Time-calibrated phylogenies reveal mediterranean and pre-mediterranean origin of the thermophilous vegetation of the Canary Islands

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Running title: *Origin of thermophilous plants from the Canary Islands*

Summary

· **Background and Aims** The Canary Islands have strong floristic affinities with the Mediterranean Basin. One of the most characteristic and diverse vegetation belt of the archipelago is the thermophilous woodland (between 200 and 900 m). This thermophilous plant community consists of many non-endemic species shared with the Mediterranean Floristic Region together with Canarian endemic species. Consequently, phytogeographic studies have historically proposed the hypothesis of a origin of the Canarian thermophilous species following the establishment of the summer-dry mediterranean climate in the Mediterranean Basin around 2.8 million years ago.

· **Methods** Time-calibrated phylogenies for 39 plant groups including Canarian thermophilous species were primarily analysed to infer colonization times. In particular, we used 26 previously-published phylogenies together with 13 time-calibrated phylogenies (including newly generated plastid and nuclear DNA sequence data) to assess whether the time interval between stem and crown ages of Canarian thermophilous lineages postdates 2.8 Ma. For lineages postdating this time threshold, we additionally conducted ancestral area reconstructions to infer the potential source area for colonization.

· **Key Results** A total of 43 Canarian thermophilous lineages were identified from 39 plant groups. Both mediterranean (16) and pre-mediterranean (9) plant lineages were found. However, we failed to determine the temporal origin for 18 lineages because a stem-crown time interval overlaps with the 2.8 Ma threshold. The spatial origin of thermophilous lineages was also heterogeneous, including ancestral areas from the Mediterranean Basin (nine) and other regions (six).

· **Conclusions** Our findings reveal an unexpectedly heterogeneous origin of the Canarian thermophilous species in terms of colonization times and mainland source areas. A substantial proportion of the lineages arrived in the Canaries before the summer-dry climate was established on the Mediterranean Basin. The complex temporal and geographical origin of Canarian thermophilous species challenges the view of the Canary Islands (and Madeira) as a subregion within the Mediterranean Floristic Region.

Keywords: thermophilous woodland, Canary Islands, Mediterranean Floristic Region, colonization times, stem age, crown age, ancestral area, extinction

INTRODUCTION

Oceanic islands emerge lifeless from the seafloor and are usually separated from continents by wide stretches of sea, which means that all of their terrestrial plants have their origin in other landmasses. The Canary archipelago is formed by seven volcanic islands situated c. 100 km off the Saharan coast (north-western Africa). Since their emergence (last 21 million years), plant lineages have colonized the islands from the mainland, grouping together into six main vegetation belts: coastal vegetation, xerophytic shrubland, thermophilous woodland, laurel forest (laurisilva), pine woodland, and alpine legume scrub (del Arco Aguilar and Rodríguez-Delgado 2018). Interestingly, the temporal origin of these floral elements is not well understood. Despite the proximity of the islands to the current Saharo-Arabian Floristic Region (Takhtajan 1986), only some elements of the coastal vegetation and xerophytic shrubland of the Canarian flora are linked to this region (Rivas-Martínez 2009). Iconic tree species of the laurel forest have been traditionally considered both subtropical in origin and surviving representatives of a once more widely distributed Tertiary-Tethyan flora (Bramwell 1976, Mai 1995); a more heterogeneous origin has been lately suggested by Kondraskov et al. 2015. Irrespective of some floristic elements connecting the Canary Islands with floristic regions of the Sahara-Arabia, East/South Africa and America (Quézel 1978, Grehan 2016), most phytogeographers agree that the Canarian flora has a predominant connection with the Mediterranean Floristic Region (MFR).

Since the 18th century, phytogeographers have been discussing whether plants of the Canaries and other Macaronesian archipelagos of the Atlantic Ocean form an independent floristic region (Engler 1879, Sunding 1979, Takhtajan 1986, Bolòs 1996) or a subregion within the MFR (Meusel 1965, Lobin 1982, Rivas-Martínez 2009, del Arco Aguilar and Rodríguez-Delgado 2018). On the one hand, high species endemicity (c. 35 %) and numerous floristic elements linked to several continental floras are considered strong arguments to accept a high-level phytogeographic classification (Macaronesian Floristic Region). On the other hand, a high percentage of Mediterranean elements and lineages are in turn understood as a clear criterion to propose a lower-level phytogeographic classification (Canarian-Madeiran subregion of the MFR). The Mediterranean element is pervasive in the six vegetation belts of the Canaries in such a way that plant lineages exhibiting traits common in mediterranean climates or having their centers of diversity in the Mediterranean Basin are particularly abundant in the pine woodland and the thermophilous woodland (Francisco-Ortega et al. 2002, Rivas-Martínez 2009, White et al. 2020, Albaladejo et al. 2021). Indeed, the thermophilous vegetation is the plant community most associated with the MFR, including some arboreal and shrubby communities named in Spanish after their dominant tree species: "sabinares" (*Juniperus turbinata* subsp. *canariensis* (Guyot & Mathou) Rivas Mart., Wildpret & P.Pérez), "almacigares" (*Pistacia atlantica* Desf.), "lentiscales" (*Pistacia lentiscus* L.), "acebuchales" (*Olea europaea* subsp. *guanchica* P.Vargas, J.Hess, Muñoz Garm. & Kadereit) (Fernández-Palacios et al. 2008, Nezadal and Welss 2009). The last three tree species have sclerophyllous leaves with flexural stiffness and strength (Schimper 1903, Read and Sanson 2003), which characterize the vegetation of the MFR (Rundel et al. 2016, Vargas 2020). All these sources of evidence suggest that phytogeographic origin of Canarian plant lineages may be predominantly associated with the MFR. If so, the question remains as to whether phylogenetic relationships and divergence times of a significant number of species from the thermophilous woodland can provide evidence of a temporal mediterranean origin, i.e., following the establishment of the mediterranean climate across the Mediterranean Basin (Carine et al. 2004, Fernández-Palacios et al. 2008, Vargas 2020).

The establishment of the mediterranean climate across southern Europe and northern Africa 2.8 million years ago (Ma) provides the opportunity to consider a relatively well-defined temporal framework. This temporal threshold (2.8 Ma) is based on independent evidence from palaeoceanographic (Hernández-Molina et al. 2014), palaeoclimatic (Hernández-Molina et al. 2014, Grant et al. 2022), palaeobotanical (Bocquet and Kiefer 1978, Suc 1984, Palmarev 1989; Tzedakis 2007, Postigo et al. 2009, Jiménez- Moreno et al. 2010) and phylogenetic (Fiz-Palacios and Valcárcel 2013 and references within it) evidence that support a 'sharp' climatic event. In particular, the establishment of the Mediterranean climate brought about a significant environmental change because of the concurrence of a drought period during the warm season. Interestingly, this threshold is close to the limit between the Pliocene and Pleistocene (2.6 Ma), as recognised by the International Cronostratigraphic Chart (https://stratigraphy.org/chart). Such a temporal threshold has been used in multiple studies to categorise Mediterranean floristic elements according to their temporal origin (paleo-mediterranean vs. neo-mediterranean; Herrera 1992, Peñuelas et al. 2001, Verdú and al. 2003). In addition, it has been used to test specific hypotheses such as the timing of colonisation of the Canary Islands by certain lineages (Vargas 2007; Salvo et al. 2010), diversification rate shifts (Fiz-Palacios and Valcárcel 2013) and karyotypic changes (Escudero et al. 2018) in combination with time-calibrated phylogenies.

The use of phylogenetic analyses based on DNA sequences to estimate the timing of evolutionary events has become a basic tool in biogeography (Sanmartín 2014). Time can be measured in absolute units when the tree is calibrated with fossils, phylogeny-based secondary calibrations and/or biogeographic events (Forest 2009, Ho and Phillips 2009; see Hipsley and Müller 2014 for alternative calibration approaches). In particular, relaxed-clock Bayesian methods can elucidate a prior distribution on the age of a node, taking into account the uncertainty associated with tree topology, branch length and calibrations (Drummond et al. 2006, Yang and Rannala 2006). This method can be applied to a large number of plant groups, thus helping describe general patterns (Pokorny et al. 2015, Vargas et al. 2018). The time-calibrated phylogenies obtained from Bayesian relaxed-clock methods are often used as input for inferring the ancestral areas from which colonisation may have occurred (e.g. Albaladejo et al 2021). These ancestral area reconstruction analyses give new possibilities for quantitative analysis in island biogeography (Lamm and Redelings, 2009). Thus, applying time-calibrated phylogenetic approaches to investigate divergence of Canarian lineages from their continental relatives may provide valuable insight into the very complex patterns of relationships between the Canary Islands and continental floras (Carine et al. 2004, Kondraskov et al. 2015, Caujapé-Castells et al. 2017, Valente et al. 2017).

Palaeoclimatic, floristic and phytogeographic studies lead us to examine the hypothesis of an origin of Canarian thermophilous species following the establishment of the mediterranean climate across the Mediterranean Basin 2.8 Ma. To test this hypothesis, we firstly analyzed the phylogenetic relationships of thermophilous Canarian lineages and their sister groups using improved phylogenetic datasets in terms of extended taxonomic and geographical sampling. Secondly, we evaluated whether ancestral thermophilous plant lineages had a temporal origin since the mediterranean climate became established around 2.8 Ma (Suc et al. 2018) based on the both newly generated and previously published time-calibrated phylogenies. Thirdly, we implemented ancestral area reconstruction analyses to assess whether colonisation of thermophilous canarian lineages had a potential source area for colonization in the Mediterranean Basin or another geographic area. In sum, we are quantifying at what degree there is a spatio-temporal biogeographic link between the Canarian Flora and the MFR.

MATERIALS AND METHODS

Study area

The thermophilous woodland is a vegetation type characteristic of the Canary Islands. It occurs between the xerophytic vegetation and the laurel forest on the windward slopes (ca. 200-500 m) and between the xerophytic vegetation and the pine woodland on the leeward slopes (ca. 300-900 m) (del Arco et al. 2006, Fernández-Palacios et al. 2008). Its climate fits into mediterranean conditions with annual rainfall between 250 and 450 mm, mostly occurring in winter, and with average temperature between 15º and 19º C, depending on elevation. The thermophilous woodland is defined by some communities dominated by tree species also found in the southern Europe and northern Africa (particularly *Juniperus turbinata*, *Pistacia atlantica*, *Pistacia lentiscus*, *Olea europaea*), which may be accompanied by endemic trees (*Gymnosporia cassinoides* (L'Hér.) Masf., *Dracaena draco* L., *Phoenix canariensis* H.Wildpret, *Sideroxylon canariense* Leyens, Lobin & A.Santos, *Visnea mocanera* L.f.). In addition, a high number of shrub and herb species characterize this vegetation belt (Fernández-Palacios et al. 2008). Unfortunately, this vegetation type is extremely rare in a pristine state because its trees have been eliminated by anthropogenic activity. Chronologically, African human groups colonized the seven the islands, who mostly settled around 2000 years ago, and then a more severe deforestation took place since colonization by European groups (Fernández-Palacios et al. 2008). As a result, currently only 11 % of the original thermophilous woodland is estimated to remain (Fernández-Palacios et al. 2008, Castilla-Beltrán et al. 2021).

Sampling strategy and DNA sequencing

In this study, stem and crown ages were inferred by extending DNA sequence datasets of 13 previously published phylogenies, which included a total of 16 thermophilous species (seven Canarian endemics, five Macaronesian endemics, four non-endemic natives) occurring in the Canary Islands. These previous datasets are heterogeneous and the published phylogenies share some of the following weak points: (1) low support for monophyletic groups including Canarian species; (2) poor sampling of potential mainland sister groups (species/populations); (3) poor sampling of species or populations from the Canary Islands; (4) lack of divergence-time estimations; and (5) need for technical improvement in terms of new methods or calibration points (Table 1). Additionally, stem and crown ages for 26 plant groups with species occurring in the Canarian thermophilous vegetation belt were directly taken from the literature (Supplementary Data Table S1). A total of 39 thermophilous plant groups (i.e., genera, rarely family) were analyzed.

To generate new data on divergence times for 16 thermophilous species, we first obtained 13 DNA sequence datasets from the most comprehensive phylogenetic studies at the genus level (occasionally at family level). Alignments were directly provided by authors of the studies or obtained from the GenBank or TreeBase databases. GenBank accession numbers and geographic origin for all downloaded sequences are available in each publication referenced in Table 1. Second, we extended taxonomic and/or population sampling of those DNA sequence datasets to infer stem and crown nodes for the Canarian species or populations. The new samples were obtained from three sources: field trips, herbarium specimens, and colleagues who contributed with field samples (Supplementary Data Table S2). We tried to sample at least one individual per island where the taxon is present depending on available material and accessibility of populations. We additionally sampled at least one individual from the most closely-related species based on taxonomic information when not available in the DNA sequence database. For non-endemic taxa, we also sampled individuals from at least two populations from nearby continental areas. Many plants of the Canary Islands have a Palearctic origin (Sunding 1979, Carine et al. 2004), and thus we focused our sampling on the archipelagos and mainland regions of Africa and Europe that are close to the Canary Islands, with particular effort on Mediterranean Iberia and northwestern Africa (Valente et al. 2017). Overall, we newly generated 262 DNA sequences from 104 samples of 33 taxa (16 representative thermophilous species and 17 close relatives) and 16 different DNA regions, which were included into the published DNA sequence datasets. Sample information for all specimens and GenBank accession numbers for all new DNA sequences are provided in Supplementary Data Table S2.

DNA was extracted from dried leaves using QIAGEN DNeasy Plant Mini Kit according to the manufacturer's protocol. The sixteen different DNA regions were amplified and sequenced based on previously published studies for each plant group (Supplementary Data Table S2). In particular, we analyzed two nuclear (ETS and ITS), one mitochondrial (PHYC) and 13 plastid DNA regions (*mat*K, *psb*A-*trn*H, *psb*B1-*psb*B2, *rbc*L, *rpl*16, *rpl*32-*trn*L, *rps*4, *trn*D-*trn*T, *trn*K, *trn*L-*trn*F, *trn*L-*trn*F, *trn*S-*trn*G, *trn*V). Primers and PCR cycles applied for each plant group are included in Supplementary Data Table S3. Amplified products were sequenced by standard Sanger sequencing at Macrogen Europe (www.macrogen.com). We used Geneious 2021.2.2 (`https://www.geneious.com`) to edit chromatograms, align sequences with the MUSCLE algorithm (Edgar 2004) and concatenate DNA regions (Table 1). The resulting alignments were checked visually and corrected where the algorithm failed to identify gaps.

Phylogenetic relationships

We applied Bayesian Inference analysis to the 13 DNA sequence datasets to infer the phylogenetic relationships of plant groups with thermophilous species in the Canary Islands. The best-fitting substitution model for each partition (DNA region) was selected using the Akaike Information Criterion implemented in jModelTest v.0.1.1 (Posada 2008). We did not test the congruence between nuclear and plastid matrices because this was already analysed in the previous phylogenetic studies. Thus, we used the phylogenetic dataset (single or combined DNA matrix) that provided the highest phylogenetic resolution in those studies (Table 1; Figs. S1-S13). MrBayes v.3.2.6 (Ronquist et al. 2012) was used in all cases on XSEDE via the CIPRES Science Gateway (`http://www.phylo.org/`) with two simultaneous runs, each with four parallel Markov chains (three hot and one cold), and sampled every 10,000 trees to obtain a total of 10 million generations. The first 25% of trees of each run were discarded (burn-in) and 50% majority-rule consensus trees were constructed. An additional approach using maximum likelihood was implemented in RAxML to obtain an alternative estimate of phylogenetic relationships and support values (see Supplementary Data, Methods S1).

Divergence times

To estimate divergence times of stem and crown nodes for plant groups with thermophilous species in the Canary Islands, we generated 13 new time-calibrated phylogenies using the Bayesian uncorrelated log-normal relaxed clock model in BEAST 1.84 (Drummond and Rambaut 2007). We used the same substitution models already applied for the phylogenetic reconstructions. For each analysis, we ran two independent chains of 100 million generations with a birth–death tree prior, which accounts for both speciation and extinction (Gernhard 2008). All molecular dating analyses in BEAST were performed using the computer cluster Trueno (CSIC, Madrid, Spain). We assessed convergence of chains and appropriate burn-ins with Tracer v.1.7.1 (Rambaut et al. 2018), combined runs using LogCombiner, and produced maximum clade credibility (MCC) trees with mean node heights in Tree Annotator.

Calibration points used to estimate divergence times were based on the fossil record and published secondary calibration points, depending on data availability for each plant group (Supplementary Data Figs. S14-S26). When reliable fossils were available, a lognormal prior on age estimates was used, since this distribution better represents the stratigraphic uncertainty associated with the fossil record (Ho and Phillips 2009). The offset of the lognormal distribution was set to the upper bound of the stratigraphic period where the fossil was found. In the absence of reliable fossils, only secondary calibration points taken from original papers were implemented to the corresponding deep nodes (Table 1). Secondary calibration points were obtained from fossil-calibrated phylogenies of higher taxonomic ranks, which included samples of our study groups (e.g., typically the family to which the genus belongs to), and were assigned normal distribution priors (Ho and Phillips 2009) in the BEAST analysis including the mean and the 95 % highest posterior density (HPD) interval from those studies. A summary of time constraints used for each DNA dataset and their provenance can be found in Supplementary Data Figs. S14-S26.

Colonization times: crown and stem ages

Colonization of the Canary Islands by a lineage have taken place at a time between the stem age and the crown age of the lineage (Fig. 1; Swenson et al. 2014, García-Verdugo et al. 2019a). The stem age, representing the time of divergence between the island lineage and the mainland sister lineage, is most commonly used as an indicator of colonization time (Fig. 1A, see examples in Keeley and Funk 2011, Spalik et al. 2014, Kondraskov et al. 2015, Grover et al. 2017, Schüßler et al. 2019). However, the stem age tends to overestimate colonization time as a result of extinction or incomplete sampling of closely related mainland lineages (Fig. 1B; Mairal et al. 2015, Pillon and Buerki 2017). Alternatively, recent studies are using the crown age, which corresponds to the onset of the divergence from the most recent common ancestor of the lineage within the archipelago, and thus a proxy for the colonization time from the mainland (Fig. 1A; Pokorny et al. 2015, García-Verdugo et al. 2019a). However, the crown age may provide an underestimate of colonization time, due to extinction of island lineages or poor sampling of the archipelago (Fig. 1C; see examples of Canarian lineages potentially affected by extinction in Sanmartín et al. 2008, and García-Verdugo et al. 2019b). Therefore, the crown age represents the minimum age (lower bound) at which colonization of the archipelago from the mainland could have occurred, whereas the stem age represents the maximum age (upper bound) of that event.

To address our working hypothesis, we compared both stem and crown ages with the 2.8 Ma threshold, which marks the establishment of mediterranean climate (Suc 1984). By considering the stem node as upper limit and the crown node as lower limit of colonization time, our approach accounts for the potential impact of lineage extinction and incomplete sampling on colonization time estimates. Based on estimates of stem and crown ages (mean and 95 % HPD intervals) from 26 previously-published and 13 newly-generated phylogenies, we classified 43 Canarian thermophilous lineages into three categories: (1) mediterranean lineages, when stem and thus crown ages postdated the 2.8 Ma threshold (i. e., both the stem and the crown node are mediterranean in time); (2) pre-mediterranean lineages, when crown and thus stem ages predated the 2.8

Ma threshold (i. e., both the stem and the crown ages are pre-mediterranean); and (3) undetermined lineages, for those groups with stem ages falling any time before this threshold (pre-mediterranean stem ages), and crown ages afterwards (mediterranean crown ages) (Fig. 2).

In the context of this hypothesis, the term "mediterranean" is referred to a window of colonization of the Canary Islands after the establishment of the mediterranean climate (temporal origin) in the Mediterranean Basin. This does not necessarily imply that the lineages colonized the thermophilous belt directly from the Mediterranean Basin.. Indeed, the closest mainland taxa for a few of the Canarian lineages are not from the Mediterranean Basin according to the literature (Supplementary Data Table S1). Although both temporal and spatial origins would have ideally to be fulfilled for a lineage to be considered "mediterranean", we classify taxa according to temporal origin rather than geographic origin to address our working hypothesis because the temporal framework allows us to integrate stem age and crown age estimates together and thus partially circumvent the impact of poor sampling, low phylogenetic resolution, extinction and fluctuant limits of the MFR over time (see Discussion).

Nodes could not be unambiguously designated as mediterranean or pre-mediterranean when their 95 % HPD intervals spanned the 2.8 Ma threshold (Fig. 2). For these nodes, a complementary approach was taken (Fig. 3). Marginal probability distributions of divergence times for such nodes were extracted from 100,000 trees using TreeStat v.1.8.4 (Rambaut and Drummond 2016). Then, we used the percentage of occurrence of node ages before or after the 2.8 Ma threshold, following the approach of Vargas et al. (2014). In other words, a node was considered mediterranean when the majority of the marginal probability distribution of the node age postdated the establishment of the mediterranean climate (2.8 Ma), and as pre-mediterranean when the majority of the marginal probability distribution of the node age predated such a threshold (Fig. 3). We chose a 50 % threshold to include the majority of probability distributions (Vargas et al. 2014). For the previously published time-calibrated phylogenies we took a different approach, in which the "mediterranean" or "pre-mediterranean" status of nodes was estimated based on mean values of node ages given by the authors.

In some cases, low phylogenetic resolution and the tree topology hinder estimation of stem and crown ages. For instance, this can happen when posterior probability (PP) of nodes is low (< 0.90), or when multiple representatives of Canarian lineages are placed at distant positions in the tree with low support. These scenarios make it difficult to distinguish between incomplete lineage sorting and multiple colonization events. In such cases, a most inclusive approach was taken, in which we considered the time estimate of the most recent common ancestor (TMRCA) of island and mainland lineages to be an upper bound. Since this TMRCA is equivalent to the stem age (when relationships are resolved), it also represents the maximum age at which the lineage may have colonized the archipelago (Valente et al. 2017).

Ancestral Area Reconstructions

To reconstruct the ancestral distribution range of the lineages with thermophilous species in the Canary Islands (both endemics and non-endemics natives), we employed a model-based maximum-likelihood approach for ancestral area optimization: the dispersal-extinction-cladogenesis (DEC) model implemented in the BioGeoBEARS R package (Matzke, 2013). For the sake of brevity and addressing our working hypothesis, biogeographical reconstructions were conducted using only three geographic areas (A= Mediterranean Basin, B = Macaronesia, C = Other regions) allowing ancestors to be present in a maximum of three areas. We set symmetric dispersal between areas, and constant dispersal rates through time. The analyses were run using the MCC tree of the 13 newly inferred time-calibrated phylogenies (see Materials and Methods, Divergence times) after pruning tips in multi-sampled species in order to represent each species with a single terminal branch. We estimated whether colonisation occurred from the Mediterranean Basin (A, AB, AC, ABC) or from other geographic areas (C, BC) by considering the most likely ancestral distribution range recovered for the stem node of the Canarian lineages (or in the TMRCA when PP of stem nodes were lower than 0.90). As a result, we interpreted that any ancestral range shared by the Mediterranean Basin and the Canary islands indicates an origin from the Mediterranean Basin.

RESULTS

Newly inferred phylogenetic relationships

Our phylogenetic reconstructions based on Bayesian Inference using MrBayes (Figs. S1-S13) and Maximum Likelihood using RAxML (results not shown) are in accordance with previous published phylogenies regarding the topological relationships for the thermophilous species occurring in the Canary Islands. However, the phylogenetic support obtained for temporal divergence using BEAST was higher in most cases (Figs. S14-S26). We following describe well supported clades obtained in BEAST.

Most of the species analyzed formed well-supported monophyletic groups (Figs. 4-6, Supplementary Data Table S1). However, we could not confirm the monophyly of Canarian populations of non-endemic species (i.e., *Ephedra fragilis* Desf., *Juniperus turbinata*, *Pistacia atlantica*, *Pistacia lentiscus*) as well as the endemics *Asparagus umbellatus* Link and *Thesium retamoides* (A.Santos) J.C.Manning & F.Forest (Figs. 4A-4E, Fig. 5C, Fig. 6D, Supplementary Data Table S1). Similarly, sister-group relationships had high statistical support (above 0.90 PP), except for the non-endemic species and for the Macaronesian endemic species *Dracunculus canariensis* Kunth (Figs. 4A-4E, Fig. 6F, Supplementary Data Table S1).

The following phylogenetic relationships within the Canarian groups or between the Canarian species and continental sister groups were documented for the first time: (i) placement of *Asparagus scoparius* Lowe within the clade of *Asparagus nesiotes* Svent. and *Asparagus plocamoides* Webb ex Svent., and of *Asparagus umbellatus* within the clade of *Asparagus fallax* Svent. and *Asparagus arborescens* Willd. ex Schult. & Schult.f.; (ii) close relationship of the two Canarian species of *Gymnosporia* (Wight & Arn.) Hook.f. (*Gymnosporia cassinoides* (L'Hér.) Masf. and *Gymnosporia cryptopetala* Reyes-Bet. & A.Santos), which are sisters to the Madeira endemic *Gymnosporia dryandrii* (Lowe) Masf.; (iii) *Chrysojasminum odoratissimum* (L.) Banfi sister to the mainland clade of *Chrysojasminum parkeri* (Dunn) Banfi, *Chrysojasminum humile* (L.) Banfi, *Chrysojasminum bignoniaceum* (Wall. ex G.Don) Banfi and *Chrysojasminum fruticans* (L.) Banfi; and (iv) the two Canarian species of *Thesium* L. (*Thesium retamoides* and *Thesium subsucculentum* (Kämmer) J.C.Manning & F.Forest) sister to the mainland *Thesium mauritanicum* Batt. (Figs 4-6).

As a result, 16 independent Canary Island colonization events were inferred for the 13 plant groups with thermophilous species analyzed in this study: 10 genera with a single colonization and two with more than one colonization (three of *Pistacia* L. and two of *Asparagus* Tourn. ex L.) (Figs. 4-6, Supplementary Data Table S4). In addition, some lineages displayed cladogenesis in the Canary Islands, including species from other vegetation zones: *Asparagus* lineage I (*A. umbellatus* in the thermophilous woodland, *A. arborescens* in the xerophytic shrubland and *A. fallax* in the laurel forest), *Asparagus* lineage II (*A. scoparius* in the thermophilous woodland, *A. nesiotes* in xerophytic shrubland and *A. plocamoides* in the pine forest), *Gymnosporia* (*G. cassinoides* and *G. cryptopetala* in the thermophilous woodland), and *Thesium* (*T. retamoides* in thermophillous woodland and *T. subsucculentum* in the xerophytic shrubland) (Figs. 4-6). For these cases (i.e., lineages that diversified in different vegetation zones of the Canary Islands), stem and crown ages considered to categorize lineages as mediterranean or pre-mediterranean were those corresponding to the entire Canarian lineage (including thermophilous and non-thermophilous species).

Colonization times

The estimated mean crown ages of the 16 Canarian lineages newly analyzed in this study ranged from 1.07 Ma within *Myrsine excelsa* D.Don to 7.99 Ma within *Sideroxylon canariense*, while mean stem ages ranged from 1.15 Ma for *Pistacia atlantica* to 37.73 Ma for *Sideroxylon canariense* (Figs. 4-6; Supplementary Data Figs. S14-S26, Table S4). These age ranges include five cases in which the TMRCA had to be used: *Asparagus lineage* II, *Ephedra fragilis*, *Juniperus turbinata* subsp. *canariensis*, *Pistacia atlantica* and *Pistacia lentiscus* lineage II. Considering the complete list of 43 lineages (including those with previously published time-calibrated phylogenies), we identified 16 mediterranean lineages, nine pre-mediterranean lineages and

18 undetermined lineages (Table 2, Supplementary Data Table S1). We following describe these results in detail.

Mediterranean lineages (stem ages < 2.8 Ma)

The newly generated phylogenies allowed identification of five thermophilous plant lineages as mediterranean with respect to their colonization times, as their stem ages postdated the 2.8 Ma threshold: *Asparagus* lineage I, *Asparagus* lineage II, *Ephedra fragilis*, *Pistacia atlantica* and *Pistacia lentiscus* lineage II (Fig. 4). Most stem ages accumulated a marginal posterior distribution clearly after the 2.8 Ma threshold, so they were assigned as mediterranean with high statistical support (Supplementary Data Table S4). The highest uncertainty was estimated for the stem nodes of *Asparagus* lineage II, in which only 61 % of the stem age distribution fell in the last 2.8 Ma. Additional studies taken from the literature provided 11 more plant lineages as mediterranean. As a result, a total of 16 of the 43 thermophilous lineages display a clear cut mediterranean origin (from youngest to oldest stem ages; Fig. 7): *Globularia* lineage (0.30 Ma), *Smilax aspera* L. (0.30), *Cistus monspeliensis* L. (0.50), *Brachypodium arbuscula* Gay ex Knoche (0.80), *Erysimum* lineage (0.80), *Pistacia atlantica* (1.15, Fig. 4C), *Ephedra fragilis* (1.29, Fig. 4E), *Convolvulus* lineage II (1.50), *Asparagus* lineage II (1.60, Fig. 4B), *Solanum* lineage (1.70), *Helianthemum* Mill. sect. *Helianthemum* (1.82), *Argyranthemum* lineage (2.20), *Olea europaea* subsp. *guanchica* (2.60), *Malva canariensis* M.F.Ray (2.78) and *Asparagus* lineage I (2.80, Fig. 4A). Although the mean stem age of *Asparagus* lineage I clearly overlaps the mediterranean threshold, the posterior distribution of trees showed that more than 60 % of the stem age distribution and 96 % of crown age distribution in the mediterranean climate period.

Pre-mediterranean lineages (crown ages > 2.8 Ma)

The newly generated phylogenies allowed identification of three of the 16 thermophilous plant lineages as pre-mediterranean, as their crown ages predated the 2.8 Ma threshold: *Sideroxylon canariense*, *Chrysojasminum odoratissimum* and *Thesium* lineage (Fig. 5). Crown ages for the *Chrysojasminum odoratissimum* lineage and *Sideroxylon canariense* accumulated a marginal posterior distribution clearly before 2.8 Ma, so they were assigned as pre-mediterranean with high statistical support (Supplementary Data Table S4). The highest uncertainty was estimated for the crown node of the *Thesium* lineage, in which only 69 % of the age distribution predated 2.8 Ma. Previously published studies revealed six additional pre-mediterranean lineages. As a result, nine of the 43 thermophilous lineages displayed a pre-mediterranean origin (from youngest to oldest crown ages; Fig. 8): *Sideritis* lineage (3.30 Ma), *Echium* lineage (3.70), *Thesium* lineage (3.86), *Chrysojasminum odoratissimum* (4.79), *Euphorbia* sect. *Aphyllis* subsect. *Macaronesicae* Molero & Barres (6.92), *Sideroxylon canariense* (7.99), *Ruta* lineage (8.10), *Crambe* lineage (8.20) and *Sonchus* lineage (8.50).

Undetermined lineages (stem ages > 2.8 Ma, crown ages < 2.8 Ma)

The temporal origin of eight of the 16 thermophilous lineages were undetermined because their stem ages predated and their crown ages postdated the 2.8 Ma threshold: *Bosea yervamora* L., *Bryonia verrucosa* Aiton, *Dracunculus canariensis, Gymnosporia* lineage, *Myrsine excelsa*, *Juniperus turbinata* subsp. *canariensis, Pistacia lentiscus* lineage I and *Rhamnus crenulata* Aiton (Fig. 6). Most of their stem and crown ages accumulated a marginal posterior distribution clearly before and after 2.8 Ma. The highest uncertainty was recorded in the crown node of *Dracunculus canariensis*, in which only 60 % of the trees fell within the last 2.8 Ma time period (Supplementary Data Table S4). Previously published studies also revealed 10 undetermined lineages. In total, the following 18 lineages were classified as undetermined (Figs. 7, 8): *Gonospermum* lineage (mean stem: 3.10 Ma; mean crown: unknown), *Gymnosporia* lineage (mean stem: 3.78 Ma; mean crown: 1.27 Ma; Fig. 6E), *Artemisia* lineage (mean stem: 3.84; mean crown: unknown), *Rhamnus crenulata* (mean stem: 3.88; mean crown: 1.71; Fig. 6B), *Pistacia lentistus* lineage I (mean stem: 3.96; mean crown: 1.15; Fig. 4D), *Myrsine excelsa* (mean stem: 3.98; mean crown: 1.07; Fig. 6G), *Juniperus turbinata* subsp. *canariensis* (mean stem: 4.91, mean crown: unknown; Fig. 6D), *Bryonia verrucosa* (mean stem: 5.19; mean crown: 1.74; Fig. 6C), *Bosea yervamora* (mean stem: 5.69; mean crown: 1.64; Fig. 6A), *Rubia fruticosa* Aiton (mean stem: 6.69; mean crown: 2.10), *Navaea phoenicea* (Vent.) Webb & Berthel. (mean stem: 6.77; mean crown: unknown), *Anagyris latifolia* Brouss. ex Willd. (mean stem: 8.20; mean crown: 1.90), *Cheirolophus* lineage (mean stem: 8.50; mean crown: 1.70), *Hypericum canariense* L. (mean stem: 10.80; mean crown: 1.90), *Dracaena* lineage (mean stem: 11.80; mean crown: 2.30), *Dracunculus canariensis* (mean stem: 12.10; mean crown: 2.76), *Dioscorea edulis* (Lowe) Campos, Wilkin & Viruel (mean stem: 13.48; mean crown: unknown), *Visnea mocanera* (mean stem: 27.00; mean crown: 2.50).

Ancestral Area Reconstructions

Biogeographical analyses supported nine lineages with stem node ranges including the Mediterranean Basin (i.e. *Asparagus* lineage II, *Bosea yervamora*, *Bryonia verrucosa, Dracunculus canariensis*, *Ephedra fragilis*, *Juniperus turbinata*, *Pistacia lentiscus, Rhamnus crenulate* and *Thesium* lineage) and six lineages with stem node ranges not including the Mediterranean Basin (i.e. *Asparagus* lineage I, *Chrysojasminum odoratissimum*, *Gymnosporia* lineage, *Myrsine excelsa, Pistacia atlantica* and *Syderoxylon canariense*) (Figs. 4-6; Supplementary Data Figs. S27-S39, Table S5). No correspondence between the temporal origin of the lineages (mediterranean vs. pre-mediterranean) and the ancestral ranges (including vs. excluding the Mediterranean Basin) was detected in three plant lineages (i.e. *Asparagus* lineage I, *Pistacia atlantica*, *Thesium* lineage).

DISCUSSION

The thermophilous woodland is considered a relatively recent ecosystem, originated after the establishment of the mediterranean climate in the Mediterranean Basin (2.8 Ma; Fernández-Palacios et al. 2008, Rivas-Martínez 2009, del Arco Aguilar and Rodríguez-Delgado 2018). In this study, we provide new divergence time estimates (i.e., stem and crown ages) based on time-calibrated phylogenies for 16 species representative of the thermophilous Canarian vegetation, which we analyzed together with previously-published results from additional 27 thermophilous plant lineages (Figs. 7, 8). In island biogeography, colonization times are more precisely considered to have taken place sometime between the stem and crown ages of the island lineage (Swenson et al. 2014, García-Verdugo et al. 2019a). Based on this phylogenetic principle, our study suggests that the Canarian thermophilous plant community is composed of lineages with an temporal origin both predating (pre-mediterranean) and postdating (mediterranean) the 2.8 Ma threshold considered for the establishment time of the mediterranean climate (Figs. 7, 8; Table 2). In addition, biogeographic reconstruction analyses showed that six of the 16 colonisation events here inferred may have occurred from areas that did not include the Mediterranean Basin by continental ancestors (Figs. 4-6). Taking all these results together, the thermophilous vegetation appears to be a complex assemblage of species with a heterogeneous origin in terms of colonization times and geographical origins.

Pre-mediterranean and mediterranean elements in the thermophilous plant community

As expected by the hypothesis of a mediterranean temporal origin for the Canarian thermophilous species, a considerable number of lineages (16) are estimated to have colonized the archipelago after the establishment of the mediterranean climate (2.8 Ma). Data from meteorological stations (https://www.acanmet.org/) between 200 and 600 m.a.s.l. and climatic variables used for species distribution modeling of thermophilous plants (Coello et al. 2020) indicate that current conditions in the Mediterranean Basin are similar to those of the thermophilous vegetation belt in the Canaries (Rivas-Martínez 2009). Since the late Pliocene (2.8 Ma), a progressive summer aridification of southern Europe and northern Africa may have produced wider distribution that may have facilitated dispersal from the MFR to other areas. There is thus a higher likelihood of dispersal and colonization to neighboring territories such as the Canarian archipelago since then (Meusel 1965, Sunding 1979). That is why trees with one of the most characteristic mediterranean-type syndromes (sclerophylly, a trait displayed mostly in leaves) may have found ideal conditions in the Canaries in the last 2.8 million years (Axelrod 1975, Verdú et al. 2003, Rundel et al. 2016, Vargas et al. 2018). Our results partly support this prediction for the sclerophyllous *Olea europaea* L., *Pistacia atlantica* and *Pistacia lentiscus* lineage II, but provide undetermined results for the sclerophyllous *Rhamnus crenulata* and *Pistacia lentiscus* lineage I. Alternatively, some other tree species (e.g., *Gymnosporia* spp., *Myrsine excelsa*, *Sideroxylon canariense*, *Visnea mocanera*) with leathery leaves and thick cuticles (typically observed in sclerophyllous species) did not display evidence for an origin postdating 2.8 Ma, which did not help support a mediterranean temporal origin for all the trees characterizing the thermophilous vegetation belt.

The relatively old stem and crown ages inferred for some plant lineages clearly indicate a pre-mediterranean origin for a considerable number of the thermophilous species (nine of 43 lineages). Indeed, the following plants appear to have already been present in the Canary Islands before the establishment of the mediterranean climate: *Sideritis* lineage*, Echium* lineage*, Thesium* lineage, *Chrysojasminum odoratissimum, Euphorbia* sect. *Aphyllis* subsect. *Macaronesicae, Sideroxylon canariense, Ruta* lineage*, Crambe* lineage and *Sonchus* lineage (Fig. 7, Table 2). Three non-mutually exclusive hypotheses can be put forward to explain the presence of pre-mediterranean lineages in the current Canarian thermophilous plant community: (i) a direct colonization from the mainland to pre-existent thermophilous vegetation in pre-mediterranean times, (ii) an indirect colonization from other Canarian vegetation types followed by a more recent species differentiation in the thermophilous vegetation and (iii) an old colonisation into non-thermophilous vegetation (on the islands) in pre-mediterranean times and long-term adaptation to thermophilous conditions *in situ* in pre-mediterranean or mediterranean times. The first hypothesis is supported by the fossil record. In particular, fossils of sclerophyllous leaves related to Miocene relicts have been found on the island of Gran Canaria (Anderson et al. 2009). These macrofossils moreover share characteristics with certain representative species of the present-day thermophilous scrub vegetation (e.g., *Cistus* L., *Gymnosporia*, *Euphorbia* L.). However, detailed anatomical investigation of fossil material is required for correct phylogenetic placement (Anderson et al. 2009). Molecular phylogenetic reconstructions and the fossil record are congruent with a Canarian palaeo-flora adapted to semi-arid conditions, scattered over dry slopes and canyons (*barrancos*) in the Canary Islands during pre-mediterranean times. This would be followed by geographical expansion of the species when the climate became more favorable. Indeed, an evolutionary process in which lineages adapted to pre-mediterranean conditions in relatively small, xeric pockets became dominant when mediterranean-like conditions were expanded has already been proposed for plants of the Mediterranean Basin (Barrón et al. 2010, Vargas et al. 2018). The second and third hypotheses are congruent with a pattern of high differentiation into species in different vegetation belts and ecological shifts into thermophilous conditions. This includes some speciation events associated with colonization of the thermophilous woodland, as documented in most of the evolutionary radiations of Canarian plants (e.g., *Sideritis* lineage*, Echium* lineage*, Euphorbia* sect. *Aphyllis* subsect. *Macaronesicae, Crambe* lineage, *Sonchus* lineage; see Supplementary Data Table S1). In any case, these three patterns of evolution could have been operating to ultimately merge into this particularly rich flora.

Impact of extinction on the inferred temporal origin of the thermophilous lineages

The time of origin (mediterranean vs. pre-mediterranean) of 25 out of 43 thermophilous lineages was successfully assigned using the approach proposed in this study, whereas 18 of them remained undetermined due to long temporal gaps between stem and crown ages spanning the 2.8 Ma threshold. These gaps entail a high uncertainty for the inference of colonization times (Cano et al. 2018, García-Verdugo et al. 2019a). The most striking case among those analyzed herein is *Dracunculus canariensis*, for which the difference between stem and crown ages was around 10 million years. An extreme case obtained from the literature is *Visnea mocanera*, which shows a difference between stem and crown ages of ca. 25 million years. Long stem-to-crown intervals have been previously found for other Macaronesian groups (e.g., *Cicer* L., *Campylanthus* Roth), an observation related to high extinction rates by recent studies (Antonelli and Sanmartín 2011, Nagalingum et al. 2011, Pokorny et al. 2015).

High extinction rates in mainland ancestral lineages as a result of abrupt climatic and geological changes (e.g., formation of the Sahara desert, Pleistocene climatic oscillations) has been the most commonly accepted explanation for the temporal gaps between stem and crown ages of Macaronesian lineages (Thiv et al. 2010, Kondraskov et al. 2015). Indeed, the Rand flora (i.e., lineages that exhibit a Canarian-eastern African disjunction) is primarily explained by widespread extinction of central-western Africa lineages rather than long-distance dispersal (Mairal et al. 2015, Pokorny et al. 2015). The extinction of lineages across the mainland may have been more pronounced in Canarian lineages of older temporal origin (i.e. pre-mediterranean and undetermined). Potential extinction coupled with the spatial uncertainty of the geographical boundaries of the MFR in the past (Suc 1984, Suc et al. 2018) makes the reconstruction of ancestral areas a suboptimal approach to evaluate the Mediterranean origin of the Canarian thermophilous species, and their results thus should be taken with caution.

García-Verdugo et al. (2019a) proposed that crown ages may be a more suitable measurement for the time of island colonization than stem ages based on the idea that stem ages are subject to higher temporal and spatial uncertainty as a result of mainland extinction. However, the analysis of crown ages suffers from the same problem of extinction and under-sampling, thus biasing the results to more recent times. The effect of island extinction in crown age estimates may be particularly pronounced in the thermophilous woodland because of multiple causes: (i) erosion and subsidence of flat, oldest islands (Fuerteventura, Lanzarote), which may previously have harbored large areas with this vegetation type (Fernández-Palacios et al. 2008, Martín Osorio et al. 2011); (ii) geological dynamics (eruptions, earthquakes, mega-landslides) (Carracedo et al. 2001, García-Olivares et al. 2017); and most importantly (iii) human land use and destruction of original vegetation (only 11 % currently preserved) between 200 and 600 m.a.s.l. (Fernández-Palacios et al. 2008, Castilla-Beltrán et al. 2021). This extreme reduction of populations, continuing even in our lifetimes, makes thermophilous vegetation the most threatened ecosystem in the Canary Islands (Castilla-Beltrán et al. 2021). This is illustrated by the few remaining individuals of non-endemic species in the thermophilous vegetation belt (*Pistacia lentiscus*, *Ephedra fragilis*), many critically endangered species (e.g., *Anagyris latifolia*, *Crambe scoparia* Svent., *Cheirolophus duranii* (Burchard) Holub, *Dracaena tamaranae* Marrero Rodr., R.S.Almeira & M.Gonzáles-Martin, *Echium handiense* Svent., *Gymnosporia cryptopetala*, *Helianthemum gonzalezferreri* Marrero Rodr., *Helianthemum bramwelliorum* Marrero Rodr., *Solanum lidii* Sunding, *Solanum vespertilio* Aiton subsp. *vespertilio*, *Thesium retamoides*, *Thesium canariense* (Stearn) J.C.Manning & F.Forest) and even several species considered already extinct (e.g., *Helianthemum aguloi* Marrero Rodr. & R.Mesa, *Thesium psilotocladum* Svent.) (Moreno 2010).

Conclusions

The approach proposed here, in which stem and crown ages are evaluated together with respect to a clear-cut threshold (2.8 Ma for the establishment of the mediterranean climate), helps test the hypotheses of temporal origins of evolutionary events even in scenarios with dramatic lineage extinction. In particular, our results provide strong evidence for a heterogeneous temporal origin of the thermophilous woodland in the Canary Islands, which harbors elements of both recent (mediterranean) and ancient Tethyan-Tertiary (pre-mediterranean) origins (Table 2). In addition, several of these colonisation events do not show ancestral areas in the Mediterranean Basin, even in some lineages postdating the establishment of the Mediterranean climate (e.g. *Asparagus* lineage I) (Figs. 4-6). This suggests a sequential history of species colonization and assemblage in the current thermophilous plant community of the Canaries, including a previously underestimated pre-mediterranean origin. A similar pattern has been identified for the laurel forest and xerophytic shrubland (Kondraskov et al. 2015, Sun et al. 2016, Salvo et al. 2010). Given that the thermophilous vegetation contains the highest number of lineages previously considered of mediterranean origin (Rivas-Martínez 2009, del Arco Aguilar and Rodríguez-Delgado 2018; but see Bolòs 1996), we hypothesize that the other five main vegetation belts contain an even lower number of mediterranean-like lineages (Vargas 2020). If this hypothesis was confirmed, the long-lasting view of Macaronesia as a subregion within the MFR would be seriously challenged. Different temporal and geographical origins resulted in a great deal of diversity of the Canarian flora in general, and the thermophilous plant community in particular. Interestingly, this is the most threatened Canarian vegetation belt (Fernández-Palacios et al. 2008; del Arco Aguilar and Rodríguez-Delgado 2018). The endangered status of a few relictual patches requires urgent prioritization for conservation and restoration at the regional, national and international levels.

SUPPLEMENTARY DATA

Supplementary data are available at https://academic.oup.com/aob and consist of the following. Figs. S1-S13. Majority rule consensus trees of the 13 plant groups analysed in this study resulting from applying Bayesian Inference in MrBayes and using previously published phylogenetic datasets (see Table 1) in combination with newly generated sequences (see Table S2). Figs. S14-S26. Time-calibrated phylogenies of the 13 plant groups analysed in this study obtained in BEAST using previously published phylogenetic datasets (see Table 1) in combination with newly generated sequences (see Table S2). Figs. S27-S39. Biogeographic reconstructions of ancestral ranges of the 13 plant groups analysed in this study resulting from applying dispersal–extinction–cladogenesis (DEC) analyses using the BioGeoBEARS R package. Table S1. Information extracted from the literature and obtained in this study for the 43 plant lineages including thermophilous species from the Canary Islands (Macaronesia) for hypothesis testing. Table S2. Studied taxa and their corresponding collection code, voucher information, island (archipelado or country), locality, collection date, collector's name (leg), DNA sequenced regions and GenBank accesion numbers. Table S3. Primers and PCR cycles used for sequencing DNA regions of the 13 plant groups analyzed in this study (genera, seldom families). Table S4. Detailed information (phylogenetic relationships and colonization times) of the 16 lineages with thermophilous species recovered by BEAST analyses of the 13 plant groups of this study. Table S5. Results of the ancestral area reconstruction under the dispersal-extinction-cladogenesis (DEC) analyses performed on the 13 newly generated time-calibrated phylogenies including thermophilous species in the Canary Islands analysed in this study. Methods S1. Details of the maximum likelihood phylogenetic analyses performed in this study.

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LITERATURE CITED

Albaladejo RG, Martín-Hernanz S, Reyes-Betancort JA, Santos-Guerra A, Olangua-Corral M, Aparicio A. 2021. Reconstruction of the spatio-temporal and ecological patterns of dispersal and diversification of *Helianthemum* sect. *Helianthemum* (Cistaceae) in the Canary Islands using Genotyping by Sequencing data. *Annals of Botany* 127: 597–611.

Anderson CL, Channing A, Zamuner AB. 2009. Life, death and fossilization on Gran Canaria – implications for Macaronesian biogeography and molecular dating. *Journal of Biogeography* 36: 2189–2201.

Antonelli A, Sanmartín I. 2011. Mass extinction, gradual cooling, or rapid radiation? Reconstructing the spatiotemporal evolution of the ancient angiosperm genus *Hedyosmum* (Chloranthaceae) using empirical and simulated approaches. *Systematic Biology* 60: 596–615.

Appelhans MS, Paetzold C, Wood KR, Wagner WL. 2020. RADseq resolves the phylogeny of Hawaiian *Myrsine* (Primulaceae) and provides evidence for hybridization. *Journal of Systematics and Evolution* 58: 823–840.

Axelrod DI. 1975. Evolution and biogeography of the Madrean-Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden* 62: 280–334.

Barrón E, Rivas-Carballo R, Postigo-Mijarra JM, et al. 2010. The Cenozoic vegetation of the Iberian Peninsula: A synthesis. *Review of Palaeobotany and Palynology* 162: 382-402.

Bocquet G, Widler B, Kiefer H. 1978. Messinian Model–A new outlook for the floristics and systematics of the Mediterranean area. *Candollea* 33: 269–287.

Bolmgren K, Oxelman B. 2004. Generic limits in *Rhamnus* L. s.l. (Rhamnaceae) inferred from nuclear and chloroplast DNA sequence phylogenies. *Taxon* 53: 383–390.

Bolòs O. 1996. Acerca de la flora macaronésica. *Anales del Jardín Botánico de Madrid* 54: 457–461.

Bramwell D. 1976. The endemic flora of the Canary Islands: distribution, relationships and phytogeography. In: Kunkel G, ed. *Biogeography and Ecology in the Canary Islands*. Dr. W. Junk: The Hague, 207-240.

Cano Á, Bacon CD, Stauffer FW, Antonelli A, Serrano-Serrano ML, Perret M. 2018. The roles of dispersal and mass extinction in shaping palm diversity across the Caribbean. *Journal of Biogeography* 45: 1432-1443.

Carine MA. 2005. Spatio-temporal relationships of the Macaronesian endemic flora: A relictual series or window of opportunity?. *Taxon* 54: 895–903.

Carine MA, Russell SJ, Santos-Guerra A, Francisco-Ortega J. 2004. Relationships of the Macaronesian and Mediterranean floras: molecular evidence for multiple colonizations into Macaronesia and back-colonization of the continent in *Convolvulus* (Convolvulaceae). *American Journal of Botany.* 91: 1070–1085.

Carracedo JC, Rodriguez Badiola E, Guillou H, De La Nuez J, Perez Torrado FJ. 2001. Geology and volcanology of La Palma and El Hierro, Western Canaries. *Estudios Geologicos* 57: 175–273.

Castilla-Beltran A, de Nascimento L, Fernandez-Palacios JM, et al. 2021. Anthropogenic transitions from forested to human-dominated landscapes in southern Macaronesia. *Proceedings of the National Academy of Sciences of the USA* 118: e2022215118.

Caujape-Castells J, Garcia-Verdugo C, Marrero-Rodriguez A, Fernandez-Palacios JM, Crawford DJ, Mort ME. 2017. Island ontogenies, syngameons, and the origins and evolution of genetic diversity in the Canarian endemic flora. *Perspectives in Plant Ecology, Evolution and Systematics* 27: 9–22.

Chen S, Kim DK, Mark WMW, Kim JH. 2013. Networks in a Large-Scale Phylogenetic Analysis: Reconstructing Evolutionary History of Asparagales (Lilianae) Based on Four Plastid Genes. *PLoS ONE* 8: e59472.

Coello AJ, Fernandez-Mazuecos M, Garcia-Verdugo C, Vargas P. 2021. Phylogeographic sampling guided by species distribution modeling reveals the Quaternary history of the Mediterranean-Canarian *Cistus monspeliensis* (Cistaceae). *Journal of Systematics and Evolution* 59: 262-277.

Davis CC, Webb CO, Wurdack KJ, Jaramillo CA, Donoghue MJ. 2005. Explosive radiation of Malpighiales supports a Mid-Cretaceous origin of modern tropical rain forests. *American Naturalist* 165: E36– E65.

del Arco Aguilar MJ, Perez-de-Paz PL, Acebes JR, et al. 2006. Bioclimatology and climatophilous vegetation of Tenerife (Canary Islands). *Annales Botanici Fennici* 43: 167–192.

del Arco Aguilar MJ, Rodriguez-Delgado O. 2018. In: Werger MJA, ed. *Vegetation of the Canary Islands*. Cham, Switzerland: Springer.

Di Vincenzo V, Gruenstaeudl M, Nauheimer L, et al. 2017. Evolutionary diversification of the African achyranthoid clade (Amaranthaceae) in the context of sterile flower evolution and epizoochory. *Annals of Botany* 122: 69–85.

Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. 2006. Relaxed phylogentics and dating with confidence. *PLoS Biology* 4: e88.

Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214.

Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.

Engler A. 1879. Versuch einer Entwicklungsgeschichte der Pflanzenwelt, insbesondere der Florengebiete seit der Tertiarperiode. I. Die extratropischen Gebiete der nordlichen Hemisphare. W. E. Verlag, Leipzig.

Escudero M, Balao F, Martin-Bravo S, Valente L, Valcarcel V. 2018. Is the diversification of Mediterranean Basin plant lineages coupled to karyotypic changes? *Plant Biology* 20: 166–175.

Fernandez-Palacios JM, Otto R, Delgado JD, et al. 2008. Los bosques termofilos de Canarias. Proyecto LIFE04/NAT/ES/000064. Excmo. Cabildo Insular de Tenerife.

Fiz-Palacios O, Valcarcel V. 2013. From Messinian crisis to Mediterranean climate: a temporal gap of diversification recovered from multiple plant phylogenies. *Perspectives in Plant Ecology, Evolution and Systematics* 15: 130–137.

Forest F. 2009. Calibrating the tree of life: fossils, molecules and evolutionary timescales. *Annals of Botany* 104: 789–794.

Francisco-Ortega J, Fuertes-Aguilar J, Kim SC, Santos- Guerra A, Crawford DJ, Jansen RK. 2002. Phylogeny of the Macaronesian endemic *Crambe* section *Dendrocrambe* (Brassicaceae) based on internal transcribed spacer sequences of nuclear ribosomal DNA. *American Journal of Botany* 88:161–169.

Garcia-Olivares V, Lopez H, Patino J, et al. 2017. Evidence for mega-landslides as drivers of island colonization. *Journal of Biogeography* 44: 1053-1064.

Garcia-Verdugo C, Caujape-Castells J, Sanmartin I. 2019a. Colonization time on island settings: Lessons from the Hawaiian and Canary Island floras. *Botanical Journal of the Linnean Society* 191: 155–163.

Garcia-Verdugo C, Caujape-Castells J, Illera JC, et al. 2019b. Pleistocene extinctions as drivers of biogeographical patterns on the easternmost Canary Islands. *Journal of Biogeography* 46: 845–859.

Gernhard T. 2008. The conditioned reconstructed process. *Journal of Theorical Biology* 253: 769–778.

Grant K, Amarathunga U, Amies J, Hu P, Qian Y, Penny T, et al. 2022. Abrupt change in North African hydroclimate and landscape evolution 3.2 million years ago. *Communications Earth & Environment* 3:11.

Grehan JR. 2016. Biogeographic relationships between Macaronesia and the Americas. *Australian Systematic Botany* 29: 447–472

Grover CE, Arick MA 2nd, Conover JL, et al. 2017. Comparative genomics of an unusual biogeographic disjunction in the cotton tribe (Gossypieae) yields insights into genome downsizing. *Genome Biology and Evolution* 9: 3328–3344.

Hernandez-Molina FJ, Stow DA, Alvarez-Zarikian CA, Acton G, Bahr A, Balestra B, et al. 2014. Onset of Mediterranean outflow into the North Atlantic. *Science* 344: 1244–1250.

Herrera CM. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *The American Naturalist* 140: 421–446.

Hipsley CA, Muller J. 2014. Beyond fossil calibrations: Realities of molecular clock practices in evolutionary biology. *Frontiers in Genetics* 5: 1-11.

Ho SYW, Phillips MJ. 2009. Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Systematic Biology* 58: 367–380.

Humboldt A. de. 1814. Atlas geographique et physique des regions equinoxiales du Nouveau Continent, fonde sur des observations astronomiques, des mesures trigonometriques et des nivellements barometriques [1814], Amsterdam-New-York, Theatrum Orbis Terrarum Ltd. et Da Capo Presse Inc, edition de 1971.

Ickert-Bond SM, Rydin C, Renner SS. 2009. A fossil-calibrated relaxed clock for *Ephedra* indicates an Oligocene age for the divergence of Asian and New World clades and Miocene dispersal into South America. *Journal of Systematics and Evolution* 47: 444–456.

Jeyarani JN, Yohannan R, Vijayavalli D, Dwivedi MD, Pandey AK. 2018. Phylogenetic analysis and evolution of morphological characters in the genus *Jasminum* L. (Oleaceae) in India. *Journal of Genetics* 97: 1225-1239.

Jimenez-Moreno G, Fauquette S, Suc JP. 2010. Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. *Review of Palaeobotany and Palynology* 162: 410–415.

Keeley SC, Funk VA. 2011. Origin and evolution of Hawaiian endemics: new patterns revealed by molecular phylogenetic studies. In: Bramwell D, Caujape-Castells, J, eds. *The biology of island floras.* Cambridge: Cambridge University Press, 57–88.

Kondraskov P, Schutz N, Schussler C, et al. 2015. Biogeography of Mediterranean hotspot biodiversity: re-evaluating the 'Tertiary Relict' hypothesis of Macaronesian Laurel forests. *PLoS One* 10: e0132091.

Lamm KS, Redelings BD. 2009. Reconstructing ancestral ranges in historical biogeography: properties and prospects. *Journal of Systematics and Evolution* 47: 369–382.

Lobin W. 1982. Untersuchung uber Flora, Vegetation und biogeographische Beziehungen der Kapverdischen Inseln. Frankfurt, M: CFS 53. 112 p.

Mai DH. 1995. Tertiare Vegetationsgeschichte Europas. Gustav Fischer, Jena, Stuttgart, New York.

Mairal M, Pokorny L, Aldasoro JJ, Alarcon M, Sanmartin I. 2015. Ancient vicariance and climate-driven extinction continental-wide disjunctions in Africa: the case of the Rand Flora genus *Canarina* (Campanulaceae). *Molecular Ecology* 24: 1335–1354.

Mansion G, Rosenbaum G, Schoenenberger N, Bacchetta G, Rossello JA, Conti E. 2008. Phylogenetic analysis informed by geological history supports multiple, sequential invasions of the Mediterranean Basin by the angiosperm family Araceae. *Systematic Biology* 57: 269–285.

Mao K, Hao G, Liu J, Adams RP, Milne RI. 2010. Diversification and biogeography of *Juniperus* (Cupressaceae): variable diversification rates and multiple intercontinental dispersals. *New Phytologist* 188: 254–272.

Martin Osorio VE, Wildpret W, De la Torre W, Scholz S. 2011. Relict ecosystems of thermophilous and laurel forest as biodiversity hotspots in Fuerteventura, Canary Islands. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* 145: 180-185.

Matzke NJ. 2013. Probabilistic historical biogeography: new models for founder- event speciation, imperfect detection, and fossils allow improved accuracy and modeltesting. *Frontiers of Biogeography* 4: 242–247.

Meusel H. 1965. Die Reliktvegetation der Kanarischen Inseln in ihren Beziehungen zur sud- undmitteleuropaischen Flora. In: Gersch M, ed. *Gesammelte Vortrage uber moderne Probleme der Abstammunslehre*, vol. 1. Jena Friedrich-Schiller-Universitat, 17–136.

Moore MJ, Soltis PS, Bell CD, Burleigh G, Soltis DE. 2010. Phylogenetic analysis of 83 plastid genes further resolves the early diversification of eudicots. *Proceedings of the National Academy of Sciences of the USA* 107: 4623–4628.

Moreno J.C. (coord.). 2010. *Lista Roja de la flora vascular espanola.* Actualizacion con los datos de la Adenda 2010 al Atlas y Libro Rojo de la Flora Vascular Amenazada. Direccion General de Medio Natural y Politica Forestal. Ministerio de Medio Ambiente y Medio Rural y Marino y Sociedad Espanola de Biologia de la Conservacion de Plantas: Madrid.

Nagalingum NS, Marshall CR, Quental TB, Rai HS, Little DP, Mathews S. 2011. Recent synchronous radiation of a living fossil. *Science* 334: 796–799.

Nauheimer L, Metzler D, Renner SS. 2012. Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist* 195: 938-950.

Nezadal W, Welss W. 2009. Aportaciones al conocimiento del bosque termofilo en el noroeste de Tenerife (Islas Canarias). In: Beltran Tejera E, Afonso-Carrillo J, Garcia Gallo A, Rodriguez Delgado O, eds. *Homenaje al Profesor Dr. Wolfredo Wildpret de la Torre. Instituto de Estudios Canarios.* La Laguna (Tenerife. Islas Canarias). Monografia LXXVIII. 229-244.

Norup MF, Petersen G, Sandie Burrows S, et al. 2015. Evolution of *Asparagus* L.(Asparagaceae): Out-of-South-Africa and multiple origins of sexual dimorphism. *Molecular Phylogenetics and Evolution* 92: 25–44.

Oberprieler CO. Ott T, Hipper A, et al. 2017. Pleistocene shaping of genetic diversity in a monsoon-affected environment: the case of *Gymnosporia* (Celastraceae) in the southern Arabian Peninsula. *Plant Systematics and Evolution* 303: 1399–1412.

Onstein RE, Carter RJ, Xing YW, Richardson JE, Linder HP. 2015. Do Mediterranean- type ecosystems have a common history?-Insights from the buckthorn family (Rhamnaceae). *Evolution* 69: 756–771.

Palmarev E. 1989. Paleontological evidences of the tertiary history and the origin of the Mediterranean sclerophyll dendroflora. *Plant Systematic and Evolution* 162: 93–107.

Penuelas J, Lloret F, Montoya R. 2001. Severe drought effects on Mediterranean woody flora in Spain. *Forest Science* 47: 214–218.

Pillon Y, Buerki S. 2017. How old are island endemics?. *Biological Journal of the Linnean Society* 121: 469–474.

Pokorny L, Riina R, Mairal M, et al. 2015. Living on the edge: Timing of Rand Flora disjunctions congruent with ongoing aridification in Africa. *Frontiers in Genetics* 6: 154.

Posada D. 2008. jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* 25: 1253–1256.

Postigo Mijarra JM, Barron E, Gomez Manzaneque F, Morla C. 2009. Floristic changes in the Iberian Peninsula and Balearic Islands (south-west Europe) during the Cenozoic. *Journal of Biogeography* 36: 2025–2043.

Quezel P. 1978. Analysis of the flora of Mediterranean and Saharan Africa. *Annals of the Missouri Botanical Garden* 65: 479–534.

Rambaut A, Drummond AJ. 2016. TreeStat v.1.8.4: Tree Statistic Calculation Tool. http://beast.community/.

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904.

Read J, Sanson GD. 2003. Characterizing sclerophylly: the mechanical properties of a diverse range of leaf types. *New Phytologist* 160: 81–99.

Rivas-Martinez S. 2009. Aportaciones al conocimiento del bosque termofilo en el noroeste de Tenerife (Islas Canarias). In: Beltran Tejera E, Afonso-Carrillo J, Garcia Gallo A, Rodriguez Delgado O, eds. *Homenaje al Profesor Dr. Wolfredo Wildpret de la Torre. Instituto de Estudios Canarios.* La Laguna (Tenerife. Islas Canarias). Monografia LXXVIII. pp.255-296.

Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck J. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.

Rose JP, Kleist TJ, Lofstrand SD, Drew BT, Schonenberger J, Sytsma KJ. 2018. Phylogeny, historical biogeography and diversification of angiosperm order Ericales suggest ancient Neotropical and East Asian connections. *Molecular Phylogenetics and Evolution* 122: 59–79.

Rundel PW, Arroyo MTK, Cowling RM, Keeley JE, Lamont BB, Vargas P. 2016. Mediterranean biomes: Evolution of their vegetation, floras, and climate. *Annual Review of Ecology, Evolution and Systematics* 47: 383–407.

Salvo G, Ho SYW, Rosenbaum G, Ree R, Conti E. 2010. Tracing the temporal and spatial origins of island endemics in the Mediterranean region: a case study from the *Citrus* family (Ruta L., Rutaceae). *Systematic Biology* 59: 705–722.

Sanmartin I, van der Mark P, Ronquist F. 2008. Inferring dispersal: a Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. *Journal of Biogeography* 35: 428–449.

Sanmartin I. 2014. Biogeography. In: Vargas P, Zardoya R, eds. *The Tree of Life.* Sunderland, US: Sinauer Associates, Inc., Publishers. 156-166.

Schaefer H, Heibl C, Renner, SS. 2009. Gourds afloat: a dated phylogeny reveals an Asian origin of the gourd family (Cucurbitaceae) and numerous oversea dispersal events. *Proceedings of the Royal Society Biological Sciences* 276: 843–851.

Schimper AFW. 1903. *Plant Geography upon a Physiological Basis.* Oxford, UK: Clarendon Press.

Schussler C, Brauchler C, Reyes-Betancort JA, Koch MA, Thiv M. 2019. Island biogeography of the Macaronesian *Gesnouinia* and Mediterranean *Soleirolia* (Parietarieae, Urticaceae) with implications for the evolution of insular woodiness. *Taxon* 68: 537–556.

Spalik K, Banasiak Ł, Feist MA, Downie SR. 2014. Recurrent short-distance dispersal explains wide distributions of hydrophytic umbellifers (Apiaceae tribe Oenantheae). *Journal of Biogeography* 41: 1559–1571.

Stride G, Nylinder S, Swenson U. 2014. Revisiting the biogeography of *Sideroxylon* (Sapotaceae) and an evaluation of the taxonomic status of *Argania* and *Spiniluma*. *Australian Systematic Botany* 27: 104–118.

Suc JP. 1984 Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature* 307: 429–432.

Suc JP, Popescu M, Fauquette S. 2018. Reconstruction of Mediterranean flora, vegetation and climate for the last 23 million years based on an extensive pollen dataset. *Ecologia mediterranea* 44: 53–85.

Sun Y, Li Y, Vargas-Mendoza CF, Wang F, Xing F. 2016. Colonization and diversification of the *Euphorbia* species (sect. *Aphyllis* subsect. *Macaronesicae*) on the Canary Islands. *Scientific Reports* 6: 34454.

Sunding P. 1979. Origins of the Macaronesian Flora. In: Bramwell D, ed. *Plants and Islands.* New York: Academic Press, 13-40.

Swenson U, Nylinder S, Munzinger J. 2014. Sapotaceae biogeography supports New Caledonia being an old Darwinian island. *Journal of Biogeography* 41: 797-809.

Takhtajan A. 1986. *Floristic regions of the world* (translation by C. Jeffrey). Edinburgh: Oliver and Boyd.

Thiv M, Thulin M, Hjertson M, Kropf M, Linder HP. 2010. Evidence for a vicariant origin of Macaronesian–Eritreo/Arabian disjunctions in *Campylanthus* Roth (Plantaginaceae). *Molecular Phylogenetics and Evolution* 54: 607–616.

Tzedakis PC. 2007. Seven ambiguities in the Mediterranean palaeoenvironmental narrative. *Quaternary Science Reviews* 26: 2042–2066.

Valente L, Illera JC, Havenstein K, Pallien T, Etienne RS, Tiedemann R. 2017. Equilibrium bird species diversity in Atlantic islands. *Current Biology* 27: 1660–1666.

Vargas P. 2007. Are Macaronesian islands refugia of relict plant lineages?: a molecular survey. In Phylogeography of southern European refugia (pp. 297-314). Springer, Dordrecht.

Vargas P, Valente LM, Blanco-Pastor JL, et al. 2014. Testing the biogeographical congruence of palaeofloras using molecular phylogenetics: snapdragons and the Madrean-Tethyan flora. *Journal of Biogeography* 41: 932–943.

Vargas P, Fernández-Mazuecos M, Heleno R. 2018. Phylogenetic evidence for a Miocene origin of Mediterranean lineages: species diversity, reproductive traits, and geographical isolation. *Plant Biology* 20: 157–165.

Vargas P. 2020. The Mediterranean Floristic Region: High Diversity of Plants and Vegetation Types. In: Goldstein MI, DellaSala DA, eds. *Encyclopedia of the World's Biomes*, vol. 3. Elsevier, 602–616.

Verdú M, Dávila P, García-Fayos P, Flores-Hernández N, Valiente-Banuet A. 2003. 'Convergent' traits of Mediterranean woody plants belong to pre-Mediterranean lineages. *Biological Journal of the Linnean Society of London* 78: 415–427.

Volz SM, Renner SS. 2008. Hybridization, polyploidy, and evolutionary transitions between monoecy and dioecy in *Bryonia* (Cucurbitaceae). *American Journal of Botany* 95: 1297–1306.

White OW, Reyes-Betancort J, Chapman MA, Carine MA. 2020. Geographical isolation, habitat shifts and hybridisation in the diversification of the Macaronesian endemic genus *Argyranthemum* (Asteraceae). *New Phytologist* 228: 1953–1971.

Xie L, Yang Z-Y, Wen J, Li D-Z, Yi, T-S. 2014. Biogeographic history of *Pistacia* (Anacardiaceae), emphasizing the evolution of the Madrean-Tethyan and the eastern Asian-Tethyan disjunctions. *Molecular Phylogenenetics and Evolution* 77: 136–146.

Yang Z, Rannala B. 2006. Bayesian estimation of species divergence timesundera molecular clock using multiple fossil calibrations with soft bounds. *Molecular Biology and Evolution* 23: 212–226.

Zhigila DA, Verboom GA, Muasya AM. 2020. An infrageneric classification of *Thesium* (Santalaceae) based on molecular phylogenetic data. *Taxon* 69: 100–123.

Table 1. List of the 16 Canarian thermophilous plant species for which colonization times were newly-inferred for this study. Taxonomic rank, DNA regions and bibliographic references of the DNA sequence datasets used are detailed, as well as calibration approach and bibliographic reference on which the strategy for calculating divergence times is based. The last column indicates the reasons why the original datasets had to be improved, namely: (1) low support for monophyletic groups formed by Canarian species; (2) poor sampling of potential mainland sister groups (species/populations); (3) poor sampling of species or populations from the Canary Islands; (4) lack of divergence-time estimations; and (5) need for technical improvement in terms of new methods or new calibration points. DNA regions marked in bold represent the regions for which we have provided new sequences in this study (more details on the samples included by genus and species in Table S2). * Macaronesian endemics; ** Canarian endemics. Species with no asterisks are non-endemic natives.

Canarian thermophilous species	**Plant group analyzed**
Asparagus scoparius Lowe*	Genus *Asparagus* Tourn. ex
Asparagus umbellatus Link*	
Bosea yervamora L.**	Family Amaranthaceae
Bryonia verrucosa Aiton**	Genus *Bryonia* L. (Cucurbit
Chrysojasminum odoratissimum (L.) Banfi*	Genus *Chrysojasminum* Ban
Dracunculus canariensis Kunth *	Genus *Arum* L. (Araceae)
Ephedra fragilis Desf.	Genus *Ephedra* Tourn. ex L.
Gymnosporia cryptopetala Reyes-Bet. & A.Santos**	Genus *Gymnosporia* (Wight
Gymnosporia cassinoides (L'Hér.) Masf.**	
Juniperus turbinata subsp. *canariensis* (Guyot & Mathou) Rivas Mart., Wildpret & P.Pérez	Genus *Juniperus* L. (Cupress
Myrsine excelsa D.Don*	Genus *Myrsine* L. (Primulac
Pistacia atlantica Desf.	Genus *Pistacia* L. (Anacardi
Pistacia lentiscus L.	
Rhamnus crenulata Aiton **	Genus *Rhamnus* L. (Rhamna
Sideroxylon canariense Leyens, Lobin & A.Santos**	Genus *Sideroxylon* L. (Sapot
Thesium retamoides (A.Santos) J.C.Manning & F.Forest**	Genus *Thesium* L. (Santalac

Table 2. List of mediterranean, pre-mediterranean and undetermined lineages (i.e. colonization events) based on the position of stem and crown ages with respect to the 2.8-million-year-threshold (i.e. establishment of the Mediterranean climate) of the complete list of 43 lineages

Mediterranean	**Pre-mediterranean**	**Undetermined**
Argyranthemum lineage	*Chrysojasminum odoratissimum*	*Anagyris latifolia*
Asparagus lineage I	*Crambe* lineage	*Artemisia* lineage

Asparagus lineage II	*Echium* lineage	*Bosea yervamora*
Brachypodium arbuscula	*Euphorbia* sect. *Aphyllis*	*Bryonia verrucosa*
Cistus monspeliensis	*Ruta* lineage	*Cheirolophus* lineage
Convolvulus lineage II	*Sideritis* lineage	*Dioscorea edulis*
Ephedra fragilis	*Sideroxylon canariense*	*Dracaena* lineage
Erysimum lineage	*Sonchus* lineage	*Dracunculus canariensis*
Globularia lineage	*Thesium* lineage	*Gonospermum* lineage
Helianthemum lineage	*Gymnosporia* lineage	
Malva canariensis	*Hypericum canariense*	
Olea europaea subsp. *guanchica*	*Juniperus turbinata* subsp. *canariensis*	
Pistacia atlantica	*Myrsine excelsa*	
Pistacia lentiscus lineage II	*Navaea phoenicea*	
Smilax aspera	*Pistacia lentiscus* lineage I	
Solanum lineage	*Rhamnus crenulata*	
Rubia fruticosa		
		Visnea mocanera

FIGURE CAPTIONS

Fig. 1. Two approaches typically used to infer colonization times on oceanic island: stem and crown ages. Brown lines represent lineages with mainland distribution while green lines represent lineages with insular distribution. **A**. Graphical representation of stem and crown ages of a hypothetical island lineage (modified from García-Verdugo et al. 2019a). **B**. Impact of assumed extinction or incomplete taxon sampling on the mainland when inferring island colonization times based on stem-age estimates. **C**. Impact of assumed extinction or incomplete taxon sampling on the archipelago when inferring island colonization times based on crown-age estimates.

Fig. 2. Classification of lineages according to divergence times for the Canarian thermophilous plant community, following the methodology proposed in this paper: (1) mediterranean lineages when stem and thus crown ages postdate the 2.8 Ma threshold; (2) pre-mediterranean lineages when crown and thus stem ages predate the 2.8 Ma threshold; and (3) undetermined lineages for those groups with stem ages before and crown ages after this temporal threshold. In these examples, 95% intervals do not span the 2.8 Ma threshold, and therefore nodes can be unambiguously designated as mediterranean or pre-mediterranean.

Fig. 3. Assignment of mediterranean vs. pre-mediterranean nodes when the 95% HPD interval spans the 2.8 Ma threshold: (1) mediterranean nodes, when most of the posterior distribution of trees ($>$ 50 %) provide node ages younger than 2.8 Ma, (2) pre-mediterranean nodes when most of the trees ($>$ 50 %) provide node ages older than 2.8 Ma.

Fig. 4. The five thermophilous lineages of mediterranean origin (stem and therefore crown ages postdate 2.8 Ma) and related Canarian and mainland species from the 13 time-calibrated phylogenies inferred in this study using BEAST. Mean stem and crown ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated. Divergence times of the most recent common ancestor (marked as TMRCA) are also indicated for those groups in which stem and crown nodes showed low phylogenetic support ($PP<0.90$, $BS<70$). Circles at the nodes represent phylogenetic relationships with high posterior Bayesian probability (PP) and/or bootstrap (BS) support values (see legend). Color of plant names indicates vegetation type. Asterisks represent new samples included in the present study. The letters in the stem node or MRCA of the Canarian lineages represent the ancestral ranges inferred for that node by the Ancestral Area Reconstruction Analysis, and correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas).

Fig. 5. The three pre-mediterranean lineages (i.e. crown and thus stem ages predate 2.8 Ma) and related Canarian and mainland species from the 13 time-calibrated phylogenies inferred in this study using BEAST.

Mean stem and crown ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated next to the corresponding nodes. The circles at the nodes represent phylogenetic relationships with high posterior Bayesian probability (PP) and/or bootstrap (BS) support values (see legend). Color of plant names indicates vegetation type. Asterisks represent new samples included in the present study. The letters in the stem node of the Canarian lineages represent the ancestral ranges inferred for that node by the Ancestral Area Reconstruction Analysis, and correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas).

Fig. 6. The seven undetermined lineages (stem ages predating and crown ages postdating 2.8 Ma) and related Canarian and mainland species for the 13 time-calibrated phylogenies inferred in this study using BEAST. Mean stem and crown ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated next to the corresponding nodes. Divergence times of the most recent common ancestor (marked as TMRCA) are indicated for those groups in which stem and crown nodes showed low phylogenetic support (PP<0.90, BS<70). The circles at the nodes represent phylogenetic relationships with high posterior Bayesian probability (PP) and/or bootstrap (BS) support values (see legend). Color of plant names indicates vegetation type. Asterisks represent new samples included in the present study. The letters in the stem node or MRCA of the Canarian lineages represent the ancestral ranges inferred for that node by the Ancestral Area Reconstruction Analysis, and correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas).

Fig. 7. Stem ages of 43 Canarian lineages including thermophilous plant species. Results from the new phylogenies obtained in this study are indicated with plant names in bold (references in Table S1). Blue bars show the 95% intervals, and mean stem ages are marked by a black line.

Fig. 8. Twenty-eight crown ages of Canarian thermophilous plant lineages (i.e., including more than one sample from the Canaries) of the 43 shown in Fig. 7. Results from the new phylogenies obtained in this study are indicated with plant names in bold, while results from previously published time-calibrated phylogenies have non-bold plant names (references in Table S1). Blue bars show the 95% intervals, and mean crown ages are marked by a black line.

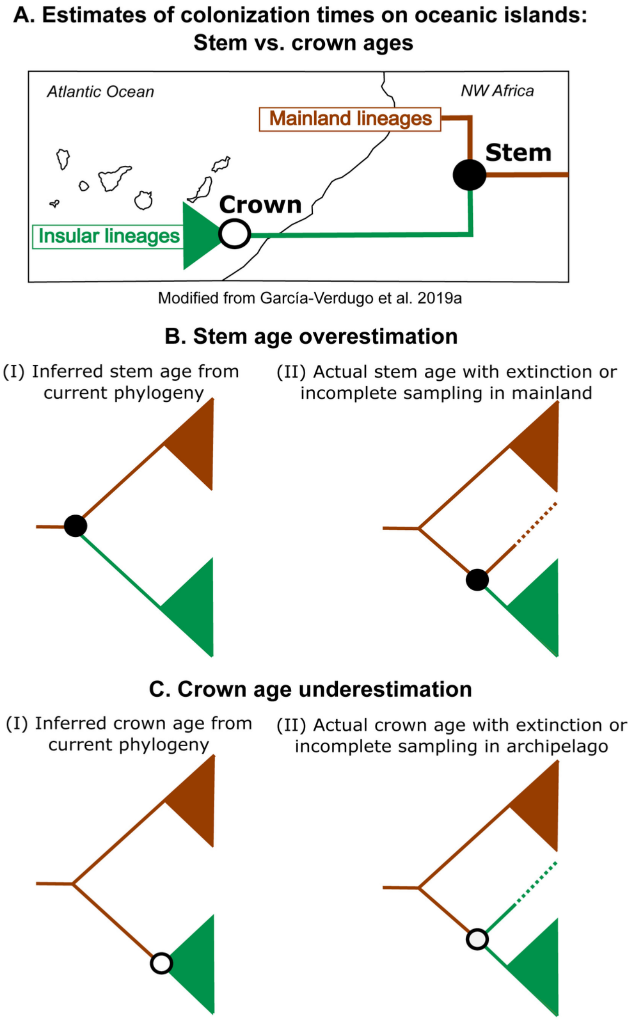

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Figure 1: This is a caption

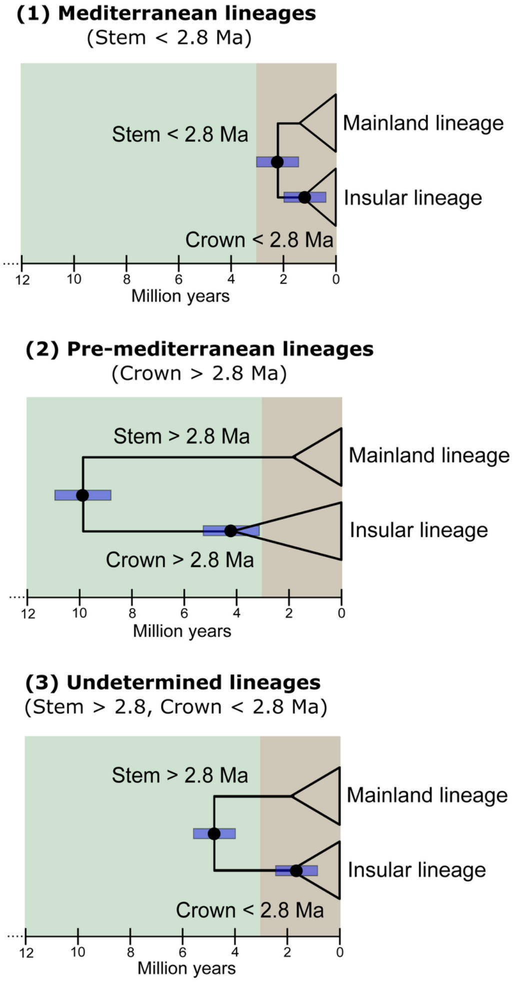

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Figure 2: This is a caption

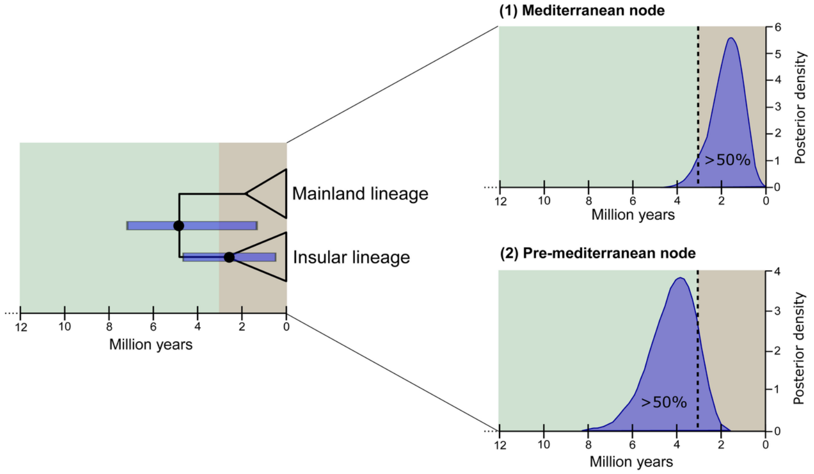

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Figure 3: This is a caption

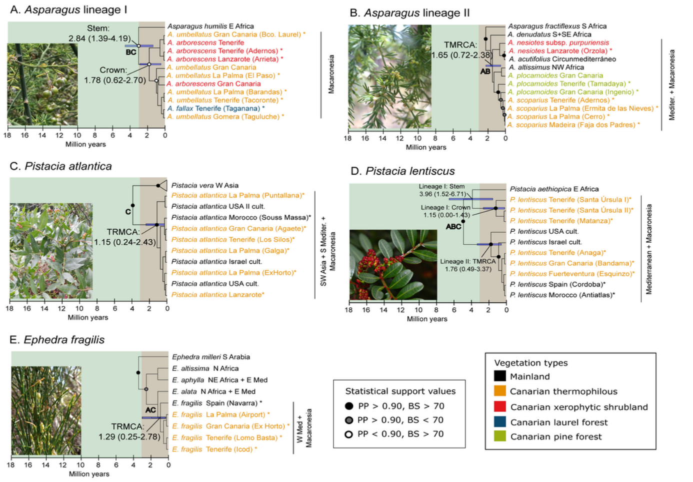

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Figure 4: This is a caption

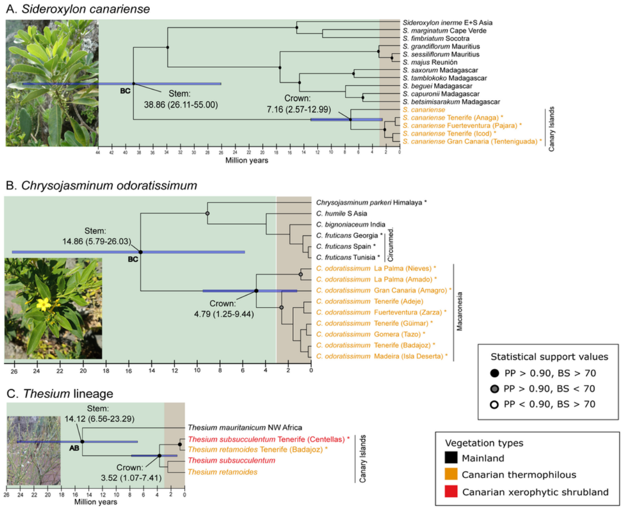

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Figure 5: This is a caption

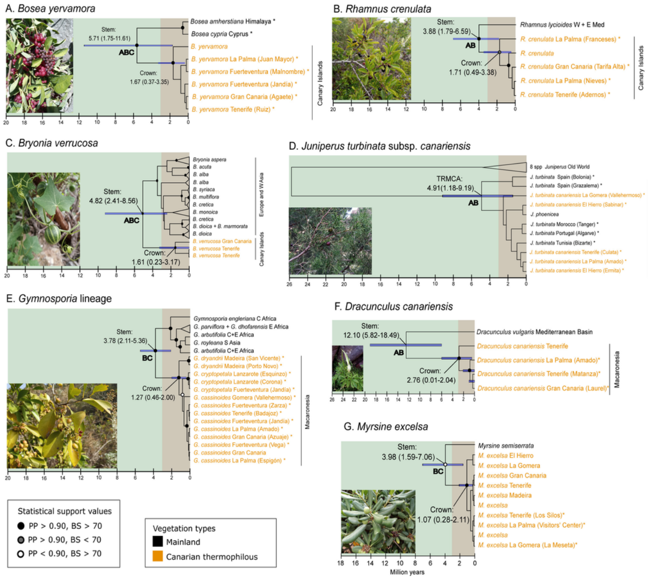

Fig. 6. The seven undetermined lineages (stem ages predating and crown ages postdating 2.8 Ma) and related Canarian and mainland species for the 13 time-calibrated phylogenies inferred in this study using BEAST. Mean stem and crown ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated next to the corresponding nodes. Divergence times of the most recent common ancestor (marked as TMRCA) are indicated for those groups in which stem and crown nodes showed low phylogenetic support (PP<0.90, BS<70). The circles at the nodes represent phylogenetic relationships with high posterior Bayesian probability (PP) and/or bootstrap (BS) support values (see legend). Color of plant names indicates vegetation type. Asterisks represent new samples included in the present study. The letters in the stem node or MRCA of the Canarian lineages represent the ancestral ranges inferred for that node by the Ancestral Area Reconstruction Analysis, and correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas).

Figure 6: This is a caption

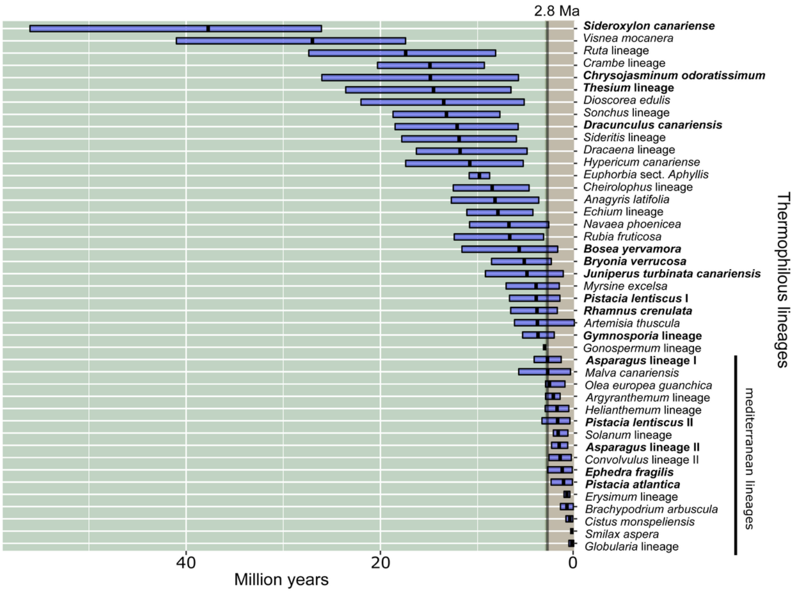

Fig. 7. Stem ages of 43 Canarian lineages including thermophilous plant species. Results from the new phylogenies obtained in this study are indicated with plant names in bold (references in Table S1). Blue bars show the 95% intervals, and mean stem ages are marked by a black line.

Figure 7: This is a caption

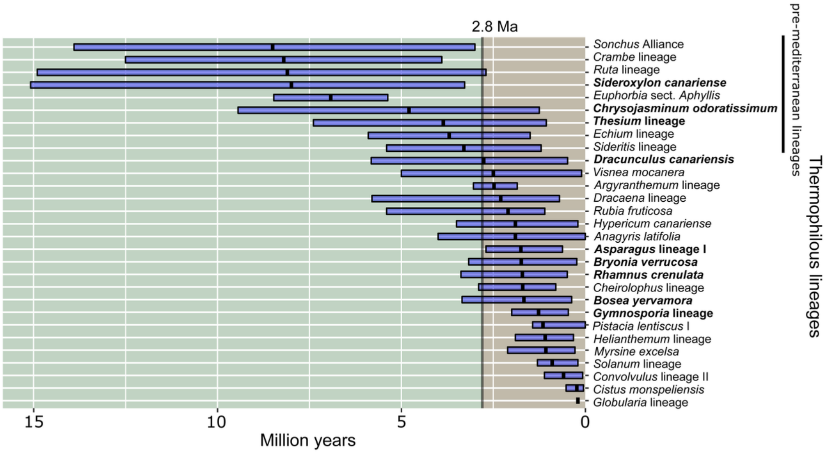

Fig. 8. Twenty-eight crown ages of Canarian thermophilous plant lineages (i.e., including more than one sample from the Canaries) of the 43 shown in Fig. 7. Results from the new phylogenies obtained in this study are indicated with plant names in bold, while results from previously published time-calibrated phylogenies have non-bold plant names (references in Table S1). Blue bars show the 95% intervals, and mean crown ages are marked by a black line.

Figure 8: This is a caption

TYPE OF ARTICLE: Original Article

Time-calibrated phylogenies reveal mediterranean and pre-mediterranean origin of the thermophilous vegetation of the Canary Islands

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Running title: *Origin of thermophilous plants from the Canary Islands*

Summary

- **Background and Aims** The Canary Islands have strong floristic affinities with the Mediterranean Basin. One of the most characteristic and diverse vegetation belt of the archipelago is the thermophilous woodland (between 200 and 900 m). This thermophilous plant community consists of many non-endemic species shared with the Mediterranean Floristic Region together with Canarian endemic species. Consequently, phytogeographic studies have historically proposed the hypothesis of a origin of the Canarian thermophilous species following the establishment of the summer-dry mediterranean climate in the Mediterranean Basin around 2.8 million years ago.
- **Methods** Time-calibrated phylogenies for 39 plant groups including Canarian thermophilous species were primarily analysed to infer colonization times. In particular, we used 26 previously-published phylogenies together with 13 time-calibrated phylogenies (including newly generated plastid and nuclear DNA sequence data) to assess whether the time interval between stem and crown ages of Canarian thermophilous lineages postdates 2.8 Ma. For lineages postdating this time threshold, we additionally conducted ancestral area reconstructions to infer the potential source area for colonization.
- **Key Results** A total of 43 Canarian thermophilous lineages were identified from 39 plant groups. Both mediterranean (16) and pre-mediterranean (9) plant lineages were found. However, we failed to determine the temporal origin for 18 lineages because a stem-crown time interval overlaps with the 2.8 Ma threshold. The spatial origin of thermophilous lineages was also heterogeneous, including ancestral areas from the Mediterranean Basin (nine) and other regions (six).
- **Conclusions** Our findings reveal an unexpectedly heterogeneous origin of the Canarian thermophilous species in terms of colonization times and mainland

source areas. A substantial proportion of the lineages arrived in the Canaries before the summer-dry climate was established on the Mediterranean Basin. The complex temporal and geographical origin of Canarian thermophilous species challenges the view of the Canary Islands (and Madeira) as a subregion within the Mediterranean Floristic Region.

Keywords: thermophilous woodland, Canary Islands, Mediterranean Floristic Region, colonization times, stem age, crown age, ancestral area, extinction

INTRODUCTION

Oceanic islands emerge lifeless from the seafloor and are usually separated from continents by wide stretches of sea, which means that all of their terrestrial plants have their origin in other landmasses. The Canary archipelago is formed by seven volcanic islands situated c. 100 km off the Saharan coast (north-western Africa). Since their emergence (last 21 million years), plant lineages have colonized the islands from the mainland, grouping together into six main vegetation belts: coastal vegetation, xerophytic shrubland, thermophilous woodland, laurel forest (laurisilva), pine woodland, and alpine legume scrub (del Arco Aguilar and Rodríguez-Delgado 2018). Interestingly, the temporal origin of these floral elements is not well understood. Despite the proximity of the islands to the current Saharo-Arabian Floristic Region (Takhtajan 1986), only some elements of the coastal vegetation and xerophytic shrubland of the Canarian flora are linked to this region (Rivas-Martínez 2009). Iconic tree species of the laurel forest have been traditionally considered both subtropical in origin and surviving representatives of a once more widely distributed Tertiary-Tethyan flora (Bramwell 1976, Mai 1995); a more heterogeneous origin has been lately suggested by Kondraskov et al. 2015. Irrespective of some floristic elements connecting the Canary Islands with floristic regions of the Sahara-Arabia, East/South Africa and America (Quézel 1978, Grehan 2016), most phytogeographers agree that the Canarian flora has a predominant connection with the Mediterranean Floristic Region (MFR).

Since the 18th century, phytogeographers have been discussing whether plants of the Canaries and other Macaronesian archipelagos of the Atlantic Ocean form an independent floristic region (Engler 1879, Sunding 1979, Takhtajan 1986, Bolòs 1996) or a subregion within the MFR (Meusel 1965, Lobin 1982, Rivas-Martínez 2009, del Arco Aguilar and Rodríguez-Delgado 2018). On the one hand, high species endemicity (c. 35 %) and numerous floristic elements linked to several continental floras are considered strong arguments to accept a high-level phytogeographic classification (Macaronesian Floristic Region). On the other hand, a high percentage of Mediterranean elements and lineages are in turn understood as a clear criterion to propose a lower-level phytogeographic classification (Canarian-Madeiran subregion of the MFR). The Mediterranean element is pervasive in the six vegetation belts of the Canaries in such a way that plant lineages exhibiting traits common in mediterranean climates or having their centers of diversity in the Mediterranean Basin are particularly abundant in the pine woodland and the thermophilous woodland (Francisco-Ortega et al. 2002, Rivas-Martínez 2009, White et al. 2020, Albaladejo et al. 2021). Indeed, the thermophilous vegetation is the plant community most associated with the MFR, including some arboreal and shrubby communities named in Spanish after their dominant tree species: "sabinares" (*Juniperus turbinata* subsp. *canariensis* (Guyot & Mathou) Rivas Mart., Wildpret & P.Pérez), "almacigares" (*Pistacia atlantica* Desf.), "lentiscales" (*Pistacia lentiscus* L.), "acebuchales" (*Olea europaea* subsp. *guanchica* P.Vargas, J.Hess, Muñoz Garm. & Kadereit) (Fernández-Palacios et al. 2008, Nezadal and Welss 2009). The last three tree species have sclerophyllous leaves with flexural stiffness and strength (Schimper 1903, Read and Sanson 2003), which characterize the vegetation of the MFR (Rundel et al. 2016, Vargas 2020). All these sources of evidence suggest that phytogeographic origin of Canarian plant lineages may be predominantly associated with the MFR. If so, the question remains as to whether phylogenetic relationships and divergence times of a significant number of species from the thermophilous woodland can provide evidence of a temporal mediterranean origin, i.e., following the establishment of the mediterranean climate across the Mediterranean Basin (Carine et al. 2004, Fernández-Palacios et al. 2008, Vargas 2020).

The establishment of the mediterranean climate across southern Europe and northern Africa 2.8 million years ago (Ma) provides the opportunity to consider a relatively well-defined temporal framework. This temporal threshold (2.8 Ma) is based on independent evidence from palaeoceanographic (Hernández-Molina et al. 2014), palaeoclimatic (Hernández-Molina et al. 2014, Grant et al. 2022), palaeobotanical (Bocquet and Kiefer 1978, Suc 1984, Palmarev 1989; Tzedakis 2007, Postigo et al. 2009, Jiménez-Moreno et al. 2010) and phylogenetic (Fiz-Palacios and Valcárcel 2013 and references within it) evidence that support a 'sharp' climatic event. In particular, the establishment of the Mediterranean climate brought about a significant environmental change because of the concurrence of a drought period during the warm season. Interestingly, this threshold is close to the limit between the Pliocene and Pleistocene (2.6 Ma), as recognised by the International Cronostratigraphic Chart (https://stratigraphy.org/chart). Such a temporal threshold has been used in multiple studies to categorise Mediterranean floristic elements according to their temporal origin (paleo-mediterranean vs. neo-mediterranean; Herrera 1992, Peñuelas et al. 2001, Verdú and al. 2003). In addition, it has been used to test specific hypotheses such as the timing of colonisation of the Canary Islands by certain lineages (Vargas 2007; Salvo et al. 2010), diversification rate shifts (Fiz-Palacios and Valcárcel 2013) and karyotypic changes (Escudero et al. 2018) in combination with time-calibrated phylogenies.

The use of phylogenetic analyses based on DNA sequences to estimate the timing of evolutionary events has become a basic tool in biogeography (Sanmartín 2014). Time can be measured in absolute units when the tree is calibrated with fossils, phylogeny-based secondary calibrations and/or biogeographic events (Forest 2009, Ho and Phillips 2009; see Hipsley and Müller 2014 for alternative calibration approaches). In particular, relaxed-clock Bayesian methods can elucidate a prior distribution on the age of a node, taking into account the uncertainty associated with tree topology, branch length and calibrations (Drummond et al. 2006, Yang and Rannala 2006). This method can be applied to a large number of plant groups, thus helping describe general patterns (Pokorny et al. 2015, Vargas et al. 2018). The time-calibrated phylogenies obtained from Bayesian relaxed-clock methods are often used as input for inferring the ancestral areas from which colonisation may have occurred (e.g. Albaladejo et al 2021). These ancestral area reconstruction analyses give new possibilities for quantitative analysis in island biogeography (Lamm and Redelings, 2009). Thus, applying time-calibrated phylogenetic approaches to investigate divergence of Canarian lineages from their continental relatives may provide valuable insight into the very complex patterns of relationships between the Canary Islands and continental floras (Carine et al. 2004, Kondraskov et al. 2015, Caujapé-Castells et al. 2017, Valente et al. 2017).

Palaeoclimatic, floristic and phytogeographic studies lead us to examine the hypothesis of an origin of Canarian thermophilous species following the establishment of the mediterranean climate across the Mediterranean Basin 2.8 Ma. To test this hypothesis, we firstly analyzed the phylogenetic relationships of thermophilous Canarian lineages and their sister groups using improved phylogenetic datasets in terms of extended taxonomic and geographical sampling. Secondly, we evaluated whether ancestral thermophilous plant lineages had a temporal origin since the mediterranean climate became established around 2.8 Ma (Suc et al. 2018) based on the both newly generated and previously published time-calibrated phylogenies. Thirdly, we implemented ancestral area reconstruction analyses to assess whether colonisation of thermophilous canarian lineages had a potential source area for colonization in the Mediterranean Basin or another geographic area. In sum, we are quantifying at what degree there is a spatio-temporal biogeographic link between the Canarian Flora and the MFR.

MATERIALS AND METHODS

Study area

The thermophilous woodland is a vegetation type characteristic of the Canary Islands. It occurs between the xerophytic vegetation and the laurel forest on the windward slopes (ca. 200-500 m) and between the xerophytic vegetation and the pine woodland on the leeward slopes (ca. 300-900 m) (del Arco et al. 2006, Fernández-Palacios et al. 2008). Its climate fits into mediterranean conditions with annual rainfall between 250 and 450 mm, mostly occurring in winter, and with average temperature between 15º and 19º C, depending on elevation. The thermophilous woodland is defined by some communities dominated by tree species also found in the southern Europe and northern Africa (particularly *Juniperus turbinata*, *Pistacia atlantica*, *Pistacia lentiscus*, *Olea europaea*), which may be accompanied by endemic trees (*Gymnosporia cassinoides* (L'Hér.) Masf., *Dracaena draco* L., *Phoenix canariensis* H.Wildpret, *Sideroxylon canariense* Leyens, Lobin & A.Santos, *Visnea mocanera* L.f.). In addition, a high number of shrub and herb species characterize this vegetation belt (Fernández-Palacios et al. 2008). Unfortunately, this vegetation type is extremely rare in a pristine state because its trees have been eliminated by anthropogenic activity. Chronologically, African human groups colonized the seven the islands, who mostly settled around 2000 years ago, and then a more severe deforestation took place since colonization by European groups (Fernández-Palacios et al. 2008). As a result, currently only 11 % of the original thermophilous woodland is estimated to remain (Fernández-Palacios et al. 2008, Castilla-Beltrán et al. 2021).

Sampling strategy and DNA sequencing

In this study, stem and crown ages were inferred by extending DNA sequence datasets of 13 previously published phylogenies, which included a total of 16 thermophilous species (seven Canarian endemics, five Macaronesian endemics, four non-endemic natives) occurring in the Canary Islands. These previous datasets are heterogeneous and the published phylogenies share some of the following weak points: (1) low support for monophyletic groups including Canarian species; (2) poor sampling of potential mainland sister groups (species/populations); (3) poor sampling of species or populations from the

Canary Islands; (4) lack of divergence-time estimations; and (5) need for technical improvement in terms of new methods or calibration points (Table 1). Additionally, stem and crown ages for 26 plant groups with species occurring in the Canarian thermophilous vegetation belt were directly taken from the literature (Supplementary Data Table S1). A total of 39 thermophilous plant groups (i.e., genera, rarely family) were analyzed.

To generate new data on divergence times for 16 thermophilous species, we first obtained 13 DNA sequence datasets from the most comprehensive phylogenetic studies at the genus level (occasionally at family level). Alignments were directly provided by authors of the studies or obtained from the GenBank or TreeBase databases. GenBank accession numbers and geographic origin for all downloaded sequences are available in each publication referenced in Table 1. Second, we extended taxonomic and/or population sampling of those DNA sequence datasets to infer stem and crown nodes for the Canarian species or populations. The new samples were obtained from three sources: field trips, herbarium specimens, and colleagues who contributed with field samples (Supplementary Data Table S2). We tried to sample at least one individual per island where the taxon is present depending on available material and accessibility of populations. We additionally sampled at least one individual from the most closely-related species based on taxonomic information when not available in the DNA sequence database. For non-endemic taxa, we also sampled individuals from at least two populations from nearby continental areas. Many plants of the Canary Islands have a Palearctic origin (Sunding 1979, Carine et al. 2004), and thus we focused our sampling on the archipelagos and mainland regions of Africa and Europe that are close to the Canary Islands, with particular effort on Mediterranean Iberia and northwestern Africa (Valente et al. 2017). Overall, we newly generated 262 DNA sequences from 104 samples of 33 taxa (16 representative thermophilous species and 17 close relatives) and 16 different DNA regions, which were included into the published DNA sequence datasets.

Sample information for all specimens and GenBank accession numbers for all new DNA sequences are provided in Supplementary Data Table S2.

DNA was extracted from dried leaves using QIAGEN DNeasy Plant Mini Kit according to the manufacturer's protocol. The sixteen different DNA regions were amplified and sequenced based on previously published studies for each plant group (Supplementary Data Table S2). In particular, we analyzed two nuclear (ETS and ITS), one mitochondrial (PHYC) and 13 plastid DNA regions (*mat*K, *psb*A-*trn*H, *psb*B1-*psb*B2, *rbc*L, *rpl*16, *rpl*32-*trn*L, *rps*4, *trn*D-*trn*T, *trn*K, *trn*L-*trn*F, *trn*L-*trn*F, *trn*S-*trn*G, *trn*V). Primers and PCR cycles applied for each plant group are included in Supplementary Data Table S3. Amplified products were sequenced by standard Sanger sequencing at Macrogen Europe (www.macrogen.com). We used Geneious 2021.2.2 (https://www.geneious.com) to edit chromatograms, align sequences with the MUSCLE algorithm (Edgar 2004) and concatenate DNA regions (Table 1). The resulting alignments were checked visually and corrected where the algorithm failed to identify gaps.

Phylogenetic relationships

We applied Bayesian Inference analysis to the 13 DNA sequence datasets to infer the phylogenetic relationships of plant groups with thermophilous species in the Canary Islands. The best-fitting substitution model for each partition (DNA region) was selected using the Akaike Information Criterion implemented in jModelTest v.0.1.1 (Posada 2008). We did not test the congruence between nuclear and plastid matrices because this was already analysed in the previous phylogenetic studies. Thus, we used the phylogenetic dataset (single or combined DNA matrix) that provided the highest phylogenetic resolution in those studies (Table 1; Figs. S1-S13). MrBayes v.3.2.6 (Ronquist et al. 2012) was used in all cases on XSEDE via the CIPRES Science Gateway (http://www.phylo.org/) with two simultaneous runs, each with four parallel Markov chains (three hot and one cold), and sampled every 10,000 trees to obtain a total of 10 million generations. The first 25% of trees of each run were discarded (burn-in) and 50% majority-rule consensus trees were constructed. An additional approach using maximum likelihood was implemented in RAxML to obtain an alternative estimate of phylogenetic relationships and support values (see Supplementary Data, Methods S1).

Divergence times

To estimate divergence times of stem and crown nodes for plant groups with thermophilous species in the Canary Islands, we generated 13 new time-calibrated phylogenies using the Bayesian uncorrelated log-normal relaxed clock model in BEAST 1.84 (Drummond and Rambaut 2007). We used the same substitution models already applied for the phylogenetic reconstructions. For each analysis, we ran two independent chains of 100 million generations with a birth–death tree prior, which accounts for both speciation and extinction (Gernhard 2008). All molecular dating analyses in BEAST were performed using the computer cluster Trueno (CSIC, Madrid, Spain). We assessed convergence of chains and appropriate burn-ins with Tracer v.1.7.1 (Rambaut et al. 2018), combined runs using LogCombiner, and produced maximum clade credibility (MCC) trees with mean node heights in Tree Annotator.

Calibration points used to estimate divergence times were based on the fossil record and published secondary calibration points, depending on data availability for each plant group (Supplementary Data Figs. S14-S26). When reliable fossils were available, a lognormal prior on age estimates was used, since this distribution better represents the stratigraphic uncertainty associated with the fossil record (Ho and Phillips 2009). The offset of the lognormal distribution was set to the upper bound of the stratigraphic period where the fossil was found. In the absence of reliable fossils, only secondary calibration points taken from original papers were implemented to the corresponding deep nodes

(Table 1). Secondary calibration points were obtained from fossil-calibrated phylogenies of higher taxonomic ranks, which included samples of our study groups (e.g., typically the family to which the genus belongs to), and were assigned normal distribution priors (Ho and Phillips 2009) in the BEAST analysis including the mean and the 95 % highest posterior density (HPD) interval from those studies. A summary of time constraints used for each DNA dataset and their provenance can be found in Supplementary Data Figs. S14-S26.

Colonization times: crown and stem ages

Colonization of the Canary Islands by a lineage have taken place at a time between the stem age and the crown age of the lineage (Fig. 1; Swenson et al. 2014, García-Verdugo et al. 2019a). The stem age, representing the time of divergence between the island lineage and the mainland sister lineage, is most commonly used as an indicator of colonization time (Fig. 1A, see examples in Keeley and Funk 2011, Spalik et al. 2014, Kondraskov et al. 2015, Grover et al. 2017, Schüßler et al. 2019). However, the stem age tends to overestimate colonization time as a result of extinction or incomplete sampling of closely related mainland lineages (Fig. 1B; Mairal et al. 2015, Pillon and Buerki 2017). Alternatively, recent studies are using the crown age, which corresponds to the onset of the divergence from the most recent common ancestor of the lineage within the archipelago, and thus a proxy for the colonization time from the mainland (Fig. 1A; Pokorny et al. 2015, García-Verdugo et al. 2019a). However, the crown age may provide an underestimate of colonization time, due to extinction of island lineages or poor sampling of the archipelago (Fig. 1C; see examples of Canarian lineages potentially affected by extinction in Sanmartín et al. 2008, and García-Verdugo et al. 2019b). Therefore, the crown age represents the minimum age (lower bound) at which colonization of the archipelago from the mainland could have occurred, whereas the stem age represents the maximum age (upper bound) of that event.

To address our working hypothesis, we compared both stem and crown ages with the 2.8 Ma threshold, which marks the establishment of mediterranean climate (Suc 1984). By considering the stem node as upper limit and the crown node as lower limit of colonization time, our approach accounts for the potential impact of lineage extinction and incomplete sampling on colonization time estimates. Based on estimates of stem and crown ages (mean and 95 % HPD intervals) from 26 previously-published and 13 newly-generated phylogenies, we classified 43 Canarian thermophilous lineages into three categories: (1) mediterranean lineages, when stem and thus crown ages postdated the 2.8 Ma threshold (i. e., both the stem and the crown node are mediterranean in time); (2) pre-mediterranean lineages, when crown and thus stem ages predated the 2.8 Ma threshold (i. e., both the stem and the crown ages are pre-mediterranean); and (3) undetermined lineages, for those groups with stem ages falling any time before this threshold (pre-mediterranean stem ages), and crown ages afterwards (mediterranean crown ages) (Fig. 2).

In the context of this hypothesis, the term “mediterranean” is referred to a window of colonization of the Canary Islands after the establishment of the mediterranean climate (temporal origin) in the Mediterranean Basin. This does not necessarily imply that the lineages colonized the thermophilous belt directly from the Mediterranean Basin.. Indeed, the closest mainland taxa for a few of the Canarian lineages are not from the Mediterranean Basin according to the literature (Supplementary Data Table S1). Although both temporal and spatial origins would have ideally to be fulfilled for a lineage to be considered "mediterranean”, we classify taxa according to temporal origin rather than geographic origin to address our working hypothesis because the temporal framework allows us to integrate stem age and crown age estimates together and thus partially circumvent the impact of poor sampling, low phylogenetic resolution, extinction and fluctuant limits of the MFR over time (see Discussion).

Nodes could not be unambiguously designated as mediterranean or pre-mediterranean when their 95 % HPD intervals spanned the 2.8 Ma threshold (Fig. 2). For these nodes, a complementary approach was taken (Fig. 3). Marginal probability distributions of divergence times for such nodes were extracted from 100,000 trees using TreeStat v.1.8.4 (Rambaut and Drummond 2016). Then, we used the percentage of occurrence of node ages before or after the 2.8 Ma threshold, following the approach of Vargas et al. (2014). In other words, a node was considered mediterranean when the majority of the marginal probability distribution of the node age postdated the establishment of the mediterranean climate (2.8 Ma), and as pre-mediterranean when the majority of the marginal probability distribution of the node age predated such a threshold (Fig. 3). We chose a 50 % threshold to include the majority of probability distributions (Vargas et al. 2014). For the previously published time-calibrated phylogenies we took a different approach, in which the "mediterranean" or "pre-mediterranean" status of nodes was estimated based on mean values of node ages given by the authors.

In some cases, low phylogenetic resolution and the tree topology hinder estimation of stem and crown ages. For instance, this can happen when posterior probability (PP) of nodes is low (< 0.90), or when multiple representatives of Canarian lineages are placed at distant positions in the tree with low support. These scenarios make it difficult to distinguish between incomplete lineage sorting and multiple colonization events. In such cases, a most inclusive approach was taken, in which we considered the time estimate of the most recent common ancestor (TMRCA) of island and mainland lineages to be an upper bound. Since this TMRCA is equivalent to the stem age (when relationships are resolved), it also represents the maximum age at which the lineage may have colonized the archipelago (Valente et al. 2017).

Ancestral Area Reconstructions

To reconstruct the ancestral distribution range of the lineages with thermophilous species in the Canary Islands (both endemics and non-endemics natives), we employed a model-based maximum-likelihood approach for ancestral area optimization: the dispersal-extinction-cladogenesis (DEC) model implemented in the BioGeoBEARS R package (Matzke, 2013). For the sake of brevity and addressing our working hypothesis, biogeographical reconstructions were conducted using only three geographic areas (A= Mediterranean Basin, B = Macaronesia, C = Other regions) allowing ancestors to be present in a maximum of three areas. We set symmetric dispersal between areas, and constant dispersal rates through time. The analyses were run using the MCC tree of the 13 newly inferred time-calibrated phylogenies (see Materials and Methods, Divergence times) after pruning tips in multi-sampled species in order to represent each species with a single terminal branch. We estimated whether colonisation occurred from the Mediterranean Basin (A, AB, AC, ABC) or from other geographic areas (C, BC) by considering the most likely ancestral distribution range recovered for the stem node of the Canarian lineages (or in the TMRCA when PP of stem nodes were lower than 0.90). As a result, we interpreted that any ancestral range shared by the Mediterranean Basin and the Canary islands indicates an origin from the Mediterranean Basin.

RESULTS

Newly inferred phylogenetic relationships

Our phylogenetic reconstructions based on Bayesian Inference using MrBayes (Figs. S1-S13) and Maximum Likelihood using RAxML (results not shown) are in accordance with previous published phylogenies regarding the topological relationships for the thermophilous species occurring in the Canary Islands. However, the phylogenetic support obtained for temporal divergence using BEAST was higher in most cases (Figs. S14-S26). We following describe well supported clades obtained in BEAST.

Most of the species analyzed formed well-supported monophyletic groups (Figs. 4-6, Supplementary Data Table S1). However, we could not confirm the monophyly of Canarian populations of non-endemic species (i.e., *Ephedra fragilis* Desf., *Juniperus turbinata*, *Pistacia atlantica*, *Pistacia lentiscus*) as well as the endemics *Asparagus umbellatus* Link and *Thesium retamoides* (A.Santos) J.C.Manning & F.Forest (Figs. 4A-4E, Fig. 5C, Fig. 6D, Supplementary Data Table S1). Similarly, sister-group relationships had high statistical support (above 0.90 PP), except for the non-endemic species and for the Macaronesian endemic species *Dracunculus canariensis* Kunth (Figs. 4A-4E, Fig. 6F, Supplementary Data Table S1).

The following phylogenetic relationships within the Canarian groups or between the Canarian species and continental sister groups were documented for the first time: (i) placement of *Asparagus scoparius* Lowe within the clade of *Asparagus nesiotes* Svent. and *Asparagus plocamoides* Webb ex Svent., and of *Asparagus umbellatus* within the clade of *Asparagus fallax* Svent. and *Asparagus arborescens* Willd. ex Schult. & Schult.f.; (ii) close relationship of the two Canarian species of *Gymnosporia* (Wight & Arn.) Hook.f. (*Gymnosporia cassinoides* (L'Hér.) Masf. and *Gymnosporia cryptopetala* Reyes-Bet. & A.Santos), which are sisters to the Madeira endemic *Gymnosporia dryandrii* (Lowe) Masf.; (iii) *Chrysojasminum odoratissimum* (L.) Banfi sister to the mainland clade of *Chrysojasminum parkeri* (Dunn) Banfi, *Chrysojasminum humile* (L.) Banfi, *Chrysojasminum bignoniaceum* (Wall. ex G.Don) Banfi and *Chrysojasminum fruticans* (L.) Banfi; and (iv) the two Canarian species of *Thesium* L. (*Thesium retamoides* and *Thesium subsucculentum* (Kämmer) J.C.Manning & F.Forest) sister to the mainland *Thesium mauritanicum* Batt. (Figs 4-6).

As a result, 16 independent Canary Island colonization events were inferred for the 13 plant groups with thermophilous species analyzed in this study: 10 genera with a single colonization and two with more than one colonization (three of *Pistacia* L. and two of *Asparagus* Tourn. ex L.) (Figs. 4-6, Supplementary Data Table S4). In addition, some lineages displayed cladogenesis in the Canary Islands, including species from other vegetation zones: *Asparagus* lineage I (*A. umbellatus* in the thermophilous woodland, *A. arborescens* in the xerophytic shrubland and *A. fallax* in the laurel forest), *Asparagus* lineage II (*A. scoparius* in the thermophilous woodland, *A. nesiotes* in xerophytic shrubland and *A. plocamoides* in the pine forest), *Gymnosporia* (*G. cassinoides* and *G. cryptopetala* in the thermophilous woodland), and *Thesium* (*T. retamoides* in thermophillous woodland and *T. subsucculentum* in the xerophytic shrubland) (Figs. 4-6). For these cases (i.e., lineages that diversified in different vegetation zones of the Canary Islands), stem and crown ages considered to categorize lineages as mediterranean or pre-mediterranean were those corresponding to the entire Canarian lineage (including thermophilous and non-thermophilous species).

Colonization times

The estimated mean crown ages of the 16 Canarian lineages newly analyzed in this study ranged from 1.07 Ma within *Myrsine excelsa* D.Don to 7.99 Ma within *Sideroxylon canariense*, while mean stem ages ranged from 1.15 Ma for *Pistacia atlantica* to 37.73 Ma for *Sideroxylon canariense* (Figs. 4-6; Supplementary Data Figs. S14-S26, Table S4). These age ranges include five cases in which the TMRCA had to be used: *Asparagus lineage* II, *Ephedra fragilis*, *Juniperus turbinata* subsp. *canariensis*, *Pistacia atlantica* and *Pistacia lentiscus* lineage II. Considering the complete list of 43 lineages (including those with previously published time-calibrated phylogenies), we identified 16 mediterranean lineages, nine pre-mediterranean lineages and 18 undetermined lineages (Table 2, Supplementary Data Table S1). We following describe these results in detail.

Mediterranean lineages (stem ages < 2.8 Ma)

The newly generated phylogenies allowed identification of five thermophilous plant lineages as mediterranean with respect to their colonization times, as their stem ages postdated the 2.8 Ma threshold: *Asparagus* lineage I, *Asparagus* lineage II, *Ephedra fragilis*, *Pistacia atlantica* and *Pistacia lentiscus* lineage II (Fig. 4). Most stem ages accumulated a marginal posterior distribution clearly after the 2.8 Ma threshold, so they were assigned as mediterranean with high statistical support (Supplementary Data Table S4). The highest uncertainty was estimated for the stem nodes of *Asparagus* lineage II, in which only 61 % of the stem age distribution fell in the last 2.8 Ma. Additional studies taken from the literature provided 11 more plant lineages as mediterranean. As a result, a total of 16 of the 43 thermophilous lineages display a clear cut mediterranean origin (from youngest to oldest stem ages; Fig. 7): *Globularia* lineage (0.30 Ma), *Smilax aspera* L. (0.30), *Cistus monspeliensis* L. (0.50), *Brachypodium arbuscula* Gay ex Knoche (0.80), *Erysimum* lineage (0.80), *Pistacia atlantica* (1.15, Fig. 4C), *Ephedra fragilis* (1.29, Fig. 4E), *Convolvulus* lineage II (1.50), *Asparagus* lineage II (1.60, Fig. 4B), *Solanum* lineage (1.70), *Helianthemum* Mill. sect. *Helianthemum* (1.82), *Argyranthemum* lineage (2.20), *Olea europaea* subsp. *guanchica* (2.60), *Malva canariensis* M.F.Ray (2.78) and *Asparagus* lineage I (2.80, Fig. 4A). Although the mean stem age of *Asparagus* lineage I clearly overlaps the mediterranean threshold, the posterior distribution of trees showed that more than 60 % of the stem age distribution and 96 % of crown age distribution in the mediterranean climate period.

Pre-mediterranean lineages (crown ages > 2.8 Ma)

The newly generated phylogenies allowed identification of three of the 16 thermophilous plant lineages as pre-mediterranean, as their crown ages predated the 2.8 Ma threshold: *Sideroxylon canariense*, *Chrysojasminum odoratissimum* and *Thesium* lineage (Fig. 5). Crown ages for the *Chrysojasminum odoratissimum* lineage and *Sideroxylon canariense* accumulated a marginal posterior distribution clearly before 2.8 Ma, so they were assigned as pre-mediterranean with high statistical support (Supplementary Data Table S4). The highest uncertainty was estimated for the crown node of the *Thesium* lineage, in which only 69 % of the age distribution predated 2.8 Ma. Previously published studies revealed six additional pre-mediterranean lineages. As a result, nine of the 43 thermophilous lineages displayed a pre-mediterranean origin (from youngest to oldest crown ages; Fig. 8): *Sideritis* lineage (3.30 Ma), *Echium* lineage (3.70), *Thesium* lineage (3.86), *Chrysojasminum odoratissimum* (4.79), *Euphorbia* sect. *Aphyllis* subsect. *Macaronesicae* Molero & Barres (6.92), *Sideroxylon canariense* (7.99), *Ruta* lineage (8.10), *Crambe* lineage (8.20) and *Sonchus* lineage (8.50).

Undetermined lineages (stem ages > 2.8 Ma, crown ages < 2.8 Ma)

The temporal origin of eight of the 16 thermophilous lineages were undetermined because their stem ages predated and their crown ages postdated the 2.8 Ma threshold: *Bosea yervamora* L., *Bryonia verrucosa* Aiton, *Dracunculus canariensis, Gymnosporia* lineage, *Myrsine excelsa*, *Juniperus turbinata* subsp. *canariensis, Pistacia lentiscus* lineage I and *Rhamnus crenulata* Aiton (Fig. 6). Most of their stem and crown ages accumulated a marginal posterior distribution clearly before and after 2.8 Ma. The highest uncertainty was recorded in the crown node of *Dracunculus canariensis*, in which only 60 % of the trees fell within the last 2.8 Ma time period (Supplementary Data Table S4). Previously published studies also revealed 10 undetermined lineages. In total, the following 18 lineages were classified as undetermined (Figs. 7, 8): *Gonospermum* lineage (mean stem:

3.10 Ma; mean crown: unknown), *Gymnosporia* lineage (mean stem: 3.78 Ma; mean crown: 1.27 Ma; Fig. 6E), *Artemisia* lineage (mean stem: 3.84; mean crown: unknown), *Rhamnus crenulata* (mean stem: 3.88; mean crown: 1.71; Fig. 6B), *Pistacia lentistus* lineage I (mean stem: 3.96; mean crown: 1.15; Fig. 4D), *Myrsine excelsa* (mean stem: 3.98; mean crown: 1.07; Fig. 6G), *Juniperus turbinata* subsp. *canariensis* (mean stem: 4.91, mean crown: unknown; Fig. 6D), *Bryonia verrucosa* (mean stem: 5.19; mean crown: 1.74; Fig. 6C), *Bosea yervamora* (mean stem: 5.69; mean crown: 1.64; Fig. 6A), *Rubia fruticosa* Aiton (mean stem: 6.69; mean crown: 2.10), *Navaea phoenicea* (Vent.) Webb & Berthel. (mean stem: 6.77; mean crown: unknown), *Anagyris latifolia* Brouss. ex Willd. (mean stem: 8.20; mean crown: 1.90), *Cheirolophus* lineage (mean stem: 8.50; mean crown: 1.70), *Hypericum canariense* L. (mean stem: 10.80; mean crown: 1.90), *Dracaena* lineage (mean stem: 11.80; mean crown: 2.30), *Dracunculus canariensis* (mean stem: 12.10; mean crown: 2.76), *Dioscorea edulis* (Lowe) Campos, Wilkin & Viruel (mean stem: 13.48; mean crown: unknown), *Visnea mocanera* (mean stem: 27.00; mean crown: 2.50).

Ancestral Area Reconstructions

Biogeographical analyses supported nine lineages with stem node ranges including the Mediterranean Basin (i.e. *Asparagus* lineage II, *Bosea yervamora*, *Bryonia verrucosa*, *Dracunculus canariensis*, *Ephedra fragilis*, *Juniperus turbinata*, *Pistacia lentiscus*, *Rhamnus crenulate* and *Thesium* lineage) and six lineages with stem node ranges not including the Mediterranean Basin (i.e. *Asparagus* lineage I, *Chrysojasminum odoratissimum*, *Gymnosporia* lineage, *Myrsine excelsa, Pistacia atlantica* and *Syderoxylon canariense*) (Figs. 4-6; Supplementary Data Figs. S27-S39, Table S5). No correspondence between the temporal origin of the lineages (mediterranean vs. pre-mediterranean) and the ancestral ranges (including vs. excluding the Mediterranean

Basin) was detected in three plant lineages (i.e. *Asparagus* lineage I, *Pistacia atlantica*, *Thesium* lineage).

DISCUSSION

The thermophilous woodland is considered a relatively recent ecosystem, originated after the establishment of the mediterranean climate in the Mediterranean Basin (2.8 Ma; Fernández-Palacios et al. 2008, Rivas-Martínez 2009, del Arco Aguilar and Rodríguez-Delgado 2018). In this study, we provide new divergence time estimates (i.e., stem and crown ages) based on time-calibrated phylogenies for 16 species representative of the thermophilous Canarian vegetation, which we analyzed together with previously-published results from additional 27 thermophilous plant lineages (Figs. 7, 8). In island biogeography, colonization times are more precisely considered to have taken place sometime between the stem and crown ages of the island lineage (Swenson et al. 2014, García-Verdugo et al. 2019a). Based on this phylogenetic principle, our study suggests that the Canarian thermophilous plant community is composed of lineages with an temporal origin both predating (pre-mediterranean) and postdating (mediterranean) the 2.8 Ma threshold considered for the establishment time of the mediterranean climate (Figs. 7, 8; Table 2). In addition, biogeographic reconstruction analyses showed that six of the 16 colonisation events here inferred may have occurred from areas that did not include the Mediterranean Basin by continental ancestors (Figs. 4-6). Taking all these results together, the thermophilous vegetation appears to be a complex assemblage of species with a heterogeneous origin in terms of colonization times and geographical origins.

Pre-mediterranean and mediterranean elements in the thermophilous plant community

As expected by the hypothesis of a mediterranean temporal origin for the Canarian thermophilous species, a considerable number of lineages (16) are estimated to have colonized the archipelago after the establishment of the mediterranean climate (2.8 Ma). Data from meteorological stations (https://www.acanmet.org/) between 200 and 600 m.a.s.l. and climatic variables used for species distribution modeling of thermophilous plants (Coello et al. 2020) indicate that current conditions in the Mediterranean Basin are similar to those of the thermophilous vegetation belt in the Canaries (Rivas-Martínez 2009). Since the late Pliocene (2.8 Ma), a progressive summer aridification of southern Europe and northern Africa may have produced wider distribution that may have facilitated dispersal from the MFR to other areas. There is thus a higher likelihood of dispersal and colonization to neighboring territories such as the Canarian archipelago since then (Meusel 1965, Sunding 1979). That is why trees with one of the most characteristic mediterranean-type syndromes (sclerophylly, a trait displayed mostly in leaves) may have found ideal conditions in the Canaries in the last 2.8 million years (Axelrod 1975, Verdú et al. 2003, Rundel et al. 2016, Vargas et al. 2018). Our results partly support this prediction for the sclerophyllous *Olea europaea* L., *Pistacia atlantica* and *Pistacia lentiscus* lineage II, but provide undetermined results for the sclerophyllous *Rhamnus crenulata* and *Pistacia lentiscus* lineage I. Alternatively, some other tree species (e.g., *Gymnosporia* spp., *Myrsine excelsa*, *Sideroxylon canariense*, *Visnea mocanera*) with leathery leaves and thick cuticles (typically observed in sclerophyllous species) did not display evidence for an origin postdating 2.8 Ma, which did not help support a mediterranean temporal origin for all the trees characterizing the thermophilous vegetation belt.

The relatively old stem and crown ages inferred for some plant lineages clearly indicate a pre-mediterranean origin for a considerable number of the thermophilous species (nine of 43 lineages). Indeed, the following plants appear to have already been present in the Canary Islands before the establishment of the mediterranean climate: *Sideritis* lineage, *Echium* lineage, *Thesium* lineage, *Chrysojasminum odoratissimum*, *Euphorbia* sect. *Aphyllis* subsect. *Macaronesicae*, *Sideroxylon canariense*, *Ruta* lineage, *Crambe* lineage and *Sonchus* lineage (Fig. 7, Table 2). Three non-mutually exclusive hypotheses can be put forward to explain the presence of pre-mediterranean lineages in the current Canarian thermophilous plant community: (i) a direct colonization from the mainland to pre-existent thermophilous vegetation in pre-mediterranean times, (ii) an indirect colonization from other Canarian vegetation types followed by a more recent species differentiation in the thermophilous vegetation and (iii) an old colonisation into non-thermophilous vegetation (on the islands) in pre-mediterranean times and long-term adaptation to thermophilous conditions *in situ* in pre-mediterranean or mediterranean times. The first hypothesis is supported by the fossil record. In particular, fossils of sclerophyllous leaves related to Miocene relicts have been found on the island of Gran Canaria (Anderson et al. 2009). These macrofossils moreover share characteristics with certain representative species of the present-day thermophilous scrub vegetation (e.g., *Cistus* L., *Gymnosporia*, *Euphorbia* L.). However, detailed anatomical investigation of fossil material is required for correct phylogenetic placement (Anderson et al. 2009). Molecular phylogenetic reconstructions and the fossil record are congruent with a Canarian palaeo-flora adapted to semi-arid conditions, scattered over dry slopes and canyons (*barrancos*) in the Canary Islands during pre-mediterranean times. This would be followed by geographical expansion of the species when the climate became more favorable. Indeed, an evolutionary process in which lineages adapted to pre-mediterranean conditions in relatively small, xeric pockets became dominant when mediterranean-like conditions were expanded has already been proposed for plants of the Mediterranean Basin (Barrón et al. 2010, Vargas et al. 2018). The second and third hypotheses are congruent with a pattern of high differentiation into species in different vegetation belts and ecological shifts into thermophilous conditions. This includes some speciation events associated with colonization of the thermophilous woodland, as documented in most of the evolutionary radiations of Canarian plants (e.g., *Sideritis* lineage, *Echium* lineage, *Euphorbia* sect. *Aphyllis* subsect. *Macaronesicae*, *Crambe* lineage, *Sonchus* lineage; see Supplementary Data Table S1). In any case, these three patterns of evolution could have been operating to ultimately merge into this particularly rich flora.

Impact of extinction on the inferred temporal origin of the thermophilous lineages

The time of origin (mediterranean vs. pre-mediterranean) of 25 out of 43 thermophilous lineages was successfully assigned using the approach proposed in this study, whereas 18 of them remained undetermined due to long temporal gaps between stem and crown ages spanning the 2.8 Ma threshold. These gaps entail a high uncertainty for the inference of colonization times (Cano et al. 2018, García-Verdugo et al. 2019a). The most striking case among those analyzed herein is *Dracunculus canariensis*, for which the difference between stem and crown ages was around 10 million years. An extreme case obtained from the literature is *Visnea mocanera*, which shows a difference between stem and crown ages of ca. 25 million years. Long stem-to-crown intervals have been previously found for other Macaronesian groups (e.g., *Cicer* L., *Campylanthus* Roth), an observation related to high extinction rates by recent studies (Antonelli and Sanmartín 2011, Nagalingum et al. 2011, Pokorny et al. 2015).

High extinction rates in mainland ancestral lineages as a result of abrupt climatic and geological changes (e.g., formation of the Sahara desert, Pleistocene climatic oscillations) has been the most commonly accepted explanation for the temporal gaps between stem and crown ages of Macaronesian lineages (Thiv et al. 2010, Kondraskov et al. 2015). Indeed, the Rand flora (i.e., lineages that exhibit a Canarian-eastern African disjunction) is primarily explained by widespread extinction of central-western Africa lineages rather than long-distance dispersal (Mairal et al. 2015, Pokorny et al. 2015). The extinction of lineages across the mainland may have been more pronounced in Canarian lineages of older temporal origin (i.e. pre-mediterranean and undetermined). Potential extinction coupled with the spatial uncertainty of the geographical boundaries of the MFR in the past (Suc 1984, Suc et al. 2018) makes the reconstruction of ancestral areas a suboptimal approach to evaluate the Mediterranean origin of the Canarian thermophilous species, and their results thus should be taken with caution.

García-Verdugo et al. (2019a) proposed that crown ages may be a more suitable measurement for the time of island colonization than stem ages based on the idea that stem ages are subject to higher temporal and spatial uncertainty as a result of mainland extinction. However, the analysis of crown ages suffers from the same problem of extinction and under-sampling, thus biasing the results to more recent times. The effect of island extinction in crown age estimates may be particularly pronounced in the thermophilous woodland because of multiple causes: (i) erosion and subsidence of flat, oldest islands (Fuerteventura, Lanzarote), which may previously have harbored large areas with this vegetation type (Fernández-Palacios et al. 2008, Martín Osorio et al. 2011); (ii) geological dynamics (eruptions, earthquakes, mega-landslides) (Carracedo et al. 2001, García-Olivares et al. 2017); and most importantly (iii) human land use and destruction of original vegetation (only 11 % currently preserved) between 200 and 600 m.a.s.l. (Fernández-Palacios et al. 2008, Castilla-Beltrán et al. 2021). This extreme reduction of populations, continuing even in our lifetimes, makes thermophilous vegetation the most threatened ecosystem in the Canary Islands (Castilla-Beltrán et al. 2021). This is illustrated by the few remaining individuals of non-endemic species in the thermophilous vegetation belt (*Pistacia lentiscus*, *Ephedra fragilis*), many critically endangered species (e.g., *Anagyris latifolia*, *Crambe scoparia* Svent., *Cheirolophus duranii* (Burchard) Holub, *Dracaena tamaranae* Marrero Rodr., R.S.Almeira & M.Gonzáles-Martin, *Echium handiense* Svent., *Gymnosporia cryptopetala*, *Helianthemum gonzalezferreri* Marrero Rodr., *Helianthemum bramwelliorum* Marrero Rodr., *Solanum lidii* Sunding, *Solanum vespertilio* Aiton subsp. *vespertilio*, *Thesium retamoides*, *Thesium canariense* (Stearn) J.C.Manning & F.Forest) and even several species considered already extinct (e.g., *Helianthemum aguloi* Marrero Rodr. & R.Mesa, *Thesium psilotocladum* Svent.) (Moreno 2010).

Conclusions

The approach proposed here, in which stem and crown ages are evaluated together with respect to a clear-cut threshold (2.8 Ma for the establishment of the mediterranean climate), helps test the hypotheses of temporal origins of evolutionary events even in scenarios with dramatic lineage extinction. In particular, our results provide strong evidence for a heterogeneous temporal origin of the thermophilous woodland in the Canary Islands, which harbors elements of both recent (mediterranean) and ancient Tethyan-Tertiary (pre-mediterranean) origins (Table 2). In addition, several of these colonisation events do not show ancestral areas in the Mediterranean Basin, even in some lineages postdating the establishment of the Mediterranean climate (e.g. *Asparagus* lineage I) (Figs. 4-6). This suggests a sequential history of species colonization and assemblage in the current thermophilous plant community of the Canaries, including a previously underestimated pre-mediterranean origin. A similar pattern has been identified for the laurel forest and xerophytic shrubland (Kondraskov et al. 2015, Sun et al. 2016, Salvo et al. 2010). Given that the thermophilous vegetation contains the highest number of lineages previously considered of mediterranean origin (Rivas-Martínez 2009, del Arco Aguilar and Rodríguez-Delgado 2018; but see Bolòs 1996), we hypothesize that the other five main vegetation belts contain an even lower number of mediterranean-like lineages (Vargas 2020). If this hypothesis was confirmed, the long-lasting view of Macaronesia as a subregion within the MFR would be seriously challenged. Different temporal and geographical origins resulted in a great deal of diversity of the Canarian flora in general, and the thermophilous plant community in particular. Interestingly, this is the most threatened Canarian vegetation belt (Fernández-Palacios et al. 2008; del Arco Aguilar and Rodríguez-Delgado 2018). The endangered status of a few relictual patches requires urgent prioritization for conservation and restoration at the regional, national and international levels.

SUPPLEMENTARY DATA

Supplementary data are available at https://academic.oup.com/aob and consist of the following. Figs. S1-S13. Majority rule consensus trees of the 13 plant groups analysed in this study resulting from applying Bayesian Inference in MrBayes and using previously published phylogenetic datasets (see Table 1) in combination with newly generated sequences (see Table S2). Figs. S14-S26. Time-calibrated phylogenies of the 13 plant groups analysed in this study obtained in BEAST using previously published phylogenetic datasets (see Table 1) in combination with newly generated sequences (see Table S2). Figs. S27-S39. Biogeographic reconstructions of ancestral ranges of the 13 plant groups analysed in this study resulting from applying dispersal–extinction–cladogenesis (DEC) analyses using the BioGeoBEARS R package. Table S1. Information extracted from the literature and obtained in this study for the 43 plant lineages including thermophilous species from the Canary Islands (Macaronesia) for hypothesis testing. Table S2. Studied taxa and their corresponding collection code, voucher information, island (archipelado or country), locality, collection date, collector's name (leg), DNA sequenced regions and GenBank accesion numbers. Table S3. Primers and PCR cycles used for sequencing DNA regions of the 13 plant groups analyzed in this study (genera, seldom families). Table S4. Detailed information (phylogenetic relationships and colonization times) of the 16 lineages with thermophilous species recovered by BEAST analyses of the 13 plant groups of this study. Table S5. Results of the ancestral area reconstruction under the dispersal-extinction-cladogenesis (DEC) analyses performed on the 13 newly generated time-calibrated phylogenies including thermophilous species in the Canary Islands analysed in this study. Methods S1. Details of the maximum likelihood phylogenetic analyses performed in this study.

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LITERATURE CITED

Albaladejo RG, Martín-Hernanz S, Reyes-Betancort JA, Santos-Guerra A, Olangua-Corral M, Aparicio A. 2021. Reconstruction of the spatio-temporal and ecological patterns of dispersal and diversification of *Helianthemum* sect. *Helianthemum* (Cistaceae) in the Canary Islands using Genotyping by Sequencing data. *Annals of Botany* 127: 597–611.

Anderson CL, Channing A, Zamuner AB. 2009. Life, death and fossilization on Gran Canaria – implications for Macaronesian biogeography and molecular dating. *Journal of Biogeography* 36: 2189–2201.

Antonelli A, Sanmartín I. 2011. Mass extinction, gradual cooling, or rapid radiation? Reconstructing the spatiotemporal evolution of the ancient angiosperm genus *Hedyosmum* (Chloranthaceae) using empirical and simulated approaches. *Systematic Biology* 60: 596–615.

Appelhans MS, Paetzold C, Wood KR, Wagner WL. 2020. RADseq resolves the phylogeny of Hawaiian *Myrsine* (Primulaceae) and provides evidence for hybridization. *Journal of Systematics and Evolution* 58: 823–840.

Axelrod DI. 1975. Evolution and biogeography of the Madrean-Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden* 62: 280–334.

Barrón E, Rivas-Carballo R, Postigo-Mijarra JM, et al. 2010. The Cenozoic vegetation of the Iberian Peninsula: A synthesis. *Review of Palaeobotany and Palynology* 162: 382-402.

Bocquet G, Widler B, Kiefer H. 1978. Messinian Model--A new outlook for the floristics and systematics of the Mediterranean area. *Candollea* 33: 269–287.

Bolmgren K, Oxelman B. 2004. Generic limits in *Rhamnus* L. s.l. (Rhamnaceae) inferred from nuclear and chloroplast DNA sequence phylogenies. *Taxon* 53: 383–390.

Bolòs O. 1996. Acerca de la flora macaronésica. *Anales del Jardín Botánico de Madrid* 54: 457–461.

Bramwell D. 1976. The endemic flora of the Canary Islands: distribution, relationships and phytogeography. In: Kunkel G, ed. *Biogeography and Ecology in the Canary Islands*. Dr. W. Junk: The Hague, 207-240.

Cano Á, Bacon CD, Stauffer FW, Antonelli A, Serrano-Serrano ML, Perret M. 2018. The roles of dispersal and mass extinction in shaping palm diversity across the Caribbean. *Journal of Biogeography* 45: 1432-1443.

Carine MA. 2005. Spatio-temporal relationships of the Macaronesian endemic flora: A relictual series or window of opportunity?. *Taxon* 54: 895–903.

Carine MA, Russell SJ, Santos-Guerra A, Francisco-Ortega J. 2004. Relationships of the Macaronesian and Mediterranean floras: molecular evidence for multiple colonizations into Macaronesia and back-colonization of the continent in *Convolvulus* (Convolvulaceae). *American Journal of Botany*. 91: 1070–1085.

Carracedo JC, Rodríguez Badiola E, Guillou H, De La Nuez J, Pérez Torrado FJ. 2001. Geology and volcanology of La Palma and El Hierro, Western Canaries. *Estudios Geológicos* 57: 175–273.

Castilla-Beltrán A, de Nascimento L, Fernández-Palacios JM, et al. 2021. Anthropogenic transitions from forested to human-dominated landscapes in southern Macaronesia. *Proceedings of the National Academy of Sciences of the USA* 118: e2022215118.

Caujapé-Castells J, García-Verdugo C, Marrero-Rodríguez Á, Fernández-Palacios JM, Crawford DJ, Mort ME. 2017. Island ontogenies, syngameons, and the origins and evolution of genetic diversity in the Canarian endemic flora. *Perspectives in Plant Ecology, Evolution and Systematics* 27: 9–22.

Chen S, Kim DK, Mark WMW, Kim JH. 2013. Networks in a Large-Scale Phylogenetic Analysis: Reconstructing Evolutionary History of Asparagales (Lilianae) Based on Four Plastid Genes. *PLoS ONE* 8: e59472.

Coello AJ, Fernández-Mazuecos M, García-Verdugo C, Vargas P. 2021. Phylogeographic sampling guided by species distribution modeling reveals the Quaternary history of the Mediterranean-Canarian *Cistus monspeliensis* (Cistaceae). *Journal of Systematics and Evolution* 59: 262-277.

Davis CC, Webb CO, Wurdack KJ, Jaramillo CA, Donoghue MJ. 2005. Explosive radiation of Malpighiales supports a Mid-Cretaceous origin of modern tropical rain forests. *American Naturalist* 165: E36– E65.

del Arco Aguilar MJ, Pérez-de-Paz PL, Acebes JR, et al. 2006. Bioclimatology and climatophilous vegetation of Tenerife (Canary Islands). *Annales Botanici Fennici* 43: 167–192.

del Arco Aguilar MJ, Rodríguez-Delgado O. 2018. In: Werger MJA, ed. *Vegetation of the Canary Islands*. Cham, Switzerland: Springer.

Di Vincenzo V, Gruenstaeudl M, Nauheimer L, et al. 2017. Evolutionary diversification of the African achyranthoid clade (Amaranthaceae) in the context of sterile flower evolution and epizoochory. *Annals of Botany* 122: 69–85.

Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. 2006. Relaxed phylogentics and dating with confidence. *PLoS Biology* 4: e88.

Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214.

Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.

Engler A. 1879. Versuch einer Entwicklungsgeschichte der Pflanzenwelt, insbesondere der Florengebiete seit der Tertiärperiode. I. Die extratropischen Gebiete der nördlichen Hemisphäre. W. E. Verlag, Leipzig.

Escudero M, Balao F, Martín-Bravo S, Valente L, Valcárcel V. 2018. Is the diversification of Mediterranean Basin plant lineages coupled to karyotypic changes? *Plant Biology* 20: 166–175.

Fernández-Palacios JM, Otto R, Delgado JD, et al. 2008. Los bosques termófilos de Canarias. Proyecto LIFE04/NAT/ES/000064. Excmo. Cabildo Insular de Tenerife.

Fiz-Palacios O, Valcárcel V. 2013. From Messinian crisis to Mediterranean climate: a temporal gap of diversification recovered from multiple plant phylogenies. *Perspectives in Plant Ecology, Evolution and Systematics* 15: 130–137.

Forest F. 2009. Calibrating the tree of life: fossils, molecules and evolutionary timescales. *Annals of Botany* 104: 789–794.

Francisco-Ortega J, Fuertes-Aguilar J, Kim SC, Santos- Guerra A, Crawford DJ, Jansen RK. 2002. Phylogeny of the Macaronesian endemic *Crambe* section *Dendrocrambe* (Brassicaceae) based on internal transcribed spacer sequences of nuclear ribosomal DNA. *American Journal of Botany* 88:161–169.

García-Olivares V, López H, Patiño J, et al. 2017. Evidence for mega-landslides as drivers of island colonization. *Journal of Biogeography* 44: 1053-1064.

García-Verdugo C, Caujapé-Castells J, Sanmartín I. 2019a. Colonization time on island settings: Lessons from the Hawaiian and Canary Island floras. *Botanical Journal of the Linnean Society* 191: 155– 163.

García-Verdugo C, Caujapé-Castells J, Illera JC, et al. 2019b. Pleistocene extinctions as drivers of biogeographical patterns on the easternmost Canary Islands. *Journal of Biogeography* 46: 845–859.

Gernhard T. 2008. The conditioned reconstructed process. *Journal of Theorical Biology* 253: 769–778.

Grant K, Amarathunga U, Amies J, Hu P, Qian Y, Penny T, et al. 2022. Abrupt change in North African hydroclimate and landscape evolution 3.2 million years ago. *Communications Earth & Environment* 3:11.

Grehan JR. 2016. Biogeographic relationships between Macaronesia and the Americas. *Australian Systematic Botany* 29: 447–472

Grover CE, Arick MA 2nd, Conover JL, et al. 2017. Comparative genomics of an unusual biogeographic disjunction in the cotton tribe (Gossypieae) yields insights into genome downsizing. *Genome Biology and Evolution* 9: 3328–3344.

Hernández-Molina FJ, Stow DA, Alvarez-Zarikian CA, Acton G, Bahr A, Balestra B, et al. 2014. Onset of Mediterranean outflow into the North Atlantic. *Science* 344: 1244–1250.

Herrera CM. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *The American Naturalist* 140: 421–446.

Hipsley CA, Müller J. 2014. Beyond fossil calibrations: Realities of molecular clock practices in evolutionary biology. *Frontiers in Genetics* 5: 1-11.

Ho SYW, Phillips MJ. 2009. Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Systematic Biology* 58: 367–380.

Humboldt A. de. 1814. Atlas géographique et physique des régions équinoxiales du Nouveau Continent, fondé sur des observations astronomiques, des mesures trigonométriques et des nivellements barométriques [1814], Amsterdam-New-York, Theatrum Orbis Terrarum Ltd. et Da Capo Presse Inc, édition de 1971.

Ickert-Bond SM, Rydin C, Renner SS. 2009. A fossil-calibrated relaxed clock for *Ephedra* indicates an Oligocene age for the divergence of Asian and New World clades and Miocene dispersal into South America. *Journal of Systematics and Evolution* 47: 444–456.

Jeyarani JN, Yohannan R, Vijayavalli D, Dwivedi MD, Pandey AK. 2018. Phylogenetic analysis and evolution of morphological characters in the genus *Jasminum* L. (Oleaceae) in India. *Journal of Genetics* 97: 1225-1239.

Jiménez-Moreno G, Fauquette S, Suc JP. 2010. Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. *Review of Palaeobotany and Palynology* 162: 410–415.

Keeley SC, Funk VA. 2011. Origin and evolution of Hawaiian endemics: new patterns revealed by molecular phylogenetic studies. In: Bramwell D, Caujapé-Castells, J, eds. *The biology of island floras*. Cambridge: Cambridge University Press, 57–88.

Kondraskov P, Schütz N, Schüßler C, et al. 2015. Biogeography of Mediterranean hotspot biodiversity: re-evaluating the 'Tertiary Relict' hypothesis of Macaronesian Laurel forests. *PLoS One* 10: e0132091.

Lamm KS, Redelings BD. 2009. Reconstructing ancestral ranges in historical biogeography: properties and prospects. *Journal of Systematics and Evolution* 47: 369–382.

Lobin W. 1982. Untersuchung über Flora, Vegetation und biogeographische Beziehungen der Kapverdischen Inseln. Frankfurt, M: CFS 53. 112 p.

Mai DH. 1995. Tertiäre Vegetationsgeschichte Europas. Gustav Fischer, Jena, Stuttgart, New York.

Mairal M, Pokorny L, Aldasoro JJ, Alarcón M, Sanmartín I. 2015. Ancient vicariance and climate-driven extinction continental-wide disjunctions in Africa: the case of the Rand Flora genus *Canarina* (Campanulaceae). *Molecular Ecology* 24: 1335–1354.

Mansion G, Rosenbaum G, Schoenenberger N, Bacchetta G, Rosselló JA, Conti E. 2008. Phylogenetic analysis informed by geological history supports multiple, sequential invasions of the Mediterranean Basin by the angiosperm family Araceae. *Systematic Biology* 57: 269–285.

Mao K, Hao G, Liu J, Adams RP, Milne RI. 2010. Diversification and biogeography of *Juniperus* (Cupressaceae): variable diversification rates and multiple intercontinental dispersals. *New Phytologist* 188: 254–272.

Martín Osorio VE, Wildpret W, De la Torre W, Scholz S. 2011. Relict ecosystems of thermophilous and laurel forest as biodiversity hotspots in Fuerteventura, Canary Islands. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* 145: 180-185.

Matzke NJ. 2013. Probabilistic historical biogeography: new models for founder- event speciation, imperfect detection, and fossils allow improved accuracy and modeltesting. *Frontiers of Biogeography* 4: 242–247.

Meusel H. 1965. Die Reliktvegetation der Kanarischen Inseln in ihren Beziehungen zur süd- undmitteleuropäischen Flora. In: Gersch M, ed. *Gesammelte Vorträge über moderne Probleme der Abstammunslehre*, vol. 1. Jena Friedrich-Schiller-Universität, 17–136.

Moore MJ, Soltis PS, Bell CD, Burleigh G, Soltis DE. 2010. Phylogenetic analysis of 83 plastid genes further resolves the early diversification of eudicots. *Proceedings of the National Academy of Sciences of the USA* 107: 4623–4628.

Moreno J.C. (coord.). 2010. *Lista Roja de la flora vascular española*. Actualización con los datos de la Adenda 2010 al Atlas y Libro Rojo de la Flora Vascular Amenazada. Dirección General de Medio Natural y Política Forestal. Ministerio de Medio

Ambiente y Medio Rural y Marino y Sociedad Española de Biología de la Conservación de Plantas: Madrid.

Nagalingum NS, Marshall CR, Quental TB, Rai HS, Little DP, Mathews S. 2011. Recent synchronous radiation of a living fossil. *Science* 334: 796–799.

Nauheimer L, Metzler D, Renner SS. 2012. Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist* 195: 938-950.

Nezadal W, Welss W. 2009. Aportaciones al conocimiento del bosque termófilo en el noroeste de Tenerife (Islas Canarias). In: Beltrán Tejera E, Afonso-Carrillo J, García Gallo A, Rodríguez Delgado O, eds. *Homenaje al Profesor Dr. Wolfredo Wildpret de la Torre. Instituto de Estudios Canarios*. La Laguna (Tenerife. Islas Canarias). Monografía LXXVIII. 229-244.

Norup MF, Petersen G, Sandie Burrows S, et al. 2015. Evolution of *Asparagus* L.(Asparagaceae): Out-of-South-Africa and multiple origins of sexual dimorphism. *Molecular Phylogenetics and Evolution* 92: 25–44.

Oberprieler CO. Ott T, Hipper A, et al. 2017. Pleistocene shaping of genetic diversity in a monsoon-affected environment: the case of *Gymnosporia* (Celastraceae) in the southern Arabian Peninsula. *Plant Systematics and Evolution* 303: 1399–1412.

Onstein RE, Carter RJ, Xing YW, Richardson JE, Linder HP. 2015. Do Mediterranean- type ecosystems have a common history?-Insights from the buckthorn family (Rhamnaceae). *Evolution* 69: 756–771.

Palmarev E. 1989. Paleontological evidences of the tertiary history and the origin of the Mediterranean sclerophyll dendroflora. *Plant Systematic and Evolution* 162: 93–107.

Peñuelas J, Lloret F, Montoya R. 2001. Severe drought effects on Mediterranean woody flora in Spain. *Forest Science* 47: 214–218.

Pillon Y, Buerki S. 2017. How old are island endemics?. *Biological Journal of the Linnean Society* 121: 469–474.

Pokorny L, Riina R, Mairal M, et al. 2015. Living on the edge: Timing of Rand Flora disjunctions congruent with ongoing aridification in Africa. *Frontiers in Genetics* 6: 154.

Posada D. 2008. jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* 25: 1253–1256.

Postigo Mijarra JM, Barrón E, Gómez Manzaneque F, Morla C. 2009. Floristic changes in the Iberian Peninsula and Balearic Islands (south-west Europe) during the Cenozoic. *Journal of Biogeography* 36: 2025–2043.

Quézel P. 1978. Analysis of the flora of Mediterranean and Saharan Africa. *Annals of the Missouri Botanical Garden* 65: 479–534.

Rambaut A, Drummond AJ. 2016. TreeStat v.1.8.4: Tree Statistic Calculation Tool. http://beast.community/.

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904.

Read J, Sanson GD. 2003. Characterizing sclerophylly: the mechanical properties of a diverse range of leaf types. *New Phytologist* 160: 81–99.

Rivas-Martínez S. 2009. Aportaciones al conocimiento del bosque termófilo en el noroeste de Tenerife (Islas Canarias). In: Beltrán Tejera E, Afonso-Carrillo J, García Gallo A, Rodríguez Delgado O, eds. *Homenaje al Profesor Dr. Wolfredo Wildpret de la Torre. Instituto de Estudios Canarios*. La Laguna (Tenerife. Islas Canarias). Monografia LXXVIII. pp.255-296.

Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck J. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.

Rose JP, Kleist TJ, Löfstrand SD, Drew BT, Schönenberger J, Sytsma KJ. 2018. Phylogeny, historical biogeography and diversification of angiosperm order Ericales suggest ancient Neotropical and East Asian connections. *Molecular Phylogenetics and Evolution* 122: 59–79.

Rundel PW, Arroyo MTK, Cowling RM, Keeley JE, Lamont BB, Vargas P. 2016. Mediterranean biomes: Evolution of their vegetation, floras, and climate. *Annual Review of Ecology, Evolution and Systematics* 47: 383–407.

Salvo G, Ho SYW, Rosenbaum G, Ree R, Conti E. 2010. Tracing the temporal and spatial origins of island endemics in the Mediterranean region: a case study from the *Citrus* family (Ruta L., Rutaceae). *Systematic Biology* 59: 705–722.

Sanmartín I, van der Mark P, Ronquist F. 2008. Inferring dispersal: a Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. *Journal of Biogeography* 35: 428–449.

Sanmartín I. 2014. Biogeography. In: Vargas P, Zardoya R, eds. *The Tree of Life*. Sunderland, US: Sinauer Associates, Inc., Publishers. 156-166.

Schaefer H, Heibl C, Renner, SS. 2009. Gourds afloat: a dated phylogeny reveals an Asian origin of the gourd family (Cucurbitaceae) and numerous oversea dispersal events. *Proceedings of the Royal Society Biological Sciences* 276: 843–851.

Schimper AFW. 1903. *Plant Geography upon a Physiological Basis*. Oxford, UK: Clarendon Press.

Schüßler C, Bräuchler C, Reyes-Betancort JA, Koch MA, Thiv M. 2019. Island biogeography of the Macaronesian *Gesnouinia* and Mediterranean *Soleirolia* (Parietarieae, Urticaceae) with implications for the evolution of insular woodiness. *Taxon* 68: 537–556.

Spalik K, Banasiak Ł, Feist MA, Downie SR. 2014. Recurrent short-distance dispersal explains wide distributions of hydrophytic umbellifers (Apiaceae tribe Oenantheae). *Journal of Biogeography* 41: 1559–1571.

Stride G, Nylinder S, Swenson U. 2014. Revisiting the biogeography of *Sideroxylon* (Sapotaceae) and an evaluation of the taxonomic status of *Argania* and *Spiniluma*. *Australian Systematic Botany* 27: 104–118.

Suc JP. 1984 Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature* 307: 429–432.

Suc JP, Popescu M, Fauquette S. 2018. Reconstruction of Mediterranean flora, vegetation and climate for the last 23 million years based on an extensive pollen dataset. *Ecologia mediterranea* 44: 53–85.

Sun Y, Li Y, Vargas-Mendoza CF, Wang F, Xing F. 2016. Colonization and diversification of the *Euphorbia* species (sect. *Aphyllis* subsect. *Macaronesicae*) on the Canary Islands. *Scientific Reports* 6: 34454.

Sunding P. 1979. Origins of the Macaronesian Flora. In: Bramwell D, ed. *Plants and Islands.* New York: Academic Press, 13-40.

Swenson U, Nylinder S, Munzinger J. 2014. Sapotaceae biogeography supports New Caledonia being an old Darwinian island. *Journal of Biogeography* 41: 797-809.

Takhtajan A. 1986. *Floristic regions of the world* (translation by C. Jeffrey). Edinburgh: Oliver and Boyd.

Thiv M, Thulin M, Hjertson M, Kropf M, Linder HP. 2010. Evidence for a vicariant origin of Macaronesian–Eritreo/Arabian disjunctions in *Campylanthus* Roth (Plantaginaceae). *Molecular Phylogenetics and Evolution* 54: 607–616.

Tzedakis PC. 2007. Seven ambiguities in the Mediterranean palaeoenvironmental narrative. *Quaternary Science Reviews* 26: 2042–2066.

Valente L, Illera JC, Havenstein K, Pallien T, Etienne RS, Tiedemann R. 2017. Equilibrium bird species diversity in Atlantic islands. *Current Biology* 27: 1660–1666.

Vargas P. 2007. Are Macaronesian islands refugia of relict plant lineages?: a molecular survey. In Phylogeography of southern European refugia (pp. 297-314). Springer, Dordrecht.

Vargas P, Valente LM, Blanco-Pastor JL, et al. 2014. Testing the biogeographical congruence of palaeofloras using molecular phylogenetics: snapdragons and the Madrean-Tethyan flora. *Journal of Biogeography* 41: 932–943.

Vargas P, Fernández-Mazuecos M, Heleno R. 2018. Phylogenetic evidence for a Miocene origin of Mediterranean lineages: species diversity, reproductive traits, and geographical isolation. *Plant Biology* 20: 157–165.

Vargas P. 2020. The Mediterranean Floristic Region: High Diversity of Plants and Vegetation Types. In: Goldstein MI, DellaSala DA, eds. *Encyclopedia of the World's Biomes*, vol. 3. Elsevier, 602–616.

Verdú M, Dávila P, García-Fayos P, Flores-Hernández N, Valiente-Banuet A. 2003. 'Convergent' traits of Mediterranean woody plants belong to pre-Mediterranean lineages. *Biological Journal of the Linnean Society of London* 78: 415–427.

Volz SM, Renner SS. 2008. Hybridization, polyploidy, and evolutionary transitions between monoecy and dioecy in *Bryonia* (Cucurbitaceae). *American Journal of Botany* 95: 1297–1306.

White OW, Reyes-Betancort J, Chapman MA, Carine MA. 2020. Geographical isolation, habitat shifts and hybridisation in the diversification of the Macaronesian endemic genus *Argyranthemum* (Asteraceae). *New Phytologist* 228: 1953–1971.

Xie L, Yang Z-Y, Wen J, Li D-Z, Yi, T-S. 2014. Biogeographic history of *Pistacia* (Anacardiaceae), emphasizing the evolution of the Madrean-Tethyan and the eastern Asian-Tethyan disjunctions. *Molecular Phylogenenetics and Evolution* 77: 136–146.

Yang Z, Rannala B. 2006. Bayesian estimation of species divergence timesundera molecular clock using multiple fossil calibrations with soft bounds. *Molecular Biology and Evolution* 23: 212–226.

Zhigila DA, Verboom GA, Muasya AM. 2020. An infrageneric classification of *Thesium* (Santalaceae) based on molecular phylogenetic data. *Taxon* 69: 100–123.

Table 1. List of the 16 Canarian thermophilous plant species for which colonization times were newly-inferred for this study. Taxonomic rank, DNA regions and bibliographic references of the DNA sequence datasets used are detailed, as well as calibration approach and bibliographic reference on which the strategy for calculating divergence times is based. The last column indicates the reasons why the original datasets had to be improved, namely: (1) low support for monophyletic groups formed by Canarian species; (2) poor sampling of potential mainland sister groups (species/populations); (3) poor sampling of species or populations from the Canary Islands; (4) lack of divergence-time estimations; and (5) need for technical improvement in terms of new methods or new calibration points. DNA regions marked in bold represent the regions for which we have provided new sequences in this study (more details on the samples included by genus and species in Table S2). * Macaronesian endemics; ** Canarian endemics. Species with no asterisks are non-endemic natives.

Canarian thermophilous species	**Plant group analyzed**	**DNA regions from published phylogenies**	**Reference for published DNA sequence dataset**	**Calibration approach**	**Reference for calibration points**	**Reasons for dataset improvement**
Asparagus scoparius Lowe* *Asparagus umbellatus* Link*	Genus *Asparagus* Tourn. ex L. (Asparagaceae)	**PHYC**, ***trn*H-*psb*A**, ***trn*D-T**, *ndh*F	Norup et al. 2015	Secondary calibration (Fig. S14)	Chen et al. 2013	1, 3, 4
Bosea yervamora L.**	Family Amaranthaceae	***mat*K**	Di Vincenzo et al. 2017	Fossil and secondary calibration (Fig. S15)	Di Vincenzo et al. 2017	2, 3
Bryonia verrucosa Aiton**	Genus *Bryonia* L. (Cucurbitaceae)	ITS, LFY, *trn*L , *trn*L-*trn*F, *psb*A-*trn*H, *trn*H2, *trn*R-*atp*A	Volz and Renner 2008	Secondary calibration (Fig. S16)	Schaefer et al. 2009	5
Chrysojasminum odoratissimum (L.) Banfi*	Genus *Chrysojasminum* Banfi (Oleaceae)	**ITS**, *mat*K, ***trn*L-F** and ***trn*H-*psb*A**	Jeyarani et al. 2018	Secondary calibration (Fig. S17)	Vargas et al. 2014	2, 3, 4
Dracunculus canariensis Kunth *	Genus *Arum* L. (Araceae)	*trn*L , *trn*F, ***mat*K**, ***trn*K**, ***rbc*L**, ***rps*16**	Mansion et al. 2008	Fossil and secondary calibration (Fig. S18)	Mansion et al. 2008, Nauheimer et al. 2012	3, 5
Ephedra fragilis Desf.	Genus *Ephedra* Tourn. ex L. (Ephedraceae)	26S, 18S, **ITS**, *atp*B, *rbc*L, ***mat*K**, ***rps*4**, ***psb*A- *trn*H**, *trn*L, *trn*L–*trn*F	Ickert-Bond et al. 2009	Fossil calibration (Fig. S19)	Ickert-Bond et al. 2009	2, 3
Gymnosporia cryptopetala Reyes-Bet. & A.Santos** *Gymnosporia cassinoides* (L'Hér.) Masf.**	Genus *Gymnosporia* (Wight & Arn.) Hook.f. (Celastraceae)	**ITS**	Oberprieler et al. 2017	Secondary calibration (Fig. S20)	Davis et al. 2005	3, 5
Juniperus turbinata subsp. *canariensis* (Guyot & Mathou) Rivas Mart., Wildpret & P.Pérez	Genus *Juniperus* L. (Cupressaceae)	**ITS**, ***mat*K**, ***rbc*L**, ***trn*L-*trn*F**, ***rps*4**, ***trn*S-*trn*G**, *trn*D-*trn*T, ***trn*V**, *pet*B-*pet*D and ***psb*B1-*psb*B2**	Mao et al. 2010	Fossil calibration (Fig. S21)	Mao et al. 2010	2, 3
Myrsine excelsa D.Don*	Genus *Myrsine* L. (Primulaceae)	**ITS**, ETS	Appelhans et al. 2020	Secondary calibration (Fig. S22)	Rose et al. 2018	3, 4
Pistacia atlantica Desf. *Pistacia lentiscus* L.	Genus *Pistacia* L. (Anacardiaceae)	**ITS**, **ETS**	Xie et al. 2014	Secondary calibration (Fig. S23)	Xie et al. 2014	2, 3
Rhamnus crenulata Aiton **	Genus *Rhamnus* L. (Rhamnaceae)	**ITS**, ***trn*L-*trn*F**	Bolmgren and Oxelman 2004	Secondary calibration (Fig. S24)	Onstein et al. 2015	2, 3
Sideroxylon canariense Leyens, Lobin & A.Santos**	Genus *Sideroxylon* L. (Sapotaceae)	**ITS**, ***trn*H-*psb*A**	Stride et al. 2014	Fossil calibration (Fig. S25)	Stride et al. 2014	3
Thesium retamoides (A.Santos) J.C.Manning & F.Forest**	Genus *Thesium* L. (Santalaceae)	**ITS**, ***mat*K**, ***rpl*32-*trn*L**, ***trn*L-*trn*F**	Zhigila et al. 2020	Secondary calibration (Fig. S26)	Moore et al. 2010	3, 4

Table 2. List of mediterranean, pre-mediterranean and undetermined lineages (i.e. colonization events) based on the position of stem and crown ages with respect to the 2.8-million-year-threshold (i.e. establishment of the Mediterranean climate) of the complete list of 43 lineages

Mediterranean	**Pre-mediterranean**	**Undetermined**
Argyranthemum lineage	*Chrysojasminum odoratissimum*	*Anagyris latifolia*
Asparagus lineage I	*Crambe* lineage	*Artemisia* lineage
Asparagus lineage II	*Echium* lineage	*Bosea yervamora*
Brachypodium arbuscula	*Euphorbia* sect. *Aphyllis*	*Bryonia verrucosa*
Cistus monspeliensis	*Ruta* lineage	*Cheirolophus* lineage
Convolvulus lineage II	*Sideritis* lineage	*Dioscorea edulis*
Ephedra fragilis	*Sideroxylon canariense*	*Dracaena* lineage
Erysimum lineage	*Sonchus* lineage	*Dracunculus canariensis*
Globularia lineage	*Thesium* lineage	*Gonospermum* lineage
Helianthemum lineage		*Gymnosporia* lineage
Malva canariensis		*Hypericum canariense*
Olea europaea subsp. *guanchica*		*Juniperus turbinata* subsp. *canariensis*
Pistacia atlantica		*Myrsine excelsa*
Pistacia lentiscus lineage II		*Navaea phoenicea*
Smilax aspera		*Pistacia lentiscus* lineage I
Solanum lineage		*Rhamnus crenulata*
		Rubia fruticosa
		Visnea mocanera

FIGURE CAPTIONS

Fig. 1. Two approaches typically used to infer colonization times on oceanic island: stem and crown ages. Brown lines represent lineages with mainland distribution while green lines represent lineages with insular distribution. **A**. Graphical representation of stem and crown ages of a hypothetical island lineage (modified from García-Verdugo et al. 2019a). **B**. Impact of assumed extinction or incomplete taxon sampling on the mainland when inferring island colonization times based on stem-age estimates. **C**. Impact of assumed extinction or incomplete taxon sampling on the archipelago when inferring island colonization times based on crown-age estimates.

Fig. 2. Classification of lineages according to divergence times for the Canarian thermophilous plant community, following the methodology proposed in this paper: (1) mediterranean lineages when stem and thus crown ages postdate the 2.8 Ma threshold; (2) pre-mediterranean lineages when crown and thus stem ages predate the 2.8 Ma threshold; and (3) undetermined lineages for those groups with stem ages before and crown ages after this temporal threshold. In these examples, 95% intervals do not span the 2.8 Ma threshold, and therefore nodes can be unambiguously designated as mediterranean or pre-mediterranean.

Fig. 3. Assignment of mediterranean vs. pre-mediterranean nodes when the 95% HPD interval spans the 2.8 Ma threshold: (1) mediterranean nodes, when most of the posterior distribution of trees (> 50 %) provide node ages younger than 2.8 Ma, (2) pre-mediterranean nodes when most of the trees (> 50 %) provide node ages older than 2.8 Ma.

Fig. 4. The five thermophilous lineages of mediterranean origin (stem and therefore crown ages postdate 2.8 Ma) and related Canarian and mainland species from the 13 time-calibrated phylogenies inferred in this study using BEAST. Mean stem and crown ages

and 95% posterior credibility intervals (blue bars and values in brackets) are indicated. Divergence times of the most recent common ancestor (marked as TMRCA) are also indicated for those groups in which stem and crown nodes showed low phylogenetic support (PP<0.90, BS<70). Circles at the nodes represent phylogenetic relationships with high posterior Bayesian probability (PP) and/or bootstrap (BS) support values (see legend). Color of plant names indicates vegetation type. Asterisks represent new samples included in the present study. The letters in the stem node or MRCA of the Canarian lineages represent the ancestral ranges inferred for that node by the Ancestral Area Reconstruction Analysis, and correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas).

Fig. 5. The three pre-mediterranean lineages (i.e. crown and thus stem ages predate 2.8 Ma) and related Canarian and mainland species from the 13 time-calibrated phylogenies inferred in this study using BEAST. Mean stem and crown ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated next to the corresponding nodes. The circles at the nodes represent phylogenetic relationships with high posterior Bayesian probability (PP) and/or bootstrap (BS) support values (see legend). Color of plant names indicates vegetation type. Asterisks represent new samples included in the present study. The letters in the stem node of the Canarian lineages represent the ancestral ranges inferred for that node by the Ancestral Area Reconstruction Analysis, and correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas).

Fig. 6. The seven undetermined lineages (stem ages predating and crown ages postdating 2.8 Ma) and related Canarian and mainland species for the 13 time-calibrated phylogenies

inferred in this study using BEAST. Mean stem and crown ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated next to the corresponding nodes. Divergence times of the most recent common ancestor (marked as TMRCA) are indicated for those groups in which stem and crown nodes showed low phylogenetic support (PP<0.90, BS<70). The circles at the nodes represent phylogenetic relationships with high posterior Bayesian probability (PP) and/or bootstrap (BS) support values (see legend). Color of plant names indicates vegetation type. Asterisks represent new samples included in the present study. The letters in the stem node or MRCA of the Canarian lineages represent the ancestral ranges inferred for that node by the Ancestral Area Reconstruction Analysis, and correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas).

Fig. 7. Stem ages of 43 Canarian lineages including thermophilous plant species. Results from the new phylogenies obtained in this study are indicated with plant names in bold (references in Table S1). Blue bars show the 95% intervals, and mean stem ages are marked by a black line.

Fig. 8. Twenty-eight crown ages of Canarian thermophilous plant lineages (i.e., including more than one sample from the Canaries) of the 43 shown in Fig. 7. Results from the new phylogenies obtained in this study are indicated with plant names in bold, while results from previously published time-calibrated phylogenies have non-bold plant names (references in Table S1). Blue bars show the 95% intervals, and mean crown ages are marked by a black line.

SUPPLEMENTARY DATA

Article title: Time-calibrated phylogenies reveal mediterranean and pre-mediterranean origin of the thermophilous vegetation of the Canary Islands

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The following Supplementary data are available for this article:

Figs. S1-S13. Majority rule consensus trees of the 13 plant groups analysed in this study resulting from applying Bayesian Inference in MrBayes and using previously published phylogenetic datasets (see Table 1) in combination with newly generated sequences (see Table S2).

Figs. S14-S26. Time-calibrated phylogenies of the 13 plant groups analysed in this study obtained in BEAST using previously published phylogenetic datasets (see Table 1) in combination with newly generated sequences (see Table S2).

Figs. S27-S39. Biogeographic reconstructions of ancestral ranges of the 13 plant groups analysed in this study resulting from applying dispersal–extinction–cladogenesis (DEC) analyses using the BioGeoBEARS R package.

Table S1. Information extracted from the literature and obtained in this study for the 43 plant lineages including thermophilous species from the Canary Islands (Macaronesia) for hypothesis testing.

Table S2. Studied taxa and their corresponding collection code, voucher information, island (archipelado or country), locality, collection date, collector's name (leg), DNA sequenced regions and GenBank accesion numbers.

Table S3. Primers and PCR cycles used for sequencing DNA regions of the 13 plant groups analyzed in this study (genera, seldom families).

Table S4. Detailed information (phylogenetic relationships and colonization times) of the 16 lineages with thermophilous species recovered by BEAST analyses of the 13 plant groups of this study.

Table S5. Results of the ancestral area reconstruction under the dispersal-extinction-cladogenesis (DEC) analyses performed on the 13 newly generated time-calibrated phylogenies including thermophilous species in the Canary Islands analysed in this study.

Methods S1. Details of the maximum likelihood phylogenetic analyses performed in this study.

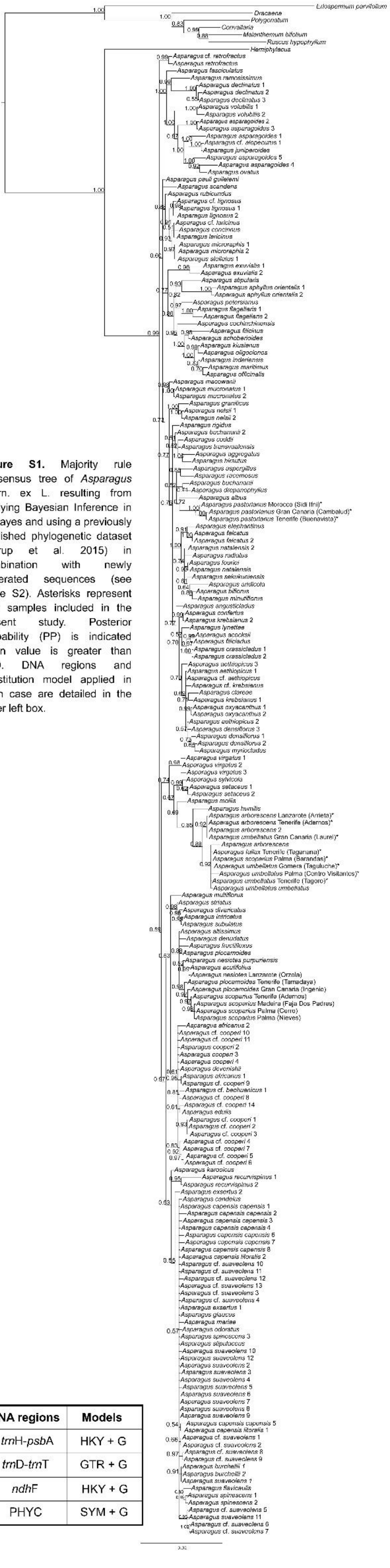


Figure S1. Majority rule consensus tree of *Asparagus* Tourn. ex L. resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Norup et al. 2015) in combination with newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA regions	Models
*trn*H-*psb*A	HKY + G
*trn*D-*trn*T	GTR + G
*ndh*F	HKY + G
PHYC	SYM + G

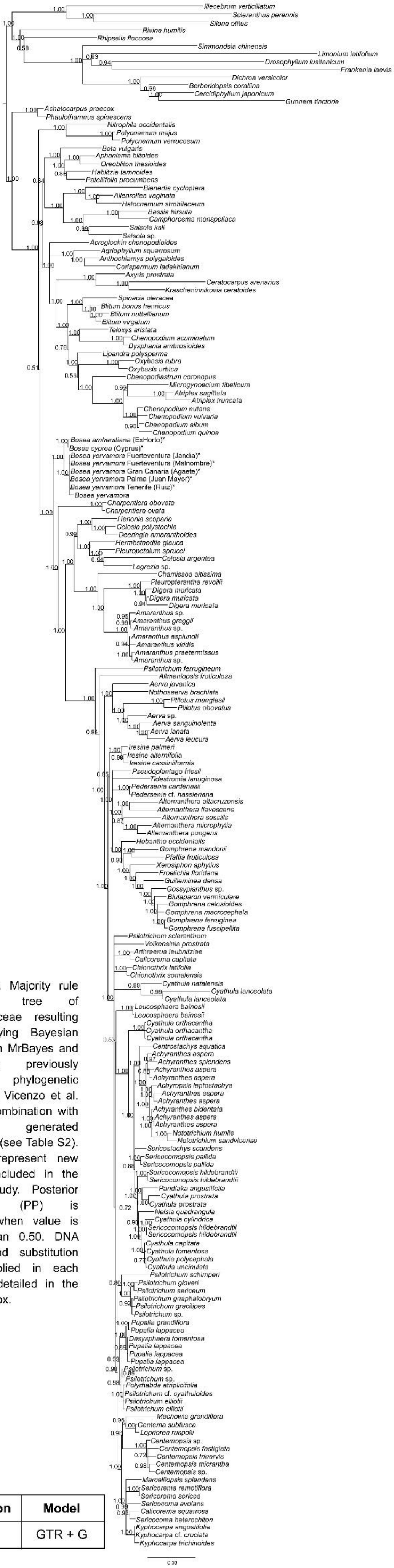


Figure S2. Majority rule consensus tree of Amaranthaceae resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Di Vicenzo et al. 2018) in combination with newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA region	**Model**
*mat*K	GTR + G

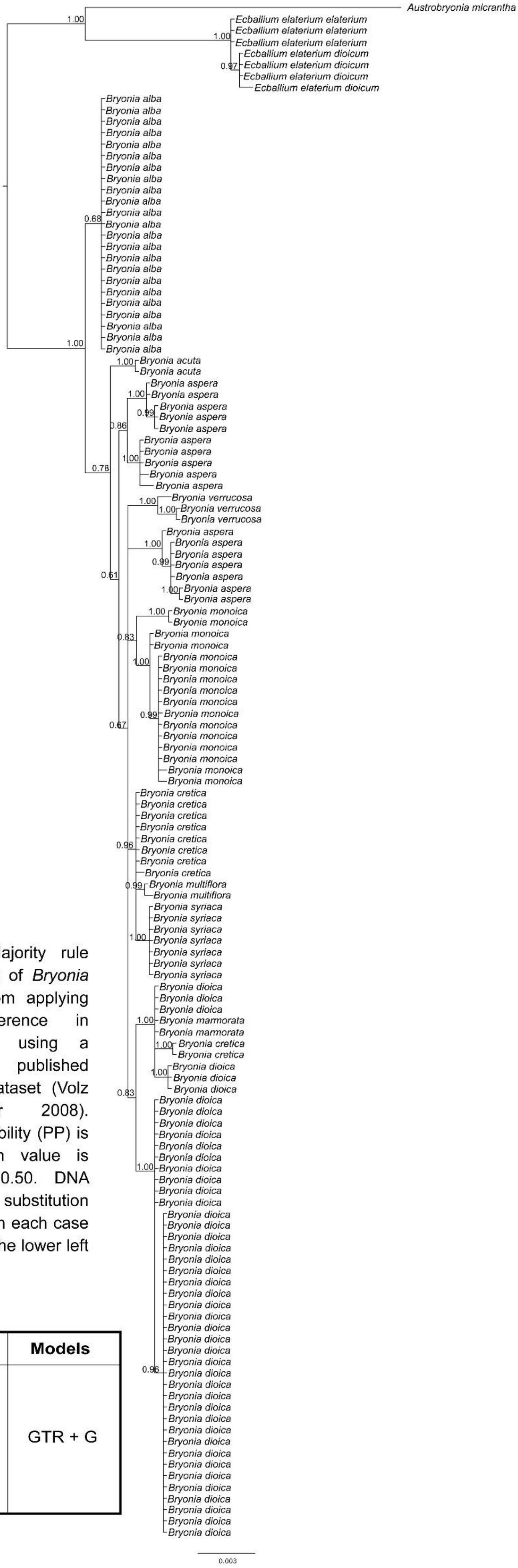


Figure S3. Majority rule consensus tree of *Bryonia* L. resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Volz and Renner 2008). Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA regions	Models
ITS LFY *trn*L *trn*L-*trn*F *psb*A-*trn*H *trn*H2 *trn*R-*atp*A	GTR + G

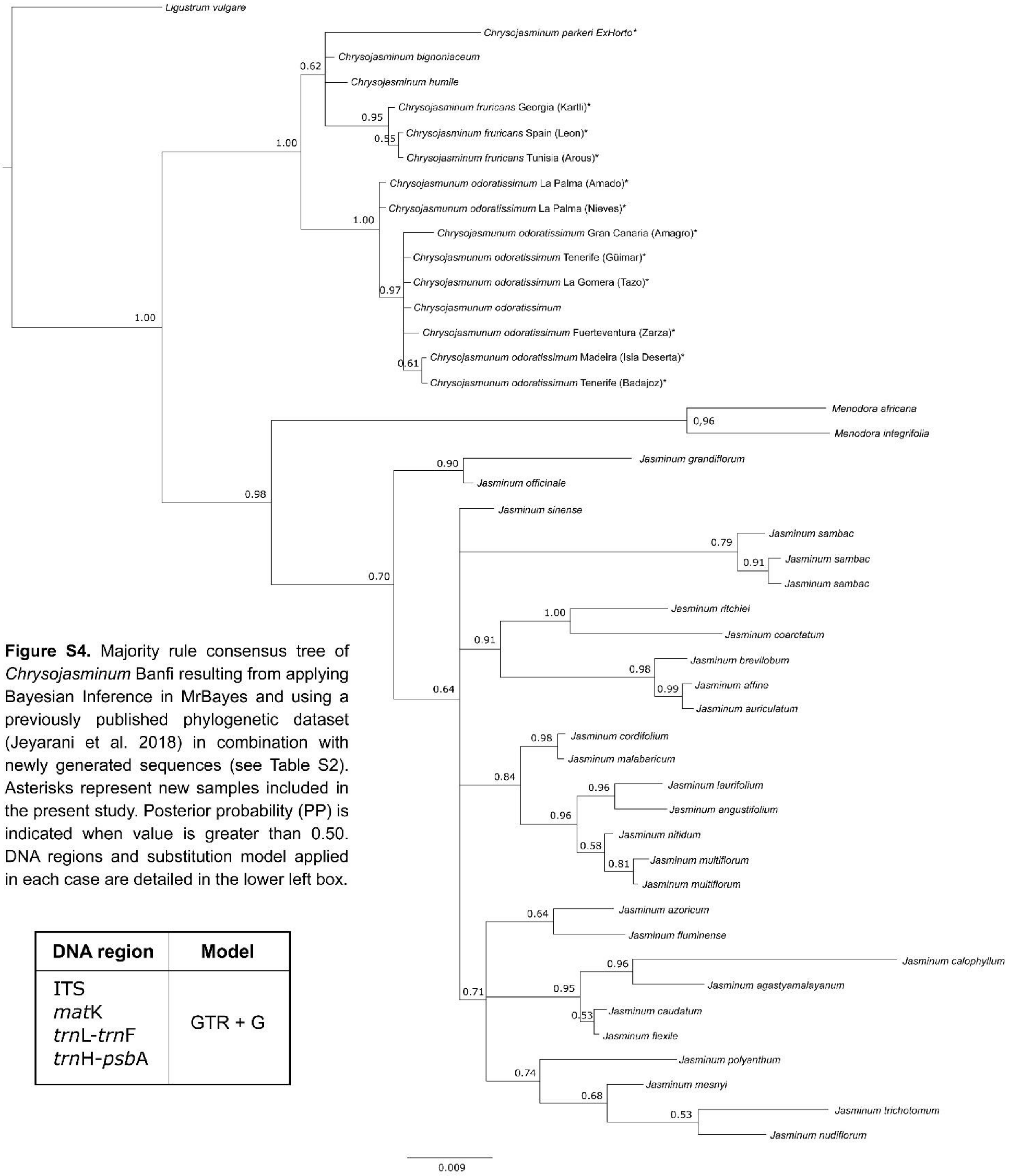


Figure S4. Majority rule consensus tree of *Chrysojasminum* Banfi resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Jeyarani et al. 2018) in combination with newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA region	Model
ITS *mat*K *trn*L-*trn*F *trn*H-*psb*A	GTR + G

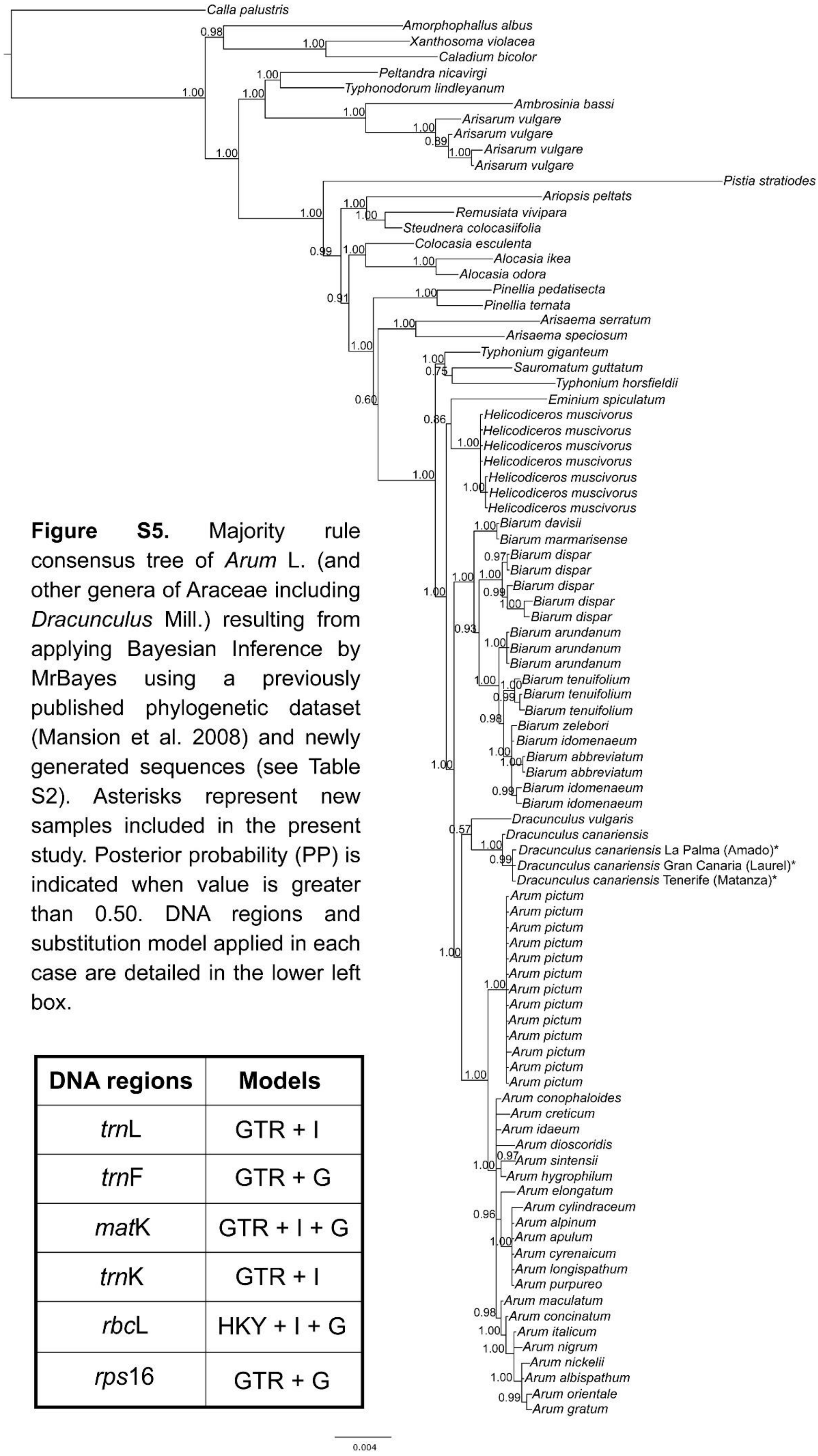


Figure S5. Majority rule consensus tree of *Arum* L. (and other genera of Araceae including *Dracunculus* Mill.) resulting from applying Bayesian Inference by MrBayes using a previously published phylogenetic dataset (Mansion et al. 2008) and newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA regions	**Models**
*trn*L	GTR + I
*trn*F	GTR + G
*mat*K	GTR + I + G
*trn*K	GTR + I
*rbc*L	HKY + I + G
*rps*16	GTR + G

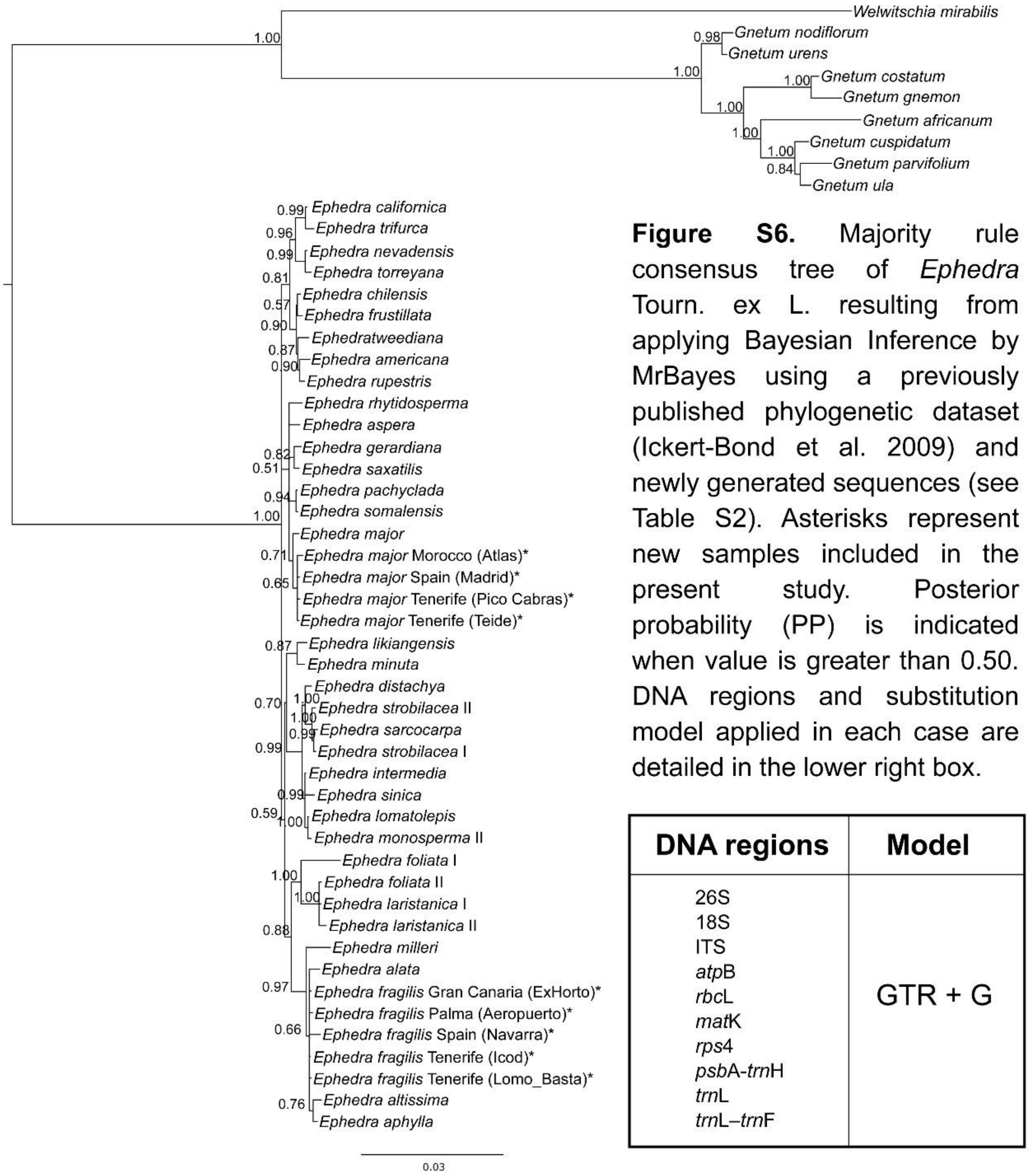


Figure S6. Majority rule consensus tree of *Ephedra* Tourn. ex L. resulting from applying Bayesian Inference by MrBayes using a previously published phylogenetic dataset (Ickert-Bond et al. 2009) and newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower right box.

DNA regions	**Model**
26S 18S ITS *atp*B *rbc*L *mat*K *rps*4 *psb*A-*trn*H *trn*L *trn*L–*trn*F	GTR + G

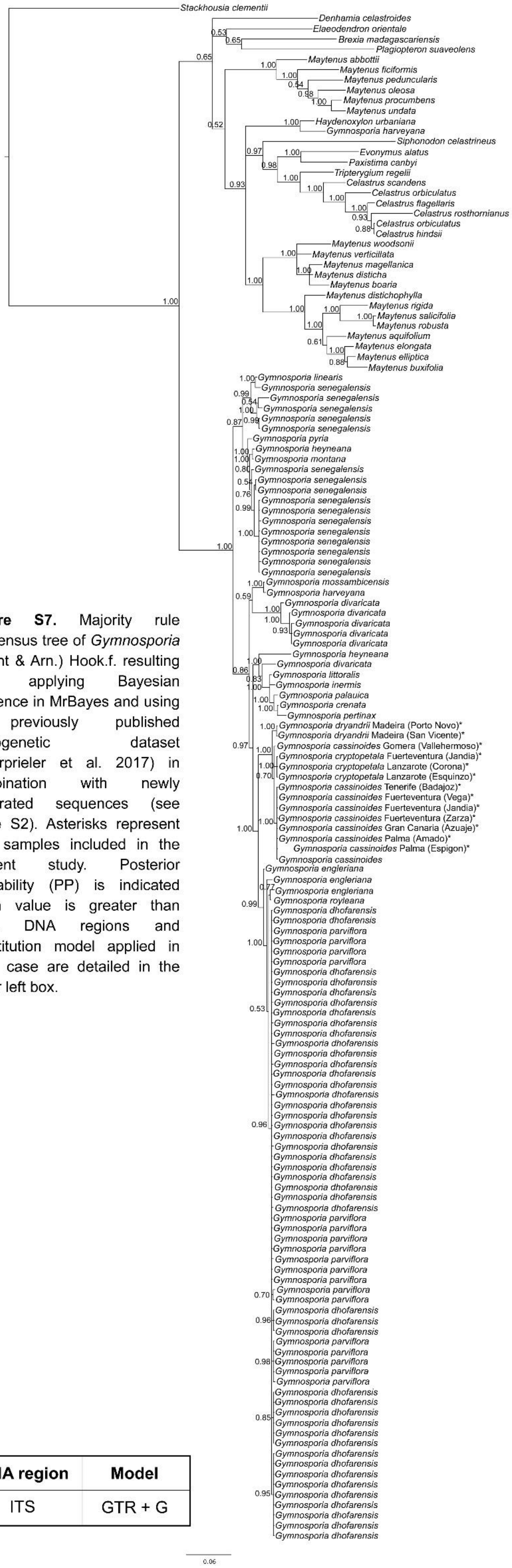


Figure S7. Majority rule consensus tree of *Gymnosporia* (Wight & Arn.) Hook.f. resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Oberprieler et al. 2017) in combination with newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA region	Model
ITS	GTR + G

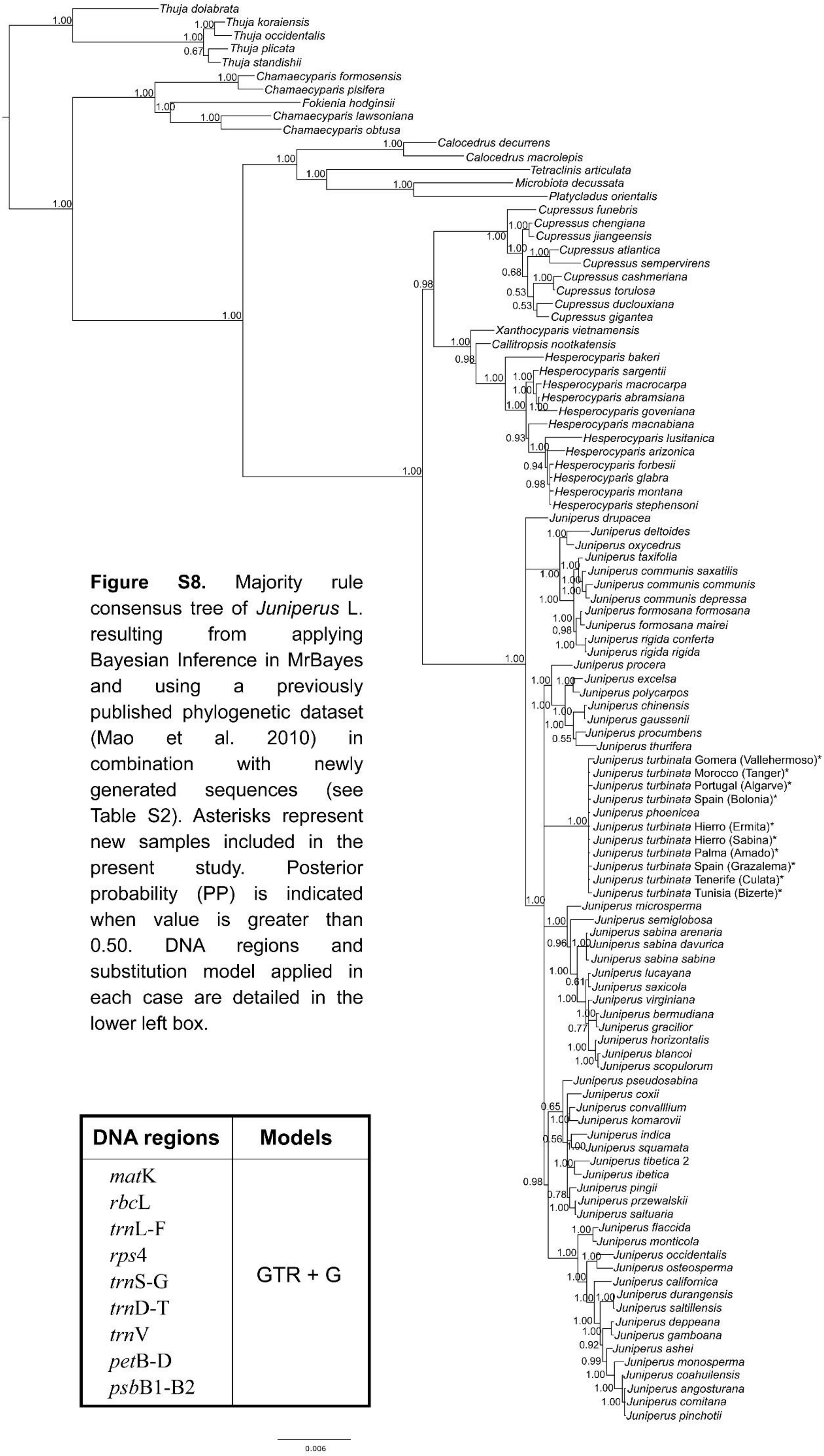


Figure S8. Majority rule consensus tree of *Juniperus* L. resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Mao et al. 2010) in combination with newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA regions	Models
*mat*K *rbc*L *trn*L-F *rps*4 *trn*S-G *trn*D-T *trn*V *pet*B-D *psb*B1-B2	GTR + G

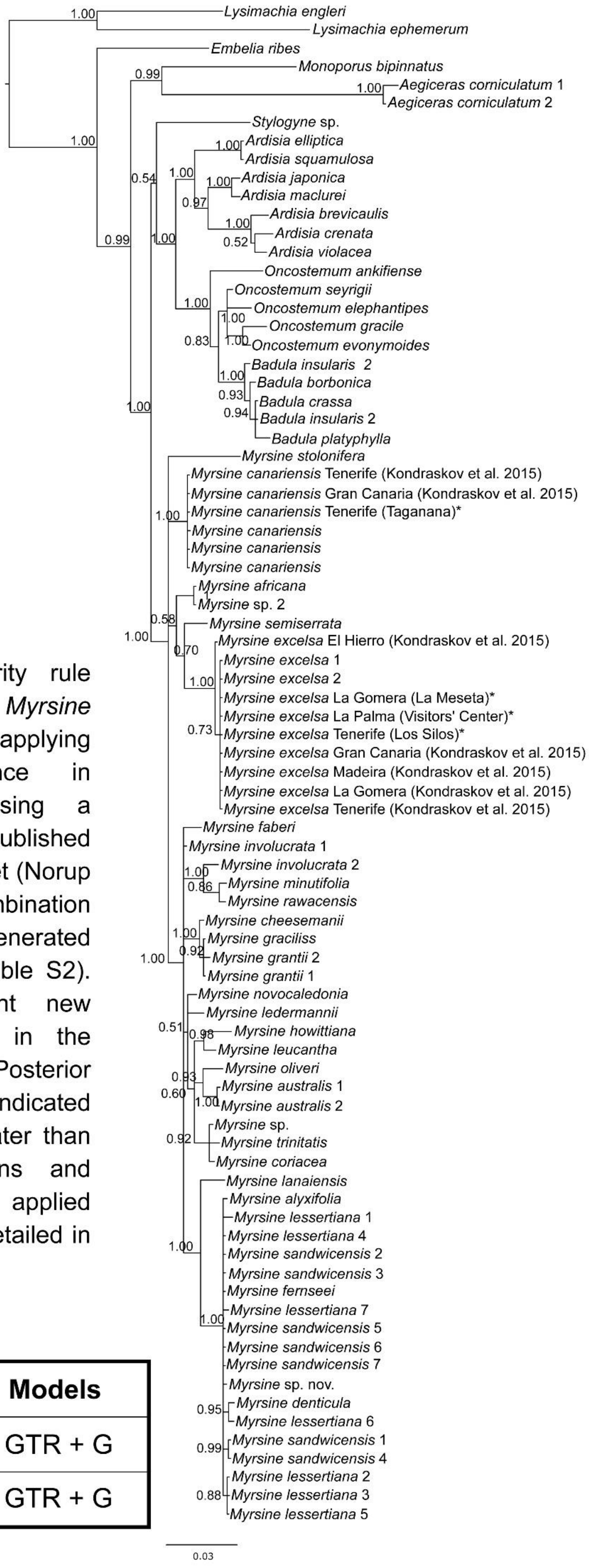


Figure S9. Majority rule consensus tree of *Myrsine* L. resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Norup et al. 2015) in combination with newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA regions	**Models**
ITS	GTR + G
ETS	GTR + G

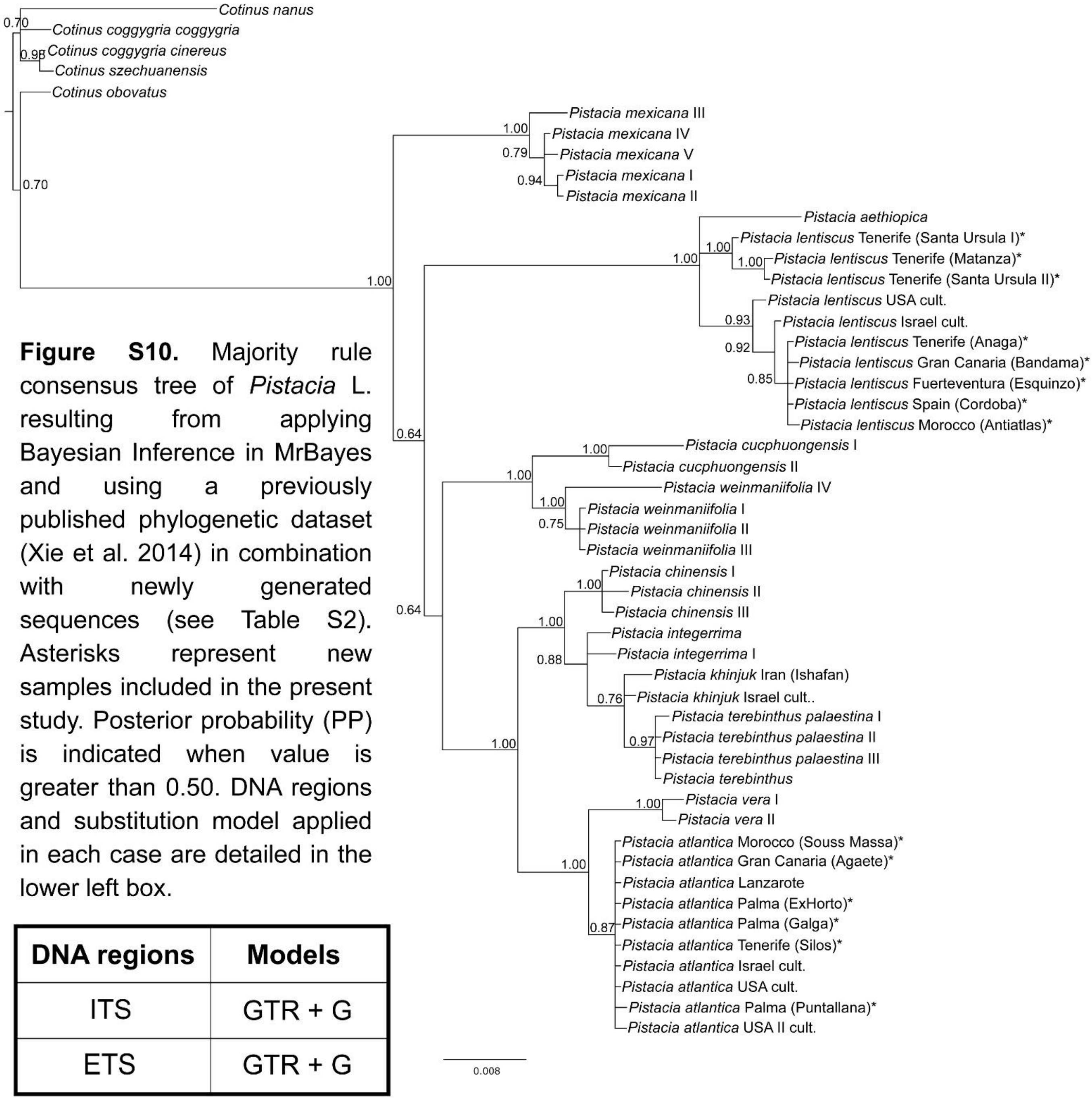
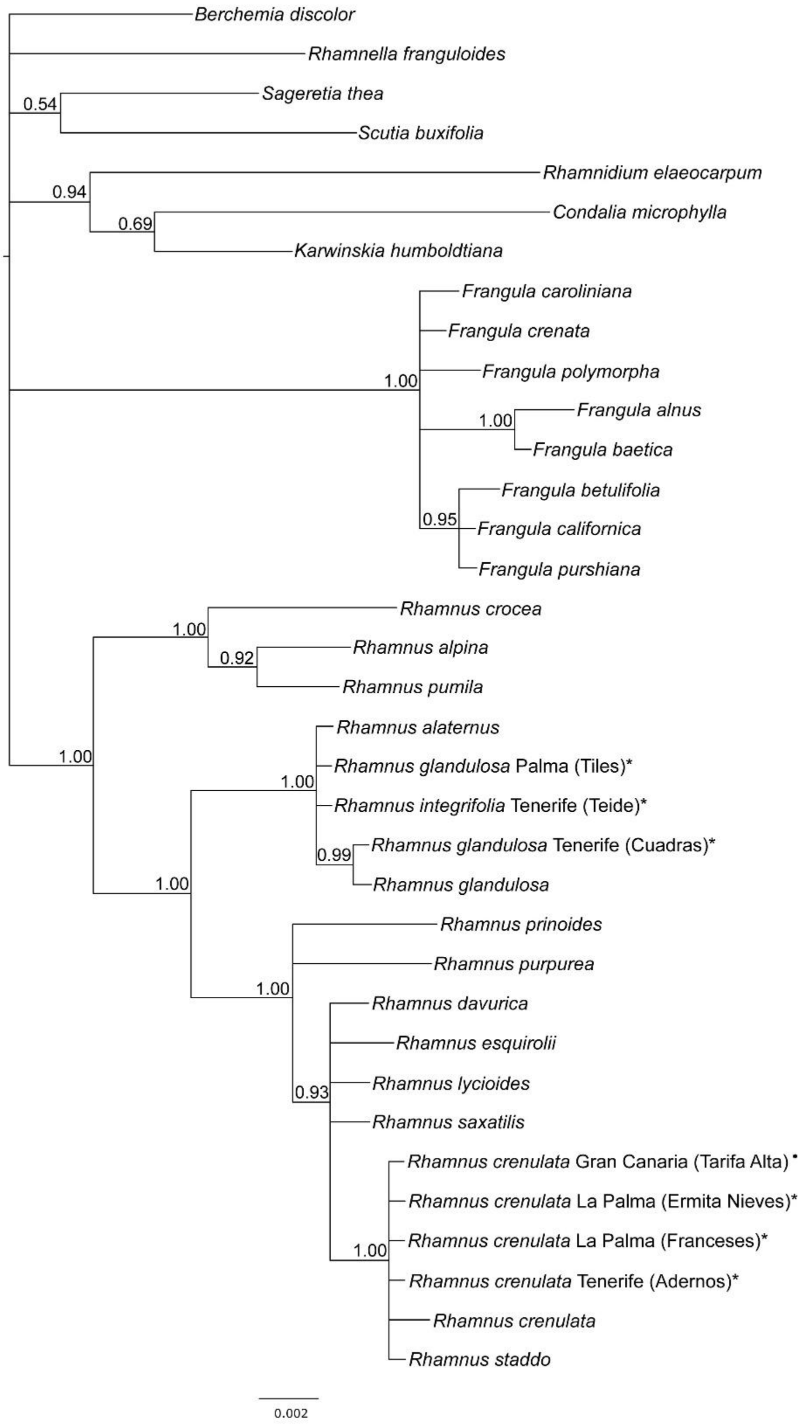


Figure S10. Majority rule consensus tree of *Pistacia* L. resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Xie et al. 2014) in combination with newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA regions	**Models**
ITS	GTR + G
ETS	GTR + G

Figure S11. Majority rule consensus tree of *Rhamnus* L. resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Bolmgren and Oxelman 2004) in combination with newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.



DNA regions	Models
ITS	GTR + G
*trn*L-*trn*F	GTR + G

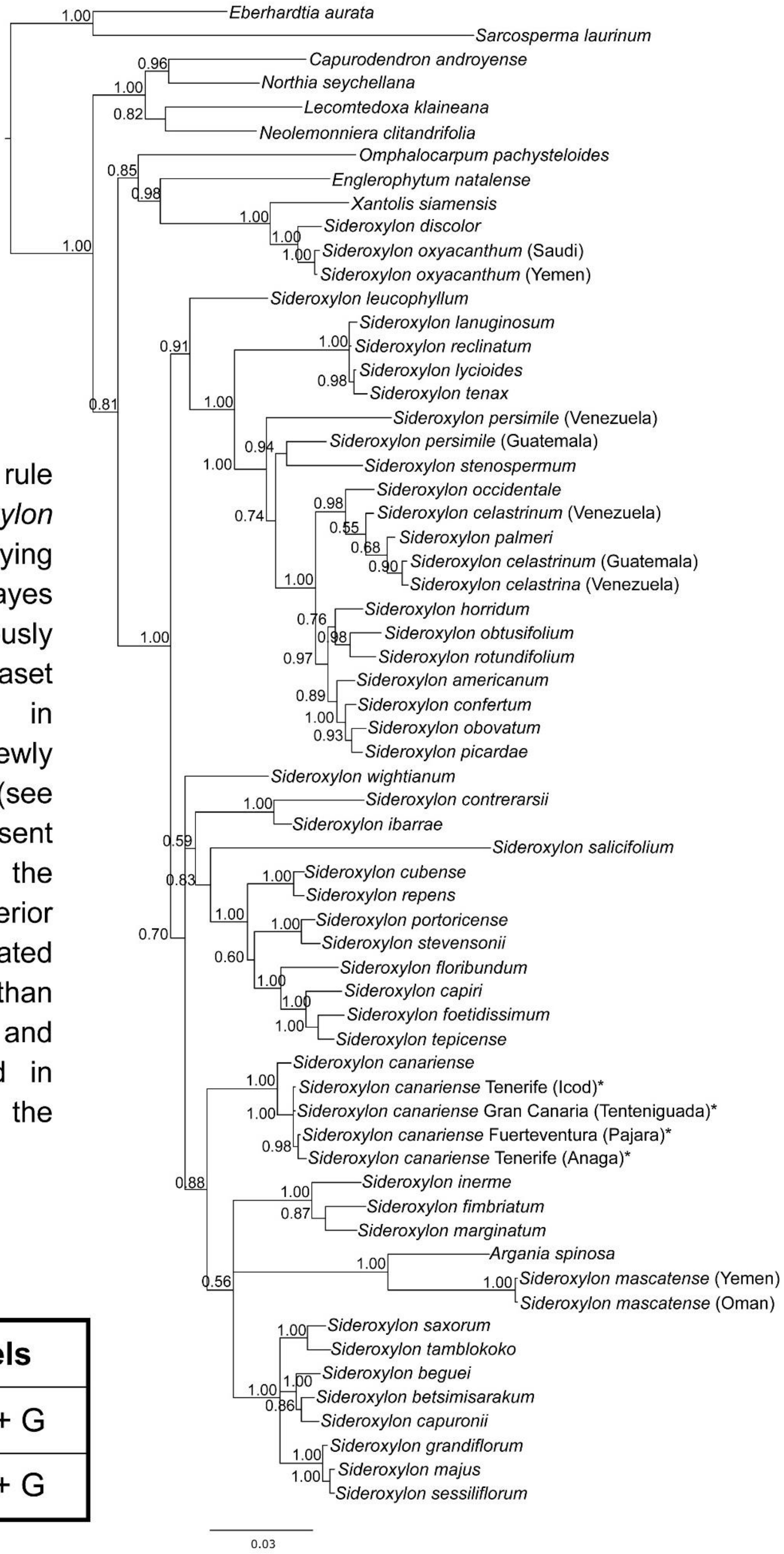


Figure S12. Majority rule consensus tree of *Sideroxylon* L. resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Stride et al. 2014) in combination with newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA regions	**Models**
ITS	GTR + G
*trn*H-*psb*A	GTR + G

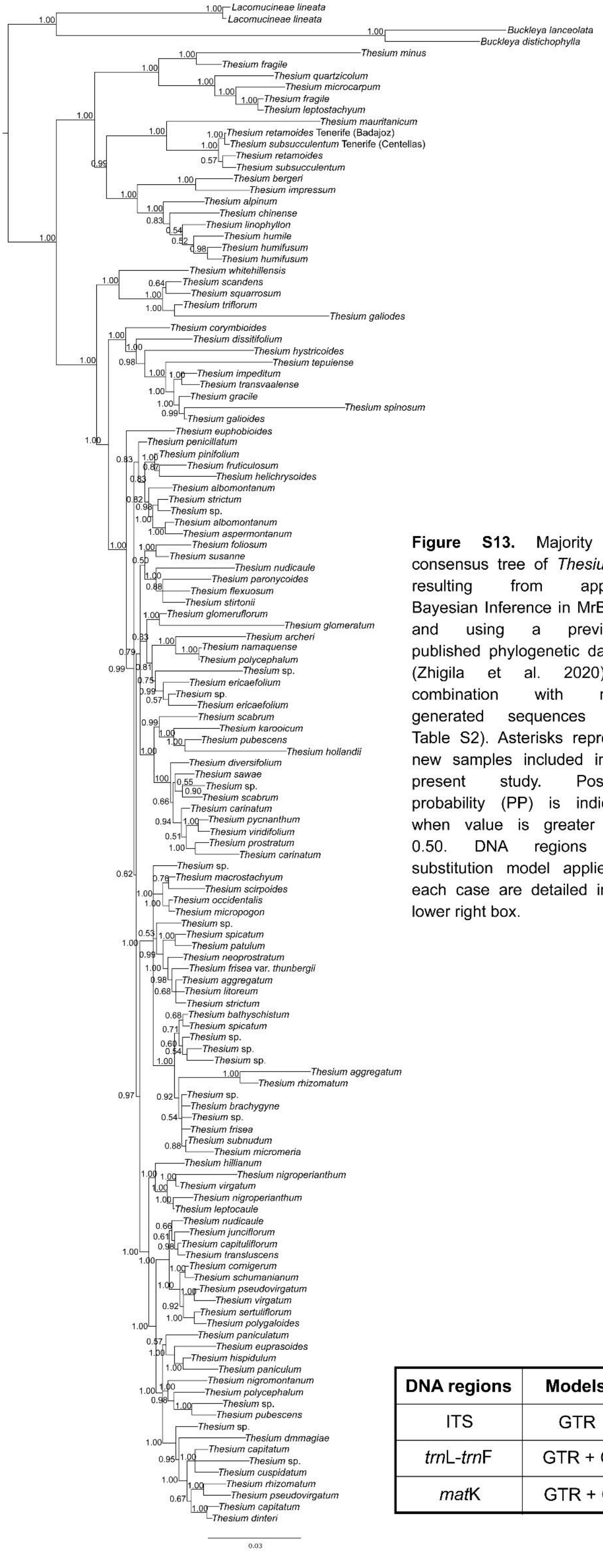


Figure S13. Majority rule consensus tree of *Thesium* L. resulting from applying Bayesian Inference in MrBayes and using a previously published phylogenetic dataset (Zhigila et al. 2020) in combination with newly generated sequences (see Table S2). Asterisks represent new samples included in the present study. Posterior probability (PP) is indicated when value is greater than 0.50. DNA regions and substitution model applied in each case are detailed in the lower right box.

DNA regions	Models
ITS	GTR
*trn*L-*trn*F	GTR + G
*mat*K	GTR + G

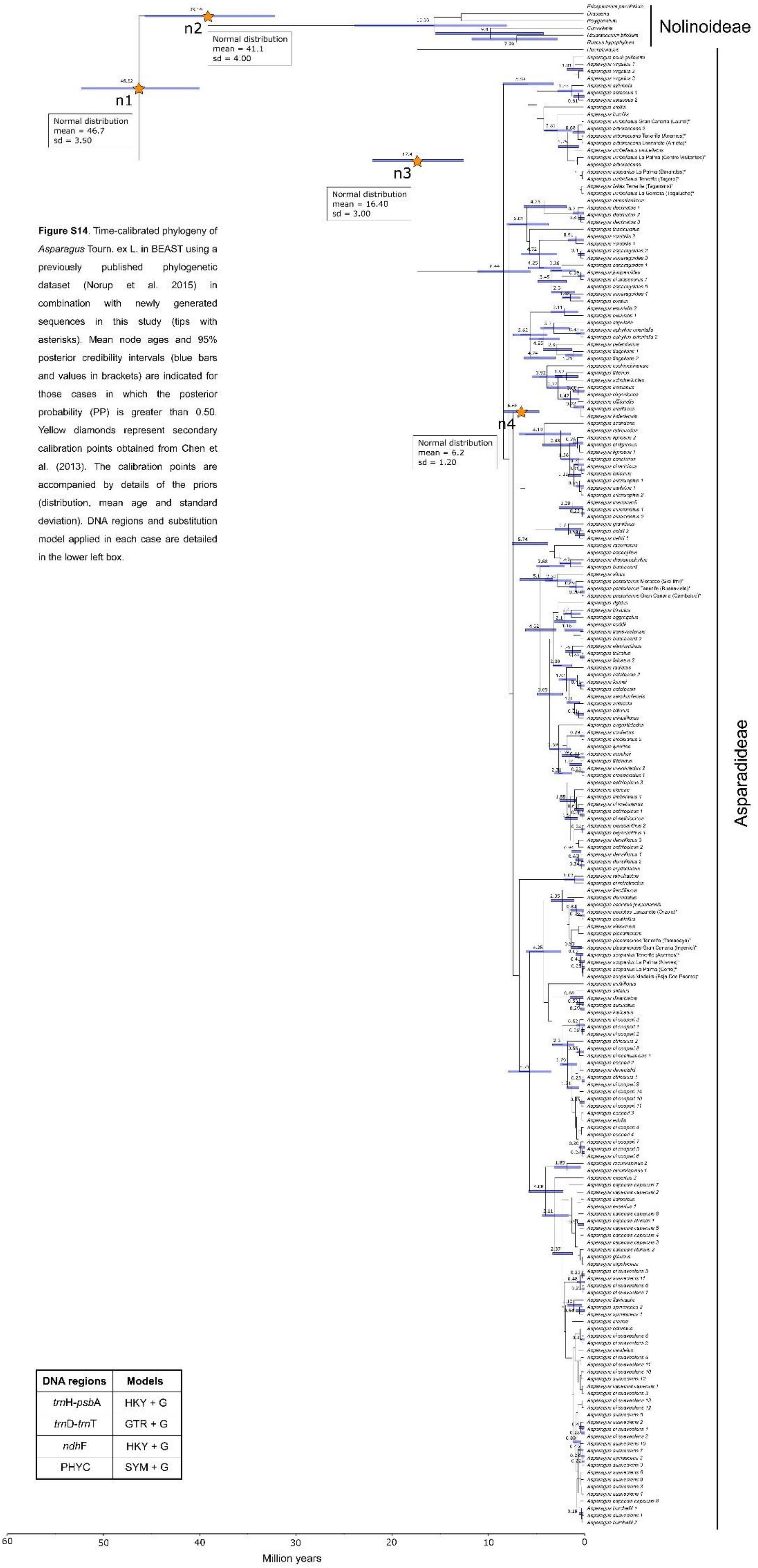


Figure S14. Time-calibrated phylogeny of *Asparagus* Tourn. ex L. in BEAST using a previously published phylogenetic dataset (Norup et al. 2015) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Yellow diamonds represent secondary calibration points obtained from Chen et al. (2013). The calibration points are accompanied by details of the priors (distribution, mean age and standard deviation). DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA regions	Models
*trn*H-*psb*A	HKY + G
*trn*D-*trn*T	GTR + G
*ndh*F	HKY + G
PHYC	SYM + G

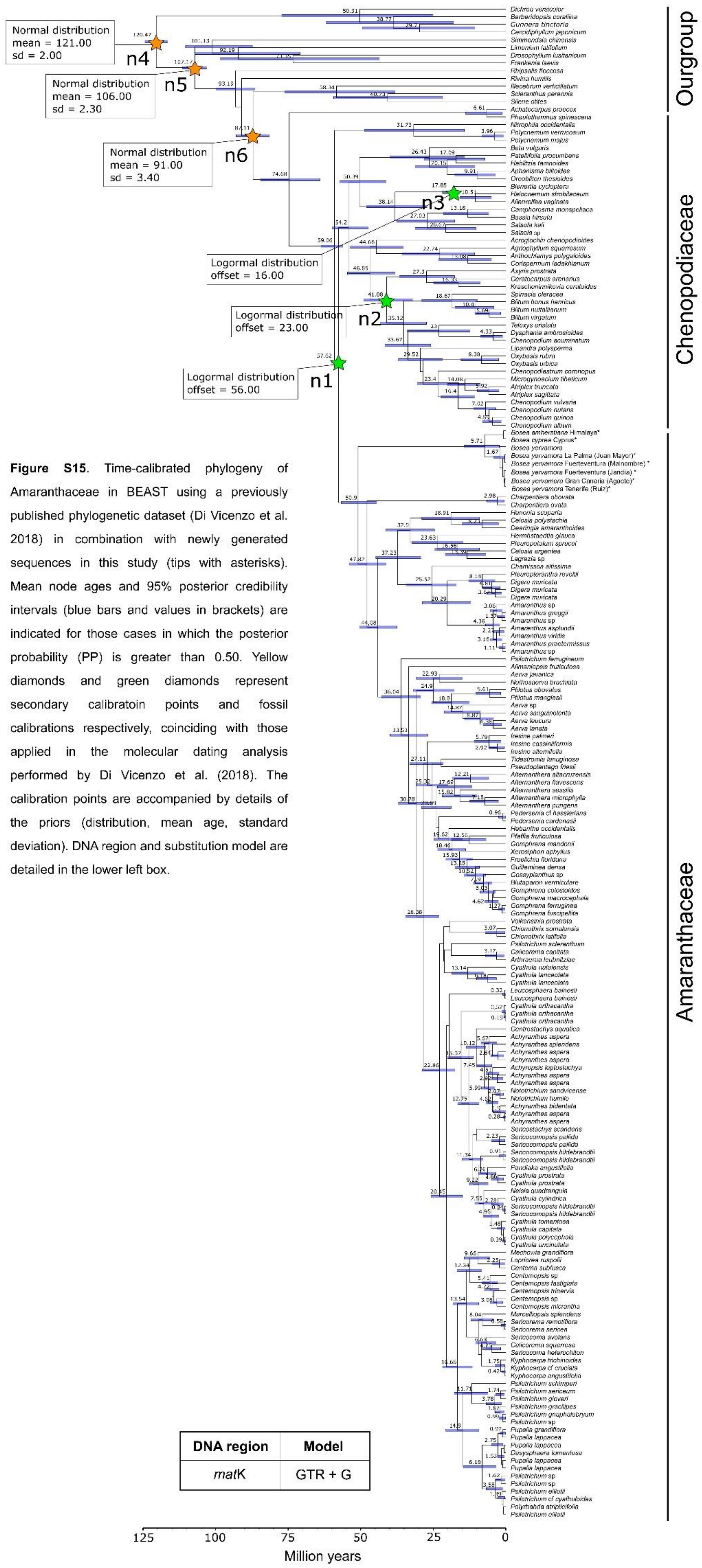


Figure S15. Time-calibrated phylogeny of Amaranthaceae in BEAST using a previously published phylogenetic dataset (Di Vicenzo et al. 2018) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Yellow diamonds and green diamonds represent secondary calibratoin points and fossil calibrations respectively, coinciding with those applied in the molecular dating analysis performed by Di Vicenzo et al. (2018). The calibration points are accompanied by details of the priors (distribution, mean age, standard deviation). DNA region and substitution model are detailed in the lower left box.

DNA region	Model
*mat*K	GTR + G

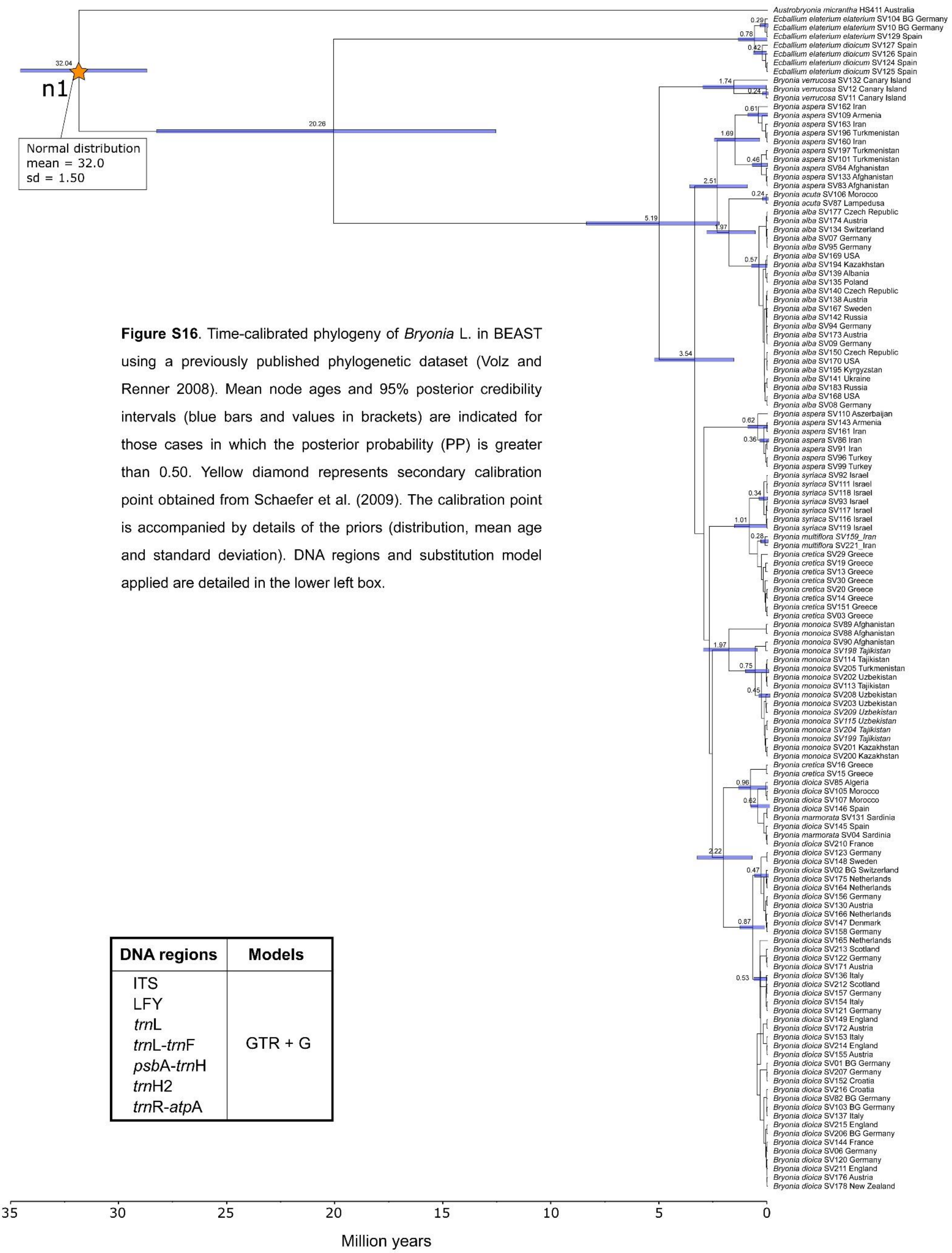
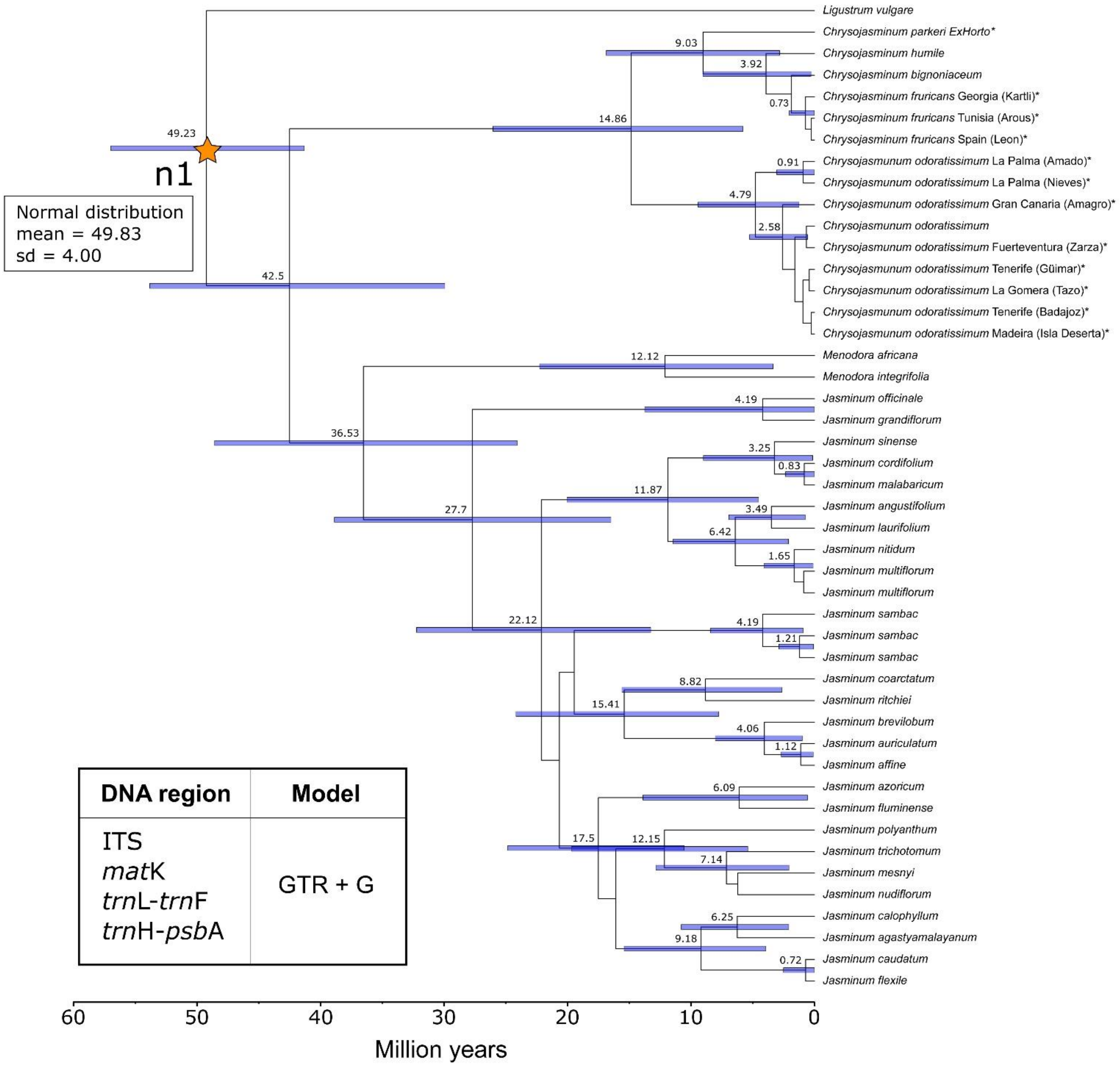


Figure S16. Time-calibrated phylogeny of *Bryonia* L. in BEAST using a previously published phylogenetic dataset (Volz and Renner 2008). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Yellow diamond represents secondary calibration point obtained from Schaefer et al. (2009). The calibration point is accompanied by details of the priors (distribution, mean age and standard deviation). DNA regions and substitution model applied are detailed in the lower left box.

DNA regions	Models
ITS LFY *trn*L *trn*L-*trn*F *psb*A-*trn*H *trn*H2 *trn*R-*atp*A	GTR + G



DNA region	Model
ITS *mat*K *trn*L-*trn*F *trn*H-*psb*A	GTR + G

Figure S17. Time-calibrated phylogeny of *Chrysojasminum* Banfi in BEAST using a previously published phylogenetic dataset (Jeyarani et al. 2018) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Yellow diamond represents secondary calibration point obtained from Vargas et al. (2014). The calibration point are accompanied by details of the priors (distribution, mean age and standard deviation). DNA region and substitution model are detailed in the lower left box.

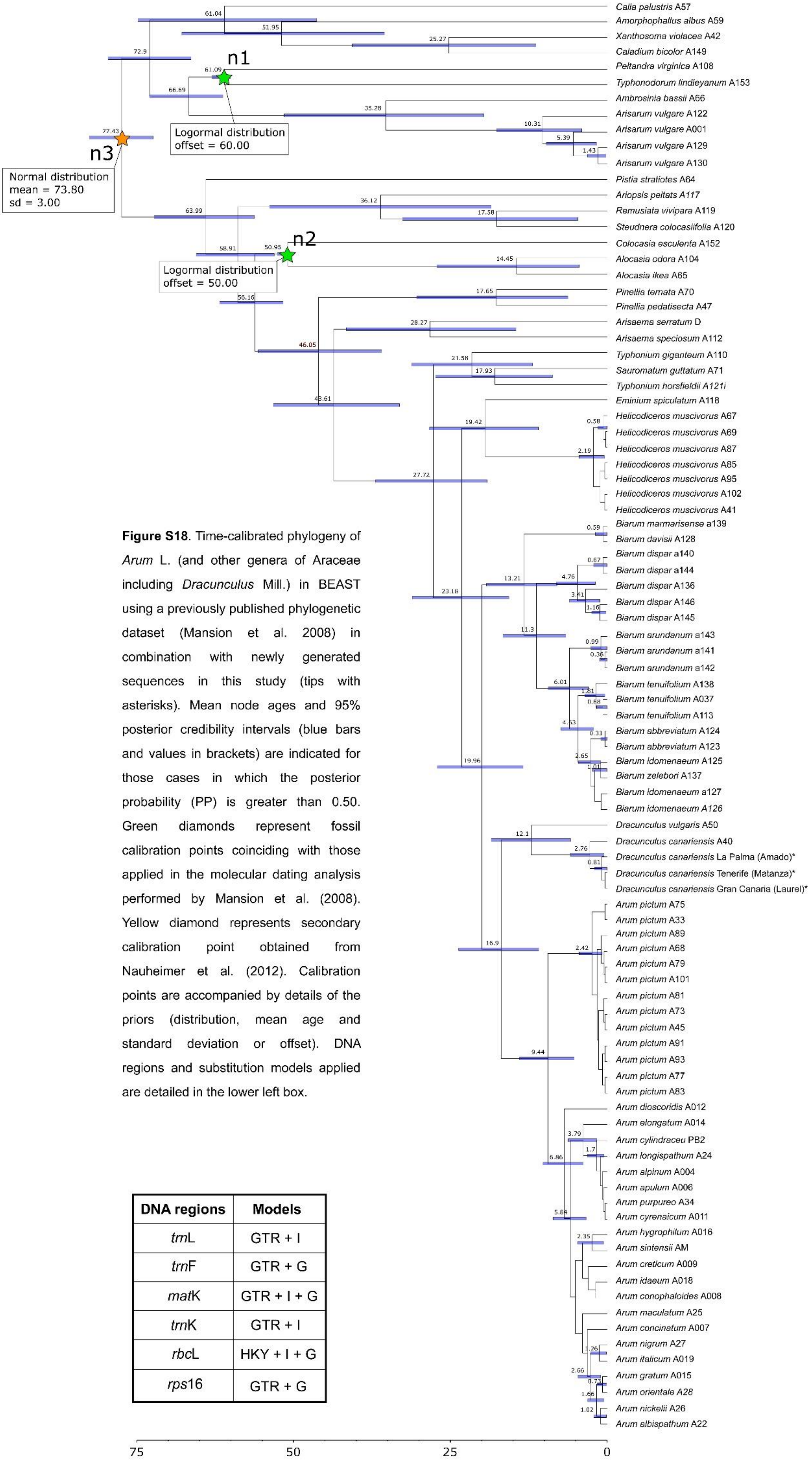
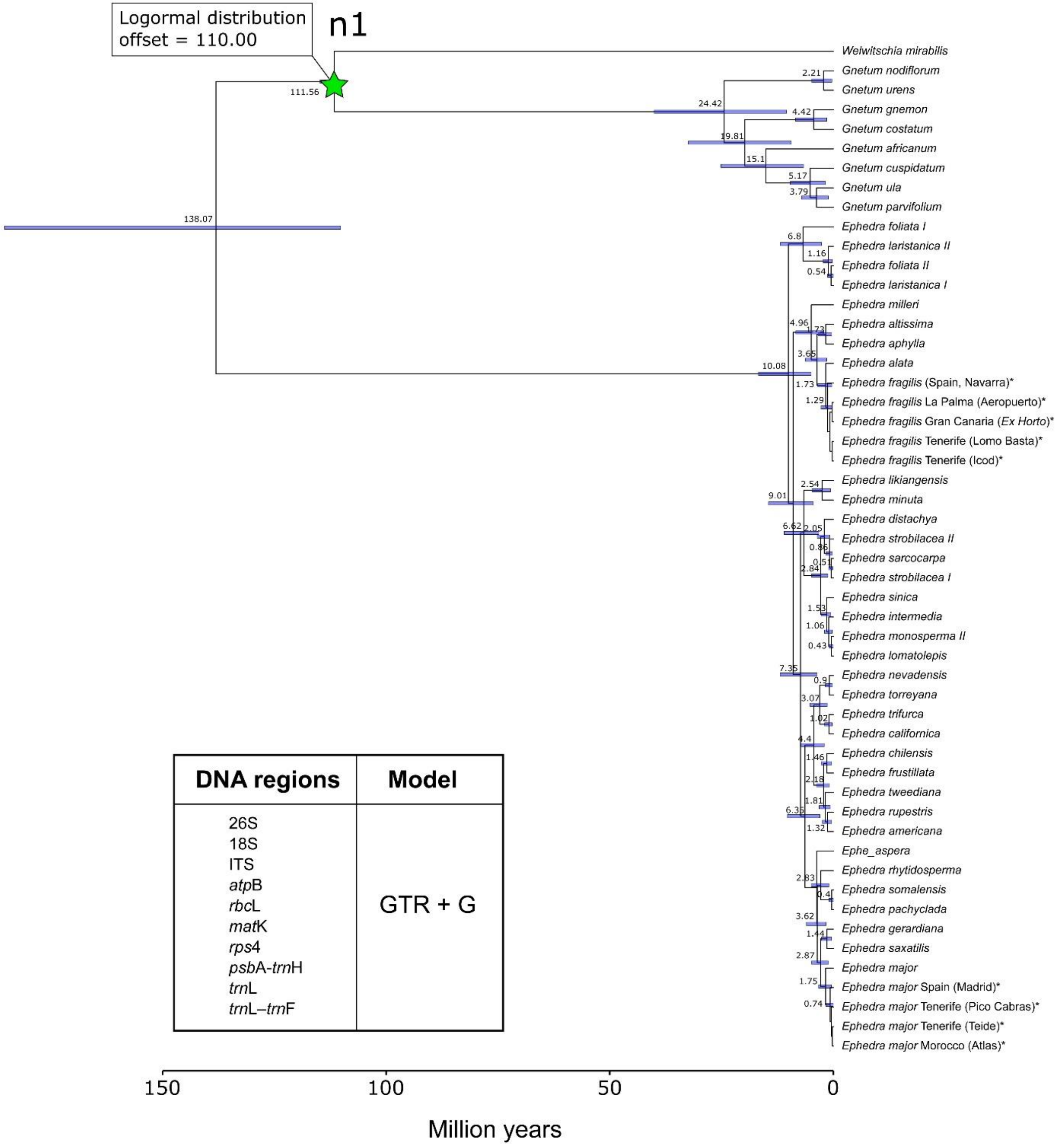


Figure S18. Time-calibrated phylogeny of *Arum* L. (and other genera of Araceae including *Dracunculus* Mill.) in BEAST using a previously published phylogenetic dataset (Mansion et al. 2008) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Green diamonds represent fossil calibration points coinciding with those applied in the molecular dating analysis performed by Mansion et al. (2008). Yellow diamond represents secondary calibration point obtained from Nauheimer et al. (2012). Calibration points are accompanied by details of the priors (distribution, mean age and standard deviation or offset). DNA regions and substitution models applied are detailed in the lower left box.

DNA regions	Models
*trn*L	GTR + I
*trn*F	GTR + G
*mat*K	GTR + I + G
*trn*K	GTR + I
*rbc*L	HKY + I + G
*rps*16	GTR + G

Figure S19. Time-calibrated phylogeny of *Ephedra* Tourn. ex L. in BEAST using a previously published phylogenetic dataset (Ickert-Bond et al. 2009) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Green diamond represents a fossil calibration point coinciding with those applied in the molecular dating analysis performed by Ickert-Bond et al. (2009). The calibration point are accompanied by details of the priors (distribution, offset). DNA regions and substitution model are detailed in the lower left box.



DNA regions	**Model**
26S 18S ITS *atp*B *rbc*L *mat*K *rps*4 *psb*A-*trn*H *trn*L *trn*L–*trn*F	GTR + G

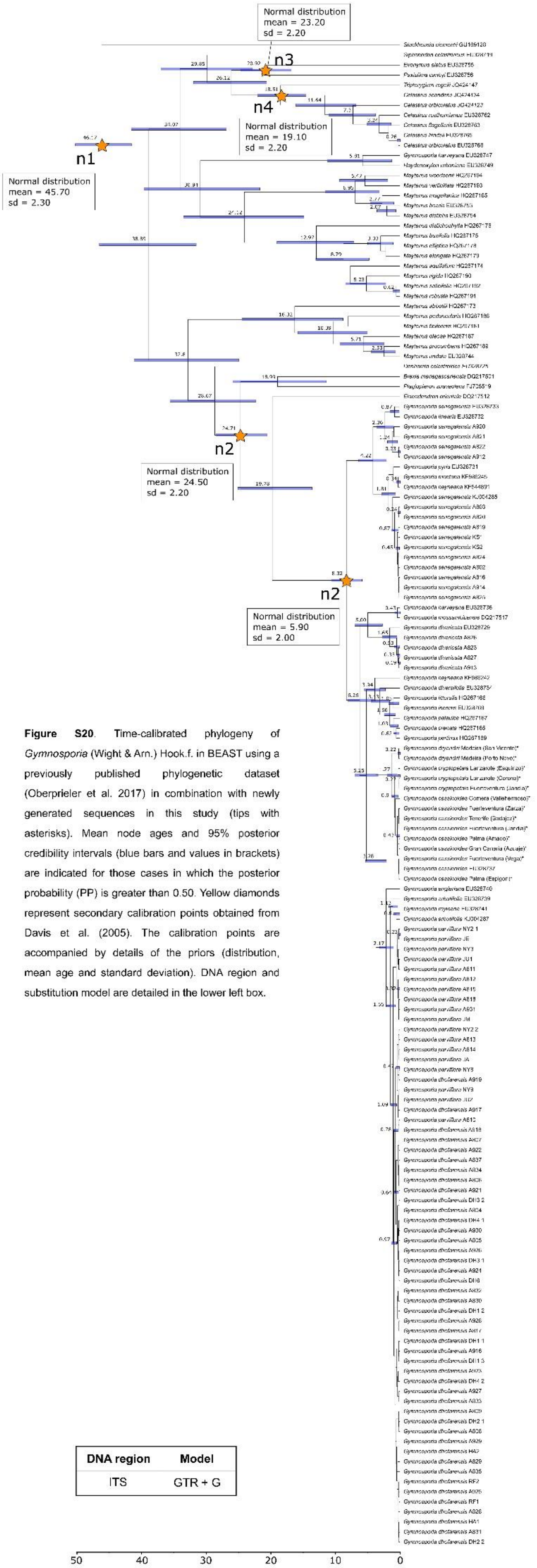
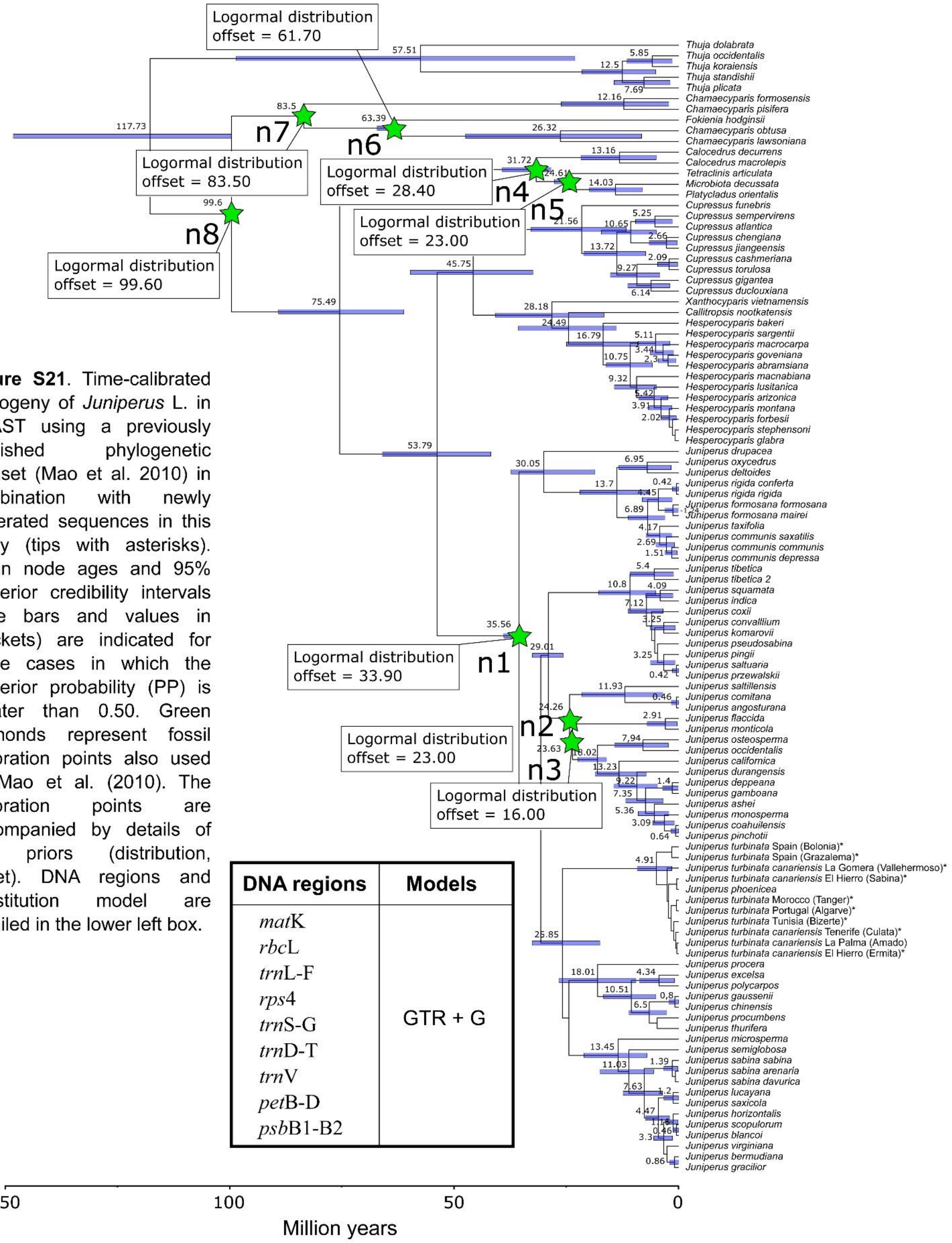


Figure S20. Time-calibrated phylogeny of *Gymnosporia* (Wight & Arn.) Hook.f. in BEAST using a previously published phylogenetic dataset (Oberprieler et al. 2017) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Yellow diamonds represent secondary calibration points obtained from Davis et al. (2005). The calibration points are accompanied by details of the priors (distribution, mean age and standard deviation). DNA region and substitution model are detailed in the lower left box.

DNA region	Model
ITS	GTR + G



DNA regions	Models
*mat*K *rbc*L *trn*L-F *rps*4 *trn*S-G *trn*D-T *trn*V *pet*B-D *psb*B1-B2	GTR + G

Figure S21. Time-calibrated phylogeny of *Juniperus* L. in BEAST using a previously published phylogenetic dataset (Mao et al. 2010) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Green diamonds represent fossil calibration points also used by Mao et al. (2010). The calibration points are accompanied by details of the priors (distribution, offset). DNA regions and substitution model are detailed in the lower left box.

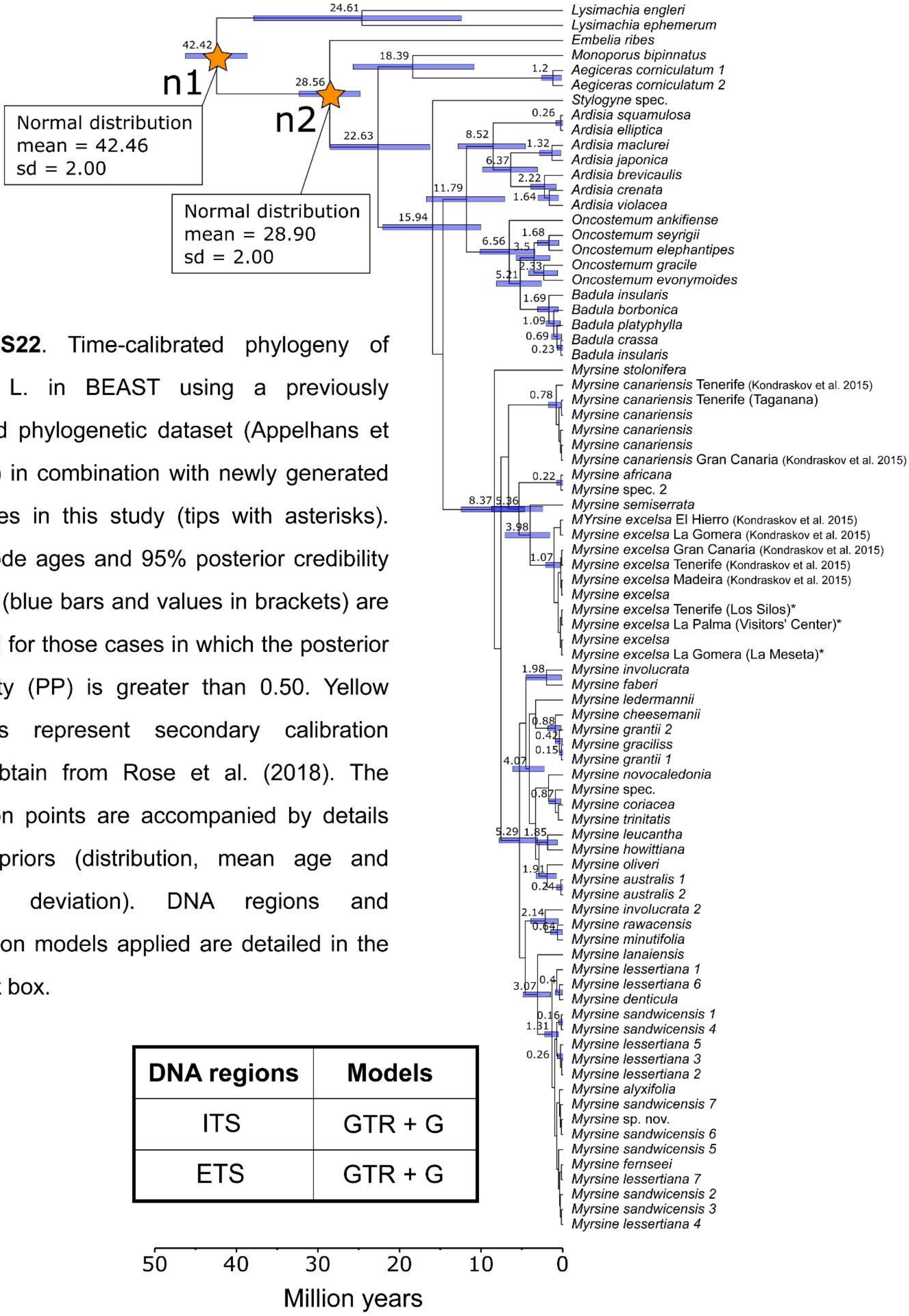
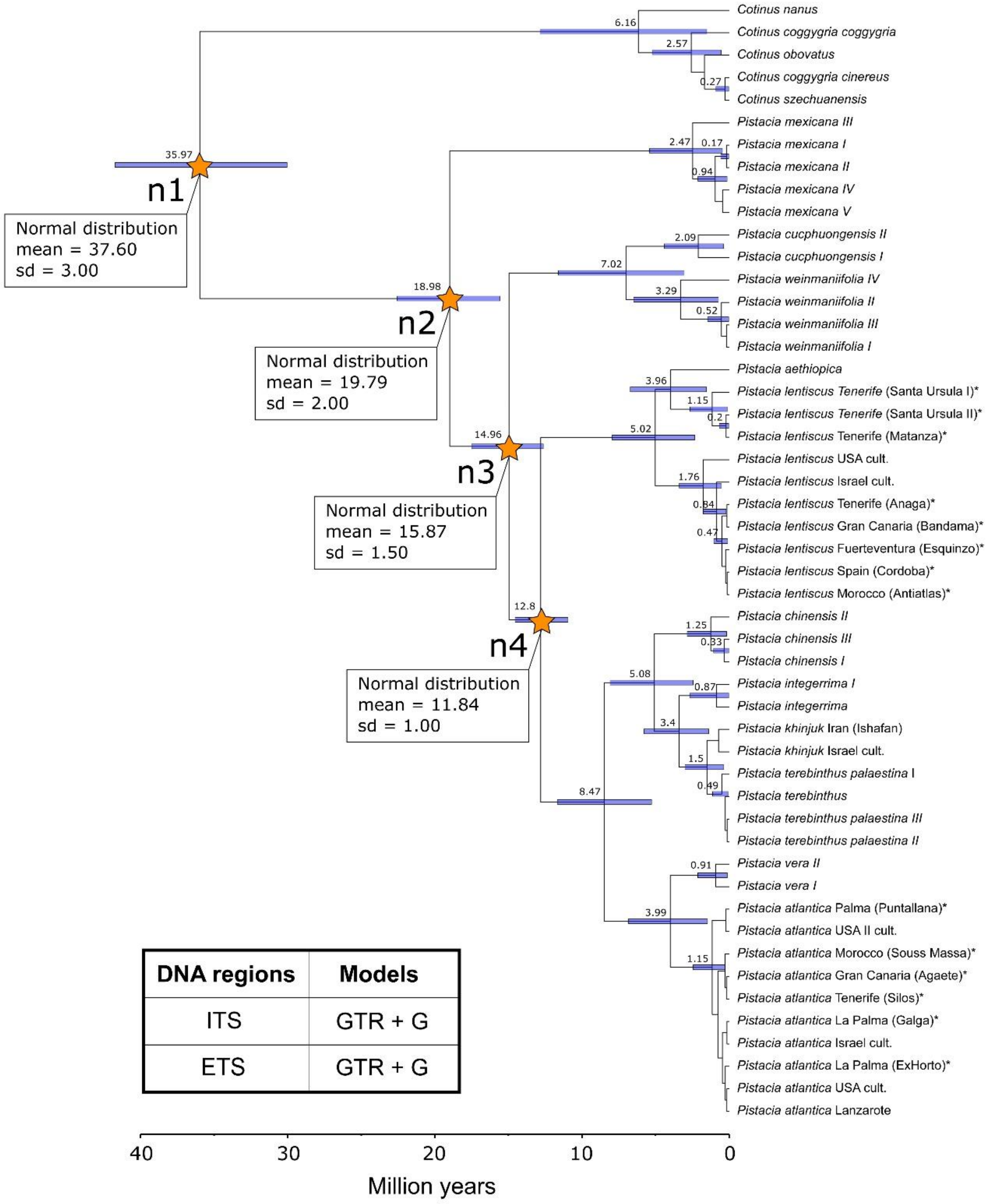


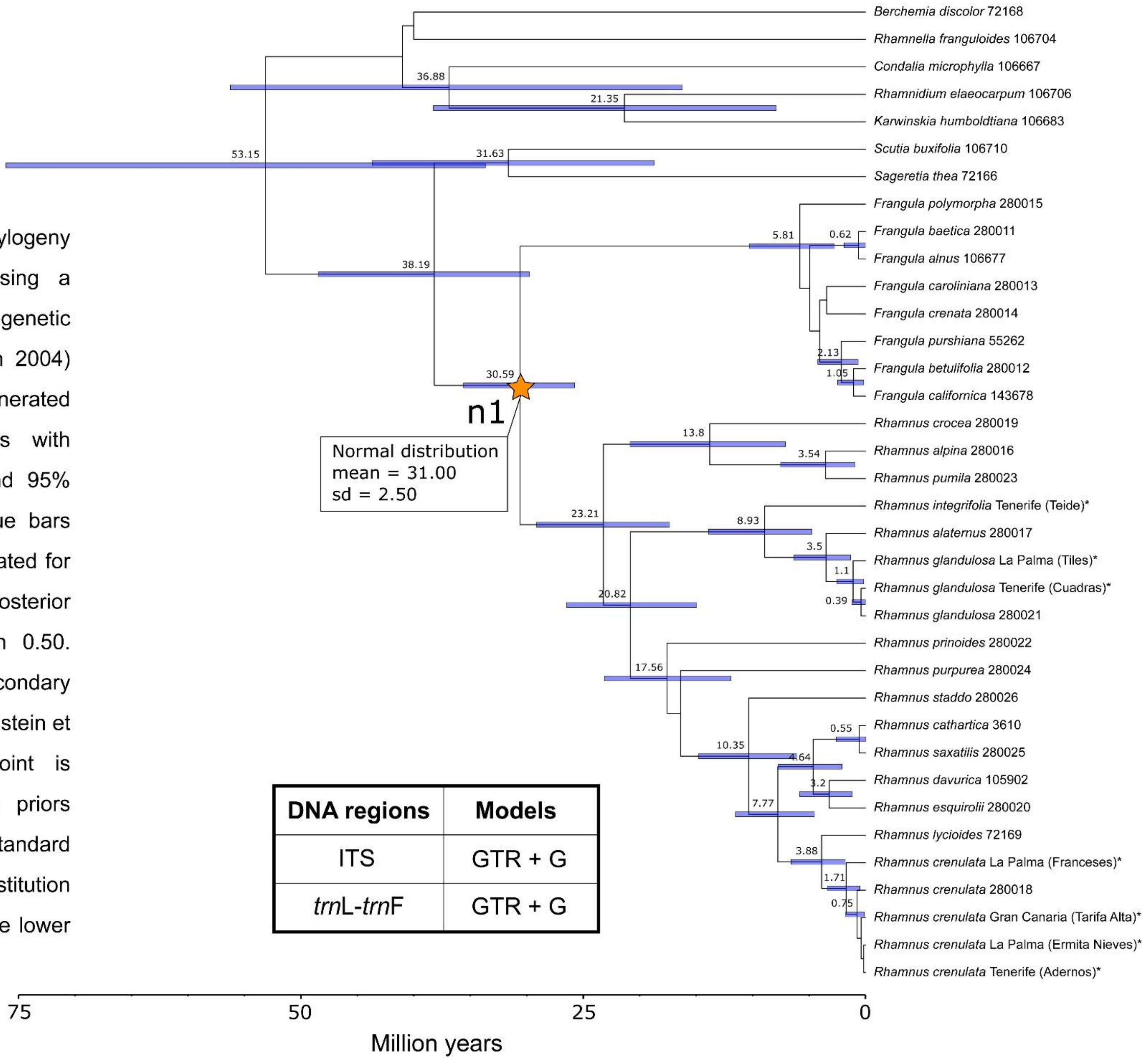
Figure S22. Time-calibrated phylogeny of *Myrsine* L. in BEAST using a previously published phylogenetic dataset (Appelhans et al. 2020) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Yellow diamonds represent secondary calibration points obtain from Rose et al. (2018). The calibration points are accompanied by details of the priors (distribution, mean age and standard deviation). DNA regions and substitution models applied are detailed in the lower left box.

DNA regions	Models
ITS	GTR + G
ETS	GTR + G



DNA regions	Models
ITS	GTR + G
ETS	GTR + G

Figure S23. Time-calibrated phylogeny of *Pistacia* L. in BEAST using a previously published phylogenetic dataset (Xie et al. 2014) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Yellow diamonds represent secondary calibration points, coinciding with those applied in the molecular dating analysis performed by Xie et al. (2014). The calibration points are accompanied by details of the priors (distribution, mean age and standard deviation). DNA regions and substitution models applied are detailed in the lower left box.



DNA regions	Models
ITS	GTR + G
*trn*L-*trn*F	GTR + G

Figure S24. Time-calibrated phylogeny of *Rhamnus* L. in BEAST using a previously published phylogenetic dataset (Bolmgren and Oxelman 2004) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Yellow diamond represents secondary calibration point obtained from Onstein et al. (2015). The calibration point is accompanied by details of the priors (distribution, mean age and standard deviation). DNA regions and substitution models applied are detailed in the lower left box.

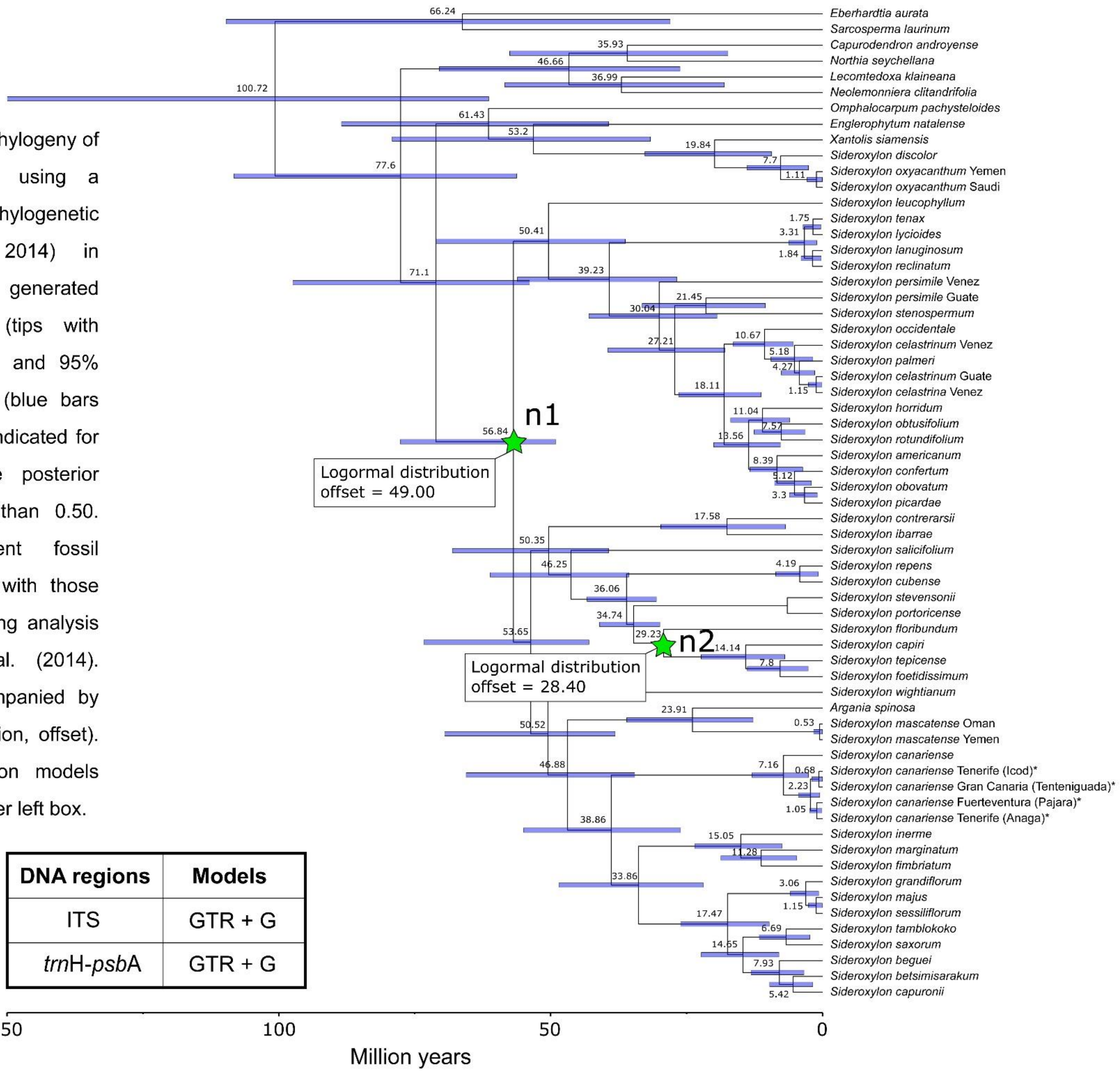


Figure S25. Time-calibrated phylogeny of *Sideroxylon* L. in BEAST using a previously published phylogenetic dataset (Stride et al. 2014) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Green diamonds represent fossil calibration points coinciding with those applied in the molecular dating analysis performed by Stride et al. (2014). Calibration points are accompanied by details of the priors (distribution, offset). DNA regions and substitution models applied are detailed in the lower left box.

DNA regions	**Models**
ITS	GTR + G
*trn*H-*psb*A	GTR + G

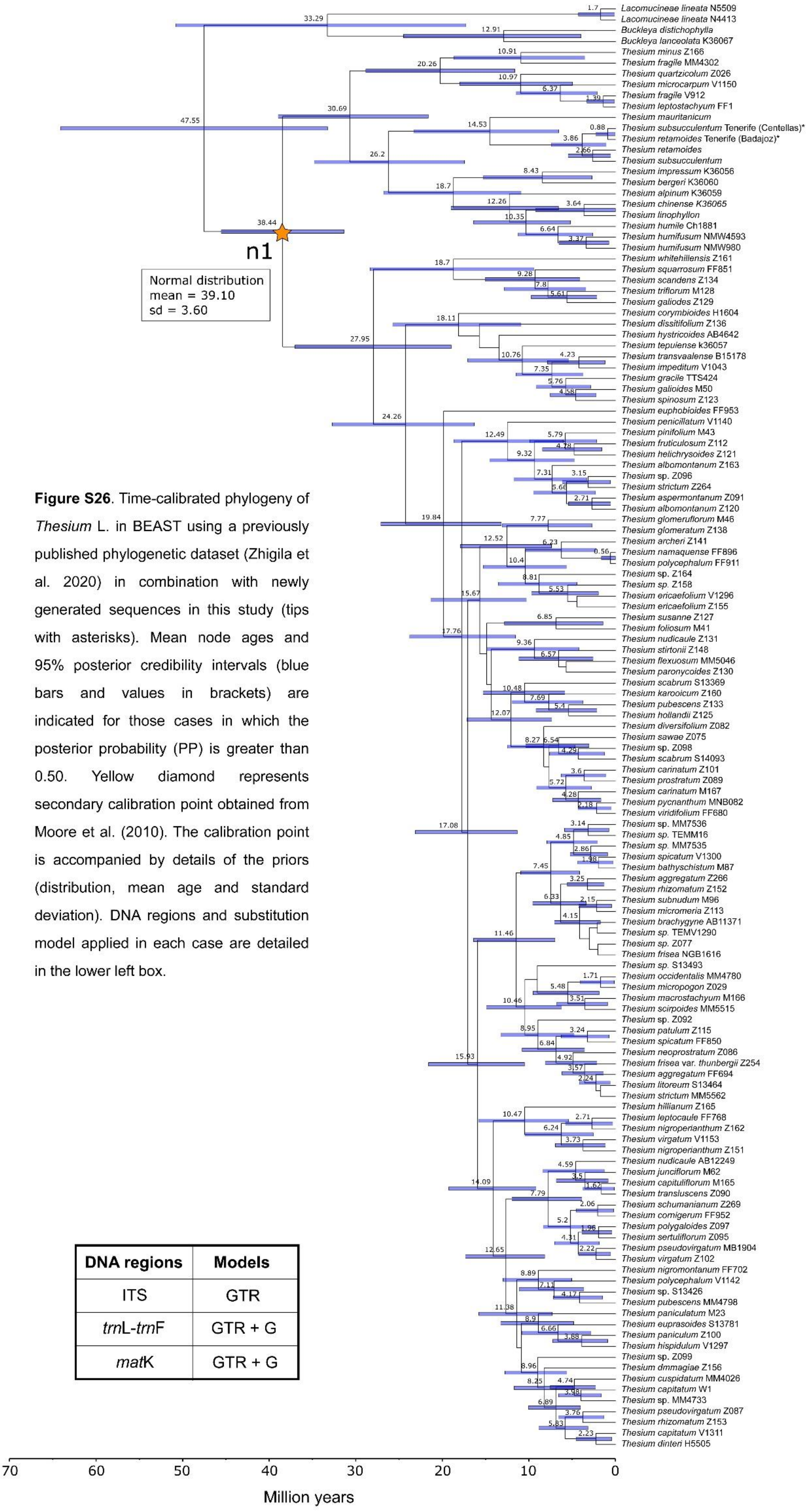


Figure S26. Time-calibrated phylogeny of *Thesium* L. in BEAST using a previously published phylogenetic dataset (Zhigila et al. 2020) in combination with newly generated sequences in this study (tips with asterisks). Mean node ages and 95% posterior credibility intervals (blue bars and values in brackets) are indicated for those cases in which the posterior probability (PP) is greater than 0.50. Yellow diamond represents secondary calibration point obtained from Moore et al. (2010). The calibration point is accompanied by details of the priors (distribution, mean age and standard deviation). DNA regions and substitution model applied in each case are detailed in the lower left box.

DNA regions	**Models**
ITS	GTR
*trn*L-*trn*F	GTR + G
*mat*K	GTR + G

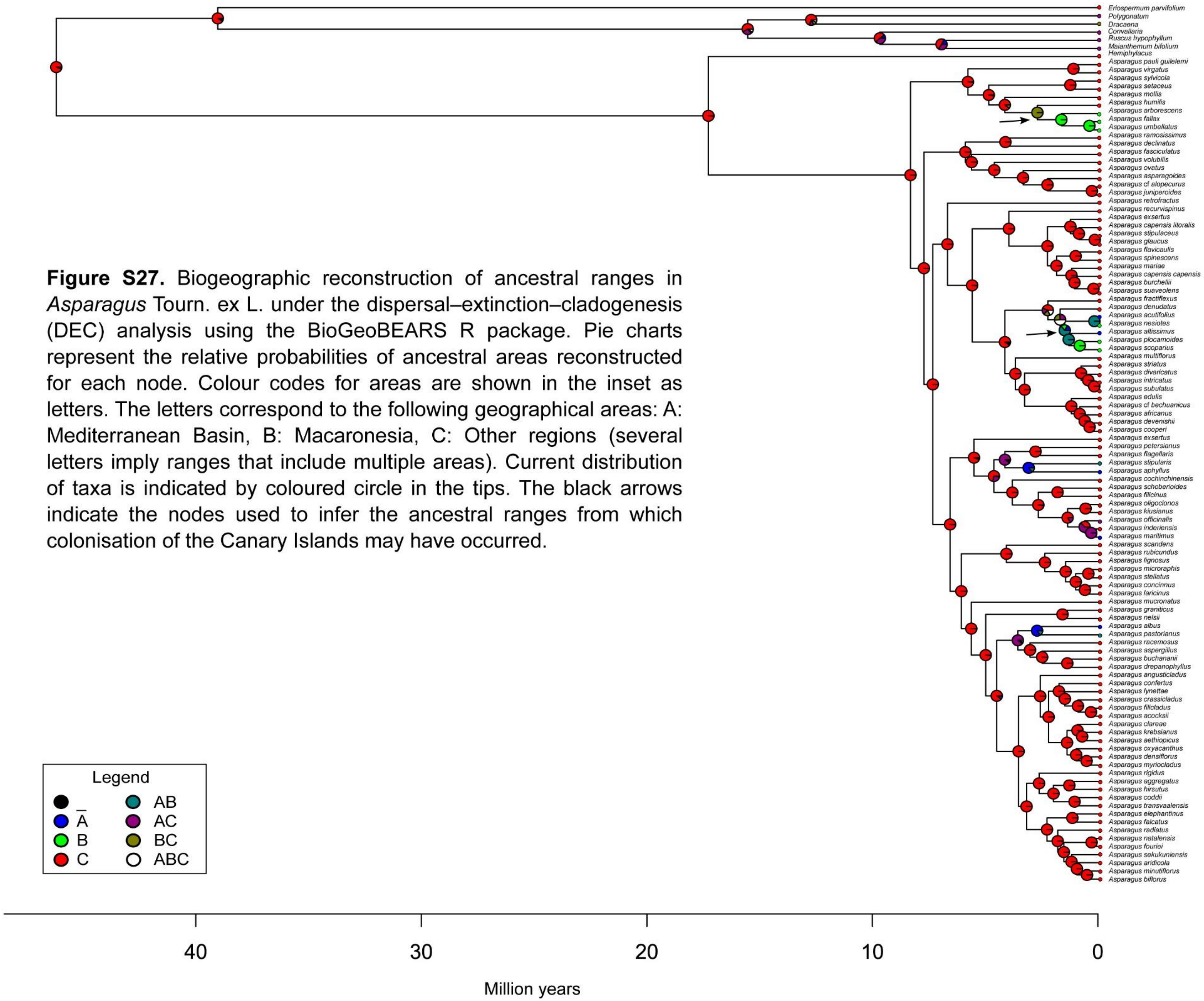


Figure S27. Biogeographic reconstruction of ancestral ranges in *Asparagus* Tourn. ex L. under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

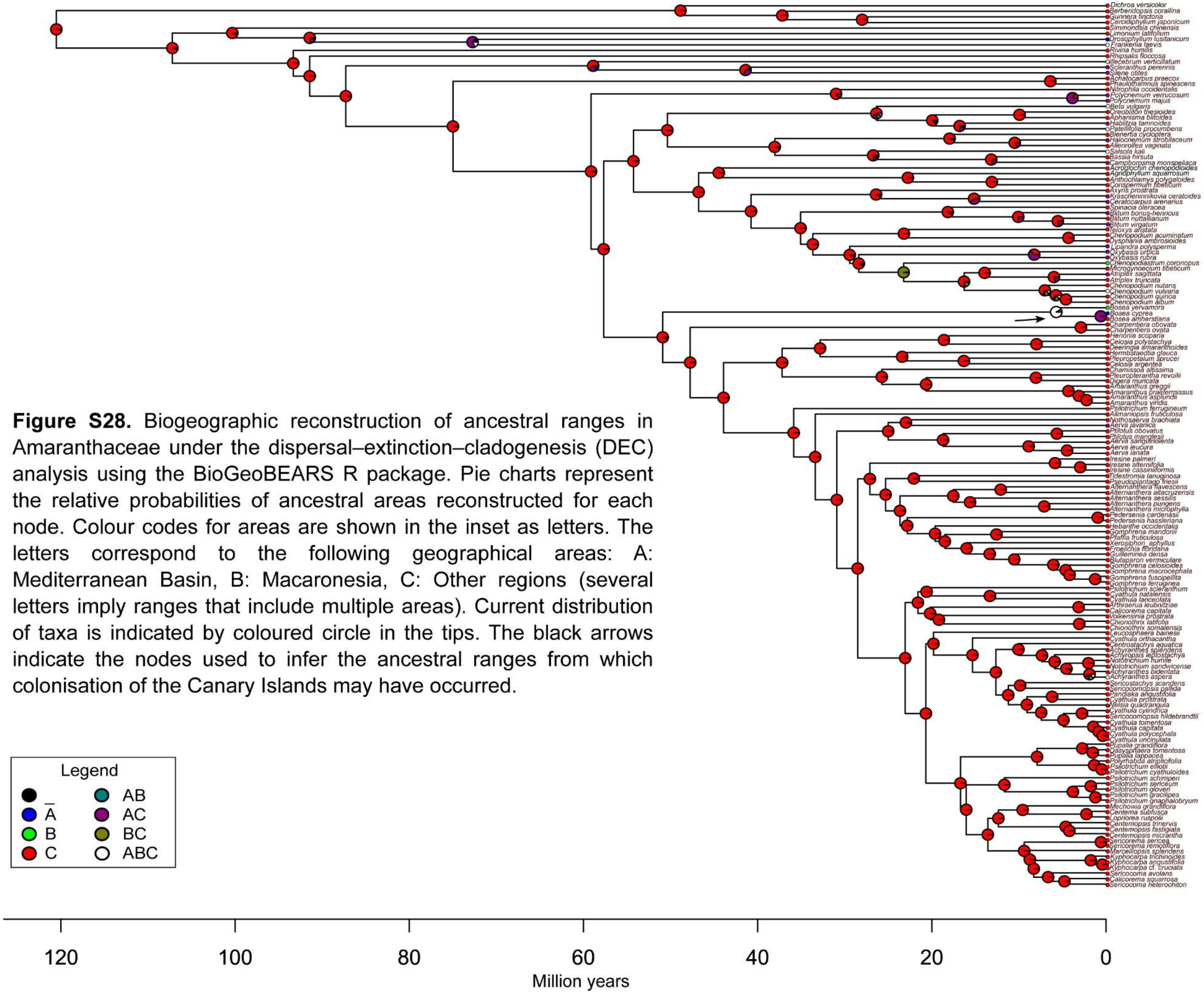


Figure S28. Biogeographic reconstruction of ancestral ranges in Amaranthaceae under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

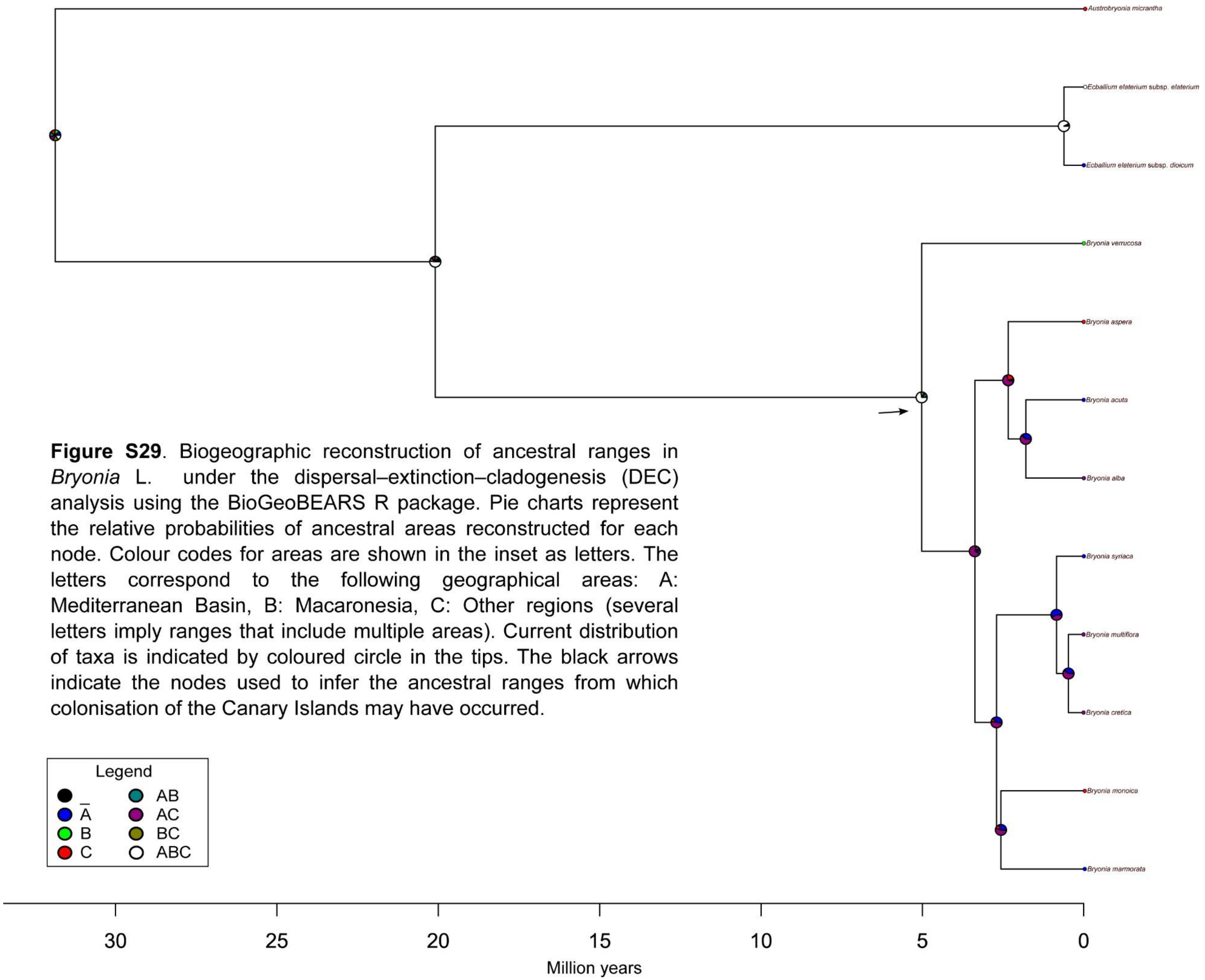


Figure S29. Biogeographic reconstruction of ancestral ranges in *Bryonia* L. under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

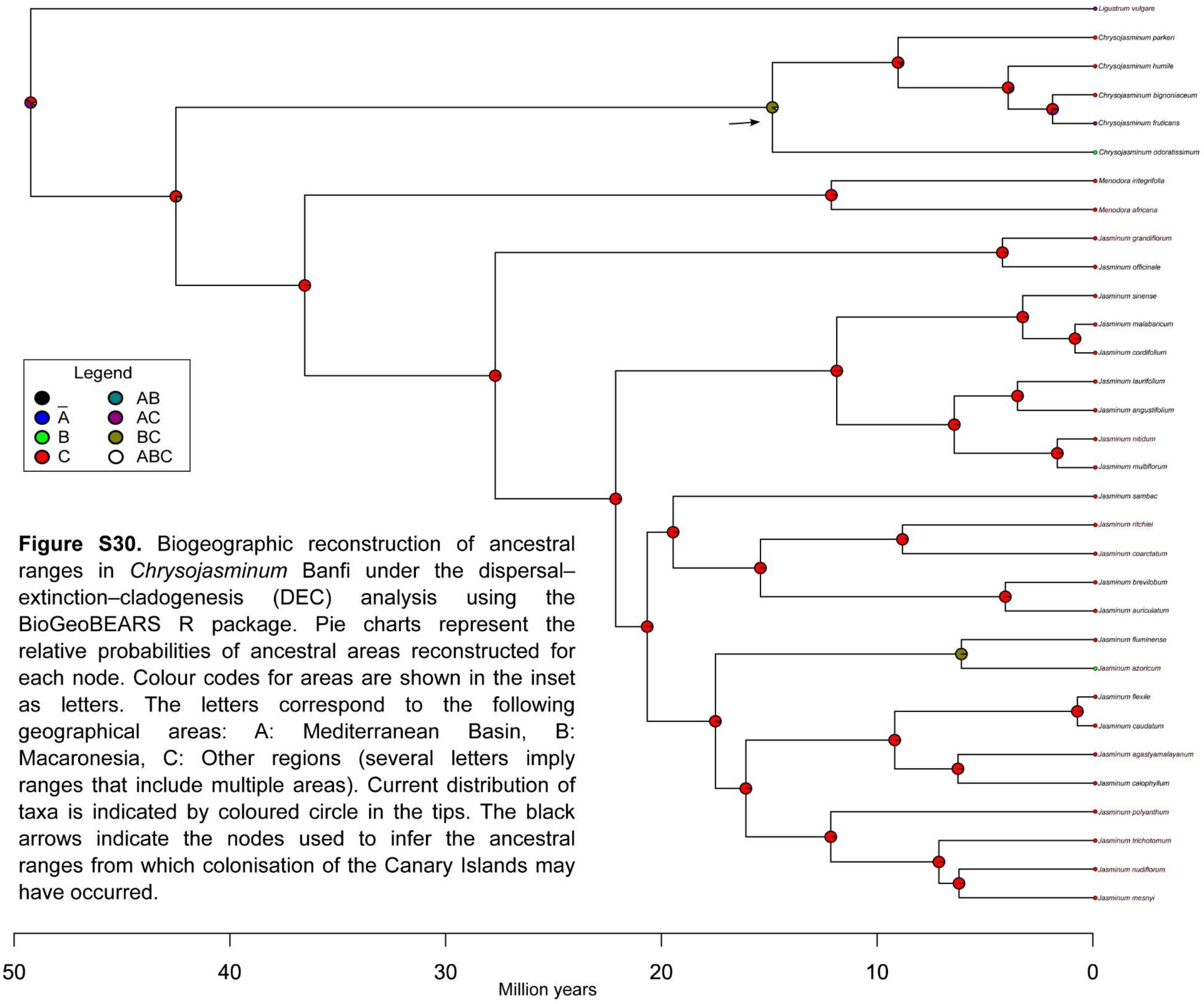


Figure S30. Biogeographic reconstruction of ancestral ranges in *Chrysojasminum* Banfi under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

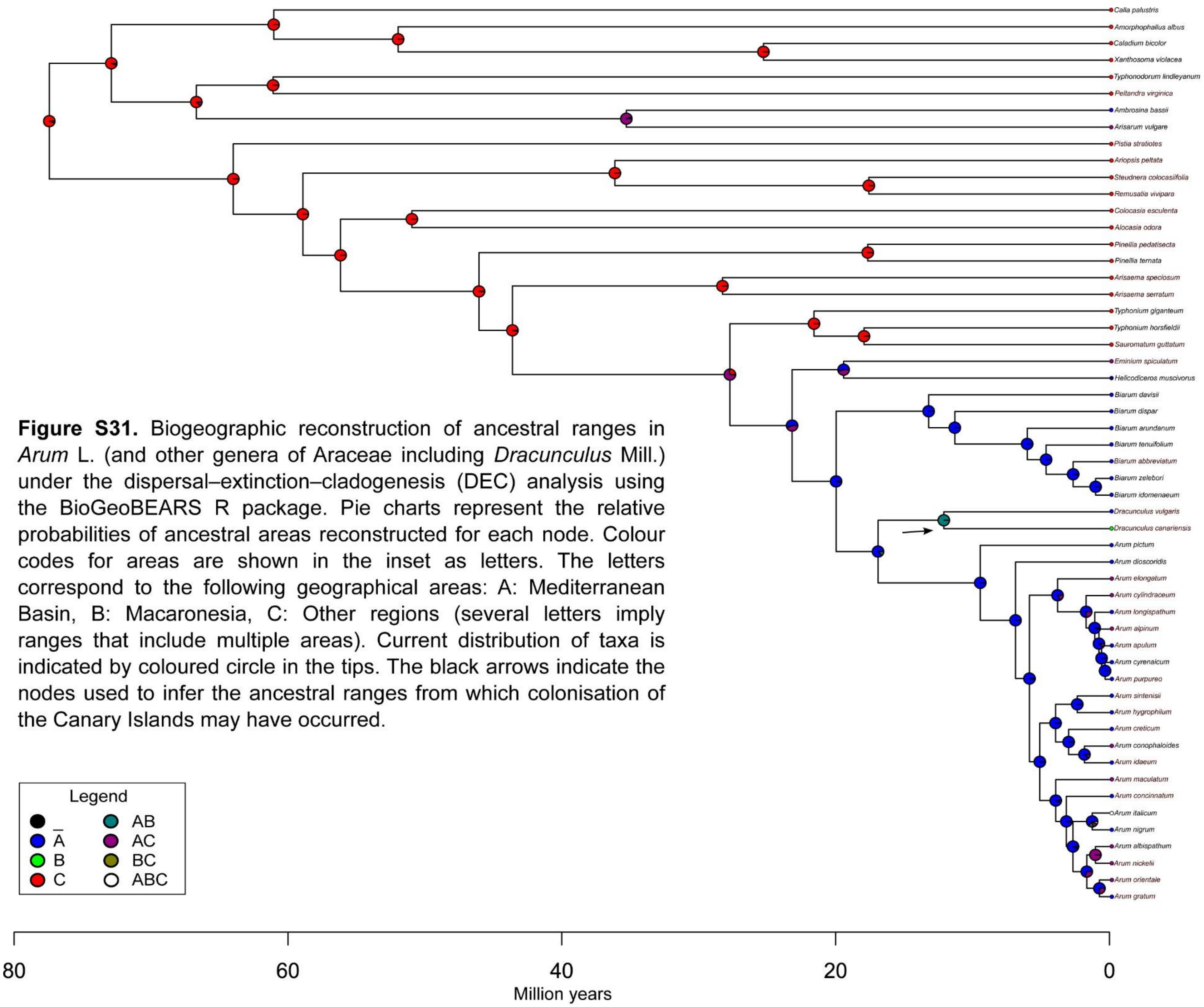


Figure S31. Biogeographic reconstruction of ancestral ranges in *Arum* L. (and other genera of Araceae including *Dracunculus* Mill.) under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

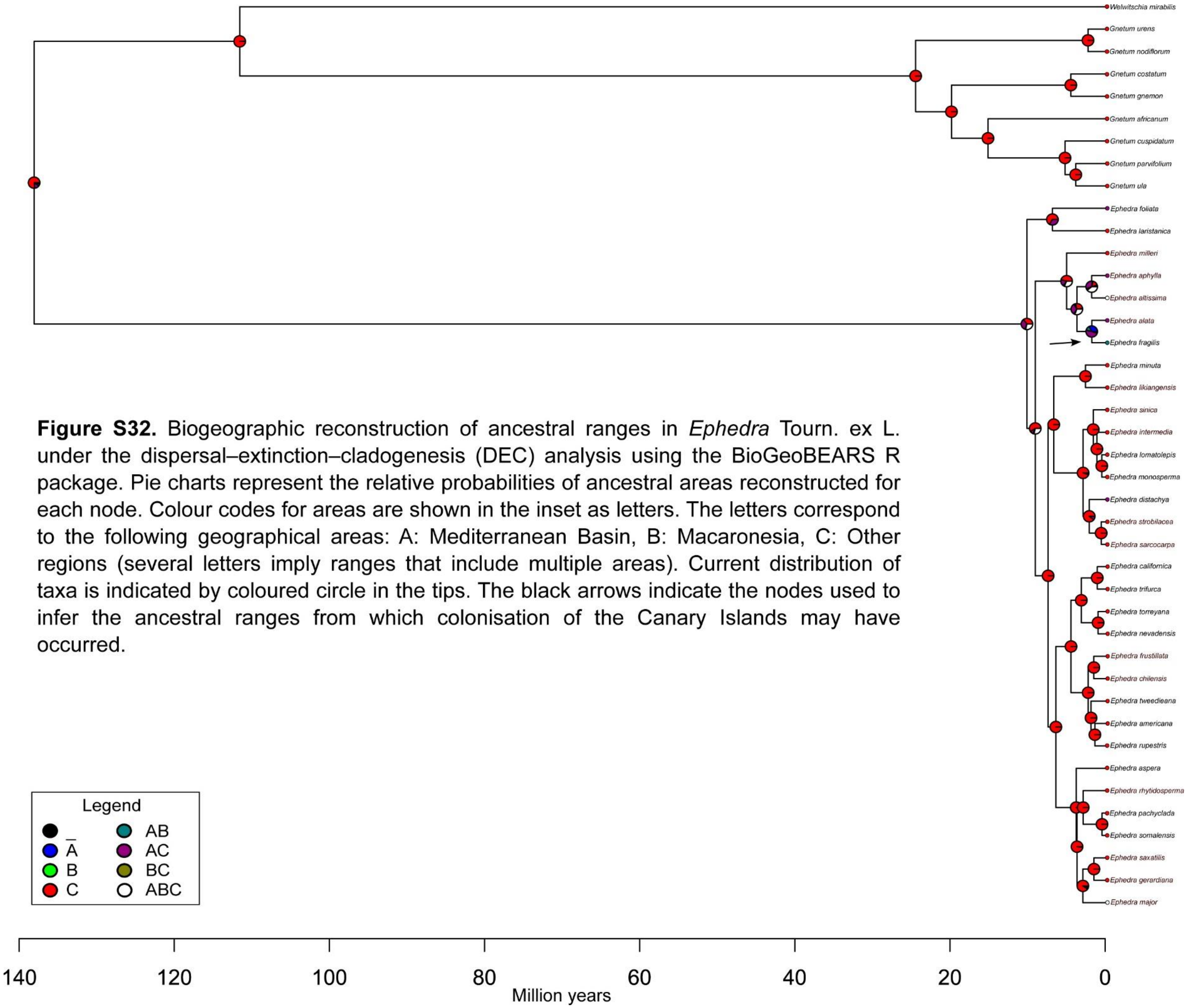


Figure S32. Biogeographic reconstruction of ancestral ranges in *Ephedra* Tourn. ex L. under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

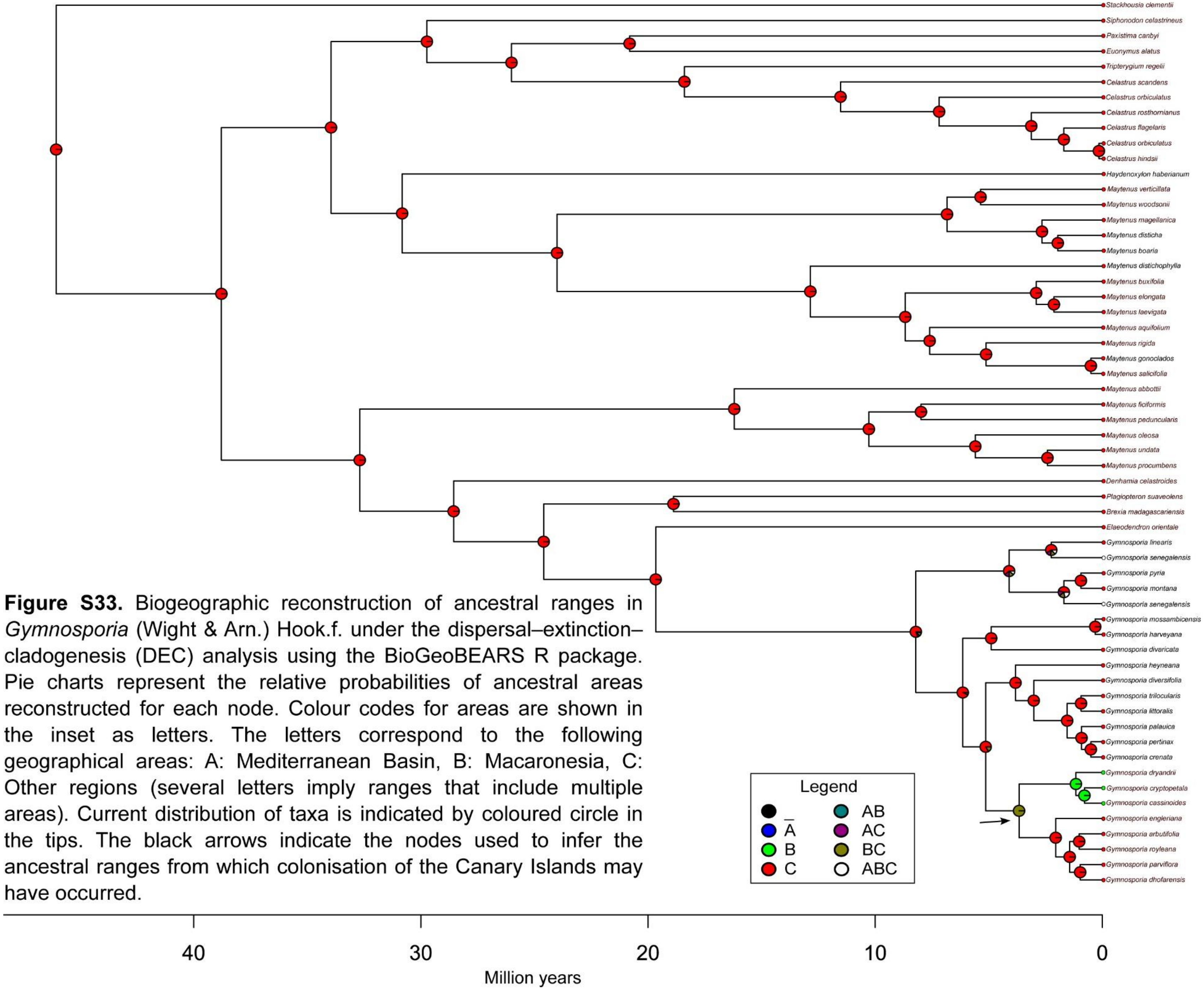


Figure S33. Biogeographic reconstruction of ancestral ranges in *Gymnosporia* (Wight & Arn.) Hook.f. under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

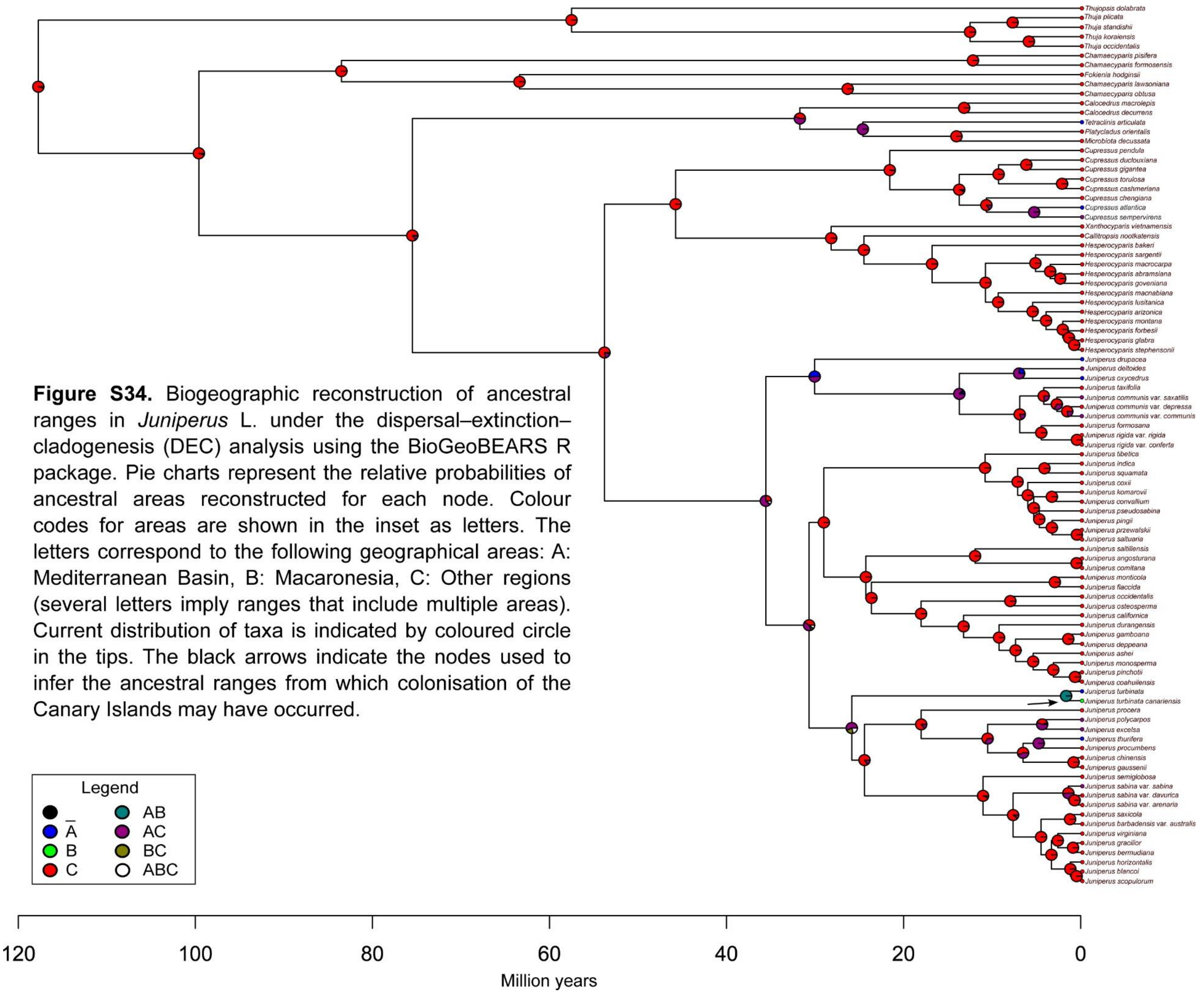


Figure S34. Biogeographic reconstruction of ancestral ranges in *Juniperus* L. under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

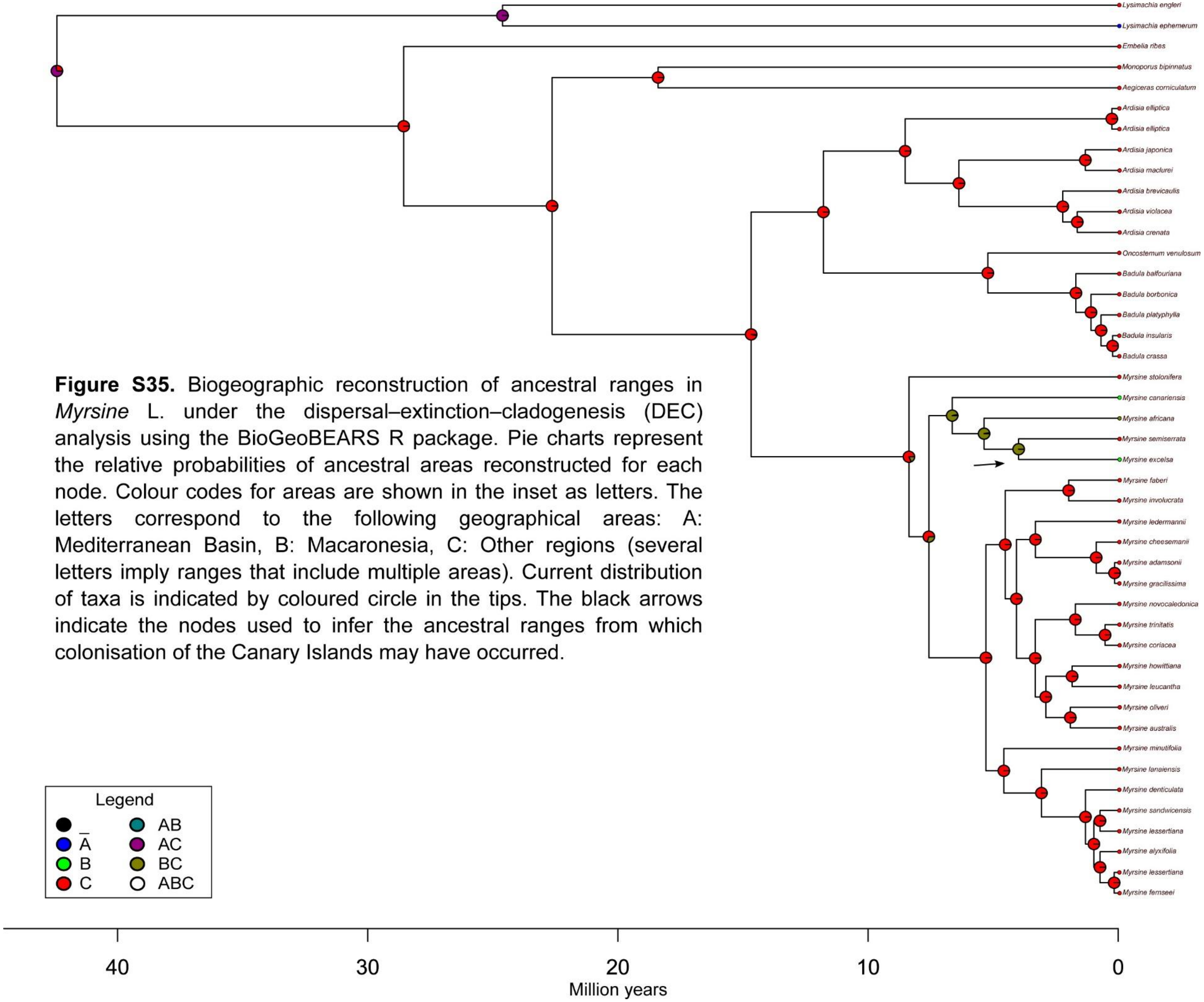


Figure S35. Biogeographic reconstruction of ancestral ranges in *Myrsine* L. under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

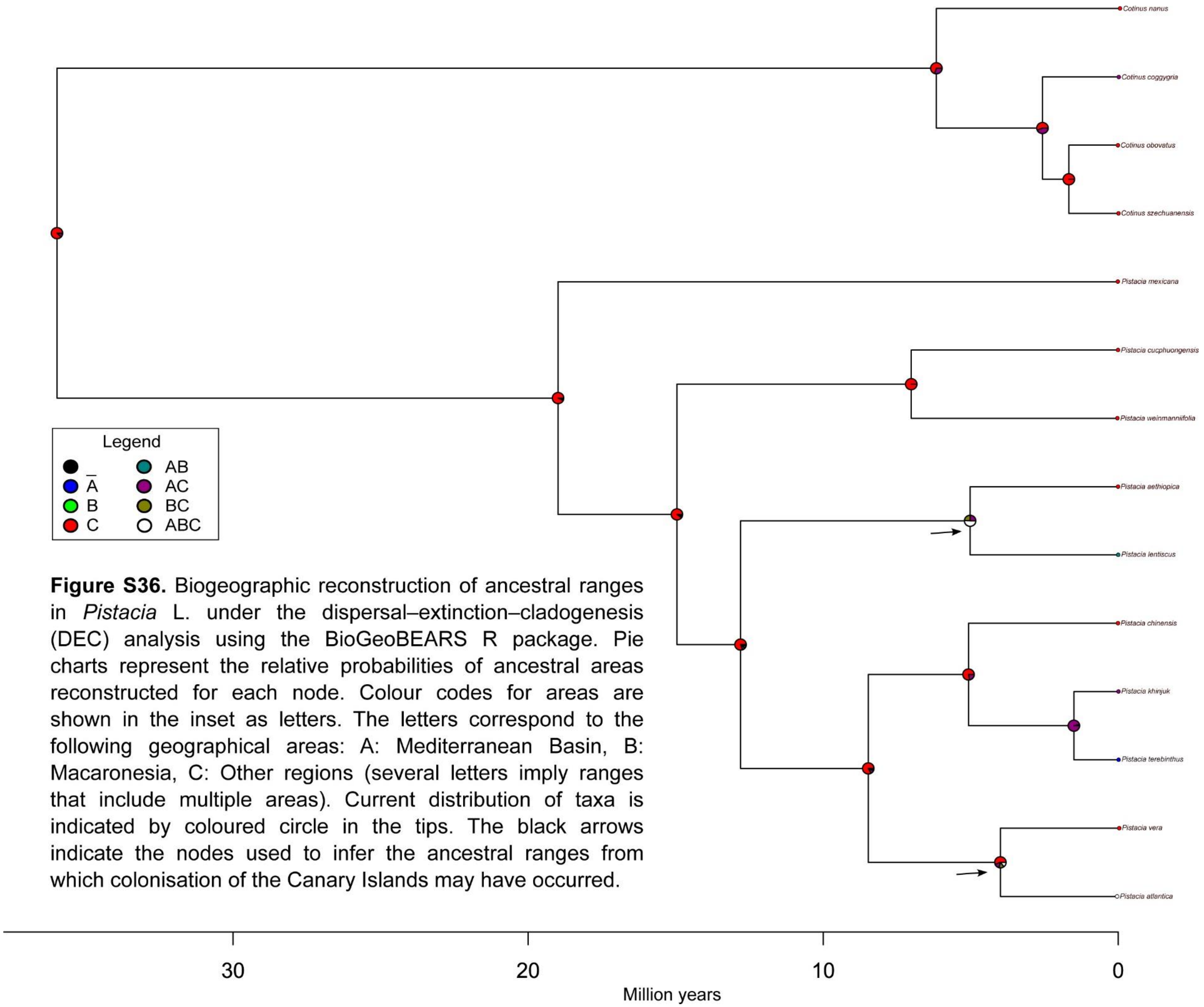


Figure S36. Biogeographic reconstruction of ancestral ranges in *Pistacia* L. under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

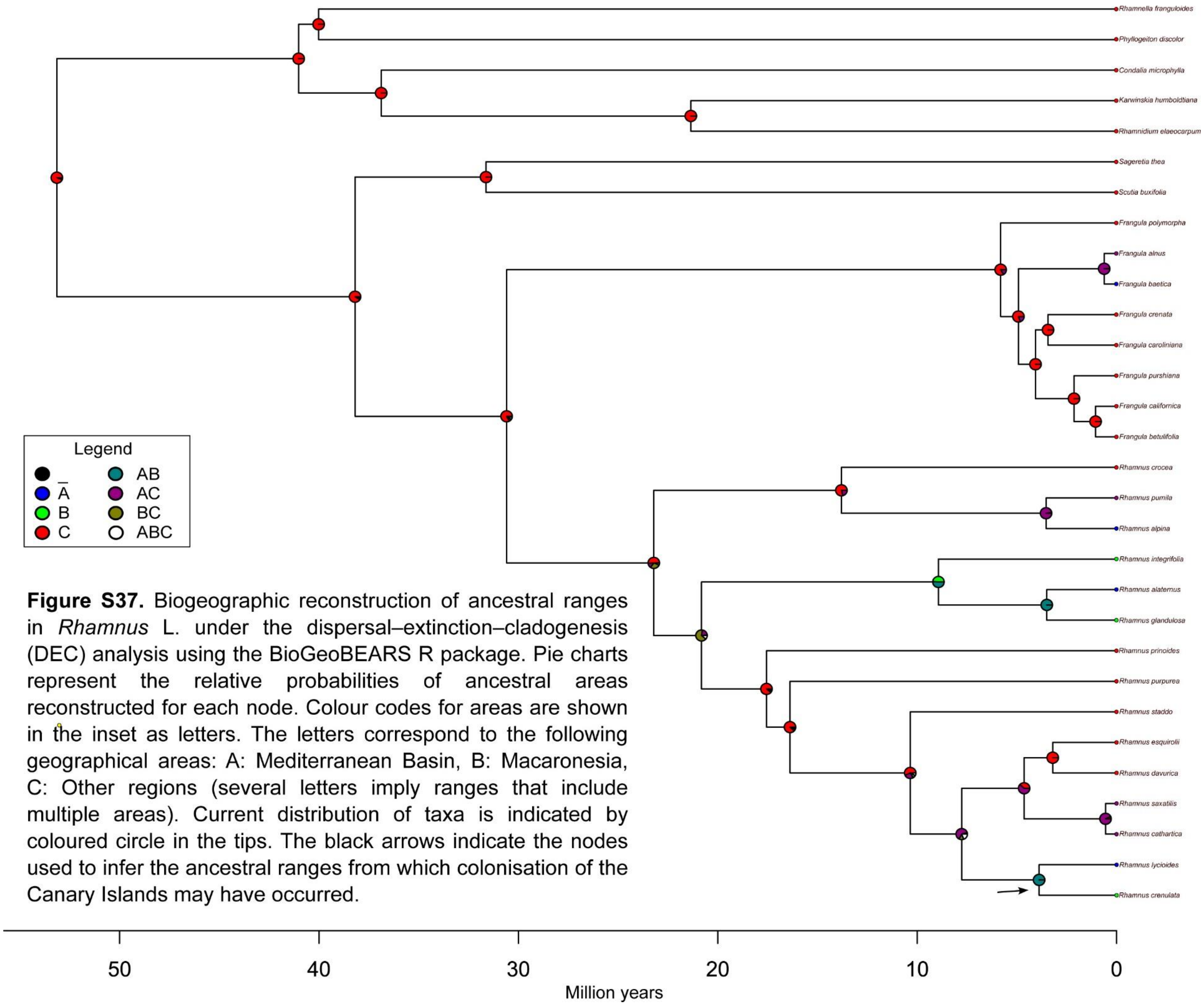


Figure S37. Biogeographic reconstruction of ancestral ranges in *Rhamnus* L. under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

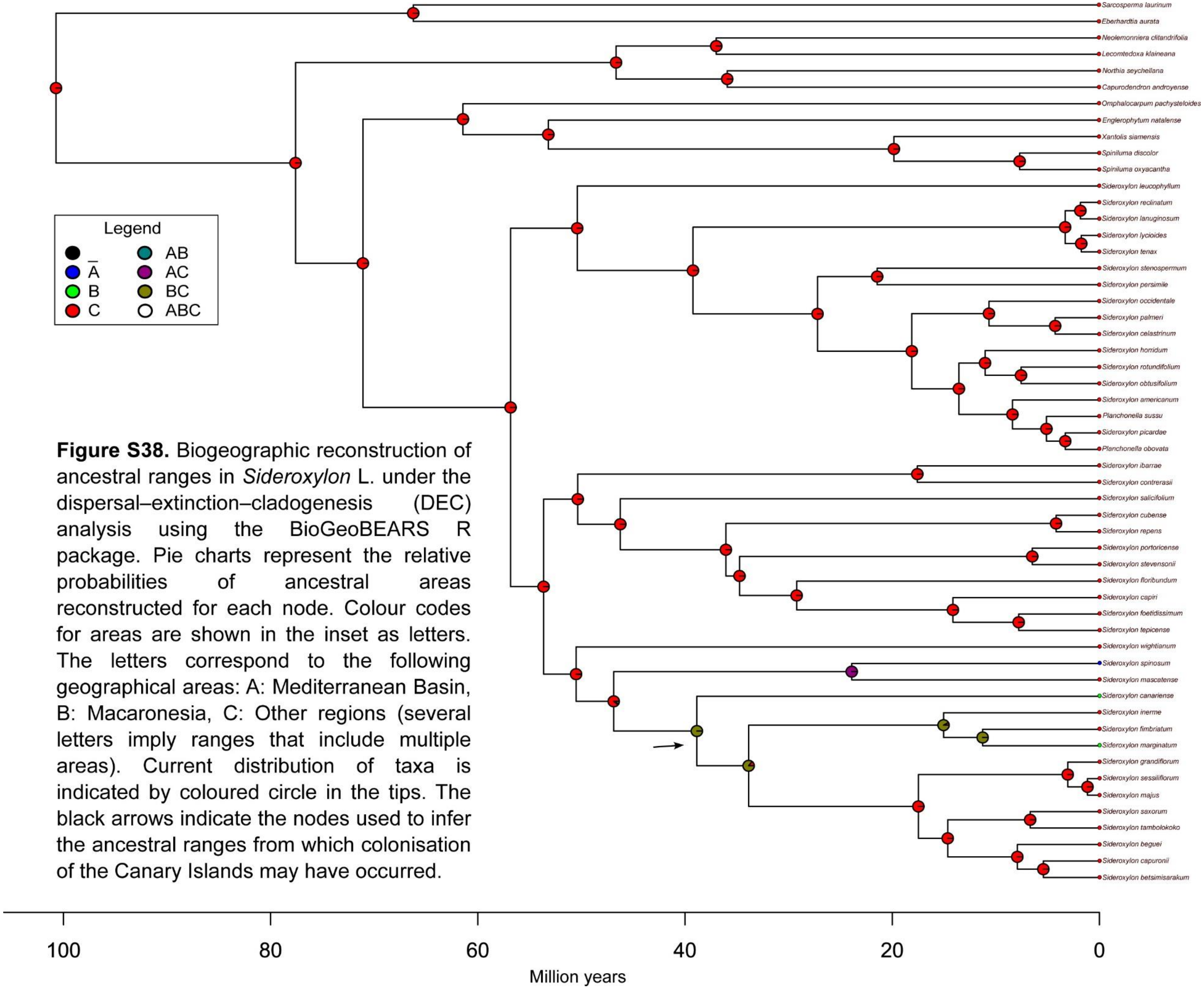


Figure S38. Biogeographic reconstruction of ancestral ranges in *Sideroxylon* L. under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

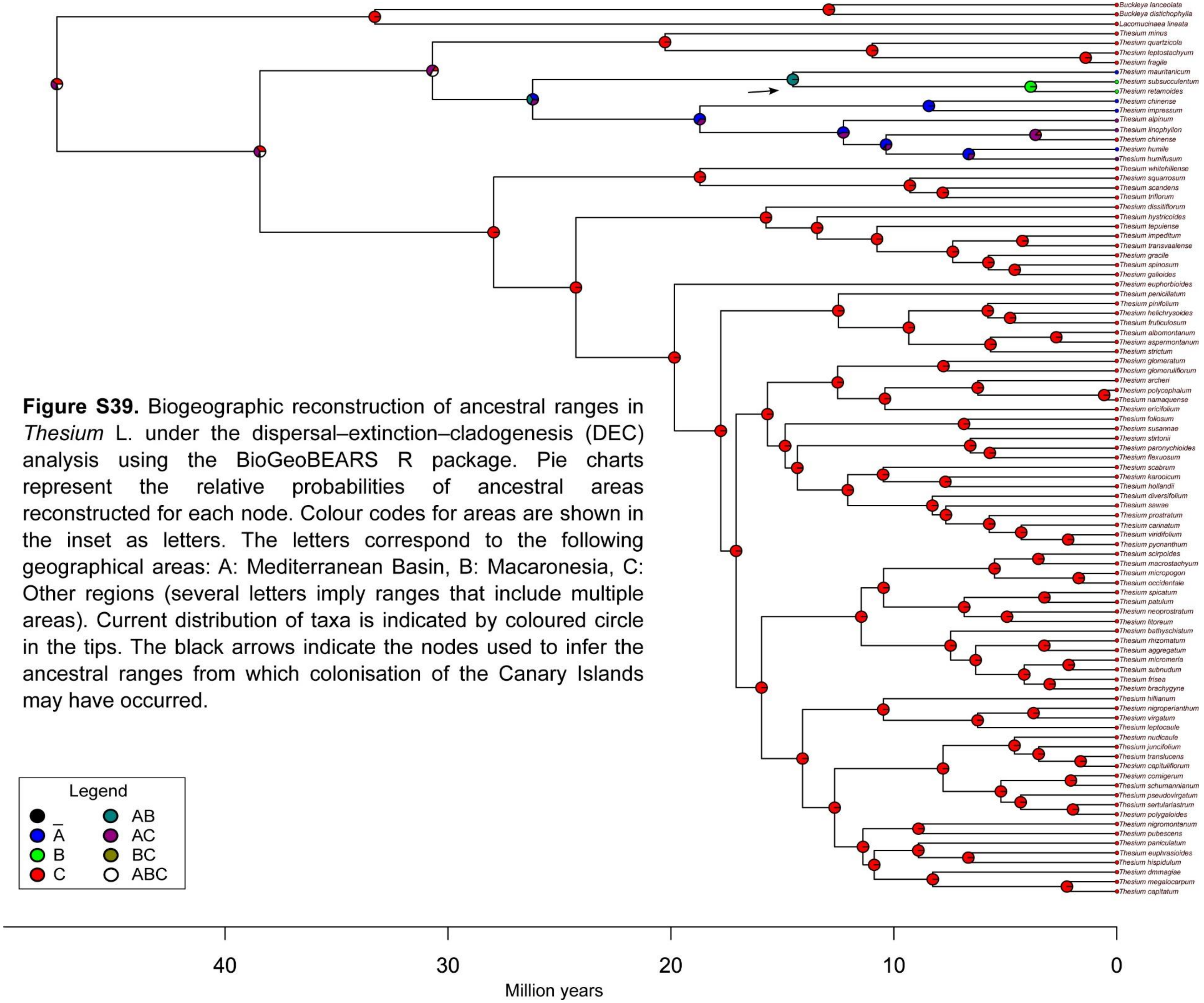


Figure S39. Biogeographic reconstruction of ancestral ranges in *Thesium* L. under the dispersal–extinction–cladogenesis (DEC) analysis using the BioGeoBEARS R package. Pie charts represent the relative probabilities of ancestral areas reconstructed for each node. Colour codes for areas are shown in the inset as letters. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). Current distribution of taxa is indicated by coloured circle in the tips. The black arrows indicate the nodes used to infer the ancestral ranges from which colonisation of the Canary Islands may have occurred.

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Table S1. Information extracted from the literature and obtained in this study for the 43 plant lineages including thermophilous species from the Canary Islands (Macaronesia) for hypothesis testing. This information include: number of species in the lineage (when more than one the species name are shown with red names highlighting thermophilous ones), sister group species names, phylogenetic support values (bootstrap support: BS; posterior probability: PP) for crown and stem nodes, distribution of the sister group (for non-endemics, distribution of the species in mainland), stem and crown ages, classification of lineages according to divergence times for the Canarian thermophilous plant community following the methodology proposed in this paper (i.e., mediterranean, pre-mediterranean and undetermined) and references (next page).

Canarian (macaronesian) lineage including termophilous species	Number of species in the lineage	Sister group	Well-supported canarian monophyletic lineage ML (BS > 70)	Well-supported thermophilous monophyletic lineage BI (PP > 0.90)	Well-supported sister-group relationship ML (BS > 70)	Well-supported sister-group relationship BI (PP > 0.90)	Sister group distribution / Non-endemic species distribution	Stem age	Crown age	Type	References
Anagyris latifolia Brouss. ex Willd.	1 spp	*Anagyris foetida* Lour.	YES (100)	YES (1.00)	YES (92)	YES (1.00)	Mediterranean (Circunmenditerranean)	8.20 (3.70-12.70)	1.9 (0.00-4.00)	Undetermined	Ortega-Olivencia and Catalan 2009 (phylogeny, molecular dating)
Argyranthemum lineage	32 spp in the lineage	*Glebionis* Cass., *Heteranthemis* Schott, and *Ismelia* Cass.	_	_	_	_	Mediterranean, Southern Iberia and Morocco, respectively	2.20 (1.50–3.00) - *Argyranthemum* spp. Francisco-Ortega et al 1997	2.48 (1.84-3.04) - White et al 2020	Mediterranean	Francisco-Ortega et al. 1997 (phylogeny, molecular dating); White et al. 2020 (phylogeny, molecular dating)
Artemisia lineage	3 spp in Macaronesia: *Artemisia thuscula* Cav. (Canary Islands), *Artemisia gorgonum* Webb (Cape Verde), *Artemisia argentea* Seb. & Maur. ex Willk. & Lange (Madeira) [also including the mainland *Artemisia arborescens* L.]	Close to *Artemisia arborescens* , *Artemisia sieversiana* Ehrh. ex Willd., *Artemisia absinthium* L.	_	NO (0.43)	_	YES (1.00)	*A. arborescens* : Mediterranean and Yemen; *A. sieversiana* : Asia, *A. absinthium* : Palearctic	3.84 (0.04-6.20) - TMRCA	?	Undetermined	Malik et al. 2017 (phylogeny, molecular dating)
Asparagus lineage I	3 spp - *Asparagus umbellatus* Link, *Asparagus arborescens* Willd. ex Schult. & Schult.f. , *Asparagus fallax* Svent.	*Asparagus humilis* Engl.	YES (86)	NO (0.54)	YES (91)	NO (0.46)	E Africa	2.80 (1.39-4.17)	1.75 (0.62-2.70)	Mediterranean*	Norup et al. 2015 (phylogeny), Chen et al. 2013 (calibration points), **this study** (molecular dating)
Asparagus lineage II	3 spp - *Asparagus nesiotes* Svent., *Asparagus scoparius* Lowe, *Asparagus plocamoides* Webb ex Svent. [also including the mainland *Asparagus altissimus* Munby and *Asparagus acutifolius* L.]	Close to *A. altissimus* , *A. acutifolius* , *A. denudatus* (Kunth) Baker, *A. fractiflexus* (Oberm.) Fellingham & N.L.Mey.	NO (51)	NO (0.10)	YES (79)	NO (0.87)	*A. altissimus* : NW Africa; *A. acutifolius* : circunmenditerranean; *A. denudatus* : E and S Africa; *A. fractiflexus* : S Africa	1.60 (0.72-2.38) - TMRCA	?	Mediterranean	Norup et al. 2015 (phylogeny), Chen et al. 2013 (calibration points), **this study** (molecular dating)
Bosea yervamora L.	1 spp	*Bosea cypria* Boiss. ex Hook.f., *Bosea amherstiana* (Moq.) Hook.f.	YES (94)	YES (1.00)	YES (100)	YES (1.00)	E Med, C Asia	5.71 (1.75-11.61)	1.67 (0.37-3.35)	Undetermined	Di Vincenzo et al. 2018 (phylogeny, calibration points), **this study** (molecular dating)
Brachypodium arbuscula Gay ex Knoche	1 spp	*Brachypodium retusum* (Pers.) P.Beauv.	_	_	YES (> 80 BS)	_	Circunmediterranean + Arabia	0.80 (1.47–0.14)	?	Mediterranean	Díaz-Pérez et al. 2018 (phylogeny, molecular dating)
Bryonia verrucosa Aiton	1 spp	Rest of *Bryonia* spp.	YES (89)	NO (polytomy)	YES (1.00)	YES (1.00)	Palearctic (N. Africa, Europe to Central Asia and W. Himalaya)	5.19 (2.41-8.56)	1.74 (0.23-3.17)	Undetermined	Volz and Renner 2008 (phylogeny), Schaefer et al. 2009 (calibration points), **this study** (molecular dating)
Cheirolophus lineage	17 spp in the lineage	*Cheirolophus uliginosus* (Brot.) Dostál	_	YES (1.00)	_	YES (1.00)	Mediterranean (Iberian Peninsula)	8.50 (4.70–12.50)	1.70 (0.80–2.90)	Undetermined	Vitales et al. 2014 (phylogeny, molecular dating)
Chrysojasminum odoratissimum (L.) Banfi	1 spp	Rest of *Chrysojasminum* spp.	YES (98)	YES (1.00)	YES (74) but clade as a whole, not species relationships)	YES (1.00)	*Chrysojasminum bignoniaceum* (Wall. ex G.Don) Banfi: India, *C. parkeri* (Dunn) Banfi: West Himalaya, *C. humile* (L.) Banfi: S. Iran to Central China and N. Myanmar, *C. fruticans* (L.) Banfi: Medit. to N. Iran	14.86 (5.79-26.03)	4.79 (1.25-9.44)	Pre-mediterranean	Jeyarani et al. 2018 (phylogeny), Vargas et al. 2014 (calibration points), **this study** (molecular dating)
Cistus monspeliensis L.	1 spp	Non-endemic	_	YES (> 0.95)	_	YES (0.90)	Mediterranean	0.50 (0.20–0.90)	0.23 (0.05-0.52)	Mediterranean	Fernández-Mazuecos and Vargas 2010 (phylogeny, molecular dating - stem node estimation); Coello et al. 2021 (molecular dating - Crown node)
Convolvulus lineage II	3 spp - *Convolvulus floridus* L.f., *Convolvulus scoparius* L.f., *Convolvulus caput-medusae* Lowe	*C. cneorum* , *C. lanuginosus* , *C. dorycnium*	YES (100, MP)	_	YES (100, MP)	_	E Mediterranean, W Asia	1.50 (0.35–2.65)	0.59 (0.07–1.11)	Mediterranean	Carine et al. 2004 (phylogeny); Carine 2005 (molecular dating)
Crambe lineage	14 spp in the lineage, 9 spp in the thermophilous (*Crambe arborea* Webb ex Christ, *Crambe laevigata* DC. ex Christ, *Crambe scaberrima* Webb ex Bramwell, *Crambe gomeraea* Webb ex Christ, *Crambe wildpretii* Prina & Bramwell, *Crambe pritzelii* Bolle, *Crambe scoparia* Svent., *Crambe tamadabensis* Prina & Marrero Rodr., *Crambe sventenii* Pett. ex Bramwell & Sunding)	Sister to *Crambe kralikii*	YES (90)	_	YES (98)	_	Mediterranean (Magrheb)	14.90 (9.30–20.30)	8.20 (3.90–12.50)	Pre-mediterranean	Francisco-Ortega et al. 2002 (phylogeny); Kim et al. 2008 (molecular dating)
Dioscorea edulis (Lowe) Campos, Wilkin & Viruel	1 spp	Sister to *Dioscorea communis* (L.) Caddick & Wilkin *and Dioscorea cretica* (L.) Campos, Wilkin & Viruel	_	_	YES (100)	NO (1.00)	W, N, E Mediterranean	13.48 (5.20-22.00)	?	Undetermined	Viruel et al. 2016 (phylogeny, molecular dating), Campos et al. in prep (phylogeny, molecular dating)
Dracaena lineage	2 spp - *Dracaena draco* (L.) L., *Dracaena tamaranae* Marrero Rodr., R.S.Almeira & M.Gonzáles-Martin	*Dracaena cochinchinensis* (Lour.) S.C.Chen	YES (100)	YES (1.00)	NO (56)	NO (0.60)	SE Asia	11.80 (4.90-16.30)	2.30 (0.70–5.80)	Undetermined*	Durán et al. 2020 (phylogeny, molecular dating)
Dracunculus canariensis Kunth	1 spp	*Dracunculus vulgaris* Schott	YES (100)	YES (1.00)	NO (56)	NO (0.80)	Mediterranean (Southern Europe, Argelia)	12.10 (5.82-18.49)	2.76 (0.48-5.82)	Undetermined	Mansion et al. 2008 (Phylogeny), Mansion et al. 2008, Nauheimer et al 2012 (calibration points), **this study** (molecular dating)
Echium lineage	27 Macaronesian spp in the lineage. *Echium handiense* Svent., *Echium giganteum* L.f. and *Echium strictum* L.f. in the thermophilous	*Echium parviflorum* St.-Lag. and *Echium sabulicola* Pomel (Böhle et al. 1996), *Echium tenue* Roth, *Echium sabulicola* Pomel (García-Maroto et al 2009)	YES (100)	YES (1.00)	YES (98, MP)	_	Mediterranean (Circunmenditerranean)	7.90 (4.30–11.10) - Kim et al 2008, 21.00 (Calibration point, García-Maroto et al 2009)	3.70 (1.50–5.90) - Kim et al 2008, 6.95 (3.04-10.86) - García-Maroto et al 2009	Pre-mediterranean	Böhle et al. 1996 (phylogeny); Kim et al. 2008 (molecular dating), García-Maroto et al. 2009 (phylogeny + molecular dating)
Ephedra fragilis Desf.	1 spp	Non-endemic	NO (polytomy)	NO (0.14)	NO (polytomy)	NO (0.59)	Mediterranean (Western Mediterranean - *E. fragilis* distribution)	1.29 (0.25-2.78) - TMRCA	?	Mediterranean	Ickert-Bond et al. 2009 (phylogeny, calibration points), **this study** (molecular dating)
Erysimum lineage	4 Macaronesian in the linage: *Erysimum bicolor* (Hornem.) DC., *Erysimum caboverdeanum* (A.Chev.) Sunding, *Erysimum scoparium* (Brouss. ex Willd.) Wettst. and *Erysimum arbuscula* (Lowe) Snogerup	*Erysimum ehrendorferi* Polatschek, *Erysimum nervosum* Pomel, *Erysimum gramineum* Pomel	_	NO (0.70)	_	NO (0.55)	Mediterranean (Magrehb)	0.80 (0.50–1.10) - *Erysimum* spp.	<1.00 - *Erysimum* spp.	Mediterranean	Moazzeni et al. 2014 (phylogeny, molecular dating)
Euphorbia sect. *Aphyllis* subsect. *Macaronesicae* Molero & Barres	11 species nearly endemic to Macaronesia. *Euphorbia regis-jubae* J.Gay, *Euphorbia lamarckii* Sweet and *Euphorbia bourgeana* J.Gay ex Boiss. are xerophilous and thermophilous specie	Sister to *Euphorbia* sect. *Aphyllis* subsect. *Africanae* Molero & Barres (see Su et al 2016)	_	YES (1.00)	_	YES (1.00)	E, C and S Africa	9.81 (8.76–10.86)	6.92 (5.37–8.47)	Pre-mediterranean*	Barres et al. 2011 (phylogeny); Sun et al. 2016 (molecular dating)
Globularia lineage	4 Macaronesian spp: *Globularia amygdalifolia* Webb, *Globularia ascanii* Bramwell & Kunkel, *Globularia salicina* Lam., *Globularia sarcophylla* Svent.	*Globularia arabica* Jaub. & Spach, *Globularia alypum* L.	YES (100)	YES (1.00)	YES (70)	NO (0.80)	N, Africa, Mediterranean	0.30 (0.10–0.60)	0.20	Mediterranean	Affenzeller et al. 2018 (phylogeny, molecular dating)
Gonospermum lineage	7 spp. Two of the species (i.e., *G. elegans* and *G. canariense*) occur primarily in the pine forest. The remaining species of the Gonosperminae are mainly found on northern slopes of the lowland scrub zone (Oleo-Rhamnetea crenulatae A. Santos).	*Tanacetum* , *Matricaria* , *Anthemis*	NO (54, MP)	_	NO (polytomy)	_	Mediterranean	3.10 - *Gonosperum* spp	?	Undetermined	Francisco-Ortega et al. 2002 (phylogeny), Oberprieler 2017 (molecular dating)
Gymnosporia lineage	3 spp - *Gymnosporia cassinoides* (L'Hér.) Masf., *Gymnosporia cryptopetala* Reyes-Bet. & A.Santos, *Gymnosporia dryandrii* (Lowe) Masf	*G. parviflora* , *G. dhofarensis* , *G. arbutifolia* , *G. engleriana* (high support)	YES (100)	YES (1.00)	YES (93)	YES (1.00)	CE Africa, S Asia	3.78 (2.11-5.36)	1.27 (0.46-2.00)	Undetermined*	Oberprieler et al. 2017 (phylogeny and calibration points), **this study** (molecular dating)
Helianthemum Mill. sect. *Helianthemum*	15 spp. *Helianthemum gonzalezferreri* Marrero Rodr. from thermophilous (probably others). Different biomes	*Helianthemum grosii* Pau & Font Quer, *Helianthemum ruficomum* (Viv.) Spreng., *Helianthemum helianthemoides* (Desf.) Grosser, Engler, Pflanzenr, *Helianthemum obtusifolium* Dunal	YES (>75)	YES (>0.95)	YES (>75)	YES (>0.95)	Mediterranean (NW Africa, Cyprus, Turkey)	1.82 (0.61–3.04)	1.09 (0.32–1.90)	Mediterranean	Martín-Hernanz et al. 2019, 2021 (phylogeny); Albaladejo et al. 2021 (molecular dating)
Hypericum canariense L.	1 spp	*Hypericum androsaemum* L., *Hypericum grandifolium* Choisy, *Hypericum hircinum* subsp. *Metroi* (Maire & Sauvage) Sauvage, *Hypericum foliosum* Aiton	NO (> 50)	NO (> 0.5)	YES (79)	YES (0.91)	Mediterranean, Azores	10.8 (5.30–17.40)	1.90 (0.20–3.50)	Undetermined	Dlugosch and Parker 2007 (phylogeny), Meseguer et al. 2013 (phylogeny, molecular dating), Pokorny et al. 2015 (molecular dating)
Juniperus turbinata subsp. *Canariensis* (Guyot & Mathou) Rivas Mart., Wildpret &	1 spp	Non-endemic	NO (polytomy)	NO (polytomy)	NO (polytomy)	NO (polytomy)	_	4.91(1.18-9.19) - TMRCA	?	Undetermined	Mao et al. 2010 (phylogeny, calibration points), **this study** (molecular dating)
Malva canariensis M.F.Ray	1 spp	*Lavatera maritima* Gouan	_	_	_	YES (1.00)	W Mediterranean	2.78 (0.44–5.76)	?	Mediterranean	Fuertes et al. 2002 (phylogeny); Villa et al. 2018 (molecular dating)
Myrsine excelsa D.Don	1 spp	*Myrsine semiserrata* Wall.	YES (100)	YES (1.00)	YES (74)	NO (0.58)	S Asia	3.98 (1.59-7.06) - This study; 4.56 (2.50-5.70) - Kondraskov et al 2015	1.07 (0.28-2.11)	Undetermined*	Appelhans et al. 2020 (phylogeny), Rose et al. 2018 (calibration points); Kondraskov et al. 2015, **this study** (molecular dating)
Navaea phoenicea (Vent.) Webb & Berthel.	1 spp	*Lavatera maritima* + *Malva canariensis*	_	_	_	YES (0.99)	Mediterranean	6.77 (2.67–10.82)	?	Undetermined	Escobar García et al. 2009 (phylogeny); Villa et al. 2018 (molecular dating)
Olea europaea subsp. guanchica P.Vargas, J.Hess, Muñoz Garm. & Kadereit	1 spp	*O. europea* L. subsp. *europaeae*	NO (polytomy)	NO (polytomy)	NO (polytomy)	NO (polytomy)	Mediterranean	2.60 (1.00–3.00)	?	Mediterranean	Besnard et al. 2009
Pistacia atlantica Desf.	1 spp	Non-endemic. Unresolved population relationships	NO (polytomy)	NO (polytomy)	NO (polytomy)	NO (polytomy)	Mediterranean (Southern and Eastern Mediterranean - *P. atlantica* distribution)	1.15 (0.24-2.43) - TMRCA	_	Mediterranean	Xie et al. 2014 (phylogeny + calibration points), **this study** (molecular dating)
Pistacia lentiscus lineage I	Population from Tenerife (Matanza, Santa Ursula)	Non-endemic - Population related to *Pistacia aethiopica* Kokwaro	_	_	NO (polytomy)	NO (polytomy)	E Africa (*P. aethiopica*)	3.96 (1.52-6.71)	1.15 (0.00-1.43)	Undetermined*	Xie et al. 2014 (phylogeny + calibration points), **this study** (molecular dating)
Pistacia lentiscus lineage II	Population from Tenerife (Anaga), Gran Canaria (Bandama) and Fuerteventura (Esquinzo)	Non-endemic - Sister to populations from Spain and Morocco	NO (polytomy)	NO (polytomy)	NO (polytomy)	YES (polytomy)	Mediterranean (Circunmenditerranean + Canary Islands - *P. lentiscus* distribution)	1.76 (0.49-3.37) - TMRCA	_	Mediterranean	Xie et al. 2014 (phylogeny + calibration points), **this study** (molecular dating)
Rhamnus crenulata Aiton	1 spp	*Rhamnus lycioides* Pall.	NO (51)	YES (0.97)	YES (90)	YES (1.00)	Mediterranean (Western and Eastern Mediterranean)	3.88 (1.79-6.59)	1.71 (0.49-3.38)	Undetermined	Bolmgren and Oxelman 2004 (phylogeny), Onstein et al. 2015 (calibration points), **this study** (molecular
Rubia fruticosa Aiton	1 spp	Sister to a clade containing 10 spp	_	YES (1.00)	_	NO (0.84)	Circunmediterranean, Horn of Africa, Azores, Madeira	6.69 (12.40-3.20)	2.10 (5.40-1.10)	Undetermined	Schaefer et al. unpublished (phylogeny and molecular dating)
Ruta lineage	3 spp - *Ruta pinnata* L.f., *Ruta oreojasme* Webb, *Ruta microcarpa* Svent.	*Ruta montana* (L.) L.	YES (100)	YES (1.00)	NO (51)	NO (0.72)	Mediterranean	17.04 (8.14–27.37)	8.10 (2.70–14.90)	Pre-mediterranean	Salvo et al. 2010 (phylogeny and molecular dating)
Sideritis lineage	27 spp. Different biomes	*Sideritis cossoniana* Ball			YES	_	Mediterranean (Morocco)	11.90 (6.00–17.80)	3.30 (1.20–5.40)	Pre-mediterranean	Barber et al. 2007 (phylogeny); Kim et al. 2008 (molecular dating)
Sideroxylon canariense Leyens, Lobin & A.Santos	1 spp	Sister to a clade containing 11 spp	YES (100)	YES (1.00)	NO (36)	YES (1.00)	Cape Verde, Socotra, C+E Asia, Reunion, Madagascar, Mauricio	37.73 (26.07-56.07)	7.99 (3.28-15.08)	Pre-mediterranean*	Stride et al. 2014 (phylogeny and calibration points), **this study** (molecular dating)
Smilax aspera L.	1 spp	Non-endemic	_	_	_	_	Paleartic + Central Europe - Distribution of *S. aspera*	< 0.30 Ma - haplotype 3 (Iberian Peninsula and Canary Islands) - TMRCA	?	Mediterranean	Chen et al. 2014 (phylogeny and molecular dating)
Solanum lineage	2 spp - *Solanum lidii* Sunding, *Solanum vespertilio* Aiton	*S. humile* , *S. tomentosum* , *S. capense*	YES (89) - MP	_	_	_	S Africa	1.70 (0.70–2.20)	0.90 (0.20–1.30)	Mediterranean*	Anderson et al. 2006 (phylogeny), Särkinen et al. 2013 (molecular dating)
Sonchus lineage	32 spp. Different biomes	*S. masguindalii* , *S. fragilis* , *S. pustulatus* (Kim et al 2008) // *S. palustris* (Kim et al 2007)			NO	_	Western Mediterranean	13.20 (7.70–18.70)	8.50 (3.00–13.90)	Pre-mediterranean	Kim et al. 1996 (phylogeny); Kim et al 2007 (phylogeny); Kim et al. 2008 (molecular dating)
Thesium lineage	4 spp - *Thesium retamoides* (A.Santos) J.C.Manning & F.Forest, *Thesium subsucculentum* (Kämmer) J.C.Manning & F.Forest, *Thesium canariense* (Stearn) J.C.Manning & F.Forest (non included in this study), *Thesium palmense* (see Rodríguez-Rodríguez et al. 2022; non included in this study)	*Thesium mauritanicum* Batt.	YES (99)	YES (1.00)	YES (100)	YES (1.00)	Mediterranean (NW Africa)	14.53 (6.56-23.57)	3.86 (1.06-7.39)	Pre-mediterranean	Zhigila et al. 2020, Rodríguez-Rodríguez et al. 2022 (phylogeny), Moore et al. 2010 (calibration points), **this study** (molecular dating)
Visnea mocanera L.f.	1 spp	Sister to all other species of the tribe Freziereae (Theaceae)	_	_	_	NO (<0.90)	Asia and America	27.00 (17.00-41.00)	2.50 (0.10-5.00)	Undetermined*	Schüßler 2020
	In red, thermophilous spp when the lineage is composed of several spp									* Non-mediterranean sister-groups distribution	

Table S2. Studied taxa (thermophilous species in bold) and their corresponding collection code, voucher information (herbarium code), island (archipelado or country), locality, collection date, collector's name (leg), DNA sequenced regions and GenBank accesion numbers.

ASPARAGUS

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	PHYC	*trn* H-*psb* A	*trn* D-*trn* T
Asparagus arborescens	3PV21	NA	Tenerife	Los Adernos (Buenavista)	09/11/2020	P Marrero, M Nogales	_	OM418819	OM418837
Asparagus arborescens	AQ1768	MA-01-00750332	Lanzarote	Arrieta, Malpaís de la Corona, La Caleta de las Aulagas	05/04/2006	C Aedo, L Medina, A Quintanar	_	OM418820	OM418838
Asparagus fallax	4PV21	NA	Tenerife	Vueltas de Taganana	27/10/2020	P Marrero, M Nogales	_	OM418821	OM418839
Asparagus nesiotes	26081	MA-01-00628064	Lanzarote	Orzola (Kanarische Inselm), Malpais de la Corona	06/02/1989	Max Nydegger	_	OM418822	OM418840
Asparagus pastorianus	5PV21	NA	Tenerife	Buenavista	09/11/2020	P Marrero, M Nogales	_	OM418823	OM418841
Asparagus pastorianus	s/n	NA	Gran Canaria	Inmediaciones de Cambalud	18/05/2021	María Olangua	OM418807	OM418824	OM418842
Asparagus pastorianus	20448	MA-01-00785968	Morocco	coast road. 28.5 km from Tiznit, N of Mirleft	06/02/2007	TM Upson, Stephen Jury	OM418808	OM418825	OM418843
Asparagus plocamoides	71PV21	NA	Tenerife	Barranco de Tamadaya (Arico)	25/01/2021	P Marrero, M Nogales	OM418809	OM418826	OM418844
Asparagus plocamoides	JC1973	MA-01-00768757	Gran Canaria	Montaña las Tierras	26/02/2008	B Ríos, Joel Calvo, Inés Álvarez	OM4188010	OM418827	OM418845
Asparagus scoparius	53PV21	NA	Tenerife	Los Adernos (Buenavista del Norte)	23/12/2020	P. Marrero/M. Nogales	OM4188011	OM418828	OM418846
Asparagus scoparius	5FP19	NA	La Palma	Sendero Mirador del Topo de las Barandas	19/02/2019	Fernando Pomeda, Daniel Pareja	OM4188012	OM418829	OM418847
Asparagus scoparius	91PV21	NA	La Palma	Lomo del Cerro	29/05/2021	Maria Olangua Corral, Sara Martín Hernanz	OM4188013	OM418830	OM418848
Asparagus scoparius	92PV21	NA	La Palma	Ermita de las Nieves	29/05/2021	Maria Olangua Corral, Sara Martín Hernanz	OM4188014	OM418831	OM418849
Asparagus scoparius	17407	MA-01-00714488	Madeira	Faja dos Padres	28/02/2004	Santiago Castroviejo Bolíbar	OM4188015	OM418832	OM418850
Asparagus umbellatus	81PV21	NA	Tenerife	Tagoro	29/04/2021	S. Martín-Hernanz, M. Nogales, P. Vargas	OM4188016	OM418833	OM418851
Asparagus umbellatus	389	MA-01-00892832	La Gomera	Gomera. Path descending from Arure	07/05/1968	LJG Van der Maesen, ERS Sventenius	OM4188017	OM418834	OM418852
Asparagus umbellatus	111PV21	NA	La Palma	Cerca del Centro de Visitantes de Caldera de Taburiente	30/05/2021	María Olangua, Sara Martín Hernanz	OM4188018	OM418835	OM418853
Asparagus umbellatus	s/n	NA	Gran Canaria	Bco del Laurel	18/05/2021	María Olangua	_	OM418836	OM418854

BOSEA

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	*trn* K/*mat* K
Bosea yervamora	73PV21	NA	Tenerife	Bco. de Ruiz, Los Realejos	26/02/2021	P Marrero, M Nogales	OM460770
Bosea yervamora	17239	MA-01-00805386	Gran Canaria	Agaete, pr. Los Berrazales	09/04/2010	Carlos Aedo Pérez	OM460771
Bosea yervamora	98PV21	NA	La Palma	Juan Mayor	29/05/2021	María Olangua, Sara Martín Hernanz	OM460772
Bosea yervamora	141PV21	NA	Fuerteventura	Barranco Malnombre (ExHorto Jardín Botánico Fuerteventura)	06/11/2021	Moritz Albersdörser	OM460773
Bosea yervamora	142PV21	NA	Fuerteventura	Riscos de Jandía	06/11/2021	Stephan Schloz	OM460774
Bosea cypria	16333	MA-01-00748044	Cyprus	Halbinsel Karpasia/Karpas, Dipkarpaz/Rizokarpaso, im Ortsgebiet an der Strrasse nach Agios Filon	08/07/2005	Robert M. Vogt	OM460775
Bosea amherstiana	s/n	BC-956022	Ex Horto Hymalaya	Barcelona, Montjuïc, near cable car	20/06/2016	S. Pyke, N. Ibáñez, J. López-Pujol & P. Farelo	OM460776

CHRYSOJASMINUM

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	ITS	*trn* L-*trn* F	*trn* H-*psb* A
Chrysojasminum odoratissimum	21PV21	NA	Tenerife	Bco. Badajoz	22/10/2020	P. Marrero, M. Nogales	OM522958	OM436792	OM436781
Chrysojasminum odoratissimum	CAN 060	MA-01-00848477	Tenerife	au dessus de Güimar en montant vers le Pico del Valle	02/05/1973	Hervé M. Burdet	_	OM436803	OM436791
Chrysojasminum odoratissimum	s/n	ORT-39768	Fuerteventura	Pico de la Zarza ex horto	01/10/2007	S. Scholz	_	OM436793	_
Chrysojasminum odoratissimum	93PV21	NA	La Palma	Ermita de las Nieves	29/05/2021	María Olangua, Sara Martín Hernanz	_	OM436794	OM436782
Chrysojasminum odoratissimum	99PV21	NA	La Palma	Finca Amado	30/05/2021	María Olangua, Sara Martín Hernanz	_	OM436795	OM436783
Chrysojasminum odoratissimum	s/n	NA	Gran Canaria	Mta. De Amagro	01/04/2021	María Olangua	_	OM436796	OM436784
Chrysojasminum odoratissimum	10873MV	MA-01-00757874	Madeira	Isla Deserta Grande, alrededores de la casa de los forestales	22/03/2007	Mauricio Velayos	OM522959	OM436797	OM436785
Chrysojasminum odoratissimum	s/n	NA	La Gomera	Bajada a Tazo	27/03/2021	María Olangua	_	OM436798	OM436786
Chrysojasminum fructicans	s/n	MA-01-00892149	Spain	León, La Balouta	01/07/2012	Carlos Manuel Romero Rodríguez	OM522960	OM436799	OM436787
Chrysojasminum fructicans	620	MA-01-00908856	Tunisia	Gouv. Ben Arous, Jebel Ressas, c. 3.5 km SW of Dawwar at Talib Áli	28/03/2014	E. Vitek, N. Ardenghi	OM522961	OM436800	OM436788
Chrysojasminum fructicans	17	MA-01-00775921	Georgia	Kartli, Mtskheta District (33). Right bank of Mtkvari River. Karsani	29/07/2004	Mukbaniani, D. Mtskhvetadze	_	OM436801	OM436789
Chrysojasminum parkeri	43	MA-01-00884036	Ex Horto	Recinto del Real Jardín Botánico. Plantas cultivadas	13/05/2014	Voluntarios RJB	OM522962	OM436802	OM436790

DRACUNCULUS

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	*mat* K	*trn* K	*rbc* L	*rpl* 16
Dracunculus canariensis	79PV21	NA	Tenerife	El Caletón (La Matanza)	07/04/2021	P. Marrero, M. Nogales	OM489535	OM489538	OM460824	OM489541
Dracunculus canariensis	17224	MA-01-00805401	Gran Canaria	pr. Moya, barranco de los Laureles	08/04/2010	Carlos Aedo Pérez	OM489536	OM489539	OM460825	OM489542
Dracunculus canariensis	34FP21	NA	La Palma	Finca Amado	22/06/2021	Fernando Pomeda	OM489537	OM489540	OM460826	_

EPHEDRA

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	ITS	*mat* K	*psb* A-*trn* H	*rps* 4
Ephedra fragilis	11PV21	NA	Tenerife	Lomo de Basta (Icod)	12/09/2020	P Marrero, M Nogales	OM478581	_	OM489665	OM541666
Ephedra fragilis	117PV21bis	NA	Tenerife	Icod	05/07/2021	P Marrero, M Nogales	OM478582	OM489662	OM489666	OM541667
Ephedra fragilis	s/n	ORT-37328	La Palma	Bajada a Aeropuerto sobre La Bajita	26/07/2003	A. Santos	OM478583	_	OM489667	_
Ephedra fragilis	s/n	NA	Gran Canaria	Ex horto Jardín Botánico Viera y Clavijo	13/05/2021	María Olangua	OM478584	OM489663	OM489668	OM541668
Ephedra fragilis	VIT 86118	SEV-264317	Spain	Navarra, Andosilla, cerro La Peña, sobre la vega del río Ega	02/07/2010	P.M. Uribe-Echebarria	OM478585	_	OM489669	_
Ephedra major	12PV21	NA	Tenerife	El Teide, Minas de San José	26/10/2020	P Marrero, M Nogales	OM478586	OM489664	OM489670	OM541669
Ephedra major	117PV21	NA	Tenerife	Pico Cabras (El Teide)	15/07/2021	Manuel Nogales	OM478587	_	OM489671	OM541670
Ephedra major	s/n	SEV-90929	Spain	Madrid, Aranjuez. N-400. Cerros del Arroyo Martín	08/06/1982	S. Laorga	OM478588	_	OM489672	OM541671
Ephedra major	17713	SEV-270374	Morocco	High Atlas, El-Ksiba to Tinghir, road from Imilchil to Tinghir, just south of pass	09/07/1997	S.L. Jury, A. Abaouz, M. Ait Lafkih & A.J.K. Griffiths	OM478589	_	_	_

GYMNOSPORIA

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	ITS
Gymnosporia cassinoides	84PV21	NA	Tenerife	Bco. de Badajoz	29/04/2021	S. Martín-Hernanz, M. Nogales, P. Vargas	OM514992
Gymnosporia cassinoides	28FP19	NA	La Palma	Sendero Espigón Atravesado Zona de La Portada	20/02/2019	Fernando Pomeda, Daniel Pareja	OM514993
Gymnosporia cassinoides	103PV21	NA	La Palma	Finca Amado	30/05/2021	María Olangua, Sara Martín Hernanz	OM514994
Gymnosporia cassinoides	AH 2533	MA-01-00733780	La Gomera	Vallehermoso, meseta de Vallehermoso	16/04/2005	A. Herrero, L. Medina, J. Leralta	OM514995
Gymnosporia cassinoides	s/n	NA	Gran Canaria	Bco de Azuaje	18/05/2021	María Olangua	OM514996
Gymnosporia cassinoides	s/n	ORT-37909	Fuerteventura	Pico de La Zarza, Jandía	12/05/2005	S. Scholz	OM514997
Gymnosporia cassinoides	143PV21	NA	Fuerteventura	Riscos de Jandía	06/11/2021	Stephan Schloz	OM514998
Gymnosporia cassinoides	144PV21	NA	Fuerteventura	Vega del Río Palmas	06/11/2021	Stephan Schloz	OM514999
Gymnosporia cryptopetala	s/n	ORT-41369	Lanzarote	Malpaís de la Corona	07/04/2009	J.A. Reyes-Betancort	OM515000
Gymnosporia cryptopetala	146PV21	NA	Lanzarote	Barranco de Esquinzo	06/11/2021	Stephan Schloz	OM515001
Gymnosporia cryptopetala	148PV21	NA	Fuerteventura	Riscos de Jandía (ExHorto)	06/11/2021	Stephan Schloz	OM515002
Gymnosporia dryandri	13627	MA-01-00757582	Madeira	pr. Porto Novo	17/03/2007	Carlos Aedo Pérez	OM515003
Gymnosporia dryandri	17397	MA-01-00714538	Madeira	San Vicente	27/02/2004	Santiago Castroviejo Bolíbar	OM515004

JUNIPERUS

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	ITS	*mat* K	*rbc* L	*trn* L-*trn* F	*rps* 4	*trn* S-*trn* G	*trn* V	*psb* B1-*psb* B2
Juniperus turbinata* subsp. *canariensis	68PV21	NA	Tenerife	Acantilados de la Culata (Guarachico)	20/01/2021	P. Marrero, M. Nogales	_	OM801629	OM801646	OM801663	OM801654	OM801672	OM801681	OM801638
Juniperus turbinata* subsp. *canariensis	100PV21	NA	La Palma	Finca Amado	30/05/2021	María Olangua, Sara Martín Hernanz	OM759832	OM801630	OM801647	OM801664	OM801655	OM801673	OM801682	OM801639
Juniperus turbinata* subsp. *canariensis	49FP21	NA	El Hierro	La Sabina	28/06/2021	Fernando Pomeda	OM759833	OM801631	OM801648	OM801665	OM801656	OM801674	OM801683	OM801640
Juniperus turbinata* subsp. *canariensis	19682	MA-01-00866694	El Hierro	Ermita de Nuestra Señora de los Reyes, montaña Tagutanta	03/01/2013	Carlos Aedo Pérez	_	OM801632	OM801649	OM801666	OM801657	OM801675	OM801684	OM801641
Juniperus turbinata	630/14	MA-01-00898926	Spain	Cádiz, Sierra de Grazalema, La Camilla	21/10/2014	F.J. Salgueiro, M. Arsita, P.L. Ortiz	OM759834	OM801633	OM801650	OM801667	OM801658	OM801676	OM801685	OM801642
Juniperus turbinata	s/n	MA-01-00909388	Tunisia	Gouv. Bizerte, coast c. 6.5km NNW Bizerte, near the Roman grottos	29/03/2014	E. Vitek, F. Abdallah	_	OM801634	OM801651	OM801668	OM801659	OM801677	OM801686	OM801643
Juniperus turbinata	JC2621	MA-01-00781962	Morocco	Tánger-Tetouan, Tleta-Oued-Laou, pr. Cap Mazari	25/06/2008	Joel Calvo, Alejandro Quintanar Sánchez	OM759835	OM801637	OM801652	OM801669	OM801660	OM801678	OM801687	OM801644
Juniperus turbinata	484	MA-01-00690874	Portugal	Algarve, Vila do Bispo, Raposeira, praia da Ingrina	06/06/2001	Sara Nisa de Oliveira, L. Medina, M. Pardo de Santayana	_	OM801635	OM801653	OM801670	OM801661	OM801679	OM801688	OM801645
Juniperus turbinata	s/n	MA-01-00779192	Spain	Cádiz, Ensenada de Bolonia	08/04/1992	L.M. Ferrero	_	OM801636	_	OM801671	OM801662	OM801680	OM801689	_

MYRSINE

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	ITS
Myrsine excelsa	14PV21	NA	Tenerife	Los Silos	19/10/2020	P Marrero, M Nogales	OM522014
Myrsine excelsa	25FP19	NA	La Palma	Alrededores Centro de Visitantes	20/02/2019	Fernando Pomeda, Daniel Pareja	OM522015
Myrsine excelsa	s/n	NA	La Gomera	La Meseta	25/03/2021	María Olangua	OM522016
Myrsine canariensis	30PV21	NA	Tenerife	Vueltas de Taganana	27/10/2020	P. Marrero, M. Nogales	OM522017

PISTACIA

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	ITS	ETS
Pistacia atlantica	28PV21	NA	Tenerife	Los Silos	19/10/2020	P. Marrero, M. Nogales	OM746110	OM801613
Pistacia atlantica	s/n	MA-01-00694792	Gran Canaria	Agaete, Los Berrazales, camino al Sao	09/04/2001	Roca, Marrero	OM746111	OM801614
Pistacia atlantica	110PV21	NA	La Palma	Ex horto Centro Visitantes Caldera de Taburiente	30/05/2021	María Olangua, Sara Martín Hernanz	OM746112	OM801615
Pistacia atlantica	2386-08	ORT-40296	La Palma	Puntallana, Bco. sobre Puerto Trigo	09/08/2008	Arnoldo Santos	_	OM801616
Pistacia atlantica	31FP21	NA	La Palma	Cubo de la Galga	19/06/2021	Fernando Pomeda	OM746113	OM801617
Pistacia atlantica	145PV21	NA	Lanzarote	NA	06/11/2021	Stephan Schloz	OM746114	OM801618
Pistacia atlantica	JC3814	MA-01-00799482	Morocco	Souss - Massa - Daraâ Anezi, Agadir-ogjgal, jbel Imzi, ladera norte	06/06/2009	Joel Calvo	OM746115	OM801619
Pistacia khinjuk	s/n	MA-01-00748956	Iran	Isfahan Province/Semirom/Vanak/Cheshme-Naz	12/06/2003	M.R. Parishani	OM746116	OM801620
Pistacia lentiscus	s/n	MA-01-00867153	Spain	Córdoba, Orilla del Arroyo Guadalnuño	11/04/2010	V.R. Invernón, M. de la Estrella	OM746117	OM801621
Pistacia lentiscus	JC0621	MA-01-00758144	Morocco	Antiatlas occidental, Ladera NE Jbel Imzi	15/04/2007	T. Buira, Joel Calvo	_	OM801622
Pistacia lentiscus	78PV21	NA	Tenerife	Barranco de la Matanza	28/03/2021	P. Marrero, M. Nogales	OM746118	OM801623
Pistacia lentiscus	165PV21	NA	Tenerife	Barranco de Santa Úrsula	03/12/2021	P. Marrero, M. Nogales	OM746119	OM801624
Pistacia lentiscus	166PV21	NA	Tenerife	Barranco de Santa Úrsula	03/12/2021	P. Marrero, M. Nogales	OM746120	OM801625
Pistacia lentiscus	167PV21	NA	Tenerife	Anaga	13/12/2021	P. Marrero, Javier Romero	OM746121	OM801626
Pistacia lentiscus	s/n	NA	Gran Canaria	Caldera de Bandama	21/05/2021	María Olangua	OM746122	OM801627
Pistacia lentiscus	147PV21	NA	Fuerteventura	Barranco de Esquinzo	06/11/2021	Stephan Schloz	OM746123	OM801628

RHAMNUS

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	ITS	*trn* L-*trn* F
Rhamnus crenulata	33PV21	NA	Tenerife	Los Adernos (Buenavista)	09/11/2020	P. Marrero, M. Nogales	OM522104	OM541906
Rhamnus crenulata	5901	MA-01-00647208	La Palma	Los Franceses	29/07/2000	Carlos Aedo Pérez	OM522105	OM541907
Rhamnus crenulata	94PV21	NA	La Palma	Ermita de las Nieves	29/05/2021	María Olangua, Sara Martín Hernanz	OM522106	OM541908
Rhamnus crenulata	s/n	NA	Gran Canaria	Tarifa Alta	09/04/2021	María Olangua Corral	OM522107	OM541909
Rhamnus glandulosa	46PV21	NA	Tenerife	Las Cuadras (Anaga)	16/12/2020	P. Marrero, M. Nogales	OM522108	OM541910
Rhamnus glandulosa	27FP19	NA	La Palma	Los Tiles, Alrededores Centro de Visitantes	20/02/2019	Fernando Pomeda, Daniel Pareja	OM522109	OM541911
Rhamnus integrifolia	35PV21	NA	Tenerife	El Teide	23/10/2020	P. Marrero, M. Nogales	OM522110	OM541912

SYDEROXYLON

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	ITS	*trn* H-*psb* A
Sideroxylon canariense	41PV21	NA	Tenerife	Batán de Arriba (Anaga)	11/11/2020	P. Marrero, M. Nogales	OM522633	OM541945
Sideroxylon canariense	MM299	MA-01-00887516	Tenerife	Las Furnias (Icod)	04/01/2015	Mario Mairal	OM522634	OM541946
Sideroxylon canariense	s/n	NA	Gran Canaria	Tenteniguada	09/04/2021	Marcos Díaz Bertrana, María Olangua Corral	OM522635	OM541947
Sideroxylon canariense	s/n	ORT-39460	Fuerteventura	Barranco de Mal Nombre (Pájara)	05/10/2006	S.Scholz	OM522636	OM541948

THESIUM

Taxa	Collection code	Voucher information	Island/archipelago/country	Locality	Collection date	Leg	ITS	*mat* K	*rpl* 32-*trn* L	*trn* L-*trn* F
Thesium retamoides	24PV21	NA	Tenerife	Bco. Badajoz	24/10/2020	P. Marrero, M. Nogales	OM730033	OM801607	OM801609	OM801611
Thesium subsucculentum	65PV21	NA	Tenerife	Punta de Juan Centellas	20/01/2021	P. Marrero, M. Nogales	OM730034	OM801608	OM801610	OM801612

Table S3. Primers and PCR cycles used for sequencing DNA regions of the 13 plant groups analyzed in this study (genera, seldom families).

ASPARAGUS

DNA region	Primers	Reference	Primer sequence	PCR cycle
PHYC	PHYC (Asparagus specific): PHYC-F1/PHYC-R1	Hertweck et al. 2015	5' CAG TTA ACC CTG CTG ATG TAC C 3' / 5' ACC TCG CCA CTT TAC AAC CT 3'	5 min at 94 C followed by 39 cycles of 94 C for 1 min, 55 C for 1 min, and 72 C for 1.5 min followed by a final extension at 72 C for 7 min.
trn H-*psb* A	trnHGUG/psbA	Shaw et al. 2005	5' CGC GCA TGG TGG ATT CAC AAT CC 3' / 5' GTT ATG CAT GAA CGT AAT GCT C 3'	initial 3 min at 94 C, followed by 32 cycles of 94 C for 1 min, 53 C for 1 min, 72 C for 1 min, and a final extension at 72 C for 7 min
trn D-*trn* T	trnDGUC/trnTGGU	Shaw et al. 2005	5' ACC AAT TGA ACT ACA ATC CC 3' / 5' CTA CCA CTG AGT TAA AAG GG 3'	initial 3 min at 94 C, followed by 34 cycles of 94 C for 1 min, 53 C for 1 min, 72 C for 1 min, and a final extension at 72 C for 5 min

BOSEA

DNA region	Primers	Reference	Primer sequence	PCR cycle
trn K/*mat* K	trnK2R		5' AAC TAG TCG GAT GGA GTA G 3'	34 cycles of 94°C (1 min.) denaturation, 52°C (1 min.) annealing, 72°C (2 min.) extension, and 72°C (15 min.) final extension
	trnKF/ ACmatK1400R	Wicke and Quandt 2009 / Müller and Borsch 2005	5' GGG TTG CTA ACT CAA TGG TAG AG 3' / 5' TTC TTC TTT GCA TTT ATT ACG 3'	
	ACmatK500F / psbA5'R	Müller and Borsch 2005 / Shaw et al. 2005	5' TTC TTC TTT GCA TTT ATT ACG 3' / 5' AAC CAT CCA ATG TAA AGA CGG TTT 3'	

CHRYSOJASMINUM

DNA region	Primers	Reference	Primer sequence	PCR cycle
ITS	ITS1 / ITS2	White et al. 1990	5' TCC GTA GGT GAA CCT GCG G 3' / 5' GCT GCG TTC TTC ATC GAT GC 3'	35 cycles (denaturation for 1 min at 94◦C, annealing for 1 min at 49◦C and 1 min of extension at 72◦C followed by a last cycle of final extension for 5 min at 72◦C).
trn L-*trn* F	trne / trnf	Taberlet et al. 1991	5' GGT TCA AGT CCC TCT ATC CC 3' / 5' ATT TGA ACT GGT GAC ACG AG 3'	35 cycles (denaturation for 1 min at 94◦C, annealing for 1 min at 49◦C and 1 min of extension at 72◦C followed by a last cycle of final extension for 5 min at 72◦C).
trn H-*psb* A	trnHGUG/psbA	Shaw et al. 2005	5' CGC GCA TGG TGG ATT CAC AAT CC 3' / 5' GTT ATG CAT GAA CGT AAT GCT C 3'	35 cycles (denaturation for 1 min at 94◦C, annealing for 1 min at 49◦C and 1 min of extension at 72◦C followed by a last cycle of final extension for 5 min at 72◦C).

DRACUNCULUS

DNA region	Primers	Reference	Primer sequence	PCR cycle
mat K	matk-F1/matK-3AR	Sang et al. 1997, Winkworth et al. 2002	5' ACTGTATCGCACTATGTATCA 3' / 5' CGT ACA STA CTT TTG TGT TTM CG 3'	1 cycle of 3 to 5 min denaturation at 94◦C, followed by 30 cycles of 30 s denaturation at 94◦C, 1 min annealing at 52◦C to 56◦C, and 1 to 2 min elongation at 72◦C, finishing with a 5- to 10-min elongation step at 72◦C to complete primer extension
trn K	tk3-MY2F/trnK-2R	Winkworth et al. 2002, Johnson and Soltis 1995	5' CAA TCA AAA TCT TCT GGA ATC 3' / 5' AAC TAG TCG GAT GGA GTA G 3'	
rbc L	rbcL-1F/ rbcL-739R	Asmussen and Chase 2001	5' ATG TCA CCA CAA ACAG AAA C 3' / 5' CCG TTA AGT AGT CGT GCA 3'	
	rbcL-636F / rbcL-Rev	Asmussen and Chase 2001	5' CGA AAT CGG TAG ACG CTA CG 3' / 5' TCC TTT TAG TAA AAG ATT GGG CCG AG 3'	
rpl 16	rps16-F / rps16-R2	Oxelman et al. 1997	5' GTG GTA GAA AGC AAC GTG CGA CTT 3' / 5' TCG GGA TCG AAC ATC AAT TGC AAC 3'	

EPHEDRA

DNA region	Primers	Reference	Primer sequence	PCR cycle
ITS	ITS1-Ep1S/ITS1-Ep2R	Ickert-Bond and Wojciechowski 2004	5' GGA CGG TCT TTG ACC AGT TTA TA 3' / 5' GCG ACG TAG GAA AGG AAA TAG 3'	initial denaturation (92C, 2 min), followed by 40 cycles of denaturation (92C, 45 sec), annealing (55C, 30 sec), and extension (72C, 30 sec), and concluding with a final extension (72C, 7 min).
mat K	trnK-Ep2/matK-Ep3R	Huang et al. 2005	5' TTC ATG AGT CAG GAG AAC 3' / 5' GTA TAT ACT TCA CAC GAT 3'	40 cycles with an annealing temperature of 47 °C and an extension period of 3min, with 10 s added to each subsequent cycle.
psb A-*trn* H	trnHGUG/psbA	Shaw et al. 2005	5' CGC GCA TGG TGG ATT CAC AAT CC 3' / 5' GTT ATG CAT GAA CGT AAT GCT C 3'	initial 3 min at 94 C, followed by 32 cycles of 94 C for 1 min, 53 C for 1 min, 72 C for 1 min, and a final extension at 72 C for 7 min
rps 4	trnSR2/rps5F	Ickert-Bond and Wojciechowski 2004	5' GCT TAC CGG GGT TCG AAT C 3' / 5' ATG TTC CCG TTA TCG AGG ACC T 3'	initial denaturation (92 C, 2 min), followed by 40 cycles of denaturation (92 C, 45 sec), annealing (55 C, 30 sec), and extension (72 C, 30 sec), and concluding with a final extension (72 C, 7 min).

GYMNOSPORIA

DNA region	Primers	Reference	Primer sequence	PCR cycle
ITS	ITS5 (P1) / ITS4?	White et al. 1990, Kim and Jansen 1994	5' GGA AGT AAA AGT CGT AAC AAG G 3' / 5' TCC TCC GCT TAT TGA TAT GC 3'	the first cycle used a longer denaturation time (3 min) than the normal cycle (1 min) at 95 °C. Each of the 30 cycles consisted of 1 min at 95 °C to denature template DNA, 1 rain at 55 °C to anneal primers to denatured template DNA, and 45 sec at 72 °C for primer extension. Primer extension time was gradually increased by 3 sec intervals during each cycle. After 30 cycles the PCR reactions were incubated at 72 °C for 7 min to complete primer extension.

JUNIPERUS

DNA region	Primers	Reference	Primer sequence	PCR cycle
ITS	Jun-ITS-F	Little et al. 2004	5' GGA AGG AGA AGT CGT AAC AAG G 3'	94°C, 5min, 37 cycles at 94°C, 1min; 56°C, 45 sec and 72°C, 1 min; finally 72°C, 7min
	Jun-ITS-R	Little et al. 2004	5' CTT TTC CTC CGC TTA TTG ATA TG 3'	
mat K	Jun-matK-F	Kusumi et al. 2000	5' CCA AAT TCG TTC TCT CTG TG 3'	**matK F-R:** 94°C, 5 min, 37 cycles of 94°C, 1 min, 53°C, 45 sec and 72°C, 1min and 20 sec, finally 72°C, 7 min; **matK F-IR2**: 94°C, 5 min, 37 cycles of 94°C, 50 sec, 54°C, 45 sec and 72°C, 1min; finally 72°C, 7 min; **matK IF2-R:** 94°C, 5 min; 37 cycles of 94°C, 50 sec, 54°C, 45 sec and 72°C, 1 min; finally 72°C, 7 min
	Jun-matK-R	Kusumi et al. 2000	5' TAT TCC ATG AGT CAG GAG AG 3'	
	Jun-matK-IF2	Kusumi et al. 2000	5' AAG GGA TCT TTC TCC ATA TC 3'	
	Jun-matK-IF4	Kusumi et al. 2000	5' ATT GCG AAC GAA ACT TCC AA 3'	
	Jun-matK-IR2	Kusumi et al. 2000	5' CTT TGG TTT CAA CCG TAT AG 3'	
	Jun-matK-IR4	Kusumi et al. 2000	5' CAG ATA TAC GAG TGC CCT AC 3'	
rbc L	Jun-rbcL-F	Little et al. 2004	5' ATG TCA CCA CAA ACA GAA ACT AAA GCA A	**rbcL F-R**: 94°C, 5 min, 37 cycles of 94°C, 1 min, 54°C, 45 sec and 72°C, 1 min and 10 sec, , finally 72°C, 7 min. **rbcL F-AR**: 94°C, 5 min, 37 cycles of 94°C, 50 sec, 55°C, 45 sec and 72°C, 1 min; finally 72°C, 7 min. **rbcL DF-R**: 94°C, 5 min; 37 cycles of 94°C, 50 sec, 55°C, 45 sec and 72°C, 1min; finally 72°C, 7 min
	Jun-rbcL-R	Little et al. 2004	5' TCA CAA GCA GCA GCT AGT TCA GGA CTC 3	
	Jun-rbcL-AR	Mao et al. 2010	5' TGA GCC AAC GAA GTA TTT GC 3'	
	Jun-rbcL-BF	Mao et al. 2010	3' GCA AAT ACT TCG TTG GCT CA 3'	
	Jun-rbcL-CR	Mao et al. 2010	5' GAA TAA GCA GGA GGA ATT CG 3'	
	Jun-rbcL-DF	Mao et al. 2010	5' CGA ATT CCT CCT GCT TAT TC 3'	
rps 4	Jun-rps4-F	Souza-Chies et al. 1997	5' ATG TCC CGT TAT CGA GGA CCT 3'	94°C 5M, 37 cicles of 94°C 50S, 56°C 45S, 72°C 1M 72°C, and finally 7M 72°C
	Jun-rps4-R	Souza-Chies et al. 1997	5' TAC CGA GGG TTC GAA TC 3'	
trn L-*trn* F	trne / trne	Taberlet et al. 1991	5' GGT TCA AGT CCC TCT ATC CC 3' / 5' ATT TGA ACT GGT GAC ACG AG 3'	94°C 5M, 37 cycles of 95°C 50S, 56°C 40S, 72°C 1M, and finally 72°C 7M
trn S-*trn* G	Jun-trnSGCU	Shaw et al. 2005	5' GCC GCT TTA GTC CAC TCA GC 3'	94°C 5M, 37 cycles of 94°C 50S, 56°C 45S, 72°C 1M, and finally 72°C 7M
	Jun-trnGUCC	Shaw et al. 2005	5' GAA CGA ATC ACA CTT TTA CCA C 3'	
trn V	Jun-trnV-F	Wang et al. 1999	5' GTA GAG CAC CTC GTT TAC AC 3'	94°C 5M, 37 cycles of 94°C 50S, 56°C 45S, 72°C 50s, and finally 72°C 7M
	Jun-trnV-R	Wang et al. 1999	5' CTC GAA CCG TAG ACC TTC TC 3'	
psb B1-*psb* B2	Jun-psbBB-F	Grivet et al. 2001	5' TGC CTT GGT ATC GTG TTC ATA C 3'	**psbB1-B2 F-R:** 94°C 5M, 37 cycles of 94°C 1M, 53°C 45S, 72°C 1M 15S, and finally 72°C, 7M **psbB1-B2 F-IR:** 94°C 5M, 37 cycles of 94°C 50S, 53°C 45S, 72°C 1M, and finally 72°C, 7M
	Jun-psbBB-R	Grivet et al. 2001	5' CYT GTC TTY TTG TAG TTG GAT 3'	
	Jun-psbBB-IF	Mao et al. 2010	5' GCA GGT CTA TTC CAT CTC AGT G 3'	
	Jun-psbBB-IR	Mao et al. 2010	5' CAC GAA CCC GTC GAT CTA TTT C 3'	

MYRSINE

DNA region	Primers	Reference	Primer sequence	PCR cycle
ITS	ITS4 / ITS5	White et al. 1990	5' TCC TCCG CTT ATT GAT ATG C 3' / 5' GGA AGT AAA AGT CGT AAC AAG G 3'	Initial denaturation of 5 min at 95 °C; 35 cycles of 1 min at 95 °C, 1 min at 52 °C, and 0:40 min at 72 °C; and final elongation of 7 min at 72 °C.

PISTACIA

DNA region	Primers	Reference	Primer sequence	PCR cycle
ITS	ITS4 / ITS5	White et al. 1990	5' TCC TCCG CTT ATT GAT ATG C 3' / 5' GGA AGT AAA AGT CGT AAC AAG G 3'	a 95 C initial hot start for 5 min, 32 cycles of 94 C for 30 s, 50 C for 40 s and 72 C for 60 s, and a final extension of 72 C for 10 min
ETS	ETS1F / 18s-IGS	Weeks et al. 2005 / Baldwin and Markos 1998	5' GAG ACA AGC ATA TGA CTA CTG GCA GGA TCA ACC AG 3' / 5' TTC GGT ATC CTG TGT TGC TTA C 3'	a 95 C initial hot start for 5 min, 32 cycles of 94 C for 30 s, 50 C for 40 s and 72 C for 60 s, and a final extension of 72 C for 10 min

RHAMNUS

DNA region	Primers	Reference	Primer sequence	PCR cycle
ITS	P17 (F)	Popp and Oxelman 2001	5´CTA CCG ATT GAA TGG TCC GGT GAA 3´	The cycling program started with a denaturation step at 95°C for 2 min followed by 38 cycles of: 95°C 30 s, 55°C 1 min, 72°C 2 min. The program was terminated with a 72°C step for 15 min.
	26S-82R (R)	Popp and Oxelman 2001	5´TCC CGG TTC GCT CGC CGT TAC TA 3´	
	P16 (F)	Popp and Oxelman 2001	5´TCA CTG AAC CTT ATC ATT TAG AGG A 3´	
	P25 (R)	Oxelman and Lidén 1995	5´GGG TAG TCC CGC CTG ACC TG 3´	
trn L-*trn* F	TRN C-F	Taberlet et al. 1991	5' CGA AAT CGG TAG ACG CTA CG 3'	The cycling program started with a denaturation step at 95°C for 2 min followed by 38 cycles of: 95°C 30 s, 55°C 1 min, 72°C 2 min. The program was terminated with a 72°C step for 15 min.
	TRN D-R	Taberlet et al. 1991	5' GGG GAT AGA GGG ACT TGA AC 3'	
	trne / trnf	Taberlet et al. 1991	5' GGT TCA AGT CCC TCT ATC CC 3' / 5' ATT TGA ACT GGT GAC ACG AG 3'	

SYDEROXYLON

DNA region	Primers	Reference	Primer sequence	PCR cycle
ITS	ITS5P / ITS4	Möller and Cronk 1997 / White et al. 1990	5' GGA AGG AGA AGT CGT AAC AAG G / 5' TCC TCCG CTT ATT GAT ATG C 3'	2-min denaturation at 95 C, followed by 35 cycles of 95 C denaturation for 30 s, 50 C annealing for 30 s, and 72 C extension for 30 s, followed by a final 8-min extension at 72 C
trn H-*psb* A	psbA3'f / trnHf	Sang et al. 1997 / Tate and Simpson 2003	5' GTT ATG CAT GAA CGT AAT GCTC 3' / 5' GCG CAT GGT GGA TTC ACA ATC C 3'	initial 3-min denaturation at 94 C, followed by two cycles of 94 C denaturation for 45 s, 50 C annealing for 45 s, and 72 C extension for 60 s, then a further 30 cycles with an annealing temperature of 45 C, followed by a final 7-min extension at 72 C

THESIUM

DNA region	Primers	Reference	Primer sequence	PCR cycle
ITS	ITS4 / ITS5	White et al. 1990	5' TCC TCCG CTT ATT GAT ATG C 3' / 5' GGA AGT AAA AGT CGT AAC AAG G 3'	an initial denaturation of 2 min at 94 C; 30 cycles each comprising 94 C for 1 min (denaturation), 48 C for 1 min (annealing) and 72 C for 1.5 min; and a final extension of 4 min at 72 C
mat K	matK-1RKIM-f / matK-3FKIM-r	Kuzmina et al. 2012	5' ACC CAG TCC ATC TGG AAA TCT TGG TTC 3' / 5' CGT ACA GTA CTT TTG TGT TTA CGA G 3'	an initial denaturation of 2 min at 94 C; 30 cycles each comprising 94 C for 1 min (denaturation), 48 C for 1 min (annealing) and 72 C for 1.5 min; and a final extension of 4 min at 72 C
rpl 32-*trn* L	trnL(UAG) / rpl32-F	Shaw et al. 2007	5' CTG CTT CCT AAG AGC AGC GT 3' / 5' CAG TTC CAA AA A AAC GTA CTT C 3'	an initial denaturation of 2 min at 94 C; 30 cycles each comprising 94 C for 1 min (denaturation), 48 C for 1 min (annealing) and 72 C for 1.5 min; and a final extension of 4 min at 72 C
trn L-*trn* F	trnc / trnf	Taberlet et al. 1991	5' CGA AAT CGG TAG ACG CTA CG 3' / 5' ATT TGA ACT GGT GAC ACG AG 3'	an initial denaturation of 2 min at 94 C; 30 cycles each comprising 94 C for 1 min (denaturation), 48 C for 1 min (annealing) and 72 C for 1.5 min; and a final extension of 4 min at 72 C

Table S4. Table S4. Detailed information (phylogenetic relationships and colonization times) of the 16 lineages with thermophilous species recovered from the BEAST analyses of 13 plant groups in this study: species comprising the Canarian (Macaronesian) lineages, continental sister groups, distribution of sister groups, stem age inferred, percentage of trees supporting a mediterranean and pre-Mediterranean stem node, stem node category assigned (i.e., mediterranean, pre-mediterranean, undetermined), crown age inferred, percentage of trees supporting a mediterranean and pre-mediterranean stem node, crown node category assigned and lineage category (next page).

Canarian (Macaronesian) lineages	Sister group	Distribution sister group	Stem age	% TREES	% TREES OUT OF 3	Category Stem node	CROWN	% TREES WITHIN	% TREES OUT OF 3	Category Crown node	Category lineage (Stem + crown)
Asparagus lineage I: ***Asparagus umbellatus***, *A. arborescens* and *A. fallax*	*A. humilis* (low support BI, high support ML)	Kenya, Tanzania, Mozambique	1.75 (1.39-4.17)	**61.24**	38.76	Mediterranean	1.75 (0.62-2.70)	**96.02**	3.98	Mediterranean	Mediterranean
Asparagus lineage II: ***Asparagus scoparius***, *A. nesiotes, A. plocamoides*	Included the mainland *A. altissimus* and *A. acutifolius* (low support). Closely related to to *A. fractiflexus* and *A. denudatus* (low support)	*A. fractiflexus*: South Africa;*A. denudatus*: South Africa; Kenya and Tanzania	1.60 (0.72-2.38) - TMRCA	**89.28**	10.72	Mediterranean	_	_	_	_	Mediterranean
Bosea yervamora	*B. cypria* and *B. amherstiana* (high support)	*B. cypria*: Cyprus; *B. amherstiana*:: Nepal, Pakistan, West Himalaya	5.71 (1.75-11.61)	7.92	**92.08**	Pre-mediterranean	1.64 (0.36-3.45)	**90.59**	9.41	Mediterranean	Undetermined
Bryonia verrucosa	The rest species of *Bryonia* (high support)	N. Africa, Europe to Central Asia and W. Himalaya	5.19 (2.41-8.56)	2.06	**97.94**	Pre-mediterranean	1.74 (0.23-3.17)	**92.11**	7.89	Mediterranean	Undetermined
Chrysojasminum odoratissimum	Polytomy with *C. parkeri*, *C. humile*, *C. bignoniaceum* and *C. fruticans* (clade well-supported but low sampling)	*C. bignoniaceum*: India; *C. parkeri*: West Himalaya; *C. humile*: S. Iran to Central China and N. Myanmar; *C. fruticans*: Medit. to N. Iran	14.86 (5.79-26.03)	0.01	**99.99**	Pre-mediterranean	4.79 (1.25-9.44)	18.08	**81.92**	Pre-mediterranean	Pre-mediterranean
Dracunculus canariensis	*D. vulgaris*	Mediterranean	12.10 (5.82-18.49)	0.01	**99.99**	Pre-mediterranean	2.76 (0.48-5.82)	**60.16**	39.84	Mediterranean	Undetermined
Ephedra fragilis	Unresolved polytomy including *E. alata*, *E. aphylla*, *E. altissima*	N Africa + Arabia	1.29 (0.25-2.78) - TMRCA	**82.16**	17.84	Mediterranean	_	_	_	_	Mediterranean
Gymnosporia lineage: ***Gymnosporia cassinoides***, ***G. cryptosepala*** and *G. dryandrii*	*G. parviflora*, *G. dhofarensis*, *G. arbutifolia*, *G. engleriana* (high support)	*G. parviflora:* Yemen and Eritrea; *G. dhofarensis*: Arabian Peninsula; *G. royleana*: S Asia; *G. arbutifolia*: C+CE Africa	3.78 (2.11-5.36)	15.23	**84.77**	Pre-mediterranean	1.27 (0.46-2.00)	**99.73**	0.27	Mediterranean	Undetermined
Myrsine excelsa	*Myrsine semiserrata* (low support)	SW Asia	3.98 (1.59-7.06)	12.34	**87.66**	Pre-mediterranean	1.07 (0.28-2.11)	**98.92**	1.08	Mediterranean	Undetermined
Juniperus turbinata (non-endemic)	Unresolved	Mediterranean	4.91(1.18-9.19) - TMRCA	13.14	**86.86**	Pre-mediterraneo	_	_	_	_	Undetermined
Pistacia atlantica (non-endemic)	*P. vera*, *P. integerrima*, *P. khinjuk* (low support)	P. atlantica: S + E Med + Macaronesia; P. vera: SW Asia; P. integerrima: E Asia; P. khinjuk: E Med, SW Asia	1.15 (0.24-2.43) - TMRCA	**97.22**	2.78	Mediterranean	_	_	_	_	Mediterranean
***Pistacia lentiscus* lineage I** (non-endemic)	*P. aethiopica* (low support)	P. aethiopica: CE Africa	3.96 (1.52-6.71)	11.04	**88.96**	Pre-mediterranean	1.15 (0.00-1.43)	**96.19**	3.81	Mediterranean	Undetermined
***Pistacia lentiscus* lineage II** (non-endemic)	Populations of *P. lentiscus* from Spain and Morocco	P. lentiscus: circunmed + Macaronesia	1.76 (0.49-3.37) - TMRCA	**89.28**	10.72	Mediterranean	_	_	_	_	Mediterranean
Rhamnus crenulata	*R. lycioides* (High support)	Mediterranean	3.88 (1.79-6.59)	16.05	**83.95**	Pre-mediterranean	1.71 (0.49-3.38)	**87.02**	12.98	Mediterranean	Undetermined
Syderoxylon canariense	Sister to a clade containing 11 spp	Cape Verde, Socotra, C+E Asia, Reunion, Madagascar, Mauricio	38.86 (26.11-55.00)	0.00	**100.00**	Pre-mediterranean	7.16 (2.57-12.99)	1.28	**98.72**	Pre-mediterranean	Pre-mediterranean
Thesium lineage: ***Thesium subsuculentum*** and *T. retamoides*	*T. mauritanicum* (High support)	N Africa	14.53 (6.56-23.57)	0.00	**100.00**	Pre-mediterranean	3.86 (1.06-7.39)	31.11	**68.89**	Pre-mediterranean	Pre-mediterranean

Table S5. Results of the ancestral area reconstruction under the dispersal-extinction-cladogenesis (DEC) analyses performed on the 13 newly generated time-calibrated phylogenies including thermophilous species in the Canary Islands analysed in this study. Log-likelihood (lnL) values corresponding to the stem node (or to the most recent common ancestor when the posterior probability of the stem node was lower than 0.90) of the lineage for each of the possible ancestral ranges (in bold the most likely) are indicated. The letters correspond to the following geographical areas: A: Mediterranean Basin, B: Macaronesia, C: Other regions (several letters imply ranges that include multiple areas). It is also indicated whether or not the Mediterranean Basin is part of the inferred ancestral range for the lineage, and whether the lineage is pre-, post- or undetermined with respect to the establishment of the Mediterranean climate.

Canarian (Macaronesian) lineages	Sister group	Null range	A	B	C	AB	AC	BC	ACB	Mediterranean Basin in the ancestral range	Temporal origin (mediterranean vs. pre-mediterranean)
Asparagus lineage I: ***Asparagus umbellatus***, *A. arborescens* and *A. fallax*	*A. humilis*	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	0.00	NO	Mediterranean
Asparagus lineage II: ***Asparagus scoparius***, *A. nesiotes, A. plocamoides*	Included the mainland *A. altissimus* and *A. acutifolius* (low support)	0.00	0.18	0.18	0.00	**0.64**	0.00	0.00	0.00	YES	Mediterranean
Bosea yervamora	*B. cypria* and *B. amherstiana*	0.00	0.00	0.00	0.00	0.00	0.00	0.09	**0.91**	YES	Undetermined
Bryonia verrucosa	The rest species of *Bryonia*	0.00	0.01	0.00	0.01	0.12	0.03	0.11	**0.73**	YES	Undetermined
Chrysojasminum odoratissimum	*C. parkeri*, *C. humile*, *C. bignoniaceum* and *C. fruticans*	0.00	0.00	0.00	0.00	0.00	0.00	**0.90**	0.10	NO	Pre-mediterranean
Dracunculus canariensis	*D. vulgaris*	0.00	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00	YES	Undetermined
Ephedra fragilis (non-endemic)	*E. alata* (low support)	0.00	0.32	0.00	0.00	0.14	**0.49**	0.01	0.04	YES	Mediterranean
Gymnosporia lineage: ***Gymnosporia cassinoides***, ***G. cryptosepala*** and *G. dryandrii*	*G. parviflora*, *G. dhofarensis*, *G. arbutifolia*, *G. engleriana*	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	0.00	NO	Undetermined
Juniperus turbinata (non-endemic)	*J. phoenicea* (low support)	0.00	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00	YES	Undetermined
Myrsine excelsa	*Myrsine semiserrata* (low support)	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	0.00	NO	Undetermined
Pistacia atlantica (non-endemic)	*P. vera* (low support)	0.00	0.00	0.00	**0.56**	0.00	0.15	0.14	0.15	NO	Mediterranean
Pistacia lentiscus (including P. lentiscus lineages I and II; non-endemic)	*P. aethiopica* (low support)	0.00	0.00	0.00	0.00	0.00	0.25	0.24	**0.51**	YES	Undetermined
Rhamnus crenulata	*R. lycioides*	0.00	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00	YES	Undetermined
Syderoxylon canariense	Sister to a clade containing 11 spp	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	0.00	NO	Pre-mediterranean
Thesium lineage: ***Thesium subsuculentum*** and *T. retamoides*	*T. mauritanicum*	0.00	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00	YES	Pre-mediterranean

METHODS S1. Details of the maximum likelihood phylogenetic analyses performed in this study

We reconstructed phylogenetic trees including the new DNA sequences and the previously-published DNA datasets using a maximum likelihood (ML) approach implemented in RaxML v.8.2.11 (Stamatakis, 2014) in Geneious. A GTR+GAMMA model and the “Rapid bootstrapping and search for the best-scoring ML tree” algorithm option was selected, and a total of 100 bootstrap replicates were performed.

LITERATURE CITED IN SUPPLEMENTARY DATA

Affenzeller M, Kadereit JW, Comes HP, 2018. Parallel bursts of recent and rapid radiation in the Mediterranean and Eritreo-Arabian biodiversity hotspots as revealed by *Globularia* and *Campylanthus* (Plantaginaceae). *Journal of Biogeography* 45: 552–566.

Albaladejo RG, Martín-Hernanz S, Reyes-Betancort JA, Santos-Guerra A, Olangua-Corral M, Aparicio A. 2021. Reconstruction of the spatio-temporal and ecological patterns of dispersal and diversification of *Helianthemum* sect. *Helianthemum* (Cistaceae) in the Canary Islands using Genotyping by Sequencing data. *Annals of Botany* 127: 597–611.

Anderson GJ, Bernardello G, Bohs L, Weese T, Santos-Guerra A. 2006. Phylogeny and biogeography of the Canarian *Solanum vespertilio* and *S. lidii* (Solanaceae). *Anales del Jardin Botanico de Madrid* 63: 159–167.

Appelhans MS, Paetzold C, Wood KR, Wagner WL. 2020. RADseq resolves the phylogeny of Hawaiian *Myrsine* (Primulaceae) and provides evidence for hybridization. *Journal of Systematics and Evolution* 58: 823–840.

Asmussen CB, Chase MW. 2001. Coding and noncoding plastid DNA in palm systematics. American Journal of Botany 88:1103–1117.

Baldwin GB, Markos S. 1998. Phylogenetic utility of the external transcribed spacer (ETS) of 18S–26S rDNA: congruence of ETS and ITS trees of *Calycadenia* (Compositae). *Molecular Phylogenetics and Evolution* 10: 449–463.

Barber JC, Finch CC, Francisco-Ortega J, Santos-Guerra A, Jansen RK. 2007. Hybridization in Macaronesian *Sideritis* (Lamiaceae): evidence from incongruence of multiple independent nuclear and chloroplast sequence datasets. *Taxon* 56: 74–88.

Barres L, Vilatersana R, Molero J, Susanna A, Galbany-Casals M. 2011. Molecular phylogeny of *Euphorbia* subg. *Esula* sect. *Aphyllis* (Euphorbiaceae) inferred from nrDNA and cpDNA markers with biogeographic insights. *Taxon* 60: 705–720.

Besnard G, Rubio de Casas R, Christin P-A, Vargas P. 2009. Phylogenetics of *Olea* (Oleaceae) based on plastid and nuclear ribosomal DNA sequences: Tertiary climatic shifts and lineage differentiation times. *Annals of Botany* 104: 143–160.

Böhle U-R, Hilger HH, Martin WF. 1996. Island colonization and evolution of the insular woody habit in *Echium* L. (Boraginaceae). *Proceedings of the National Academy of Sciences of the USA* 93: 11740–11745.

Bolmgren K, Oxelman B. 2004. Generic limits in *Rhamnus* L. s.l. (Rhamnaceae) inferred from nuclear and chloroplast DNA sequence phylogenies. *Taxon* 53: 383–390.

Carine MA, Russell SJ, Santos-Guerra A, Francisco-Ortega J. 2004. Relationships of the Macaronesian and Mediterranean floras: molecular evidence for multiple colonizations into Macaronesia and back-colonization of the continent in *Convolvulus* (Convolvulaceae). *American Journal of Botany*. 91: 1070–1085.

Carine MA. 2005. Spatio-temporal relationships of the Macaronesian endemic flora: A relictual series or window of opportunity?. *Taxon* 54: 895–903.

Chen C, Qi ZC, Xu XH, et al. 2014. Understanding the formation of Mediterranean-African-Asian disjunctions: Evidence for Miocene climate-driven vicariance and recent long-distance dispersal in the Tertiary relict *Smilax aspera* (Smilacaceae). *New Phytologist* 204: 243–255.

Chen S, Kim DK, Mark WMW, Kim JH. 2013. Networks in a Large-Scale Phylogenetic Analysis: Reconstructing Evolutionary History of Asparagales (Lilianae) Based on Four Plastid Genes. *PLoS ONE* 8: e59472.

Coello AJ, Fernández-Mazuecos M, García-Verdugo C, Vargas P. 2021. Phylogeographic sampling guided by species distribution modeling reveals the Quaternary history of the Mediterranean-Canarian *Cistus monspeliensis* (Cistaceae). *Journal of Systematics and Evolution* 59: 262–277.

Davis CC, Webb CO, Wurdack KJ, Jaramillo CA, Donoghue MJ. 2005. Explosive radiation of Malpighiales supports a Mid-Cretaceous origin of modern tropical rain forests. *American Naturalist* 165: E36– E65.

Di Vincenzo V, Gruenstaeudl M, Nauheimer L, et al. 2017. Evolutionary diversification of the African achyranthoid clade (Amaranthaceae) in the context of sterile flower evolution and epizoochory. *Annals of Botany* 122: 69–85.

Díaz-Pérez A, López-Álvarez D, Sancho R, Catalán P. 2018. Reconstructing the origins and the biogeography of species' genomes in the highly reticulate allopolyploid-rich model grass genus *Brachypodium* using minimum evolution, coalescence and maximum likelihood approaches. *Molecular Phylogenetics and Evolution* 127: 256–271.

Dlugosch KM, Parker IM. 2007. Molecular and quantitative trait variation across the native range of the invasive species *Hypericum canariense*: evidence for ancient patterns of colonization via pre-adaptation?. *Molecular Ecology* 16: 4269–4283.

Durán I, Marrero A, Msanda F, et al. 2020. Iconic, threatened, but largely unknown: Biogeography of the Macaronesian dragon trees (*Dracaena* spp.) as inferred from plastid DNA markers. *Taxon* 69: 217–233.

Escobar García P, Schönswetter P, Fuertes Aguilar J, Nieto Feliner G, Schneeweiss GM. 2009. Five molecular markers reveal extensive morphological homoplasy and reticulate evolution in the *Malva* alliance (Malvaceae). *Molecular Phylogenetics and Evolution* 50: 226–239.

Fernández-Mazuecos M, Vargas P. 2010. Ecological rather than geographical isolation dominates Quaternary formation of Mediterranean *Cistus* species. *Molecular Ecology* 19: 1381–1395.

Francisco-Ortega J, Crawford DJ, Santos-Guerra A, Jansen RK. 1997. Origin and evolution of *Argyranthemum* (Asteraceae: Anthemideae) in Macaronesia. In: Givnish TJ, Sytsma KJ, eds. Molecular evolution and adaptive radiation. Cambridge: Cambridge University Press, 406–431.

Francisco-Ortega J, Fuertes-Aguilar J, Kim SC, Santos-Guerra A, Crawford DJ, Jansen RK. 2002. Phylogeny of the Macaronesian endemic *Crambe* Section *Dendrocrambe* (Brassicaceae) based on internal transcribed spacer sequences of nuclear ribosomal DNA. *American Journal of Botany* 89: 1984–1990.

Fuertes Aguilar J, Francisco-Ortega J, Santos-Guerra A, Ray MF, Jansen RK. 2002. Chloroplast and nuclear molecular evidence for multiple colonizations of *Lavatera* (Malvaceae) in the Canary Islands. *Systematic Botany* 27: 74–83.

García-Maroto F, Mañas-Fernández A, Garrido-Cárdenas JA, et al. 2009. Delta 6-desaturase sequence evidence for explosive Pliocene radiations within the adaptive radiation of Macaronesian *Echium* (Boraginaceae). *Molecular Phylogenetics and Evolution* 52: 563–574.

Hertweck KL, Kinney MS, Stuart SA, et al. 2015. Phylogenetics, divergence times and diversification from three genomic partitions in monocots. *Botanical Journal of the Linnean Society* 178: 375–393.

Huang J, Giannasi DE, Price RA. 2005. Phylogenetic relationships in Ephedra (Ephedraceae) inferred from chloroplast and nuclear DNA sequences. *Molecular Phylogenetics and Evolution* 35: 48–59.

Ickert-Bond SM, Rydin C, Renner SS. 2009. A fossil-calibrated relaxed clock for *Ephedra* indicates an Oligocene age for the divergence of Asian and New World clades and Miocene dispersal into South America. *Journal of Systematics and Evolution* 47: 444–456.

Ickert-Bond SM, Wojciechowski MF. 2004. Phylogenetic relationships in *Ephedra* (Gnetales): evidence from nuclear and chloroplast DNA sequence data. *Systematic Botany* 29: 834–849.

Jeyarani JN, Yohannan R, Vijayavalli D, Dwivedi MD, Pandey AK. 2018. Phylogenetic analysis and evolution of morphological characters in the genus *Jasminum* L. (Oleaceae) in India. *Journal of Genetics* 97: 1225–1239.

Johnson LA, Soltis DE. 1995. Phylogenetic inference in Saxifragaceae sensu-stricto and *Gilia* (Polemoniaceae) using matK sequences. *Annals of the Missouri Botanical Garden* 82:149–175.

Kim KJ, Jansen RK. 1994. Comparisons of phylogenetic hypotheses among different data sets in dwarf dandelions (*Krigia*, Asteraceae): additional information from internal transcribed spacer sequences of nuclear ribosomal DNA. *Plant Systematics and Evolution* 190: 157–185.

Kim SC, Crawford DJ, Francisco-Ortega J, Santos-Guerra A. 1996. A common origin for woody *Sonchus* and five related genera in the Macaronesian islands: molecular evidence for extensive radiation. *Proceedings of the National Academy of Sciences of the USA* 93: 7743–7748.

Kim SC, Lee C, Mejías JA. 2007. Phylogenetic analysis of chloroplast DNA matK gene and ITS of nrDNA sequences reveals polyphyly of the genus *Sonchus* and new relationships among the subtribe Sonchinae (Asteraceae: Cichorieae). *Molecular Phylogenetics and Evolution* 44: 578–597.

Kim SC, McGowen MR, Lubinsky P, Barber JC, Mort ME, Santos-Guerra A. 2008. Timing and tempo of early and successive adaptive radiations in Macaronesia. *PLoS One* 3: e2139.

Kusumi J, Tsumura Y, Yoshimaru H, Tachida H. 2000. Phylogenetic relationships in Taxodiaceae and Cupressaceae sensu stricto based on *mat*K gene, *chl*L gene, *trn*L-*trn*F IGS region, and *trn*L intron sequences. *American Journal of Botany* 87: 1480–1488.

Kuzmina ML, Johnson KL, Barron HR, Herbert PDN.2012. Identification of vascular plants of Churchill, Manitoba, using a DNA barcode library. *BMC Ecology* 12: 25.

Little DP, Schwarzbach AE, Adams RP, Hsieh C-F. 2004. The circumscription and phylogenetic relationships of *Callitropsis* and the newly described genus *Xanthocyparis* (Cupressaceae). *American Journal of Botany* 91: 1872–1881.

Malik S, Vitales D, Hayat MQ, Korobkov AA, Garnatje T, Vallès J. 2017. Phylogeny and biogeography of *Artemisia* subgenus *Seriphidium* (Asteraceae: Anthemideae). *Taxon* 66: 934–952.

Mansion G, Rosenbaum G, Schoenenberger N, Bacchetta G, Rosselló JA, Conti E. 2008. Phylogenetic analysis informed by geological history supports multiple, sequential invasions of the Mediterranean Basin by the angiosperm family Araceae. *Systematic Biology* 57: 269–285.

Mao K, Hao G, Liu J, Adams RP, Milne RI. 2010. Diversification and biogeography of *Juniperus* (Cupressaceae): variable diversification rates and multiple intercontinental dispersals. New Phytologist. 188: 254–272.

Martín-Hernanz S, Albaladejo RG, Lavergne S, Rubio E, Grall A, Aparicio A. 2021. Biogeographic history and environmental niche evolution in the Palearctic genus *Helianthemum* (Cistaceae). *Molecular Phylogenetics and Evolution* 163: 107238.

Martín-Hernanz S, Aparicio A, Fernández-Mazuecos M, et al. 2019. Maximize Resolution or Minimize Error? Using Genotyping-By-Sequencing to Investigate the Recent Diversification of *Helianthemum* (Cistaceae). *Frontiers in Plan Science* 10: 1416.

Meseguer AS, Aldasoro JJ, Sanmartin I. 2013. Bayesian inference of phylogeny, morphology and range evolution reveals a complex evolutionary history in St. John's wort (*Hypericum*). *Molecular Phylogenetics and Evolution* 67: 379–403.

Moazzeni H, Zarre S, Pfeil BE, et al. 2014. Phylogenetic perspectives on diversification and character evolution in the species-rich genus *Erysimum* (Erysimeae; Brassicaceae) based on a densely sampled ITS approach. *Botanical Journal of the Linnean Society* 175: 497–522.

Möller M, Cronk QCB. 1997. Origin and relationships of *Saintpaulia* (Gesneriaceae) based on ribosomal DNA internal transcribed spacer (ITS) sequences. *American Journal of Botany* 84: 956–965.

Moore MJ, Soltis PS, Bell CD, Burleigh G, Soltis DE. 2010. Phylogenetic analysis of 83 plastid genes further resolves the early diversification of eudicots. *Proceedings of the National Academy of Sciences of the USA* 107: 4623–4628.

Müller K, Borsch T. 2005. Phylogenetics of Amaranthaceae based on matK/trnK sequence data: evidence from parsimony, likelihood, and Bayesian analyses. *Annals of the Missouri Botanical Garden* 66–102.

Nauheimer L, Metzler D, Renner SS. 2012. Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist* 195: 938–950.

Norup MF, Petersen G, Burrows S, et al. 2015. Evolution of *Asparagus* L.(Asparagaceae): Out-of-South-Africa and multiple origins of sexual dimorphism. Molecular Phylogenetics and Evolution. 92: 25–44.

Oberprieler CO. Ott T, Hipper A, et al. 2017. Pleistocene shaping of genetic diversity in a monsoon-affected environment: the case of *Gymnosporia* (Celastraceae) in the southern Arabian Peninsula. *Plant Systematics and Evolution* 303: 1399–1412.

Onstein RE, Carter RJ, Xing YW, Richardson JE, Linder HP. 2015. Do Mediterranean- type ecosystems have a common history?-Insights from the buckthorn family (Rhamnaceae). *Evolution* 69: 756–771.

Ortega-Olivencia A, Catalán P. 2009. Systematics and evolutionary history of the circum-Mediterranean genus *Anagyris* L. (Fabaceae) based on morphological and molecular data. *Taxon* 58: 1290–1306.

Oxelman B, Liden M, Berglund D. 1997. Chloroplast rps16 intron phylogeny of the tribe Sileneae (Caryophyllaceae). *Plant Systematics and Evolution* 206:393–410.

Oxelman B, Lidén M. 1995. Generic boundaries in the tribe Sileneae (Caryophyllaceae) as inferred from nuclear rDNA sequences. *Taxon* 44: 525–542.

Pokorny L, Riina R, Mairal M, et al. 2015. Living on the edge: Timing of Rand Flora disjunctions congruent with ongoing aridification in Africa. *Frontiers in Genetics* 6: 154.

Popp M, Oxelman B. 2001. Inferring the history of the polyploid *Silene aegaea* (Caryophyllaceae) using plastid and homoeologous nuclear DNA sequences. *Molecular phylogenetics and evolution* 20: 474–481.

Rodríguez-Rodríguez P, Fernández de Castro AG, Pérez de Paz PL, Curbelo L, Palomares A, Mesa R, Acevedo A, Sosa PA. 2022. Evolution and conservation genetics of an insular hemiparasitic plant lineage at the limit of survival: the case of *Thesium* sect. *Kunkeliella* in the Canary Islands. *American Journal of Botany* 109: 419–436.

Salvo G, Ho SYW, Rosenbaum G, Ree R, Conti E. 2010. Tracing the temporal and spatial origins of island endemics in the Mediterranean region: a case study from the *Citrus* family (Ruta L., Rutaceae). *Systematic Biology* 59: 705–722.

Sang T, Crawford DJ, Stuessy TF. 1997. Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). *American journal of Botany* 84: 1120–1136.

Särkinen T, Bohs L, Olmstead RG, Knapp S. 2013. A phylogenetic framework for evolutionary study of the nightshades (Solanaceae): a dated 1000-tip tree. *BMC Evolutionary Biology* 13: 214.

Schaefer H, Heibl C, Renner, SS. 2009. Gourds afloat: a dated phylogeny reveals an Asian origin of the gourd family (Cucurbitaceae) and numerous oversea dispersal events. *Proceedings of the Royal Society Biological Sciences* 276: 843–851.

Schüßler CS. 2020. *No Tertiary relicts? A biogeographical study on the Macaronesian laurel forest species in Daucus (Apiaceae), Geranium (Geraniaceae), Gesnouinia (Urticaceae), Phyllis (Rubiaceae), Semele (Asparagaceae) and Visnea (Pentaphylacaceae)*. PhD Thesis, Faculty of Natural Sciences and Mathematics of the Ruperto Carola, University Heidelberg, Germany.

Shaw J, Lickey EB, Beck JT, et al. 2005. The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American journal of botany* 92: 142–166.

Shaw J, Lickey EB, Schilling EE, Small RL. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. *American journal of botany* 94: 275-288.

Souza-Chies TT, Bittar G, Nadot S, Carter L, Besin E, Lejeune B. 1997. Phylogenetic analysis of Iridaceae with parsimony and distance methods using the plastid gene *rps*4. *Plant Systematics and Evolution* 204: 109–123.

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313.

Stride G, Nylinder S, Swenson U. 2014. Revisiting the biogeography of *Sideroxylon* (Sapotaceae) and an evaluation of the taxonomic status of *Argania* and *Spiniluma*. *Australian Systematic Botany* 27: 104–118.

Sun Y, Li Y, Vargas-Mendoza CF, Wang F, Xing F. 2016. Colonization and diversification of the *Euphorbia* species (sect. *Aphyllis* subsect. *Macaronesicae*) on the Canary Islands. *Scientific Reports* 6: 34454.

Taberlet P, Gielly L, Pautou G, Bouvet J. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant molecular biology* 17: 1105–1109.

Tate JA, Simpson BB. 2003. Paraphyly of *Tarasa* (Malvaceae) and diverse origins of the polyploid species. *Systematic Botany* 28: 723–737.

Vargas P, Valente LM, Blanco-Pastor JL, et al. 2014. Testing the biogeographical congruence of palaeofloras using molecular phylogenetics: snapdragons and the Madrean-Tethyan flora. *Journal of Biogeography* 41: 932–943.

Villa I, Fernández de Castro AG, Fuertes-Aguilar J, Nieto-Feliner G. 2018. Out of North Africa by different routes. Phylogeography and species distribution model of the western Mediterranean *Lavatera maritima* (Malvaceae). *Botanical Journal of the Linnean Society* 187: 441–455.

Viruel J, Segarra-Moragues JG, Raz L, et al. 2016. Late Cretaceous–Early Eocene origin of yams (*Dioscorea*, Dioscoreaceae) in the Laurasian Palaearctic and their subsequent Oligocene–Miocene diversification. *Journal of Biogeography* 43: 750–762.

Vitales D, Garnatje T, Pellicer J, Vallès J, Santos-Guerra A, Sanmartín I. 2014. The explosive radiation of *Cheirolophus* (Asteraceae, Cardueae) in Macaronesia. *BMC Evolutionary Biology* 14: 118.

Volz SM, Renner SS. 2008. Hybridization, polyploidy, and evolutionary transitions between monoecy and dioecy in *Bryonia* (Cucurbitaceae). *American Journal of Botany* 95: 1297–1306.

Wang XR, Tsumura Y, Yoshimaru H, Nagasaka K, Szmidt AE. 1999. Phylogenetic relationships of Eurasian pines (Pinus, Pinaceae) based on chloroplast rbcL, matK, rpl20-rps18 spacer, and trnV intron sequences. *American Journal of Botany* 86: 1742–1753.

Weeks A, Daly DC, Simpson BB. 2005. The phylogenetic history and biogeography of the frankincense and myrrh family (Burseraceae) based on nuclear and chloroplast sequence data. *Molecular Phylogenetics and Evolution* 35: 85–101.

White OW, Reyes-Betancort J, Chapman MA, Carine MA. 2020. Geographical isolation, habitat shifts and hybridisation in the diversification of the Macaronesian endemic genus *Argyranthemum* (Asteraceae). *New Phytologist* 228: 1953–1971.

White TJ, Bruns T, Lee SJWT, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *PCR protocols: a guide to methods and applications* 18: 315–322.

Wicke S, Quandt D. 2009. Universal primers for the amplification of the plastid *trn*K/*mat*K region in land plants. *Anales del Jardín Botánico de Madrid* 66: 285–288.

Winkworth RC, Grau J, Robertson AW, Lockhart PJ. 2002. The origins and evolution of the genus *Myosotis* L. (Boraginaceae). *Molecular Phylogenetics and Evolution* 24:180–193.

Xie L, Yang Z-Y, Wen J, Li D-Z, Yi, T-S. 2014. Biogeographic history of *Pistacia* (Anacardiaceae), emphasizing the evolution of the Madrean-Tethyan and the eastern Asian-Tethyan disjunctions. *Molecular Phylogenenetics and Evolution* 77: 136–146.

Zhigila DA, Verboom GA, Muasya AM. 2020. An infrageneric classification of *Thesium* (Santalaceae) based on molecular phylogenetic data. *Taxon* 69: 100–123.