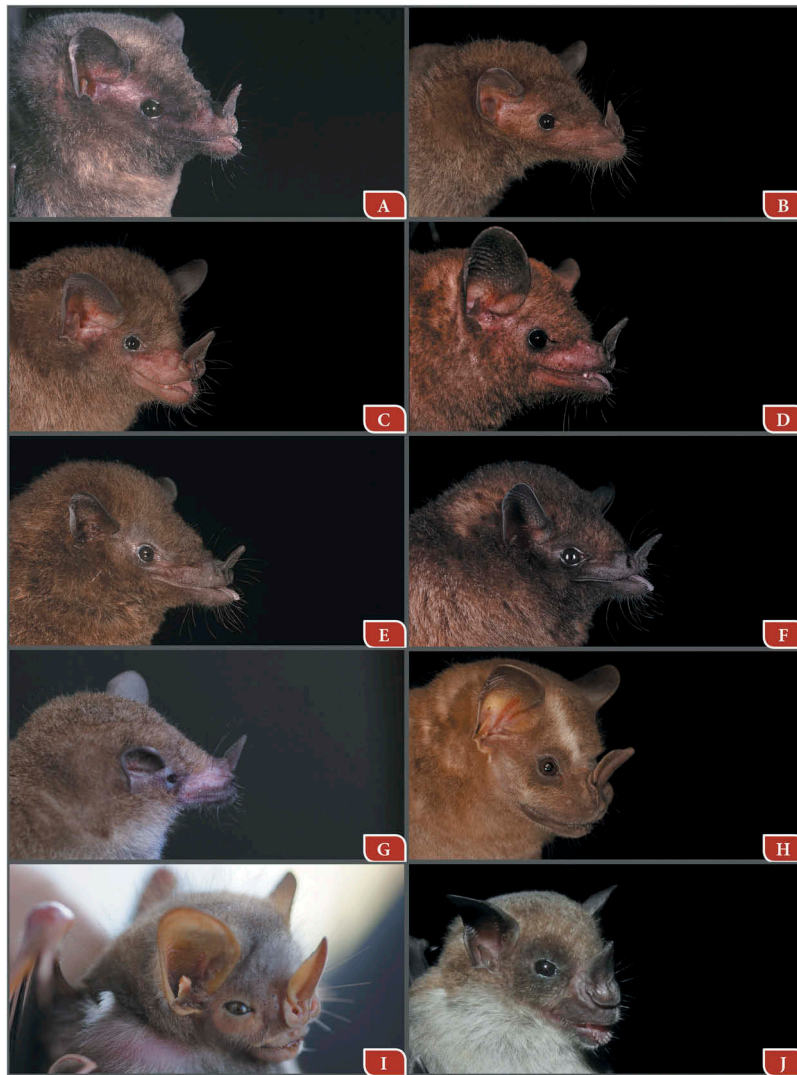
Figure 4. Bats identified as pollinators of Bromeliaceae: (a) *Anoura caudifer* (Glossophaginae subfamily), (b) *Anoura geoffroyi* (Glossophaginae), (c) *Glossophaga commissarisi* (Glossophaginae), (d) *Glossophaga soricina* (Glossophaginae), (e) *Hylonycteris underwoodi* (Glossophaginae), (f) *Lichonycteris obscura* (Glossophaginae), (g) *Lonchophylla bokermanni* (Lonchophyllinae), (h) *Artibeus lituratus* (Stenodermatinae), (i) *Pygoderma bilabiatum* (Stenodermatinae), (j) *Phyllostomus discolor* (Phyllostominae). Photographic credits: **A, B, C, D, E, F, H**: Marco Tschapka. **G, I**: Lena Geise. **J**: Pedro A. Aguilar-Rodríguez.

Some non-glossophagine bats, such as *P. discolor* (Queiroz et al. 2016; and see also reports of frugivorous bats in; Martinelli 1994, 1997), cannot forage for nectar during hovering-flight, and instead perch upside down from the inflorescence to gain access.

High plant abundance and high nectar production make bromeliads an important resource for bats, birds and insects (Howell and Burch 1974; Siqueira Filho 2003; Maguiña Conde 2016; Maguiña and Amanzo 2016; Morales 2016; Cordero-Schmidt et al. 2017). In the Maquiné river valley in Brazil, *Anoura caudifer* were found to feed on an unidentified *Vriesea* species for six months, accounting for over 50% of their total diet during the austral summer and almost 18% of their diet over the course of the year (Barros et al. 2013). Due to the local high abundance of *Werauhia gladioliflora* and its high nectar volume, the energy

density offered by this plant in Costa Rica reaches up to 349.3 kJ/ha/day during the peak flowering season, thus constituting one of the most efficient foraging options for bats (Tschapka 2004). Up to 28% of the chiropterophilous plants found within the home ranges of *Glossophaga commissarisi* in Costa Rica were *W. gladioliflora*, making it the most important plant resource for this bat (Rothenwöhrer et al. 2011).

Conclusions and future directions

Chiropterophily has evolved in different lineages of the Bromeliaceae family, with evidence for convergent evolution occurring across different phylogenetic clades. Key traits of chiropterophily, such as nocturnal anthesis and the length of floral structures, allow bats to act as the principal or occasionally the secondary

pollinator of chiropterophilous species (Rosas-Guerrero et al. 2014); however, most studies of such species have not specifically evaluated the contributions of other floral visitors in terms of pollination success. The short evolutionary time span of the bat-bromeliad interaction has probably led to the maintenance of some 'generalist' floral characteristics that currently correspond to a bimodal pollination system between primarily nocturnal and diurnal pollinators. In a few clades, more specialised flowers seem to have evolved relatively rapidly; for example, in *Werauhia*, possibly the most specialised bat-pollinated genus in the family, which is only *ca.* 5 mya (Givnish et al. 2014).

Bat visitation has been reported in more than 40 species from four of the eight recognised bromeliad subfamilies. Some bat-pollinated species may have been overlooked in other subfamilies or presumed to be moth-pollinated (Gardner 1986; Rauh 1986, 1987, 1990; Aguilar-Rodríguez et al. 2016). Only 24 (35%) of the references presented in Table S1 actually represent in-depth studies on the reproductive biology of Bromeliaceae. Of these, only seven (10%) were conducted during the last 10 years, but even this relatively small number of studies yielded five chiropterophilic species previously unreported in the literature. This emphasises the importance of field-work for determining the extent of the distribution of this pollination syndrome within the family.

Pollination by vertebrates is considered to be an important driver of speciation within the Bromeliaceae (Givnish et al. 2014) and nectar-feeding bats may therefore have played a significant role in the origin of some species, although this remains to be investigated in detail. The genus *Werauhia*, with 92 species (Gouda et al. 2017), seems to be particularly well adapted to bat pollination, (see also Utley, 1983; von Helversen and von Helversen, 1975) and offers interesting options for comparisons between species from differing regions, elevations and morphology; currently, detailed information on the pollination system is only available for *Werauhia gladioliflora*. In addition, the speciose genus *Stigmatodon*, formerly included in *Vriesea*, shows floral characteristics, including nocturnal anthesis, pale and greenish petals and musty scent (Barfuss et al. 2016), which suggest that all of its 18 species might be bat-pollinated, although supporting field evidence to date is limited.

As is the case with almost all plant-pollinator interactions, only scarce information exists regarding the contribution of bats to genetic population structure within bromeliad species (i.e. Wendt et al. 2002; Barbará et al. 2007; Paggi et al., 2007;

Lexer et al. 2016) or even their role in hybridisation between species sharing habitats or pollinators (Wendt et al. 2001; Palma-Silva et al. 2011; Versieux et al. 2012; Queiroz et al., 2015). The effect of pollinators on species cohesion could be particularly important considering the lack of other prezygotic reproductive barriers among many bromeliad species (Wendt et al. 2008, but see also Matallana et al. 2016).

The presence of bat pollination among species of the Bromeliaceae family is associated with environmental conditions and elevation (Kessler and Krömer 2000 ; Kessler 2002) and most of the reported species are epiphytic or lithophytic. Borges et al. (2016), suggest that plant families living in habitats with low water availability are more likely to develop crepuscular or nocturnal anthesis as a strategy to reduce nectar loss through evaporation. In addition, species living in arid regions (including *Encholirium* and *Puya*) and epiphytic species grow under environmental water stress (Ruzana Adibah and Ainuddin 2011). In this context, future work should focus on whether high altitude and precipitation are truly associated with pollination by bats among epiphytic species, and whether drier environmental conditions favour bat pollination in large bromeliad species such as those of the genera *Alcantarea* and *Encholirium*.

In order to understand the role of bat pollination in a bromeliad species visited by several pollinators over its geographical distribution, it is important to quantify the relative contribution of each pollinator species to reproduction within local populations. If a bromeliad flower has extended anthesis, lasting from afternoon until early morning, it may be visited by animals other than or in addition to bats. With regard to nectar-feeding bats, different species may carry a species-specific pollen load (King et al. 2013) and dissimilarities in size and behaviour might result in differences in the relative contributions of each species to seed set, and thus may ultimately modify the breeding system of the species. There are bromeliad species that seem to be self-incompatible and therefore depend on pollinators for reproduction (*e.g. Encholirium* spp.; Christianini et al. 2013; Hmeljevski et al. 2017), while others are self-compatible and even capable of autonomous self-pollination (*T. heterophylla*; Aguilar-Rodríguez et al. 2016, *W. gladioliflora*, Tschapka and von Helversen 2007).

Finally, it is to be emphasised that the interaction between bromeliads and nectar-feeding bats presents a multitude of interesting ecological and

evolutionary aspects, ranging from pollinator behaviour to local adaptations and population genetic consequences. Bromeliad species occur in different habitats all over the Neotropics, in high numbers and often large population sizes. These characteristics allow interesting studies that will help further our understanding of wider patterns and ecological roles within different habitats as well as the evolutionary relationships that exist within the bromeliad family.

Acknowledgements

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

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