Heringeriana
Jardim Botânico de Brasília
https://revistas.jardimbotanicodf.org/index.php/heringeriana
ISSN 2359-165X

Original article

A review of Inflorescences in Myrteae (Myrtaceae): Concepts, Terminology and Usage

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Received 24 January 2025 | **Accepted** 25 June 2025 | **Published** 14 October 2025

How to cite: Kubo, M.T., Sano, P.T. & Lucas, E.J. (2025) "A review of Inflorescences in Myrteae (Myrtaceae): Concepts, Terminology and Usage" Heringeriana Special Issue Myrtaceae (2025): e918069. doi.org/10.70782/heringeriana.v19i1.918069

Abstract: Myrtaceae is a diverse family with a center of diversity in South America, Australia and Southeast Asia, whose ecological and evolutionary histories have been the focus of various studies. Such diversity also reflects into a rich variety of morphological, developmental, and evolutionary aspects, including the architecture of inflorescences. Here, we propose a systematic survey of the literature to better understand the profile and the approaches of scientific studies about inflorescences in general and then, specifically in myrtaceous plants of the tribe Myrteae. We found that most published works in this field focus on Monocotyledons, with China and the USA leading in number of publications. Transversal studies across plant families or focusing on important crops/models yield more citations. Ecological studies on inflorescences (especially pollination) have a strong theoretical framework, while structural, developmental, and evolutionary areas lack a common body of references. Scientific production is biased towards economically important plant families, neglecting biodiverse ones like Myrtaceae. Our results point out to the necessity of efforts toward a terminological unification/clarification and of morphological and ontogenetical studies to better circumscribe and describe inflorescences in myrtaceous plants, making results comparable allowing broader studies that may have important impacts in different fields of research.

Keywords: Neotropical, inflorescence architecture, systematic review.

Resumo: **(Revisão de inflorescências em Myrteae (Myrtaceae): conceitos, terminologia e uso)** Myrtaceae é uma família diversa com centro de diversidade na América do Sul, Austrália e Sudeste Asiático, cujas histórias ecológicas e evolutivas têm sido foco de diversos estudos. Essa diversidade também se reflete em uma rica variedade de aspectos morfológicos, de desenvolvimento e evolutivos, incluindo a arquitetura das inflorescências. Propomos aqui um levantamento sistemático da literatura para melhor compreender o perfil e as abordagens dos estudos científicos sobre inflorescências em geral e, em seguida, especificamente em mirtáceas da tribo Myrteae. Descobrimos que a maioria dos trabalhos publicados nesta área concentra-se nas Monocotiledôneas, com a China e os EUA liderando em número de publicações. Estudos transversais entre famílias de plantas ou com foco em plantas cultivadas/modelos importantes geram mais citações. Os estudos ecológicos sobre inflorescências (especialmente referentes à polinização) têm uma estrutura teórica forte, enquanto as áreas estruturais, de desenvolvimento e evolutivas carecem de um corpo comum de referências. A produção científica é tendenciosa para famílias de plantas economicamente importantes, negligenciando aquelas biodiversas como Myrtaceae. Nossos resultados apontam para a necessidade de esforços de unificação/esclarecimento terminológico e de estudos morfológicos e ontogenéticos para melhor circunscrever e descrever inflorescências nas mirtáceas, tornando os resultados comparáveis e permitindo estudos mais amplos que possam ter impactos importantes em diferentes campos de pesquisa.

Palavras-chave: Neotrópicos, arquitetura de inflorescência, revisão sistemática.

Introduction

Myrtaceae encompasses 3,800-5,671 species of 132 genera, with diversification centers in South America, Australia and Southeast Asia (Govaerts et al., 2017; Wilson et al., 2001). Myrtaceae plays an important ecological role in tropical forest domains across the world. In Brazil, this is particularly well documented in the Atlantic Forest Domain, the second largest rainforest of South America (Oliveira-Filho & Fontes, 2000) and a world hotspot of biodiversity (Murray-Smith et al., 2009). Myrtaceae, specifically tribe Myrteae (Lucas et al., 2019), to which all but one of the c. 2500 South American native Myrtaceae species belong, is the richest tree family in the Atlantic Forest and Cerrado Domains (Mori et al., 1983; Leitão Filho, 1987; Peixoto & Gentry, 1990; Landrum & Kawasaki, 1997; Oliveira-Filho & Fontes, 2000; Oliveira-Filho et al., 2006). Myrtaceae is an important indicator of total tree diversity and vegetation subtypes in these regions and has been used as a model for biome evolutionary, ecological and conservation studies (e.g. Murray-Smith et al. 2009, Lucas et al. 2015. Myrtaceae species have important economical uses such as timber (*Eucalyptus* spp.), spices (*Pimenta dioica* (L.) Merr.and *Syzygium aromaticum* (L.) Merr. & L.M.Perry) and fruit source (*Psidium guajava* L.), for example. Despite this importance in tropical biomes, Myrtaceae is a disproportionate contributor to the 'taxonomic gap' (Raposo et al., 2020) throughout the tropics as difficulties in identification of both species and genera hamper efforts to manage and conserve the fragile environments in which species occur (Landrum & Kawasaki, 1997).

Inflorescence architecture and/or typology have helped taxonomists circumscribe taxa at different hierarchical levels (McVaugh, 1956; McVaugh, 1968; Lucas et al., 2019). Nonetheless, classification and description of inflorescences are controversial due to terminological confusion that leads to uncertainty when comparing traits throughout taxa (e.g. Endress 2010). Much taxonomic confusion in Myrtaceae is linked to poor understanding of what comprises an inflorescence, or homologous units of it, and yet, the last thorough studies on Myrtaceae inflorescence were carried out by (Briggs & Johnson, 1979) and (Weberling, 1988b), the latter with a focus on the order Myrtales.

A robust overview of the scientific literature regarding inflorescence architecture, morphology, development, and evolution is badly needed to precisely understand the value of the inflorescence for accurate species classification and so to address the taxonomic gap. To undertake a review on this topic in Myrtaceae, with a focus on tribe Myrteae, an angiosperm wide context was necessary. By systematically mapping literature focused first on angiosperm, then Myrtaceae inflorescences, the aim of this study is to interrogate existing literature to learn: 1) who and where were/are the researchers working specifically on angiosperm inflorescences? 2) what are the main foci of published inflorescence research in angiosperms? 3) how are angiosperm inflorescence studies distributed across families? Are Myrtaceae inflorescences studies abundant?. Focusing on tribe Myrteae, we further investigate 4) what are the main studies on inflorescence of the tribe Myrteae and are they being used by the researchers?. The final aim of this work is (5) to summarize inflorescence concepts and terminology and their application to Myrteae inflorescences.

Material and Methods

Angiosperm literature

To address questions 1-3, articles were selected using the Web of Science (WOS) Core collection, from 1900 to 2023, and searching Title & Keyword Plus® for occurrences of (inflorescence* AND pattern) or (inflorescence* AND morpholog*) or (inflorescence* AND evolution) or (inflorescence* AND term*); herein referred to as search parameters A. To address study questions 2-3, we manually extracted the following information from articles published between 2011-2021: (a) Family of the plant studied (Plant families followed POWO 2023, when the study involved more than one family it was scored as "multiple"); (b) main research methods, classified as Anatomy, Morphology, Ontogeny, Taxonomy, Crop/ornamental (studies focusing on plants with economical interest and human use); Model Organisms (e.g. studies focusing on *Arabidopsis thaliana* (L.) Heynh., *Antirrhinum majus* L., *Oryza sativa* L., *Zea mays* L., *Triticum* sp., *Solanum lycopersicum* L.); Molecular approaches; Phytochemical; Evolutionary and Phylogenetics; Ecological; Review; Other (e.g. computational modelling, physics). More than one method could be scored from a single document.

Myrtaceae literature

To address questions 4-5 on references for inflorescence terminology in Myrtaceae, we searched WOS collection for occurrences of (Myrtaceae AND new species), then manually filtered those working within Myrteae; herein referred to as search parameters B. Then we extracted references cited in articles from 2015-2020 e as sources for morphological terminology. Raw results were analysed using the Bibliometrix package (Aria & Cuccurullo, 2017) in the R environment (Team, 2023) to recover the following information, with analysis steps numbered for convenience:

Descriptive analyses: (1) Average Citations per Year, default settings; (2) Annual Scientific production, assessed using Compound Annual Growth Rate (CAGR), a geometric progression ratio with constant rate; (3) two Word Clouds were generated, one using author's keywords, the other using Keywords Plus®, and font size measured by frequency; synonyms as (floral development = flower development), (inflorescence = inflorescences) and (*Arabidopsis* = *Arabidopsis thaliana* = *Arabidopsis-thaliana*), had their results combined, and terms used as query in the database (inflorescence, evolution, pattern, term, morphology) were removed; (4) A three-field plot was used to summarize the relationship between three metadata fields using a Sankey Plot; two combinations were made: (i) Authors/ Author's Country/ Author's keywords and (ii) Author's affiliation/ Author's keywords/ Cited references; number of items in each field was restricted to the top 10.

Data analyses: (5) Most Relevant Authors were assessed using a fractional authorship approach, quantifying individual author's contribution in documents co-authored assuming uniform contribution by all authors; (6) Author's

Production over Time was created plotting the number of documents per year; (7) Most Local Cited Authors ranks the top ten authors in the collection with most citations; (8) Top Documents by Local Citations measures the number of times a document from our collection was cited within our collection; (9) Most Local Cited References retrieves the most cited document listed as reference independent of whether it is included in our collection; (10) Conceptual Structure was addressed by factorial analysis using Multiple Correspondence Analysis (MCA), where distance between words corresponds to the number of documents in which they appear together, and Co-occurrence Network, where a co-occurrence matrix is constructed with vertex as words, vertex size corresponds to term occurrence and links width between vertices corresponds to co-occurrences. Both strategies used field Keywords Plus® as query, all other settings were used as default (clustering algorithm: Walktrap; Normalization by association); (11) Thematic evolution was measured using the "abstract" field and 4 time slices (1910-1997, 1998-2007, 2008-2013, 2014-2019 and 2020-2023), using thematic maps in which each cluster is plotted along Callon centrality and density axes, and quadrants are divided in "niche themes", i.e. highly developed and isolated themes; "motor themes", i.e. with a high developmental degree and central to the research theme; "emerging or declining themes", i.e. weakly developed and peripherical; and "basic and transversal themes", i.e. important themes for the research field but not strongly developed; a list of synonyms was created and non-relevant words in the abstract were removed (e.g. found, suggest, study) (Cobo et al., 2015); (12) Co-citation analysis was conducted using "paper" field, filtered for years (i)1910-1991, (ii) 1991-2005, (iii) 2005-2012, and (iv) 2012-2023, clustering algorithm used was Walktrap, and remaining parameters were set as default.

Results

Angiosperm literature

The total number of publications retrieved using search parameters A was 801, ranging from 1910 to 2023, from 2317 authors. Most documents were original articles (84.89%) followed by review articles (8.99%). The annual production and average citation per year are shown in Figure 1a, with two periods indicated as experiencing an increase in scientific production (1989-1991 and 2002-2005). Average citations per year, Figure 1b, indicate that three references published in 1978, 2005 and 2012 (i.e. (Pyke, 1978; Heisler et al., 2005; Andrés & Coupland, 2012), have the highest accumulation of total average citations per year.

Most used keywords are summarized in Figure 2; using the author's key words, "flower" ranks first (8.5% of hits), followed by "development", "pollination", "phylogeny" and "*Arabidopsis*" (6.9, 5.6, 4.2 and 3.4% of hits, respectively). Using Keywords Plus® as a parameter, "flower" also ranked first (7.2% of hits), followed by the terms "*Arabidopsis*" (7.0% of hits), "expression" (4.9% of hits), "inflorescence architecture" (4.8% of hits) and "plant" (4.5% of hits).

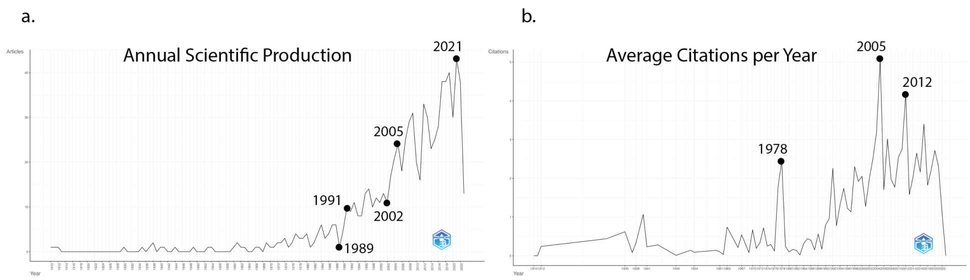

Figure 1: Descriptive overview of the data collected. a. Annual scientific production, with important jumps in production between 1989-1991 and 2002-2005; peaking in 2021. b. Average citations per year, note the three peaks, meaning that studies published in those years are accumulating more than average total citations per year.

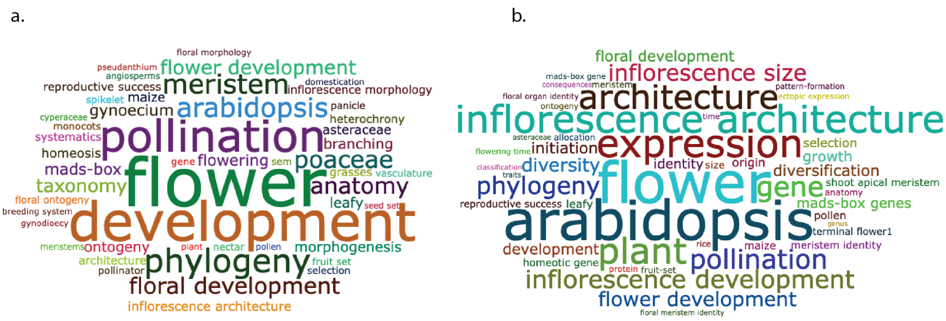

Figure 2: Word Cloud presenting the 50 most frequent keywords in the documents retrieved excluding searched words. Font size is proportional to frequency. a. using Author's keywords. b. using Keywords Plus®.

In Figure 3a, the relationship between the 10 top ranked authors, countries and keywords used is shown. A predominance of researchers from the Northern hemisphere is observed, with only Argentina and Brazil from the South hemisphere figuring among them, the latter without any incoming connection. On the other hand, the second plot (Figure 3b), assessing relationships between affiliation, keywords and cited references, shows that only Universidad Nacional del Litoral (Argentina) appears as one of the top ranked institutions. Besides "inflorescence", keywords not primarily searched for appeared, such as "development", "pollination", "flower" and "meristem" in both plots (Figure 3).

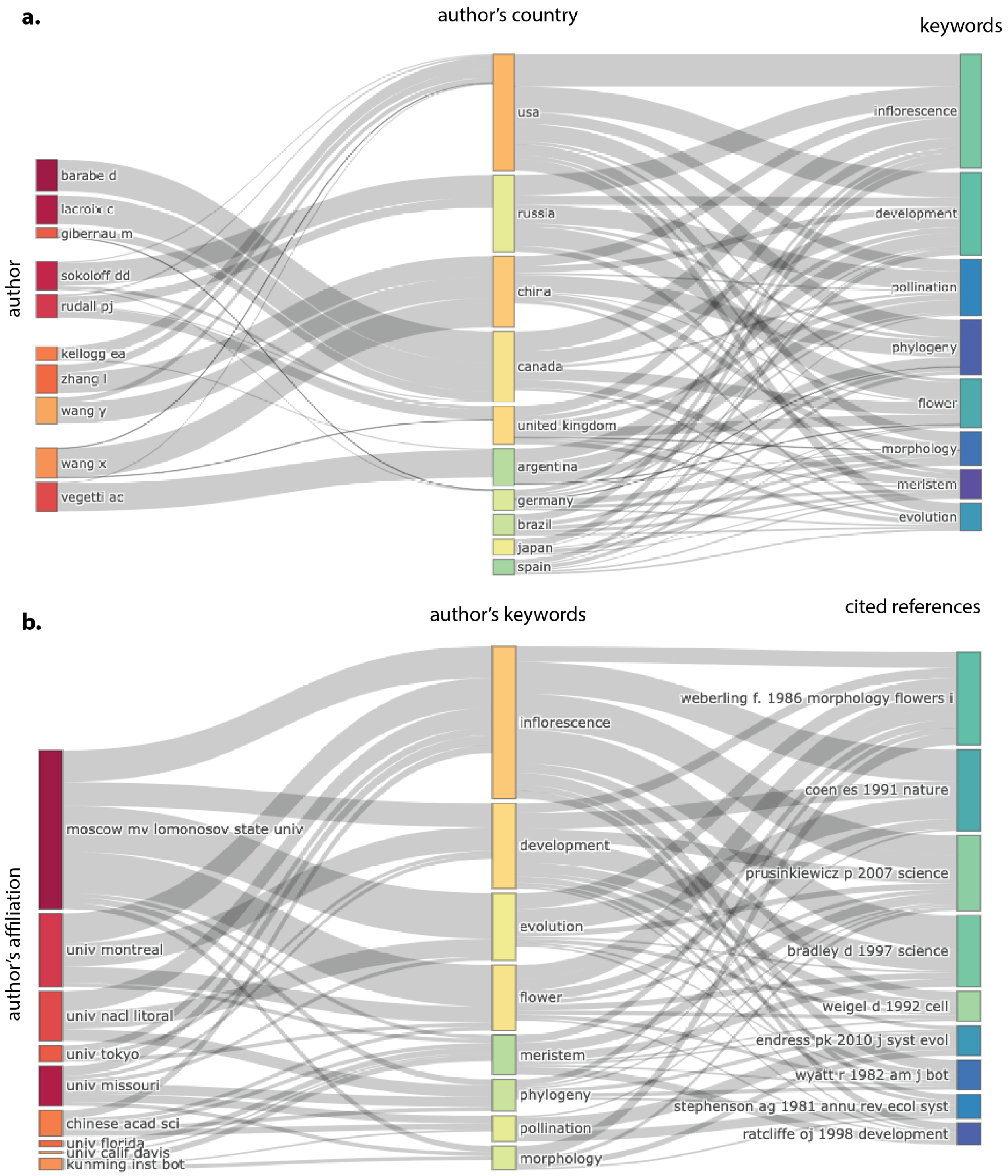

Figure 3: Three-field plots for the collection summarized in a Sankey plot showing relationships between the top 10 ranked items of three fields. a. Author – Author's Country – Author's keywords. b. Author's affiliation – Author's keywords – Cited References. Nodes are represented by rectangles and width of the line linking them is proportional to the importance of the relationship.

Between 2011 and 2021, a total of 463 documents were returned; manually extracted information is summarized in Figure 4. Families in which model plants are included figure in most studies, namely Poaceae (e.g. *Oryza sativa*), Brassicaceae (e.g. *Arabidopsis thaliana*), Fabaceae (e.g. *Medicago truncatula* Gaertn.), Asteraceae (e.g. *Gerbera* sp.) and Solanaceae (*Solanum lycopersicum*). The only top-ranking family that was not linked to a model species or an economically exploited one was Cyperaceae, but it was also the only that did not present any study using molecular data.

The most productive author in our survey was D. Barabé (18), followed by C. Lacroix (15), D.D. Sokoloff (14), P.J. Rudall (12) and A.C. Vegetti (12) (see Supplementary Material 1 for top ten authors and Supplementary Material 2 for timeline of publications). The most cited authors in the publications reviewed here were involved in studies of inflorescence trait development and evolution (e.g. P.J. Rudall, P.K. Endress), genetic control of those traits (R. Koes, E. Coen, Y. Erasmus, K. Goto), a combination of such fields (E.A. Kellogg) or computational modelling (e.g. P. Prusinkiewicz) (see Supplementary Material 3). Local citation scored Prusinkiewicz (2007) and Endress (2010) as the documents with highest impact among surveyed publications, followed by studies focusing on gene expression and function in *Arabidopsis thaliana*, as Hanano & Goto (2011) and Alvarez et al. (1992). The most cited reference documents were also related to genetic control, such as Weigel et al. (1992), Bradley et al. (1997), and Coen & Meyerowitz (1991); or inflorescence architecture and evolution, with Prusinkiewicz et al. (2007), Weberling (1988a, 1988b) and Endress (2010).

Conceptual structure co-occurrence analysis network presented three clusters with centralities in "evolution", "expression" and "patterns" (Figure 5). The conceptual structure map of Keywords Plus® using a factorial approach also resulted in three clusters of themes (Figure 6). The thematical evolution in the research field was assessed by analysing the abstracts of documents and is summarized in Figure 7. "Inflorescence" appears as a motor theme since the first time slice (Figure 7B) and remains in this position up until the last time slice, where J-cluster is divided in two and "inflorescence" becomes a niche theme (Figure 7K), while "development", "flowering" and "architecture" become transversal themes (Figure 7L). "Meristem", "model", "gene", and "expression" first appear in 2008-2013 as emerging themes (Figure 7F), merging with "inflorescence" in 2014-2019 as a motor theme (Figure 7J), and later diverging again from it by 2020-2023, becoming a transversal theme.

Co-citation of papers using different time frames analyses (Figure 8) presented the changes in co-citation network during periods with jumps in science production or peaks of cited documents (Figure 1). Analysing data from 1910-1991, we found five clusters, with Stephenson (1981), Willson & Rathcke (1974) and Willson & Price (1977) standing out; from 1991-2005, the network remained with five clusters, now separated in two main groups, one remained with Willson & Price (1977), and the other with a very dense cluster with published works from S.J. Mayo and D. Barabé; from 2005-2012, one main cluster dominates the plot with Weigel et al. (1992); and from 2012-2023, the same cluster continues as the most dense, but with no clear leading document (in number of citations) while Prusinkiewicz et al. (2007) appears in a cluster close to the former, and also connected to another cluster with Endress (2010) as the most cited paper.

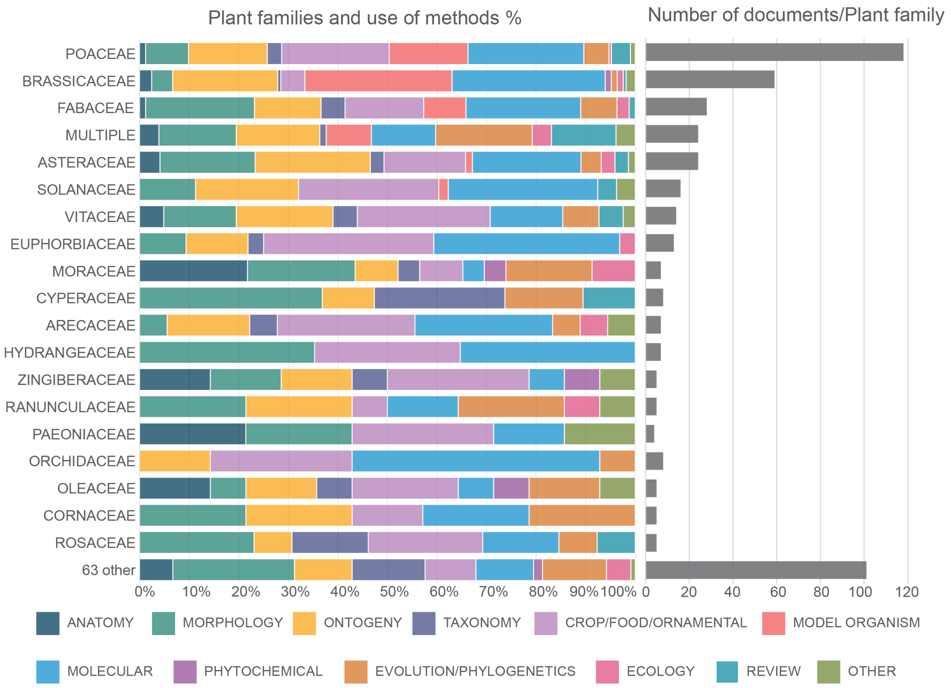

Figure 4: Documents from 2011-2021 divided by plant family and main methods used. On the left, stacked bar chart by family showing the percentage of each method. On the right, total number of documents divided by family.

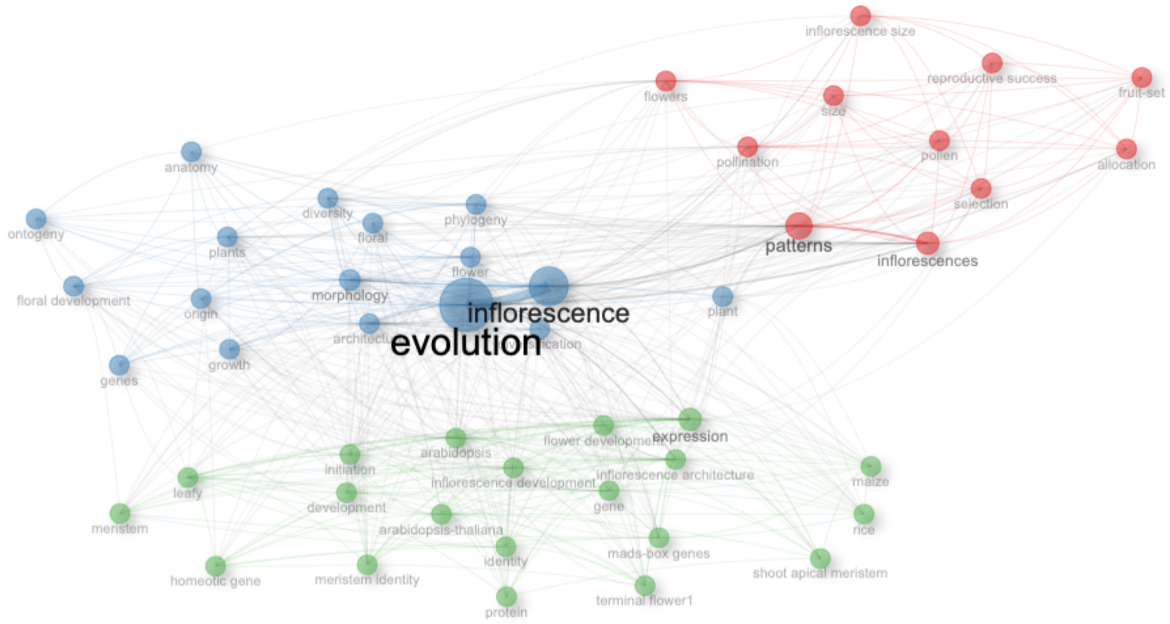

Figure 5: Network analysis plot using co-occurrence of Keywords Plus® showing three clusters (different colours). Bubble dimensions correspond to occurrence, and connections width to link strength.

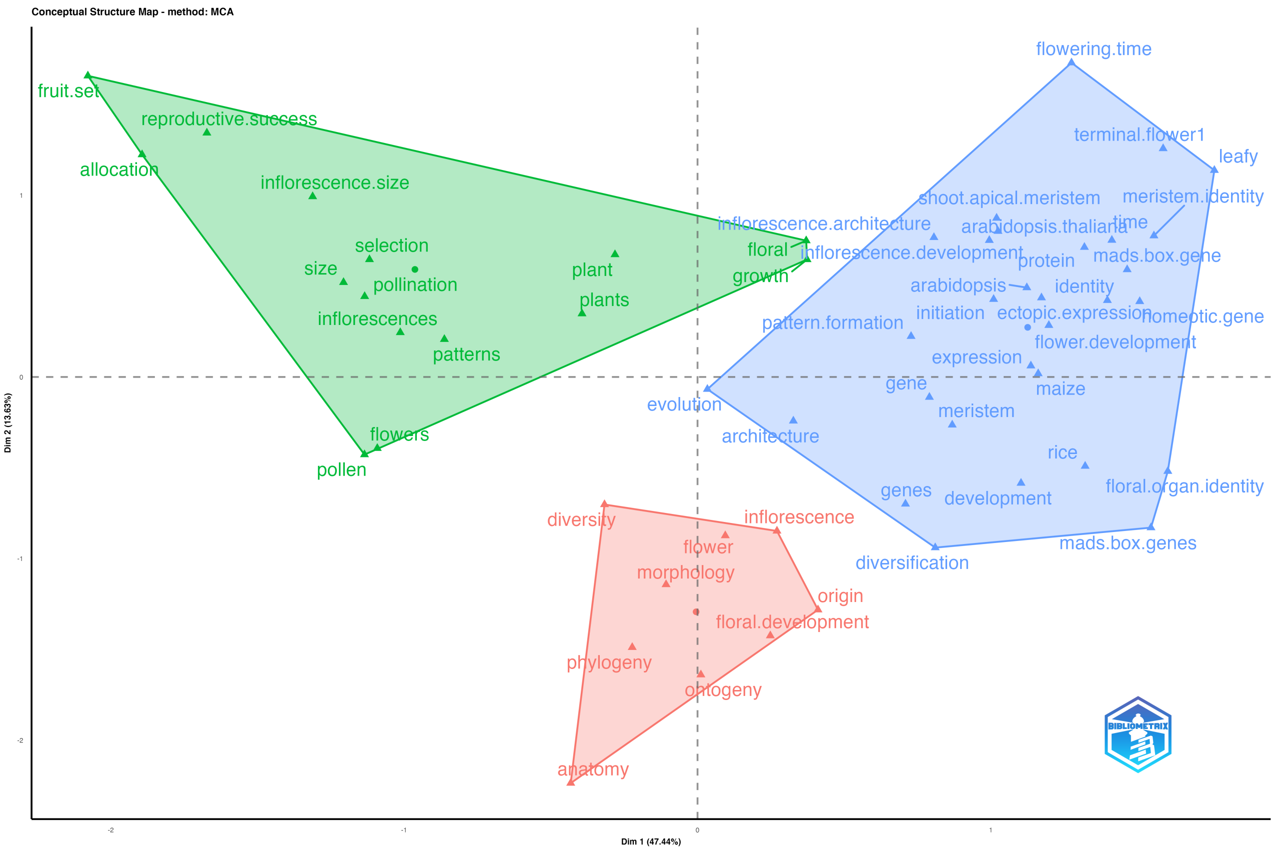

Figure 6: Conceptual Structure Map using factorial approach. A division in three clusters was made after analysing the Topic Dendrogram (Supplementary Material 4). Colours represent different cluster of topics, identified by hierarchical clustering.

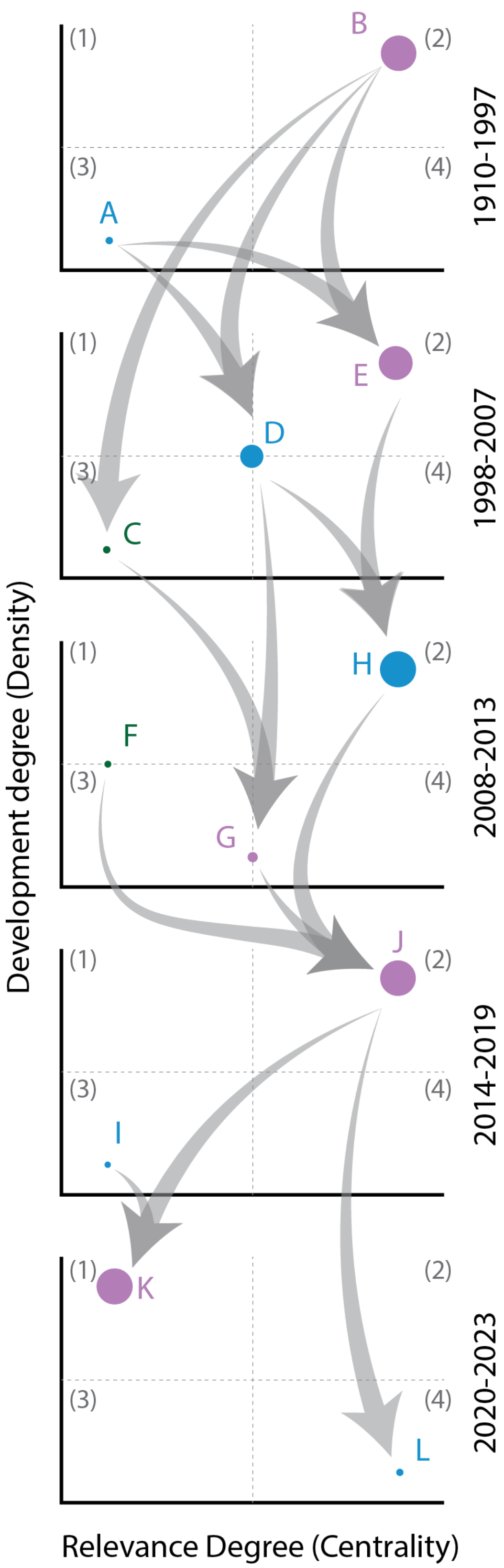

Figure 7: Thematic evolution of documents in collection assessed by abstract analysis in five periods of time. Colours differentiate clusters of words; size of circle is proportional to cluster words occurrences. Gray arrows indicate themes dividing or merging. The four quadrants are (1) Niche themes, (2) Motor themes, (3) Emerging or Declining themes and (4) Basic or Transversal themes. Cluster names are given with the top 5 words: A. Species, morphology, development, growth, leaves; B. Flower, plant, inflorescence, female, production; C. Female, stamens, male, zone, carpels; D. Species, reproductive, pollen, size, production; E. Flower, inflorescence, development, plant, morphology; F. Gene, expression, *Arabidopsis*, model, meristem; G. Plant, flowering, reproductive, patterns, pollen; H. Flower, inflorescence, development, species, morphology; I. Species, morphology, evolution, production, structures; J. Flower, plant, inflorescence, development, gene; K. Flower, inflorescence, plant, species, morphology; L. Gene, development, expression, flowering, architecture.

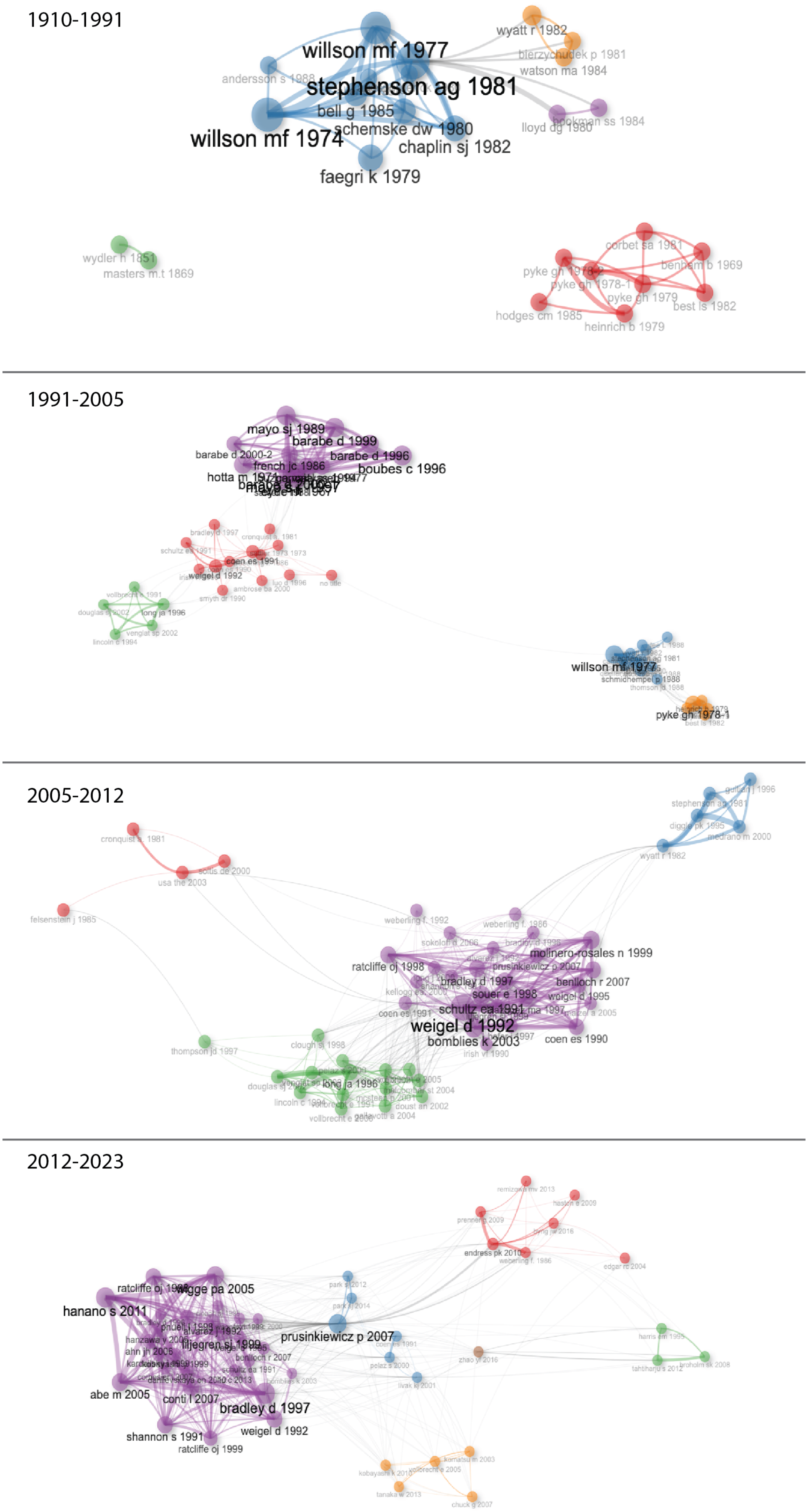

Figure 8: Co-citation analysis by "paper" in different periods to assess changes in the network of cited references in our documents collection over time. Colours differentiate clusters; size of circle is proportional to number of citations; width of links is proportional to strength of connection.

Myrtaceae literature

The search in WOS database for parameters B resulted in 197 documents. The co-citation network is presented in Figure 9. In the three clusters, Briggs & Johnson (1979) is the only publication dealing specifically with inflorescences. It is clustered with taxonomical treatments in Myrtaceae (e.g. Berg 1857; McVaugh 1968, 1969; Landrum & Kawasaki 1997; Wilson et al. 2001) and phylogenetic studies in *Eugenia* (Mazine et al., 2014) and Myrteae (Lucas et al., 2007). Other sources of terminology, such as glossaries of Radford et al. (1974), Hickey & King (1973) and Beentje (2012), are in a different cluster (green), with other historical taxonomic works (e.g. Berg 1855; De Candolle 1827), taxonomic studies in *Eugenia* (e.g. Mazine et al. 2016), phylogenetic and taxonomic studies in *Myrcia* (Lucas et al. 2011, 2018) and new species descriptions (Sobral et al. 2012, 2015, 2016). In the documents from 2015-2020, glossaries were the most cited as source for morphological terminology (52.3%), followed by citation of other published works in new species (23.4%) and morphological studies (13.2%) (Figure 10). Gonçalves & Lorenzi (2011), Hickey & King (2000), Briggs & Johnson (1979) are the most cited globally. A total of 22 works of new species were cited as basis for morphological description, of those Snow et al. (2012) was the most cited (22 species described), although only auto-citation (Snow et al. 2015, 2016). 51 of the described species in the period analysed had no document explicitly cited as reference for morphological terminology.

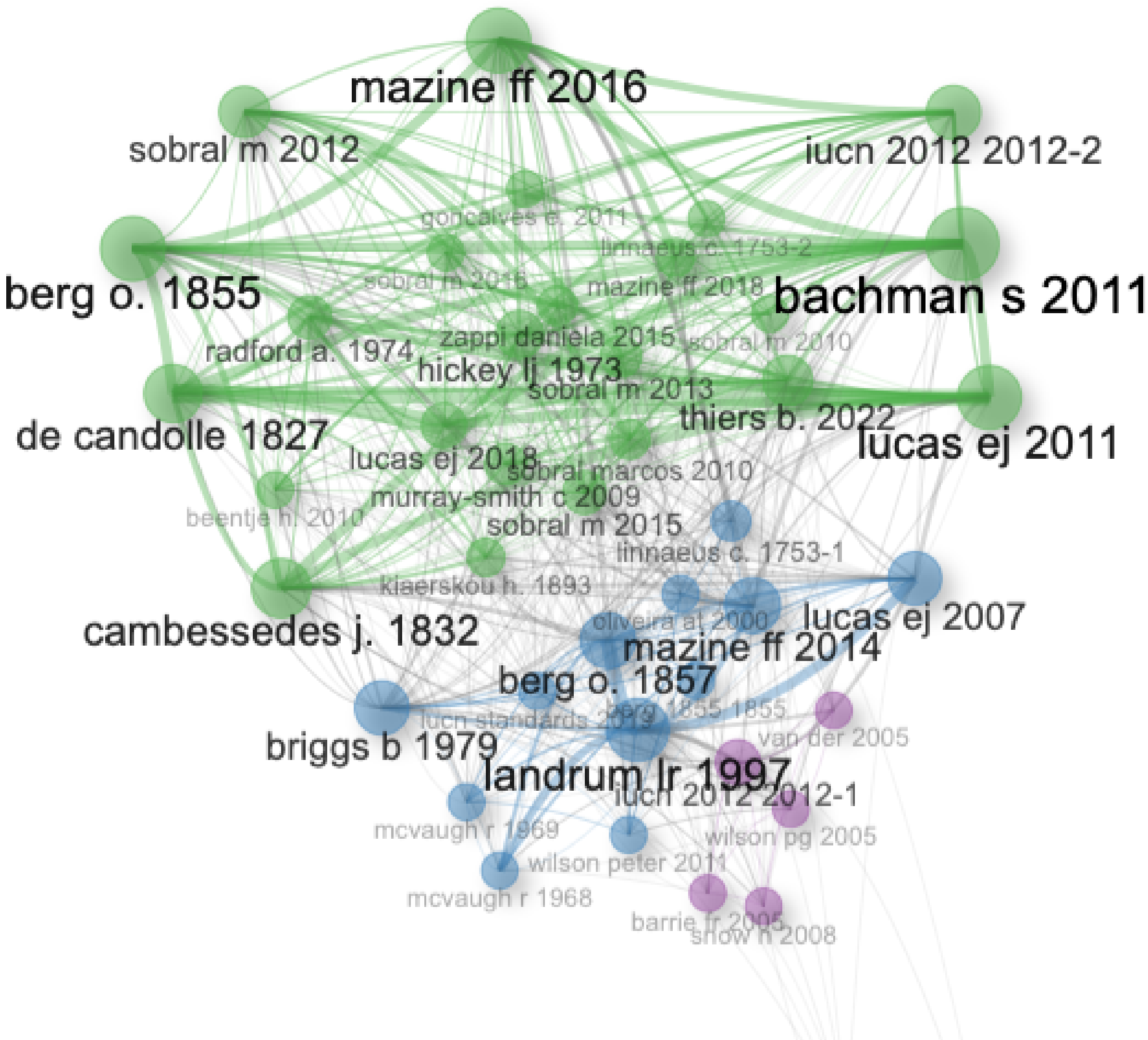

Figure 9: Co-citation network from published studies between 1974-2023 describing new species in Myrteae. Colours indicate clusters; circle and font size are proportional to number of citations; width of links is proportional to strength of connections.

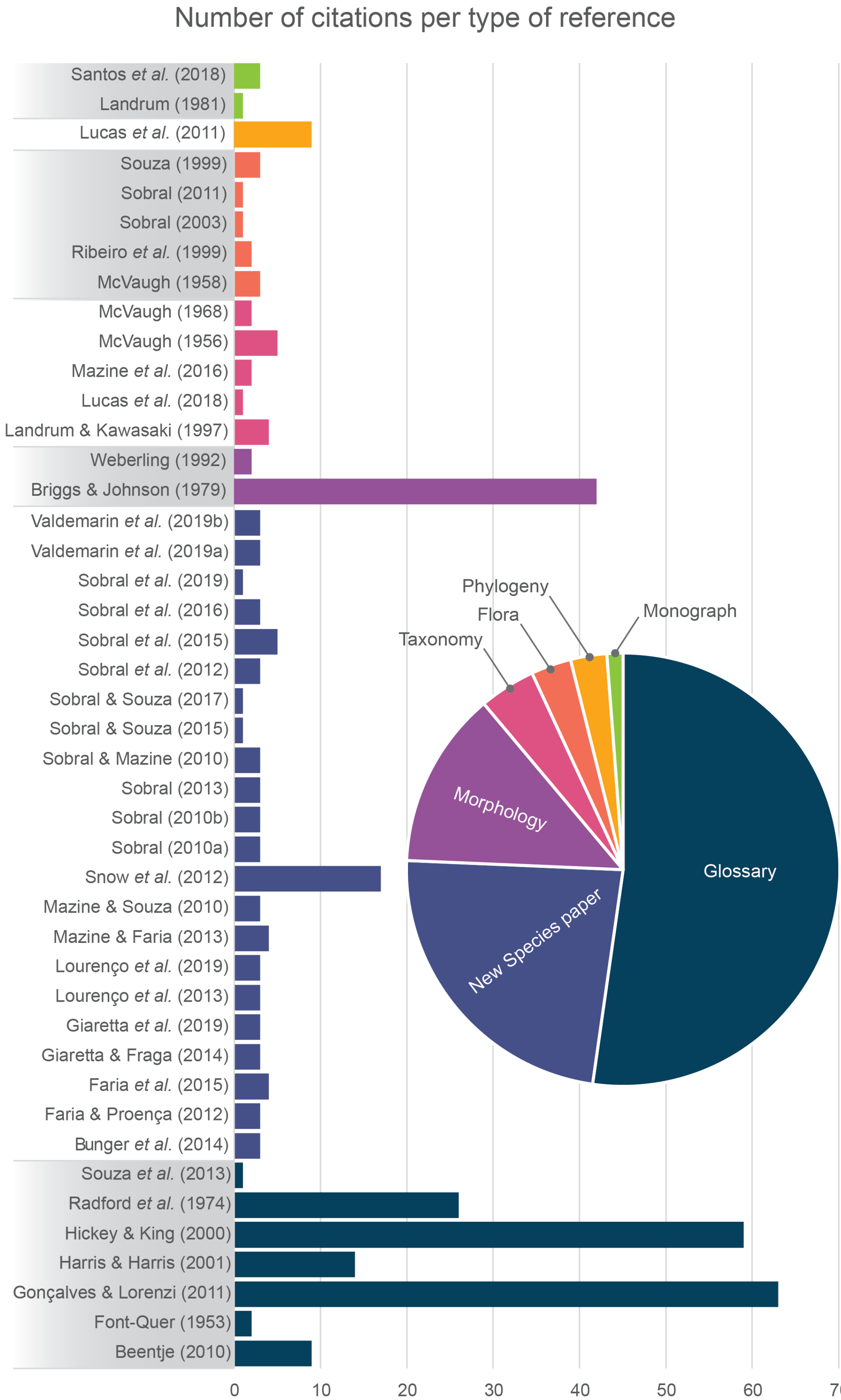

Figure 10: Distribution of citations in inflorescence description of new species in Myrteae from 2015-2020, divided by nature of the studies. New species papers are other new species publications cited as references; Morphology are studies focused on plant morphology; Taxonomy are taxonomical revisions.

Discusssion

Our analysis of the literature concerning inflorescences in angiosperms (parameters A) showed the following:

Inflorescence researchers in angiosperms

The most prolific authors in our collection of published studies focused mostly on a single family, Araceae (D. Barabé and C. Lacroix) and Poaceae (E.A. Kellogg and A.C. Vegetti) (see Figure 3 and Supplementary Material 1 and 5). In contrast, P.J. Rudall documented the inflorescence of various plant families (e.g. Poaceae, Rapateaceae, Salicaceae, Orchidaceae), but with focus on evolution and development in Monocotyledons, often in collaboration with D.D. Sokoloff. Of the top ten most prolific authors, X. Wang is the latest to publish in the field, first contributing in 2017 and with, at least, one published paper every year since, apart from 2020, mostly related to gene identification, function and expression in economically important or model plants (e.g. rice, tomato, pepper, *Arabidopsis*).

The three-field plot (Figure 3a) reinforces the impact of the collaborative works of D. Barabé and C. Lacroix (working on Araceae) and D. Sokoloff and P. Rudall (working on Monocotyledons), highlighting the hegemony of researchers from the northern hemisphere in the field. The former authors are noted to collaborate only with Canadian authors, and the latter, while collaborating with a more international suite of authors, these institutions are still restricted to the northern hemisphere, including the USA, Russia, China, and UK. Abelardo Vegetti is the only author in the top ten most cited, affiliated to a South American country (Supplementary Material 3). This makes the Universidad Nacional del Litoral (Argentina) the highest ranking and only South American author's institution (Figure 3). The situation described corroborates a predominance of researchers from the global North found in other lines of Life Sciences, such as forestry carbon sequestration (Huang et al., 2019), climate change (Fu & Waltman, 2022), and biodiversity (Tydecks et al., 2018). Marks et al. (2023) led a comprehensive study on Plant Science and found that the geographic distribution of publications is highly concentrated in institutions from China and USA. Karlsson et al. (2007) highlight that, on top of this discrepancy in number of published works, most published studies are focused on temperate environments with relatively fewer in the tropics. This focus on local or regional problems also means that comprehensive, larger-scale analyses are rare.

The most cited local (referenced documents that are also part of our collection) and global (referenced documents that may or may not be in our collection) references also have names in common, such as E. Coen, P. Prusinkiewicz and P.K. Endress. The remaining global references are either on genetic control of plant development, following E. Coen (e.g. Weigel et al. 1992; Bradley et al. 1997 and Ratcliffe et al. 1998) or a more ecological approach to architecture of inflorescence impacting pollination and fruit production (e.g. Wyatt 1982; Stephenson et al. 1981). Weberling (1983) - an earlier edition to Weberling (1989) - presented links with all keywords but pollination, with somewhat weaker link strength (width) to "meristem" and "phylogeny" when compared to the other keywords (Figure 3b). Endress (2010) presented another study focusing on inflorescence definition, description and terminological clarification with its strongest link with "pollination", showing how inflorescence definition supports different fields of research. The same is true for Wyatt (1982), which has no link to "pollination", the keyword more easily related to ecology, but has strong links to "evolution" and "development".

The co-citation network evolution shows that between 1910-1991, research was divided in seven clusters, with citations of M.F. Willson and A.G. Stephenson clearly dominating (Figure 8). The main theme of these articles is related to inflorescence function and its impacts on reproductive success and pollination, a more ecological approach. Between 1991-2005, a new set of clusters appeared with S.J. Mayo and D. Barabé leading the largest and densest cluster (in purple, Figure 8 – 1991-2005), focused on morphology and anatomy/ontogeny, with loose connection to the "ecology" cluster (in blue and orange), but with closer and more links to the other two clusters (in red and green), comprising authors working on gene identification, function and expression (e.g. E.S. Coen, D. Weigel, J.A. Long). In works published between 2005-2012, clusters related to genetic research grew considerably and include studies focusing on structural traits and evolution of inflorescences (Weberling (1992); Kellogg (2000); Sokoloff et al. (2006); Prusinkiewicz et al. (2007)), reestablishing links to ecological studies (Wyatt, 1982). In our last time slice (2012-2023), these evolutionary works are separated into another cluster (in red, Figure 8 – 2012-2023) and Prusinkiewicz et al. (2007) bridge this cluster with genetic research (in purple), resonating with the aim of the paper (see section on Transient model). This shift in co-cited documents throughout the years can help us understand how the view of the angiosperm inflorescence changed over time. From our data, it appears that the field moved from a more functional and ecological approach, with those seminal works of Willson and Sphenson disappearing from the network in the last time slice. Two lines of research are noted to then be established, one dealing with the genetic control of inflorescence development and architecture, mainly focused on model plants and another focused on a more morphological and conceptual approach, often contributing to the field of systematics. Despite links between studies inside the 'genetic' cluster being much stronger, we observe that many links remain between these and morphological and conceptual studies, many of those mediated by works that couple gene function with ontogenetics and meristem function. These inter-cluster links reflect the importance of understanding the biological meaning and consequence of genes studied.

Main themes and methods in inflorescence research

As expected, the most frequent keywords appearing in the Word Cloud (Figure 2) were those used as queries in our search in the database. Terms like "pollination" and "development", some plant groups (e.g. "grasses", "asteraceae", "monocots") and some model plants (e.g. "*Arabidopsis*", "maize", "rice"), are amongst the terms predominant in the Word Cloud. This result emphasizes the common interest in the inflorescence and associated funding available to those concerned with crops. Considering the angiosperm families and methods most frequently appearing in the literature between 2011-2021, Poaceae and Brassicaceae were the most studied families, with most works using ontogenetic and/or molecular approaches (Figure 4). Morphological, ontogenetical and molecular approaches were the most used, with few families without any published work in this period using these methodologies (e.g. Orchidaceae-Morphology and Hydrangeaceae-Ontogeny). Many of the studies used species with economic importance, from important crops to improvement of ornamental plants. This pattern is found in other fields of plant science, with more effort and funding directed to model organisms and crops studies than to other plants (Marks et al., 2023). When species richness is considered, even Myrtales and Asterales, which figure in the top 20 most cited plant orders, are underrepresented, as studies are focused on few species with economical value (e.g. *Eucalyptus*, in Myrtaceae, and *Helianthus annuus* L., in Asteraceae), whereas Poales, Brassicales and Solanales are overrepresented (Marks et al., 2023).

Considering the co-occurrence of the article's keywords, our results can be divided into three main themes (1) "evolution", (2) "patterns" and (3) "expression" (Figure 5). In the "evolution" cluster, we found terms related to structure, morphology, and ontogeny; in "patterns" cluster, terms are more related to ecology; and in the "expression" cluster, terms related to genetic studies and model plants were found. This division in three main themes is in accordance with the main lines of research found when assessing the authors and references. The "evolution" cluster shares more co-occurrences (see number of gray links from node of one cluster to the other) with the other two clusters than they do between themselves. However, connections between "evolution" and "expression" appeared divided between nodes, while connections between "evolution" and "patterns" were concentrated on nodes closer to "evolution". Assessing the data by a factorial approach (MCA) allowed us to construct a topic dendrogram (Supplementary Material 4) and visualize that the topics could be partitioned in three groups. By plotting this partition in a conceptual structure map, it was possible to see that the term "evolution" is the one closest to the origin, meaning that most documents deal with evolution (Cuccurullo et al., 2016). The clusters have similar composition of terms from the co-occurrence analysis, with the main difference that "evolution" now is part of the same cluster as "expression".

Considering the thematic evolution analysis (Figure 7), the "inflorescence" theme appeared immediately as a motor theme in the first time slice. As already noted when assessing co-citation, the occurrence of this theme along with themes concerning reproduction and pollination, both connected with "production", indicates that inflorescence research is frequently connected to its function. We also note a shift of the "inflorescence" theme from motor to niche theme in the last time slice (2020-2023), is linked to the shift of the centrality of the field to genetical approaches (plotted as basic or transversal themes). Themes like "reproduction", "production" and "pollen" (more closely related to the ecological approach) then disappear from the plot. This indicates that morphologically oriented themes have specialized and are often isolated from genetic themes, as observed by the separation of clusters in Figure 8 - 2005-2012 and 2012-2023. The transversality of genetic approaches in inflorescence research may be partially explained by technological advances and cost reduction that improved accessibility to genetic sequencing. However, this preference and biased importance given to publications using genetic approaches may deepen the inequality of production between northern and the southern hemispheres (Tydecks et al., 2018; Marks et al., 2023). Wealthier countries have more access to cutting edge technology than developing countries, and researchers from the latter, despite being from where biodiversity is richest, can be relegated to data gathering or minor roles in publications (Tydecks et al., 2018).

Myrtaceous inflorescence studies

Our analyses of the Myrtaceae literature (parameters B), with manual extraction of reference works in inflorescence morphology and evolution in Myrteae, indicate an evolution of understanding and allows us to summarize as follows. McVaugh (1956) builds on the discussion of myrtaceous inflorescences of Bentham (1869). Bentham (1869) stated that inflorescences were usually helpful for distinguishing taxa, e.g. inferring relationship between genera. Nonetheless, Bentham (1869), never references the terminology and inflorescence descriptions used are vague, as when describing Myrcia inflorescences as "usually more compound" (Bentham (1869); p. 156), or when "simple" and "compound" inflorescences are distinguished by the presence of ramification subtended by the bracteole. McVaugh (1956), (1968) focuses on Neotropical Myrtaceae and dedicates an entire section to the discussion of myrtaceous inflorescences in both works, stating that on top of providing recognizable characters, those are usually preserved in all herborized fertile specimens. McVaugh (1956) defines the terminology used to describe inflorescences, as raceme, myrcioid panicle and dichasium, also used in McVaugh (1968). But it is Briggs & Johnson (1979) and, later, Weberling (1988b) who analyse the morphology of myrtaceous inflorescences in depth and consider it in light of specialized inflorescence literature, such as Wilhelm Troll (1897-1978). These multiple works by different authors proliferated terms and conceptual complexity, with more than 70 terms listed in Briggs & Johnson's (1979) glossary and 100 in Weberling

(1989), where the terminology previously used by Weberling (1988b) is systematically defined in a glossary, making practical use of them often unmanageable (Endress, 2010).

To add to the confusion, the same terms might have different meanings depending on the author. If we take the three main inflorescence types recognized by McVaugh (1956, 1968) — raceme, panicle and dichasium — and compare the definitions between McVaugh (1956), (1968), Briggs & Johnson (1979) and Weberling (1989) the difficulties one faces while describing an inflorescence become evident (original definitions can be found in Supplementary material 6). To define raceme, the authors agree about the indefinite (or blastotelic) nature of the primary axis and that secondary axes are solitary flowers with elongated pedicels. Conversely, McVaugh (1956), (1968) gives weight to the morphology of the phyllomes (i.e. an inclusive term for leaf, bracts, bracteoles, prophylls, etc., in Briggs & Johnson 1979) both in primary and secondary axes; however, Briggs & Johnson (1979) and Weberling (1988b), (1989) do not mention anything regarding phyllomes in the primary axis and the former explicitly states that their presence in the secondary axes are facultative. Panicle, according to the three authors, is a determinate (or anthotelic) inflorescence; McVaugh (1956) and Weberling (1989) also describe it as compound (i.e. when there are branching orders higher than one, Weberling 1989) and that all axes are determinate. On the other hand, Briggs & Johnson's (1979) only condition for the second order axes is that they must not be thyrsoids (thyrses with terminal flower); McVaugh (1956) goes further and describes how the elongation and ramification of successive branch orders must be in a panicle. Regarding the dichasium, McVaugh (1956) and Briggs and Johnson (1979)'s descriptions are similar, although the latter uses a different terminology, which requires familiarity to understand ("cymose", "pronodate", "internode"), rather than the descriptive language of McVaugh (1956). The significant difference with Weberling (1989)'s definition is the use of "cymose": to Briggs & Johnson (1979) the dichasium is a cymose inflorescence, while to Weberling (1989) it may be only similar to a cymose branching pattern. In Briggs & Johnson (1979), "cyme" is described as " (adj. cymose . . .) – an inflorescence in which the main and all of the subsequent axes are pronodate and each is terminated by a flower (. . .)" (p. 243), and in Weberling (1989), "cyme" is a "cymose partial inflorescence; which develops no further leaves apart from the prophylls and thus has only one or two possibilities for lateral branches" and "cymose" as "branching pattern of inflorescences, where the branching only takes place from the axil of the prophylls" (Glossary, XVI). These differences are subtle and linked to different concepts for delimiting inflorescences and partial inflorescences between the authors, although both partially follow Troll (1964), (1969).

Inflorescence delimitation

The flexibility of the architecture of the myrtaceous inflorescence poses difficulties of delimitation (McVaugh 1956; Endress 2010). The same axillary meristem may give rise to shoots that resemble vegetative ones, but which, in some nodes, may exhibit flower-bearing axes, while retaining normal leaves (expanded foliar organs, "frondose phyllomes" *sensu* Briggs & Johnson 1979); or, it can give rise to a modified branch system, with bracts ("bracteose phyllomes", *sensu* Briggs & Johnson 1979). This difference in leaf morphology has been used to circumscribe the inflorescence by McVaugh (1956), (1968), though to Briggs & Johnson (1979), the position of the phyllome is more important than its shape.

Briggs & Johnson (1979) and Weberling (1989) bring definitions for inflorescence, influenced by Troll's school, limiting its use to accommodate the diversity observed in nature. On the other hand, those authors apply more precise terms such as "conflorescence", "partial inflorescence", "superconflorescence" and "uniflorescence" in the former, and "main florescence", "synflorescence", "partial florescence", "partial inflorescence", "coflorescence" by the latter. Briggs & Johnson (1979) reject some of Troll's terms adopted by Weberling (1989), such as "conflorescence" and "synflorescence" (see discussion in their Apendix I, p.236-240), because they were applicable only to herbaceous systems. They also reject the typological view (monotelic vs polytelic), maintaining only descriptive terms used by Troll (1964), (1969).

Bentham (1869) and McVaugh (1956) describe a characteristic type of flowering axis that bears solitary flowers in basal nodes, subtended by bracts, and continues vegetative growth in the apex, with regular leaves that do not subtend flowers. McVaugh (1968) names such inflorescence as "Stenocalyx type", which later is named "auxotelic" in Briggs & Johnson (1979), and "proliferation" in Weberling (1988b), (1989). Another aspect of myrtaceous inflorescences that was not mentioned in McVaugh's studies, but is addressed in Briggs & Johnson (1979) and Weberling (1988b), (1989), is the occurrence of accessory branches, i.e. when more than one axis is subtended for the same phyllome; they can be solitary flowers or branched axes; may be more than one; and vary in architecture (Briggs & Johnson 1979; Weberling 1988b, 1989).

Inflorescence evolution

Concerning the evolution of inflorescence architecture, the ancestral myrtaceous inflorescence was first described as one in which axes of all orders terminated in a flower (McVaugh, 1956). The same author, however, in a later study, hypothesizes a solitary flower, with two bracteoles, subtended by an expanded leaf in an indeterminate axis, which later underwent specialization by different paths (McVaugh, 1968). Briggs & Johnson (1979) advocates for a flexible decussate patterned system, in which the presence of terminal flower or reversion to vegetative growth was possible. Weberling (1988b), on the other hand, returns to the hypothesis that the ancestral inflorescence had a terminal flower, naming it a "monotelic thyrsoid". Following works from Troll (1964), (1969), Weberling (1988b), (1989) uses the term "monotelic" to describe the typological inflorescence with axis terminating in a terminal flower, and opposed to "polytelic" (i.e. without a terminal flower); and adopting Briggs & Johnson (1979) terminology, refers to a thyrse (axis with many nodes, bearing lateral cymes) which has a terminal flower (hence the suffix -oid, thyrsoid).

Bibliographical references for inflorescence terminology in new species description

It is interesting to note that detailed morphological studies such as Briggs & Johnson (1979), although written more than 40 years ago, remain one of the most cited references when describing a new Myrtaceous species, even though the level of detail provided can make it difficult to use their terminology (Endress, 2010). A result of such a situation where the available system provides useful structure but an unusable level of detail is a tendency for researchers to adopt more generic derivations of terms. Examples of such simplifications include the addition of suffixes such as those ending in "-form" or "-ose" (e.g. "corymbiform", "cymose"). These derived terms are common in new species descriptions and also present in more general glossaries (e.g. Hickey & King 1973). This simplification makes terminology easier to use however, as already stated, terms may have different meanings and concepts depending on the source used (Endress 2010; Claßen-Bockhoff & Bull-Hereñu 2013). As a result,over simplifying descriptive terms can result in diversity being overlooked, or overly standardized. Regardless of the choice for a more detailed or simplified description, it is recommended that terminology used should be explicitly described and sources of definitions cited for meaningful comparative and evolutionary conclusions to be drawn.

Summary of inflorescence concepts in selected works

In a previous section we briefly reviewed concepts and some of the terminologies used by authors working on myrtaceous inflorescences (McVaugh 1956, 1968; Briggs & Johnson 1979; Weberling 1988b, 1989). Here we will explore, consider and discuss more recent concepts and studies that examine inflorescence architecture and development using different methodologies and conceptual frameworks, namely Prusinkiewicz et al. (2007), Endress (2010), which appeared as top cited in our literature systematic review, and Claßen-Bockhoff & Bull-Hereñu (2013), proposing yet another framework to understand inflorescence based on ontogeny.

The transient model

The aim of Prusinkiewicz et al. (2007), was to understand why, from the multitude of forms possible by the iterative nature of plant structure, there are only a handful of patterns observed. They acknowledge the existence of three types of inflorescences (following Troll 1964, 1969; Weberling 1992), panicles, racemes and cymes. The premise of their work is that these differences in inflorescence architectures reflect fundamental genetic changes. They create a model, named the transient model, coupling theoretical modelling and plant developmental knowledge.

Final inflorescence architecture is the product of meristem identities maintenance or modification and, according to the model of Prusinkiewicz et al. (2007), the variable responsible underlying one or the other outcome is the level of vegetativeness (veg). The meristem identity remains vegetative as long as veg levels are high; on the other extreme, meristem identity shifts to floral when veg levels are low. The time it takes for the meristem to go from one extreme to the other, they call T, and meristems are at states A and B, before reaching the floral identity (each in its own time, TA or TB). The transient part of their model is that all axillary meristems start development at state B (immature meristem), with two possible pathways: they can revert to A (mature meristem) or change into a flower meristem. By changing relationships between TA and TB, they were able to recreate those three inflorescence types: TA = TB results in a panicle; TA > TB in racemes; and TA < TB in cymes. Their model also incorporated two genes from Arabidopsis thaliana with known roles in inflorescence architecture, TERMINAL FLOWER 1 (TFL1) and LEAFY (LFY), with the latter repressing veg in meristems, while the former upregulating veg.

Prusinkiewicz et al. (2007) using the transient model morphospace, tested different constraints that could have shaped inflorescence architecture. They found that cymes and racemes are more frequent in temperate climates and panicles in tropical. Also, well delimited growth seasons tend to favor the panicle, whereas variable growth seasons favor racemes and cymes.

Inflorescence descriptive framework

Endress (2010) reviewed inflorescence terminology and organized a simple framework of definitions drawing extensively on work on inflorescences by other authors (e.g. Troll 1964, 1969; Briggs & Johnson 1979; Weberling 1989). Terminology adopted from Briggs & Johnson 1979 includes the use of phyllome, pherophyll and prophyll, terms, in turn, based on Troll (1964), (1969) to describe leaf-like structures by position instead of shape, avoiding terms that had different use in the literature, such as bract and bracteoles.

Endress (2010) recognized two main branching patterns: (1) racemose, where the 1st-order axis may bear many (not limited) 2nd-order axes, but no axes of higher order; and (2) cymose, with 1st-order axis limited to two 2nd-order axes, each subtended by a phyllome (and there are no other phyllomes), but there is no limitation of branching orders. If the inflorescence has the 1st-order axis with racemose branching pattern and 2nd-order with cymose, it can be called a thyrse (or thyrsoid if there is a terminal flower). Panicles are recognized as a pattern in-between the racemose and cymose patterns, without the limitations of both and with flexible arrangements, making it hard to define. The second attribute that is analysed when classifying a racemose inflorescence is the differential elongation of axes. Depending on the relationship between 1st- and 2nd-order lengths, Endress (2010) accepts the following terms: (1) raceme (1st = 2nd, both elongated); (2) spike (1st > 2nd); (3) umbel (1st < 2nd); and (4) head (1st = 2nd, both short). Another pattern of inflorescence elaboration described results from the repetition of branching patterns in higher order axes.

The ontogenetic concept

Claßen-Bockhoff & Bull-Hereñu (2013) assessed species from 105 genera of angiosperms and classified the meristems in FM (Flower Meristem), FUM (Floral Unit Meristem), IM (Inflorescence Meristem), RM (Reproductive meristem), and VM (Vegetative Meristem). They also used the concept of Seasonal Growth Unit (Briggs & Johnson, 1979), but named it FSS (Flowering Shoot System). Other terms used were FU (Floral Unit), RU (Reproductive Unit).

IMs are defined as meristems that share some development traits with VMs, e.g. the order of differentiation of lateral primordia, but an IM is usually larger than a VM and may have altered phyllotaxis. The axillary meristems of an axis formed from an IM develop immediately and influence subtending phyllome expansion. FMs differ in their determinate nature and unique organogenesis. FUMs are structurally closer to FMs than to IMs, despite producing many flowers.

Under this concept, the auxotelic inflorescence (*sensu* Briggs & Johnson 1979) is not considered an inflorescence in the ontogenetic concept because it is not a single RM that gives rise to the FM. By changing the focus from the mature inflorescence to the ontogeny, they propose a four-step framework to analyse inflorescences by identifying: (1) the FSS; (2) the RUs position in FSS; (3) the type of RU; and (4) the developmental processes. In this view, inflorescences are only products of IMs, not FSSs or FUs. Also, cymes originate from FUMs and not FUs.

Claßen-Bockhoff & Bull-Hereñu (2013) reduce inflorescence classification terminology to four types: (1) compound racemes; (2) simple racemes; (3) panicles; and (4) botryoids. The concept of determinate and indeterminate inflorescences is again used but named “closed” and “open” inflorescences. Finally, they propose a way of describing FSSs and RUs based on meristem position by formulas, mimicking flower formulas.

Although both Endress (2010) and Claßen-Bockhoff & Bull-Hereñu (2013) try to find answers to the arduous job of classifying the diversity of forms found in nature, they do it by very different paths and arrive at very different conclusions. The Claßen-Bockhoff & Bull-Hereñu (2013) ontogenetic concept of inflorescence is logical, as they address the difficulty of defining the inflorescence, by going to its origin, the developmental processes that are responsible for the mature form of the inflorescence. Circumscription of inflorescences as the product of IMs is a reasonable and straightforward approach to compare inflorescence development between taxa. However, the level of detail needed to draw such conclusions, e.g. previous knowledge of ontogenetic pathways in the species, and technology required (the use of Scanning Electron Microscopy, for example), are not methods widely and equally available to all scientists, nor is such information available in all plant families. Such discrepancies further deepen the division between ontogenetic, morphological and taxonomic studies and with each field using a different terminology. The resulting segregation of research groups, often with limited access to cutting edge technologies is likely to discourage research in poorly known organisms and diminishes the citation of reports on the few studies that do take place.

Conclusions

Morphological, anatomical and ontogenetical traits of reproductive structures support our understanding of evolutionary history and taxonomy in angiosperms, as demonstrated by Reinheimer & Vegetti (2008), in Poaceae; Pessoa et al. (2012), in Orchidaceae; and Schmid (1972), Carrucan & Drinnan (2000), Bohte & Drinnan (2005), Vasconcelos et al. (2015), in Myrtaceae. Nonetheless, inflorescences studies struggle with out of date and/or multiple definitions for the same term (e.g. morphology vs. ontogeny), and/or proliferation of terms/definitions to accommodate morphological diversity, that have led to terminological confusion (Endress, 2010).

Most published works sampled here have Monocotyledons as study group, with continuous and consistent efforts, and recent diversification of approaches, including molecular ones. As with other research lines in Life Sciences, most productive countries are in the global North, with China and USA leading most studies.

Citation patterns indicate that working transversally in plant families, i.e. mastering a methodology and varying the model studied, or working with plant families of important crops or model organisms (e.g. Poaceae), favors authors in relation to number of citations. Ecological and functional approaches to inflorescences, such as studies focused on pollination, appear to be better structured in terms of theoretical references, with a clear set of referenced works most used by the scientific community, than structural, developmental, or evolutionary areas. Those areas do not present a clear network of co-citations, which may be due to a lack of common framework that could make studies more comparable. It is possible to observe, in recent years, some efforts in this direction, with more conceptual works being cited and morphological approaches, that are important to contextualize results of motor themes as genetic and developmental approaches.

Thematic and methodological analyses show that scientific production is biased toward the study of economically important plant families, which is detrimental to the most biodiverse ones. Surprisingly, despite being very speciose, myrtaceous plants are not reported in any of the inflorescence literature surveyed from 2011 to 2021 (parameters A), as efforts are focused on few species (e.g. *Eucalyptus*). Even though the literature surveyed could be separated in 3 main themes, reflecting different methodological approaches, it can be observed that evolutionary analyses are important for most of the literature surveyed, as they correlate somewhat closely to the other themes.

By surveying the description of new species, a lack of a common bibliography to address inflorescence terminology became clear. The use of previous new species descriptions and general morphological glossaries instead of more specific literature to describe inflorescences may be the result of the complexity of such works, with confusing and conflicting terminology or too specific/expensive methods (e.g. electron microscopy). Even so, continued use of Briggs & Johnson (1979), a highly complex work, suggests that researchers are open to using specific literature. Unifying or, at least, clarifying the source of terminology and framework to describe inflorescences would improve our capacity to compare, spot similarities and differences throughout Myrteae, crucial to help us answer questions in evolution, diversity, and ecology.

Much taxonomic confusion in Myrtaceae is linked to poor understanding of what comprises an inflorescence, or homologous units of it, and yet, the last thorough studies of Myrtaceae inflorescence were conducted by Briggs & Johnson (1979) and Weberling (1988b), the latter assessing Myrtales. We consider the ontogenetic concept of Claßen-Bockhoff & Bull-Hereñu (2013) an important contribution to the delimitation and architecture of inflorescences, however, it is not practical for everyday use. In this respect, the approaches of Endress (2010) and Briggs & Johnson (1979) are more widely usable. We suggest that the Seasonal Growth Unit (SGU) concept of Briggs & Johnson (1979) and adopted by Claßen-Bockhoff & Bull-Hereñu (2013) as FSS, allied with the framework of Endress (2010), is the system of inflorescence description best suited for use in Myrteae. In this way, we maintain that analyses restricted to the products of a meristem (the origin of the SGU), using the position system to describe phyllomes inside the SGU, and adopting the clear and precise definitions of branching and iteration of Endress (2010), should be encouraged. The advantage of using this more descriptive language is that it avoids terminology that may cause confusion (as described in raceme, panicle and dichasium) and allows exceptions to accommodate the diversity of forms we find in nature. Ontogenetic evidence will continue to be of value and importance, especially when exploring the disambiguation of similar morphologies with different evolutionary histories. As technology becomes more accessible and more of our biodiversity is studied under such methodologies, it can greatly contribute to our understanding of inflorescences architecture and evolution.

Acknowledgements

The authors would like to thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the scholarship (140639/2017-9) during the first author´s PhD; the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) for the PrInt-USP international scholarship (88887.367998/2019-00); the National Geographic Society (EC-85521R-21) and the Bentham-Moxon Trust (BMT31-2019) for funding; and Dr Jascieli Bortolini for assistance with the systematic review methodology. PTS would also like to thank FAPESP (2023/12044-4) and CNPq (313151/2023-7) for grants received. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) - Finance Code 001.

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