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REVIEW

Advances and perspectives on the evolutionary history and diversification of Neotropical Myrteae (Myrtaceae)

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Myrtaceae are one of the largest families of flowering plants and are widely distributed in the Neotropics, where they are mainly represented by the tribe Myrteae. Myrteae are the most species-rich tribe of Myrtaceae and include groups with significant ecological and economic importance. Myrteae are considered to be a model group for biodiversity studies in the Neotropics, and so understanding the history of their diversification in this area is extremely important. The last decade has witnessed an increase in macro- and microevolutionary studies of the group, and summarizing this knowledge is now crucial to plan future steps in research on Myrteae. Here we provide the first overview of evolution and diversification studies on Myrteae, highlighting recent advances in understanding their evolutionary history. We discuss biogeography, phylogeny, phylogeography, population genetics, genomics and cytology in light of current knowledge. Finally, we provide perspectives and open hypotheses to be tested in future studies to fill gaps in the evolutionary knowledge of specific groups/taxa in Myrteae.

ADDITIONAL KEYWORDS: evolutionary trends – Neotropics – phylogenetics – South America – species diversity – systematics.

INTRODUCTION

Myrtaceae are a predominantly pantropical family of flowering plants (Wilson *et al.*, 2005), mostly distributed in the Southern Hemisphere (Thornhill *et al.*, 2015). They are divided into two subfamilies, Psiloxyloideae and Myrtoideae, and boast high species diversity. Centres of species diversity for Myrtaceae are in Australia, Southeast Asia, tropical and subtropical regions of South America and Africa (Wilson *et al.*, 2001). According to Thornhill *et al.* (2015), Myrtaceae originated in Gondwana, *c*. 90 Mya, during the Late Cretaceous. During this period, the Antarctic continent was still partially linked with South America, Australia, New Zealand and New Caledonia, and early diversification in Myrtaceae occurred through migration and long-distance dispersal that followed the fragmentation of the continents (Thornhill *et al.*, 2015; Vasconcelos *et al.*, 2017a). Fourteen of the 17 tribes of Myrtaceae occur in Australia (Thornhill *et al.*, 2015). The Neotropics harbour, predominantly,

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species from a single tribe: Myrteae (Wilson *et al.*, 2005; Lucas *et al.*, 2007). Despite this low diversity of tribes, the Neotropics have a high diversity of species of Myrtaceae since Myrteae are the most species-rich tribe, including 51 genera and *c*. 2500 species, representing approximately half of the species diversity in the family (Lucas *et al.*, 2007; Wilson, 2011; Vasconcelos *et al.*, 2017; WCVP, 2021).

Myrteae have broad ecological and socio-economic importance in the Neotropics. They are one of the most representative groups in the Atlantic Forest, in terms of number of species, and they include many species that provide food, shelter and habitat for associated fauna (Beech *et al.*, 2017; Ulloa *et al.*, 2017; Castuera-Oliveira *et al.*, 2020). Furthermore, species can be used for regeneration of degraded areas due to attraction of dispersers, which favour the maintenance of ecosystem services (Backes & Irgang, 2002; Pizo, 2002; Gomes *et al.*, 2017). Myrteae also stand out due to their economic importance because most species have nutritional, agro-industrial and medicinal characteristics and are of interest to the food, cosmetic and pharmacological industries (Sardi *et al.*, 2017). Commercial exploitation of fruits and leaves of species of Myrteae in the Neotropics is mostly focused on their antioxidant and phytochemical features. Fruits of Myrteae are rich in important nutrients for health and are often consumed by humans (Pereira *et al.*, 2012; De Carvalho *et al.*, 2014; Cascaes *et al.*, 2015; Faleiro *et al.*, 2016; Sardi *et al.*, 2017; Sisay & Gashaw, 2017; Araújo *et al.*, 2019; Schmidt *et al.*, 2019).

The past decade has witnessed an increase in macro- and microevolutionary studies of Neotropical Myrteae, and summarizing this knowledge will be helpful in planning future steps in the research agenda for the group. This review describes and discusses current knowledge of evolution of Myrteae in the Neotropics based on a detailed survey of the literature in this area. We focus on studies of phylogeny, biogeography, phylogeography, population genetics, genomics and cytogenetics. Phylogenetic studies provide speciation patterns and divergence times among species. Macroevolutionary patterns (e.g. gradual and rapid change, extinctions and adaptive radiations) can be observed on a phylogenetic tree, revealing the evolution of the diversity of life. Microevolutionary mechanisms (e.g. mutation, migration, genetic drift and natural selection) provide species diversity information via studies of population genetics and phylogeography. Cytogenetic studies can clarify processes involved in species diversification and establishment in new habitats, in conjunction with changes in ploidy. Increased availability of genomic data has promoted advances in population genetics, phylogeography and phylogenetics, further revealing diversification processes and patterns. Empirical studies in all these areas connect micro- and macroevolution, elucidating the underlying mechanisms driving species diversification patterns in Myrteae at a variety of scales. This review provides an up-to-date compilation and discussion of literature clarifying the known evolutionary history and diversification of Neotropical Myrteae. Finally, we propose future lines of investigation based on gaps of knowledge in these groups.

CURRENT STATUS OF RESEARCH

To compile the database used in this review, a systematic survey of the Web of Science (Institute of Scientific Information, Thomson Scientific) (https://apps.webofknowledge.com/) was performed on 26 June 2020, searching for publications using combinations of terms shown in the Supporting Information (Table S1).

As we have focused our discussion mainly on the Neotropical tribe Myrteae, we did not consider studies in which species ranges were outside the Neotropics. Thus, from a total of 3036 articles retrieved, 95 empirical studies (Table 1; Supporting Information, Table S2) published between 1947 and June 2020 were included in this review. From the 95 retrieved articles, we recorded the following general information: (i) research field (phylogeny, biogeography, phylogeography, population genetics, cytogenetics, genomics); (ii) sampled species; (iii) tools or methodologies used, such as molecular markers or staining; and (iv) main results. We used this information to describe the number of articles discussing macro- and microevolution in Myrteae. Our goal was to identify how many species and genera have been studied in the tribe so far and to synthethize the underlying mechanisms of diversification of the Neotropical flora.

Species nomenclature and synonyms were standardized for species occurring in Brazil using the Flora do Brasil 2020 resource (Proença *et al.*, 2020). The World Checklist of Selected Plant Families (WCVP, 2021) was used for extra Brazilian taxa (Supporting Information, Table S3).

Of the 95 articles, 26 were categorized as 'phylogeny', 14 as 'biogeography', two as 'phylogeography', 29 as 'population genetics', 26 as 'cytogenetics' and 12 as 'genomics' (Table 1). Considering the cumulative number of studies in these areas, phylogeography is the only category that has not seen an increase in the number of studies through time (Table 1; Fig. 1). The 95 articles include studies of 27 and 440 of the 29 genera and 2164 species of Neotropical Myrteae, respectively (WCVP, 2021) (Table 2; Supporting Information, Table S4). Concerning taxa studied, phylogenetic and biogeographic studies were the most representative, including all 27 sampled genera and 414 and 390 of the sampled species, respectively (Fig. 2; Table 1). Population genetics studies concerned nine genera and

13 species, whereas phylogeographic studies included only one genus (*Eugenia* P.Micheli ex L.) and two species. Although cytogenetics is the earliest featured research field (Atchison, 1947) in this review, only 16 genera and 86 species have been evaluated to date. Genomics studies that examine the structure and function of the genome, only started in the past decade (i.e. 2010 onwards) and seven genera and 14 species have been studied to date (Fig. 2; Table 1).

Table 1. Summary of article numbers included for each research area in this review after manual curation

Research field	Number of articles	Number of genera	Number of species
Phylogeny	26	27	414
Biogeography	14	27	390
Genomics	12	7	14
Population genetics	29	9	13
Phylogeography	2	1	2
Cytogenetics	26	16	86
Total*	95	-	-

*This does not represent the sum of the number of articles assigned to each area because some articles cover more than one research area.

The most representative genera addressed in the 95 articles retrieved were *Myrcia* DC. ex Guill., *Eugenia*, *Myrceugenia* O.Berg and *Psidium* L., with 182 (23.67%), 142 (14.98%), 33 (73.33%) and 21 (23.33%) species studied, respectively (Tables 1, 2; Supporting Information, Table S4). A possible explanation is that these are large genera including many species with economic importance for the food or chemical industries (Cascaes *et al.*, 2015). Although *Myrcia* was the most representative genus studied, *Eugenia uniflora* L. was the most representative species, appearing in 37 of 95 studies, followed by *Eugenia dysenterica* (Mart.) DC., included in 19 articles (Supporting Information, Table S5).

Studies concerning Neotropical Myrteae evolution increased twofold in the past 5 years (Fig. 1). Nonetheless, two genera [*Acca* O.Berg *sensu* Lucas *et al.*, 2019, not including *Feijoa sellowiana* (O.Berg) O.Berg, and *Amomyrtella* Kausel (Maurin *et al.*, 2021)] and 1724 species are not included in any evolutionary study. Further investigations are necessary to answer questions regarding the evolution of the Neotropical species and genera of Myrteae and of

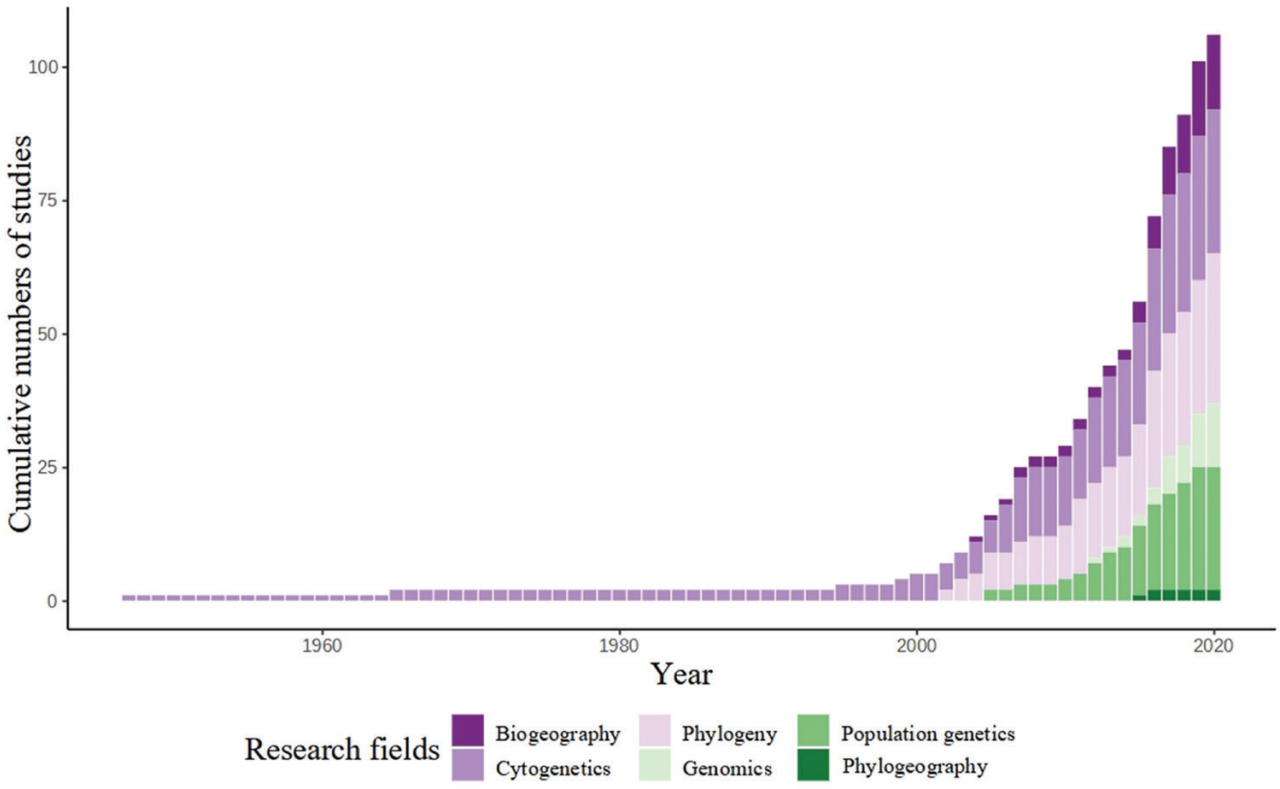


Figure 1. Cumulative increase through time of number of articles on selected topics of studies on evolution of Neotropical Myrtaceae. The cumulative number of articles represents the sum of assigned ones to each area. Note: some articles cover more than one research area and are counted more than once.

Table 2. Number of species sampled in each genus in the articles retrieved using the terms present in the Supporting Information (Table S1)

Genus	Number of species
Accara O.Berg	1
Algrizea Proença & NicLugh.	2
Amomyrtus (Burret) D.Legrand & Kausel	2
Blepharocalyx O.Berg	2
Calycolpus O.Berg	2
Campomanesia Ruiz & Pav.	12
Chamguava Landrum	1
Curitiba Salywon & Landrum	1
Eugenia L.	142
Feijoa O.Berg	1
Legrandia Kausel	1
Luma A.Gray	2
Mosiera Small	1
Myrceugenia O.Berg	33
Myrcia DC. ex Guill.	182
Myrcianthes O.Berg	4
Myrciaria O.Berg	9
Myrrhinium Schott	1
Myrteola O.Berg	1
Neomitranthes D.Legrand	1
Nothomyrcia Kausel	1
Pimenta Lindl.	4
Plinia Plum. ex L.	7
Psidium L.	21
Siphoneugena O.Berg	2
Temu O.Berg	1
Ugni Turcz.	3
Total	440

the phytophysionomies in which they occur. We also indicate an urgent need for more phylogeographical studies to further uncover the processes responsible for generating species diversity in this tribe in the Neotropics. Phylogeographical studies will also help understand the effects of environmental factors in species evolution and the impact of past climatic changes on species distribution and population structure.

MACROEVOLUTION AND DIVERSIFICATION

PHYLOGENETICS

Beginning in the early 1990s, phylogenetic study in Myrtaceae systematics has tracked that of the angiosperms. The first molecular studies of taxonomic relationships in Myrtaceae were carried out by Australian researchers focused on the iconic genus *Eucalyptus* L'Hér., with the earliest studies finding plastid DNA haplotype variation to be informative at higher taxonomic levels (e.g. Sale *et al.*, 1993). At lower taxonomic levels, discordance between plastid DNA and phenetic data implied reticulate evolution (Steane *et al.*, 1998). The first studies examining family level relationships were those of Gadek *et al.* (1996) and Wilson *et al.* (2001) who used the plastid *matK* gene to study tribal relationships. In 2005, proceedings from a Melbourne conference celebrating 150 years of systematic botany in Australia included: (1) the currently generally accepted tribal classification of Wilson *et al.* (2005); (2) the first study of *Eugenia* phylogenetics using nuclear ITS (Merwe *et al.*, 2005); and (3) a preliminary study of relationships in Myrteae (Lucas *et al.*, 2005) based on combined nuclear and plastid data. Subsequent studies increased numbers of taxa and markers used both at the tribal level in Myrteae (e.g. Lucas *et al.*, 2005; Vasconcelos *et al.*, 2017) and in studies focused on genera (Murillo-A *et al.*, 2012; Mazine *et al.*, 2014, 2018; Santos *et al.*, 2017; Amorim *et al.*, 2019), or clades in them [e.g. *Myrcia* section *Aulomyrcia* (O.Berg) Griseb.: Staggemeier *et al.*, 2015a; *Eugenia* section *Phyllocalyx* Nied.: Bünger *et al.*, 2016; *Myrcia* section *Sympodiomyrcia* M.F.Santos & E.Lucas: Santos *et al.*, 2016, *Myrcia* section *Calyptranthes* (Sw.) A.R.Lourenço & E.Lucas: Wilson *et al.*, 2016]. These endeavours continue, based on Sanger sequencing and phylogenomic approaches using genome skimming (*Myrcia*: Lima *et al.*, 2021), targeted enrichment (*Eugenia*: Giaretta *et al.*, in prep.; Maurin *et al.*, 2021) and whole-genome sequencing (*Syzygium* P. Browne ex Gaertn.: Low *et al.*, in prep.).

MOLECULAR MARKERS AND MORPHOLOGICAL TRAITS

To identify molecular markers that were used in macroevolutionary studies, we selected only articles regarding phylogenetic reconstruction of a significant pool of Neotropical species (eight or more) and focused on macro- rather than microevolution. Following these criteria and using the terms MYRTACEAE AND PHYLOGEN*, 26 publications contributed to phylogenetic studies in Neotropical Myrtaceae, the first published in 2004 and last in 2019 (Table 1; Supporting Information, Table S2).

Ten molecular markers are most frequently used for phylogenetic reconstruction in Myrteae: two nuclear regions [ITS (in 92.3% of the studies) and ETS (in 42.3% of the studies)]; and eight plastid regions (Fig. 3). Of the plastid regions, *psbA-trnH* is the most frequently used plastid marker (in 76.9% of the studies); *rbcL* was used in early papers (Sytsma *et al.*, 2004) but later abandoned in favour of more rapidly evolving markers such as *ndhF* and *matK* that were found to be more informative (Sytsma *et al.*, 2004).

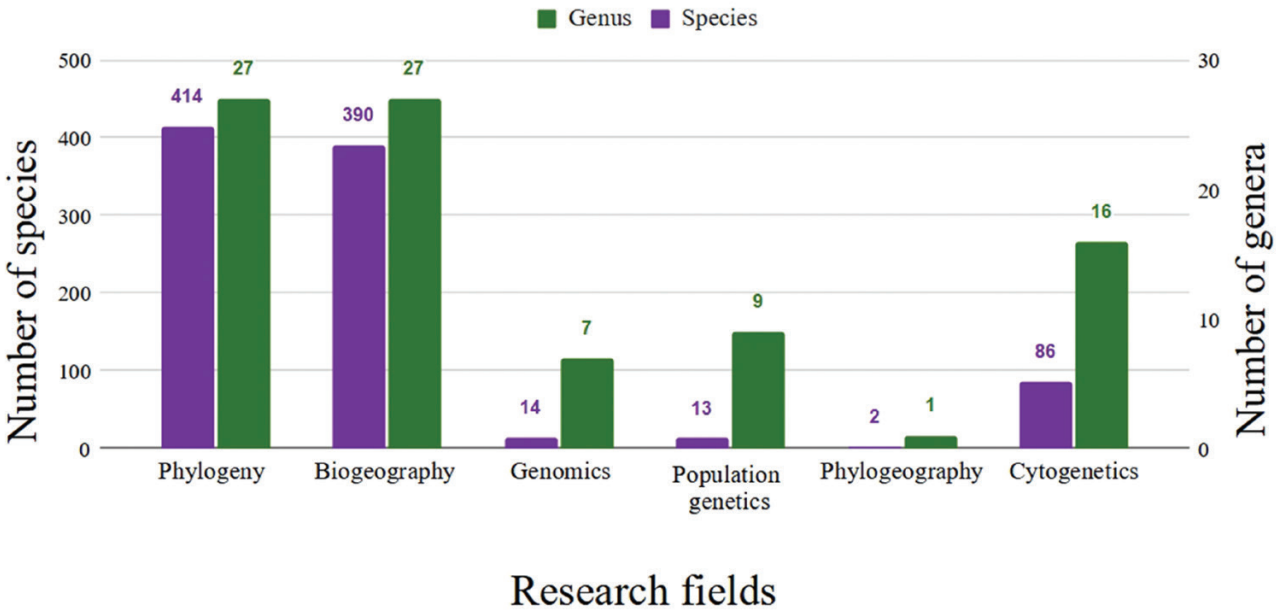


Figure 2. Number of species and genera of Neotropical Myrtaceae (i.e. tribe Myrteae) studied in the articles reviewed here. Values on bars represent the number of sampled species or genera.

Morphological characters in Neotropical Myrtaceae are plastic with high levels of homoplasy (Lucas *et al.*, 2007). For that reason, morphological data has never been used explicitly in phylogenetic tree inference. Instead, morphological characters have been used to discuss congruence with molecular-based inferences, to support or refute taxonomic understanding (e.g. Pimentel *et al.*, 2014; Vasconcelos *et al.*, 2015, 2017b; Harthman *et al.*, 2018), a process of 'reciprocal illumination' (Hennig, 1999).

Newly available information and more studies often bring more questions than answers to the systematic and evolutionary understanding of Myrteae. Even though most generic delimitation is supported by molecular data, many traits traditionally used to diagnose natural groups are shown to be highly homoplastic due to parallel or convergent evolution (Lucas *et al.*, 2005, 2007; Vasconcelos *et al.*, 2015, 2017b, 2019a, b, c; Giaretta *et al.*, 2019). Consequently, taxa previously recognized at ranks higher than species (i.e. subtribes, genera, sections) have been found to be para- or polyphyletic after molecular analyses (Lucas *et al.*, 2007, 2011; Snow *et al.*, 2011; Mazine *et al.*, 2014; Staggemeier *et al.*, 2015a). Such ambiguity is not restricted to Myrteae, and it is frequently found in other diverse tropical plant groups, e.g. *Miconia* Ruiz & Pav. (Michelangeli *et al.*, 2004), *Croton* L. (Berry *et al.*, 2005) and *Mimosa* L. (Simon *et al.*, 2011).

It is difficult to find single morphological characters that are taxonomically diagnostic in Myrteae. However, in combination, imperfectly shared morphological traits can be useful for diagnosis of clades and supra-specific taxa (Lucas *et al.*, 2007, 2011, 2018; Mazine *et al.*, 2014, 2016; Staggemeier *et al.*, 2015a; Vasconcelos *et al.*, 2015). The evolution of selected morphological characters has been examined over phylogenetic trees to consider the evolutionary history and/or systematic relevance of the trait (e.g. Lucas *et al.*, 2007; Vasconcelos *et al.*, 2015; Amorim *et al.*, 2019; Giaretta *et al.*, 2019). Hypotheses of trait evolution also allow estimation of the strength of the response of a set of species to external pressures such as ecological factors (Staggemeier *et al.*, 2010, 2015b; Pimentel *et al.*, 2014; Vasconcelos *et al.*, 2019a).

Morphological traits frequently studied by those interested in the systematics and evolution of Myrteae (McVaugh, 1958, 1968; Landrum, 1981a; Landrum & Kawasaki, 1997; Lucas *et al.*, 2007, 2018, 2019; Vasconcelos *et al.*, 2019c) are briefly summarized. Most diagnostic characters involve reproductive organs operating under more acute selective pressure to maximize pollination and dispersal efficiency and effectiveness (Vasconcelos & Proença, 2015).

Cortex (bark) composition, branching pattern, indumentum and wood anatomy are vegetative characters that can be useful for identification of sterile material, particularly to genus level [but see Santos *et al.* (2013, 2015), who did not find anatomical differences in wood of closely related genera of *Plinia* Plum. ex L.]. These traits are correlated with the environment in which individuals are found and systematic use can be limited to taxa endemic to a given ecoregion. Bark can be consistently corky in species from xerophytic environments, flaky or highly

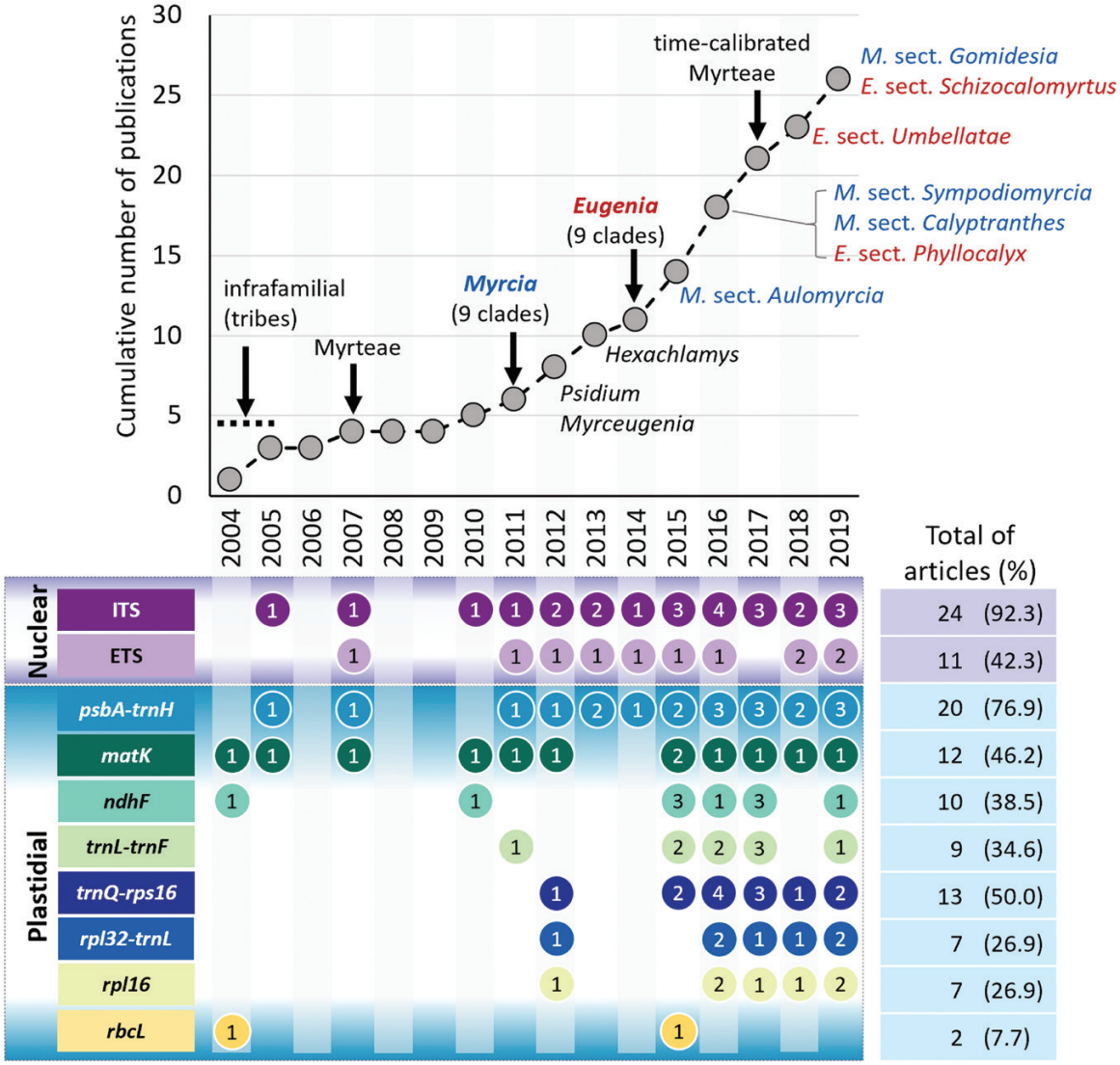


Figure 3. Cumulative number of publications on phylogenetics of Neotropical Myrtaceae over time and profiled use of nuclear and/or plastid molecular markers. Lucas *et al.* (2011) and Mazine *et al.* (2014) were key papers splitting the two mega-genera, *Myrcia* and *Eugenia*, into smaller, workable units (sections) enabling further studies focused on individual sections.

smooth in forest species. Vegetative branching systems only stabilize in mature individuals, but Myrteae usually have monopodial branching (e.g. *Eugenia*, *Decaspermum* J.R.Forst. & G.Forst.), or sometimes sympodial (e.g. *Myrcia* section *Sympodiomyrcia*, *Pimenta* Lindl.). Pubescence in Myrteae is variable in position, colour and length, but hairs are mostly basifixed and simple. Exclusively dibrachiate hairs or a mixture of dibrachiate and simple, can be diagnostic of species in some groups (*Myrcia* section *Calyptranthes*: McVaugh, 1958, 1968; *Myrceugenia*: Landrum, 1981b). The presence of scalariform perforation plates in vessel elements of the wood of some genera of Myrteae is strongly correlated with ranges in high elevation environments prone to frost (e.g. *Myrteola* O.Berg, *Temu* O.Berg; Lucas *et al.*, 2007).

Flowers of Myrteae are superficially similar, but possess characters used with varying degrees of accuracy for distinguishing taxa and subtle variations never fully explored in the context of systematics and macroevolutionary dynamics but discussed by Vasconcelos *et al.* (2015, 2019c, and references therein). The number of perianth parts varies from four to five, occasionally six, with the number strongly conserved in some genera (e.g. four in *Eugenia*: Mazine *et al.*, 2016), or a most common arrangement (e.g.

usually five in *Myrcia*: Lucas *et al.*, 2018), or with four, five or six possible in the same genus (e.g. *Psidium*: Landrum, 2017). The shape and pubescence of the floral disc and the degree to which a tubular hypanthium is extended beyond it have been used diagnostically (Proença, 1990; Lucas *et al.*, 2018). The degree of fusion of the calyx lobes and method of opening of buds with a completely fused calyx, circumscribed multiple genera later shown to be polyphyletic (e.g. *Myrcia* section *Calyptranthes*: Wilson *et al.*, 2016; *Eugenia* section *Calycorectes* (O.Berg) Mattos: Giaretta *et al.*, 2019), with the remarkable parallel evolution involved discussed by Vasconcelos *et al.* (2017b). Characters of the gynoecium such as locule and ovary number or placentation were commonly used by 19th and 20th century taxonomists for setting generic boundaries (e.g. de Candolle, 1828; Berg, 1857-1859; McVaugh, 1958, 1968).

These characters are strongly interdependent, and the evolution of the different arrangements was described by Vasconcelos *et al.* (2019c). Ovary characters are not strongly correlated with phylogeny of Myrteae, but are successfully used as part of suites of characters to define genera (e.g. peltate placentation in *Pimenta*: Landrum, 1986; two locules in *Eugenia*: Mazine *et al.*, 2016; two ovules per locule in *Myrcia*: Lucas *et al.*, 2019). Characters of the androecium have been used to distinguish informally named groups of genera of Myrteae depending on the folding or otherwise of stamens in the bud also related to hypanthium extension (Vasconcelos *et al.*, 2015). Anther morphology can also be diagnostic, for example, the anthers of *Myrcia* section *Gomidesia* (O.Berg) B.S.Amorim & E.Lucas can have displaced thecae that are not reflexed at dehiscence and variable presence of oil glands at the apex (Amorim *et al.*, 2019), whereas *Eugenia* spp. associated with *Eugenia feijoi* O.Berg have enlarged anthers with pollen divided between internal chambers (Giaretta *et al.*, pers. comm.).

The disposition of the inflorescence in Myrteae influences how flowers are presented to pollinators and is used extensively to define genera and species in the tribe. Architecture of the inflorescence of Myrtaceae was discussed by McVaugh (1956), who noted the topologically flexible 'frondo-bracteose panicle' that can present flowers apparently singly or branching to varying degrees. Briggs & Johnson (1979) carried out the most extensive review of the inflorescence and emphasized the importance of the 'seasonal growth unit' (SGU) as a unit of comparison of inflorescence, and the difference between essentially racemose or cymose development of the flowers. Ontogenetic studies and the differential effects of gene expression on inflorescence development are currently underway to better understand the environmental vs. genetic factors that influence inflorescence type.

Traits associated with species reproductive biology support systematic arrangement of Myrteae. Cryptic dioecy, in which flowers appear hermaphrodite but are functionally unisexual (via unviable pollen or a vestigial style), has been recorded in *Eugenia*, *Myrcia*, *Decaspermum*, *Pimenta* and *Psidium* (Nic Lughadha & Proenca, 1996; Soares-Silva & Proença, 2006), although, apart from a high incidence of dioecy in South African *Eugenia* (Van Wyk & Lowrey, 1988), phylogenetic or biogeographical patterns have been little discussed. An elongated style appears to reduce self-pollination in some groups (e.g. *Myrcia*, *Eugenia* section *Umbellatae* O.Berg; Vasconcelos *et al.*, 2019c), whereas the variable nature of the placenta and compitum (fused tissue of a syncarpous ovary through which pollen tubes grow) may influence pollen competition (Harthman *et al.*, 2018).

Characters of fruits and seeds have been much relied on for understanding the systematics of Myrtaceae, with the presence of the fleshy fruit originally distinguishing the subfamily Myrtoideae from the subfamily Leptospermoideae, although Myrtoideae now have a quite different circumscription (Wilson *et al.*, 2005). In Neotropical Myrtaceae, fruit morphology and display vary between genera, but this variation remains unexplored in the context of phylogenetic patterns or in the context of the heterogeneous distribution of species diversity in Myrteae. The nature of the embryo and seed coat were the basis for the original division of the tribe into three (now mostly defunct) subtribes by Berg (1857-1859). Details of that tripartite system and variations from it are discussed by Lucas *et al.* (2005, 2007), but the main divergences are in the degree to which the cotyledons and hypocotyl are enlarged into green, laminate, folded structures or swollen, starchy, homogeneous tissue. Species with enlarged embryos tend to have larger seeds with thin, papery seed coats, whereas species with less developed embryos have more seeds with harder bony testa (Landrum & Kawasaki, 1997). Species with larger seeds tend to have fewer per fruit than those with smaller seeds (Staggemeier *et al.*, 2010), presumably expending more energy in specialized seed production, but producing fewer of them. The shape of embryo and nature of the seed testa show some degree of phylogenetic structure and have been suggested to affect fruiting patterns in Neotropical Myrtaceae (Staggemeier *et al.*, 2015b).

When and where?

Fossils, data and dating of species divergence

A robust time-calibrated phylogenetic tree is a key step for addressing hypotheses in macroevolution (e.g. diversification rates and/or ancestral state reconstructions) and biogeography (ancestral range estimation, importance of vicariance and/or dispersal

models) that have implicit time assumptions. Calibration is usually accomplished by selecting fossil remains with features of extant clades and using age information to define calibration points as priors in dating analyses (Forest, 2009). In Myrteae, given extreme morphological homogeneity, choosing appropriate fossils for calibration can be tricky and consequently represents a potential and important source of bias in analyses that depends on a time-calibrated tree. Recent studies and reviews on the theme are available and tests using a combination of different sets of fossils can point to more reliable age estimates (e.g. Thornhill *et al.*, 2015; Vasconcelos *et al.*, 2017a).

In general, fossil records of Myrteae can be divided into microfossils (pollen) and macrofossils (mainly wood, leaves and seeds). Microfossils have been proved to be powerful in explaining divergence ages in Myrtaceae. A recent morphological review of the widespread genus of fossil pollen *Myrtacedeites* Cookson and Pike, which ranges from the Cretaceous to the Holocene, has revealed a series of morphological features that can be confidently assigned to extant tribes of Myrtaceae (Thornhill & Macphail, 2012). The oldest remains of the species that most closely resembles Myrteae (*Myrtacedeites verrucosus* Stover and Partridge) are from the Mid-Late Eocene (*c*. 41 Mya), and their geographical distribution is compatible with the current distribution of the tribe (i.e. mainly in Australia, Zealandia and South America; Thornhill & Macphail, 2012). These fossils have been used to calibrate the tribe in two studies (Thornhill *et al.*, 2015; Vasconcelos *et al.*, 2017a), indicating that Myrteae are a Late Eocene group, with most subtribes arising in the Oligocene (30-20 Mya).

The most recurrent macrofossil used to calibrate Myrteae are the fossil fruits and seeds of *Paleomyrtinaea princetonensis* Pigg, Stockey & Maxwell (Pigg *et al.*, 1993; Manchester, 1999), from North America. By using this fossil to calibrate the crown node of Myrteae, studies recover an estimated origin for Myrteae at *c.* 55 Mya (Late Palaeocene) and a Mid-Late Eocene origin (*c*. 40 Mya) for the major groups (i.e. subtribes and species-rich genera). Recent scepticism in using *Paleomyrtinaea princetonensis* Pigg, Stockey & Maxwell for fossil calibration comes from comparative analyses using a mixed data set of micro- and macrofossils (Thornhill *et al.*, 2015; Vasconcelos *et al.*, 2017a), from ambiguous morphological characterization of this fossil (which could also resemble some Lythraceae, as suggested by anonymous reviewers from previous calibration studies) and from its geographical position where no extant species of Myrteae occur [although this could be a relict from periods of warmer climate (Willis & McElwain, 2014)]. In a biogeographical context, these older ages are dubious for increasing the amount of long-distance dispersal and establishment events needed to explain the current distribution of the tribe (see Vasconcelos *et al.*, 2017a).

Despite the popularity of *Paleomyrtinaea princetonensis* in calibration analyses, most macrofossils assigned to Myrteae are from wood and leaf remains (e.g. Pujana, 2009; Oskolski *et al.*, 2013). Calibration using these macrofossils, however, also yields the same effect in pushing ages of backbone nodes to older periods (e.g. Murillo-A *et al.*, 2016; Vasconcelos *et al.*, 2017). A careful review of wood and leaf traits that can be used to diagnose tribes and subtribes in light of the current classification would be very welcome to improve the utility of these fossils in calibration.

Ancestral range estimation and biogeography

Geological time sequence of barrier formation, reliable fossil dating and robust estimates of phylogenetic relationships have allowed analytical advances in biogeographical approaches contributing to the understanding of Neotropical Myrtaceae distribution. Evidence from studies at the infrafamilial level indicate that Myrteae originated and diversified in Australasia between 77-56 Mya (Sytsma *et al.*, 2004) and 40 Mya (Vasconcelos *et al.*, 2017a) when Australia was still connected to South America via warm-temperate Antarctic land bridges (Estrella *et al.*, 2019). The separation of Australasian and Neotropical Myrteae has been estimated at *c*. 40-50 Mya (Sytsma *et al.*, 2004; Thornhill *et al.*, 2015; Vasconcelos *et al.*, 2017a). After the opening of the Drake Passage (37 Mya), Antarctica underwent glaciation and with the progressive isolation of this region to more southern latitudes, light levels, climate and landscape changed from subtropical, warm temperate forests (up to the Eocene), to complete establishment of Arctic vegetation during the Miocene (Willis & McElwain, 2014). Glaciation of Antarctica, marine transgressions, uplift of the Andes and formation of the dry diagonal in South America are remarkable events shaping Myrteae history in South and Central America (Santos *et al.*, 2017; Mazine *et al.*, 2018; Amorim *et al.*, 2019; Lima *et al.*, 2021).

Configuration of areas is crucial for biogeographical analysis (Morrone, 2014; Estrella *et al.*, 2019). Five articles pose broad biogeographical questions (Sytsma *et al.*, 2004; Lucas *et al.*, 2007; Thornhill *et al.*, 2015; Vasconcelos *et al.*, 2017a; Estrella *et al.*, 2019), configuring areas of endemism at a continental scale to reduce numbers of areas and so combinations of possible ancestral areas.

Thornhill *et al.* (2015) attributed Australia+New Zealand as the ancestral range for Myrteae, but they did not include species of Myrteae from New Caledonia in their analysis. In a recent study using a wider molecular

and taxonomic sampling of Myrteae Vasconcelos *et al.* (2017a) identified New Caledonia and New Zealand as the most probable ancestral range for the tribe with subsequent migration to South America where this lineage underwent most of its diversification. Estrella *et al.* (2019) reanalysed the data of Vasconcelos *et al.* (2017a) to examine the effect of modifying ancestral distribution areas on biogeographic estimations (i.e. including those of extinct lineages that do not overlap with extant ranges). To test this effect Estrella *et al.* (2019) included Antarctica as a new area in the DEC model (i.e. Antarctica was set as a predefined area in the analyses not only as a posterior route for dispersal), finding increased biogeographical precision at all nodes and suggesting Australia and New Zealand as the most likely area where Myrteae first evolved.

The modern distribution of Myrteae, with diversity centres in the Caribbean, the Guiana Highlands and central-eastern Brazil, is apparently better explained by events of vicariance and short migration (Sytsma *et al.*, 2004; Vasconcelos *et al.*, 2017a; Estrella *et al.*, 2019) rather than long-distance dispersal. However, long-distance dispersal events were crucial in the history of specific clades such as *Eugenia* section Commerson ex De Candolle *Jossinia* (Merwe *et al.*, 2005; Vasconcelos *et al.*, 2017a; Mazine *et al.*, 2018). Dispersal appears the main process driving biogeographic shift at local spatial scales (e.g. in *Myrcia*; Amorim *et al.*, 2019), whereas vicariance and extinction have less influence at a continental scale (Staggemeier *et al.*, 2015a).

Studies focusing on Neotropical Myrteae have reconstructed the biogeography of *Myrceugenia* (Murillo-A *et al.*, 2016), *Myrcia s.l.* (Santos *et al.*, 2017; Amorim *et al.*, 2019) and *Eugenia* (Bünger *et al.*, 2016; Mazine *et al.*, 2018). Between four and ten ancestral areas were used in each study. Non-tropical zones in southern South America were important to first radiations of extant Neotropical Myrteae lineages (Lucas *et al.*, 2007; Vasconcelos *et al.*, 2017a), including *Eugenia* (Mazine *et al.*, 2018) and *Myrceugenia* (Murillo-A *et al.*, 2016). These areas, such as subtropical and temperate Chilean forests, now have colder climates and are less species rich, but still boast high genus-level endemism including *Luma* A.Gray, *Amomyrtus* (Burret) D.Legrand & Kausel, *Legrandia* Kausel and *Ugni* Turcz. (Lucas *et al.*, 2019).

The Mid Oligocene (27.9 to 32.8 Mya) is the most likely period for the first diversification events in Eugeniinae. Early diversification in this group is associated with dry ecoregions and non-tropical southern South America (Mazine *et al.*, 2018). The earliest lineages of *Eugenia* are older than *Myrcia* and potentially reached Amazonia from the Atlantic Forest before the formation of the Dry Diagonal Zone in the Miocene (Mazine *et al.*, 2018). Most ancestral lineages of extant *Eugenia* sections arose in the Atlantic Forest (Bünger *et al.*, 2016; Mazine *et al.*, 2018). The Atlantic Forest was also identified as the most important area explaining the origins of *Myrcia s.l.* (Santos *et al.*, 2017; Amorim *et al.*, 2019). The southern portion of this phytogeographic domain acted as a secondary cradle for several lineages, with many clades diversifying there during the Miocene (Santos *et al.*, 2017). In analysing phylogeny and diversification times in *Myrcia* section *Aulomyrcia*, Staggemeier *et al.* (2015a) suggested strong links between Amazonian and northern Atlantic Forest species, and between the latter and southern Atlantic Forest ones. The Amazonian forest and the Caribbean region have been important for diversification of some *Myrcia* lineages (sections *Calyptranthes*, *Myrcia* and *Aulomyrcia*; Santos *et al.*, 2017; Amorim *et al.*, 2019) and of three subgroups of *Eugenia* section *Umbellatae* (Mazine *et al.*, 2018).

The colonization of the Cerrado by *Myrcia* spp. is relatively recent, ranging between 7.7 and 1.0 Mya (Santos *et al.*, 2017; but see Lima *et al.*, 2021), in contrast with older Cerrado lineages reported for *Eugenia* (16.7–9.2 Mya; Bünger *et al.*, 2016). Amorim *et al.* (2019) showed that *Myrcia* colonized the Brazilian Cerrado through multiple unidirectional range expansions from the Atlantic Forest, although Lima *et al.* (2021) showed reversals to the Atlantic Forest in at least one clade [section *Aguava* (Raf.) D.F.Lima & E.Lucas]. Campo rupestre has been included as an endemism area in some studies (Santos *et al.*, 2017) or considered part of the Cerrado/Dry Diagonal Zone (Amorim *et al.*, 2019). Although many species occur in this area, endemism levels are not as high (Vasconcelos *et al.*, 2020).

Mechanisms of speciation

To date, mechanisms of speciation have seldom been explicitly investigated in Neotropical Myrtaceae. However, traits that can promote reproductive isolation (and thus lead to the establishment of new species from segregated populations) can be inferred from studies in several related fields. Traits linked to reproductive strategies, for instance, can provide some insights into speciation processes. Vasconcelos *et al.* (2019a) suggested that reproductive isolation by changes in pollination strategies is unlikely to be among the major drivers of Myrteae speciation, given the exceptional homogeneity of the flowers in this group. Phenology has also been shown to have high phylogenetic signal in some clades (*Myrcia* section *Gomidesia*; Staggemeier *et al.*, 2015b), so it is also unlikely that this feature strongly affects reproductive isolation in Myrteae, as congeneric species usually present flowers at the same time of the year.

Because pollinators are frequently shared among congeneric and sympatric species (Gressler *et al.*, 2006, and references therein), speciation by hybridization and allopolyploidy can potentially contribute to speciation in Myrteae, in which post-zygotic barriers are weak or non-existent (Costa & Forni-Martins, 2007b; Lima *et al.*, 2015). Hybridization is also inferred by the contrast between the phylogenetic structure resulting from nuclear and plastid data (Lucas *et al.*, 2007; Vasconcelos *et al.*, 2017a). However, reproductive biology studies also show that species are frequently allogamous (e.g. Proença & Gibbs, 1994; Telles *et al.*, 2003), with mechanisms for avoiding selfing and non-conspecific pollen that usually act after fertilization (i.e. post-zygotic isolation; e.g. diminished fruit-set: Nic Lughadha, 1998; flower abortion: Finatto *et al.*, 2011). More studies focusing specifically on hybridization should be performed, as this has been proved to be an important mechanism of speciation in other closely related groups (e.g. *Eucalyptus*; Matsumoto & Marin-Morales, 2001).

Many genera of Myrteae present strong geographical structure among species of individual clades (e.g. *Eugenia* section *Umbellatae*; Mazine *et al.*, 2018), inferring that local speciation may be relevant. Studies in other groups have found that fleshy-fruited lineages in forested areas (a frequent combination in Myrteae) can have restricted dispersal abilities, but occasional stochastic events can lead to rampant allopatry and speciation [Givnish (2010), as discussed in other families of Myrtales; Reginato *et al.* (2020)]. This pattern is supported by population-level studies in widespread species of Myrteae that indicate strong correlation between genetic structure and geography (e.g. Telles *et al.*, 2003; Zucchi *et al.*, 2005; Barbosa *et al.*, 2015; Lima *et al.*, 2021).

Finally, autopolyploidy could also be an important speciation mechanism as it is frequently observed in species of several genera. For instance, Costa & Forni-Martins (2006a) confirmed that almost half of the species of the subtribes Pimentinae, Myrtinae, Ugniinae and Blepharocalycinae can form polyploids. Polyploids have also been frequently recorded in *Eugenia* (e.g. Costa & Forni-Martins, 2006a). Polyploidy can accelerate barriers to gene flow between populations of different ploidy, thus contributing as a speciation mechanism. Polyploids in Myrteae have also been observed to have a higher capacity of colonizing new niches (Silveira *et al.*, 2016; Tuler *et al.*, 2019), further increasing the chances of reproductive isolation and the selection of new forms that lead to speciation.

Diversification factors

Measurements of speciation and extinction rates through time help to understand present-day diversity patterns in Myrteae. Suggestions of potential processes that could explain high diversity of Myrtaceae in the Neotropics include those of Biffin *et al.* (2010), the first study to explore the evidence for and drivers of elevated diversification rates among tribes. Biffin *et al.* (2010) proposed fleshy fruits as a key innovation promoting speciation in Myrteae and Syzygieae. Vasconcelos *et al.* (2017a) found accelerating diversification rates in Neotropical Myrteae in the crown nodes of the *Eugenia*, *Psidium* and *Myrcia+Plinia* groups, which might contribute to the higher diversity of the tribe in the Neotropics (Lucas *et al.*, 2007). Vasconcelos *et al.* (2017a) suggested differences in characters related to embryo morphology, seed traits and cytogenetics as possible explanations for higher diversification in these groups. However, key innovations do not always explain high diversity as Vasconcelos *et al.* (2019a) found morphological stasis in flower traits of the hyper-diverse genus *Myrcia* (*c.* 770 species). Vasconcelos *et al.* (2019a) found constant and homogeneous accumulation of species over time throughout the different ecological niches occupied during evolution of *Myrcia*; differences in species diversity between clades were better explained by clade ages suggesting the genus is in a long-lasting adaptive peak.

Studies mapping ontogenetic, morphological or anatomical characteristics across phylogenetic trees have, however, suggested floral traits of importance to the diversification of Myrteae (Vasconcelos *et al.*, 2015, 2018, 2019c). Vasconcelos *et al.* (2015) showed that stamen position and hypanthial extension are important characters to understand floral evolution in Myrteae and may be linked to shifts in pollination strategy (Vasconcelos *et al.*, 2015) and to diversification dynamics. Most flowers in Myrteae are bee pollinated (Gressler *et al.*, 2006), and bird pollination is uncommon and occurs only in species-poor clades (such as *Feijoa* O.Berg and *Myrhinium* Schott; Nadra *et al.*, 2018), suggesting this specialization has not been advantageous for diversification of Myrteae (Vasconcelos *et al.*, 2019c). Another important floral trait to understand diversification of Myrteae is hyper-style elongation resulting from a heterochronic pattern that can be related to high species diversity in *Eugenia* section *Umbellatae*, the largest section of *Eugenia* (Vasconcelos *et al.*, 2018). Vasconcelos *et al.* (2019c) stressed the importance of studying the whole flower system as a single unit under natural selection as changes in one floral whorl lead to spatial changes affecting the development of the next whorl.

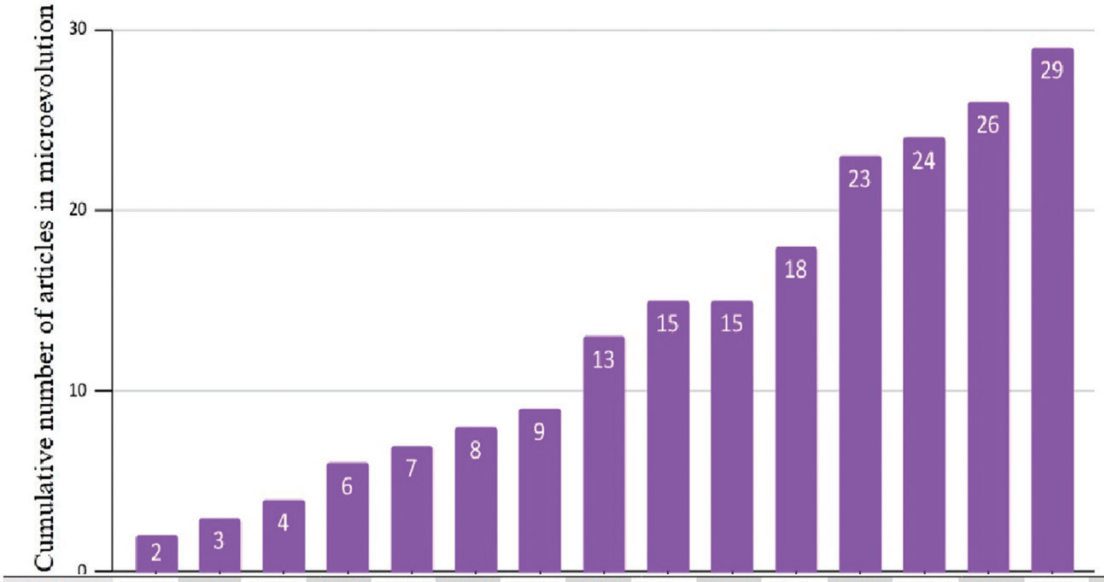
Morphological and ecological characters can explain accelerated rates of speciation relative to extinction resulting in species-rich groups. One way to explicitly identify trait dependent diversification is modelling the diversification rates associated with the evolution of a character over the phylogeny (Maddison *et al.*, 2007; Goldberg *et al.*, 2011; FitzJohn, 2012). State speciation and extinction (SSE) models show that geographical area of distribution is also relevant to understanding diversification dynamics in Myrteae. Staggemeier *et al.* (2015a) found region-dependent diversification rates for *Myrcia* section

Aulomyrcia. In the simplest scenario considered in this latter study, where only extinction rates were free to vary in the models (i.e. speciation and dispersal rates were set as equal, not varying between areas), extinction rates were lower within glacial refugia suggesting such areas were implicated in the high current levels of species diversity in the Atlantic Forest biodiversity hotspot. Staggemeier *et al.* (2015a) also described a second scenario, using a model under which all parameters are allowed to vary, indicating that range expansion from unstable areas to refugia contributed to the highest levels of species diversity in a Bahian refugium and that speciation and extinction rates were higher in climatic unstable regions. Bünger *et al.* (2016) also found that climatically stable areas were important to understand diversification in *Eugenia* section *Phyllocalyx*.

MICROEVOLUTION AND POPULATION LEVEL DYNAMICS

Population genetics

The first studies addressing population genetics based on molecular markers in Neotropical Myrtaceae were published in 2002 (Jensen *et al.*, 2002; Margis *et al.*, 2002). Since then, studies in this area have increased, mostly based on studies of SSR markers (Fig. 4). We evaluated 29 publications that sampled 13 species of Myrteae (Supporting Information, Table S6) with most studies including *Eugenia dysenterica* (Mart.) DC. (ten studies), *Nothomyrcia fernandeziana* (Hook. & Arn.) Kausel (five studies) and *E. uniflora* (four studies). Factors responsible for population structure differ among the species studied. Of the 13 species, 11 show population structure due to factors such as tree density, presence of rivers and human activities. In *Myrciaria dubia* (Kunth) McVaugh, Nunes *et al.* (2017) found low gene flow among natural populations in the Amazon. These results were associated with tree density that can act as a barrier to gene flow. For other species, rivers can both act as a barrier or facilitate gene flow. Boaventura-Novaes *et al.* (2018) found two large and structured *E. dysenterica* populations in the Cerrado savanna: one in the north-west, the other in the south-east. The Corumbá and Paranaíba rivers separate these two populations and were shown to be responsible for the lack of gene flow between them. In *Luma apiculata* (DC.) Burret, the rivers facilitated



Markers	2002	2003	2004	2005	2007	2008	2010	2011	2013	2014	2015	2016	2017	2018	2020	Total articles (%)
AFLP	1		1						1							3 (10.3)
Allozyme	1							2				1				4 (13.8)
cpMarker			1									1				2 (6.9)
Isozyme				1	1			1								3 (10.3)
ISSR								1			2					3 (10.3)
RAPD				1				1								2 (6.9)
SSR		1				1	1	2	2		2	4	1	2	3	19 (65.5)

Figure 4. Cumulative number of microevolution articles, focused on populations of Neotropical Myrtaceae over time, profiling use of different molecular markers.

gene flow among upstream populations (Caldiz & Premoli, 2005). These authors verified that rivers promote dispersal and fixation of propagules in small populations of *L. apiculata* and low levels of population structure result. On the other hand, in this species, large populations are more structured than small ones due to the Wahlund effect (Caldiz & Premoli, 2005). This effect is also found in *Legrandia concinna* (Phil.) Kausel (Martínez Araneda *et al.*, 2011), in which small populations contain as much diversity as large populations. However, in *Myrciaria floribunda* (H.West ex Willd.) O.Berg (Franceschinelli *et al.*, 2007) this is not the case; small populations have lower diversity than large populations, indicating that the diversity is maintained in different ways in different species.

Studied species of Myrteae that demonstrate no population structure were *Campomanesia adamantium* (Cambess.) O.Berg (Crispim *et al.*, 2018) and *Psidium guineense* Sw. (Silva *et al.*, 2016). However, Crispim *et al.* (2018) observed a reduction in gene flow among the Cerrado population due to fragmentation and isolation by large, agricultural monocultures. The same was observed in *E. dysenterica*, also occurring in the Cerrado (Boaventura-Novaes *et al.*, 2018). Fragmentation of natural populations by agriculture has led to increased frequency of rare alleles, reduced vigour and seed germination and elevated levels of homozygosity and inbreeding depression in *E. dysenterica* populations (Zucchi *et al.*, 2003; Chaves *et al.*, 2011; Telles *et al.*, 2013).

These results improve understanding of factors promoting population structure in species of Myrteae and the spatial distribution of genetic diversity. Such information is of importance to those developing conservation strategies for these species (Diniz *et al.*, 2020). Diniz-Filho *et al.* (2016c) published an R script suggesting individual and population numbers necessary to maintain and conserve optimal natural genetic diversity in *E. dysenterica*. Similar methodologies can be developed for other species, assisting delimitation of areas of high conservation significance. To implement such techniques in Myrteae, however, the need for accurate species spatial genetic distribution data can be an obstacle. This is due to the existence of widespread species complexes, such as *Myrcia selloi* (Spreng.) N.Silveira (Lima *et al.*, 2015). The *M. selloi* species complex covers diverse geographical areas, making taxonomic delimitation difficult. Taxonomic progress in the *M. selloi* complex was achieved following analysis of population structure (Lima *et al.*, 2015) that, allied with ecological and morphological data, instigated taxonomic adjustment in the species that comprise the complex, *Myrcia tomentosa* (Aubl.) DC., *Myrcia laruotteana* Cambess. and *M. selloi*, and synonymization of *M. lajeana* D.Legrand under *M. laruotteana*. Of the 13 species sampled, five occur in the Atlantic Forest, four in the Andes, two in the Cerrado and one in the Chaco, with *M. selloi* occurring in both the Atlantic Forest and Cerrado. Population sampling of other species and species complexes in the tribe is desirable, ensuring wide sampling accross ecoregions.

Phylogeographical patterns

The phylogeographic study of Neotropical taxa has increased in the past years (Turchetto-Zolet *et al.*, 2013); however, the species-rich Myrtaceae are poorly represented. Until now, the only two phylogeographic studies of Myrtaceae have focused on *E. uniflora*, a widely distributed Atlantic Forest species (Turchetto-Zolet *et al.*, 2016) and *E. dysenterica*, widely distributed in the Cerrado (Lima *et al.*, 2017).

Turchetto-Zolet *et al.* (2016) analysed plastid markers from 313 individuals from across the distribution of *E. uniflora* and found two divergent lineages with an estimated divergence time of *c.* 4.9 Mya. That study also showed a phylogeographic break between these groups of populations, located south of the city of Torres, in the State of Rio Grande do Sul (*c.* 29°-30°S), recognized as an important phytogeographical boundary (Turchetto-Zolet *et al.*, 2016). This phylogeographic break separated the two lineages, one distributed in the south of Brazil and Argentina (riparian forest and restinga) and the other in the south-east and north-east of Brazil (restinga). Distinct demographic and genetic diversity patterns were found for these two groups of haplotypes. The south-east and north-east populations had experienced population growth and low genetic diversity, but southern populations experienced relative historical demographic stability and high genetic diversity.

Lima *et al.* (2017) sampled 333 individuals of *E. dysenterica* in the Cerrado and by analysing plastid and nuclear markers demonstrated population stability over time and species dispersion in the northern, western and south-eastern regions of Brazil, favoured by the existence of a historic refuge in the savanna of central Brazil (Cerrado) during the Pleistocene. This refuge is likely to have been a key factor in the establishment of the uninterrupted dispersion of the lineage among populations of *E. dysenterica*.

Ecological niche modelling (ENM) was performed on both *E. uniflora* (Turchetto-Zolet *et al.*, 2016) and *E. dysenterica* (Lima *et al.*, 2017). Fragmentation of the distribution of *E. uniflora* during cool periods and broader and more connected distribution in warm periods during the Pleistocene were reported. *Eugenia dysenterica* was potentially distributed across a large area, extending over central-western Brazil through the last glaciation. These studies describe phylogeographic and demographic patterns

in biodiverse and fragile biomes and demonstrate the effects of past climate changes in the genetic diversity and population structure of these species. The high population structure and lineage divergence found in *E. uniflora*, associated with the phytogeographical changes in the Atlantic Forest, demonstrate that microevolutionary dynamics can influence lineage diversification in this family. Further phylogeographic studies with species of Myrtaceae will continue to develop these eco-evolutionary pictures, contributing to our understanding of the high levels of species diversity found in tropical Myrtaceae.

CYTOGENETICS

To retrieve cytological data beyond the search carried out using Web of Science, we supplemented the search with data from the Chromosome Counts Database (CCDB), IPCN Chromosome Reports and the Plant DNA C-values Database. Traits searched for were chromosome number, karyotypic characterization (conventional and molecular cytogenetic), meiotic behaviour, pollen morphology and viability and genome size estimation.

Karyological traits such as chromosome number, morphology and size and DNA content (2C value) have been successfully employed in studies of different angiosperm families to investigate inter- and intraspecific relationships and to better understand the evolutionary history of taxa (Stace, 2000; Bareka *et al.*, 2008; Goldblatt & Manning, 2008; Guerra, 2012).

Cytogenetic studies involving Neotropical species are scarce and usually restricted to chromosome counts (Table 1; Fig. 5). Many genera are poorly investigated and some do not yet have chromosome numbers determined (Costa & Forni-Martins, 2006b, 2007b; Jara-Seguel *et al.*, 2013).

Until 2004, chromosome number was reported for < 5% of the fleshy-fruited species of Myrteae from the Neotropics (Costa, 2004). Although several studies have been carried out since then, according to our review, availability of cytological data remains limited. In fact, our search indicates that cytogenetic data exist for only 3.97% (86) of Neotropical species of Myrtaceae. This apparent reduction is due to recent taxonomic revisions that have led to several synonymizations (Fig. 5). There is no cytogenetic data available for 13 genera of Myrteae (Fig. 5; Supporting Information, Table S7): *Acca*; *Algrizea* Proença & NicLugh.; *Amomyrtella*; *Amomyrtus*, *Calycolpus* O.Berg; *Chamguava* Landrum; *Curitiba* Salywon & Landrum; *Legrandia*; *Mosiera* Small; *Neomitranthes* D.Legrand; *Nothomyrcia* Kausel; *Siphoneugena* O.Berg and *Temu.*

The ancestral base chromosome number suggested for Myrtaceae is $x = 11$, observed in almost all the genera of this family; however, $x = 12$ is also reported as a secondary base number (Atchison, 1947; Raven, 1975; Costa & Forni-Martins, 2006a). Events of dysploidy and polyploidy have driven genome evolution in Myrtaceae. Costa & Forni-Martins (2006a) referred to hybridization associated with polyploidy in speciation of Brazilian Myrtaceae. Euploidy was important in the diversification of Myrteae (Andrade & Forni-Martins, 1998). Polyploid species from $x = 11$ and intraspecific polyploid series can be found in several genera (Supporting Information, Fig. S1). At least 26 species of *Eugenia* P.Micheli ex L. have chromosome numbers determined and wide variation can be observed: $2n = 22, 33, 44, 66$ (Costa & Forni-Martins, 2006a; Rice *et al.*, 2015; Silveira *et al.*, 2016; CCDB; IPCN Chromosome Reports). According to Costa & Forni-Martins (2007a), 22.5% of *Eugenia* spp. are polyploids, but in our literature review we found a higher number; polyploidy has been reported for 12 of the 26 species

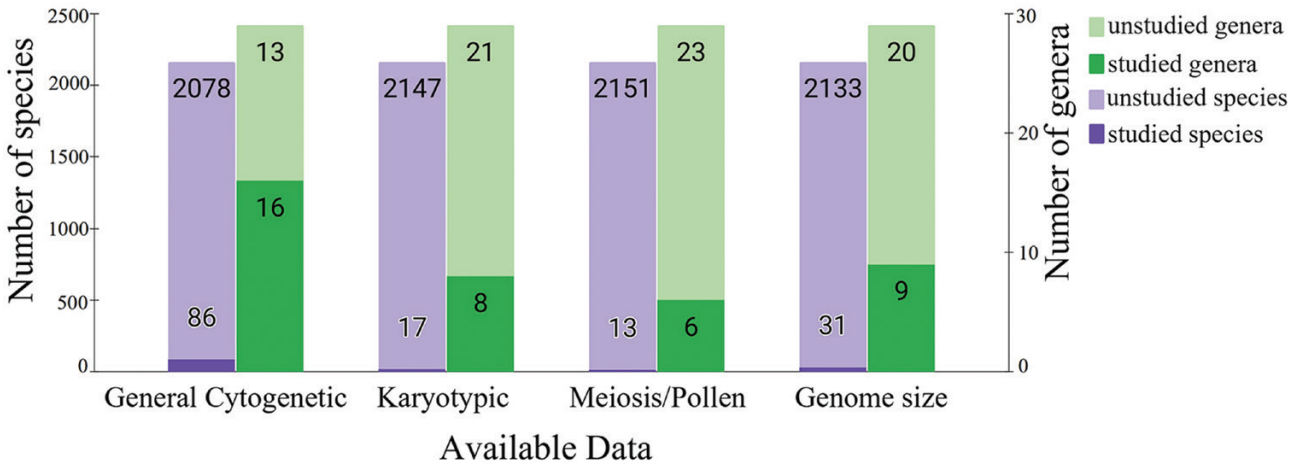


Figure 5. Cytogenetic data available for Myrteae based on currently accepted genera and species.

of *Eugenia* investigated. Intraspecific cytotypes are also found in some species, like *Eugenia hyemalis* DC. (2*n* = 22 and 44), *Eugenia pitanga* (O.Berg) Kiaersk. (2*n* = 22 and 44) and *Eugenia punicifolia* (Kunth) DC. (2*n* = 22, 33 and 44) (Silveira *et al.*, 2016). Dysploid *Eugenia* spp. with 2*n* = 24, 42, 45, 46 and 54 have also been reported (see Costa & Forni-Martins, 2006b).

Psidium L. is a genus in which most studied species are polyploid (85.7%), with only two exclusively diploid species recorded: *Psidium cauliflorum* Landrum & Sobral and *Psidium oblongatum* O.Berg (Costa & Forni-Martins, 2006a, b; Souza *et al.*, 2015; Tuler *et al.*, 2019). Literature reports for *Psidium* state 2*n* = 22, 33, 44, 55, 66, 77 and 88 (Hirano & Nakasone, 1969; Costa & Forni Martins 2006a, b, 2007a; Eder-Silva *et al.*, 2007; Coser *et al.*, 2012; Marques *et al.*, 2016; Tuler *et al.*, 2019). Souza-Perez & Speroni (2017) investigated female gametophyte ontogeny of *Psidium cattleyanum* Sabine and showed that the disploporic origin of the embryo sac explains varying ploidies found in natural populations (2*n* = 44, 55, 66, 77, 88, including odd ploidies), the absence of diploids and low pollen viability can be explained by the disploporic origin of the embryo sacs.

Variation in chromosome number relative to the basic number *x* = 11 also includes dysploid cytotypes. Souza *et al.* (2015) found wide variation in chromosome numbers (2*n* = 44, 46, 48, 55, 58, 66 and 82) of accessions of *P. cattleyanum*. Likewise, *Psidium guajava* L. includes many dysploid populations (2*n* = 21, 22, 28, 20, 32 and 34) or polyploid series (2*n* = 22, 33, 44 and 88). Considering this available data, polyploidy and dysploidy seem to have played important roles in diversification of *Psidium* (Costa & Forni-Martins, 2006b; Marques *et al.*, 2016).

Despite the noticeable effects of polyploidy and dysploidy on chromosome numbers in some genera, stability of the basic number *x* = 11, and especially the diploid status, can be evidenced in most genera (Costa & Forni-Martins, 2006a, 2007a). Among the 16 genera of Myrteae with reported chromosome numbers, nine have exclusively diploid species. *Myrciaria* O.Berg, for example, has no polyploids or cytotypes reported with all the six species studied presenting 2*n* = 22.

Variation in chromosomes (chromosome number, morphology and structure) can provide information for biosystematics and evolutionary studies. Nevertheless, the constancy of the basic number in Myrtaceae and the small size of the chromosomes have restricted the use of cytotaxonomy in this family (Atchison, 1947; Oudjehih & Abdellah, 2006; Costa & Forni-Martins, 2007a). Studies related to chromosome morphology and karyotype architecture are scarce, probably due to their small size, usually ranging from 0.6 µm to 2.0 µm, rarely reaching 3.0 µm (Vijayakumar & Subramanian, 1985; Silveira *et al.*, 2006; Costa & Forni-Martins, 2007b; Jara-Seguel *et al.*, 2013; Marques *et al.*, 2016). In general, species of Myrteae show homogeneity in chromosome sizes and morphology resulting in moderately symmetrical karyotypes (intra- and interchromosomal symmetry). Although karyotypic variation is not as substantial as in other families such as Iridaceae (Goldblatt & Takei, 1997; Alves *et al.*, 2011; Moraes *et al.*, 2015; Alencar *et al.*, 2018; Báez *et al.*, 2019), differences found in some taxa indicate that karyomorphological data may contribute to their characterization (Guerra, 2012). The degree of asymmetry of a karyotype indicates the evolutionary status of a taxa. More symmetrical karyotypes point to a more primitive position (Alves *et al.*, 2011; Moraes *et al.*, 2015). Although there are few karyomorphological data for Myrteae (only seven articles for 17 species), the described karyotypes are moderately symmetrical when compared to those of dry-fruited taxa, which are highly symmetrical, evidencing the most derived condition of fleshy-fruited taxa. Certainly additional karyotypic studies are necessary including more species of Myrteae to better understand genome evolution. The use of other cytogenetic tools for morphological analysis, like chromosome banding and fluorescence *in situ* hybridization (FISH), will allow better characterization and differentiation of the taxonomic groups. Chromosome banding data are reported only for *P. cattleyanum* and *F. sellowiana* in the thesis of Medina (2014). Regarding molecular cytogenetic analysis, we found just those data obtained by Costa (2009) in his thesis in which DNA 45S probes were used to investigate nine *Psidium* spp., two species of *Campomanesia* Ruiz & Pav. and one *Pimenta* sp.

Information about meiotic stability and pollen viability is important for conservation and breeding purposes, both traits indicating reproductive success. Studies using these kinds of data are found especially in economically relevant (fruit and ornamental) Brazilian native species of Myrtaceae (Loguercio & Battistin, 2004; Franzon & Raseira, 2004; Almeida *et al.*, 2012; Guerra *et al.*, 2016; Tedesco *et al.*, 2019). To our knowledge, data regarding microsporogenesis and/or pollen viability exist for only six Neotropical Myrtaceae genera [*Campomanesia* (two species), *Eugenia* (five species), *Myrciaria* (one species), *Plinia* (one species), *Psidium* (three species) and *F. sellowiana*] (Franzon & Raseira, 2004; Costa & Forni-Martins, 2006a, b; Almeida *et al.*, 2012; Guerra *et al.*, 2016; Tedesco *et al.*, 2019). These studies report highly stable meiosis, regular chromosome pairing and segregation, with 82-100% normal meiotic cells. Meiotic indices (% of normal tetrads) and pollen viability are generally > 85%, reaching 100% in some species. Such regularity in meiosis is expected in diploid and even polyploid species; however, there is little data about microsporogenesis at odd ploidies. Singhal *et al.* (1985)

reported low pollen stainability and meiotic abnormalities in a triploid sample of *E. uniflora*.

Genome size data has been widely used, along with karyotypic data, in several studies addressing cytotaxonomic, cytogeographic and phylogenetic approaches. However, there are few estimates of C-value in Myrtaceae (Marhold *et al.*, 2010; Dagher-Kharrat *et al.*, 2013; Carta & Peruzzi, 2016; Moura *et al.*, 2018; Souza *et al.*, 2019). In the Angiosperm DNA C-values database (Leitch *et al.*, 2019) there are 52 records of C-value estimates for Myrtaceae, the majority obtained from Costa *et al.* (2008). In our search for genome size data, we found estimates for nine genera and 31 species (1.43% of species of Myrteae; Fig. 5). The mean value for these sampled species is 2C = 1.02 pg, therefore a very small genome size (*sensu* Leitch, 1998; Soltis *et al.*, 2003). Costa *et al.* (2008) determined for the first time the genome size of 30 species of Neotropical fleshy-fruited taxa (from the three subtribes) (28 diploids, $2n = 22$; two tetraploids, $2n = 44$). The DNA content (2C value) varied from 0.478 pg in *Myrciaria glazioviana* (Kiaersk.) G.M.Barroso ex Sobral (diploid) to 1.167 pg in *P. cattleyanum* (tetraploid). More recently, four other studies reported genome size data, all of them in *Psidium* spp. (Coser *et al.*, 2012; Souza *et al.*, 2015; Marques *et al.*, 2016; Tuler *et al.*, 2019). As mentioned previously, *Psidium* is a genus with high variability in ploidy, with polyploid series ranging from $3x$ to $8x$. Such variability is also observed in DNA content, with records ranging from the diploid *P. oblongatum* with 2C = 0.98 pg to the octoploid *Psidium longipetiolatum* D.Legrand with 2C = 5.12 pg. In this genus, there is a relationship between ploidy and genome size. Considering the monoploid genome ($x = 11$), the 1Cx value of *Psidium* spp. Apparently exhibits a moderate increase in DNA content according to the ploidy (*c.* 0.5 pg in diploids and > 0.6 pg in octoploids; Souza *et al.*, 2015; Tuler *et al.*, 2019).

Cytogenetic data can make important contributions to taxonomic, evolutionary, conservation and breeding studies in Myrtaceae. However, much remains unknown. Considering the large number of non-investigated species, efforts should be made to obtain information about chromosome number, karyotypic characterization (including chromosome banding and FISH tools) and genome size estimates for several species and genera of Neotropical Myrtaceae.

GENOMIC AND TRANSCRIPTOMIC APPROACHES

The use of genomic and transcriptomic techniques in combination with other well-established approaches has revolutionized the study of evolution at both macro- and microevolutionary scales (Sands, 2019). These approaches have produced a high quantity and density of genetic polymorphism data that can be used in population genetic, phylogeographic and demographic analyses (Gagnaire, 2020). Whole genome and plastome sequencing has facilitated significant advances in the systematic study of angiosperms, underpinning phylogenetic reconstructions conducted at both deep and fine scale, employing data sets of several taxa and genes. Importantly, high-throughput sequencing has also contributed to probe development for use in FISH for chromosome studies (Soltis *et al.*, 2013). At the macroevolutionary scale, genomic data has been successfully applied to improve phylogenetic analysis and systematics in a variety of plants (Ran *et al.*, 2018).

In Myrtaceae, most studies using genomic approaches have been performed in the model species *Eucalyptus grandis* W.Hill ex Maiden and, until now, there is no reference genome sequenced for a Neotropical species of Myrtaceae. High-throughput sequencing was employed to generate partial genome sequencing of *Campomanesia xanthocarpa* (Mart.) O.Berg (Petry *et al.*, 2019) and *E. uniflora* (Sarzi *et al.*, 2019; Stefenon *et al.*, 2019). Draft genomes of *C. xanthocarpa* and *E. uniflora* allowed identification and characterization of SSR markers for use in population level studies in these and other Neotropical species of Myrtaceae. Repetitive elements in the genome of these species were characterized, demonstrating a higher number of *Copia* elements than *Gypsy* elements (Petry *et al.*, 2019; Stefenon *et al.*, 2019). Transcriptome analysis was employed for *E. uniflora* (Guzman *et al.*, 2014) and *P. cattleyanum* (Vetö *et al.*, 2020), providing a reference transcriptome for each species. Guzman *et al.* (2014) identified genes potentially involved in terpenoid biosynthesis in *E. uniflora*, and Vetö *et al.* (2020) identified genes involved in fruit colour in *P. cattleyanum*. Using high-throughput sequencing of small RNA and RNA-seq libraries, Guzman *et al.* (2012) identified miRNAs and their potential targets in *E. uniflora*. These genomic and transcriptomic studies provided data sources such as molecular markers, gene expression and regulation and candidate genes involved in the phenotypic variation, which could in the future be explored in population genomics, local adaptation and phenotype/genotype association studies, contributing to improved understanding of evolution in Neotropical Myrtaceae.

The availability of > 6800 sequenced plastid genomes from land plants has allowed us to perform comparative analyses associated with phylogenetic analysis, enhancing our understanding of plant evolution. Until now, the complete sequence of the plastid genome is available for 14 species of Myrteae: *Plinia trunciflora* (O.Berg) Kausel (Eguiluz *et al.*, 2017a), *E. uniflora*

(Eguiluz *et al.*, 2017b), *Psidium guajava* L. (Jo *et al.*, 2016), *Campomanesia xanthocarpa* (Mart.) O.Berg. (Machado *et al.*, 2020), *Eugenia brasiliensis* Lam., *Eugenia pyriformis* Cambess, *Eugenia nitida* Cambess, *Myrcianthes pungens* (O.Berg) D.Legrand, *Plinia edulis* (Vell.) Sobral, *Psidium cattleyanum* Sabine (Rodrigues *et al.*, 2020), *P. galapageium* Hook and *Psidium* sp. (Reatini *et al.*, 2018), *Feijoa sellowiana* (Machado *et al.*, 2017) and *Myrcia amethystina* (O.Berg) Kiaersk. (GenBank:MW353255). Generally, the sequenced plastomes of these species are highly conserved regarding gene content and organization and genome structure. Some differences could be observed in genome length, protein-coding genes and non-coding regions. Rodrigues *et al.* (2020), comparing the plastomes of *E. brasiliensis*, *E. pyriformis*, *E. nitida*, *M. pungens*, *Plinia edulis* and *Psidium cattleyanum*, identified intergenic regions with high sequence diversity with potential for intra- and interspecific genetic population genetic and phylogeographic studies. Comparing the substitution rates of each plastid DNA locus between *F. sellowiana* and *E. uniflora*, Machado *et al.* (2017) found positive selection for eight genes associated with the large subunit of the ribosome (*rpl122*), RNA polymerase subunit (*rpoC2*), NADH dehydrogenase (*ndhD*, *ndhF*, *ndhH*), photosystem I (*psaA*), *matK* and one gene with unknown functions (*ycf1*). The availability of the plastomes of these species and the results from comparative analyses among them will improve taxonomic coverage in further phylogenetic analyses to further understand evolution in Neotropical Myrtaceae.

CONCLUSIONS AND FUTURE DIRECTIONS

This review consolidates information on the evolution of Neotropical Myrtaceae. It highlights significant advances in research, but also shows that some areas are neglected and that some species show difficult maintenance of intraspecific diversity due to anthropic activities. Although phylogenetic studies based on molecular markers have increased in the past years, providing new insights into the macroevolution in the family, population-level studies have only been performed on a few species. Thus, there are gaps in knowledge of microevolutionary processes, making it difficult to link macro- and microevolutionary scales. Also, further genomic and cytogenetic studies are required to answer basic questions related to genome structure and evolution in the group, providing important information on the evolution of the family.

Here, we suggest several open questions to be addressed in future studies to fill gaps in the evolutionary knowledge of specific groups/taxa in Neotropical Myrtaceae. First, further studies are needed on the evolution and systematic relevance of vegetative characters, such as bark tissues, leaf traits and chemical composition (Padovan *et al.*, 2014), and reproductive characters such as fruit display and composition, especially for species and genera that have been less well studied. A review of leaf and woody characters to better classify and verify calibration points based on fossils is also recommended. Hybridization studies in closely related taxa are also necessary to understand how mechanisms of speciation occur in these species.

Second, more studies are necessary to obtain population genetic data, like those already obtained for *E. dysenterica* and *E. uniflora*. This data can be integrated with phenotypic (Zamudio *et al.*, 2016), climatic (Turchetto-Zolet *et al.*, 2016; Santos *et al.*, 2018), geological (Mäder *et al.*, 2013), landscape ecology (Capurucho *et al.*, 2013) and reproductive data, allowing greater understanding of factors (Li *et al.*, 2018) that promoted diversification and structuring of species and genera in Neotropical Myrtaceae.

In cytogenetics, information on number of chromosomes, karyotype characterization, banding, FISH and genome size are necessary for an alarming 2078 of 2164 species that do not have any data, mainly in the genera *Acca*, *Algrizea*, *Amomyrtella*, *Amomyrtus*, *Calycolpus*, *Chamguava*, *Curitiba*, *Legrandia*, *Mosiera*, *Neomitranthes*, *Nothomyrcia*, *Siphoneugena* and *Temu*. Important biological questions from this and other plant families can be answered using these data and will contribute to the conservation and use of these species.

Finally, the reduction of costs and the development of robust methodologies for sequencing, assembly and analysis of gene expression in plastid genomes have enabled comparative approaches (Rodrigues *et al.*, 2020). The integration of other data sets (e.g. environmental, geological, reproductive or phenotypic) will identify biotic and abiotic pressures that influence speciation within a population and ultimately elucidate macroevolutionary patterns across evolutionary time.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Figure S1. Number of species and genera with information on polyploidy and ploidy in Neotropical Myrteae.
Table S1. Summary of the retrieved articles, including the total number of articles on 2 July 2020.
Table S2. Articles used in this revision that investigated Neotropical Myrteae species with DOI/site, year, authors and major area of study reported.
Table S3. Nomenclature of the species described by the authors of the articles used in this review, followed by their taxonomic update and status.
Table S4. The number of Myrteae species by genus occurring in the Neotropical region following World Checklist of Selected Plant Families (WCVP, 2021).
Table S5. The Neotropical Myrteae species most studied in evolution articles recovered for this revision.
Table S6. Species investigated in microevolutionary studies with their respective DOI and citation.
Table S7. Number of Myrteae species with studies in any cytogenetics category by genus.