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**Exploring the universe of the pollen flowers:
Classification, traits, and distribution**

Doctoral thesis

Lilian Rodrigues Ferreira de Melo

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**Exploring the universe of the pollen flowers:
Classification, traits, and distribution**

The thesis was presented to the Federal University of Uberlândia, as part of the requirements for obtaining a PhD in Ecology, Conservation and Biodiversity.

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Resumo

A polinização é um processo fundamental para a reprodução e evolução das plantas com flores. Os custos e benefícios associados à polinização podem influenciar a seleção natural e moldar os traços florais ao longo do tempo, resultando em uma impressionante variedade de formas, cores e estruturas florais em diferentes espécies. Essa interação pode levar à coevolução, onde as características de ambos os grupos são moldadas ao longo do tempo, otimizando a eficiência da polinização. Porém, em algumas flores, como as flores de pólen, esses custos e benefícios são pagos na mesma moeda, que neste caso são os grãos de pólen. Em sua definição original, essas flores foram chamadas de “flores de pólen” pelo botânico Stefan Vogel (1978), em contraste com outras flores que também oferecem outro recurso, como néctar, óleo ou resina. A principal função do pólen é permitir a transferência dos gametas masculinos para o órgão reprodutor feminino da flor. Enquanto algumas plantas dependem do vento ou da água para a dispersão do pólen, outras dependem da polinização de insetos, pássaros, morcegos ou outros animais. A classificação inicial das flores de pólen foi introduzida por Vogel (1978), que propôs três tipos florais distintos: Magnolian, Papaver e Solanum. Em nosso primeiro capítulo, fornecemos uma revisão abrangente do notável e altamente significativo trabalho de Vogel (1978) na área de Biologia da Polinização. Além disso, reavaliamos e propomos um sistema de classificação atualizado para flores de pólen. Esta classificação revisada incorpora uma gama mais ampla de famílias botânicas conhecidas por possuírem flores de pólen. Nossa abordagem leva em consideração a filogenia das angiospermas e utiliza novas ferramentas e metodologias que não estavam disponíveis na era de Vogel. No segundo capítulo, resumimos em um contexto funcional e evolutivo o que se sabe sobre diversidade morfológica, padrões de coloração e especialização estaminal em Melastomataceae. Primeiro, cobrimos informações sobre a morfologia das anteras, incluindo tipos de deiscência, presença ou ausência de pedoconectivos, apêndices, glândulas, tricomas e rostro. Em seguida, discutimos a variabilidade na forma e comprimento do estame e seu potencial papel funcional na reprodução. Finalmente, o papel geral das características do estame na divisão da carga de pólen entre a reprodução da planta e a recompensa do polinizador, bem como estratégias alternativas, é explorado como uma explicação adaptativa para a diversidade de estames em Melastomataceae. No terceiro capítulo dessa tese, focamos em estimar a distribuição geográfica das espécies de Melastomataceae que compreende um grupo notavelmente diverso de plantas com flores que prosperam em diferentes regiões do mundo, com uma concentração particular no Neotrópico. Investigamos o tamanho da flor e o dimetrismo dos estames e sua correlação entre fatores abióticos como temperatura, precipitação e altitude com a distribuição dessas espécies.

Palavras-chaves: atributos florais; síndrome de polinização; *buzz pollination*; estames; Neotrópico.

Abstract

Pollination is a fundamental process for the reproduction and evolution of flowering plants. The costs and benefits associated with pollination can influence natural selection and shape floral traits over time, resulting in an impressive variety of shapes, colors, and floral structures in different species. This interaction can lead to coevolution, where the traits of both groups are shaped over time, optimizing pollination efficiency. However, in some flowers, such as pollen flowers, these costs and benefits are paid in the same coin, in this case with the pollen grains. In their original definition, these flowers were called “pollen flowers” by the botanist Stefan Vogel (1978), in contrast to other flowers that also offer another resource such as nectar, oil, or resin. The main function of pollen is to allow the transfer of male gametes to the female reproductive organ of the flower. While some plants rely on wind or water for pollen dispersal, others rely on pollinating insects, birds, bats, or other animals. The initial classification of pollen flowers was introduced by Vogel (1978), who proposed three distinct floral types: Magnolian, Papaver, and Solanum. In our first chapter, we provide a comprehensive review of Vogel's (1978) remarkable and highly significant work in the area of Pollination Biology. Furthermore, we reassess and propose an updated classification system for pollen flowers. This revised classification incorporates a broader range of botanical families known to possess pollen flowers, as well as additional floral traits. Our approach takes into account the phylogeny of angiosperms and uses new tools and methodologies that were not available during Vogel's era. In the second chapter, we summarize in a functional and evolutionary context what is known about morphological diversity, color patterns, and stamen specialization within Melastomataceae. First, we cover information on anther morphology, including dehiscence types, presence or absence of pedoconnectives, appendages, oil-glands, trichomes and rostrum. Then, we discuss variability in stamen shape and length, and their potential functional role in reproduction. Finally, the general role of stamen traits in dividing the pollen load between plant reproduction and pollinator reward, as well as alternative strategies, is explored as an adaptive explanation for the stamen diversity in Melastomataceae. In the third chapter of our study, we focused on analyzing the geographic distribution of Melastomataceae species that comprises a remarkably diverse group of flowering plants that thrive in different regions of the world, with a particular concentration in the Neotropic. We investigated different flower sizes and degrees of stamens dimetrisism and its correlation between abiotic factors such as temperature, precipitation, and altitude with the geographic distribution of these traits.

Keywords: floral traits; pollination syndrome; buzz pollination; stamens; Neotropic.

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General Introduction

Pollination is a fundamental process for the reproduction and evolution of flowering plants (Stebbins 1970). The costs and benefits associated with pollination can influence natural selection and shape floral traits over time, resulting in an impressive variety of shapes, colors, and floral structures in different species (Waser 1983). To secure this process, the plant spends a lot of energy, both in pollen production and in the maintenance of specific structures to attract pollinators (Barônio et al. 2018). Plants and pollinators can coevolve, resulting in a mutualistic relationship, where both groups benefit from the interaction (Kiestler 1984; Thompson et al. 2021). Some work, for example, has already shown that flowers can develop specific shapes that fit perfectly with pollinators' body parts, making pollen collection more efficient (*safe sites*), while pollinators have specific behaviors to exploit these flowers (Koch et al. 2017; Dellinger et al. 2019; Russell et al. 2021). This interaction can lead to coevolution, where the traits of both groups are shaped over time, optimizing pollination efficiency (Kiestler 1984; Thompson and Pagel 2001; Thompson et al. 2021). However, in some flowers, such as pollen flowers, these costs and benefits are paid in the same coin, in this case with the pollen grains. In the original definition, such flowers receive this name in contrast to other flowers that offer another resource such as nectar, oil, or resin (Vogel 1978).

The initial classification of pollen flowers was introduced by Vogel (1978), who proposed three distinct floral types: Magnolian, Papaver, and Solanum. This classification was established based on the morphological traits of the flowers, including the number of stamens, androecium morphology, floral symmetry, and the pollinators involved. Some flowers were categorized as strictly melittophilous, relying exclusively on bees for pollination, while others had surplus pollen available for beetles, for instance. In our first chapter, we provide a comprehensive review of Vogel's (1978) remarkable and highly significant work in the area of Pollination Biology. Additionally, we reevaluate and propose an updated classification system for pollen flowers. We evaluate the distribution of these families over the angiosperms phylogeny and utilizes novel data and tools that were not available during Vogel's era to cluster families with similar traits in a new classification. This revised classification incorporates a broader range of botanical families known to possess pollen flowers, as well as additional floral traits.

Pollen flowers play a crucial role in plant reproduction and the preservation of biodiversity (Lunau et al. 2014). Some floral traits are particularly significant when discussing pollen flowers and their interactions, including the stamens, anther types, and the anthers dehiscence (Melo et al. 2021). These traits provide valuable insights into the pollinators capable of collecting this essential resource (Lunau et al. 2015; Telles et al. 2020). Since pollen is the sole resource offered by these flowers, pollen grains hold even greater value and face the dilemma of dual function (Pollen Dilemma). They serve a food resource for pollinators or their offspring, while simultaneously containing the male gametes necessary for plant reproduction (Harder and Thomson 1989; Lunau et al. 2015; Oliveira et al. 2020). In the second chapter, we delve into the specific traits of the stamens (related to morphology, color, and function) found within the Melastomataceae family, which represents a large radiation of pollen flowers.

The Melastomataceae family encompasses a remarkably diverse group of flowering plants that thrive in various regions across the globe, with a particular concentration in the Neotropical regions. Many species within the Melastomataceae family are endemic, meaning they are exclusively found in specific geographic areas characterized by distinct environmental and climatic conditions (Reginato et al. 2022; Ulloa-Ulloa et al. 2022). These conditions can significantly influence floral traits and the distribution patterns of these species. Many Melastomataceae plants rely on pollinating animals for their reproductive success, and the geographical distribution of these pollinators is also influenced by climatic factors. In the third chapter of our study, we focus on estimating the geographic distribution of Melastomataceae species with different flower and stamens sizes. Additionally, we investigate the correlation between abiotic factors such as temperature, precipitation, and altitude with the spatial distribution of these species. By examining these relationships, we aim to gain insights into how abiotic factors shape the distribution patterns of floral attributes in Melastomataceae.

Thus, the main objective of this thesis was to explore the universe of pollen flowers through three different studies. In addition to being unprecedented, this work significantly contributes to our understanding of the pollen flowers diversity and the evolutionary history of floral traits. By investigating the classification, traits, and distribution of these pollen flowers, we have gained a deeper understanding of how interactions between mutualists and environmental factors influence the evolution and distribution of floral traits over time.

References

- Barônio GJ, Cunha Guimarães BM, Oliveira LC, Melo LRF, Antunes PR, Cardoso RKDOA, Araújo TN (2018) Entre flores e visitantes: estratégias de disponibilização e coleta de recursos florais. *Oecologia Australis*, 22(4).
- Bastos B, Bacci LF, Reginato M, Bochner T, Goldenberg R (2022) Limited dispersal ability and restricted niche characterize “depauperons” in Melastomataceae. *Perspectives in Plant Ecology, Evolution and Systematics*, 57, 125701. <https://doi.org/10.1016/j.ppees.2022.125701>
- Buchmann SL (1983) Buzz pollination in angiosperms. *Buzz pollination in angiosperms.*, 73-113.
- Dafni A, Kevan PG (1997) Flower size and shape: implications in pollination. *Israel Journal of Plant Sciences*, 45(2-3), 201-211.
- Dellinger AS, Artuso S, Pamperl S, Michelangeli FA, Penneys DS, Fernández-Fernández DM, Schönenberger J (2019) Modularity increases rate of floral evolution and adaptive success for functionally specialized pollination systems. *Communications Biology*, 2(1), 453.
- Harder LD, Thomson JD (1989) Evolutionary options for maximizing pollen dispersal of animal-pollinated plants. *The American Naturalist*, 133(3), 323-344.
- Kiester AR, Lande R, Schemske DW (1984) Models of coevolution and speciation in plants and their pollinators. *The American Naturalist*, 124(2), 220-243.
- Koch L, Lunau K, Wester P (2017) To be on the safe site—Ungroomed spots on the bee’s body and their importance for pollination. *PLoS One*, 12(9), e0182522.
- Lunau K, Maier EJ (1995) Innate colour preferences of flower visitors. *Journal of Comparative Physiology A*, 177, 1-19.
- Lunau K, Piorek V, Krohn O, Pacini E (2015) Just spines—mechanical defense of malvaceous pollen against collection by corbiculate bees. *Apidologie*, 46, 144-149.
- Oliveira LC, Teixido AL, Trevizan R, Brito VL (2020) Bee-mediated selection favors floral sex specialization in a heterantherous species: strategies to solve the pollen dilemma. *Plants (Basel, Switzerland)*, 9(12), 1685. <https://doi.org/10.3390/plants9121685>
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos*, 120(3), 321-326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Reginato M, Almeda F, Michelangeli FA, Goldenberg R, Fritsch PW, Stone RD, Penneys DS (2022) Historical Biogeography of the Melastomataceae. In *Systematics, Evolution, and Ecology of Melastomataceae* (pp. 87-105). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-030-99742-7_4
- Renner SS (1989) A survey of reproductive biology in Neotropical Melastomataceae and Memecylaceae. *Annals of the Missouri Botanical Garden*, 496-518.
- Russell AL, Fetters AM, James EI, Ashman TL (2021) Pollinator effectiveness is affected by intraindividual behavioral variation. *Oecologia*, 197, 189-200.
- Stebbins GL (1970) Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. *Annual review of ecology and systematics*, 1(1), 307-326.

Telles FJ, Klunk CL, Maia FRD, Brito VLG, Varassin IG (2020) Towards a new understanding of the division of labour in heterantherous flowers: the case of *Pterolepis glomerata* (Melastomataceae). *Biological Journal of the Linnean Society*, 131(1), 1-11.

Thompson JN, Pagel M (2001) Coevolution. *Encyclopedia of life sciences*. London: Nature Publishing Group, 1-5.

Thompson JN, Segraves KA, Althoff DM (2021) Coevolution and Macroevolution. In: Nuño de la Rosa, L., Müller, G.B. (eds) *Evolutionary Developmental Biology*. Springer, Cham. https://doi.org/10.1007/978-3-319-32979-6_125

Ulloa Ulloa C, Almeda F, Goldenberg R, Kadereit G, Michelangeli FA, Penneys DS, Veranso-Libalah MC (2022) Melastomataceae: Global diversity, distribution, and endemism. In *Systematics, Evolution, and Ecology of Melastomataceae* (pp. 3-28). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-030-99742-7_1

Vogel S (1978) Evolutionary shifts from reward to deception in pollen flowers. The pollination of flowers by insects.

Waser NM (1983) The adaptive nature of floral traits: ideas and evidence. *Pollination biology*, 1, 241-285.

Westerkamp CH (1996) Pollen in bee-flower relations some considerations on melittophily. *Botanica Acta*, 109(4), 325-332.

Westerkamp CH (1997) Keel blossoms: bee flowers with adaptations against bees. *Flora*, 192(2), 125-132.

Chapter 1

Pollen flower classification then and now: Vogel (1978) revisited

Pollen flower classification then and now: Vogel (1978) revisited

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Abstract

“Pollen flower” describes flowers that present pollen as the main or only resource available for their pollinators. Such flowers are mainly pollinated by bees and present a series of morphological and functional adaptations, especially in their male reproductive organs, related to their tight interaction with pollinators. In 1978, these adaptations led the botanist Stefan Vogel to classify pollen flowers into three types: *Magnolian*, *Papaver* and *Solanum*. However, Vogel’s classification was based on limited access to data from that time and, for that reason, it did not encompass all the variability of floral traits and ecological interactions that pollen flowers are currently known to present. In this study, we revisit the pollen flower classification by Vogel to assess whether it encompasses the currently known diversity of pollen flowers and propose a new classification. To that end, we first inferred a floral morphospace using the five original floral traits and families described by Vogel. This analysis was then repeated including new plant families currently known to present pollen flowers. Finally, we repeated the same analysis considering all plant families with pollen flowers and eight additional traits that are currently known to be important for pollen flower pollination, such as stamen dimorphism, flowers grouped or isolated, floral display, and the presence of contrasting stamen color in relation to the petals. Next, we used cluster analyses to contrast it with the original categorization proposed by Vogel. Pollen flowers were identified in 75 of the 420 angiosperm families recognized in the APG IV, and our analysis allowed the identification of three functional groups of pollen flowers that are different from the original ones proposed by Vogel. The first group presents flowers that have anthers with longitudinal dehiscence, shed or exposed pollen grains, radial symmetry, many stamens, and commonly brush-blossom floral display. The second group also has flowers with anthers with longitudinal dehiscence, but their flowers are mostly grouped, small, and with reduced petals and few stamens. In addition, this group encompasses plants that present ambophily as a reproductive strategy, a condition not analyzed in Vogel's work. The last group presents anther dehiscence of the poricidal type and the pollen grains are released through small portions. These flowers often have few stamens that contrast with the petal’s colors, radial symmetry, and a shooting-star floral display. The new proposed classification is more objective and allows pollen flowers to be compared using only their morphological traits which are more accessible than the type of pollinator that visits them.

Key-words: ambophily, floral traits, pollination syndrome, buzz pollination

Introduction

Despite their high variability in flower morphology, all angiosperm species produce pollen grains as the male gamete carriers during their sexual reproduction. Pollen grains may also be directly consumed by pollinators creating an evolutionary dilemma: pollen is needed as a nutritive resource for pollinators and for plant reproduction (Westerkamp 1996; Luo et al. 2008). Such dilemma is deeper in flowers that offer only or mainly pollen as a resource for pollinators. In its original definition, these flowers were called “pollen flowers” by the botanist Stefan Vogel (1978), in contrast to other flowers that offer, for example, nectar, oil, or resin. Although the evolutionary transitions between pollen flowers and those that have other types of floral resources have been discussed since the beginning of the 19th century (Stäger 1902; Beutler 1953), it was in this seminal paper that Vogel firstly described their evolutionary trends, presenting a classification based in both flower morphology and their potential pollinators.

In his 1978 publication, Vogel described the morphological traits in pollen flowers, especially of the male reproductive organs, based on presumed floral adaptations to pollinators, especially bees. He classified all variability in pollen flowers in three basic floral types called: *Magnolian*, *Papaver*, and *Solanum*. According to Vogel, the *Magnolian* type would represent the most “ancestral” pollen flower. The high amount of pollen in this group is due to primary polyandry, inherited from anemophilous ancestors. This supposition was also shared by Cronquist (1968), who believed that an androecium with many stamens was more primitive than those observed in oligandric flowers. The main representatives of this floral type are found in the orders Magnoliales and Nymphaeales and the pollen grains, released by small stamens, are directly eaten by beetles. The *Papaver* type is also polyandric. In such flowers, pollen is predominantly used by female bees not to be directly eaten but to feed their offspring and, for this reason,

this type was considered a specialization within the melittophily syndrome. Polyandric families such as Papaveraceae and Ranunculaceae represent this floral type, in addition to members of Ochnaceae, Dilleniaceae, and Cistaceae. Finally, the *Solanum* type comprised all oligandric, and often zygomorphic, pollen flowers. This type was considered strictly melittophilous and floral visitors have a morphological match with flowers during the visit. Pollen is released in small portions like a cloud, from the mechanical vibratory movements produced by the bees. Still according to Vogel (1978), although some of these oligandric pollen flowers, such as Primulales, Melastomataceae, and Commelinales, probably never had nectaries, many ancestral representatives of the *Solanum* type are derived from oligandric nectar flowers, which sometimes still show a rudimentary and non-functional nectary.

Over the past years, there have been significant advancements in our understanding of floral trait evolution and plant-pollinator interactions (e.g., Hetherington-Rauth and Johnson 2020; Phillips et al. 2020; Mackin et al. 2021). However, it is surprising to note that there has been limited exploration regarding pollen flower classification since Vogel's groundbreaking research, which is now more than four decades old. Vogel mentions 37 flowering plant families to exemplify his pollen flower types and their interaction with pollinators. Though this shows an extensive knowledge of the subject, it is noteworthy that his categorization was based on the angiosperm classification systems contemporary to his time (e.g., Cronquist 1981; Takhtajan 1980). Furthermore, Vogel emphasized an evolutionary hierarchy between his three floral types (from the most 'primitive' - *Magnolian*, to the most 'modern' or 'derived' - *Solanum*) which is no longer coherent with our current understanding of the evolution of floral traits (Omland et al. 2008). Studies have shown that several conditions can interfere with the evolution of floral traits (Mackin et al. 2021; Trunschke et al. 2021) and, given that

different traits are under different selective pressures (eg. Melo et al. 2021; Kriebel et al. 2022), we cannot generalize whole clades as being more or less evolved. Moreover, there is little information about the distribution of pollen flowers in modern phylogenies, which precludes our understanding of whether different pollen flower types evolved sequentially, as proposed by Vogel, or independently, appearing several times in different clades.

In this study, we review Vogel's seminal work on the classification of pollen flowers. Our aims are: 1) review which families of angiosperms have species with pollen flowers in the current classification of the Angiosperm Phylogeny Group IV (APG IV); 2) analyze the phylogenetic distribution of pollen flowers in modern family-level angiosperm phylogenies to understand how they evolved and; 3) analyze whether the floral types coined by Vogel have statistical support, based on our current knowledge of pollen flower biology.

Methods

Angiosperm families with pollen flowers

To compile a comprehensive list of flowering plant families that present species with pollen flowers, published data was sampled by searching papers published from 1978 until 2022. We used the Angiosperm Phylogeny Group IV (henceforward APG IV, Chase et al. 2016) classification, which recognizes 64 orders and about 416 families, as a reference for our search, using each family name as a search term until all 416 families were covered. The review was performed using mainly two platforms: Angiosperm Phylogeny website (Stevens 2001 onwards), and Google Scholar (130 works were analyzed, including books and papers) (supporting information - Table S1). In addition, taxonomical publications with species descriptions and herbarium photos available online

(nybg.org) and, Re flora (reflora.jbrj.gov.br) were consulted to confirm some morphological traits. Family names cited before 2016, including those in Vogel (1978), needed synonymization because taxonomic classification has changed over time and some families or genera have been split or merged into other groups (Stevens 2001 onwards).

Trait data scoring

To perform a statistical reevaluation of the pollen flower types described by Vogel (1978), we compared three morphospaces. The first included only the three floral traits and angiosperm families mentioned by Vogel (1978). The second uses only the three floral traits mentioned by Vogel but includes both the original families cited by him plus those recovered as having pollen flowers in our literature review from the 1978-2022. Finally, the third morphospace includes all families (original Vogel plus our review) and uses eight additional floral traits that were found to be relevant to pollen flower pollination along our review. By comparing the three morphospaces, we observed how adding new possibilities of trait combinations could cluster new pollen-flower groups (more details below).

From each plant family sampled, we recovered the following three floral traits, which were mentioned by Vogel in his original work: (1) type of anther dehiscence (poricidal or longitudinal), (2) pollen release (shed, exposed or small portions) and (3) number of stamens (polyandric or oligandric). Pollinator's type and behavior, criteria investigated by Vogel, was not included in the analysis because they are extrinsic factors not directly linked to floral morphology. We did, however, take note of primary pollinators (bees, beetles, or others) and their interactions with the flower when this information was available (supporting information - Table S1).

With this information gathered, we select additional traits that are currently known to influence the behavior of pollinators in pollen flower and could improve floral type classification. The new traits annotated were: (1) presence of stamen dimorphism (Luo et al. 2008; Vallejo-Marin et al. 2009), (2) isolated or grouped flowers (Krick and Ackerman 2015; Costa et al. 2017; Timerman and Barrett 2018), (3) floral display as “shooting-star”, “brush-blossom” or none (Russell et al., 2016), (4) presence of reduced petals, (5) presence of color contrasting stamen in relation to the petal color (Lunau et al. 2017; Dellinger et al. 2021; Melo et al. 2021), (6) radial or zygomorphic floral symmetry (Stebbins 1974, Marazzi et al. 2007; Vallejo-Marín et al. 2010b), (7) diurnal or nocturnal anthesis (Cordeiro et al. 2021), and (8) presence of other floral resources (e.g., thermogeny and oil gland) (Silberbauer-Gottsberger et al. 2001). These new floral traits were selected based on their morphological relevance and functional importance during flower pollinator interaction (e.g., Stebbins 1951, Sargent et al. 2004; Endress 2011; Paterno et al. 2020; supporting information - Table S1).

The scoring was performed at the family level, i.e., the attributed value refers to the existence of at least one species or genus with those traits - as listed in supporting information - Table 1. For example, although we know that not all Fabaceae species have pollen flowers, the family was included in our list because some genera and species within this family have pollen flowers. In fact, in this case, there are two clearly distinct types of pollen flowers within the family, which is why we call them Fabaceae 1 (e.g., *Acacia* and *Swartzia*) and Fabaceae 2 (e.g., *Cassia*, *Chamaecrista* and *Senna*). With the exception of Fabaceae where at least two types of pollen flowers are clearly present, all other families were represented by a single data point.

Morphospaces and Cluster Analysis

To visualize how families are distributed in the morphospace, we performed non-metric multidimensional scaling (NMDS) based on floral traits considering the Euclidean distances between data points, using the *metaMDS* function of the *vegan* package (Oksanen et al. 2022) to find a stable solution. We used several random starts and the *geom_jitter* function of the *ggplot2* package (Wickham 2016), which adds a small amount of random variation to the location of each point, for visualization.

Subsequently, to assess whether there was statistical support for clustering of families in the morphospace, a k-means cluster analysis was performed based on the family scores on the NMDS1 and NMDS2 axis of the morphospace. K-mean clustering is a simple non-supervised algorithm that estimates the best position of the centroid for each previously defined k clusters on the morphospace by minimizing the distances between the centroid and the data points (Frades and Matthiesen 2009). At the end of the process, a given data point (family) is ascribed to its nearest centroid, defining the clusters. To search for the optimal cluster number, we used a gap statistic which compares the total intracluster variation for different values of k (in our case from 2 to 10) with their expected values under a null reference distribution generated by Monte Carlo simulations (Tibshirani et al. 2001). The gap statistic is easily computed using the function *clusGap* from the *cluster* package (Maechler et al. 2022). The optimal number of clusters is the one with highest gap statistic which can be assessed using the function *fviz_gap_stat* from the package *factoextra* (Kassambara and Mundt 2020). We did not include Vogel's floral types for the new families found in the review as a trait in the cluster analysis. In this way, we do not create a bias to reinforce one type or another, nor the Vogel's own ideas when he created the classification. All analyses were performed in the R environment (R Core Team 2020).

Phylogenetic distribution of pollen flowers

We used the family-level phylogeny of seed plants made by Qian and Zhang (2014) to visualize the distribution of families with different pollen flower types over the angiosperm phylogeny. This phylogeny included 425 families of angiosperms – (12 gymnosperms families were removed). This phylogeny was chosen because it is appropriate for phylogenetic analyses of functional traits at the family-level and the closest family-level phylogeny to the current classification (APG IV) used to review families with pollen flowers. We indicated the presence of the different flower pollen type in this family-level phylogeny using iTOL - Interactive Tree of Life (Letunic and Bork 2021).

Results

Pollen flower types based on morphological traits

Vogel's original work described species or genera of pollen flowers in 38 botanical families, of which eight belonged to the *Magnolian* type, 11 to the *Papaver* type and 18 to the *Solanum* type. In our review, we identified 78 families presenting pollen flowers and belonging to 28 angiosperm orders. The 40 newly recognized families encompass species with pollen flowers in at least one of their genera. The families Corsiaceae, Rhabdodendraceae, Clethraceae, Calceolariaceae, and Hydnoraceae present species with pollen flowers, but they were removed from subsequent analyses due to limited morphological data.

We identified a clear clustering in the morphospace built using the original three floral traits and 38 families of pollen flowers proposed in Vogel's original work (Fig. 1A). However, when all 73 families with pollen flowers are analyzed for these traits, an overlap between clusters is observed, showing that the original traits alone do not allow a clear

distinction between pollen flower types proposed by Vogel when current pollen flower diversity is considered (Fig. 1B). Finally, when analyzing the morphospace containing all 73 families and adding the eight additional floral traits, we recover three clear clusters, suggesting three floral types (Fig. 1C). These new clusters, however, do not coincide with Vogel's original types in terms of traits nor taxonomic representation at the family level.

In general, the vast majority of pollen flowers analyzed are bisexual, presenting gynoecium and androecium in the same flower. The first group of pollen flowers, is composed of plant families that present flowers with anthers with longitudinal dehiscence, shed or exposed pollen grains, radial symmetry, many stamens (polyandric) and commonly brush-blossom floral display (Fig. 2A). Families such as Myrtaceae, Lythraceae, Papaveraceae, Magnoliaceae, Nymphaeaceae, among others belong to this group (Table 1S). The second group is composed of families that also have flowers with anthers with longitudinal dehiscence. However, in this group, their flowers are mostly grouped, small and with reduced petals and few stamens (oligandric). Pollen grains in at least 50% of the families in this group are exposed (Fig. 2B). The families Araceae, Canellaceae, Cyperaceae, Ruppiaceae, among others, belong to this group (Table SI 1). The last group comprises families that mostly have anthers with poricidal dehiscence and the pollen grains being released through small portions. In addition, they often have few stamens (oligandric), which contrast with the petal's colors, radial symmetry, and a shooting-star floral display. Some families may also have grouped flowers (Fig. 2C). This group includes families such as Melastomataceae, Primulaceae, Commelinaceae, Iridaceae, Ochnaceae, Solanaceae and Fabaceae 2 (supporting information - Table SI 1).

Distribution of pollen flowers in the angiosperm phylogeny

A visualization of the phylogenetic distribution of pollen flowers over the angiosperm phylogeny suggests that there is no common origin for pollen flowers. They

have probably arisen several times independently, under different pressures and environmental contexts (Fig. 3). Group 1 is more concentrated within the ANA grade and the Magnoliids and Monocots clades. Group 2, on the other hand, is represented by families in several clades throughout the phylogeny, from Magnoliids to Asterids. Finally, Group 3 also has a more restricted distribution to clades of early diversification (Fig. 3).

Discussion

The three pollen flower types originally proposed by Vogel do not comprise all the morphological diversity of pollen flowers currently known. By including new information on floral diversity and angiosperm classification of the last 50 years, our results recovered 40 additional families with pollen flowers than what had been described in Vogel's 1978 seminal work. This means a significant increase in sampling, which also allowed us to refine the interpretation of floral types based on their shared morphology. Our results show that, considering recent data on floral traits linked to interaction with pollinators, pollen flowers are better classified in three new functional types. These previously unveiled morphological combinations, together with the pollination systems that they may be associated, is likely to facilitate our understanding of the ecology and evolution of pollen flowers.

The role of pollination biology studies in understanding pollen flower classification

Pollination syndromes and floral biology had been debated long before the first studies on pollen flowers (Stäger 1902; Vogel 1954; Werth 1956; van der Pijl 1961; Faegri and van der Pijl 1966) and the types proposed by Vogel were important for understanding the interaction between these flowers and their pollinators. However, Vogel grouped families that are very morphologically distinct together based mainly on the fact that they tend to be pollinated by similar functional group of pollinators (e.g.,

Araceae and Magnoliaceae as *Magnolian* type due to beetle pollination), rather than classifying them in terms of individual floral traits, which in turn can be easily measured and compared.

Including information about the pollination biology in this type of categorization may be impractical because, despite the conserved floral morphology within species, floral visitors can be diverse and vary with location (Lefebvre et al. 2018; Dellinger et al. 2021). However, information on pollination biology can be used *a posteriori* to interpret morphological groupings, as we will see below. Currently, some plant-pollinator interactions in pollen flowers are already well known and described (e.g., Melastomataceae and bees; Konzmann et al. 2020; Bochorny et al. 2021; Passos et al. 2022; Valadão-Mendes et al. 2022). However, others need more studies and observations, such as plants that show ambophily, as Cyperaceae (Costa and Machado 2012). This family is characteristically anemophilous, but there are some reports of species adapted to entomophily as well. For example, reproductive tests indicated that *Rhynchospora ciliata* is self-incompatible and that ambophily enhances its reproductive success (Costa and Machado 2012). Ambophily, i.e., plants that are pollinated either by biotic or abiotic vectors (Culley et al. 2002), are not addressed by Vogel in his work. But in our literature review we identified at least 10 families with flowers that offer only pollen as floral resource for insect pollinators that may also spread their pollen through wind (e.g., Cyperaceae and Ranunculaceae) or water (Hydrocharitaceae and Ruppiaceae) (Tanaka et al. 2004; Duan et al. 2009; Costa et al. 2017) - (supporting information - Table SI 1). As stated earlier, information about the pollination systems of these families are still scarce and further investigations are needed. It is also necessary to understand if the plant is truly adapted to the two pollination modes or if they are adapted to aquatic ecosystems (Taylor et al. 2018), or to the wind such as some anemophilous systems (Tanaka et al. 2004). In

addition, some plants, like some of the families mentioned above (Cyperaceae and Hydrocharitaceae), can act in more than one pollination pathway, and thus ensure greater reproductive success (Tanaka et al. 2004; Costa and Machado 2012; Costa et al. 2017).

Pollen flowers classification in a new perspective

Vogel's classification leaves little room for trait combinations that do not strictly follow one of his originally proposed pollen flower types. Therefore, families or clusters that have unpredicted trait combinations are not classifiable in his system. For example, the genus *Dalechampia* (Euphorbiaceae) has species with both poricidal anthers and polyandry, not fitting into any of Vogel's floral types (Armbruster et al. 2012). Although we also found three functional clusters of pollen flowers, our classification is perhaps more flexible because the new clusters include previously unclassifiable families. Also, the new classification is more objective, and the plants can be compared depending on their morphological traits, and not directly on the type of pollinator that visits them.

Among the families presented by Vogel in 1978, Group 1 in our new proposal, brought together 8 families of the *Papaver* type (Aizoaceae, Cactaceae, Cistaceae, Fabaceae 1 (*Acacia* and *Swartzia*), Hypericaceae, Papaveraceae, Ranunculaceae, Theaceae), and 6 families of the *Magnolian* type (Annonaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae, Nymphaeaceae). In addition to these, 9 new families containing a set of specific characteristics of the group are presented. It is interesting to note that this group brought together two of the families that named two of the three original floral types of Vogel that is, Papaveraceae and Magnoliaceae. The fact that they belong to the same group in our new classification says a lot about the similarities in their floral traits. Unlike Group 2, the flowers in Group 1 usually have large and striking petals. The stamens are many, sometimes contrasting with the petals, and are often highlighted in a brush-blossom display, which favors the contact of floral visitors

with the anthers with longitudinal dehiscence. Thus, we can think that this group has the most morphologically generalist pollen flowers (*sensu* Ollerton et al. 2011), as they are attractive (considering their colors, shapes, and sizes) to different pollinator groups, and the pollen grains are easily accessible. For the flowers analyzed from these families, visits from beetles, bees, flies, thrips, and other small insects were reported in the literature (Endress 1986; Bhunia and Mondal 2012; Erbar 2014).

According to our newly proposed classification, Group 2 is not very representative for the families originally presented by Vogel. Only three families cited by Vogel were classified in this group (Philydraceae, formerly *Solanum* type, and Araceae and Pandanaceae, formerly *Magnolian* type). In addition to these, all the other 18 families belonging to this group were not considered by Vogel's seminal paper, including Juncaginaceae, Piperaceae, Poaceae, Zosteraceae, among others (supporting information - Table SI 1). It is worth to mention that they were not considered at the time of Vogel's work perhaps because they were seen only as anemophilous flowers. However, some more recent studies have proposed that the floral structures do offer resources and allow legitimate interactions with animal pollinators in Cyperaceae, Poaceae and Trimeniaceae (Bernhardt et al. 2003; Wolowski and Freitas 2015; Costa et al. 2017). The main morphological traits of the flowers of this cluster are related to the pollination systems in which these pollen flowers are involved. For example, although many of these flowers have reduced petals (thus being less attractive than other flowers), longitudinal dehiscence leaves pollen grains more exposed to visitors (shed or exposed) and grouped flowers promote a relative increase in the availability of this resource during the plant-pollinator interaction. The works reviewed reported visits by beetles, flies, hoverflies, bees, some small insects and even vertebrates (Table 1S) in flowers of this group, such as

the pollination of *Freycinetia reineckeii* (Pandanaaceae) by *Pteropus marianensis* (Pteropidae – flying foxes) (Cox 1990).

There are 28 families in Group 3, including 18 families that belonged to Vogel's *Solanum* type; two families, classified as *Papaver* type (Begoniaceae and Ericaceae) and 7 new families included by our review (Asphodelaceae, Euphorbiaceae, Iridaceae, Mayacaceae, Pittosporaceae, Pontederiaceae and Tecophilaeaceae). Most families in Group 3, unlike the other two groups, have anthers with poricidal dehiscence. In this way, pollen is not easily accessible and is released in small portions like a cloud by mechanical vibratory movements of bees. Vogel already presented the *Solanum* type as being the most specialized (he called it strictly ‘mellitophilous’) and our results corroborated this idea. Poricidal anthers may exclude some visitors (pollen eating beetles and flies), which corroborates a more specialized interaction (De Luca and Vallejo-Marín 2013). This interaction is known as *buzz pollination* and occurs in species from 65 angiosperm families (De Luca and Vallejo-Marín 2013; Vallejo-Marín 2019). In addition, poricidal anthers can also help increase the efficiency of pollen transfer by releasing pollen into specific areas of the pollinator's body called “safe sites” (Koch et al. 2017).

It is worth mentioning that during the review, we noticed that *buzz pollination* occurs in families that do not belong to Group 3. Thus, this pollination mode is not exclusive to plants with poricidal anthers. The vibratory behavior performed by bees may also occur in some plants that have a longitudinal opening anther, such as the flowers of the genus *Swartzia* (Fabaceae 1) that are visited by carpenter bees (*Xylocopa*) (Lopes and Machado 1996; Pinheiro et al. 2018, Basso-Alves et al. 2022). Other studies also mention the use of vibration in the pollination of other species with non-poricidal anthers (Buchmann 1985; Oliveira and Sazima 1990; Fidalgo and Kleinert 2009; Nevard et al. 2021), as well as Vogel himself (1978).

Another important trait found in many species from Group 3 is heteranthery, which occur in 16 families of angiosperms (Vallejo-Marín 2010). When this sampling is reduced to families that contain pollen flowers, it results in 12 families (Aizoaceae, Commelinaceae, Techophilaceae, Dilleniaceae, Malvaceae, Bixaceae, Fabaceae 2 (*Cassia*, *Senna* and *Chamaecrista*), Lythraceae, Malpighiaceae, Melastomataceae, Lecythidaceae and Solanaceae). As small stamens often offer pollen grains for bees' collection and large stamens destinate pollen for pollination, the presence of two stamen sets within the same pollen flower has been mostly interpreted as a functional division of labor (Luo et al. 2008; Vallejo-Marín et al. 2009). The fact that a flower has this division of labor into two sets of stamens further reinforces the presence of a well-specialized plant-pollinator relationship (Dellinger et al. 2019; Telles et al. 2020; Nunes et al. 2021). In addition, in some cases, we can observe the presence of a set of stamens that present color contrast in relation to the petal, while the other set has a cryptic color, such as *Microlicia cordata* (Melastomataceae) (Velloso et al. 2018). In other cases, the difference in size between the sets of stamens (isometric, subdimetric or dimetric) may be more relevant than the color contrast (as seen in Brito et al. 2021; Melo et al. 2021). Finally, flowers that have a shooting-star floral display, such as *Dodecatheon* (Primulaceae), highlight their stamens at the front. Even though these flowers have few stamens, they are prominently to floral visitors (Harder and Barclay 1994).

The floral traits associated to type 3 flowers are seen as an evolutionary convergence to the “solanoid” floral form which has been pointed out several times in the past (Delpino 1868, cited in (Macior 1964; Faegri 1986; Harder and Barclay 1994). Some common traits of these flowers are reflected petals, prominent stamen cone, poricidal anthers and absence of nectar (Endress 1994; Matthews and Endress 2002). The evolution of poricidal dehiscent anthers likely had a significant impact on the ability of different

types of pollinators to remove pollen (Buchmann 1983; De Luca and Vallejo-Marín 2013; Nunes and Vallejo-Marín 2022). In addition, vibrating pollen release is not associated with a single type of floral morphology (Buchmann 1983). However, some floral morphologies such as “solanoïd” or “*Solanum type*” appear to have evolved specifically in response to pollen collection by sonicating bees and represents an adaptative peak for *buzz-pollinated* plants (Faegri 1986; Vogel 1978; Harder and Barclay 1994; Matthews and Endress 2002; De Luca and Vallejo-Marín 2013). In that way, our Group 3 is perhaps the closest representation of the more classic view of pollen flower in the context originally proposed by Vogel.

Pollen flowers in the angiosperm phylogeny

Group 1 pollen flowers originate from the most basal angiosperm families (Grade ANA + Magnoliids + Chloranthales). They can be found in certain families of the order Ranunculales, as well as in Myrtales and Caryophyllales. Although most prevalent in the early stages of phylogeny, this type of flower has arisen multiple times throughout evolutionary history. Many families within group 1 are classified as Magnolian type according to the classification proposed by Vogel (1978). In his work, he suggested that these flowers probably predated nectar flowers and could be the oldest pollen flowers. Recently, Sauquet and colleagues presented a paper on the ancestral flower of angiosperms and their early diversification, where they reconstructed the most recent common ancestor of all extant angiosperms. This reconstructed flower bears a remarkable resemblance to the flowers found in group 1, marking a significant milestone in our understanding of the origin of floral diversity and the evolution of angiosperms (Sauquet et al., 2017).

Families with this type of pollen flowers are found in the Monocots and Commelinidae phylogeny. Also, they can be found in Fabidae, Malvidae, Myrtales,

Ericales, and other groups. We did not observe evidence of common origin for the pollen flowers of this group. Families belonging to Group 2 are not present among basal angiosperms. The diversification of these flowers is probably influenced by several biotic and abiotic factors in their respective habitats (*e.g.*, pollinators, temperature) and the emergence of important innovations (traits flexibility) that may have facilitated the adaptation and diversification of these plants as suggested by Onstein (2019).

Group 3 families tend to appear earlier on the phylogeny. They can be found in the clades Canellales, Piperales, Monocots, Pandanales, Poales and Ranunculales, but not among the more advanced groups. Its emergence is less frequent and concentrated in clades that share a common origin. This indicates that they form a more conserved group within the evolutionary history of pollen flowers. It is important to note that most of the families mentioned in this group were not included in Vogel's work and were only recognized for having pollen flowers after the revision made in that work.

Conclusion

Vogel's work in 1978 was undoubtedly significant for classifying flower types based on their interactions with pollinators. However, we now find that this classification, as proposed by Vogel, is insufficient considering our current understanding of the vast diversity of pollen flowers. Attempting to fit all recognized pollen flowers into the existing floral types of Magnolian, Papaver, and Solanum would be impractical and insufficient. In our research, we present a new perspective on the classification of pollen flowers. Rather than relying mainly on pollinator interaction, we advocate the analysis of individual morphological features, spanning the full spectrum of known pollen flower diversity. By expanding the sampling of floral morphology characters, we can allow for a wider range of combinations between these characters. In conclusion, our research

suggests a move away from Vogel's classification and encourages a more inclusive and comprehensive classification of pollen flowers based on morphological traits.

Figures

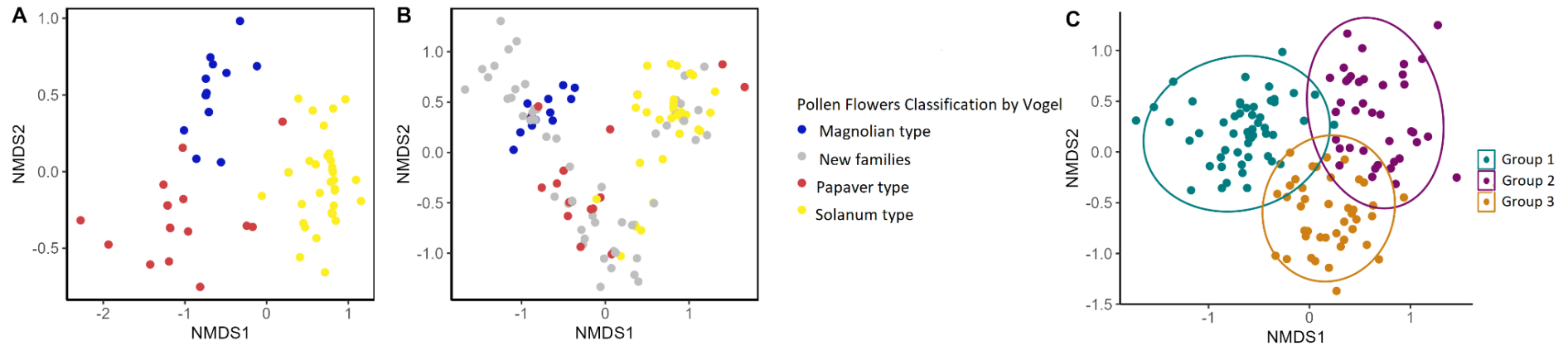


Fig.1. (A) Morphospace based on three floral traits proposed by Vogel (1978) and including the 38 families of pollen flowers mentioned by him. **(B)** Morphospace based on the same three floral traits as in A, but this time including both Vogel's (1978) original families plus 35 new families found to have pollen flowers in our review. **(C)** Morphospace based on 11 morphological traits and including all 73 families. The families included in each of the three highlighted clusters (Groups 1, 2, and 3) do not coincide with those present in each of Vogel's original classification of pollen flowers (*Magnolian*, *Papaver* and *Solanum*).

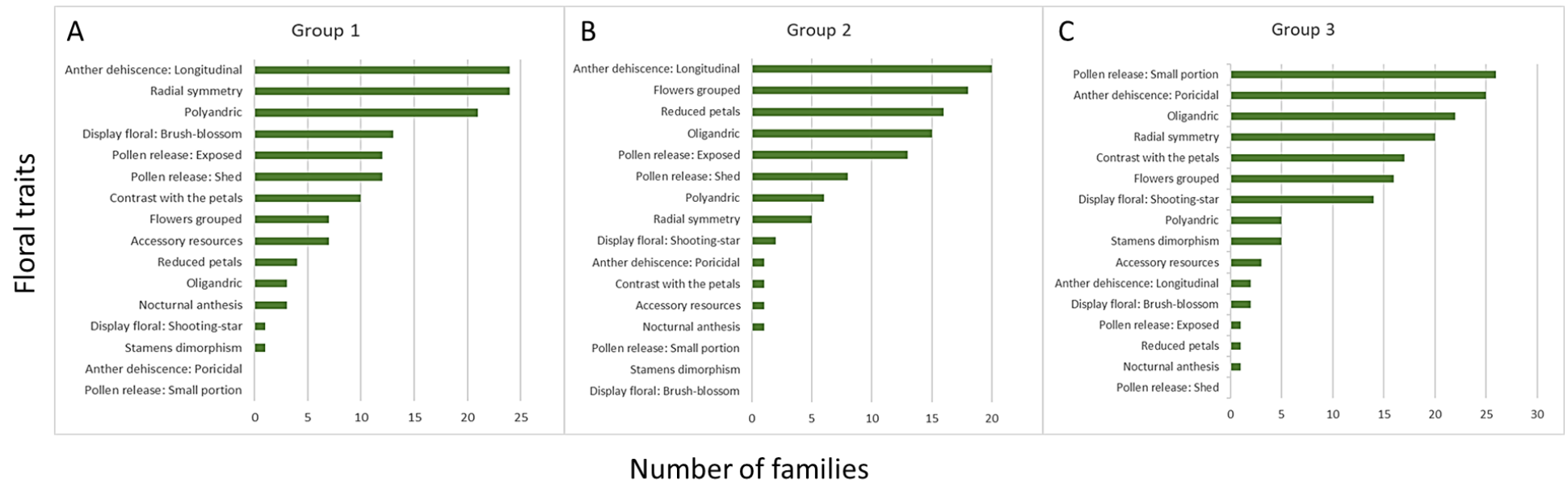


Fig.2. Most important floral traits composing each pollen flower group in our reviewed analyses using 11 floral traits in 73 families. The predominance of floral traits **(A)** for the 24 families within group 1, **(B)** for the 21 families within group 2, and **(C)** for the 28 families within group 3.

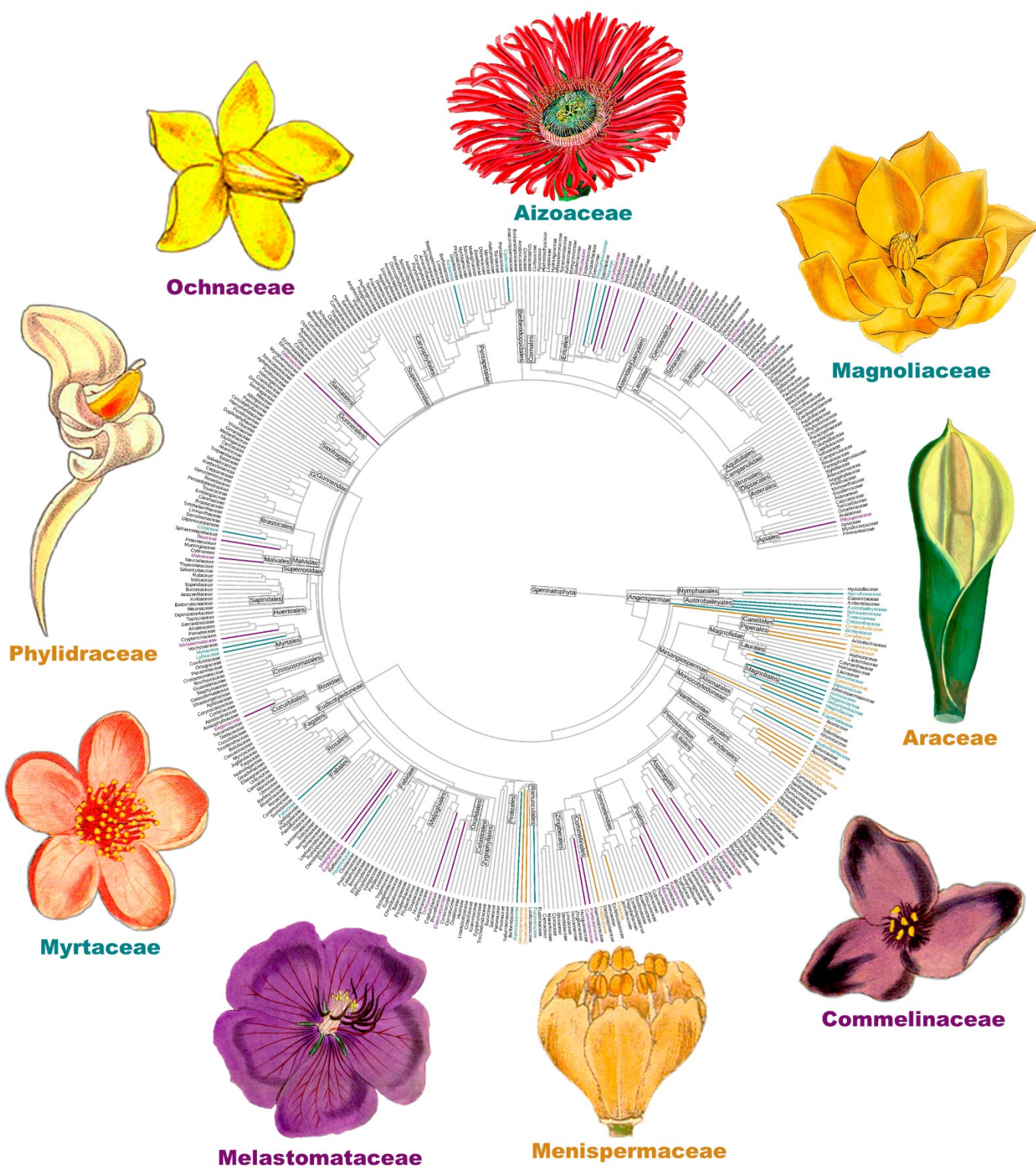


Fig. 3. Families of the three groups of pollen flowers proposed in the new classification, along the Phylogeny of Angiosperm Families (Quian & Zhang, 2014 - adapted). The illustrations are available in Watson and Dallwitz (1992) onwards. Version: 25th July 2023. (Illustrations edited by João Pedro Santos Pereira).

References

- Asar Y, Ho SYW, Sauquet H (2022) Early diversifications of angiosperms and their insect pollinators: were they unlinked? *Trends Plant Sci.* <https://doi.org/10.1016/j.tplants.2022.04.004>
- Basso-Alves JP, da Silva RF, Coimbra G, Leitão SG, et al (2022). Heteromorphic stamens are differentially attractive in *Swartzia* (Fabaceae). *AoB Plants*, 14(5), plac041.
- Benton MJ, Wilf P, Sauquet H (2022) The Angiosperm Terrestrial Revolution and the origins of modern biodiversity. *New Phytol.* 233:2017–2035
- Bernhardt P, Sage T, Weston P, et al (2003) The pollination of *Trimenia moorei* (Trimeniaceae): Floral volatiles, insect/wind pollen vectors and stigmatic self-incompatibility in a basal angiosperm. *Ann Bot* 92:445–458. <https://doi.org/10.1093/aob/mcg157>
- Beutler R (1953) Nectar. *Bee World* 34:106–116. <https://doi.org/10.1080/0005772X.1953.11094798>
- Bhunia D, Mondal AK (2012) Studies on production, morphology and free amino acids of pollen of four members in the genus *Nymphaea* L. (Nymphaeaceae). *Int J Sci Nat* 3:705–718
- Bochorny T, Bacci LF, Dellinger AS, et al (2021) Connective appendages in *Huberia bradeana* (Melastomataceae) affect pollen release during buzz pollination. *Plant Biol* plb.13244. <https://doi.org/10.1111/plb.13244>
- Brito VLG, Fendrich TG, Smidt EC, et al (2016) Shifts from specialised to generalised pollination systems in *Miconieae* (Melastomataceae) and their relation with anther morphology and seed number. *Plant Biol (Stuttg)* 18:585–593. <https://doi.org/10.1111/plb.12432>
- Brito VLG, Leite FB, Telles FJ, Jorge LR, Sazima M (2021) The attractive role of floral elements in heterantherous species without pronounced stamen differences. *Arthropod-Plant Interactions*, 15(1), 23-31.
- Buchmann SL (1983) Buzz pollination in angiosperms. *Handb Exp Pollinat Biol* 73–113
- Buchmann SL (1985) Bees Use Vibration to Aid Pollen Collection from Non-Poricidal Flowers Author(s): Stephen L. Buchmann Reviewed work (s): Source: *Journal of the Kansas Entomological Society*, Vol. 58, No. 3 (Jul, 1985), pp. 517-525 Published by: Allen Pres. *J Kansas Entomol Soc* 58:517–525
- Buchmann SL, Hurley JP (1978) A biophysical model for buzz pollination in angiosperms. *J Theor Biol* 72:639–657. [https://doi.org/10.1016/0022-5193\(78\)90277-1](https://doi.org/10.1016/0022-5193(78)90277-1)
- Cardoso JCF, Viana ML, Matias R, et al (2018) Towards a unified terminology for angiosperm reproductive systems. *Acta Bot Brasilica* 32:329–348. <https://doi.org/10.1590/0102-33062018abb0124>
- Chase MW, Christenhusz MJM, Fay MF, et al (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot J Linn Soc* 181:1–20. <https://doi.org/10.1111/boj.12385>

- Cordeiro GD, Liporoni R, Caetano CA, et al (2021) Nocturnal Bees as Crop Pollinators. <https://doi.org/10.3390/agronomy11051014>
- Costa ACG & Machado IC (2012) Flowering dynamics and pollination system of the sedge *Rhynchospora ciliata* (Vahl) Kükenth (Cyperaceae): does ambophily enhance its reproductive success? *Plant Biol* 14:865–1010. <https://doi.org/https://doi.org/10.1111/j.1438-8677.2012.00574.x>
- Costa ACG, Thomas WW, Machado IC (2017) Comparative floral biology of *Rhynchospora ciliata* (Vahl) Kükenth and *R. pubera* (Vahl) Boeckeler (Cyperaceae): the role of white involucre bracts in attracting pollinating insects. *Plant Species Biol* 32:403–411. <https://doi.org/10.1111/1442-1984.12173>
- Cox PA (1990) Pollination and the Evolution of Breeding Systems in Pandanaceae. *Ann Missouri Bot Gard* 77:816–840
- Culley TM, Weller SG, Sakai AK (2002) The evolution of wind pollination in angiosperms. *Trends in Ecology & Evolution*, 17, 361–369.
- Daumann E (1971) Zum problem der Täuschblumen. *Preslia* 43:304–317
- De Luca PA, Vallejo-Marín M (2013) What's the “buzz” about? The ecology and evolutionary significance of buzz-pollination. *Curr Opin Plant Biol* 16:429–435. <https://doi.org/10.1016/j.pbi.2013.05.002>
- Dellinger AS, Pérez-Barrales R, Michelangeli FA, et al (2021) Low bee visitation rates explain pollinator shifts to vertebrates in tropical mountains. *New Phytologist*, 231(2), 864-877.
- Dellinger AS, Pöllabauer L, Loreti M, Czurda J & Schönenberger J (2019) Testing functional hypotheses on poricidal anther dehiscence and heteranthery in buzz-pollinated flowers. *Acta ZooBot Austria*, 156, 197-214.
- Duan YW, Zhang TF, He Y, Liu JQ (2009) Insect and wind pollination of an alpine biennial *Aconitum gymnanthum* (Ranunculaceae). *Plant Biology*, 11, 796–802.
- Endress PK (1986) Reproductive structures and phylogenetic significance of extant primitive Angiosperms. *Plant Syst Evol* 152:1–28. <https://doi.org/10.1007/BF00985348>
- Endress PK (1994) Floral structure and evolution of primitive angiosperms: Recent advances. *Plant Syst Evol* 192:79–97. <https://doi.org/10.1007/BF00985910>
- Erbar C (2014) Nectar secretion and nectaries in basal angiosperms, magnoliids and non-core eudicots and a comparison with core eudicots. *Plant Divers Evol* 131:63–143. <https://doi.org/10.1127/1869-6155/2014/0131-0075>
- Faegri K (1986) The solanoid flower. *Trans Bot Soc Edinburgh* 45:51–59. <https://doi.org/10.1080/03746608608684993>
- Faegri K, Van Der Pijl L (1966) *The principles of pollination ecology*, Pergamon P. New York, NY, USA
- Fidalgo OA, Kleinert AMP (2009) Reproductive biology of six Brazilian Myrtaceae: Is there a syndrome associated with buzz-pollination? *New Zeal J Bot* 47:355–365
- Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Disponível em: <

<http://floradobrasil.jbrj.gov.br/>

- Frades I, Matthiesen R (2009) Overview on Techniques in Cluster Analysis. *Bioinformatics Methods in Clinical Research*, 81–107. doi:10.1007/978-1-60327-194-3_5
- Grant EL, Wallace HM, Brooks PR, et al (2021) Floral attraction and flower visitors of a subcanopy, tropical rainforest tree, *Fontainea picrosperma*. 10468 | *Ecol Evol* 11:10468–10482. <https://doi.org/10.1002/ece3.7850>
- Harder LD, Barclay RMR (1994) The Functional Significance of Poricidal Anthers and Buzz Pollination: Controlled Pollen Removal From *Dodecatheon*. *Funct Ecol* 8:509. <https://doi.org/10.2307/2390076>
- Harder LD, Prusinkiewicz P (2013) The interplay between inflorescence development and function as the crucible of architectural diversity. *Ann Bot* 112:1477–1493. <https://doi.org/10.1093/aob/mcs252>
- Hetherington-Rauth MC, Johnson MT (2020) Floral Trait Evolution of Angiosperms on Pacific Islands. *The American Naturalist*, 196, 87 - 100. <https://www.nybg.org/plant-research-and-conservation/collections-resources/>
- Jabbour F, Espinosa F, Dejonghe Q, Péchon T Le (2022) Development and Evolution of Unisexual Flowers: A Review. *Plants* 11
- Kassambara A, Mundt F (2020) Factoextra: extract and visualize the results of multivariate data analyses. R Package Version 107
- Koch L, Lunau K, Wester P (2017) To be on the safe site – Ungroomed spots on the bee's body and their importance for pollination. *PLoS One* 12:1–16. <https://doi.org/10.1371/journal.pone.0182522>
- Konzmann S, Hilgendorf F, Niester C, et al (2020) Morphological specialization of heterantherous *Rhynchanthera grandiflora* (Melastomataceae) accommodates pollinator diversity. *Plant Biol* 22:583–590. <https://doi.org/10.1111/plb.13102>
- Krick J, Ackerman JD (2015) Adding ecology to particle capture models: Numerical simulations of capture on a moving cylinder in crossflow. *J Theor Biol* 368:13–26. <https://doi.org/10.1016/j.jtbi.2014.12.003>
- Kriebel R, Drew BT, González-Gallegos JG, et al (2022) Stigma shape shifting in sages (*Salvia*: Lamiaceae): hummingbirds guided the evolution of New World floral features. *Botanical Journal of the Linnean Society*, 2022, 199, 428–448
- Lefebvre V, Villemant C, Fontaine C, et al. (2018) Altitudinal, temporal and trophic partitioning of flower-visitors in Alpine communities. *Sci Rep* 8, 4706 <https://doi.org/10.1038/s41598-018-23210-y>
- Letunic I, Bork P (2021). Interactive Tree Of Life (iTOL) v5: an online tool for phylogenetic tree display and annotation, *Nucleic Acids Research*, Volume 49 <https://doi.org/10.1093/nar/gkab301eractive>
- Lopes AVDFE, Machado ICS (1996) Biologia floral de *Swartia pickelii* Killip ex Ducke (Leguminosae-Papilionoideae) e sua polinização por *Eulaema* spp. (Apidae-Euglossini). *Rev Bras Botânica* 19:17–24
- Lunau K, Konzmann S, Winter L, et al (2017) Pollen and stamen mimicry: the alpine

- flora as a case study. *Arthropod Plant Interact* 11:427–447. <https://doi.org/10.1007/s11829-017-9525-5>
- Luo Z, Zhang D, Renner SS (2008) Why two kinds of stamens in buzz-pollinated flowers? Experimental support for Darwin's division-of-labour hypothesis. *Funct Ecol* 22:794–800. <https://doi.org/10.1111/j.1365-2435.2008.01444.x>
- Macior LW (1964) An experimental study of the floral ecology of *Dodecatheon meadia*. *Am J Bot* 51:96–108. <https://doi.org/10.1002/j.1537-2197.1964.tb06605.x>
- Mackin CR, Peña JF, Blanco MA, et al (2021) Rapid evolution of a floral trait following acquisition of novel pollinators. *J Ecol* 109:2234–2246. <https://doi.org/10.1111/1365-2745.13636>
- Maechler M, Rousseeuw P, Struyf A, Hubert M HK (2022) cluster: Cluster Analysis Basics and Extensions. R Package version 213
- Marazzi B, Conti E, Endress PK (2007) Diversity in Anthers and Stigmas in the Buzz - Pollinated Genus *Senna* (Leguminosae, Cassiinae). *Int J Plant Sci* 168:371–391
- Melo LRF, Vasconcelos T, Reginato M, et al (2021) Evolution of stamen dimetrisism in Melastomataceae, a large radiation of pollen flowers. *Perspect Plant Ecol Evol Syst* 48:125589. <https://doi.org/10.1016/j.ppees.2021.125589>
- Merran LM, Endress PK (2002) Comparative floral structure and systematics in Oxalidales (Oxalidaceae, Connaraceae, Brunelliaceae, Cephalotaceae, Cunoniaceae, Elaeocarpaceae, Tremandraceae). *Bot J Linn Soc* 140:321–381. <https://doi.org/10.1046/j.1095-8339.2002.00105.x>
- Nunes CEP, Nevard L, Montealegre-Z F, Vallejo-Marín M (2021) Variation in the natural frequency of stamens in six morphologically diverse, buzz-pollinated, heterantherous *Solanum* taxa and its relationship to bee vibrations. *Botanical Journal of the Linnean Society*, 197(4), 541-553.
- Nunes CEP, Vallejo-Marín M (2022) How Much Pollen Do Beelike Floral Vibrations Remove from Different Types of Anthers? *International Journal of Plant Sciences*, 183(9), 768-776.
- Oksanen J, Blanchet FG, Friendly M, et al (2019) Package 'vegan' Community ecology package, version, 2(9).
- Oliveira PEAM, Sazima M (1990) Pollination biology of two species of *Kielmeyera* (Guttiferae) from Brazilian cerrado vegetation. *Plant Syst Evol* 172:35–49. <https://doi.org/10.1007/BF00937796>
- Omland KE, Cook LG, Crisp MD (2008) Tree thinking for all biology: the problem with reading phylogenies as ladders of progress. *Bioessays* 30(9): 854-67. <https://doi.org/10.1002/bies.20794>
- Passos LS, Telles FJ, Goldenberg R, Amano E, Maia FR. 2022. What is the role of stamen appendages in the buzz-pollinated *Huberia insignis* (Melastomataceae)? *Flora*, 152113, ISSN 0367-2530. <https://doi.org/10.1016/j.flora.2022.152113>.
- Phillips RD, Peakall R, van der Niet T, Johnson SD (2020) Niche Perspectives on Plant-Pollinator Interactions. *Trends in plant science*, 25(8), 779–793. <https://doi.org/10.1016/j.tplants.2020.03.009>

- Pinheiro M, Brito VLG, Sazima M (2018) Pollination biology of melittophilous legume tree species in the Atlantic Forest in Southeast Brazil. *Acta Botanica Brasilica*, 32, 410-425.
- R Core Team (2020). R: A language and environment for statistical computing. R Foundation for
- Silberbauer-Gottsberger I, Webber AC, Küchmeister H, Gottsberger G (2001) Convergence in beetle-pollinated Central Amazonian Annonaceae, Araceae, Arecaceae, and Cyclanthaceae. *Life Forms Dyn. Trop. For.* 346:165–183
- Stäger R (1902) Chemischer Nachweis von Nektarien bei Pollenblumen und Anemophilen. *B B Z* 12:34–43
- Stebbins GL (1951) Natural Selection and the Differentiation of Angiosperm Families. *Soc Study Evol* 5:299–324
- Stebbins GL (1974) *Flowering Plants: Evolution Above the Species Level*. Harvard University Press, Cambridge, Mass.
- Stevens PF (2001 onwards). Angiosperm Phylogeny Website. Version 14, July 2017 [and more or less continuously updated since]. will do. <http://www.mobot.org/MOBOT/research/APweb/.7>
- Tanaka N, Uehara K, Murata J (2004) Correlation between pollen morphology and pollination mechanisms in the Hydrocharitaceae. *J Plant Res* 117:265–276. <https://doi.org/10.1007/s10265-004-0155-5>
- Taylor ML, Altrichter KM, Aeilts LB (2018) Pollen ontogeny in *Ruppia* (Alismatidae). *Int J Plant Sci* 179:217–230. <https://doi.org/10.1086/696535>
- Telles FJ, Klunk CL, Maia FR da, et al (2020) Towards a new understanding of the division of labour in heterantherous flowers: The case of *Pterolepis glomerata* (Melastomataceae). *Biol J Linn Soc* 131:1–11. <https://doi.org/10.1093/biolinnean/blaa107>
- Tibshirani R, Walther G, Hastie T (2001) Estimating the number of clusters in a data set via the gap statistic. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 63(2), 411-423.
- Timerman D, Barrett SCH (2018) Divergent selection on the biomechanical properties of stamens under wind and insect pollination. *Proc R Soc B Biol Sci* 285:. <https://doi.org/10.1098/rspb.2018.2251>
- Trunschke J, Lunau K, Pyke GH, et al (2021) Flower Color Evolution and the Evidence of Pollinator-Mediated Selection. *Front Plant Sci* 12:1–20. <https://doi.org/10.3389/fpls.2021.617851>
- Vallejo-Marín M (2019) Evolutionary tinkering allows buzz pollinated plants to escape from an adaptive dead-end. *New Phytol* 221:618–620. <https://doi.org/10.1111/nph.15474>
- Vallejo-Marín M, Da Silva EM, Sargent RD, Barrett SCH (2010) Trait correlates and functional significance of heteranthery in flowering plants. *New Phytol* 188:418–425. <https://doi.org/10.1111/j.1469-8137.2010.03430.x>
- Vallejo-Marín M, Manson JS, Thomson JD, Barrett SCH (2009) Division of labour

- within flowers: Heteranthery, a floral strategy to reconcile contrasting pollen fates. *J Evol Biol.* <https://doi.org/10.1111/j.1420-9101.2009.01693.x>
- van der Pijl L. (1961) Ecological aspects of flower evolution. II. Zoophilous flower classes. *Evolution* (N Y) 15:44–59
- Velloso MSC, Brito VLG, Caetano APS, Romero R (2018) Anther specializations related to the division of labor in *Microlicia cordata* (Spreng.) Cham. (Melastomataceae). *Acta Bot Brasilica* 32:349–358. <https://doi.org/10.1590/0102-33062017abb0358>
- Vogel S (1954) Blütenbiologische Typen als Elemente der Sippengliederung, dargestellt anhand der Flora Südafrikas. *Bot Stud* 1:1–338
- Vogel S (1978) Evolutionary shifts from reward to deception in pollen flowers. *Pollinat. Flowers by Insects* 89–96
- Watson and Dallwitz (1992) onwards. The families of flowering plants: descriptions, illustrations, identification, and information retrieval. Version: 25th July 2023
- Werth E (1956) *Bau und Leben der Blumen*. Stuttgart Enke
- Westerkamp C (1996) Pollen in Bee-Flower Relations Some Considerations on Melittophily*. *Bot Acta* 109:325–332. <https://doi.org/10.1111/j.1438-8677.1996.tb00580.x>
- Wickham et al. (2019) Welcome to the Tidyverse. *J Open Source Softw* 4:. <https://doi.org/https://doi.org/10.21105/joss.01686>
- Wickham H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4. <https://ggplot2.tidyverse.org>.
- Wolowski M, Freitas L (2015) An overview on pollination of the Neotropical Poales. *Rodriguesia* 66:329–336. <https://doi.org/10.1590/2175-7860201566204>

Supplementary information

Table SI 1 – List of species or genera analyzed within each family considering traits proposed by Vogel.

Orders	Families	Genus	Species	Author	pollen flower type	Dehiscence anthers	Pollen release	Pollinator	Visitors behaviour	Pollinati on type	Number of stamens	Reference
Ericales	Actinidiaceae	<i>Saurauia</i>		Willd.	papaver	poricidal		bees	buzz	biotic	10 to 100	Cane, 1993
Caryophyllales	Aizoaceae	<i>Sesuvium</i>	<i>Sesuvium portulacastrum</i>	L.	papaver	longitudinal	exposed	bees	forage	biotic	6 to 120	Percival, 1974
Magnoliales	Annonaceae	<i>Annona</i>	<i>Annona squamosa</i>	L.	magnolian	longitudinal	shed	beetles	actively eat	biotic	25 to 100	Kishore et al., 2012
Alismatales	Araceae	<i>Philodendron</i>	<i>Philodendron bipinnatifidum</i>	Schott	magnolian	poricidal	shed	beetles	actively eat	biotic	1 to 12	Pellmyr & Patt, 1986
Austrobaileyales	Austrobaileyaceae	<i>Austrobaileya</i>	<i>Austrobaileya scandens</i>	White	new	longitudinal	shed	flies	actively eat	biotic	12 to 25	Endress, 1986
Cucurbitales	Begoniaceae	<i>Begonia</i>	<i>Begonia integerrima</i>	Spreng.	papaver	poricidal	small portion	bees	buzz	biotic	4 to 100	Wyatt & Sazima, 2011
Malvales	Bixaceae	<i>Bixa</i>	<i>Bixa orellana</i>	L.	solanum	poricidal	small portion	bees	buzz	biotic	50 to 150	Rocha & Polatto, 2017
Lamiales	Byblidaceae	<i>Byblis</i>	<i>Byblis gigantea</i>	Lindl.	new	poricidal		bees		biotic	5	Conran et al., 2002
Caryophyllales	Cactaceae	<i>Opuntia</i>			papaver		exposed	bees	forage	biotic	15 to 100	Osborn et al., 1986
Lamiales	Calceolariaceae	<i>Calceolaria</i>	<i>Calceolaria comulcana</i>	C.Romero, Bussmann & Puppo	new			bees		biotic		Romero-Hernández et al., 2017
Canellalles	Canellaceae	<i>Cinnamodendron</i>	<i>Cinnamodendron dinisii</i>	Schwacke	new	longitudinal		bees		biotic		Diniz & Buschini, 2015
Canellalles	Canellaceae	<i>Canella</i>			new	longitudinal						Erbar, 2014
Chloranthales	Chloranthaceae	<i>Chloranthus</i>	<i>Chloranthus serratus</i>	Thunb.	new	longitudinal		thrips		biotic		Yi-Bo & Zhen-Yu, 1999
Chloranthales	Chloranthaceae	<i>Chloranthus</i>	<i>Chloranthus fortunei</i>	A. Gray	new	longitudinal		thrips		biotic		Yi-Bo & Zhen-Yu, 1999
Ranunculales	Circaeasteraceae	<i>Circaeaster</i>	<i>Circaeaster agrestis</i>	Maxim.	new	longitudinal				biotic	1 to 2	Susan W. Nicolson, Massimo Nepi p61; 2008
Malvales	Cistaceae	<i>Cistus</i>	<i>Cistus salvifolius</i>	L.	papaver	longitudinal	exposed	bees	forage	biotic	3 to 100	Nansen & Korie, 2000
Ericales	Clethraceae	<i>Clethra</i>	<i>Clethra alnifolia</i>	L.	new	longitudinal		bees		biotic	10	Martínez et al., 2016
Ericales	Clethraceae	<i>Rariglanda</i>	<i>Rariglanda jerseyensis</i>	Martinez & Choo	new			bees		biotic		Martínez et al., 2017
Commelinales	Commelinaceae	<i>Murdannia</i>	<i>Murdannia nudiflora</i>	(L.) Brenan	solanum	poricidal	small portion	bees		biotic	1 to 6	Veena & Nampy, 2019
Commelinales	Commelinaceae	<i>Dichorisandra</i>	<i>Dichorisandra thyrsiflora</i>	J.C.Mikan	solanum	poricidal		bees	buzz	biotic		Russel et al., 2015
Liliales	Corsiaceae	<i>Corsia</i>		Becc.	new	longitudinal		fly/fungi		biotic	6	Mennes et al., 2015
Pandanales	Cyclanthaceae	<i>Cyclanthus</i>	<i>Cyclanthus bipartitus</i>	Poit. ex A. Rich.	new	longitudinal		beetles		biotic	10 to 150	Silberbauer-Gottsberger et al., 2001

Poales	Cyperaceae	<i>Rhynchospora</i> <i>a</i>	<i>Rhynchospora ciliata</i>	(Vahl) Kukenth	new	longitudinal		bees; wind		biotic and abiotic	3 to 22	Costa; 2017
Magnoliales	Degeneriaceae	<i>Degeneria</i>		I.W. Bailey & A.C.Sm.	magnolian	longitudinal	shed	beetles		biotic	30 to 50	Erbar, 2014
Dilleniales	Dilleniaceae	<i>Hibbertia</i>	<i>Hibbertia fasciculata</i>	R.Br. ex D C.	solanum	poricidal	small portion	insects	buzz	biotic	15 to 150	Bernhardt, 1986
Dilleniales	Dilleniaceae	<i>Hibbertia</i>	<i>Hibbertia cistiflora</i>	N.A.Wakef .	solanum	poricidal		bees	buzz	biotic		Russel et al., 2015
Oxalidales	Elaeocarpaceae	<i>Sloanea</i>		L.	new	poricidal	small portion	bees	buzz	biotic	12 to 100	Matthews & Endress 2002
Oxalidales	Elaeocarpaceae	<i>Tetralthea</i>		Sm.	solanum	poricidal		bees	buzz	biotic		Russel et al., 2015
Ericales	Ericaceae	<i>Conostephium</i> <i>m</i>		Benth.	new	poricidal		bees	buzz	biotic	8 to 10	Houston & Ladd, 2002
Ericales	Ericaceae	<i>Sprengelia</i>	<i>Sprengelia incarnata</i>	Sm.	new	poricidal		bees	buzz	biotic		Jonhson & McQuillan, 2011
Malpighiales	Euphorbiaceae	<i>Dalechampia</i>			new	poricidal	small portion	bees	buzz	biotic	1 to 1000	Armbruster et al, 2012
Magnoliales	Eupomatiaceae	<i>Eupomatia</i>	<i>Eupomatia laurina</i>	R.Br.	magnolian	longitudinal	shed	beetles		biotic	25 to 100	Erbar, 2014
Fabales	Fabaceae	<i>Swartzia</i>	<i>Swartzia apetala</i>	Raddi	solanum	longitudinal		bees	buzz	biotic		Moço & Pinheiro, 1999
Fabales	Fabaceae	<i>Cassia</i>	<i>Cassia alata</i>	L.	solanum	poricidal		bees	buzz	biotic		Zafar & Raju, 2006
Fabales	Fabaceae	<i>Senna</i>	<i>Senna multijuga</i>	Rich.	new	poricidal	small portion	bees	buzz	biotic		Wolowski & Freitas, 2010
Fabales	Fabaceae	<i>Chamaecrista</i>	<i>Chamaecrista desvauxii</i>	Collad.	new	poricidal	small portion	bees	buzz	biotic		Nogueira et al 2018
Fabales	Fabaceae	<i>Acacia</i>	<i>Acacia retinodes</i>	Schltldl.	papaver	longitudinal		bees	buzz	biotic		Bernhardt et al., 1984
Gentianales	Gentianaceae	<i>Exacum</i>	<i>Exacum affine</i>	Balf. f.	solanum	poricidal	small portion	bees	buzz	biotic	4 to 12	Russel et al., 2015
Lamiales	Gesneriaceae	<i>Ramonda</i>	<i>Ramonda myconi</i>	(L.) Rchb.	solanum	poricidal		bees		biotic	2 to 5	Harder & Barclay, 1994
Laurales	Gomortegaceae	<i>Gomortega</i>	<i>Gomortega nitida</i>	Ruiz & Pavon	new	longitudinal		Syrphids		biotic	5 to 10	Heo et al., 2004
Magnoliales	Himantandraceae	<i>Galbulimima</i>	<i>Galbulimima baccata</i>	F.M.Bailey	magnolian	longitudinal		beetles		biotic		Erbar, 2014
Magnoliales	Himantandraceae	<i>Galbulimima</i>	<i>Galbulimima belgraveana</i>	(F.Muell.) Sprague	magnolian	longitudinal		beetles		biotic		Erbar, 2014
Piperales	Hydnoraceae	<i>Hydnora</i>	<i>Hydnora africana</i>	Thunb.	new	longitudinal		beetles	actively eat	biotic	3 to 10	Bolin et al., 2009
Alismatales	Hydrocharitaceae	<i>Egeria</i>	<i>Egeria densa</i>	Planch.	new	longitudinal		insects		biotic	4 to 100	Tanaka et al., 2004
Alismatales	Hydrocharitaceae	<i>Blyxa</i>	<i>Blyxa japonica</i>	Maxim. ex Asch. & Gürke	new	longitudinal		insects		biotic		Tanaka et al., 2004
Alismatales	Hydrocharitaceae	<i>Ottelia</i>	<i>Ottelia alismoides</i>	(L.) Pers.	new	longitudinal		insects		biotic		Tanaka et al., 2004
Alismatales	Hydrocharitaceae	<i>Stratiotes</i>	<i>Stratiotes aloides</i>	L.	new	longitudinal		insects		biotic		Tanaka et al., 2004
Alismatales	Hydrocharitaceae	<i>Hydrocharis</i>	<i>Hydrocharis dubia</i>	Backer	new	longitudinal		insects		biotic		Tanaka et al., 2004

Malpighiales	Hypericaceae	<i>Hypericum</i>	<i>Hypericum roeperianum</i>	G.W.Schim p. ex A.Rich.	papaver		exposed	bees	forage	biotic		Bartos̃ et al., 2015
Asparagales	Hypoxidaceae	<i>Hypoxis</i>	<i>Hypoxis camerooniana</i>	Baker	solanum	longitudinal	small portion	bees; flies	buzz	biotic	4 to 6	http://floradobrasil.jbrj.gov.br/
Asparagales	Iridaceae	<i>Ixia</i>	<i>Ixia scillaris</i>	L.	new							Goldblatt et al 2000
Alismatales	Juncaginaceae	<i>Tetroncium</i>		Willd.	new	longitudinal		wind		abiotic	3 to 8	Watson & Dallwitz, 1992
Ericales	Lecythidaceae	<i>Gustavia</i>	<i>Gustavia augusta</i>	L.	new	poricidal		bees	buzz	biotic	40 to 1000	Mori & Cornejo, 2013
Myrtales	Lythraceae	<i>Lagerstroemia</i>	<i>Lagerstroemia indica</i>	L.	solanum	longitudinal	exposed	bees	forage	biotic	4 to 35	Odintsova, 2008
Magnoliales	Magnoliaceae	<i>Liriodendron</i>	<i>Liriodendron chinense</i>	(Hemsl.) S arg.	magnolian	longitudinal	shed	beetles; bees, bumblebees	actively eat	biotic	50 to 200	Erbar, 2014
Magnoliales	Magnoliaceae	<i>Liriodendron</i>	<i>Liriodendron tulipifera</i>	L.	magnolian	longitudinal		beetles; bees, bumblebees		biotic		Erbar, 2014
Magnoliales	Magnoliaceae	<i>Magnolia</i>	<i>Magnolia grandiflora</i>	L.	magnolian	longitudinal		beetles		biotic		Erbar, 2014
Malpighiales	Malpighiaceae	<i>Hiptage</i>		Gaertn.	solanum			bees		biotic	10	Davis & Anderson, 2010
Malvales	Malvaceae	<i>Apeiba</i>		Aubl.	solanum			bees	buzz	biotic	5 to 100	Brunken et al., 2012
Malvales	Malvaceae	<i>Keraudrenia</i>	<i>Keraudrenia velutina</i>	Steetz.	solanum	poricidal		bees	buzz	biotic		Russel et al., 2015/ Faegri 1986
Malvales	Malvaceae - Tiliaceae	<i>Sparmannia</i>	<i>Sparmannia africana</i>	L.f.	solanum					biotic		vogel, 1978
Myrtales	Melastomataceae	<i>Rhynchanthera</i>	<i>Rhynchanthera grandiflora</i>	DC.	new	poricidal	small portion	bees	buzz	biotic	4 to 100	konzmann et al „2020
Myrtales	Melastomataceae	<i>Pleroma</i>	<i>Pleroma raddianum</i>	Triana	solanum	poricidal		bees	buzz	biotic		Pereira et al, 2011
Myrtales	Melastomataceae	<i>Osbeckia</i>	<i>Osbeckia wynaadensis</i>	C. B. Clarke	solanum	poricidal	small portion	bees	buzz	biotic		Simi 2018
Myrtales	Melastomataceae	<i>Rhexia</i>	<i>Rhexia virginica</i>	L.	solanum	poricidal	small portion	bees	buzz	biotic		Larson & Barrett, 1999
Myrtales	Melastomataceae	<i>Meriania</i>	<i>Meriania longifolia</i>	(Naudin) Cogn.	solanum	poricidal	small portion	bees	buzz	biotic		Delinger et al 2019
Myrtales	Melastomataceae	<i>Clidemia</i>	<i>Clidemia capitellata</i>	(Bonpl.) D. Don	new	poricidal	small portion	bees	buzz	biotic		Melo et al., 1999
Myrtales	Melastomataceae	<i>Trembleya</i>	<i>Trembleya laniflora</i>	Cong.	solanum	poricidal	small portion	bees	buzz	biotic		Soares & Morellato, 2016
Myrtales	Melastomataceae	<i>Melastoma</i>	<i>Melastoma malabathricum</i>	L.	solanum	poricidal	small portion	bees	buzz	biotic		Luo et al., 2008
Ranunculales	Menispermaceae			Juss.	new	longitudinal		insects		biotic	1 to 40	Kessler, 1993.
Laurales	Monimiaceae	<i>Wilkiea</i>	<i>Wilkiea huegeliana</i>	(Tul.) A.DC.	new	longitudinal		thrips		biotic	10 to 150	Williams et al., 2001
Magnoliales	Myristicaceae	<i>Myristica</i>		Gronov.	magnolian	longitudinal	shed	beetles	actively eat	biotic	2 to 30	Erbar, 2014
Ericales	Myrsinaceae	<i>Ardisia</i>	<i>Ardisia elliptica</i>	Thumb.	solanum			bees	buzz	biotic	3 to 6	Yong et al., 2019
Myrtales	Myrtaceae	<i>Eugenia</i>	<i>Eugenia uniflora</i>	L.	new	longitudinal		bees		biotic	4 to 150	Diniz & Buschini, 2016
Myrtales	Myrtaceae	<i>Myrcia</i>	<i>Myrcia multiflora</i>	DC.	new	poricidal		bees	buzz	biotic		Fidalgo & Kleinert, 2009

Myrtales	Myrtaceae	<i>Gomidesia</i>	<i>Gomidesia schaueriana</i>	O.Berg.	new	poricidal		bees	buzz	biotic		Fidalgo & Kleinert, 2009
Myrtales	Myrtaceae	<i>Blepharocalyx</i>	<i>Blepharocalyx salicifolius</i>	(Kunth) O.Berg.	new	poricidal		bees	buzz	biotic		Proença & Gibbs, 1994
Nymphaeales	Nymphaeaceae	<i>Nymphaea</i>	<i>Nymphaea pubescens</i>	Willd.	magnolian	longitudinal	shed	insects	actively eat	biotic	40 to 80	Bhunja & Mondal, 2012
Nymphaeales	Nymphaeaceae	<i>Nymphaea</i>	<i>Nymphaea nouchali</i>	Burm.f.	magnolian	longitudinal	shed	insects	actively eat	biotic	40 to 80	Bhunja & Mondal, 2012
Nymphaeales	Nymphaeaceae	<i>Nymphaea</i>	<i>Nymphaea stellata</i>	Willd.	magnolian	longitudinal	shed	insects	actively eat	biotic	40 to 80	Bhunja & Mondal, 2012
Nymphaeales	Nymphaeaceae	<i>Nymphaea</i>	<i>Nymphaea pulchella</i>	DC.	magnolian		shed	bee	actively eat	biotic	40 to 80	Chalegre et al., 2020
Nymphaeales	Nymphaeaceae	<i>Nymphaea</i>	<i>Nymphaea rubra</i>	Roxb. ex Andrews	magnolian	longitudinal	shed	insects	actively eat	biotic		Bhunja & Mondal, 2012
Malpighiales	Ochnaceae	<i>Sauvagesia</i>		L.	new	poricidal	small portion	bees	buzz	biotic	10 to 100	Nadia & Machado, 2005
Malpighiales	Ochnaceae	<i>Rhabdophyllum</i>		Tiegh.	new	poricidal		bees	buzz	biotic		Schneider et al, 2014
Malpighiales	Ochnaceae	<i>Ouratea</i>		Aulb.	solanum	poricidal		bees	buzz	biotic		Schneider et al, 2014
Malpighiales	Ochnaceae	<i>Idertia</i>		Farron	new	poricidal		bees	buzz	biotic		Schneider et al, 2014
Malpighiales	Ochnaceae	<i>Campylospermum</i>		Tiegh.	new	poricidal		bees	buzz	biotic		Schneider et al, 2014
Malpighiales	Ochnaceae	<i>Luxemburgia</i>		A.St.-Hil.	solanum	poricidal		bees	buzz	biotic		Schneider et al, 2014
Malpighiales	Ochnaceae	<i>Philacra</i>		Dwyer	new	poricidal		bees	buzz	biotic		Matthews et al 2012
Pandanales	Pandanaceae	<i>Freycinetia</i>		Gaudich.	new	longitudinal		vertebrate		biotic	10 to 100	Cox, 1990
Pandanales	Pandanaceae	<i>Pandanus</i>		Parkinson	new	longitudinal		wind		abiotic		Cox, 1990
Pandanales	Pandanaceae	<i>Sararanga</i>		Hemsl.	new	longitudinal		insect		biotic		Cox, 1990
Pandanales	Pandanaceae	<i>Scisphila</i>	<i>Sciaphila nana</i>	Blume	new	longitudinal		fly		biotic		Funamoto, 2019
Ranunculales	Papaveraceae				papaver	longitudinal	exposed	bees		biotic	16 to 200	Yang et al., 2019
Ericales	Pentaphragaceae	<i>Ternstroemia</i>	<i>Ternstroemia laevigata</i>	Wawra	new	longitudinal		bees	buzz	biotic	5	Bittrich et al., 1993
Commelinales	Philydraceae	<i>Helmholtzia</i>	<i>Helmholtzia acorifolia</i>	F.Muell.	solanum	longitudinal		insects		biotic	1	Nicolson, Nepi 2007
Piperales	Piperaceae	<i>Peperomia</i>			new	longitudinal		hoverflies, bees and beetles		biotic	1 to 10	Erbar, 2014
Poales	Poaceae	<i>Merostachys</i>	<i>Merostachys riedeliana</i>	Rupr. ex Döll	new	longitudinal		insects		biotic		Wolowski & Feitras, 2016
Alismatales	Posidoniaceae	<i>Posidonia</i>	<i>Posidonia australis</i>	J.D.Hooker	new	longitudinal		water		abiotic	3	Sinclair et al., 2014
Alismatales	Potamogetonaceae	<i>Althenia</i>	<i>Althenia orientalis</i>	(Tzvelev) Garcia-Mur. & Talavera	new	longitudinal		water		abiotic	4	Severova et al., 2019
Ericales	Primulaceae	<i>Dodecatheon</i>		(L.) A.R.Mast & Reveal	new			bees	buzz	biotic	3 to 9	Harder & Barclay, 1994

Ericales	Primulaceae	<i>Cyclamen</i>		L.	new			bees	buzz	biotic		Mast & Reveal, 2007
Ericales	Primulaceae	<i>Lysimachia</i>		L.	new			bees	buzz	biotic		Anderberg et al., 2007
Ranunculales	Ranunculaceae	<i>Anemone</i>	<i>Anemone pavonina</i>	Lam.	papaver	longitudinal		beetles; bees		biotic	15 to 100	Streinz et al., 2019
Ranunculales	Ranunculaceae	<i>Thalictrum</i>		L.	papaver	longitudinal		wind, small insects		biotic and abiotic		Wang et al., 2019
Poales	Rapateaceae	<i>Cephalostemon</i>	<i>Cephalostemon riedelia</i>	Körn.	solanum	poricidal	small portion	bees	buzz	biotic	6	Wolovski & Feitras, 2015; Russel et al., 2015
Caryophyllales	Rhabdodendraceae	<i>Rhabdodendron</i>	<i>Rhabdodendron macrophyllum</i>	(Spruce ex Benth.) Huber	new	longitudinal		bees		biotic		Nelson & Prance, 1984
Alismatales	Ruppiaceae	<i>Ruppia</i>		L.	new	longitudinal		water		abiotic	2	Taylor et al., 2018
Piperales	Saururaceae	<i>Saururus</i>	<i>Saururus chinensis</i>	(Lour.) Baill.	new	longitudinal		wind and insects		biotic and abiotic	3 to 8	Erbar, 2014; Tanaka, 1979
Alismatales	Scheuchzeriaceae	<i>Scheuchzeria</i>	<i>Scheuchzeria palustris</i>	L.	new	longitudinal		wind		abiotic	6	Volkova et al., 2016
Austrobaileyales	Schisandraceae (Illiciaceae)	<i>Illicium</i>	<i>Illicium floridanum</i>	Ellis	new	longitudinal	shed	beetles	actively eat	biotic	4 to 80	Thien et al., 1983
Austrobaileyales	Schisandraceae (Illiciaceae)	<i>Illicium</i>	<i>Illicium micranthum</i>	Dunn.	new	longitudinal	shed	beetles	actively eat	biotic	5 to 80	Thien et al., 1983
Austrobaileyales	Schisandraceae (Illiciaceae)	<i>Illicium</i>	<i>Illicium anisistrum</i>	L.	new	longitudinal	shed	beetles	actively eat	biotic	6 to 80	Thien et al., 1983
Laurales	Siparunaceae	<i>Siparuna</i>	<i>Siparuna guianensis</i>	Aublet	new	longitudinal		flies; gall insects		biotic	2 to 100	Renner et al., 1997
Solanales	Solanaceae	<i>Solanum</i>		L.	solanum	poricidal	small portion	bees	buzz	biotic	5	Vallejo-Marín, 2019
Solanales	Solanaceae	<i>Lycianthes</i>		(Dunal) Hassl.	new	poricidal		bees	buzz	biotic		Smith & Knapp, 2002
Dioscoreales	Taccaceae	<i>Tacca</i>		J.R.Forst. & G.Forst.	new	longitudinal		insects		biotic	6	Watson & Dallwitz, 1992
Asparagales	Tecophilaeaceae	<i>Cyanella</i>		D.Royen	new	poricidal	small portion	bees	buzz	biotic	3 to 6	Dulberger & Ornduff, 1980
Asparagales	Tecophilaeaceae	<i>Conanthera</i>	<i>Conanthera bifolia</i>		new	poricidal		bees	buzz	biotic		Russel et al., 2015
Ericales	Theaceae	<i>Ternstroemia</i>		Mutis ex L.f.	new	longitudinal		bees	buzz	biotic	5 to 100	Bittrich et al., 1993
Austrobaileyales	Trimeniaceae	<i>Trimenia</i>	<i>Trimenia moorei</i>	Oliv.	new	longitudinal	shed	flies; bees	actively eat	biotic	7 to 23	Bernhardt et al., 2003
Canellales	Winteraceae	<i>Drimys</i>	<i>Drimys angustifolia</i>	Miers	new	longitudinal	shed	beetles, flies, thrips	actively eat	biotic	15 to 100	Endress, 2010; Erbar, 2014
Alismatales	Zosteraceae	<i>Zostera</i>	<i>Zostera marina</i>	L.	new	longitudinal		water		abiotic	1	Ackerman, 1997

Hydrocharitaceae	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0
Hypericaceae	1	0	0	0	1	1	0	1	1	1	0	0	1	1	0
Hypoxidaceae	3	0	0	1	0	0	0	1	1	0	0	0	1	0	0
Iridaceae	3	1	0	1	0	0	0	0	1	0	1	0	1	0	0
Juncaginaceae	2	0	0	0	1	0	0	1	0	0	0	1	0	0	0
Lecythidaceae	3	1	0	1	0	1	0	0	0	0	1	0	1	1	0
Lytraceae	1	0	0	0	1	1	1	1	0	1	1	0	1	0	0
Magnoliaceae	1	0	1	0	0	1	0	0	0	1	1	0	1	0	1
Malpighiaceae	3	1	0	1	0	0	1	1	1	0	1	0	0	0	1
Malvaceae	3	1	0	1	0	0	0	1	1	0	1	0	1	0	1
Mayaceae	3	1	0	1	0	0	0	0	0	0	1	0	1	0	0
Melastomataceae	3	1	0	1	0	0	1	1	0	0	1	0	1	0	1
Menispermaceae	2	0	0	0	1	0	0	1	0	0	0	0	1	0	0
Monimiaceae	1	0	0	0	1	1	0	1	0	0	1	1	1	0	0
Myristicaceae	2	0	1	0	0	1	0	1	0	0	0	0	0	0	0
Myrsinaceae	3	0	0	0	1	0	0	1	1	0	1	0	1	0	0
Myrtaceae	1	1	0	0	1	1	0	1	0	1	0	1	1	0	0
Nymphaeaceae	1	0	1	0	0	1	0	0	0	0	1	0	1	1	1
Ochnaceae	3	1	0	1	0	1	0	1	1	0	0	0	1	0	0
Pandanaceae	2	0	1	0	0	1	0	1	0	0	0	1	0	0	0
Papaveraceae	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0
Pentaphragaceae	1	0	0	0	1	1	0	1	0	0	0	0	1	0	0
Philydraceae	2	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Piperaceae	2	0	1	0	0	1	0	1	0	0	0	1	0	0	0
Pittosporaceae	3	1	0	1	0	0	0	0	0	0	1	0	0	0	0
Poaceae	2	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Pontederiaceae	3	1	0	1	0	0	1	1	0	0	1	0	1	0	0
Posidoniaceae	2	0	1	0	0	0	0	1	0	0	0	1	0	0	0
Potamogetonaceae	2	0	0	0	1	0	0	1	0	0	0	1	0	0	0
Primulaceae	3	1	0	1	0	0	0	0	1	0	0	0	0	0	0
Ranunculaceae	1	0	0	0	1	1	0	0	0	1	1	0	1	0	1
Rapateaceae	3	1	0	1	0	0	0	0	0	0	0	0	1	0	0
Ruppiaceae	2	0	0	0	1	0	0	0	0	0	0	1	0	0	0

Saururaceae	2	0	0	0	1	1	0	1	0	0	0	1	0	0	0
Scheuchzeriaceae	2	0	0	0	1	0	0	1	0	0	0	1	1	0	0
Schisandraceae	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1
Siparunaceae	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Solanaceae	3	1	0	1	0	0	0	0	1	0	1	0	1	0	0
Taccaceae	2	0	0	0	1	0	0	1	1	0	0	1	1	0	0
Tecophilaeaceae	3	1	0	1	0	0	0	0	1	0	1	0	1	0	0
Theaceae	1	0	0	0	1	0	0	0	0	1	1	0	1	0	0
Trimeniaceae	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0
Winteraceae	1	0	1	0	0	1	0	0	0	0	1	0	1	0	1
Zosteraceae	2	0	0	0	1	0	0	1	0	0	0	1	0	0	0

Chapter 2

Stamen Diversity in Melastomataceae: Morphology, Color, and Function

Stamen Diversity in Melastomataceae: Morphology, Color, and Function

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Abstract

Melastomataceae stand out for their great variability of stamen traits. Most species in the family rely on pollen as the sole reward for pollinators and adaptations associated with this strategy render the family an excellent model group to explore the interactions between pollinators and stamen morphology, color and function through evolutionary time. In this chapter, we summarize in a functional and evolutionary context what is known about morphological diversity, color patterns, and stamen specialization within Melastomataceae. First, we cover information on anther morphology, including dehiscence types, presence or absence of pedoconnectives, appendages, oil-glands, trichomes and rostrum. Then, we discuss variability in stamen shape and length, and their potential functional role in reproduction. Finally, the general role of stamen traits in dividing the pollen load between plant reproduction and pollinator reward, as well as alternative strategies, is explored as an adaptive explanation for the stamen diversity in Melastomataceae.

Keywords: Appendages, dehiscence, dimorphism, heteranthery, pedoconnective, rostrum, secretory structures.

Introduction

Melastomataceae present a large diversity in stamen traits. In this family, stamens display a striking variation in size, shape, color, dehiscence type and presence (or absence) of connective extensions and appendages (Fig. 1). In fact, by using statistical tests on floral disparity (i.e., morphological diversity), Dellinger et al. (2019c) have shown that the androecium is significantly more disparate than the other floral organs in the group. For that reason, stamens have had a key role in studies of floral evolution (Caetano et al. 2020; Melo et al. 2021), diversification patterns (Goldenberg et al. 2008; Reginato and Michelangeli 2016; Dellinger et al. 2021a), pollination ecology (Luo et al. 2008; Dellinger et al. 2014; Brito et al. 2016; Dellinger et al. 2019a; Dellinger et al. 2019b; Dellinger et al. 2019c; Konzmann et al. 2020; Telles et al. 2020), reproductive biology (Luo et al. 2009; Santos et al. 2012; Brito et al. 2017; Velloso et al. 2018; Oliveira et al. 2020) and systematics (Goldenberg et al. 2012; Da Rocha et al. 2017; Fontelas and Romero 2020) in the family.

The high morphological variability has traditionally been interpreted as an adaptive response to selective pressures imposed by pollinators. Most of Melastomataceae flowers produce pollen as the only reward available to their pollinators and this creates a conflicting demand between producing pollen grains to reward pollinators and for sexual reproduction (Luo et al. 2008). This “pollen dilemma” (Lunau et al. 2015) is behind some of the most characteristic traits of Melastomataceae stamens, such as poricidal anthers and stamen dimorphism (e.g., Oliveira et al. 2020; Melo et al. 2021). In addition, most species of Melastomataceae are pollinated by bees that are able to vibrate their thoracic muscles during pollen collection, a mechanism called buzz pollination (Buchmann 1983; Vallejo-Marin 2019).

Certain stamen specializations also characterize the small but still significant number of species in the family that present other pollination strategies, such as species of Merianieae and Pyxidanthaeae that produce nectar and are pollinated by vertebrates (Lumer 1980; Dellinger et al. 2019b). (see more in Chapter 26 of this book). Finally, shifts from specialist to generalist pollination systems may also affect the morphology of stamens, as in the case of some species in Miconieae where anthers have large openings associated with non-vibratory small insects (e.g., Goldenberg et al. 2008; Kriebel and Zumbado 2014; Brito et al. 2016; Gavrutenko et al. 2020).

In addition to their role in the ecology and evolution of Melastomataceae species, variations in stamens color and morphology can also be important diagnostic characters in taxonomic studies of the family (Fig. 2). Stamen's traits play a key role in identifying and differentiating family members at the level of tribes, genera and species (e.g., Goldenberg et al. 2008; Penneys and Judd 2011; Michelangeli et al. 2013; Reginato and Michelangeli 2016; Goldenberg et al. 2016; Da Rocha et al. 201; Bacci et al. 2020) (see more in Section II). In this chapter, we will discuss and summarize what is known about morphological diversity and color patterns of stamens within Melastomataceae, in a functional and evolutionary context.

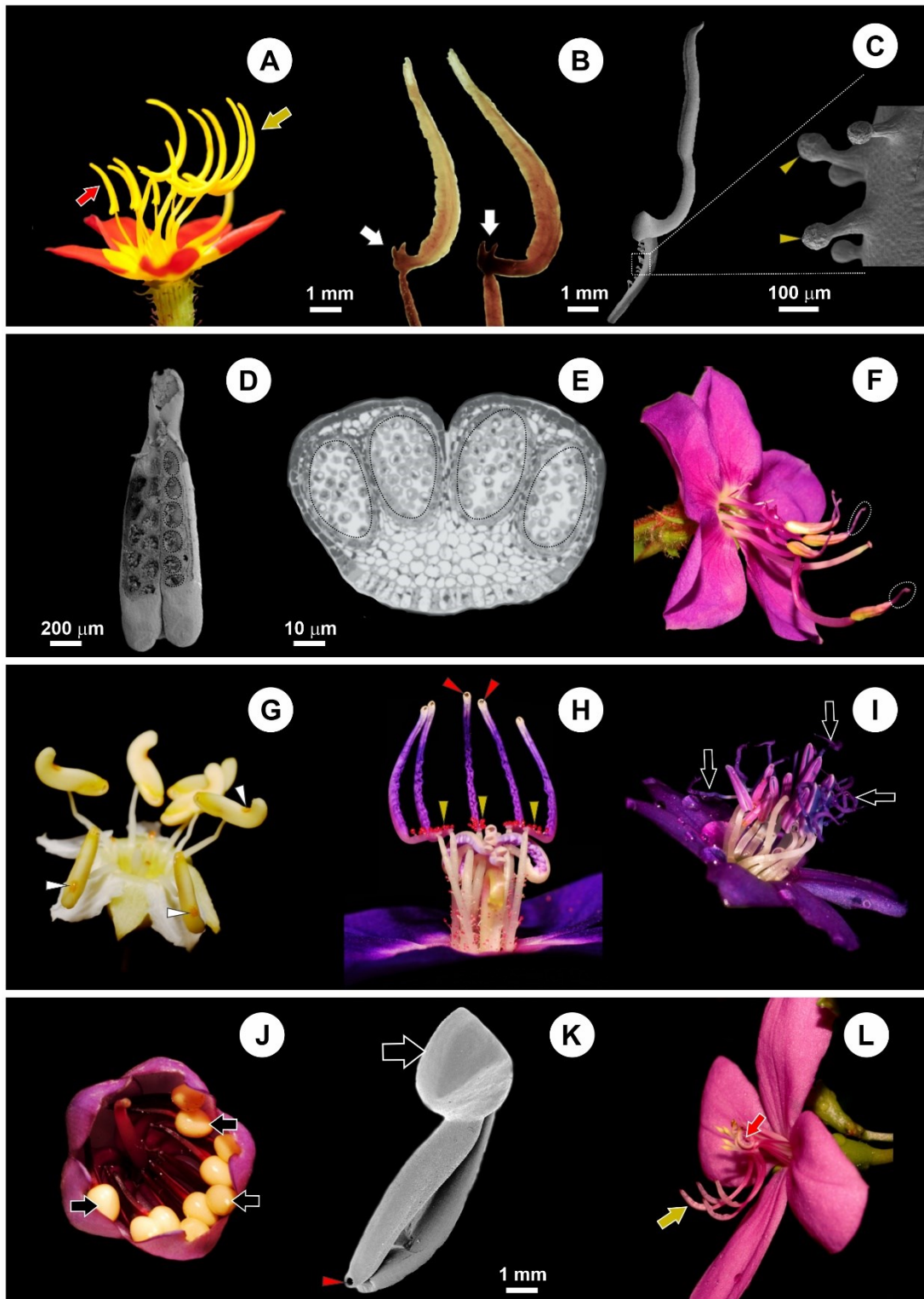


Figure 1. A. Flower of *Cambessedesia hilariana*, showing the dimetric stamens with the feeding (red arrow) and pollination (yellow arrow) stamens; B. Stamens of *Comolia vernicosa*. White arrows indicate ventral staminal appendages; C. Stamen of *Macairea radula*, evidencing the staminal glands (yellow arrowheads); D. Ventral view of the stamen of *Microlicia insignis*, showing the multiple sporangia (dotted lines); E. Transverse section of the anther of *Miconia fallax*, evidencing the four sporangia (dotted lines); F. Flower of *Rhyncanthera grandiflora*. Dotted lines surround the rostrum; G. Flower of *Mouriri cearensis*, highlighting the oil glands (white arrowheads); H. Flower of *Pleroma costatocalyx*, showing the glandular trichomes (yellow arrowheads) and the poricidal anthers (red arrowheads); I. Flower of *Dolichoura spiritusantensis*, evidencing the dorsal staminal appendages; J. Flower of *Axineae* sp., showing the bulbous staminal appendages (black arrows); K. Stamen of *Axinea confusa*, evidencing the bulbous staminal appendage (black arrow) and the poricidal anther (red arrowhead); L. Flower of *Arthrostemma* sp., showing the dimetric stamens with the feeding (red arrow) and pollination (yellow arrow) stamens.

2) The androecium of Melastomataceae

Melastomataceae flowers often exhibit a diplostemonous androecium with a variable number of stamens distributed between the antepetalous (opposite to petals) and antesepalous (opposite to sepal) whorls (Renner 1993) (Fig. 1A). The presence of one entire whorl of stamens reduced to staminodia, or their complete loss resulting in haplostemony, are relatively uncommon but phylogenetically scattered in Melastomataceae. They are observed in tribes Cyphostyleae (Michelangeli et al. 2011), Dissochaeteae (Kartonegoro et al. 2018), Lavoisiereae (Renner 1990; Almeda and Pacifico 2018), Marcetiae (Almeda and Robinson 2011; Almeda et al. 2016; (Rocha et al. 2017), Melastomateae (Alvear and Almeda 2019), Pyxidanthaeae (Almeda 2000), and Sonerileae (Cellinese 1997). Although in haplostemonous flowers the stamens are usually those from the antesepalous whorl, the opposite occurs in *Monochaetum* (Gleason 1929, Alvear and Almeda 2019) and some species of *Dissochaeta* (Kartonegoro et al. 2018). Curiously, antesepalous staminodia with undeveloped thecae, but well-developed filaments and appendages are present in some species of *Dissochaeta* (Kartonegoro et al. 2018). These staminodes may have assumed new functions such as increasing the flower attractivity by their colorful appendages as observed in other clades of angiosperms (Walker-Larsen and Harder 2000). However, the possible functional role of staminodia has not yet been addressed in Melastomataceae.

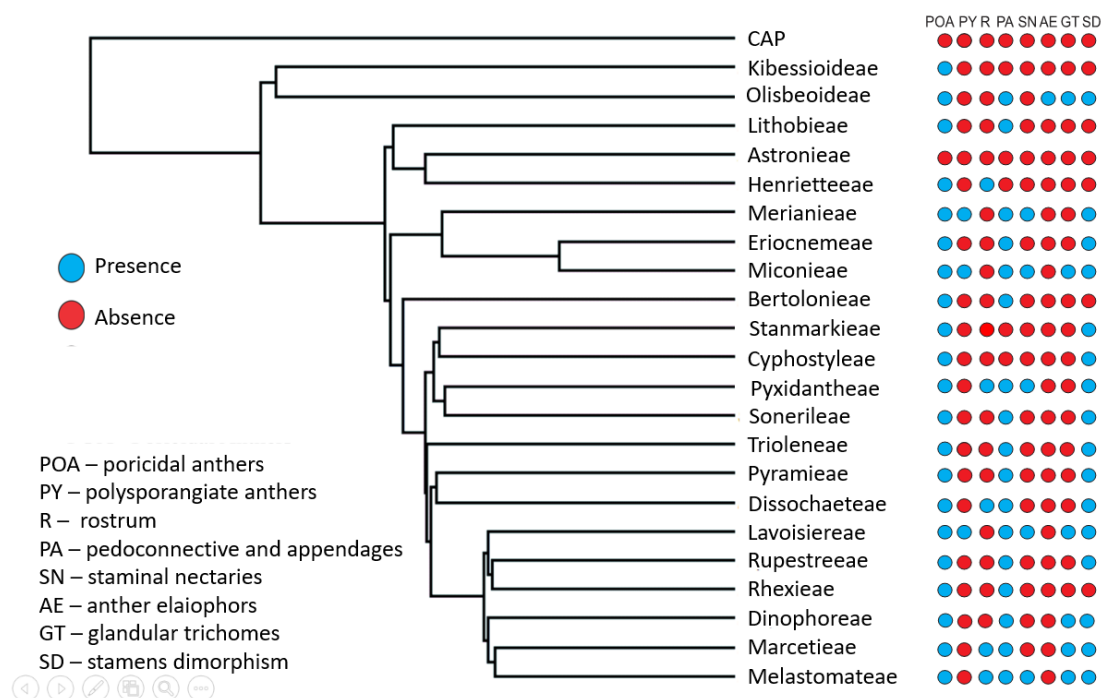


Figure 2. The presence and/or absence of several traits in Melastomataceae tribes currently recognized by Penneys et al. - (See Chapter 5 - An overview of Melastomataceae classification and phylogenetics - for more information about the classification).

A pleiostemonous androecium with more than double the number of stamens than petals, may be found in a few genera of Melastomataceae, such as in *Astrocalyx* (Astronieae) (Mancera et al. 2017), *Henriettea* (Henrietteae) (Penneys et al. 2010), *Miconia* (Miconieae) (Kriebel 2016; reported as *Conostegia*), and *Plethiandra* (Dissochaeteae) (Kadereit 2005). A study involving floral development in *Miconia* indicates that there are at least two developmental patterns leading to pleiostemony: 1. by a single large stamen occurring in each antesealous position and several smaller ones positioned in each antepetalous position; 2. by *dédoublement*, where each or most of stamen primordia splits in two parts (Wanntorp et al. 2011).

Most Melastomataceae lineages exhibit stamens with a terminal anther that sits on a filament, which is a common pattern in angiosperms (Endress 1994). At maturity, anthers generally open by one or two pores, a condition shared by most species within the family (Clausing and Renner 2001a) (see details in subsection “Anther dehiscence”). Each anther comprises two thecae and a connective, the sterile zone which connect the thecae and link the anther to the filament. The anther connective tissue is enlarged and massive in Olisbeoideae and Kibessioideae, the first-branching lineages of the family (Clausing and Renner 2001a, Fig. 2). Additionally, Olisbeoideae has connectives with a

concave dorsal oil-gland (see details in subsection “Stamen secretory structures”) (Buchmann and Buchmann 1981; Renner 1993; Clausen and Renner 2001), but it may be reduced or absent in some taxa (Morley 1976; Stone 2014; Stone and Cheek 2018).

A basal-ventral extension of the anther connective, termed pedoconnective (*sensu* Jacques-Félix 1953) may be found between connective and filament. The pedoconnective works like a hinge, increasing anther flexibility and facilitating bees to hold the stamens while they apply vibrations. Moreover, this structure standardizes bee position during the visit, optimizing pollination (see details in subsection “pedoconnective and appendages”) (Clausen and Renner 2001a). The pedoconnective is uniquely shared by the clade formed by Marcetieae, Melastomateae, Lavoisiereae and Rhexieae (Clausen and Renner 2001a; Michelangeli et al. 2013), but it may be highly reduced or even lost in some taxa (Michelangeli et al. 2013; Rocha et al. 2017; Verano-Libalah et al. 2017). This staminal structure appears to be a key innovation, leading to high levels of species diversity in the respective clades (Kriebel 2008). The anther connective and/or the pedoconnective may also have ventral (Fig. 3) and/or dorsal appendages, such as in Pyramieae (Bochorny et al. 2019), Henrietteae (Penneys et al. 2010), Marcetieae (Rocha et al. 2018), Melastomateae (Michelangeli et al. 2013), Merianieae (Mendoza-Cifuentes and Fernández-Alonso 2010), Lavoisiereae (Fritsch et al. 2004), and Pyramieae (Bochorny et al. 2019). These appendages vary widely in morphology (Fig. 3) (Fritsch et al. 2004; Mendoza-Cifuentes and Fernández-Alonso 2010; Goldenberg et al. 2012; Michelangeli et al. 2013; Rocha et al. 2016; Verano-Libalah et al. 2017; Bochorny et al. 2019) and may play different functions (see details in subsection “pedoconnective and appendages”) (Dellinger et al. 2014; Bochorny et al. 2021).

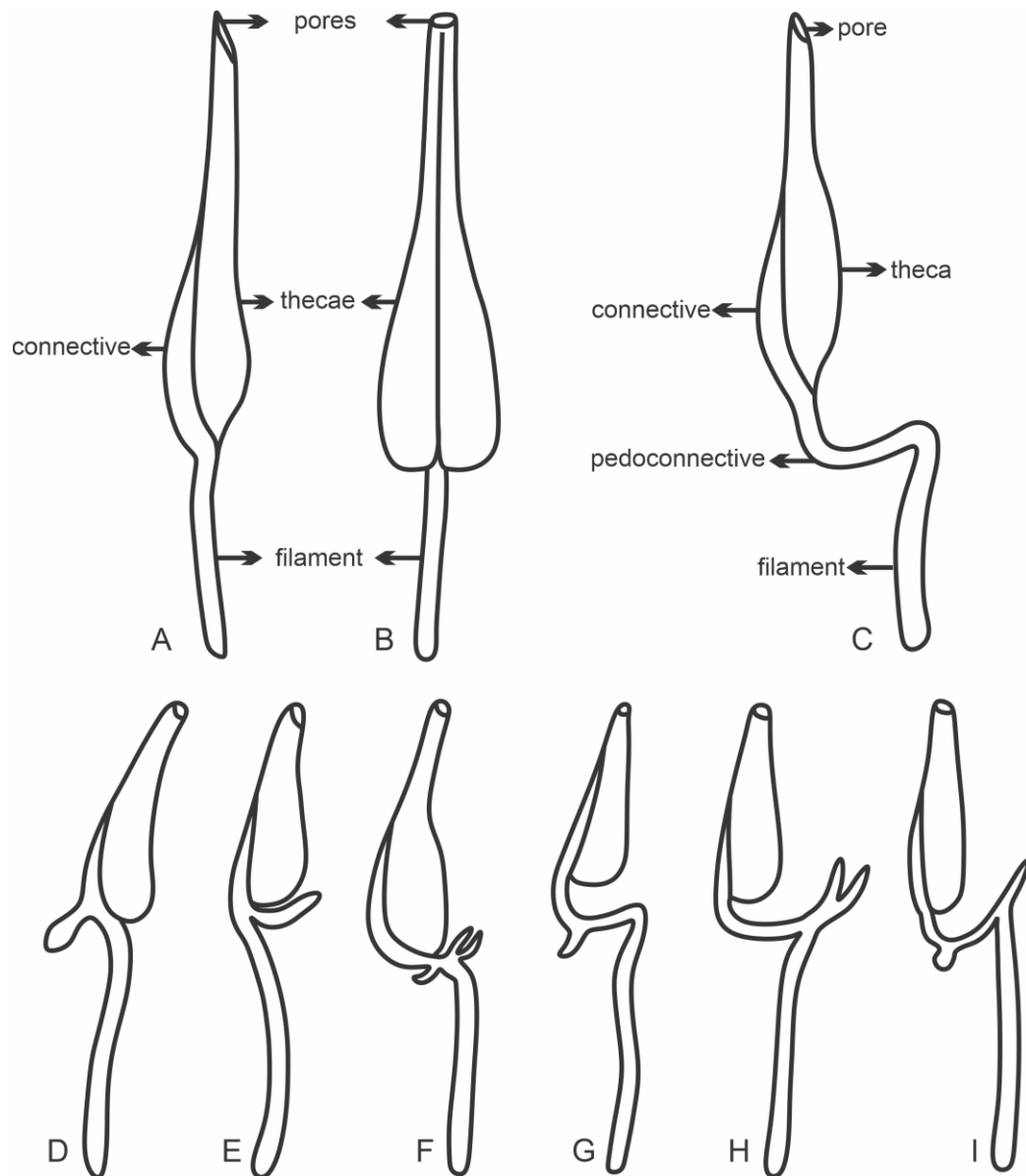


Figure 3. Stamens in Melastomataceae. A-B. Stamens without connective extensions in lateral (A) and ventral (B) views. C. Lateral view of a stamen with a pedoconnective. D-I. Stamens in lateral view, showing the diversity of staminal appendages. Stamens with dorsal (D) and ventral (E) appendages. Stamen with dorsal and ventral appendages (F). Stamen with a dorsal appendage in the pedoconnective (G). Stamen with a ventral appendage in the pedoconnective (H). Stamen with ventral and dorsal appendages in the pedoconnective (I).

3) Diversity, structure and function of stamens traits

3.1) *Stamens dimorphism / Heteranthery*

Stamens within a flower are usually similar in appearance. However, some species can have two or three structurally distinct types of stamens that also differ in their function. This conspicuous morphological differentiation of stamens and anthers within a flower is known as heteranthery or stamen dimorphism. Studies show that this condition

occurs in at least 20 families distributed in 12 orders and has evolved numerous times independently (Vallejo-Marin et al. 2010; Barrett 2021; Melo et al. 2021). In Melastomataceae, heteranthery is common and raises intriguing questions about how different types of stamen interfere with reproductive success. These differences can be expressed in different ways, such as differences in the size of stamens and anthers, their colors, or as different volatiles emitted by each type of stamen (Velloso et al. 2018; Solis-Montero et al. 2018; Gavrutenko et al. 2020; Melo et al. 2021). When the stamens are similar in shape and size, they are called isomorphic; whereas when there are two types of stamens, they are called dimorphic. Sometimes, the difference is not very pronounced and therefore these stamens are called subisomorphic.

3.1.1) *Stamens dimetrisism*

Melo et al. (2021) called stamen dimetrisism the dimorphism that refers exclusively to the difference in size between the stamens of the same flower. Stamen is composed of filament and anthers, and this difference in size can vary in both structures or only in one of them. When the stamens are of the same size, they are called isometric (e.g., *Rhexia parviflora*); those that differ by up to one third in size from the other are called subdimetric (e.g., *Comolia stenodon*), while sets of stamens that are at least twice the size of the other are called dimetric e.g., *Siphanthera cordifolia*) (Melo et al. 2021).

When stamens are not isometric, the antepetalous stamens are often smaller than the antesealous ones, with exceptions in *Miconia dissitiflora* (Almeda 1989), *Monochaetum* (Alvear and Almeda 2019), and species of *Dissochaeta* (Kartonegoro et al. 2018) and *Meriania* (Mendoza-Cifuentes and Fernández-Alonso 2010; Dellinger et al. 2021b) where larger antepetalous stamens are observed (see more in Chapter 3). In terms of functionality, Fritz Müller (1882) assumed that fertilization in pollen-flowers is almost always achieved by the pollen grains from the longer stamens, while the smaller stamens serve to attract and feed pollen-eating bees. Some contemporaneous naturalists, including Darwin, observed and exchanged letters about this curious condition, which generated several speculations (Darwin 1887). This division of function between stamens was then called the “Division of labor hypothesis”. This hypothesis has been overlooked for over a hundred years and only in 2008 was brought back to the literature by Luo et al. (2008) studying the species *Melastoma malabathricum*, and, since then, has been corroborated by several authors even in other plant families (Vallejo-Marin et al. 2009; Amorim et al.

2017; Telles et al. 2020; Saab et al. 2021). This morphological condition can be a strategy to maximize pollen delivery since longer stamens place pollen in safe sites on the bee's body (i.e., the bee's back which it cannot reach when grooming) (Koch et al. 2017).

Currently, it is understood that the production of pollen grains as the only floral resource in pollen flowers favored the evolution of mechanisms such as stamen dimetrisism (Vallejo-Marín et al. 2011; Veena and Nampy 2020). However, it has been recently noted that stamen dimetrisism is not restricted to buzz-pollinated flowers in Melastomataceae. Some flowers that are not buzz-pollinated, such as those of some species in tribe Merianieae, can also present stamen dimetrisism. Although the underlying driving forces may be similar, in those cases different stamen sizes have been linked to staggered pollen release and evolution *de-novo* in passerine-pollinated species (Dellinger et al. 2021b).

Although the evolution of stamen dimetrisism clearly provides an advantage in securing successful pollination, most of the Melastomataceae species can be considered isometric (Melo et al. 2021). Stamen dimetrisism is not a conserved trait in the evolutionary history of the Melastomataceae clade. It is labile over evolutionary time and converges to two adaptive peaks, depending or not on pollinators. In the first case, when plants depend on pollinators to set seeds, stamen dimorphism evolved with greater phenotypic variation of stamen size. In the second case, plants that are independent of pollinators to set seeds evolved flowers with isomorphic stamens. To complement the observation made by Melo et al. (2021), it would be interesting to investigate whether species with variation in stamen size are located in specific regions in the world, with greater bee pollinator diversity as well and higher climatic instability.

3.1.2) Color differences between stamen types

In addition to the morphological variation in stamens size, many species of Melastomataceae show variation in stamen color within the same flower (Fig. 1L). This variation in stamen color together with the color of petals and the contrast with the background can interfere in the attraction of certain pollinators. In this way, the division of labor can be reinforced since one set of stamens (feeding) may signal the availability of resources for visitors with a more contrasting and attractive color, while the other set (pollination) goes unnoticed due to the similarity in coloration with the petals or the background (e.g., *Microlia cordata*). In this interaction, the pollinating agents move

directly to the set of stamens that best signal the resource, causing pollen grains from the other set to be used only for pollination, thus ensuring the plant's reproductive success (Melo et al. 2018; Velloso et al. 2018). During buzz pollination, the anther itself can attract the pollinators with their highlighted color, attracting pollinators due to the contrast against the background (Lunau 2006). Yellow anthers in particular mimic the color of pollen grains and trigger innate responses in pollen-collecting bees and flies (Fig. 1L) (Luo et al. 2009; Lunau et al. 2017). Possibly, the yellow anthers present in most of the Miconieae clade are a consequence of ancestral modes of specialized pollination, while the presence of white anthers may be indicative of generalized pollination (Gavrutenko et al. 2020). Thus, during short-distance signaling for pollinators, the anther color will be an important and more reliable indicator of pollination mode than the petal color (Gavrutenko et al. 2020).

3.1.3) *Scent differences between stamen types*

Differences in scent produced by short and long stamens within the same flower is poorly studied and has never been reported in Melastomataceae. Solís-Montero et al. (2018) showed that floral volatiles emitted by dimorphic anthers in *Solanum rostratum* (Solanaceae) may also represent a type of heteranthery that involves chemical differentiation (i.e., the proportion of volatile compounds). In this case, the presence of certain volatiles and their concentration levels in each anther type influences bee preference for feeding anthers over pollinating anthers. It is clear that some studies need to be done to better clarify this differentiation and the perception capacity of possible pollinators in Melastomataceae.

3.2) *Anther dehiscence*

The anthers of the majority of angiosperms dehisce through longitudinal slots along the stamens, exposing pollen grains. In such flowers, pollen grains are automatically taken up when in direct contact with a pollinators' body. However, roughly 6% of all angiosperms represented by different and evolutionarily independent families present anthers that dehisce through small pores, including most species of Melastomataceae (Buchmann 1983; Clausen and Renner 2001a; Vallejo-Marín et al. 2010). It is estimated that 96-98% of all Melastomataceae species present pollen flowers

with poricidal anthers that are buzz-pollinated (Renner 1989; see more in Chapter 26). Anther pores may contribute to pollen dose in Melastomataceae, i.e., the control of pollen release along flower life-span (Brito et al. 2021) and pollen targeting on the bee body (Konzmann et al. 2020).

Pores may also have an additional role in restricting pollen-harvesting only to buzzing bees acting as a mechanical barrier to non-buzzing bees and other pollen collecting insects. However, it is common to see non-buzzing bees (e.g., Apidae: Meliponini) chewing or even milking anthers to get pollen grains in Neotropical Melastomataceae with small pores (Renner 1983). Some species in the tribes Kibessioideae, Olisbeoideae, Miconieae, Marcetieae, and the Astronieae + Henrietteae clade present an anther dehiscence that differ from the rest of the family (Clausing & Renner 2001a). Anthers in *Memecylon* open by slits and by short, drop-shaped slits in *Mouriri* (both Olisbeoideae, Clausing and Renner 2001a). In Astronieae, anthers also dehiscence through slits. Also, some *Miconia* species in sections *Cremanium*, *Chaenopleura*, *Chaenantha* and *Miconia* have anthers that dehiscence by 1-2 slit-like or broad pores (Renner 1989; Gavrutenko et al. 2020). In such cases, this specific dehiscence may favor spontaneous pollen release by non-vibratory animals and it is associated to generalization in pollination strategies (Goldenberg and Shepherd 1998; Varassin et al. 2008; Kriebel and Zumbado 2014; Brito et al. 2016; Brito et al. 2017). Despite there is no reason to believe that such enlarged and modified pore dehiscences act as a filter to buzzing bees (Renner 1989; Oliveira 2016; Brito et al. 2017), anther pore modifications in some Melastomataceae lineages may be correlated with shifts in pollination systems (Varassin et al. 2008; Brito et al. 2016). However, there are no consistent modifications in pore dehiscence (i.e., size or position) following the pollination shifts that occurred in Merianieae (Fig.1K) (Dellinger et al. 2019b).

Even though poricidal anthers are also found in other buzz-pollinated flowers in Ericaceae (Hermann and Palser 2000), Leguminosae (Marazzi 2007), and Solanaceae (Bohs 2005), the ontogeny of anther dehiscence in Melastomataceae appears to be quite particular (Goldenberg 2003; Cortez et al. 2014). Cortez et al. (2014) pointed out three stages for pore opening: 1) the intersporangial septum breakage, which allow that the two microsporangia of each theca release pollen grains through the apical pore(s); 2) the gradual separation of the border region between the groups of epidermal cells with and without a cuticle and; 3) the subsequent and complete degeneration of the pore epidermal

cells that lack cuticle. Therefore, the lack of the cuticle in the pore region seems to be crucial in pore opening and restricts this phenomenon to occur only during or after flower anthesis. Although studies on anther development to date have been restricted to species of Miconieae, it is possible that the same developmental mechanism operates in all species of Melastomataceae, since the presence of poricidal dehiscence is present in most of the family (Clausing and Renner 2001a).

3.3) *Sporangia number*

The anthers of angiosperms are often composed of four microsporangia organized pairwise in each theca (Fig. 1E). The microsporangia, or pollen sacs, correspond to the site of pollen development (Endress 2011). This typical tetrasporangiate arrangement is also the most common pattern in Melastomataceae (Tobe and Raven 1983; Cortez et al. 2015). In general, the anthers exhibit four intact microsporangia during stamen development, but commonly a bilocular appearance is observed in mature anthers (Renner 1993; Cortez et al. 2015). It occurs due to the degeneration of the septum between the microsporangia of each theca, resulting in two perceptible pollen sacs at this stage (Cortez et al. 2015).

In addition to the tetrasporangiate condition, bisporangiate and polysporangiate (Fig. 1D e 1E) anthers have also been reported in Melastomataceae. Bisporangiate anthers have, to date, only been found in *Miconia latecrenata* (Cortez et al. 2015). On the other hand, polysporangiate anthers have been reported in at least 74 species of *Microlicia*, *Meriania* and *Miconia*. This trait has evolved independently several times within the family in a similar morphological fashion: parenchymatous longitudinal and/or transverse septa divide the microsporangia into several small locules (Baumgratz et al. 1996; Lima et al. 2019; Caetano et al. 2020). Although polysporangiate anthers seem to be an adaptive trait, its functional role is still under debate. Some authors have associated the presence of multiple sporangia with a better nutritional condition for pollen development (Lima et al. 2019). Another hypothesis suggests that the compartmentalized polysporangiate anthers would modify the pattern of pollen release, which would make the grains available to more visitors (Baumgratz 1996).

3.4) *Accessory structures*

3.4.1) *Rostrum*

The term rostrum designates a beak-like structure (Harris and Harris 2001). In Melastomataceae, anthers which exhibit a beaked apex have been denominated rostrate (Cogniaux 1891; Fritsch et al. 2004; Penneys et al. 2010; Michelangeli et al. 2013; Martins and Almeda 2017; Kartonegoro et al. 2018; Rocha et al. 2018). The anther rostrum consists of an apically tubular and elongated constriction, with a distal pore (Fig. 1F). This type of anther apex, although uncommon in most angiosperms, occurs associated with poricidal anthers in other buzz-pollinated groups, such as in species of Elaeocarpaceae, Ericaceae and Malvaceae (Luteyn 1989; Matthews and Endress 2002; Marazzi 2007; Shepherd and Wilkins 2017). The rostrum likely functions in directing pollen ejection during buzz pollination (Marazzi et al. 2007; Konzmann et al. 2020). Moreover, it is possible that this structure may also influence both the speed of pollen ejection and the amount of pollen released (Marazzi et al. 2007). In Melastomataceae, rostrate anthers are found in some species of Dissochaeteae (Kartonegoro et al. 2018), Henrietteae (Penneys et al. 2010), Marcetieae (Rocha et al. 2016), and Melastomateae (Veranso-Libalah et al. 2017), and it is shared among Lavoisiereae members (Fritsch et al. 2004).

3.4.2) *Pedoconnective and staminal appendages*

There is a striking diversity of dorsal and ventral appendages that originates from the connective tissue in the stamens of Melastomataceae (Fig 3). Staminal appendages can be positioned at the base of the thecae or in the pedoconnective and may vary in size, shape, colour as well as their intra-staminal position. The tribes Dissochaeteae, Lavoisiereae, Marcetieae, Melastomateae, Merianieae, Rhexieae, and Pyramieae have evolved staminal appendages (Renner 1993; Clausen and Renner 2001; Michelangeli et al. 2013; Kartonegoro et al. 2018; Rocha et al. 2018; Bochorony et al. 2019). Although staminal appendages have been used in species identification and classification in these groups (Renner 1993; Clausen and Renner 2001a; Michelangeli et al. 2013), there is little evidence of homology and it is often difficult to compare them among taxa (Rocha et al. 2016). These staminal appendages can be either vascularized or not (Wilson 1950) and

may be linked to a plethora of functional roles in Melastomataceae, including flower development and pollination.

During Melastomataceae flower ontogeny, the anthers of the incurved stamens develop early in small chambers in the hypanthium and the development of the pedoconnectives and their ventral appendices follow at a later phase (Basso-Alves 2016). On the other hand, dorsal appendages seem to have an earlier development, being visible as a protrusion at early stages of stamen development (Dellinger 2013). The most common functional role attributed to staminal appendages, as the ones found in Melastomataceae and Pyramieae, is to serve as mechanical handles for buzzing bees, which would optimize the transmission of vibrations as well as help on the positioning of such pollinators (Fig. 1I) (Renner 1989; Luo et al. 2008; Bochorny et al. 2021). Surprisingly, however, the removal of long ‘whip-like’ dorsal appendages in *Huberia bradeana* had no effect in the vibrational behavior of the buzzing bees during their visits, but reduced the amount of pollen grains released by the flowers (Bochorny et al. 2021). Even though these authors did not detect any specific improvement in stamen vibration in flowers that did not have their staminal appendages removed, this result suggests that these appendages may optimize pollen release by altering the vibrational mechanical properties of stamens with no direct influence on bee vibrational behavior. Moreover, as the amount of pollen received by the stigmas did not differ among treatments, it is reasonable to think that such appendages evolved in response to a male fitness component, shedding light on this understudied structure (Minnaar et al. 2019).

One of the most astonishing cases of the functional role carried by staminal appendages in Melastomataceae occurs in the genus *Axinaea* (Dellinger et al. 2014). In these flowers, the dorsal appendage is enlarged and aerated, rich in hexoses, and it is actively consumed by passerine birds (Fig. 1J). These appendages also function as bellows structures that eject air flows through the anther tube, affecting pollen release and causing its deposition on the bird’s head and beak. This is the only known case of such a specialized pollination system involving a food body reward associated with stamens in eudicots. The evolution of this structure may have promoted the diversification of *Axinaea* within the tribe Merianieae by leading to a departure from the buzz pollination adaptive plateau (Dellinger et al. 2019b).

The removal of ventral appendages of the pedoconnective in controlled experiments also led to a potential decrease in flower fitness as a consequence of the

reduction in bee attraction in both *Melastoma malabathrichum* and *Desmocelis villosa* (Luo et al. 2008; Ferreira and Araújo 2016). In both cases, the appendages are conspicuously yellow and may have affected bee flower discrimination after their removal by disrupting their intrafloral color pattern. In fact, yellow appendages in long stamens are similar to the yellow anthers in short stamens when considering their color contrast in relation to the corolla background in *Microlicia cordata* (Velloso et al. 2018). On the other hand, the anthers of long stamens are color camouflaged against the corolla background in the same flowers. The intrafloral color pattern created by the yellow ventral appendages of long stamens together with anthers with different colors may reinforce the division of labor among stamens in such flowers.

3.4.3) *Stamen secretory structures*

Three main types of secretory structures can be associated with stamens of Melastomataceae: staminal nectaries, anther elaiophores and glandular trichomes. Staminal nectaries are a common feature in few Melastomataceae species that produce nectar as a floral resource. Many of these species are pollinated by vertebrates or generalist insects and are associated with areas where bees are not abundant (e.g., higher altitudes) (Stein and Tobe 1989; Dellinger et al. 2021a). These staminal nectaries can be classified as non-structural, since they are not histologically differentiated (see Chapter 3 of this book). The position of the nectaries along the stamens, as well as the way in which nectar is secreted by these structures, may vary depending on the genus. In *Blakea* and *Huilaea*, for instance, nectar is secreted by modified stomata located on the dorsal surface of the anther appendage (Varassin et al. 2008). Nectar is also secreted by modified stomata in stamens of *Brachyotum*, but in this genus they appear to be distributed along the entire connective (Varassin et al. 2008). In *Meriania*, nectar is secreted through porous or tissue ruptures and phloem sap leakage along the filaments (Varassin et al. 2008; Dellinger et al. 2019b; Dellinger et al. 2019c). In all cases, species that produce nectar through staminal nectaries often have significantly thicker vascular bundles in the stamens. The nectar secreted by staminal nectaries usually forms small drops between stamens and corolla where it is accessed by pollinators (Stein and Tobe 1989; Varassin et al. 2008; Dellinger et al. 2019c).

Anther elaiophores are a characteristic feature of, and possibly restricted to, members of tribe Olindebeoideae (Buchmann and Buchmann 1981). These multilayered

epithelial oil glands can be identified as a darker spot usually located below the pore on the abaxial side of the anther (Fig. 1G). The oils produced by these structures have been described as bright yellow and rich in fatty acids. They are typically produced in less quantities than those of typical oil flowers and, perhaps for that reason, there is some controversy around their actual functional role. Some authors regard oil produced by *Olisbeoideae*'s elaiophores as possible resources for pollinators (Buchmann and Buchmann 1981; Oliveira 2016). Renner (1989), however, noted that bees actively collecting this secretion are too small to make stigmatic contact while harvesting. Other possible functions for elaiophores that have been mentioned in the literature include scent production and the visual enhancement of stamen attractiveness for pollinators (Morley 1976; Renner 1989).

Glandular trichomes are observed on stamens of several genera across the family, including species of *Macairea*, *Miconia* and *Tibouchina* (Mendoza and Ramirez 2006; Goldenberg et al. 2008; Oliveira 2019) (Fig. 1H). In *Macairea radula*, these structures are also described as oil producers and, although they are typically called “glandular trichomes”, recent micro-morphological analysis revealed that they are technically not trichomes, but actually glandular emergences (Oliveira 2019). As with the elaiophores in *Olisbeoideae*, the role of oil production by these structures is yet to be fully understood. Although bees were observed to collect oil from glandular trichomes of *Macairea radula* during buzz pollination, oil was only a secondary resource (Fig. 1C). More studies on the role of oil production by Melastomataceae flowers and their role in pollination, including more field observations, are clearly needed.

4) Conclusion

In this chapter, we described the intriguing diversity of stamens in Melastomataceae. Structural changes in size and shape of stamens are visible from the earliest stages of androecium development and can play an important ecological role in the mature flower by regulating their interaction with pollinators. Much of this structural diversity, including presence of poricidal anthers, stamen dimetrisism, some types of appendices and rostrum, appear to be linked to adaptations to the prevalent buzz-pollination syndrome. Other characteristics, such as presence of stamen nectaries, bulbous anthers and large anther pores, however, have probably evolved in response to shifts to other forms of pollination, such as by vertebrates and generalist insects. Most

importantly, we show that the functional role of several structures discussed here, including trichomes and oil glands, remain poorly understood. Therefore, more studies on morphology, ecology and evolution of stamen traits are necessary in the family. In particular, we highlight eight questions that remain open to be answered by future studies that focus on understanding the role of stamen diversity in the ecology and evolution of Melastomataceae: (1) What is the functional role of staminodia, such as those observed in *Dissochaeta*? (2) Is the pedoconnective a key-innovation in the groups that present this structure? (3) Are any of the adaptations associated with stamen morphology and size, such as stamen dimetrisism, more common in certain environments and regions of the world? (4) What are the groups that present staminal dimorphism in terms of scent and how does this trait impact the success of pollination? (5) What is the function of polysporangiate anthers in the reproductive biology of Melastomataceae? (6) Is there any difference in the mechanical functioning of ventral and dorsal staminal appendages, or between slender and bulky ones, during buzz-pollination? (7) Why is there such a diversity in appendages among all Melastomataceae species pollinated by buzzing bees? (8) How important is oil production in the pollination of Melastomataceae species that present staminal elaiophores? New studies should also explore the role of stamen diversity, as well as other floral traits, in the diversification of the family, contributing to understanding the drivers of diversity in this speciose tropical clade.

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References

- Almeda F (1989) Five new berry-fruited species of tropical American Melastomataceae. *Proceedings of the California Academy of Sciences* 46:137–150
- Almeda F (2000) The hexandrous species of *Topobea* (Melastomataceae). *Proceedings of the California Academy of Sciences* 52:97–109
- Almeda F, Michelangeli FA, Viana PL (2016) *Brasilianthus* (Melastomataceae), a new monotypic genus endemic to ironstone outcrops in the Brazilian Amazon. *Phytotaxa* 273:269–282. <https://doi.org/10.11646/phytotaxa.273.4.3>
- Almeda F, Pacifico R (2018) Neotropical *Poteranthera* (Melastomataceae: Microlicieae) Revisited. *Systematic Botany* 43:552–556. <https://doi.org/10.1600/036364418X697274>
- Almeda F, Robinson OR (2011) Systematics and phylogeny of *Siphanthera* (Melastomataceae). *Systematic Botany* 93:1–101
- Alvear M, Almeda F (2019) Revision of *Monochaetum* (Melastomataceae: Melastomateae) in Colombia. In: *Systematic Botany Monographs*. p 202
- Amorim T, Marazzi B, Soares AA, Forni-Martins ER, Muniz CR, Westerkam, C (2017) Ricochet pollination in *Senna* (Fabaceae) – petals deflect pollen jets and promote division of labour among flower structures. *Plant Biology*, 19: 951–962. <https://doi.org/10.1111/plb.12607>
- Bacci LF, Amorim AM, Michelangeli FA, Goldenberg R (2020) Flower morphology is correlated with distribution and phylogeny in *Bertolonia* (Melastomataceae), an herbaceous genus endemic to the Atlantic Forest. *Molecular Phylogenetics and Evolution* 149:106844. <https://doi.org/10.1016/j.ympev.2020.106844>
- Barrett SC (2021) Heteranthery. *Current Biology*, 31(12)
- Basso-Alves JP (2016) Morfologia comparada da flor de Melastomataceae Juss. Campinas, São Paulo, Brazil. Retrieved from <http://repositorio.unicamp.br/jspui/handle/REPOSIP/331428>
- Baumgratz JFA, Souza MLDR, Woodgyer EM, Nic Lughadha EM (1996) Polysporangiate anthers: Described for the first time in Melastomataceae. *Kew Bull* 51:133–144. <https://doi.org/10.2307/4118750>
- Bochorny T, Bacci LF, Dellinger AS, et al (2021) Connective appendages in *Huberia bradeana* (Melastomataceae) affect pollen release during buzz pollination. *Plant Biology* plb.13244. <https://doi.org/10.1111/plb.13244>
- Bochorny T, Michelangeli FA, Almeda F, Goldenberg R (2019) Phylogenetics, morphology and circumscription of Cambessedesieae: A new neotropical tribe of Melastomataceae. *Botanical Journal of the Linnean Society* 190:281–302. <https://doi.org/10.1093/botlinnean/boz018>
- Bohs L, Weese T, Myers N, et al (2007) Zygomorphy and heteranthery in *Solanum* in a phylogenetic context. *Acta Hort* 745:201–223. <https://doi.org/10.17660/ActaHortic.2007.745.8>

- Brito VLG, Fendrich TG, Smidt EC, et al (2016) Shifts from specialised to generalised pollination systems in Miconieae (Melastomataceae) and their relation with anther morphology and seed number. *Plant Biology (Stuttg)* 18:585–593. <https://doi.org/10.1111/plb.12432>
- Brito VLG, Maia FR, Silveira FAO, et al (2017) Reproductive phenology of Melastomataceae species with contrasting reproductive systems: contemporary and historical drivers. *Plant Biology* 19:806–817. <https://doi.org/10.1111/plb.12591>
- Bruce A. Stein and Hiroshi Tobe (1989) Floral nectaries in Melastomataceae and their systematic and evolutionary implications source: *Annals of the Missouri Botanical Garden*, 76: 2
- Buchmann SL (1983) Buzz pollination in angiosperms. *Handbook of Experimental Pollination Biology* 73–113
- Caetano APS, Reginato M, Goldenberg R, et al (2020) Structure and evolution of polysporangiate anthers in Melastomataceae. *Perspect Plant Ecology Evolution Systematic* 46:125556. <https://doi.org/10.1016/j.ppees.2020.125556>
- Cellinese N (1997) A New *Sonerila* (Melastomataceae) from central Kalimantan, Borneo. *Missouri Botanical Garden*, 7:103–105
- Clausing G, Renner SS (2001a) Molecular phylogenetics of Melastomataceae and Memecylaceae: implications for character evolution. *American Journal of Botany* 88:486–498. <https://doi.org/10.2307/2657114>
- Clausing G, Renner SS (2001b) Evolution of growth form in epiphytic Dissochaeteae (Melastomataceae). *Organisms Diversity & Evolution* 1:45–60. <https://doi.org/10.1078/1439-6092-00004>
- Cortez PA, Caetano AP de S, Carmello-Guerreiro SM, Teixeira SP (2014) Elucidating the mechanism of poricidal anther dehiscence in *Miconia* species (Melastomataceae). *Morphology, distribution, functional ecology of plants* 209:571–579. <https://doi.org/10.1016/j.flora.2014.07.002>
- Cortez PA, Caetano APS, Carmello-Guerreiro SM, Teixeira SP (2015) Anther wall and pollen development in Neotropical species-rich *Miconia* (Melastomataceae). *Plant Systematics and Evolution* 301:217–230. <https://doi.org/10.1007/s00606-014-1067-z>
- Darwin C (1887) The life and letters of Charles Darwin including an autobiographical chapter, vol. 3 (ed. F. Darwin). London, UK: John Murray
- Dellinger AS, Penneys DS, Staedler YM, et al (2014) A specialized bird pollination system with a bellows mechanism for pollen transfer and staminal food body rewards. *Current Biology* 24:1615–1619. <https://doi.org/10.1016/j.cub.2014.05.056>
- Dellinger AS, Pöllabauer L, Loreti M, Czurda J, Schönenberger J (2019a) Testing functional hypotheses on poricidal anther dehiscence and heteranthery in buzz-pollinated flowers. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien. Zoologisch-Botanische Gesellschaft in Wien*. 156. 197-214.
- Dellinger AS, Chartier M, Fernández-Fernández D, et al (2019b) Beyond buzz-pollination – departures from an adaptive plateau lead to new pollination syndromes. *New Phytologist* 221:1136–1149. <https://doi.org/10.1111/nph.15468>

- Dellinger AS, Scheer LM, Artuso S, Fernández-Fernández D, Sornoza F, Penneys DS, Tenhaken R, Dötterl S, Schönenberger J (2019c) Bimodal pollination systems in andean Melastomataceae involving birds, bats, and rodents. *The American Naturalist* 194(1):104-116. <https://doi.org/10.1086/703517>
- Dellinger AS, Pérez-Barrales R, Michelangeli FA, et al (2021a) Low bee visitation rates explain pollinator shifts to vertebrates in tropical mountains. *New Phytologist*, 231: 864-877. <https://doi.org/10.1111/nph.17390>
- Dellinger AS, Artuso S, Fernández-Fernández DM, Schönenberger J (2021b) Stamen dimorphism in bird-pollinated flowers: Investigating alternative hypotheses on the evolution of heteranthy. *Evolution*, 75: 2589-2599. <https://doi.org/10.1111/evo.14260>
- Endress PK (2011) Evolutionary diversification of the flowers in angiosperms. *American Journal of Botany* 98:370–396. <https://doi.org/10.3732/ajb.1000299>
- Ferreira QIX, De Araújo FP (2016) Economia de pólen favorecida pela heteranteria em *Desmocelis villosa* (Melastomataceae). *Rodriguesia* 67:347–355. <https://doi.org/10.1590/2175-7860201667206>
- Fontelas JC, Romero R (2020) Two new species of *Microlicia* D. Don (Melastomataceae, Microlicieae) from Chapada dos Veadeiros, Goiás, Brazil. *PhytoKeys* 164: 115-126. <https://doi.org/10.3897/phytokeys.164.57569>
- Fritsch PW, Almeda F, Renner SS, et al (2004) Phylogeny and circumscription of the near-endemic Brazilian tribe Microlicieae (Melastomataceae). *American Journal of Botany* 91:1105–1114. <https://doi.org/10.3732/ajb.91.7.1105>
- Gavrutenko M, Reginato M, Kriebel R, et al (2020) Evolution of floral morphology and symmetry in the Miconieae (Melastomataceae): Multiple generalization trends within a specialized family. *International Journal of Plant Sciences* 181:732–747. <https://doi.org/10.1086/708906>
- Gleason HA (1929) the genus *Monochaetum* in South America. *American Journal of Botany* 16:502–522. <https://doi.org/10.1002/j.1537-2197.1929.tb09498.x>
- Goldenberg AR, Teixeira SP, Martins AB (2003) Anther dehiscence and circumscription of *Miconia* sect. *Hypoxanthus* (Melastomataceae). *International Journal of Plant Sciences* 58:195–203
- Goldenberg R, Bacci LF, Bochner T (2016) Behuria, Bertolonia, Cambessedesia, Huberia e Mouriri, e chave para identificação de gêneros de Melastomataceae no Estado do Paraná. *Rodriguesia* 67:445–454. <https://doi.org/10.1590/2175-7860201667215>
- Goldenberg R, Baumgratz JFA, Souza MLD (2012) Taxonomia de Melastomataceae no Brasil: retrospectiva, perspectivas e chave de identificação para os gêneros. *Rodriguesia* 63:145–161. <https://doi.org/10.1590/S2175-78602012000100011>
- Goldenberg R, Penneys DS, Almeda F, et al (2008) Phylogeny of *Miconia* (Melastomataceae): Patterns of Stamen Diversification in a Megadiverse Neotropical Genus. *International Journal of Plant Sciences* 169:963–979. <https://doi.org/10.1086/589697>
- Goldenberg R, Shepherd GJ (1998) Studies on the reproductive biology of

- Melastomataceae in “Cerrado” vegetation. *Plant Systematics and Evolution* 211:13–29. <https://doi.org/10.1007/BF00984909>
- Hermann PM, Palser BF (2000) Stamen development in the Ericaceae. In: anther wall, microsporogenesis, inversion, and appendages. *American Journal of Botany* 87(7): 934–957.
- Kadereit G (2005) Revision of *Plethiandra* hook.f.: a polystaminate, east Asian genus of Melastomataceae. *Edinburgh Journal of Botany*, 62(3), 127–144. doi:10.1017/S0960428606000175
- Kartonegoro A, Veldkamp JF, Hovenkamp P, van Welzen P (2018) A revision of *Dissochaeta* (Melastomataceae, Dissochaeteae). *PhytoKeys* 178:1–178. <https://doi.org/10.3897/phytokeys.107.26548>
- Koch L, Lunau K, Wester P (2017) To be on the safe site – Ungroomed spots on the bee’s body and their importance for pollination. *PLoS One* 12:1–16. <https://doi.org/10.1371/journal.pone.0182522>
- Konzmann S, Hilgendorf F, Niester C, et al (2020) Morphological specialization of heterantherous *Rhynchanthera grandiflora* (Melastomataceae) accommodates pollinator diversity. *Plant Biology* 22:583–590. <https://doi.org/10.1111/plb.13102>
- Kriebel R, Zumbado MA (2014) New reports of generalist insect visitation to flowers of species of *Miconia* (Miconieae: Melastomataceae) and their evolutionary implications. *Brittonia* 66:396–404. <https://doi.org/10.1007/s12228-014-9337-1>
- Lima JF, Romero R, Simão DG (2019) Polysporangiate anthers in *Microlicia* D. Don (Melastomataceae Juss.). *Feddes Repertorium* 130:9–18. <https://doi.org/10.1002/fedr.201800006>
- Lumer C (1980) Rodent Pollination of *Blakea* (Melastomataceae) in a Costa Rican Cloud Forest. *Brittonia* 32:512. <https://doi.org/10.2307/2806163>
- Lunau K (2006) Stamens and mimic stamens as components of floral colour patterns. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 127:13–41. <https://doi.org/10.1127/0006-8152/2006/0127-0013>
- Lunau K, Piorek V, Krohn O, Pacini E (2015) Just spines - mechanical defense of malvaceous pollen against collection by corbiculate bees. *Apidologie* 46: 144–149. <https://doi.org/10.1007/s13592-014-0310-5>
- Lunau K, Konzmann S, Winter L, et al (2017) Pollen and stamen mimicry: the alpine flora as a case study. *Arthropod Plant Interact* 11:427–447. <https://doi.org/10.1007/s11829-017-9525-5>
- Luo Z, Zhang D, Renner SS (2008) Why two kinds of stamens in buzz-pollinated flowers? Experimental support for Darwin’s division-of-labour hypothesis. *Functional Ecology* 22:794–800. <https://doi.org/10.1111/j.1365-2435.2008.01444.x>
- Luo ZL, Gu L, Zhang DX (2009) Intrafloral differentiation of stamens in heterantherous flowers. *Journal of Systematics and Evolution*. 47:43–56. <https://doi.org/10.1111/j.1759-6831.2009.00002.x>
- Lutelyn JL. (1989) New variety and nomenclatural changes in Neotropical *Gaultheria* (Ericaceae). *Springer behav New York Botanical Garden* 41:10–16

- Marazzi B, Conti E, Endress PK (2007) Diversity in anthers and stigmas in the buzz-pollinated genus *Senna* (Leguminosae, Cassiinae). *International Journal of Plant Sciences*, 168:371–391
- Martins AB, Almeda F (2017) A monograph of the Brazilian endemic genus *Lavoisiera* (Melastomataceae: Microlicieae) *Phytotaxa*, 315, 1-194.
- Matthews ML, Endress PK (2002) Comparative floral structure and systematics in Oxalidales (Oxalidaceae, Connaraceae, Brunelliaceae, Cephalotaceae, Cunoniaceae, Elaeocarpaceae, Tremandraceae). *Botanical Journal of the Linnean Society* 140:321–381. <https://doi.org/10.1046/j.1095-8339.2002.00105.x>
- Melo LRF, Guimarães BM da C, Barônio GJ, et al (2018) Como as abelhas percebem as flores e por que isso é importante? *Oecologia Australis* 22:362–389. <https://doi.org/10.4257/oeco.2018.2204.03>
- Melo LRF, Vasconcelos T, Reginato M, et al (2021) Evolution of stamen dimetrisism in Melastomataceae, a large radiation of pollen flowers. *Perspectives in Plant Ecology, Evolution and Systematics* 48:125589. <https://doi.org/10.1016/j.ppees.2021.125589>
- Mendoza H, Ramirez B (2006) Guía ilustrada de géneros Melastomataceae y Memecylaceae de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; Univerisad del Cauca. Bogotá D. C.
- Mendoza-Cifuentes H, Fernández-Alonso JL (2010) Evaluación de caracteres del cáliz y de los estambres en la tribu Merianieae (Melastomataceae) y definición de homologías. *Revista de la Academia Colombiana de Ciencias* 34: 143–172.
- Michelangeli FA, Nicolas A, Morales-P ME, David H (2011) Phylogenetic Relationships of Allomaiaeta, Alloneuron, Cyphostyla, and Wurdastom (Melastomataceae) and the Resurrection of the Tribe Cyphostyleae. *International Journal of Plant Sciences* 172:1165–1178. <https://doi.org/10.1086/662032>
- Michelangeli FA, Guimaraes PJF, Penneys DS, et a (2013) Phylogenetic relationships and distribution of New World Melastomeae (Melastomataceae). *International Journal of Plant Sciences* 171:38–60. <https://doi.org/10.1111/j.1095-8339.2012.01295.x>
- Minnaar C, de Jager ML, Anderson B (2019) Intraspecific divergence in floral-tube length promotes asymmetric pollen movement and reproductive isolation. *New Phytologist* 224:1160–1170. <https://doi.org/10.1111/nph.15971>
- Morley T (1976) Memecyleae (Melastomataceae). New York Botanical Garden Press on behalf of the Organization for Flora Neotropica.
- Müller F (1882) Two kinds of stamens with different functions in the same flower. *Nature* 26:386. <https://doi.org/10.1038/026386b0>
- Oliveira FS (2016) Ecologia da polinização e análise da composição química do óleo floral de duas espécies de Mouriri (Melastomataceae) e sua importância na atração dos visitantes florais. Programa de Pós-graduação em Rede de Biodiversidade e biotecnologia da Amazônia Legal. Amazonas, Brazil.
- Oliveira LC (2019) Oferta de recursos e polimorfismos florais em uma flor de pólen. Universidade Federal de Uberlândia. Minas Gerais, Brazil

- Oliveira LC, Teixido AL, Trevizan R, Brito VLG (2020) Bee-mediated selection favors floral sex specialization in a heterantherous species: strategies to solve the pollen dilemma. *Plants* 9:1–16. <https://doi.org/10.3390/plants9121685>
- Penneys DS, Michelangeli FA, Judd WS, Almeda F (2010) Henrietteae (Melastomataceae): A new neotropical berry-fruited tribe. *Systematic Botany* 35:783–800. <https://doi.org/10.1600/036364410X539862>
- Penneys DS, Judd WS (2011) Phylogenetics and morphology in the Blakeae (Melastomataceae). *International Journal of Plant Sciences* 172:78–106. <https://doi.org/10.1086/657284>
- Reginato M, Michelangeli FA (2016) Diversity and constraints in the floral morphological evolution of *Leandra* s.str. (Melastomataceae). *Annals of Botany* 118:445–458. <https://doi.org/10.1093/aob/mcw116>
- Renner S (1983) The widespread occurrence of anther destruction by *Trigona* bees in Melastomataceae. *Biotropica* 15: 251–256. <https://doi.org/10.2307/2387649>
- Renner S (1989) A survey of reproductive biology in neotropical Melastomataceae and Memecylaceae. *Annals of the Missouri Botanical Garden*. 76:496
- Renner S (1990) A revision of *Rhynchanthera* (Melastomataceae). *Nordic Journal of Botany* 9:601–630. <https://doi.org/10.1111/j.1756-1051.1990.tb00551.x>
- Renner S (1993) Phylogeny and classification of the Melastomataceae and Memecylaceae. *Nordic Journal of Botany* 13:519–540. <https://doi.org/10.1111/j.1756-1051.1993.tb00096.x>
- Rocha MJR, Batista JAN, Guimarães PJF, Michelangeli FA (2016) Phylogenetic relationships in the Marcetia alliance (Melastomeae, Melastomataceae) and implications for generic circumscription. *Botanical Journal of the Linnean Society* 181:585–609. <https://doi.org/10.1111/boj.12429>
- Rocha MJR, Guimarães PJF, Michelangeli FA, Nogueira Batista JA (2017) Taxonomy of Marcetiae: A New Neotropical tribe of Melastomataceae. *International Journal of Plant Sciences* 179:000–000. <https://doi.org/10.1086/694932>
- Saab GS, Mansano VF, Nogueira A, Maia IC, Bergamo PJ, Paulino JV (2021) A sophisticated case of division of labour in the trimorphic stamens of the *Cassia fistula* (Leguminosae) flower, *AoB PLANTS*, 13:5 <https://doi.org/10.1093/aobpla/plab054>
- Santos APM, Fracasso CM, Luciene dos Santos M, et al (2012) Reproductive biology and species geographical distribution in the Melastomataceae: a survey based on New World taxa. *Annals of Botany* 110:667–679. <https://doi.org/10.1093/aob/mcs125>
- Shepherd, KA and Wilkins CF (2017) A revision of the *Lasiopetalum floribundum* group (Malvaceae), including recognition of four new species. *Nuytsia* 28. 273–298.
- Solís-Montero L, Cáceres-García S, Alavez-Rosas D, et al (2018) Pollinator preferences for floral volatiles emitted by dimorphic anthers of a buzz-pollinated herb. *Journal of Chemical Ecology* 44:1058–1067. <https://doi.org/10.1007/s10886-018-1014-5>
- Telles FJ, Klunk CL, Maia FR da, et al (2020) Towards a new understanding of the

- division of labour in heterantherous flowers: The case of *Pterolepis glomerata* (Melastomataceae). *Biological Journal of the Linnean Society* 131:1–11. <https://doi.org/10.1093/biolinnean/blaa107>
- Tobe H, Raven P (1983) An embryological analysis of Myrtales: Its definition and characteristics. *Missouri Botanical Garden Press* 70:71–94
- Vallejo-Marín M, Manson JS, Thomson JD, Barrett SCH (2009) Division of labour within flowers: Heteranthery, a floral strategy to reconcile contrasting pollen fates. *Journal of Evolutionary Biology* <https://doi.org/10.1111/j.1420-9101.2009.01693.x>
- Vallejo-Marín M, Da Silva EM, Sargent RD, Barrett SCH (2010) Trait correlates and functional significance of heteranthery in flowering plants. *New Phytologist*. <https://doi.org/10.1111/j.1469-8137.2010.03430.x>
- Vallejo-Marín M (2019) Evolutionary tinkering allows buzz pollinated plants to escape from an adaptive dead-end. *New Phytologist* 221:618–620. <https://doi.org/10.1111/nph.15474>
- Varassin IG, Penneys DS, Michelangeli FA (2008) Comparative anatomy and morphology of nectar-producing Melastomataceae. *Annals of Botany* 102:899–909. <https://doi.org/10.1093/aob/mcn180>
- Veena V, Nampy S (2020) Heteromorphic stamen: a strategy in nectarless entomophilous plants to increase pollination efficiency? An investigation with regard to three species of Commelinaceae. *Plant Systematics and Evolution* 306:82. <https://doi.org/10.1007/s00606-020-01710-7>
- Velloso MSC, Brito VLG de, Caetano APS, Romero R (2018) Anther specializations related to the division of labor in *Microlicia cordata* (Spreng.) Cham. (Melastomataceae). *Acta Botanica Brasilica* 32:349–358. <https://doi.org/10.1590/0102-33062017abb0358>
- Veranso-Libalah MC, Stone RD, Fongod AGN, et al (2017) Phylogeny and systematics of African Melastomateae (Melastomataceae). *Taxon* 66:584–614. <http://doi.wiley.com/10.12705/663.5>
- Vogel S (1978) Evolutionary shifts from reward to deception in pollen flowers. *Pollination of Flowers by Insects* 89–96. London: Academic Press.
- Wilson CL (1950) Vasculature of the stamen in the Melastomaceae, with some phyletic implications. *American Journal of Botany* 37: 431–444. <https://doi.org/10.1002/j.1537-2197.1950.tb08193.x>

Chapter 3

Distribution of flower size and stamen dimetrism in Melastomataceae across the Neotropical region

Geographical distribution of flower size and stamen dimetrisism in Melastomataceae across the Neotropical region

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Abstract

The Neotropics is a region where Melastomataceae, an immensely diverse group of flowering plants (173 genera and about 5,858 species), thrives, mainly in tropical and subtropical regions. Within the Neotropics, this family has a wide distribution, demonstrating its remarkable adaptability and impressive biodiversity, with many Melastomataceae species found in the region being endemic. This suggests that such plants may require specific environmental conditions in order to grow and survive. In the third chapter of our study, we evaluate the geographical distribution of Melastomataceae species in terms of their flower sizes and the stamen dimetrisism. We also investigated the correlation between abiotic factors such as temperature, precipitation, and altitude with the distribution of these floral traits. We used the phylogenetic inference and phylogenetic comparative methods to test whether petal length and SDI are correlated with climate and elevation throughout the evolution of the Neotropical Melastomataceae. The analyses used 289 species with data on stamen length and 731 species with data on petal length, a proxy for flower size, as well as geographical distribution data for all these species. The distribution of stamen dimetrisism in the Melastomataceae family throughout the Neotropics is influenced by precipitation. Although a positive correlation between higher SDI values and large flowers has already been shown in the literature, in this work we did not find a relationship between the flower size distribution and the abiotic factors considered, only between SDI values and wetter regions.

Keywords: abiotic factors, climatic variability, floral traits, pollen flowers, pollination, elevational gradient.

Introduction

The Neotropics are characterized by their high plant diversity occurring in ecosystems such as rainforests, cloud forests and savannas (Rangel 1995; Martinelli 2007; Raven et al. 2020). The distribution of plants in the Neotropics is influenced by several factors, including climate, topography, historical and geological events, (Chaverri-Polini 1998; Martinelli 2007). For instance, the formation of the Andes Mountains has created a major barrier that influences plant distribution (Antonelli and Sanmartín 2011). The Neotropics are also known for their high levels of endemism (Vasconcelos et al. 2020) and studies indicate that high levels of precipitation and temperature are correlated with high species richness (Antúnez et al. 2021; Serna-González et al. 2021; Yao et al 2022). In addition, other studies have demonstrated biotic exchange between Neotropical biomes and altitudinal zones within the same biome, showing that altitude is also a driver in species distribution (Miola et al. 2021; Pérez-Escobar et al. 2022; Presley and Willig 2023). Plants interact with other organisms, including animals, and microorganisms, which also influence their distribution patterns (Martinelli 2007; Raven et al. 2020). Therefore, it is expected that plant distribution in the Neotropics is also influenced by ecological interactions such as competition, predation, and mutualism. However, how each of these biotic and abiotic factors influences plant distributions and traits is still poorly understood.

The Neotropics is a region where Melastomataceae, an immensely diverse group of flowering plants (173 genera and about 5,858 species), thrives, mainly in tropical and subtropical regions (Chaverri-Polini 1998; Ulloa Ulloa et al. 2022). Within the Neotropics, this family has a wide distribution, demonstrating its remarkable adaptability and impressive biodiversity, with many species found in the region being endemic (Bochorny et al. 2022; Pérez-Escobar et al. 2022). This suggests that such plants may require specific environmental conditions in order to grow and survive. Some Melastomataceae species have specialized pollination mechanisms, depending on specific insects or birds for successful reproduction. In these cases, the local occurrence of these pollinators may impact floral trait evolution in species occurring in an area (Dellinger et al. 2019). Most of the flowers of the Melastomataceae family are pollinated by bees and consist mainly of pollen flowers (Reginato et al. 2020).

Studies have already shown that vibrating bees favor the evolution of stamen dimetrisism in Melastomataceae flowers, which are dependent on these insects for their reproduction. Because of the dependence on these pollinators, it is essential to understand what role their distribution played in the evolution of Melastomataceae flowers and their traits (Settele et al. 2016; Melo et al. 2021). Bees have a bimodal distribution across the globe with diversity peaking in dry areas (Orr et al. 2021). In this sense, we understand that there is a negative relationship between precipitation and bee richness, suggesting that moisture may have a limiting effect on the distribution of bees (Ollerton 2017). The study also showed that this distributional pattern contrasts with other pollinator groups that tend to be richer near the equatorial tropics (Kindlmann et al. 2007; Orr et al. 2021). Therefore, given this co-dependency, we believe that Melastomataceae flowers with a higher SDI (Stamens Dimetrisism Index), which tend to be more dependent on bees for reproduction, will also be found in the same areas (Ollerton 2017; Melo et al. 2021). This dimetrisism, as well as stamen dimorphism in general, may be associated with specific pollination strategies that depend on pollinators with specialized sizes and behaviors in pollen grain removal (Konzmann et al. 2020; Melo et al. 2021; Melo et al. 2022).

The presence of dimorphic stamens also can be influenced by factors such as genetic variation, and selective pressures, beyond ecological interactions with pollinators (Ollerton 2017; Dellinger et al. 2022). Plants that are pollinated by vibration, for example, are visited by vibrating bees capable of extracting pollen grains from poricidal anthers, whereas other types of anther dehiscence do not require this type of specialized pollinator (Melo et al. 2022; Passos et al. 2022). Buzz pollination is a fascinating adaptation that demonstrates the diversity of reproductive strategies and the intricate relationships between plants and their pollinators.

In this sense, we use Melastomataceae species distribution data (Reginato et al. 2020) and morphological data for SDI (Melo et al. 2021), and petal length to: (1) estimate the geographic distribution of stamen dimetrisism and petal length in the Melastomataceae family; and (2) investigate how the abiotic factors like temperature, precipitation, and altitude - are related to the distribution of traits (stamen dimetrisism and petal size). Our hypotheses are: species with larger petal size and SDI would be present in drier regions with higher elevation and lower temperatures, while species with SDI and smaller petals would be in lower altitude regions, with higher precipitation rates and higher temperatures.

Methods

Distribution and climatic data

To visualize the distribution of Melastomataceae species with different petal sizes and SDI values, and to gather climatic data to test our hypotheses, shapefiles representing the distribution of Melastomataceae species were downloaded from the database of Reginato et al. (2020). In that study, they used filtered occurrence data to model the distribution of 1395 Melastomataceae species. Range sizes were estimated for all species based on their filtered records and climatic niche models, based on the 19 climatic variables from the WorldClim (2.5 spatial resolution; Fick and Hijmans 2017). To assess associations between floral traits and climate, we downloaded layers for mean annual temperature (bio1, $\times 10^\circ\text{C}$), mean annual precipitation (bio12, mm^3) and altitude (m) from the Worldclim dataset. The *raster* (Hijmans 2016), *maptools* (Bivand and Lewin-Koh, 2013), and *sp* (Pebesma and Bivand 2005) R packages were used to create the maps and overlay the shapefiles with the climatic layers. We then extracted climatic values for each point where the shapefile intersected with each climatic layer and calculated the median values for each species based on the three layers of interest.

Morphological data

Values of Stamens Dimetrisism Index (SDI) for 336 species of Melastomataceae were downloaded from Melo et al. (2021). We also updated this data with stamen data from new species descriptions that were published between 2019 and April 2023. After this effort, we got information on stamen size for a total of 438 species. Of these, 289 species had data for both stamen length and distribution and were thus kept for further analyses (supporting Information Table SI 1). Petal length data, a proxy for flower size, were collected for 1936 species of Melastomataceae. Of those, 731 species also had distribution data, and these were therefore selected for further analyses (supporting Information Table SI 2). These data were extracted from published articles through a data mining method, which consists of searching and compiling information using artificial intelligence that allows the location of the terms of interest (Reginato et al. in review). Through this method, the logarithm of the average petal length (mm) was collected. These data were then checked individually and manually, confronted with the source articles when there was doubt or divergence, in order to avoid errors. All species names were

updated according to the *MelNames* website database (Renner et al. 2007 onwards). As there is a greater concentration of Melastomataceae species in the Neotropical region in our dataset compared to the scarcity of species in other areas, we will focus our results and discussion on this region.

Phylogenetic data

For this study, we used the phylogenetic analysis of Melastomataceae performed by Penneys et al. (2022), based on DNA sequence data from the ETS and ITS core ribosomal regions in combination with seven plastid regions (*accD-psaI* + *atpF-atpH* + *ndhF* + *psbK-psbL* + *rbcL* + *rpl16* + *trnS-trnG*), covering 2973 terminals (of which 32 form the outgroup), 2435 melastome species and 158 of the 177 currently recognized genera.

Phylogenetic Linear Model

We used the phylogenetic inference of Penneys et al. (2022) and phylogenetic comparative methods to test whether petal length and SDI are correlated with climate and elevation throughout the evolution of the Neotropical Melastomataceae. We used the *ape* package (Paradis and Schliep 2019) to load the phylogenetic tree and the *phylolm* - package version 2.6.2 - to fit a phylogenetic logistic regression. In this function, the likelihood is calculated with an algorithm that is linear in the number of tips in the tree, considering the following evolutionary models: Brownian motion which assumes that traits evolve randomly (*BM*); Orsntein-Uhlenbeck with the ancestral state estimated at the base/root of the phylogeny (*OUfixedRoot*); Orsntein-Uhlenbeck with a stationary ancestral state distribution (*OURandomRoot*); *Pagel's lambda*, which scales the tree from its original form to a "star" phylogeny and thus quantifies whether the data fit a tree-based model or one where all species are independent; *kappa*, which scales branch lengths between their original values and mimics a speciation model of evolution (but only if all species are sampled and there has been no extinction); *delta*, which captures changes in the rate of trait evolution over time; and *Brownian motion with trend*. The phylogenetic linear regression was performed considering the evolutionary history of the species and comparing the AIC values between the evolutionary models.

Results

Geographical distribution of floral size and stamens dimetrisism index

Our results show that, considering the 289 species sampled, high mean values of stamen dimetrisism are concentrated mainly in the southeastern and northeastern regions of Brazil, along the Serra do Espinhaço and in the Atlantic Forest region (Fig. 1A). Furthermore, considering 731 species of Melastomataceae, it was observed that larger flowers are more common in South America, especially in Colombia and Venezuela, and in Central America, mainly in Costa Rica and Panama (Fig. 1B). The maps show that the diversity of species with large flowers tends to be higher in areas of higher altitude. On the other hand, smaller flowers were found to be more widely distributed in areas of lower altitude in South America, Mesoamerica, and Southeast United States. Species with medium or high SDI values tend to be more concentrated in certain regions, such as southeastern Brazil, but also in Central America. Lower SDI values, however, are more widely distributed throughout the Neotropics. The wide range of habitats in which Melastomataceae species can thrive is highlighted by this diverse distribution across different ecosystems.

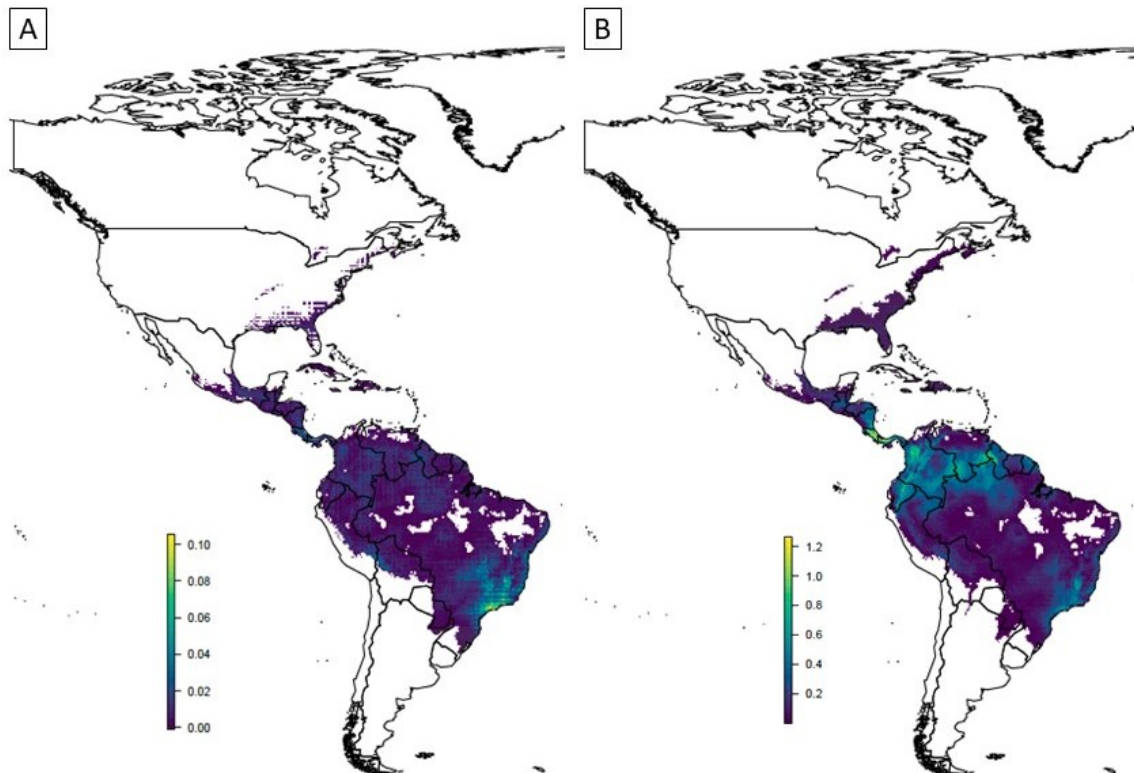


Figure 1: A - SDI distribution | B – Floral size distribution

Phylogenetic linear regression

The best model (“lambda”) shows a positive relationship between SDI values and precipitation ($t = 2.7278$; $R^2 = 0.02948$; $p = 0.006$), but not with temperature and altitude (supporting information Table SI 3). For flower size, the best model (“lambda”) did not show any significant relationship between flower size and the abiotic variables, considering the evolutionary history (Fig.2) - the results of the other models can be found on the supporting information Table SI 3 and SI 4.

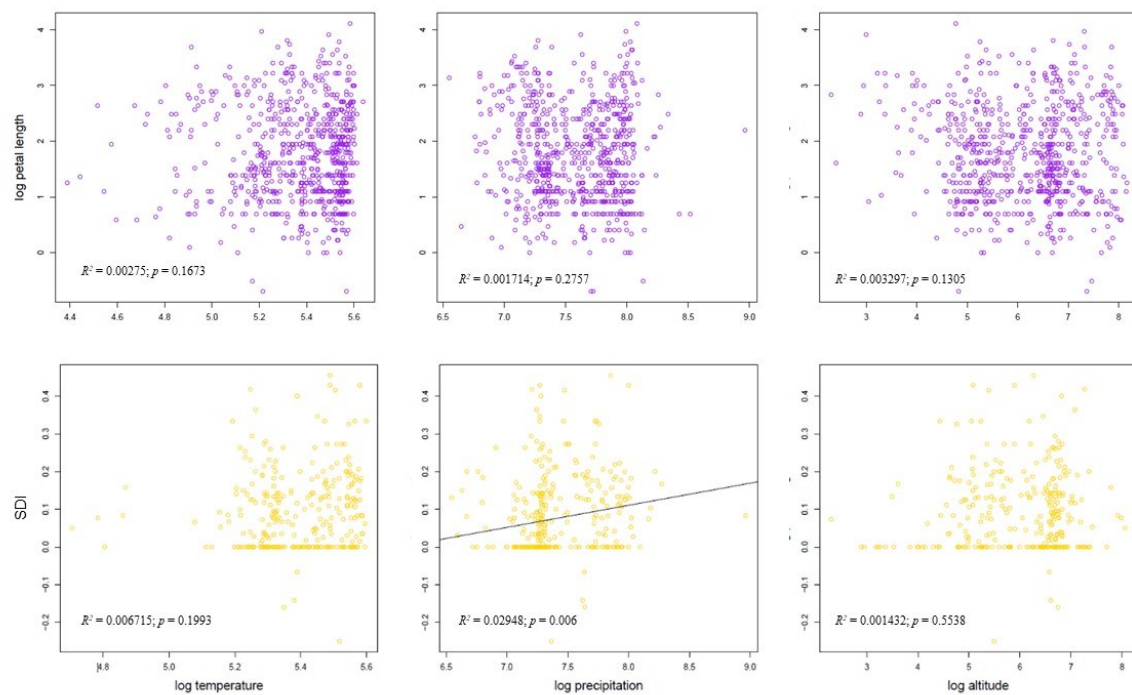


Figure 2: Phylogenetic linear regression considering the best model "lambda" for both traits. The purple dots show the distribution of flower size (petal length) with no significant result, while the yellow dots show the distribution of SDI values. The logarithm of precipitation is positively correlated with the SDI.

Discussion

Geographical distribution of floral size and stamens dimetrisism

Our analyses allow us to identify the uneven distribution of stamen dimetrisism and petal size in Melastomataceae species, and thus to better understand their evolutionary history in the face of abiotic factors such as temperature and precipitation at different altitudes. They also allow us to discuss biotic factors that may indirectly determine this distribution, such as the presence of specific pollinators, which play a crucial role in

understanding the distribution and diversification of the family (Dellinger et al. 2023). This understanding contributes to our knowledge of plant-pollinator interactions in diverse ecosystems by shedding light on the co-evolutionary processes between plants and their pollinators (Bochorny et al. 2021; Dellinger et al. 2023).

Despite the pantropical nature of the family, most genera have a restricted distribution (Reginato et al. 2022; Ulloa-Ulloa et al. 2022). In the Neotropical region alone, there are more than 80 genera and 3500 species of Melastomataceae. In contrast, the entire Old World Melastomataceae has about 89 genera and about 2,000 species (Ulloa-Ulloa et al. 2022). From the analysis of the maps, we observed that among the sampled species, the largest flowers are predominantly found in Central and South America (Fig. 1). Several studies exploring biographical history, interactions with pollinators, and taxonomic descriptions of genera such as *Axinaeae*, *Triolena*, *Pleroma*, *Tibouchina*, *Blakea*, and *Lavoisiera* provide further evidence of the prevalence of large flowers in these regions (Mendonza and Ramirez 2006; Penneys and Judd 2011; Brito et al. 2015; Bacci et al. 2019; Fernández-Fernández et al. 2020; Pacífico and Almeda, 2022; Reginato et al. 2022). Despite the maps suggesting a positive relationship between altitude and flower size, our analyses with phylogenetic correction indicate that there is not (Fig. 1).

In this work, no relationship between the distribution of flower size and the abiotic factors considered was observed when considering the phylogeny, despite the indication on the maps. This may indicate that the spatial variation of this trait is more related to biotic factors, such as pollinator dependence. Melo et al. (2021) showed that flower size in Melastomataceae is positively correlated with higher stamen dimetrisism index (SDI), and smaller flowers with lower SDI are less dependent on pollinators for reproduction. Other studies have also shown the wide distribution of some genera with small flowers, including *Acisanthera*, *Aciotis*, *Comolia*, *Conostegia*, *Dissochaeta*, *Macairea*, *Miconia*, *Mouriri*, and *Memecylon* (Kriebel 2016; Kartonegoro et al. 2022; Oliveira et al. 2022; Reginato et al. 2022).

The potential indirect effect of abiotic factors in shaping plant-pollinator interactions

Variations in average temperature and water availability have a direct impact on which animals can survive and pollinate in certain locations (Lawson and Rand 2019).

Considering that some animals, such as vertebrates, are endothermic and therefore more resistant to climate variation, it is expected that they will be found in high elevation ecosystems. Among Melastomataceae, this relationship exists in a minority of species. Therefore, both biotic (the presence or exchange of pollinators) and abiotic (temperature and precipitation) factors may influence the distribution of species along the elevational gradient, as proposed by Cruden (1972). Plants that depend on pollinators and are present in these places, have flowers with some traits as an attractive resource for their interactors (*e.g.*, bulbous stamen, nutritious tissue, striking colors, larger sizes) (Dellinger et al. 2014; Dellinger et al. 2022; Luna et al. 2023). On the other hand, ectothermic animals, such as invertebrates, being less resistant to extreme conditions, would be present in places with milder conditions. These insects are the pollinators for the majority of Melastomataceae species. Though this distribution pattern is expected, some work has shown that bees decrease in abundance and richness along elevation gradients, while flies replace bees as the dominant floral visitors in higher elevation systems (McCabe and Cobb 2021). In addition, other works have shown that bumblebees and some flies are able to regulate their body temperature and manage to survive in cold regions (Oyen and Dillon 2016).

The high diversity of bee species in arid and warm regions can facilitate our comprehension of the reason why areas with high temperatures exhibit greater stamen dimorphism - as shown on the maps. However, the result of phylogenetic regression does not support this pattern. This may be due to the strong interdependence between these insects and the flowers that rely on them to ensure their reproductive success. Furthermore, it is observable higher levels of SDI in locations with high precipitation. In this case, a greater difference in stamen size in places with high rainfall may indicate a greater specialization in the interactions. Humidity can be detrimental to the quality and collection of pollen grains, but in these flowers with high stamen dimorphism, the division of labour between the anthers may be a solution (Orr et al. 2021; Melo et al. 2021). Most Melastomataceae flowers have poricidal anthers, which are divided between feeding and pollinating anthers. The first provides the resource that, thanks to their vibrational capacity, are able to collect the pollen grains, while the second protects the male gametes, which are used for plant reproduction and must therefore be deposited in safe sites (Luo et al. 2008; Telles et al. 2020).

The distribution of Melastomataceae species is directly influenced by the availability of pollinators (mainly bees) and may be under greater selection pressure due to the presence of these pollen vectors in the regions where they occur. Furthermore, there

are species that are independent of pollinators for reproductive success, such as apomictic species, but which are also subject to environmental variation such as climate (temperature and precipitation) and availability of water and nutrients (soil conditions). Thus, apomictic species are understood to be associated with wide distributions, whereas sexual species have more restricted distributions (Santos et al. 2012; Oyen and Dillon 2016; Caetano et al. 2018; Melo et al. 2021; Luna et al. 2023).

Future research is needed to deepen our understanding of the factors that influence these distribution patterns and the significance of larger flowers in specific geographic regions, as well as to better understand the importance of stamen dimetrisism in the distribution of Melastomataceae in the Neotropics. The influence of latitude was not considered in this study, but more recent research indicates that it can be a good predictor in species distribution analyses, especially when related to climatic and biotic factors in elevational gradients (Dellinger et al. 2023).

Conclusion

The distribution of stamen dimetrisism in the Melastomataceae family throughout the Neotropics is influenced by precipitation. Although a positive correlation between higher SDI values and large flowers has already been shown in the literature, in this work we did not find a relationship between the flower size distribution and the abiotic factors considered, only between SDI values and wetter regions. More studies are needed considering other abiotic factors, such as latitude and also the biotic factors and interactions present in ecosystems so that we can have more clarity about which selection factors actually have an impact on the distribution of these traits.

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References

- Antonelli A, Sanmartín I (2011) Why are there so many plant species in the Neotropics? *Taxon*, 60: 403-414. <https://doi.org/10.1002/tax.602010>
- Antúnez P, Wehenkel C, Kukunda CB, Hernández-Díaz JC (2021) Climatic variables differentially influence neotropical plant species of conservation concern. *Journal of Sustainable Forestry*, 42, 43 - 58. <https://doi.org/10.1080/10549811.2021.1944878>

- Bacci LF, Michelangeli FA, Goldenberg R (2019) Revisiting the classification of Melastomataceae: implications for habit and fruit evolution. *Botanical Journal of the Linnean Society*, 190(1), 1-24 <https://doi.org/10.1093/botlinnean/boz006>
- Benites VM, Simas FNB, Schaefer CEGR, Santos HG, Mendonça BAF (2007) Soils associated to rock outcrops in the highlands of Serras da Mantiqueira and Espinhaço, southeastern Brazil. *Revista Brasileira de Botânica* 30. <https://doi.org/10.1590/S0100-84042007000400003>
- Bochorny T, Bacci LF, Dellinger AS, Michelangeli FA, Goldenberg R, Brito VD (2021) Connective appendages in *Huberia bradeana* (Melastomataceae) affect pollen release during buzz pollination. *Plant Biology*, 23(4), 556-563. <https://doi.org/10.1111/plb.13244>
- Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Bolker BM (2017) *glmmTMB* balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal*, 9(2), 378-400. <https://doi.org/10.1101/132753>
- Caetano APS, Cortez PA, Teixeira SP, Oliveira PE, Carmello-Guerreiro SM (2018) Unusual diversity of apomictic mechanisms in a species of *Miconia*, Melastomataceae. *Plant Systematics and Evolution*, 304(3), 343-355. <https://doi.org/10.1007/s00606-017-1480-1>
- Chaverri-Polini A (1998) Mountains, biodiversity and conservation. *Unasylva-FAO*-, 47-54.
- Cruden RW (1972) Pollinators in high elevation ecosystems: relative effectiveness of birds and bees. *Science*, 176, 1439-1440.
- Dellinger AS, Pérez-Barrales R, Michelangeli FA, Penneys DS, Fernández-Fernández DM, Schoenenberger J (2021) Low bee visitation rates explain pollinator shifts to vertebrates in tropical mountains. *New Phytologist*, 231(2), 864-877.
- Dellinger AS, Hamilton AM, Wessinger CA, Smith SD (2023) Opposing patterns of altitude-driven pollinator turnover in the tropical and temperate Americas. *The American Naturalist*, 202(2), 000-000. <https://doi.org/10.1086/725017>
- Dellinger AS, Kopper C, Kagerl K, Schönenberger J (2022) Pollination in Melastomataceae: a family-wide update on the little we know and the much that remains to be discovered. In *Systematics, Evolution, and Ecology of Melastomataceae*. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-030-99742-7_26
- Hartig F (2017) Package ‘DHARMa’. R package.
- Ho LST, Ane C (2014) A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology* 63(3):397-408. <https://doi.org/10.1093/sysbio/syu005>
- Kartonegoro A, Kadereit G, Veranso-Libalah MC (2022) Systematics and phylogeny of Dissochaeteae. In *Systematics, Evolution, and Ecology of Melastomataceae*. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-030-99742-7_16
- Kindlmann P, Dixon AFG (2007) Inverse latitudinal gradients in species diversity. In *Scaling Biodiversity*, D. Storch, P.A. Marquet, and J.H. Brown, eds. (Cambridge: Cambridge University Press). <https://doi.org/10.1017/CBO9780511814938.014>
- Konzmann S, Hilgendorf F, Niester C, Rech AR, Lunau K (2020) Morphological specialization of heterantherous *Rhynchanthera grandiflora* (Melastomataceae) accommodates pollinator diversity. *Plant Biology*, 22(4), 583-590. <https://doi.org/10.1111/plb.13102>
- Kreft H, Jetz W (2007) Global patterns and determinants of vascular plant diversity. *Proc. Natl. Acad. Sci. U.S.A.* 104: 5925–5930. <https://doi.org/10.1073/pnas.0608361104>
- Lauriano MH, Romero R (2022) Melastomataceae Juss. do Complexo de Serras da Bocaina e de Carrancas, Estado de Minas Gerais, Brasil: inventário e comparação florística. *Hoehnea*, 49. <https://doi.org/10.1590/2236-8906-54/2021>
- Lawson DA, Rands SA (2019) The effects of rainfall on plant–pollinator interactions. *Arthropod-Plant Interactions* 13, 561–569 <https://doi.org/10.1007/s11829-019-09686-z>

- Luna P, Villalobos F, Escobar F, et al. (2023) Temperature dissimilarity drives flower–visitor interaction turnover across elevation in the Mexican Transition Zone. *Journal of Biogeography*. <https://doi.org/10.1111/jbi.14684>
- Luo Z, Zhang D, Renner SS (2008) Why two kinds of stamens in buzz-pollinated flowers? Experimental support for Darwin's division-of-labour hypothesis. *Functional Ecology*, 22(5), 794-800. <https://doi.org/10.1111/j.1365-2435.2008.01444.x>
- Martinelli G (2007) Mountain biodiversity in Brazil. *Brazilian Journal of Botany*, 30, 587-597. <https://doi.org/10.1590/S0100-84042007000400005>
- McCabe LM, Cobb NS (2021) From bees to flies: global shift in pollinator communities along elevation gradients. *Frontiers in Ecology and Evolution*, 8, 626124.
- Miola DT, Ramos VD, Silveira FA (2021) A brief history of research in campo rupestre: identifying research priorities and revisiting the geographical distribution of an ancient, widespread Neotropical biome. *Biological Journal of the Linnean Society*, 133(2), 464-480. <https://doi.org/10.1093/biolinnean/blaa175>
- Oliveira LC, Matias R, Furtado MT, Romero R, Brito VLG (2022) What explains the variation in length of stamens and styles in a pollen flower? a study exemplified by *Macairea radula* (Melastomataceae). *Plant Systematics and Evolution*, 308(2), 15. <https://doi.org/10.1007/s00606-022-01808-0>
- Ollerton J (2017) Pollinator diversity: distribution, ecological function, and conservation. *Annu. Rev. Ecol. Evol. Syst.* 48, 353–376. <https://doi.org/10.1146/annurev-ecolsys-110316-022919>
- Orr MC, Hughes AC, Chesters D, Pickering J, Zhu CD, Ascher JS (2021) Global patterns and drivers of bee distribution. *Current Biology*, 31(3), 451-458. <https://doi.org/10.1016/j.cub.2020.10.053>
- Oyen KJ, Giri S, Dillon ME (2016) Altitudinal variation in bumble bee (*Bombus*) critical thermal limits. *Journal of Thermal Biology*, 59, 52-57. <https://doi.org/10.1016/j.jtherbio.2016.04.015>
- Pacifico R, Almeda F (2022) Lavoisiereae: A Neotropical tribe with remarkable endemism on eastern Brazilian mountaintops. In *Systematics, evolution, and ecology of Melastomataceae* (pp. 385-408). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-030-99742-7_19
- Paradis E, Schliep K (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528.
- Passos LS, Telles FJ, Goldenberg R, Amano E, Maia FR (2022) What is the role of stamen appendages in the buzz-pollinated *Huberia insignis* (Melastomataceae)? *Flora*, 293, 152113. <https://doi.org/10.1016/j.flora.2022.152113>
- Pérez-Escobar OA, Zizka A, Bermúdez MA, Meseguer AS, Condamine FL, Hoorn C, Hooghiemstra H, Pu Y, Bogarín D, Boschman LM, Pennington RT, Antonelli A, Chomicki G (2022) The Andes through time: evolution and distribution of Andean floras. *Trends in plant science*, 27(4), 364–378. <https://doi.org/10.1016/j.tplants.2021.09.010>
- Presley SJ, Willig MR (2023) Gradients and the Structure of Neotropical Metacommunities: Effects of Disturbance, Elevation, Landscape Structure, and Biogeography. In: Myster, R.W. (eds) *Neotropical Gradients and Their Analysis*. Springer, Cham. https://doi.org/10.1007/978-3-031-22848-3_15
- Rangel JO (1995) La diversidad florística en el espacio andino de Colombia. In *Biodiversity and conservation of neotropical montane forests*, proceedings (SP Churchill, H. Balslev, E. Forero & JL Luteyn, eds). New York Botanical Garden, New York (pp. 187-205).
- Raven et al. (2020) The distribution of biodiversity richness in the tropics. *Science Advances* .6, eabc6228 <https://doi.org/10.1126/sciadv.abc6228>
- Ribeiro KT, Medina BMO, Scarano FR (2007) Species composition and biogeographic relations of the rock outcrop flora on the high plateau of Itatiaia, SE-Brazil. *Revista Brasileira de Botânica* 30:623-639. <https://doi.org/10.1590/S0100-84042007000400008>
- Santos APM, Fracasso CM, Luciene dos Santos M, Romero R, Sazima M, Oliveira PE (2012) Reproductive biology and species geographical distribution in the Melastomataceae: a survey based on New World taxa. *Annals of Botany*, 110(3), 667-679. <https://doi.org/10.1093/aob/mcs125>

- Serna-González M, Urrego-Giraldo LE, Santa-Ceballos JP, Suzuki-Azuma H (2021) Flowering, floral visitors and climatic drivers of reproductive phenology of two endangered magnolias from neotropical Andean forests. *Plant Species Biology*. <https://doi.org/10.1111/1442-1984.12351>
- Settele J, Bishop J, Potts SG (2016) Climate change impacts on pollination. *Nat. Plants* 2, <https://doi.org/10.1038/nplants.2016.92>
- Telles FJ, Klunk CL, Maia FRD, Brito VLG, Varassin IG (2020) Towards a new understanding of the division of labour in heterantherous flowers: the case of *Pterolepis glomerata* (Melastomataceae). *Biological Journal of the Linnean Society*, 131(1), 1-11. <https://doi.org/10.1093/biolinnean/blaa107>
- Trevizan R, Caetano APS, Brito VLG, Oliveira PE, Telles FJ (2023) Stamen and pollen heteromorphism linked to the division of labour in Melastomataceae species. *Flora*, 152315. <https://doi.org/10.1016/j.flora.2023.152315>
- Ulloa Ulloa C, Almeda F, Goldenberg R, Kadereit G, Michelangeli FA, Penneys DS, Veranso-Libalah MC (2022) Melastomataceae: Global diversity, distribution, and endemism. In *Systematics, Evolution, and Ecology of Melastomataceae* (pp. 3-28). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-030-99742-7_1
- Vasconcelos TNC, Alcantara S, Andrino CO, Forest F, Reginato M, Simon MF, Pirani JR (2020) Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient Neotropical mountains *Proc. R. Soc.* <https://doi.org/10.1098/rspb.2019.2933>
- Wilkinson GN, Rogers CE (1973) Symbolic descriptions of factorial models for analysis of variance. *Applied Statistics*, 22, 392–399. <https://doi.org/10.2307/2346786>
- Yao Z, Xin Y, Yang L, Zhao L, Ali A (2022) Precipitation and temperature regulate species diversity, plant coverage and aboveground biomass through opposing mechanisms in large-scale grasslands. *Frontiers in plant science*, 13, 999636. <https://doi.org/10.3389/fpls.2022.999636>

Supporting Information

Table S11 – List of 289 species with stamen dimetrisism index (SDI) values and mean annual temperature (bio1, x10°C), mean annual precipitation (bio12, mm³), and altitude (m) from the Worldclim dataset.

Species	SDI	temperature	precipitation	altitude
<i>Aciotis_acuminifolia</i>	0.076923077	261	2392	145
<i>Aciotis_circaeifolia</i>	0.0625	269	2244	66
<i>Aciotis_indecora</i>	0.042253521	258	2653	139
<i>Aciotis_paludosa</i>	0	223	1294	268
<i>Aciotis_rubricaulis</i>	0.156626506	240	2596	528
<i>Acisanthera_hedyotoidea</i>	0.210526316	243	1617	106
<i>Acisanthera_limnobios</i>	0.428571429	242	1435	362
<i>Acisanthera_quadrata</i>	0.166666667	238	1601	228
<i>Acisanthera_uniflora</i>	0.034482759	267	2417	223
<i>Acisanthera_variabilis</i>	0.066666667	205	1443	725
<i>Allomaieta_ebejicosana</i>	0	166	2477.5	2213.5
<i>Allomaieta_pancurana</i>	0	217	2831.5	1269.5
<i>Allomaieta_zenufanasana</i>	0	204.5	3281.5	1498
<i>Alloneuron_ulei</i>	0.103448276	247	3570	332
<i>Arthrostemma_ciliatum</i>	0.272727273	240	2271	497
<i>Arthrostemma_primaevum</i>	0.417721519	190	1346	1431
<i>Axinaea_affinis</i>	0.076923077	119.5	1164	2934
<i>Axinaea_costaricensis</i>	0	188	2304	1431
<i>Axinaea_macrophylla</i>	0.083333333	129	1473.5	2743
<i>Behuria_comosa</i>	0	217	1249	513
<i>Bellucia_grossularioides</i>	0.014409222	265	2274	146
<i>Bellucia_spruceana</i>	0.014245014	259	2695	180
<i>Bertolonia_maculata</i>	0	240	1228	121
<i>Bertolonia_mosenii</i>	0	181	1553	692
<i>Blakea_storkii</i>	0.135135135	206	2932	1122
<i>Blakea_wilsoniorum</i>	0	199	2982	1255
<i>Bredia_quadragularis</i>	0.333333333	180	1746	188
<i>Calvoa_orientalis</i>	0	232	1624	778
<i>Calycogonium_bissei</i>	0	224.5	1553	531.5
<i>Cambessedesia_corymbosa</i>	0.230769231	201	1437	900
<i>Cambessedesia_eichleri</i>	0.1	234	1166	302
<i>Cambessedesia_espora</i>	0.095238095	206	1439	853
<i>Cambessedesia_gracilis</i>	0.2	205	789	1056
<i>Cambessedesia_hilariana</i>	0.142857143	215	1357	802
<i>Cambessedesia_membranacea</i>	0.263157895	231	1001	764
<i>Centradenia_floribunda</i>	0.1	224	1644.5	920.5
<i>Centradenia_grandifolia</i>	0.19047619	197	1918.5	1240
<i>Centradenia_inaequilateralis</i>	0.333333333	238	2292.5	484.5
<i>Chaetostoma_armatum</i>	0.28	199	1401	860
<i>Charianthus_nodosus</i>	0.108910891	241	2493	284

<i>Clidemia_biserrata</i>	0.047619048	232	1262	367
<i>Clidemia_capitellata</i>	0	244	1986	336
<i>Clidemia_debilis</i>	0.074074074	235	1122	229
<i>Clidemia_epibaterium</i>	0	261	2809	135
<i>Clidemia_heteroneura</i>	0.027027027	262	3093	142
<i>Clidemia_japurensis</i>	0	263	2509	121
<i>Clidemia_rubra</i>	0	263	2482	188
<i>Clidemia_sericea</i>	0	251	2219	331
<i>Clidemia_urceolata</i>	0	208	1335	642
<i>Comolia_microphylla</i>	0.125	265	2098	140
<i>Comolia_ovalifolia</i>	0.034482759	243	1345.5	99
<i>Comolia_smithii</i>	0.186046512	262	2680.5	102
<i>Comolia_vernicosa</i>	0.176470588	261	2204	112
<i>Comolia_villosa</i>	0.181818182	266	2091	102
<i>Conostegia_bigibbosa</i>	0.052631579	173.5	3039	1666.5
<i>Conostegia_bracteata</i>	0.130434783	255	3004	209
<i>Conostegia_brenesii</i>	0.074074074	206	3517	1111
<i>Conostegia_caelestis</i>	0.047619048	242	2477	332
<i>Conostegia_centronioides</i>	0.186440678	233	2121	517
<i>Conostegia_cinnamomea</i>	0.133333333	255	2725	230.5
<i>Conostegia_cuatrecasii</i>	0	247	2737	323
<i>Conostegia_extinctoria</i>	0.11627907	219	2773.5	1185
<i>Conostegia_icosandra</i>	0.161290323	244	2337	290.5
<i>Conostegia_jaliscana</i>	0	184	1236	1564
<i>Conostegia_lasiopoda</i>	0.2	254	3706	283
<i>Conostegia_micrantha</i>	0.222222222	247	2772	276
<i>Conostegia_montana</i>	0.090909091	249	2762	220
<i>Conostegia_monteleagreana</i>	0.2	193	2886.5	1562.5
<i>Conostegia_oerstediana</i>	0.125	206	2905	1117
<i>Conostegia_pittieri</i>	0.125	191.5	2900	1356
<i>Conostegia_plumosa</i>	0.128205128	249	1698	294
<i>Conostegia_polyandra</i>	0.166666667	259	3917	37
<i>Conostegia_pyxidata</i>	0.142857143	230	2465	640
<i>Conostegia_rhodopetala</i>	0.181818182	249	3043	311
<i>Conostegia_rubiginosa</i>	0.083333333	266	7807	85.5
<i>Conostegia_rufescens</i>	0.076923077	243	3053	423
<i>Conostegia_setosa</i>	0.157894737	256	2980	170
<i>Conostegia_speciosa</i>	0.238095238	256	2219	160
<i>Conostegia_subcrustulata</i>	0.111111111	255	2731.5	161
<i>Conostegia_superba</i>	0.179487179	229	2634	761
<i>Conostegia_tenuifolia</i>	0.176470588	245	2804	337
<i>Conostegia_volcanalis</i>	0.066666667	213	1503.5	1047
<i>Conostegia_xalapensis</i>	0.272727273	247	1822	362
<i>Desmoscelis_villosa</i>	0.176470588	239	1503	462
<i>Dolichoura_spiritusanctensis</i>	0	227.5	1189	337
<i>Henriettea_martiusii</i>	0	269	2633	83

<i>Henriettea_uniflora</i>	0	253	937	299
<i>Huberia_ovalifolia</i>	0	233	1168	199
<i>Lavoisiera_alba</i>	0.136363636	199	1439.5	936
<i>Lavoisiera_caryophyllea</i>	0.095238095	204	1441	815.5
<i>Lavoisiera_cordata</i>	0.084745763	203	1450	841
<i>Lavoisiera_crassifolia</i>	0.263157895	210	1273	782
<i>Lavoisiera_imbricata</i>	0.076923077	204	1408	866
<i>Lavoisiera_macrocarpa</i>	0.133333333	204	1444	814
<i>Lavoisiera_mucorifera</i>	0.227272727	205	1390	829
<i>Lavoisiera_pulchella</i>	0.092307692	173	1410	883
<i>Lavoisiera_subulata</i>	0.161290323	204	1437	812
<i>Leandra_amplexicaulis</i>	0.139896373	188	1464	731
<i>Leandra_aspera</i>	0.083798883	184.5	1349.5	1043.5
<i>Leandra_aurea</i>	0	200	1435	799
<i>Leandra_cancellata</i>	0	199	1453	914
<i>Leandra_eichleri</i>	0	169	1528	903
<i>Leandra_erostrata</i>	0	191	1436	857
<i>Leandra_foveolata</i>	0	197	1427	797
<i>Leandra_glazioviana</i>	0.166666667	191	1494	713
<i>Leandra_hirta</i>	0	201	1368	601
<i>Leandra_lapae</i>	0.085271318	177.5	1762.5	766.5
<i>Leandra_melastomoides</i>	0.058823529	201	1423	742
<i>Leandra_pennipilis</i>	0	189	1536	1028
<i>Leandra_polystachya</i>	0.04	190	1496	889
<i>Leandra_quinquedentata</i>	0	183	1527	812
<i>Leandra_reversa</i>	0	206	1344	521
<i>Leandra_salicina</i>	0	201	1482	965
<i>Leandra_sericea</i>	0.125827815	190	1449	776
<i>Leandra_tetraquetra</i>	0.066666667	178	1584	715
<i>Leandra_therezopolitana</i>	0.065989848	160.5	1800	1324.5
<i>Leandra_ulaei</i>	0.141176471	182	1568	467
<i>Leandra_umbellata</i>	0.259259259	202	1436	806
<i>Leandra_variabilis</i>	0	190	1495	631.5
<i>Lijndenia_danguyana</i>	0.133333333	200	1952	735
<i>Lijndenia_roborea</i>	0.133333333	238	2815	33
<i>Macairea_radula</i>	0.346405229	233	1435.5	636
<i>Maieta_guianensis</i>	0	257	2753	207
<i>Marcetia_acerosa</i>	0.363636364	193	1400	1183
<i>Marcetia_taxifolia</i>	0.090909091	212	1265	744
<i>Medinilla_stephanostegia</i>	0	187	2135.5	1586
<i>Medinilla_suberosa</i>	0	236	2406	74
<i>Memecylon_batekeanum</i>	0	242.5	1943	459.5
<i>Memecylon_buxifolium</i>	0	259	1095	24
<i>Memecylon_erythranthum</i>	0	253	1166	146
<i>Memecylon_flavovirens</i>	0	204	1161	1318
<i>Memecylon_germainii</i>	0	239	1637	687.5

<i>Memecylon_greenwayi</i>	0	233	2242.5	213.5
<i>Memecylon_sitanum</i>	0	258	2259	47
<i>Meriania_brevipedunculata</i>	-0.06626506	219	2072	716
<i>Meriania_parvifolia</i>	-0.141304348	217	2047	738
<i>Meriania_purpurea</i>	0.019138756	251	1909	247
<i>Meriania_squamulosa</i>	-0.15942029	210.5	2079.5	850
<i>Merianthera_bullata</i>	0.127272727	208	1262	693
<i>Merianthera_eburnea</i>	0.184	209	899	886
<i>Merianthera_parvifolia</i>	0.125	235	1193	278
<i>Merianthera_verrucosa</i>	0.117647059	207	1284	718
<i>Miconia_alata</i>	0.175438596	265	2307	124
<i>Miconia_albicans</i>	0	235	1402	479
<i>Miconia_alborufescens</i>	0	220	1254	780
<i>Miconia_argyrophylla</i>	0.14893617	264	2188	160
<i>Miconia_baumgratziana</i>	0	203	1395	568
<i>Miconia_brasiliensis</i>	0	200	1413	598.5
<i>Miconia_brunnea</i>	0	198	1461.5	701
<i>Miconia_budlejoides</i>	0	200	1408	619
<i>Miconia_capixaba</i>	0.079365079	203	1301	769
<i>Miconia_chamissois</i>	0	227	1413	621
<i>Miconia_chartacea</i>	0	200	1493	859
<i>Miconia_chrysophylla</i>	0.076923077	258	2254	213
<i>Miconia_ciliata</i>	0.230769231	254	1922	250
<i>Miconia_cinerascens</i>	0.253333333	187	1560	703
<i>Miconia_cinnamomifolia</i>	0.027027027	200	1416	698
<i>Miconia_corallina</i>	0.027777778	192	1475	927
<i>Miconia_crassinervia</i>	0.125	258	2400	243
<i>Miconia_cubatanensis</i>	0	197	1493	848
<i>Miconia_cuspidata</i>	0.272727273	253	1809	297
<i>Miconia_cyathanthera</i>	0.189189189	197	1501	990
<i>Miconia_discolor</i>	0.009009009	196	1470	650
<i>Miconia_dispar</i>	0.12962963	260	2014	169
<i>Miconia_egensis</i>	0.106796117	255	2241	226
<i>Miconia_elegans</i>	0	227	1424	760
<i>Miconia_fasciculata</i>	0.037037037	198	1421	618
<i>Miconia_ferruginata</i>	0.017857143	225	1444	768
<i>Miconia_gratissima</i>	0	261	2189	234
<i>Miconia_hirtella</i>	0	226	1431	837
<i>Miconia_holosericea</i>	0.165289256	258	2127	213
<i>Miconia_ibaguensis</i>	0.049180328	231	1495	605
<i>Miconia_kollmannii</i>	0.023255814	201	1303	812
<i>Miconia_latecrenata</i>	0.01754386	197	1420	706
<i>Miconia_lepidota</i>	0.125	261	2149	136
<i>Miconia_ligustroides</i>	0.090909091	205	1396	781
<i>Miconia_longispicata</i>	0.206349206	264	2414	159
<i>Miconia_lourteigiana</i>	0.189189189	256	1931	233

<i>Miconia_lymanii</i>	0.035714286	186	1716.5	556.5
<i>Miconia_macrocarpa</i>	0.212121212	204	1644	972
<i>Miconia_macrothyrsa</i>	0.058823529	237	1490	609
<i>Miconia_mirabilis</i>	0	241	1649	191
<i>Miconia_nervosa</i>	0.03030303	255	2462	211
<i>Miconia_octopetala</i>	0.025380711	237	1621	148
<i>Miconia_paniculata</i>	0.1	184	1504	767
<i>Miconia_paradoxa</i>	0	210	1208	836
<i>Miconia_penduliflora</i>	0.044776119	230	1436	452
<i>Miconia_pepericarpa</i>	0.034482759	209	1438	848
<i>Miconia_phanerostila</i>	0.082568807	263	2515.5	192
<i>Miconia_poeppigii</i>	0.12	262	2403	128
<i>Miconia_prasina</i>	0.2	255	2131	243
<i>Miconia_punctata</i>	0.218390805	257	2663	209
<i>Miconia_radulaefolia</i>	0.106060606	261	2818	149
<i>Miconia_regelii</i>	0.191489362	259	2047	162
<i>Miconia_rimalis</i>	0	216	978	660
<i>Miconia_rubiginosa</i>	0	230	1638	627
<i>Miconia_sclerophylla</i>	0	203	1094	972
<i>Miconia_staminea</i>	0	230	1249.5	83
<i>Miconia_stenostachya</i>	0.130434783	236	1504	487
<i>Miconia_subcompressa</i>	0.223140496	229.5	1944	557.5
<i>Miconia_tetrandra</i>	0	232	1687.5	399.5
<i>Miconia_theizans</i>	0	201	1439	934
<i>Miconia_tomentosa</i>	0	259	2410	193
<i>Miconia_tristis</i>	0	196	1435	711
<i>Miconia_umbellata</i>	0.415525114	246	1762	219
<i>Miconia_willdenowii</i>	0.033333333	199	1390	744
<i>Microlicia_fulva</i>	0.142857143	206	1419	862
<i>Microlicia_isophylla</i>	0.142857143	198	1453	872
<i>Microlicia_minima</i>	0	206	829	1022.5
<i>Mouriri_guianensis</i>	0.333333333	261	1436	156
<i>Nepsera_aquatica</i>	0.325842697	256	2338	117
<i>Ossaea_amygdaloides</i>	0	198	1423	623
<i>Ossaea_marginata</i>	0	211	1509	328
<i>Ossaea_sanguinea</i>	0.15	186	1533	686
<i>Pachyanthus_clementis</i>	0	250	1499	137
<i>Pachyanthus_poiretii</i>	0.131707317	241	1578	178.5
<i>Pachyanthus_tetramerus</i>	0.05785124	242	1498	125
<i>Pachyanthus_wrightii</i>	0.073446328	252	1382	10
<i>Plagiopetalum_esquirolii</i>	0.157894737	130	1215	2401
<i>Pleiochiton_blepharodes</i>	0	191	1515.5	644
<i>Pleiochiton_ebracteatum</i>	0.155555556	182	1604	668
<i>Pleroma_oleifolia</i>	0.117647059	193	1455	843
<i>Pseudodissochaeta_septentrionalis</i>	0	223	1377	683
<i>Pterolepis_alpestris</i>	0.032258065	204	1417	828

<i>Pterolepis_glomerata</i>	0.037037037	231	1247	241
<i>Pterolepis_polygonoides</i>	0.2	237	864	435
<i>Pterolepis_repanda</i>	0.078125	207	1449	858
<i>Pterolepis_rotundifolia</i>	0.117647059	198	895	1093
<i>Pterolepis_trichotoma</i>	0.272727273	251	1773	212
<i>Rhexia_alifanus</i>	0	192	1402	25
<i>Rhexia_aristosa</i>	0	181	1275	55
<i>Rhexia_cubensis</i>	0	219	1299.5	19
<i>Rhexia_lutea</i>	0	192	1382	26
<i>Rhexia_mariana</i>	0	185	1355	54
<i>Rhexia_nashii</i>	0	208	1317	29
<i>Rhexia_nuttallii</i>	0	222	1288	18
<i>Rhexia_parviflora</i>	0	189	1589	60
<i>Rhexia_petiolata</i>	0	192	1341	34
<i>Rhexia_virginica</i>	0	122	1183	63
<i>Rhynchanthera_grandiflora</i>	0.142857143	241	1575	544
<i>Rhynchanthera_serrulata</i>	0.333333333	270	2261	84
<i>Salpinga_margaritacea</i>	0.090909091	205	1803.5	312.5
<i>Siphanthera_arenaria</i>	0	207	1304	817
<i>Siphanthera_cordata</i>	0.4	219	1451	912
<i>Siphanthera_cordifolia</i>	0.454545455	242	2571.5	528.5
<i>Siphanthera_dawsonii</i>	0.2	221	1545	955
<i>Siphanthera_fasciculata</i>	0.428571429	265	2984	161
<i>Siphanthera_foliosa</i>	0.142857143	229	1466	713
<i>Siphanthera_gracillima</i>	0.142857143	207	1473	932
<i>Siphanthera_hostmannii</i>	0.2	257	2571	270
<i>Siphanthera_paludosa</i>	0.181818182	204	1477	779
<i>Siphanthera_subtilis</i>	-0.25	249	1580	242
<i>Tetrazygia_decorticans</i>	0	252	1489	123
<i>Tibouchina_aegopogon</i>	0.111111111	229	1482	797
<i>Tibouchina_arborea</i>	0.294117647	191	1340	806
<i>Tibouchina_aspera</i>	0.083333333	267	2284	109
<i>Tibouchina_barnebyana</i>	0.081081081	218	787	602
<i>Tibouchina_blanchetiana</i>	0.03125	217	731	732
<i>Tibouchina_candolleana</i>	0.135135135	210	1440	875
<i>Tibouchina_cardinalis</i>	0.038461538	198	1467	918
<i>Tibouchina_collina</i>	0.272727273	198	1471	924
<i>Tibouchina_corymbosa</i>	0.066666667	239	1150	187
<i>Tibouchina_estrellensis</i>	0.142857143	200	1400	741
<i>Tibouchina_fissinervia</i>	0.137254902	228	1160.5	413
<i>Tibouchina_fothergillae</i>	0.072555205	197	1460	783
<i>Tibouchina_frigidula</i>	0.03125	198	1497	923
<i>Tibouchina_gracilis</i>	0.066666667	209	1442	562
<i>Tibouchina_granulosa</i>	0.111111111	202	1460	721
<i>Tibouchina_hieracioides</i>	0	196	1508	927
<i>Tibouchina_laevicaulis</i>	0	221	1491	986

<i>Tibouchina_macrochiton</i>	0	241	1172	79
<i>Tibouchina_martialis</i>	0.263157895	184	1463	870
<i>Tibouchina_nodosa</i>	0.019607843	233	1552	813
<i>Tibouchina_oreophila</i>	0	216	857	618
<i>Tibouchina_pereirae</i>	0.15	215	758	802
<i>Tibouchina_salviaefolia</i>	0.111111111	258	1512	95.5
<i>Tibouchina_sellowiana</i>	0.238095238	187	1496	711
<i>Tibouchina_semidecandra</i>	0.214285714	198	1459	867
<i>Tibouchina_stenocarpa</i>	0.058823529	216	1434	753
<i>Tibouchina_trichopoda</i>	0.230769231	190	1557	658
<i>Tibouchina_urceolaris</i>	0.170731707	239	1183	149
<i>Tibouchina_velutina</i>	0.130434783	226	696	493
<i>Tococa_bullifera</i>	0	260	2697	168
<i>Tococa_coronata</i>	0	263	2813	119
<i>Tococa_guianensis</i>	0	258	2648	183
<i>Tococa_subciliata</i>	0.035971223	267	2322	102
<i>Trembleya_parviflora</i>	0	204	1418	846
<i>Wurdastom_cuatrecasasii</i>	0	207	2541	1373
<i>Wurdastom_hexamera</i>	0	206	1852	1425

Table SI2 – List of 731 species with the logarithm of the average petal length (mm) and mean annual temperature (bio1, $\times 10^{\circ}\text{C}$), mean annual precipitation (bio12, mm^3), and altitude (m) from the Worldclim dataset.

Species	petal length	temperature	precipitation	altitude
<i>Acanthella_sprucei</i>	15	267	2901.5	177
<i>Aciotis_acuminifolia</i>	3.5	261	2392	145
<i>Aciotis_annua</i>	4	266	2649	113
<i>Aciotis_circaeifolia</i>	7.5	269	2244	66
<i>Aciotis_indecora</i>	4	258	2653	139
<i>Aciotis_paludosa</i>	5.5	223	1294	268
<i>Aciotis_polystachya</i>	2.5	259	2850	175
<i>Aciotis_purpurascens</i>	5	258	2546	184
<i>Aciotis_rubricaulis</i>	6	240	2596	528
<i>Acisanthera_alsinaefolia</i>	15	213	1428	551
<i>Acisanthera_uniflora</i>	6	267	2417	223
<i>Acisanthera_variabilis</i>	6	205	1443	725
<i>Adelobotrys_adscendens</i>	12	244	2706	456
<i>Adelobotrys_barbata</i>	17	267	3248	114
<i>Adelobotrys_permixta</i>	13	229	1812	725
<i>Adelobotrys_scandens</i>	12.5	259	2902	177
<i>Adelobotrys_spruceana</i>	10	261	2900	136
<i>Allomaieta_ebejicosana</i>	8	166	2477.5	2213.5
<i>Allomaieta_grandiflora</i>	22	237	2695.5	919.5
<i>Allomaieta_pancurana</i>	2.1	217	2831.5	1269.5
<i>Anaectocalyx_bracteosa</i>	14	156	1037	2140
<i>Appendicularia_thymifolia</i>	3.6	259	2448	104
<i>Arthrostemma_ciliatum</i>	30	240	2271	497
<i>Arthrostemma_primaevum</i>	16	190	1346	1431
<i>Astronia_ferruginea</i>	1	238	3068	206
<i>Axinaea_affinis</i>	180	119.5	1164	2934
<i>Axinaea_alata</i>	20	141	991	2988
<i>Axinaea_costaricensis</i>	15	188	2304	1431
<i>Axinaea_floribunda</i>	8	135.5	1440	2667.5
<i>Axinaea_grandifolia</i>	12	127.5	1293	2657
<i>Axinaea_macrophylla</i>	9	129	1473.5	2743
<i>Axinaea_sclerophylla</i>	24	157	1096	2336
<i>Barthea_barthei</i>	22	177.5	3374.5	1145.5
<i>Bellucia_arborescens</i>	8	264	2826	132
<i>Bellucia_grossularioides</i>	28	265	2274	146
<i>Bellucia_mespiloides</i>	15	256	2403	151
<i>Bellucia_pentamera</i>	25	254	2512	264
<i>Bellucia_spruceana</i>	15	259	2695	180
<i>Bertolonia_mosenii</i>	10	181	1553	692
<i>Blakea_adscendens</i>	17	172	1384	2111.5
<i>Blakea_albertiae</i>	28	233	2947.5	790
<i>Blakea_brunnea</i>	53	183	2958.5	1507.5
<i>Blakea_bullata</i>	18	165	1333.5	2207

<i>Blakea_calycosa</i>	25	252	2994	235
<i>Blakea_calycularis</i>	13	249	2449	283
<i>Blakea_chlorantha</i>	8.5	205	2869.5	1090
<i>Blakea_cordata</i>	13	257	2930.5	208
<i>Blakea_costaricensis</i>	44	254	3065	191
<i>Blakea_crinita</i>	22	263	2863	141
<i>Blakea_dodsonorum</i>	6	247	2049	179
<i>Blakea_foliacea</i>	35	247	3001	360
<i>Blakea_fragrantissima</i>	14	198	3091	1251
<i>Blakea_fuchsioides</i>	23	230	3115	709
<i>Blakea_gerardoana</i>	12	182.5	2806.5	1501.5
<i>Blakea_gracilis</i>	25	202	2861.5	1150
<i>Blakea_grandiflora</i>	38	252	3093	216
<i>Blakea_guatemalensis</i>	21	202	3182	1192.5
<i>Blakea_henripittieri</i>	8.5	199	2772	1420
<i>Blakea_herrerae</i>	7	262	2936.5	154
<i>Blakea_hexandra</i>	7	263	2403.5	101
<i>Blakea_intricata</i>	23	172	2806	1719
<i>Blakea_litoralis</i>	30	244	3252	414
<i>Blakea_maurofernandeziana</i>	25	250	3087	195
<i>Blakea_micrantha</i>	4.56	138	2025	2583
<i>Blakea_pauciflora</i>	16	217	2976	956
<i>Blakea_penduliflora</i>	20	177.5	2893	1611
<i>Blakea_purpusii</i>	12	230	4173	988
<i>Blakea_repens</i>	10	208	2260.5	1308
<i>Blakea_rosea</i>	15	257	2772	222
<i>Blakea_schlimii</i>	17	165	1010	1963
<i>Blakea_storkii</i>	42	206	2932	1122
<i>Blakea_subconnata</i>	20	240	2624	395
<i>Blakea_subpanduriformis</i>	17	166	1396	2176
<i>Blakea_tapantiana</i>	21	221	3138	796
<i>Blakea_tuberculata</i>	38	237	3118	553
<i>Blakea_venusta</i>	17	190.5	3853.5	1371.5
<i>Blakea_watsonii</i>	16	251	2635	280
<i>Blakea_wilburiana</i>	18	262	2948	158
<i>Blakea_wilsoniorum</i>	30	199	2982	1255
<i>Blastus_borneensis</i>	3	213	2057	1098.5
<i>Blastus_cochinchinensis</i>	4	186	2974	818
<i>Blastus_pauciflorus</i>	4	175	1513	320
<i>Brachyotum_benthamianum</i>	18	142	1054	2589
<i>Brachyotum_confertum</i>	13	138	975	2667
<i>Brachyotum_fictum</i>	16	135	1135	2751
<i>Brachyotum_fraternum</i>	14	107	1082	3187
<i>Brachyotum_incrassatum</i>	20	163.5	1162.5	2232.5
<i>Brachyotum_ledifolium</i>	17	134	1591	2672
<i>Brachyotum_lindenii</i>	16	139	1793	2583

<i>Brachyotum_microdon</i>	23	160	700	2549
<i>Brachyotum_rostratum</i>	12	113	907	3201
<i>Bredia_fordii</i>	14	167	1334	493
<i>Bredia_microphylla</i>	9	174	1668	517.5
<i>Cambessedesia_corymbosa</i>	7	201	1437	900
<i>Cambessedesia_espora</i>	6	206	1439	853
<i>Cambessedesia_hilariana</i>	7	215	1357	802
<i>Castratella_piloselloides</i>	9	123	1047.5	2847
<i>Centradenia_floribunda</i>	11	224	1644.5	920.5
<i>Centradenia_grandifolia</i>	11	197	1918.5	1240
<i>Centradenia_inaequalateralis</i>	9	238	2292.5	484.5
<i>Chaetolepis_anisandra</i>	8	124	1338	2811
<i>Chaetolepis_cufodontisii</i>	10	112	2903	2683
<i>Chaetolepis_lindeniana</i>	5	144	1057	2340.5
<i>Chaetolepis_microphylla</i>	4	128	1259	2743
<i>Chaetostoma_armatum</i>	12.5	199	1401	860
<i>Charianthus_nodosus</i>	14.25	241	2493	284
<i>Clidemia_almedae</i>	2	244	3305	438
<i>Clidemia_alternifolia</i>	2	263	2989	134
<i>Clidemia_aphanantha</i>	2.5	257	2478	106
<i>Clidemia_atrata</i>	5	197	1546.5	747
<i>Clidemia_biserrata</i>	4.5	232	1262	367
<i>Clidemia_bullosa</i>	4	260	2297	159
<i>Clidemia_capitata</i>	2.5	231	2571	724
<i>Clidemia_capitellata</i>	6	244	1986	336
<i>Clidemia_charadrophylla</i>	1	223	2202	801
<i>Clidemia_ciliata</i>	4	198	1988	1511
<i>Clidemia_clandestina</i>	1	241	3013.5	601.5
<i>Clidemia_conglomerata</i>	5.5	258	2400	124
<i>Clidemia_costaricensis</i>	5.5	228	2958.5	737.5
<i>Clidemia_crenulata</i>	3	252	3139.5	326
<i>Clidemia_cruegeriana</i>	1.2	237.5	1649	486
<i>Clidemia_debilis</i>	2.5	235	1122	229
<i>Clidemia_dentata</i>	6.5	246	2480	383
<i>Clidemia_discolor</i>	2	254	3018	216
<i>Clidemia_epibaterium</i>	3	261	2809	135
<i>Clidemia_epiphytica</i>	3	257	2881.5	157
<i>Clidemia_fendleri</i>	2.5	264	1135	210
<i>Clidemia_fluminensis</i>	6	232	1194	50
<i>Clidemia_folsomii</i>	4.5	261	2578.5	128
<i>Clidemia_fulva</i>	9	250	2562	221
<i>Clidemia_globuliflora</i>	7	152	2916	2035.5
<i>Clidemia_heptamera</i>	7	226	1828	762
<i>Clidemia_heteroneura</i>	1.4	262	3093	142
<i>Clidemia_involucrata</i>	3.5	249	2063.5	424
<i>Clidemia_japurensis</i>	2.5	263	2509	121

<i>Clidemia_laevifolia</i>	8	264	2149	162
<i>Clidemia_laxiflora</i>	3	217	1614	1069
<i>Clidemia_mortoniana</i>	6.5	209.5	2841.5	1093
<i>Clidemia_myrmecina</i>	7	258	3161.5	401
<i>Clidemia_novemnervia</i>	5.5	267	2358	130
<i>Clidemia_octona</i>	10	246	2251	423
<i>Clidemia_ostrina</i>	1.7	251	2956.5	490
<i>Clidemia_petiolaris</i>	7	251	2193.5	177
<i>Clidemia_pustulata</i>	6	263	2121	163
<i>Clidemia_rodriguezii</i>	2	179	2905	1561
<i>Clidemia_rubra</i>	3	263	2482	188
<i>Clidemia_septuplinervia</i>	2	256	2848	157
<i>Clidemia_sericea</i>	2.8	251	2219	331
<i>Clidemia_sessiliflora</i>	2.5	220	2706.5	1029
<i>Clidemia_setosa</i>	5	248	2596	254
<i>Clidemia_spectabilis</i>	7	228	3123	725
<i>Clidemia_strigillosa</i>	3.5	259	2560	192
<i>Clidemia_tenebrosa</i>	5	250	3016.5	313
<i>Clidemia_tetrapetala</i>	6	183	2917	1499
<i>Clidemia_urceolata</i>	7	208	1335	642
<i>Clidemia_utleyana</i>	2	247	3198	439.5
<i>Comolia_leptophylla</i>	12	274	2770	109
<i>Comolia_microphylla</i>	7	265	2098	140
<i>Comolia_smithii</i>	12	262	2680.5	102
<i>Comolia_villosa</i>	12	266	2091	102
<i>Conostegia_bigibbosa</i>	11.25	173.5	3039	1666.5
<i>Conostegia_bracteata</i>	7	255	3004	209
<i>Conostegia_brenesii</i>	6.5	206	3517	1111
<i>Conostegia_caelestis</i>	10	242	2477	332
<i>Conostegia_centronioides</i>	9	233	2121	517
<i>Conostegia_cinnamomea</i>	4.25	255	2725	230.5
<i>Conostegia_cuatrecasii</i>	12	247	2737	323
<i>Conostegia_extinctoria</i>	5	219	2773.5	1185
<i>Conostegia_icosandra</i>	9	244	2337	290.5
<i>Conostegia_jaliscana</i>	8	184	1236	1564
<i>Conostegia_lasiopoda</i>	8	254	3706	283
<i>Conostegia_micrantha</i>	5.25	247	2772	276
<i>Conostegia_montana</i>	5.25	249	2762	220
<i>Conostegia_monteleagreana</i>	5	193	2886.5	1562.5
<i>Conostegia_oerstediana</i>	11	206	2905	1117
<i>Conostegia_pittieri</i>	14	191.5	2900	1356
<i>Conostegia_plumosa</i>	6	249	1698	294
<i>Conostegia_polyandra</i>	9.5	259	3917	37
<i>Conostegia_rhodopetala</i>	8.3	249	3043	311
<i>Conostegia_rubiginosa</i>	9	266	7807	85.5
<i>Conostegia_rufescens</i>	11	243	3053	423

<i>Conostegia_setosa</i>	7	256	2980	170
<i>Conostegia_speciosa</i>	7.25	256	2219	160
<i>Conostegia_subcrustulata</i>	5	255	2731.5	161
<i>Conostegia_superba</i>	6.5	229	2634	761
<i>Conostegia_tenuifolia</i>	8.25	245	2804	337
<i>Conostegia_volcanalis</i>	15	213	1503.5	1047
<i>Conostegia_xalapensis</i>	8	247	1822	362
<i>Cyphotheca_montana</i>	11	188	1261	1402
<i>Desmoscelis_villosa</i>	9	239	1503	462
<i>Dissochaeta_annulata</i>	20	270	2925	50
<i>Dissochaeta_divaricata</i>	10	269	1758	106
<i>Dissochaeta_reformata</i>	25	270	2093	50
<i>Dissochaeta_viminalis</i>	5	194	2614.5	1460.5
<i>Ernestia_maguirei</i>	8.5	186	1243	1585.5
<i>Ernestia_ovata</i>	9	193	1457	1660
<i>Ernestia_tenella</i>	9	264	2853	205
<i>Graffenrieda_cucullata</i>	7	200	1981	1522
<i>Graffenrieda_galeottii</i>	6	242	3161	581
<i>Graffenrieda_gracilis</i>	3.5	228	2651	913
<i>Graffenrieda_hitchcockii</i>	7	271	2695	182
<i>Graffenrieda_intermedia</i>	5	213	2113	1130
<i>Graffenrieda_miconioides</i>	6	253	2540	328
<i>Graffenrieda_micrantha</i>	3	249	2992	352
<i>Graffenrieda_moritziana</i>	4	228	936	727
<i>Graffenrieda_rotundifolia</i>	15	281	2248	75
<i>Graffenrieda_sessilifolia</i>	11	247.5	3012	522
<i>Graffenrieda_weddellii</i>	14	242	1654	471
<i>Henriettea_flavescens</i>	4	257	2780.5	93
<i>Henriettea_granulata</i>	5	268	2239	110
<i>Henriettea_martiusii</i>	15	269	2633	83
<i>Henriettea_odorata</i>	2.8	207	2717	1204
<i>Henriettea_patrisiana</i>	5	270	1780	137
<i>Henriettea_ramiflora</i>	10	262	2152	223
<i>Henriettea_rimosa</i>	3	263	1736.5	196
<i>Henriettea_sessilifolia</i>	8	236.5	1229.5	435.5
<i>Henriettea_spruceana</i>	9	262	2906	103
<i>Henriettea_succosa</i>	11	245	1425	117
<i>Henriettea_tuberculosa</i>	2	250	3130	374.5
<i>Henriettea_uniflora</i>	7.2	253	937	299
<i>Heterocentron_elegans</i>	13	189	1756	1194
<i>Heterocentron_muricatum</i>	13	210	2210	1229
<i>Huberia_consimilis</i>	25	217	899	549
<i>Huberia_ovalifolia</i>	31	233	1168	199
<i>Lavoisiera_alba</i>	22	199	1439.5	936
<i>Lavoisiera_caryophyllea</i>	25	204	1441	815.5
<i>Lavoisiera_cordata</i>	25	203	1450	841

<i>Lavoisiera_crassifolia</i>	28	210	1273	782
<i>Lavoisiera_imbricata</i>	27	204	1408	866
<i>Lavoisiera_macrocarpa</i>	45	204	1444	814
<i>Lavoisiera_mucorifera</i>	18	205	1390	829
<i>Lavoisiera_pulchella</i>	18	173	1410	883
<i>Lavoisiera_subulata</i>	14	204	1437	812
<i>Leandra_agrestis</i>	3	256	2405	145
<i>Leandra_amplexicaulis</i>	6	188	1464	731
<i>Leandra_aristigera</i>	2.4	257	2930	215
<i>Leandra_aspera</i>	4.2	184.5	1349.5	1043.5
<i>Leandra_aurea</i>	5.8	200	1435	799
<i>Leandra_australis</i>	4.3	185	1582	636
<i>Leandra_barbinervis</i>	4.8	183	1580	781
<i>Leandra_brackenridgei</i>	4	203	1696	291
<i>Leandra_breviflora</i>	4	209	1415	488
<i>Leandra_calvescens</i>	4	171	1702	806
<i>Leandra_capilliflora</i>	2.6	236	1210	121
<i>Leandra_capitata</i>	5.2	232	1186	240
<i>Leandra_carassana</i>	4.7	177	1583	834
<i>Leandra_catharinensis</i>	3	163	1673	885
<i>Leandra_clidemioides</i>	2	229	1596	524
<i>Leandra_collina</i>	3.5	208	2012	225
<i>Leandra_cordigera</i>	3.2	184	1701.5	879
<i>Leandra_cristata</i>	1.9	204.5	1303	762.5
<i>Leandra_cuneata</i>	2.2	238	1305	141
<i>Leandra_dichotoma</i>	2.5	243	2486	457
<i>Leandra_divaricata</i>	2.5	258	2130	180
<i>Leandra_echinata</i>	6	200	1647	607
<i>Leandra_edentula</i>	1.2	222	1945	832
<i>Leandra_eichleri</i>	4	169	1528	903
<i>Leandra_erostrata</i>	3.6	191	1436	857
<i>Leandra_fallax</i>	2.6	182	1527	736
<i>Leandra_fontanae</i>	5	215	1243	590.5
<i>Leandra_foveolata</i>	4.5	197	1427	797
<i>Leandra_glabrata</i>	3	194	1444	871
<i>Leandra_glazioviana</i>	9	191	1494	713
<i>Leandra_gracilis</i>	2.5	183	1627	712.5
<i>Leandra_granatensis</i>	2.5	255	2913.5	152
<i>Leandra_gynoverrucosa</i>	7	180	1558	1101
<i>Leandra_hatschbachii</i>	3.3	178	1593	631.5
<i>Leandra_hirta</i>	4.2	201	1368	601
<i>Leandra_hirtella</i>	2.8	176	1565	800
<i>Leandra_humilis</i>	3.7	178	1575	808
<i>Leandra_ionopogon</i>	5.2	232	1204	179
<i>Leandra_itatiaiae</i>	5.5	186	1695	661
<i>Leandra_laevigata</i>	4.5	175	1563	820

<i>Leandra_lapae</i>	4	177.5	1762.5	766.5
<i>Leandra_lasiopetala</i>	3.5	221	3087	884
<i>Leandra_loligomorpha</i>	4	244	1090.5	96
<i>Leandra_longicoma</i>	2	255	2806	235
<i>Leandra_magdalenensis</i>	2	171	1487	1137
<i>Leandra_melanodesma</i>	2.5	172	1916	1901
<i>Leandra_melastomoides</i>	6.5	201	1423	742
<i>Leandra_mexicana</i>	2.5	252	2625	156
<i>Leandra_miconiastrum</i>	3	198	1457	741
<i>Leandra_micropetala</i>	0.5	262	2264	125
<i>Leandra_microphylla</i>	3	173	1479	849
<i>Leandra_mollis</i>	4.6	178.5	1454.5	994
<i>Leandra_multiplinervis</i>	5.7	180	1544	919
<i>Leandra_multisetosa</i>	2.3	182	1470	942
<i>Leandra_neurotricha</i>	3	192	1535.5	981
<i>Leandra_nianga</i>	4	204	1334	591
<i>Leandra_pallida</i>	3.3	168	1593	917
<i>Leandra_pennipilis</i>	4	189	1536	1028
<i>Leandra_phelpsiae</i>	0.6	176	3402	1750
<i>Leandra_pilonensis</i>	4.5	178	1544	743
<i>Leandra_planifilamentosa</i>	3.5	162	1565	890
<i>Leandra_polyadena</i>	0.5	184	2224	1586
<i>Leandra_polystachya</i>	5	190	1496	889
<i>Leandra_purpurascens</i>	4	186	1497	756
<i>Leandra_quinquedentata</i>	4.5	183	1527	812
<i>Leandra_refracta</i>	4.2	180	1511.5	767
<i>Leandra_regnellii</i>	2.5	181	1615	712
<i>Leandra_reitzii</i>	4	177	1588	711
<i>Leandra_reversa</i>	3.6	206	1344	521
<i>Leandra_ribesiaeflora</i>	3.7	172	1859.5	814
<i>Leandra_riedeliana</i>	2	196	1474	941
<i>Leandra_riograndensis</i>	2	161	1702	924
<i>Leandra_rufescens</i>	1.3	243	1535	81
<i>Leandra_salicina</i>	5	201	1482	965
<i>Leandra_sericea</i>	4.8	190	1449	776
<i>Leandra_solenifera</i>	2.8	255	2533	272
<i>Leandra_strigilliflora</i>	3.7	224	1225	328
<i>Leandra_subseriata</i>	2	169	1677	2006
<i>Leandra_subulata</i>	5.5	247	3129	356
<i>Leandra_sulfurea</i>	5.7	183	1632	864
<i>Leandra_tetraquetra</i>	3	178	1584	715
<i>Leandra_therezopolitana</i>	4	160.5	1800	1324.5
<i>Leandra_ulaei</i>	5.8	182	1568	467
<i>Leandra_umbellata</i>	9	202	1436	806
<i>Leandra_variabilis</i>	3	190	1495	631.5
<i>Leandra_vesiculosa</i>	3	146	1884	1662

<i>Leandra_xanthocoma</i>	5	185	1535	774
<i>Leandra_xantholasia</i>	4.5	189	1483	731
<i>Leandra_xanthostachya</i>	4.5	173	1575	887
<i>Macairea_lasiophylla</i>	8	250	2520	449
<i>Macairea_multinervia</i>	14	264	2383	69
<i>Macairea_pachyphylla</i>	8.5	238	2401	641
<i>Macairea_radula</i>	8.5	233	1435.5	636
<i>Macairea_thyrsiflora</i>	11	265	2538	141
<i>Macrocentrum_anfractum</i>	6	232	1629	630
<i>Macrocentrum_cristatum</i>	10	252	2439	180
<i>Macrocentrum_droseroides</i>	5.5	226	1944	782
<i>Macrocentrum_fasciculatum</i>	9	222	1805	847
<i>Macrocentrum_gesneriaceum</i>	8	225	1804.5	780.5
<i>Macrocentrum_minus</i>	7	223	1900.5	816.5
<i>Macrocentrum_neblinae</i>	7	221	3114	975
<i>Macrocentrum_repens</i>	4.5	226	1776	762
<i>Macrocentrum_vestitum</i>	7	225	2227	778
<i>Maguireanthus_ayangannae</i>	5.8	230	2481	693
<i>Maieta_guianensis</i>	8	257	2753	207
<i>Maieta_poeppigii</i>	8	257	2725	193
<i>Marcetia_eimeariana</i>	3	179	984	1503
<i>Marcetia_taxifolia</i>	7	212	1265	744
<i>Mecranium_alpestre</i>	1.3	214	2102	789
<i>Mecranium_amygdalinum</i>	3.8	247	1367	230
<i>Mecranium_axillare</i>	2	239	2106	313
<i>Mecranium_birimosum</i>	2.5	217	2101	738
<i>Mecranium_crassinerve</i>	3.5	217	2084	747
<i>Mecranium_haemanthum</i>	3.3	219.5	1584.5	642
<i>Mecranium_haitiense</i>	3.9	219	2073.5	708.5
<i>Mecranium_integrifolium</i>	2.2	250	1388.5	177
<i>Mecranium_microdictyum</i>	1.6	217	2072	747
<i>Mecranium_ovatum</i>	1.6	216	1567.5	730
<i>Mecranium_puberulum</i>	1.8	247	1463	257
<i>Mecranium_revolutum</i>	1.4	217	2118	729
<i>Mecranium_septentrionale</i>	1.4	222.5	1501	638.5
<i>Mecranium_tricostatum</i>	2.4	217	2072	747
<i>Mecranium_tuberculatum</i>	3.1	230	2075	527
<i>Melastoma_cyanoides</i>	10	233	2240.5	295.5
<i>Melastoma_dodecandrum</i>	20	170	1489	390
<i>Melastoma_imbricatum</i>	35	206	2071	1243
<i>Melastoma_intermedium</i>	14	176	2809	1102
<i>Melastoma_orientale</i>	8	270	2122	59
<i>Melastoma_saigonense</i>	20	271	1582	29.5
<i>Melastoma_sanguineum</i>	50	243	2045	20
<i>Memecylon_caeruleum</i>	2	270	2102	52
<i>Memecylon_impressivenum</i>	2	228	2447	273

<i>Memecylon_pauciflorum</i>	3	265	1217	94
<i>Memecylon_perditum</i>	3.5	233	2494.5	195
<i>Memecylon_polyanthum</i>	2	216	1626	840
<i>Memecylon_scutellatum</i>	2.5	246	1541.5	21
<i>Memecylon_sejunctum</i>	4	231	2313	209.5
<i>Memecylon_xiphophyllum</i>	2.5	233	2704	177
<i>Meriania_brevipedunculata</i>	22	219	2072	716
<i>Meriania_calyptrata</i>	10	212.5	2409	228.5
<i>Meriania_franciscana</i>	10	177	1550.5	1962.5
<i>Meriania_haemantha</i>	40	136	1417	2595
<i>Meriania_longifolia</i>	40	196	1616	1518
<i>Meriania_macrophylla</i>	18	151	1905	2343.5
<i>Meriania_parvifolia</i>	11	217	2047	738
<i>Meriania_phlomoides</i>	16	182	2696.5	1766
<i>Meriania_robusta</i>	24	230	1129.5	37
<i>Meriania_sclerophylla</i>	18	215	1866	982
<i>Meriania_subumbellata</i>	12	152	978	2189
<i>Meriania_tomentosa</i>	10	144	1268	2567
<i>Meriania_urceolata</i>	17	262	2548	207
<i>Merianthera_bullata</i>	25	208	1262	693
<i>Merianthera_burlemarxii</i>	30	238	1163	227
<i>Merianthera_eburnea</i>	23.5	209	899	886
<i>Merianthera_parvifolia</i>	34	235	1193	278
<i>Merianthera_pulchra</i>	18.7	240	1136	188
<i>Merianthera_sipolisii</i>	28	208	1247	827
<i>Merianthera_verrucosa</i>	15.8	207	1284	718
<i>Miconia_abbreviata</i>	2.5	254	2633	253
<i>Miconia_acuminata</i>	4.8	260	2418	125
<i>Miconia_aeruginosa</i>	3	185	1792	1717.5
<i>Miconia_affinis</i>	3	243	2151	357
<i>Miconia_aggregata</i>	1.2	154	1349	2380
<i>Miconia_alata</i>	2.5	265	2307	124
<i>Miconia_albertii</i>	3.9	85	1311	3297
<i>Miconia_albertobrenesii</i>	4	227	2936	790
<i>Miconia_albicans</i>	3	235	1402	479
<i>Miconia_alboglandulosa</i>	2.5	244	3072.5	396
<i>Miconia_alborufescens</i>	2.8	220	1254	780
<i>Miconia_aliquantula</i>	3	260	2444	98
<i>Miconia_alternans</i>	3	257	2400	197
<i>Miconia_alternifolia</i>	4.1	243	1644	250
<i>Miconia_amilcariana</i>	1.1	135	1070.5	2507
<i>Miconia_ampla</i>	8	253	2752	251
<i>Miconia_amplinodis</i>	2	186	3361	1459.5
<i>Miconia_andreana</i>	2	155	1963	2321
<i>Miconia_angelana</i>	2.5	197	1486	950
<i>Miconia_apiculata</i>	3.15	217	2084	747

<i>Miconia_aplostachya</i>	2.5	268	2446	120
<i>Miconia_aponeura</i>	7	248	2665	568
<i>Miconia_appendiculata</i>	3.5	254	3106	154
<i>Miconia_approximata</i>	2.5	254	3020	163
<i>Miconia_araguensis</i>	15.3	148	1748	2417
<i>Miconia_arboricola</i>	3	256	2972	180
<i>Miconia_argentea</i>	3	256	2249	115
<i>Miconia_argyrophylla</i>	2.5	264	2188	160
<i>Miconia_asperrima</i>	2.7	178	2089.5	1928
<i>Miconia_astroplocama</i>	3	233	2412	646.5
<i>Miconia_barbinervis</i>	4	250	2840	272
<i>Miconia_barkeri</i>	6.7	217	2073.5	738
<i>Miconia_benthamiana</i>	9	222	2924.5	986
<i>Miconia_biolleyana</i>	1.5	250	3437	355
<i>Miconia_biperulifera</i>	2	135	2746	2339
<i>Miconia_brachybotrya</i>	3	245	2714	422
<i>Miconia_bracteata</i>	6	250	2463	187.5
<i>Miconia_brevithecata</i>	1.3	208	2118	1148
<i>Miconia_bubalina</i>	5.1	253	2408	270
<i>Miconia_buxifolia</i>	1.8	99	1334.5	3138.5
<i>Miconia_calycina</i>	5.4	228	2117	460
<i>Miconia_campestris</i>	4	263	2228	138
<i>Miconia_capixaba</i>	1.7	203	1301	769
<i>Miconia_carnea</i>	2.5	139	3092	2212
<i>Miconia_cataractae</i>	1.9	117	1408	2895
<i>Miconia_caudata</i>	3	194	2042	1633
<i>Miconia_centrodesma</i>	1.8	242	2750	547
<i>Miconia_ceramicarpa</i>	3.5	262	2367	112
<i>Miconia_cernua</i>	3.5	80.5	877.5	3515.5
<i>Miconia_chamissois</i>	3	227	1413	621
<i>Miconia_charleswrightii</i>	4.2	257.5	2595	36
<i>Miconia_chionophila</i>	3	94	963	3463
<i>Miconia_chrysophylla</i>	2	258	2254	213
<i>Miconia_ciliata</i>	2.5	254	1922	250
<i>Miconia_cladonia</i>	2.5	147	1825	2447
<i>Miconia_commutata</i>	3.3	256	2899.5	197.5
<i>Miconia_complanata</i>	1	165.5	1348.5	2119.5
<i>Miconia_concinna</i>	2.5	160.5	2461.5	1920
<i>Miconia_corallina</i>	2	192	1475	927
<i>Miconia_coriacea</i>	2.5	208.5	1588	703
<i>Miconia_corymbiformis</i>	4.5	127	1068	2857.5
<i>Miconia_costaricensis</i>	2	191	2665	1615
<i>Miconia_cremadena</i>	3	148	3025.5	2081.5
<i>Miconia_crocata</i>	1.5	264	2275	121
<i>Miconia_cuspidatissima</i>	2.5	148	3038	2139
<i>Miconia_decurrans</i>	4	255	2682	256

<i>Miconia_desmantha</i>	3	214	1545	1041
<i>Miconia_diaphanea</i>	2	259	2366	162
<i>Miconia_dielsiana</i>	5	250	1444	211.5
<i>Miconia_dispar</i>	3	260	2014	169
<i>Miconia_dissita</i>	1.5	217.5	2975.5	942.5
<i>Miconia_dodecandra</i>	8.5	216	1556	829
<i>Miconia_dolichopoda</i>	2.8	164	1919	2145
<i>Miconia_dolichorrhyncha</i>	1.25	253	2478	279
<i>Miconia_donaeana</i>	6	247	2513	281.5
<i>Miconia_dorsiloba</i>	3	255	3096	221
<i>Miconia_egensis</i>	2.5	255	2241	226
<i>Miconia_elaeoides</i>	2.2	119	1211	2891
<i>Miconia_elata</i>	2.5	256	2744	243
<i>Miconia_eriodonta</i>	4	269	2403.5	40
<i>Miconia_erosa</i>	5.3	162.5	2560	2211.5
<i>Miconia_evanescent</i>	2	238	2985	511
<i>Miconia_ferruginea</i>	4.4	232	1475	785
<i>Miconia_floribunda</i>	6	170	1905	2067
<i>Miconia_fragilis</i>	2	260	2328	103
<i>Miconia_funcckii</i>	19	243	935	486
<i>Miconia_galeiformis</i>	2.2	156	1240	2764
<i>Miconia_goniostigma</i>	4	208	2755	1268
<i>Miconia_gracilis</i>	3	244	2705	495
<i>Miconia_grandidentata</i>	2	218	3075.5	905.5
<i>Miconia_gratissima</i>	6	261	2189	234
<i>Miconia_hemenostigma</i>	1.5	176	1197	1824
<i>Miconia_holosericea</i>	8	258	2127	213
<i>Miconia_hondurensis</i>	3.5	253	2637	130
<i>Miconia_howardiana</i>	6.2	255	874	261
<i>Miconia_hypnioides</i>	5	217	2072	747
<i>Miconia_hypoleuca</i>	2.3	239	1226	116
<i>Miconia_ibaguensis</i>	3	231	1495	605
<i>Miconia_impetiolaris</i>	2.5	254	2276	138
<i>Miconia_intricata</i>	8	257	3751.5	106
<i>Miconia_kollmannii</i>	1.3	201	1303	812
<i>Miconia_kriegeriana</i>	3.2	164	1441	1371
<i>Miconia_krugii</i>	3.2	235	1494	436
<i>Miconia_lacera</i>	4	254	2585	175
<i>Miconia_laevigata</i>	3	239	1568	495
<i>Miconia_lanceolata</i>	3.2	168	1681	1461
<i>Miconia_lappacea</i>	5.1	253	2509	192
<i>Miconia_lateriflora</i>	2.5	259	2465	142
<i>Miconia_laxivenula</i>	3.5	222	2655.5	846.5
<i>Miconia_lepidota</i>	2	261	2149	136
<i>Miconia_livida</i>	2.5	192	2162	1438
<i>Miconia_lonchophylla</i>	5.5	185	2015	1684

<i>Miconia_longibracteata</i>	2.5	188.5	2919	1447
<i>Miconia_longifolia</i>	1.5	257	2535	188
<i>Miconia_longispicata</i>	2.5	264	2414	159
<i>Miconia_loreyoides</i>	3.5	225	3233.5	850.5
<i>Miconia_lourteigiana</i>	2	256	1931	233
<i>Miconia_luteola</i>	2.4	172	1671	1384
<i>Miconia_macayana</i>	2.6	217	2084	747
<i>Miconia_macrothyrsa</i>	3	237	1490	609
<i>Miconia_magdalenae</i>	2	258	2608	405
<i>Miconia_marginata</i>	1	255	2936	196
<i>Miconia_matthaei</i>	3	250	2343	295
<i>Miconia_melanotricha</i>	7	178	2907.5	1599
<i>Miconia_melinonis</i>	9	267	2368	49
<i>Miconia_meridensis</i>	13	205	1073	1219.5
<i>Miconia_mesmeana</i>	2	204	1113	1213
<i>Miconia_mexicana</i>	7	209	1528	1107
<i>Miconia_mirabilis</i>	10	241	1649	191
<i>Miconia_mulleola</i>	2	195	1958	1598
<i>Miconia_multispicata</i>	5	250	2580	345
<i>Miconia_myriantha</i>	22.3	265	2206	144
<i>Miconia_myrtillifolia</i>	3	135	1686.5	2634
<i>Miconia_neei</i>	1.6	163	772	2402
<i>Miconia_neocoronata</i>	2	259	4570	123
<i>Miconia_nervosa</i>	5	255	2462	211
<i>Miconia_nitidissima</i>	7	97	899	3265
<i>Miconia_nutans</i>	3.5	216	2655	1125
<i>Miconia_oinochrophylla</i>	3	253	2716.5	146
<i>Miconia_oraria</i>	2	257	4999	133
<i>Miconia_ossaeifolia</i>	1.5	215.5	2073.5	771.5
<i>Miconia_paleacea</i>	4	248	2641	291
<i>Miconia_pittieri</i>	2	194	2909	1318.5
<i>Miconia_plukenetii</i>	7.9	254	2199.5	165
<i>Miconia_poeppigii</i>	3	262	2403	128
<i>Miconia_polita</i>	3.4	226	2006	757
<i>Miconia_prasina</i>	3	255	2131	243
<i>Miconia_procumbens</i>	1.5	249	2693	345
<i>Miconia_pseudorigida</i>	5.7	230	2465	640
<i>Miconia_pterocaulon</i>	2.8	258	2830	232
<i>Miconia_pteroclada</i>	5	218	1569	673
<i>Miconia_pubipetala</i>	7.5	264	1843	151
<i>Miconia_pulvinata</i>	2.9	195	1925	1563
<i>Miconia_punctata</i>	2.8	257	2663	209
<i>Miconia_pycnoneura</i>	3.3	216	2442.5	623.5
<i>Miconia_pyramidalis</i>	4.3	252	1560.5	172
<i>Miconia_pyrifolia</i>	2.6	249	1941	292
<i>Miconia_quinquenervia</i>	1.25	252	2638	255

<i>Miconia_radulaefolia</i>	34	261	2818	149
<i>Miconia_reducens</i>	6.5	248	3131	457.5
<i>Miconia_regelii</i>	1.5	259	2047	162
<i>Miconia_reitziana</i>	1.5	248	2799	238
<i>Miconia_resimoides</i>	2	199.5	2444	1612.5
<i>Miconia_rubiginosa</i>	3	230	1638	627
<i>Miconia_rufa</i>	5.5	218	1565	651
<i>Miconia_rufescens</i>	5	261	1905	255
<i>Miconia_rugosa</i>	5	260	2865	184
<i>Miconia_salicifolia</i>	1.8	108	1207	3078
<i>Miconia_samanensis</i>	2.9	252	1748	176
<i>Miconia_sanctiphilippi</i>	8	245	1012	467
<i>Miconia_schlechtendalii</i>	2.5	225	1531	885
<i>Miconia_schnellii</i>	2	134	2878.5	2350
<i>Miconia_selleana</i>	6.2	182	1670.5	1243
<i>Miconia_septentrionalis</i>	5	254	1122	217.5
<i>Miconia_serrulata</i>	9	257	2707	189
<i>Miconia_simplex</i>	5	257	3023	193
<i>Miconia_sintenisii</i>	8.2	233	2213	363.5
<i>Miconia_skeaniana</i>	4.2	217	1576	691
<i>Miconia_smaragdina</i>	4.3	209	2685	1290
<i>Miconia_solearis</i>	4	246	3375	361
<i>Miconia_spiciformis</i>	4	257	3781	155
<i>Miconia_spinulosa</i>	3.1	187	1097	1476
<i>Miconia_splendens</i>	3.7	258	2633	194
<i>Miconia_squamulosa</i>	3	127	1115	2790
<i>Miconia_staminea</i>	9	230	1249.5	83
<i>Miconia_stenobotrys</i>	2.8	133	1021.5	27
<i>Miconia_stenostachya</i>	4	236	1504	487
<i>Miconia_stevensiana</i>	3	255	2855	66
<i>Miconia_subcompressa</i>	6.3	229.5	1944	557.5
<i>Miconia_superba</i>	11	259	1977	283
<i>Miconia_sylvatica</i>	3	220	1532	823
<i>Miconia_tamana</i>	1.3	124	992	2652
<i>Miconia_theizans</i>	1.3	201	1439	934
<i>Miconia_tillettii</i>	2	249	2474.5	334.5
<i>Miconia_tinifolia</i>	2.3	139	1590	2592
<i>Miconia_tomentosa</i>	8	259	2410	193
<i>Miconia_tovarensis</i>	2	138	1323	2553
<i>Miconia_trimera</i>	2	254	2552	118
<i>Miconia_trinervia</i>	3.1	257	2711	211
<i>Miconia_tschudyoides</i>	2.9	193	1408	760
<i>Miconia_ulmarioides</i>	28	139	1208	2548
<i>Miconia_urticoides</i>	1.5	230	2590	1002
<i>Miconia_valerioana</i>	3.5	217.5	2955.5	933.5
<i>Miconia_variabilis</i>	4	241	3366	472

<i>Miconia_viscidula</i>	3.1	236.5	1493	429.5
<i>Miconia_xenotricha</i>	3.5	217	2084	747
<i>Microlicia_fulva</i>	5	206	1419	862
<i>Microlicia_isophylla</i>	10	198	1453	872
<i>Monochaetum_bonplandii</i>	14	140	1304	2537
<i>Monochaetum_discolor</i>	15	143	894	2505
<i>Monochaetum_floribundum</i>	7	205	1692	1184
<i>Monochaetum_humboldtianum</i>	30	192	1308	1173
<i>Monochaetum_lineatum</i>	11	151	1233	2412
<i>Monochaetum_meridense</i>	14	91.5	1368	3248
<i>Monochaetum_polyneurum</i>	18	148	1079	2275
<i>Monochaetum_tenellum</i>	17	149	1456	2314
<i>Monochaetum_uribei</i>	12	125	1170	2788
<i>Monochaetum_vulcanicum</i>	22	233	2613	550
<i>Monolena_primuliflora</i>	24	236	2688	690
<i>Mouriri_collocarpa</i>	9.3	271	2233	95
<i>Mouriri_crassifolia</i>	14.5	266	2540	52
<i>Mouriri_cyphocarpa</i>	10	255	2893	121
<i>Mouriri_dumetosa</i>	11	269	2558	52
<i>Mouriri_gleasoniana</i>	6.3	253	2559	168
<i>Mouriri_guianensis</i>	7	261	1436	156
<i>Mouriri_helleri</i>	6.7	251	1866.5	142
<i>Mouriri_myrtilloides</i>	7	252	2175	200
<i>Mouriri_nervosa</i>	6.5	264	2261	145
<i>Mouriri_sagotiana</i>	5	266	2399	84
<i>Necramium_gigantophyllum</i>	2.5	237	1677	500
<i>Nepsera_aquatica</i>	7.5	256	2338	117
<i>Opisthocentra_clidemoides</i>	9	266	3135.5	125
<i>Osbeckia_chinensis</i>	17	248	1622	101
<i>Osbeckia_nepalensis</i>	25	186	1592	1301.5
<i>Osbeckia_stellata</i>	28	160	1224	1538
<i>Ossaea_amygdaloides</i>	3.6	198	1423	623
<i>Ossaea_cabraliensis</i>	3.8	233	1157	202.5
<i>Ossaea_capillaris</i>	3	238	2319	685
<i>Ossaea_cinnamomifolia</i>	4.2	189	1472	1223
<i>Ossaea_coriacea</i>	3.5	187	1508.5	1176.5
<i>Ossaea_marginata</i>	4	211	1509	328
<i>Ossaea_quadrisulca</i>	3.2	234	2319	675.5
<i>Ossaea_sanguinea</i>	4	186	1533	686
<i>Ossaea_suprabasalis</i>	2.5	195	1327	921
<i>Ossaea_warmingiana</i>	3	192	1534	1049
<i>Pachyanthus_clementis</i>	12	250	1499	137
<i>Pachyanthus_poiretii</i>	17	241	1578	178.5
<i>Pachyanthus_wrightii</i>	17	252	1382	10
<i>Pachycentria_constricta</i>	7	258	2216	228
<i>Pachycentria_pulverulenta</i>	5	274	1948	11

<i>Pachyloma_huberioides</i>	20	269	2669	105
<i>Phainantha_laxiflora</i>	6.5	225	1814	784
<i>Phainantha_shuariorum</i>	9	222	2375	1054.5
<i>Phyllagathis_oligotricha</i>	4	164	1578	932
<i>Physeterostemon_thomasi</i>	7.2	218	1248	440
<i>Pilocosta_campanensis</i>	11	238	2894.5	640.5
<i>Pilocosta_nana</i>	14	239	2667	447
<i>Pilocosta_nubicola</i>	15	203	2850	1192
<i>Pilocosta_oerstedii</i>	12	243	3074	456
<i>Plagiopetalum_esquirolii</i>	10	130	1215	2401
<i>Pleiochiton_amorimii</i>	6.2	234	1278	196
<i>Pleiochiton_blepharodes</i>	8	191	1515.5	644
<i>Pleiochiton_ebracteatum</i>	6.7	182	1604	668
<i>Pleiochiton_micranthum</i>	4.4	174.5	1450.5	1064
<i>Pleiochiton_parasiticum</i>	6	184	1678	765
<i>Pleiochiton_roseum</i>	5	175	1603	905
<i>Pleiochiton_setulosum</i>	4.5	186	1511	876
<i>Pleroma_oleifolia</i>	11	193	1455	843
<i>Pseudodissochaeta_septentrionalis</i>	10	223	1377	683
<i>Pternandra_coerulescens</i>	6	265	1755	38
<i>Pternandra_echinata</i>	13	270	2132	42
<i>Pterogastra_divaricata</i>	14	268	2528	204
<i>Pterolepis_alpestris</i>	13	204	1417	828
<i>Pterolepis_glomerata</i>	12	231	1247	241
<i>Pterolepis_polygonoides</i>	8	237	864	435
<i>Pterolepis_repanda</i>	22	207	1449	858
<i>Pterolepis_rotundifolia</i>	15	198	895	1093
<i>Pterolepis_trichotoma</i>	12	251	1773	212
<i>Quipuanthus_epipetricus</i>	17	246	2253.5	521.5
<i>Rhexia_alifanus</i>	25	192	1402	25
<i>Rhexia_aristosa</i>	22	181	1275	55
<i>Rhexia_cubensis</i>	20	219	1299.5	19
<i>Rhexia_lutea</i>	15	192	1382	26
<i>Rhexia_mariana</i>	20	185	1355	54
<i>Rhexia_nashii</i>	25	208	1317	29
<i>Rhexia_nuttallii</i>	12	222	1288	18
<i>Rhexia_parviflora</i>	13	189	1589	60
<i>Rhexia_salicifolia</i>	12	194	1559	29
<i>Rhexia_virginica</i>	20	122	1183	63
<i>Rhynchanthera_bracteata</i>	30	254	1939	190
<i>Rhynchanthera_grandiflora</i>	25	241	1575	544
<i>Rhynchanthera_serrulata</i>	15	270	2261	84
<i>Salpinga_secunda</i>	11	259	2847	163
<i>Sandemania_hoehnei</i>	4.5	261	2175	124
<i>Sarcopyramis_bodinieri</i>	4	161	3142	1318
<i>Schwackaea_cupheoides</i>	7	257	1841	208

<i>Siphanthera_arenaria</i>	5	207	1304	817
<i>Siphanthera_cordata</i>	4.5	219	1451	912
<i>Siphanthera_cordifolia</i>	4	242	2571.5	528.5
<i>Siphanthera_dawsonii</i>	2	221	1545	955
<i>Siphanthera_foliosa</i>	3	229	1466	713
<i>Siphanthera_hostmannii</i>	1.7	257	2571	270
<i>Sonerila_cantonensis</i>	10	201.5	1396.5	470
<i>Sonerila_obliqua</i>	8	227	2449	764
<i>Sporoxeia_sciadophila</i>	9	136	1327.5	2332.5
<i>Tetrazygia_decorticans</i>	5.5	252	1489	123
<i>Tetrazygia_elaeagnoides</i>	12	269	2189	70
<i>Tetrazygia_paralongicollis</i>	6.1	251	946	362.5
<i>Tibouchina_aegopogon</i>	18	229	1482	797
<i>Tibouchina_aspera</i>	15	267	2284	109
<i>Tibouchina_bipenicillata</i>	20	226	2224	952
<i>Tibouchina_fraterna</i>	14	221	2198	918.5
<i>Tibouchina_llanorum</i>	13	254	1516	174
<i>Tibouchina_striphnocalyx</i>	61	266	3238	118
<i>Tococa_aristata</i>	10	225	1812	787
<i>Tococa_bolivarensis</i>	11	228	2943	810
<i>Tococa_broadwayi</i>	10	238	1654	472
<i>Tococa_bullifera</i>	6.5	260	2697	168
<i>Tococa_capitata</i>	7	261	2779	126
<i>Tococa_caquetana</i>	3.5	257	2861	203
<i>Tococa_carolensis</i>	11	216	1815	1220
<i>Tococa_caudata</i>	3.5	261	2583	119
<i>Tococa_cordata</i>	14	263	2989	132
<i>Tococa_coronata</i>	11	263	2813	119
<i>Tococa_guianensis</i>	15	258	2648	183
<i>Tococa_macrophysca</i>	9	263	3046	141
<i>Tococa_macrosperma</i>	25	264	2907	124
<i>Tococa_nitens</i>	13	264	2094	220
<i>Tococa_perclara</i>	9	245	1231	446.5
<i>Tococa_platyphylla</i>	13	202	2565	1417
<i>Tococa_quadrialata</i>	13	247	2384	415
<i>Tococa_raggiana</i>	11	191	2947	1562
<i>Tococa_rotundifolia</i>	14.5	266	3272	116
<i>Tococa_stellata</i>	13	256	2942	244
<i>Tococa_subciliata</i>	11	267	2322	102
<i>Tococa_symphyandra</i>	8	213	2968	1141
<i>Trembleya_parviflora</i>	10	204	1418	846
<i>Tryssophyton_merumense</i>	11	226.5	2011.5	755
<i>Votomita_guianensis</i>	6.5	251	2481	280
<i>Warneckea_masoalae</i>	4.5	226.5	2501	316.5

Table SI3 – Phylogenetic Linear Regression

Petal: flower size; bio1: temperature; bio12: precipitation; alt: altitude						
Model	Parameters	AIC	<i>logLik</i>	<i>p</i>	<i>t</i>	<i>R</i> ²
BM	Petal ~ temperature	1613.4	-803.7	0.0967	1.6633	0.003976
	Petal ~ precipitation	1614.4	-804.2	0.19359	-1.3013	0.002438
	Petal ~ altitude	1616	-805	0.73487	-0.3388	0.0001656
OUrandomRoot	Petal ~ temperature	1370.7	-681.3	0.67971	0.4130	0.0002461
	Petal ~ precipitation	1365.3	-678.7	0.01812	2.3689	0.008032
	Petal ~ altitude	1370.8	-681.4	0.834	-0.2096	6.339e-05
OUfixedRoot	Petal ~ temperature	1370.7	-681.3	0.67971	0.4130	0.0002461
	Petal ~ precipitation	1365.3	-678.7	0.01812	-2.3689	0.008032
	Petal ~ altitude	1370.8	-681.4	0.834	-0.2096	6.339e-05
lambda	Petal ~ temperature	1050	-521	0.1673	1.3823	0.00275
	Petal ~ precipitation	1050.8	-521.4	0.2757590	-1.0908	0.001714
	Petal ~ altitude	1049.7	-520.9	0.1305	-1.5140	0.003297
kappa	Petal ~ temperature	1107.2	-549.6	0.2193	1.2295	0.002176
	Petal ~ precipitation	1102.9	-521.4	0.01581	-2.4191	0.008374
	Petal ~ altitude	1106.6	-549.3	0.1447	-1.4602	0.003067
delta	Petal ~ temperature	1550.9	-771.5	0.1046	1.6252	0.003797
	Petal ~ precipitation	1551.8	-771.9	0.1804	-1.3410	0.002588
	Petal ~ altitude	1553.5	-772.7	0.7144	-0.3661	0.0001934
EB	Petal ~ temperature	1615.4	-803.7	0.0967	1.6633	0.003976
	Petal ~ precipitation	1616.4	-804.2	0.19359	-1.3013	0.002438
	Petal ~ altitude	1618	-805	0.73487	-0.3388	0.0001656

Table SI4 – Phylogenetic Linear Regression

SDI: Stamen dimetrisism index; bio1: (*log*) temperature; bio12: (*log*) precipitation; alt: (*log*) altitude

Model	Parameters	AIC	<i>logLik</i>	<i>p</i>	<i>t</i>	<i>R</i> ²
BM	SDI ~ temperature	-377.2	191.6	0.4145	0.8173	0.002719
	SDI ~ precipitation	-380.2	193.1	0.05744	1.9090	0.01466
	SDI ~ altitude	-376.8	191.4	0.6102	-0.5105	0.001063
OUrandomRoot	SDI ~ temperature	- 444.4	226.2	0.2135	1.2474	0.006311
	SDI ~ precipitation	- 445.9	229.9	0.08316	1.7397	0.0122
	SDI ~ altitude	-442.9	225.5	0.74565	0.3247	0.0004303
OUfixedRoot	SDI ~ temperature	-444.4	226.2	0.2135	1.2474	0.006311
	SDI ~ precipitation	-445.9	226.9	0.08316	1.7397	0.0122
	SDI ~ altitude	-442.9	225.5	0.74565	0.3247	0.0004303
lambda	SDI ~ temperature	-457.6	232.8	0.1993	1.2869	0.006715
	SDI ~ precipitation	-463.4	235.7	0.006837	2.7278	0.02948
	SDI ~ altitude	-456.3	232.2	0.5538	-0.5928	0.001432
kappa	SDI ~ temperature	-420	214	0.3566	0.9236	0.00347
	SDI ~ precipitation	-424.6	216.3	0.02084	2.3258	0.0216
	SDI ~ altitude	-419.5	213.8	0.5327	-0.5259	0.001591
delta	SDI ~ temperature	-401.8	204.9	0.3907	0.8598	0.003008
	SDI ~ precipitation	-404.7	206.3	0.05658	1.9156	0.01476
	SDI ~ altitude	-401.2	204.6	0.01476	-0.4736	0.0009146
EB	SDI ~ temperature	-375.2	191.6	0.4145	0.8173	0.002719
	SDI ~ precipitation	-378.2	193.1	0.05744	1.9090	0.01466
	SDI ~ altitude	-374.8	191.4	0.6102	-0.5105	0.001063

Final Considerations

The first chapter, based on the work of Vogel's 1978, allowed us to propose a departure from Vogel's classification and encourage a more inclusive classification of pollen flowers based on morphological traits. In the second chapter we described the fascinating diversity of stamens in Melastomataceae. Structural variation in stamen size and shape is evident from the earliest stages of androecium development and can play an important ecological role in the mature flower by regulating its interaction with pollinators. Much of this structural diversity, including the presence of poricidal anthers, stamen dimetrisism, some types of appendages and the rostrum, appears to be related to adaptations to the widespread buzz pollination syndrome. Most importantly, we show that the functional roles of several of the structures discussed here, including trichomes and oil glands, remain poorly understood. Finally, the family Melastomataceae, a large radiation of pollen flowers, includes a remarkably diverse group of flowering plants that thrive in different regions of the world, with a particular concentration in the Neotropics. In the third chapter we focused on estimating the geographic distribution of Melastomataceae traits, taking into account flower size and stamen dimetrisism. We also investigated the correlation between abiotic factors such as temperature, precipitation and altitude with the spatial distribution of these floral traits.