Pollination in Melastomataceae: a family-wide update on the little we know and the much that remains to be discovered

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Abstract
Conducting a literature review of the past 31 years, we here present an update of pollinator observations in Melastomataceae following Renner’s seminal work of 1989. The number of species with documented pollinators has more than doubled, to 272 species across 14 of the 18 major tribes. We detected a strong geographic bias, however, with 90% of observations from New-World species, despite 35% of Melastomataceae species diversity contained in the Old World. Further, we report that shifts from the common and most widespread pollination strategy (buzz pollination by bees, ca. 95.5% of species) have occurred both in the New- and Old-World tropics, and likely more than 20 times. These include shifts to nectar-foraging vertebrates (2.5%, 6 tribes), food-body-foraging vertebrates (0.9%, 1 tribe), and to generalized pollination systems (1.1%, possibly 2 tribes). Pollinator shifts commonly associate with floral trait changes, including, for instance, reward type, pollen release mechanisms, and corolla shape. We emphasize the need for more pollination biological studies particularly of Old-World species and the four hitherto unstudied clades, as well as comparative investigations across tribes and biogeographic regions to understand the extraordinary success of buzz pollination and the drivers of pollinator shifts in the family.

I. Introduction
Animal pollinators are regarded as key drivers of floral diversity and diversification across angiosperms (Sauquet & Magallón 2018). Particularly in the world’s biodiversity hotspots, such as the tropical Andes, the Atlantic Rainforest, Madagascar, Sundaland or the Cape Floristic Region, pollinators may have played a key role in plant speciation by mediating reproductive isolation among incipient species (in addition to abiotic factors, fruit dispersers, etc; van der Niet & Johnson 2012; Lagomarsino et al. 2016). Our understanding of the phylogenetic history of plant radiations is continuously improving through rapid advances in sequencing technologies, allowing to more
completely and reliably resolve even recent speciation events. At the same time, information on the natural history of many of these species remains fragmentary or even inexistent (Hortal et al. 2015). Data on biotic interactions such as pollination is time-consuming to collect and requires careful, continuous field observations in order to differentiate illegitimate flower visitors (i.e. any animal visiting a flower but not performing pollination) from legitimate pollinators (those visitors that touch both female and male reproductive organs). Even among pollinators, however, there may be important differences in pollination efficiency, i.e. in the amount of pollen they transfer, as even frequently visiting pollinators may be poor pollinators if they only transfer small amounts of pollen (King et al. 2013).

Accurately collecting comparative empirical field data on pollination forms the backbone for placing any macroevolutionary study on floral traits into a meaningful pollination ecological context. Pollination syndromes represent a tool for such approaches (Dellinger 2020). Pollination syndromes are defined as suites of floral traits which have evolved under distinct pollinator selection regimes, i.e. in adaptation to a specific functional group of pollinators (Fenster et al. 2004). If detailed empirical pollinator observations are available for a subset of species spanning the taxonomic and morphological diversity of a plant lineage, pollination syndromes may be used – with care! - to predict the most likely pollinators of species for which no empirical observations are available (Dellinger 2020). One crucial pre-condition for such predictions to be reliable, however, is the identification of the floral traits most strongly associating with distinct pollination strategies in the clade studied. These floral traits may differ among clades and may be highly system specific (Dellinger et al. 2019a).

In Melastomataceae, the last systematic review of the pollination ecological literature was done more than 30 years ago (Renner 1989). In this seminal review, Renner presented data on 126 Neotropical Melastomataceae species and their animal pollinators. The most common (and possibly ancestral) pollination strategy across the family is buzz pollination by bees, and Renner estimated 98% of species to be buzz-pollinated. Buzz pollination represents a functionally highly specialized pollination strategy, where bees apply vibrations to flowers to extract pollen (Buchmann 1983). Buzz pollination is common across angiosperms (ca. 8% of species), and has evolved multiple times independently (De Luca & Vallejo-Marín 2013). With more than 5000 species likely being bee-pollinated, Melastomataceae may form the largest radiation of buzz-pollinated flowers (Melo et al. 2021). In addition to buzz pollination, Renner reported observations by colleagues on shifts to alternative pollination strategies such as hummingbird-, bat- or rodent-pollination in the four Neotropical tribes Blakeeeae, Melastomateae, Merianieae and Miconieae. These pollinator shifts generally go along with changes in reward type through the secretion of nectar (Varassin et al. 2008; Dellinger et al. 2019a). In the past 31 years, field investigations on pollination in Melastomataceae...
have led to the discovery of several unexpected new pollination systems. In the Merianieae genus *Axinaea*, for example, passerine birds visit the nectarless flowers, and are rewarded by nutritional staminal food bodies, which, at the same time, function as bellows-like air-filled pollen expulsion organs (Dellinger et al. 2014). Further, recent fieldwork has shown that nectar-producing Merianieae commonly rely on pollination by mixed assemblages of both diurnal and nocturnal pollinators, such as diurnal hummingbirds and nocturnal rodents (Dellinger et al. 2019b). In the tribe Miconieae, in turn, several cases of generalist pollination have been reported, where nectar-secreting species are visited by a large number of insect taxa (Brito et al. 2016). In contrast to the New-World Melastomataceae, Old-World Melastomataceae have never been subject to a systematic literature review on pollination.

It is our aim in this chapter to provide an update of the published pollination records for both New- and Old-World Melastomataceae and to pinpoint tribes and geographic areas which are in particular need for future fieldwork. We then discuss broad patterns of floral trait convergence across the family based on recent work on pollination syndromes in Merianieae (Dellinger et al. 2019a). Using machine-learning algorithms and multivariate statistics, Dellinger et al. (2019a) had differentiated three distinct pollination syndromes in Merianieae: a bee-buzz syndrome, a mixed-vertebrate syndrome and a passerine syndrome. Each of these syndromes is associated with a characteristic set of floral traits. We discuss the most significant of these traits and point out obvious floral trait convergences across Melastomataceae. These floral traits may serve as guides for scientists working in distinct Melastomataceae tribes to correctly predict the most probable pollinators and identify particularly interesting species for field investigations. We emphasize, however, that no prediction can substitute empirical fieldwork (Hortal et al. 2015). Finally, we give a new estimate for the percentage of buzz-pollinated versus other pollination systems in Melastomataceae based on the reviewed literature and discuss drivers of pollinator shifts across the family.

II. Updated literature survey on empirical pollinator observations in Melastomataceae

1. Methods

We performed a systematic survey of the published literature from 1990 to 2020 (following Renner’s seminal work published in 1989) by searching Web of Science using the search terms “Melastomataceae & pollinat*” on 10.10.2020 (197 hits, 70 relevant). We repeated the Web of Science search on 18.12.2020 adding the following country/continent words: “Africa”, “Australia*”, “India*”, “Borneo”, “China”, “Madagascar”, “Philippines”, “Sri Lanka”, “South East Asia” (37 hits, zero
relevant) or specific genera which had not been covered in the first search (12 relevant hits). In order to better cover the South American (particularly Brazilian) literature, we also searched SciELO (30.11.2020, 21 hits, three new and relevant) and for Asian/Chinese literature the Wanfang database (07.12.2020, 103 hits, zero new). In a pre-screening, we considered all papers containing information on flower visitors as relevant. Next, we checked whether the authors of the paper had differentiated illegitimate visitors from pollinators. Given the specialized morphology of Melastomataceae, important primary pollinators may usually be those which are capable of activating the sophisticated pollen expulsion mechanisms. We grouped these as “primary pollinators” and classified them as “buzzing bees” (including oil-collecting bees in Olisbeoideae, see below), “nectar-foraging vertebrates”, “food-body-foraging vertebrates” and “generalist insects”. In the rare cases where authors had classified flower visitors as pollinators that are clearly not capable of triggering pollen release (i.e. small beetles which may occasionally touch both the stamens and the stigma), we classified those as “uncertain or secondary pollinators”. Finally, we also included “pollen thieves, robbers and illegitimate visitors” if they were specified by the authors. We also checked primary sources cited by previous authors and critically differentiated actual field observations from predictions based on floral traits. Finally, we added personal observations on flower visitors or nectar secretion by ourselves and colleagues (Yannick Klomberg, Fabián Michelangeli, Luan Passos, Darin Penneys, Mauricio Posada, Peter Quakenbush).

Next, we went through the obtained lists to correct species names so that they correspond to recent systematic changes following Michelangeli et al. 2021 and http://www.melastomataceae.net/. For calculating the percentage of available pollinator records per genus and the major 18 tribes (plus the monotypic Lithobieae), we followed the species number per tribe estimates provided in Michelangeli et al. 2021. Further, to evaluate whether the number of species with documented pollinators correlates with species diversity per continent, we used continent-wide species number estimates given by Michelangeli (2021). Please note that estimates from Michelangeli 2021 and Michelangeli et al. 2021 differ slightly, but do not change the outcome of our survey. Further, in our pollinator list, we identified those bee genera for which buzzing behaviour has been documented (Cardinal et al. 2018) and marked them in Supplementary Table 1. Finally, to visualize general patterns of pollinator shifts across Melastomataceae, we redrew the phylogenetic tree produced by Reginato et al. 2020. For illustrative purposes, we randomly subsampled each tribe (to 6.5% of species) so that tribes are represented proportionally (R-package phytools (Revell 2012)). We marked tribes where pollinator shifts have occurred.

2. Results
Our review more than double the documented pollination reports provided in Renner (1989) to a total of 272 (4.7% of Melastomataceae). While in some clades, floral visitors have been observed in a substantial portion (> 10%) of their species (Eriocnemeae – 14.3%, Henrietteeae – 11.6%, Marcetieae – 10.1%), no visitor observations at all are available in other clades (Cypostyleae, Dissochaeteae, Lithobieae, Trioleneae) as well as in 16 unplaced species (corresponding to 3.8% of recognized species). Within clades, visitor observations are unevenly distributed, with only 55 of the currently accepted 177 Melastomataceae genera having one or more records (Table 1).

Of the 272 visitor records, 243 stem from the Americas (6.5% of the approximately 3723 New-World species) and 29 from the Old-World tropics (1.4% of the 2027 Old-World species). Most observations are available from known Melastomataceae diversity hotspots in the Brazilian Atlantic Rainforest and the Cerrado (131 observations), the tropical Andes (40 observations), and Costa Rica (35 observations). Among the Old-World species, 1.8% of the ca. 1352 Australasian/Indomalayan species count with pollinator observations, and only 0.8% of the 644 Afrotropical species (including Madagascar). Speciose Old-World lineages such as Sonerileae are largely deficient of observations (1.5% of species with observations). This pattern persists when comparing lineages distributed in both the New and Old World such as Melastomateae: 10.1% of New-World species have documented floral visitors, while only 3.0% of Old-World species do (Table 1).

Consistent with previous reports, buzz pollination by bees is by far the most common pollination strategy in Melastomataceae, with a total of 212 out of the 272 visitor records, documented in 14 out of the 15 clades with flower visitor observations, and reported for 48 (out of 175) genera. Studies where bee-pollinators were identified to lower taxonomic levels show that most Melastomataceae species were visited by a diversity of different buzzing bee taxa (Supplementary Table 1), including the genera Bombus, Xylocopa, Melipona, Eulaema, Euglossa and Augochloropsis. Other buzzing but also non-buzzing bees such as Apis mellifera or Trigona were commonly reported as secondary pollinators or pollen robbers, as well as occasionally visiting small beetles (often Curculionidae), ants or syrphid flies (note that syrphid flies may be important pollinators in generalist Miconieae, however). These visitors may contribute to pollination to a small extent if they touch the stigma when moving around the flower, i.e. to change buzzing position on single anthers, or when collecting residual pollen grains previously expelled by a buzzing bee and lying on petals (Mesquita-Neto et al. 2018; Konzmann et al. 2020).

Shifts to nectar-foraging vertebrate pollinators have been documented in 37 species. These encompass 32 species in the four New-World tribes already reported by Renner (Blakeeae: seven spp., Merianieae: nine spp., Miconieae: eleven spp., Melastomateae: five spp.) and, thanks to new observations by Darin Penneys and Peter Quakenbush, five species in the Old-World tribes.
Astronieae (three spp.) and Sonerlieae (two spp., Supplementary Table 1). In New-World Blakeeae, Melastomateae and Merianieae, mixed assemblages of vertebrates were reported to visit flowers of the same species, such as hummingbirds or flowerpiercers during daytime and rodents or bats during night time. Detailed observations on the pollination efficiency of these different taxonomic pollinator groups have only been conducted in Merianieae (Dellinger et al. 2019b). In the investigated Merianieae species, both diurnal and nocturnal visitors act as effective pollinators, and the same may hold true for the other tribes. In Miconieae, flower visitation by either hummingbirds (in the Andes) or bats (in the Greater Antilles) was reported (Supplementary Table 1). Miconieae further count with a report of otherwise very rare lizard flower visitation (and possibly pollination) in the Lesser Antilles (Timmerman et al. 2008, Supplementary Table 1). While it is possible that these Miconieae species are indeed only visited by either diurnal or nocturnal pollinators, we caution that this may simply be a result of lack of observations at other times of the day. Similarly, in four species of the Melastomateae genus Brachyotum, only diurnal pollinators (hummingbirds and flowerpiercers) have been reported. Again, this may either be due to a lack of nocturnal observations, or it may be the result of the very narrow pseudo-tubular corolla, which is characteristic for the genus and probably limits access to birds with narrow bills and long tongues. In Old-World Astronieae, passerines such as sunbirds, spiderhunters, longbills, and honeyeaters were observed to visit flowers of two species of Beccarianthus (Penneys & Quakenbush, pers. com.). In addition, the same bird taxa were also reported in one species of Astronia (Mack & Wright 1996, Supplementary Table 1). Based on floral traits, bat-pollination is further expected for Beccarianthus pulcherrimus (Penneys 2013). In two Medinilla species (Sonerileae), nectar-foraging passerine bird visitors have also been reported in the Western Ghats of India (Sasidharan & Sujanapal 2005) and are expected for more species also in Madagascar (Quakenbush, pers. com.). To date, there are no indications of shifts to nectar-foraging vertebrate pollinators in mainland Africa. As with some of the New-World species, it remains unclear whether the shifted species are adapted to pollination by only one pollinator group or mixed assemblages of vertebrates. Generally, the few available observations on Old-World species are anecdotal and detailed comparative studies on the pollination biology of all of these Old-World clades are highly needed.

Pollination by food-body foraging vertebrates (birds) is restricted to the tribe Merianieae and reported for six species of the genera Axinaea and Merania. This pollination strategy is associated with the evolution of bulbously inflated stamen appendages, which function in visual pollinator attraction, rewarding (food body) and pollen expulsion through a bellows mechanism activated when the bulbous appendages are compressed by the bird’s bill (Dellinger et al. 2014). Any birds capable of activating the bellows mechanism may serve as pollinators, including passerines (tanagers, flowerpiercers, Dellinger et al. 2014) and parrots (yellow-eared parrot, Posada, pers. com.). Pollinator
observations are only available for Andean species, but floral morphology is suggestive of pollination by food-body foraging vertebrates also in species from the Atlantic Rainforest (Dellinger et al. 2019a).

In 13 species of the tribe Miconieae (some of which are nectar-secreting), generalist pollination (i.e. by representatives of several functional pollinator groups) has been documented (Brito et al. 2016, Supplementary Table 1). These generalist visitor assemblages may be highly diverse and include more than 80 insect taxa such as bees, wasps, flies and beetles. In tribe Melastomateae (Pleroma hospitum), visitation of various insects has been reported (Bergamo et al. 2020). There also is one report of generalist insect visitation (grasshoppers, flies, beetles) in Old-World Pterandra multiflora (Kibessioideae, Momose et al. 1998, Supplementary Table 1). Since no details on reward type and pollen expulsion mechanisms are given in these publications, however, we treat these reports with care.

III. Pollination syndromes: linking convergent floral traits to pollinator behaviour

For a general description of the Melastomataceae flower, please see Chapter 3.

1. Bee buzz pollination

Melastomataceae represent the largest radiation of buzz-pollinated flowers (Melo et al. 2021), and have likely evolved in tight connection with the diversity of buzzing bees. Like most other buzz-pollinated flowers, Melastomataceae are characterized by high numbers of pollen grains (e.g. 300’000-1’000’000 pollen grains per flower in Merianieae, Dellinger et al. 2021) and pollen as sole reward. Unlike most others, however, they are functionally and morphologically exceptionally diverse. Many buzz-pollinated lineages across angiosperms share a single floral phenotype: the Solanum-type flower, with anthers forming a cone in the centre of a flower with reflexed petals (Vogel 1978; Faegri 1986; Russell et al. 2016; Vallejo-Marin et al. 2019). Bee behaviour is relatively stereotypical on this Solanum-type flower, with buzzing bees grasping the anther cone with their legs and mandibles to apply vibrations (Vallejo-Marin et al. 2019). The Solanum-type flower does also occur in Melastomataceae (i.e. Miconia, Graffenrieda), but, more commonly, buzz-pollinated Melastomataceae flowers are open, bowl-shaped flowers with zygomorphically arranged, often heterantherous stamens and highly variable in size (Fig. 1, Dellinger et al. 2019a; Melo et al. 2021). This exceptional floral diversity is commonly referred to as ‘adaptive plateau’ (floral trait combinations guaranteeing high evolutionary success of a lineage; Reginato & Michelangeli 2016; Dellinger et al. 2019c), and may represent adaptations to distinct bee pollinators.

Recent studies have showcased the diversity of interactions between buzzing bees and Melastomataceae flowers (Mesquita-Neto et al. 2018; Konzmann et al. 2020). While buzzing bees
have generally been regarded as one functional pollinator group, Mesquita-Neto et al. (2018) proposed to separate them into two functional groups depending on their behaviour: bees which buzz single stamens versus bees which buzz the entire androecium at once. This buzzing behaviour strongly depends on the relative size-match between the bee and the flower and bees may change from single stamen buzzing to whole androecium buzzing in different Melastomataceae flowers (Mesquita-Neto et al. 2018). Generally, only bees large enough to grasp all stamens at once can vibrate the entire flower (Mesquita-Neto et al. 2018). In very large, sturdy flowers (i.e. Andean *Meriania*), however, even large bees may only buzz single stamens by grasping single stamens by the conspicuous connective appendage (Dellinger et al. 2021). Further, to correctly evaluate whether a buzzing bee is a primary pollinator, one does not only need to consider the buzzing behaviour, but also whether the bee contacts the stigma. Large bees buzzing all stamens are usually likely to touch the stigma, but also small, single-stamen-buzzing bees may touch the stigma if they move around the flower to adjust their buzzing position (Konzmann et al. 2020).

Besides these legitimate buzzing interactions, pollen theft (gleaning: licking pollen out of the apical pore), and pollen robbing (destructive anther cutting), are commonly observed in non-buzzing *Trigona* bees (Renner 1983; Rego et al. 2018). Both gleaning and anther-cutting bees usually contribute little to pollination, and particularly the latter may even negatively impact reproductive success (Rego et al. 2018). Whether such interactions induce adaptive trade-offs, and, consequently, lead to the evolution of strategies discouraging flower visitation by pollen robbers in Melastomataceae, as has been reported for nectar robbers in other plant families (e.g. Barlow et al. 2017), provides a challenging avenue for future research.

Further, in some species in the early-diverging clades Olisbeoideae, Kibessioideae and Astronieae, but also in some Miconieae, anthers dehisce through short longitudinal slits (Goldenberg et al. 2008). Longitudinal dehiscence may, in theory, open flowers to pollination by non-buzzing bees and other insects. Correspondingly, in the Kibessioideae genus *Pterandra*, floral visitation by beetles, grasshoppers and flies was reported (Momose et al. 1998, Supplementary Table 1). Anecdotal observations in Astronia indicate generalization, with flower visitation by non-buzzing *Apis dorsata*, ants, butterflies and beetles, but no detailed pollination studies are available (Quakenbush, pers. com.). All Olisbeoideae species with pollination studies, on the other hand, were buzz-pollinated (Supplementary Table 1). In most species, the dehiscence slits remain relatively short and pore-like, possibly confining species on buzz pollination (Oliveira et al. 2016). More work particularly in the three early-diverging clades is needed to evaluate whether these short slits in combination with pollen rewards may lead to more generalized insect pollination, or whether generalization trends are mostly driven by the evolution of nectar rewards (Brito et al. 2016).
Besides the exceptional diversity in floral architecture, Melastomataceae flowers are also highly variable in colour (Fig. 1). One notable feature in regard to flower colour is the common contrast between the corolla and the androecium (Fig. 2). In many lineages, petals are pink while (parts of) stamens are yellow and hence stick out markedly also in the colour vision of bees (Fig. 2, Velloso et al. 2018). It is possible that this colour contrast helps bees to quickly find the optimal buzzing position in each flower and provides a direct visual cue to pollen (which is usually white or yellow and hidden inside the stamens; Lunau 2000). Particularly in heterantherous species (species presenting two distinct sets of stamens), such colour contrasts may be important in focusing the bee’s foraging on the specific colour-contrast-stamens (Telles et al. 2020). Importantly, although often only appendages are coloured differently in human vision, the entire androecium may contrast when photographed with a UV-sensitive lens (Fig. 2). Further, colour patterns may not only function at the within-flower level in Melastomataceae but be adaptive even at the plant level. Brito et al. (2015) demonstrated that in **Tibouchina pulchra**, the retention of old flowers, which have undergone a colour change from white to pink, functions to increase visibility of and visitation to fertile first-day flowers.

In contrast to flower colour, floral scent has never been studied systematically in bee-pollinated Melastomataceae. Certain lineages, such as Blakeeae, have strongly scented flowers with sweet, heavy perfumes (Penneys & Judd 2013). A rose-like fragrance dominated by phenylethyl alcohol was reported in **Blakea maurofernandeziana**, and a lemon-like scent composed of monoterpenes in **B. anomala** (Wester et al. 2016). In Merianieae, we found weak, rose-like scents in **Meriania maxima**, dominated by the terpenoid β-Barbatene, and floral fragrances of **Graffenrieda penneysii** were dominated by (E)-β-Caryophyllene*, in addition to 23 terpenoids and unknown substances, but no floral scent was noticeable to the human nose (Scheer 2019). This lack in broad-scale floral scent data in Melastomataceae clearly limits our understanding of the role of traits involved in pollinator attraction (and possible pollen-robber deterrence) in the family in general. Recent investigations in buzz-pollinated **Solanum rostratum** have revealed, for example, that heterantherous stamens differ in the proportion of emitted scent compounds, with pollinating stamens producing high amounts of scents particularly attractive to bees (Solís-Montero et al. 2018). Future studies in Melastomataceae quantifying floral scents are hence direly needed in order to work out the potentially integrated and interrelated adaptive role of floral attraction traits. Further, observations in **Tibouchina** and **Meriania** indicate scent emission from stamens (Pereira et al. 2011; Dellinger, pers. obsv.), but systematic comparative data are hitherto lacking.

The androecium represents the morphologically and architecturally most diverse organ type in Melastomataceae flowers (Dellinger et al. 2019a, also see Chapter 27). Generally, poricidal anther dehiscence is believed to have evolved as pollen-dosing strategy to alleviate the pollen dilemma.
arising through the dual function of pollen as reward and male reproductive agent in pollen-rewarding flowers (Konzmann et al. 2019). Our understanding of how differences in stamen traits in Melastomataceae contribute to pollen dosing in response to bee buzzes is in its infancy, however. Many buzz-pollinated species bear conspicuous connective appendages of different colour, size, shape and structure. Renner (1989) suggested that these appendages serve as handles for bees to grasp when applying vibrations, and this was also confirmed by our observations in Merianieae (Dellinger et al. 2019a). In addition, recent experimental investigations have highlighted more refined functions of stamen appendages as pollen dosing devices (Bochorny et al. 2021). Clipping the cork-screw-shaped connective appendages off stamens of Huberia bradeana (Pyramieae), for example, led to a significantly lower percentage of pollen released per buzz than when flowers were intact (Bochorny et al. 2021). Hence, appendages enhance pollen release in this species, possibly as an adaptation to low bee visitation rates. Further, many buzz-pollinated Melastomataceae species have sturdy stamens with strongly corrugated thecal walls (thickening of endothecial cells), which may, again, influence pollen release dynamics (Dellinger et al. 2019a). The Merianieae species Adelobotrys ascendens, for example, is heterantherous, with one set of stamens having corrugated thecal walls and the other having smooth walls. Artificially vibrating A. ascendens flowers, we found that higher proportions of pollen are released from the short, smooth anthers than from the long, corrugated anthers (Dellinger et al. 2019d). Further, stamen traits such as pore size and orientation of the anther tip (bearing the pore) critically influence how and in which direction pollen is released (Dellinger et al. 2019d; Konzmann et al. 2020). Experimentally removing the anther tip in Rhynchanthera grandiflora, for example, led to unfocused pollen scattering, while an intact anther tip accurately placed pollen on the bee’s back (Konzmann et al. 2020).

Recently, much attention has been given to heteranthery, common in some Melastomataceae lineages (Melo et al. 2021). While heteranthery has classically been explained through Darwin’s ‘division-of-labour’ hypothesis, with one stamen type (feeding stamens) functioning in pollinator rewarding and the other in pollination (pollination stamens), recent investigations indicate that the functioning may be more complex. Konzmann et al. (2020) proposed that differently sized stamen types allow Melastomataceae flowers to exploit a wider range of differently sized buzzing bee pollinators, particularly if pollen is scattered widely across the bee’s body. Size-matching between flower and bee is critical for successful pollen transfer (Solis-Montero & Vallejo-Marín 2018), but the relation between bee-buzzing position, pore and stigma location have rarely been investigated. Some recent, exciting findings in Macairea radula (Marcetieae) indicate strong selection gradients imposed by bees on style dimorphism and intermediate levels of heteranthery, favouring flowers with high amounts of pollen grains (Oliveira et al. 2020). Taken together, more experimental work on species differing in traits potentially influencing pollen release dynamics and pollen deposition, such
as appendage size and shape, anther length and structure, pore size and orientation or stigma-pore distances are required to more deeply resolve the functional significance of these traits.

2. Pollination by nectar-foraging vertebrates

As we show here, shifts from bee-pollination to nectar-foraging vertebrate pollinators have occurred repeatedly, at least 15 times (and possibly more often): Astronieae: at least twice (in Astronia and Beccarianthus); Blakeeae: at least twice (in former Chalybea and Blakea); Melastomateae: possibly three times (in Brachyotum, Chaetogastra and possibly Pleroma, Guimarães et al. 2019); Merianieae: possibly three times (all in Meriania, Dellinger et al. 2021); Miconieae: possibly five times (twice in Caribbean Miconia, three times in Miconia III (plus one shift from generalist pollination in section Cremanium, Goldenberg et al. 2008; Kriebel & Zumbado 2014; but see Reginato et al. 2020 for different topology)); Sonerileae: possibly three times (in Medinilla, Catanthera, Driessenia), Fig. 1, Supplementary Table 1). Shifts to vertebrate pollinators occurred both in New-World and Old-World lineages and are associated with clear changes in floral traits, most prominently in reward type (from pollen to nectar) and pollen expulsion mechanism from buzzing to non-vibratile pollen release (Stein & Tobe 1989; Varassin et al. 2008; Dellinger et al. 2019b). There is continued controversy about the location of nectar secretion, which also differs among clades (i.e. petal nectaries in Sonerileae and possibly some Miconieae, staminal non-structural nectar secretion in other clades, Fig. 2, Vogel 1997). Field investigations are required to accurately determine the onset of nectar secretion and the location of nectar release. For example, while hypanthial nectaries have been proposed in Merianieae based on microtome sections (Varassin et al. 2008), we did not find any nectar in the hypanthium using bagging experiments in the field. Instead, in many species, nectar oozed out of horizontal dorsal filament ruptures, which formed within the first hours of anthesis when inflexed stamens folded outwards (Dellinger et al. 2019b, Fig. 2). We observed similar necrotic ruptures at the point of stamen inflexion in other nectar producing species such as Chaetogastra grossa, Brachyotum ledifolium and B. lindenii (both Melastomateae, Fig. 2; also reported in Pleroma cleistoflorum (Ule 1896) or Miconia sintenisii (Miconieae, also see Vogel 1997). Nectar drops formed in bagged flowers on these ruptures (Vogel 1997; Kopper 2021). In some flowers of Meriania, we detected stomata on connective appendages, but never observed nectar to be extruded by these stomata (Dellinger et al. 2019b). We hence disagree with Varassin et al. (2008) and argue that, at least in Merianieae, stomata are not involved in nectar production but, potentially, in scent release (see below). Nectar-sugar composition has, to our knowledge, only been studied in Merianieae. In these species, we found a textbook-example of pollination syndromes, with species pollinated by specialized nectar-feeding birds (hummingbirds) producing sucrose-rich nectar while species pollinated by generalist birds (flowerpiercers) produced nectar rich in hexose sugars.
(Dellinger et al. 2019b). Whether these patterns hold true also for other tribes and Old-World Astronieae and Sonerileae remains to be investigated.

Melastomataceae flowers pollinated by nectar-foraging vertebrates are further characterized by pendant flowers with pseudo-tubular (e.g. Astronia, Brachyotum, Miconia (former Charianthus)) or pseudo-campanulate (e.g. Blakea, Merania) corollas (Varassin et al. 2008; Dellinger et al. 2019a). At least in Merianieae, the positioning of these flowers is indicative of the pollinators: flowers projected from the surrounding foliage by long inflorescence stalks are pollinated by hovering pollinators (hummingbirds and bats) while flowers close to surrounding twigs and leaves are usually pollinated by perching birds or rodents (Dellinger et al. 2019b). Since vertebrates cannot buzz stamens, we observed convergent traits facilitating non-vibratile pollen release. While most species have retained poridical anthers (Astronieae have short slits), thecal walls have softened so that externally applied pressure when vertebrates insert their mouthparts into the flowers to take up nectar, triggers pollen release (“salt-shaker” mechanism, Stiles 1992; Dellinger et al. 2019a; b). In Chaetogastra grossa, we recently observed pollen release through a “bounce” mechanism, where the bifid elongated dorsal stamen appendage functions as a spring, bouncing back and triggering pollen release when the pollinator retracts its head from the flower (Kopper 2021). Otherwise, stamen appendages are often reduced in nectar-secreting species and are not directly involved in the pollination process (Dellinger et al. 2019a).

Floral scents have been studied in detail only in vertebrate pollinated species of Pyxidantheae and Merianieae (Wester et al. 2016; Dellinger et al. 2019b). Wester et al. found passerine- and rodent-pollinated Pyxidantheae to be unscented. In Merianieae, hummingbird- and bat-pollinated Merianieae had scent profiles dominated by aliphatics and terpenoids, while scents of hummingbird- and rodent-pollinated species were dominated by aliphatics only (Dellinger et al. 2019b). Importantly, rodent-pollinated Merania sanguinea released solvent-like odours (3-hexanone, 1-hexen-3-one), which are otherwise only known from rodent-pollinated African Cytinaceae (Johnson et al. 2011). We have, however, noticed such scents in ground-flowering, nectar-producing Miconieae and the potential function of these compounds in communication with mammal pollinators provides an exciting avenue for future work. Flowers of Chaetogastra grossa produce garlic-like odours, while we did not notice any odour in the flowers of Brachyotum. No data on floral scents is available from Old-World vertebrate-pollinated species. Finally, the location of scent production remains unknown; dissecting anthetic flowers of Merania sanguinea in the field and putting organs into separate Eppendorf tubes for one hour, we found only tubes containing stamens to be scented. Whether the scent is produced by the tissue underlying the stomata on the connective appendage, or comes from the nectar, remains unclear.
Finally, numerous Old-World lineages merit further investigation. Flower morphology of several lineages in Sonerileae is indicative of pollinator shifts. The Asian genus *Catanthera*, for example, contains species with pseudo-campanulate corollas and exerted styles, which may potentially be pollinated by birds. The species *Driessenia phasmolacuna* has cauliflorous, pseudo-campanulate white flowers (Lin 2019), possibly also indicative of a shift to vertebrate (potentially bat) pollinators.

3. Pollination by food-body foraging vertebrates

Food-body rewards have, to date, only been documented in the Merianieae, where they have evolved at least three times from bee pollination in the genera *Axinaea* and *Meriania* (Dellinger et al. 2014; Valverde et al. in prep). In these food-body-rewarding species, bulbous connective appendages are co-opted into multifunctional organs serving as attractor cue and sugar reward for passerine birds (tanagers) and as “bellows”-organ for effecting pollen release (Dellinger et al. 2014). These flowers are further characterized by urceolate corollas and long, exerted styles. As in bee-pollinated species, stamen appendages form a marked colour-contrast against the corolla in most species. Stamen thecal walls are usually sturdy but smooth, likely facilitating pollen release when the bellows mechanism is activated (Dellinger et al. 2014). We believe that the rarity of this pollination mechanism across Melastomataceae may be due to a constraint for the complex bellows mechanism to evolve (Dellinger et al. 2021). Possibly, markedly enlarged, sturdy connective appendages as occurring in Merianieae are a pre-requisite for this pollination strategy to evolve. Pyxidantheae have similarly sturdy stamens, but lack the enlarged appendage.

4. Generalist pollination systems

Generalist pollination strategies have, to date, only been studied in detail in *Miconia*, where they evolved at least four times (clades *Miconia* III, *Miconia* IV and *Leandra*, see Chapter 11). In contrast to the other pollinator shifts, they are not always associated with changes in reward type (Brito et al. 2016). Some species produce minute nectar droplets (Kriebel & Zumbado 2014). Varassin et al. (2008) and Kriebel & Zumbado (2014) suggest nectar secretion through small stomata in the proximal part of the stamen connective, and Kriebel & Zumbado (2014) and Brito et al. (2017) found small amounts of nectar on the petals and ‘lower parts of the anthers’ during field investigations. In *M. corymbiformis*, we found nectar secretion by filament ruptures, at the point of filament inflexion in bud stage (Fig. 2, also see Vogel 1997). Generally, nectar secretion did also increase the number of different visitor guilds documented on flowers (Brito et al. 2016). Most importantly, all species investigated show adaptations facilitating pollen release with non-vibrating insects, such as enlarged stamen pores, dehiscence through slits and shorter anthers (Brito et al. 2016). Detailed field investigations are required in the early-diverging tribes Olisbeoideae, Kibessioideae and Astronieae to clarify whether non-poricidal dehiscence in these clades is associated with generalized pollination.
strategies. Further, generalist Miconieae flowers are small, often completely white and may produce sweet fragrances. At least from our current understanding, there seems to be some overlap between specialization on nectar-foraging vertebrates and generalization. The Antillean species *M. sintenisii*, for example, has been reported as bat pollinated (Judd 2007), but also as generalist (Kriebel & Zumbado 2014). In Ecuadorian cloud forests, we have observed bees, flies, wasps and hummingbirds as visitors of nectar-secreting *M. corymbiformis*, with insects likely being the primary pollinators (Dellinger, pers. obsv., Supplementary Table 1). Investigating under which conditions and selection regimes species adapt to a generalist (insect) pollination strategy or specialize on nectar-feeding vertebrates, and to what extent these two strategies overlap (i.e. in section *Chaenopleura*) provides a challenging and exciting avenue for future work.

5. Potential other syndromes and unclear cases

There are several lineages in Melastomataceae with trait combinations potentially indicating pollination strategies not reported yet. For example, several species with herbaceous habit and often closed flowers have evolved in shady, moist environments across the Bertolonieae, Melastomateae, Trioleneae, Sonerileae and Merianieae (Bacci et al. 2019). In three species (*Bertolina paranaensis*, *B. mosenii*, Bertoloneae; *Salpinga secunda*, Merianieae), flower visitation by buzzing bees has been observed (Passos et al., submitted, Michelangeli, pers. com.), and it is possible that buzz pollination also is common in the other tribes. In addition, however, notable cases of autonomous self-pollination have been reported in Bertolonieae (Passos et al., submitted), Trioleneae (Warner 1981) and Miconieae (Kopper 2021), where pollen germinates within the stamens and grows towards the stigma. Vivipary has further been reported for Betoloneae, Merianieae and Trioleneae (Bacci et al. 2021). Clearly, additional fieldwork is needed to clarify whether there is a common reproductive strategy associated with the growth in the moist, shaded herbaceous understorey (or with closed flowers). As a cautious side-note, a peculiar anecdotal observation of ‘predatophily’ is available for one such species, *Sonerila pulnyensis*, where flower movement caused by a small frog catching flower-visiting insects supposedly triggers pollen release (Karuppusamy 2019).

Further, while buzz pollination has been reported for seven species in Olisbeoideae (Supplementary Table 1), many species in the tribe are characterized by a small oil gland on each stamen (Buchmann & Buchmann 1981; Stone et al. 2008). Renner (1984) reported *Melipona* bees to actively collect this oil, but after further investigations, rejected this finding (Renner 1989). More recently, buzzing bees (*Melipona subnitida*) were again observed to actively collect the oil from stamens of *Mouriri guianensis* and to use it to seal the entrance to their nest overnight (Oliveira et al. 2016). Since Olisbeoideae are sister to all other Melastomataceae, investigating the adaptive role of
this oil- and pollen-rewarding (and occasional loss thereof in Memecylon, Stone et al. 2008) may provide important insights into the early evolution of Melastomataceae flowers.

Other interesting and unexplored lineages include taxa from the high-elevation Andes such as Bucquetia, Castratella, Chaetolepis (all Melastomateae), and the ground-flowering cushion plants Miconia chionophila (Andean) and Miconia sphagnicola (Antillean). While the three high-elevation genera are possibly buzz-pollinated with typical poricidal anthers, the two Miconia species have anthers dehiscing by slits, which, together with their ground-flowering habit, may point towards two other cases of pollinator shifts or selfing. In another ground-flowering cushion species from the Brazilian Itatiaia mountains, Pleroma cleistoflora (Melastomateae), flowers do not open during anthesis, (Ule 1896). Although one may assume autonomous selfing or apomixis in such flowers, Ule (1896) reported the flowers as protandrous, with well-developed reproductive organs. Further, he documented nectar secretion through filament ruptures and often found flowers destroyed, with parts of petals lying on the ground (Ule 1896). During 14 days of field observations, he could not document any pollinators (Ule 1896; sic Renner 1989). Again, the combination of characters (ground-flowering, nectar production) and no floral visits during daytime may indicate nocturnal rodent pollination, although we have also observed tanagers destroying Melastomataceae flowers while foraging (Dellinger, pers. obsv.). Finally, Ule (1896) reported nectar secretion and campanulate corollas in two species, Pleroma itatiaiae and P. hospitum, closely related and occurring in the same area as P. cleistoflora, supporting the idea of additional pollinator shifts in this group. Indeed, Bergamo et al. (2020) recently reported flower visitation of various insect taxa to P. hospitum, suggesting a generalized pollination strategy in Melastomateae.

Finally, apomixis has been reported in Miconieae (Santos et al. 2012) and Microlicieae (Viana et al. 2021). Importantly, apomixis does not necessarily preclude insect visitation in Melastomataceae (Maia et al. 2016). It is hence possible that pseudogamous apomixis (apomicts in need of fertilization of polar nuclei through pollen, Hörandl 2010) went undetected by bagging experiments in other tribes (i.e. Merianieae).

IV. Concluding remarks: evolutionary trends and drivers of pollinator shifts

Buzz pollination by bees clearly is the most common pollination strategy across Melastomataceae and, given that it also occurs in Olisbeoideae, the earliest-diverging lineage of the family (Reginato et al. 2020), it may be the ancestral condition for the family as a whole. On the other hand, since the early-diverging lineages (Olisbeoideae, Kibessioideae, Astronieae) sometimes have anthers dehiscing through short slits, potentially indicating more generalized pollination strategies, explicit phylogenetic analyses of pollination strategies and floral trait evolution are required.
Pollinator shifts have happened in at least six tribes, more than 20 times and both in the Old- and New-world tropics. In total, combining available pollinator records and information based on floral traits (pollination syndromes), we estimate that at least 4.5% of species have shifted from buzz pollination to alternative pollination strategies (146 (2.5%) pollinated by nectar-foraging vertebrates, 52 (0.9%) by food-body-foraging vertebrates, and 61 (1.1%) generalist species (Table 1)). This leaves approximately 5,485 species (95.5%) as bee-pollinated. Obviously, these are vague estimates given that flower visitor observations are only available for 268 species, and we believe that future fieldwork may reveal a higher percentage of species which have shifted pollination strategy.

Pollinator shifts clearly associate with growth in high-elevation ecosystems and islands in all tribes, with notable exceptions in some Miconieae (e.g. Brito et al. 2016). The tropical Andes, mountain tops of the Atlantic Rainforest, Antillean mountains as well as the Whestern Ghats and island mountains in the Philippines contain species which have shifted pollination strategy (Supplementary Table 1). No pollinator observations are available from Madagascar, but pseudo-campanulate corollas in several Malagasy Medinilla species are indicative of pollinator shifts (Quakenbush, pers. com.). Surprisingly, there is no indication of pollinator shifts on the African continent, despite relatively high Melastomataceae species richness in mountainous areas such as Mount Cameroon (Reginato et al. 2020). Again, this may simply be the result of extremely scarce observation data for African species, or point to a different evolutionary history i.e. shaped by dry and wet periods rather than mountain uplift (Veranso-Libalah et al. 2018). Other than that, the recurring association between elevation and pollinator shifts across Melastomataceae is likely driven by the cooler, windy and often rainy weather conditions prevalent in mountains, effectively reducing bee-pollination efficiency (Brito et al. 2012; Dellinger et al. 2021).

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References


Figure 1. Flower diversity and pollinator shifts across Melastomataceae. Buzz-bee-pollinated flowers are most common (inner circle, grey letters), with generally reflexed corollas and actino- or zygomorphically arranged, often visually contrasting androecia offering pollen rewards. Shifts to nectar-foraging vertebrates have occurred in six tribes (Astronieae, Sonerileae, Pyxidantheae, Melastomateae, Merianieae, Miconieae; outer circle, red letters) and go along with shifts to nectar rewards and pseudo-tubular or pseudo-campanulate corollas. Shifts to food-body-foraging vertebrates occurred only in tribe Merianieae (outer circle, yellow letter), with the evolution of bulbously-inflated sugary stamen appendages and bowl-shaped to urceolate corollas. Shifts to generalist pollination are documented in tribe Miconieae (outer circle, green letter), often with nectar secretion, open corollas, actinomorphic androecia and enlarged stamen pores. The 18 tribes are represented corresponding to their size, number and proportion of species per tribe with flower visitor observations are given. Shifts are indicated by * approximately where they occurred on the phylogeny (note that in Merianieae, two additional shifts to nectar-foraging vertebrates and two additional shifts to food-body-foraging vertebrates occurred, but are not indicated due to limited
Figure 2. Flower colour-contrast in buzz-bee-pollinated *Meriania maguirei* and common sites of nectar secretion in Pyxidantheae, Merianieae, Melastomateae and Miconieae. (A) Flower of *Meriania maguirei* viewed in normal light and (B) through a UV-sensitive lens, with the entire androecium clearly visually contrasting against the corolla. (C) Pseudo-campanulate, pendant flower of *Blakea chlorantha*, nectar accumulating between corolla and filaments. (D) Ventral filament rupture in *B. chlorantha*, and site of nectar secretion. (E) Flower of *Meriania tomentosa*, with petals partly removed, nectar accumulation on dorsal filament ruptures which form within the first six hours of anthesis. (F) Longitudinal section of filament of *M. tomentosa*, the dorsal filament rupture reaches the vascular bundle, from which nectar is secreted. (G) Pseudo-campanulate flower of
Chaetogastra grossa, arrow indicating site of nectar secretion at ventral filament bent. (H) Detail of (G), reaching vascular bundle. (I) Pseudo-tubular flower of Brachyotum sp. (J) Ventral filament ruptures on stamen of Brachyotum sp. (K) Detail of (J), reaching vascular bundle. (L) Generalist Miconia corymbiformis with nectar secretion from filament ruptures indicated by arrow. (M) Detail of (L), reaching vascular bundle. (N) Nectar-secreting Miconia barbipetiolata, nectar droplets aggregating in each involute petal tip (arrows). (O) Involute petal of M. barbipetiolata with necrotic tissue rupture through vascular bundles, likely site of nectar secretion. Scale bars: A, B, C, E, G, I, L, N – 1 cm; D – 200 µm; F, H – 100 µm; O – 300 µm; K, L – 500 µm.

Table 1. Number of species per tribe with flower visitor observations in relation to clade size (number of genera, number of species) and distribution (OW – Old World; NW – New World, following Michelangeli et al. 2020); we separated pollinators into four major groups. * indicate most probable pollination syndrome (based on general floral morphology), *? indicates uncertainty in pollination syndrome.

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