

And the twain shall meet at the end: a phylogeny of *Myrcianthes* (Myrtaceae, Myrteae) with phytogeographic and morphological insights

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Abstract

Background and aims – *Myrcianthes* is a New World genus of Myrtaceae with 36 species, diverse in the Andes, and often dominant in montane forests. It is found from the Pacific to the Atlantic, from sea level to 3729 m, and its total latitudinal range is almost 62°. Its old age, combined with a wide ecological and geographic range, and the many narrow-endemic species, make it of phytogeographic and evolutionary interest.

Material and methods – Altitudinal, geographic, and wood anatomy data of the genus were compiled from literature and online herbaria and curated to eliminate errors and produce a reliable dataset. ML and Bayesian phylogenetic trees based on ITS, ETS, *matK*, and *psbA-trnH* of 11 *Myrcianthes* species, in a matrix of 123 species, were constructed. The Bayesian tree was calibrated with three macrofossils and three secondary calibration points and used to infer biogeographic history and to estimate ancestral ranges using BioGeoBEARS.

Key results – *Myrcianthes* has the widest combined altitudinal/latitudinal range in Myrtaceae. Narrow-endemic species are concentrated either in the high-latitude lowlands or the low-latitude highlands. *Myrcianthes* diverged from *Eugenia* in the early Oligocene but did not diversify before the mid-Miocene (later than *Eugenia*). *Myrcianthes* diversified from the south into South America, Central America, and the Caribbean. Its ancestral range emerged as the Chacoan/Paraná dominions, consistent with the extinct temperate/subtropical austral forest. After splitting from *M. coquimbensis*, endemic to Chile, the main clade divided into a lowland clade (most diverse in eastern South America) and a highland clade (most diverse in the Andes). The clades are sympatric near the inferred root of the tree and probably meet again in Colombia and Venezuela. *Myrcianthes* wood anatomy appears to differ from that of *Eugenia* by the occurrence of helical thickenings in the vessels and absence of prismatic crystals in the axial parenchyma, but sampling is still incomplete.

Keywords

Andes, ancestral range, fossil calibration, Gondwana, Neotropics, phylogenetic tree, wood anatomy

INTRODUCTION

Myrcianthes O.Berg is a New World genus of 36 species that is noteworthy for its exceptionally wide altitudinal and

latitudinal range (Landrum and Grifo 1988; Proença et al. 2011; Parra-O. and Bohórquez-Osorio 2016; Kawasaki et al. 2019). It is one of the dominant genera in the montane forests of the northern Andes (Valencia and Jorgensen

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1992; Worthy et al. 2019), where tree species richness has been shown to decrease with increasing altitude (Worthy et al. 2019). *Myrcianthes* is distributed from southern Florida and Mexico to Argentina, Bolivia, Brazil, Chile, and Uruguay, with its main centre of distribution in the Andes (Grifo 1992; Parra-O. and Bohórquez-Osorio 2016). Previous molecular phylogenies place *Myrcianthes* as sister to the megadiverse *Eugenia* L. (Lucas et al. 2007; Vasconcelos et al. 2017; Mazine et al. 2018; Giaretta et al. 2022), and together they compose the subtribe Eugeniinae, the oldest lineage within tribe Myrteae (NMWG 2024). *Myrcianthes* is characterized morphologically by a woody habit, frequently rather coriaceous or thickened leaves, flowers in 1–31-flowered dichotomous inflorescences, tetramerous or more rarely pentamerous white flowers with many stamens (Fig. 1A, C, F), and 2–3-locular ovaries with 5–30 ovules per locule (Landrum and Grifo 1988; Grifo 1992). The fruits are globose to wide-ellipsoid (Fig. 1D, E), 1(–6)-seeded, and the embryo has two free, well-developed, rather fleshy cotyledons; the hypocotyl in the mature seed is composed of a small plumule and radicle that together are up to half the length of the cotyledons (adapted from Grifo 1992 and Proença et al. 2023). It is probably bee pollinated (Nadra et al. 2018), whilst fruits are dispersed by birds or more rarely monkeys or rodents (Voss and Sander 1980; Chitolina and Sander 1981;

Brown et al. 1984; Pizo 2002; Parra-O. and Bohórquez-Osorio 2016; Parra-O. and Díaz-Rueda 2024).

The chloroplast genome of *Myrcianthes pungens* (O.Berg) D.Legrand is available (Rodrigues et al. 2020), but there is no phylogeny focusing on the genus, although there is a recent phylogeny of tribe Myrteae, which includes 10 *Myrcianthes* species (NMWG 2024). In our study, we present a dated phylogeny of 11 *Myrcianthes* species calibrated with three macrofossils and three secondary calibration points in Myrtales. We also produced a robust and reliable occurrence dataset to study the biogeography of the genus and infer ancestral ranges.

Myrceugenia O.Berg and *Myrcianthes* are the only myrtaceous genera to occur in Chile, in the Yungas forests that run along the eastern foot of the Andes and in the Atlantic Forest (Proença et al. 2024). The Chilean myrtaceous flora is composed of nine genera, all endemic to Chile except for *Myrceugenia* and *Myrcianthes* (Landrum 1988). Most other Neotropical myrtaceous genera occur in the Atlantic Forest, or in the Atlantic Forest and Yungas, with one exception, genus *Amomyrtella* Kausel that is endemic to the Yungas forests. The rest of the Americas, i.e. northern South America, Central America, the Caribbean, and Florida, have been colonized only by myrtaceous genera that also occur in the Brazilian Atlantic Forest (Lucas et al. 2019). Therefore,

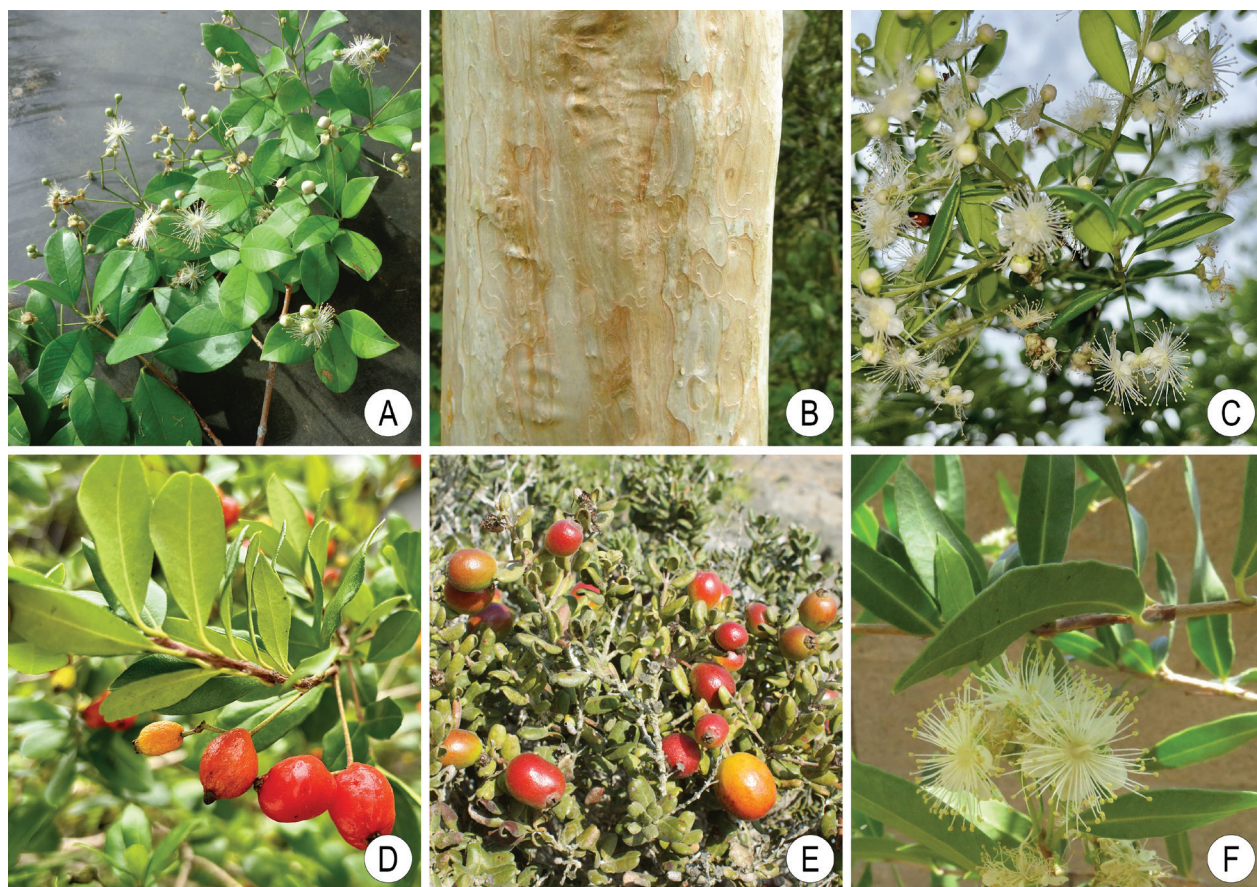


Figure 1. *Myrcianthes* species sampled in the study. A, B. *M. cruciata*. C, D. *M. fragrans*. E. *M. coquimbensis*. F. *M. cisplatensis*. Photos by Marta Farias (A), Fabiano Dantas (B), Paulo Gaem (C), Les Landrum (D, E, F).

we asked the question if *Myrcianthes* would show a similar phylogenetic structure to that of *Myrceugenia* that has strong geographic structuring into western and eastern clades, with the Chilean western clades basal to the Atlantic Forest clade (Murillo-A. et al. 2016).

MATERIAL AND METHODS

Geographic and altitudinal distribution

The material cited in the *Myrcianthes* monograph of Grifo (1992) was the core of the database (42% of the records). Google Earth was used to georeference all collections that had detailed geographic data. This was complemented with specimens with original geographic coordinates downloaded from SpeciesLink (<https://specieslink.net/>). Herbarium records that recorded country centroid coordinates were eliminated or, if enough geographic information was provided, refined to exact localities. The database was also complemented with data from Tropicos (<http://www.tropicos.org>) for Central America. All records were exported into BRAHMS v.7.9.14 (<https://herbaria.plants.ox.ac.uk/bol/brahms>), which was used for data curation. Duplicate records, those unidentified to species level without images, or those whose identification were considered unreliable, were excluded. The BRAHMS tool “look for similar/identical records” (using different combinations of collector names, collection numbers, and day, month and year of collection) was used to eliminate or combine duplicates. Reliable identifications were those made by specialist taxonomists or by generalist taxonomists with excellent knowledge of local floras. Altitudes were obtained from herbarium records; altitudes given in feet were converted to meters. Where an altitudinal range was given on the specimen, the lower limit was used to calculate mean altitude per species, therefore mean altitudes probably underestimate the true values (Suppl. material 1, Table S1). The final dataset is available from the corresponding author. Preliminary maps were made in BRAHMS v.7.9.14, in Google Earth and visually checked against geographic distributions reported by Grifo (1992) to detect possible incongruities. Final maps for publication were generated in QGIS v.3.40.3-Brisbane (QGIS 2024) and R v.4.1.1, using packages sf v.1.0–20 (Pebesma 2018), raster v.3.6–32 (Hijmans 2025), sp v.1.4–5 (Bivand et al. 2013), and phytools v.2.4–4 (Revell 2012).

To compare latitudinal and altitudinal distributions of *Myrcianthes* with other New World genera of Myrtaceae, we first checked distributions on Plants of the World Online (POWO 2024, <https://powo.science.kew.org/>) (that uses TDWG regions) for all New World Myrtaceae genera. This revealed that only *Eugenia*, *Myrcia* DC., and *Psidium* L. had similar wide distributions. These genera are all absent from Chile where *Myrcianthes* occurs but roughly match it in extending from Mexico and Florida in

the north to Uruguay and Argentina in the south. The next step was to establish extreme latitudinal and altitudinal records in country and regional floras (i.e. for Argentina: Legrand 1962; Rotman 1995, 2005; for Uruguay: Legrand 1943, 1968; for the USA, Florida: Landrum 2022). Online records, particularly SpeciesLink, the NY and MO herbaria, and the map searches and altitudinal searches in CoTRAM – Cooperative Taxonomic Resource for American Myrtaceae (<https://cotram.org/>) were also consulted. For *Psidium*, the first author’s personal database of ca 6,000 records was consulted (Proença et al. 2022). We applied the term narrow-endemic to species with a known distributional range < 1° latitude × longitude, a common minimum geographic unit adopted in biogeographic studies (Vieira et al. 2008; Diniz-Filho et al. 2009).

Phylogeny, dating, and ancestral range

We sampled 123 species, of which 11 were *Myrcianthes* species (ca one third of the species in the genus; Suppl. material 2, Table S2). To encompass geographic variability, we included two to three vouchers of the following species: *M. cisplatensis* (Cambess.) O.Berg, *M. ferreyrae* (McVaugh) McVaugh, *M. fragrans* (Sw.) McVaugh, and *M. pungens* (O.Berg) D.Legrand (Suppl. material 2, Table S2). To encompass phylogenetic variability within Myrtaceae, representatives from all sections of *Eugenia*, sister genus of *Myrcianthes* and the only other genus of subtribe Eugeniinae (Mazine et al. 2018), were included (19 species), as well as representatives of nine other Myrteae subtribes (44 species in 34 genera). To encompass phylogenetic variability outside of tribe Myrteae and attain better sampling for dating the lineages, we included representatives of other Myrtaceae tribes (26 species in 20 genera) and of seven other Myrtelean families (23 species in 15 genera).

A total of 403 sequences of the internal and external transcribed spacer (ITS and ETS, respectively) of the ribosomal nuclear region and two plastid markers (*matK* and *psbA-trnH*) were already available. Ten new sequences were generated for this study; the remainder were downloaded from GenBank (Suppl. material 2, Table S2). All molecular data were combined (3650 bp) into one matrix with two partitions, the first partition representing the nuclear sequences (1768 bp), while the second representing the plastid sequences (1882 bp). Mantel correlations (in which a value of 1 would indicate identical trees with identical bootstrap values; Legendre and Legendre 1998) were recently calculated for these four markers compared to a nine-marker phylogenetic tree (all trees 0% missing data) for 53 species of tribe Myrteae (NMWG 2024). This 53-species tree was totally resolved, and all bootstrap values (henceforward BS; Soltis and Soltis 2003) were > 75. The correlation values for these four markers were 0.97, 0.97, 0.96, and 0.91, respectively, suggesting that they are highly informative (at least under the condition of 0% missing data).

To construct the phylogenetic tree, we applied Maximum Likelihood (ML) analysis to a matrix with 11 *Myrcianthes* species (ca 1/3 of the genus); the missing data was 25% for *Myrcianthes*. ML analysis was performed with RAXML v.8.2.12 (Stamatakis 2014) using the rapid bootstrap algorithm with 1000 replicates, combined with a search of the best-scoring ML tree under default parameters via the CIPRES platform (Miller et al. 2010). Concatenation of sequences from different accessions was done when the morphology and geographic locality among vouchers showed a reasonable match; geographically distant samples were not concatenated.

The matrix was used to explore temporal divergence among species. To calibrate the tree, we used the Bayesian inference approach implemented in BEAST2 (Drummond et al. 2012) via the CIPRES platform (Miller et al. 2010) using two partitions and the best nucleotide substitution model estimated separately for each partition. The GTR + G + I model was found to be best for both partitions, according to the Akaike information criterion (AICc) calculated in jModelTest v.2.1.4 (Darriba et al. 2012). An uncorrelated relaxed molecular clock, assuming a lognormal distribution of rates and a Yule model, was applied.

Four runs of 200,000,000 generations were performed, sampling one tree every 1000th generation. Parameter convergence was confirmed by examining their posterior distributions in TRACER v.1.7.2 (Rambaut et al. 2018). The MCMC sampling was considered sufficient when effective sampling size (ESS) of each parameter was > 184. A maximum clade credibility tree with median branch lengths and a 95% highest posterior density interval on nodes was built using TreeAnnotator v.2.6.0 (Drummond et al. 2012), based on the remaining set of trees after burn-in (for each run a burn-in of 25% was applied).

Fossil selection for calibration

The presence of stenopalynous taxa, with certain pollen types widely scattered across the family, makes identification of suitable microfossils for tree time-calibration extremely problematic in Myrtaceae (Barth and Barbosa 1972; Patel et al. 1984; Thornhill and Macphail 2012). Vasconcelos et al. (2017) found that macrofossils (fruits, leaves, and wood) produced significantly older dates than fossil pollen confidently attributed to Myrteae (see Thornhill and Macphail 2012). Myrteae phylogenetic trees dated using both approaches had crown dates for the nine New World clades that were, on average, 14 my older when macrofossils rather than microfossils were used for calibration (Vasconcelos et al. 2017). In dating their phylogeny of *Myrceugenia*, Murillo-A. et al. (2016) concentrated on macrofossils.

Therefore, we calibrated our tree with three macrofossils within Myrteae and three secondary calibration points in other Myrtales families (Gonçalves et al. 2020) (Suppl. material 3, Table S3). Gonçalves et al. (2020) focused on Vochysiaceae, sister family of Myrtaceae, and calibrated their phylogenetic tree based on a combination of fossil

pollen in Myrtaceae (*Myrtaceidites lisamae* Hammen ex Boltenh.) and macrofossils in other Myrtales families (see also Gonçalves et al. 2020 and Suppl. material 3, Tables S4, S5). Three macrofossils fulfilled the criteria listed by Parham et al. (2012) as desirable for correct calibration.

The first fossil wood selected for calibration was *Myrceugenelloxylon antarcticum* I. Poole, R.J. Hunt & Cantrill (Poole et al. 2001, 2003) as calibration for the *Luma*+*Temu* crown node. This fossil from Seymour Island, in the James Ross Basin, Antarctica was considered by the describing authors to be closest to extant *Luma*. Seymour Island had its stratigraphy reviewed (Crame et al. 2004) and the Cretaceous/Tertiary boundary was narrowly established at the 1458 m level; the James Ross Basin is richly fossiliferous and the Maastrichtian succession there is possibly the thickest in the Southern hemisphere (Francis et al. 2006). The fossil taxon has been recorded from the Maastrichtian, the Paleocene, and the middle Eocene (Poole and Cantrill 2006). The calibration of the *Luma* stem node by *M. antarcticum* is strongly supported by presence of scalariform perforation plates (a basal feature) with numerous bars, a lack of helical thickenings in the vessels, vasicentric tracheids and crystals, together with a suite of secondary characters (Suppl. material 3, Table S4) in which it is contrasted to the two extant species of *Luma*. Several other fossils considered to be similar and possibly related to *M. antarcticum* (Oskolski et al. 2013) that range from the Maastrichtian to the Oligocene (Poole et al. 2001, 2003; Poole and Cantrill 2006; Pujana 2009) have also been included in the table as they show a reduction in the number of bars on the scalariform perforation plates and an increase in vessel density compared to present-day values in *Luma*.

The second fossil used in the calibration was the wood of *Myrtineoxylon maomingense* Oskolski, X.X. Feng & J.H. Jin (Oskolski et al. 2013, spelled as “*maomingensis*”) for the crown node of subtribes Decasperminae+Myrtinae. This fossil from the Maoming Bay, China, was considered by the describing authors to be closest to extant *Octamyrtus* Diels (subtribe Decasperminae; Lucas et al. 2019) and to *Calycolpus* O.Berg (subtribe Myrtinae; Lucas et al. 2019). The Maoming Bay has a well-developed Paleogene stratum but the Youganwo Formation that yielded the fossil wood is considered Late Eocene based on fossil vertebrates, palynological zonation (Jin 2008), and a preliminary magnetostratigraphic study (Junda et al. 1994). *Myrtineoxylon maomingense* is characterized by solitary vessels (> 80%), simple perforation plates, alternate intervessel pits, vested, vessel-ray pits bordered, vasicentric tracheids, fibres with distinct bordered pits, diffuse and diffuse-in-aggregate axial parenchyma, forming short tangential lines, in 3–8 cell strands, and ray 1–3-seriate, heterocellular rays, the absence of crystals in axial parenchyma or in ray cells, and lack of helical thickenings in the vessels (Oskolski et al. 2013). The fossil is also compared to a somewhat similar Maastrichtian fossil, *Fulleroxylon armendarisense* Estrada-Ruiz, Upchurch, Wheeler & Mack from New Mexico (Estrada-

Ruiz et al. 2012), and to extant *Octamyrtus pleiopetala* Diels (Ingle and Dadswell 1953) and *Calycolpus glaber* O.Berg (Détienne and Jacquet 1983) (Suppl. material 3, Table S5).

The third calibration point was based on macrofossils of leaves, buds, flowers, and capsules of *Eucalyptus frenguelli* from Chubut Province, Argentina (Gandolfo et al. 2011), one of the most biodiverse Cenozoic fossil deposits in the world. It could be attributed to the genus *Eucalyptus* L'Hér. with a high degree of confidence due to the leaf shape, venation, and presence of oil glands, as well as the operculate flower buds, the infructescence structure, and the valvate capsular fruits.

Re-interpretation of the Myrtaceae wood anatomy (Schmid and Baas 1984; Rancusi et al. 1987; Dias-Leme et al. 1995; Sonsin et al. 2014) in the light of the current knowledge of Myrteae phylogeny (Vasconcelos et al. 2017; Amorim et al. 2019) has shown strong phylogenetic conservatism. This is particularly obvious for the distribution of scalariform perforation plates and helical thickenings in the vessels due to a very wide survey of these two characters across Myrtaceae done by Schmid and Baas (1984), and for crystalliferous elements in the axial parenchyma (Santos et al. 2015).

Ancestral range reconstruction

The biogeographic history of *Myrcianthes* was inferred from a dated phylogeny using BioGeoBEARS v.1.1.2 (Matzke 2013, 2014) to reconstruct ancestral ranges within the genus. We fitted all six models available in the package (DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, BAYAREALIKE+J), and compared their fit with the Akaike Information Criterion corrected for sample size (AICc). These models consider scenarios involving speciation, extinction, dispersal, and founder-event speciation (i.e. jump dispersal) to explain the biogeography of a group (Matzke 2014). To code the biogeographic areas, we gathered the distribution points of all species (718 occurrence points, see Suppl. material 5, Figs S4–S6) and then plotted these points over the map of the biogeographic provinces for the Neotropical region produced by Morrone et al. (2022) using QGIS v.3.40 (QGIS 2024). We used the Morrone et al. (2022) delimitations of the five dominions or transition zones: Andean region, Chacoan dominion, Paraná dominion, South Brazilian dominion, and South American transition zone. We also modified the original map to minimise the number of areas and to adjust area limits to the diversity of *Myrcianthes*. Therefore, for *M. fragrans*, a species with a wide range but the only species distributed in northwestern South America and Central America, we grouped five Morrone et al. (2022) biogeographic regions (Antillean subregion, Brazilian subregion Mesoamerican dominion, Pacific dominion, Boreal Brazilian dominion, and Mexican transition zone) as “Northwest of Latin America”. Most terminals (six species) were endemic to a single area (90 to 100% of points inside a single dominion; Suppl. material 3, Table S6), three species occurred in two

dominions, and two species in three dominions. Low occurrence points (below 10% in any one dominion) were visually inspected on the QGIS maps (Suppl. material 5, Figs S4, S5, S6) and were found to be mostly borderline to the main dominion(s), so they were not considered in the ancestral reconstruction, except in the case of *M. cisplatensis*. Eight percent (8%) of the distribution points of *M. cisplatensis* were in the South Brazilian dominion. Although this was marginally below the 10% cut-off value, the points were internal as well as marginal to the South Brazilian dominion and formed an arc beyond the greatest concentration of points in its two main dominions (Paraná and Chacoan; Suppl. material 5, Fig. S5). Therefore, this species was scored as present in the South Brazilian dominion.

The default configuration of BioGeoBEARS was implemented with unconstrained analysis and no time stratification nor different dispersal scalars between areas. In order to reduce the state space, range size was set to the maximum range observed in the data (three areas). Using the best model selected, the probability of possible range configuration at each internal node was estimated and mapped onto the calibrated tree to provide a general picture of the biogeographic origin of each clade.

Taxonomy and morphology

Species names and circumscriptions for *Myrcianthes* follows Grifo (1992) and the continuously updated World Checklist of Vascular Plants (Govaerts et al. 2021a). Three names that are listed by Govaerts et al. (2021b) as accepted have not been included in this study: *Myrcianthes bradeana* Mattos is a synonym of *Eugenia cappariidifolia* DC. (Mazine and Faria 2022); *M. esnardiana* (Urb. & Ekman) Alain was excluded from *Myrcianthes* by Grifo (1992); and *M. storkii* (Standl.) McVaugh was treated as a synonym of *M. rhopaloides* by Grifo (1992).

Morphological data was gathered from the taxonomic descriptions in Grifo (1992) for all species that were described before 1992. For more recently described species, morphological data was gathered from original descriptions (Sobral et al. 2012; Parra-O. and Bohórquez-Osorio 2016; Kawasaki et al. 2019; Proença et al. 2023), i.e. respectively *M. riparia* Sobral, Grippa & T.B.Guim., *M. roncesvallensis* Parra-Os. & Bohórq.-Os., *M. rubra* B.Holst & M.L.Kawas, and *M. cruciata* M.Ibrahim & Proença. Characters discussed in the text are those considered of taxonomic importance in Neotropical Myrtaceae (Landrum and Kawasaki 1997; Lucas et al. 2019).

Wood anatomy

Wood anatomy data was gathered from the literature. The species *Myrcianthes cruciata* M.Ibrahim & Proença was published together with the characterization of its wood anatomy, and an overview of the wood anatomy of the genus *Myrcianthes* (Rebollar et al. 1993; Ramírez-Martínez et al. 2017; Proença et al. 2023). For *Eugenia*, wood anatomy data was taken from the personal

database of wood anatomical characters of Myrtaceae tribe Myrteae compiled by one of us (J.S.-O.) based on the following literature: Santos and Marchiori (2011), Santos et al. (2014, 2015), Schmid and Baas (1984), Sonsin et al. (2014), and data available on the InsideWood (2004–) website, that aims to be a comprehensive database of anatomical characters of extant and fossil wood following the IAWA traits and classification (IAWA Committee 1989). When images of slides were available on InsideWood (2004–), these were also examined. When choosing fossil woods for calibration, we focused on characters that are considered of taxonomic importance (type of porosity, vessel grouping, type of perforation plate, size and position of intervessel pits, vessel diameter, vessel density, borders of vessel-ray pits, type of axial parenchyma and ray width; Baas et al. 2000). For the comparison between *Myrcianthes* and *Eugenia* only characters that varied between these genera, or between species of these two genera, are shown; characters that did not vary (the majority) are not shown.

RESULTS

Geographic and altitudinal distribution

The geographic and altitudinal database is stored in BRAHMS and includes 1,228 georeferenced records of the 36 currently accepted species of the genus and

is available from the corresponding author. A list of extreme latitudinal and altitudinal records of *Myrcianthes* is available for each species in Suppl. material 1, Table S1 and for other genera in Suppl. material 3, Table S7. *Myrcianthes* is distributed from 29°02'N (Florida, USA) to 34°47'S (Maldonado, Uruguay; total latitudinal range 63°48') and from near sea level to ca 3729 m a.s.l. (Oruro, Bolivia) (Fig. 2). Its closest rivals are its sister genera, the megadiverse *Eugenia* (> 1000 species), *Myrcia* (ca 800 species), and *Psidium* (ca 100 species). *Eugenia* occurs from ca 28°14'N (Florida, USA) to 32°57'S (Vergara, Uruguay) or possibly 34°36'S (Reserva Ecológica Costanera Sur, Buenos Aires, Argentina); total latitudinal range 61°12' (or possibly 62°50') and from sea level to ca 2900 m a.s.l. (Imbabura, Ecuador) (Suppl. material 3, Table S7). *Myrcia* occurs from 25°43'N (Florida, USA) to 31°16'S in Salto, Uruguay; total latitudinal range ca 57° and from sea level to possibly 3100 m a.s.l. (2950–3100; Pasco, Peru). *Psidium* occurs from ca 27°02'N (Chihuahua, Mexico) to 37°50'S (Buenos Aires, Argentina; total latitudinal range 64°52') and from sea level to 2840 m a.s.l. (Ecuador, Pichincha). Thus, of the three comparable genera, *Psidium* surpasses *Myrcianthes* in latitudinal amplitude by ca 1°04' (less than 2% of the total range of *Myrcianthes*) but has an altitudinal range that is 75% of that of *Myrcianthes*. *Eugenia* and *Myrcia* have both narrower latitudinal and altitudinal distributions than *Myrcianthes*. Therefore, *Myrcianthes* is confirmed to have a broader latitudinal/

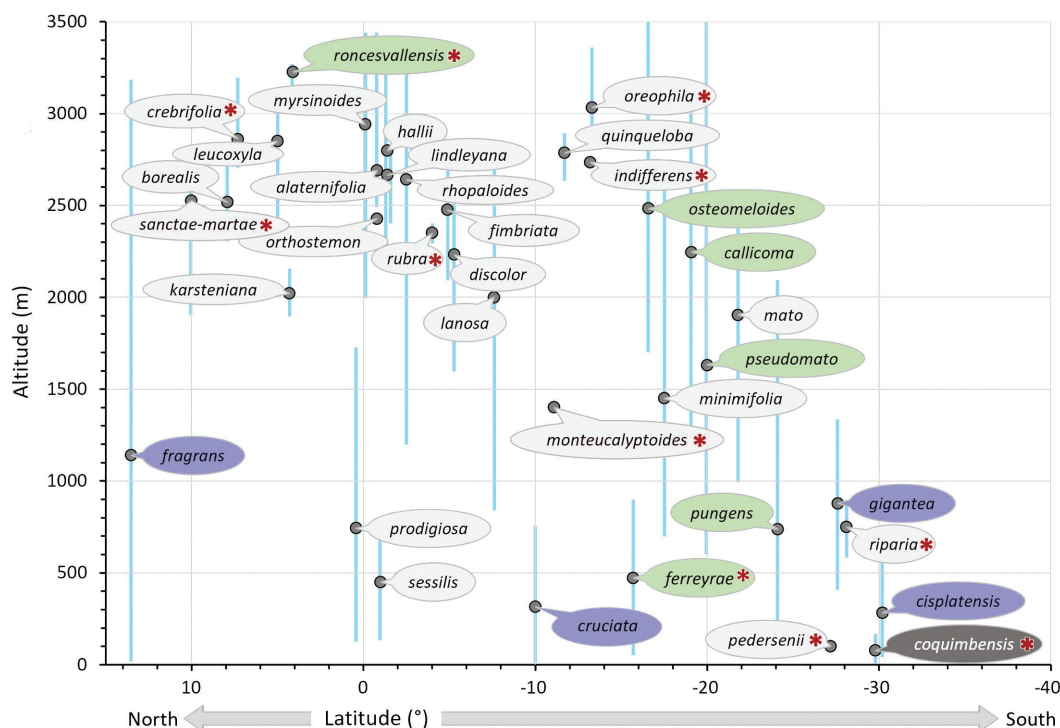


Figure 2. Relationship between average latitude and average altitude for accepted *Myrcianthes* species. Bars represent altitudinal intervals (bars for *M. osteomeloides* and *M. pseudomato* are truncated at 3500 m). Species with asterisks are narrow endemics restricted to < 1° of latitude; pale grey balloons are species not included in the phylogeny; the dark grey balloon is the sister species to all other sampled species; violet balloons are lowland clade species; green balloons are highland clade species.

altitudinal distribution than any other Neotropical genus of Myrtaceae (Suppl. material 3, Table S5).

Plotting the latitudinal and altitudinal averages (with interval bars for minimum and maximum values of altitude) allows a rough overview of the geographic/altitudinal ecospace (G/A ecospace) of each species in the Americas (Fig. 2). This enabled us to conclude that all species in the more easterly, lowland clade have their midpoint between 100 and 1200 m and their maximum altitude below 1400 m, with the exception of *M. fragrans*, which characterizes this clade as essentially lowland. All species in the more westerly (mostly Andean) clade have midpoints between 700 and 3200 m, which characterizes this clade as essentially highland (Fig. 2).

Narrow-endemic species occur in two different areas of the G/A ecospace. The first suite of narrow endemics (four species) appears in the right-hand corner, at the more southerly latitudes and lower altitudes. The second suite of narrow-endemic species are scattered over the lower latitudes (7°N–13°S) and have their altitudinal midpoints above 2300 m, i.e. they are cloud forest species, with the possible exception of *M. monteucalyptoides* Proença & L.V.S.Jenn. (recorded altitude 1460 m) although the original authors questioned this altitude since the type locality, Tarma, Peru, is located at ca 3000 m and the nearest locality in the vicinity of Tarma with the altitude cited on the type specimen is 50 km distant (Proença et al. 2011).

Phylogeny, dating, and ancestral range

Two-thirds of the 36 *Myrcianthes* species remain unsampled in the phylogeny and they are mainly from the Andes suggesting where future efforts should be focused, as well as the Guyanas. *Myrcianthes* emerged as a monophyletic genus with high bootstrap support in the ML tree (96 BS; Fig. 3; Suppl. material 4, Fig. S1) and maximum support in the Bayesian tree (1 PP; Suppl. material 4, Fig. S2). It was recovered as sister to *Eugenia* with maximum bootstrap support (100 BS) and maximum Bayesian support (1 PP). *Myrcianthes coquimbensis* (Barnéoud) Landrum & Grifo emerged as sister to the rest of the genus, which then splits into two clades (Figs 3, 4; Suppl. material 4, Fig. S3; Suppl. material 5, Fig. S4 for the non-collapsed tree). We have called these two clades the highland clade and lowland clade, respectively, based on the dominant altitudinal distribution in each clade (Fig. 2).

Divergence time estimates (Fig. 4) indicated that *Myrcianthes* diverged from *Eugenia* ca 32 mya. *Myrcianthes coquimbensis* is sister to the rest of the genus and the divergence is deep, dated at ca 24 mya. The two *Myrcianthes* clades have more or less similar ages. The highland clade is slightly older (ca 13.7 my old) than the lowland clade (ca 11.4 my old). However, the sampled species of the highland clade diversified later than those of the lowland clade species.

The model that conferred the best likelihood on our *Myrcianthes* dataset was BAYAREALIKE+J with an AICc

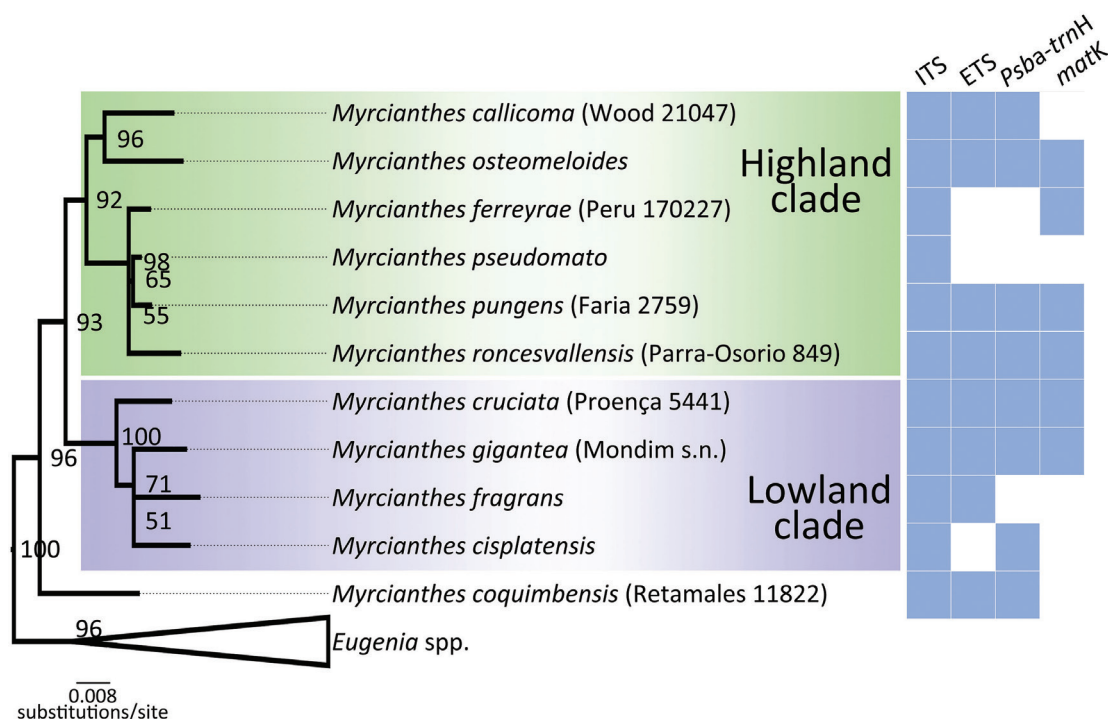


Figure 3. ML tree of *Myrcianthes* based on ITS, ETS, *psbA-trnH*, and *matK*. Bootstrap values are to the right of the nodes. The green clade contains highland species, while the purple clade contains lowland species. Presence of sequences is represented by blue squares, while missing data are blank squares.

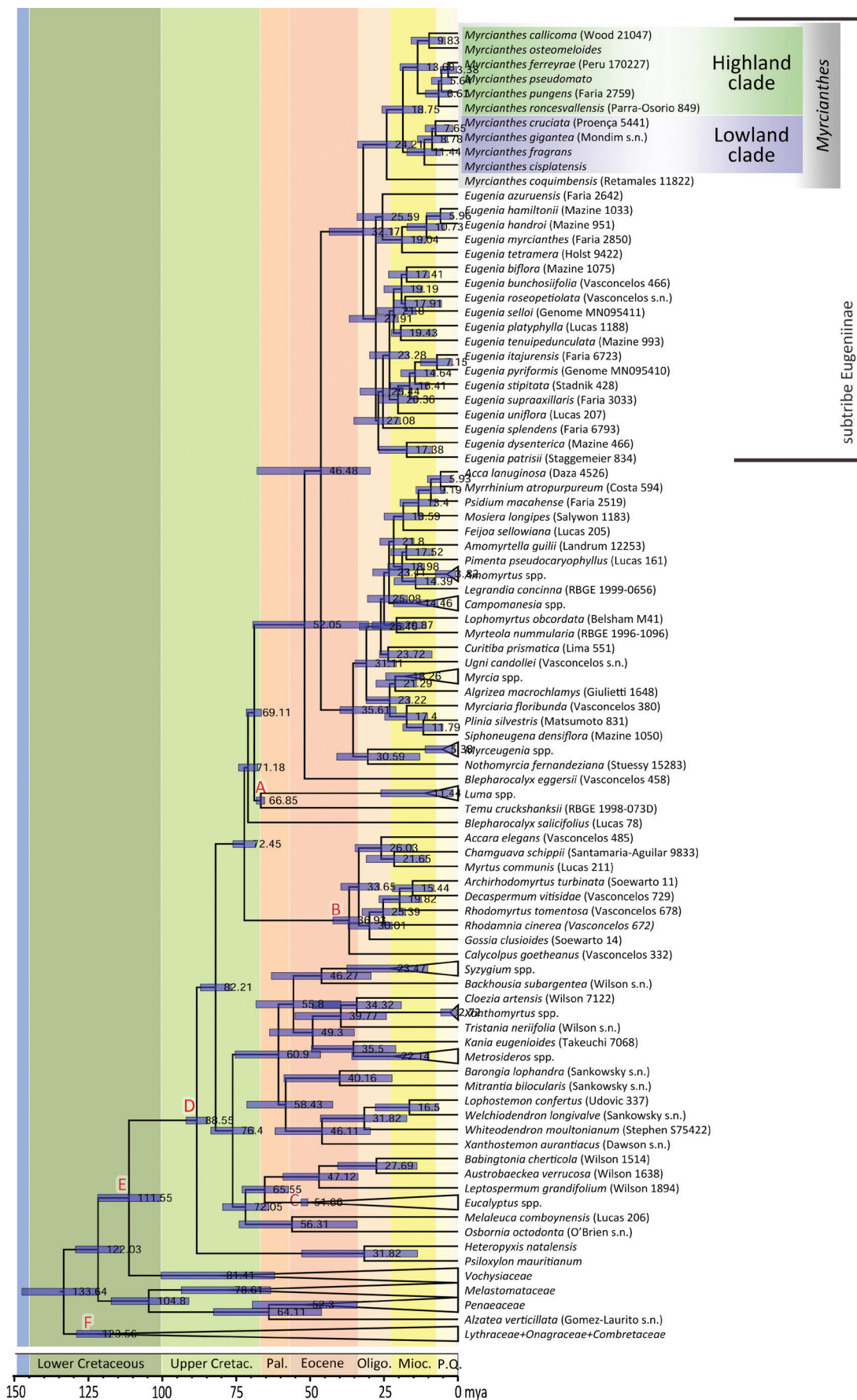


Figure 4. Divergence time tree based on ITS, ETS, *psbA-trnH*, and *matK*. Ages are to the right of the nodes. For posterior probability values, see Suppl. material 4, Fig. S2. A, B, C, D, E, F = calibration points, see Suppl. material 3, Table S3 for fossils used.

Table 1. Comparison of biogeographic models on *Myrcianthes*, constrained to the maximum number of areas equals three. Best model in bold.

	Ln L	Number	Parameter estimates			AIC	AICc	AICc weights
			Dispersal (<i>d</i>)	Extinction (<i>e</i>)	Founder effect (<i>j</i>)			
DEC	-33.28	2	0.013	0.010	0.000	70.57	72.07	0.076
DEC+J	-32.18	3	0.011	0.003	0.064	70.37	73.80	0.032
DIVALIKE	-33.89	2	0.016	1E-12	0.000	71.79	73.29	0.041
DIVALIKE+J	-32.32	3	0.013	1E-12	0.063	70.63	74.06	0.028
BAYAREALIKE	-34.56	2	0.015	0.062	0.000	73.11	74.61	0.021
BAYAREALIKE+J	-28.96	3	0.004	1E-7	0.117	63.93	67.36	0.801

of 67.36 (80% of probability), while the next closest model (DEC) had an AICc of 72.07, and all the rest were > 73.29 (Table 1). The BAYAREALIKE+J model is similar to the Bay Area model implemented in Landis et al. (2013) but BioGeoBEARS allows the inclusion of a founder event and jump speciation captured by the *j* parameter (Matzke 2013) that permits a daughter lineage to have a different area from the direct ancestor. The addition of *j* parameter improves the log likelihood of resulting inferences of ancestral areas in comparison to a model with only two free parameters (Table 1), showing jump speciation (i.e. dispersal between non-adjacent areas) as an important pattern in range variation of *Myrcianthes*. The Chacoan and Paraná dominion are highly likely to be the ancestral range for most *Myrcianthes* species (Fig. 5) including the ancestral node of each of the clades (highland and lowland). In the lowland clade, subsequent nodes show shifts into the South Brazilian dominion and into the Northwest of Latin America. These shifts are estimated to date from ~12–9 mya. In the highland clade, the first diversification occurred ~10 mya in the South Brazilian dominion, specifically in the Yungas province where we found two species (*Myrcianthes callicoma* McVaugh and *M. osteomeloides* (Rusby) McVaugh, Fig. 5) endemic to this province. The second diversification of the highland clade occurred ~6 mya; this node was recovered as being from Chacoan-Paraná-South American transition zone, with two of its four species emerging as endemic to the South American transition zone (*Myrcianthes ferreyrae* and *M. roncesvallensis*).

Taxonomy and morphology

We examined the floral characters from the literature (Grifo 1992; Proença et al. 2011, 2023) but could not find any obvious lowland/highland split for type of inflorescence, number of sepals (4, 5, or 4–5), number of stamens, disk size (1.5–8 mm in diameter but most species 2–4 mm), or number of ovules per locule (5–30). Although no clear-cut lowland/highland dichotomy in floral morphology was found, we did detect a tendency for species with more austral distributions to have fewer ovules per locule (see Discussion).

Wood anatomy

Five species of *Myrcianthes* have been sampled from previous studies on wood anatomy (Schmid and Baas 1984; Rebollar et al. 1993; Richter and Dallwitz 2000; Santos et al. 2015; Ramírez-Martínez et al. 2017; Proença et al. 2023). Although most wood characters were uniform within the genus, four characters differed among *Myrcianthes* species and two differed between *Myrcianthes* and its sister genus *Eugenia* (Table 2). Two wood anatomy characters that are apparently conserved in *Eugenia* varied between species and clades of *Myrcianthes*: 1) helical thickenings (absent in *Eugenia*) are often found in *Myrcianthes*; 2) prismatic crystals in the axial parenchyma (universal in *Eugenia*) are either present or absent in *Myrcianthes*.

DISCUSSION

Geographic and altitudinal distribution

Myrcianthes coquimbensis (Fig. 1E), sister to all other *Myrcianthes*, is in the extreme right-hand corner of the G/A ecospace (high latitude, low altitude) and is a narrow-endemic species restricted to maritime scrub in Coquimbo, Chile. The G/A ecospace close to *M. coquimbensis* is occupied by six species (Fig. 2). Three of these are also narrow-endemic species and occur between 16° and 34°S. Two of these are of unknown phylogenetic affinities: *M. riparia* (restricted to one river basin in southern Brazil; Sobral et al. 2012) and *M. pedersenii* D.Legrand (restricted to fields in Misiones, Paraguay; Grifo 1992). The third, *M. ferreyrae* (restricted to “lomas”, which are “fog oases” of vegetation in the desert belt in Arequipa, Peru; Song et al. 2023) is a member of the older, highland clade (Figs 2, 6A). The other three species are relatively widespread (*M. cisplatensis*, Figs 2, 6B; *M. pungens*, Figs 2, 6A; *M. gigantea* D.Legrand, Figs 2, 6B) and were sampled for the phylogenetic reconstruction, belonging to both the lowland and highland clades (Fig. 7). Moreover, two of them are the only species of the genus to straddle the Chaco sensu Cabrera and Willink (1973) – not the Chacoan Dominion of Morrone et

Table 2. Wood anatomical features of *Myrcianthes* (only of sampled species) compared to its sister genus *Eugenia*. *M. coq.* = *Myrcianthes coquimbensis*; *M. cru.* = *Myrcianthes cruciata*; *M. cis.* = *Myrcianthes cisplatensis*; *M. fra.* = *Myrcianthes fragrans*; *M. gig.* = *Myrcianthes gigantea*; *M. pun.* = *Myrcianthes pungens*.

Wood anatomical features	<i>Myrcianthes</i> basal species	<i>Myrcianthes</i> Lowland clade					<i>Myrcianthes</i> Highland clade	<i>Eugenia</i> spp.
	<i>M. coq.</i>	<i>M. cru.</i>	<i>M. cis.</i>	<i>M. fra.</i>	<i>M. gig.</i>		<i>M. pun.</i>	
Helical thickenings in the vessels	0	0	+	+?	+		0	0 (31 spp.)
Parenchyma apotracheal forming irregular lines or bands	?	+	+	+?	0		+	0 (2 spp.) + (17 spp.)
Prismatic crystals in the axial parenchyma	?	0	0	+	+		+	+ (19 spp.)
Crystals in idioblasts	?	0	0	0	0		+	0 (9 spp.) + (10 spp.)

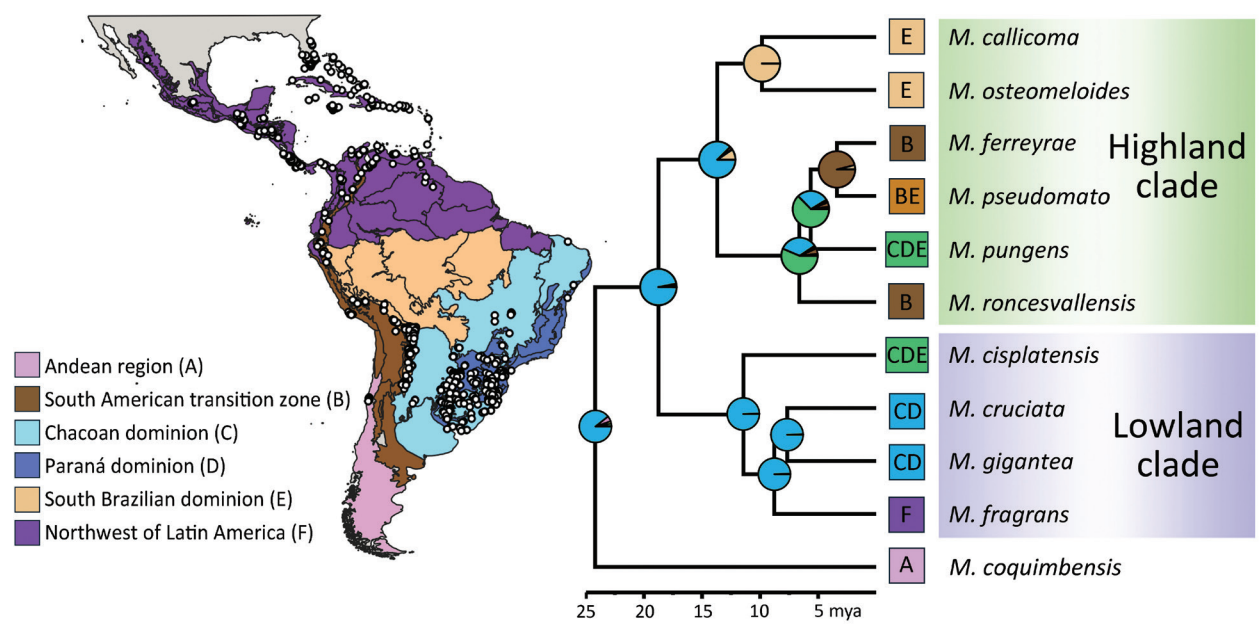


Figure 5. Ancestral range reconstruction of *Myrcianthes*. Regions, dominions, and transition zone (areas A–E) according to Morrone et al. (2022); see Methods for area F.

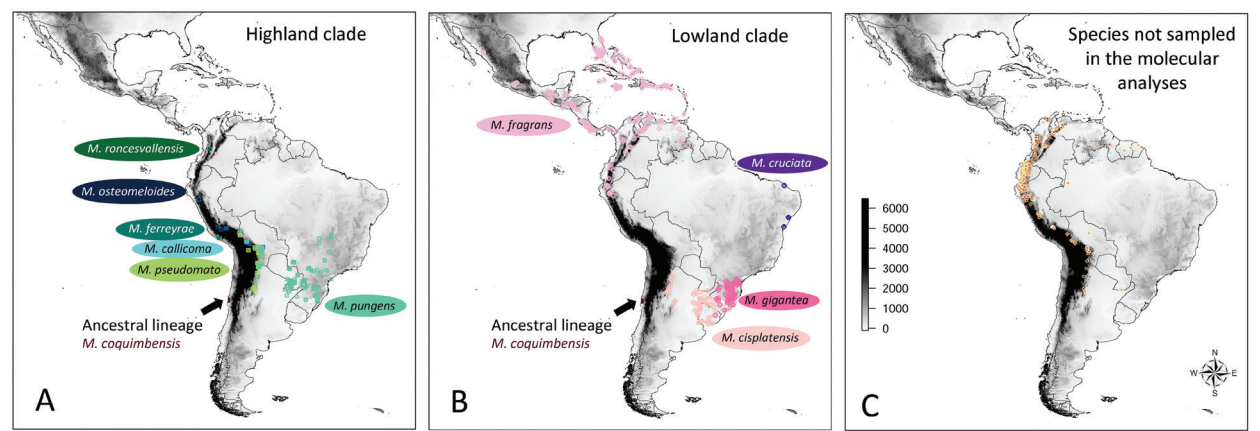


Figure 6. Geographic distribution of *Myrcianthes*. **A.** Highland clade species represented in the phylogenetic tree. **B.** Lowland clade species represented in the phylogenetic tree. **C.** Not sampled species showing major geographic overlap with the sampled species, except for *M. prodigiosa* (Guyana Highlands and peri-Amazonia in Bolivia and Brazil).

al. (2022) that covers the whole South American dry diagonal of Caatinga, Cerrado, and Chaco. The area now occupied by the Chaco has been a barrier to wet forest species expansion since the Miocene; first by marine transgressions and in the late Miocene by the uplift of the western hills that created a barrier to NE winds that led to extreme desertification (Pascual and Ortiz-Jaureguizar 1990). Although the possibility of later long-distance dispersal cannot be discarded, it seems more likely that these two species predated these events: *M. cisplatensis* (lowland clade), is the most southerly *Myrcianthes* species and sister to the rest of the lowland clade, and *M. pungens* (highland clade) is also the most southerly species of its clade. *Myrcianthes gigantea* (lowland clade) is the last of the six species within the G/A ecospace (near *M. coquimbensis*) and is restricted to southern Brazil and Uruguay but is distributed somewhat further north than *M. cisplatensis* (Fig. 6B).

The lowland clade has a broad latitudinal range (Fig. 6B), but a relatively narrow altitudinal range, while the highland clade has a somewhat narrower latitudinal range, but an altitudinal range that is approximately three times broader than the former (Fig. 2). This is congruent with the rising of the Andes providing opportunities for this clade to colonize higher altitudes, which were unavailable in eastern South America. A latitudinal gradient is also perceptible, i.e. species generally occur at low altitudes in the southern part of *Myrcianthes*' range but reach higher altitudes as they approach the equator. *Myrcianthes fragrans* was found to be the species with the widest altitudinal range (Fig. 2). It occurs in

northern South America, the Greater and Lesser Antilles, Mexico, and Florida. *Myrcianthes fragrans* overlaps both altitudinally (ca 1500–2000 m) and geographically (5°–8°N and 70°–72°W) with several putative (based on geographic distribution) highland clade species in Colombia and Venezuela (e.g. *M. hallii* (O.Berg) McVaugh, *M. karsteniana* (O.Berg) McVaugh, and *M. leucoxylla* (Ortega) McVaugh). *Myrcianthes fragrans* is exclusive to the Northern Andean zone and does not extend beyond the Amotape-Huancabamba North-South Biogeographical barrier (Luebert and Weigend 2014 and references therein).

Phylogeny, dating, and ancestral range

Our results for *Myrcianthes* show that the genus is monophyletic and confirm prior studies that it is sister to *Eugenia* (Lucas et al. 2007; Vasconcelos et al. 2017; Giaretta et al. 2022), with the mean date for the split estimated at ca 32.1 mya (middle Eocene). The date of the split is congruent with the mean age of 33.2 my estimated for the Eugeniinae lineage based on a very large sample of tribe Myrteae (NMWG 2024). The Eocene was marked by climatic stability (Morrone et al. 2022) and extensive dispersal of other plant clades since the beginning of this period has been postulated (e.g. the clusioid clade; Ruhfel et al. 2016).

We also confirm the finding of Retamales (2017) that the Chilean endemic *M. coquimbensis* is sister to the rest of the genus. *Myrcianthes coquimbensis* split from the main *Myrcianthes* lineage in the late Oligocene (ca 24.2 mya), but the main *Myrcianthes* lineage did not diversify before

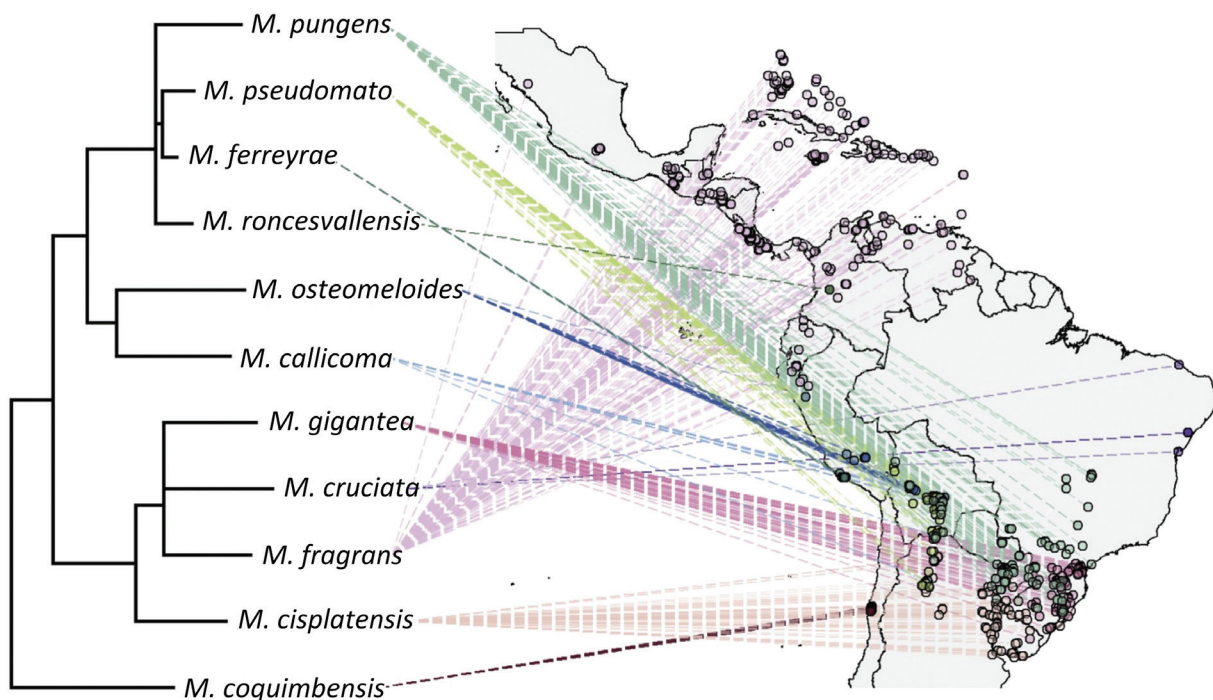


Figure 7. ML tree plotted against 718 unique occurrences for the 11 sampled species of *Myrcianthes*. Dark brown = *M. coquimbensis*; blueish, greenish = highland clade species; pinkish, purplish = lowland clade species.

the middle of the Miocene (later than *Eugenia*). The main *Myrcianthes* lineage subsequently split into two major clades that we have called lowland and highland clades for simplicity, with the former more easterly and the latter mostly Andean (Figs 5–7). The clades overlap at the base of the tree in Uruguay and southern Brazil (Fig. 5), and probably meet again in northern South America (in the Cordillera Oriental, Colombia and in Parque Nacional El Ávila, Cundinamarca, Venezuela), although this scenario depends on the unproven assumption that the sympatric species, collected within a few kilometres of *M. fragrans* (*M. hallii*, *M. karsteniana*, and *M. leucoxylla*) belong to the highland clade. A similar pattern, of two separate clades, had been found in another ancient myrtaceous genus with a compatible distribution, *Myrceugenia*, and, as we had hypothesized, both genera apparently had their origin in Chile. The Western clade of *Myrceugenia* diversified mainly in Chile and western Argentina (14 species) but, in contrast to *Myrcianthes*, did not colonize the Andes to any significant degree (Murillo-A. et al. 2016). The Eastern clade of *Myrceugenia*, on the other hand, diversified much more in the east (38 species in Uruguay, eastern Argentina, and southeastern Brazil; Vieira et al. 2025) than did *Myrcianthes*. A single species, *Myrceugenia linda* F.C.S.Vieira & Proença, occurs in the Yungas forests of Bolivia (Proença et al. 2024). Although *Myrceugenia* is much more diverse in the east than in the west, the genus only extends to ca 13°S in the Bahia highlands, Brazil (SpeciesLink 2022). This is the opposite of what happened in *Myrcianthes*, in which, although there was little speciation in the east, there was a significant range expansion (due to *M. fragrans*). It is possible of course that speciation did occur, but the species have not survived.

Vasconcelos et al. (2017) suggested a quick northerly vertical expansion of tribe Myrteae into South America soon after its initial diversification; the only exception was *Myrcianthes* (based on *M. fragrans*) that required a long-distance dispersal event (LDDE) into the Caribbean to explain its current distribution. Here, we were able to show, with a larger sample of the genus (including north-eastern Brazilian *M. cruciata* that was not described until 2023), that the origin of *Myrcianthes* is also southern (Chacoan-Paraná dominion, Fig. 5) with a northerly expansion as in other Myrteae, corroborating the long-held theory that Myrtaceae diversified from south to north (Berry 1915; Vasconcelos et al. 2017). Barreda et al. (2021) found that Myrtaceae was an important component of the Patagonian palaeoflora from the Cenozoic to the early Miocene, decreasing in diversity during the middle Miocene (~16–12 mya) with global cooling, and becoming extinct in Patagonia by the late Miocene (~12–6 mya). Landrum (1981) postulated that during the late Oligocene (~25–23 mya), *Myrceugenia* grew across South America in a temperate/subtropical austral forest, and our study corroborates that theory and suggests a similar pattern for *Myrcianthes*. An interesting parallel was also found between the *Myrcianthes* lowland clade and *Drymis* Juss., a genus also belonging to an

ancient southern Gondwanan family (Winteraceae). Similar to *Myrcianthes*, *Drymis* showed two vicariant clades, one endemic to Chile and the other in the Brazilian Atlantic Forest and the Northern Andes (Marquinez et al. 2009), i.e. both *Drymis* and the *Myrcianthes* lowland clade appear to have reached the northern Andes from Atlantic Forest ancestors.

The highland clade is represented in our study by six species (Figs 5, 6A) that occur in Argentina, Uruguay, southern and central Brazil, Bolivia, Paraguay, and the Andes at least to Colombia (based on the inclusion of *M. roncesvallensis* in the highland clade). The recently published NMWG (2024) tree with a “where we stand with the Myrteae phylogeny” approach looked at most of the same species of *Myrcianthes* (it did not include *M. coquimbensis*) but had significantly more missing data than our study, as nine molecular markers were used. Their *Myrcianthes* reconstructed phylogenetic tree was highly congruent to ours for the highland clade. They found a strongly supported (94 BS) highland clade composed of the same two subclades.

The highland clade crown is slightly older (ca 13.7 my old) than the lowland clade crown (ca 11.4 my old). Miocene diversification of the *Myrcianthes* highland clade in the Andes is congruent with increased uplift rates in the Eastern Cordillera, Cordillera Real, and Cordillera de Merida from the late Miocene onwards (van der Hammen 1988; Villamil 1999; Mora et al. 2008). The highland clade shows two well-supported subclades, one Central Andean and the other with a wider range. The Central Andean subclade, with two species, *M. callicoma* and *M. osteomeloides* from Argentina, Bolivia, and Peru, ranges from ca 26° to 13° S (crown ca 9.8 my old). A period starting at ca 13 mya was marked by rapid uplift of the Central Andes and several clades, e.g. in *Peperomia* Ruiz & Pav. (Piperaceae) diversified in the Central Andes during this period (Luebert and Weigend 2014). The wider-ranging clade, composed of *M. ferreyrae*, *M. pseudomato* (D.Legrand) McVaugh, *M. pungens*, and *M. roncesvallensis* from Argentina, Bolivia, Brazil, Paraguay, Peru, and Colombia ranges from ca 30°S to 4°N and diverged later (crown ca 6.6 my old). This would be congruent with the late Miocene climatic instability of the Central Andes, particularly the period between ca 7.9–6 mya (Uba et al. 2007). During this period, the uplift of the Eastern Cordillera in Colombia reached elevations high enough to produce an orographic barrier that intercepted moisture-laden winds and increased rainfall on the Eastern flanks (Mora et al. 2008), which might have favoured this essentially subtropical/montane genus. This division into two subclades could be an artefact of the low level of sampling in the highland clade or indicate that the highland clade of *Myrcianthes* underwent more than one radiation; further sampling is needed.

The lowland clade of *Myrcianthes* is represented by four species in our study (Figs 6B, 7) that occur in the Atlantic Forest, from Rio Grande do Sul to Ceará, but reaching northern South America, the Caribbean, southern

Mexico, and Florida. Three species of the lowland clade (*M. cisplatensis*, *M. cruciata*, and *M. gigantea*) have relatively narrow distributions, but the fourth, *M. fragrans*, as mentioned above, is widely distributed (Fig. 6; Suppl. material 5, Fig. S6). *Myrcianthes fragrans* is the most northerly species of the lowland clade and of the genus. Conversely, *M. cisplatensis* is the most southerly species of the lowland clade and of the genus and is basal to the other three species of the lowland clade. The lowland clade was not recovered by NMWG (2024). They found that a clade formed by lowland species *M. gigantea* plus two accessions of *M. fragrans* was sister to the rest of the genus (35 BS), and another clade formed by lowland species *M. cruciata* plus *M. cisplatensis* (58 BS) was sister to the highland clade. We attribute this difference to the higher proportion of missing data in the NMWG tree as their bootstrap values were much lower than ours. In fact, NMWG (2024: 8) stresses that: "...given the low support of some relationships at both higher and lower taxonomic levels, it is important to emphasize that our supermatrix tree should not be considered as the final word in terms of phylogenetic relationships within Neotropical Myrtaceae. It is rather a first step towards evaluating sampling gaps..."

Taxonomy and morphology

Reproductive morphology

The number of ovules per locule in *Myrcianthes* is 5–30 but in the most austral, lowland species, numbers of ovules per locule ranged between 5–15: *M. cisplatensis* (up to 15), *M. coquimbensis* (5–11), *M. pedersenii* (6–8), *M. riparia* (up to 9), and *M. sessilis* McVaugh (ca 8). Reconstruction of ancestral character states on a larger sample of species would be necessary to state with confidence that a low number of ovules per locule is the ancestral state.

Convergence between *Myrcianthes* and basal lineages of *Eugenia*

A recent phylogenomic reconstruction of *Eugenia* recovered *Myrcianthes* as its sister genus (Giaretta et al. 2022), as was also found in our study. These authors also found that *E. splendens* O.Berg is sister to the rest of *Eugenia* and it was reported by Vasconcelos et al. (2018) as having many ovules per locule (average = 34.3, $n = 3$ flowers) but specimens examined for the Flora do Morro do Chapéu (Bahia) examined by one of us (J.E.Q.F.) had 7–10 ovules per locule, and the original description describes it as pauci-ovulate (Berg 1857).

After this first split-off of *E. splendens*, the phylogenomic reconstruction (Giaretta et al. 2022) recovered a 4-species clade designated by them as the *Eugenia* "*Pilotheicum-Pseudeugenia*" clade as sister to all remaining *Eugenia*. This "*Pilotheicum-Pseudeugenia*" clade included species formally included in basal lineages of *Eugenia*, i.e. *Eugenia* sect. *Pilotheicum* and *Eugenia* sect. *Pseudeugenia*, well-known for frequently having a low number of ovules per locule (sometimes very low, 1–4 fide Mazine et al. 2018). *Eugenia* sect. *Pilotheicum* has dichasial inflorescences and

free cotyledons, characters that are virtually unknown in other sections (Faria 2014; Mazine et al. 2018) but are very common in *Myrcianthes* (Grifo 1992). Three of the four species that emerged in the "*Pilotheicum-Pseudeugenia*" clade have a low number of ovules per locule, compatible with those found within the more southerly species of *Myrcianthes*: *E. dysenterica* Mart. ex DC. (1–2; Proença and Gibbs 1994), *E. pohliana* DC. (5; Vasconcelos et al. 2018), and *E. pyriformis* Cambess. (2–9; Faria 2014).

Interestingly, it has recently come to light that *E. splendens* forms a clade (0.94 PP, Faria 2014; 31 BS, NMWG 2024) with *Eugenia* subg. *Hexachlamys*. Giaretta et al. (2022) noted that *E. subg. Hexachlamys* was not sampled in their study due to unsuccessful recovery; however, if *E. splendens* is a morphologically cryptic member of *E. subg. Hexachlamys* (as suggested by the molecular data), it may have inadvertently been sampled through the inclusion of *E. splendens* in their study. *Eugenia splendens* has never, as far as we are aware, been referred to *E. subg. Hexachlamys* based on its morphology; it was not, for example, included in a study that specifically targeted the relationship between *Hexachlamys* O.Berg and *Eugenia* (Cruz et al. 2013). This is not surprising since *E. splendens* has small, black, one-seeded fruits, an embryo with completely free cotyledons and an unusually well-developed hypocotyl that reaches to half the length of the embryo, as well as a complete absence of bracteoles, all good matches for *Myrcianthes*, with the last three characters rare in *Eugenia*. It is worth noting in this context that, in the most inclusive phylogeny of *Eugenia* to date (103 samples; Mazine et al. 2018), only if *E. splendens* is excluded does *E. subg. Pseudeugenia* show strong support; its inclusion brought BS support of this subgenus down from 94 to 45. Likewise, its sister clade (*E. subg. Eugenia* + *E. subg. Hexachlamys*) showed weak support (38 BS) although both of the subgenera themselves were well supported. In short, although the three subgenera of *Eugenia* are well supported (Mazine et al. 2018), i.e. *E. subg. Hexachlamys* (100 BS; three species), *E. subg. Eugenia* (97 BS; 87 species), and *E. subg. Pseudeugenia* excluding *E. splendens* (94 BS; four species), backbone resolution of their relationship remains poor due to the inclusion of *E. splendens* in the analysis. The inclusive phylogeny recently published (NMWG 2024) recovered *E. splendens* as part of a clade that also included *E. subg. Hexachlamys* and *E. sect. Pseudeugenia*, but bootstrap support for this clade was low. Additional sequencing of species within *E. subg. Hexachlamys* (and including *E. splendens*) is clearly essential to establish this subgenus' circumscription, and its position relative to the other two subgenera of *Eugenia* and to *Myrcianthes*.

Diversification of *Myrcianthes* in comparison to *Eugenia*

Myrcianthes did not diversify before the middle of the Miocene, the only exception being the splitting off of *M. coquimbensis* from the main lineage (which occurred at the end of the Oligocene). *Eugenia*, on the other hand,

showed significant diversification in the late Oligocene, and, by the end of the Oligocene/early Miocene all the main lineages had already diverged; this pattern is similar to that found by The Neotropical Myrtaceae Working Group (NMWG 2024) based on a much wider sample of *Eugenia*.

Wood anatomy

There is a very broad study across the Myrtaceae of helical thickenings in the vessels (Schmid and Baas 1984). Their results have been re-interpreted in the light of the most recent Myrteae phylogeny (NMWG 2024) and currently recognized tribes and subtribes (Lucas et al. 2019; Wilson et al. 2022). Helical thickenings occur in tribe Xanthomyrteae (in *Xanthomyrtus* Diels) and in tribe Myrteae (in eight genera). In tribe Myrteae, helical thickenings occur in the two most basal subtribes, the Decaspermiae (*Gossia* N.Snow & Guymier; Schmid and Baas 1984) and the Myrtinae (*Myrtus* L. and *Mosiera* Small; Schmid and Baas 1984; Fahn et al. 1986), and in three other subtribes, the Luminae (*Luma* A.Gray and *Myrceugenia*; Rancusi et al. 1987), the Eugeniinae (*Myrcianthes*; Schmid and Baas 1984; Ramírez-Martínez et al. 2017), and the Myrciinae (*Myrcia* sect. *Myrcia*; Santos and Marchiori 2011). The function and phylogenetic significance of helical thickenings (synonym: spiral thickenings) in the vessels has been the object of much debate (Baas 1973; van den Oever et al. 1981; Carlquist 1982). It was proposed by these authors that they are an adaptation to episodes of drought, ground freezing (physiological drought), or other sorts of water stress that can cause air bubbles (embolisms) to form in the vessels and block water movement. Helical thickenings in the vessels of the wood are considered a specialized anatomical feature, and do not appear in the fossil record until the Eocene, first reaching modern levels of incidence in Oligocene fossil floras (Wheeler and Baas 1991). Kohonen and Helland (2009) have convincingly demonstrated using physical models that helical thickenings in the vessels do increase vessel wettability (as predicted by Carlquist 1982) and lead to the formation of regular-shaped air bubbles that shrink much faster than the irregular bubbles that form in vessels that lack helical thickenings, thus restoring water flow more rapidly.

Most species of *Myrcianthes* sampled in the study by Schmid and Baas (1984) showed helical thickenings in the vessels. *Myrcianthes cisplatensis* (lowland clade, with helical thickenings) is the most southerly species of *Myrcianthes* (reaching 34.9°S; average altitude 282.5 m) and is a small tree (4–6 m; Grifo 1992). *Myrcianthes gigantea* (lowland clade, with helical thickenings) reaches similar latitudes (32.9°S; average altitude 878 m) and is a much taller tree (5–15 m; Grifo 1992). *Myrcianthes cruciata* (lowland clade, ranging from 3.9°S to 13.1°S; average altitude 305 m), is a tall northern Atlantic Forest tree (13–18 m; Proença et al. 2023) and lacks helical thickenings. *Myrcianthes fragrans* (lowland clade, most

wide-ranging species of the genus) is (possibly) variable for this character: trees studied in Mexico showing helical thickenings (Ramírez-Martínez et al. 2017) but in other trees studied in Florida and Mexico no helical thickenings were reported (InsideWood 2004–; Rebollar et al. 1993). A review of *Myrcianthes* wood anatomy (Proença et al. 2023) suggested that the voucher specimen for the study of Ramírez-Martínez et al. (2017), that reported helical thickenings in *M. fragrans*, might have been misidentified, as its wood anatomy differs markedly from other species of the genus in vessel size, vessel density, and the reduced to apparently simple borders of the ray-vessel pits, besides the presence of helical thickenings. The third most southerly species of *Myrcianthes* (reaching 30.1°S; average altitude 77 m) is *M. coquimbensis* (sister species to the rest of the genus, lacking helical thickenings). *Myrcianthes coquimbensis* is a densely branched shrub (Fig. 1E) up to 1.5 m tall from coastal scrub vegetation (Landrum 1988; Landrum and Grifo 1988). *Myrcianthes mato* (Griseb.) McVaugh (clade unknown, with helical thickenings) reaches 27.5°S (average altitude 1904 m) and is a small tree (3–8 m; Grifo 1992). Under these climatic conditions and habits, it is possible that the retention of ancestral helical thickenings occurred in *M. cisplatensis*, *M. mato*, and *M. gigantea*, all trees from cool subtropical or montane forests, has been advantageous, but not in *M. coquimbensis*, a shrub growing in maritime rocky scrub at sea level nor in *M. cruciata*, a tree but adapted to lowland tropical rainforest. The difference in this character across *Myrcianthes* is perhaps not surprising, if the wide altitudinal and latitudinal range of the genus is considered, with many of its species restricted to specific altitudinal ranges (Grifo 1992; Worthy et al. 2019; this study). This scenario is congruent with the literature. Global studies of helical thickenings reported higher percentages in temperate, high latitude floras than in tropical floras (van der Graaff and Baas 1974) and higher percentages of helical thickenings in seasonal cool temperate or montane habitats (Wheeler and Baas 1991). In Brazil, a trend for helical thickenings to be prevalent at higher latitudes or in colder climates was also observed, although it was not statistically significant for the sampled species (Alves and Angyalossy-Alfonso 2000).

CONCLUSIONS

Myrcianthes emerges as a promising model genus to study dispersal of ancient Gondwanan clades in the Americas. The different wood anatomy characters of *Myrcianthes* as compared to those of *Eugenia* are likely to be a combination of phylogenetic signal and ecological selection and merit further additional sampling and investigation. Our biogeographic hypothesis, based on a still incomplete phylogeny, will be presented here as a challenge. The genus was probably reasonably diverse in the Oligocene, when paleoclimatic and palaeogeographic events reduced its species or populations to the first suite of endemics that still persist in highly specialized, local conditions such as

M. coquimbensis, *M. pedersenii*, and *M. riparia*; these three species are probably paleo-endemics. Two clades escaped this scenario by dispersing northwards. The lowland, less diverse clade adapted to lowland conditions and advanced through the Atlantic Forest of Brazil, with one species, *M. fragrans*, eventually reaching northern South America and occupying the Caribbean and southern Florida and Mexico. The highland, more diverse clade advanced through the Andes, where it successfully diversified along an altitudinal gradient, giving rise to several relatively wide-spread species, and to a second suite of narrow-endemic species, most of which are cloud forest species; these are more likely to be neo-endemics, at least relative to the first suite. *Myrcianthes fragrans*, a lowland clade species, is morphologically highly variable with five different ecotypes and a vast synonymy (Grifo 1992). This species has the widest altitudinal range in the genus and overlaps with putative highland clade species in Colombia and Venezuela. We suspect that interspecific crosses may have occurred between *M. fragrans* and highland clade species, allowing *M. fragrans* to incorporate genes that favoured colonization of highland habitats in the northern hemisphere, such as the montane forests of Chiapas, Mexico. Many questions remain to be answered. Will the two unsampled southerly narrow endemics align with *M. coquimbensis* or with the lowland or highland clades? What is the phylogenetic position of *M. prodigiosa* McVaugh that has a peri-Amazonian distributions in Colombia, the Guyana highlands, extreme western Brazil, and Bolivia? What are the phylogenetic positions and wood anatomy characteristics of the many unsampled Andean species? What is the phylogenetic signal versus environmental selection of wood anatomy features within the genus? Finally, why did *Myrcianthes* not diversify in the Atlantic Forest, where its sister genus *Eugenia* (apparently morphologically and ecologically very similar) is one of the most diverse and successful genera?

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SUPPLEMENTARY MATERIALS

Supplementary material 1

Table S1. Species with geographic and altitudinal extremes and averages, and countries of occurrence.

<https://doi.org/10.5091/plecevo.152818.suppl1>

Supplementary material 2

Table S2. Species, vouchers, and GenBank accession numbers for molecular markers.

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Supplementary material 3

Table S3. Fossils and secondary calibration points used in the divergence time estimation analysis.

Table S4. Similarities between chosen fossil 1 (bold) and most similar modern wood.

Table S5. Similarities between chosen fossil 2 (bold) and most similar modern wood

Table S6. Percentage of occurrences in each neotropical bioregion adapted from the Morrone et al. (2022) classification.

Table S7. Vouchers for extreme latitudes and altitudes of widespread Neotropical genera of Myrtaceae.

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Supplementary material 4

Figure S1. Maximum likelihood tree based on ITS, ETS, *psbA-trnH*, and *matK*. Bootstrap values to the right of nodes. All tips are shown.

Figure S2. Bayesian phylogenetic tree based on ITS, ETS, *psbA-trnH*, and *matK*. Posterior probability values to the right of the nodes. Some *Myrcianthes* vouchers combined to compose one terminal per species. A, B, C, D, E, F = calibration points (see Table S3). All tips are shown.

Figure S3. Bayesian phylogenetic tree based on ITS, ETS, *psbA-trnH*, and *matK*. Ages to the right of the nodes. For posterior probability values, see Fig. S2. A, B, C, D, E, F = calibration points (see Table S3). All tips are shown.

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Supplementary material 5

Figure S4. Geographic distribution of *Myrcianthes ferreyrae*, *M. osteomeloides*, *M. pungens*, and *M. roncesvallensis*. Colours highlighting species names correspond to dots.

Figure S5. Geographic distribution of *Myrcianthes callicoma*, *M. cisplatensis*, *M. coquimbensis*, and *M. cruciata*. Colours highlighting species names correspond to dots.

Figure S6. Geographic distribution of *Myrcianthes fragrans*, *M. gigantea*, and *M. pseudomato*. Colours highlighting species names correspond to dots.

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