



An overview on pollination of the Neotropical Poales

Marina Wolowski¹ & Leandro Freitas^{2,3}

Abstract

Current phylogenetic hypotheses support that ancestral Poales were animal-pollinated and that subsequent shifts to wind pollination have occurred. Ten of the 16 Poales families are widely distributed in the Neotropics, however a comprehensive understanding of their pollination systems' diversity is still lacking. Here we surveyed studies on pollination biology of Neotropical species of Poales. Poaceae, Cyperaceae and Juncaceae are predominantly wind-pollinated but insect pollination also occurs. Thurniaceae and Typhaceae fit on anemophily but empirical data are missing. Pollen flowers with poricidal anthers have evolved independently in Mayacaceae and Rapateaceae. Pollen- and nectar-flowers occur in Xyridaceae, which are mainly pollinated by bees. Eriocaulaceae flowers secrete minute quantity of nectar and are pollinated by “diverse small insects”. Pollination of Bromeliaceae is carried out by a great variety of animal groups, mainly hummingbirds, and includes anemophily. The diversity in floral forms is very high within the order but more constant within the families. This trend indicates that many events of species diversification may have occurred without divergence in the pollination mode. Still, parallel shifts in pollination modes are found, including possible reversals to wind- or animal-pollination, changes in the type of pollinators (e.g. from hummingbirds to bee or bats) and the arising of ambophily.

Key words: ambophily, ecology, evolution, floral biology, monocots.

Introduction

The order Poales represents about one third of the monocots, with ca. 20,000 species distributed in 16 families (APG III 2009), and has one of the highest diversification rates among the angiosperm orders (Magallón & Castillo 2009). The order probably originated in the late Cretaceous in wet nutrient-poor sunny habitats and diversified into distinct habitat conditions (wetlands, forest understory, epiphytic habitats) during the Paleogene, with major diversification into fire-adapted vegetation in seasonal climates and low atmospheric CO₂ in the Neogene (Linder & Rudall 2005). Thus, diversification into these habitats was associated with CO₂-concentrating mechanisms (Bouchenak-Khelladi *et al.* 2014). Despite the high diversity within Poales and several morphological and molecular studies that established well-supported phylogenetic relationships within the order (Givnish *et al.* 2010; Bouchenak-Khelladi *et al.* 2014), empirical knowledge on its pollination ecology is dispersed

over the literature among studies of one or few species and concentrated in Bromeliaceae.

A first overview about the evolution of pollination modes in the light of the current phylogenetic hypotheses within the order indicated that ancestral Poales were animal pollinated and that five subsequent shifts to wind pollination have occurred, which were correlated with shift to open habitats and small, inconspicuous, unisexual, and nectarless flowers (Givnish *et al.* 2010). However a comprehensive understanding of the diversity of pollination systems in the families of Poales is still lacking (but see Benzing 2000; Givnish *et al.* 2010; Oriani 2011). Ten of the Poales families are widely distributed in the Neotropical region (see Stevens 2001). From these, Cyperaceae, Juncaceae, Poaceae and Typhaceae are worldwide distributed, Eriocaulaceae is pantropical (to temperate, but especially at Guayana Shield and Southeastern Brazil) and Xyridaceae is pantropical (to warm temperate). While Bromeliaceae, Mayacaceae, Rapateaceae and Thurniaceae are almost exclusive

¹ Universidade Estadual de Campinas, Depto. Biologia Vegetal, C.P. 6109, 13083-970, Campinas, SP, Brazil.

² Jardim Botânico do Rio de Janeiro, R. Pacheco Leão 915, 22460-040, Rio de Janeiro, RJ, Brazil.

³ Author for correspondence: lfreytas.jbot@gmail.com

distributed in the Neotropics, and one species of each family in Africa. Although Restionaceae is distributed within the Indo-Pacific region, there are representatives in Chile.

Here, we surveyed published studies, dissertations and theses with information on pollination biology and breeding system of Neotropical species of Poales. Specifically, we aimed to evaluate if family diversity is associated with biotic pollination. Besides, we provided an overview on the pollination modes in Poales families.

Methods

We reviewed published studies primarily using the databases ‘Institute for Scientific Information Web of Science®’ and ‘Scientific Electronic Library Online - SciELO’, without date limit. We used the following keyword combination: “family name AND pollinat*” and “family name AND reproduc*”. Then, we sought for dissertations and theses from the online collection of Coordination of Improvement of Higher Education Personnel (CAPES), and from personal library collections of the authors, which also included books and papers. We did not include the keyword “Neotrop*” in the search because the quantity of results were low. Then, we used as criterion the selection of studies conducted on native species of Poales from the Neotropics (Olson *et al.* 2001). Other criteria were the studies containing data, or descriptive information, on pollination biology and/or breeding system, e.g., empirical data on biotic or abiotic pollen vectors, pollination experiments as fruit set after hand self or cross-pollination and natural pollination. Our search resulted in studies available from 1971 through 2014. In total our dataset was composed of 79 studies (two book chapters, five unpublished dissertations and theses, and 72 papers) that described features of pollination biology of the native Poales species from the Neotropics. These studies counted 227 species. Bromeliaceae had strong representation in the studies of the Neotropical Poales with 78.4% of the records, while other families were under represented (11.9% in Poaceae, 4.4% in Cyperaceae, 2.2% in Eriocaulaceae, 1.8% in Xyridaceae, and 1.3% in Rapateaceae), while no studies were recorded for Juncaceae, Mayacaceae, Thurniaceae, and Typhaceae.

For each study/species, we compiled data on pollination syndrome (based on floral morphology sensu Faegri & van der Pijl 1979), pollination system (based on empirical observation of pollen

vectors - wind; animal; ambophily - *sensu* Culley *et al.* 2002); pollinator taxa (scientific names and taxonomic group); sexual system (hermaphrodite; monoecy; andromonoecy); mating system (self-compatible; self-incompatible); floral reward (nectar; pollen); floral attractiveness (floral scents; colour). We obtained the phylogenetic hypothesis for the Neotropical families of Poales using the angiosperm APG III (APG III 2009) consensus tree (R20120829) from Phylomatic (Webb & Donogue 2004). Then, we plot the predominant pollination mode as wind, animal, ambophily for each family on the phylogenetic hypothesis and the secondary pollination mode (i.e. other systems restricted for some species or genera of the family) (Fig. 1). We estimated the Neotropical species’ richness of each family following Smith *et al.* (2004), and performed t-Test to evaluate if biotic pollination increases diversity (species richness was log-transformed to achieve parametric assumptions).

Results and Discussion

Animal pollination stands as the ancestral pollination mode of Poales evidenced by the earliest diverging lineage of Bromeliaceae (Givnish *et al.* 2010). Birds are by far the main group of pollinators of the bromeliads (131 of surveyed species, 72.5%), followed by bats (10.7%) and bees (7.6%). Within the birds, hummingbirds pollinated most of the species (97.9%), and passerine birds pollinated exclusively only two species of *Puya*. Mixed pollination systems, i.e. pollination by different functional groups of pollinators, count for 9.2% of the bromeliads. For instance, hummingbirds, bees and butterflies were recorded in flowers of *Dyckia pseudococcinea* (= *Dyckia martinellii* B.R. Silva & Forzza) (Martinelli 1994), bats, hummingbirds, bees and moths in *Encholirium horridum* L.B.Sm. (Hmeljevski 2013); and bats, bees and moths in *Pitcairnia albiflos* Herb. (Wendt *et al.* 2001). Further examples include pollination by hummingbirds (Canela 2006) and bats (Sazima *et al.* 1995) in *Vriesea longicaulis* Mez, and flowers of *Aechmea nudicaulis* (L.) Griseb. that were mainly pollinated by hummingbirds (Sazima *et al.* 1996; Buzato *et al.* 2000; Araujo *et al.* 2004; Canela 2006; Machado & Semir 2006; Piacentini & Varassin 2007), but were also visited by bees (Schmid *et al.* 2011). Indeed hummingbirds and bees was the most frequent combination (58.3%) of mixed pollination systems in Bromeliaceae, recorded in *Aechmea nudicaulis* (Schmid *et al.*

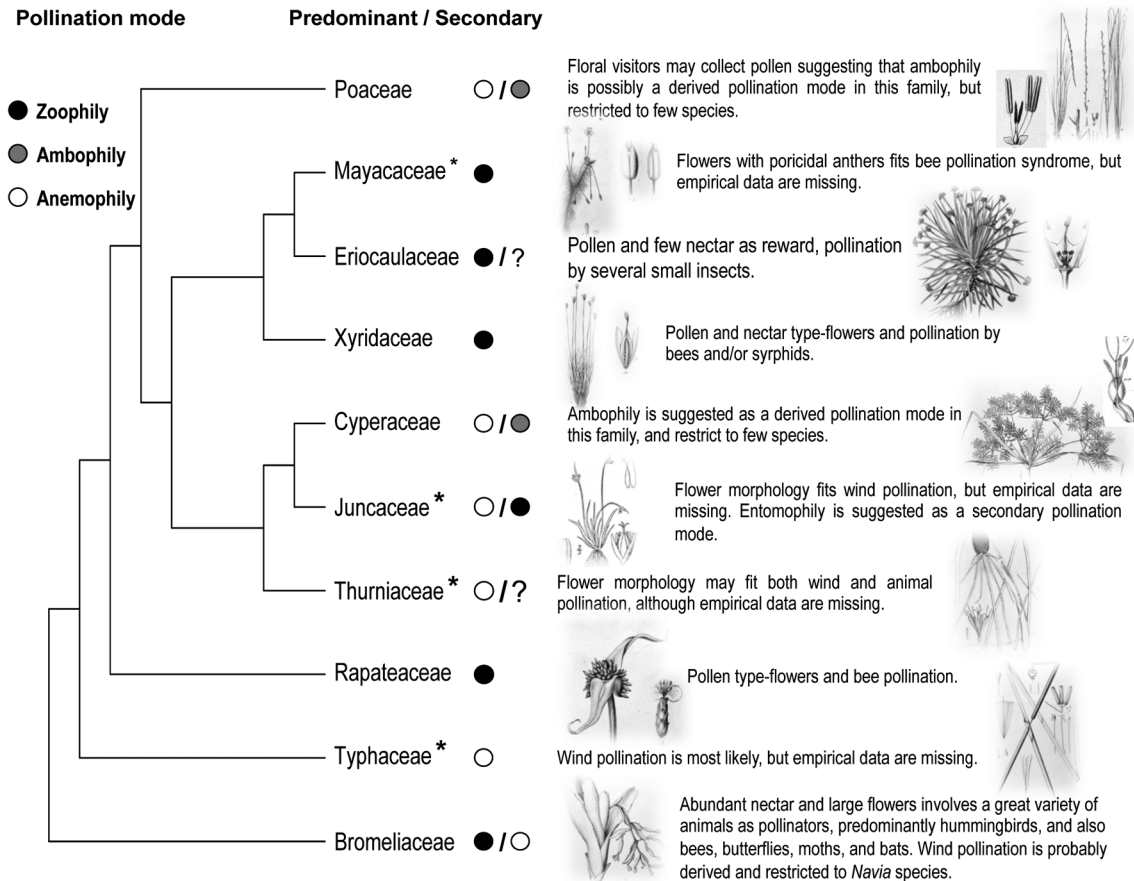


Figure 1 – Distribution of the predominant pollination mode (abiotic or biotic) in each family and the likely secondary pollination mode in Bromeliaceae, Cyperaceae, and Poaceae along the phylogenetic hypotheses of the Neotropical Poales. Families denoted with asterisk have no empirical data on pollination biology. Illustrations from: Britton, N.L., and A. Brown. 1913. An illustrated flora of the northern United States, Canada and the British Possessions. Vol. 1: 475. (Juncaceae); Hooker, Joseph Dalton. 1883. Hooker’s Icones Plantarum v 15, plates 1407–1408 in Watson, L. and Dallwitz M.J. 1992 onwards. The families of flowering plants: descriptions, illustrations, identification, and information retrieval. Version: 19th August 2014. (<<http://delta-intkey.com>>) (Thurniaceae); and Flora Brasiliensis (all other families).

2011), *Bromelia antiacantha* Bertol. (Canela & Sazima 2005), *Cryptanthus diana*e Leme (Siqueira-Filho 2003), *Lymania smithii* R.W.Read (Siqueira-Filho 2003), *Neoregelia johannis* (Carrière) L.B.Sm. (Buzato *et al.* 2000; Guerra *et al.* 2010), *Pitcairnia staminea* Lodd. (Wendt *et al.* 2001), and *Vriesea jonghei* (K. Koch) E.Morren (Snow & Snow 1986).

Although some Bromeliaceae have small and inconspicuous flowers that are associated to insect- or wind-pollination, most are large and showy and bear massive septal nectaries: such traits may explain the high dependence on vertebrates as pollinators (Benzing 2000), which

is an unusual pattern within angiosperm families. In fact, pollination by birds, predominantly by hummingbirds, may have arisen two or three times independently in the family, from insect pollination (Givnish *et al.* 2014). Reversions to insect pollination seems to have occurred at least seven times in Bromelioideae (Givnish *et al.* 2014), reflected in the predominance of bee pollination in this subfamily (60%). While bat pollination evolved from bird-pollinated ancestors, at least four times (Givnish *et al.* 2014), and is concentrated in Tillandsioideae (92.7%). This indicated several independent events of pollination shifts, a question

that has been underexplored in pollination studies of the family. Moreover, pollination by wind is expected in some *Navia* species with tiny flowers (Benzing 2000). In this medium-sized genus predominates species with ornithophilous flowers and the probable shift to pollination by wind from pollination by vertebrates is unique among angiosperms (see Culley *et al.* 2002).

There is extensive knowledge on the breeding system of three of the subfamilies of Bromeliaceae (reviewed first by Matallana *et al.* 2010). Overall 76 species in our review (71% of 107 spp.) were self-compatible, 30 species (29%) were self-incompatible, and two species (*Tillandsia geminiflora* Brogn. and *Vriesea longicaulis* Mez) had divergent results among studied sites. Self-incompatibility was concentrated in Bromelioideae: 74.2% of all self-incompatible bromeliads species and 56.1% of the subfamily species. Pitcairnioideae and Tillandsioideae were predominantly self-compatible: 86% and 88% of species, respectively. The self-incompatibility system was recorded for 14 species with predominance of possible gametophytic self-incompatibility (85.7%), and occurrence of possibly sporophytic self-incompatibility in two species.

Breeding system in the extremely diverse Bromeliaceae is puzzling, because other high diverse families are predominantly self-incompatible (Asteraceae, Solanaceae, Rubiaceae, Igc *et al.* 2008). Besides the family may have experienced reversion from self-compatibility to self-incompatibility, as the earlier divergent Tillandsioideae is predominantly self-compatible in contrast to Bromelioideae. Reversals to outcrossing are generally viewed as theoretically unlikely because of the concurrent reduction in outcrossing rate and inbreeding depression, but few direct tests have been conducted (Igc & Busch 2013).

Although Bromeliaceae is a family with extensive knowledge about pollination among the neotropical Poales, this is extremely concentrated within the largest three subfamilies Bromelioideae, Pitcairnioideae, and Tillandsioideae. Only eight species were studied from other three subfamilies, Brocchinioideae (Ramirez 1989), Hechtioideae (Ramírez Morillo *et al.* 2008), and Puyoideae (Bernardello *et al.* 1991; González-Gómez & Valdivia 2005; Hornung-Leoni *et al.* 2013), and we are still lacking information about two subfamilies, Lindmanioideae and Navioideae, which is a gap, considering that these five subfamilies represent 13% of Bromeliaceae richness.

Wind pollination first evolved in Typhaceae, at the divergence between all other Poales. Remarkable floral traits of Typhaceae are the unisexual flowers in terminal inflorescence, with male flowers at the base and female flowers near the apex, and the inconspicuous tepals. These floral traits, and also inhabiting open areas, are associated with wind pollination as stated by Givnish *et al.* (2010). However, there is no empirical data on floral biology and pollen movement promoted by wind within and among inflorescences of Typhaceae in time and space.

Rapateaceae is considered animal-pollinated. Its showy yellow flowers, presence of sweet scent, lack of nectar, and poricidal anthers suggest pollination by bees. In fact, Oriani (2011) observed bees visiting the flowers of *Stegolepis guianensis* Klotzsch ex Körn. while Renner (1989) recorded buzz pollination by bumblebees and carpenter bees in *Saxofridericia compressa* Maguire and *Stegolepis neblinensis* Maguire, both on the Tepuis of the Guayana Shield. Other floral visitors (halictid bees, euglossine bees and weevils) were also observed (Givnish *et al.* 2014), although their role as pollinators is unknown. Thus, addressed questions and refined pollination studies are still missing for this modest rich family with ca. 80 species in the Neotropics.

Following the evolution of the more recent clades, the cyperid/xyrid lineage diverged from the Poaceae lineage with the retaining of animal pollination in the xyrids (Xyridaceae, Eriocaulaceae, Mayacaceae) and evolution of wind pollination in the cyperids (Cyperaceae, Juncaceae, Thurniaceae), with probably posterior evolution of ambophily in the latter. Within the xyrids clade, there is empirical evidence of animal pollination in genera *Abolboda* and *Xyris* (Xyridaceae). The two *Abolboda* species studied in a Brazilian savanna are self-compatible and pollinated by bees, which forage for nectar and pollen (Oriani & Scatena 2011). While the two *Xyris* species offer only pollen as reward for bees and syrphids in high altitude grasslands vegetation within the Atlantic Forest domain (Freitas & Sazima 2006). At this same site, *Paepalanthus paulensis* Ruhland and *P. polyanthus* (Bong.) Kunth (Eriocaulaceae) offer nectar and pollen as reward and are pollinated by several insects (Freitas & Sazima 2006). Among species of *Comanthera* studied at rupestrian fields in the Brazilian savannas, *C. curralensis* (Moldenke) L.R.Parra & Giul. was pollinated

by flies, while two species (*C. elegans* (Bong.) L.R.Parra & Giul. and *C. mucugensis* (Giul.) L.R.Parra & Giul.) were pollinated by many species from several insect orders: Diptera, Hymenoptera, and Coleoptera, among others (Ramos *et al.* 2005; Oriani *et al.* 2009). Some insects collected pollen, and nectar, which is probably produced by the appendices of pistillate flowers (Ramos *et al.* 2005). These *Comanthera* species are monoecious and self-compatibility was reported in *C. mucugensis* (Ramos *et al.* 2005). Although both families offer nectar as reward, nectaries probably evolved independently in these lineages: from petal appendages, staminodes, pistillodes, and pistils in Eriocaulaceae, and associated with stylar appendages in Xyridaceae (Givnish *et al.* 2010 and references therein). Distinctly, nectaries are absent in Mayacaceae flowers. Besides, showy petals and poricidal anthers characterize pollen-type flowers pollinated by bees. However pollination studies are lacking for this low-diverse family (3 to 9 species in the Neotropics, Smith *et al.* 2004).

Likewise in the cyperids clade, there is no empirical information on pollination in Neotropical Juncaceae and Thurniaceae. Overall, wind pollination would be predominant in the cyperids' clade, but ambophily may have evolved in a few species or groups. In fact, pollination by wind and by insects is found in Juncaceae, as well as self-fertilization and cleistogamy (Knuth 1899; Huang *et al.* 2013), and small bees visit flowers of Thurniaceae (M. Alves, personal observation). Notably both wind- and insect-pollination were recorded in Cyperaceae (e.g., species of *Rhynchospora* in Thomas 1984; Costa & Machado 2012 and references therein). In the monoecious and self-incompatible *Rhynchospora ciliata* (Vahl) Kük., anthers reflect UV-light, which may act as floral attractiveness, and bees feed on pollen, but both abiotic and biotic pollination enhance reproductive success. Moreover, for other species of *Rhynchospora* insect pollination was recorded by Thomas (1984), which observed bees and other insects collecting pollen. It is important to know whether ambophily is a remarkable feature of the whole clade, which would bring new insights into the evolution of pollination systems in Poales.

Concurrently, wind pollination also evolved independently in Poaceae. Despite its high diversity, few pollination studies were conducted with native Poaceae in the Neotropics. Although floral traits of anemophily are remarkable in Poaceae (i.e.

inconspicuous flowers, exposed anthers, plumose stigmas) and wind pollination was already measured (e.g., *Setaria lachnea* (Nees) Kunth, Exner *et al.* 2010), biotic vectors may also play a role in the pollination of some Poaceae. Insects of distinct orders (e.g. Hymenoptera, Coleoptera, and Diptera) were recorded collecting pollen in male flowers of the woody bamboo *Merostachys riedeliana* Rupr. ex Döll (Guilherme & Ressel 2001), which can be moved to female flowers, or these insects can simply enhance pollen dispersion in the air, especially in habitats with low air streams (e.g. understory of tropical and subtropical forests), or acting as pollen thieves. Likewise, insects were also observed visiting flowers of the understory herbs of the genera *Lasiacis*, *Olyra*, and *Pariana* (Soderstrom & Calderón 1971; Seres & Ramirez 1995; Dorea 2011).

It is most parsimonious that shifts from animal to wind pollination occurred at least three times in lineages of Poales that are currently distributed in the Neotropics rather than several reversals from an abiotic pollinated ancestral (see Givnish *et al.* 2010). Yet, shifts in pollination mode were not related to species diversification among families of Poales in the Neotropics (Fig. 2, t-Test = 0.573, d.f. = 7.236, p-value = 0.584). While there seems to be a relationship with small flowers ending in wind pollination in more derived groups, the floral morphology of Typhaceae would break it down. Thus, the support of this early divergent clade leaves questions about how it would be the probable ancestor.

Concerning the sexual system of the Neotropical families of Poales reviewed here, there is a tendency for association of bisexual flowers with biotic pollination registered in

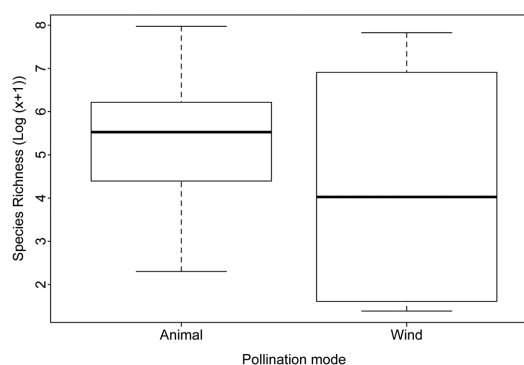


Figure 2 – Species richness per pollination mode of the Neotropical Poales families.

Bromeliaceae, Rapataceae, and Xyridaceae. While, the separation of male and female functions in unisexual flowers or inflorescences is associated with wind pollination (or ambophily) observed in Cyperaceae and Poaceae. Although Eriocaulaceae is an exception because of unisexual flowers and pollination by insects, and even in Poaceae there is a wide variety of sexual system (e.g., monoecious species with bisexual or unisexual flowers and andromonoecious species). The association of animal pollination to bisexual flowers and wind pollination to unisexual flowers was reported for the angiosperms as a whole (Friedman & Barrett 2008, 2009b). While the evolution of monoecy is interpreted as a mechanism that promote outcrossing (Charlesworth & Charlesworth 1978), Friedman and Barrett (2009a) proposed that it provides reproductive assurance due to geitonogamy in self-compatible species of *Carex* (Poaceae) pollinated by wind. In fact, wind pollination may commonly have evolved among the angiosperms to provide reproductive assurance when pollinators are scarce, thus alleviating pollen limitation (Friedman & Barrett 2009b).

Although more refined analyses could be run considering phylogenetic relationships among species, the scarcity of empirical data on pollination biology for Neotropical Poales other than bromeliads is the main impediment for a better comprehension of the diversity of pollination systems and its role in the evolution of the order. Even in the light of the paucity of extensive data some intriguing findings have been previously pointed, for instance, the predominance of self-compatibility and vertebrate-pollination in Bromeliaceae (Benzing 2000; Matallana *et al.* 2010) and the multiple origins of wind pollination (Givnish *et al.* 2010). Other notable aspect is the high diversity in floral forms within the order that results in pollination by wind, vertebrates, small bees and flies or large bees in search of pollen (buzz-pollination), and bees or diverse small insects in search of nectar. In contrast, concerning pollination modes there is high constancy in floral morphology within families; even in Bromeliaceae that probably shelters the highest diversity of pollination modes in the order, gross floral morphology is not so variable as observed in other large zoophilous families, for example, Fabaceae and Solanaceae (Endress 1994; Knapp 2002). Givnish *et al.* (2010) pointed that some attributes such as vigorous vegetative spread, adaptation to patchy disturbances, and/or positive feedback on conspecific abundance appear

to provide a logical explanation for the distribution of wind pollination in members of Poales. These attributes may also be important in zoophilous groups of Poales if it is assumed that many events of species diversification may have occurred without divergence in the pollination mode. Despite this general constancy in floral morphology within the families, parallel shifts in pollination modes are present in many clades as wind pollination in Typhaceae, the cyperid clade, and Poaceae and pollen type-flowers in Rapataceae and Mayacaceae that fit bee pollination. Moreover, possible reversals to wind- or animal-pollination, changes in the type of pollinators in zoophilous groups (e.g. from hummingbirds to bee or bats, Sazima *et al.* 1995; Canela 2006; Schmid *et al.* 2011) and the arising of pollination by wind and animals (ambophily) (Costa & Machado 2012) were also observed.

In conclusion, we have a dichotomy in the overview of pollination biology in Neotropical Poales. At one side, Bromeliaceae probably accumulates more case studies on pollination than any other family in the Neotropics (e.g., Wolowski *et al.* 2013; Wolowski *et al.* 2014). In opposition, empirical data on pollination are available for a few Neotropical species of the other families of Poales. Thus, the pollination of Neotropical Poales is still an open field for research, and basic case studies in those families with scarce information and phylogenetically oriented studies, are a great opportunity for biologists interested in both monocot evolution and pollination biology.

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