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Abstract

The concept of pollination syndromes is used to study and analyze convergences in floral trait combinations across flowering plants. Pollination syndromes are based on the assumption that pollinators with similar behavior, morphology and sensory system (functional group) exert similar selective pressure on a flower, leading to convergent floral phenotypes irrespective of phylogenetic affinities. In one of the largest plant families worldwide, Melastomataceae (ca. 5400 sp.), pollination syndromes have only been described in one tribe of ca. 300 species, the Merianieae. For Merianieae, three well differentiated pollination syndromes ("buzz-bee", "passerine", "mixed-vertebrate") were reported. Importantly, these syndromes were best characterized by highly system-specific traits and only to a lesser extent by floral traits important in traditional pollination syndrome studies. To date, it remains unclear whether these specialized pollination syndromes are applicable also to other Melastomataceae tribes.

In my thesis, I hence tested whether the three pollination syndromes put forward for Merianieae ("buzz-bee", "passerine", "mixed-vertebrate") are also found in three other Neotropical Melastomataceae tribes (Melastomeae, Blakeeae, Miconieae), and whether the same traits are important in differentiating syndromes across these tribes. Further, I investigated which traits differ between the three pollination syndromes and whether the different pollination syndromes differ in morphological diversity (i.e. disparity). To answer these questions, I collected flowers and observed pollinators during a fieldtrip to Costa Rica and Colombia in February and March 2020 and compiled a trait matrix of 74 functional traits across 59 species of the four Neotropical tribes (Melastomeae, Blakeeae, Miconieae, Merianieae) where pollinator shifts occurred. I used statistical classification methods (Random Forest Analyses) to sort flowers into pollination syndromes, and multivariate statistics based on a dissimilarity matrix to test for differences between and within the different pollination syndromes.

I found that two of the three pollination syndromes ("buzz-bee" and "mixed-vertebrate") found in Merianieae were also clearly detected in the three other tribes while the "passerine" pollination syndrome only occurs in the tribe Merianieae. Note, that I had one species (*Brachyotum ledifolium*) in my data set that was exclusively pollinated by hummingbirds, hence I excluded this syndrome from disparity and trait importance analyses. All syndromes were significantly different from each other, except for the "hummingbird" syndrome. Like in Merianieae, I found that system-specific traits were of high importance in differentiating the three pollination syndromes ("known mode of pollen expulsion", "reward type", "corolla shape"). Furthermore, I found the highest disparity within the "buzz-bee" syndrome, followed by the "mixed-vertebrate" syndrome. I could not reliably classify four species (*Tibouchina mollis, Miconia reducens, Clidemia epiphytica, Aciotis levyana*) into either of the four pollination syndromes ("buzz-bee", "mixed-vertebrate", "passerine" and "hummingbird") either because of missing data (e.g. *T. mollis*) or because the species may actually exhibit other syndromes (*Miconia reducens*). I found strong evidence for an extreme case of self-pollination in *Miconia reducens*, and possibly, a "selfing" syndrome needs to be included in future studies in Melastomataceae pollination syndromes. *Aciotis levyana* and *Clidemia epiphytica* on the other hand, possibly belong to a "generalists" syndrome (some generalist species occur in the tribe Miconieae) or may be pollinated by some other functional pollinator group (i.e. tiny flies or coleoptera). In conclusion, the highly system-specific floral traits identified as important in delineating pollination syndromes in Merianieae appear useful also across Melastomataceae. Additional fieldwork and wider taxon sampling are required, however, as well as the potential consideration of additional (i.e. selfing, generalist) syndromes.

Keywords: pollination syndromes, pollinator shifts, Melastomataceae, Merianieae, Blakeeae, Melastomeae, Miconieae, floral functional traits

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1. Introduction

"Pollination syndromes" are defined as suites of floral traits which have evolved repeatedly across angiosperms in adaptation to distinct functional pollinator groups (i.e., a group of pollinators which exerts similar selective pressures on flowers due to similarities in behavior/morphology/dietary preferences/sensory systems, Fenster et al. 2004). Flowers that are pollinated by the same functional group have evolved convergent floral trait combinations (Ashworth et al. 2015), while flowers being pollinated by different functional groups have evolved different trait combinations (Fenster et al., 2004). Pollination syndromes have been developed to classify flowers under a functional ecological perspective (Ollerton et al. 2009) by their most efficient pollinator (pollinator that contributes the most to pollen transfer between conspecifics, Rosas-Guerrero et al. 2014), irrespective of their phylogenetic relationship (Schiestl & Johnson 2013). They may also be used to predict pollinators (Lagomarsino et al. 2017, Rosas-Guerrero et al. 2014) for species where no direct pollinator observations are available (Dellinger et al. 2018).

Several studies show strong support for the concept of pollination syndromes (Lagomarsino et al. 2017, Dellinger et al. 2018), even across angiosperms (Rosas-Guerrero et al. 2014). Other studies have raised concerns, however, about the liability of this concept (Hingston & McQuillan 2000, Ollerton et al. 2009). Major points of criticism are: the over-simplification of complex animal-plant interactions, the focus of studies on specialized systems, using pollination syndromes to predict pollinators for clades where no empirical pollinator observations are available, the lack of a unified terminology/methodology of how to score traits and the focus on only a few floral traits (summarized by Dellinger 2020). Promising solutions to some of these problems have been proposed, however. While most studies focused on a few sets of traits, often "easy to score" attraction traits, it pays off to include additional traits (e.g. efficiency traits) specific for the studied

syndrome in the analyses to improve the predictions of confirmed and unknown pollinators (Dellinger et al. 2020). The detailed assessment of the pollinator community of a species, for example, helps to correctly identify the most efficient pollinator (Rosas-Guerrero et al. 2014). Also, a more detailed recording of traits (Abrahamczyk et al., 2017) was shown to improve the ability to predict pollination syndromes and make up for some of the shortcomings of this concept (Dellinger 2020). Dellinger (2020) concludes that the concept of pollination syndromes is robust, both at large and small scales, as long as the known shortcomings of this concept are accounted for. Each study system has its own specific trait combinations and morphological peculiarities, which need to be identified before developing trait categories (Dellinger 2020). In order to guarantee high predictive accuracy, the floral traits most clearly discriminating syndromes in each plant group need to be identified (Dellinger et al. 2018).

The concept of pollination syndromes traditionally distinguishes between eleven functional pollinator groups: bee, bird, bat, fly, wasp, moth, butterfly, long-tongued fly, beetle, carrion fly and nonflying mammal (Delpino, 1890, Vogel, 1954, Ollerton et al. 2009, Rosas-Guerrero et al. 2014, Dellinger 2020). All traditional syndromes can be further divided (Philips et al. 2020). The moth syndrome, for example, can be divided into long- and short-tongue moths (Whittall & Hodges 2007). Another example for further subdividing a traditional syndrome is the bee syndrome, where the “buzz-bee” sub-syndrome may be differentiated (Michener 1962, Endress 1996). The “buzz-bee” syndrome is characterized by tubular poricidal anthers (i.e. anthers opening by a small apical pore), pollen as the only reward and pollen release only when bees apply specific vibrations to the anthers (Renner 1989, Buchmann 1983, Endress 1996). Buzz-pollinated flowers tend to possess large, showy, often yellow anthers and the apical part of the filament is often enlarged and brightly colored. Single anthers or the entire androecium form a resonating chamber, from which pollen can be removed (Endress 1996). In monosymmetric flowers the filaments are often arching, aligning

the anthers close to the median plane of the flower (Endress 1996). Generally, buzz-pollinated flowers are morphological highly diverse (Dellinger et al. 2018). In some families (e.g. Melastomataceae, Ericaceae, Gesneriaceae) the endothecium of the anthers is thickened (Endress 1996, Cortez et al. 2014). In Melastomataceae this trait often co-occurs with crumpled or ruminated thecal wall structure (Dellinger et al. 2018). This has been interpreted as a mechanism for pollen dosage (Caetano et al. 2020; i.e. in addition to mostly tubular anthers), since pollen is held back by the irregular cell wall structure.

Another important evolutionary and ecological process related to pollination syndromes are pollinator shifts. Pollinator shifts are defined as shifts form one functional pollinator group to another functional group (Thomas & Wilson 2008). There are two basic mechanisms for pollinator shifts. Intrinsic mechanisms where the floral morphology changes and the environment stays the same and extrinsic mechanisms where the environment changes and then the flower adapts. Examples for extrinsic causes are pollinator shifts along elevational gradients (Arroyo et. al 1982, Renner 1989, Varassin et al. 2008, Lefebvre et al. 2018), when a pollinator disappears from a community or when plants expand their distribution (Thomas & Wilson 2008). Per definition, pollinator shifts lead to significant changes in selection regimes on flowers (Smith & Kriebel 2018, Dellinger et al. 2019a). Consequently, pollinator shifts affect a large number of different floral traits, including traits involved in pollinator attraction as well as traits ensuring successful pollen removal and deposition by the most efficient pollinator(s) (Galen 1989, Bradshaw & Schemske 2003). Bradshaw & Schemske (2003) showed, for example, that a single major mutation e.g. in floral color, can result in a shift of pollinators (intrinsic cause). Further, pollinator shifts may lead to reproductive isolation between individuals or populations and hence play an important role in speciation (Harder & Barrett 2006, Whittall & Hodges 2007, Smith 2017). Divergent selective pressure on the

reproductive traits, exerted by distinct functional pollinator groups, is considered as the main mechanism of floral diversification (Barrett 2013).

Pollinator shifts may lead to the formation of distinct pollination syndromes even among closely related taxa, thereby increasing flower diversity in a clade. Disparity is a measure to quantify such morphological diversity (Wills et al. 1994, Foote 1997). High disparity might help taxa to adapt to changing environments more easily, since they have a broader spectrum of possible phenotypes to explore (Foote 1997, Chevin et al. 2010). Chartier et al. (2014) found the highest disparity across angiosperms within the early diverging clades (early diverging angiosperms, monocots, early diverging eudicots) while the lowest disparity was found within the malvids (containing Melastomataceae, Myrtales), lamiids, and campanulids and intermediate disparity was found in the basal superrosids, superasterids and fabids. Some lineages where all taxa are essentially pollinated by the same functional pollinator group are characterized by low disparity (e.g. Malpighiaceae, Davis et al. 2014 or *Myrica*, Vasconcelos et al. 2018), which is attributed to stabilizing selection of their pollinators (Davis et al. 2014). In contrast to these findings, Dellinger et al. (2018) demonstrated that the "buzz-bee" pollination syndrome within Merianieae (Melastomataceae) is highly disparate. Furthermore, studying disparity of only subsets of floral traits (i.e. corolla, attraction traits) may inform on their function in the pollination process. Chartier et al. (2017), for example, found that the androecium was significantly more disparate than the corolla or the gynoecium in Ericales, possibly a result of divergent pollinator selection pressures.

Shifts to another functional pollinator group are accompanied by changes in traits mediating the attraction or the efficiency of a pollinator (e.g. Armbruster 1988). Most macroevolutionary studies on pollination focus on attraction traits (e.g. corolla color) in their analyses (e.g. Lagomarsino et al. 2017, Rosas Guerrero et al. 2014, Dellinger et al. 2014, Dellinger et al. 2018) while efficiency traits (e.g. distance of anther pore to stigma) have received less attention (Dellinger et al. 2020).

Generally, attraction traits are of known importance in mediating pollinator shifts and have been central in characterizing pollination syndromes (Armbruster et al., 2005). Interestingly, Dellinger et al. (2018) found that attraction traits (e.g. exposure of flower, display size, scent, color, flower symmetry and timing of anthesis) may be of less importance in differentiating pollination syndromes than efficiency traits (e.g. flower shape and orientation, position of reproductive organs). These findings are supported by a recent meta-analysis, where Caruso et al. (2018) found that pollinator mediated selection is strongest on efficiency traits. Efficiency traits are more likely to contribute to pollinator-mediated diversification than attraction traits (Caruso et al. 2018). This suggests, consistent with Dellinger et al. (2018), that efficiency traits may be more or at least equally important in differentiating the different pollination syndromes. Opedal (2019) found that attraction traits show higher evolvability (the rate at which a trait can adapt e.g. to new pollinators) than efficiency traits. The rate at which traits can adapt to different pollinators are different between attraction and efficiency traits, with efficiency traits adapting more slowly (Opedal 2019, Dellinger et al. 2019). This finding suggests, in contrast to Dellinger et al. (2018) and Caruso et al. (2018), that attraction traits may be of higher importance in differentiating the different pollination syndromes than efficiency traits. It seems that attraction traits can adapt faster to new pollinators (and in fact induce pollinator shifts), while efficiency traits adapt more slowly, but are particularly important when species diversify within their new pollination syndrome (Caruso et al. 2018, Opedal 2019).

The Melastomataceae, the study system I chose for my Master thesis, are a large (about 5400 species), pantropically distributed family most diverse in the New World (about 3500 species) and classified into eight tribes (Renner 1993). The basic melastome flower is usually bisexual and 4-6-merous (Weber et al. 2001). The hypanthium is cup-shaped and bears the perianth and the stamens on a torus near the base of the calyx lobes. The calyx is fused, often with protruding lobes, while

the petals are free (Weber et al. 2001). Most Melastomataceae flowers are pentamerous and possess twice as many stamens as petals, arranged in two whorls. The stamens can be isomorphic or dimorphic, and usually open via terminal pores (poricidal anthers) (Weber et al. 2001). In many species the connective is strongly modified and forms appendages of various types (Weber et al. 2001, Dellinger et al. 2018). Genera with inferior ovaries produce berries, while genera with superior ovaries produce capsular fruits (Weber et al. 2001).

Melastomataceae remain relatively poorly studied with regard to pollination. So far, pollination syndromes have only been studied systematically in one tribe, the Merianieae (Dellinger et al. 2018). Renner (1989) distinguished between buzz-pollination and species pollinated by nectar collecting pollinators (birds, bats, rodents, hummingbirds, bees). Most Melastomataceae are buzz-pollinated by bees (98%, Renner 1989). Bees that buzz Melastomataceae flowers are very diverse in terms of size and/or behavior on the flower (Vogel 1975), which could explain the high morphological diversity of buzz-pollinated flowers in Merianieae and possibly across Melastomataceae. Buzz-pollinated species are characterized by pollen as the only reward, a landing platform provided by the androecium, enlarged and stiffened connective appendages, and, in some clades, strong morphological differentiation into two sets of stamens (heteranthery, Renner 1989). Another characteristic trait of buzz-pollinated Melastomataceae – also present in most buzz-pollinated flowers in other taxonomic groups - are tubular poricidal anthers, from which pollen may only be extracted through vibration buzzes (Buchmann 1983, Endress 1996).

In four Neotropical tribes (Merianieae, Blakeeae, Melastomeae, Miconieae), a small number of species have shifted from bee to vertebrate pollination (ca. 2% of melastome species; Renner 1989, Varassin et al. 2008, Dellinger et al. 2014). Since most of these species are visited by mixed assemblages of vertebrate pollinators normally associated with distinct functional groups (i.e. nectar-foraging passerine birds, bats, rodents, hummingbirds), Dellinger et al. (2018) merged the

nectar foraging pollinators into a single functional group, associated with a characteristic "mixed-vertebrate" syndrome. This syndrome is characterized by a shift from pollen to nectar rewards, changes in the mechanism of pollen release (from vibrations to a "salt-shaker" mechanism, see below), and pseudo-campanulate corolla shapes (as opposed to mostly reflexed corollas). Nectar-rewarding seems to be achieved through different mechanisms (Dellinger et al. 2019a, Varassin et al. 2008). In Merianieae and some other lineages, nectar is produced in the vascular bundle and secreted either directly by small cuticular openings on the filaments or via filament ruptures (Renner 1989, Vogel 1997, Dellinger et al. 2019a). Varassin et al. (2008), on the other hand, also found nectary stomata on the inner hypanthium surface on the ovary apex and on the dorsal side of the connective. Nectar aggregates on the pseudo-campanulate corolla behind the stamens (Dellinger et al. 2018). To facilitate pollen release with the non-vibrating nectar-foraging pollinators, the anther pores are enlarged, and stamen thecae are soft and easily deformable and have changed from an often dorsal ("bee-buzz" syndrome) to a lateral position. Further, they are mostly reflexed, and flowers are pendent, so that pollen may fall out of the anthers more easily when nectar-foraging pollinators insert their mouthparts into the flower and strive against the anthers (i.e. "salt-shaker" mechanism, Dellinger et al. 2019a).

Further, in addition to the nectar collecting pollinators described by Renner (1989), Dellinger et al. (2014) and Dellinger et al. (2018) found another functional pollinator group in the tribe Merianieae: passerine birds, which associate with a distinct "passerine" syndrome. Also, the "passerine" syndrome is characterized by changes in reward type (food-bodies provided by the stamen appendages) and type of pollen expulsion mechanism (appendage works as air pump (bellows) organ). The so called "bellows" pollen expulsion mechanism is activated when the foraging passerine birds rip out single stamens from the flower by the appendage, and the compression of the bulbous appendage causes the ejection of a pollen cloud through the anther pore (Dellinger et al.

2014). “Passerine”-syndrome species are further mostly characterized by urceolate corolla shapes. Although not formally tested yet, pollinator shifts in Melastomataceae seem to associate with occurrence at high elevations. Both species within the “mixed-vertebrate” and the “passerine” syndrome start to occur at an altitude of about 1600 m and can be found up to 3400 m, while bee-pollinated species also occur at sea level (Renner 1989, Dellinger, unpublished).

In contrast to “traditional” pollination syndromes known from other plant clades, pollination syndromes in Merianieae, and possibly Melastomataceae, are characterized by unusual, system-specific floral trait combinations. For example, the complex pollen expulsion mechanisms and unusual rewarding structures were identified as the two traits most reliably differentiating pollination syndromes in Merianieae (Dellinger et al. 2018). It is possible, however, that additional pollination syndromes exist across Melastomataceae. In the tribe Miconieae, for example, several species show generalist pollinator assemblages, with more than 100 different insect species foraging on the flowers (Brito 2016, Gavrutenko et al. 2020). In addition, self-pollination and apomixis are common across Melastomataceae, possibly related to distinct floral trait combinations (Renner 1989).

Species, within the tribe Merianieae that shifted from buzz-pollination to other pollination syndromes retained the tubular poricidal anthers (Dellinger et al. 2014, Dellinger et al. 2018), which possibly represents an evolutionary constraint not only in Merianieae, but in Melastomataceae (Dellinger et al. 2019b). This evolutional constraint most likely hindered the evolution towards “traditional” pollination syndromes, for example towards anthers that open via longitudinal slits (Dellinger et al. 2019a, Dellinger et al. 2019b). Strong floral modularity (i.e. independent evolution of distinct floral traits) in Merianieae allowed to overcome this constraint and facilitated the evolution into new pollination syndromes. In order to explore these ideas, studying pollination syndromes across a broad set of Melastomataceae species is necessary.

In my master thesis I tested whether the three highly system-specific pollination syndromes put forward for Merianieae (Dellinger et al. 2018) also apply to the other three Melastomataceae tribes where pollinator shifts to vertebrates have occurred (Renner 1989), and whether the same traits are important in differentiating these syndromes. I investigated the morphological adaptions to shifts from buzz-pollination to different groups of vertebrate pollinators (e.g. rodents, bats, birds) in four tribes (Melastomeae, Blakeeae, Miconieae, Merianieae). In addition, I compared floral morphology within the different pollination syndromes with a focus on the buzz-pollination syndrome. Finally, I newly described the pollination syndromes for three of the investigated tribes. To avoid known shortcomings of the pollination syndrome concept in my thesis, I inspected flowers of each tribe before developing trait categories, with a focus on morphological features that may play an important role in attracting pollinators or facilitating pollination. In addition to traits traditionally used in pollination syndrome studies (floral color, reward type, floral orientation, floral size, corolla shape etc., Dellinger 2020), I included traits that are specific for the tribes I studied (e.g. appendages shape, structure of thecal wall, pollen grain diameter etc.). To increase the number of species with documented pollinators, and hence reliably relate floral traits to pollinators, I performed video observations during day and the night on species without known pollinators.

2. Objectives and hypotheses

The overall objective of my Master thesis was to characterize pollination syndromes in the three tribes Blakeeae, Melastomeae and Miconieae, and determine whether patterns of floral trait changes and disparity detected in Merianieae also apply to these other tribes. All of these analyses are vital to establish whether the pollination syndrome concept indeed is a useful and reliable tool for predicting pollinators also in other Melastomataceae groups. Specifically, I tested the hypothesis

(Hyp. 1) that the three tribes Blakeeae, Melastomeae and Miconieae show the same three pollination syndromes as put forward for Merianieae. Second, I tested the hypothesis (Hyp. 2a) that species pollinated by the same functional pollinator group converge in pollination syndrome (i.e. multivariate character space) both within and among tribes. Further, I tested (Hyp. 2b) whether the same floral traits (i.e. stamen morphology, reward type, and floral shape) important in differentiating pollination syndromes in Merianieae can be used to discriminate syndromes in the other three tribes. I calculated floral disparity to test (Hyp. 3) whether the "buzz-bee" syndrome is morphologically more diverse than the other syndromes, and whether the androecium is the most disparate floral part. Next, I tested pollination syndromes to predict pollinators for species with unknown pollinators (Hyp. 4). Finally, I assessed the association between pollination syndrome and altitude where my study species were collected, to test whether (Hyp. 5) pollinator shifts associate with growth at high elevations.

3. Material and Methods

3.1 Selection of study taxa

It was my aim to sample both bee- and vertebrate-pollinated species from the Neotropical tribes Blakeeae, Melastomeae and Miconieae. With more than 5000 species, a sampling providing the required breadth and depth across Melastomataceae would not be feasible within the scope of a Master thesis. I focused on species growing in Costa Rica, since the University of Vienna is running a research station in Costa Rica, offering ideal conditions to study Melastomataceae. In addition, I conducted fieldwork in Colombia, given recently established collaborations of my co-supervisor Agnes Dellinger with the Universidad del Valle (Cali, Colombia). From each of the three tribes with documented pollinator shifts (Blakeeae, Melastomeae, Miconieae), I pre-selected ten species where pollinator observations were available from the published literature (summarized by Renner 1989).

*Table 1: Species list of collected samples including the species found in Dellinger et al. 2018 (tribe Merianieae). Additional information: Tribe, Altitude (m), Pollinator observation, Pollination syndrome, Origin of samples (Comments). Buzz = "buzz-bee", Mix = "mixed-vertebrate", Pass = "passerine", HB = "hummingbird". * indicates personal or video observations, otherwise pollinators had already been documented.*

Species	Author	Tribe	Altitude (m)	Video Observation	Pollinator	Data Source
Blakea anomala	Donn. Sm.	Blakeae	1502	No	Buzz	Collected in Costa Rica
Blakea austin-smithii	Standl.	Blakeae	Unknown	No	Mix	Literature, Wester et al. 2016
Blakea chlorantha	Almeda	Blakeae	1583	No	Mix	Collected in Costa Rica
Blakea florifera	Gleason	Blakeae	1883	Yes	Buzz *	Collected in Colombia
Blakea gregii	Almeda	Blakeae	Unknown	No	Mix	Literature, Wester et al. 2016
Blakea litoralis	L.O. Williams	Blakeae	114	Yes	Buzz *	Collected in Costa Rica
Blakea maurofernandeziana	Penneys & Almeda	Blakeae	60	Yes	Buzz *	Collected in Costa Rica
Blakea setosa	(Triana) Penneys & Judd	Blakeae	1376	No	Unknown	Collected in Colombia
Blakea superba	(Naudin) Penneys & Judd	Blakeae	1879	Yes	Buzz *	Collected in Colombia
Aciotis levyana	(Mart. ex DC.) Triana	Melastomeae	70	Yes	Unknown	Collected in Costa Rica
Arthrostemma cf. ciliatum	Pav. ex D. Don	Melastomeae	1377	No	Unknown	Collected in Colombia
Brachyotum ledifolium	(Desr.) Triana	Melastomeae	Unknown	No	HB	Alcohol material, University of Vienn (previous sampling trip)
Brachyotum lindenii	Cuatrec., Danguy & Cherm.	Melastomeae	Unknown	No	Mix	Alcohol material, University of Vienn (previous sampling trip)
Monochaetum cf. floribundum	(Schltdl.) Naudin	Melastomeae	Unknown	No	Buzz	Collected in Costa Rica
Monochaetum cf. vulcanicum	Cogniaux, Célestin Alfred	Melastomeae	Unknown	No	Buzz	Collected in Costa Rica
Monochaetum linearifolium	Almeda	Melastomeae	1840	No	Buzz	Collected in Costa Rica
Tibouchina cf. ciliaris	Vent.	Melastomeae	1990	No	Unknown	Collected in Colombia
Tibouchina grossa	L. f.	Melastomeae	2635	Yes	Mix *	Collected in Colombia
Tibouchina lepidota	(Bonpl.) Baill.	Melastomeae	2008	No	Unknown	Collected in Colombia
Tibouchina mollis	(Bonpl.)	Melastomeae	2754	No	Unknown	Collected in Colombia
Tibouchina oroensis	Gleason, Henry Allan	Melastomeae	Unknown	No	Buzz	Alcohol material, University of Vienn (previous sampling trip)
Tibouchina urvilleana	DC.	Melastomeae	1796	Yes	Unknown	Collected in Colombia
Adelobotrys adscendens	(Sw.) Triana	Merianieae	593	No	Buzz	Data from Dellinger et al. 2018
Axinaea confusa	E. Cotton & Borchs	Merianieae	1800	No	Pass	Data from Dellinger et al. 2018
Axinaea costaricensis	Cogniaux, Célestin Alfred	Merianieae	2600	No	Pass	Data from Dellinger et al. 2018
Axinaea macrophylla	(Naudin) Triana	Merianieae	2400	No	Pass	Data from Dellinger et al. 2018
Axinaea sclerophylla	Triana	Merianieae	2750	No	Pass	Data from Dellinger et al. 2018
Graffenrieda cucullata	(Triana) L.O. Williams	Merianieae	1362	No	Buzz	Data from Dellinger et al. 2018
Meriania aff sanguinea	Wurdack	Merianieae	3100	No	Mix	Data from Dellinger et al. 2018

Meriania cf costata	Wurdack	Merianieae	2900	No	Mix	Data from Dellinger et al. 2018
Meriania drakei	Wurdack	Merianieae	2052	No	Buzz	Data from Dellinger et al. 2018
Meriania furvanthera	Wurdack	Merianieae	2800	No	Mix	Data from Dellinger et al. 2018
Meriania longifolia	Naudin	Merianieae	1259	No	Buzz	Data from Dellinger et al. 2018
Meriania macrophylla	(Benth.) Triana	Merianieae	1860	No	Pass	Data from Dellinger et al. 2018
Meriania maguirei	Wurdack	Merianieae	2850	No	Buzz	Data from Dellinger et al. 2018
Meriania maxima	Markgr.	Merianieae	1888	No	Buzz	Data from Dellinger et al. 2018
Meriania phlomoides	(Triana) Almeda	Merianieae	1414	No	Mix	Data from Dellinger et al. 2018
Meriania pichinchensis	Wurdack	Merianieae	1930	No	Mix	Data from Dellinger et al. 2018
Meriania quintuplinervis	Naudin	Merianieae	2140	No	Mix	Data from Dellinger et al. 2018
Meriania sanguinea	Wurdack	Merianieae	2850	No	Mix	Data from Dellinger et al. 2018
Meriania speciosa	(Bonpl.) Naudin	Merianieae	1875	No	Buzz	Data from Dellinger et al. 2018
Meriania tomentosa	Wurdack	Merianieae	1700	No	Mix	Data from Dellinger et al. 2018
Clidemia cf. epiphytica	Triana	Miconieae	113	No	Unknown	Collected in Costa Rica
Clidemia dentata	Pav. ex D. Don	Miconieae	64	No	Unknown	Collected in Costa Rica
Clidemia globuliflora	(Cogn.) L.O. Williams	Miconieae	1749	No	Unknown	Collected in Costa Rica
Conostegia oerstediana	O. Berg ex Triana	Miconieae	1530	Yes	Buzz *	Collected in Costa Rica
Conostegia subcrustulata	(Beurl.) Triana	Miconieae	70	Yes	Buzz *	Collected in Costa Rica
Leandra subseriata	Naudin	Miconieae	2475	Yes	Buzz *	Collected in Costa Rica
Miconia andreana	Kuntze	Miconieae	1878	Yes	Buzz *	Collected in Colombia
Miconia argentea	(Sw.) DC.	Miconieae	Unknown	No	Buzz	Collected in Costa Rica
Miconia barbata	(Borhidi) Judd, Bécquer & Majure	Miconieae	1990	Yes	Unknown	Collected in Colombia
Miconia cf. lacera	(Bonpl.) Naudin	Miconieae	64	Yes	Buzz *	Collected in Costa Rica
Miconia cf. reducens	Triana	Miconieae	1376	No	Unknown	Collected in Colombia
Miconia donaeana	Naudin	Miconieae	100	No	Buzz *	Collected in Costa Rica
Miconia goniostigma	Triana	Miconieae	1998	No	Unknown	Collected in Colombia
Miconia notabilis	Triana	Miconieae	1946	No	Unknown	Collected in Colombia
Miconia schlimii	Triana	Miconieae	92	No	Buzz *	Collected in Costa Rica
Miconia tonduzii	Cogniaux, Célestin Alfred	Miconieae	2573	No	Buzz *	Collected in Costa Rica
Miconia trinervia	(Sw.) D. Don ex Loudon	Miconieae	64	Yes	Buzz *	Collected in Costa Rica

I employed the following selection criteria prior to my fieldwork: each tribe should be represented by bee pollinated species and species which shifted pollinators; distribution in Costa Rica or Colombia; flowering time in February/March, because my fieldwork was done during that period of time in Costa Rica and Colombia (see below). To determine the distribution and flowering time of the species, I used the website tropicos (https://www.tropicos.org/). I did not find all of the pre-selected species in the field, but I was able to supplement them with other species which fulfill the criteria mentioned above (4 found, 26 substituted, 9 additional). In addition, I included 20 species of the tribe Merianieae found in Dellinger et al. (2018). My final data set contained 59 species of the 4 four Neotropical tribes that shifted pollinators (Fig. 1).

3.2. Fieldwork – Pollinator observations and collection of flower material

I performed fieldwork in Costa Rica and Columbia from 16th February to 16th March 2020. In Costa Rica, I worked at the Tropical Field Station La Gamba (Golfito region, https://www.lagamba.at/), where numerous Melastomataceae species grow. In addition, I carried out sampling trips to lowland (Piedras Blancas, Vulcan Arenal) and mountain rainforests (Cerro de la Muerte, Finca Truchas Selva Madre, Monteverde) to collect floral material and observe pollinators in order to identify possible pollinator shifts along elevational gradients. In Colombia, I worked at "El Refugio" (https://elrefugionatura.jimdofree.com/) located in the Western Cordillera, near the city of Cali and at the Finca Mira Lejos close to Bogotá. In both reserves, Colombian Melastomataceae species have been cultivated and the reserves provide access to pristine rainforest in the surroundings.

I collected fully anthetic flowers of each of the selected study species (Figs 1-4) and recorded the GPS position as well as the altitude. From each species, I collected at least three anthetic flowers and fixed them in 70% EtOH.

Figure 1: Photographs of species of the tribe Blakeeae; A-D:" buzz-bee" syndrome; E-F: "mixed-vertebrate" syndrome; BB = Buzz-Bee, MV = Mixed-Vertebrate.

Figure 2: Photographs of species of the tribe Melastomeae; A, B, D-G: "buzz-bee" pollination; C: "mixed-vertebrate" syndrome; BB = Buzz-Bee, MV = Mixed-Vertebrate, UNK = Unknown.

Figure 3: Photographs of species of the tribe Miconieae; A: unknown pollination syndrome; B-E: "buzz-bee" syndrome; BB = Buzz-Bee, UNK = Unknown.

Figure 4: Photographs of species of the tribe Miconieae; A: "mixed-vertebrate" syndrome; B-D, F, G: "buzz-bee" syndrome; E: possibly "self-pollination"; BB = Buzz-Bee, MV = Mixed-Vertebrate, UNK = Unknown.

Traits that may get lost during fixation or transport like flower color, petal gloss, presence of nectar or relative organ arrangement in flowers of very soft tissue, I scored in the field. These traits are indicated with * in Table 2. I used magnifying glasses, a caliper ruler, a binocular microscope and the Natural Color System (NCS 1989) to score the traits in the field. To determine the pollen-release mechanism, I tried to mimic buzzing the flowers using an electric toothbrush and a vibrating speaker that can be tuned to chosen frequency and amplitude (Dellinger, unpublished). To mimic nectar foraging vertebrates, I used a 10µl capillary to see if pollen is released when the anthers are touched, as known from the "salt-shaker" mechanism (Dellinger et al. 2019a).

In order to reliably relate floral traits to pollinators, and hence delineate pollination syndromes, I also conducted pollinator observations using video cameras for 14 selected species (Table 1, Table 2).

Table 2: List of observed species.

Species	Tribe	Number of days filmed
Aciotis levyana	Melastomeae	1
Blakea florifera	Blakeae	3
Blakea litoralis	Blakeae	1
Blakea maurofernanderiana	Blakeae	1
Blakea superba	Blakeae	1
Conostegia oerstediana	Miconieae	1
Conostegia subcrustulata	Miconieae	1
Leandra subseriata	Miconieae	0,5
Miconia andreana	Miconieae	1
Miconia barbata	Miconieae	2
Miconia barbata	Miconieae	1
Miconia cf. lacera	Miconieae	1
Miconia trinervia	Miconieae	1
Miconia trinervia	Miconieae	1
Tibouchina grossa	Melastomeae	2
Tibouchina urvilleana	Melastomeae	3

Using this approach, I could confirm reported pollinators and detect possible unknown pollinators. I used two video cameras (Sony HDR-CX330) to film freshly opened flowers between 6 am and 6 pm (tropical day) and an infrared night shot camera (Sony FDR-AX100E) to monitor possible

nocturnal visitors between 6 pm and 12 pm (Dellinger et al. 2018). I positioned the cameras between 20 cm and 60 cm away from the flowers. I reviewed the videos using QuickTime Player at 2x or 4x speed and scored pollinators into functional groups (buzzing bees, generalist insects, hummingbirds, bats, rodents, passerine birds). In the following text, I will use the term "pollinator" either for pollinators, confirmed in previous published studies, or documented effective pollen release and touching the stigmas through my video or personal observation.

For 15 selected species I documented the duration of anthesis by labeling 10 buds of different developmental stages and taking pictures in the morning (8 am) and in the evening (6 pm) for 2 to 6 days, depending on the speed of bud development and duration of anthesis. Further, I checked for nectar production, and took samples if nectar was present using 10µl capillaries. I analyzed the nectar sugar concentration using a refractometer.

Finally, to assure correct species identification, I collected two herbarium vouchers for each species (one to be deposited in a local herbarium (e.g. in Cali (Colombia) or San José (Costa Rica) and one transferred to the herbarium of the University of Vienna). I have deposited the Colombian collections in the herbarium in Cali and duplicates await shipping to Austria. Unfortunately, the Costa Rican vouchers got lost on the flight back to Vienna. I verified species identification in the herbaria of the Universidad del Valle (Cali, Colombia) by comparing my collected vouchers with herbarium vouchers from the herbaria of the Universidad del Valle. In addition, I used the Melastomataceae of Central America webpage (https://melas-centroamerica.com/) and expert consultation (Fabián Michelangeli, Eduardo Chacón, Eduardo Calderón).

I was accompanied during field work by my co-supervisor Dr. Agnes Dellinger. Dr. Dellinger has obtained the required research and export permits for collecting plant material and helped finding and identifying plants and classifying floral traits.

3.3 Floral traits studied

I have selected 17 floral traits of the traits identified as most important (Table 3) in separating the three pollination syndromes in the tribe Merianieae (Dellinger et al. 2018). In addition, I have selected 57 traits that may be of evolutionary importance or are commonly used in studies on pollination syndromes (Table 3 & Apx. 1, Dellinger 2020). I performed trait scoring under a functional perspective (targeting trait function during the pollination process), explicitly not focusing on purely systematic or non-functional characters.

The final trait-matrix consisted of 74 traits, of which 7 are general traits (e.g. orientation, reward type, merism), 6 corolla specific traits, 47 traits specific for the androecium, 6 traits specific for the gynoecium and 8 mixed traits, where more than one of these categories applies (e.g. distance of stigma to anther pores). In total there are 16 attraction and 58 efficiency traits in the trait-matrix. I chose the traits in consideration of their functional role when interacting with a pollinator and to describe morphological characters that may be crucial during pollination.

I categorized traits following criteria developed for Merianieae (Dellinger et al. 2018), but I defined new categories for species that did not fit into any of the existing categories.

*Table 3: Floral character code. 17 most important traits separating the three pollination syndromes in the tribe Merianieae and 57 traits that may be of evolutionary importance. * indicates that this trait was scored in the field, # indicates 17 most important traits separating the three pollination syndromes in the tribe Merianieae.*

Floral Character	Number
Mode of pollen expulsion	1*#
Reward type	2*#
Orientation of flower	3*#
Inflorescence or single flower	4*
Floral size	5*
Merism	6*
Site of interaction	7
Petal gloss	8*#
Corolla height	9*#
Ratio between diameter:height	10#
Corolla shape	11*#
Corolla colour	12*
Petal surface	13
Androecial position relative to style (symmetry)	14*
Robustness of stamens	15*
Filament ruptures large anthers	16#
Filament ruptures small anthers	17
Length of large stamen filament	18*
Lenght of small stamen filament	19*
Shape of large stamen filament	20*
Shape of small stamen filament	21*
Large stamen filament position relative to style	22*
Small stamen filament position relative to style	23*
Lenght of large stamen anther	24*
Lenght of small stamen anther	25*
Anther colour of large stamen	26*
Anther colour of small stamen	27*
Shape of large stamen anther	28*
Shape of small stamen anther	29*
Large stamen anther position relative to style	30*
Small stamen anther position relative to style	31*
Structure of large stamen appendage	32#
Structure of small stamen appendage	33
Large Stamen appendage shape	34*#
Small Stamen appendage shape	35*#
Sec appendage shape, large stamen	36
Sec appendage shape, small stamen	37

Floral Character	Number
Colour of large stamen appendage	38*
Colour of small stamen appendage	39*
Appendage orientation	40*
Functional position of appendage	41*
Structure of adaxial thecal wall, large stamen	42*#
Structure of adaxial thecal wall, small stamen	43*#
Connective vs anthere position	44*
Functional thecal position	45
Location of thecal end of large stamen	46*
Location of thecal end of small stamen	47
Thecae separated	48
Width of large anther pore opening	49
Width of small anther pore opening	50
Hight of large anther pore opening	51
Hight of small anther pore opening	52
Orientation of pore opening of large stamen	53
Orientation of pore opening of small stamen	54*
Number of pores	55
Pollen grain diameter large stamens	56#
Pollen grain diameter small stamens	57#
Colour contrast thecae - large stamen appendage	58*
Colour contrast thecae - small stamen appendage	59
Stamen colour dimorphism	60*
Relative position of stigma vs corolla opening	61*#
Stigma shape	62#
Stigma diameter	63#
Style curvature	64*#
Style lenght	65*
Colour contrast between stigma - style	66*
Level of anthere pore	67*#
Distance of stigma to anther pores of large stamens	68*
Distance of stigma to anther pores of small stamens	69*
Funct. orientation of pore of large stamen and stigma	70*
Funct. orientation of pore of small stamen and stigma	71*
Colour contrast corolla - stamens	72*
Colour contrast style - corolla	73*
Colour contrast androecium – gynoecium	74*

3.4 Laboratory work to code floral trait combination

To score the remaining floral traits (Table 3) I used high-resolution 3D images of whole flowers obtained by High Resolution X-ray Computed Tomography (HRXCT, Staedler et al. 2013), Scanning Electron Microscopy (SEM) for detailed surface images, and light microscopy for pollen measuring.

For HRXCT scans, I infiltrated all samples for at least two weeks in 70% ethanol with 1% PTA (phosphotungstic acid) to allow saturation of the tissues with the contrasting agent (PTA). Just before scanning, I mounted the samples in plastic containers and stabilized them with acrylic pillow foam (an x-ray translucent material; Staedler et al. 2013). I added 2 mm of 70% ethanol at the bottom of each container to create a saturated atmosphere to prevent the samples from drying and potential shrinkage during scanning. I performed the scanning on a MicroXCT-200 system (Zeiss Microscopy) using the LFO-Detector, the source at 40kV/200µA, and exposure time between 1 sec and 3 sec. I reconstructed the 3D images via the software XMReconstructor 8.1.6599 (Zeiss Microscopy). I analyzed and processed the reconstructed tomography files in the 3D-imaging software AMIRA (version 6.4.0).

I used SEM for detailed images of floral organ surfaces and to identify possible nectar releasing structures on stamens and the inner hypanthium wall. I dehydrated the samples over an ethanol series, critical point dried them using a Leica EM CPD300, coated them with gold using a Sputter Coater (BAL-TEC SCD 050), then mounted them onto aluminum stubs and scanned them in a JEOL JSM IT300 Scanning Electron Microscope.

To measure the pollen grain diameter, I used a light microscope (Olympus BX50).

3.5 Statistical data analysis

For the statistical analyses, I included additional data from 20 species (Table 4) of the tribe Merianieae (Dellinger et al. 2018). This led to the final dataset of 59 species, covering all four Neotropical tribes with documented pollinator shifts. Of these 59 species, 45 species had documented pollinators while in 14 species pollinators were unknown. This set-up allowed to test and apply pollination syndromes as predictive tool in my own dataset (see below).

Table 4: Species list of additional data found in Dellinger et al. 2018.

Species	Syndrome	Tribe
Adelobotrys adscendens	bee	Merianieae
Axinaea confusa	passerine	Merianieae
Axinaea costaricensis	passerine	Merianieae
Axinaea macrophylla	passerine	Merianieae
Axinaea sclerophylla	passerine	Merianieae
Graffenrieda cucullata	bee	Merianieae
Meriania aff, sanguinea	mixed vertebrate	Merianieae
Meriania costata	mixed vertebrate	Merianieae
Meriania drakei	bee	Merianieae
Meriania furvanthera	mixed vertebrate	Merianieae
Meriania longifolia	bee	Merianieae
Meriania macrophylla	passerine	Merianieae
Meriania maguirei	bee	Merianieae
Meriania maxima	bee	Merianieae
Meriania phlomoides	mixed vertebrate	Merianieae
Meriania pichinchensis	mixed vertebrate	Merianieae
Meriania quintuplinervis	mixed vertebrate	Merianieae
Meriania sanguinea	mixed vertebrate	Merianieae
Meriania speciosa	bee	Merianieae
Meriania tomentosa	mixed vertebrate	Merianieae

To identify the most important traits differentiating functional pollinator groups, and to predict pollinators of species with unknown pollinators, I used the statistical classification method of random forests (randomForest v2.3; Liaw & Wiener 2002) following Dellinger et al. (2018). I tested floral trait adaptations to the following pollinator groups: “buzz-bee”, “mixed-vertebrate”, “passerine” and “hummingbird”. Note that “mixed-vertebrate” encompasses different combinations of vertebrate pollinators (i.e. hummingbirds and bats, flowerpiercers and rodents, Dellinger et al. 2019a), while “hummingbird” refers to flowers of the genus *Brachyotum* where only hummingbirds

have been reported (Renner 1989). I included the pollination syndrome "hummingbird" in the analyses although I found only one species that was exclusively pollinated by hummingbirds (*Brachyotum ledifolium*). I ran additional models attempting to subdivide the "buzz-bee" syndrome based on bee body size further (see below).

A random forest is a machine learning approach, where a "forest" composed of many decision trees is constructed, asking "yes" or "no" questions in order to separate pre-defined groups (i.e. functional pollinator groups). Depending on the quality of the question asked (i.e. the importance of the trait), the split of the data set is more or less pronounced. If the pollinators are known, a random-forest model can be trained to predict these pollinators based on the trait matrix. This allows for direct validation of the prediction accuracy of the model. If the training model is accurate, it may then be used to predict pollinators for species where pollinators have never been observed.

In my study, I built a total of 100 random forests, each forest consisting of 500 trees. Each tree was constructed using four random traits to predict the functional pollinator group of each species. In order to assess prediction accuracy, I counted how often a functional pollinator group was correctly predicted for each species across the 100 forests and calculate the error rates of each model. The traits that are not used in a particular decision tree constitute the out-of-bag (OOB) observations and can be used to estimate classification error and the importance of each variable. To calculate the relative importance of a trait for correctly predicting pollinators, the OOB observations are randomly permuted and passed down the decision trees to get new predictions. The trait importance is the difference between the misclassification rate for the randomly permuted OOB and the original OOB data, divided by the standard error (Cutler et al. 2007). The Gini index is a measure for unequal distributions (variance, Cutler et al. 2007). The higher the Gini index the more misclassifications would occur if a trait is excluded from the model (Tat 2017). Note that in the context of the Gini index, an equal distribution does not correspond to the equal distribution in probability statistics.

When fitting a classification tree, an optimization is carried out to select a node, a predictor variable and a cut-off that result in the most homogenous subgroups for the data and is measured by the Gini index (Breiman et al. 1984). The splitting is continued until further subdivisions no longer reduce the Gini index. The more the Gini index for a trait decreases at each split, the more important this trait is (Tat 2017).

I tested six random forest models using different trait combinations and different subsets of species. Since random forest analyses do not allow for missing data in the training model, I ran two different models to remove missing data from the dataset. First (M1), I excluded all traits containing missing data for species with confirmed pollinators. M1 contained 18 traits and 45 species with known pollinators and 14 species with unknown pollinators. Second (M2), I removed all species that contained missing data for at least one trait, in order to analyze the whole trait matrix. M2 consisted of all traits, except "anther color" (not recorded for Merianieae). M2 contains 72 traits, 31 species with known pollinators and 14 species without confirmed pollinators. I also ran a model (M3) where I aimed to divide the "buzz-bee" syndrome into sub-syndromes (i.e. bees of different sizes), using the traits from M1 (best to predict syndromes for species lacking pollinator observations, see Results). I discriminated between small (< 1cm), medium (1-2cm) and large bees (>2cm), since I suspected that bees of different body sizes may exert different selective pressures on the flower. I based these discriminations on video material and personal observations.

To predict pollinators for species without confirmed pollinators, where the other models failed to predict certain species due to missing data, I ran two additional models. First (M4), I excluded all traits containing missing data for species with and without confirmed pollinators (15 traits, 45 known pollinators, 14 unknown species). Second (M5) I excluded all species containing missing data for species without confirmed pollinators (17 traits, 45 known pollinators, 11 unknown species). I trained both M4 and M5 on species with known pollinators before I applied them to

predict pollinators. Finally, in model M6, I again aimed to predict bee-pollinated species into sub-syndromes. M6 consisted of 26 species with known pollinators, 14 species without confirmed pollinators and 62 traits. I evaluated the quality of the model by comparing the prediction accuracy and error rates of known pollinators.

To test whether the four pollination syndromes differ significantly from each other, I used a PERMANOVA on a dissimilarity matrix based on the floral traits of M1 and M2, calculated following Chartier et al. (2017). To account for conducting multiple analyses on the same data set (comparison of four pollination syndromes) I performed a post hoc test with a pairwise Bonferroni correction. Furthermore, I calculated the mean pairwise dissimilarity within each syndrome, to compare whether the different syndromes differ in disparity. To investigate whether efficiency and attraction traits differ in disparity I performed disparity analyses using first only efficiency traits and second only attraction traits. Since the "hummingbird" syndrome was only represented by one specimen in my dataset (*Brachyotum ledifolium*; but note that the genus *Brachyotum* consists of ca. 45 potentially mostly hummingbird-pollinated species), I excluded this species from these calculations.

To visualize the morphological disparity between and within the pollination syndromes, I performed principal coordinate analyses (PCoA) on dissimilarity matrices. I constructed separate PCoAs based on different predicted results obtained from the random forest analyses. I performed a PCoA on the dissimilarity matrix based on M1 and M2 and colored species according to the prediction results to visualize morphospace occupation for both species with known and unknown pollinators. To visualize the power of the different organ modules (androecium, gynoecium, corolla) in separating the different pollination syndromes, I performed three PCoAs on the dissimilarity matrices based on subsets containing traits of only one of these organ modules. Finally, to visualize the power of efficiency and attraction traits in separating the different pollination syndromes, I performed a PCoA

on the dissimilarity matrix first based on efficiency traits only and second based on attraction traits only.

To test for differences in the disparity of each organ module (corolla: 6 traits, androecium: 47 traits, gynoecium: 6 traits) depending on the pollination syndrome, I calculated the partial disparity of each organ module for each pollination syndrome. Since the "hummingbird" syndrome was only represented by one specimen in my dataset, I excluded this species from these calculations.

Finally, I visualized the association between pollination syndromes and elevation using a Box-Plot and by plotting the elevation of the sampled species. For the visualization I used a subset of species for which I was able to evaluate the elevation (Table 1).

I carried out all statistical testing in R-Studio (Version 1.1.447, R Core Team, 2018). I used the packages "randomForest" (v2.3; Liaw & Wiener 2002), "vegan" (v2.5-6; Oksanen et al. 2019) and "rgl" (v0.99.16; Adler et al. 2018). I based my analyses on R-scripts provided by Marion Chartier and Agnes Dellinger.

4. Results

4.1 New empirical pollinator observations and literature data

I was able to document pollinators for the first time for 13 species and found an additional functional pollinator group in one species. The 13 newly documented pollinators all belong to the functional group of buzzing bees (Apidae). I further divided the buzzing bees by size and behavior (buzzing single stamens or buzzing the whole androecium, Table 5).

For one species (*Tibouchina grossa*), me and my co-supervisor were able do document an additional pollinator to the two functional groups (hummingbird, bat) that were reported by Vogel (1957). We

were able to document flowerpiercers (*Diaglossa sp.*, Fig. 5), activating the pollen release mechanism when foraging for nectar.

Pollinators were either documented on video or via personal observations by me or my co-supervisor Dr. Agnes Dellinger.

To further analyse floral traits in conjunction with pollinator data, I collated my own field observations with published pollinator data. In total, I had 26 "buzz-bee" pollinated species, 13 "mixed-vertebrate" pollinated species, five "passerine" pollinated species and one exclusively "hummingbird" pollinated species in my dataset.

Within the tribe Blakeeae I found five "buzz-bee" pollinated species and three "mixed-vertebrate" pollinated species. Within the tribe Melastomeae I found five "buzz-bee" pollinated species, two "mixed-vertebrate" pollinated species, and one exclusively "hummingbird" pollinated species, while within the tribe Miconieae I found nine "buzz-bee" pollinated species. Within the tribe Merianieae I had seven "buzz-bee" pollinated species, eight "mixed-vertebrate" pollinated species, and five "passerine" pollinated species. I found the "passerine" syndrome only within the tribe Merianieae.

Table 5: New empirical pollinator observations. Single = single anthers are buzzed, all = buzzing the whole androecium. "Large" and "small" indicate the size of the pollinator.

Species	Syndrome	New Pollinator	Method
Blakea florifera	Buzz-Bee	Apidae (large), single	Video
Blakea litoralis	Buzz-Bee	Apidae (large), single	Video
Blakea maurofernandiana	Buzz-Bee	Apidae (large), single	Video
Blakea superba	Buzz-Bee	Apidae (small), single	Video
Conostegia oerstediana	Buzz-Bee	Apidae (large), single	Pers. Obs
Conostegia subcrustulata	Buzz-Bee	Apidae (small), all	Video
Leandra subseriata	Buzz-Bee	Apidae (small), all	Pers. Obs
Miconia andreana	Buzz-Bee	Apidae (small), single	Video
Miconia donaeana	Buzz-Bee	Apidae (large), single	Pers. Obs
Miconia lacera	Buzz-Bee	Apidae (small), single	Video
Miconia schlimii	Buzz-Bee	Apidae (large), all	Pers. Obs
Miconia tonduzii	Buzz-Bee	Apidae (small), single	Video
Miconia trinervia	Buzz-Bee	Apidae (small), single	Video
Tibouchina grossa	Mixed Vertebrate	Diglossa	Pers. Obs

4.2. Random forest analyses

4.2.1 Training model

I found that M1 was the best model to predict the pollination syndromes for species with confirmed pollinators, followed by M2 (Table 6).

Table 6: Mean error rates and standard deviation per pollination syndrome for all random forest models (M1 – M6, 100 bootstrap runs per model). OBB = out of bag error rate, HB = hummingbird, Mixed = mixed-vertebrate, Pass = passerine.

M1	OOB	Bee	HB	Mixed	Pass
Mean Error	0.028889	0	1	0.02308	0
SD	0.010235	0	0	0.03543	0

M2	OOB	Bee	HB	Mixed	Pass
Mean Error	0.046977	0	1	0.090901	0
SD	0.003272	0	0	0	0

M3	OOB	HB	Large Bee	Medium Bee	Mixed	Pass	Small Bee
Mean Error	0.299377	1	0.243181	0.64683	0.00385	0.62766	NA
SD	0.019105	0	0.05458	0.04584	0.01685	0.10203	NA

M4	OOB	Bee	HB	Mixeed	Pass
Mean Error	0.101667	0.069054	1	0.04231	0.22273
SD	0.018307	0.018141	0	0.04287	0.11587

M5	OOB	Bee	HB	Mixed	Pass
Mean Error	0.027556	0	1	0.01769	0
SD	0.009539	0	0	0.03253	0

M6	OOB	Large Bee	Medium Bee	Small Bee
Mean Error	0.551154	0.46	0.72111	0.42308
SD	0.037099	0.03374	0.05802	0.12938

The models where I divided the bee syndrome even further by separating the bees by size (M3, M6) showed high error rates when trying to predict the three different bee syndromes with confirmed pollinators (Table 6).

When using M2, all pollination syndromes were predicted correctly in each bootstrap for species with confirmed pollinators (Table 7). All species within the “buzz-bee” and “passerine” syndromes with confirmed pollinators were always predicted correctly in each bootstrap of M1. Within the

"mixed-vertebrate" syndrome all species with confirmed pollinators were predicted correctly in each bootstrap except for *Brachyotum lindenii* (errorate = 0.82, predicted as hummingbird syndrome 24 times of 100 bootstrap runs). The model M1 was not able to predict the hummingbird syndrome for the species with confirmed pollinator (prediction accuracy = 0, Table 7).

Table 7: Predicted pollination syndromes for species with confirmed pollinators. Pred. Accur. = Prediction accuracy = 1: all 100 bootstraps predicted the same syndrome. Error = 0: syndrome was not predictable. Left M1, right M2.

Species	Confirmed Pollinator	Pred. Accur.
Adelobotrys adscendens	bee	1
Axinaea confusa	passerine	1
Axinaea costaricensis	passerine	1
Axinaea macrophylla	passerine	1
Axinaea sclerophylla	passerine	1
Blakea anomala	bee	1
Blakea austin-smithii	mixed vertebrate	1
Blakea chlorantha	mixed vertebrate	1
Blakea florifera	bee	1
Blakea gregii	mixed vertebrate	1
Blakea litoralis	bee	1
Blakea maurofernanderiana	bee	1
Blakea superba	bee	1
Brachyotum ledifolium	hb	0
Brachyotum lindenii	mixed vertebrate	0.82
Conostegia oerstediana	bee	1
Conostegia subcrustulata	bee	1
Graffenrieda cucullata	bee	1
Leandra subseriata	bee	1
Meriania aff, sanguinea	mixed vertebrate	1
Meriania costata	mixed vertebrate	1
Meriania drakei	bee	1
Meriania furvanthera	mixed vertebrate	1
Meriania longifolia	bee	1
Meriania macrophylla	passerine	1
Meriania maguirei	bee	1
Meriania maxima	bee	1
Meriania phlomoides	mixed vertebrate	1
Meriania pichinchensis	mixed vertebrate	1
Meriania quintuplinervis	mixed vertebrate	1
Meriania sanguinea	mixed vertebrate	1
Meriania speciosa	bee	1
Meriania tomentosa	mixed vertebrate	1
Miconia andreana	bee	1
Miconia argentea	bee	1
Miconia donaeana	bee	1
Miconia lacera	bee	1
Miconia schlimii	bee	1
Miconia tonduzii	bee	1
Miconia trinervia	bee	1
Monochaetum cf, floribundum	bee	1
Monochaetum cf, vulcanicum	bee	1
Monochaetum linearifolium	bee	1
Tibouchina grossa	mixed vertebrate	1
Tibouchina oroensis	bee	1

Species	Confirmed Pollinator	Pred. Accur.
Adelobotrys adscendens	bee	1
Axinaea confusa	passerine	1
Axinaea costaricensis	passerine	1
Axinaea macrophylla	passerine	1
Axinaea sclerophylla	passerine	1
Blakea anomala	bee	1
Blakea chlorantha	mixed vertebrate	1
Blakea florifera	bee	1
Blakea litoralis	bee	1
Blakea maurofernanderiana	bee	1
Blakea superba	bee	1
Brachyotum ledifolium	hb	1
Brachyotum lindenii	mixed vertebrate	1
Conostegia oerstediana	bee	1
Conostegia subcrustulata	bee	1
Graffenrieda cucullata	bee	1
Leandra subseriata	bee	1
Meriania aff, sanguinea	mixed vertebrate	1
Meriania costata	mixed vertebrate	1
Meriania drakei	bee	1
Meriania furvanthera	mixed vertebrate	1
Meriania longifolia	bee	1
Meriania macrophylla	passerine	1
Meriania maguirei	bee	1
Meriania maxima	bee	1
Meriania phlomoides	mixed vertebrate	1
Meriania pichinchensis	mixed vertebrate	1
Meriania quintuplinervis	mixed vertebrate	1
Meriania sanguinea	mixed vertebrate	1
Meriania speciosa	bee	1
Meriania tomentosa	mixed vertebrate	1
Miconia andreana	bee	1
Miconia argentea	bee	1
Miconia donaeana	bee	1
Miconia lacera	bee	1
Miconia schlimii	bee	1
Miconia tonduzii	bee	1
Miconia trinervia	bee	1
Monochaetum cf, floribundum	bee	1
Monochaetum cf, vulcanicum	bee	1
Monochaetum linearifolium	bee	1
Tibouchina grossa	mixed vertebrate	1
Tibouchina oroensis	bee	1

When using M1, I identified seven traits of high importance in differentiating pollination syndromes (Reward type, Known mode of pollen expulsion, Corolla shape, Position of style relative to corolla, Orientation of flower in inflorescence, Corolla color, Robustness of stamens). Within these seven traits, I detected a rapid decline of importance from the two most important traits to the next three most important traits and to the two least important traits (Fig. 5).

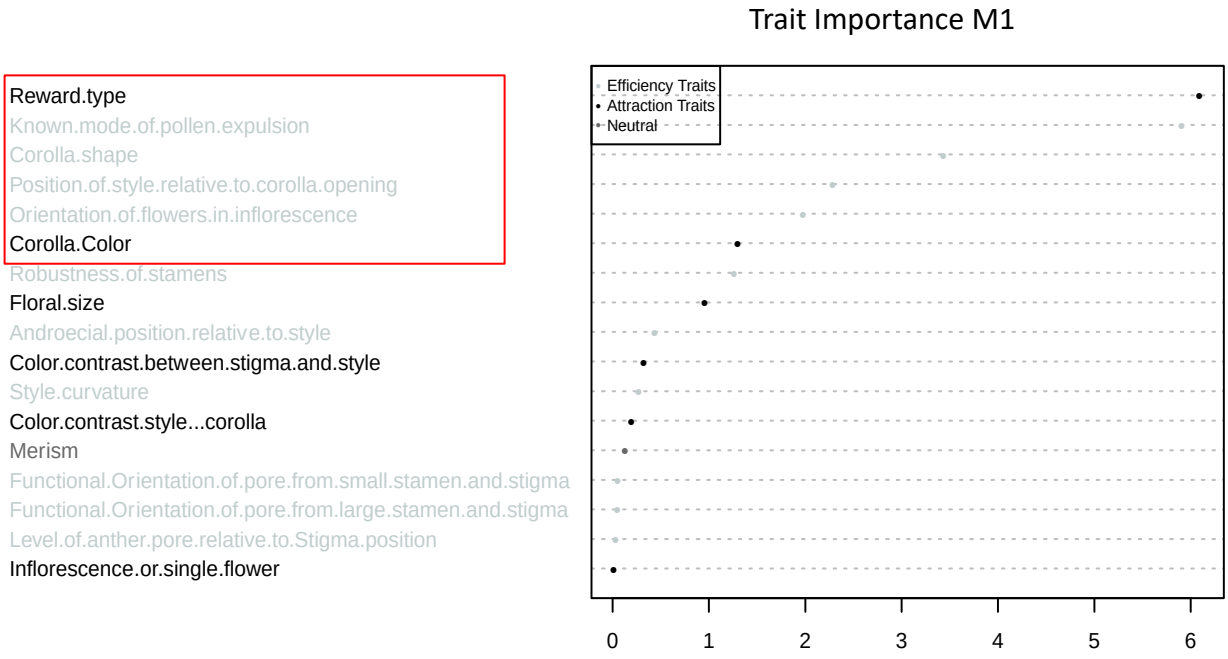

Figure 5: Trait importance (MeanGini) for discriminating the three pollination syndromes ("buzz-bee", "mixed-vertebrate" and "passerine" syndrome:: "buzz-bee", "mixed-vertebrate" and "passerine" using M1 (18 traits); red square indicates the most important trait;. MeanGini of 100 bootstraps; the traits are grouped into "efficiency" and "attraction" traits or, if both categories are interacting (e.g. distance of anther pore to stigma), into "both"; x-axis = trait importance.

I found that, except for the traits that were excluded in M1 (Ratio of corolla height and diameter, Structure of stamen filaments, Pollen grain diameter), the same traits were of high importance in M2 in differentiating pollination syndromes. Also, I found that only one trait was of less importance in M2: "corolla color" (Fig. 6). Further, I detected in M2 a rapid decline in trait importance within the seven most important traits. However, in comparison to M1, I detected only two steps of decreasing trait importance (between the first and the next five most important traits).

Similar traits are of high importance when comparing the different syndromes using M1 (Table 8). Nevertheless, “corolla color” seems to be more important in the “buzz-bee” syndrome while in the “mixed-vertebrate” and in the passerine syndrome the trait “robustness of stamens” is more important (Table 8). Using M2, similar traits are of high importance when comparing the different syndromes, except for the trait “structure of stamen filaments” (Table 9). Note, that this trait is indirectly also a reflects the trait “reward type” (nectar is secreted via filament ruptures in some species). This trait was important for differentiating the “mixed-vertebrate” syndrome and of intermediate importance for the “buzz-bee” syndrome. Also, fewer traits were of high importance in the “buzz-bee” and the “passerine” syndrome, compared to the “mixed-vertebrate” (Table 9). The two most important traits across pollination syndromes and tribes were “reward type” and “known mode of pollen expulsion” (Figs 5, 6 & Tables 8, 9).

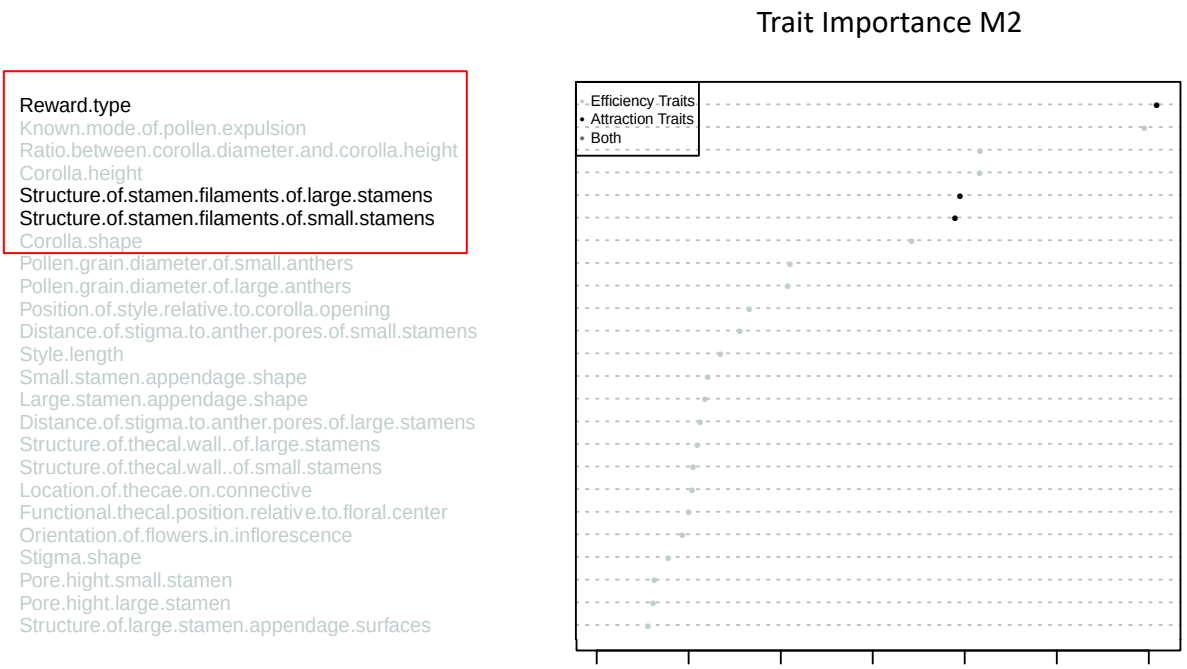

Figure 6: Trait importance (MeanGini) for discriminating the three pollination syndromes (“buzz-bee”, “mixed-vertebrate” and “passerine” syndrome); 24 most important traits of M2 (74 traits in total); red square indicates the most important traits; MeanGini of 100 bootstraps; the traits are grouped into “efficiency” and “attraction” traits or, if both categories are interacting (e.g. distance of anther pore to stigma), into “both”; x-axis = trait importance.

Table 8: Trait importance (ranked by mean Gini index) for each pollination syndrome, based on M1. Bee = Buzz-Bee, Mix = Mixed-Vertebrate, Pass = Passerine

Character	meanGini_Bee
Reward type	14,0787
Known mode of pollen expulsion	13,6877
Corolla shape	8,18550
Position of style relative to corolla opening	6,73659
Corolla Color	5,10015
Floral size	2,36824
Orientation of flowers in inflorescence	2,27689
Color contrast between stigma and style	1,75532
Androecial position relative to style	1,15931
Functional Orientation of pore from small stamen and stigma	1,06400
Functional Orientation of pore from large stamen and stigma	0,98518
Merism	0,76489
Style curvature	0,58719
Color contrast style corolla	0,41827
Robustness of stamens	0,1655
Inflorescence or single flower	-0,04191
Level of anther pore relative to Stigma position	-0,65451

Character	meanGini_Mix
Reward type	15,6042
Known mode of pollen expulsion	15,1410
Position of style relative to corolla opening	10,2155
Corolla shape	9,15186
Robustness of stamens	9,04012
Orientation of flowers in inflorescence	8,77592
Androecial position relative to style	3,52901
Corolla Color	3,09133
Floral size	2,75450
Merism	2,23859
Functional Orientation of pore from small stamen and stigma	1,27529
Functional Orientation of pore from large stamen and stigma	1,18216
Color contrast between stigma and style	1,16430
Inflorescence or single flower	0,72731
Style curvature	0,53868
Color contrast style corolla	0,07743
Level of anther pore relative to Stigma position	-0,38193

Character	meanGini_Pass
Reward type	13,8426
Known mode of pollen expulsion	13,5132
Corolla shape	10,7215
Orientation of flowers in inflorescence	10,4110
Robustness of stamens	8,89487
Androecial position relative to style	3,59765
Style curvature	3,57463
Corolla Color	2,19742
Merism	2,06985
Position of style relative to corolla opening	1,93190
Floral size	1,47440
Color contrast style corolla	1,17917
Color contrast between stigma and style	0,62682
Functional Orientation of pore from small stamen and stigma	0,43197
Level of anther pore relative to Stigma position	0,42020
Functional Orientation of pore from large stamen and stigma	0,39333
Inflorescence or single flower	0,29281

Table 9: Trait importance (ranked by mean Gini index) for each pollination syndrome, based on M2. Bee = Buzz-Bee, Mix = Mixed-Vertebrate, Pass = Passerine.

character	meanGini_Bee
Known mode of pollen expulsion	8,00201
Reward type	7,93528
Ratio between corolla diameter and corolla height	6,66352
Corolla height	6,34387
Structure of stamen filaments of small stamens	5,96548
Structure of stamen filaments of large stamens	5,93254
Corolla shape	5,36184
Pollen grain diameter of large anthers	5,12267
Pollen grain diameter of small anthers	5,07254
Style length	3,23074
Structure of thecal wall of small stamens	3,07563
Functional thecal position relative to floral center	3,07413
Structure of thecal wall of large stamens	3,02548
Position of style relative to corolla opening	3,01398
Location of thecae on connective	2,97614
Distance of stigma to anther pores of small stamens	2,61757
Stigma shape	2,15018
Large stamen appendage shape	1,95224

character	meanGini_Mix
Structure of stamen filaments of small stamens	7,3913
Structure of stamen filaments of large stamens	7,2351
Known mode of pollen expulsion	7,0956
Reward type	7,0913
Corolla height	6,264
Ratio between corolla diameter and corolla height	6,1441
Corolla shape	4,6614
Position of style relative to corolla opening	4,3512
Structure of thecal wall of small stamens	3,0495
Robustness of stamens	2,9717
Structure of thecal wall of large stamens	2,9557
Orientation of large stamen anther	2,8333
Functional thecal position relative to floral center	2,6792
Location of thecae on connective	2,6635
Orientation of small stamen anther	2,6205
Orientation of flowers in inflorescence	2,371
Petal surface	1,8198
Petal gloss	1,733

character	meanGini_Pass
Reward type	6,12718
Known mode of pollen expulsion	6,10744
Corolla shape	5,48127
Distance of stigma to anther pores of small stamens	4,57543
Pollen grain diameter of large anthers	4,29784
Pollen grain diameter of small anthers	4,28022
Small stamen appendage shape	4,00880
Large stamen appendage shape	3,94640
Distance of stigma to anther pores of large stamens	3,83683
Orientation of flowers in inflorescence	3,29890
Structure of large stamen appendage surfaces	2,74416
Structure of stamen filaments of small stamens	2,73619
Structure of stamen filaments of large stamens	2,70086
Ratio between corolla diameter and corolla height	2,67834
Structure of small stamen appendage surfaces	2,66938
Style length	2,54326
Robustness of stamens	2,26063
Orientation of small stamen anther	2,16669

4.2.2 Predicting pollinators for species without confirmed pollinator

I used the models M1 and M2 to predict pollinators for species without confirmed pollinators, since these models most accurately predicted the pollinators for species with confirmed pollinators (comp. Tables 6 – 9). In addition, I ran the models M4 and M5 in order to predict pollinators for species without confirmed pollinators where the other models were not able to predict the pollinators due to missing data. Finally, I ran the model M3, including the further divided bee pollinators, to see if this model was able to predict pollinators for species that were not able to be predicted by the other models.

Model M1 was able to predict most pollination syndromes for species without confirmed pollinators with a low error rate (Table 10). This model was also able to produce more precise predictions than the other models (comp. Tables 10, 11, 12). Given that *M. barbata* is a nectar secreting species and occasional hummingbird visits have been reported for closely related *Miconia* species not included in my sample, I argue that model M1 is more accurately predicting pollination syndromes.

Table 10: Predicted pollination syndromes for species without confirmed pollinator. 1 = each of the 100 bootstraps predicted the same syndrome, 0 = syndrome was not predicted for this species, HB = hummingbird. Left: M1, right M2.

Species	bee	hb	pass	mixed vertebrate
Aciotis levyana	0	0	0	0
Arthrostemma cf, ciliatum	1	0	0	0
Blakea setosa	1	0	0	0
Clidemia cf, epiphytica	0	0	0	0
Clidemia dentata	1	0	0	0
Clidemia globuliflora	1	0	0	0
Miconia barbata	0.04	0	0	0.96
Miconia cf, reducens	0	0	0	0
Miconia goniostigma	1	0	0	0
Miconia notabilis	1	0	0	0
Tibouchina cf, ciliaris	1	0	0	0
Tibouchina lepidota	1	0	0	0
Tibouchina mollis	0	0	0	0
Tibouchina urvilleana	1	0	0	0

Species	bee	hb	pass	mixed vertebrate
Aciotis levyana	0	0	0	0
Arthrostemma cf, ciliatum	1	0	0	0
Blakea setosa	1	0	0	0
Clidemia cf, epiphytica	0	0	0	0
Clidemia dentata	1	0	0	0
Clidemia globuliflora	1	0	0	0
Miconia barbata	1	0	0	0
Miconia cf, reducens	0	0	0	0
Miconia goniostigma	1	0	0	0
Miconia notabilis	1	0	0	0
Tibouchina cf, ciliaris	1	0	0	0
Tibouchina lepidota	1	0	0	0
Tibouchina mollis	0	0	0	0
Tibouchina urvilleana	0	0	0	0

Table 11: Predicted pollination syndromes for species without confirmed pollinator using M3. 1 = each of the 100 bootstraps predicted the same syndrome, 0 = syndrome was not predicted for this species, HB = hummingbird.

Species	small bee	hb	passerine	mixed vertebrate	medium bee	large bee
Aciotis levyana	0	0	0	0	0	0
Arthrostemma cf, ciliatum	0	0	0	0	1	0
Blakea setosa	0	0	0	0	0	1
Clidemia cf, epiphytica	0	0	0	0	0	0
Clidemia dentata	1	0	0	0	0	0
Clidemia globuliflora	0.33	0	0	0	0.67	0
Miconia barbata	0	0	0	1	0	0
Miconia cf, reducens	0	0	0	0	0	0
Miconia goniostigma	0.99	0	0	0	0.01	0
Miconia notabilis	0	0	0	0	0	1
Tibouchina cf, ciliaris	0.19	0	0	0	0.64	0.17
Tibouchina lepidota	0	0	0	0	0	1
Tibouchina mollis	0	0	0	0	0	0
Tibouchina urvilleana	0	0	0	0	0	1

Table 12: Predicted pollination syndromes for species without confirmed pollinator using M4 und M5. 1 = each of the 100 bootstraps predicted the same syndrome, 0 = syndrome was not predicted for this species, HB = hummingbird. Left: M4 – reward type was excluded (missing data in M. reducens, important trait). Right: M5

Species	bee	hb	pass	mixed vertebrate
Aciotis levyana	1	0	0	0
Arthrostemma cf, ciliatum	1	0	0	0
Blakea setosa	1	0	0	0
Clidemia cf, epiphytica	1	0	0	0
Clidemia dentata	1	0	0	0
Clidemia globuliflora	1	0	0	0
Miconia barbata	1	0	0	0
Miconia cf, reducens	1	0	0	0
Miconia goniostigma	1	0	0	0
Miconia notabilis	1	0	0	0
Tibouchina cf, ciliaris	1	0	0	0
Tibouchina lepidota	1	0	0	0
Tibouchina mollis	1	0	0	0
Tibouchina urvilleana	1	0	0	0

Species	bee	hb	pass	mixed vertebrate
Arthrostemma cf, ciliatum	1	0	0	0
Blakea setosa	1	0	0	0
Clidemia dentata	1	0	0	0
Clidemia globuliflora	1	0	0	0
Miconia barbata	0.2	0	0	0.8
Miconia goniostigma	1	0	0	0
Miconia notabilis	1	0	0	0
Tibouchina cf, ciliaris	1	0	0	0
Tibouchina lepidota	1	0	0	0
Tibouchina mollis	1	0	0	0
Tibouchina urvilleana	1	0	0	0

I could not predict pollinators of four species (*Miconia reducens*, *Tibouchina mollis*, *Aciotis levyana* and *Clidemia epiphytica*) without confirmed pollinators using M1 since these species contained missing data. Hence, I ran model M4 (where I had removed the missing traits; note that the most important traits "reward type" and "known mode of pollen expulsion" were also removed) to predict these four species. Using M4, all species were predicted as bee pollinated (Table 12). It is possible that an additional syndrome exists in *M. reducens*. I found strong evidence for an extreme case of self-pollination in this species, where the anthers are strongly curved towards the stigma, the pollen tube germinates within the anthers and grows directly towards the stigma (Fig. 7).

Figure 7: Scanning Electron Microscope (SEM) picture and stereomicroscopic picture of Miconia reducens; *Extreme case of self-pollination in* Miconia reducens; *left: SEM picture of pollen tubes growing out of the anther pore (100µm); right: stereomicroscopic picture of anthers (ripped off the filaments) and attached to the stigma by pollen tubes (arrowhead).*

4.3. Visualizing pollination syndromes and testing for differences in morphospace occupation

4.3.1 Visualizing pollination syndromes

I identified the model M1 to be the best regarding its ability to predict pollination syndromes both for species with and without confirmed pollinators. I hence derived syndrome predictions from this model, resulting in 35 species in the "buzz-bee" syndrome, 14 species in the "mixed-vertebrate" syndrome, 5 species in the "passerine" syndrome, and 1 species in the "hummingbird" syndrome. Four species remained without confirmed or predicted pollinators (*Miconia reducens, Tibouchina mollis, Aciotis levyana* and *Clidemia epiphytica*)

All syndromes were significantly different from each other, except for the "hummingbird" syndrome. (Table 13).

Table 13: PERMANOVA on significant differences between pollination syndromes M1. ns = not significant. Upper part of the table shows F-values, lower part of the table shows significance.

-	Bee	HB	Mixed	Pass
Bee	NA	3.675	45.583	9.48
HB	ns	NA	1.962	11.268
Mixed	*	ns	NA	26.39
Pass	*	ns	*	NA

The grouping into the four pollination syndromes (“buzz-bee”, “passerine”, “mixed-vertebrate”, “hummingbird”) explained 50% of the variance of the selected trait combination. The first three axes of the PCoA explained ca. 64% of variance. Also, the PCoA displays the significant separation of the three pollination syndromes clearly (Fig. 8).

When comparing M2 to M1, the grouping into the four pollination syndromes (“buzz-bee”, “passerine”, “mixed-vertebrate”, “hummingbird”) explained only 38% of the variance of the selected trait combination. Also, the first three axes of the PCoA explained ca. 60% of variance (Fig. 9).

When including the predicted species without confirmed pollinators in the PCoA using the traits from M1, the grouping into the four pollination syndromes (“buzz-bee”, “passerine”, “mixed-vertebrate”, “hummingbird”) explained 47% of the variance of the selected trait combination. the first three axes of the PCoA explained ca. 59% of variance (Fig. 10). The species that remained unpredictable all fell either into the “buzz-bee” space or into the “mixed-vertebrate” space and hence confirm predictions obtained through models M4 and M5 (Fig. 10).

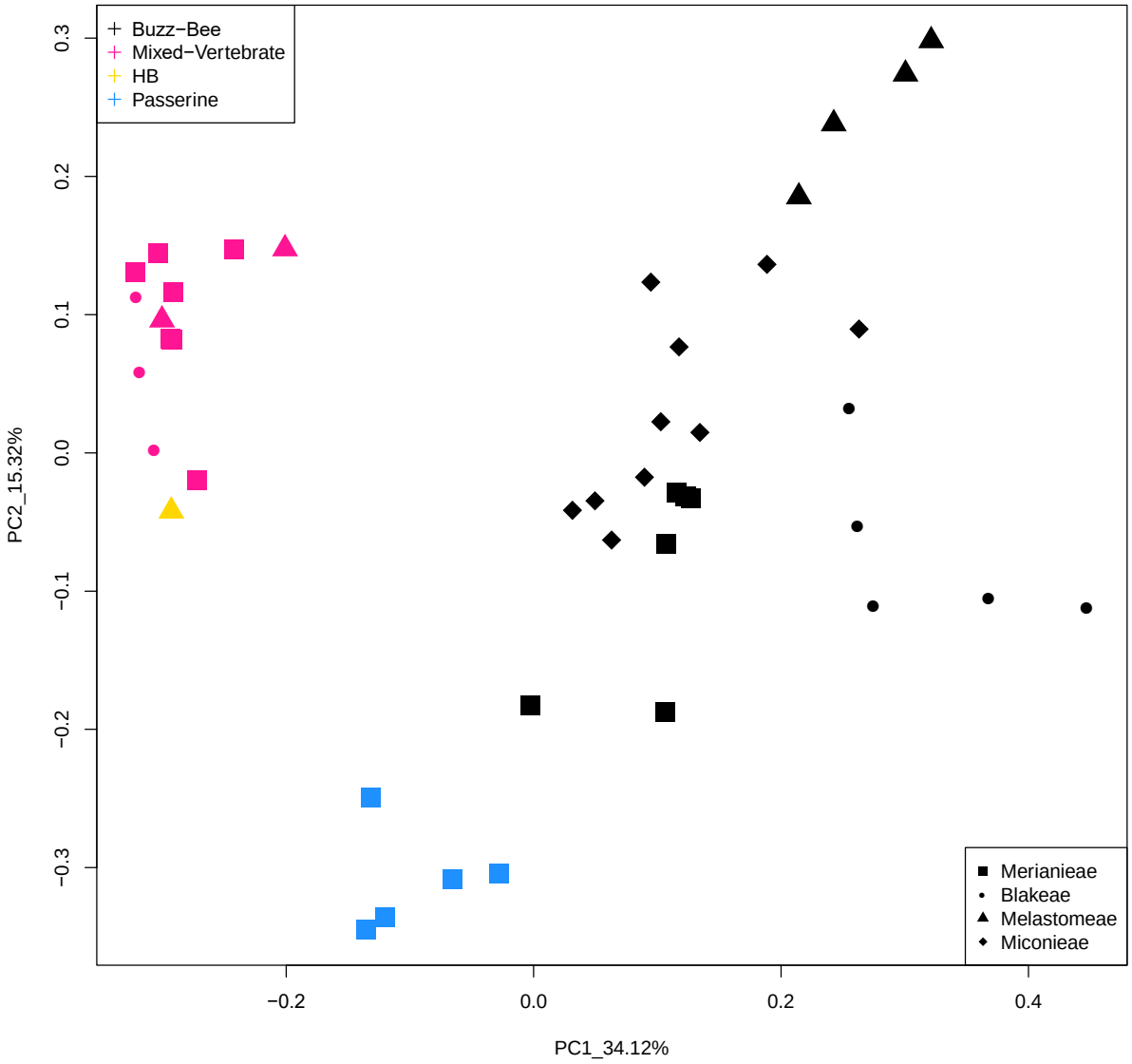

Figure 8: Morphospace of species of the four tribes that shifted pollinators and their pollination syndromes, only species with confirmed pollinators: "buzz-bee", "mixed-vertebrate", "passerine" and "hummingbird" syndrome using the traits of M1 (18 traits). Species of different tribes converge in shape space depending on their pollination syndrome; the "buzz-bee", "mixed-vertebrate" and "passerine" syndromes are clearly separated from each other, the "hummingbird" syndrome falls within the "mixed-vertebrate" syndrome HB = hummingbird.

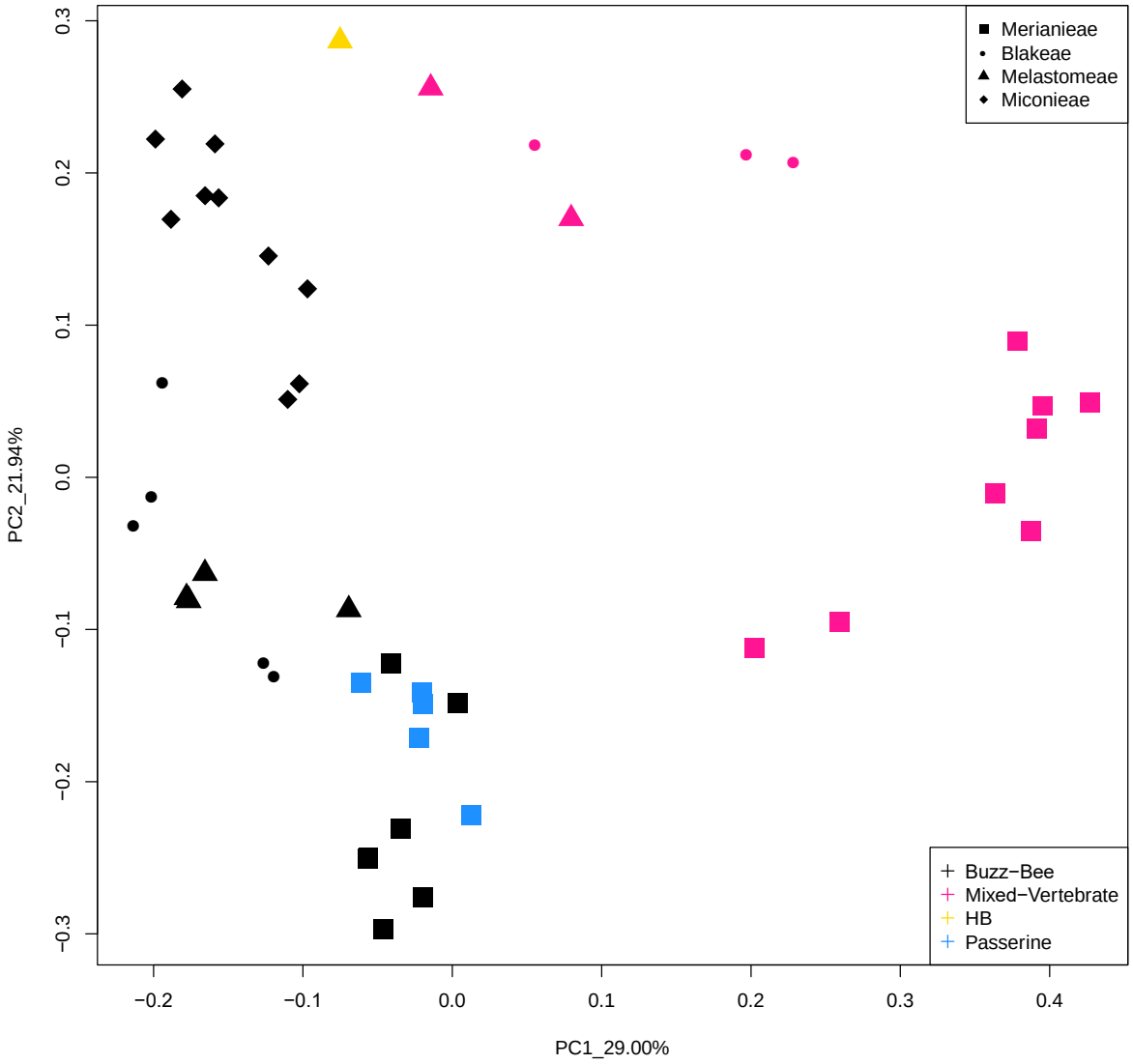

Figure 9:Morphospace of species of the four tribes that shifted pollinators and their pollination syndromes, only species with confirmed pollinators: "buzz-bee", "mixed-vertebrate", "passerine" and "hummingbird" syndromes using M2 (72 traits); species of different tribes converge in shape space depending on their pollination syndrome; the "buzz-bee", "mixed-vertebrate" and "passerine" syndromes are clearly separated from each other ("passerine" syndrome is clearly separated from "buzz-bee" syndrome on the 3rd axis, the "hummingbird" syndrome falls within the "mixed-vertebrate" syndrome; HB = hummingbird.

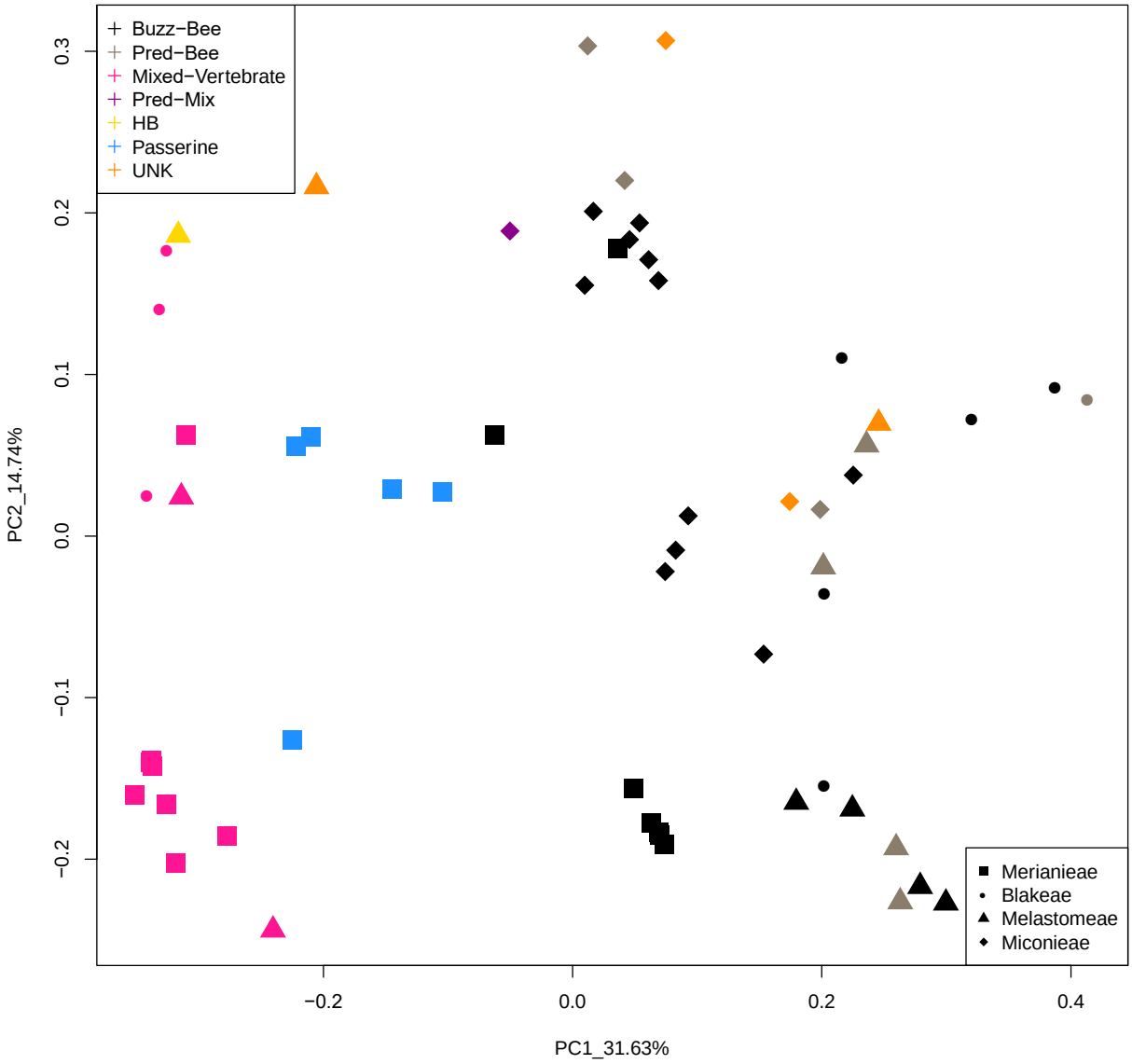

Figure 10: Morphospace of species of the four tribes that shifted pollinators and their pollination syndromes, species with confirmed and predicted pollinators: "buzz-bee", "mixed-vertebrate", "passerine" and "hummingbird" syndromes using traits of M1 (18 traits); the "buzz-bee", "mixed-vertebrate" and "passerine" syndromes are clearly separated from each other, the "hummingbird" syndrome falls within the "mixed-vertebrate" syndrome, the species with predicted pollinators fall within the "buzz-bee" and the "mixed-vertebrate" morphospace; HB = hummingbird, UNK = unpredictable syndrome, Pred. = prediction.

4.3.2 Disparity of the pollination syndromes

I calculated morphological diversity (disparity) for all species (confirmed and predicted pollinators) using the traits from M1. The "buzz-bee" syndrome was the most disparate (MaxDisp. = 0.693, MeanDisp. = 0.411), followed by the "mixed-vertebrate" syndrome (MaxDisp. = 0.553, MeanDisp. = 0.230) and the "passerine" syndrome (MaxDisp. = 0.304, MeanDisp. = 0.158). I could not assess disparity in the "hummingbird" syndrome since it was only represented by a single species in my dataset. The four species for which the pollinator could not be predicted by M1 also showed high disparity (MaxDisp. = 0.518, MeanDisp. = 0.413, Fig. 10).

4.4. Organ modules and contribution to overall disparity

When comparing the disparity of the three different organ modules ("corolla" 6 traits, "androecium" 47 traits, "gynoecium" 6 traits) the module "corolla" had the highest disparity, followed by the module "androecium" and the module "gynoecium" (Table 14). As when considering the whole flower, the "buzz-bee" syndrome was the most diverse when analyzing each organ module separately, followed by the "mixed-vertebrate" syndrome and the "passerine" syndrome (Table 14).

Table 14: Disparity of the three different organ modules of the three different pollination syndromes: "buzz-bee", "mixed-vertebrate" and "passerine". Eucl. = Euclidian distance, PD = pairwise dissimilarity.

Corolla	Bee	Mixed	Pass
Eucl	0.0426	0.0228	0.0072
PD	54.55	29.14	9.27

Androecium	Bee	Mixed	Pass
Eucl	0.0544	0.0414	0.0060
PD	49.93	38.07	5.55

Gynoecium	Bee	Mixed	Pass
Eucl	0.0737	0.0748	0.0088
PD	44.11	44.8	5.25

Nevertheless, it should be mentioned that using only one organ module would not be sufficient to accurately separate the four pollination syndromes ("buzz-bee", "passerine", "mixed-vertebrate", "hummingbird") on the first two axes of the PCoA (Fig. 11).

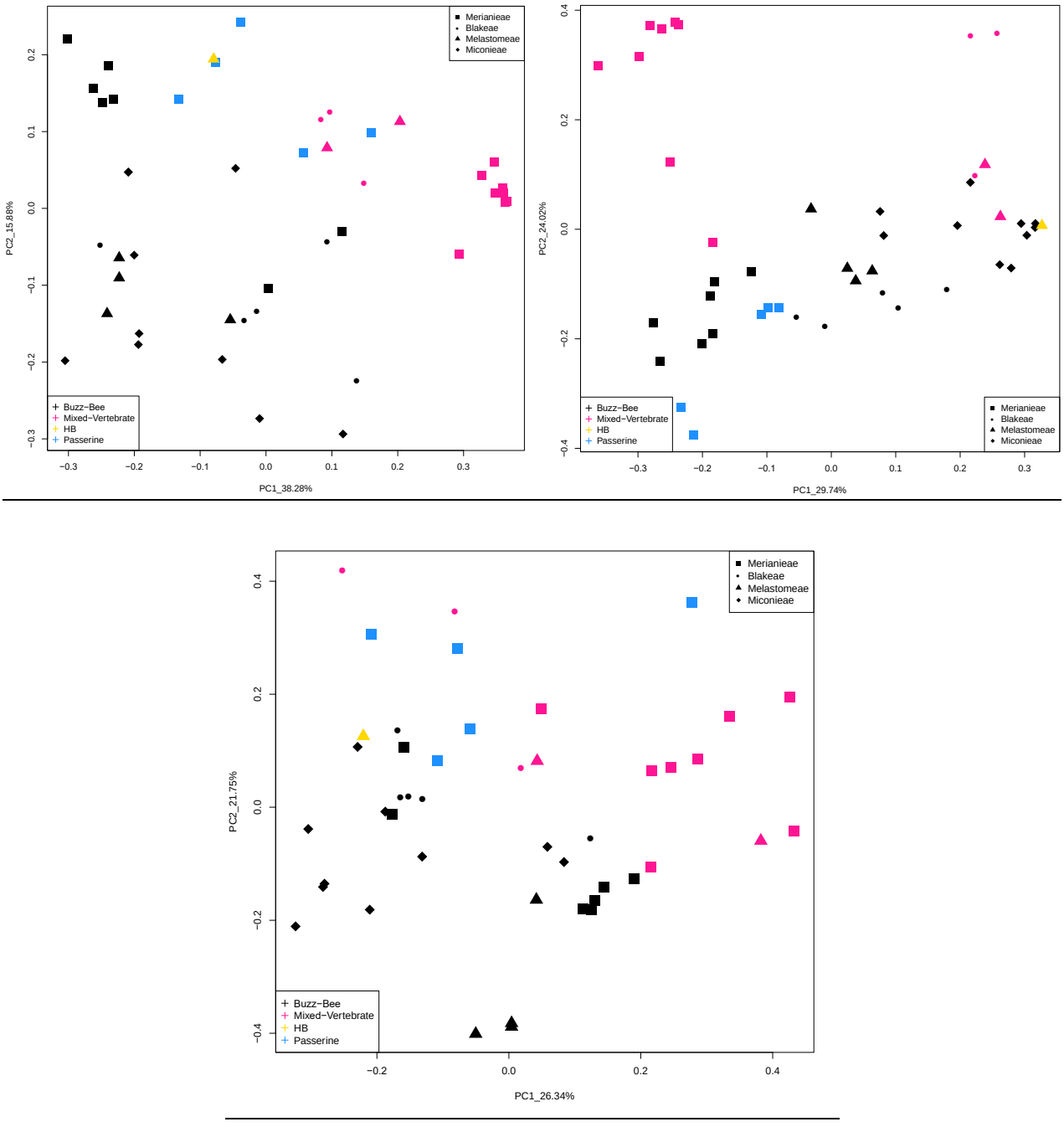

Figure 11: Morphospace of species of the four tribes that shifted pollinators and their pollination syndromes: "buzz-bee", "mixed-vertebrate", "passerine" and "hummingbird" using only traits of the three organ modules; top left: Corolla traits only, some species of the "passerine" and the "mixed-vertebrate" syndrome fall within the same morphospace, the "buzz-bee" syndrome is separated from the other syndromes; top right: androecium traits, the different pollination syndromes are not clearly separated from each other, some species of the "mixed-vertebrate" and "passerine" syndrome fall within the "buzz-bee" syndrome morphospace; bottom: gynoecium traits, the different pollination syndromes are not clearly separated from each other, some species of the "mixed-vertebrate" and "passerine" syndrome fall within the "buzz-bee" syndrome morphospace; The first 2 axes are not sufficient to separate the four pollination syndromes. HB = hummingbird.

4.5 Comparing efficiency and attraction traits

I compared the explained variance of efficiency and attraction traits and visualized how well the three pollination syndromes are separated using only efficiency or attraction traits. Except the hummingbird syndrome, all other syndromes were significantly different from each other when only assessing attraction or efficiency traits (Table 15 & 16). Visually, efficiency traits separated the three pollination syndromes better than attraction traits (Fig. 12).

Table 15: PERMANOVA on significant differences between pollination syndromes using only efficiency traits. ns = not significant. Upper part of the table shows F-values, lower part of the table shows significance.

-	bee	hb	mixed vertebrate	passerine
bee	NA	2.037	26.337	6.550
hb	ns	NA	2.261	11.246
mixed vertebrate	*	ns	NA	15.25
passerine	*	ns	*	NA

Table 16: PERMANOVA on significant differences between pollination syndromes using only attraction traits. ns = not significant. Upper part of the table shows F-values, lower part of the table shows significance.

-	bee	hb	mixed vertebrate	passerine
bee	NA	1.685	16.804	4.213
hb	ns	NA	2.416	9.404
mixed vertebrate	*	ns	NA	13.221
passerine	*	ns	*	NA

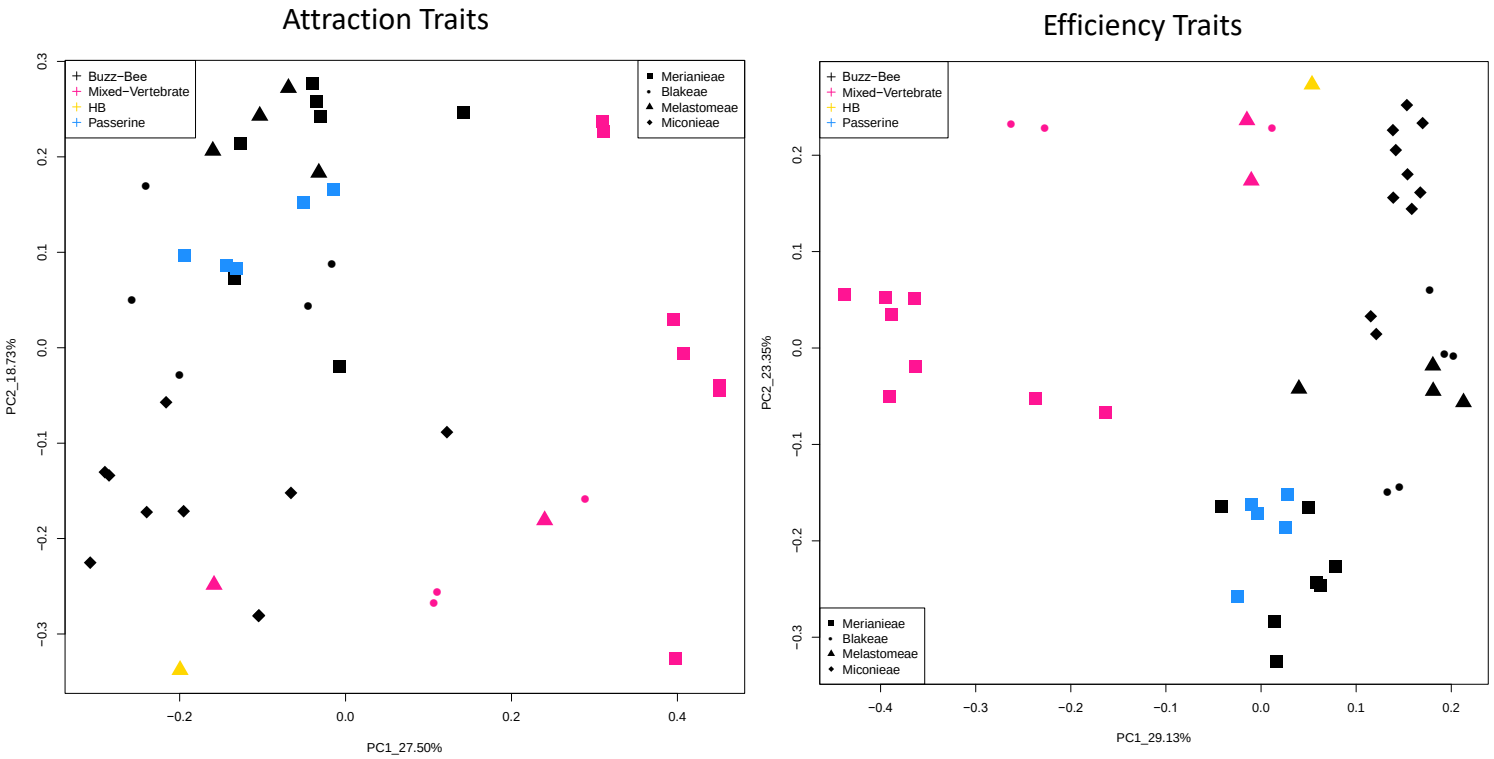

Figure 12: Morphospace of the four tribes that shifted pollinators and the three pollination syndromes; "buzz-bee", "mixed-vertebrate" and "passerine" using only attraction (left) and only efficiency (right) traits; right: efficiency traits clearly separate the "mixed-vertebrate" syndrome from the "buzz-bee" and the "passerine" syndrome, some of the "passerine" syndrome species fall within the "buzz-bee" syndrome morphospace, left: the different syndromes are not that clearly separated by the first two axes, some of "mixed-vertebrate" and the "buzz-bee" syndrome species fall within the same morphospace and some of the "passerine" syndrome species fall within the "buzz-bee" syndrome; in both morphospace the only exclusively hummingbird pollinated species falls within the "buzz-bee" and the "mixed-vertebrate" syndrome.

The grouping into the four pollination syndromes explained 39% of the variance when using only efficiency traits and 34% when using only attraction traits. The first three axes of both PCoAs explained ca. 61% of the variance.

4.6 Trait differences between the three pollination syndromes

In the following section, I only describe traits of the pollination syndromes: “buzz-bee”, “mixed-vertebrate” and “hummingbird”. The traits for the pollination syndrome “passerine” were described by Dellinger et al. (2018).

4.6.1 Reward type

I found 36 species offering pollen as reward, all were confirmed “buzz-bee” pollinated species or were predicted to belong to the “buzz-bee” syndrome. I found 15 species offering nectar as reward. 13 of those were confirmed “mixed-vertebrate” pollinated species. One species (*Miconia barbata*) was predicted to belong to the “mixed-vertebrate” syndrome and the only exclusively hummingbird pollinated species (*Brachyotum ledifolium*) also offered nectar. For three species (*Miconia reducens*, *Aciotis levyana*, *Clidemia epiphytica*), I was not able to determine the reward type (Apx. 1). Neither artificial buzzing nor touching the anthers with a 10µl capillary led to pollen expulsion, but pollen was present in all species.

4.6.2 Known mode of pollen expulsion

The 36 species belonging to the “buzz-bee” syndrome released pollen when vibrated by pollinators or manually. I found 14 species releasing pollen via the “salt-shaker” mechanism previously described for the “mixed-vertebrate” syndrome. The only exclusively hummingbird pollinated species (*Brachyotum ledifolium*) also possesses the salt-shaker pollen-release mechanism (Apx. 1). In one species (*Tibouchina grossa*), pollinated by mixed assemblages of vertebrates, I found a different pollen release mechanism, which I termed “bounce-mechanism”. *T. grossa* has a conspicuous, V-shaped, connective appendage (Figs 13, 15). The appendage is positioned directly above the rupture in the filament where nectar is secreted, and the flowers are oriented horizontally.

When the pollinators (bats, hummingbirds, flowerpiercers) are foraging for nectar located on the filament between the filament and the appendage (Fig. 13), they lift up the V-shaped appendage, which functions as a lever, away from the filament, thereby lowering the thecae. When the pollinators move their heads out of the flower again, the appendage bounces back down towards the filament, and the thecae are moved back up rapidly. This rapid movement causes pollen release, pollen is catapulted out of the anther onto the pollinator (Figs 13, 15, 20).

Figure 13: Photographs and Scanning Electron Microscopy (SEM) pictures of Tibouchina grossa (flower length = 33mm, flower diameter = 32mm); A: photography of longitudinal *section of flower, the whit arrow indicates the location of nectar secretion, the black arrow indicates the location of the appendage; B: photography of a flower* in *front view, showing the abaxial androecial position; C: SEM picture of filament rupture where nectar is secreted (100µm); D: SEM picture of V-shaped appendage (200 µm).*

4.6.3 Corolla shape

I found that all species within the "buzz-bee" syndrome possess flowers with either an open or a reflexed corolla, while all species within the "mixed-vertebrate" syndrome possess flowers with

either a pseudo-campanulate, bowl or a tube-shaped corolla (Fig. 14). The only exclusively hummingbird pollinated species (*Brachyotum ledifolium*) has a narrow corolla tube, shaped like a cigar, constricting the diameter of the flower to a point where only hummingbird bills can enter (Apx. 1).

4.6.4 Appendage

I found that all species within the "buzz-bee" syndrome possess appendages of various shapes and sizes. Appendages are strongly reduced or missing in most species within the "mixed-vertebrate" syndrome (i.e. *Blakea chlorantha*, Fig. 17). Nevertheless, one species within the "mixed-vertebrate" pollination syndrome, *Tibouchina grossa*, possesses a V-shape appendage (Figs 13 & 15). The only exclusively hummingbird pollinated species (*Brachyotum ledifolium*) does not have an appendage (Apx. 1).

Figure 14: Photographs of flowers showing the change of corolla shapes with a shift from buzz-bee pollination to other pollination syndrome; A: Blakea maurofernandiana *with an open corolla shape (flower length = 7mm, flower diameter = 30mm); B:* Miconia gonisostiga *with reflexed petals (flower length = 1mm, flower diameter = 9mm); C:* Tiboucina grossa *with a pseudo-campanulate corolla (flower length = 33mm, flower diameter = 32mm); D:* Blakea chlorantha *with a bowl-shaped corolla (flower length = 10mm, flower diameter = 12mm); E:* Axinea lehmanni *with an open corolla and bulbous appendages; A-B: buzz-bee syndrome, C-D: mixed-vertebrate syndrome, E: passerine syndrome.*

4.6.5 Structure of stamen filaments

Consistent with the literature (Dellinger et al. 2018), I found that all species within the "buzz-bee" syndrome possess smooth filaments. Species within the "mixed-vertebrate" syndrome show marked ruptures in stamen filaments (Figs 13 & 19) from which nectar is secreted. This finding is consistent with the literature (Vogel 1997, Dellinger et al. 2018, 2019a). The only exclusively hummingbird

pollinated species (*Brachyotum ledifolium*) has smooth filaments, hence the exact location of nectar secretion in this species remains unclear (Apx. 1).

4.6.6 Structure of thecae wall

Consistent with Dellinger et al. (2018), I found that species within the "buzz-bee" syndrome can either possess thecae with smooth (21 species) or ruminate (15 species) wall structure (Fig. 15). Within the "mixed-vertebrate" syndrome, thecal walls are smooth (4 species) or crumpled (7 species) (Fig. 15). The only exclusively hummingbird pollinated species (*Brachyotum ledifolium*) had smooth thecal walls (Apx. 1).

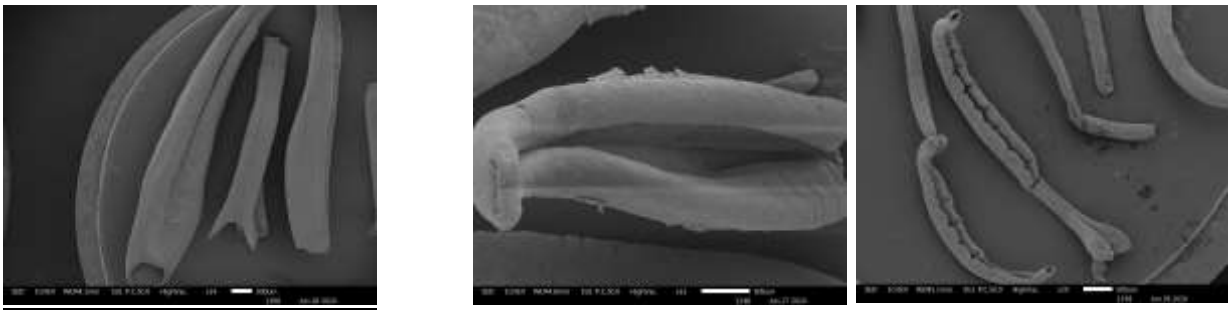

Figure 15: Scanning Electron Microscope pictures ofanthers; showing the Change of the structure of thecal wall with a shift from buzz-bee pollination to other pollination syndromes; left: Tibouchina grossa *("mixed-vertebrate" syndrome) with smooth thecal walls (500 µm); the middle image shows* Blakea maurofernandiana *("buzz-bee" syndrome) with smooth thecal walls (500µm); the right image shows* Tibouchina ciliaris ("buzz-bee" syndrome) with ruminate thecal walls (*500µm).*

4.7 Pollination syndromes in the Neotropical Melastomataceae tribes with pollinator shifts

In the following, I describe major pollination syndrome patterns for Blakeeae, Melastomeae and Miconieae. Pollination syndromes for Merianieae have been described and represent the reference for my descriptions (Dellinger et al. 2018). My syndrome descriptions are based on the set of taxa which I could include in my thesis, and I emphasize that a wider sampling may require the inclusion of additional traits and somewhat alter syndrome circumscriptions in the future.

4.7.1 Pollination syndromes in Blakeeae:

Species within the tribe Blakeeae can be classified in the “buzz-bee” or the “mixed-vertebrate” syndrome. No species with the “passerine” pollination syndrome is known so far within the tribe Blakeeae.

The “buzz-bee” syndrome species I sampled are characterized by buzz-pollination, pollen as sole reward for the pollinators, and an open corolla. The flowers are oriented upright or horizontally. Further, the androecium of my sampled species is always in an adaxial (zygomorphic) position relative to the floral center (Fig. 16). The stamens are isomorphic, sturdy, possess small knob-like or thread-like dorsal appendages, two anther pores (with extrorse or introrse pollen release) and a smooth thecal wall. The anthers are often dorsiventrally broadened, the thecae are fused with each other except for the first and the last thecae forming a half circle around the style, and are directed towards the floral center (Fig. 16). The style is free and bent upwards towards the stamens with a convex or conical stigma.

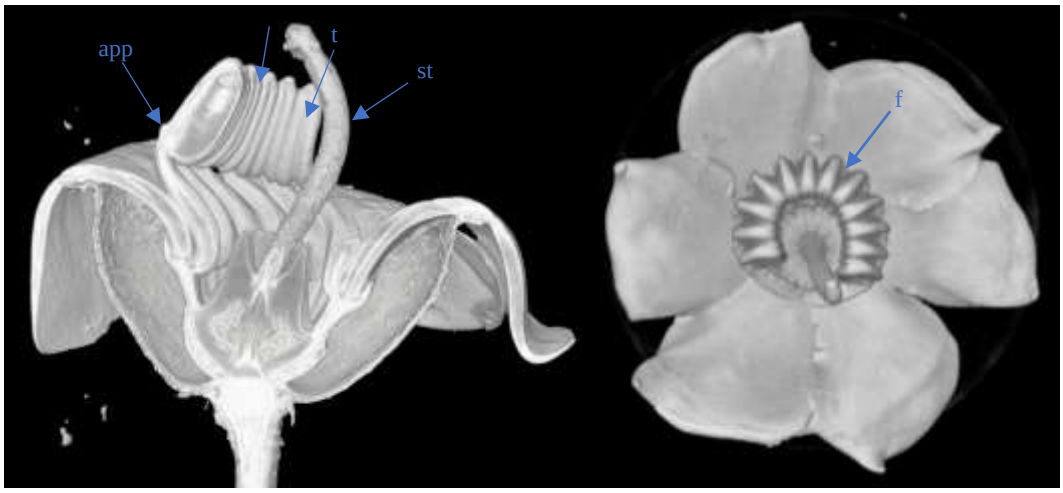

Figure 16: Tomography-based 3D models of Blakea florifera *(flower length = 4mm, flower diameter = 26mm); left: longitudinal section through a flower of* Blakea florifera *showing a tiny knob-like appendage, two anther pores with introrse pollen release, smooth thecal wall and a free style, the arrows indicate appendage, anther pores, thecal wall and free curved style (app = appendage, p = pore, t = thecae, st = style,); the right* image shows Blakea setosa *with adaxial androecial position and fused thecae, the arrow indicates fused thecae (f = fused thecae).*

The only Blakeeae species within the “mixed-vertebrate” syndrome I found in the field (*Blakea chlorantha)* is characterized by the typical “salt-shaker” mechanism of pollen release, nectar as

reward type and a pseudo-campanulate pendant corolla. The androecium forms a circle around the style. The stamens are flexible, possess two apical pores (the only species with 2 pores within the pollination syndrome "mixed-vertebrate"), tiny knob-like appendages, a smooth thecal wall and ruptures in the filaments where nectar is secreted. The thecae are located on the ventral side of the stamens. The style is partly enclosed and straight with a convex stigma (Fig. 17). In addition to *B. chlorantha* I included two species from the literature (*Blakea austin-smithii*, *Blakea gregii*, Wester et al. 2016) that are "mixed-vertebrate" pollinated. Since I did not have access to floral material of these species, I was not able to score all traits of the floral character code (Apx.). These two species are also characterized by the typical "salt-shaker" mechanism of pollen release, nectar as reward and a pseudo-campanulate pendant corolla. The androecium forms a circle around the style. The stamens are flexible, the style is straight and partly enclosed (Apx. 1).

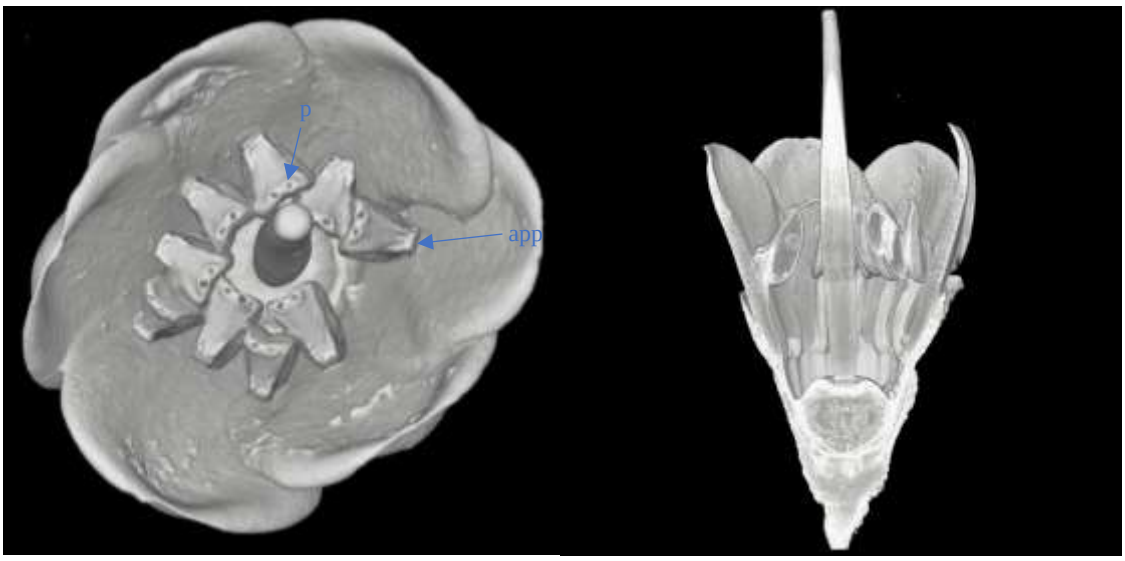

Figure 17: Tomography-based 3D models of Blakea chlorantha *(flower length = 10mm, flower diameter = 12mm); left: top view of a flower showing actinomorphic androecial position, tiny knob-like appendages and two apical pores, the arrows indicate anther pores and appendage (app = appendage, p = pore); the right image showing a longitudinal section of a flower showing a partly enclosed style and a part of the actinomorphic androecium.*

4.7.2 Pollination syndromes in Melastomeae

Species within the tribe Melastomeae can be classified as "buzz-bee" or "mixed-vertebrate" syndrome. An exclusively hummingbird-pollinated species (*Brachyotum ledifolium*) was included

in my dataset (but pertaining to a genus of approximately 50 morphologically highly similar species, Renner 1989). I classified this species into a separate "hummingbird" syndrome, although statistical support for this syndrome was low (see Discussion). No species with the pollination syndrome "passerine" is known so far within the tribe Melastomeae.

Within the "buzz-bee" syndrome of my sampled species in the tribe Melastomeae, the species are characterized by pollen release through vibrations, pollen as the reward type, and open, reflexed or bowl-like corollas. The androecium is either in an adaxial (zygomorphic) position or forms a circle (actinomorphic) around the style and can be highly heterantherous. The stamens are sturdy, possess a large variety of appendage shapes and sizes that are morphologically directed towards to floral center (except *Monochaetum* – directed outside the flower) but are functionally usually directed outside the flower. Further, the stamens possess only one pore with apical, introrse or extrorse pollen release and the thecal wall can be ruminate or smooth. The thecae are morphologically directed towards the floral center but can be directed outside the flower in heterantherous species. The style is free and bent or hooked with a convex or conical stigma (Fig. 18).

Figure 18: Photographs of flowers; left: Tibouchina ciliaris *(flower length = 3mm, flower diameter = 21mm), a strongly heterantherous species; the middle image shows* Tibouchina mollis *(flower length = 2mm, flower diameter = 19mm) with an actinomorphic androecium; the right image shows* Tibouchina lepidota *flower length = 4mm, flower diameter = 43mm) with a hooked style and thecae that are directed outside of the flower.*

Species within the "mixed-vertebrate" syndrome of my sampled species in the tribe Melastomeae are characterized by "salt-shaker" pollen release (*Brachyotum lindenii*) or by a "bounce-mechanism", newly described here (*Tibouchina grossa*, see above). Further, the species within the

"mixed-vertebrate" syndrome are characterized by nectar as reward (in *T. grossa* 13%Vol sucrose Fig. 19) and bowl-like (*T. grossa*) or tubular (*B. lindenii*) corollas. The androecium is actinomorphic (*B. lindenii*) or zygomorphic with the stamens directed towards the abaxial side of the flower (*T. grossa*). The stamens are flexible, possess no appendages (*B. lindenii*) or a V-shape appendage (*T. grossa*) that is directed towards the floral center. Further, the stamens possess only one pore with pollen release in introrse (*T. grossa*) or apical direction (*B. lindenii*); the structure of the thecal wall is smooth. The thecae are directed towards the floral center (*B. lindenii*) or are positioned laterally (*T. grossa*). The style is partly (*T. grossa*) or completely enclosed (*B. lindenii*) by the corolla and can be straight (*B. lindenii*) or bent (*T. grossa*) with a convex (*B. lindenii*) or enlarged, capitat (*T. grossa*) stigma (Fig. 20). The flowers of *T. grossa* start to open slowly in the morning, are fully anthetic in the evening and stay open at least until the next morning.

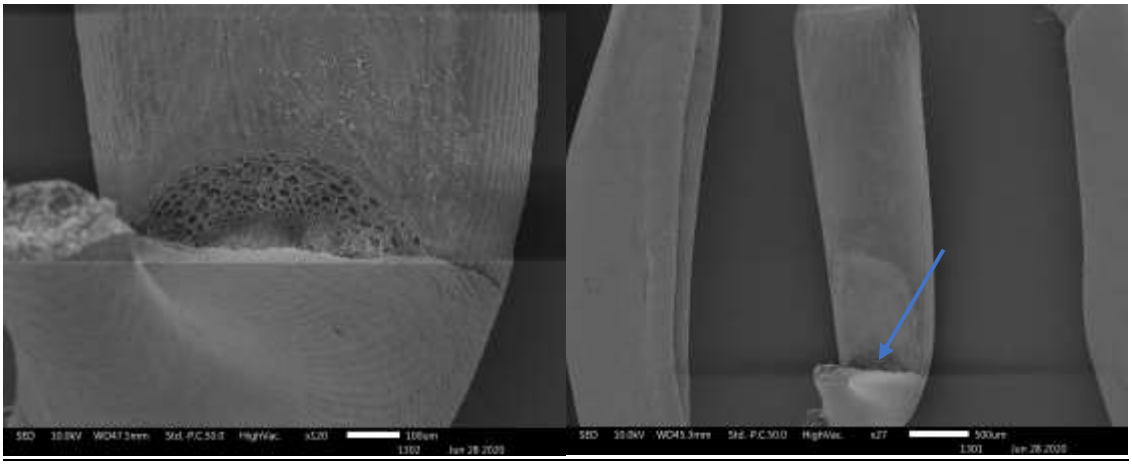

Figure 19: Scanning Electron Microscope picture of Tibouchina grossa*; left: detail of filament rupture where nectar is secreted (100 µm); the right image shows a total view of a filament, the arrow indicates the filament rupture (500 µm).*

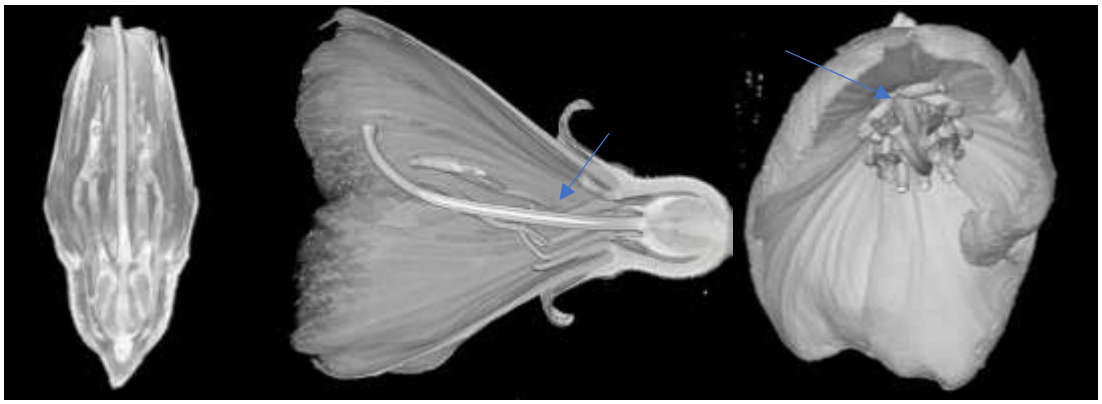

Figure 20: Tomography-based 3D models of flowers; left: longitudinal section through flower of Brachyotum ledifolium *(flower length = 14mm, flower diameter = 5mm)* showing part of actinomorphic androecium and *enclosed style; middle and right:* Tibouchina grossa *(flower length = 33mm, flower diameter = 32mm), the middle image shows a flower in longitudinal section, the arrow indicates a v-shaped stamen appendage; the right image shows a flower with its anthers mostly arranged in the lower part of flower.*

The only species that was pollinated exclusively by hummingbirds (*Brachyotum ledifolium*) is similar to the "mixed-vertebrate" pollination syndrome, except for the corolla shape. The corolla in this species is pseudo-tubular throughout anthesis so that only hummingbirds can forage for nectar (Dellinger, pers. obsv., Fig 20). This being said, no nocturnal pollinator observations exist for this species to date. Hence, at the moment, we cannot exclude with certainty visits by nocturnal pollinators, and hence correct classification as "mixed-vertebrate".

4.7.3 Pollination syndromes in Miconieae

I classified the species within the tribe Miconieae as "buzz-bee" or "mixed-vertebrate" syndrome. I found no species with the "passerine" syndrome. Although I did not formally test for it, Miconieae may also include a "self-pollination" and a "generalist" syndrome (Brito 2016, Gavrutenko et al. 2020), or even an additional insect-pollination syndrome (i.e. "fly" syndrome, Mauricio Posada, pers. com. to Agnes Dellinger).

Species within the "buzz-bee" syndrome are characterized by buzz-pollination, pollen as only reward and open, reflexed or bowl-like corollas. The flowers are usually small, and the androecium

can be adaxial, abaxial or actinomorphic (Fig. 21). The stamens are sturdy and often lack an appendage. If an appendage is present, it is often knob-like, but always small in size (Fig. 21) and can be oriented laterally, ventrally or dorsally in relation to the floral center. Further, the stamens only possess one pore (Fig. 21), except for *Miconia trinervia* which has two anther pores. The thecae are directed towards the floral center and the thecal wall can be smooth or ruminate. Some species show heteranthery (e.g. *Miconia notabilis*) The style is freely exposed from the corolla and can be bent, hooked or straight with a convex, corymbose or capitate stigma (Fig. 21).

Figure 21: Tomography-based 3D models of flowers; left: Miconia goniostigma *(flower length = 1mm, flower diameter = 9mm), showing actinomorphic androecial position, reflexed petals, one anther pore and stamp like stigma, the arrow indicates the appendage; the middle image shows* Miconia lacera *(flower length = 1mm, flower diameter = 5mm) with adaxial androecial position and open corolla shape; the right image shows* Miconia donaeana *(flower length = 1mm, flower diamerter = 12mm) with one anther pore and ruminate thecal walls.*

The only species that was predicted to be within the "mixed-vertebrate" syndrome (*Miconia barbata*) in the tribe Miconieae is characterized by "salt-shaker"-like pollen release, nectar as reward (13,5% Vol. sucrose)) and an open corolla shape. The androecium is actinomorphic, and the stamens are flexible, possess no appendage and only one anther pore that is located apically on the anther. Further, the structure of the anther wall is smooth, and the thecae are directed towards the floral center. The style is free and straight with a convex stigma shape (Fig. 22).

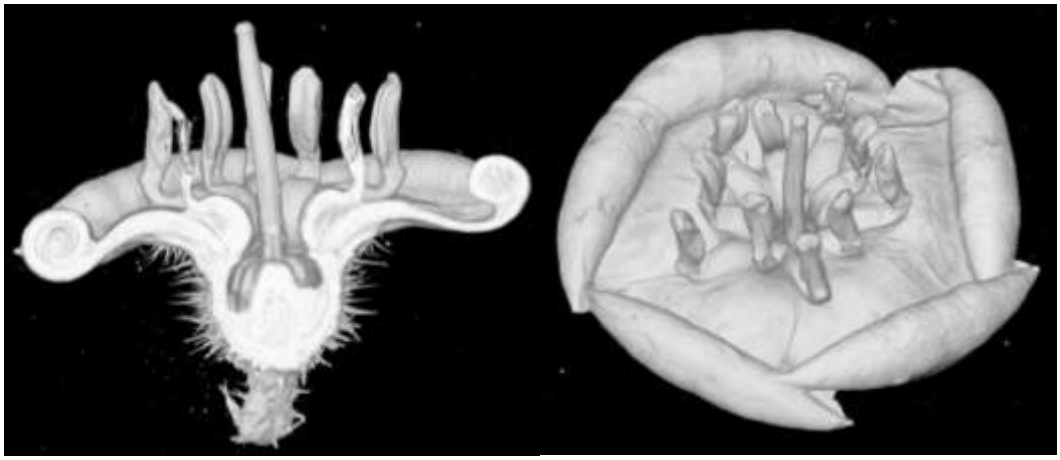

Figure 22: Tomography-based 3D models of flowers of Miconia barbata *(flower length = 2mm, flower diameter = 13mm); left: longitudinal section through a flower showing smooth structure of thecal wall, extrorse single pores and free style; right: showing actinomorphic androecial position and open corolla shape with rolled up petal tips where nectar is secreted.*

In *Miconia reducens*, I found strong evidence for an extreme case of self-pollination, where the pollen tube germinates within the anther and grows directly into the stigma (Fig. 7).

In my data set, I did not have any species included that fall into the "generalist" pollination system also occurring in Miconieae. However, there are several species within the tribe Miconieae which are visited by generalist insect pollinator assemblages (Brito 2016, Gavrutenko et al. 2020). Some of these generalist species (i.e. *Miconia crocea*) may also be visited by short-billed hummingbirds (Dellinger, pers. obsv.). A broad sampling across Miconieae would be necessary to clarify affinities between the "mixed-vertebrate"-pollinated species and the generalist species in order to see whether these pollination systems can be differentiated into two separate syndromes, or whether they form a big continuous syndrome.

4.8 Pollinator shifts and the relation to altitude

In my sample, vertebrate-pollinated species start to appear at an elevation of about 1300m. "Buzz-bee" pollination can be found along the entire altitudinal gradient analyzed, from sea-level up to almost 3000m, while "passerine", "mixed-vertebrate", and "hummingbird" pollinated species are only found at elevations that range from 1300m to over 3000m (Fig. 23).

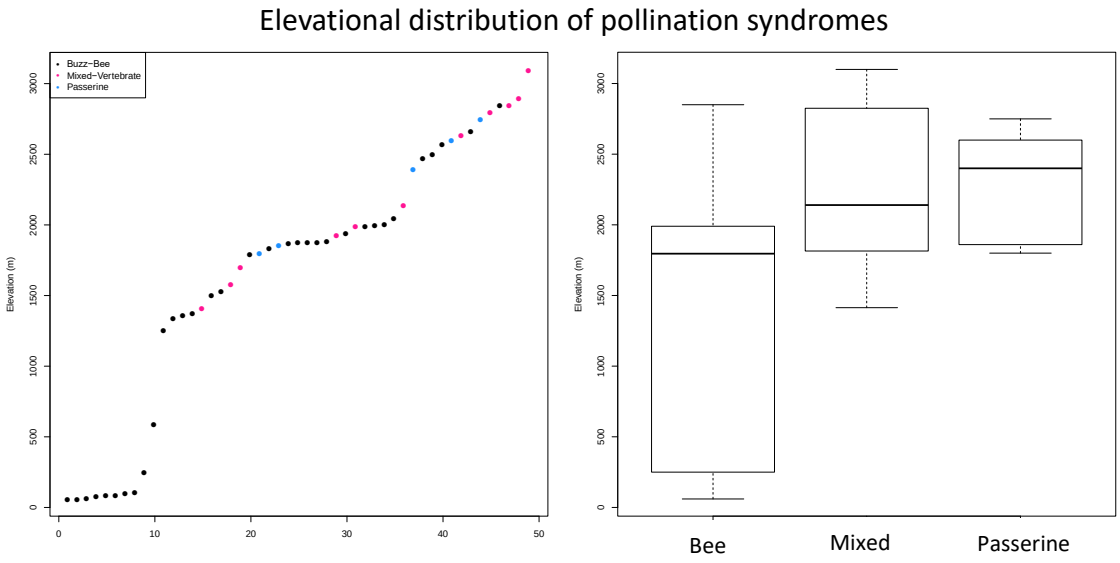

Figure 23: Elevational distribution of pollination syndromes; left: plotted elevation of each species and pollination syndrome; right: boxplot of elevational distribution of the three pollination syndromes; pollinator shifts to vertebrate pollination start to occur at an elevation of about 1300m; buzz-bee pollination can be found from sea-level up to almost 3000m while vertebrate pollination is only found at an elevation between 1300m to over 3000m.

5. Discussion

Overall, I detected two well differentiated pollination syndromes in the Melastomataceae tribes Blakeeae, Melastomeae and Miconieae: “buzz-bee” pollination and “mixed-vertebrate” pollination. These syndromes were best characterized by the same floral traits as pollination syndromes in the tribe Merianieae (Dellinger et al. 2018). I did not find any species in these three tribes falling into the “passerine” pollination syndrome also occurring in Merianieae. The floral traits identified as most important in separating pollination syndromes in Merianieae (i.e. “reward type” and “known mode of pollen expulsion”) were also most informative in differentiating syndromes in the other tribes. By showing that Merianieae pollination syndromes may be extrapolated to other Melastomataceae tribes, my results support the concept of pollination syndromes as useful tool to study floral traits in the context of pollination at macroevolutionary scales (Ashworth et al. 2015, Dellinger 2020). As long as detailed, system-specific floral functional traits are studied, pollination syndromes may indeed be used to predict pollinators of species where no empirical pollinator observations are available (Ollerton et al. 2009, Dellinger 2020). In the following, I discuss the major findings of my study in more detail.

5.1 Differences in disparity between syndromes and organ modules

Among the different syndromes, the “buzz-bee” syndrome was the most disparate. However, also among the species with unknown pollinators (no observations and no predictions), I found high disparity. This finding indicates that several undetected pollination syndromes, like “self-pollination” in *M. reducens* or possibly a “generalist” syndrome within the other unpredictable species may be present. Furthermore, my limited dataset has not captured the entire diversity of flower morphologies found across Melastomataceae.

Differences in disparity between pollination syndromes remains poorly investigated and may arise for different reasons. First, distinct functional pollinator groups may interact differently with flowers, some functional groups showing more variability in their interaction behavior than others. In Melastomataceae, buzzing bees are attracted by and actively interact with anthers and stamen appendages when vibrating them to extract pollen rewards. Stamens are hence exceptionally diverse in size, color and shape in the "buzz-bee" syndrome (12 of 13 character states of stamen appendage shape are found within the "buzz-bee" syndrome!) and may represent adaptations to distinct subgroups of buzzing bees varying in their behavior on the flower. Pollinators within the "mixed-vertebrate" syndrome, on the other hand, do not actively manipulate the anthers when foraging for nectar, but passively touch both the anthers and the corolla. Accordingly, stamen appendages are reduced in size in many "mixed-vertebrate" species. The passerine birds pollinating some species in the tribe Merianieae, on the other hand, again directly interact with a the specialized bulbous stamen appendage that was co-opted into food bodies (Dellinger et al. 2014). These bulbous stamen appendages are relatively homogeneous in shape and the behavior of the passerine birds is similar across different species (Dellinger et al. 2014). To date, there is little comparative data on disparity from other lineages where pollinator shifts have occurred (Dellinger et al. 2018), and whether there are consistent differences in disparity between syndromes also in other lineages remains unknown. Alternatively, differences in disparity may be a mere result of differences in species numbers: buzz-pollination occurs in ca. 98% of Melastomataceae, while relatively few species have shifted pollinators (Renner 1989).

When comparing the disparity of the three different organ modules ("corolla", "androecium", "gynoecium"), the module "corolla" had the highest disparity, followed by the module "androecium", and then the module "gynoecium". The "buzz-bee" syndrome showed the highest disparity in each organ module (Table 14). Subjectively, the organ module "androecium" was the

most diverse (reflected by 47 traits recorded, versus six in the other two modules; also see above), followed by the organ modules "corolla" and "gynoecium". Such bias may arise when recoding floral traits qualitatively as done here, i.e. through a highly refined categorization, potentially missing functional aspects. Since the corolla traits were scored with 6 categories at most, this bias can be ruled out here. Another explanation could be that some of the androecium traits are uniform and hence generate pseudo-similarity.

Generally, the androecium is under high selective pressure, since it is crucial for efficient pollen release and thereby for reproduction (Bawa & Beach 1981). In general, the perianth has been reported as less diverse than the reproductive organs in other groups (Endress & Matthews 2005, Chartier et al. 2017). This could also explain why the "buzz-bee" syndrome is the most diverse, since buzzing bees interact with many parts of the androecium, while pollinators of the other syndromes interact with only few parts of the androecium. To test for significant differences, one would have to proceed as mentioned in the section "Comparing efficiency and attraction traits".

5.2 High disparity of the buzz-bee syndrome

As mentioned above, I found that the "buzz-bee" syndrome shows the highest disparity. This finding is consistent with the findings of Dellinger et al. (2018). One explanation for this high disparity could be the high modularity found in the "buzz-bee" syndrome of Merianieae (Dellinger et al. 2019b), which could also apply for other buzz-bee-pollinated tribes within the family. This is particularly important in the light of high floral uniformity found in other buzz-pollinated groups, such as the mega-genus *Solanum* (Solanaceae; Endress 1996) or *Myrcia* (Myrtaceae; Vasconcelos et al. 2018). To maximize intraspecific pollen transfer it is advantageous to be specialized on a specific pollinator (Brosi 2016). The "buzz-bee" syndrome encompasses 98% of Melastomataceae species (Renner 1989), and the buzzing-behavior occurs in more than 50% of bee species (Cardinal

et al. 2018), thus the morphological diversity of buzzing-bees is high. Many different bee species are known to buzz Melastomataceae flowers but differ in size and/or behavior on the flower (Vogel 1975, Renner 1989). It therefore can be expected that the "buzz-bee" pollination syndrome represents various slightly different selective pressures. Although we lack comparative experimental testing, different Melastomataceae flowers within the "buzz-bee" syndrome possibly represent adaptations to distinct bee species. The "buzz-bee" syndrome is a highly specialized system and most Melastomataceae radiated within this syndrome (98% of Melastomataceae are "buzz-bee" pollinated, Renner 1989). Shifts to other pollination syndromes have been constrained by retaining poricidal anthers (Dellinger et al. 2019b). Without this morphological constraint, the other pollination syndromes could also be more disparate.

5.3 Hummingbird pollination syndrome

The statistical support for this pollination syndrome was low, since I had only one species in my trait matrix that was exclusively hummingbird pollinated (*Brachyotum ledifolium*). The other *Brachyotum* species, *B. lindenii*, in my dataset was pollinated by hummingbirds and flowerpiercers (Stiles et al. 1992), thus possibly belonging to the "mixed-vertebrate" syndrome. More species of the genus *Brachyotum* need to be studied both in the field and morphologically to evaluate whether the genus *Brachyotum* is exclusively hummingbird pollinated (suggested by Renner, 1989), or whether it is better included in the "mixed-vertebrate" syndrome. Furthermore, it could be tested whether *Brachyotum* is a genus where shifts from bimodal "mixed-vertebrate" pollination to specialized hummingbird pollination occur. Note that *Brachyotum* belongs to the tribe Tibouchineae, where species belonging to the "mixed-vertebrate" syndrome are known (e.g. *T. grossa*) and that Stiles et al. (1992) also reported flowerpiercers visiting *Brachyotum ledifolium*. The most important trait in differentiating exclusively hummingbird pollinated species from the

"mixed-vertebrate" syndrome is the corolla shape. The hummingbird pollinated species *Brachyotum ledifolium* possesses a narrowly tubular corollas allowing only hummingbird bills to enter the flower and forage for nectar. Further field investigations are required to verify the reports of flowerpiercer-pollination in *Brachyotum* (Stiles et al. 1992). Flowerpiercers are common nectar robbers (Irwin et al. 2010) and it is possible that flowerpiercers act primarily as nectar robbers by piercing holes into the corolla, but do not effect pollination (Dellinger, pers. obsv.).

5.4 "Unpredictable" species – shortcomings of pollination syndrome concept?

Using M4, all species were predicted as bee pollinated (Table 12). This is plausible for all species except for *Miconia barbata* and *Miconia reducens*. *M. barbata* does produce nectar and possesses a "salt-shaker" pollination mechanism. Thus, it most likely belongs to the "mixed-vertebrate" syndrome, which is also supported by the fact that no nectar producing, bee-pollinated Melastomataceae species is known to date. Hence removing the reward type from the prediction algorithm likely caused an erroneous classification of this species. The model M1, which was the best in predicting pollination syndromes both for species with and without confirmed pollinators, was not able to predict the pollinators of four species (*Miconia reducens*, *Tibouchina mollis*, *Aciotis levyana* and *Clidemia epiphytica*), due to missing data. However, there may be several reasons for this (not able to score traits or pollination syndrome not included in training data). As reported for other species (*Monolena,* Melastomataceae; Warner 1981, *Arabidopsis,* Brassicaceae; Johnson & McCormick 2001), I found strong evidence for an extreme case of self-pollination in *Miconia reducens*. The anthers are strongly curved towards the stigma, the pollen tube germinates within the anther and grows directly onto the stigma (Fig. 7). Since I do not have a "selfing" syndrome in the training dataset, this extraordinary selfing-mechanism may explain the disability of the model to predict a pollination syndrome for this particular species. Other models that I tested (M2, M4),

predicted *Tibouchina mollis* as belonging to the "buzz-bee" syndrome.. This prediction is likely correct since *T. mollis* strongly resembles other "buzz-bee" pollinated *Tibouchina* species. *Aciotis levyana* and *Clidemia epiphytica* could either be "generalists" like described for some species in the tribe Miconieae (Gavrutenko et al. 2020), again not included in my training dataset, or be pollinated by some other functional pollinator group like tiny flies or coleoptera. *Aciotis levyana* has a tiny white flower with an open corolla shape, an actinomorphic androecium, a knob-like appendage and no nectar production. The stamens possess only one anther pore and the thecal structure is smooth. *Clidemia epiphytica* has a tiny flower with a red calyx and white petals. The corolla shape is open, the androecium is actinomorphic, the stamens possess no appendage, and no nectar is produced. The stamen pore is a slit that is oriented introrsely and the thecal structure is smooth. Also, the flowers are only open for a few hours in the early morning (00:00 am – 08:00 am). Another explanation for the disability of the model to predict the functional pollinator group for these four species could be that I was not able to score the traits "reward type" and "known mode of pollen expulsion" for *Miconia reducens*, *Aciotis levyana*, and *Clidemia epiphytica*. For *Tibouchina mollis* I had 17 traits with missing data, since this sample did not make it back to Vienna for further analyses. These problems highlight the need to study a broad taxonomic sampling, combined with empirical pollinator observations and a detailed and complete trait-matrix specific for the studied group in order to reliably apply pollination syndromes (Dellinger 2020). Generally, however, I conclude that pollination syndromes work well in Melastomataceae, provided that the analyses are based on a detailed set of functional floral traits, as in my thesis.

5.5 Pollinator shifts and high elevation

I observed that pollinator shifts from buzz-bee to vertebrate pollination start to appear at an elevation of about 1300m (Fig. 23), this is consistent with other authors mentioning this pattern (e.g. Renner

1989, Varassin et al. 2008). Similar patterns have also been reported in other plant groups (e.g. Arroyo et al. 1982). I found "buzz-bee" pollinated flowers from sea-level up to almost 3000m. Cruden (1972) reported that at high elevations, birds are more efficient during the rainy season, while during the dry season, the effectiveness of birds and bees is equal. Thus, the higher number of bird pollinated species at higher elevations may be a result of competitive advantage gained through greater reproductive success (Cruden 1972). This finding could explain the recurring shifts from bee to bird pollination at high elevations. It does not explain, however, why many bee-pollinated species persist at high elevations. Evolutionary constraints in flower morphology could be one reason, but not likely in the highly divers Melastomataceae (Dellinger et al. 2019b). Further research is needed to fully explain why some lineages within the "buzz-bee" syndrome shifted pollinator at an altitude of about 1300m upwards and why some remained "buzz-bee" pollinated.

5.6 Comparing random forest models and trait importance

I chose all traits carefully with a special focus on functionally important traits and traits that might play an important role in attracting pollinators. I also selected traits that might be of evolutionary importance in Melastomataceae (Renner 1989, Dellinger et al. 2014, Dellinger et al. 2018, Dellinger et al. 2019a) and across angiosperms (Endress 1996, Ollerton 2009, Rosas Guerrero et al. 2014, Dellinger et al. 2020). The trait categories followed categories developed for Merianieae (Dellinger et al. 2018), but I defined new categories for species that differ from Merianieae in their morphological features.

I tested six different trait combinations in random forest models including two models (M3, M6) where I tried to subdivide the "buzz-bee" syndrome further by differentiating the bees in large, medium, and small species. However, I was not able to tease apart the "buzz-bee" syndrome using this approach (Table 6 & 11). Recently, a functional division of buzzing bees into "single-anther-

buzzing" and "whole-flower-buzzing" was proposed (Mesquita-Neto et al. 2017). Possibly, additional field data could help to differentiate such groups.

All other trait combinations produced less accurate syndrome predictions than the model M1. Although the models M4 and M5 were able to predict more pollination syndromes for species without confirmed pollinators (comp. Table 10 & 12), I chose model M1 to be the best to predict syndromes for species without confirmed pollinators for two reasons. First, in model M5 three species (*Aciotis levyana*, *Clidemia epiphytica*, *Miconia reducens*) were excluded (Table 12), due to missing data. Second, in model M4, *Miconia barbata* was predicted as "buzz-bee" syndrome (Table 12), although this species shows strong evidence to be "mixed-vertebrate" pollinated ("salt-shaker" mechanism, nectar, Fig. 22).

When comparing the trait importance of M1 and M2, only the trait "corolla color" was of less importance in M2, except for the traits that were excluded in M1 (Table 8 & 9). Since, I used more traits in M2 than in M1, this could explain why this trait was of less importance in M2. Also, this trait was found to be of little importance in Dellinger et al. (2018), except for hummingbird pollination (Fenster et al. 2004, Cronk & Ojeda 2007). Further, it was shown that floral color can be of high importance in syndrome classification but can also be highly uninformative or misleading (Dellinger et al. 2020).

When comparing the trait importance of M1 to the trait importance reported in Dellinger et al. (2018), the traits which were of high importance in discriminating the three different pollination syndromes were similar. The most important traits in my thesis and in Dellinger et al (2018) were, "reward type" and "known mode of pollen expulsion". The traits "stigma shape" and "petal gloss", which were excluded from M1, were of less importance in M2 than in Dellinger et al. (2018). Petal gloss can be a highly subjective trait, depending on the scoring method (pictures, in the field or following Whitney et al. 2012). While strong petal gloss was only found in vertebrate-pollinated

Merianieae, it was common in the pollination syndrome "mixed-vertebrate" and in some "buzz-bee" species (*Miconia goniostigma, Miconia lacera, Blakea maurofernandiana* and *Clidemia globuliformes*). Possibly, this trait is only important in differentiating pollination syndromes within Merianieae (Dellinger et al. 2018), but not across Melastomataceae. The trait "stigma shape" is possibly of less importance in M2 because I included three other tribes in addition to Merianieae and this trait possibly only is important in differentiating pollination syndromes within Merianieae, similar to the trait "petal gloss" (Dellinger et al. 2018). Another explanation could be that this trait might only be important in discriminating the "passerine" syndrome from the other syndromes, but I found no species in the other three tribes that were "passerine" pollinated. Overall, "stigma shape" ranked only among the 18 most important traits in the "buzz-bee" syndrome (Table 9). Within the "buzz-bee" syndrome, all four possible stigma shapes were found (Apx. 1). Species within the "mixed-vertebrate" syndrome had capitate or convex stigma shapes, while species within the "passerine" syndrome possessed convex or conical stigma shapes (Apx. 1). One mechanism to maximize reproductive output is to increase stigma size (Cruden 2000). Large stigma area increases pollen contact site with the pollinator and more pollen can be deposited in one visit (Cruden 2000). Flowers with large pollinators and pollinators that only shortly contact the reproductive parts of a flower (e.g. bat, hummingbird – "mixed vertebrate" syndrome), may hence evolve larger stigmas (Cruden 2000). This is also supported by my data. I found large stigmas in the "mixed-vertebrate" and "hummingbird" syndrome, but also some of the "buzz-bee" syndrome species can possess large stigmas. Another way to increase the number of pollen grains that can be deposited on the stigma is to decrease pollen size or to increase the duration of receptivity (Cruden 2000). In my thesis, I did not score these traits.

The trait "structure of stamen filaments" is most important within the pollination syndrome "mixed-vertebrate" (Table 9), because this is the only syndrome where ruptures are present, and nectar is

secreted from these ruptures in most of the species (not in *Brachyotum lindenii*, *Meriania costata*, *Meriania furvanthera*, *Meriania sanguinea*, *Meriania* aff. *sanguinea*) and can therefore be used as proxy for reward type. This is consistent with Vogel (1997), Dellinger et al. (2018), and Dellinger et al. (2019a). Varassin et al. (2008) on the other hand, reported nectary stomata on the inner hypanthium surface in the tribe Merianieae, on the dorsal side of anther connectives in Blakeeae on the inner surface of the ovary apex in the tribe Miconieae and on the dorsal side of the anther connective in *Brachyotum*. In my thesis I only looked at stamen filaments as source for nectar production. In *Miconia barbata,* I found nectar that aggregated in the distally rolled in petal tips (Fig. 22), but whether this nectar is secreted from ruptures (Fig. 19), from the petals or the ovary apex remains to be investigated. All nectar-secreting Merianieae species without filament ruptures possess small intercellular holes on the proximal-lateral side of filament and/or ruptures on the filament/connective joint (Dellinger et al. 2019). Within the "buzz-bee" syndrome, this trait is of intermediate importance (Table 9), while within the "passerine" syndrome, this trait seems to be of little importance (Table 9). The traits "appendage shape" and "orientation of flower" are more important in the "passerine" syndrome (Table 9) and thereby ranking back the trait "structure of stamen filaments".

5.7 Comparing efficiency and attraction traits

I compared the explained variance of efficiency and attraction traits and tried to separate the three pollination syndromes using only efficiency or attraction traits, respectively. Efficiency traits separated the three pollination syndromes better than attraction traits (comp. Table 15 & 16 and Fig. 12).

I used more efficiency traits than attraction traits, this could explain the difference in the power of this subsets to separate the three pollination syndromes. Nevertheless, the explained variance, when

grouping the species into the four pollination syndromes, using either efficiency or attraction traits only, was similar (Fig. 12). These similar percentages of explained variance could also be due to the different numbers of efficiency and attraction traits. To really test for significant differences between efficiency and attraction traits, one would have to select a subset from these traits by a loop that selects different sets of traits randomly from the trait matrix to account for different numbers of traits. Finally, it should be mentioned that the function of a trait can change between the different syndromes. In the "buzz-bee" syndrome, for example, the colorful anthers attract pollinators (Renner 1989) and appendages serve as handles for the bees to grasp while buzzing (Renner 1989, Dellinger et al. 2018 and pers. obs.). In the "mixed-vertebrate" syndrome stamen appendages are often not involved in pollinator attraction and pollen transfer (but see *T. grossa*), since the reward is nectar aggregating on the petals (Dellinger et al. 2018).

6. Conclusion

6.1 Hypothesis 1

First, I wanted to determine whether the three tribes Blakeeae, Melastomeae and Miconieae show the same three pollination syndromes as Merianieae. The three pollination syndromes "buzz-bee", "passerine" and "mixed-vertebrate" that were confirmed by Dellinger et al. 2018 were also clearly detected and significantly different from each other in my data set (Fig. 8, Table 13). I found the "passerine" syndrome only within the tribe Merianieae. Additionally, I had one species in my data set (*Brachyotum ledifolium*) exclusively pollinated by hummingbirds. The "hummingbird" syndrome was not significantly different from the other pollination syndromes (Table 11)

6.2 Hypothesis 2

Second, I wanted to identify which traits change with a shift from buzz-pollination to other syndromes. The most important traits that change with a shift from buzz-pollination to vertebrate pollination are: reward type, pollen expulsion mechanism, corolla shape, structure of stamen filaments and appendage shape. These traits are the same as found in Dellinger et al. 2018 for the tribe Merianieae alone.

6.3 Hypothesis 2a

Third, I investigated whether there are morphological similarities among and within the different pollination syndromes of the three different tribes. Species that are pollinated by the same functional pollinator group were characterized by the same functional trait combination. Thus, species from different tribes possessed the same functional trait combination if they were pollinated by the same functional pollinator group (Fig. 8). Hence, species were not separated by tribes, but rather by functional pollinator groups based on functional traits (Fig. 8). Consequently, the pollination syndrome concept can be successfully applied in Melastomataceae, since adaptation to different functional pollinator groups resulted in strong floral functional trait convergence independent from phylogenetic relationships (Fig. 8). Species within the "buzz-bee" syndrome are characterized by pollen release when high-frequency vibrations are applied, various appendage shapes and sizes, and are sometimes heterantherous (not in *Blakea* in my sampled species). Species within the "passerine" syndrome, which only evolved in the tribe Merianieae, are characterized by pollen release when the appendage is compressed by foraging passerines, bulbous appendages, and tubular or pseudo-campanulate corollas. Species within the "mixed-vertebrate" syndrome are characterized by pollen release when the anthers are touched laterally (salt-shaker) or when the anther bounces back after the appendage is released from the foraging pollinator (bounce mechanism). Appendages are often smaller in size, except for *T. grossa* and possess pseudo-campanulate or bowl-shaped corollas. The

only exclusively hummingbird pollinated species (*Brachyotum ledifolium*) is similar to the "mixed-vertebrate" pollination syndrome, except for the corolla shape. The corolla in this species is narrowed throughout anthesis so that only hummingbirds can forage for nectar (Dellinger, pers. obs., Fig. 20).

Also, among the different pollination syndromes some species share some traits. For example, zygomorphic as well as actinomorphic androecial arrangements are present in species within the "buzz-bee" and within the "mixed-vertebrate" syndrome (see Apx. 1).

6.4 Hypothesis 2b

Fourth, I identified the most important traits discriminating the pollination syndromes and the most important traits specific for each syndrome. The seven most important traits discriminating the four pollination syndromes ("buzz-bee", "passerine", mixed-vertebrate", "hummingbird") are: reward type, known mode of pollen expulsion, corolla shape, position of style relative to corolla, orientation of flower in inflorescence, corolla color, and robustness of stamens (Fig. 5). The most important traits to describe the "buzz-bee" syndrome are: known mode of pollen expulsion, reward type, ratio between corolla height and diameter, corolla height, structure of stamen filaments, corolla shape, and pollen grain diameter (Tab 8 & 9). The most important traits to describe the "passerine" syndrome are: reward type, known mode of pollen expulsion, corolla shape, orientation of stigma to anther pore, pollen grain diameter, and appendage shape (Tab 8 & 9). The most important traits to describe the "mixed-vertebrate" syndrome are: structure of stamen filaments, known mode of pollen expulsion, reward type, corolla height, ratio between corolla height and diameter, and corolla shape (Tab 8 & 9).

6.5 Hypothesis 3

Fifth, I investigated whether the three pollination syndromes differ in morphological diversity (disparity). In accordance with Dellinger et al. (2018), I also found the "buzz-bee" syndrome to be

morphologically most diverse, possibly a result of adaptation to the large diversity of different buzzing bee species. My analyses detected the corolla to be morphologically most diverse. Subjectively, however, I consider the androecium as most diverse (47 traits), and particularly so in the "buzz-bee" syndrome.

6.6 Hypothesis 4

Sixth, I predicted pollinators for species without confirmed pollinators. The model M1 was able to predict most pollinators for species lacking empirical pollinator observations with high accuracy. *Brachyotum lindenii* was predicted as "mixed-vertebrate" pollinated while *Brachyotum ledifolium* was exclusively pollinated by hummingbirds. Additional empirical fieldwork is necessary to assess whether *Brachyotum* is indeed "mixed-vertebrate" and "hummingbird" pollinated, respectively, or form a purely hummingbird-pollinated clade. Also, these results demonstrate the close affinity between the "mixed-vertebrate" and the potential "hummingbird" syndrome. The model was not able to predict the pollinators for four species lacking empirical pollinator observations due to missing data: *Miconia reducens, Tibouchina mollis, Aciotis levyana* and *Clidemia epiphytica* (Table 10).

6.7 Hypothesis 5

Finally, I assessed the association between pollination syndrome and altitude. I found clear evidence that vertebrate-pollinated species occur at higher elevations while "buzz-bee" syndrome species are found both at low and high elevations.

7. Outlook

The first step of further research should be to include more species (ideally 10% per tribe) as well as species from different geographical regions (e.g. South East Asia) into the data matrix. Further, floral traits should be analyzed in a phylogenetic context. Furthermore, given the prevalence of the "buzz-bee" syndrome across Melastomataceae, this pollination system should be investigated more closely to identify possible differences between lowland and mountain species and answer the question why some "buzz-bee" species shifted pollinators at high elevations while others remained "buzz-bee" pollinated. Also, more refined tests on significant differences in disparity of the three different organ modules and the role of efficiency and attraction traits are necessary in order to determine their role in floral evolution in Melastomataceae. Finally, other pollination syndromes than described in this thesis should be identified and incorporated in the Random Forest prediction models (e.g. the pollination syndromes "self-pollination" and "generalist").

8. Literature

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Appendix:

Zusammenfassung

Das Konzept der Bestäubungssyndrome wird verwendet, um Blüten gemäß ihrem effizientesten Bestäuber zu klassifizieren, unabhängig von Verwandtschaftsverhältnissen. Das Konzept basiert auf der Theorie, dass Bestäuber aufgrund von Ähnlichkeiten in ihrem Verhalten, ihrer Morphologie, ihrer sensorischen Systemen etc., einen ähnlichen Selektionsdruck auf eine Blüte ausüben und diese Blüten daher konvergente Merkmale aufweisen. Bis jetzt wurden Bestäubungssyndrome in der Familie Melastomataceae nur in der Tribus Merianieae getestet. In dieser Tribus wurden drei signifikant unterschiedliche Syndrome gefunden: „buzz-bee“, „mixed-vertebrate“, „passerine“ (Dellinger et al. 2018). In meiner Masterarbeit untersuche ich, ob die drei Bestäubungssyndrome, die für die Merianieae beschrieben worden sind, auch in drei anderen Neotropischen Triben der Melastomataceae (Melastomeae, Blakeeae, Miconieae) vorkommen (Renner 1989). Weiters untersuche ich, ob in diesen drei Triben dieselben Blütenmerkmale wichtig sind, um die unterschiedlichen Syndrome voneinander zu unterscheiden. Ich arbeite heraus, in welchen Blütenmerkmalen sich die verschiedenen Syndrome unterscheiden und ob es Unterschiede in der morphologischen Diversität (Disparität) zwischen den verschiedenen Syndromen gibt. Für Arten, für die es keine bestätigten Bestäuberbeobachtungen gibt, versuche ich, die Bestäubungssyndrome vorherzusagen und schließlich untersuche ich, ob Bestäuberwechsel entlang von Höhengradienten stattfinden.

Um diese Fragen zu beantworten, habe ich während meiner Feldarbeit in Costa Rica und Kolumbien im Februar und März 2020 Blüten gesammelt und Bestäuber beobachtet und eine Datenmatrix aus 74 funktionellen Blütenmerkmalen für 59 Arten erstellt. Die Daten habe ich mittels *Random Forest* Analysen und multivariater Statistik analysiert. Um die Stärke der morphologischen Unterschiede

zwischen den Syndromen zu testen habe ich eine PERMANOVA mit einer *Pairwise Bonferroni* Korrektur durchgeführt und habe die Unterschiedlichkeit innerhalb jedes Syndroms berechnet.
Zwei der drei Merianieae-Syndrome („buzz-bee“ und „mixed-vertebrate“) habe ich auch in den drei anderen Triben gefunden. Die Syndrome sind signifikant unterschiedlich von einender. Weiters waren dieselben Merkmale von hoher Wichtigkeit („pollen expulsion mechanism“, „known mode of reward type“, „corolla shape“) um die verschiedenen Syndrome zu unterscheiden. Die wichtigsten Merkmale, in denen sich die verschiedenen Syndrome unterscheiden sind: „pollen expulsion mechanism“, „known mode of reward type“, „corolla shape“ und „structure of stamen filaments“. Der größte Unterschied habe ich im „buzz-bee“-Syndrom gefunden, gefolgt vom „mixed-vertebrate“-Syndrom. Bestäuberwechsel beginnen ab einer Seehöhe von 1300m. Das „Buzz-bee“-Syndrom kommt vom Meeresniveau bis über 3000 m Seehöhe vor. Weitere Analysen sind nötig, um auf signifikante Unterschiede zwischen den verschiedenen Organ-Modulen (Androecium, Gynoecium, Corolla) zu testen und um die Rolle von „attraction“ und „efficiency“ Merkmalen besser zu verstehen.

Floral Character Code

I coded 74 floral traits with a focus on traits that are of direct functional relevance during pollination, i.e., traits at the level of floral architecture and floral mode (sensu Endress 1996). I did not include floral traits at the level of floral organization (e.g., number organs, phyllotaxis, type of placentation, etc.) because they are neither directly relevant for pollination nor are they variable at the taxonomic level of this study.

General:

1. Known mode of pollen expulsion – evaluated in the field by pollinator observations and experimental manipulation using capillaries, to mimic birds' bills, and an electric toothbrush as well as an application for artificial buzzes to mimic buzzing bees (Dellinger et al. 2018)
0) Buzzing (pollen released when vibrations are applied)

1) Bellows-mechanism

2) Salt-shaker (flowers are pending, and pollen is released when anthers are moved)

3) Bounce-Mechanism (stamen is pushed downwards when the appendage is moved upwards – when released, the stamen bounces upwards and pollen is released)

2. Reward type (traditional pollination syndrome character)

0) Pollen

1) Nectar

2) Food body

3. Orientation of flowers in inflorescence relative to the ground - evaluated on photos and in the field and considering the majority of flowers in an inflorescence (traditional pollination syndrome character)

0) Multiple (multiple directions, any orientation of flower possible)

1) Upright-horizontal (Flowers are oriented upright and horizontal)

2) Nodding (all flowers nodding, corolla opening facing towards the ground)

3) Upright (all flowers upright, corolla opening faces away from ground)

4) Horizontal (90° tilted, style perpendicular to ground)

5) Capitulum (Flowers together form a capitulum; flowers are oriented in all directions in and ordered fashion)

4. Inflorescence or single flower – evaluated on fresh flowers and photos

0) Inflorescence

1) Single Flower

5. Floral size – Diameter of flower measured with a caliper rule in the field on fresh, anthetic flowers (numeric (mm))

6. Merism - evaluated on photos and in the field; if individuals with variable merism were present, the most common condition was coded unless different types of merism were equally abundant (an increase in merism was mostly observed in bee pollinated species)

7. Site of interaction that triggers pollen release - evaluated in the field by pollinator observations and video analyses.

0) Appendage

1) Connective

2) Thecae

Corolla:

8. Petal gloss - evaluated on flowers in the field and on photos if high quality photos were available (traditional pollination syndrome character, pollinator attraction)

0) Matt

1) Gloss (reflecting sunlight)

9. Corolla length – measured on longitudinal sections of 3D-models of flowers in AMIRA from the hypanthium rim to the most distal point of the corolla (numeric (mm)); (traditional pollination syndrome character)

10. Ratio between corolla diameter and corolla length – numeric (traditional pollination syndrome character, indicative of flower shape or tube width)

11. Corolla shape - assessed at anthesis, evaluated on photos and fresh material (traditional pollination syndrome character, important for fit with pollinator and physical restriction of flower access in many other plant lineages)

0) Flat (flowers open, petals forming a landing platform, tips can be reflexed)

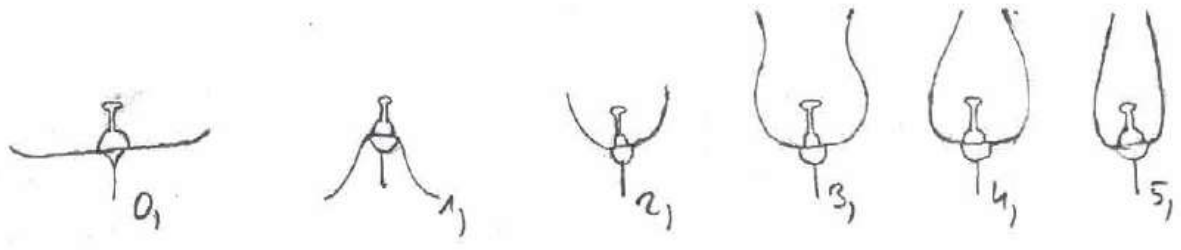
1) *Solanum*-type (flowers open, petals strongly reflexed, not forming a landing platform)

2) Bowl-shaped or campanulate-salverform (flowers relatively open but petals not flat, forming an open bowl (no constrictions))

3) Campanulate (bell-shaped, widening towards opening)

4) Urceolate (bell-shaped, opening narrower than the maximum corolla diameter)

5) Tube-shaped (petals forming a narrow corolla tube, not widened at the opening)



12. Corolla color – evaluated on photos and in the field, using the Natural Color System (traditional pollination syndrome character)

0) White

1) Cream pink
2) Red
3) Salmon
4) Fuchsia
5) Orange
6) Lilac
7) Light burgundy
8) Dark violet
9) Pink
10) Green
11) Dark purple
12) Cream

13. Petal surface - SEM was used to assess the shape of epidermis cells on the adaxial petal surface (with bee pollinated flowers usually having conical cells (mostly long papillate, enhancing grip and visibility), and bird pollinated flowers usually having flat surface cells (see Papiorek et al. 2014 for more details))

0) Smooth

1) Short papillate

2) Long papillate

Androecium:

14. Androecial position relative to style – evaluated on fresh flowers and photos, viewed from the front.

0) Adaxial (stamens form a half circle above the style, zygomorphic)

1) Abaxial (stamens from a half circle below the style, zygomorphic)

2) Actinomorphic (full circle around the style)

15. Robustness of stamens – evaluated on fresh flowers and on pickled material

0) Sturdy (anthers do not move when touched with a needle)

1) Flexible (anthers move when touched with needle)

16. Structure of stamen filaments of large stamens – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Filaments have been found to constitute the location of nectar

secretion, evaluated using light microscopy and SEM; (filament ruptures have been detected as sites of nectar secretion (Dellinger et al., 2019b))

0) Dorsal ruptures (necrotic horizontal slits on the dorsal side)

1) Small intercellular holes on proximal lateral side of filament and/or rupture on filament/connective joint

2) Smooth

3) Punctures (rounded necrotic surface damages; down to vascular bundle in some species)

4) Papillate

17. Structure of stamen filaments of small stamens – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same value was assigned as in 16 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Filaments have been found to constitute the location of nectar secretion, evaluated using light microscopy and SEM; (filament ruptures have been detected as sites of nectar secretion (Dellinger et al., 2019b))

0) Dorsal ruptures (necrotic horizontal slits on the dorsal side)

1) Small intercellular holes on proximal lateral side of filament and/or rupture on filament/connective joint

2) Smooth

3) Punctures (rounded necrotic surface damages; down to vascular bundle in some species)

4) Papillate

18. Length of large stamen filament – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size) measured in the filed using a caliper rule, from the base of the filament to the beginning of the connective. (numeric (mm))

19. Length of small stamen filament – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same value was assigned as in 18 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). measured in the filed using a caliper rule, from the base of the filament to the beginning of the connective. (numeric (mm))

20. Large stamen filament shape (Functional) – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens

(large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated on fresh flowers and on pickled material.

0) Straight

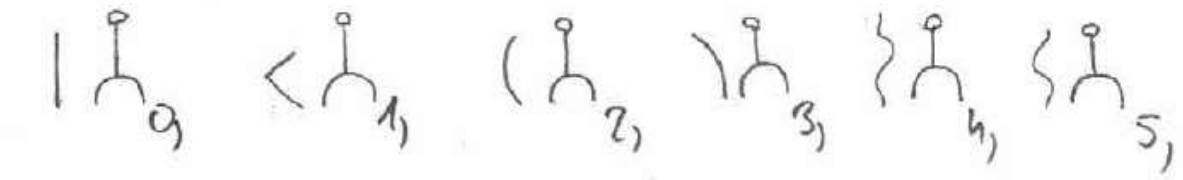
1) Kneed

2) Bent Inwards (Convex, apex of the curve points away from floral center)

3) Bent Outwards (Concave, apex of the curve points towards floral center)

4) Wave (More than 2 curves)

5) S-Shape (first convex than concave)



21. Small stamen filament shape (Functional) – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 20 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Evaluated on fresh flowers and on pickled material.

0) Straight

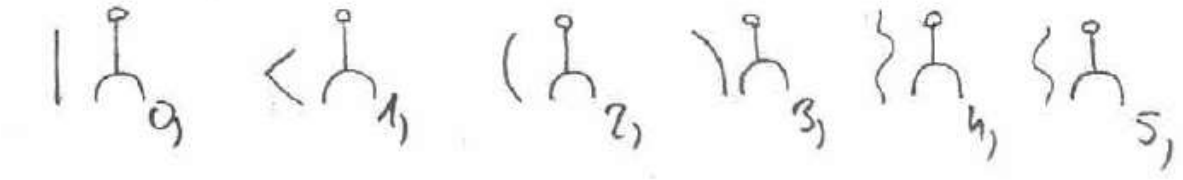
1) Kneed

2) Bent Inwards (Convex, apex of the curve points away from floral center)

3) Bent Outwards Concave, apex of the curve points towards floral center)

4) Wave (More than 2 curves)

5) S-Shape (first convex than concave)

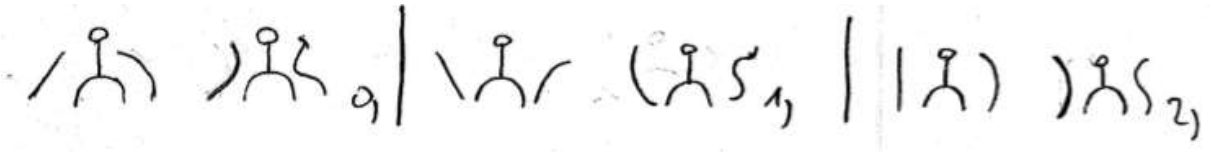


22. Functional position of large stamen filament relative to floral center, lateral view – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated on fresh flowers and on pickled material.

0) Inwards (Anther tilted towards the axis of the floral center)

1) Outwards (Anther tilted away from the axis of the floral center)

2) Parallel (Filaments parallel to the axis of the floral center)

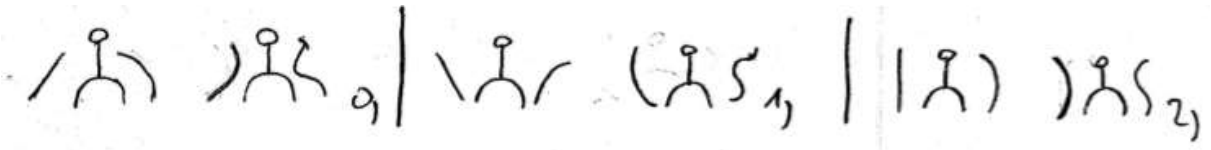


23. Functional position of small stamen filament relative to floral center, lateral view – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 21 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). evaluated on fresh flowers and on pickled material.

0) Inwards (Anther tilted towards the axis of the floral center)

1) Outwards (Anther tilted away from the axis of the floral center)

2) Parallel (Filaments parallel to the axis of the floral center)



24. Length of large stamen anther – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Measured in the field using a caliper rule, from the bottom of the thecae to the top. (numeric (mm))

25. Length of small stamen anther – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same value was assigned as in 24 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Measured in the field using a caliper rule, from the bottom of the thecae to the top. (numeric (mm))

26. Anther Color of large stamen - in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated on photos and in the field, using the Natural Color System (not for Merianieae – only contrast corolla vs. stamens and stamen color dimorphism)

0) Yellow

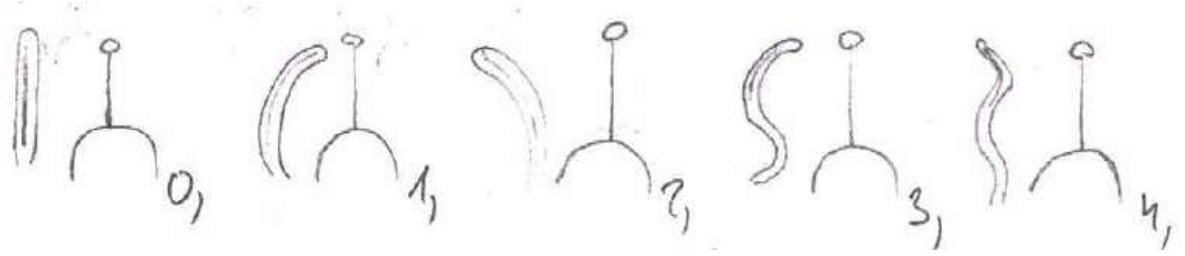
1) Cream

2) White

3) Light Yellow
4) Dark Violet
5) Deep Royal Purple
6) Pink
7) Light Pink
8) Cream Pink
9) Burgundy
10) Purple
11) Dark Burgundy

27. Anther Color of small stamen - in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 26 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Evaluated on photos and in the field, using the Natural Color System (not for Merianieae – only Contrast corolla vs. stamens and Stamen color dimorphism)
0) Yellow
1) Cream
2)White
3) Light Yellow
4) Dark Violet
5) Deep Royal Purple
6) Pink
7) Light Pink
8) Burgundy
10) Purple
11) Dark Burgundy

28. Shape of large stamen anther (Functional) - in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated on fresh flowers and on pickled material, anther viewed from the side.
0) Straight
1) Bent Inwards (Convex, apex of the curve points away from floral center)
2) Bent Outwards (Concave, apex of the curve points towards floral center)
3) S-Shape (first convex than concave)
4) Wave (more than 2 curves)



29. Shape of small stamen anther (Functional) – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 28 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Evaluated on fresh flowers and on pickled material, anther viewed from the side.

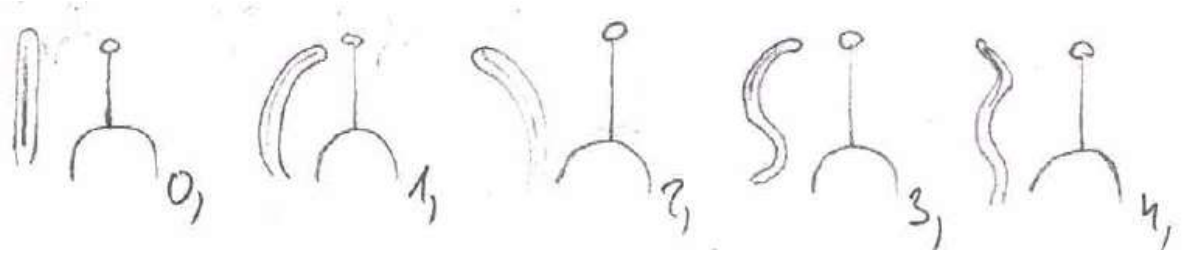
0) Straight

1) Bent Inwards (Convex, apex of the curve points away from floral center)

2) Bent Outwards (Concave, apex of the curve points towards floral center)

3) S-Shape (first convex than concave)

4) Wave (more than 2 curves)

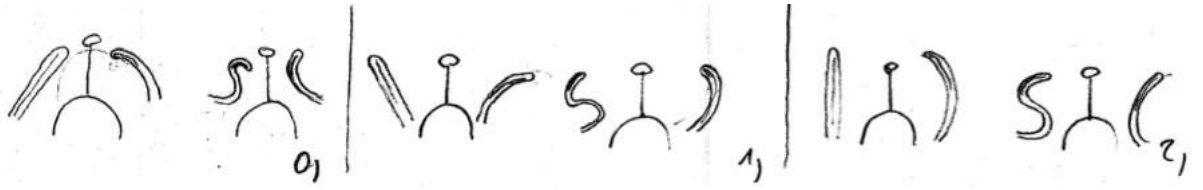


30. Functional orientation of large stamen anther relative to floral center, lateral view - in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated on fresh flowers, pickled material and on photos.

0) Inwards (Anther tilted towards the axis of the floral center, independent from pore opening or thecae location on connective)

1) Outwards (Anther tilted away from the axis of the floral center, independent from pore opening or thecae location on connective)

2) Parallel (Anthers parallel to the axis of the floral center)



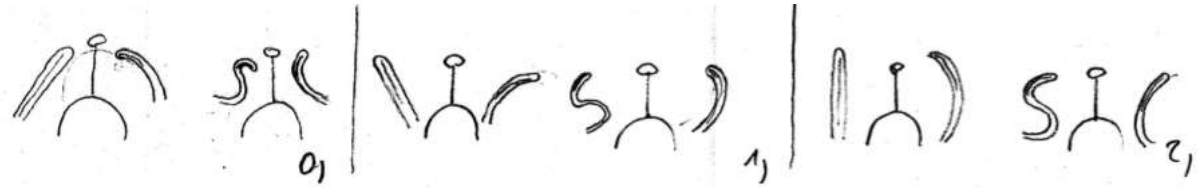
31. Functional orientation of small stamen anther relative to floral center, lateral view – in heterantherous species, small stamens were measured separately; in flowers with isomorphic

stamens, the same state was assigned as in 30 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Evaluated on fresh flowers, pickled material and on photos.

0) Inwards (Anther tilted towards the axis of the floral center, independent from pore opening or thecae location on connective)

1) Outwards (Anther tilted away from the axis of the floral center, independent from pore opening or thecae location on connective)

2) Parallel (Anthers parallel to the axis of the floral center)



32. Structure of large stamen appendage surfaces – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated on SEM (appendage surface structures may influence the grip for pollinators applying vibrations)

0) Smooth (no protrusions or groves)

1) Smooth-pitted (generally smooth, but some depressions)

2) Cauliflower (both horizontal and vertical grooves, like cauliflower)

3) Mixed-bumpy (in *M. tomentosa*-group, appendages that have features of sulcate/cauliflower but also smooth parts and a generally bumpy surface)

4) Sulcate (mainly vertical grooves but overall even surface (without cauliflower protrusions)

5) Papillate (papillae on appendage)

6) No App

33. Structure of small stamen appendage surfaces– in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 32 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size) evaluated on SEM (appendage surface structures may influence the grip for pollinators applying vibrations)

0) Smooth (no protrusions or groves)

1) Smooth-pitted (generally smooth, but some depressions)

2) Cauliflower (both horizontal and vertical grooves, like cauliflower)

3) Mixed-bumpy (in M. tomentosa-group, appendages that have features of sulcate/cauliflower but also smooth parts and a generally bumpy surface)

4) Sulcate (mainly vertical grooves but overall even surface (without cauliflower protrusions)

5) Papillate (papillae on appendage)

6) No App

34. Large stamen appendage shape – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). evaluated on fresh flowers and on pickled material (stamen appendages are sites of interaction with the pollinator (to obtain the reward) at least in bee and passerine pollinated species (Renner 1989, Dellinger et al. 2014))

0) Acuminate (e.g. Graffenrieda, *Blakea litoralis*; small spine, separate from thecae)

1) Bulbous-acuminate (e.g. *Meriania macrophylla*)

2) Bulbous (e.g. in Axinaea, similar width:length, ratio 0.5 to > 1)

3) Crown (severals Merianias, similar to pyramidal but ending in a rugged tip

(instead of an acuminate one))

4) Fusiform (elongated, width:length < 0.25; more direct transition into thecae)

5) Pyramidal (triangular acuminate pyramid, width:length > 0.33, including species

with more distant thecae (e.g. *Meriania sanguinea* but also *Meriania haemantha* ssp

haemantha)

6) Knob like (e.g. *Miconia notabilis*, *Blakea setosa, Clidemia dentata*)

7) Upside-down heart (e.g. *Tibouchina ciliaris*)

8) V-Shape (e.g. *Tibouchina grossa*)

9) Thread-like downwards (Thread-like – thread points downwards, towards flower, e.g. *Blakea maurofernandiana*)

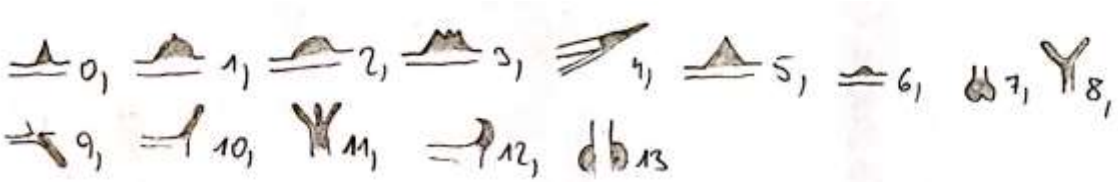
10) Thread-like upwards (Thread-like – thread points upwards, away from flower, e.g. *Monochaetum vulcanicum* small stamens)

11) Trident (e.g. *Arthrostemma ciliatum*)

12) Hooked

13) Lateral flaps (e.g. *Miconia argentea*)

14) No App



35. Small stamen appendage shape – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 34 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). evaluated on fresh flowers and on pickled material.

0) Acuminate (e.g. Graffenrieda, *Blakea litoralis*; small spine, separate from thecae)

1) Bulbous-acuminate (e.g. *Meriania macrophylla*)

2) Bulbous (e.g. in Axinaea, similar width:length, ratio 0.5 to > 1)

3) Crown (severals Merianias, similar to pyramidal but ending in a rugged tip

(instead of an acuminate one))

4) Fusiform (elongated, width:length < 0.25; more direct transition into thecae)

5) Pyramidal (triangular acuminate pyramid, width:length > 0.33, including species

with more distant thecae (e.g. *Meriania sanguinea* but also *Meriania haemantha* ssp

haemantha)

6) Knob like (e.g. *Miconia notabilis*, *Blakea setosa, Clidemia dentata*)

7) Upside-down heart (e.g. *Tibouchina ciliaris*)

8) V-Shape (e.b. *Tibouchina grossa*)

9) Thread-like downwards (Thread-like – thread points downwards, towards flower, e.g. *Blakea maurofernandiana*)

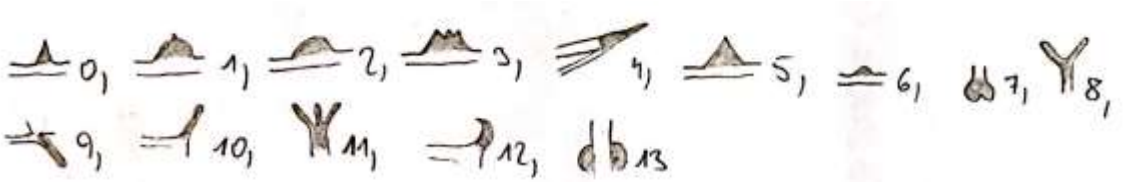
10) Thread-like upwards (Thread-like – thread points upwards, away from flower, e.g. *Monochaetum vulcanicum* small stamens)

11) Trident (e.g. *Arthrostemma ciliatum*)

12) Hooked

13) Lateral flaps (e.g. *Miconia argentea*)

14) No App



36. Secondary dorsal appendage shape of large stamen– in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated on pickled material (stamen appendages are sites of interaction with the pollinator (to obtain the reward) at least in bee and passerine pollinated species (Renner 1989, Dellinger et al. 2014))

0) Bifurcate (bifurcated, often elongated)

1) Knob (protrusion bending upwards (away from connective strand, not towards pore (compare "nose")), sitting on connective strand; found in *M. tomentosa* group)

2) Nose (rounded structure bending towards pore, sitting on connective strand; found e.g. in *M. haemantha*)

3) Absent (no secondary appendage present)

37. Secondary dorsal appendage shape of small stamen – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 36 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Evaluated on pickled material (stamen appendages are sites of interaction with the pollinator (to obtain the reward) at least in bee and passerine pollinated species (Renner 1989, Dellinger et al. 2014))

0) Bifurcate (bifurcated, often elongated)

1) Knob (protrusion bending upwards (away from connective strand, not towards pore (compare "nose")), sitting on connective strand; found in *M. tomentosa* group)

2) Nose (rounded structure bending towards pore, sitting on connective strand; found e.g. in *M. haemantha*)

3) Absent (no secondary appendage present)

38. Color of large stamen appendage - in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). evaluated on photos and in the field, using the Natural Color System (traditional pollination syndrome character, visual attraction)

0) Yellow

1) Cream

2) Fuchsia

3) Dark violet

4) Pink

5) White

6) Yellow – Pink

7) Purple

8) Dark Burgundy

9) No App

39. Color of small stamen appendage – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 38 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Evaluated on photos and in the field, using the Natural Color System (traditional pollination syndrome character, visual attraction)

0) Yellow

1) Cream

2) Fuchsia

3) Dark violet

4) Pink

5) White

6) Yellow – Pink

7) Purple

8) Dark Burgundy

9) No App

40. Appendage orientation (morphological) – evaluated on fresh flowers and on pickled material (not in analyses).

0) Lateral

1) Ventral (towards floral center)

2) Dorsal (towards floral margin)

3) No App

41. Functional orientation of appendage relative to floral center - evaluated on fresh flowers and on pickled material.

0) Ventral

1) Dorsal

2) Lateral

3) No App

42. Structure of thecal wall, of large stamens – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated in the field with binocular microscopes, on pickled material, SEM and sections (possibly related to pollen release/pollen dosing)

0) Ruminate (sturdy and strongly folded, made up by more than one tightly arranged cell layer (possibly a remaining)

1) Smooth (sturdy but NOT folded, made up by one tightly arranged cell layer and strong cuticle and remnants of tapetum)

2) Crumpled (soft and flexible, made up by one more loosely arranged cell layer)

43. Structure of thecal wall, of small stamens – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 42 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Evaluated in the field with binocular microscopes, on pickled material, SEM and sections (possibly related to pollen release/pollen dosing)

0) Ruminate (sturdy and strongly folded, made up by more than one tightly arranged cell layer (possibly a remaining)

1) Smooth (sturdy but NOT folded, made up by one tightly arranged cell layer and strong cuticle and remnants of tapetum)

2) Crumpled (soft and flexible, made up by one more loosely arranged cell layer)

44. Location of thecae on connective – evaluated on fresh and pickled material (location is related to the mechanism of pollen release, pollen is released more easily on laterally attached thecae)

0) Ventral (thecae face floral center)

1) Dorsal (thecae face floral margin)

2) Lateral (thecae attached at sides of connective strand, pollen chambers supinated)

45. Functional thecal position relative to floral center – evaluated on fresh flowers and on pickled material.

0) Ventral

1) Dorsal

2) Lateral

46. Location of thecal end (end of pollen chambers) in relation to appendage of large stamens – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). evaluated on pickled and fresh material (possibly related to pollen release)

0) Base (thecae end at appendage base, actual end of pollen chamber often only visible in cross-sections)

1) Offset (thecae end a few mm/cm away from appendage base, only connective strand reaches appendage base)

47. **Location of thecal end (end of pollen chambers) in relation to appendage of small stamens** – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 46 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). evaluated on pickled material (possibly related to pollen release)

0) Base (thecae end at appendage base, actual end of pollen chamber often only visible in cross-sections)

1) Offset (thecae end a few mm/cm away from appendage base, only connective strand reaches appendage base)

48. Thecae separated into two pollen sacs by septum– evaluated on cross sections of stamens using microtome sectioning/light microscopy and cross-sections of stamens of HRXCT-scans of flowers in AMIRA (possibly related to pollen release/pollen dosing)

0) Yes

1) No

49. Pore width of large stamens – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). 3 stamens/species measured on 3D models of flowers in AMIRA, mean taken (numeric (mm)); (possibly related to pollen release/pollen dosing)

50. Pore width of small stamens - in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 49 (small

stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). 3 stamens/species measured on 3D models of flowers in AMIRA, mean taken (numeric (mm)); (possibly related to pollen release/pollen dosing)

51. Pore length of large stamens – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). 3 stamens/species measured on 3D models of flowers in AMIRA, mean taken (numeric (mm)); (possibly related to pollen release/pollen dosing)

52. Pore length of small stamens - in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 51 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). 3 stamens/species measured on 3D models of flowers in AMIRA, mean taken (numeric (mm)); (possibly related to pollen release/pollen dosing)

53. Functional Orientation of pore opening of large stamens relative to floral center - in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated on pickled and fresh material.

0) Apical

1) Introrse

2) Extrorse

54. Functional Orientation of pore opening of small stamens relative to floral center - in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 53 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Evaluated on pickled and fresh material.

0) Apical

1) Introrse

2) Extrorse

55. Number of anther pores - evaluated on fresh flowers and on pickled material.

56. Pollen grain diameter of large anthers – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens

(large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). 10 pollen grains/species measured in 70% ethanol using a fluorescence microscope, mean taken (numeric (μm)); (possibly related to pollen release/pollen dosing)

57. Pollen grain diameter of small anthers – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 56 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). 10 pollen grains/species measured in 70% ethanol using a fluorescence microscope, mean taken (numeric (μm)); (possibly related to pollen release/pollen dosing)

58. Color contrast of large stamen thecae and large stamen appendage – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated on photos and in field (traditional pollination syndrome character, visual attraction)

0) Yes

1) No

2) Weak

3) No App

59. Color contrast of small stamen thecae and small stamen appendage – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 58 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Evaluated on photos and in field (traditional pollination syndrome character, visual attraction)

0) Yes

1) No

2) Weak

3) No App

60. Stamen color dimorphism – evaluated on photos and in field (heteranthery is known to be an important trait in buzz-pollination (Vallejo-Marín et al., 2010)

0) Yes

1) No

Gynoecium:

61. Position of style relative to corolla opening – evaluated on fresh and pickled material, viewed from the front/side (traditional pollination syndrome character, related to fit between flower and pollinator)

0) Free (style visible in its full length) 80-100%

1) Partly enclosed (upper quarter of the style usually visible) > 20%

2) Enclosed (style mostly enclosed by petals, not (or only tip of stigma) visible) < 20%

62. Stigma shape - interpreted when placing the style upright and looking at the stigma from the side in SEM (possibly related to pollen pick-up)

0) Corymbose (umbrella-shape, overarching the width of the style but usually shorter than wide, sometimes almost rounded like a ball)

1) Convex (bump, shorter than wide, but not overarching style width)

2) Conical (elongated, as long or longer than wide, not overarching style width)

3) Stamp (almost flat, about as wide as the style, neither narrowing nor widening)

63. Stigma diameter – measured on 3D scans of flowers, mean taken (numeric (mm)); (possibly related to pollen pick-up, Cruden 2000)

64. Style curvature – evaluated on pickled material (possibly governs pollen pick-up from pollinator; e.g. a hooked style would only pick up pollen if the pollinator positioned itself directly underneath)

0) Curved

1) Hooked

2) Straight (Style straight, independent from its position relative to the ground)

65. Style length – measured from the top of the ovary to the end of the stigma, using a caliper rule on fresh floral material in the field (numeric (mm))

66. Color contrast between stigma and style – evaluated on photos and in the field (visual attraction)

0) No

1) Yes

Mixed:

67. Level of anther pore relative to Stigma position - evaluated on fresh flowers and pickled material (determines site of pollen release in relation to the stigma), flower viewed in lateral view.

0) Higher (anther pores higher than stigma)

1) Lower (anther pores lower than stigma)

2) Same Level as stigma

3) Higher/Lower (in strongly dimorphic species)

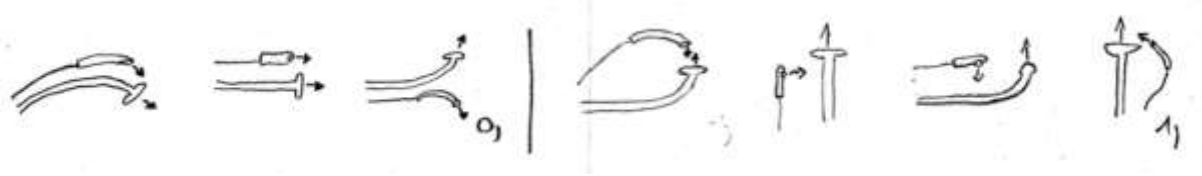
68. Distance of stigma to anther pores of large stamens – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Measured on fresh flowers using a caliper rule. In radially symmetric flowers 3 measurements were taken and the average was calculated. In zygomorphic flowers the maximum and minimum distance was measured. (numeric (mm))

69. Distance of stigma to anther pores of small stamens – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 66 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Measured on fresh flowers using a caliper rule. In radially symmetric flowers 3 measurements were taken and the average was calculated. In zygomorphic flowers the maximum and minimum distance was measured. (numeric (mm))

70. Functional orientation of pore from large stamen and stigma – in heterantherous species, large stamens were measured separately; in isomorphic species, the same value/score was used for all stamens (large stamens are bigger than small stamens in their overall appearance, independent from anther and appendage size). Evaluated on fresh flowers and pickled material using binocular microscopy.

0) Pore points away from stigma

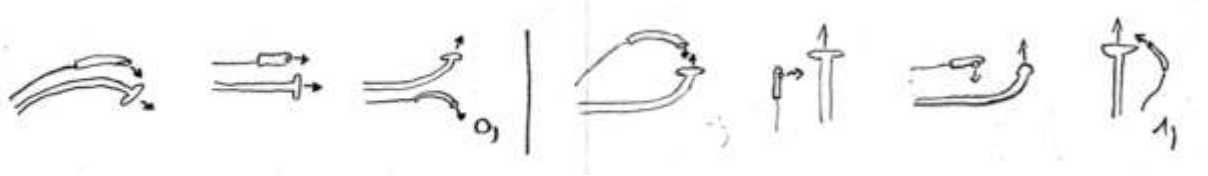
1) Pore faces stigma



71. Functional orientation of pore from small stamen and stigma – in heterantherous species, small stamens were measured separately; in flowers with isomorphic stamens, the same state was assigned as in 68 (small stamens are smaller than large stamens in their overall appearance, independent from anther and appendage size). Evaluated on fresh flowers and pickled material using binocular microscopy.

0) Pore points away from stigma

1) Pore faces stigma



72. Color contrast corolla - stamens – based on photos and in the field (traditional pollination syndrome character, important for pollinator attraction)

0) Yes

1) No

2) Weak

73. Color contrast style – corolla – evaluated on photos and in the field (visual attraction)

0) No

1) Yes

2) Weak

74. Color contrast androecium – gynoecium – evaluated on photos and in the field (visual attraction)

0) No

1) Yes

2) Weak

Apx. 1: Trait matrix

Species	ID	Presumed pollinato	Known mode of pol	Reward type	Orientation of flow	Inflorescence or sin
Adelobotrys adscen	AD	bee	buzz	pollen	0	0
Axinaea confusa	AD	passerine	bellows	food body	0	0
Axinaea costaricens	AD	passerine	bellows	food body	0	0
Axinaea macrophyll	AD	passerine	bellows	food body	0	0
Axinaea sclerophyll	AD	passerine	bellows	food body	0	0
Graffenrieda cucull	AD	bee	buzz	pollen	1	0
Meriania costata	AD	mixed vertebrate	salt-shaker	nectar	2	0
Meriania drakei	AD	bee	buzz	pollen	4	0
Meriania furvanthe	AD	mixed vertebrate	salt-shaker	nectar	2	0
Meriania longifolia	AD	bee	buzz	pollen	4	0
Meriania maguirei	AD	bee	buzz	pollen	4	0
Meriania maxima	AD	bee	buzz	pollen	4	0
Meriania phlomoid	AD	mixed vertebrate	salt-shaker	nectar	2	0
Meriania pichinche	AD	mixed vertebrate	salt-shaker	nectar	2	0
Meriania quintuplin	AD	mixed vertebrate	salt-shaker	nectar	2	0
Meriania sanguinea	AD	mixed vertebrate	salt-shaker	nectar	2	0
Meriania tomentos	AD	mixed vertebrate	salt-shaker	nectar	2	0
Meriania aff, sangu	AD	mixed vertebrate	salt-shaker	nectar	2	0
Meriania macrophy	AD	passerine	bellows	food body	0	0
Meriania speciosa	AD	bee	buzz	pollen	1	0
Blakea superba	BLASUP	bee	buzz	pollen	4	0
Blakea florifera	BLAFLO	bee	buzz	pollen	4	0
Miconia andreana	MICAND	bee	buzz	pollen	0	0
Tibouchina urvillea	TIBURV		buzz	pollen	4	0
Miconia barbata	MICBAR		salt-shaker	nectar	1	0
Tibouchina cf, ciliar	TIBCIL		buzz	pollen	1	0
Miconia cf, reducen	MICRED		NA	NA	4	0
Miconia goniostigm	MICGON		buzz	pollen	1	0
Tibouchina lepidota	TIBLEP		buzz	pollen	4	1
Miconia notabilis	MICNOT		buzz	pollen	4	0
Blakea setosa	BLASET		buzz	pollen	4	0
Arthrostemma cf, c	ARTCIL		buzz	pollen	4	0
Tibouchina grossa	TIBGRO	mixed vertebrate	bounce-mechanism	nectar	4	0
Tibouchina mollis	TIBMOL		buzz	pollen	1	0
Miconia lacera	MICLAC	bee	buzz	pollen	3	0
Miconia schlimii	MICSCH	bee	buzz	pollen	4	0
Blakea mauroferna	BLAMAU	bee	buzz	pollen	4	0
Conostegia subcrus	CONSUB	bee	buzz	pollen	1	0
Aciotis levyana	ACILEV		NA	NA	1	0
Conostegia oersted	CONOER	bee	buzz	pollen	4	0
Miconia trinervia	MICTRI	bee	buzz	pollen	3	0
Clidemia dentata	CLIDEN		buzz	pollen	1	0
Miconia donaeana	MICDON	bee	buzz	pollen	1	0
Blakea litoralis	BLALIT	bee	buzz	pollen	1	1
Miconia argentea	MICNOT	bee	buzz	pollen	0	0
Monochaetum cf, v	MONVUL	bee	buzz	pollen	4	1
Clidemia cf, epiphyt	CLIEPI		NA	NA	4	0
Monochaetum line	MONLIN	bee	buzz	pollen	4	1
Leandra subseriata	LEASUB	bee	buzz	pollen	1	0
Miconia tonduzii	MICTON	bee	buzz	pollen	4	0
Monochaetum cf, fl	MONFLO	bee	buzz	pollen	4	0
Clidemia globuliflor	CLIGLO		buzz	pollen	5	0
Blakea anomala	BLAANO	bee	buzz	pollen	4	1
Blakea chlorantha	BLACHLO	mixed vertebrate	salt-shaker	nectar	2	0
Brachyotum lindeni	BRALIN	mixed vertebrate	salt-shaker	nectar	2	0
Brachyotum ledifoli	BRALED	hb	salt-shaker	nectar	2	0
Tibouchina oroensi	TIBORO	bee	buzz	pollen	4	1
Blakea gregii	BLAGRE	mixed vertebrate	salt-shaker	nectar	2	0
Blakea austin-smith	BLAAU	mixed vertebrate	salt-shaker	nectar	2	0

Floral size	Merism	Site of Interaction t	Petal gloss	Corolla height	Ratio between coro	Corolla shape
10,03	5	appendages	0	8,7	1,152	2
11,46	5	appendages	0	5,9	1,942	5
20,75	5	appendages	0	6,8	3,049	5
23,07	5	appendages	0	21,32	1,082	5
18,53	5	appendages	0	15,34	1,208	5
14,58	6	connective	0	2,28	6,407	4
14,79	5	thecae	1	19,33	0,765	2
49,23	5	appendages	0	4,9	10,046	1
16,18	6	thecae	1	17,3	0,935	2
53	5	appendages	0	4,07	13,022	1
35,2	5	appendages	0	3,38	10,429	1
67	5	appendages	0	3,84	17,448	1
15,88	5	thecae	1	13,92	1,14	2
16,36	6	thecae	1	18	0,909	2
16,37	5	thecae	1	16,65	0,983	2
15,46	5	appendages	1	12,66	1,221	2
18,61	5	thecae	1	20,02	0,93	2
20,5	5	appendages	1	17,5	1,171	2
23	5	appendages	NA	15	1,533	3
68	5	appendages	0	5	13,6	1
44,67	6	appendages	0	4,78	9,35	0
26,34	6	appendages	0	4,1	6,42	0
5,34	5	thecae	0	0,99	5,39	0
86	5	NA	0	NA	NA	0
13,34	5	thecae	0	1,77	7,54	0
21,34	5	NA	0	3,49	6,11	0
10,07	5	NA	0	2,97	3,39	0
9,34	5	NA	1	0,99	9,43	1
43	5	NA	0	4,05	10,62	0
25,67	8	NA	0	2,46	10,43	0
73	6	NA	0	7,05	10,35	0
29	4	NA	0	3,48	2,78	0
32,67	5	appendages	0	33,12	0,986	2
19,34	5	NA	0	NA	NA	0
4,67	5	thecae	1	1,07	4,36	0
14,34	5	NA	0	NA	NA	0
30	6	appendages	1	6,71	4,47	0
11	5	thecae	0	0,55	20	0
4,34	4	NA	0	1,14	3,81	2
25	8	thecae	0	0,55	45,45	0
4,34	4	appendages	0	0,87	4,99	0
12,34	5	NA	0	2,52	4,9	0
12,34	5	NA	0	1,28	9,64	0
49,34	6	appendages	0	4,86	10,15	0
5,34	5	NA	0	0,76	7,03	1
29,67	4	appendages	0	3,72	7,98	0
9,67	4	NA	0	0,84	11,51	0
20,67	4	appendages	0	2,26	9,15	0
3,67	5	thecae	0	0,56	6,55	1
4,67	5	NA	0	2,59	1,8	2
11,67	4	appendages	0	0,5	23,34	0
13	5	NA	1	1,69	7,69	0
27	6	appendages	0	7,06	3,82	2
12,34	6	thecae	0	9,8	1,26	2
5	5	thecae	0	15,05	0,33	5
5,5	5	thecae	0	13,69	0,4	5
40,5	5	appendages	0	3,79	10,69	0
14	6	thecae	0	17	0,824	2
10	6	thecae	0	14	0,714	2

Corolla Color	Petal surface	Androecial position	Robustness of stam	Structure of stamen	Structure of stamen	Length of large sta
0	0	1	0	2	2	7,09
1	1	1	0	2	2	5,12
2	0	1	0	2	2	5,44
2	1	1	0	2	2	NA
1	1	1	0	2	2	8,63
0	0	2	0	2	2	1,96
3	0	1	1	1	1	10,93
4	2	1	0	2	2	14,49
3	0	1	1	1	1	6,9
4	2	1	0	3	3	6,7
4	1	1	0	2	2	11,19
4	1	1	0	2	2	18,62
0	0	1	1	0	0	6,76
3	0	1	1	0	0	NA
3	0	1	1	0	0	9,46
2	0	1	1	1	1	8,37
3	0	1	1	0	0	10,93
2	0	1	1	1	1	NA
4	0	1	0	2	2	NA
4	2	1	0	2	2	9,34
3	0	0	0	2	2	8
6	0	0	0	2	2	3,67
7	1	2	1	2	2	2,34
8	NA	0	1	2	2	15
0	0	2	1	2	2	1,34
0	2	0	1	2	2	6
9	0	1	1	2	2	2,34
0	2	2	0	4	4	3,33
9	0	0	1	2	2	7,34
0	1	0	1	2	2	8
0	0	0	0	2	2	7,34
9	1	0	1	2	2	5
2	0	1	1	0	0	11
10	NA	2	NA	NA	NA	11
0	0	1	1	2	2	1,34
0	0	0	1	2	2	7
9	0	0	0	2	2	8
9	0	1	1	2	2	2,34
0	1	2	1	2	2	1,34
0	1	0	1	2	2	4
0	2	2	1	2	2	2,67
0	0	2	1	2	2	2,34
0	2	0	1	4	4	7,34
9	1	0	0	2	2	8,34
0	1	2	1	2	2	1,67
9	1	0	1	2	2	9,67
0	0	2	1	2	2	2
1	0	0	1	2	2	5,67
0	1	2	1	2	2	2
0	1	2	1	2	2	3,34
1	2	0	1	2	2	3,67
0	0	2	1	2	2	2
0	0	0	0	2	2	6,34
10	0	2	1	0	0	2,34
11	0	2	1	2	2	7
12	1	2	1	2	2	6,5
8	2	0	1	2	2	8,5
10	NA	2	1	NA	NA	6
10	NA	2	1	NA	NA	4,5

Length of small sta	Large stamen filam	Small stamen filam	Large stamen filam	Small stamen filam	Length of large sta	Length of small sta
5,8	1	1	1	1	7,22	5,2
4,21	1	1	1	1	7,66	7,44
4,66	1	1	1	1	9,71	8,84
NA	1	1	1	1	NA	NA
5,36	1	1	1	1	11,69	10,48
1,96	0	0	1	1	NA	NA
10,93	1	1	1	1	17,01	16,55
14,49	1	1	1	1	11,79	11,59
6,9	1	1	1	1	8,65	8,25
6,7	1	1	1	1	10,82	10,79
11,19	1	1	1	1	13,84	13,81
18,62	1	1	1	1	15,69	13,55
6,76	1	1	1	1	10,45	9,81
NA	1	1	1	1	NA	NA
9,46	1	1	1	1	NA	NA
8,37	1	1	1	1	7,8	7,57
10,93	1	1	1	1	12,1	10,67
NA	1	1	1	1	NA	NA
NA	1	1	1	1	NA	NA
9,34	1	1	1	1	13,28	13,28
8	2	2	1	1	9,33	9,33
3,67	2	2	1	1	4,67	4,67
2,34	5	5	2	2	2	2
10	3	0	2	2	15,34	13
1,34	5	5	2	2	2,67	2,67
5	2	2	2	2	6	5
2,34	0	0	2	2	2,67	2,67
3,33	3	3	1	1	3	3
7,34	2	2	2	2	7,34	7,34
6,67	2	2	1	1	7,67	6
7,34	0	0	1	1	7	7
5	3	3	2	2	6	3,34
11	5	5	2	2	7	7
11	5	5	2	2	5,34	5,34
1,34	0	0	2	2	2	2
7	0	0	2	2	1,34	1,34
8	2	2	1	1	8,34	8,34
2,34	5	5	2	2	2,67	2,67
1,34	2	2	2	2	1,34	1,34
4	3	3	2	2	3	3
2,67	3	3	1	1	2,34	2,34
2,34	3	3	2	2	4,34	4,34
7,34	2	2	2	2	6,67	6,67
8,34	2	2	1	1	5,34	5,34
1,67	3	3	1	1	2,67	2,67
8,67	2	0	1	1	5,67	1,9
1	5	5	2	2	1	1
7	0	0	1	1	7,34	4,67
2	5	5	2	2	2	2
3,34	5	5	2	2	2	2
3,67	2	2	1	1	5,34	5
2	3	3	2	2	2	2
6,34	2	2	2	2	6,34	6,34
2,34	0	0	2	2	4,34	4,34
7	1	1	2	2	6	6
6,5	2	2	2	2	6	6
8,5	2	2	1	1	7	7
6	NA	NA	NA	NA	6	6
4,5	NA	NA	NA	NA	4,5	4,5

Anther color of larg	Anther color of sma	Shape of large stam	Shape of small stam	Orientation of large	Orientation of smal	Structure of large st
NA	NA	1	1	0	0	0
NA	NA	0	0	0	0	0
NA	NA	0	0	0	0	0
NA	NA	0	0	0	0	0
NA	NA	0	0	0	0	0
NA	NA	1	1	0	0	0
NA	NA	0	0	1	1	3
NA	NA	1	1	0	0	2
NA	NA	0	0	1	1	3
NA	NA	1	1	0	0	2
NA	NA	1	1	0	0	2
NA	NA	1	1	0	0	4
NA	NA	0	0	1	1	3
NA	NA	0	0	1	1	3
NA	NA	0	0	1	1	3
NA	NA	1	1	1	1	3
NA	NA	0	0	1	1	3
NA	NA	1	1	1	1	4
NA	NA	1	1	2	2	0
NA	NA	1	1	0	0	2
0	0	1	1	0	0	4
1	1	0	0	2	2	4
3	3	0	0	2	2	6
5	4	1	1	2	2	1
0	0	2	2	2	2	0
6	0	2	2	0	0	0
7	7	1	1	2	2	6
0	0	0	0	0	0	5
0	0	3	3	0	0	2
8	8	2	2	0	2	1
1	1	0	0	0	0	4
6	0	1	1	2	2	0
6	6	4	4	2	2	5
0	0	3	3	2	2	NA
8	8	1	1	2	2	6
0	0	0	0	2	2	6
0	0	1	1	0	0	4
0	0	0	0	0	0	6
4	4	3	3	2	2	0
0	0	0	0	2	2	6
2	2	1	1	1	1	1
2	2	1	1	2	2	0
10	10	2	2	2	2	5
0	0	0	0	2	2	5
2	2	1	1	1	1	0
7	0	1	0	0	2	4
2	2	0	0	2	2	6
9	0	1	0	0	2	4
0	0	0	0	2	2	6
6	6	0	0	0	0	0
6	0	1	0	0	0	5
1	1	0	0	0	0	6
0	0	0	0	2	2	0
11	11	0	0	2	2	0
NA	NA	0	0	2	2	6
NA	NA	0	0	2	2	6
4	4	2	2	1	1	1
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA

Structure of small s	Large stamen appe	Small stamen appe	Secondary dorsal a	Secondary dorsal a	Color of large stam	Color of small stam
0	3	3	0	0	0	0
0	2	2	3	3	0	0
0	2	2	3	3	0	0
0	2	2	3	3	0	0
0	2	2	3	3	0	0
0	0	0	3	3	0	0
3	3	3	1	1	3	3
2	5	5	3	3	0	0
3	3	3	1	1	3	3
2	5	5	3	3	1	1
2	5	5	2	2	0	0
4	5	4	2	2	0	0
3	3	3	1	1	1	1
3	3	3	1	1	1	1
3	3	3	1	1	1	1
3	5	5	2	2	0	0
3	3	3	1	1	1	1
4	4	4	3	3	0	0
0	2	0	0	0	3	3
2	5	5	3	3	0	0
4	9	9	3	3	0	0
4	6	6	3	3	4	4
6	14	14	3	3	9	9
1	7	7	3	3	4	4
0	6	6	3	3	0	0
0	7	7	3	3	0	0
6	14	14	3	3	9	9
5	5	5	3	3	0	0
2	8	8	3	3	0	0
1	10	6	3	3	5	5
4	6	6	3	3	5	5
0	11	11	3	3	0	0
5	8	8	3	3	6	6
NA	6	6	3	3	0	0
6	14	14	3	3	9	9
6	14	14	3	3	9	9
4	9	9	3	3	0	0
6	14	14	3	3	9	9
0	6	6	3	3	3	3
6	14	14	3	3	9	9
1	6	6	3	3	5	5
0	6	6	3	3	1	1
5	6	6	3	3	7	7
5	0	0	3	3	1	1
0	13	13	3	3	5	5
5	12	10	3	3	0	0
6	14	14	3	3	9	9
5	12	10	3	3	0	0
6	14	14	3	3	9	9
0	7	7	3	3	4	4
5	12	10	3	3	0	0
6	14	14	3	3	9	9
0	5	5	3	3	0	0
0	6	6	3	3	8	8
6	14	14	3	3	9	9
6	14	14	3	3	9	9
1	7	7	3	3	0	0
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA

Functional orientati	Structure of thecal	Structure of thecal	Location of thecae	Functional thecal p	Location of thecal e	Location of thecal e
1	0	0	0	0	0	0
1	1	1	0	0	0	0
1	1	1	0	0	0	0
1	1	1	0	0	0	0
1	1	1	0	0	0	0
1	0	0	0	0	1	1
1	2	2	1	2	1	1
1	1	1	0	0	0	0
1	2	2	1	2	1	1
1	1	1	0	0	0	0
1	0	0	0	0	0	0
1	0	0	0	0	0	0
1	2	2	1	2	1	1
1	2	2	1	2	1	1
1	2	2	1	2	1	1
1	2	2	0	0	0	0
1	2	2	1	2	1	1
1	1	1	0	0	0	0
1	1	1	0	0	0	0
1	1	1	0	0	0	0
1	1	1	0	0	0	0
1	1	1	0	0	0	0
3	1	1	0	0	0	0
1	0	0	0	1	1	0
1	1	1	0	0	0	0
1	0	0	0	1	1	0
3	0	0	0	0	0	0
1	1	1	0	0	0	0
1	0	0	0	1	0	0
0	0	0	0	1	0	0
1	1	1	0	0	0	0
1	0	0	0	0	1	0
0	1	1	2	2	0	0
1	0	0	0	0	0	0
3	0	0	0	0	0	0
3	0	0	0	0	0	0
1	1	1	0	0	0	0
3	1	1	0	0	0	0
0	1	1	0	0	1	1
3	1	1	0	0	0	0
1	1	1	0	0	0	0
1	0	0	0	0	0	0
1	0	0	0	0	0	0
1	1	1	0	0	0	0
2	1	1	0	0	0	0
1	0	1	0	0	0	0
3	1	1	0	0	0	0
1	1	1	0	0	0	0
3	1	1	0	0	0	0
0	1	1	0	0	0	0
1	1	1	0	0	0	0
3	1	1	0	0	0	0
1	1	1	0	0	0	0
1	1	1	0	0	0	0
3	1	1	0	0	0	0
3	1	1	0	0	0	0
1	0	0	0	1	1	1
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA

Thecae separated i	Pore width large sta	Pore width small st	Pore hight large sta	Pore hight small sta	Orientation of pore	Orientation of pore
0	0,187	0,11	0,076	0,093	2	0
0	0,191	0,191	0,17509	0,17509	2	2
0	0,281	0,281	0,279827	0,279827	2	2
0	0,235	0,235	0,11529	0,11529	2	2
0	0,195	0,195	0,2402344	0,2402344	2	2
0	0,228	0,228	0,2549405	0,2549405	2	2
0	0,273	0,273	0,258748833	0,258748833	2	2
0	0,476	0,476	0,336133333	0,336133333	2	2
0	0,334	0,334	0,297954	0,297954	2	2
0	0,291	0,291	0,3113014	0,3113014	2	2
0	0,379	0,379	0,3192675	0,3192675	2	2
0	0,288	0,355	0,248	0,321	2	2
0	0,379	0,379	0,3236565	0,3236565	0	0
0	0,382	0,382	0,194118	0,194118	0	0
0	0,321	0,321	0,250992	0,250992	0	0
0	0,386	0,386	0,336755	0,336755	0	0
0	0,438	0,438	0,367702667	0,367702667	0	0
0	0,349	0,349	0,376	0,376	0	0
0	NA	NA	NA	NA	2	2
0	0,368	0,368	0,266762333	0,266762333	2	2
0	0,24	0,24	0,34	0,34	2	2
0	0,13	0,13	0,17	0,17	1	1
0	0,13	0,13	0,14	0,14	0	0
1	0,35	0,22	0,28	0,28	1	1
1	0,11	0,11	0,1	0,1	0	0
1	0,19	0,16	0,17	0,14	2	2
1	0,25	0,25	0,15	0,15	2	2
0	0,25	0,25	0,15	0,15	2	2
1	0,18	0,18	0,17	0,17	2	2
1	0,28	0,26	0,14	0,18	2	2
0	0,09	0,09	0,1	0,1	1	1
1	0,18	0,17	0,14	0,14	1	1
1	1,04	1,04	1,34	1,34	1	1
NA	NA	NA	NA	NA	1	1
0	0,16	0,16	0,12	0,12	1	1
0	0,14	0,14	0,14	0,14	0	0
0	0,21	0,21	0,16	0,16	2	2
0	0,26	0,26	0,14	0,14	1	1
0	0,11	0,11	0,09	0,09	0	0
0	0,21	0,21	0,16	0,16	0	0
0	0,13	0,13	0,15	0,15	0	0
0	12	0,12	0,9	0,9	2	2
1	0,24	0,24	0,13	0,13	0	0
0	0,34	0,34	0,14	0,14	1	1
0	0,31	0,31	0,21	0,21	1	1
0	0,37	0,27	0,25	0,21	1	2
0	3	0,3	0,084	0,084	1	1
1	0,24	0,17	0,17	0,17	1	2
0	0,24	0,24	0,14	0,14	0	0
0	0,21	0,21	0,19	0,19	0	0
1	0,2	0,17	0,19	0,13	2	2
1	0,18	0,18	0,14	0,14	2	2
0	0,11	0,11	0,15	0,15	1	1
1	0,21	0,21	0,2	0,2	0	0
1	0,24	0,24	0,16	0,16	0	0
1	0,2	0,2	0,19	0,19	0	0
1	0,19	0,19	0,18	0,18	2	2
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA

Number of anther p	Pollen grain diamet	Pollen grain diamet	Color contrast large	Color contrast smal	Stamen color dimor	Position of style rel
1	11,11	11,11	0	0	0	1
1	17,27	17,27	0	0	1	0
1	17,18	17,18	0	0	1	0
1	18,04	18,04	0	0	0	1
1	17,87	17,87	0	0	1	1
1	11,61	11,61	1	1	0	0
1	29,27	29,27	1	1	0	2
1	14,06	14,06	0	0	0	0
1	17,82	17,82	1	1	0	2
2	13,52	13,52	0	0	0	0
1	16,87	16,87	0	0	0	0
1	16,87	16,87	0	0	1	0
1	16,86	16,86	1	1	0	2
1	17,43	17,43	1	1	0	2
1	13,02	13,02	1	1	0	2
1	19,92	19,92	0	0	0	2
1	17,39	17,39	1	1	0	2
1	19,37	19,37	0	0	0	2
1	16,64	16,64	0	0	1	1
1	13,14	13,14	0	0	0	0
2	8,93	8,93	1	1	0	0
2	10,31	10,31	0	0	1	0
1	6,27	6,27	3	3	1	0
1	10,1	9,96	0	0	0	0
1	7,73	7,73	1	1	1	0
1	7,67	7,87	0	1	0	0
1	7,16	7,16	3	3	1	0
1	11,53	11,53	1	1	1	0
1	10,25	10,25	1	1	1	0
1	9,1	7,93	2	2	1	0
2	8,44	8,44	1	1	1	0
1	10,84	10,85	0	1	0	0
1	10,59	10,59	2	2	1	2
NA	NA	NA	0	0	1	0
1	7,39	7,39	3	3	1	2
1	7,6	7,6	3	3	1	0
2	10,5	10,5	1	1	1	0
1	7,29	7,29	3	3	1	0
1	7,67	7,67	1	1	1	1
1	6,19	6,19	3	3	1	0
2	7,62	7,62	1	1	1	0
1	7,38	7,38	1	1	1	0
1	7,5	7,5	1	1	1	0
2	9,58	9,58	0	0	1	0
1	6,62	6,62	1	1	1	0
1	7,96	8,6	0	1	0	0
1	7	7	3	3	1	0
1	7,81	7,96	0	1	0	0
1	6,47	6,47	3	3	1	0
1	7,33	7,33	1	1	1	1
1	8,21	8,31	0	1	0	0
1	6,18	6,18	3	3	1	0
2	7,21	7,21	1	1	1	1
2	8,19	8,19	1	1	1	1
1	9,85	9,85	3	3	1	1
1	9,43	9,43	3	3	1	1
1	7,77	7,77	0	0	1	0
NA	NA	NA	NA	NA	NA	2
NA	NA	NA	NA	NA	NA	1

Stigma shape	Stigma diameter	Style curvature	Style length	Color contrast betw	Level of anther por	Distance of stigma t
0	0,509	1	5,74	0	1	3,69
1	0,562	0	17,81	0	1	16,23
2	0,501	0	17,25	0	1	14,37
1	0,305	0	NA	0	1	NA
1	0,781	0	21,38	0	1	18,16
2	0,252	0	7,07	0	1	NA
1	1,139	0	26,17	1	1	10,5
0	1,01	1	16,31	1	1	9,18
3	0,911	0	20,29	1	1	6,55
0	0,661	1	12	1	1	10,43
0	1,141	1	12,95	1	1	9,55
0	0,981	1	23,79	1	1	16,3
3	1,209	0	15,53	0	1	6,26
3	2,612	0	NA	1	1	NA
3	0,995	0	21,44	1	1	NA
3	1,475	0	11,11	1	2	3,36
3	1,737	0	20,98	1	1	7,95
3	0,85	1	NA	1	1	NA
2	NA	0	NA	1	1	NA
0	0,89	1	16,7	1	1	12,46
1	0,35	0	15,67	0	1	4
1	1,11	0	12,67	0	1	6,67
1	0,73	2	3,67	0	1	1,34
1	0,97	1	32,67	1	3	14,5
1	0,46	2	6	0	1	3
1	0,97	1	7	0	2	4
0	0,98	1	4	0	2	0,1
3	1,41	2	5,34	0	1	1,34
1	1,22	1	13,34	1	1	6,34
0	1,65	1	11,2	0	3	7
1	0,824	1	16,5	0	1	8,5
2	0,39	1	6	0	1	17
3	1,85	0	30	1	3	9
1	NA	0	13,34	1	2	5,5
1	0,54	1	2,67	0	2	1
0	1,76	0	9,34	1	1	0,95
0	1,92	0	16,67	1	1	6
1	0,74	0	4,67	0	0	2
2	0,28	0	5,34	0	1	2,5
3	3,79	0	6,67	0	0	3,5
1	0,52	0	5,34	0	2	3
1	0,84	2	6,67	0	1	2,5
1	0,87	0	11,34	1	1	6,5
1	2,01	0	13,13	0	1	3,5
0	0,98	2	6	0	2	4
1	0,61	1	6,34	1	3	4,5
1	0,43	2	4,67	0	1	2,5
1	0,5	1	8,34	1	3	3
1	0,33	0	7,34	0	1	3,5
0	0,86	2	4,34	0	1	1,5
1	0,39	1	6	1	0	3
1	0,44	2	6,34	0	1	2
1	0,45	0	10	0	1	5
1	0,59	2	15,67	1	1	8
1	0,74	2	19,5	1	1	8,5
1	0,65	2	16	0	1	6
1	0,52	1	14,5	1	1	7
NA	NA	2	16	0	1	NA
NA	NA	2	17	0	1	NA

Distance of stigma t	Functional Orientat	Functional Orientat	Color contrast corol	Color contrast style	Color contrast andr	oecium – gynoecium
2,32	0	0	0	0	2	
15,15	0	0	0	1	1	
15,1	0	0	0	0	1	
NA	0	0	0	0	1	
18,61	0	0	0	0	1	
NA	0	0	0	0	1	
9,72	0	0	0	1	1	
9,29	0	0	0	0	1	
5,64	0	0	0	2	1	
10,22	0	0	0	0	1	
9,16	0	0	0	0	1	
14,06	0	0	0	0	1	
5,82	0	0	1	0	0	
NA	0	0	0	0	1	
NA	0	0	0	0	1	
3,1	0	0	0	0	1	
7,8	0	0	0	0	1	
NA	0	0	0	0	1	
NA	0	0	0	0	1	
13,3	0	0	0	0	1	
4	0	0	0	2	1	
6,67	1	1	0	2	2	
1,34	0	0	0	1	2	
13	0	0	2	2	2	
3	0	0	0	2	1	
7	0	0	0	2	1	
0,1	1	1	2	1	1	
1,34	0	0	0	0	1	
6,34	0	0	0	2	1	
10	0	0	2	0	1	
8,5	1	1	2	2	0	
1,5	0	0	0	1	1	
9	0	0	2	0	2	
5,5	1	1	0	2	1	
1	0	0	0	2	1	
0,95	0	0	0	2	1	
6	0	0	0	2	1	
2	0	0	0	1	1	
2,5	0	0	0	0	1	
3,5	0	0	0	2	1	
3	0	0	1	0	0	
2,5	0	0	2	0	0	
6,5	0	0	0	0	1	
3,5	1	1	0	2	1	
4	0	0	1	0	0	
8	0	0	0	2	2	
2,5	1	1	1	0	0	
9	0	0	0	2	1	
3,5	0	0	0	0	1	
1,5	1	1	0	0	1	
3,5	0	0	0	2	1	
2	0	0	1	0	0	
5	1	1	0	2	1	
8	0	0	0	0	1	
8,5	0	0	NA	1	NA	
6	0	0	NA	0	NA	
7	0	0	1	0	1	
NA	0	0	NA	0	NA	
NA	0	0	NA	0	NA	