

PHYLOGENETIC AND BIOGEOGRAPHIC ANALYSIS IN *MYRCIA* SECT. *MYRCIA* (*MYRCIA* S.L., MYRTACEAE) WITH FOCUS ON HIGHLY POLYPHYLETIC *MYRCIA SPLENDENS*

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Premise of research. *Myrcia* s.l. is the largest exclusively Neotropical genus of Myrtaceae, comprising about 800 species. This large genus is divided into 10 clades, most of these recently published as sections. One section, *Myrcia* sect. *Myrcia*, has 114 species distributed from Mexico to Uruguay, with species diversity centers in the Atlantic Forest, Amazon, and Cerrado. This section includes one of the most difficult to circumscribe species of the Neotropical flora, *Myrcia splendens*, with the same distribution as the genus and currently with almost 170 synonyms. Phylogenetic relationships and biogeographic patterns in *Myrcia* sect. *Myrcia* are examined for the first time using molecular data.

Methodology. Phylogenetic inference is based on maximum likelihood and Bayesian analysis of internal transcribed spacer (nuclear), *ndhF*, *psbA-trnH*, *trnL-trnF*, and *trnQ-rps16* (plastid) sequences obtained by sequencing a morphologically and geographically representative sample. Phylogenetic relationships, divergence time estimates, and biogeographic patterns are investigated using BEAST and BioGeoBEARS.

Pivotal results. Results show that *Myrcia* sect. *Myrcia* is monophyletic as morphologically circumscribed. Internal relationships indicate morphologically distinct lineages, but the widespread and taxonomically unruly *M. splendens* emerges as polyphyletic. Lineages from Central America and the Amazon are sister to multiple dispersals to disparate biomes and subsequent colonization of the Cerrado. Further field and laboratory studies are necessary to understand the extreme morphological plasticity of this section, with a particular focus on improving taxonomic delimitations in *M. splendens*.

Conclusions. This article represents the largest sample of *Myrcia* sect. *Myrcia* examined to date. The results presented here demonstrate the monophyly of the section and confirm the nonmonophyly of the widespread *M. splendens*, with multiple accessions emerging in independent clades from different biomes. The mean estimated age for *Myrcia* sect. *Myrcia* is 22.4 mya, and the four clades of focus in this article are estimated to have originated in the Miocene.

Keywords: Amazon, Atlantic Forest, Cerrado, molecular dating, Myrteae.

Online enhancements: appendixes.

Introduction

Tribe Myrteae (ca. 2500 species) comprises all American species of Myrtaceae except the Chilean *Metrosideros stipularis* (Hook.

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& Arn.) Hook.f. (Wilson et al. 2005; Pillon et al. 2015). Tribe Myrteae includes groups with unusually complex taxonomic delimitation (McVaugh 1968), such as *Myrcia*, the largest exclusively Neotropical genus of Myrtaceae (Lucas et al. 2011). Until the beginning of the twenty-first century, the species of *Myrcia* were included in five genera—*Calyptanthes* Sw., *Gomidesia* O.Berg, *Marlierea* Cambess., *Mitranthes* O.Berg., and *Myrcia* DC.—differentiated by characters of the calyx, mode of opening the flowers, and branching pattern (Berg 1855–1856; McVaugh 1956).

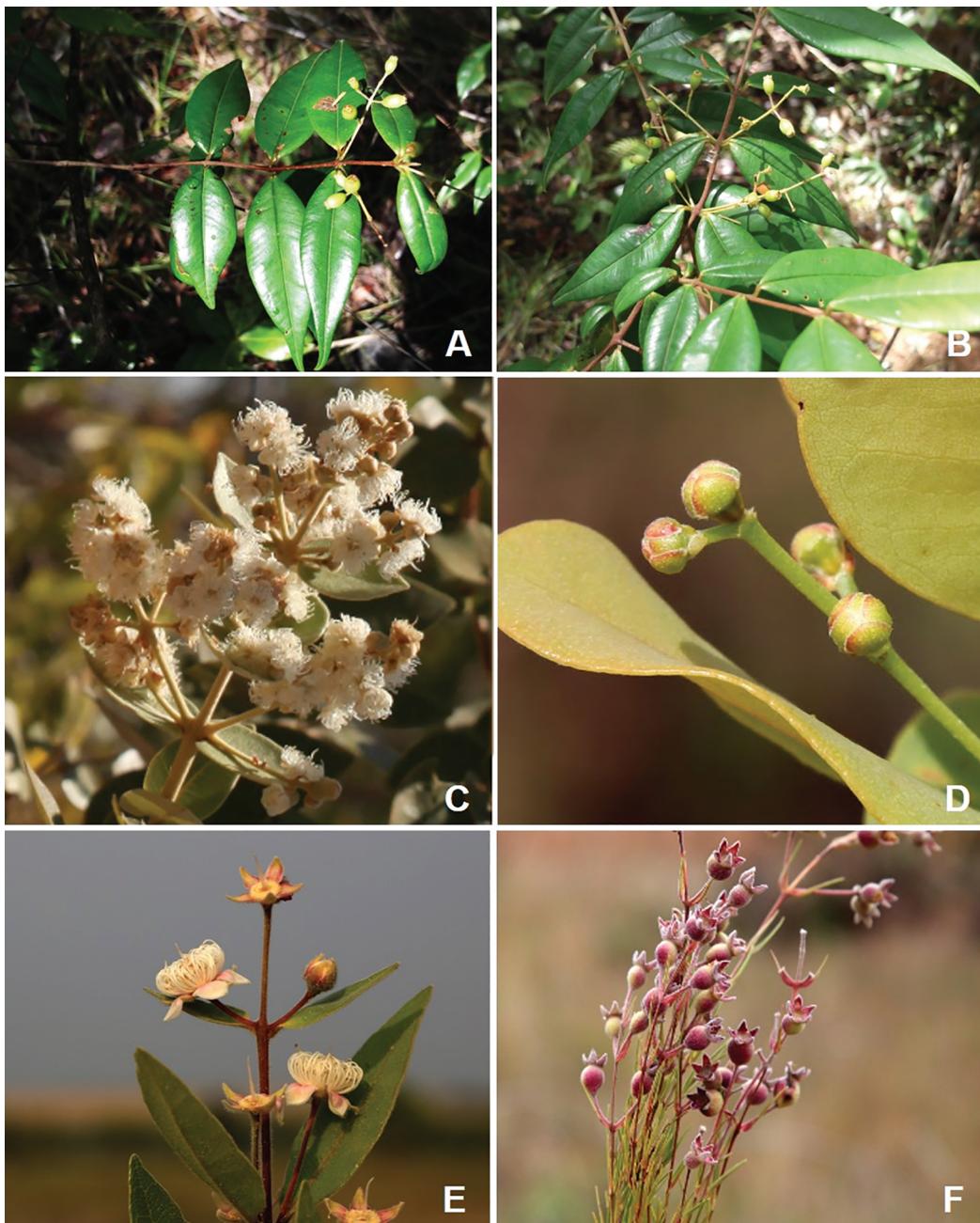


Fig. 1 Diagnostic features of *Myrcia* sect. *Myrcia*. *A*, Cylindrical fruits in *M. sylvatica*. *B*, Cylindrical fruits in *M. splendens*. *C*, Dense, pale indument of *M. bella*. *D*, Dense, pale indument of *M. ochrooides*. *E*, Thickened staminal disc of *M. suffruticosa*. *F*, Subglobose fruits and enlarged calyx lobes of *M. linearifolia*. Photographs by Ana Isa F. B. Lima (*A, B*) and José Henrique Moreira da Costa (*C–F*).

In the phylogenetic hypothesis of Myrteae proposed by Vasconcelos et al. (2017b), based on Bayesian inference (BI) and maximum likelihood (ML) analyses of one nuclear and seven plastid regions, the *Myrcia* s.l. clade emerges as monophyletic. A new subgeneric classification has recently been published (Lucas et al. 2018) that is based on recent phylogenetic studies in *Myrcia* s.l. (Lucas et al. 2011; Staggemeier et al. 2015; Wilson et al. 2016; Lima et al. 2021) and supplemented by the biogeographical investigations of the largest *Myrcia* samples to date by Santos et al.

(2017) and Amorim et al. (2019). One of the resulting sections is *Myrcia* sect. *Myrcia*; encompassing 114 species (L. Lima dos Santos, unpublished data), it is the most widespread section of *Myrcia*, occurring from southern Mexico to the Lesser Antilles and south to the north of Argentina. Most species of *Myrcia* sect. *Myrcia* occur in Brazil (78 species), in the Amazon, Atlantic Forest, and Cerrado phytogeographic domains (Santos et al. 2020). *Myrcia* sect. *Myrcia* species are mostly pollinated by bees and dispersed by mammals and birds (Vasconcelos et al. 2019b). The most

recent diagnosis of *Myrcia* sect. *Myrcia* (Lucas et al. 2018) describes generally pentamerous flowers with free perianth parts, a pubescent staminal ring comprising 60% or more of the total disc width, a hypanthium that is not elevated or is scarcely elevated above the surface of the ovary, with the ovary externally pubescent or sericeous or setose, two-locular with two ovules per locule and cylindrical fruits, with some subglobose exceptions (fig. 1). However, after the publication of *Myrcia elevata* M.F. Santos (Santos et al. 2015), the concept of the section must be expanded, as *M. elevata* emerged in the *Myrcia* sect. *Myrcia* clade despite the calyx tearing at anthesis, the staminal ring being relatively thin, and the hypanthium being elevated above the ovary by more than 2 mm. In these characters, *M. elevata* is reminiscent of *Myrcia* sect. *Aulomyrcia* (O. Berg) Griseb. However, *M. elevata* has a pubescent staminal ring and disc (vs. glabrous in *Myrcia* sect. *Aulomyrcia*).

McVaugh (1968) published a section, *Myrcia* sect. *Armeriela*, now in synonymy of *Myrcia* sect. *Aulomyrcia*, to include species such as *M. elevata* that he considered characteristic of both sections *Aulomyrcia* and *Myrcia*. Expanding the concept of section *Armeriela*, McVaugh (1969) included *M. calycampa*, *M. gonini*, and *M. tafelbergica*. Species corresponding to this group are also discussed by Holst (2002) as the “Calycampe complex.” Lucas et al. (2016), in preparing a taxonomic revision of *Myrcia* sect. *Aulomyrcia*, reported a group of unplaced species (*M. calycampa*, *M. elevata*, *M. gonini*, *M. intonsa*, *M. ramageana*, and *M. tafelbergica*). Lucas et al. (2016) hesitated to place these species in *Myrcia* sect. *Aulomyrcia* and listed them as species uncertainly placed in the genus. It is now desirable to test the position of these species within *Myrcia* sect. *Myrcia* because of their possession of characters such as pale to rufous hair covering hypanthia and hairy staminal rings, both arrangements associated with the latter section.

Despite significant advances in the taxonomy and systematics of *Myrcia* as a result of focused systematic studies and taxonomic revisions of its constituent clades (e.g., Lucas et al. 2016; Lourenço et al. 2018; Santos et al. 2018), *Myrcia* sect. *Myrcia* remains one of the most unmanageable sections. This complexity is due to (1) the exceptionally close morphological similarity of species complexes in areas such as the Amazon (e.g., *M. paivae*, *M. splendens*, *M. servata*, and *M. sylvatica*) and Cerrado (e.g., *M. albottomentosa*, *M. bella*, *M. cardiaca*, and *M. uberavensis*) and (2) the unusually high levels of phenotypic plasticity of diagnostic characters. Both geographically and ecologically, *Myrcia* sect. *Myrcia* species exhibit extremely different morphotypes of the same species that may have radically different characteristics (e.g., leaf shape/size, indument, floral disc width, or fruit shape; fig. 1). In this study, a morphotype is defined as a recurring morphological form, often associated with a particular geography and possibly genetically identifiable at the population level. At the extremes of the spectrum, it is hard to imagine that these forms are anything other than distinct species. However, with alarming regularity, specimens occur without one clear character state or another; species boundaries are stretched and blurred to the extreme.

A further problem that contributes to the difficulty of species management in this section is related to its most widespread and morphologically variable species, *M. splendens*. This is one of the most collected species of the Brazilian flora (CRIA 2019); it is the fifth most commonly collected of all species in the Amazon (ter Steege et al. 2019) and the most commonly collected native Myrtaceae species in the Americas (GBIF 2019). As a result of

blurred character state boundaries, a challenging number of species with very similar characters have been considered at some time as synonyms of *M. splendens* (e.g., *M. deflexa*, *M. eximia*, and *M. piauiensis*). The wide distribution of *M. splendens* from Mexico to tropical South America (WCSP 2019) matches that of the section, and the species complex includes ca. 170 synonymized names. On first examination, some of these synonyms appear to be clearly distinct morphotypes (e.g., *M. fallax*, *M. formosiana*, and *M. rostrata*), and their synonymization is sometimes met with skepticism. Swartz (1788) described *Myrtus splendens* on the basis of material from Hispaniola. According to its protologue, *M. splendens* is characterized by having virgate (erect) branchlets, elliptic and acuminate leaves, and axillary inflorescence peduncles. De Candolle (1828) later transferred this species to *Myrcia* on the basis of characteristics of the embryo. Since then, *M. splendens* sensu De Candolle (1828) has changed significantly. Multiple species of *Myrcia* described at the same time subsequently exhibit variation from the original concept, but although this variation can be extreme, it is rarely continuous. For example, De Candolle (1828) and Berg (1855–1856, 1857–1859) described 29 and 124 species of *Myrcia*, respectively, that are now included in synonymy of *M. splendens*.

The purpose of the work presented here is to produce a phylogenetic analysis of *Myrcia* sect. *Myrcia* and to interpret this in light of morphology and historical biogeography. The main aims of this study are, first, to test the monophyly of the section with an improved sampling and to examine the taxonomic and evolutionary/ecological significance of key diagnostic characteristics. Second, we discuss the internal relationships of the clade with particular focus on the widely distributed *M. splendens*. Third, we also examine the biogeographic history of the group to determine patterns of species dispersal and consider their significance in light of the evolution of tropical biomes. A taxonomic revision of the Brazilian species of *Myrcia* sect. *Myrcia* is underway (L. Lima dos Santos, J. S. Santos, E. Lucas, and M. F. Sales, unpublished manuscript), and the phylogenetic analysis presented here will eventually be incorporated into wider ecological and evolutionary hypotheses regarding Neotropical biomes and guide the taxonomic revision of the group.

Material and Methods

Taxonomic and Molecular Sampling

We sampled 127 species of Myrteae, of which 113 are *Myrcia*, including 48 *Myrcia* sect. *Myrcia* samples representing 32 species (from a total of 114; app. A1). This sample encompasses as much morphological and geographical variation in *Myrcia* sect. *Myrcia* as possible. *Myrtus communis* was used as outgroup taxon in all analyses following Lucas et al. (2011). To encompass the morphological and geographical variation of *Myrcia splendens*, a sample was selected that balanced availability with representation. Eleven individuals of *M. splendens* were included from across the species’ wide range, including material from the Brazilian Atlantic Forest, Amazon, and Cerrado; French Guiana; Costa Rica; and Dominican Republic. Every effort was made to also include multiple morphotypes for the species, capturing as much variation as possible and, where possible, matching names of previously accepted species. In these cases, the previous name is included in parentheses in the sample name in appendix A1 (e.g., “as *M.*

formosiana"). Species names and nomenclature used in this work follow ongoing taxonomic revision of the group (L. Lima dos Santos, J. S. Santos, E. Lucas, and M. F. Sales, unpublished manuscript) developed from the World Checklist of Selected Plant Families (WCSP 2019) and Santos et al. (2020). The internal transcribed spacer (ITS) of the ribosomal nuclear region and four plastid markers (*psbA-trnH*, *trnL-trnF*, *ndhF*, and *trnQ-rps16*) were used for the reconstruction of phylogenetic hypotheses. Around 30% of these sequences were newly generated for this study, and ca. 70% were obtained from other studies (Lucas et al. 2007, 2011; Staggemeier et al. 2015; Santos et al. 2016; Lima et al. 2021).

DNA Sequencing

Total DNA was extracted from 0.3 g of silica gel-dried leaves using a modified 2X cetyltrimethyl ammonium bromide protocol (Doyle and Doyle 1987). Amplification and purification of target DNA regions were executed according to the protocols outlined in Lucas et al. (2007, 2011) using internal primers when necessary. The GeneAmp 9700 PCR system (Applied Biosystems, Foster City, CA) was used for DNA amplification; primers and polymerase chain reaction conditions followed those used by Santos et al. (2016) and are listed in table 1. Sequencing reactions were conducted using the Mastercycler nexus (Eppendorf, Hamburg), implementing 26 cycles, each of 10 s at 96°C, 5 s at 50°C, and 4 min at 60°C. Sequences were read on a 3730 DNA analyzer (Applied Biosystems) and assembled and edited in Geneious 8.1 (Kearse et al. 2012); sequences were aligned using MUSCLE (Edgar 2004), using the default settings. Subsequently, ambiguous base calls were double-checked by eye against raw sequence data, and base calls were manually adjusted when wrongly called by the MUSCLE algorithm. All sequences were deposited in GenBank, and the DNA samples were deposited in the DNA and tissue collections at RBG Kew (app. A1).

Phylogenetic Analyses

For the combined data set, data were divided into two partitions: one including the nuclear marker ITS and the other including the four plastid regions combined. This approach was implemented because markers of the chloroplast genome are maternally inherited as

a single unit, and treating them as one unit has been shown to be effective in previous studies (e.g., Staggemeier et al. 2015; Santos et al. 2017). MrModeltest version 2.2 was used to estimate the optimal nucleotide substitution model for each partition, according to the Akaike information criterion (Nylander 2004). RAxML version 7.6.3 (Stamatakis 2006) was used to perform a ML analysis on each partition, using the default parameters and the rapid bootstrap algorithm with 1000 replicates, retaining the best-scoring ML tree for each partition. These individual analyses were compared by eye, and no topological incongruence with strong statistical support was detected; thus, the ITS and plastid data were combined in subsequent analyses. *Myrcia neovelutina* (voucher: Simon 1689) was removed from downstream analyses because it was represented only by an ITS sequence. A phylogenetic analysis was performed with the combined data set of 127 taxa using ML and the same parameters as for the individual analyses. BI, as implemented in MrBayes version 3.2.1 (Ronquist et al. 2012), was performed on the combined data using the best-fit models for each partition. Four Markov chain Monte Carlo chains were run twice for 15 million generations sampling every one-thousandth generation to approximate posterior probabilities. Convergence between runs was established using Tracer version 1.4 (Rambaut et al. 2013) to check for convergence and to check that chains had reached stationarity, deemed when the sufficient effective sample size was higher than 200 as implemented by Santos et al. (2016). Following previous phylogenetic protocols in *Myrcia* (e.g., Staggemeier et al. 2015; Wilson et al. 2016), 10% of the trees were removed as burn-in while calculating a 50% majority-rule consensus tree (halfcompat option) with posterior probability distributions using the sumt command in MrBayes. The final combined alignment is available as a NEXUS file in appendix A2 (apps. A2–A6 are available online). All outputs of the phylogenetic analyses were viewed using FigTree version 1.3.1 (Rambaut 2014). Both Bayesian and ML analyses were run on the CIPRES portal (Miller et al. 2010).

Dating and Historical Biogeography

Divergence times were estimated using a Bayesian approach implemented in BEAST version 1.8.3 (Drummond et al. 2012)

Table 1

Characteristics of the Five Regions Used in Phylogenetic Analyses and Protocols for Amplification and Sequencing

	ITS	<i>ndhF</i>	<i>psbA-trnH</i>	<i>trnL-trnF</i>	<i>trnQ-rps16</i>
Size of fragments (bp)	632	708	417	662	1332
Amplification protocol	2 min at 94°C; 30 cycles of 1 min at 94°C, 1 min at 50°C and 1.5 min at 72°C; at the end, 4 min at 72°C	5 min at 80°C; 35 cycles of 1 min at 95°C, 1 min at 50°C, and 5 min at 65°C; at the end, 4 min at 65°C	Same as <i>ndhF</i>	Same as <i>ndhF</i>	Same as <i>ndhF</i>
Sequencing protocol	26 cycles of 10 s at 96°C, 5 s at 50°C, 4 min at 60°C	Same as ITS	Same as ITS	Same as ITS	Same as ITS
Primers	AB101F, AB102R	ndhF1252F, ndhF2063R	<i>psbA(F)</i> , <i>trnH(R)</i>	External: <i>trnL</i> (c), <i>trnL</i> (f); internal: <i>trnL</i> (d), <i>trnL</i> (e)	External: <i>trnQ(F)</i> , <i>rps16xi(R)</i> ; internal: <i>MYtrnQ(R)</i> , <i>MYrps16(F)</i>
Primers reference	Sun et al. 1994	Biffin et al. 2006	Hamilton 1999	Taberlet et al. 1991	Murillo et al. 2012

Note. ITS = internal transcribed spacer.

using the combined data set. Following previous protocols in *Myrcia* (e.g., Santos et al. 2017), an uncorrelated relaxed molecular clock was implemented with the Yule speciation model. Sampling was performed every one-thousandth generation out of four total runs of 50 million generations each. Results were checked on Tracer version 1.6 (Rambaut et al. 2013), again using an effective sample size of >200 to show that chains had reached stationarity. A burn-in of 10% was used to remove trees produced before stationarity. TreeAnnotator version 1.8 (Drummond et al. 2012) was used to build a maximum clade credibility tree presenting 95% posterior probability at nodes. Because of the absence of reliable fossils of *Myrcia* species, calibration points were taken from a dated analysis of Myrteae (Vasconcelos et al. 2017b). Normal prior means were used because of the absence of the context of the fossil record, giving calibrations of 25.58 and 35.36 mya for the crown nodes of *Myrcia* s.l. and the Neotropical lineage, respectively.

The R package BioGeoBEARS (Matzke 2013; R Core Team 2019) was used to reconstruct the historical biogeography of *Myrcia* sect. *Myrcia* on the dated phylogenetic tree. The most likely area of origin and center of diversification of *Myrcia* has been shown to be the Atlantic Forest of eastern Brazil (Santos et al. 2017; Amorim et al. 2019). To focus on the biogeographical history of section *Myrcia*, reduce biogeographic ambiguity from missing outgroup taxa, and save computing time, the topology

used for the biogeographical analysis was reduced using the drop.tip function of the R package ape (Paradis et al. 2004). The remaining sample comprised only *Myrcia* sect. *Myrcia* (44 samples) and representative samples of each major lineage for the rest of *Myrcia* (10 samples). Where duplicate samples identified as the same species were used, only one accession was included from each putative ancestral area (AA), unless the samples were not sister to each other. The remaining phylogenetic tree comprised a total of 54 samples. Log likelihood (LnL) values were compared for BioGeoBEARS analyses with and without allowance for jump speciation where species can disperse to nonadjacent areas (DEC vs. DEC+J). LnL values were higher for DEC without J (DEC: LnL = -63.03; DEC+J: LnL = -102.48), suggesting that jump speciation has not been a substantial factor in *Myrcia* sect. *Myrcia* dispersal. The DEC approach (Ree and Smith 2008) was therefore adopted for this analysis. The following four AAs, based on those used by Santos et al. (2017), were used, spanning the distribution range of *Myrcia* sect. *Myrcia*: Amazon forest, Atlantic Forest (a combination of lowland Atlantic Forest and montane Atlantic Forest sensu Santos et al. 2017), Caribbean, and Cerrado (fig. 2). After testing analyses splitting the Atlantic Forest into northern and southern portions following the studies of Santos et al. (2017) and Amorim et al. (2019), patterns were not found to differ significantly. To simplify interpretation and facilitate the analysis, the Atlantic Forest phytogeographic

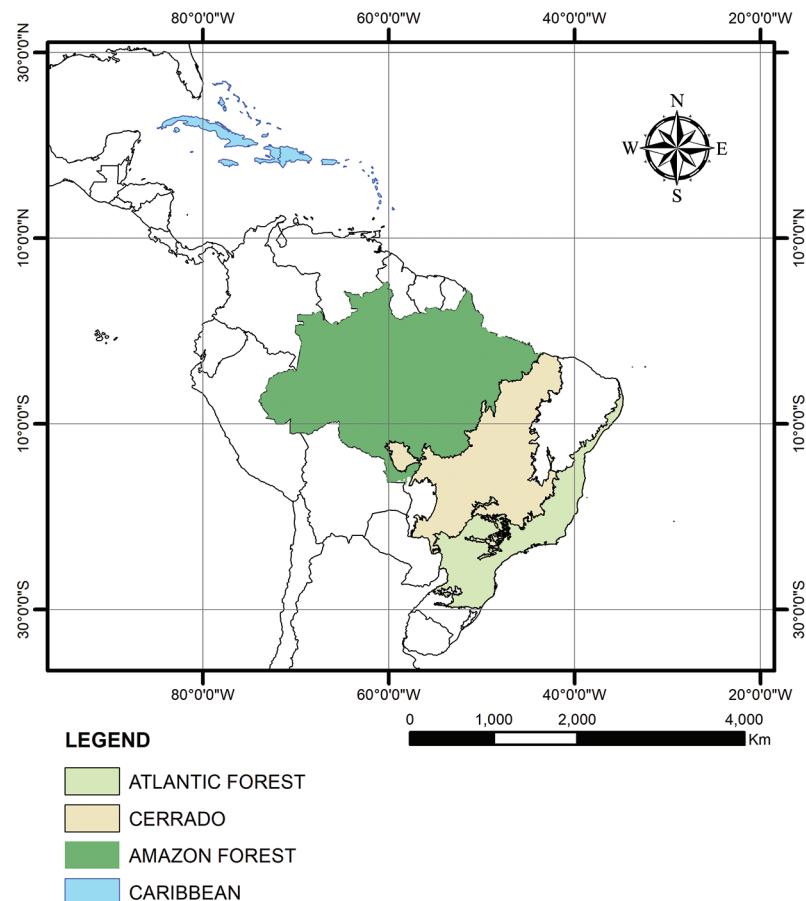


Fig. 2 Biogeographic areas defined for this study.

domain was maintained as a single region. AAs were compiled as a presence/absence matrix. In the case of widespread species such as *M. splendens*, species were scored in more than one AA. Accessions from Costa Rica were scored as occurring in the Amazon biogeographic area because of the similarity of ombrophilous rain forest habitat and similarity of species occurrences between these areas (McVaugh 1969; Barrie et al. 2009). Data files implemented in the BioGeoBEARS analysis (species presence/absence per region: distribution; time stratification: time_periods; relative probability of dispersal between each area: dispersal; and area adjacency through time: adjacency_through_time) are available in appendix A3.

Results

Phylogenetic Relationships of Myrcia Sect. Myrcia

The combined length of the two partitions was 3772 bp; of this, 3140 bp comprise the chloroplast DNA (cpDNA) partition and 632 bp represent the nuclear partition. In the cpDNA and nuclear partitions, 47.3% and 55% of the characters varied, respectively. The best model estimated for both nuclear and cpDNA partitions was GTR+I+G. Trees obtained from the ML analyses of ITS and plastid data are presented in appendixes A4 and A5. Phylogenetic trees obtained from the combined analysis of ITS and plastid data using BI and ML indicate mostly congruent relationships (figs. 3, 4) with no statistically supported contradictions. Taking strong statistical support to be posterior probability (PP) >0.95 and bootstrap (BS)>75%, both reconstructions place all inferred species of *Myrcia* sect. *Myrcia* in a monophyletic group with high support (PP: 1, BS: 91).

Internal Relationships and Myrcia splendens

Internal relationships within *Myrcia* sect. *Myrcia* have overall low statistical support (i.e., BS < 50% and PP < 0.75). Nodes with statistical support are marked in bold on figures 3 and 4 and considered further in “Discussion.” Despite the lack of support at internal nodes, the patterns recovered demonstrate groups of species that correspond to geography and morphology. These clades are informally lettered A–D and are indicated on figures 3 and 4 by colored boxes.

Dating and Historical Biogeography

The dated phylogenetic tree generated from the BEAST analysis with AA/range probabilities from the biogeographical reconstruction using BioGeoBEARS presented as pie charts is presented in figure 5. The topology of the reconstruction differs little from those produced using ML and BI, only in the placement of some species not included in any informal grouping. *Myrcia anceps* moves to become sister to clades C and D; *M. splendens* CR2 moves sister to *M. ochroides*, with the resulting clade being sister to group B; and *M. suffruticosa* emerges within group C. These results indicate that the mean estimated age for *Myrcia* sect. *Myrcia* is 22.4 mya with a 95% confidence interval (CI) of 24.9–19.9 mya (Oligocene/early Miocene). The four clades of focus in this work are estimated to have originated in the Miocene. A summary of node ages, CIs, estimated AAs/ranges, and probabilities for these key nodes are provided in table 2. AA/range probabilities for each node are listed in appendix A6.

Discussion

Phylogenetic Relationships of Myrcia Sect. Myrcia and Morphological Trends

The monophyly of *Myrcia* sect. *Myrcia* is confirmed with high support. Relatively low statistical support for internal nodes within the group is characteristic of similar analyses within *Myrcia* (e.g., Santos et al. 2017) and is thought to be due to incomplete genetic distinction of lineages (Lucas et al. 2011). Given that speciation is believed to be steady rather than accelerated (Vasconcelos et al. 2019a), it is surprising that lineage distinction is incomplete to this degree. Vasconcelos et al. (2019a) also found that *Myrcia* has undergone relatively little morphological diversification over its evolutionary history (i.e., has reached an adaptive plateau). It seems that the low level of discontinuous variation in morphological characters is matched by a similarly low level of genetic discontinuity despite evidence that the group has not experienced accelerated speciation. Nevertheless, consistent and useful patterns are supported by morphology (often based on characters taken in combination) and geography and are further explored below.

The most consistent diagnostic characters for *Myrcia* sect. *Myrcia* are cylindrical fruits (fig. 1A, 1B); the presence of sericeous indument on the outside of the calyx, hypanthium, and often other parts of the plant (fig. 1C, 1D); and the presence of thick, erect hairs on an expanded staminal ring (fig. 1E). According to Lucas et al. (2018), *Myrcia* sects. *Gomidesia* and *Myrcia* share the latter two of these characters. However, in *Gomidesia*, anthers have dislocated thecae (vs. symmetrical in *Myrcia*) and a thinner staminal ring, taking up no more than 40% of the disc (Lucas et al. 2011, 2018; Amorim et al. 2019). The nonmonophyly of the widespread *M. splendens* is confirmed (figs. 3, 4) with high support (PP: 1, BS: 91), with multiple accessions emerging in independent clades from different biomes and a Central American accession appearing sister to the rest of the section.

Within section *Myrcia*, four groups are further noted. The moderately to well-supported (PP: 0.98, BS: 63) clade A (figs. 3, 4, light orange box), or “*isaiana* group,” is composed of *M. bergiana*, *M. isaiana*, *M. megaphylla*, *M. retorta*, and *M. salzmannii*. These species occur in the Atlantic Forest (although *M. retorta* also occurs in the Cerrado) and have subglobose fruits in contrast to all of the other species sampled that have the cylindrical fruits more characteristic of the section (fig. 1A). Clade A is also remarkable in having several species with unusually large flowers and leaves, often with a dense indument; the species of this group have clear delimitation and are quite distinct from, and not likely to be confused with, *M. splendens*.

Between clades A and B is a lineage consisting only of the Cerrado species *M. ochroides*, again a species with larger flowers than usual in *Myrcia* sect. *Myrcia* and an unusual paniculate architecture that is especially stout and open, with apparently perfectly oppositely branching dichasias. Perfectly opposite branching is characteristic of *Myrcia* sects. *Calyptanthes* and *Sympodiomyrcia* (Santos et al. 2018) and is unusual in *Myrcia* sect. *Myrcia*.

Clade B (figs. 3, 4, dark green box) receives low to moderate support (PP: 0.33, BS: 76) and is composed entirely of Amazonian and Caribbean species. This clade contains *M. coumetae*, a riverine species characterized by large flowers and fruits, with a very evident hairy disc and thickened staminal ring. *Myrcia elevata* also occurs in this clade, a highly unusual species with a closed calyx

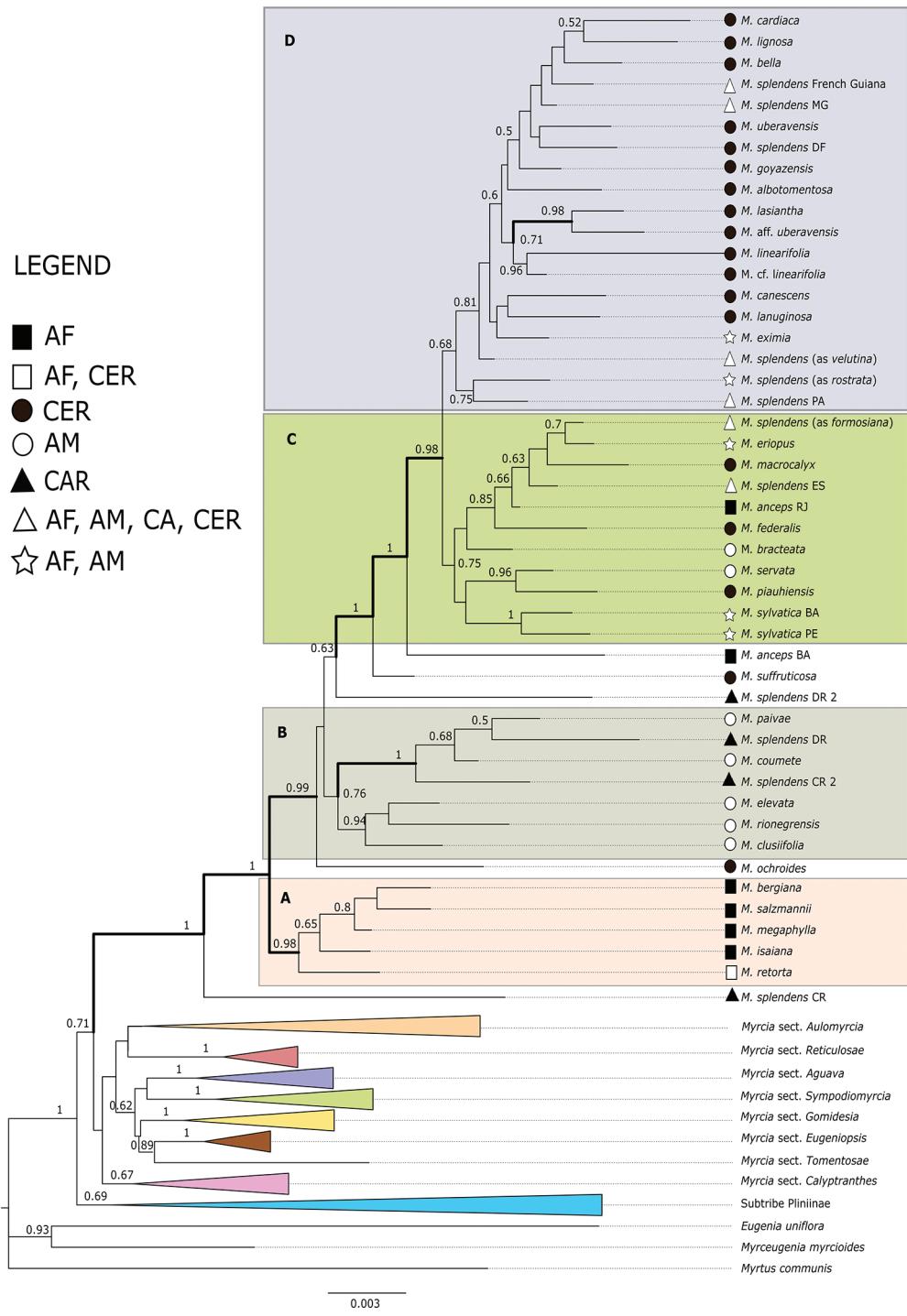


Fig. 3 Consensus tree of *Myrcia* sect. *Myrcia* obtained from Bayesian analysis of five DNA regions (internal transcribed spacer, *ndhF*, *psbA*-*trnH*, *trnL*-*trnF*, and *trnQ*-*rps16*). Posterior probabilities (Bayesian PPs) are indicated at nodes, with branches in bold representing PP ≥ 0.8 . Symbols at tips represent broad range distributions as indicated in the legend. Colored, lettered boxes indicate clades A–D mentioned in “Discussion.” AF = Atlantic Forest; AM = Amazon; CAR = Caribbean; CE = Cerrado; PA = Pará; BA = Bahia; CR = Costa Rica; DF = Distrito Federal; DR = Dominican Republic; ES = Espírito Santo; MG = Minas Gerais.

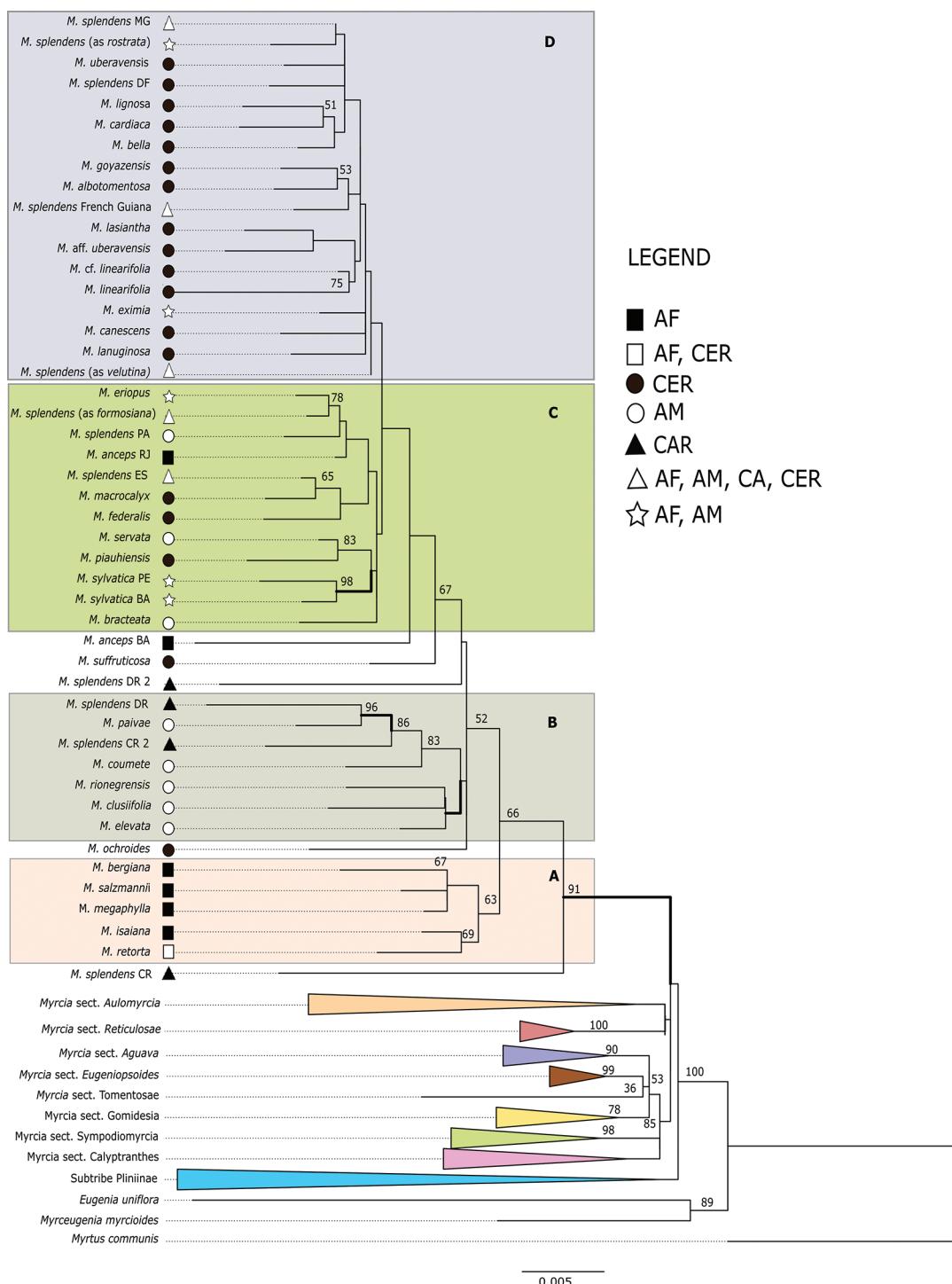


Fig. 4 Phylogenetic tree of *Myrcia* sect. *Myrcia* obtained from maximum likelihood analyses of five DNA regions (internal transcribed spacer, *ndhF*, *psbA-trnH*, *trnL-trnF*, and *trnQ-rps16*). Bootstrap percentages (maximum likelihood BPs) are indicated at nodes, with branches in bold representing BP ≥ 90 . Symbols at tips represent broad range distributions as indicated in the legend. Colored, lettered boxes indicate clades A–D mentioned in “Discussion.” AF = Atlantic Forest; AM = Amazon; CAR = Caribbean; CE = Cerrado; PA = Pará; BA = Bahia; CR = Costa Rica; DF = Distrito Federal; DR = Dominican Republic; ES = Espírito Santo; MG = Minas Gerais.

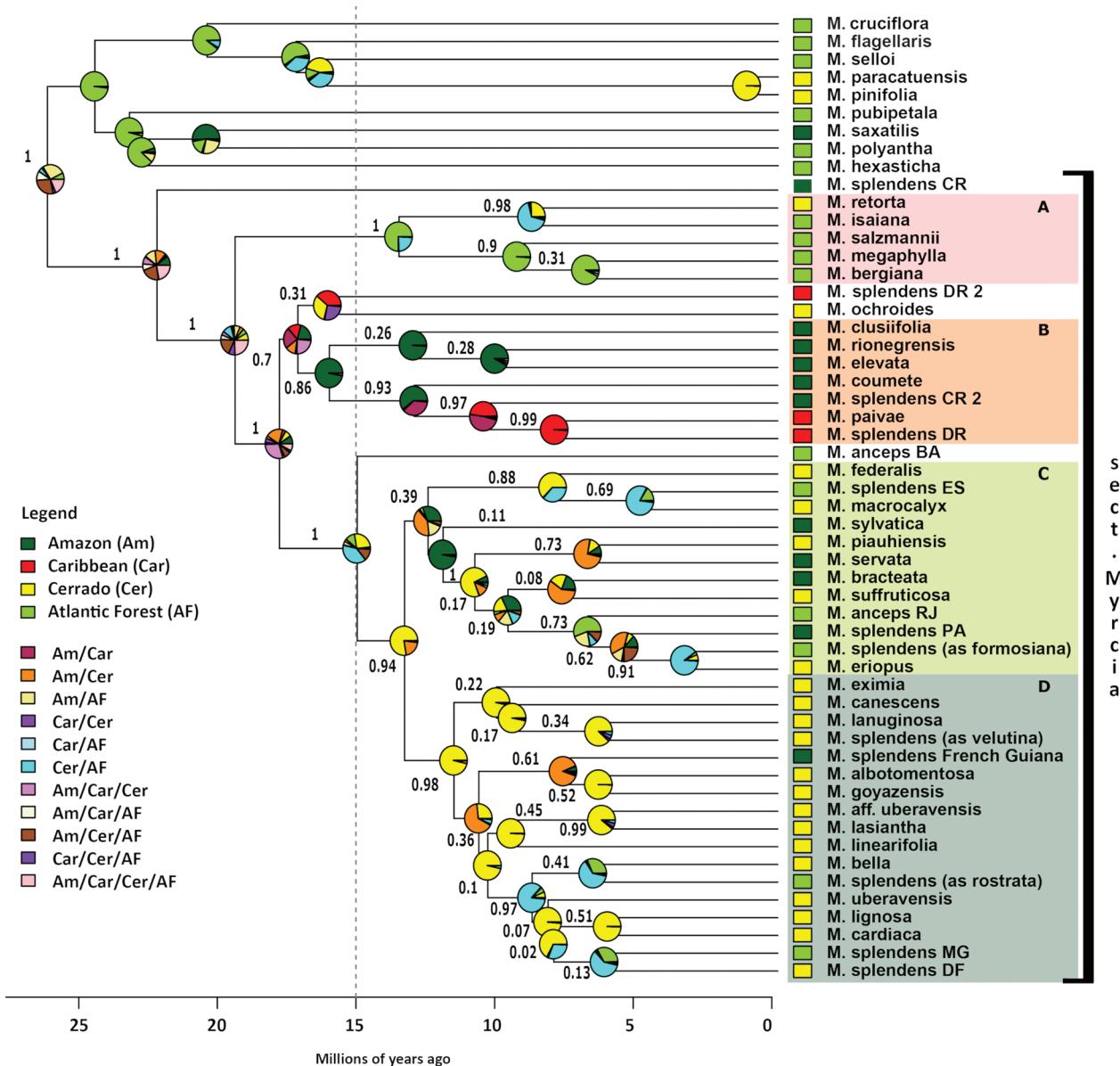


Fig. 5 Biogeographic inference of *Myrcia* sect. *Myrcia* resulting from BioGeoBEARS analysis using a pruned BEAST dated tree. Pie charts reflect ancestral area/range probabilities colored according to each biogeographical area or group of areas as represented in the legend. Clades in colored boxes correspond to those highlighted in figures 3 and 4. Numbers above the branches are posterior probabilities from the BEAST analysis.

in the bud that tears at anthesis, which is quite exceptional in *Myrcia* sect. *Myrcia*. *Myrcia rionegrensis* and *M. clusiifolia* also occur in this clade; leaves of these species could be mistaken for *M. splendens*, but closer examination shows distinct differences in the costate hypanthium of *M. rionegrensis*, and both have globose (rather than cylindrical) fruits. *Myrcia paivae* was suggested by McVaugh (1968) to be of hybrid origin, implicating *M. splendens* and *M. sylvatica* as parents. There is no evidence of this hybridization in the results presented here, with *M. splendens* accessions emerging in multiple clades, often with high statistical support, and *M. sylvatica* occurring in a clade different from *M. paivae*. Compared with *M. paivae*, *M. sylvatica* is distinguished by the smaller leaf size, lower density of glands in the leaves,

and reduction of the inflorescence and flower size. The accession of *M. splendens* (as *M. rufidula*) from the Dominican Republic has an overall morphology reminiscent of *M. sylvatica* and *M. rostrata*. Clade B is sister to the rest of *Myrcia* sect. *Myrcia* (PP: 0.63, BS: 35).

Three independent lineages emerge sequentially sister to the clade of remaining species. One is a *M. splendens* accession from the Dominican Republic (DR2) that resembles a common morphotype of Atlantic Forest and Cerrado riverine forests with elliptic or obovate leaves, strongly impressed lateral veins, and a sulcate hypanthium (PP: 1, BS: 67). This is followed by an accession of *M. suffruticosa*, a distinct subshrub from the Cerrado with short dichasia, frequently reduced to a single central flower, and

Table 2

Summary of Node Ages, Confidence Intervals (CIs), Estimated Ancestral Areas/Ranges, and Ancestral Area/Range Probabilities (AAPs) for *Myrcia* Sect. *Myrcia* and Key Nodes within It

Clade	Node	Age (mya)	95% CI	Most likely ancestral area	AAP
<i>Myrcia</i> sect.					
<i>Myrcia</i>	64	22.39	19.85–24.86	AM/CAR/CER/AF	.32
A	104	13.66	8.71–18.51	AF	.75
B	97	16.17	13.21–19.17	AM	.97
C	85	12.61	12.65–17.87	CER/AM	.4
D	69	11.68	9.24–14.21	CER	.96

Note. AF = Atlantic Forest; AM = Amazon; CAR = Caribbean; CER = Cerrado.

woody, rhizomatous roots, or xylopodia (PP: 1, BS: 31). Sister to the clade of remaining species, divided here into clades C and D, is a sample of *M. anceps* from Bahia (PP: 0.98, BS: 19).

Clade C (figs 3, 4, light green box) comprises species of disparate morphologies from a mix of phytogeographic domains, often occurring in more than one vegetation type. Again, species of this clade vary from *M. splendens* in relatively few characters. *Myrcia anceps* with distinct flattened rachises appears paraphyletic with a specimen from the forests of Rio de Janeiro emerging here and separate from the Bahian collection already mentioned. The specimens of *M. eriopus* and of *M. splendens* (as *formosiana*) in clade C were collected from the same vicinity in Rio de Janeiro. *Myrcia bracteata* and *M. eriopus* share similar long pubescence, differing in the presence of bracts and Amazonian distribution of the former. *Myrcia piauiensis*, *M. federalis*, and *M. macrocalyx* are Cerrado species. The former has relatively large, thickened leaves covered with a short, stiff indumenta and can also occur in the Atlantic Forest, while the latter two have linear leaves and enlarged calyx lobes of varying degrees of pubescence and are endemic to the Cerrado. McVaugh (1969) noted the morphological plasticity and similarity of a group of Amazonian species, including *M. sylvatica*, *M. paivae*, *M. splendens*, and *M. servata*, and suggested that these species were the result of hybridization and introgression. There is no evidence to support this in the results presented here; these species do not emerge in the same clade in analyses based on combined data or in those based on only nuclear or plastid DNA.

Clade D (figs. 3, 4, purple box) includes the majority of Cerrado endemic species sampled. These species share similarity of leaf form, with relatively small leaves. Leaves are narrow with sparse indument in some (e.g., *M. linearifolia*, *M. lignosa*) or oval, rounded, or cordate with dense, pale indumentum in others (e.g., *M. albotomentosa*, *M. bella*, *M. canescens*, *M. cardiaca*, *M. lanuginosa*, *M. lasiantha*, and *M. uberavensis*). Swollen, woody rootstocks, presumably to survive burning events, are also common in this clade (e.g., *M. lignosa*, *M. linearifolia*). These traits can be adaptations to survive in the Cerrado. The tendency for environmental selection of such morphological traits to tolerate drought and heat and the subsequent speciation were noted by Vasconcelos et al. (2019a). Two specimens of *M. splendens* emerge in clade D: one collected in French Guiana, close to Cayenne, and one from

Cerrado riverine forest in Minas Gerais, Brazil. An accession of *M. splendens* from the Amazonian state of Pará switches between clade D in the ML analysis and clade C in the Bayesian analysis, a result of the extremely low levels of variation between sequences of species in *Myrcia* sect. *Myrcia*.

The single ITS sequence of *M. neovelutina* (previously *Myrcia* sect. *Aulomyrcia* sensu Lucas et al. 2016) is noted in this discussion because of its unusual phenotype. *Myrcia neovelutina* has indument covering the whole disc, more usual in *Myrcia* sect. *Gomidesia* (Lucas et al. 2018) and sometimes difficult to distinguish from *Myrcia* sect. *Myrcia*. However, *M. neovelutina* has a deeply tearing four-lobed calyx. McVaugh (1956) diagnosed *M. neovelutina* (as *Marlierea velutina*), emphasizing the tearing calyx and the similarity of the indument to that of *Gomidesia*. The importance of the results presented in the current work are that a group of ca. 20 species from the Amazon basin and Caribbean, previously thought allied to *Myrcia* sect. *Aulomyrcia* (or the now defunct section *Armeriella*) on account of the tearing calyx, can be seen in fact to form part of *Myrcia* sect. *Myrcia*. This group of species has short, pale to rufous hairs covering the hypanthia and axes of the inflorescence (L. Lima dos Santos, J. S. Santos, E. Lucas, and M. F. Sales, unpublished manuscript). These Amazonian species are hard to access and many remain understudied and without good quality tissue for DNA extraction. However, the placement here of both *M. elevata* and *M. neovelutina* within *Myrcia* sect. *Myrcia* strongly suggests that these species form part of *Myrcia* sect. *Myrcia* and that the closed calyx is even more homoplastic in *Myrcia* than previously thought (Vasconcelos et al. 2017a; Giaretta et al. 2019). The type species of section *Armeriella* is *M. inaequiloba* (DC.) McVaugh, a species proved to be part of *Myrcia* sect. *Aulomyrcia* (Staggemeier et al. 2015); therefore, no nomenclatural change is required at the sectional level.

Internal Relationships and M. splendens

Low supports similar to those reported here have been recorded in other phylogenetic analyses of Myrtleae published to date, where half or more nodes receive such low values (e.g., Lucas et al. 2011; Staggemeier et al. 2015; Bunger et al. 2016; Wilson et al. 2016; Santos et al. 2017; Vasconcelos et al. 2017b; Mazine et al. 2018).

Myrcia sect. *Myrcia* includes several species very similar to *M. splendens* in general aspect, delimited on the basis of few but apparently distinct features. Despite the obvious similarities of these species and occasional character overlap, diagnostic characters are generally consistent, and the taxa are kept as distinct entities. *Myrcia anceps*, for example, is distinguished from *M. splendens* in its flattened branchlets, *M. pseudosplendens* is distinguished only by its furrowed fruits, and *M. eriopus* is distinguished by its sinuous, hirsute inflorescence branchlets. However, as often found in cryptic species, variation within the concept of *M. splendens* is also wide, particularly among its specific synonyms. For the purpose of this work, we assume the definition of a cryptic species from Bickford et al. (2007, p. 149) and others—that two or more species are cryptic “if they are, or have been, classified as a single nominal species because they are at least superficially morphologically indistinguishable.” Continuous trait variation is particularly notable regarding the size and shape of the leaves that grade seamlessly from one extreme to another. Characters that diagnose *Myrcia* sect. *Myrcia* species can often be seen to constitute a

gradient; while a single specimen may appear distinct, when large numbers of morphotypes are examined from different collections and biomes, species boundaries dissolve. Faced with this situation, it is tempting to conclude that the various *M. splendens* morphotypes are merely intermediate forms of morphological “extremes” that should not be recognized as different species but rather as a cryptic species. Taxonomy is further aggravated by the co-occurrence of morphotypes not sister in the phylogeny in the same geographical area (e.g., the tips “*M. splendens* as *formosiana*” and “*M. splendens* as *rostrata*”), further emphasizing that geography alone cannot distinguish these forms (Chenuil et al. 2019). This unpredictable and unmanageable pattern also fits the characteristics of cryptic species that are thought to be recently diverged or in the process of divergence, having not yet achieved reproductive isolation (Stebbins 1950). The situation of *M. splendens* here diverges from the classical definition of a cryptic species, as crucially, *M. splendens* is not recognized using morphological or molecular characters. The *M. splendens* complex of morphotypes cannot be shown to be monophyletic but must be managed as a cryptic species in which continuous trait variation is common as a result of combinations of unknown evolutionary pressures. Struck et al. (2018) review limitations in defining cryptic species consistently and outline the influence of parallel and convergent evolution on complexes such as *M. splendens*. Future studies are required to explore these patterns and processes at greater depth, such as at the population level, to finally understand this complex and manage it appropriately.

In summary, despite low support for clades within *Myrcia* sect. *Myrcia*, results show morphological and geographical patterns that provide the first step in understanding and managing this complex group. *Myrcia splendens* has morphotypes different enough to be considered separate species, evolving from the same common ancestor as other lineages that retain the basic *M. splendens* morphotype. The typical *M. splendens* phenotype appears to have been widely distributed throughout the contiguous forests of the Eocene and to have migrated to the Caribbean on at least three separate occasions. Likewise, other relatively widespread species, such as *M. anceps*, defined by its flattened rachis, may not be monophyletic species but merely transient morphotypes, appearing sporadically in different biomes.

Dating and Historical Biogeography

Even though the biogeographic origin of *Myrcia* sect. *Myrcia* is not returned with certainty by the analysis presented here, general biogeographical patterns corroborate findings from previous studies of *Myrcia* (Staggemeier et al. 2015; Wilson et al. 2016; Santos et al. 2017; Vasconcelos et al. 2017b; Amorim et al. 2019; Lima et al. 2021) with a few exceptions. In contrast with studies of other sections of *Myrcia* (Staggemeier et al. 2015; Santos et al. 2017; Amorim et al. 2019; Lima et al. 2021) or *Eugenia* (Bunger et al. 2016; Mazine et al. 2018), there is little indication of geographic structure in the phylogenetic reconstruction of *Myrcia* sect. *Myrcia*.

Santos et al. (2017) note that the genus *Myrcia* may be particularly adapted to montane areas above 800 m. In that case, ancestral *Myrcia* may have shared this habitat and other corresponding adaptations, such as a tendency for an arboreal habit and larger leaves. While this pattern may be seen in some groups (e.g., *Myrcia* sect. *Sympodiomyrcia*) and in *Myrcia* as a whole, it is not reflected in *Myrcia* sect. *Myrcia*, where higher altitude species are rare.

The likely ancestral range of all 10 *Myrcia* sections are the expansive humid forests of the Paleocene and Eocene (ca. 50 mya) that linked today’s Atlantic coastal and Amazon forests (Ortiz-Jaureguizar and Cladera 2006). This is supported by the high number of possible AA combinations (fig. 5). As those forests slowly separated as a result of oceanic transgressions from the Eocene to the mid-Miocene (55–11 mya; Ortiz-Jaureguizar and Cladera 2006), Andean orogeny (23 mya to present; Hoorn et al. 2010), and the resulting formation of the dry diagonal formed by the Caatinga, Cerrado, and Chaco (16–4 mya; Ratter et al. 1997; Simon et al. 2009), new niches became available for colonization by taxa speciating in the Miocene (24–5 mya). The estimated date for the age of *Myrcia* sect. *Myrcia* returned here falls well within the CI of Santos et al. (2016; 36.1–21.1 mya). Speciation events within *Myrcia* sect. *Myrcia* (table 2) are all estimated to have taken place during the Miocene, a geological period during which the global angiosperm flora underwent rapid diversification (e.g., *Eugenia* [Mazine et al. 2018], Myrtaceae [Thornhill et al. 2015], *Astragalus* [Azani et al. 2019], Mediterranean flora [Vargas et al. 2018]).

Previous phylogenetic and biogeographic studies in *Myrcia* (e.g., Staggemeier et al. 2015; Wilson et al. 2016; Santos et al. 2017; Amorim et al. 2019) show an Atlantic Forest origin for the genus *Myrcia*, with a tendency for older lineages to emanate from the Amazon and/or Central America. The explanation regarding the latter pattern may lie in the contiguous forests of the Eocene. The pattern is corroborated here for *Myrcia* sect. *Myrcia*, where the lineage with the oldest crown node, clade B (16.17 mya; 95% CI: 19.17–13.21), has the highest probability of ancestral range in the Amazon forest, and the ancestral range of the lineage arising from the earliest branching nodes, a specimen of *M. splendens* from Central America (Costa Rica), appears to have also been from this area. Younger clades A (13.7 mya; 95% CI: 18.5–8.7), C (12.61 mya; 95% CI: 17.9–12.7), and D (11.7 mya; 95% CI: 14.2–9.2) are most likely to have originated in the Atlantic Forest, Cerrado/Amazon forests, and Cerrado, respectively. The relatively recent date associated with speciation of clade D in the Cerrado supports other recent studies (e.g., Bunger et al. 2016; Santos et al. 2017) that show that the biota of this physiognomy originated around 10 mya (Simon et al. 2009; Simon and Pennington 2012) as a result of colonization from the Atlantic Forest.

The appearance of pollen of angiosperm lineages of Gondwanan origin from Maastrichtian sediments (ca. 76 mya) along the southern Atlantic coast of South America (Morley 2003) suggests that the eastern portion of the continent was the earliest to be forested (Pennington and Dick 2004), spreading northwestward to form the contiguous forests of the Eocene that reached the Amazon. In this case, the tendency for older *Myrcia* lineages to occur in the Amazon appears to be a result of lineage isolation as the contiguous forests of the Eocene were slowly cleaved by subsequent geological events as well as lower rates of extinction in Amazonian lineages, all of which have given rise to the concept that Amazonia is a “museum” for Neotropical trees (Schley et al. 2018). The ridges of the Serra do Mar and Serra da Mantiqueira that run parallel along the Brazilian Atlantic coast support a hugely heterogeneous patchwork of niches and vegetation types that support the extraordinarily high species diversity levels seen in the Atlantic Forest. Myrtaceae species diversity is also high in the adjacent Cerrado biome and its associated riverine gallery forests and

higher-altitude campo rupestre vegetation. The Amazon forest boasts significant numbers of Myrtaceae species, including several endemics; nevertheless, total Myrtaceae species diversity is lower in the Amazon compared with the Atlantic Forest and Cerrado (224, 709, and 254 species, respectively; Flora do Brasil 2020). In this way and as described, *Myrcia* and *Myrcia* sect. *Myrcia* lineages isolated in the Amazon remained more effectively undisturbed, while Atlantic Forest lineages, exposed to constantly changing environments and the opening and closing of niches, were able to diverge and form new species (Stebbins 1974; but see Gentry 1982).

A clear biogeographic implication of this analysis is the successful adaptation of *Myrcia* sect. *Myrcia* clade D to the Cerrado biome. The date of this event, between 14 and 9 mya, corresponds to estimates from Simon et al. (2009) and Ratter et al. (1997), fitting better with the earlier estimates of the latter, and is in agreement with other Myrtaceae studies, such as Mazine et al. (2018) who found a similar age for Cerrado lineages of *Eugenia*. Morphological characteristics of this clade are typical adaptations to dry biomes, such as the presence of woody rootstocks, or xylopodia, for water storage and to assist regeneration after fire; dense, pale pubescence to reflect sunlight and regulate temperature; and leathery leaves to retain water (Simon and Pennington 2012). Species of this clade also often have enlarged flowers or flowers with enlarged sepals (fig. 1F). Future investigations are necessary to explore possible adaptations to Cerrado-specific pollinators, such as large solitary bees or beetles (e.g., Oliveira and Gibbs 2000). Cerrado species with adaptations to dry environments are not exclusive to clade D, however, with *M. retorta* and *M. suffruticosa* emerging in other clades, indicating apparent multiple migrations into drier niches.

Conclusions

Findings of this study must be interpreted with caution because of the relatively small sample, both in terms of molecular regions and species included. Nevertheless, this is the largest sample of *Myrcia* sect. *Myrcia* examined to date, and the results presented here will be of importance to those seeking to manage Neotropical biomes. In addressing the aims of the study, demonstrating the monophyly of *Myrcia* sect. *Myrcia*, and examining the characters of its species and their historical biogeography, some conclusions can be drawn.

Species delimitation in *Myrcia* sect. *Myrcia* remains very difficult, and this is particularly the case for *M. splendens*. It is difficult to underestimate the extreme discontinuity of morphological characters in *Myrcia* sect. *Myrcia*. A single morphotype is relatively distinct; however, as numbers of collections from different biomes are observed, the morphological continuum becomes clear. This complex morphological pattern is also observed in other *Myrcia* species groups (e.g., *Myrcia* sect. *Tomentosae*; Lima et al. 2015). For the foreseeable future, authors will likely continue to use the current names associated with characters known to be unreliable plastic, such as flattened branchlets, presence/absence of bracteoles, sinuosity of the branches of the inflorescence, degree of sulcation of the exterior of the hypanthium, degree of pubescence on any part of the plant, leaf size, and lamina texture (degree of raising of lamina between veins). There is an acute need for studies at a greater scale—for example, phylogenomic studies, population studies to observe gene flow between morphotypes, or examination of genome sizes to observe trends in ploidy. Very few characters have diagnostic use in placing species into the lettered clades identified in this work. Subglobose rather than cylindrical fruits and relatively few large flowers are most likely to be found in species of clade A. Woody rootstocks, leaves drying bright green (suggesting tolerance to heavy metals in soils; Chenery 1948), and other characters associated with adaptation to xerophytic environments (Simon and Pennington 2012) are more likely to be found in clade D. In addition to laboratory-based studies, pushing the frontier of understanding in *Myrcia* sect. *Myrcia* requires more field studies. In particular, sampling is necessary in the western Amazon of Bolivia, Colombia, Peru, and Venezuela, where species discussed here under *Myrcia* sect. *Armeriella* sensu McVaugh (1968) are found. Also, gaps in the current knowledge of *Myrcia* sect. *Myrcia* exist in the eastern Brazilian Amazon. Along with collection of specimens, field observation of physiology, phenology, and pollination studies are also much needed.

Acknowledgments

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Appendix A1

Vouchers for DNA Samples Used in the Biogeographic and Phylogenetic Analysis, with Kew DNA Bank Numbers

Algrizea macrochlamys (DC.) Proen  a & NicLugh., Giulietti, A.M. 1648 (16833), K; *Calyptranthes concinna* DC., Lucas, E. 171 (41398), K; *Calyptranthes multiflora* Poepp. Ex O. Berg, Ara  o, A.C. 1885 (41410), K; *Calyptranthes thomasiana* O.Berg, Pollard, B.J. 1195 (19048), K; *Eugenia uniflora* L., Lucas, E. 207 (9077), K; *Marlierea aff. subacuminata* Kiaersk., Staggemeier, V.G. 742 (43201), K, UB; *Marlierea antonia* (O.Berg) D.Legrand, Santos, M.F. 840 (43245), SPF, K; *Marlierea caudata* McVaugh, Zappi, D. 1506 (42097), K; *Marlierea dimorpha* O.Berg, Folli, D. 6649 (43447), K; *Marlierea eugeniopsoides* (D.Legrand & Kausel) D.Legrand, Lucas, E. 61 (16813), K; *Marlierea excoriata* Mart., Matsumoto, K. 825 (31629), K, UEC; *Myrcia neoglabra* E.Lucas & C.E.Wilson, Staggemeier, V.G. 935 (43174), UB, K, R, RB, IAN, EAFM, UFG, HUFSJ; *Marlierea glazioviana* Kiaersk., Matsumoto, K. 799 (31631), K, UEC; *Marlierea neuwiediana* (O.Berg) Nied., Staggemeier, V.G. 793 (43206), UB, K, UFG, RB; *Marlierea regeliania* O.Berg, Matsumoto, K. 814 (31628), K, UEC; *Marlierea sucrei* G.M.Barroso & Peixoto, Matsumoto, K. 824 (31625), K, UEC; *Marlierea sucrei* G.M.Barroso & Peixoto, Staggemeier, V.G. 916 (43170), UB, K; *Marlierea tomentosa* Cambess., Matsumoto, K. 798 (31627), K, UEC; *Marlierea umbraticola* (Kunth) O.Berg, Souza, M.A.D. sn (43175), INPA; *Myrciogenia myrcioides* (Cambess.) O.Berg, Lucas, E. 82

(16821), ESA, HUEM, K; *Myrcia amazonica* DC., Neto, L.A. 3007 (43456), INPA 213000; *Myrcia amazonica* DC., Prévost, M.F. 4751 (19063), K; *Myrcia* aff. *plusiantha* Kiaersk., Staggemeier, V.G. 737 (43199), K, UB, UFG, RB, IAN; *Myrcia* aff. *truncata* Sobral, Lucas, E. 1189 (43440), K; *Myrcia* aff. *uberavensis* O. Berg, Vasconcelos, T. (46274), K; *Myrcia albotomentosa* DC., Lima, D.F. 504 (46122), K; *Myrcia amazonica* DC., Lucas, E. 59 (16195), K; *Myrcia amazonica* DC. [as detergens], Lucas, E. 189 (19060), K; *Myrcia anceps* (Spreng.) O. Berg, Lima, D.F. 438 (46267), K; *Myrcia anceps* (Spreng.) O. Berg (19681), K; *Myrcia bella* Cambess., Lima, D.F. 379 (46123), K; *Myrcia bergiana* O. Berg, Lima, D.F. 409 (46271), K; *Myrcia bracteata* (Rich.), Prévost 4712 (16830), K; *Myrcia canescens* O. Berg, Faria, J.E.Q. 1692 (46115), UB; *Myrcia cardiaca* O. Berg, Vasconcelos, T.N. 274 (46129), K; *Myrcia* cf. *linearifolia* Cambess., Lima, D.F. 506B K; *Myrcia clavija* Sobral, Lucas, E. 244 (19682), K; *Myrcia clusiantha*, Carvalho, F.A. 1594 (43273), INPA; *Myrcia clusiifolia* (Kunth) DC., Goldenberg, R. 1909 (46279), RB; *Myrcia coumetae* (Aubl.) DC., Lucas, E. 107 (16209), K; *Myrcia cuprea* (O. Berg) Kiaersk., Staggemeier, V.G. 862 (43198), K, UB; *Myrcia decorticans* DC., Staggemeier, V.G. 799 (43165), UB, K; *Myrcia elevata* M.F. Santos, M. F. Santos 763 (43254), K; *Myrcia eriopus* DC., Lucas, E. 258 (19685), K; *Myrcia eumecephylla* (O. Berg) Nied., Matsumoto, K. 803 (31626); *Myrcia eximia* DC., Vasconcelos, T.N. 407 (46262), K; *Myrcia federalis* Bezerra & Faria, J. E. Q. Faria 2445 (46114), HUEFS, UB; *Myrcia flagellaris* (D. Legrand) Mattos, Lucas, E. 83 (16820), ESA, HUEM, K; *Myrcia follii* G.M. Barroso & Peixoto, Staggemeier, V.G. 907 (43166), UB, K, CVRD, UFG, RB; *Myrcia glaziovii* Mattos & D. Legrand, Vasconcelos, T.N. 501 (46269), K; *Myrcia goyazensis* Cambess., Lima, D. F. 500 (46281), K; *Myrcia grandis* McVaugh, Staggemeier, V.G. 850 (43167), UB, K, UFG, RB, INPA; *Myrcia hexasticha* Kiaersk., Lucas, E. 194 (19061), K; *Myrcia hirtiflora* DC., Lucas, E. 1181 (43436); *Myrcia inaequiloba* (DC.) Lemée, Lucas, E. 105 (16208), K; *Myrcia isaiana* G.M. Barroso & Peixoto, Lucas, E. 60 (16196), K; *Myrcia lanuginosa* O. Berg, Lima, D. F. 494 (46124), K; *Myrcia lasiantha* DC., Lima, D. F. 525 (46125), K; *Myrcia laxiflora* Cambess., Meirelles, J. 307 (43209), CEPEC, RB; *Myrcia lignosa* Villaruel, J. R. I. Wood 27034, K; *Myrcia linearifolia* Cambess., J. R. I. Wood s.n., K; *Myrcia macrocalyx* Faria & Soares-Silva, J. Bringel 755 (46116), K; *Myrcia magnifolia* (O. Berg) Kiaersk., Lucas, E. 1182 (43439), K; *Myrcia megaphylla* M. F. Santos & Sobral, Santos, M.F. 721 (43267), SPF, K; *Myrcia minutiflora* Sagot, Sasaki, D. 2394 (43203), K; *Myrcia multiflora* (Lam.) DC., Staggemeier, V.G. 422 (43161), UB, IAN, HUF SJ; *Myrcia multiflora* (Lam.) DC., Staggemeier, V.G. 863 (43168), UB, K; *Myrcia multiflora* (Lam.) DC., Staggemeier, V.G. 867 (43169), UB; *Myrcia ochrooides* O. Berg, J. E. Q. Faria 2147 (46117), UB; *Myrcia paivae* O. Berg, Vasconcelos, T.N. 516 (46120), K; *Myrcia paracatuensis* Kiaersk., Mello-Silva, R. 1713 (12209), HUFU, K, SPF; *Myrcia paulii-jonesii* Aguillar, D. Santam. & A. Estrada, Vasconcelos, T.N. 520 (46119), K; *Myrcia piauhiensis* O. Berg, J. E. Q. Faria 1452 (46261), UB; *Myrcia pimifolia* Cambess., R. M. S. 1713, K; *Myrcia polyantha* DC., Staggemeier, V.G. 797 (43204), UB, K; *Myrcia pseudomarlierea* Sobral, Souza, M.C. 1139 (43214), RB; *Myrcia pubipetala* Miq., Lucas, E. 86 (16203), ESA, K; *Myrcia racemosa* (O. Berg) Kiaersk., Lucas, E. 63 (16198), K; *Myrcia racemosa* (O. Berg) Kiaersk., Staggemeier, V.G. 751 (43162), UB; *Myrcia retorta* Cambess., K; *Myrcia riococensis* G.M. Barroso & Peixoto, Staggemeier, V.G. 917 (43171), UB, K, UFG, RB, CVRD; *Myrcia rionegrensis* L.L. Santos & T.V. Nogales, Vasconcelos, T.N. 337, K, UFP; *Myrcia salzmannii* O. Berg, Vasconcelos, T.N. 459 (46275), K; *Myrcia saxatilis* (Amshoff) McVaugh, Lucas, E. 98 (16207), K; *Myrcia selloi* (Spreng.) N. Silveira, Lucas, E. 110 (19054), K; *Myrcia servata* McVaugh, Santos, M.F. 700 (43269), K; *Myrcia* sp. 1, Lima, D. F. 415 (46268), K.; *Myrcia* sp. 10, Souza, M.C. 1126 (43217), RB; *Myrcia* sp. 11, Staggemeier, V.G. 740 (43219), UB; *Myrcia* sp. 12, Staggemeier, V.G. 792 (43164), UB, K, UFG; *Myrcia* sp. 13, Lucas, E. 1169 (43438); *Myrcia* sp. 14, Staggemeier, V.G. 764 (43163), UB, K, UFG, RB, SPF, IAN, H RCB; *Myrcia* sp. 15, Staggemeier, V.G. 927 (43173), UB, K, UFG, IAN; *Myrcia* sp. 16, Lucas, E. 1192 (43442); *Myrcia* sp. 17, Souza, M.C. 1131 (43216), RB; *Myrcia trimera* E. Lucas & Sobral, Lucas, E. 1190 (43441), HURB, K, RB; *Myrcia* sp. 19, Staggemeier, V.G. 901 (43205), UB, K, UFG; *Myrcia* sp. 2, Vasconcelos, T.N. 519 (46273), K; *Myrcia* sp. 3, Vasconcelos, T.N. 527 (46278), K; *Myrcia* sp. 4, Prévost, M.F. 4749 (19064), K; *Myrcia* sp. 5, Caddah, M.K. 555 (43260), SPF, INPA; *Myrcia* sp. 6, Staggemeier, V.G. 845 (43202), UB, K, UFG, IAN; *Myrcia* sp. 7, Staggemeier, V.G. 762 (43197), K, UB, UFG; *Myrcia* sp. 8, Staggemeier, V.G. 896 (43218), UB, K, UFG, IAN; *Myrcia* sp. 9, Lucas, E. 1159 (43443); *Myrcia splendens* (Sw.) DC, Prevost, 4716 (16831), K; *Myrcia splendens* (Sw.) DC., Lima, D. F. 469 (46270), K; *Myrcia splendens* (Sw.) DC., Lucas, 165 (19059), K; *Myrcia splendens* (Sw.) DC., Lucas, E. 73 (16202), ESA, HUEM, K; *Myrcia splendens* (Sw.) DC., R. Goldenberg 1914 (46280), RB; *Myrcia splendens* (Sw.) DC., Vasconcelos, T.N. 250 (46263), K; *Myrcia splendens* (Sw.) DC., Vasconcelos, T.N. 528 (46276), K; *Myrcia splendens* (Sw.) DC., Vasconcelos, T.N. 586 (46264), K; *Myrcia splendens* (Sw.) DC., Vasconcelos, T.N. 591 (46265), K; *Myrcia splendens* (Sw.) DC., Vasconcelos, T.N. 757 (46266), K; *Myrcia splendens* (Sw.) DC., Wood, 15435 (16834), K; *Myrcia suffruticosa* O. Berg, Mello-Silva 1690 (12208), K; *Myrcia sylvatica* (G. Mey) DC., L. Lima 844 (46128), PEUFR; *Myrcia sylvatica* (G. Mey) DC., Vasconcelos, T.N. 437 (46282), K; *Myrcia tetraphylla* Sobral, Staggemeier, V.G. 926 (43172), UB, K, UFG, HUF SJ, RB, R, CVRD; *Myrcia sessilissima* M.F. Santos, Santos, M.F. 641 (43266), K, SPF; *Myrcia uberavensis* O. Berg, Lima, D. F. 473 (46121), K; *Myrcia blanchetiana* (O. Berg) Mattos, Santos, M.F. 819 (43270), K, SPF; *Myrcia trimera* E. Lucas & Sobral, Lucas, E. 1156 (43437), ESA, HURB; *Myrtus communis* L., Lucas, E. 211 (10347), K; *Plinia cordifolia* (D. Legrand) Sobral, Mazine, F. 957 (20679), ESA, K; *Siphoneugena densiflora* O. Berg, Mazine, F. 1050 (20681), ALCB, HUEM, ESA, K, MBM, SPF.

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