



# Biogeography, phylogenetic relationships and morphological analyses of the South American genus *Mutisia* L.f. (Asteraceae) shows early connections of two disjunct biodiversity hotspots

Andrés Moreira-Muñoz<sup>1</sup> · Rosa A. Scherson<sup>2</sup> · Federico Luebert<sup>2,3</sup> · María José Román<sup>2</sup> · Marcelo Monge<sup>4</sup> · Mauricio Diazgranados<sup>5</sup> · Herman Silva<sup>6</sup>

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## Abstract

The Andes is recognized as one of the most biodiverse places on Earth, promoting in its uplift process a series of recent rapid diversification events in different biotic groups like birds, mammals, insects and vascular plants. The uplift of the Andes during the Cenozoic acted as a barrier for many biotic groups, as a scenario for radiation processes due to occupancy of different niches and as a corridor for others. Connections between the Andes and the Atlantic Forest showed intermittent phases along the Cenozoic, affecting the distribution patterns and diversification of different biotic groups. Nowadays, the Andes and the Atlantic Forest are both considered globally relevant biodiversity hotspots. Floristic groups thriving in both hotspots are crucial for a better understanding of their biogeographic history, as well as for informing future conservation actions. *Mutisia* (Asteraceae), a genus comprising 63 perennial shrubs and vines endemic to South America, shows a marked West-East disjunction: Most species occupy almost the whole Andean chain from Colombia to Patagonia, while a second group encompasses four species distributed in eastern Brazil and the surrounding areas of Paraguay, Uruguay and Argentina. We reconstructed the phylogeny of the genus to assess its possible biogeographic history. We analysed three DNA regions, i.e. the chloroplast *trnL-trnF* intergenic spacer and the nuclear ribosomal internal and external transcribed spacers, ITS and ETS. Using maximum likelihood and Bayesian inference, gene trees were reconstructed, and a concatenated phylogenetic tree was inferred. Divergence times were estimated by means of BEAST, and the ancestral areas were inferred using BioGeoBEARS. An ancestral reconstruction of morphological traits was also performed, as well as maps representing current richness hotspots within the genus. Phylogenetic analyses strongly support the monophyly of *Mutisia*, with two well-supported main clades:

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✉ Andrés Moreira-Muñoz  
andres.moreira@pucv.cl

- <sup>1</sup> Instituto de Geografía, Pontificia Universidad Católica de Valparaíso, Av. Brasil, 2241 Valparaíso, Chile
- <sup>2</sup> Departamento de Silvicultura y Conservación de la Naturaleza, Universidad de Chile, 9206 Santiago, Chile
- <sup>3</sup> Nees Institute for Biodiversity of Plants, Uni Bonn, Meckenheimer Allee 170, D-53115 Bonn, Germany
- <sup>4</sup> Programa de Pós-graduação em Biologia Vegetal, Federal University of Uberlândia, Uberlândia, MG 38400-902, Brazil
- <sup>5</sup> Natural Capital & Plant Health department, Royal Botanic Gardens, Kew, Wakehurst Place, Ardingly, West Sussex RH17 6TN, UK
- <sup>6</sup> Laboratorio de Genómica Funcional & Bioinformática, Facultad de Ciencias Agronómicas, Universidad de Chile, Av. Santa Rosa 11315, 8820808 La Pintana, Santiago, Chile

clade A, with presence of Atlantic-central-northern Andes species, and clade B, with central/southern Andes species. Dating analyses suggest that a main clade separation occurred at the early Miocene, followed by the separation of the Atlantic clade A2 by the late Miocene, and more recent radiations occurred in the central, northern and southern Andes during the Pliocene. Results are in tune with other angiosperm taxa that also underwent rapid radiations, possibly related to environmental and pollinator changes. The biogeographic history of *Mutisia* is related to morphological adaptations, history and geographic factors acting since the Miocene along the Andes and adjacent areas. Threat assessments and conservation actions for the genus shall include the whole distribution range, including low-range northern and southern Andes species, as well as the distinctive Atlantic Forest clade.

**Keywords** Andean uplift · Atlantic Forest · BioGeoBEARS · Biogeography · Compositae · Conservation · Molecular dating

## Introduction

Mountain chains worldwide harbour about one-quarter of the terrestrial biota in about just a tenth of the Earth's continental surface (Hoorn et al. 2018). Key features making mountains so diverse are the following: (a) elevational gradient, (b) geodiversity (physiographic and climatic) and (c) prolonged isolation of peaks and valleys. These features reflect a complex interplay between orogeny, climate changes and geomorphologic processes over millions of years. The understanding of this complexity constitutes one of the big challenges for modern biogeography (Antonelli et al. 2018), and it is relevant for informing conservation actions (Whittaker et al. 2005). Among the mountain systems on Earth, the Andes are recognized as one of the most biodiverse, promoting in its uplift process a series of recent rapid diversification in different biotic groups such as birds, mammals, insects and vascular plants (Diazgranados and Barber 2017; Hazzi et al. 2018; Madriñán et al. 2013).

Two globally recognized biodiversity hotspots cover the whole Andes: the Tropical Andes (TA) and the Chilean Winter Rainfall and Valdivian Forests (CWR) (Mittermeier et al. 2011; Moreira-Muñoz 2014). A third disjunct Neotropical biodiversity hotspot is the Atlantic Forest (AF), separated from the two others by the arid Cerrado and Chaco domains (Oliveira-Filho et al. 2006; Fig. 1). Many biotic groups share related taxa between the Andes and the Atlantic Forest (Luebert and Weigend 2014; Moreira-Muñoz 2011). A better understanding of the processes underlying the evolutionary trajectories of disjunct groups present in these hotspots helps us unravel Neotropical biogeography and better informing conservation actions, especially where the superposing of biodiversity conservation and human activities is showing increasing conflicts due to global climatic changes and regional land use changes plus infrastructure megaprojects (Mansilla et al. 2019; Molotoks et al. 2017).

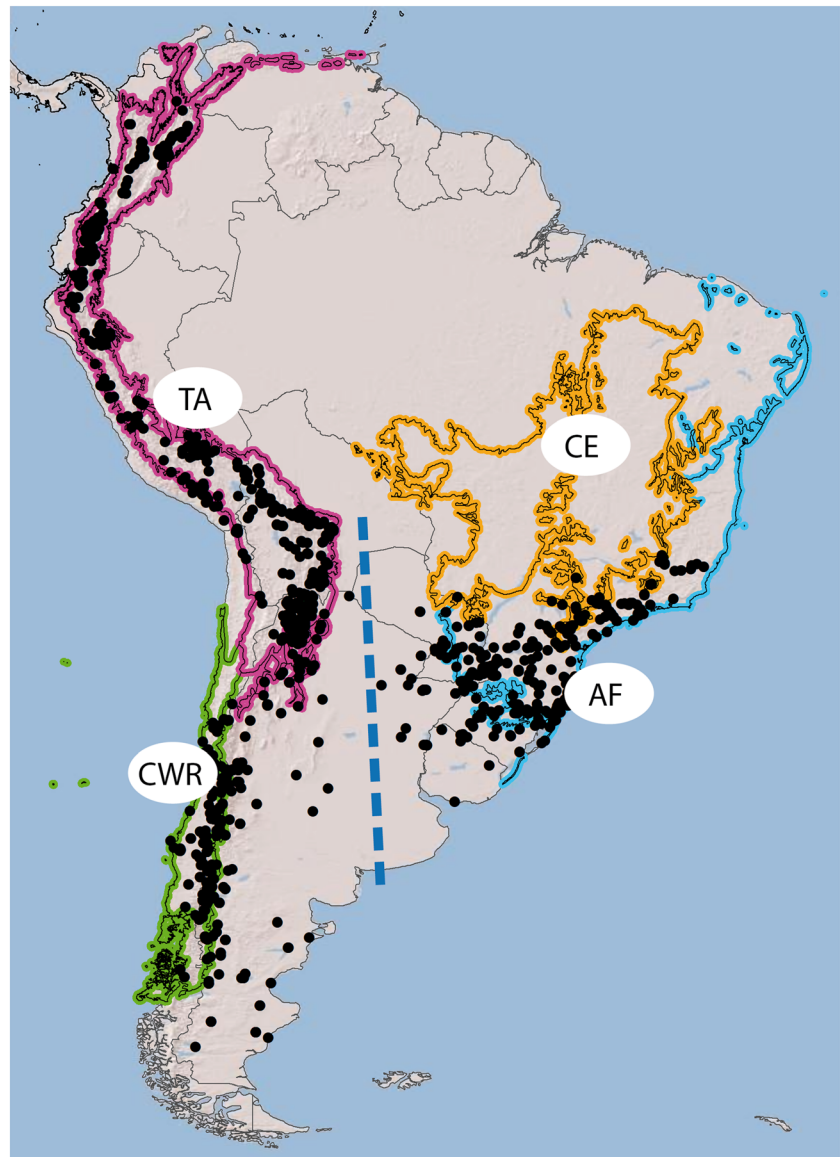
Regarding biogeography and evolutionary processes, mountain systems generate local diversification along the altitudinal gradient, but they also affect adjacent areas through dispersal events, enhancing diversification in neighbouring regions (Chazot et al. 2018). In this sense, the Andes are intrinsically related to the evolution of the Amazon basin, through the transition from cratonic to Andean-dominated landscapes since the Oligocene (Hoorn et al. 2010a, 2010b). Temporal connections between the Andean orogeny and Neotropical diversity have been explored through dated phylogenies for more than a decade for different groups (Albert et al. 2006; Antonelli et al. 2009; Brumfield and Edwards 2007). Estimating Andean uplift pulses is a complex issue: Different methods and approaches intend to discover the interplay between tectonic and climatically controlled processes (Barnes et al. 2012; Ehlers and Poulsen 2009; Fiorella et al. 2015; Flantua et al. 2019; Garziona et al. 2017; Martínez et al. 2020; Rohrmann et al. 2016).

Although with regional differences, current evidence suggest that the Andes underwent a marked uplift process starting around 40 Ma during the middle Eocene, due to the subduction of the Nazca Plate under the South American Plate (Armijo et al. 2015). The subsequent uplift pulses of the Central Andean Plateau were at least three: latest Oligocene-early Miocene, middle-late Miocene and late Miocene-early Pliocene and early Pliocene (Garziona et al. 2017; Lamb 2016). These pulses most probably mediated the biotic interchange between the Andes and the Atlantic Forest, originating current disjunct distributions. Among vascular plants, the Andes-Atlantic Forest disjunction is found in several non-related angiosperm taxa (Moreira-Muñoz 2011), such as *Alstroemeria* L. (Chacón et al. 2012), *Escallonia* Mutis (Zapata 2013), *Azara* Ruiz & Pav. (Sleumer 1980), *Mutisia* L.f. (Cabrera 1965) and *Perezia* Lag. (Simpson et al. 2009), being the latter two, members of the Asteraceae.

The pronounced uplift of the Andes since the early Miocene fostered angiosperms' diversification through the generation of vicariant barriers, and the availability of new high-altitude niches, as occurred in different angiosperm families such as Solanaceae (Särkinen et al. 2012), Loasaceae (Strelin et al. 2017) and Fabaceae (Contreras-Ortiz et al. 2018; Scherson et al. 2008). Genera within these families experienced rapid Pliocene speciation associated with diversification of flower morphology and pollination syndromes (Achimón et al. 2018; Scherson et al. 2008). Similar diversification times have been found for several genera in the Asteraceae family such as *Nassauvia*, *Chaetanthera*, *Leucheria* and *Perezia* (Grossi et al. 2017; Hershkovitz et al. 2006; Jara-Arancio et al. 2017; Nicola et al. 2019; Simpson et al. 2009), the tribe Gochnatieae (Funk et al. 2014) and the subtribe Espeletiinae (Diazgranados and Barber 2017; Pouchon et al. 2018), among others.

Due to its disjunct distribution along the Andes and in eastern Brazil, the diversified genus *Mutisia* L. f. (Asteraceae) offers a unique opportunity for better understanding evolutionary processes between the Andean biodiversity hotspots and the Atlantic Forest hotspot. The Asteraceae (or Compositae) is one of the most diverse and widespread plant families along the Andes in South America. The family's putative origin has been proposed in Patagonia, with posterior dispersals along the continent and beyond (Stuessy et al. 1996; Barreda et al. 2012). Nowadays, the family occupies almost all environments, from the wet and hot intertropics to the subantarctic biome. *Mutisia*, the type genus of the Mutisieae tribe and the Mutisioideae subfamily (Katinas et al. 2008a), comprises vines or subshrubs, with attractive bilabiate flowers (Fig. 2). The subfamily Mutisioideae is considered particularly relevant for disentangling evolutionary processes within the Asteraceae, due to its basal placement in the family along with the Barnadesioideae (Ortiz et al. 2009). Within the

**Fig. 1** Collection localities of *Mutisia* species extracted from GBIF, Chilean herbaria (SGO and CONC) and team collections, plotted upon four biodiversity hotspots: (1) Tropical Andes (TA), (2) Chilean Winter Rainfall and Valdivian Forests (CWR), (3) Atlantic Forest (AF) and (4) Cerrado (CE). Disjunct distribution of Andean and AF species is marked with a dotted line



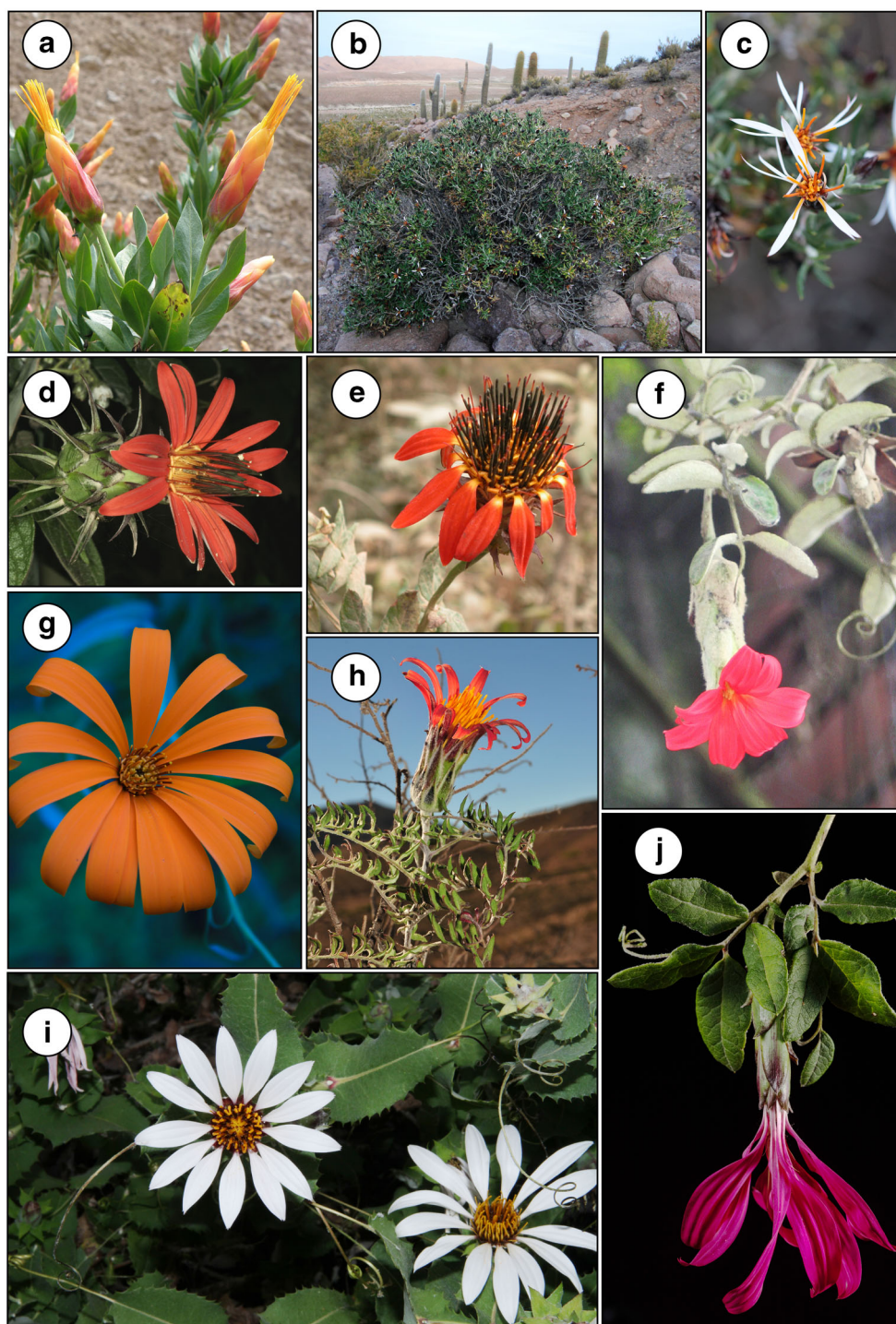
Mutisioideae, the tribe Mutisieae is distributed in South America, Africa and Australia, while the Nassauvieae and Onoserideae are tribes restricted to the Neotropics, some of them reaching subantarctic latitudes (e.g. *Nassauvia* Comm. ex Juss.) (Grossi et al. 2017). The tribe Mutisieae is an early diverging clade within the Compositae (Mandel et al. 2019; Panero and Crozier 2016), and paleobotanic findings tend to reinforce this idea: Morphological features from fossils found in Patagonia resemble taxa phylogenetically close to Mutisioideae sensu lato (Barreda et al. 2012).

The genus *Mutisia* currently encompasses 63 species that grow in South America within two main disjunct areas: the whole Andean chain from Colombia to Patagonia and the Atlantic Forest in eastern Brazil and the surrounding areas of Paraguay, Uruguay and Argentina (Cabrera 1965; Monge 2011). From an ecological point of view, the members of the

genus occupy a broad gradient of Andean ecosystems (e.g. Andean forests, Yungas, páramos, semi-deserts, Altiplano), as well as the Atlantic Forest, from sea level up to 4.500 m (Fig. 1). The main Andean distribution of the genus encompasses around 59 species, while the eastern Brazilian distribution is composed by a group of four very distinctive species (Monge 2011; Moreira-Muñoz et al. 2012) (Figs. 1 and 2).

The members of *Mutisia* have some traits that are very uncommon or unique in the family, such as the vine habit, pinnatifid leaves with tendrils and big radiated capitula with colourful flowers, ranging from red to pink, magenta, orange, yellow and white. Characters used for the division in sections were chromosome number, life form, winged stems, leaf entire/pinnatifid, capitula size, flower morphology and appendices within bracts. Cabrera (1965) divided the genus in six sections, some of them previously considered

**Fig. 2** Morphological diversity in *Mutisia* species pertaining to different sections: **a** *M. orbignyana* (section *Isantha*); **b, c** *M. ledifolia* (section *Fruticosa*); **d** *M. coccinea* (section *Mutisia*); **e** *M. campanulata* (section *Mutisia*); **f** *M. clematis* (section *Mutisia*); **g** *M. decurrens* (section *Guariruma*); **h** *M. hamata* (section *Guariruma*); **i** *M. ilicifolia* (section *Ovata*); and **j** *M. grandiflora* (section *Mutisia*). Photos by Henry Gonzales (**a**), Andrés Moreira-Muñoz (**b, c, g, h, i**), Marcelo Monge (**d**), Gustavo Shimizu (**e**), Mauricio Diazgranados (**f**), Ricardo Jaramillo (**j**)



subgenera: *Isantha* Cabrera, *Holophyllum* Less., *Fruticosa* Cabrera, *Guariruma* (Cass.) Cabrera, *Ovata* Cabrera and *Mutisia* Less. Floral morphology has been considered especially important because fertile disc florets are usually assumed to be ancestral to other types. Cabrera (1965) suggested that *Isantha* was the putative oldest evolutionary section, due to its capitula with isomorphic flowers, different to

the rest of the genus. This section encompasses three species from Argentina, Bolivia and Peru (*M. kurtzii*, *M. orbignyana* and *M. linifolia*) (Fig. 2). The scarlet colour of the ligules of derived taxa like the ones from section *Mutisia* is typically considered suited for ornithophily. The inclined and pendent flowers make them attractive to hummingbirds (Vogel 2015). On the other hand, entomophilous species are to be found

mostly within sections *Ovata*, *Guariruma* and *Holophyllum* (Vogel 2015). The habit and leaf morphology also vary within different sections: *Isantha* and *Fruticosa* encompass shrubby species with entire leaves (Fig. 2), whereas most species and subspecies in *Ovata*, *Guariruma* and *Mutisia* are vines with pinnatifid leaves (Fig. 2). However, the systematic value of these characters and the monophyly of *Mutisia* and its sections remain to be evaluated in the light of molecular phylogenetics, because no phylogenetic study has been conducted so far in the genus. Only few species of *Mutisia* have been included in previous, broader phylogenetic studies (Panero and Funk 2008), which suggest that *Mutisia* is sister to monospecific *Pachylaena* D. Don ex Hook. & Arn.

In this study, we analysed the biogeographic history of the genus *Mutisia* as a principal member of the current disjunction between the Andean and Atlantic Forest biodiversity hotspots. Our specific aims were as follows: (1) to assess the species richness of the genus along the Andes and the Atlantic Forest; (2) to analyse the phylogenetic relationships of the species in *Mutisia*, testing its monophyly, the relationships among sections and its putative sister relation to the genus *Pachylaena*; (3) to estimate divergence times and ancestral ranges of Andean and Atlantic Forest species; and (4) to infer ancestral character states that have been considered of systematic value. Finally, we discuss the results in relation to several challenges in conservation actions within the two biodiversity hotspots hosting the distribution of the genus.

## Materials and methods

### Diversity patterns

The majority of the species data and their occurrence records (8154) were obtained from the Global Biodiversity Information Facility (GBIF), under the Creative Commons Attribution Non Commercial (CC-BY-NC) 4.0 License (Supplementary file 1). Additional data of herbarium specimens and photographic vouchers were provided by Moreira-Muñoz (1879) and Diazgranados (1511). After deleting records without coordinates, with dubious coordinates (including coordinates of country centroids) and duplicates, and reconciling the taxonomy based on Plants of the World Online (<http://www.plantsoftheworldonline.org/>), we obtained a database with 62 species and 2653 clean georeferenced records.

We used SDMtoolbox 2.4 (Brown 2014; Brown et al. 2017), a python-based ArcGIS toolbox for spatial analyses, to estimate species richness (SR), weighted endemism (WE) and corrected weighted endemism (CWE). SR is the sum of unique species per cell. WE corresponds to the sum of the reciprocal of the total number of cells each species in a grid cell is found in. The CWE is simply the WE divided by the

total number of species in a cell. Both WE and CWE emphasize areas that have a high proportion of species with restricted ranges, but in the latter, the areas are not necessarily species rich.

SR, WE and CWE were estimated with a geographic resolution of 0.1 degrees, using ArcMap 10.7. The raster output in tiff format for each analysis was converted into a point shapefile, and an interpolation by a Gaussian process regression (kriging) was performed with a spherical semivariogram and a search radius of 100 cells. The resulting layer was classified using Natural Breaks (Jenks) with 25 classes.

### Taxon sampling for phylogenetic reconstruction and outgroup selection

A total of 43 ingroup taxa (41 species plus one variety and one form), representing 65% of the genus diversity, were sampled in this study. Sequences for three of the ingroup taxa and most outgroups were obtained from GenBank based on already published data (Wagstaff and Breitwieser 2002; Katinas et al. 2008b; Gruenstaeudl et al. 2009; Luebert et al. 2009; Baird et al. 2010; Pelsner et al. 2010; Wagstaff et al. 2011; Jara-Arancio et al. 2018; Sancho et al. 2018; Xu et al. 2018a, b), and the rest of the species were collected in the field, mainly in Central Chile. Vouchers were deposited in several herbaria, namely, B, BONN, GB, LPB, SPU, SGO and UEC. Outgroup taxa were selected to cover the diversity of Mutisioideae based on previous studies (e.g. Luebert et al. 2009; Pasini et al. 2016; Sancho et al. 2018), including especially *Pachylaena atriplicifolia* D. Don ex Hook. & Arn., the putative sister species to *Mutisia* (Panero and Funk 2008; Pasini et al. 2016). We therefore included representatives of the Mutisieae, Nassauvieae and Onoserideae, attempting to cover the generic diversity of these tribes. We also included four species of Barnadesioideae and four representatives of the remaining subfamilies of Asteraceae. All trees were rooted with two species of Calyceraceae, the sister family to Asteraceae (Tank and Donoghue 2010). This outgroup sampling enabled us to place two fossil calibrations for divergence time estimations (see below). All employed sequences with voucher information and GenBank accession numbers are listed in Supplementary file 2.

### DNA extraction, amplification and sequencing

Genomic DNA was isolated from silica gel-dried or herbarium leaves using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA) following the manufacturer's recommendations. Two nuclear rDNA regions were amplified: The internal transcribed spacer (ITS) region was obtained using primers ITS4 and ITS5 (White et al. 1990) and the external transcribed spacer (ETS) region using primers 18S-ETS (Baldwin and Markos 1998) and Ast8 (Markos and Baldwin 2001). In

addition, the chloroplast DNA spacer *trnL-trnF* was amplified using primers “C” and “F” (Taberlet et al. 1991).

For all regions, polymerase chain reaction (PCR) amplification was performed with 12.5  $\mu$ L GoTaq Colorless Master Mix (Promega), 2.5  $\mu$ L of each 10  $\mu$ M primer, 2.5  $\mu$ L of 1 mg/ml BSA, 2  $\mu$ L of DNA template and distilled nuclease free water for a 25  $\mu$ L reaction. The PCR reaction followed the protocols of Bonifacino and Funk (2012) for ITS and ETS and Taberlet et al. (1991) for *trnL-trnF*. All PCR reactions consisted on 35 cycles. Products were purified and sequenced using Applied Biosystems sequencers ABI3700 and ABI3730XL at Macrogen Inc. (Seoul, Korea), using the primers described previously at a 3  $\mu$ M concentration. Both forward and reverse strands were sequenced. Electropherograms of the sequenced products were edited and assembled into contigs using the DNA Baser v4 sequence assembly software (Heracle BioSoft SRL, Pitesti, Romania). Identity of the contigs was confirmed using the BLAST tool implemented in the National Centre for Biotechnology Information website (<http://www.ncbi.nlm.nih.gov/>). The contig sequences were exported as FASTA text files to the alignment software.

### Phylogenetic analyses

For all analyses, the three DNA regions were aligned separately using the L-INS-i method in MAFFT version 7 (Katoch and Standley 2013) followed by manual adjustments and then combined in Mesquite version 3.04 (Maddison and Maddison 2018). The aligned matrix consisted of 76 taxa and 2236 characters. The GTR+I+G model of sequence evolution was used for all regions. In addition to performing analyses for each individual gene, a combined analysis using both a Bayesian approach and maximum likelihood was done in which each region was considered a separate partition. The Bayesian inference was conducted using MrBayes 3.2 (Ronquist et al. 2012). Analyses consisted on two independent runs of 10 million generations with four chains each (three heated and one cold). Trees were saved every 1000 generations in each run. Twenty five percent of the trees were discarded as burn-in. Convergence of the Markov chains was assessed using the following indicators: (1) a stable value of the log likelihood of the cold chain in two separate runs, (2) a value approaching zero for the standard deviation between runs and (3) a value approaching 1.0 for the potential scale reduction factor (PSRF) for each parameter in the model. A 50% majority rule consensus tree was constructed from the non-discarded trees. Support for clades was provided by posterior probabilities estimated from default priors. Maximum likelihood inference was carried out using RaxML version 8 (Stamatakis 2014) with random seeds and allowing the program to estimate the model parameters. Support for clades was provided by rapid bootstrapping search over 1000 iterations. All phylogenetic

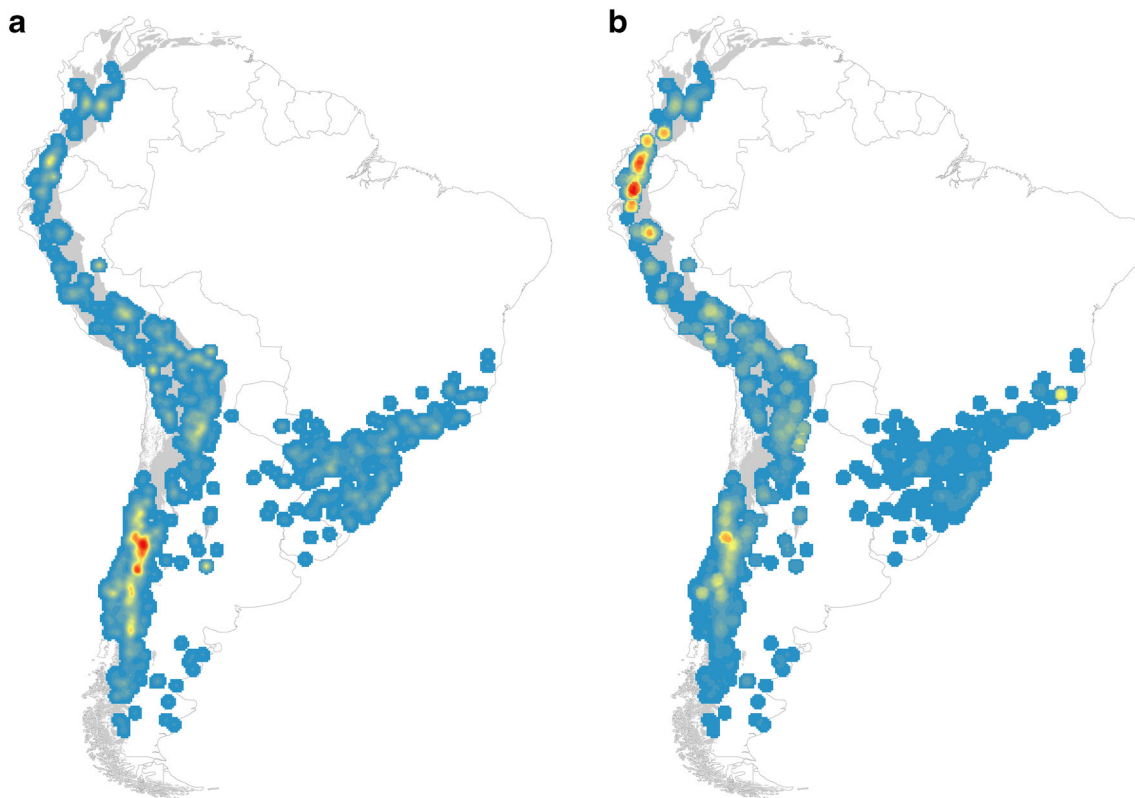
analyses and the model-fitting tests were run in CIPRES (Miller et al. 2010). Clades were considered well-supported when their posterior probability was equal or higher than 95%, and bootstrap support was equal or higher than 90%.

### Divergence time estimation and biogeographical analysis

In order to estimate divergence times, two fossil calibrations were employed. Fossil pollen described from the Campanian/Maastrichtian of Antarctica (83–66 Ma) was originally considered to be related to *Dasyphyllum* Kunth (Barnadesioideae; Barreda et al. 2015). However, its placement in Barnadesioideae appears to be uncertain (Panero 2016; Barreda et al. 2016). Based on these references, we placed a conservative calibration point on the crown node of the Asteraceae using a lognormal distribution with an offset of 66 Ma and log mean of 1.6 Ma which render a median age of 70.95 Ma. A second Asteraceae fossil was described from the middle Miocene of Patagonia and assigned to the Mutisioideae (Barreda et al. 2010, 2012). We therefore placed a calibration point on the stem node of Mutisioideae, which corresponds to the crown node of Asteraceae excluding Barnadesioideae. We used a lognormal distribution, offset of 47.5 Ma and log mean of 1.5, which gives a median age of 51.98 Ma.

We used an uncorrelated clock approach implemented in BEAST v.1.8.4 (Drummond and Rambaut 2007) to estimate divergence times based on the three-marker dataset. Partitions were unlinked with respect to site and clock models. We used the same substitution models as in the MrBayes analysis (i.e. GTR+I+G model). A lognormal clock prior was set for all partitions, and Yule process tree prior was chosen. The Markov chain lasted for 100 million generations sampling every 5000 generations. Convergence was checked with Tracer v.1.7 (Rambaut et al. 2018) ensuring that the ESS was above 200 for all parameters and 10% of the trees were discarded as burn-in. The maximum clade credibility tree with median ages was selected with Tree Annotator v.1.8.4, and the parameters were mapped onto that tree with a posterior probability limit of 0.95.

Ancestral range estimation was conducted with the R package BioGeoBEARS v.1.1.2 (Matzke 2013) using the DEC model originally described by Ree and Smith (2008). We restrained ourselves from employing the DEC+J model (Matzke 2014) in light of recent criticism (Ree and Sanmartín 2018). This analysis was carried out for the clade including *Mutisia* and its sister group, as recovered in the BEAST analysis. We defined five areas that encompass the distribution of this clade: A, northern Andes (N Amotape-Huancabamba zone); B, central Andes (S Amotape-Huancabamba zone to 28° S); C, southern Andes (S 28° S); D, Patagonia (S Argentina and adjacent Chile); and E, Atlantic Forest (SE Brazil and adjacent areas). We set the maximum range size to 2, because this is the maximum number of areas



**Fig. 3** Diversity patterns of *Mutisia*. **a** Species richness map, showing the Andes of Central Chile as the richest area. **b** Corrected weighted endemism map, with the Andes of Ecuador standing out

currently occupied by any species of *Mutisia*, and we set no dispersal constraints. The final results were plotted in R together with the BEAST analysis using the R packages ape v.5.2 (Paradis et al. 2004), phyloch v.1.5-5 (Heibl 2008) and strap 1.4 (Bell and Lloyd 2014).

### Inference of ancestral morphological states and phylogenetic signal

To understand how morphology correlates to phylogeny, five morphological traits were selected to infer the ancestral character states: habit, leaf shape, leaf apex, colour of the ray and colour of the disc flower. These characters were selected, because they have been employed as diagnostic in previous infrageneric classifications (Cabrera 1965). All traits were treated as discrete variables (Supplementary file 3). Character values for these traits were coded based on collected materials, photographs taken in the field, information obtained in the literature (Cabrera 1965, Ulloa Ulloa and Jørgensen 1996, Monge and Semir 2020) and herbarium specimens and complemented with images stored in the GBIF (2018) digital repository.

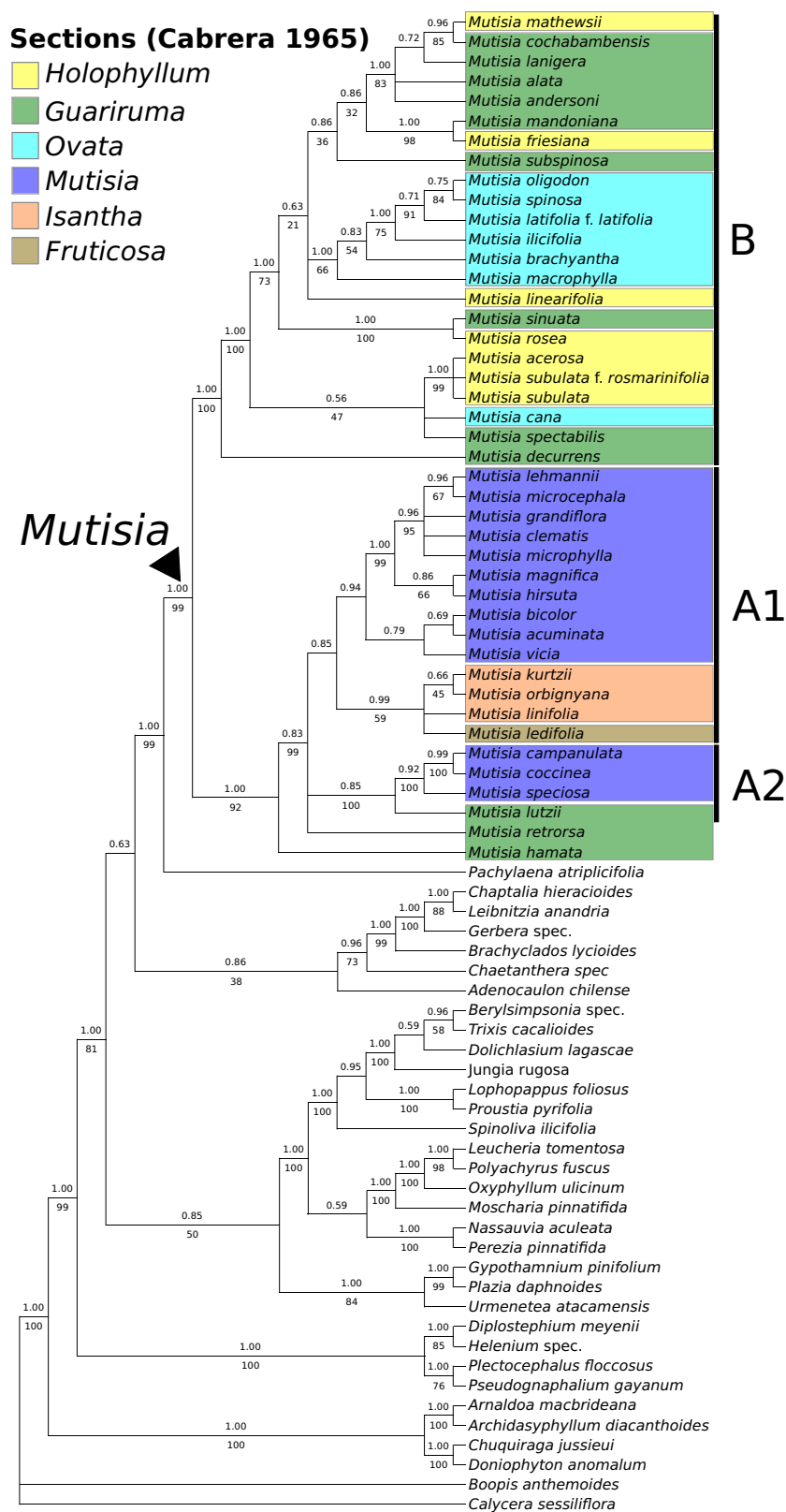
In order to reconstruct ancestral character states accounting for phylogenetic uncertainty and uncertainty in trait values, we used stochastic trait mapping on the phylogeny of *Mutisia* through SIMMAP (Bollback 2006) using the function make.simmap on the package Phytools (Revell 2012) available in R (R Core team

2018). To do that, we used a fully dichotomous tree, where polytomies were arbitrarily transformed in dichotomies. We performed 1000 stochastic trait mapping simulations on the maximum clade credibility tree and plotted the posterior probability of each trait value on the respective node. We selected the best model of trait rate change for each trait using the *ace* function, with the “type = discrete” parameter, from the R package ape (Paradis and Schliep 2019) based on AICc values. All species for which we were unable to code the morphological character states were excluded from the analysis. The phylogenetic signal is the statistical nonindependence among species trait values due to the degree of phylogenetic relatedness (Revell et al. 2008). To estimate this, we selected the function “fitDiscrete” with parameter  $\lambda$  (Pagel 1999) from the R package Geiger (Pennell et al. 2014).

## Results

### Diversity patterns

Based on the clean dataset of georeferenced records (2653 records for 62 species; 98.5% of taxonomic coverage), the centre of species diversity is clearly located along the Andes in Central Chile, between 32 and 37° S, at the core of the Chilean Winter Rainfall and Valdivian Forests (CWR) hotspot (Fig. 3a), encompassing around 19 species



**Fig. 4** Bayesian phylogram obtained by combining nuclear and chloroplast information (ITS, ETS and trnL-F). Thick branches represent clades with higher than 0.95 posterior probabilities (pp) and above 95% bootstrap support (as obtained from a ML analysis). Asterisks represent clades with higher than 0.95 pp but less than 95% bootstrap support. Coloured boxes represent the sections described by Cabrera (1965). The species that are not in boxes have been described after Cabrera's classification. Brackets indicate the main clades mentioned in the text

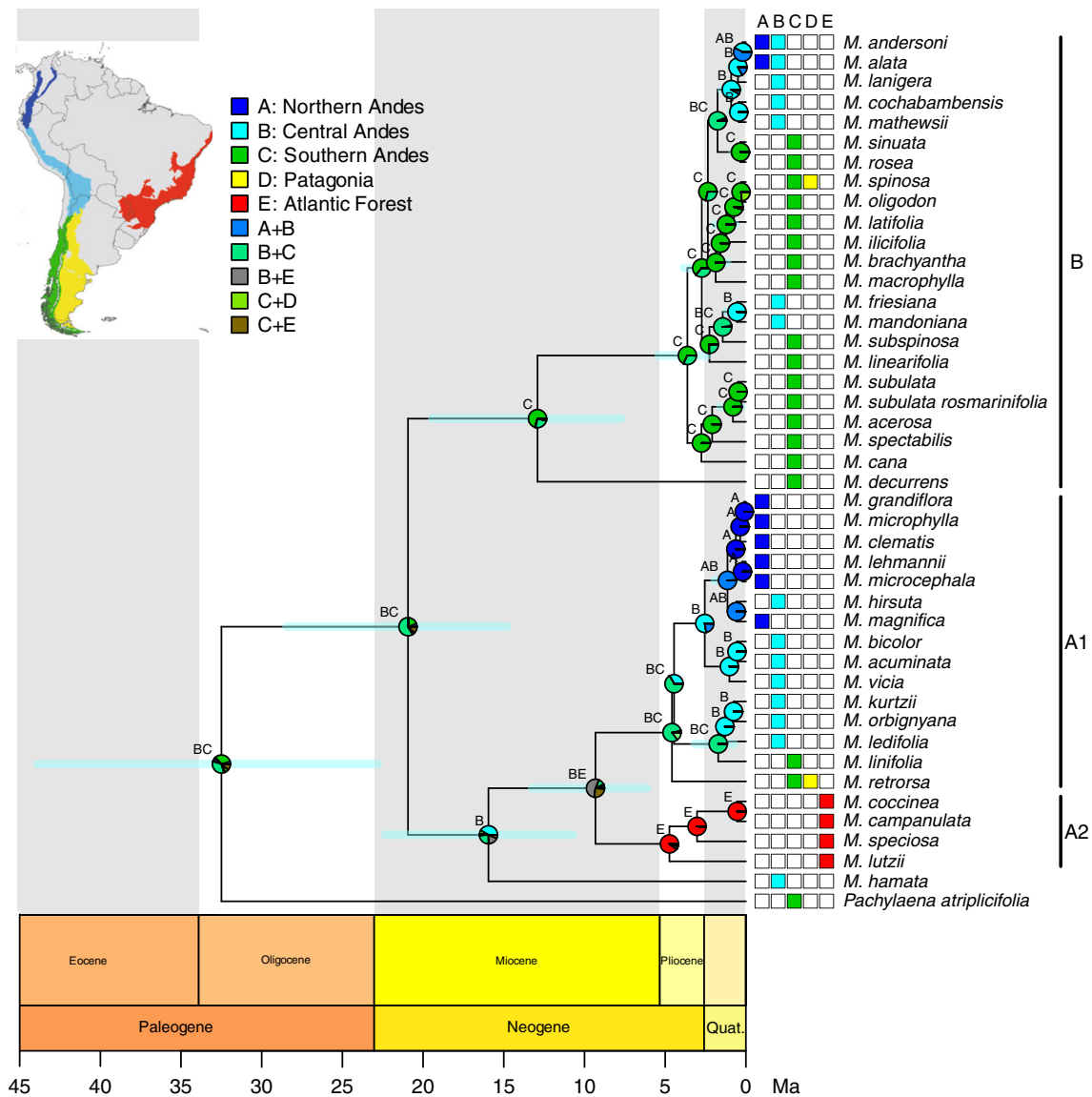


(Moreira-Muñoz et al. 2012). Because of the high species richness, this area is also one of the centres for endemic species of the genus. When estimating the weighted endemism and correcting for the species richness (CWE, Fig. 3b), the Andean region in Ecuador clearly stands out: Most of the 17 species of *Mutisia* reported in this country exhibit narrow distribution areas.

**Phylogenetic analyses**

The nuclear combined dataset (ITS + ETS) provided sufficient information to resolve the phylogenetic relationships with

high support for all major clades. The chloroplast dataset was unable to resolve relationships with high support, but no conflict was observed between the investigated molecular signals of the two cellular compartments. Therefore, we decided to combine the nuclear and chloroplast datasets (ITS + ETS and cpDNA) for the final phylogenetic reconstruction (Fig. 4). *Mutisia* is monophyletic in all the analyses (1 pp/99 bs), with *Pachylaena* as its sister taxon (1 pp/99 bs). Relationships for the backbone tree are well-resolved, and two well-supported main clades were recovered, i.e. clades A and B (Fig. 4). *Mutisia hamata* is the sister species of clade A, which in turn is composed by two clades: A1, comprising species with



**Fig. 5** Divergence times and ancestral range estimates of *Mutisia* and *Pachylaena*. Major clades and the current distribution of species in areas A to E are indicated right and left of the taxon names, respectively. Node bars are 95% HPD intervals of divergences times from the posterior distribution of the BEAST analysis. Pie charts at

nodes represent the probabilities of different ancestral areas as obtained from the DEC analysis and most likely are indicated with letters. Biogeographic units: **A** blue, northern Andes; **B** light blue, central Andes (Altiplano + Yungas); **C** green, southern Andes; **D** yellow, Patagonia; **E** red, Atlantic Forest

mixed origins, with a clade from the northern Andes and a few species from northern South America, and A2 with species from south-eastern Brazil and adjacent areas (*M. lutzii*, *M. speciosa*, *M. coccinea* and *M. campanulata*). *Mutisia decurrens* is the sister species of clade B, which includes all species from the southern Andes (Chile and Argentina) and species from the central Andean Altiplano.

The sections described by Cabrera (1965) were depicted in different colours in the inferred phylogeny (Fig. 4). All sections except for *Isantha* are non-monophyletic in our analyses, even though this must be taken with caution due to incomplete taxon sampling of the genus. *Isantha*, the section that grouped all species bearing capitula with isomorphic flowers, had been described as the basal-most section by Cabrera (1965). In our analyses, however, this section appears in a more derived position, suggesting that capitula with isomorphic flowers might not be a basal condition in this group.

### Divergence times and biogeographical analysis

Divergence time estimates are supplied in Fig. 5 and in Supplementary file 3. The stem node of *Mutisia* was estimated to be 32.5 Ma (95% HPD 22.8–43.9) (Oligocene/Eocene), with an estimated crown node age of 20.9 Ma (95% HPD 14.8–28.5) (late Oligocene/early Miocene). The age crown nodes of clades A and B were estimated to be 15.9 Ma (95% HPD 10.7–22.4) (middle Miocene) and 12.9 Ma (95% HPD 7.7–19.4) (both middle Miocene), respectively. The diversification of all major clades of *Mutisia* is estimated to have taken place from the Miocene to the Pleistocene, between 22 and 2.3 Mya. The main diversification of *Mutisia* occurred in the last 5 Mya.

Ancestral range estimations (Fig. 5) suggest that the ancestor of *Mutisia* originated in the central and southern Andes during the Oligocene/Miocene transition and formed two separate groups during the early Miocene: one restricted to the central Andes (clade A) and the other to the southern Andes (clade B). Within clade A, the Atlantic Forest was colonized by a central Andean ancestor during the middle Miocene and became separated from each other during the late Miocene, in parallel with a recolonization of the southern Andes, also from a central Andean ancestor. The northern Andes would have been reached during the Pliocene from a central Andean ancestor. Patagonia would have been colonized once, probably by a southern Andean ancestor. Within clade B, most lineages remained restricted to the southern Andes, and two independent colonisations of the central Andes appear to have taken place during the Pleistocene. From one of these central Andean ancestors, the northern Andes would have been colonized during the late Pleistocene.

### Morphological evolution and phylogenetic signal

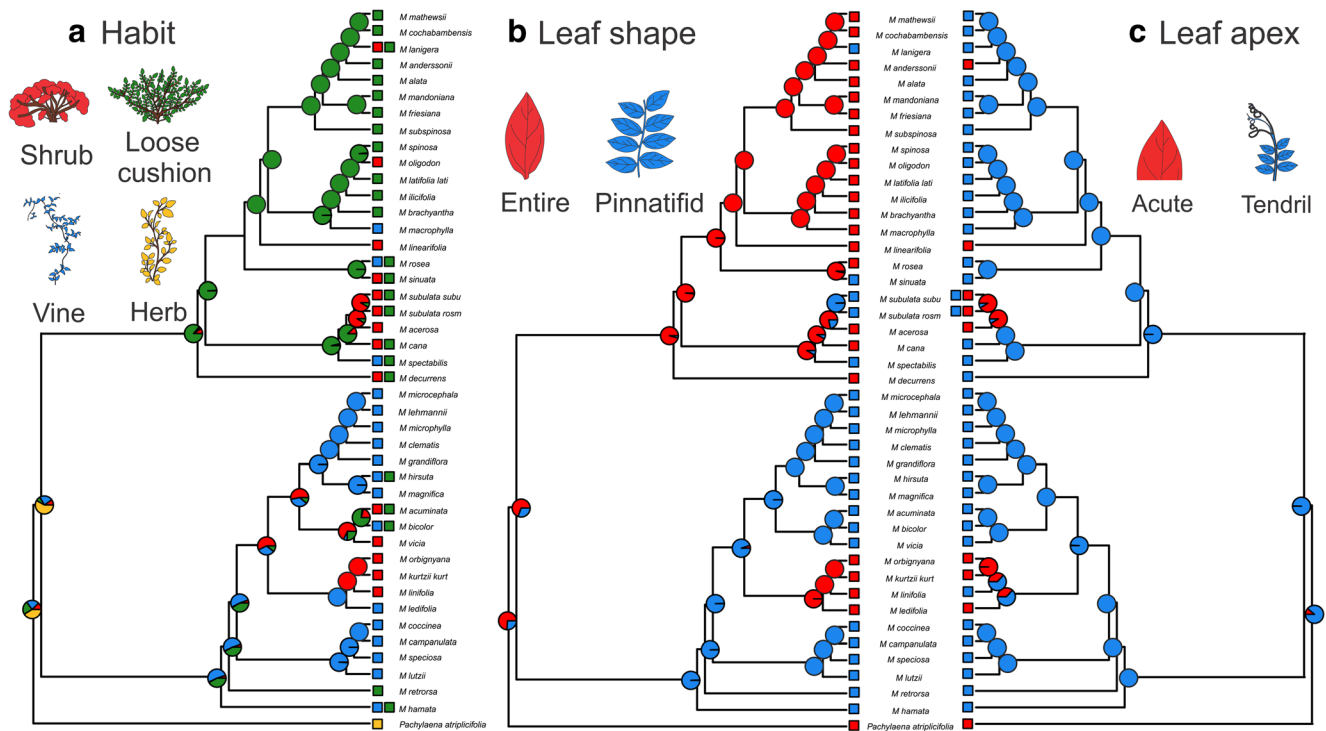
The inference of ancestral traits in *Mutisia* indicates that the most recent common ancestor of the genus had tendrils, entire leaves, and herbaceous habit, but the reconstruction of other traits is uncertain. The estimated transition rates between characters states are available in Supplementary file 4. The reconstruction of all five traits showed a similar pattern, with repeated changes within each clade. The vine habit arose in *Mutisia* independently at least five times and in both clades A and B (Fig. 6a). The ancestral habit of clade A is uncertain, but clade A2 appears to have had a vine habit. Clade A1 shows higher support for ancestral shrubby habit, and the ancestral character state of clade B is loose cushion, with low support (Fig. 6a). Pinnatifid leaf shape evolved independently at least four times in *Mutisia*, also in both clades, even though there is a predominance of pinnatifid leaf shape in clade A and a predominance of entire leaf shape in clade B (Fig. 6b). Leaves with tendrils is a synapomorphy of *Mutisia*, and there are four reversions to acuminate apex, two in clade A1 and three in clade B (Fig. 6c). There is one species (*M. subulata*) with both states, acuminate apex and tendrils. This species has basal leaves without tendrils, but they are present in apical leaves.

Estimates of the phylogenetic signal for all analysed morphological traits are provided in Table 1. The habit showed the highest values of phylogenetic signal ( $\lambda = 95$ ), while the colour of the disc flower has the lowest phylogenetic signal ( $\lambda = 0.50$ ). The inference of ancestral colour of flowers was not recovered for deep nodes, likely due to the high polymorphism present in several species (Supplementary file 4).

## Discussion

### Phylogenetic relationships

Our results provide the first comprehensive hypothesis on phylogenetic relationships and morphological evolution in *Mutisia*. The phylogeny resulting from the combined datasets has considerable broader sampling and higher support than any previous phylogeny proposed for this group (e.g. Panero and Funk 2008). The genus *Mutisia* is monophyletic in all datasets, with *Pachylaena* as its sister group, coinciding with previous studies (Pasini et al. 2016; Katinas et al. 2009; Panero and Funk 2008). According to Pasini et al. (2016), the clade *Pachylaena* + *Mutisia* is the sister group of the remaining Mutisieae, which is also suggested here, even though with low support. Two major, well-supported clades can be recognized in *Mutisia*, here designated as clades A and B. Relationships within the genus are mostly well-resolved and show very little congruence with the original sections



**Fig. 6** Stochastic trait mapping of *Mutisia* and *Pachylaena*. **a** Habit. **b** Leaf shape. **c** Leaf apex. Trait values are indicated to the left and right of the taxon names. Pie charts at nodes represent the probabilities of

different ancestral trait values obtained from SIMMAP reconstruction. In (a) the habit was coded as a shrub

proposed by Cabrera (1965). In fact, all the sections described in his revision of the genus appear to be non-monophyletic in our analysis. Cabrera (1965) considered sections *Isantha* and *Fruticosa* as basal; however, these two sections form a moderately supported group, nested in clade A1.

Most of *Mutisia* section *Ovata* is monophyletic in this analysis within clade B, except for *M. cana*. The species in this section show broad ovate leaves with tendrils, and they are all from southern South America (Chile and Argentina). The presence of tendrils arose in the most recent common ancestor of *Mutisia*, so this is a synapomorphic trait of the genus, and there were only five reversions to acute apex. The association between loose cushion habit and the presence of tendrils might

be an adaptation to the harsh habitats where those species occur.

The remaining sections are non-monophyletic and appear scattered in the phylogeny, propounding that a broad sectional re-circumscription in *Mutisia* is required. Most of the conspicuous morphological traits used by Cabrera (1965) in his classification, such as habit, leaf shape and tendrils, are homoplastic, and therefore, it would not be appropriate to use them in a classification based on monophyly, as we have shown here. These characters likely evolved several times with repeated changes in each clade of the genus. Next generation sequence approaches and an increase in taxon sampling could help to further resolve nodes with weak support towards a definitive infrageneric classification of the genus.

The vast majority of *Mutisia* with shrubby habit have entire leaf blades, but some shrubs have pinnatifid leaves. The species with entire leaf blades also show typical xeromorphic traits, such as coriaceous leaf blade, tough, varnished, with acicular (needle-like) shape. These traits prevent desiccation, increasing the reflection of high luminosity, reducing the leaf area and isolating the leaf tissues from the environment (Damascos et al. 2008). In contrast, the species with vine habit mostly have pinnatifid leaves, and they mostly occur in wet Yungas, Atlantic Forest and central Andes. The colour of ray and disc flowers presented moderately low phylogenetic constraints. However, there is a strong colour lability in *Mutisia*

**Table 1** Estimates of best model of rate change between trait values and phylogenetic signal for morphological traits based on I statistics, with parameters  $\lambda$ , log likelihood (l) and AIC (l)

	Best model	$\lambda$	log likelihood (l)	AIC (l)
Habit	ER	0.95	- 54.32	112.65
Leaf shape	ER	0.89	- 21.938	47.87
Leaf apex	ARD	0.71	- 23.22	63.84
Colour of the ray flower	ER	0.96	- 81.52	167.36
Colour of the disc flower	ER	0.50	- 76.25	156.82

flowers, especially in the ray flowers. Flower colour lability is a well-known pattern in several groups of Angiosperms (Reginato and Michelangeli 2016; Serrano-Serrano et al. 2017), and it is frequently associated with pollination syndromes. Unfortunately, there are just few studies of pollination biology in *Mutisia*, in which six species were reported to be visited by hummingbirds (Buzato et al. 2000); other eight are cited as ornithophilous (Vogel 2015); and three others are visited by bees, flies and butterflies (Arroyo et al. 1982).

As in the case of other non-related taxa like *Anarthrophyllum* (Fabaceae) (Achimón et al. 2018), floral features related to the pollination syndromes could have influenced the more recent diversification of both clades A and B from the Pliocene onwards. Indeed, several high-Andean species of hummingbirds show a similar distribution range, as the case of *Oreotrochilus estella* (Andean Hillstar), showing a similar central Andes distribution as *M. hamata* (the sister to the A clade). Furthermore, diversification of several hummingbird clades took place in the context of the Andean uplift (Chaves et al. 2011; McGuire et al. 2014). However, these coincidences alone do not imply that shifts towards hummingbird pollination have a causal effect on diversification (Abrahamczyk and Renner 2015) and this relationship thus remains to be tested in *Mutisia*.

## Historical biogeography

The origin and diversification of *Mutisia* can be related to specific geologic/climatic events since the early Miocene (Table 2). On the base of our ancestral range estimations, divergence between *Mutisia* and *Pachylaena* occurred in the central and southern Andes during late Oligocene/early Miocene (14.8–28.5 Ma), in relation to one of the strongest uplift pulses (around 23 Ma) (Hoorn et al. 2010b). This is consistent with the idea of Cabrera (1965), who proposed that the centre of origin of *Mutisia* was likely the central Andes. The probable herbaceous ancestral habit of *Mutisia* is, however, elusive. The outgroup (*Pachylaena*) shows herbaceous habit, but all possible habits appear as having roughly the same likelihood at the base of the *Mutisia* clade.

Clades A and B diverged during the Miocene, when there was still suitable habitat connectivity between the Andes and the Atlantic Forest (Prates et al. 2017). Early biogeographic connections between the AF and Amazonia have been widely explored (Costa 2003; Ledo and Colli 2017; Ströher et al. 2019), but possible early connections between the AF and the Andes remain less explored. Biogeographic analyses with highly disjunct, narrowly distributed anole lizards suggest that there were fragments of suitable habitat connecting the Atlantic Forest to western South America along the Miocene (Prates et al. 2017). In plants, the apparent disjunct pattern between the southern Andes and the southern AF is likely the result of a wide range of possible biogeographic histories,

some going back to the late Oligocene and some as recent as the Pleistocene, as shown in a study comparing ten disjunct plant groups (Luebert et al. 2020). In all cases, climatic niche differentiation was detected, but that seems to be clade-specific rather than connected to any common factor. However, none of these groups is distributed in the central or in the northern Andes as is the case of *Mutisia*.

The ancestor of the Atlantic species of *Mutisia* seems to have colonized the AF from the central Andes during the middle Miocene, with a subsequent vicariant event originating the actual Andes/Atlantic disjunction. The Miocene development of the Amazonian-Mega Wetland (Hoorn et al. 2010a) may have had an important effect at its southern part on the (dis)connection between the Andes and the AF. Similar ages as in *Mutisia* have been recovered in other groups having a similar distribution pattern, but the sequence of biogeographic events appears to be clade-specific. In *Alstroemeria*, disjunctly distributed in the southern and central Andes and the AF, the colonization of the AF took place during the middle Miocene, but from a southern Andean ancestor (Chacón et al. 2012). In *Drimys*, disjunct among southern Andes, northern Andes and the AF but notably absent in the central Andes, Marquinez et al. (2009) suggested a middle Miocene separation between the southern Andes and the other areas, followed by an unresolved split between the northern Andes and AF. In *Escallonia*, widely distributed in the Andes and AF, the southern Andes appear to have been colonized by a northern Andean ancestor, followed by a colonization of the AF by a southern Andean ancestor (Zapata 2013). Unfortunately, divergence times have not been estimated in *Escallonia* due to lack of a reliable fossil record (Zapata 2013).

The definitive separation of the Atlantic clade (A2) might have taken place during the late Miocene/early Pliocene, related to another uplift pulse and the consolidation of the arid diagonal. This issue might have been the cause of possible extinctions of species of the Cerrado and the Chaco domains. While there is evidence of more recent reconnections between the Andes and the Atlantic Forest through the Cerrado and Chaco (i.e. in several pulses along the Pleistocene-Holocene (Cabanne et al. 2019; Trujillo-Arias et al. 2017, 2018), the disjunction in *Mutisia* was already established, as it was in other similar cases such as *Alstroemeria* and *Drimys* (see above).

While the central and southern Andes appear to be part of the ancestral range of *Mutisia*, the northern Andes were colonized more recently in its evolutionary history. Two arrivals in the northern Andes out of central Andean ancestors were inferred by the DEC analysis, one in each clade and both during the Quaternary. The idea that the northern Andean distribution of *Mutisia* is the product of secondary radiations from central Andean ancestors was already suggested by Cabrera (1965). In clade A the central Andes appear to be the ancestral area of both southern and northern Andean species, with an earlier dispersal into the southern Andes (late Miocene) and a later colonization of the northern Andes (late Pliocene to Pleistocene). This

**Table 2** Summary of putative environmental events affecting evolutionary events within *Mutisia*

Geological epoch	Evolutionary events in <i>Mutisia</i>	Diversification and habitat conditions	Environmental events
Late Oligocene/early Miocene	Stem age of <i>Mutisia</i> estimated to be 32.5 Ma, with an estimated crown age of 20.9 Ma	Diversification of modern montane plant taxa (genera) (Hoom et al. 2010b; Luebert and Weigend 2014)	Andean building first peaked by the late Oligocene to early Miocene (~ 23 Ma) (Hoom et al. 2010b)
Middle Miocene	Crown age of clades A and B estimated to be 15.9 Ma and 12.9 Ma	Presence of suitable habitat connecting the Atlantic Forest to the Andes (Prates et al. 2017), in accordance with the mid-Miocene Climatic Optimum (Armijo et al. 2015)	Intense peaks of Andean mountain building occurred during the late middle Miocene (~ 12 Ma) (Hoom et al. 2010b) During middle Miocene, gradual uplift of the Eastern Cordillera creates lake Pebas, a huge watershed separating the Amazonas from the Andes (Antonelli et al. 2009).
Late Miocene to Pleistocene	Diversification of major clades of <i>Mutisia</i> estimated between 5 and 2.3 Mya In clade A, early divergence of <i>M. hamata</i> around 16 Ma Divergence of clades A1 and A2 around 9 Ma In clade B, early divergence of <i>M. decurrens</i> around 13 Ma	Andean uplift reinforced pre-existing climatic regime and promoted further aridification within the Altiplano and along the Pacific coast (Rohmann et al. 2016) Increase of plant diversity between ~ 7 and 5 Ma, shortly after the wetlands were replaced by forested habitats in the contact between the Andes and Amazonas (Hoom et al. 2010a)	Reorganization of subtropical ecosystems and hydroclimate in South America between 15 and 35° S (late Miocene) (Carrapa et al. 2019)
Pliocene	Within the Atlantic Forest, divergence between <i>M. lutzii</i> , <i>M. speciosa</i> and the clade including <i>M. coccinea</i> and <i>M. campanulate</i> (clade A2)	Between 4.7–4.2 Ma, permanently humid climate with broad rainforest coverage in western equatorial South America (Grimmer et al. 2018) Earliest evidence of a Puna-like ecosystem (Martínez et al. 2020)	Puna-Altiplano Plateau rising from 2500 to 4000 m a.s.l. (~ 5 Ma to present) (Garziona et al. 2017; Lamb 2016)
Quaternary	Main diversification of <i>Mutisia</i> occurred in the last 2.5 Mya Speciation events within central Andes and southern Andes species in clade B Speciation events within species from northern Andes and central Andes in clade A1	Expansion of arid environments facilitating differentiation through isolation by distance (Achimón et al. 2018)	Pleistocene glacial-interglacial interplay affected distribution ranges and possibly promoted speciation. During LGM the snow line of the E-cordillera of Peru and Bolivia was at 1200 m (present line at ~ 4400 m) (De la Riva et al. 2010)

corresponds to the scenario proposed by Cabrera (1965) for the whole of *Mutisia*. In contrast, in clade B the colonization had been progressed from south to north along the Andes since the middle Miocene, with two colonization events of the central Andes, one of which gave rise to northern Andean species. Altogether, this is coincident with the general Andean uplift trend that progressed from south to north (Gregory-Wodzicki 2000), confirming a tendency observed in other plant groups that may have used the Andes as a dispersal corridor (Luebert and Weigend 2014). These results further suggest that the high levels of diversity and endemism in *Mutisia* in the northern Andes may be the result of recent diversifications, while the high diversity and endemism in Central Chile (southern Andes) is likely the product of relatively older colonisations and in situ diversifications. The trend towards an ancient distribution in the southern Andes and a later colonization of the central and northern Andes has also been shown in other Andes-AF disjunct lineages (e.g. *Astroemeria* and *Drimys*; see above) and has been proposed for

other South American plant groups as distinct as *Perezia* (Simpson et al. 2009) and *Viviania* (Palazzesi et al. 2012). However, the opposite (i.e. an origin in the northern Andes followed by a colonization of the southern Andes) has been suggested for *Escallonia* (Zapata 2013; see above), and other studies likely showing various historical developments of the Andean flora are yet to come out. This reinforces the conclusion of several multi-lineage comparisons (e.g. Luebert and Weigend (2014), Simpson (2014) and Luebert et al. (2020) in South America; Pokorny et al. (2015) and Mairal et al. (2017) in Africa) that similar biogeographic patterns do not necessarily reflect similar underlying biogeographical processes and likely go back to lineage-specific evolutionary histories.

### Conservation implications

The northern (mainly Ecuador) and the southern Andes (mainly Central Chile) can be considered hotspots of biodiversity

for *Mutisia*. Both zones show currently high levels of human impacts, including deforestation, land use changes and urban and agriculture sprawl, as well as intense and ample wildland fires (Bowman et al. 2019). Specifically in the core of the southern spot of richness for *Mutisia*, protected areas are, unfortunately, scarce (Luebert and Plischoff 2017), generating uncertainty regarding potential threats for several species of the genus. While the Tropical Andes hotspot faces many challenges, its long-term conservation relies on the recognition of the interplay between its biodiversity and the Andean culture, including nowadays community-based tree planting practices for forest restoration (da Silva Tomadon et al. 2019; Wilson and Coomes 2019).

In conclusion, our results show the monophyly of the genus *Mutisia*, being its sister group the herbaceous genus *Pachylaena*, diverging during the early Oligocene. A relative early separation between two main clades happened later: the northern/central Andes-Atlantic clade (clade A) and the central/southern Andes clade (clade B) during early Miocene. Then, a posterior separation of the Atlantic clade (A2) from the northern/central Andes clade (A1) at the Miocene/Pliocene transition occurred, followed by a diversification of most species during the Pleistocene. Clade A1 currently includes species distributed in the Ecuadorian and Colombian highlands (páramos and high-Andean forest). It also includes a subclade of the three species bearing capitula with isomorphic flowers (section *Isantha*), which is not the most primitive group as was hypothesized by Cabrera (1965). Our findings suggest a middle Miocene separation of the Andes and Atlantic Forest species, lending support to the early separation of these two main South American biodiversity hotspots.

Andean orogeny likely triggered the diversification and biogeography of genus *Mutisia*, through the arising of vicariant barriers, which also acted as corridors. The uplift of the Andes provided new topographic and climatic conditions and promoted putative specific association to pollinators, favouring further speciation within the genus. As in the case of other Andean taxa, floral features linked to pollination syndromes would have influenced the more recent diversification of both clades A and B from the Pliocene onwards. Nowadays, the genus richness is higher in the Ecuadorian Andes and the southern Andes. Species hotspots identified in this study may contribute with further evidence to support not just the conservation of the *Mutisia* species but also specific areas that are key for the preservation of Andean biodiversity and its unique evolutionary history.

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**Authors' contributions** AM-M, RAS, MM, FL conceived the study. AM-M, FL, MM, MD studied and collected exemplars in the field. RAS, MJR, HS prepared and performed material extraction and analyses. FL, AM-M, MM and MD did complementary analyses and prepared all figures. AM-M, RAS, MM, FL drafted the manuscript. All authors have read and approve the final version of this manuscript.

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