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DISENTANGLING THE BIOGEOGRAPHICAL ORIGINS OF THREATENED SPECIES OF THE MACARONESIAN BRYOPHYTHE FLORA

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CERTIFICA:

Que el presente trabajo titulado "**DISENTANGLING THE BIOGEOGRAPHICAL ORIGINS OF THREATENED SPECIES OF THE MACARONESIAN BRYOPHYTHE FLORA**" se ha realizado bajo su dirección durante el curso académico 2018-2019 en el Departamento de Departamento de Botánica, Ecología y Fisiología Vegetal de la Universidad de La Laguna, por el Lcdo. Felipe Lisandro Monzón Cabrera para optar a los créditos correspondientes al "Trabajo de Fin de Máster" del Máster Oficial de Biodiversidad Terrestre y Conservación en Islas de la misma Universidad.

AUTORIZA:

La lectura de este trabajo por considerar que reúne los requisitos de calidad necesarios para la presentación del mismo ante la comisión que le sea asignado al efecto.

La Laguna, a 5 de Septiembre de 2019

Fdo.: Jairo Patiño LLorente

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ABSTRACT

Historical biogeographic knowledge of island colonization is unevenly spread across insular regions and taxonomic groups. While in the case of vascular plants, the biogeographical origins of a limited number of insular floras are relatively well known, there is still a long way to go to reach a similar knowledge for insular bryophyte floras. Most of this knowledge is highly concentrated in a few archipelagos distributed across the Northeastern Atlantic Ocean, a region known as Macaronesia. The Macaronesian bryophyte flora has been thus object of a number of publications focussing on phylogenetic and biogeographic aspects, but aspects such as the geographic origins of its bryophyte flora remains largely unknown. This contrast with the case of the Macaronesian angiosperm flora, for which there is mounting evidence that the main species pools are inferred to have been in the Mediterrean and northern regions in Europe. In the present Master Thesis, we implement an integrative biogeographical quantitative-approach in order to improve our understanding on the evolutionary origins and post-colonization diversification events of the Macaronesian bryophyte flora. Specifically, we target species groups that include threatened bryophyte taxa, which have been analysed in BEAST and *BioGeoBEARS* in order to estimate their colonization and divergence times and their ancestral areas, respectively. Our results support the role of the Macaronesian archipelagos as a crossroad for bryophyte species pools from different geographic origins, with a principal influence of Palearctic, Nearctic and Neotropical regions. The dating approach also provides preliminary evidence for the apparent predominance of neoendemic species in detriment of palaeoendemic species, which departs from previous hypotheses on the origins of the Macaronesian flora, in particular for species associated with the different types of the laurel forest. The implications of our findings for island plant conservation are discussed.

KEYWORDS

Ancestral area estimation, bryophytes, colonization, diversification, island biogeography, island conservation, long distance dispersal, Macaronesia, threated species.

INTRODUCTION

Oceanic islands have been object of study for researchers since the introduction of the evolution concept by Charles Darwin and Alfred Russel Wallace, who focused on the Galapagos and Malayan archipelagos, respectively. Volcanic islands are *de novo* creation, devoid of biota and, hence, species must arrive by dispersal events. Avoiding the debate about the two central ideas of historical biogeography – vicariance versus dispersal (Quieroz, 2005), species must use different mechanism to colonize oceanic islands through anemocory, zoocory or talasocory, among others. Herein, we focus on a spore-producing plant group, bryophytes, that produces small propagules, and highlight wind (anemocory) as the main vehicle driving the passively dispersion of such a small diaspores (Muñoz et al., 2004); these two features provide part of the context of the present Master Thesis. Nowadays, researchers distinguished two processes of propagule dispersion: Short Distance Dispersal (SDD) and Long Distance Dispersal (LDD), disseminating propagules within population limits and outside them, respectively (Jordano, 2017). In the context of oceanic islands, propagules must often disperse by LDD out of their population range limits to colonize new territories, but this phenomenon implies that spores must survive the transport being exposed to UV radiation, drought and frequently dry freezing (Sundberg, 2013). Although the presumed resistance to these extreme conditions needs to be tested in many bryophyte groups, it is assumed that, a large number of bryophyte species indeed have the capability for wind LDD and therefore the potential to cope with these extreme environmental conditions (Van Zanten & Gradstein, 1988).

Biogeographical dynamics are gaining interest on oceanic islands around the world, allowing us to shed light into the mechanisms that drive community assembly and speciation, while controlling variables such as distribution, environment and species diversity (Whittaker et al., 2017). There is indeed an increasing number of studies addressing floristic affinities between islands and the nearly mainland at various spatial and temporal scales, in diverse groups like angiosperms, pteridophytes and bryophytes. In the case of the vascular flora from Juan Fernandez, for instance, phylogenetics clearly suggests that the overall affinities of the archipelago are of South American origin (Bernardello et al., 2006). Early studies on the Galapagos flora concluded that, although the majority of endemic and native plants seem to have South American ancestors, a small component has a North American (mostly Mexican) or Caribbean origin (Andrus et al., 2009). In the Hawaiian flora, the geographical regions acting as species pool sources are predominantly Indo-Malayan, North American, East Asian, Neotropical and Australasian, by this order (Price & Wagner, 2018), pointing to a very complex historical biogeography and multiple origins. Finally, the Macaronesian archipelagos of the Azores, Madeira and the Canary Islands evidenced floristic relationships with European, North African and southwest Asian floras, conversely to Cape Verde, which showed a stronger relationship with Sub-Saharan floras (Carine, 2005; Carine et al., 2010), where the differences in their origins was hypothesized to be the result of “windows of opportunities” for colonization and speciation (Carine, 2005). More in detail, Azores, Madeira and Canary Islands show strong affinities with the Mediterranean flora but with some influence of African flora elements and occasionally with Eurosiberian and Asiatic flora lineages (Carine et al., 2010). Unlike the vascular flora, recent biogeographical bryophyte studies have demonstrated Nearctic affinities in the genera *Orthotrichum*

(Vigalondo et al., 2019) and Neotropical origin in the case of the liverwort, *Leptoscyphus azoricus* (Devos & Vanderpoorten, 2009), pointing to the possibility that the main species pools for the Macaronesian bryophyte flora, or at least for a portion of it, could be very different, or at least not mainly found in the Mediterranean region.

Once an oceanic island is colonized, it has been historically proposed that insular lineages typically lack the capacity to disperse back to and re-establish in continental areas (reviewed in Patiño et al., 2015). However, gene flow on many bryophyte species does not stop following the colonization of islands, and there is evidence that the interchange of genetic material can continue and that reverse colonization events from islands to continental landmasses could be more frequent than previously thought (reviewed in Patiño & Vanderpoorten, 2015; Patiño & Vanderpoorten, 2018). Such levels of gene flow in bryophyte impose that insular speciation events can be only possible in the case of discrete LDD events with gene-flow disruption (Vanderpoorten et al., 2007). Furthermore, oceanic islands are useful for studying speciation because their well-defined boundaries and isolation make it easier to distinguish within-island cladogenesis or anagenesis than on continental regions (Kisel & Timothy, 2010). These evolutionary concepts, cladogenesis and anagenesis, have been recently redefined, and suggested an alternative terminology that better describes the geographical relationships of insular sister species (Emerson & Patiño, 2018).

Macaronesia as an ideal laboratory for island biogeography and island conservation

Macaronesia is a biogeographical insular region that comprises the oceanic archipelagos of the Azores, Madeira, Selvagens, Canaries and Cape Verde located in the Atlantic Ocean between 15 and 30°N (Carine, 2005). This region is defined based on the existence of many shared elements of flora and fauna, in addition to other geographical, cultural and political features. The very first delimitation of Macaronesia as a floristic region, by *Philip Barker Webb (1793-1854),* included the Madeiran, Selvagens and Canarian archipelagos from the nearby continental areas, being Engler in 1879 the first one who also included the Azorean archipelago within this distinct biogeographic unit (Vanderpoorten et al., 2007; Fernández-Palacios et al., 2011). Posterior authors included Cape Verde and continental territories of Northwestern Africa into this region (Sunding, 1979, reference from Fernández-Palacios et al., 2017). Macaronesia have resulted in more than 25.000 terrestrial species, on a surface of about 15.000 km^2 spread over 40 islands (Fernández-Palacios et al., 2017), which provides an ideal scenario for evolutionary and biogeographic questions, such as the study of the origins of its biota.

The geological configuration and climatological conditions of the Macaronesia has not always been, as we perceive it nowadays (Fernández-Palacios et al., 2011). The existence of seamounts in the vicinity of the actual Macaronesian islands indicate that, the previous configuration of those Atlantic archipelagos known as Palaeo-Macaronesia was different, helping us to explain certain distribution range patterns that we observe nowadays. The colonization of PalaeoMacaronesia could have been started since the formation of Ormonde and Gettysburg (65-67 Ma) and Lars (68 Ma) (Fernández-Palacios et al., 2011). In the particular case of bryophytes, we find interesting cases that would match with the PalaeoMacaronesia hypothesis. Among those, the Madeiran endemic moss *Hedenasiastrum percurrens* diverged about 40 million years, that is well before

Madeira actually emerged, 5.2 million years ago (Ma) (Agoin et al., 2009). Therefore, its condition of continental palaeoendemic (i.e. lineages that evolved somewhere else and differ only slightly from extinct mainland ancestors), such as the case of *Alophosia azorica* (Vanderpoorten et al., 2007), has been proposed (Vanderpoorten et al., 2011). However, the Macaronesian endemic element is probably dominated by neoendemics (i.e. new insular lineages that evolved through *in-situ* speciation events), which may have resulted from much more recent dispersal events (Vanderpoorten et al., 2010).

There is a traditional perception of Macaronesia as a refugium for the vascular flora, in particularly for species associated with the laurel forest that spread across south Europe and North Africa during the Tertiary. Glacial extinctions resulted in local extinctions promoting disjunction distributions for a number of Macaronesian plant groups, which have been used to support the hypothesis that much of the Macaronesian vascular flora is relictual (Carine et al., 2004, 2010). Therefore, it is not surprising that there are instances of laurel forest species that were extirpated from the mainland, becoming Macaronesian palaeoendemics (Vargas, 2007; Carine et al., 2010; but see Kondraskov et al., 2015). However, paleogeographical and paleontological data do not indeed provide irrefutable evidence for the Engler refugium hypothesis (Vanderpoorten et al., 2007), and the perception of islands as evolutionary dead-ends (Heaney, 2007) has been increasingly challenged. Indeed, a recent meta-analysis showed that Macaronesian laurel forest lineages exhibit a cornucopia of colonization time windows and geographic origins, including the Mediterranean, Paleotropic, Neotropic and source areas within Macaronesia (Kondraskov et al., 2015). The tertiary relict condition of the Macaronesian laurel forest has been thus questioned, providing speciation times that do not fit with Engler's hypothesis (Kondraskov et al., 2015). In the particular case of bryophytes, phylogenetic evidence has shown even more challenging scenarios. For instance the Macaronesian archipelagos have played roles: (i) sources of genetic diversity via reverse colonization from the island to the continental landmasses (Patiño & Vanderpoorten, 2015) and for the more recent postglacial recolonization of Western Europe (Laenen et al., 2011); and even (ii) as gates for *de novo* colonization of Western Europe during the Pleistocene (Patiño et al., 2015). Colonization of Macaronesia could have thus occurred through a combination of both relictual series and more recent windows of opportunity (sensu Carine, 2005).

Oceanic islands are of fundamental importance for the conservation of biodiversity because they exhibit high endemism rates coupled with exceptional concentration of range-restricted taxa, higher extinction rates and their potential role to act as sources of biodiversity for other archipelagos and continental areas (Whitakker et al., 2017). It is currently accepted that conservation efforts should focus on areas where there is greatest need and where the payoff from safeguard measures would be greatest (Myers et al., 2000), an idea which helped to define the worldwide diversity hotspots. Of the 36 hotspots identified by Conservation International in 2005, 12 are island ecosystems, and here we focus on the insular regions that are included within the Mediterranean Biogeographic Hotspot (Médail & Myers 2004). The most recent perception of oceanic islands as sources of biodiversity for continents, together with the view of islands as key climatic refugia in the face of future climate change (Patiño et al.,2015), supposed a new incentive for island plant conservation. Recently, there has been an increasing awareness that it is mandatory to go beyond the traditional taxonomic diversity approach to thus incorporate the putative large gains offered in conservation biology by the other facets of biodiversity, such as evolutionary diversity (Pollock et al. 2015). This means that the dimension of evolutionary diversity and evolutionary rarity (sensu Medail and Baumel 2018) needs to be considered through the lens of the phylogenetic attributes (e.g. palaeoendemism vs. neoendemism) and biogeographical origins, because of their potential use in conservation prioritization (Pollock et al. 2015, 2017).

Molecular biogeography and phylogenetics, primary biological disciplines in evolutionary patterns, have had a secondary role in conservation and management (Redding et al. 2014; Pollock et al. 2015; Graham et al. 2018). Recently, however, authors have increasingly incorporated phylogeny-aware analyses in biological conservation issues due to the given the wide range of applications of phylogenetic theory in evolutionary biology (reviewed in Tucker et al. 2017). This is a pending subject in bryology as just a few cases have been applied to conservation issues and even less to island bryophyte species (Patiño et al., 2013). In this respect, there is a number of phylogenetic studies of Macaronesian bryophyte flora to be considered which focused on a broad variety of objectives: resolve species complexes, identify new species, reveal misidentified species, analyses number of colonization events, analyses the mechanisms for in situ radiation events or identify ongoing speciation processes, among others. The heterogeneity in the nature of these phylogenetic studies was therefore wide but, luckily, genetic markers used were largely common, at least in their sequencing technology (Sanger sequencing).

General and specific goals of the Master Thesis

In this Master Thesis, we have tried to reanalyze a number of published datasets with the objectives of, through a unified analytical method, shedding light in our understanding of the evolutionary origins of the Macaronesian bryophyte flora, in particular in groups that present threatened species (i.e. endangered, vulnerable). We mostly focus our compilation to laurel forest bryophyte species because: most of the threatened and endemic species occur in potential areas of different types of laurel forests (Vanderpoorten et al., 2010; González-Mancebo et al. 2012); and because such a sampling strategy opens the door to test its palaeoendemic origin. This Master Thesis is part of a bigger initiative leaded by the mentor, Dr. Patiño, and Dr. Vanderpoorten from the University of Liege, and should be considered as a contribution to a much broader research program. In this context, despite they have all the necessary phylogenetic data to perform dating analyses and ancestral range reconstructions, there are a number of taxonomical studies that focused on genera such as *Tylimanthus* (Stech et al., 2011), *Metzgeria* (Fuselier et al., 2011), *Amphidium* (Sim-Sim et al., 2017), *Odontoschisma* (Aranda, 2014) or *Homalothecium* (Hedenas et al., 2014) that completely neglected questions related to their historical biogeography. We considered the availability of these datasets as an opportunity to perform the present study.

The specific objectives of the present study are to:

> (1) Carry out a bibliographic review of the literature containing phylogenetic and biogeographic bryophyte information, and compile a phylogenetic database.
>
> (2) Apply an analytical unified approach (i.e. dating and ancestral area estimation analyses) to the compiled phylogenetic datasets in order to make comparisons.
>
> (3) Perform a meta-analysis of the colonization time and geographical origins of the most recent common ancestors (MRCA) of the Macaronesian lineages, along with their time of diversification, when possible.
>
> (4) Discuss the main results in the framework of the future conservation of this iconic insular flora, providing complementary arguments for the conversation and management of Macaronesian bryodiversity.

In this respect, we tested three hypotheses: (a) given the LDD capabilities of bryophytes, their geographic sources should be mainly inferred to be in distant species pool like the Neotropics, in detriment of the closer ones like the Palearctic; (b) Macaronesian endemics should be more often palaeoendemics than neoendemics due to their strong relationship with a presumably relict forest formation (but see Kondraskov et al. 2015); and (c) threatened species should be more often neoendemics than palaeoendemics as one would expect that their effective population size and distribution ranges could be more limited due to their shorter time window for evolution.

Finally, we must acknowledge that, we have excluded the archipelagos of Cape Verde and Selvagens from the Master Thesis due to a number of reasons. In both cases, the lack of phylogenetic datasets could be considered as the ultimate reason for their exclusion from this meta-analysis. Furthermore, in the case of Cape Verde, such a decision is partially due to its predominant floristic affinities with sub-Sahara Africa (Vanderpoorten et al., 2007). While in the case of Selvagens, an archipelago formed 27 Ma that is strongly eroded (Fernández-Palacios et al, 2011), and the complete absence of laurel forest motived us to exclude it from the Master Thesis.

MATERIALS AND METHODS

Species list

First, we compiled a species list, with the 764 species and subspecies of mosses, liverworts and hornworts, present in the Macaronesian archipelagos shown on Supplementary Material 1 (Macaronesian unified checklist), by using the available checklists for the Azores (Borges et al., 2010), Madeira (Borges et al., 2008) and the Canary Islands (Datos de Biodiversidad de Canarias -Gobierno de Canarias-). This number of bryophyte species registered became an increase of 38 species and subspecies from the previous number of 726 bryophyte species given in a similar compilation (Gonzalez-Mancebo et al., 2013; Fernández-Palacios et al., 2017). The species number of species by archipelago change (in respect to Gonzales-Mancebo et al., 2013) for Azores, increasing from 451 to 472 species, Madeira increasing from 461 to 519 and the Canary Islands increasing from 485 to 523 species.

Geographic background, data sampling and molecular markers: Criteria of selection

The phylogenetic datasets analyzed in the present Master Thesis have been extracted from information compiled from the literature or produced in the lab by the supervisor of the Master Thesis, Dr. Patiño. We follow three main criteria of selection for the selection of each phylogenetic dataset, as follows: (1) the inclusion of specimens of species native to or endemic to Macaronesia; (2) the consideration of a sampling that encompasses at least 60% of taxa in the neighboring regions or closely phylogenetic related taxa; and (3) the use of genetic markers that provide a relatively well resolved phylogeny, at least for the Macaronesian clade/s and their sister clade/s (i.e. bootstrap > 80% and/or posterior probabilities > 0.9). Based on these three criteria, we performed an exhaustive search on digital libraries of academic content, which include phylogenetic data from any of the species listed in Supplementary Material 3 (Summary of sequence information). Then, we carried out a more restrictive selection of the more than 500 articles initially downloaded, only considering phylogenetic studies that contain sequences from Macaronesian archipelagos, ending up with a selection of about 80 papers. Finally, we pruned our initial selection of papers to those that contain at least one sequence of any Macaronesian species under threat from archipelagos, according to the Red Lists of Madeira and the Canary Islands (Sim-Sim et al., 2014; Gonzales-Mancebo et al., 2012), and the European Red List of Mosses, Liverworts and Hornworts (Hodgetts et al. 2019). The endemic condition of each species selected was also checked and incorporated into our database Supplementary Material 2 (Endemic & Threatened species).

Following the three main criteria described before, the selection of genetic markers used on this Master Thesis, was made on the basis of their availability and suitability. For the nuclear regions, we employed nrITS or ITS, and in a few cases, we differentiated between ITS-1 and ITS-2. For the chloroplast genome, we used rps4, trnG, atpB or psbA, among others. Articles source was summarized on Supplementary Material 3 (Summary of sequence information). After performing the different filtering steps mentioned in the former section (Geographic background, data sampling and molecular markers: Criteria of selection), we downloaded 28 datasets, from which we finally had to discard 13 datasets due to different problems of sequence quality or misleading results obtaining therefore 15 datasets included on the present study by their quality standards. Once the selection of sequences was finished, we created a database with all the relevant information. The complete database is accessible available upon request to the supervisor of the Master Thesis (Dr. Patiño), and herein we provide a summary of such a database Supplementary Material 3 (Summary of sequence information).

Data analysis

- Sequence processing and phylogenetic analyses

The very first step was to compile the sequences from each dataset identified in the literature, or from alignments provided by the supervisor, Dr. Patiño and Dr. Vanderpoorten. We prepared the raw data on *Notepad ++* (available at https://notepad-plus-plus.org/download/v7.6.4.html) by organizing the sequences by molecular markers – i.e. we separated the nuclear and chloroplast markers, using a *"fasta"* format. Then, we used the program *Sequence matrix* (Meier et al., 2006) to concatenate the different markers of each dataset, annotating the order of the markers in the "*nexus*" files that were subsequently created. To align by hand, the different sequences, we used *PhyDE-1* (Müller et al., 2006; available at http://www.phyde.de/docu/docu.html). In order to obtain a suitable dataset without poorly aligned positions and divergent regions of DNA, the concatenated dataset was polished in *GBLOCKS-0.91b* (Castresana, 2000), using the default options, but changing only the allowed gap positions from none allowed gap positions to with half, to thus maintain a better percentage of the phylogenetic informative positions in the blocks recovered. In the case of the following datasets indicated by genera (*Lejeunea, Exsertotheca, Orthotrichum and Dicranum*), was necessary the adjustment of the parameter "*minimum number of sequences for a flank position"*, selecting the higher values to avoid the loss of high quantities of sequences information. Once finished the filtering steps of each alignment, we apply *FaBox* (Villesen, 2007), in order to select the unique haplotypes from all datasets uploaded to avoid redundant phylogenetic information, which could decrease the robustness of the inferences of our posterior analyses. We then rechecked visually each alignment in PhyDE-1.

Subsequently, the best-fitting partition scheme and substitution model for each partition identified were inferred in *PartitionFinder2.1.1* (Lanfear et al., 2012, 2016) on Cipres Science Gateway (available at https://www.phylo.org), using the greedy algorithm under a Bayesian information criteria for linked branch lengths. The partitions obtained are provided in supplementary material 4 (Evolution models & phylogenetic marker). Then, the best partition scheme was updated each nexus file accordingly.

Phylogenetic analyses and divergence times were estimated using Bayesian inference (BI). We ran strict clock and uncorrelated lognormal relaxed clock analyses of each species-level (i.e. interspecific) and population-level (i.e. intraspecific) molecular dataset respectively, using BEAST v.1.8 (Drummond et al., 2012). Because the inclusion of identical sequences results in many zero-length branches at the tip of the tree and can cause the model to oversplit the dataset (Reid & Carstens, 2012), we reduced our list of specimens to haplotypes using FaBox (see above). We ran BEAST analyses with the same best partitions scheme and substitutions models obtained in PartitionFinder. Two chains were run for a variable number of generations (from 50 to 100 million generations) and sampled every 20^4 generations under a speciation Birth-Death and a Yule speciation model for the species-level datasets, and under a Coalescent Constant Size and Exponential Growth model for the population-level datasets, respectively. Convergence and mixing of the two chains were assessed by checking that all parameters had reached stationarity and sufficient (> 200) effective sample sizes (ESS) using Tracer v.1.6 (Rambaut et al., 2014), and between 10% and 25% of the trees were discarded as burn-in, depending on the quality of the results. It is worthy to note that, given the difficulties encountered throughout the process and the quality of the resulting trees, we allowed values under 100 ESS for the datasets of *Exertotheca* and *Leucodon*. Based on Marginal likelihood estimates (MLEs) and Bayes factors, we selected the best combination of parameters for each dataset, which were assessed using path-sampling (PS, Lartillot & Philippe, 2006) and stepping-stone (SS, Xie et al., 2011) methods. The resulting MLEs were averaged across the two replicate runs to generate a single PS and SS value for each model. The obtained MLEs for each combination of parameters per dataset were ranked, and Bayes factors were then calculated. After discarding the burn-in steps, tree files from the two independent runs of the selected model were combined using LogCombiner 1.8.4 (Drummond et al., 2007) and the resulting maximum clade credibility (MCC) tree was summarized in TreeAnnotator 1.8.4 (Drummond et al., 2007) and viewed in FigTree v.1.4.4 (available on https://github.com/rambaut/figtree/releases).

In the significant absence of fossils in bryophytes, in particular in lineages occurring across the Macaronesian region (Vanderpoorten et al., 2010). Ultrametric trees were dated in this Master Thesis under two different absolute nucleotide substitution rates: (i) the substitution rate for the chloroplast regions was set to $5 \times 10{-}4$ subst./sites/my and SD of $1 \times 10{-}4$ with a normal prior; and (ii) the substitution rate for the nuclear regions was set to 0.00135± 0.005 substitutions/site/million years with a normal prior distribution and truncated with upper and lower bounds of 0.4-3 -- 8.3E−3 subst./sites/my (Bechteler et al., 2017). Therefore, datasets with nuclear and chloroplast sequence markers, must be unlinked for the options defining the substitution model and the clock model. Once the input files were ready to be processed, we ran the analysis in **BEAST v1.8.4** (Drummond et al., 2012), on ***Cipres Science Gateway***, taking between eight hours and one week of computation time, depending on the number of generations and number of terminals selected for each dataset.

- Ancestral area estimation

The MCC tree were used to perform an ancestral area estimation analysis, but first removing the outgroups. Distribution data of specimens was compiled from herbarium labels and each haplotype was assigned to one or several of the following main floristic regions traditionally considered in bryophyte biogeography and represented in Figure 1 (adapted from van der Wijk et al. 1959; and see Vanderpoorten et al. 2010). We identified by letters Azores (Z), Madeira (M), Canary Islands (C), Macaronesia (K), Palearctic (E), Paleotropic (F), Nearctic (U), Neotropic (S), Oceania (O) and Indo-Malaya (A). We performed ancestral area estimations across each dataset with the R package BioGeoBEARS (Matzke, 2014). In BioGeoBEARS, the Lagrange DEC model (Dispersal-Extinction-Cladogenesis) can be implemented, which includes dispersal (d) and extinction (e) as free parameters, and a model (DEC+J) that includes an additional parameter J, which takes founder-event speciation into account (see Matzke, 2014). Since different approaches to estimate ancestral areas are based on different assumptions, one can compare these two versions of the DEC model with a likelihood version of the Dispersal-Vicariance Analysis (DIVALIKE), and a likelihood version of the range evolution model of the Bayesian Binary Model (BAYAREA), with the option of also adding founder-event speciation to either of them. However, in a recent study, Ree & Sanmartín (2018) proposed that DEC+J might be a poor model of founder-event speciation and statistical comparisons of its likelihood with a pure DEC model may be inappropriate. Consequently, we refrained from implementing the DEC+J in the present study and focused on the classical versions of the three biogeographical models implemented in BioGeoBEARS (DEC, DIVALIKE, BAYAREA). These three models were estimated under a maximum likelihood framework, and compared in terms of how well they fitted the data using the Akaike's Information Criterion (AIC; Matzke 2013, 2014).

- Statistical analysis

On one hand, Kruskal–Wallis tests were carried out in order to test the differences in the time of colonization across the different conservation groups considered in the present study: endemic and threatened species. Post hoc (Nemenyi) test were then carried out, using the 'posthoc.kruskal.nemenyi.test' function in the PMCMRplus R package (available at https://cran.r-project.org/web/packages/PMCMRplus/index.html). All statistical analyses were carried out in R version 3.5.1 (2018-07-02) -- "Feather Spray" (Development Core Team at http://cran.r-project.org).

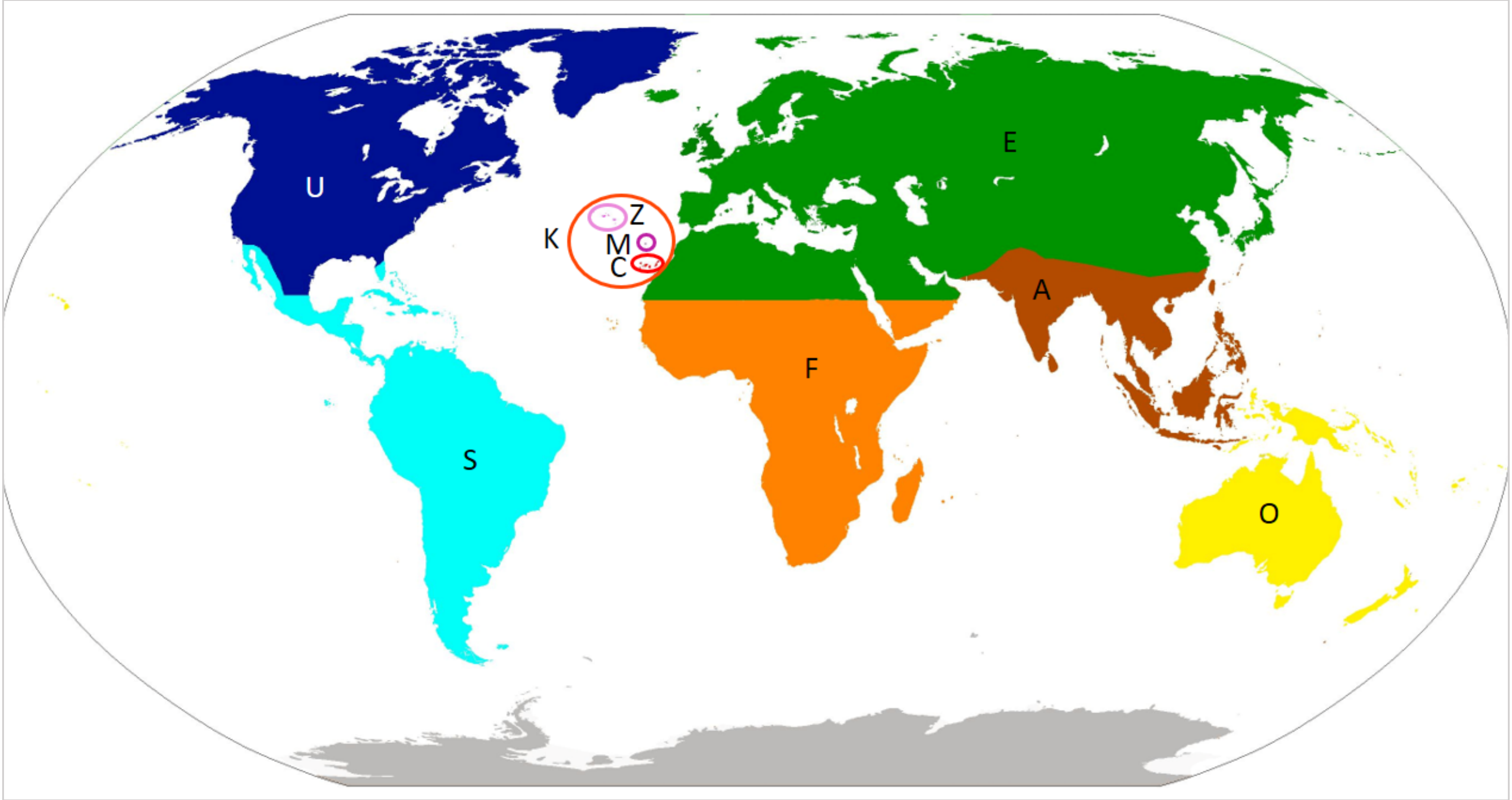

Figure 1: Geographic Floristic regions. *(A) Indo-Malaya, (C) Canary Islands, (E) Palearctic, (F) Paleotropic, (K) Macaronesia, (M) Madeira, (O) Oceania, (S) Neotropics, (U) Nearctic and (Z) Azores. The regionalization is an adaptation of the classification of the world biogeographic regions defined by van der Wijk et al. (1959) with subsequent refinements (Tan & Pócs, 2000) The color of each region corresponds to the pattern color established for figures and Supplementary Materials representing the results of the ancestral range reconstructions performed in the present Master Thesis.*

RESULTS

Following the different selection criteria, a total of 15 phylogenetic bryophyte datasets were included in the present study, adding up to 42 Macaronesian species, being 21 of them endangered species and 15 of them endemic (Table 1; Supplementary Material 2). These 42 taxa included 27 moss and 15 liverwort species, with 14 endangered mosses species and 7 endangered liverworts. In addition, only 4 endemic liverworts species were analyzed, in comparison with the 11 endemic mosses species included. From the original 744 download sequences (Supplementary Material 3), 618 phylogenetic sequences were finally analyzed, with 262 belonging to liverworts and 356 to mosses.

Model selection and dating analyses

Based on Bayes Factors (BFs) comparisons, a number of models with different combination of priors were selected for each dataset as the best-fit models (details provided in Supplementary Material 5). As a result, we obtained nine datasets for which the best-fitting model was Birth-Death process, five for the Yule process model and one for the Coalescent Constant Size model. To confirm the suitable selection of priors, we checked the correct mixing and convergence (ESS > 200; see Methods) of the two runs per dataset. All the analyses reached an appropriate level of convergence and good mixing, but we had three exceptions exemplified by the genera *Tetrastichium, Leucodon* and *Exsertotheca*. These three datasets failed to reach a good mixing. One potential problem of these three datasets could have been the low number of sequences coupled with the low variability of the markers used. We decided to included them in the meta-analysis using the best-fit combinations of priors according to our BFs approach because the resulting trees showed to have robust posterior probabilities values. However, the inferences resulting from these three datasets should be considered with caution.

Once obtained the MCC tree, we extracted the node ages and the 95% Highest Posterior Density [HPD] of the nodes from stem and crown branches, here interpreted as colonization and diversification events (see Table 1). Three species of the genus *Metzgeria* are the oldest lineages in our database, as the colonization of Macaronesia (see Figure 2.1) is dated between 22.2 Ma and 23.3 Ma as mean age of colonization for the three independent colonization events. Those three colonization events presented HPD very similar: 10.6-41.14 Ma; 9.6-42.3 Ma and 8.4-43.4 Ma, respectively, pointing to a considerable source of uncertainty in the dating analyses. Other old lineages are *Frullania microphyllla* with 20.1 Ma (HPD: 11.5-31.8 Ma) and *Amphidium mougeotii* with 19.2 Ma (HPD: 9.0-32.22 Ma). Conversely, the most recent events of colonization were inferred in *Rhynchostegiella trichophylla* with 0.44 Ma (HPD: 0.002-0.98 Ma)*,* *Odontoschisma denudatum* with 0.76 Ma (HPD: 0.02-2.34 Ma) and *Bryoxiphium madeirensis* with 0.77 Ma (HPD: 0.18-2 Ma). On the other hand, the oldest Macaronesian diversification events (Figure 2.2) were inferred to begin in *Metzgeria conjugata* with 16.98 Ma (HPD: 7.59-31.08 Ma) and *Metzgeria furcata with* 10.48 Ma (HPD: 4.2-20.93 Ma). The rest of diversification events were relativity recent, under 4 Ma, being 22 of them more recent than one million year (Table 1). *Rhynchostegiella bourgeana* showed the most recent diversification event (0.27 Ma, HPD: 0-0.9 Ma).

Species	Threat Category	Endemic Status	Probable Geographic Source (colonization)	Probable Geographic Source (MRCA)	Mean Colonization Age	HPD Colonization age	Posterior Probability	Mean Age Diversification Age	HPD Diversification Age	Posterior Probability	Number of Back-Colonization Events
Alleniella complanata	Not	Not	Palearctic	Palearctic	8.12	2.76-15.69	0.63	0.54	0.01-1.85	1	0
Amphidium mougeotii	Not	Not	Palearctic	Palearctic	19.26	9.08-32.22	0.34	0.87	0.004-3.00	1	0*
Amphidium lapponicum	Not	Not	Uncertain	Nearctic	1.64	0.31-4.09	0.94	_ _ _	_ _ _	_ _ _	0
Amphidium curvipes	Vulnerable[1]	Canary Islands & Madeira	Uncertain	Palearctic	11. 3252	4.63-19.50	0.93	2.11	0.52-4.65	1	0
Bryoxiphium madeirensis	Endangered[1]	Madeira	Nearctic	Nearctic	1.87	0.77-2.47	0.48	_ _ _	_ _ _	_ _ _	0
Bryoxiphium madeirensis	Endangered[1]	Madeira	Nearctic	Nearctic	0.77	0.18-1.69	0.12	_ _ _	_ _ _	_ _ _	0
Bryoxiphium madeirensis	Endangered[1]	Madeira	Nearctic	Nearctic	1.49	0.77-2.47	0.19	0.50	0.06-1.25	0.96	0
Dicranum canariense	Not	Not	Palearctic	Palearctic	3.12	1.23-5.78	1	1.39	0.37-3.10	0.99	0
Dicranum scottianum	Near Threatened[1]	Not	Palearctic	Palearctic	3.12	1.23-5.78	1	1.87	0.37-4.13	0.59	0
Dicranum scoparium (Madeira)	Vulnerable[2]	Not	Palearctic	Palearctic	1.95	0.64-3.85	0.06	1.57	0.35-2.95	1	0
Dicranum scoparium (Macaronesia)	Vulnerable[2]	Not	Palearctic	Palearctic	5.30	2.36-9.40	0.99	_ _ _	_ _ _	_ _ _	2
Exsertotheca intermedia	Near Threatened[1]	Macaronesia	Palearctic	Palearctic	6.56	2.47-12.25	1	1.44	0.20-3.59	1	0
Leucodon canariensis	Vulnerable[1] Near Threatened[2]	Macaronesia	Macaronesia	Macaronesia	7.04	3.40-12.68	1	0.38	0.02-1.06	1	0
Leucodon sciuroides	Not	Not	Palearctic	Palearctic	1.39	0.50-2.78	1	0.75	0.21-1.66	0.97	0
Leucodon treleasei	Near Threatened[1] Vulnerable[2]	Macaronesia	Macaronesia	Macaronesia	7.47	3.53-13.24	0.99	0.55	0.05-1.53	1	0
Lewinskya acuminata	Data Deficient[1]	Not	_ _ _	_ _ _	5.08	1.49-11.05	1	2.03	0.30-5.28	0.73	0
Neckera cephalonica	Not	Not	Palearctic	Palearctic	3.67	1.10-7.65	0.99	_ _ _	_ _ _	_ _ _	0
Neckera pumila	Not	Not	Palearctic	Palearctic	3.67	1.10-7.65	0.99	1.16	0.02-3.49	0.96	0

Orthotrichum handiense	Endangered[2]	Canary Islands	Nearctic	Nearctic	11.63	4.84-20.93	1	0.70	0.00-1.14	0.33	0
Orthotrichum shevockii	Not	Not	Nearctic	Nearctic	15.31	8.00-25.15	0.77	7.42	3.52-13.21	0.99	1
Pelekium atlanticum	Near Threatened[1] Vulnerable[2]	Macaronesia	Paleotropical	Neotropical	16.29	7.22-30.35	0.59	_ _ _	_ _ _	_ _ _	0
Rhynchostegiella azorica	Not	Azores	Uncertain	Palearctic	3.63	1.45-6.23	0.83	0.81	0.11-1.79	1	0
Rhynchostegiella bourgeana	Vulnerable[2]	Canary Islands	Uncertain	Macaronesia	6.70	3.37-11.07	1	0.27	0-0.90	1	0
Rhynchostegiella litorea	Near Threatened[2]	Not	Uncertain	Macaronesia	3.63	1.45-6.23	0.83	0.91	0.17-1.90	1	0
Rhynchostegiella pseudolitorea	Not	Canary Islands & Madeira	Uncertain	Palearctic	1.77	0.67-3.08	0.41	0.80	0.16-1.62	0.99	0
Rhynchostegiella spA	Not	Not	Uncertain	Uncertain	0.46	0.03-0.92	0.96	_ _ _	_ _ _	_ _ _	1
Rhynchostegiella teneriffae	Near Threatened[2]	Not	Macaronesia	Macaronesia	2.77	0.73-3.07	1	1.79	0.73-3.07	1	1
Rhynchostegiella trichophylla	Not	Canary Islands & Madeira	Macaronesia	Macaronesia	0.44	0.002-0.98	0.69	_ _ _	_ _ _	_ _ _	0
Tetrastichium fontanum	Near Threatened[1] Vulnerable[2]	Not	Neotropical	Neotropical	9.57	3.44-20.19	1	6.62	2.37-13.82	0.95	1
Tetrastichium virens	Critically endangered[2]	Not	Neotropical	Neotropical	9.57	3.44-20.19	1	4.54	0.83-10.93	0.91	0
Frullania calcarifera	Not	Not	Palearctic	Palearctic	6.05	3.22-9.63	0.99	4.29	2.08-7.54	0.90	0
Frullania microphyllla	Not	Not	Macaronesia	Macaronesia	20.18	11.50-31.85	1	3.51	1.39-6.86	1	0
Frullania polysticta	Near Threatened[1]	Macaronesia	Macaronesia	Macaronesia	10.04	5.44-16.04	0.46	1.31	0.46-2.73	1	0
Frullania sergiae	Vulnerable[1]	Madeira	Nearctic	Nearctic	6.05	3.22-9.63	0.99	_ _ _	_ _ _	_ _ _	0
Frullania tamarisci	Not	Not	Nearctic	Nearctic	4.67	2.64-7.56	0.99	2.80	1.29-4.88	1	0
Frullania teneriffae	Not	Not	Palearctic	Palearctic	9.77	5.82-15.07	0.99	2.50	1.12-4.44	1	0
Lejeunea flava	Vulnerable[2]	Not	Neotropical	Neotropical	4.75	2.67-7.57	1	3.46	9.34-20.90	0.75	0
Lejeunea laetevirens	Not	Not	Neotropical	Neotropical	4.88	1.84-9.38	1	_ _ _	_ _ _	_ _ _	0
Leptoscyphus azoricus	Not	Not	Neotropical	Neotropical	1.39	0.97-6.31	0.99	_ _ _	_ _ _	_ _ _	0

Leptoscyphus cuneifolius	Vulnerable[1]	Not	Palearctic	Palearctic	3.98	1.54-10.01	1	_ _ _	_ _ _	_ _ _	0
Metzgeria conjugata	Vulnerable[1,2]	Not	Nearctic	Nearctic	23.30	10.69-41.14	1	16.98	7.59-31.08	0.99	0
Metzgeria conjugata	Vulnerable[1,2]	Not	Nearctic	Nearctic	1.42	0.0001-3.21	0.19	_ _ _	_ _ _	_ _ _	0
Metzgeria furcata (Azores)	Not	Not	Nearctic	Nearctic	22.52	8.42-43.49	0.47	_ _ _	_ _ _	_ _ _	0
Metzgeria furcata (Canarias)	Not	Not	Palearctic	Palearctic	22.55	9.65-42.31	1	10.48	4.20-20.93	1	1
Odontoschisma denudatum	Endangered[1]	Not	Palearctic	Palearctic	0.76	0.02-2.34	1	_ _ _	_ _ _	_ _ _	0
Tylimanthus azoricus	Not	Azores	Neotropical	Neotropical	2.65	0.39-5.75	0.88	_ _ _	_ _ _	_ _ _	0
Tylimanthus madeirensis	Vulnerable[1]	Madeira	Neotropical	Neotropical	5.84	2.45-9.72	0.97	1.63	0.35-3.71	1	0

Table 1: Summary with the results of the dating analyses. *This table summarizes the results of the dating analyses for each of the Macaronesian species included in our datasets. alphabetically. In the column where the treat category is specified, we designed with (1) the references for the Madeiran Red-List and (2) the reference for the Canary Island Red-List, with no coincidence with the European Red List. Each colonization and diversification time correspond to the MCC trees represented in Supplementary Materials 7. MRCA: most recent common ancestor.*

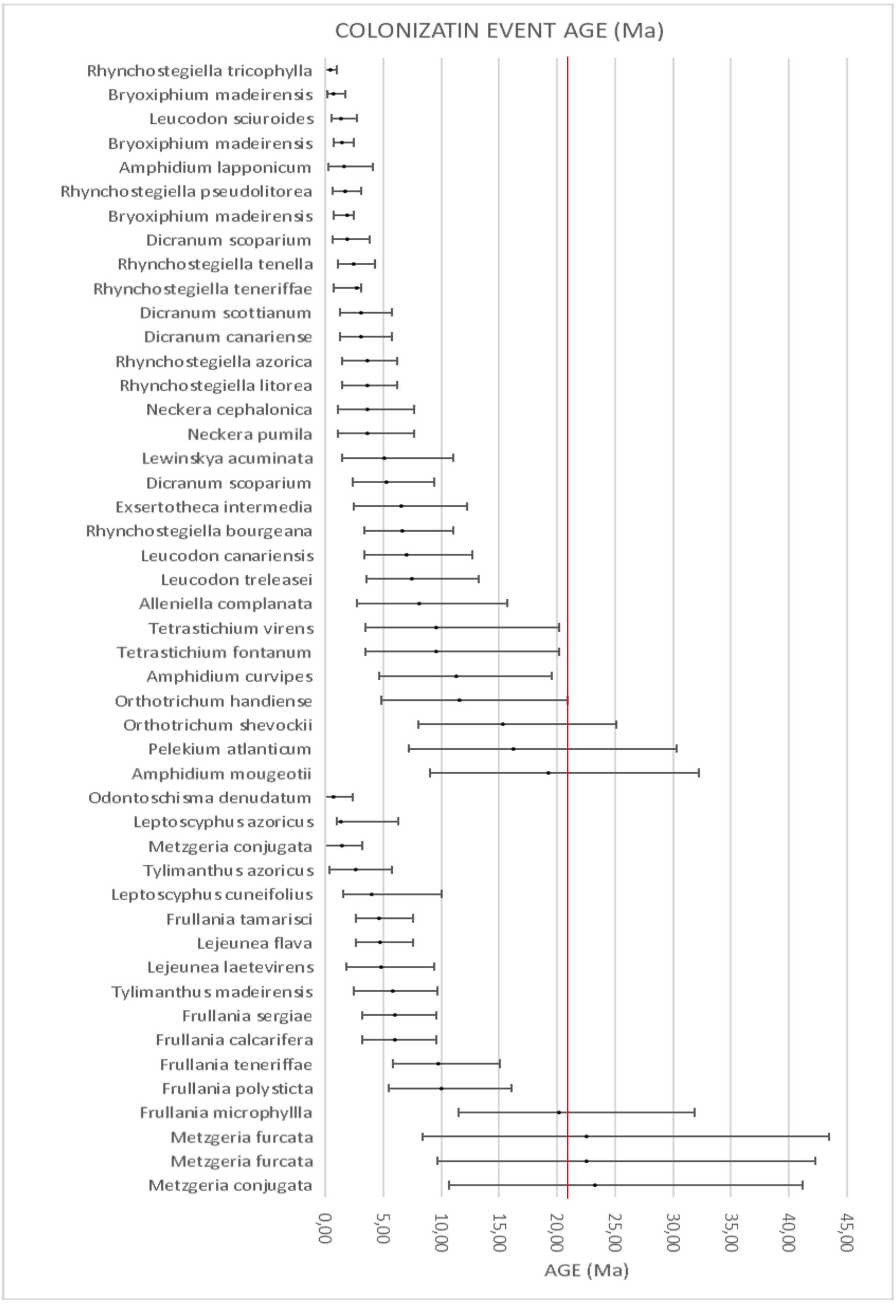

Figure 2.1: Dates of the colonization events of Macaronesia for the bryophyte species analyzed. *The estimated mean age of colonization events (i.e. stem age) of Macaronesia and HPD ranges are represented for each taxon analyzed (Ma). The dates correspond to the MCC trees summarized in Table 1 and Supplementary Material 7. The red line represent the oldest extant emerged Macaronesian island, Fuerteventura, included in the framework of the present study. Ma = million of years ago.*

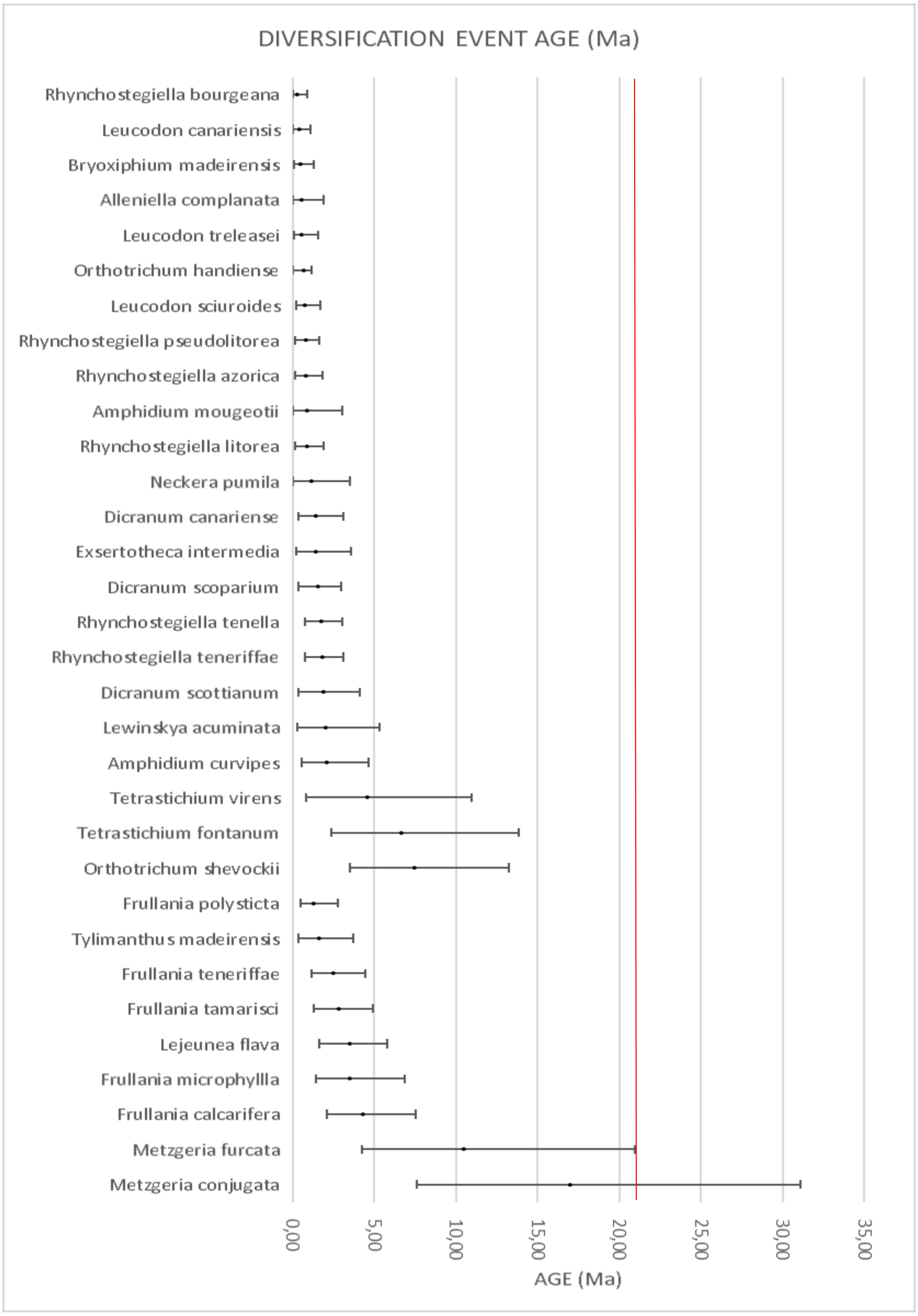

***Figure 2.2: Dates of the diversification events of the Macaronesian bryophyte species analyzed.** The estimated mean age of diversification events (i.e. crown age) of Macaronesian lineages and HPD ranges are represented for each taxon analyzed (Ma). The dates correspond to the MCC trees summarized in Table 1 and Supplementary Material 7. The red line represents the oldest extant emerged Macaronesian island, Fuerteventura, included in the framework of the present study. Ma = million of years ago.*

The tests performed to evaluate the differences in colonization time of the MRCA (crown clade) for endemic species and for threatened species resulted in the rejection of the second hypothesis, since there were no significant differences (Supplementary Material 8), between endemic and not endemic (Kruskal-Wallis chi-squared test = 0.024, df = 1, p-value = 0.877), and between threatened and not threatened species (Kruskal-Wallis chi-squared test = 0.110, df = 1, p-value = 0.740). However, due to the low number of presumably palaeoendemic species identified in the present study, basically *Frullania polysticta* and *Pelekium atlanticum*, we do not have statistical support to test the third hypothesis. Our analyses failed to confirm the relationships between the endemic and the threat condition, and with the colonization time, respectively.

Ancestral range estimation

Regarding the ancestral area estimation analyses, we had tested the fitting of the three different models implemented in *BioGeoBEARS*. We summarized the best-fit models for each dataset in Supplementary Material 6, which shows that the best-fitting model was DEC for five datasets and the DIVALIKE for ten datasets. We failed to select the BAYAREALIKE as the best-fit model for any of the datasets. Among all the parameters describing the performance of the results obtained in *BioGeoBEARS* analyses, we provided the log-likelihoods (lnL), number of parameters (n), rate of dispersal (d), rate of extinction (e) and Akaike´s information criterions for small sample size (AICc) of ancestral areas estimations in Supplementary Material 7; wherein the actual ancestral range reconstructions are provided.

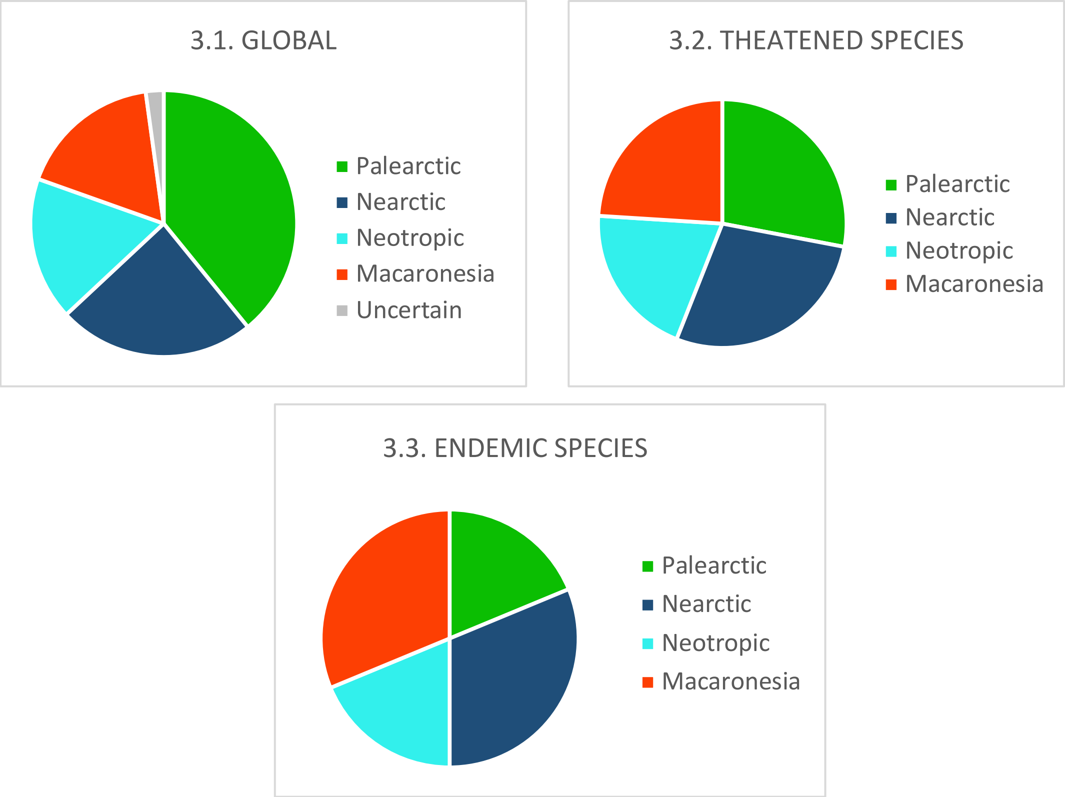

Figure 3: Source areas (in proportion) of Macaronesian bryophyte lineages as inferred study. *Figure 3.1 shows the source regions for the MRCA of the Macaronesian species represented in our Master Thesis datasets. Figure 3.2 shows the source regions for the MRCA of threatened Macaronesian species analyzed. Figure 3.3 shows the source regions for the MRCA of Macaronesian endemic species analyzed. Information on the species for each of those categories can be found in Table 1. The color pattern follows Figure 1.*

A total of 47 independent colonization events from mainland to Macaronesia, implying an average number of colonization events per species of 1.14, were inferred, as opposed to only eight independent back-colonization events from Macaronesia to mainland (Table 1). The ancestral ranges estimated by *BioGeoBEARS*, when looking at the nodes that provide information for the colonization event (i.e. stem clades) shows that the predominant pool species are inferred to be of Palearctic origin (15), followed by Nearctic (12), Neotropical (7) and Macaronesian (6) origins. We also obtained a high number of datasets with an inferred uncertain origin (7), so we looked into the MRCA (i.e. crown clade) to evaluate whether the levels of uncertainty were reduced. At the MRCA level, we found 18 cases of Palearctic, 11 cases of Nearctic, 8 cases of Neotropical, 8 cases of Macaronesian origin (Figure 3.1). We also present the same results, but organized by the functional groups defining the category of threat (Figure 3.2) and endemism (Figure 3.3.), obtaining similar results to the ones described for Figure 3.1.

We performed similar analyses but considering the main lineages of bryophytes, mosses (Figure 4) and liverworts (Figure 5), separately. Important differences between these two main groups of bryophytes observed were: (i) the highest dominance of the Palearctic element in mosses (Figure 4.1) in comparison with the strongest signature of Neotropical and Nearctic elements in liverworts (Figure 5.1); and (ii) these differences were in general applicable to the functional groups of threat and endemic species (Figures 4.2, 4.3, 5.2 and 5.3).

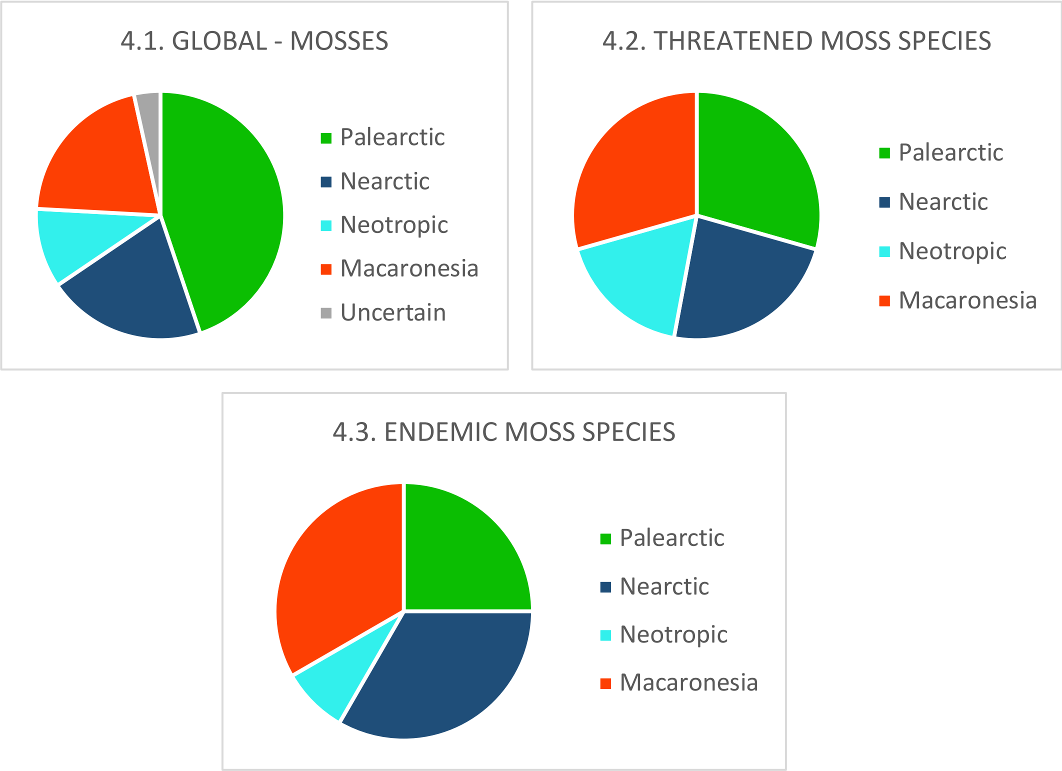

Figure 4: Source areas (in proportion) of Macaronesian Mosses lineages. *Figure 4.1 shows the source regions for the MRCA of the Macaronesian species represented in our Master Thesis datasets. Figure 4.2 shows the source regions for the MRCA of threatened Macaronesian species analyzed. Figure 4.3 shows the source regions for the MRCA of Macaronesian endemic species analyzed. Information on the species for each of those categories can be found in Table 1. The color pattern follows Figure 1.*

DISCUSION

Colonization and diversification in the Macaronesian archipelagos

According to our integrative dating approach, all the colonization events of Macaronesian bryophyte lineages, but three lineages belonging to the genus *Metzgeria*, were estimated under 21 Ma, and therefore, younger than Fuerteventura, the oldest island considered within our datasets (Fernández-Palacios et al., 2011). The results obtained from the datasets compiled in the present Master Thesis therefore seem to support the predominance of neoendemics,- i.e. the result of *in-situ* speciation-, within the Macaronesian flora, in agreement with our second hypothesis. The colonization times estimated in the present Mater thesis, however, does not allow us to completely rule out the existence of two palaeoendemics among the analyses species, *Frullania polysticta* and *Pelekium atlanticum*. These are linages whose estimated colonization times could match the estimated ages provide for different PalaeoMacaronesian islands (Fernández-Palacios et al., 2011), reinforcing their putative palaeoendemic condition. Furthermore, the age ranges defined by the HPD intervals from BEAST analyses in 12 of

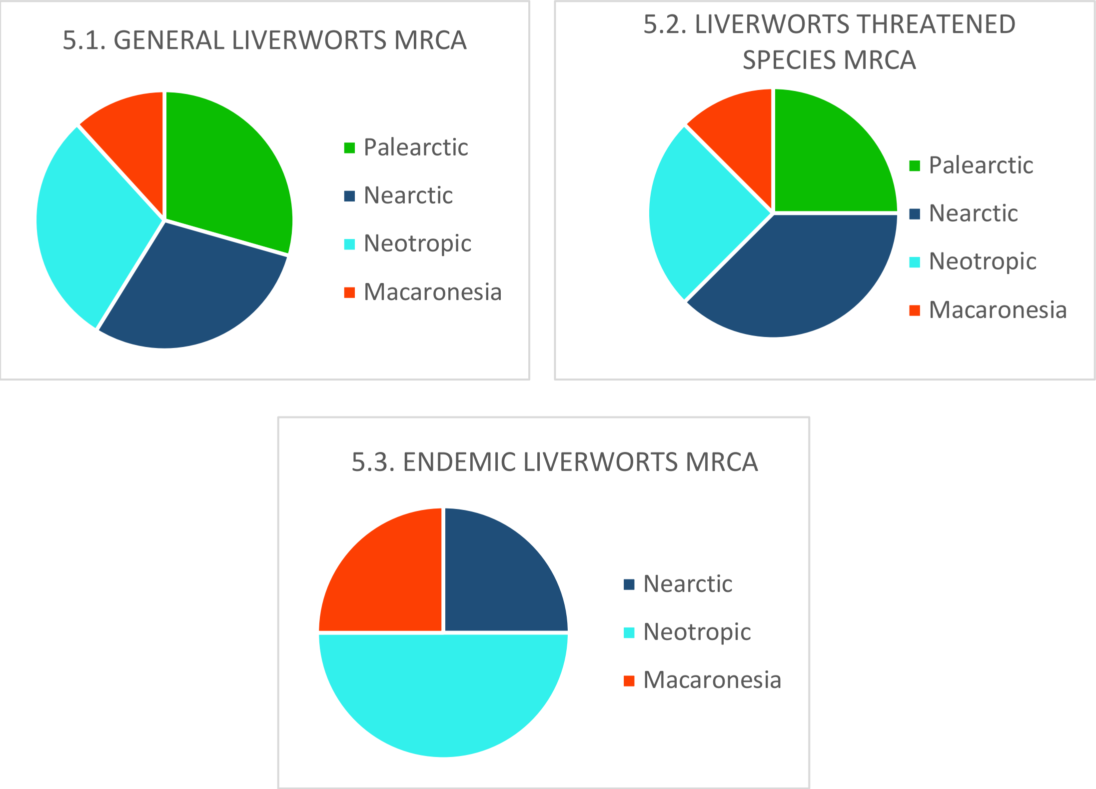

Figure 5: Source areas (in proportion) of Macaronesian Liverworts lineages as inferred in the present study. *Figure 5.1 shows the source regions for the MRCA of the Macaronesian species represented in our Master Thesis datasets. Figure 5.2 shows the source regions for the MRCA of threatened Macaronesian species analyzed. Figure 5.3 shows the source regions for the MRCA of Macaronesian endemic species analyzed. Information on the species for each of those categories can be found in Table 1. The color pattern follows Figure 1.*

the 47 colonization events reached time windows older than 21 Ma (as shown on Figure 3.1), but in non-endemic taxa mostly. This is the case of the three lineages of *Metzgeria*, whose upper bounds were about 40 Ma (HPD: 10.6-41.14 Ma; 9.6-42.3 Ma and 8.4-43.4 Ma), along with *Amphidium mougeotii* (HPD: 9.0-32.22 Ma). The limited number of palaeoendemics could be perhaps related to a more obvious fact, that is, that a relict taxon, which had a continental distribution in the past, could have gone extinct from the source region and colonized the island in a time more recent than 21 Ma. However, here, we followed the classic approach to designate a palaeoendemic (e.g. Vargas, 2007; Devos & Vanderpoorten, 2009), but acknowledging the limitations of such an approach.

Following the colonization and establishment on oceanic Islands, a number of bryophyte species exhibited diversification events on Macaronesia, at least according to the datasets that we compiled and show in Table 1. Specifically, 33 out of the 47 colonization events inferred from our datasets exhibit the presence of diversification events (Supplementary Material 7). Species such as *Exsertotheca intermedia, Alliela complanata or Leucodon canariensis* showed relatively high levels of genetic diversification across the Macaronesian archipelagos. In the case of *Rhynchostegiella azorica*, the beginning of the diversification in this Azorean endemic started about 0.81 Ma (HPD: 0.11-1.79), which matches the results of a previous analysis (Patiño et al., 2017). However, as mentioned for *Dicranum scoparium* where lineage diversification was strongly related to the extra-effort sampling (Lang et al., 2014; 2015), we should be aware that our results are sensitive to sampling bias. However two features make that our inferences on diversification are robust: first, we reduced each dataset to the haplotype level, obtaining for instance for the case of *D. scoparium* an estimated time for the beginning of the diversification in the insular clade of 1.57 Ma (HPD: 0.35-2.95 Ma). The beginning of the diversification events were thus estimated to have started less than 17 Ma. The three of the most recent diversification events inferred in our analyses were *Rhynchostegiella bourgeana* (0.27 Ma, HPD: 0-0.90 Ma), *Leucodon canariensis* (0.38 Ma, HPD: 0.02-1.06 Ma) and *Leucodon treleasei* (0.55 Ma, HPD: 0.05-1.53 Ma)*,* which have the common characteristic of being endemic species to Macaronesia. This evidence, along with the colonization event inferred to be of Macaronesian origin as well (stem clade in Table 1), points to their neoendemic condition. In summary, we do not have enough evidence to support our hypothesis that endemic species should be palaeoendemics more frequently than neoendemics. Conversely, our study provides support for a higher frequency of neoendemics and, at some extent, would support the results obtained by Kondraskov et al. (2015), pointing the establishment of most species in the Plio-Pleistocene and suggesting a massive species turnover before this time.

Source areas for the Macaronesian bryophyte flora

Our findings show strong Palearctic affinities within the group of species analyzed (Figure 3.1), based on the ancestral range estimations supporting a Palearctic origin for a number of species. In total 18 lineages were inferred to have a Palearctic origin, followed by 11 cases with a Nearctic origin, 8 cases for a Neotropical origins and 8 cases for a Macaronesian *in situ* speciation event. These results, which reinforce the Palearctic origin of a bulk of the Macaronesian bryophyte flora, do not suppose a definitive confirmation of the biogeographical pattern, as we have not tested a representative sampling of all Macaronesian bryophyte species, among other reasons. Based on pure floristic affinities of its non-vascular flora, Macaronesia was partitioned into two classified two groups: Cape Verde was nested within a Sub-Saharan African clade whereas the Azores, Madeira and the Canary Island were closely related to a Holarctic clade composed of European, North African and Asian assemblages (Vanderpoorten et al., 2007). This pattern mirrors the floristics affinities observed in Macaronesian angiosperms, mainly with the Mediterranean vascular flora (Carine et al., 2010). In turn, our results also support partially our first hypothesis on how potential distant species pools, in our case located in America (Nearctic and Neotropics depending on the species), seems to have played a crucial role in the assembly of the Macaronesia bryophyte flora, greatly thanks to the high LDD capabilities presumed for bryophytes. The pattern of exhibiting remote geographic sources is particularly relevant for species associated with different types of laurel forests, as previously hypothesized by Vanderpoorten et al. (2010).

As just a few examples, we corroborated the American species sources for Macaronesian species, such as the cases *Orthotrichum shevockii* (Vigalondo et al., 2019) and *O. handiense* (Patiño et al., 2013), which were both in our analyses and the respective former studies inferred to be of Nearctic origin. The phylogenetic inferences provided for the genus *Tylimanthus* in a former publication (Stech et al., 2006), supporting a Neotropical origin for *Tylimanthus madeirensis* and *Tylimanthus azoricus*, were reinforced by our analyses. Finally, it is remarkable the predominance of the Palearctic element for the inferred species sources of threatened species and endemic species (Figure 3), conversely to our initial presumptions. However, if we sum up the contributions of the Nearctic and Neotropics, then, the American affinities would arise as the predominant source region for the Macaronesian species included in the present Master Thesis. And this is particularly evident, for the case of the liverworts and, in particular, for threatened liverworts (Figure 5). This result therefore supports indirectly the recent observation that, despite being extremely efficient dispersers, bryophytes can exhibit limitations to disperse at scales over 100 km, which likely marks the limits of regional dispersal, beyond which an increasingly smaller proportion of spores can effectively travel (Vanderpoorten et al., 2019).

Macaronesia as a biogeographic crossroad

In general, the role of Macaronesia as a crossroad for its bryophyte flora is relatively logical and supported by the heterogeneity of the MRCA origins shown in the present Master Thesis (Figure 3). Former evidence of such a role of the Macaronesian islands has been provided for the angiosperm flora, with species sources having been inferred in the Eurosiberian, African, Indo-Malayan and South African regions, in addition to the principal Mediterranean affinities already mentioned above (Carine et al., 2010). The role of oceanic archipelagos as crossroads of different geographic species pool sources is not exclusive to Macaronesia. For instance, in the pacific Hawaiian archipelago, it has been recently demonstrated that the largest source category was widespread involving taxa that occur in at least several regions, followed by the Indo-Malayan and Neotropical regions, pointing to the tremendous heterogeneity in the geographic sources of the Hawaiian flora (Price et al., 2018).

Among our datasets, the concept of Macaronesia as a crossroad of propagules sources is best exemplified by our results on *Frullania*, among others. Our analysis suggest a Neotropical origin for *F. sergiae and F. tamarisci*, a Palearctic origin for *F. calcarifera* and *F. teneriffae* and a Macaronesian in situ speciation origin for *F. microphyllla* and *F. polysticta*. The original publication by Heinrichs et al. (Heinrichs et al., 2010), who did not perform quantitative biogeographical analyses, reached very different conclusions, establishing the origins of *Frullania azorica, F. polysticta and F. teneriffae* in the Nearctic, and of *F. sergiae, F. calcarifera* and *F. microphyllla* in the Palearctic.

These results, far for being a dead-end, are an incentive for conservation. Multiple colonization events along with back-colonization events from the Macaronesian islands to neighboring continental areas, and de novo colonization events of the mainland has been described for bryophyte flora (e.g. (Laenen et al., 2011; Patiño & Vanderpoorten, 2015; Patiño et al., 2016; Patiño et al., 2017) and reanalyzed and confirmed in this Master Thesis. At least, 7 new back-colonization events, not inferred before, were recorded in this Master Thesis increasing genetic biodiversity on the mainland. For instance, in the genus *Bryoxiphium*, we inferred other example of reverse colonization from Macaronesia to North America, inferring a total of three different back colonization events (Supplementary Material 7), increasing in one the total events described in a previous publication (Patiño et al, 2016).

<u>Remaining uncertainties and future research</u>

The majority of lineages have been well resolved, but there are limitations in our approach that need to be considered in the future steps of the initiative leaded by the Dr. Patiño and Dr. Vanderpoorten, in which this Master Thesis is framed.

The *first uncertainty* resides on the review nature of this Master Thesis, where we had to adapt our selection of datasets to the availability of phylogenetic information. In this context, we have faced problems related to the limitation in the sampling of both geographic regions and molecular markers that could have made the results of our analyses not as reliable as we would have wished in a few study cases, such as the genera *Tetrastichium* or *Lejeunea*. The increasing number of phylogenetic bryophyte publications that different research groups are currently working on will for sure turn upside this situation, by improving future inferences of the historical biogeography of the Macaronesian bryophyte flora. In this respect, it is promising the application of new molecular technologies (genomics) in bryology.

The second shortcoming is related to the differences observed between former publications and the results shown in the present Master Thesis. On the one hand, former studies focusing on *Odontoschisma* (Aranda et al., 2013) and *Metzgeria* (Fuselier et al., 2011) did not provide the split times of lineages for Macaronesian clades, despite having performed dating analyses, which prevent us of being able to carry out quantitative comparisons. On the other hand, we have found cases where the dating analyses provided significantly depart from each other. For instance, in *Bryoxiphium madeirense*, an earlier publication (Patiño et al., 2016) dated the colonization events approximately between 5-3 Ma, noticeably higher than our estimations (see Table 1). In this respect, the use of substitution rates has a strong and expected impact on the estimates (Villarreal & Renner 2014; Bechteler et al., 2017) and, due to the lack of fossils in bryophytes, the present Master Thesis calls for the need of an updated review on substitution rates across a broad variety of bryophyte clades, in order to be able to obtain more replicable and reliable phylogenetic-based divergence times.

Finally, perhaps, the main limitation resides in the fact that numerous lineages including many distinctive endemic genera and species have not had sufficient or any phylogenetic study to determine their ancestral origin. It seems very likely that we could not obtain enough evidence to test the second and third initial hypotheses appropriately, since the final sample of threatened and endemic species was not quite limited (21 of them endangered species and 15 of them endemic). Future research using more sophisticated techniques, such as population-level studies of widespread species and genomic approaches will help to clarify these questions.

Conservation implications

Macaronesian endangered bryophytes species are in a problematic situation for a number of reasons. First, their actual but also the potential occupancy area is often very restricted, given that habitat area on the Macaronesian islands as in other oceanic archipelagoes are limited by definition. Secondly, another important factor that affects many of the species analyzed in the present Master Thesis is the very restricted suitable areas of laurel forest, which continue to be threatened by different factors (Gonzales-Mancebo et al., 2012). As has been estimated by (Del Arco et al., 2010), the potential area of laurel forest has been reduced to less than 10% in the Canary Islands. In this respect, our results suggest that one of the main source regions displaying a role as the species pool for species associated with the laurel forest might be in the American continent (i.e. Nearctic and Neotropics), which is particularly notable for Macaronesian threatened species (Figure 3). In addition, adapting our first hypothesis, endangered liverworts species shows an apparent stronger relation to the American continent than endangered mosses species (Figures 4.2. and 5.2), which opens the door for the discussion of a potential criterium for prioritization based on the vicinity of propagule sources. Such a criterium might be used for prioritization in cases where, for instance, the effective population size and occupancy areas were equally limited.

The traditional perception of the Macaronesia as refugium of Palaeoendemism has been increasingly challenged. Oceanic Islands are not perceived anymore as biodiversity dead-ends (Carine et al., 2004; Heaney, 2007), as they represent dynamic refugia and migratory stepping-stones for effectively dispersive species (Hutsemekers et al., 2011). As mentioned earlier in this Discussion, our results provide support to this emergent paradigm and, for instance, for *Rhynchostegiella teneriffae* and *Metzgeria furcata* for the first case, and *Tetrastichium fontanum* for the second case, among others, provide support for the pattern of reverse colonization from the islands to the mainland and for *de novo* colonization of continental regions from islands (sensu Patiño & Vanderpoorten, 2015), respectively. An integrative management and conservation of insular territories should consider in future actions the prioritization of potential propagules areas that present high and singular levels of genetic diversity.

The present Master Thesis has been an attempt to unify and reanalyse a large portion of the available phylogenetic knowledge of threatened and endemic species in the Macaronesian region. Moreover, we failed to test the third hypothesis that threatened species should be more often neoendemics than palaeoendemics, greatly due to the low sampling size for palaeoendemics recognized in our database (n= 2). Therefore, the fact that all the threatened species included in this work are neoendemics is merely circumstantial and no strong conclusions should be drawn from these results. In conclusion, our work represents a small but significant step further, and much more is pending to be done in order to gain a more comprehensive understanding of the origins of the Macaronesian bryophyte flora, and their possible ramifications for the conservation and management of this valuable floristic element.

CONCLUSIONS

1. Throughout this Master Thesis, we have compiled a database based on research literature containing phylogenetic and biogeographic information of bryophyte species, mostly associated with laurel forest, where the category of threat and the status of endemism were considered.
2. We subjected the different datasets compiled to an integrative-quantitative biogeographical approach in order to answer a general question on what geographic origins of the Macaronesian bryophyte flora are.
3. In the 15 phylogenetic bryophyte datasets finally considered in the present Master Thesis, 262 and 356 sequences corresponded to liverworts and mosses, respectively, adding up to 42 Macaronesian species being 21 of them endangered species and 15 of them endemic. These 42 taxa included 27 moss and 15 liverwort species, with 14 endangered mosses and seven endangered liverwort species. In addition, our database included four endemic liverwort and 11 endemic moss species.
4. A total of 42 colonization events we retrieved from the phylogenies analyzed. The most important regions accounting for the origins of the Most Recent Common Ancestor (MRCA, crown clade) with 18 lineages was inferred to be the Palearctic, followed by 11 cases with a Nearctic origin, 8 cases with a Neotropical origin and 8 cases with a Macaronesian *in situ* speciation event, which reflects the strong heterogeneity in the MRCA origins and, therefore, the role of Macaronesia as a crossroad for its bryophyte flora.
5. Our findings support partially our first hypothesis on how potential distant species pools, in our case located in America (Nearctic and Neotropics depending on the species), seem to have played a crucial role in the assembly of the Macaronesia bryophyte flora, greatly thanks to their high LDD capabilities.
6. When liverworts and mosses were analyzed separately, we found important differences in their biogeographic origins. Among them, the highest dominance of the Palearctic element in mosses contrasted with the strongest signature of Neotropical and Nearctic elements in liverworts.
7. Our biogeographical inferences seem to support the predominance of neoendemics,- i.e. species that are the result of *in-situ* speciation-, within the Macaronesian bryophyte flora, in agreement with our second hypothesis.

8. We could not obtain enough evidence and statistical power to test the third initial hypothesis appropriately, since the final sample size for the number of inferred palaeondemics was quite limited.
9. Our results provide arguments to set up possible complementary criteria in order to establish priorities of conservation from the often biogeographical perspective, when species show similar levels of treat.
10. This Master Thesis represents a humble contribution to our understanding of the origins of the Macaronesian bryophyte flora, and their possible ramifications for the conservation and management of this valuable floristic element. Future research in this framework should consider aspects such as a more appropriated and comprehensive sampling strategy and the application of genomic technologies such as high-throughput restriction-site-associated DNA sequencing, which altogether will open avenues of research in order to not only reconstruct the historical biogeography of island bryophyte floras, but also to shed light into the evolutionary mechanisms underlying their evolutionary pathways.

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SUPPLEMENTARY MATERIAL 1:

Macaronesian unified checklist

SPECIES & SUBSPECIES	AZORES	CANARY ISLANDS	MADEIRA & SELVAGENS
Acanthocoleus aberrans	1	1	1
Acaulon fontiquerianum		1	
Acaulon mediterraneum		1	
Acaulon muticum		1	1
Acaulon triquetrum		1	1
Acrobolbus wilsonii	1		1
Adelanthus decipiens	1		1
Aloina aloides		1	1
Aloina ambigua	1	1	1
Aloina brevirostris		1	
Aloina humilis		1	
Aloina rigida	1	1	1
Alophosia azorica	1		1
Amblystegium confervoides	1		
Amblystegium serpens	1	1	
Amphidium lapponicum		1	
Amphidium mougeotii	1	1	1
Amphidium tortuosum		1	1
Anacolia webbii		1	1
Anastrophyllum minutum	1		
Andoa berthelotiana	1	1	1
Andreaea alpestris			1
Andreaea crassifolia		1	
Andreaea heinemannii		1	1
Andreaea rothii			1
Andreaea rupestris	1		1
Aneura pinguis	1	1	1
Anoectangium aestivum	1	1	1
Anomobryum julaceum	1	1	1

Anomodon viticulosus		1	
Anthoceros agrestis		1	1
Anthoceros caucasicus	1	1	1
Anthoceros punctatus	1	1	1
Antitrichia californica		1	1
Antitrichia curtipendula		1	1
Aphanolejeunea azorica	1		1
Aphanolejeunea madeirensis	1		1
Aphanolejeunea microscopica	1	1	1
Aphanolejeunea sintenisii	1	1	1
Archidium alternifolium	1	1	1
Asterella Africana	1	1	1
Athalamia spathysii		1	
Atrichum angustatum	1	1	1
Atrichum tenellum	1		
Atrichum undulatum	1	1	1
Aulacomnium androgynum		1	
Aulacomnium palustre	1		
Barbilophozia attenuate	1		
Barbula convolute	1	1	1
Barbula unguiculata	1	1	1
Bartramia pomiformis	1	1	1
Bartramia stricta	1	1	1
Bazzania azorica	1		
Bazzania trilobata			1
Blepharostoma trichophyllum	1		
Blindia acuta	1		1
Brachymenium notarisii	1	1	1
Brachytheciastrum dieckii		1	
Brachytheciastrum velutinum	1	1	1
Brachythecium albicans	1		1
Brachythecium mildeanum	1		
Brachythecium percurrens			1
Brachythecium rivulare	1	1	1

Brachythecium rutabulum	1	1	1
Brachythecium salebrosum	1	1	
Breutelia azorica	1		
Bryoerythrophyllum campylocarpum			1
Bryoerythrophyllum inaequalifolium	1	1	
Bryoerythrophyllum recurvirostrum		1	1
Bryoxiphium madeirense			1
Bryoxiphium norvegicum	1		
Bryum alpinum			1
Bryum apiculatum		1	
Bryum argenteum	1	1	1
Bryum caespiticium			1
Bryum canariense	1	1	1
Bryum capillare			1
Bryum cellular		1	
Bryum creberrimum	1		
Bryum dichotomum	1	1	1
Bryum donianum			1
Bryum dunense		1	
Bryum funckii		1	
Bryum gemmiferum		1	
Bryum gemmilucens		1	
Bryum gemmiparum	1	1	1
Bryum kunzei	1		
Bryum mildeanum	1		1
Bryum moravicum		1	
Bryum muehlenbeckii			1
Bryum pseudotriquetrum			1
Bryum radiculosum	1	1	1
Bryum rubens			1
Bryum ruderale	1	1	1
Bryum sauteri	1	1	1
Bryum subapiculatum	1	1	1
Bryum tenuisetum	1	1	

Bryum torquescens	1	1	1
Bryum valparaisense		1	
Bryum violaceum		1	
Calliergonella cuspidate	1	1	1
Calypogeia argute	1	1	1
Calypogeia azorica	1		1
Calypogeia azurea			1
Calypogeia fissa	1	1	1
Calypogeia integristipula	1		
Calypogeia muelleriana	1		1
Calypogeia neesiana	1		
Calypogeia sphagnicola	1	1	1
Calypogeia suecica	1	1	
Campylopus atrovirens	1		
Campylopus brevipilus	1		
Campylopus cygneus	1		
Campylopus flaccidus	1		
Campylopus flexuosus	1	1	1
Campylopus fragilis	1	1	1
Campylopus incrassatus	1		1
Campylopus introflexus	1	1	1
Campylopus pilifer	1	1	1
Campylopus pyriformis	1		1
Campylopus shawii	1		
Campylopus subulatus	1		
Campylostelium pitardii		1	
Campylostelium strictum		1	1
Cephalozia bicuspidata	1	1	1
Cephalozia catenulata			1
Cephalozia connivens	1		1
Cephalozia crassifolia	1		1
Cephalozia lunulifolia	1		1
Cephaloziella baumgartneri	1	1	1
Cephaloziella calyculata	1	1	

Cephaloziella dentata	1	1	1
Cephaloziella divaricata	1	1	1
Cephaloziella granatensis			1
Cephaloziella hampeana	1	1	1
Cephaloziella rubella	1	1	1
Cephaloziella stellulifera		1	1
Cephaloziella turneri	1	1	1
Ceratodon conicus		1	
Ceratodon purpureus	1	1	1
Cheilolejeunea cedercreutzii	1		
Cheilothela chloropus	1	1	
Chiloscyphus coadunatus	1	1	
Chiloscyphus fragrans	1	1	
Chiloscyphus minor	1		
Chiloscyphus pallescens	1		1
Chiloscyphus polyanthos	1		1
Chiloscyphus profundus	1	1	
Cinclidotus fontinaloides		1	1
Cirriphyllum crassinervium		1	1
Cirriphyllum piliferum	1		
Cladopodiella francisci	1		1
Cololejeunea minutissima	1	1	1
Cololejeunea schaeferi		1	1
Colura calyptrifolia	1	1	1
Conocephalum conicum	1	1	1
Conocephalum salebrosum	1		
Corsinia coriandrina	1	1	1
Cratoneuron filicinum		1	1
Crossidium aberrans		1	
Crossidium crassinerve		1	1
Crossidium davidai		1	
Crossidium geheebii		1	
Crossidium squamiferum		1	1
Cryphaea heteromalla	1	1	

Cryptoleptodon longisetus			1
Ctenidium molluscum	1	1	
Cyclodictyon laetevirens	1	1	1
Cynodontium bruntonii	1	1	
Daltonia stenophylla	1		
Daltonia stenophylla			1
Dialytrichia fragilifolia			1
Dialytrichia mucronata	1	1	1
Dichodontium flavescens			1
Dichodontium pellucidum			1
Dicranella heteromalla	1	1	1
Dicranella howei	1	1	1
Dicranella humilis			1
Dicranella rufescens			1
Dicranella schreberiana	1		
Dicranella staphylina		1	
Dicranella subulata	1		
Dicranella varia	1	1	1
Dicranoweisia cirrata	1	1	1
Dicranoweisia crispula	1		
Dicranum bonjeanii	1		
Dicranum canariense	1	1	1
Dicranum flagellare	1	1	1
Dicranum fuscescens			1
Dicranum majus	1		
Dicranum montanum			1
Dicranum scoparium	1	1	1
Dicranum scottianum	1		1
Didymodon acutus	1	1	1
Didymodon australasiae		1	
Didymodon fallax		1	1
Didymodon insulanus	1	1	1
Didymodon luridus	1	1	1
Didymodon nicholsonii		1	

Didymodon rigidulus	1	1	1
Didymodon sicculus		1	
Didymodon tophaceus	1	1	1
Didymodon umbrosus		1	
Didymodon vinealis	1	1	1
Diphyscium foliosum	1	1	1
Diplophyllum albicans	1	1	1
Ditrichum flexicaule			1
Ditrichum pallidum	1		
Ditrichum punctulatum	1		1
Ditrichum pusillum		1	
Ditrichum subulatum	1	1	1
Drepanolejeunea hamatifolia	1	1	1
Dryptodon decipiens		1	
Dryptodon torquatus		1	
Dryptodon trichophyllus		1	
Dumortiera hirsute	1	1	1
Echinodium prolixum			1
Echinodium renauldii	1		
Echinodium setigerum			1
Echinodium spinosum		1	1
Encalypta streptocarpa		1	
Encalypta vulgaris		1	1
Entosthodon attenuates	1	1	1
Entosthodon commutatus		1	
Entosthodon convexus		1	1
Entosthodon durieui		1	
Entosthodon fascicularis		1	1
Entosthodon krausei			1
Entosthodon kroonkurk		1	
Entosthodon longicolle		1	
Entosthodon muhlenbergii	1	1	1
Entosthodon obtusus	1	1	1
Entosthodon pulchellus	1	1	1

Entosthodon schimperi		1	
Ephemerum cohaerens	1		
Ephemerum serratum			1
Epipterygium tozeri	1	1	1
Eucladium verticillatum	1	1	1
Eurhynchium striatum	1		1
Exormotheca pustulosa	1	1	1
Fabronia pusilla		1	1
Fissidens adianthoides	1	1	1
Fissidens asplenioides	1	1	1
Fissidens azoricus	1		
Fissidens bryoides	1	1	1
Fissidens coacervatus	1	1	1
Fissidens crassipes	1	1	1
Fissidens crispus	1	1	1
Fissidens curvatus	1	1	1
Fissidens dubius	1	1	1
Fissidens exilis		1	
Fissidens fontanus			1
Fissidens gracilifolius			1
Fissidens luisieri			1
Fissidens microstictus			1
Fissidens monguillonii	1		1
Fissidens nobreganus			1
Fissidens ovatifolius		1	1
Fissidens polyphyllus		1	1
Fissidens pusillus	1		1
Fissidens rivularis	1	1	1
Fissidens serratus	1	1	1
Fissidens serrulatus	1	1	1
Fissidens sublimbatus		1	
Fissidens sublinaefolius	1		
Fissidens sublineaefolius			1
Fissidens taxifolius	1	1	1

Fissidens viridulus	1	1	1
Fontinalis antipyretica	1	1	1
Fossombronia angulosa	1	1	1
Fossombronia caespitiformis	1	1	1
Fossombronia echinata	1	1	1
Fossombronia husnotii			1
Fossombronia pusilla	1	1	1
Frullania azorica	1	1	1
Frullania dilatata		1	1
Frullania ericoides		1	1
Frullania fragilifolia	1	1	1
Frullania microphyllla	1	1	1
Frullania polysticta		1	1
Frullania sergiae			1
Frullania tamarisci	1	1	1
Frullania teneriffae	1	1	1
Funaria hygrometrica	1	1	1
Funariella curviseta		1	
Geocalyx graveolens	1		1
Gigaspermum mouretii		1	
Glyphomitrium daviesii	1		1
Gongylanthus ericetorum	1	1	1
Goniomitrium seroi		1	
Grimmia anodon		1	
Grimmia arenaria			1
Grimmia cribosa		1	
Grimmia crinite		1	
Grimmia curviseta		1	
Grimmia decipiens			1
Grimmia donniana			1
Grimmia elongate	1		
Grimmia funalis		1	1
Grimmia hartmanii	1		
Grimmia incurve	1		

Grimmia laevigata	1	1	1
Grimmia lisae	1	1	1
Grimmia longirostris		1	
Grimmia montana	1	1	1
Grimmia nutans		1	
Grimmia orbicularis		1	1
Grimmia ovalis		1	1
Grimmia pulvinata	1	1	1
Grimmia ramondii		1	1
Grimmia tergestina		1	
Grimmia torquata			1
Grimmia trichophylla			1
Grimmia ungeri		1	
Gymnocolea inflate	1	1	1
Gymnostomum aeruginosum		1	1
Gymnostomum calcareum	1	1	1
Gymnostomum viridulum	1	1	1
Gyroweisia reflexa		1	1
Gyroweisia tenuis	1		1
Habrodon perpusillus		1	1
Harpalejeunea molleri	1	1	1
Hedwigia ciliata		1	1
Hedwigia stellate		1	1
Herbertus dicranus	1		
Herbertus sendtneri	1		
Herzogiella striatella	1		
Heterocladium flaccidum	1		
Heterocladium heteropterum	1	1	1
Heterocladium wulfsbergii	1	1	1
Heteroscyphus denticulatus	1	1	1
Homalia lusitanica	1	1	1
Homalia webbiana	1	1	1
Homalothecium aureum		1	1
Homalothecium lutescens		1	

Homalothecium mandonii		1	
Homalothecium sericeum	1	1	1
Hookeria lucens	1		1
Hygroamblystegium fluviatile	1		1
Hygroamblystegium humile	1		1
Hygroamblystegium tenax	1	1	1
Hygroamblystegium varium	1	1	1
Hygrobiella laxifolia	1		1
Hygrohypnum luridum	1		
Hylocomium splendens	1	1	1
Hymenostylium recurvirostrum		1	1
Hyocomium armoricum	1		1
Hypnum andoi	1	1	
Hypnum cupressiforme	1	1	1
Hypnum imponens	1		
Hypnum jutlandicum	1	1	1
Hypnum uncinulatum	1	1	1
Leptophascum leptophyllum			1
Imbribryum alpinum	1	1	
Isopterygiopsis pulchella			1
Isopterygium tenerum	1		
Isothecium algarvicum		1	1
Isothecium alopecuroides	1	1	
Isothecium myosuroides	1	1	1
Isothecium prolixum	1		
Jamesoniella rubricaulis	1		
Jubula hutchinsiae	1	1	1
Jungermannia atrovirens	1	1	1
Jungermannia callithrix	1	1	1
Jungermannia gracillima	1	1	1
Jungermannia hyaline	1	1	1
Jungermannia leiantha		1	1
Jungermannia pumila	1	1	1
Kiaeria blyttii	1		

Kindbergia praelonga	1	1	1
Kurzia pauciflora	1		1
Leiocolea heterocolpos		1	
Leiocolea turbinate		1	
Lejeunea canariensis		1	1
Lejeunea cavifolia		1	1
Lejeunea eckloniana	1	1	1
Lejeunea flava	1	1	1
Lejeunea hibernica	1		1
Lejeunea laetevirens		1	
Lejeunea lamacerina	1	1	1
Lejeunea mandonii		1	1
Lejeunea patens	1		1
Lepidozia cupressina	1	1	1
Lepidozia pearsonii	1		
Lepidozia reptans	1		1
Lepidozia stuhlmannii	1		
Leptobarbula berica	1		1
Leptobryum pyriforme	1	1	1
Leptodictyum riparium	1	1	1
Leptodon longisetus		1	
Leptodon smithii		1	1
Leptodontium flexifolium			1
Leptophascum leptophyllum	1	1	
Leptoscyphus azoricus	1		
Leptoscyphus cuneifolius	1		1
Lescuraea mutabilis		1	
Leskea polycarpa		1	
Leucobryum albidum	1	1	
Leucobryum glaucum	1	1	1
Leucobryum juniperoideum	1		1
Leucodon canariensis	1	1	1
Leucodon sciuroides	1	1	1
Leucodon treleasei	1	1	1

Loeskeobryum brevirostre	1		
Lophocolea bidentate			1
Lophocolea fragrans			1
Lophocolea heterophylla			1
Lophocolea minor			1
Lophozia bantriensis			1
Lophozia bicrenata	1	1	1
Lophozia excise		1	
Lophozia heterocolpos			1
Lophozia incisa	1		
Lophozia longiflora	1		
Lophozia sudetica			1
Lophozia ventricosa	1		
Lunularia cruciate	1	1	1
Mannia androgyna	1	1	1
Mannia fragans			1
Marchantia paleacea	1	1	1
Marchantia polymorpha	1	1	1
Marchesinia mackaii	1	1	1
Marsupella adusta	1		1
Marsupella emarginata	1	1	1
Marsupella funckii	1	1	1
Marsupella profunda	1	1	1
Marsupella sparsifolia	1		
Marsupella sphacelata	1		
Marsupella sprucei			1
Metzgeria conjugata		1	1
Metzgeria fruticulosa			1
Metzgeria furcata	1	1	1
Metzgeria leptoneura	1	1	1
Metzgeria temperate		1	1
Microbryum davallianum		1	1
Microbryum starckeanum		1	1
Microcampylopus laevigatus	1	1	1

Microlejeunea ulicina	1	1	1
Mnioloma fuscum	1		
Mnium hornum	1		1
Mylia taylorii	1		
Myurium hochstetteri	1	1	1
Nardia geoscyphus	1	1	1
Nardia scalaris	1	1	1
Neckera cephalonica	1	1	1
Neckera complanata	1	1	1
Neckera crispa	1	1	1
Neckera intermedia	1	1	1
Neckera menziesii		1	
Neckera pennata		1	
Neckera pumila	1	1	1
Nobregaea latinervis			1
Nowellia curvifolia	1		1
Odontoschisma denudatum	1		1
Odontoschisma prostratum	1		1
Oedipodiella australis		1	1
Orthodontium gracile			1
Orthodontium pellucens		1	1
Orthotrichum acuminatum		1	
Orthotrichum affine		1	1
Orthotrichum alpestre		1	
Orthotrichum anomalum		1	
Orthotrichum cupulatum		1	1
Orthotrichum diaphanum	1	1	1
Orthotrichum handiense		1	
Orthotrichum lyellii		1	1
Orthotrichum pallens			1
Orthotrichum patens		1	
Orthotrichum pumilum		1	
Orthotrichum rupestre		1	1
Orthotrichum striatum		1	

Orthotrichum tenellum	1	1	1
Oxymitra incrassata		1	
Oxyrhynchium hians		1	
Oxyrhynchium pumilum		1	
Oxyrhynchium schleicheri		1	
Oxyrhynchium speciosum		1	
Oxyrrhynchium hians	1		1
Oxyrrhynchium pumilum	1		1
Oxyrrhynchium schleicheri			1
Oxyrrhynchium speciosum	1		1
Pallavicinia lyellii	1		1
Palustriella commutata			1
Palustriella falcata			1
Paraleucobryum longifolium			1
Pelekium atlanticum		1	1
Pelekium minutulum			1
Pellia endiviifolia			1
Pellia epiphylla	1		1
Phaeoceros carolinianus	1	1	1
Phaeoceros laevis	1	1	1
Phascum cuspidatum			1
Philonotis arnellii	1		1
Philonotis caespitosa	1	1	
Philonotis calcarea	1	1	
Philonotis fontana	1	1	1
Philonotis hastate	1		
Philonotis marchica	1		1
Philonotis rigida	1	1	1
Philonotis tomentella	1	1	
Phymatoceros bulbiculosus	1	1	1
Physcomitrium pyriforme	1	1	1
Plagiochasma rupestre	1	1	1
Plagiochila bifaria	1	1	1
Plagiochila exigua	1	1	1

Plagiochila longispina	1		
Plagiochila maderensis		1	1
Plagiochila papillifolia	1		
Plagiochila porelloides		1	1
Plagiochila punctata	1	1	1
Plagiochila retrorsa	1		1
Plagiochila spinulosa		1	1
Plagiochila stricta		1	1
Plagiochila virginica		1	1
Plagiomnium affine		1	1
Plagiomnium rostratum	1	1	1
Plagiomnium undulatum	1	1	1
Plagiothecium denticulatum			1
Plagiothecium nemorale	1	1	1
Plagiothecium succulentum	1	1	1
Plasteurhynchium meridionale	1	1	1
Plasteurhynchium striatulum		1	
Platyhypnidium riparioides	1	1	1
Pleuridium acuminatum	1	1	1
Pleuridium subulatum	1	1	1
Pleurozium schreberi	1		1
Pogonatum aloides	1	1	1
Pogonatum nanum	1	1	1
Pogonatum urnigerum	1	1	1
Pohlia andalusica	1		
Pohlia annotina	1	1	1
Pohlia bulbifera	1		
Pohlia cruda	1	1	
Pohlia elongate		1	1
Pohlia melanodon	1	1	
Pohlia nutans	1		1
Pohlia proligera	1		1
Pohlia wahlenbergii		1	
Polytrichastrum formosum	1	1	1

Polytrichum commune	1	1	1
Polytrichum juniperinum	1	1	1
Polytrichum piliferum	1	1	1
Porella arboris-vitae		1	
Porella canariensis	1	1	1
Porella cordaeana		1	1
Porella inaequalis			1
Porella obtusata	1	1	1
Porella platyphylla		1	
Pseudephemerum nitidum	1		
Pseudocrossidium hornschuchianum	1	1	
Pseudocrossidium revolutum	1	1	1
Pseudoscleropodium purum	1	1	1
Pseudotaxiphyllum elegans	1	1	1
Pseudotaxiphyllum laetevirens	1		1
Pterigynandrum filiforme		1	1
Pterogonium gracile	1	1	1
Pterygoneurum ovatum			1
Pterygoneurum subsessile		1	
Ptychomitrium nigrescens	1	1	1
Ptychomitrium polyphyllum	1	1	1
Ptychostomum bornholmense		1	
Ptychostomum capillare	1	1	
Ptychostomum donianum	1	1	
Ptychostomum imbricatulum	1	1	
Ptychostomum pallens		1	
Ptychostomum pallescens		1	
Ptychostomum pseudotriquetrum	1	1	
Ptychostomum rubens	1	1	
Pylaisia polyantha		1	
Pyramidula tetragona		1	
Racomitrium aciculare	1	1	1
Racomitrium aquaticum	1	1	1
Racomitrium ellipticum		1	

Racomitrium elongatum	1		1
Racomitrium ericoides	1		
Racomitrium fasciculare	1		1
Racomitrium heterostichum	1	1	1
Racomitrium lanuginosum	1	1	1
Radula aquilegia	1	1	1
Radula carringtonii	1	1	1
Radula complanata	1		
Radula holtii	1	1	1
Radula jonesii		1	1
Radula lindenbergiana	1	1	1
Radula nudicaulis	1		1
Radula wichurae	1	1	1
Reboulia hemisphaerica	1	1	1
Rhabdoweisia crispata		1	
Rhabdoweisia fugax	1	1	1
Rhamphidium purpuratum	1	1	1
Rhizomnium punctatum	1		1
Rhynchostegiella bourgeana	1	1	
Rhynchostegiella curviseta	1		1
Rhynchostegiella durieui	1		1
Rhynchostegiella litorea		1	1
Rhynchostegiella macilenta		1	1
Rhynchostegiella tenella	1		1
Rhynchostegiella teneriffae		1	1
Rhynchostegiella trichophylla		1	
Rhynchostegium confertum	1	1	1
Rhynchostegium megapolitanum	1	1	1
Rhynchostegium murale		1	
Rhytidiadelphus loreus	1		1
Rhytidiadelphus squarrosus	1		1
Rhytidiadelphus subpinnatus	1		
Rhytidiadelphus triquetrus			1
Riccardia chamedryfolia	1	1	1

Riccardia incurvata			1
Riccardia latifrons	1		1
Riccardia multifidi	1	1	1
Riccardia palmate	1		1
Riccia atlantica			1
Riccia atromarginata		1	1
Riccia beyrichiana	1		
Riccia bicarinata		1	
Riccia bifurca		1	1
Riccia boumanii		1	
Riccia cavernosa		1	1
Riccia ciliata		1	1
Riccia ciliifera		1	1
Riccia crinite		1	
Riccia crozalsii	1	1	1
Riccia crystallina	1	1	1
Riccia glauca	1	1	
Riccia gougetiana		1	1
Riccia huebeneriana	1		
Riccia lamellose		1	1
Riccia ligula	1	1	
Riccia macrocarpa		1	1
Riccia nigrella	1	1	1
Riccia papillosa		1	
Riccia sorocarpa	1	1	1
Riccia subbifurca	1	1	1
Riccia trabutiana	1	1	1
Riccia warnstorfii	1		1
Riella affinis		1	
Riella cossoniana		1	
Riella notarisii		1	
Saccogyna viticulosa	1	1	1
Sanionia uncinata		1	
Scapania compacta	1	1	1

Scapania curta	1	1	1
Scapania gracilis	1	1	1
Scapania nemorea	1	1	1
Scapania paludosa	1		
Scapania scandica	1		
Scapania subalpine			1
Scapania umbrosa			1
Scapania undulata	1	1	1
Schistidium agassizii	1		1
Schistidium apocarpum	1	1	1
Schistidium confertum		1	
Schistidium flaccidum		1	
Schistidium frigidum		1	
Schistidium rivulare	1		1
Schistidium strictum			1
Sciuro-hypnum plumosum	1	1	1
Sciuro-hypnum populeum	1		
Scleropodium cespitans		1	
Scleropodium touretii	1	1	1
Scopelophila ligulata	1	1	
Scorpiurium circinatum	1	1	1
Scorpiurium deflexifolium		1	1
Sematophyllum substrumulosum	1	1	1
Southbya nigrella		1	1
Southbya tophacea	1	1	1
Sphaerocarpos michelii		1	
Sphaerocarpos texanus	1	1	
Sphagnum affine	1		
Sphagnum auriculatum	1		1
Sphagnum capillifolium	1		
Sphagnum centrale	1		
Sphagnum compactum	1	1	1
Sphagnum cuspidatum	1		
Sphagnum girgensohnii	1		

Sphagnum inundatum	1		
Sphagnum magellanicum	1		
Sphagnum nitidulum	1		
Sphagnum palustre	1		
Sphagnum papillosum	1		
Sphagnum recurvum	1		
Sphagnum rubellum	1		
Sphagnum squarrosum	1		
Sphagnum subnitens	1		1
Splachnobryum obtusum	1		
Syntrichia bogotensis			1
Syntrichia fragilis		1	1
Syntrichia laevipila	1	1	1
Syntrichia minor		1	
Syntrichia montana		1	
Syntrichia norvegica			1
Syntrichia papillosa		1	
Syntrichia princeps		1	1
Syntrichia ruralis	1	1	1
Syntrichia virescens		1	
Targionia hypophylla	1	1	1
Targionia lorbeeriana	1	1	1
Telaranea azorica	1	1	
Telaranea europaea	1	1	1
Tetrastichium fontanum	1	1	1
Tetrastichium virens	1	1	1
Thamnobryum alopecurum	1	1	1
Thamnobryum fernandesii			1
Thamnobryum maderense		1	1
Thamnobryum rudolphianum	1		
Thuidiopsis sparsa			1
Thuidium delicatulum	1		
Thuidium tamariscinum	1		1
Timmiella anomala		1	

Timmiella barbuloides	1	1	1
Timmiella flexiseta		1	
Tortella alpicola		1	
Tortella bambergeri		1	
Tortella flavovirens	1	1	1
Tortella fragilis	1	1	
Tortella humilis			1
Tortella inflexa	1	1	
Tortella limbata		1	1
Tortella nitida	1	1	1
Tortella squarrosa	1	1	
Tortella tortuosa	1	1	1
Tortula acaulon		1	
Tortula ampliretis		1	
Tortula atrovirens	1	1	1
Tortula bogosica	1	1	
Tortula bolanderi		1	1
Tortula brevissima		1	
Tortula canescens	1	1	1
Tortula cuneifolia	1	1	1
Tortula inermis		1	
Tortula Israelis		1	
Tortula lanceolata			1
Tortula lindbergii		1	
Tortula marginata	1	1	1
Tortula muralis	1	1	1
Tortula pallida		1	
Tortula protobryoides		1	
Tortula revolvens	1	1	
Tortula solmsii	1	1	1
Tortula subulata		1	1
Tortula truncate	1	1	1
Tortula vahliana	1	1	
Tortula viridifolia		1	

Trematodon perssoniorum	1		
Trichocolea tomentella	1		
Trichodon cylindricus		1	
Trichostomum brachydontium	1	1	1
Trichostomum crispulum	1	1	1
Trichostomum tenuirostre			1
Trichostomum triumphans	1		1
Tritomaria exsecta		1	1
Tylimanthus laxus	1		
Tylimanthus madeirensis			1
Ulota calvescens	1	1	1
Ulota crispa	1	1	1
Warnstorfia fluitans	1	1	
Weissia brachycarpa	1		
Weissia condensa	1	1	1
Weissia controversa	1	1	1
Weissia longifolia		1	1
Zygodon conoideus	1	1	1
Zygodon forsteri			1
Zygodon rupestris	1	1	1
Zygodon viridissimus	1	1	1
Total general: 764	**472**	**523**	**519**

***Supplementary Material 1: Macaronesian unified checklist**. This table summarizes the unification of Macaronesian bryophyte flora checklist. Subspecies have been removed from this checklist. Original sources: Borges, 2008; Borges, 2010 and Banco de Datos de Biodiversidad de Canarias (Gobierno de Canarias).*

SUPPLEMENTARY MATERIAL 2:

Endemic & Threatened species

DATASET (BY GENUS)	MACARONESIAN SPECIES	THREATENED SPECIES	ENDEMIC SPECIES
Frullania	*F. polysticta* *F. teneriffae* *F. calcarifera* *F. sergiae* *F. tamarisci* *F. microphyllla*	*F. sergiae* *F. polysticta*	*F. polysticta*: Macaronesian *F. sergiae*: Madeira
Lejeunea	*L. laetevirens* *L. flava*	*L. flava*	_ _ _
Leptoscyphus	*L. azoricus* *L. cuneifolius*	*L. cuneifolius*	_ _ _
Metzgeria	*E. conjugata* *M. furcata*	*E. conjugata*	_ _ _
Odontoschisma	*O. denudatum*	*O. denudatum*	_ _ _
Tylimanthus	*T. madeirensis* *T. azoricus*	*T. madeirensis*	*T. madeirensis*: Madeira *T. azoricus*: Azores
Amphidium	*A. mougeotii* *A. lapponicum* *A. curvipes*	*A. curvipes*	*A. curvipes*: Madeira and Canary islands
Bryoxiphium	*B. madeirensis*	*B. madeirensis*	*B. madeirense*: Madeira
Dicranum	*D. canariense* *D. scottianum* *D. scoparium*	*D. scoparium*	_ _ _
Exsertotheca	*Neckera pumila* *N. cephalonica* *E. intermedia* *Alleniella complanata*	*E. intermedia*	*E. intermedia*: Macaronesian
Leucodon	*L. treleasei* *L. canariensis* *L. sciuroides*	*L. canariensis* *L. treleasei*	*L. treleassi*: Macaronesian *L. canariensis*: Macaronesian
Orthotrichum	*O. handiense* *O. shevockii* *Lewinskya acuminata*	*O. handiense* *L. acuminata*	*O. handiense*: Canary Islands
Pelekium	*P. atlanticum*	*P. atlanticum*	*P. atlanticum*: Macaronesian
Rhynchostegiella	*R. litorea* *R. pseudolitorea* *R. bourgeana* *R. azorica* *R. teneriffae* *R. tenella* *R. tricophylla*	*R. bourgeana* *R. litorea* *R. teneriffae*	*R. tricophylla*: Madeira and Canary Islands *R. azorica*: Azores *R. pseudolitorea*: Madeira and Canary Islands *R. bourgenana*: Canary Islands
Tetrastichium	*T. fontanum* *T. virens*	*T. fontanum* *T. virens*	_ _ _
TOTAL SPECIES	42	21	15

Supplementary Material 2: Endemic & threatened species*. This table summarises species status between native macaronesian species, endemic species and threatened species, on relation with the reference databases.*

SUPPLEMENTARY MATERIAL 3:

Summary of sequences information

DATASET (BY GENUS)	INITIAL Nº SEQUENCES	FINAL Nº SEQUENCES	MACARO-NESIAN SPECIES	Nº THREA-TENED SPECIES	Nº ENDEMIC SPECIES	MARKERS	ORIGINAL PUBLICATION
Frullania	43	43	6	2	2	ITS, rbcL, atpB and trnL-F	Hentschel et al., 2009 Heinrichs et al., 2010
Lejeunea	63	63	2	1	0	ITS, trnL and rbcL	Heinrichs et al., 2013
Leptoscyphus	51	41	2	1	0	rps4, atpB and trnL	Devos et al., 2009
Metzgeria	65	58	2	1	0	atpIH-trnG	Fuselier et al., 2009 & 2011
Odontoschisma	21	19	1	1	0	atpB, rbcL, rps4 and trnF-L	Aranda et al., 2013
Tylimanthus	39	38	2	1	2	atpB, rbcL, psbA and psbT	Stech et al., 2010
Amphidium	32	24	3	1	1	ITS, trnL and rps4	Sim-Sim et al., 2017
Bryoxiphium	44	44	1	1	1	rps4, trnG, trnL and rpoC1	Patiño et al., 2016
Dicranum	68	66	3	1	0	ITS, rps4, psbA, trnT, trnH, trnL-F, rps19, rpsl2 and rpoB	Lang et al., 2014 & 2015
Exsertotheca	47	20	4	1	1	ITS and trnL-F	Draper et al., 2011
Leucodon	30	19	3	2	2	ITS, rbcL, atpB, trnG and trnT-E	Stech et al., 2011
Orthotrichum	74	70	2	2	1	ITS, rbcL, atpB, rps4 and trnL-F	Sawiki et al., 2009 Medina et al., 2013 Patiño et al., 2013 Vigalondo et al., 2016 & 2019
Pelekium	47	47	1	1	1	3 anonymous locus and trnL-F	Norhazrina et al., 2016
Rhynchostegiella	74	46	7	3	4	atpB, psbT, trnL, Ho and PAD	Patiño et al., 2015 & 2017
Tetrastichium	46	20	2	2	0	rps4 and trnL	Boon-Chuan Ho, 2012 Patiño et al., 2015
TOTAL	744	618	41	21	15		

Supplementary Material 3: Summary and sequence information*. This is a summary of sequence sources used for the elaboration of datasets, also includes a relation of the markers used on the original papers and the adaptation of information to our Master Thesis. The number of endemic and threatened species is indicated as a summary of the information extracted from the sources.*

SUPPLEMENTARY MATERIAL 4:

Evolution models & phylogenetic markers

SPECIES	MARKS	EVOLUTION MODEL
Frullania	ITS	TN93+I+G+X
	trnL-trnF-atpB-rbcL	GTR+I+G+X
Lejeunea	ITS	TN93+I+G+X
	rbcL	HKY+I+G+X
	trnL	GTR+G+X
Leptoscyphus	rps4-atpB-trnL	GTR+G+X
Metzgeria	atpIH-trnG	GTR+G+X
Odontoschisma	trnF-trnL	HKY+I+X
	atpB-rbcL-rps4	GTR+G+X
Tylimanthus	atpB-rbcL	GTR+I+G+X
	psbA-psbT	HKY+G+X
Amphidium	ITS	GTR+G+X
	rps4-trnL	GTR+G+X
Bryoxiphium	rpoC1	HKY+I+G+X
	rps4-trnG	TN93+I+G+X
Dicranum	ITS	HKY+G+X
	trnT-trnH-rps4-psbA	HKY+I+G+X
	trnL-trnF	GTR+G+I+X
	rps19-rpl19-rpoB	TN93+I+G+X
Exsertotheca	ITS	GTR+I+X
	trnL-trnF	GTR+I+X
Leucodon	ITS	HKY+G+X
	atpB-rbcL-trnT-trnE-trnG	GTR+X
Orthotrichum	ITS	TN93+I+G+X
	trnL-trnF	TN93+I+G+X
	rps4-atpB-rbcL	GTR+I+G+X
Pelekium	Nuclear CharSet1	TN93+G+X
	Nuclear CharSet2	HKY+I+G+X
	trnL	HKY+G+X
Rhynchostegiella	atpB-psbT-trnC	GTR+I+G+X
	HO-PAD	HKY+G+X
Tetrastichium	rps4-trnL	GTR+I+G+X

Supplementary Material 4: Evolution models & phylogenetic markers. *This is a summary table of the final partition of the phylogenetic markers used for our analysis and their fit evolution model estimated on PartitionFinder.*

SUPPLEMENTARY MATERIAL 5:

Bayes Factor calculation summary

Datasets	Tree priors	MLE path sampling	2ln (BF)	stepping stone sampling	2ln (BF)	correct mixing
Frullania	BD	-5835.7931	0	-5406.011	0	Yes
	YULE	-7043.6592	2415.7322	-7045.2435	3278.465	Yes
Lejeunea	BD	-7768.4531	0	-7768.56805	0	Yes
	YULE	-7781.5932	26.2802	-7782.86465	28.5932	Yes
Leptoscyphus	BD	-5274.3162	0	-5274.76915	0	Yes
	YULE	-5290.3262	32.0199	-5291.89355	34.2488	Yes
Metzgeria	BD	-5243.3137	0	-5243.54955	0	Yes
	YULE	-5261.3310	36.0346	-5263.0127	38.9263	Yes
Odontoschisma	BD	-3605.5496	0	-3605.74405	0	Yes
	YULE	-3623.4196	35.7401	-3623.5896	35.6911	Yes
Tylimanthus	BD	-5538.7727	268.775	-5538.832878	410.6831	Yes
	YULE	-5404.3849	0	-5333.491293	0	Yes
Amphidium	BD	-3259.3351	0	-3259.716	0	No
	YULE	-3280.6176	42.565	-3282.4192	45.4064	Yes
Bryoxiphium	CS	-4580.7953	0	-4580.8072	0	Yes
	EG	-4600.1910	38.7914	-4600.1558	38.6972	Yes
Dicranum	BD	-6915.3776	0	-6915.91875	0	Yes
	YULE	-6931.0525	31.3499	-6932.3914	32.9453	Yes
Exsertotheca	BD	-2320.9297	0	-2320.9762	0	No (better)
	YULE	-2344.2194	46.5795	-2345.4202	48.888	No
Leucodon	BD	-3852.6180	0	-3852.56675	0	No
	YULE	-3875.6543	46.0726	-3876.1426	47.1517	No (better)
Orthotrichum	BD	-7129.6602	0	-7130.64445	0	Yes
	YULE	-7151.9726	44.6247	-7153.7125	46.1361	Yes
Pelekium	BD	-10273.9154	48.3607	-10273.7384	46.393	Yes
	YULE	-10249.7350	0	-10250.5419	0	Yes
Rhynchostegiella	BD	-5605.2030	1274.8224	-5606.0298	2221.3746	Yes
	YULE	-4967.7918	0	-4495.34255	0	Yes
Tetrastichium	BD	-1398.9515	0	-1399.11695	0	No
	YULE	-1414.4988	31.0946	-1413.5896	28.9453	Yes

Supplementary Material 5: Bayes Factor calculation summary. *This is a summary table of MCC trees, estimated on Cipres by BEAST analysis. The final selection tree prior is highline with blue colour.*

SUPPLEMENTARY MATERIAL 6:
Akaike's information criterion summary

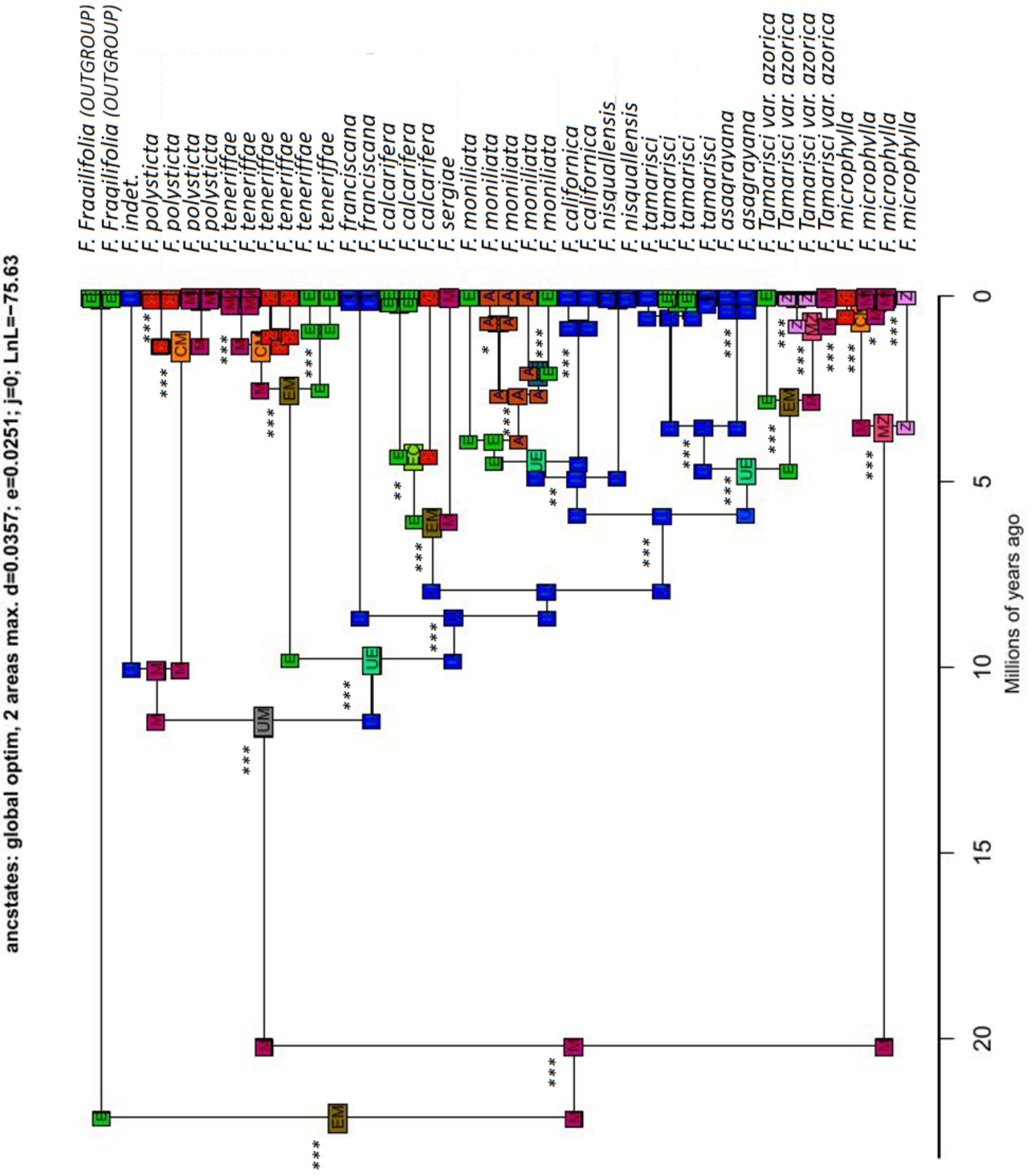
SPECIES	MODELS	LnL	numparams	d	e	j	AICc	AICc_wt
Frullania	DEC	-81.52	2	0.035	0.037	0	167.3	0.0015
	DIVALIKE	-75.68	2	0.036	0.025	0	155.7	0.50
	BAYAREALIKE	-101.4	2	0.065	0.17	0	207.1	3.4e-12
Lejeunea	DEC	-126.2	2	0.010	0.010	0	256.5	6.1e-06
	DIVALIKE	-114.9	2	0.0077	0.0012	0	233.9	0.50
	BAYAREALIKE	-142.8	2	0.011	0.075	0	289.8	3.6e-13
Leptoscyphus	DEC	-32.15	2	0.012	1.0e-12	0	68.75	0.029
	DIVALIKE	-29.37	2	0.014	1.0e-12	0	63.2	0.47
	BAYAREALIKE	-41.45	2	0.016	0.092	0	87.35	2.7e-06
Metzgeria	DEC	-191.9	2	0.010	0.010	0	388	0.31
	DIVALIKE	-192.4	2	0.010	0.010	0	389	0.19
	BAYAREALIKE	-202.9	2	0.014	0.037	0	410.1	5.0e-06
Odontoschisma	DEC	-20.27	2	0.0041	1.0e-12	0	45.35	0.047
	DIVALIKE	-18.01	2	0.0040	1.0e-12	0	40.81	0.45
	BAYAREALIKE	-31.09	2	0.0046	0.024	0	66.97	9.5e-07
Tylimanthus	DEC	-35.47	2	0.0017	1.0e-12	0	75.29	0.032
	DIVALIKE	-32.8	2	0.0019	1.0e-12	0	69.94	0.47
	BAYAREALIKE	-47.85	2	0.0024	0.018	0	100.1	1.4e-07
Amphidium	DEC	-58.93	2	0.013	0.0098	0	122.5	0.0030
	DIVALIKE	-53.82	2	0.013	1.0e-12	0	112.3	0.50
	BAYAREALIKE	-78.02	2	0.032	0.16	0	160.7	1.5e-11
Bryoxiphium	DEC	-69,3229	2	0.059	0.000	0	142,95	0,001
	DIVALIKE	-62,6049	2	0.066	1,00E-12	0	129,52	0,499
	BAYAREALIKE	-89,8797	2	0.094	0.406	0	184,07	7,131
Dicranum	DEC	-62.84	2	0.0044	1.0e-12	0	129.9	0.47
	DIVALIKE	-65.49	2	0.0059	1.0e-12	0	135.2	0.033
	BAYAREALIKE	-109.9	2	0.0052	0.035	0	223.9	1.8e-21
Exsertotheca	DEC	-41.33	2	0.010	0.010	0	87.4	0.47
	DIVALIKE	-44.27	2	0.029	1.0e-12	0	93.28	0.025
	BAYAREALIKE	-63.58	2	0.043	0.20	0	131.9	1.0e-10
Leucodon	DEC	-38.53	2	0.032	0.022	0	81.93	0.48
	DIVALIKE	-41.66	2	0.036	0.013	0	88.17	0.021
	BAYAREALIKE	-52.63	2	0.10	0.36	0	110.1	3.6e-07
Orthotrichum	DEC	-85.87	2	0.0068	1.0e-12	0	175.9	0.060
	DIVALIKE	-83.88	2	0.0075	1.0e-12	0	171.9	0.44
	BAYAREALIKE	-132.1	2	0.0080	0.035	0	268.3	5.3e-22
Pelekium	DEC	-93.36	2	0.0040	0.011	0	191	0.023
	DIVALIKE	-90.32	2	0.0039	0.0065	0	184.9	0.48
	BAYAREALIKE	-96.98	2	0.0048	0.028	0	198.3	0.0006
Rhynchostegiella	DEC	-44.18	2	0.034	1.0e-12	0	92.53	0.43
	DIVALIKE	-45.93	2	0.060	1.0e-12	0	96.04	0.074
	BAYAREALIKE	-63.5	2	0.052	0.17	0	131.2	1.7e-09
Tetrastichium	DEC	-49.8	2	0.028	1.0e-12	0	104.3	0.055
	DIVALIKE	-47.72	2	0.035	1.0e-12	0	100.1	0.44
	BAYAREALIKE	-61.42	2	0.041	0.22	0	127.5	5.0e-07

Supplementary Material 6: Akaike's information criterion summary. *This is a summary table estimation ancestral model calculated on BioGeoBEARS. The final selection model is highline with blue colour.*

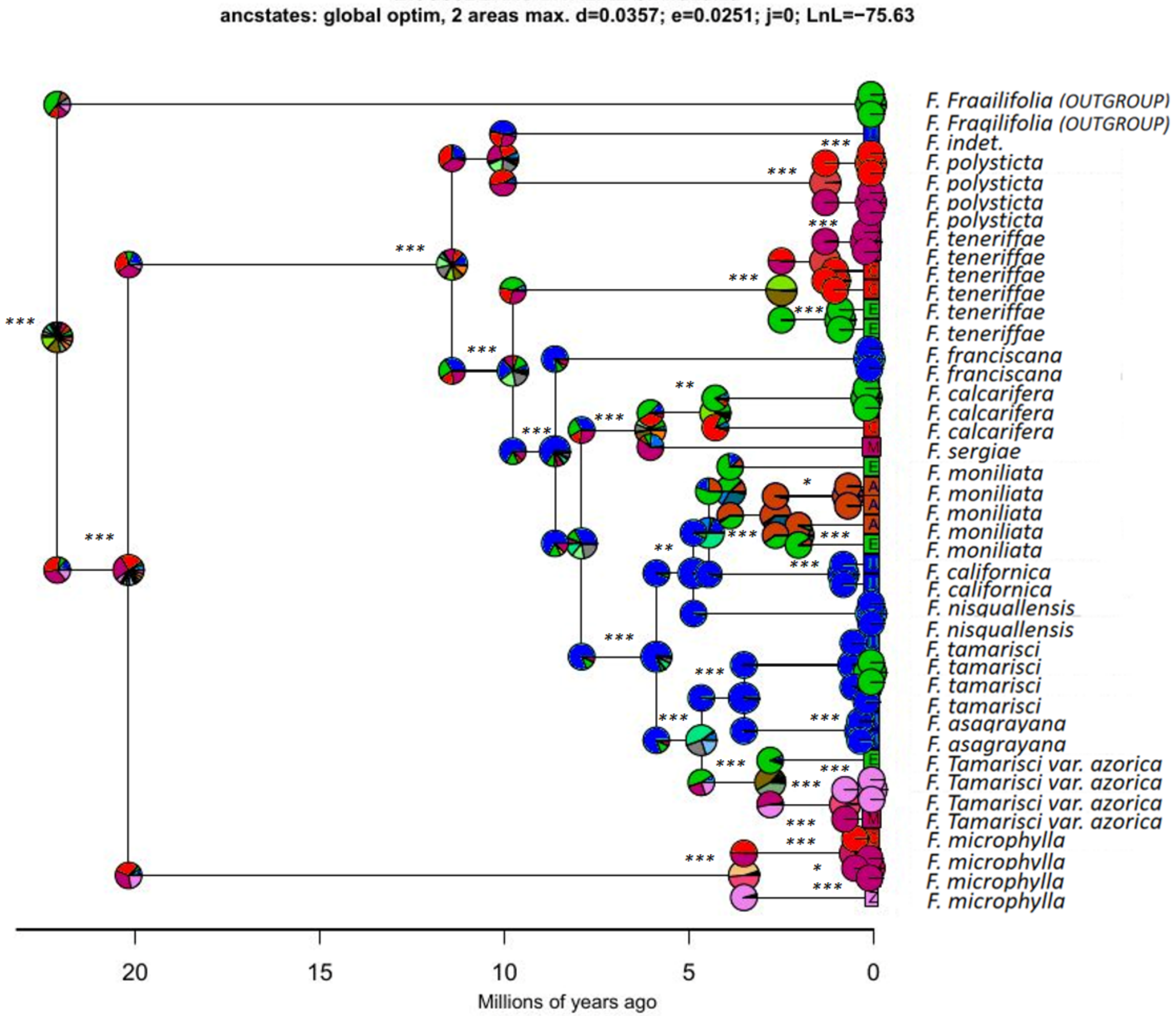
SUPPLEMENTARY MATERIAL 7:

“BioGeoBEARS” ancestral areas reconstruction

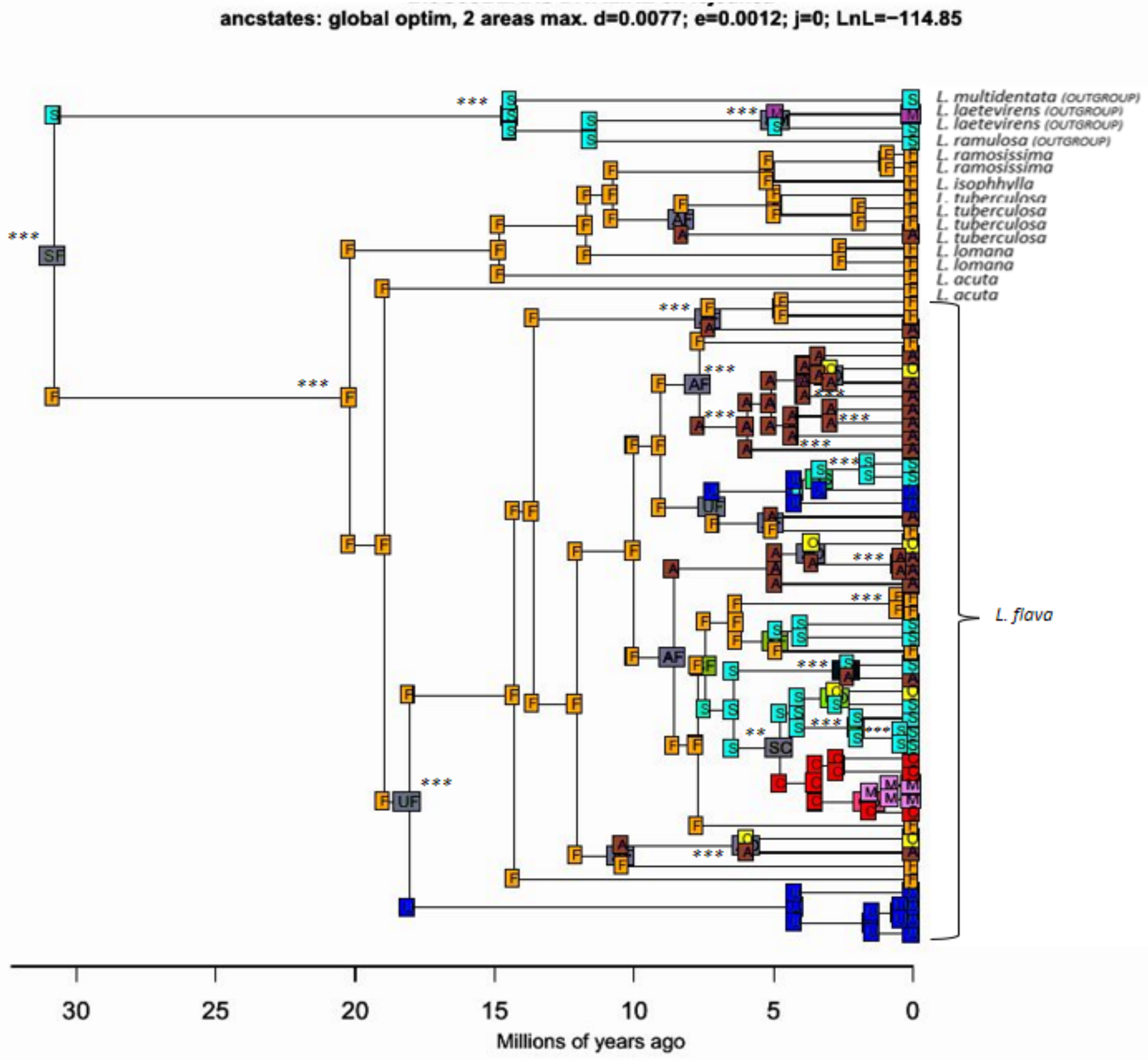
BioGeoBEARS 1.1: DIVALIKE on *Frullania*



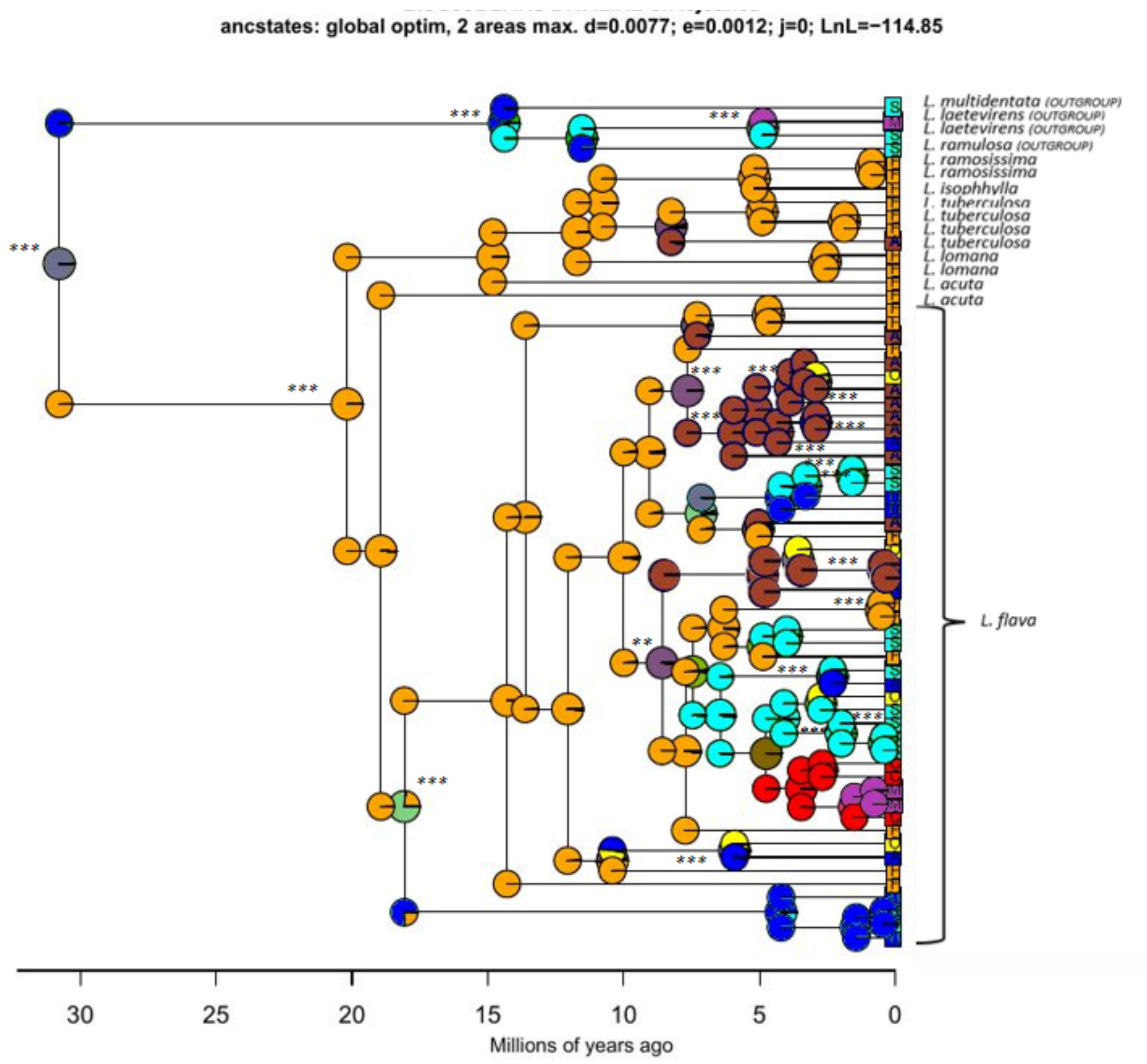
BioGeoBEARS 1.2: DIVALIKE on *Frullania*



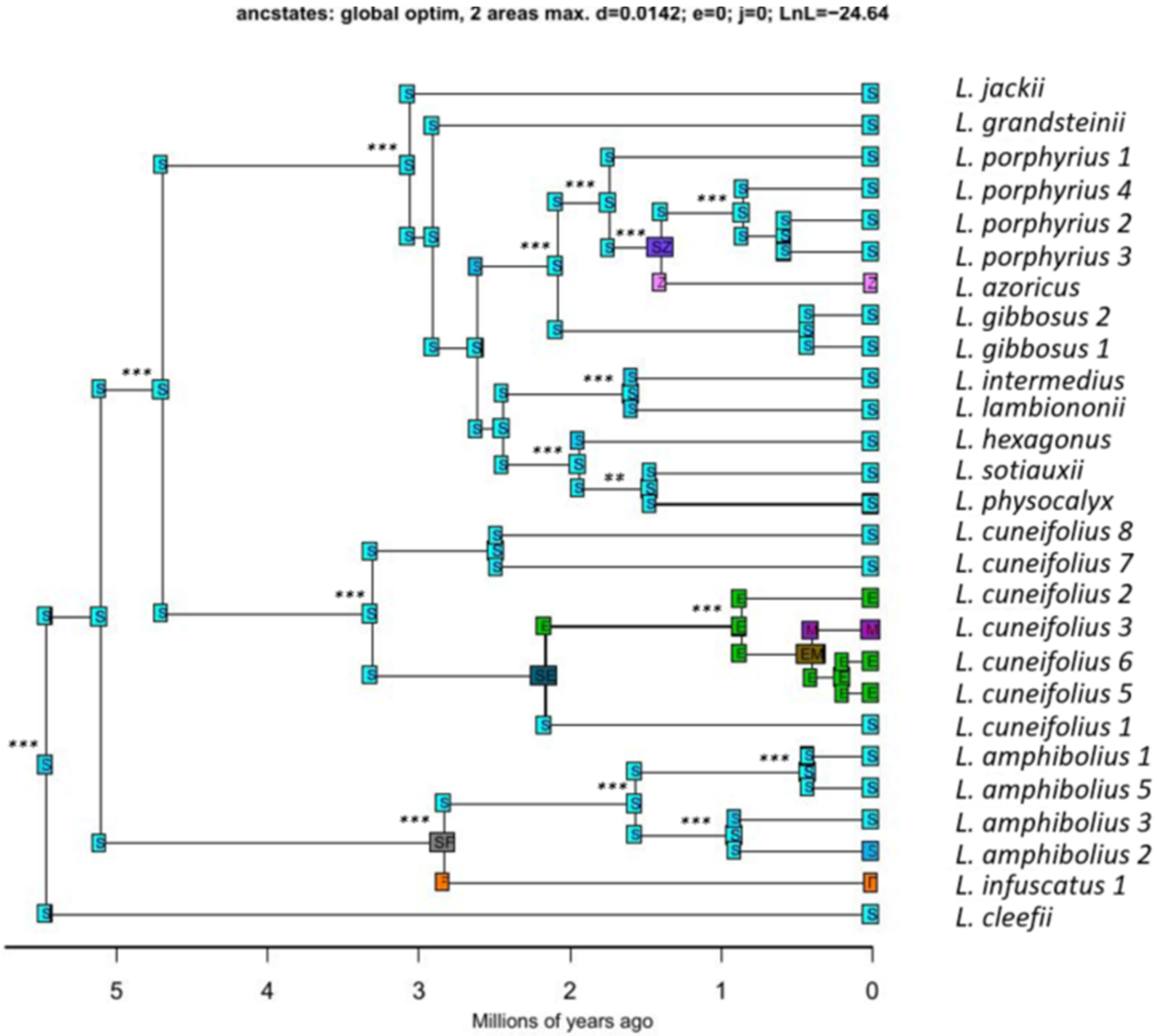
BioGeoBEARS 2.1: DIVALIKE on *Lejeunea*



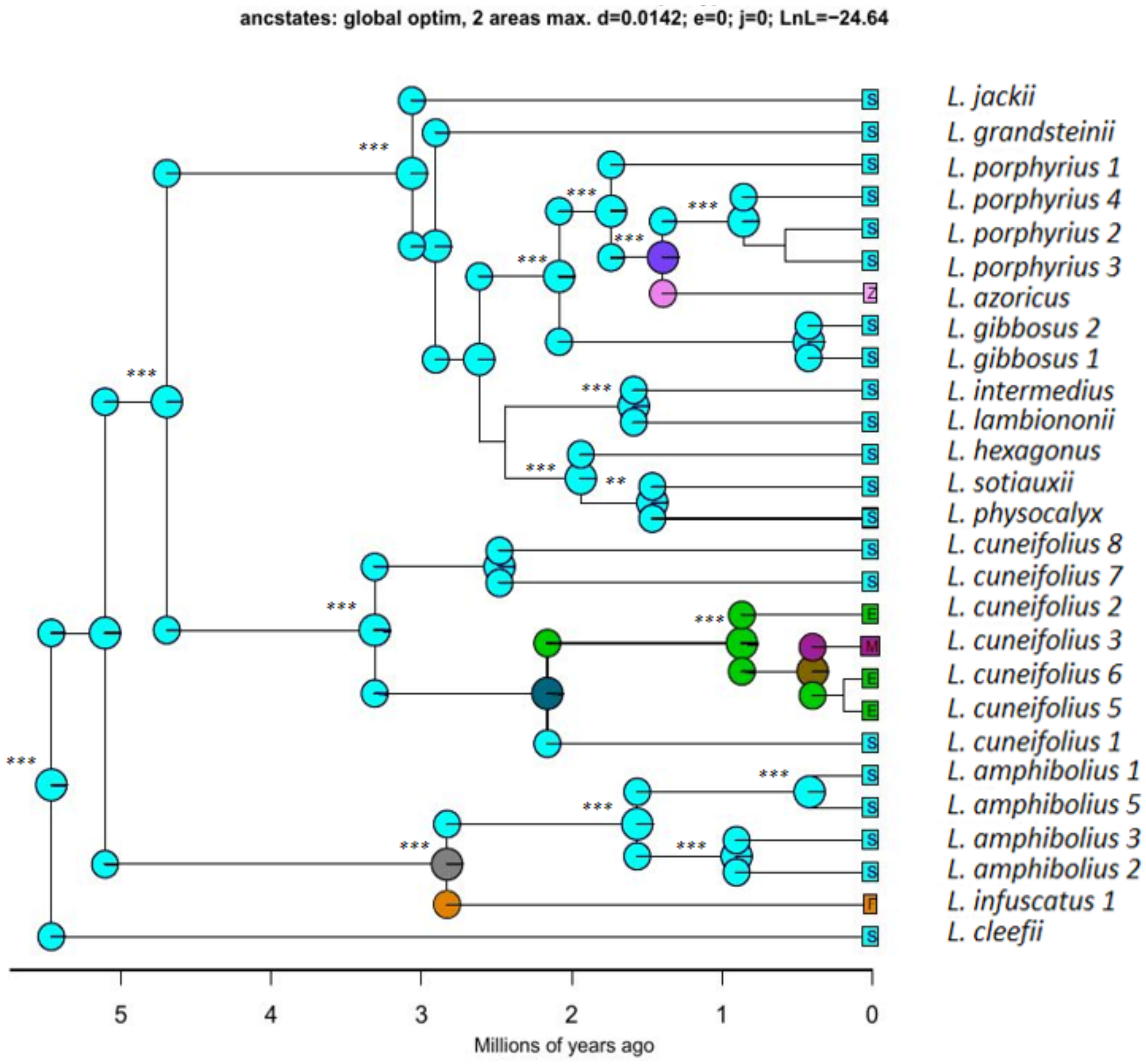
BioGeoBEARS 2.2: DIVALIKE on *Lejeunea*



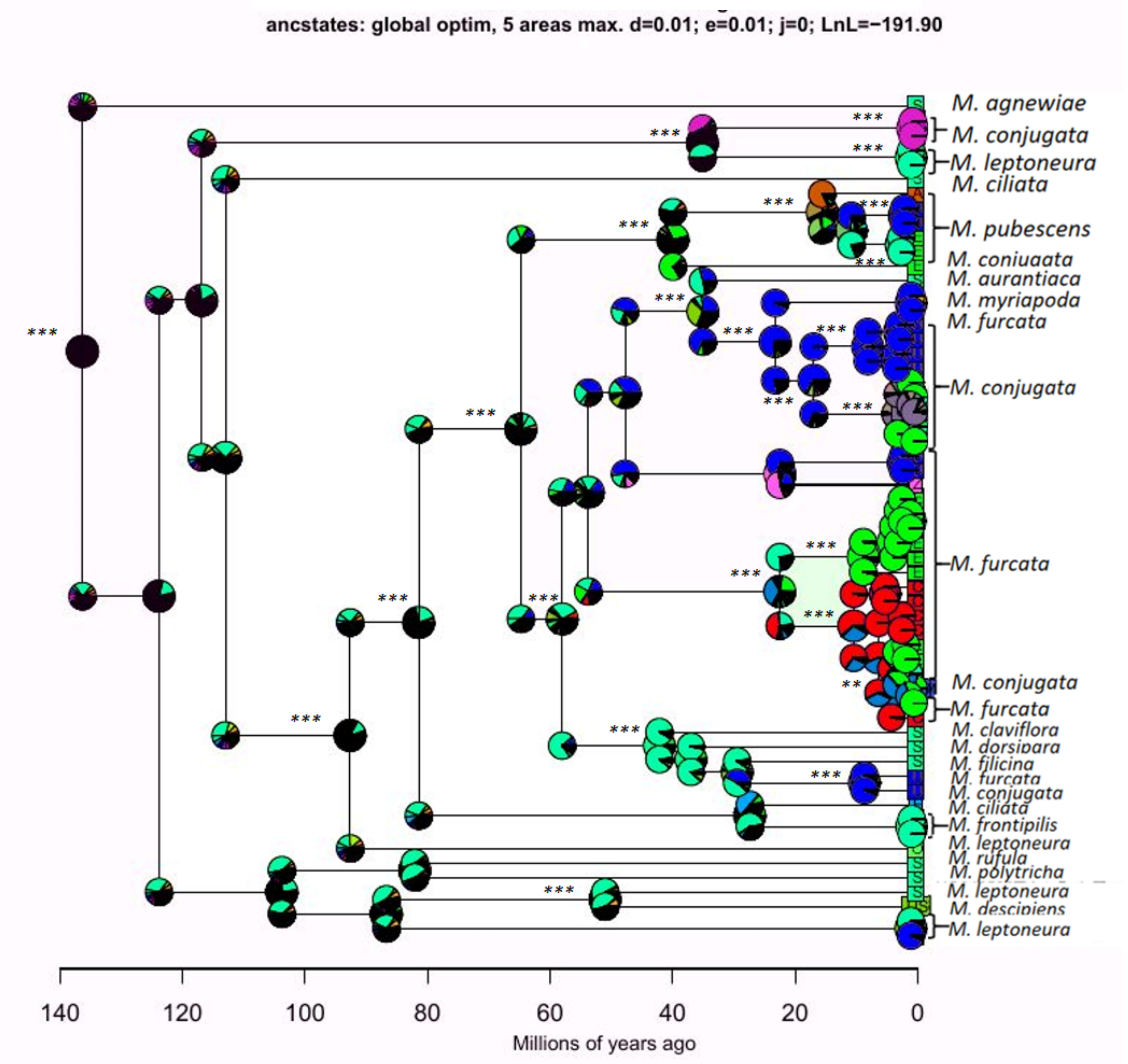
BioGeoBEARS 3.1: DIVALIKE on *Leptoscyphus*



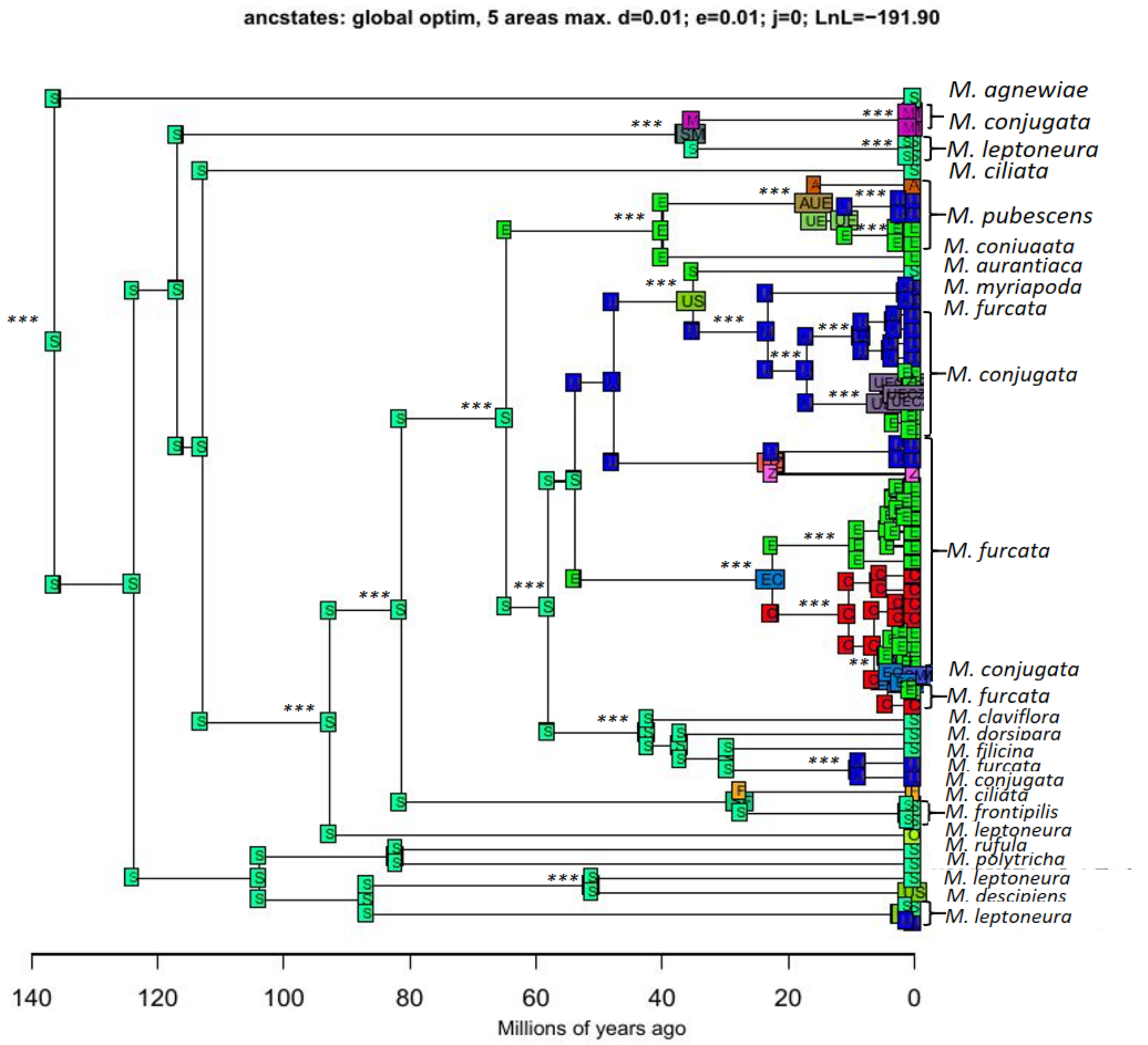
BioGeoBEARS 3.2: DIVALIKE on *Leptoscyphus*



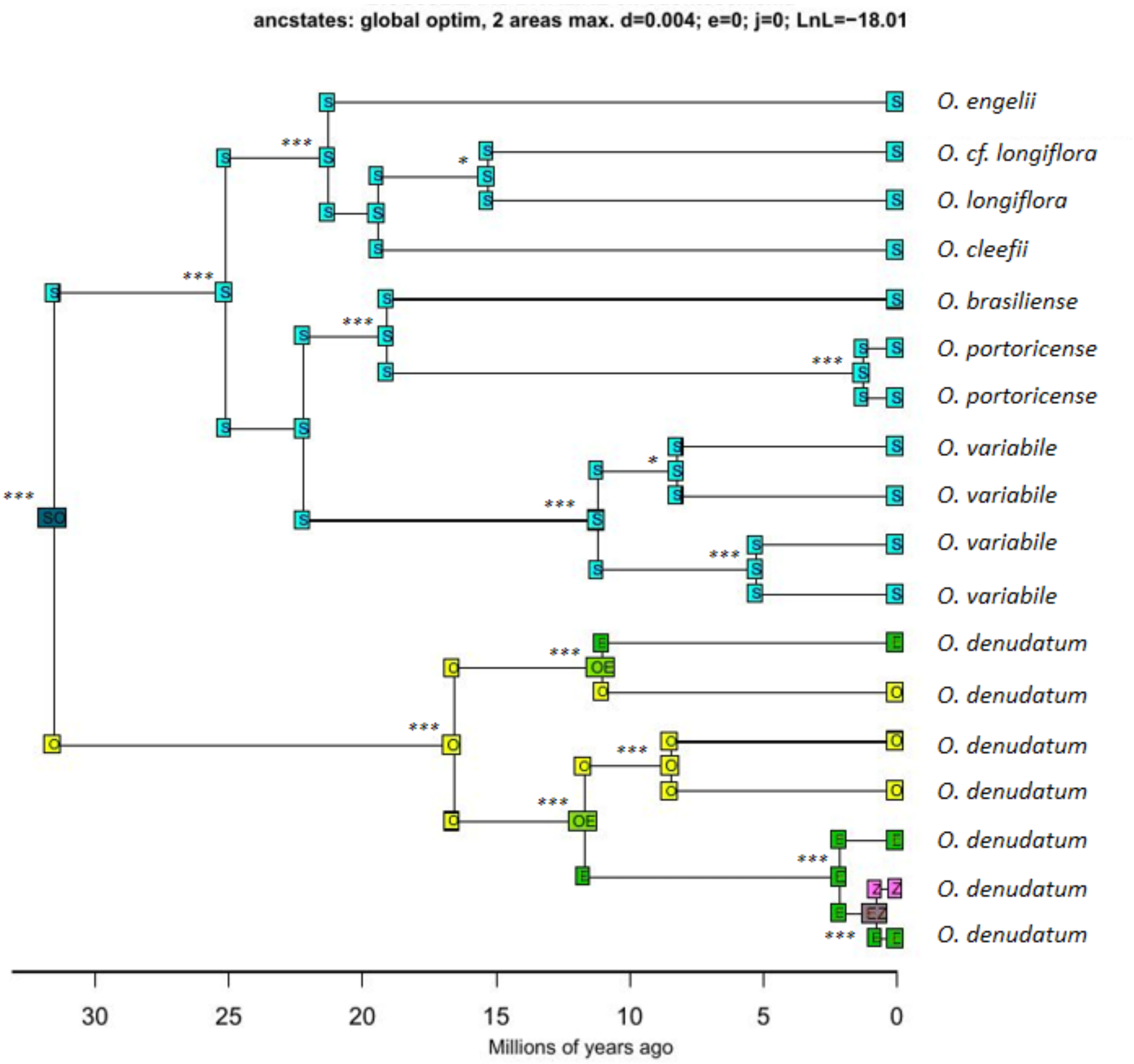
BioGeoBEARS 4.1: DEC on *Metzgeria*



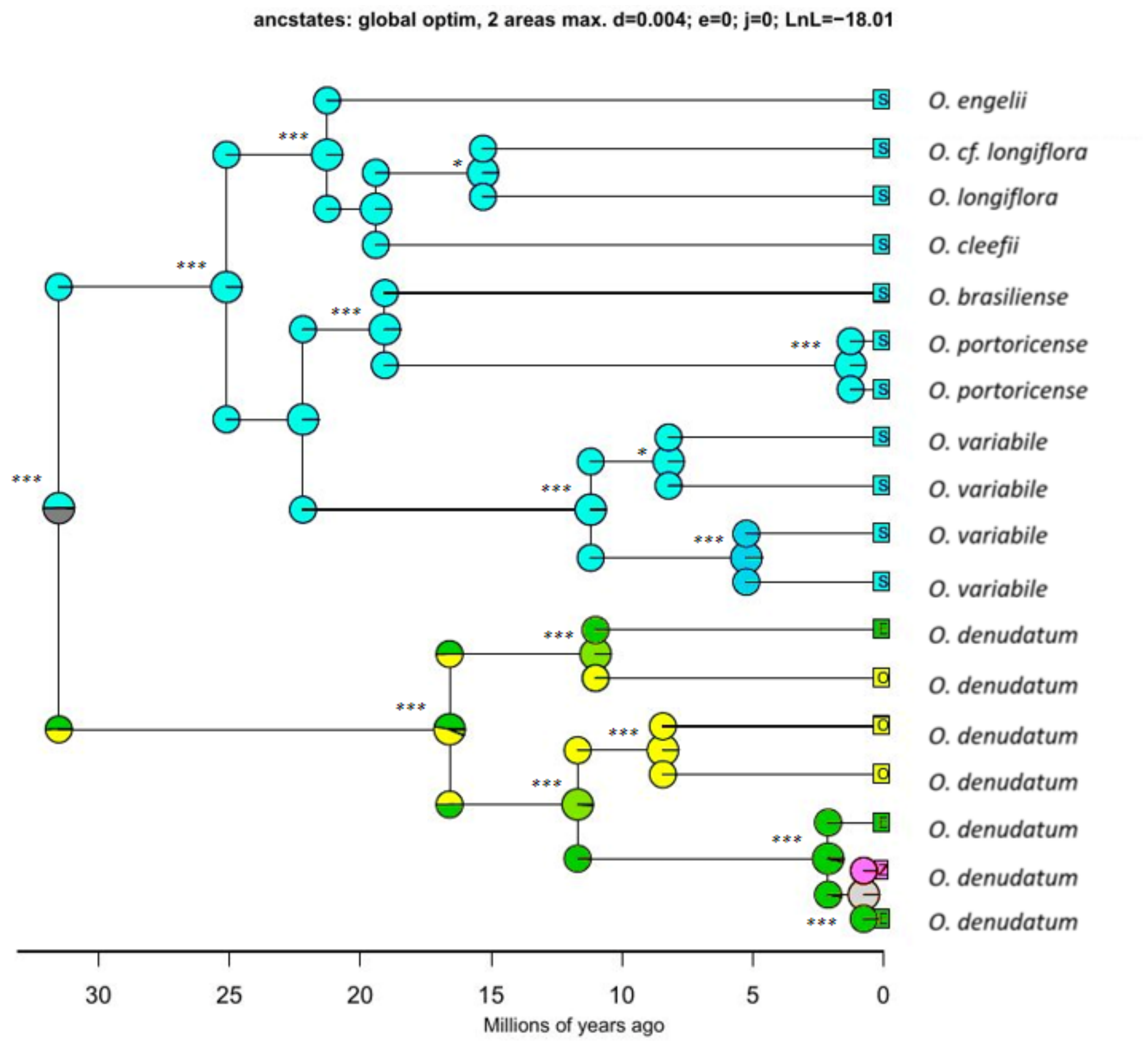
BioGeoBEARS 4.2: DEC on *Metzgeria*



BioGeoBEARS 5.1: DIVALIKE on *Odontoschisma*

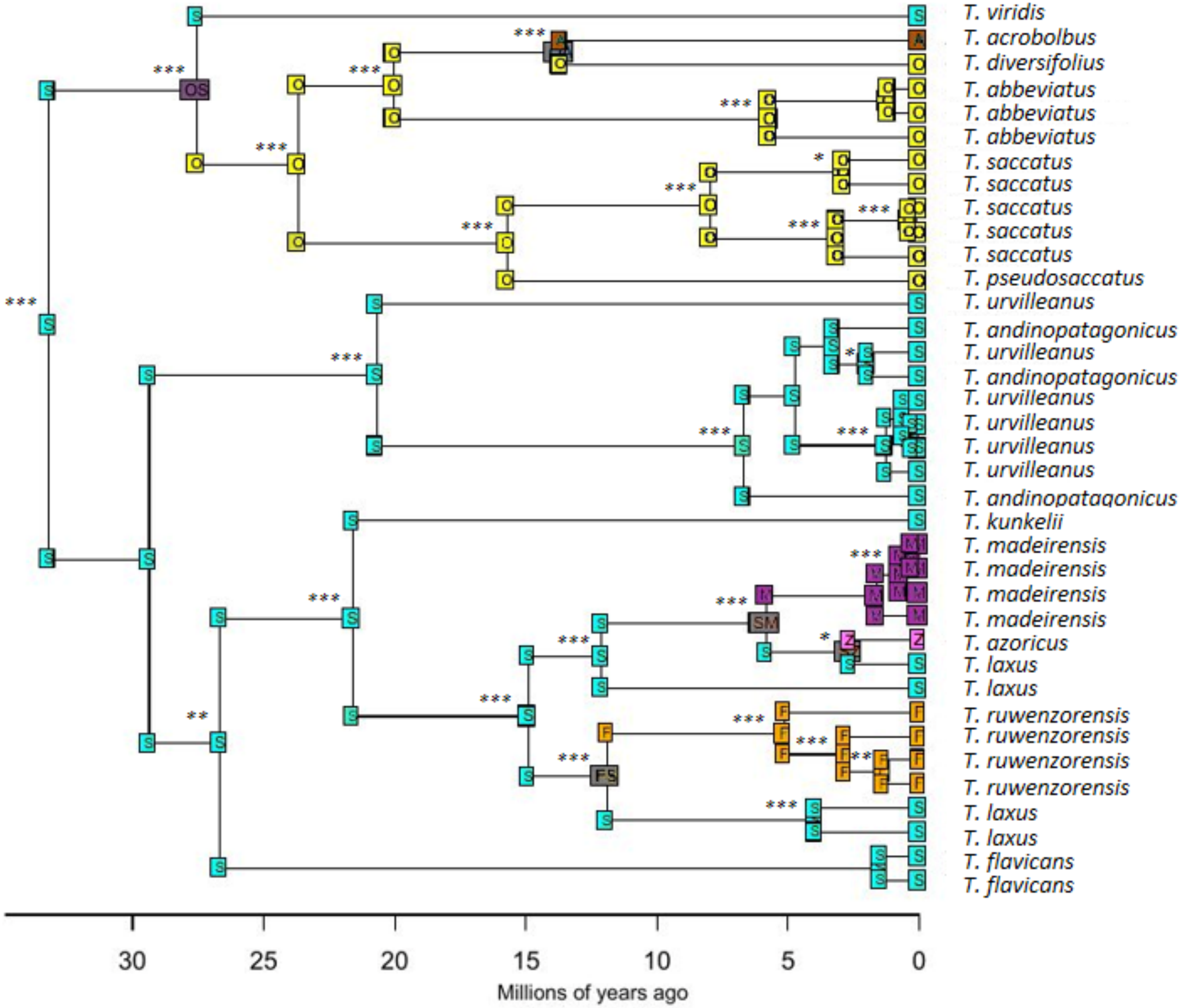


BioGeoBEARS 5.2: DIVALIKE on *Odontoschisma*

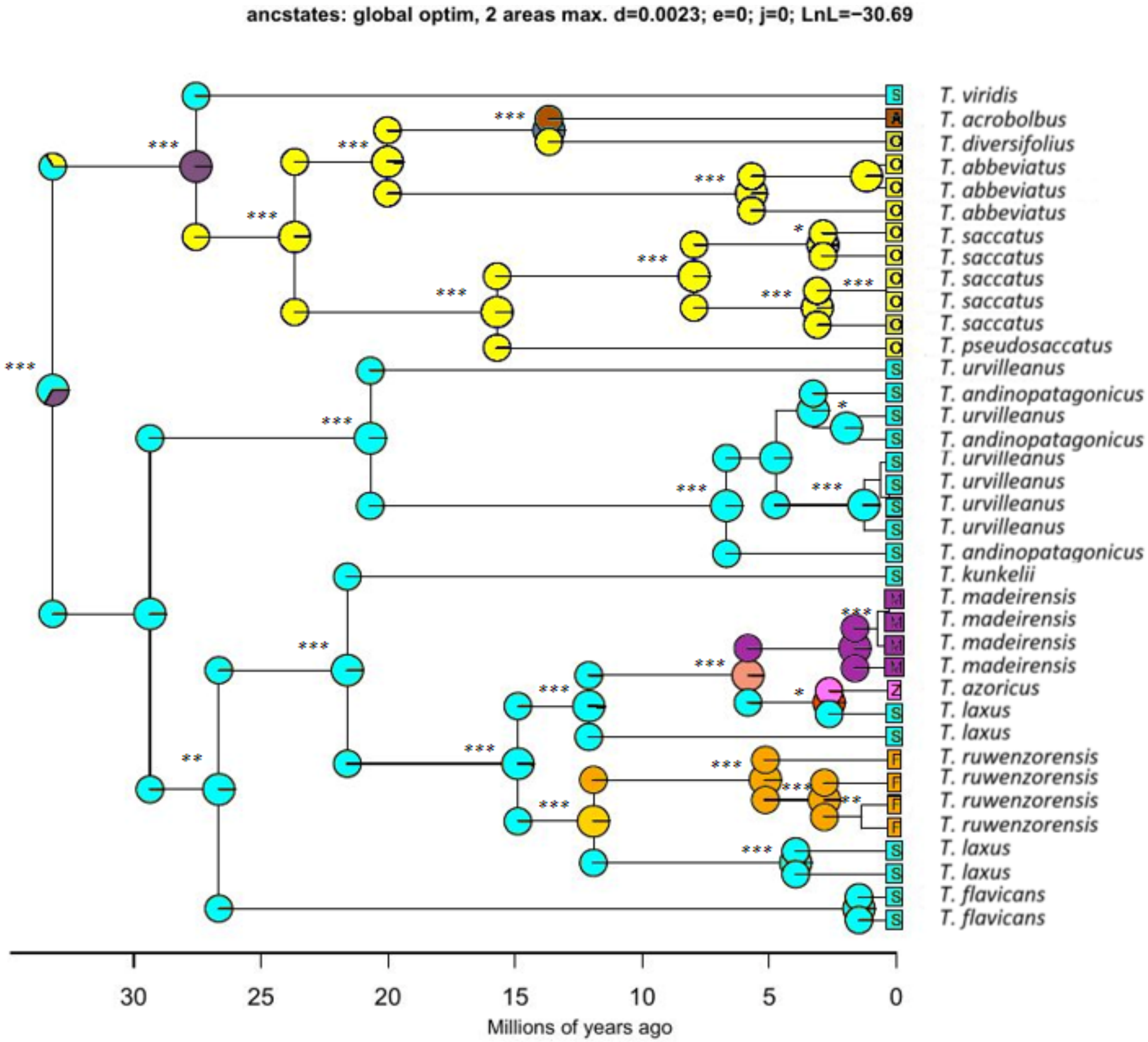


BioGeoBEARS 6.1: DIVALIKE on *Tylimanthus*

ancstates: global optim, 2 areas max. d=0.0023; e=0; j=0; LnL=−30.69

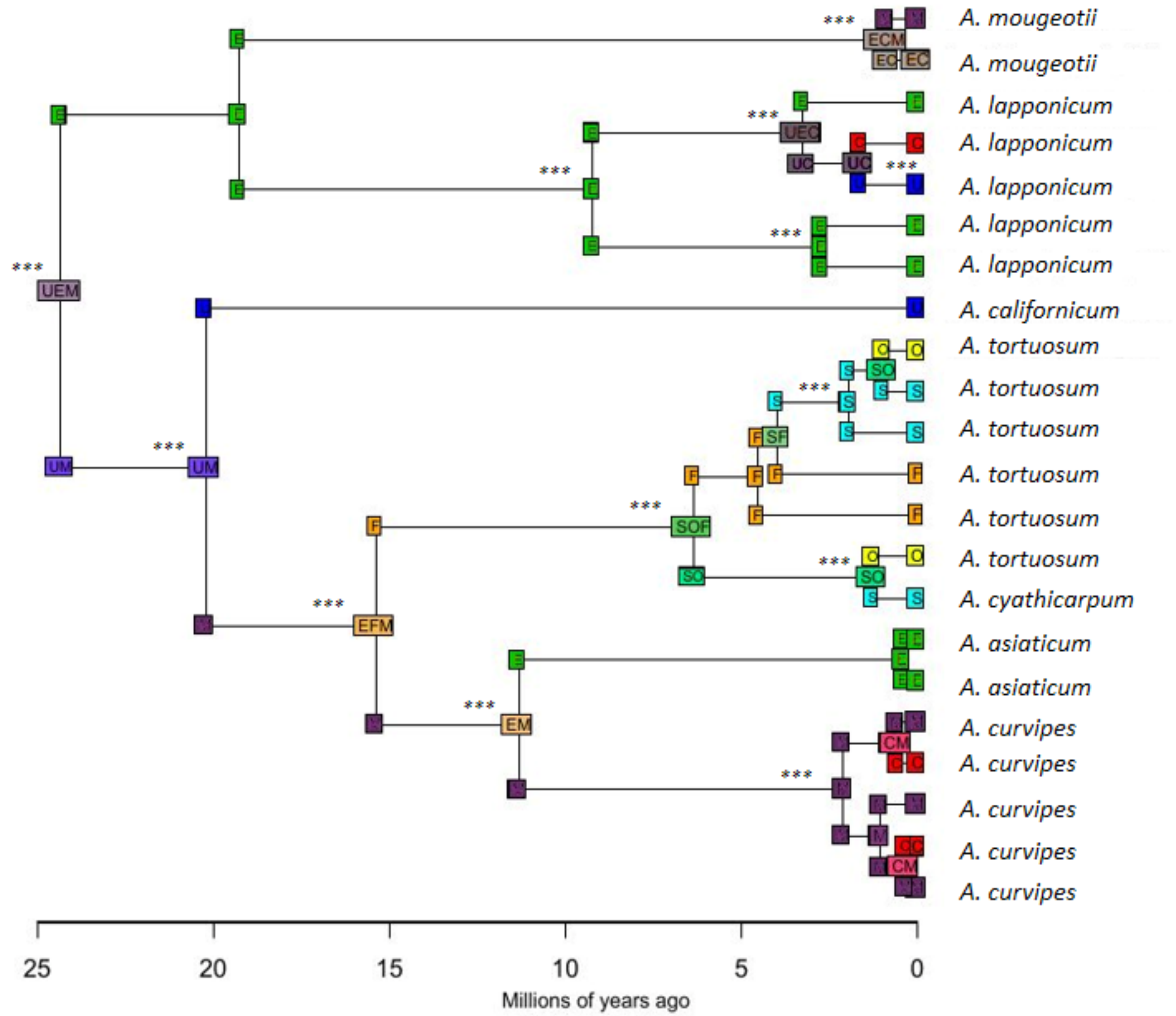


BioGeoBEARS 6.2: DIVALIKE on *Tylimanthus*

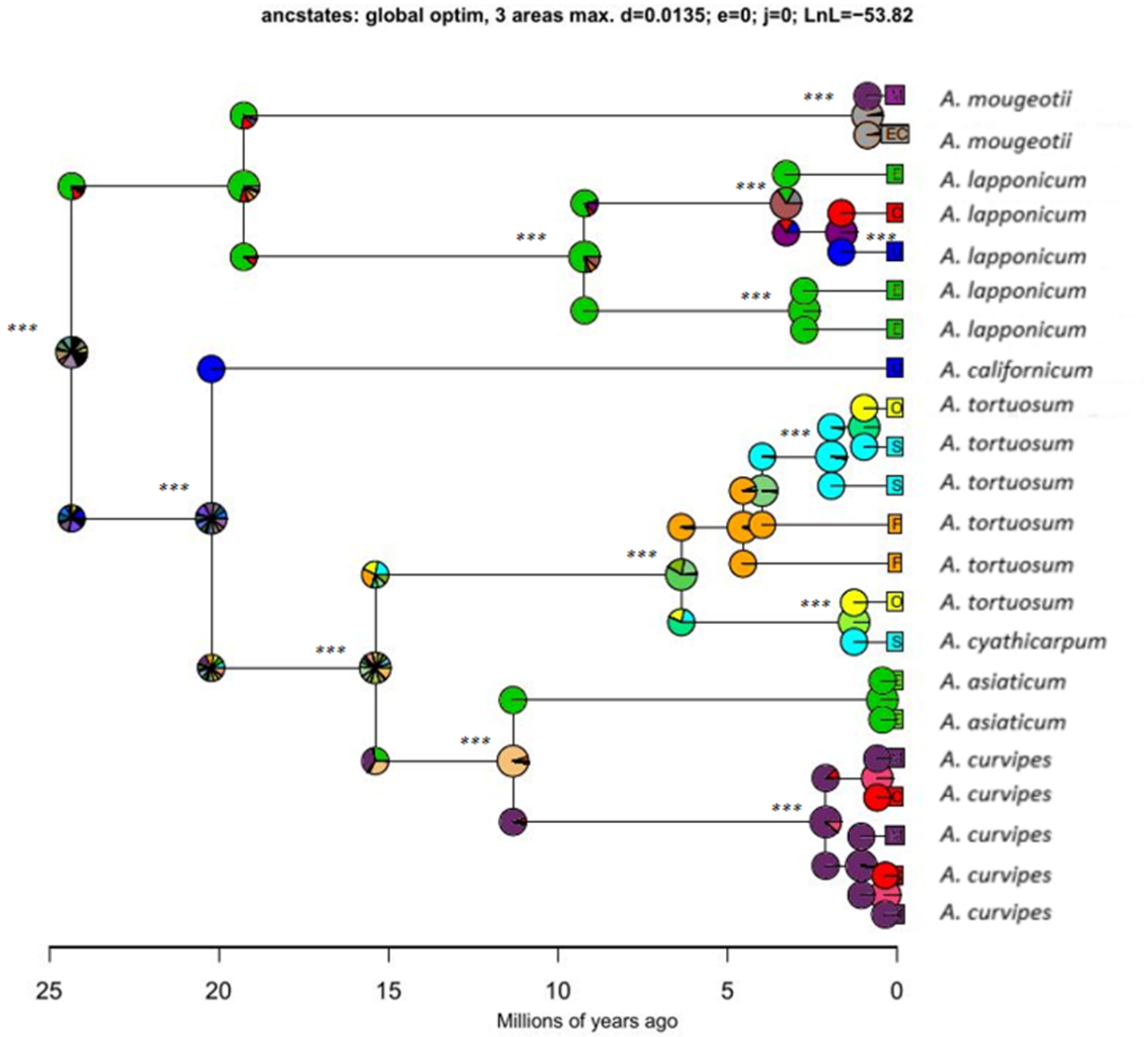


BioGeoBEARS 7.1: DIVALIKE on *Amphidium*

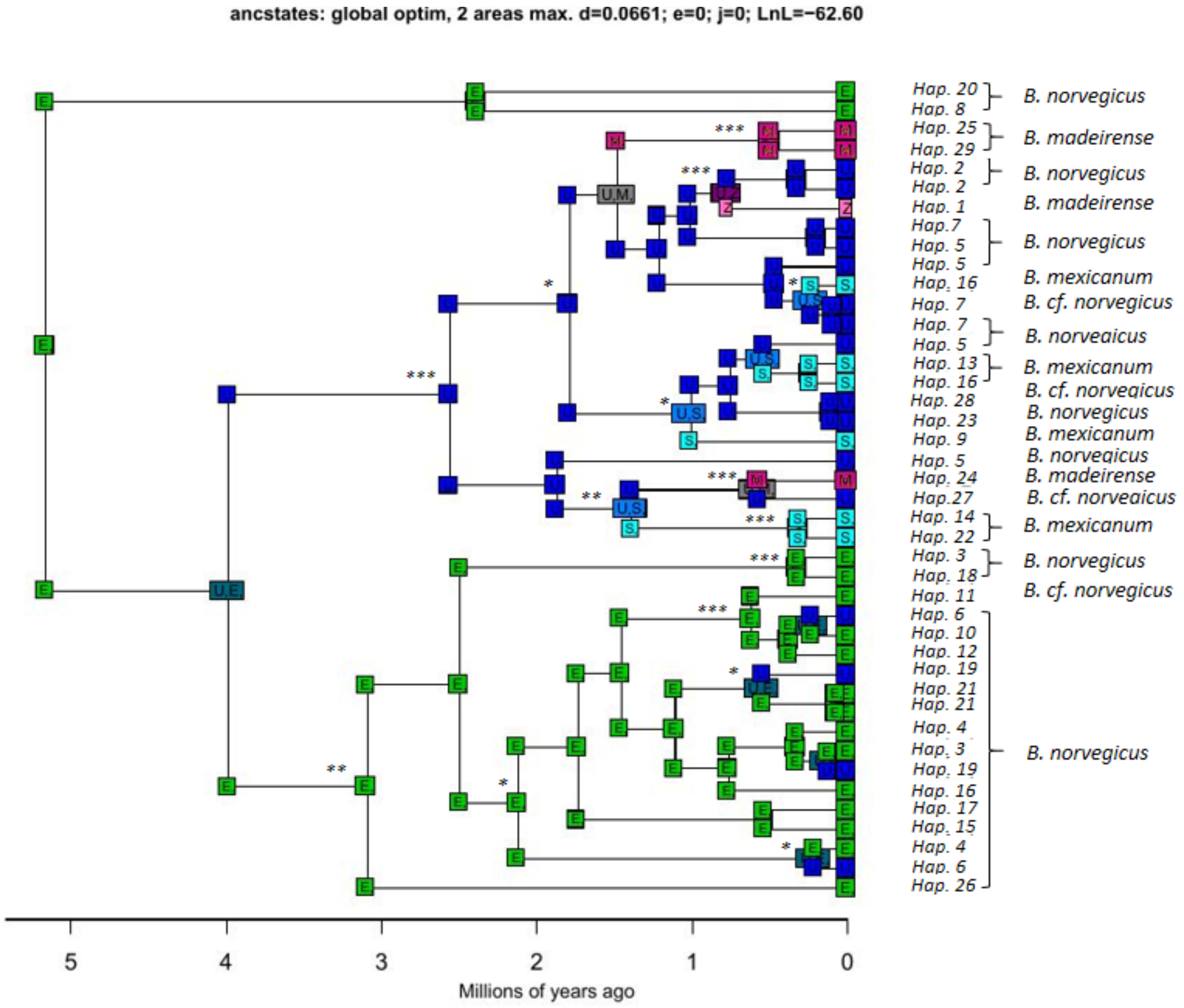
ancstates: global optim, 3 areas max. d=0.0135; e=0; j=0; LnL=−53.82



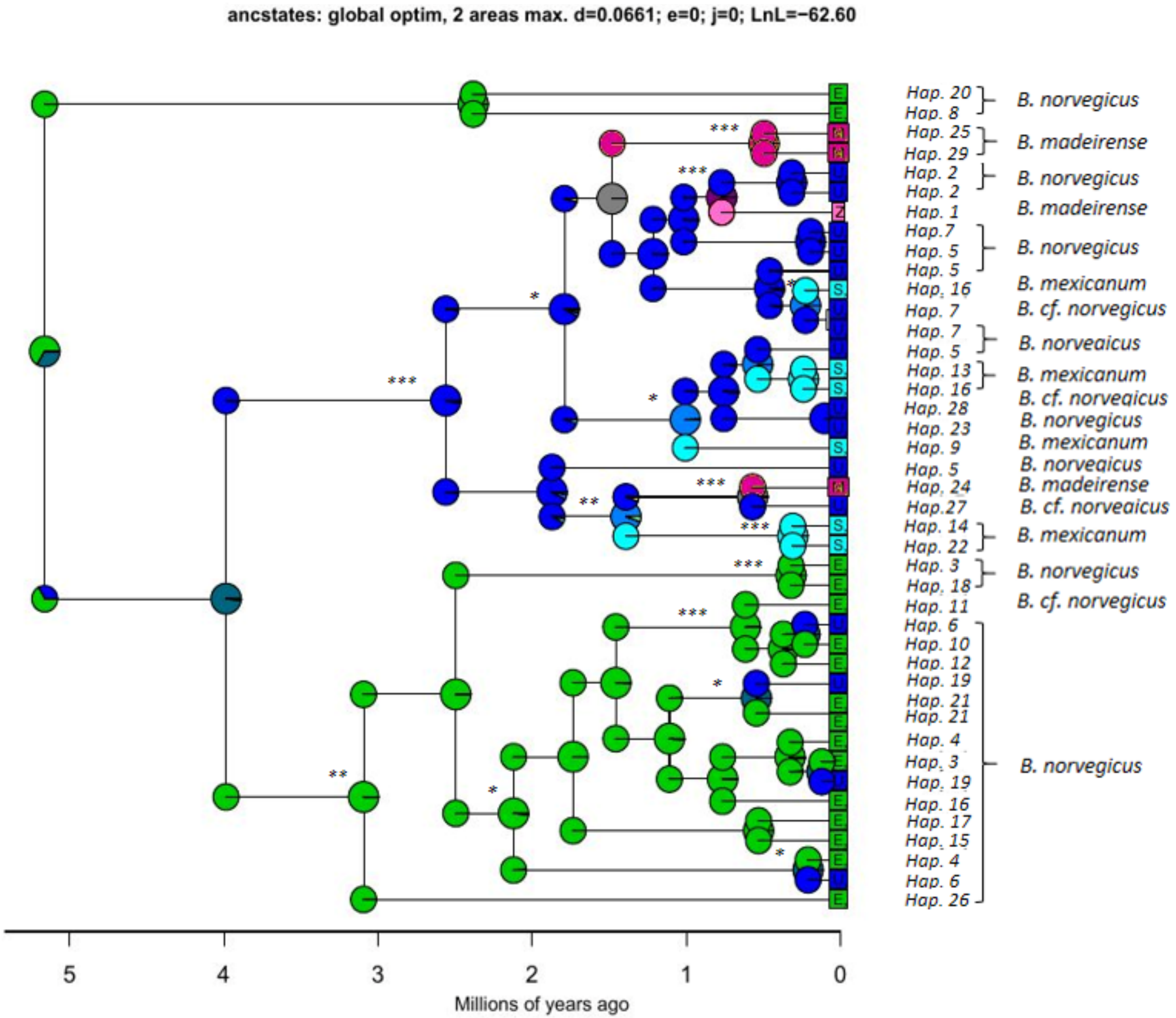
BioGeoBEARS 7.2: DIVALIKE on *Amphidium*



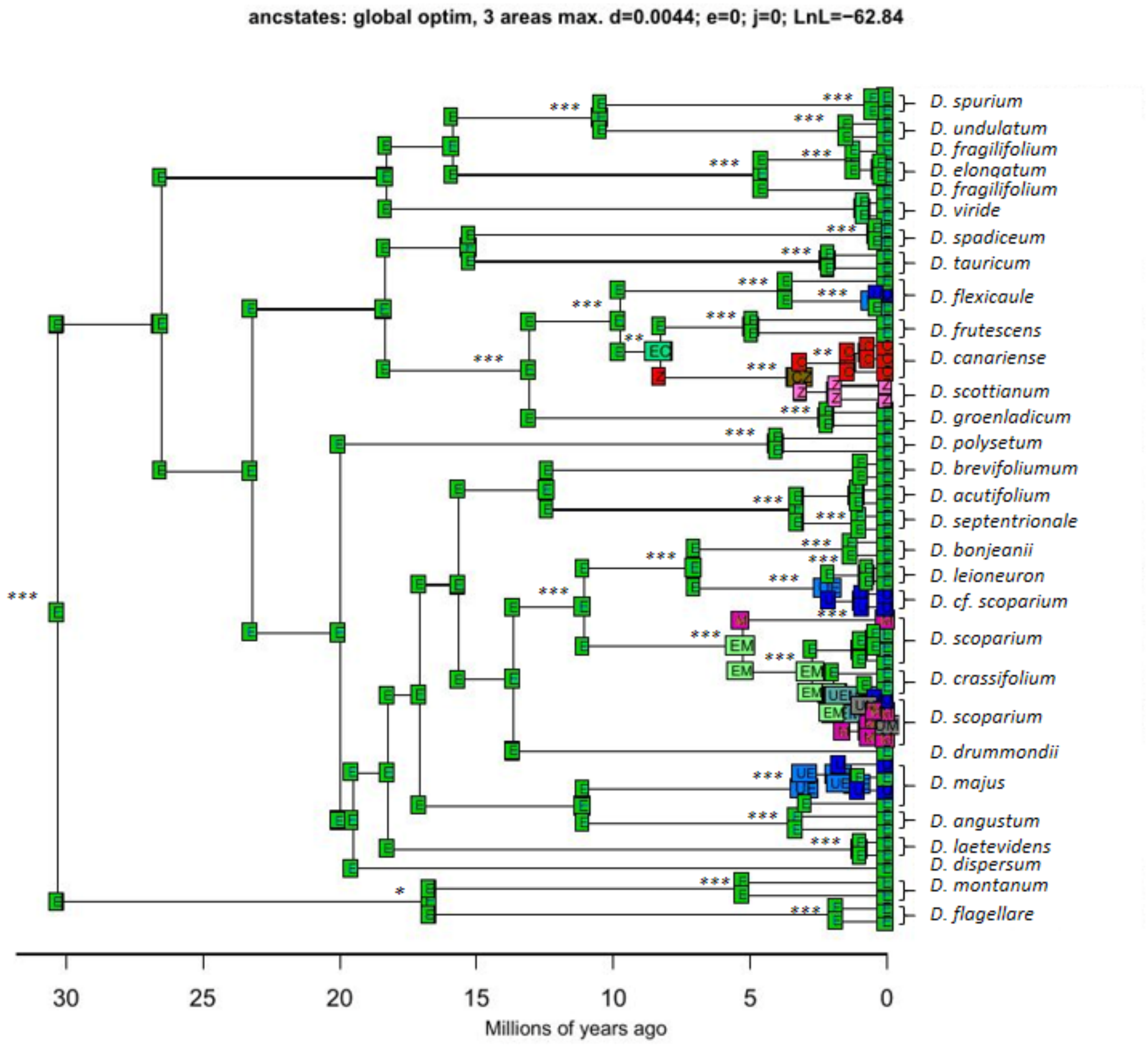
BioGeoBEARS 8.1: DIVALIKE on *Bryoxiphium*



BioGeoBEARS 8.2: DIVALIKE on *Bryoxiphium*

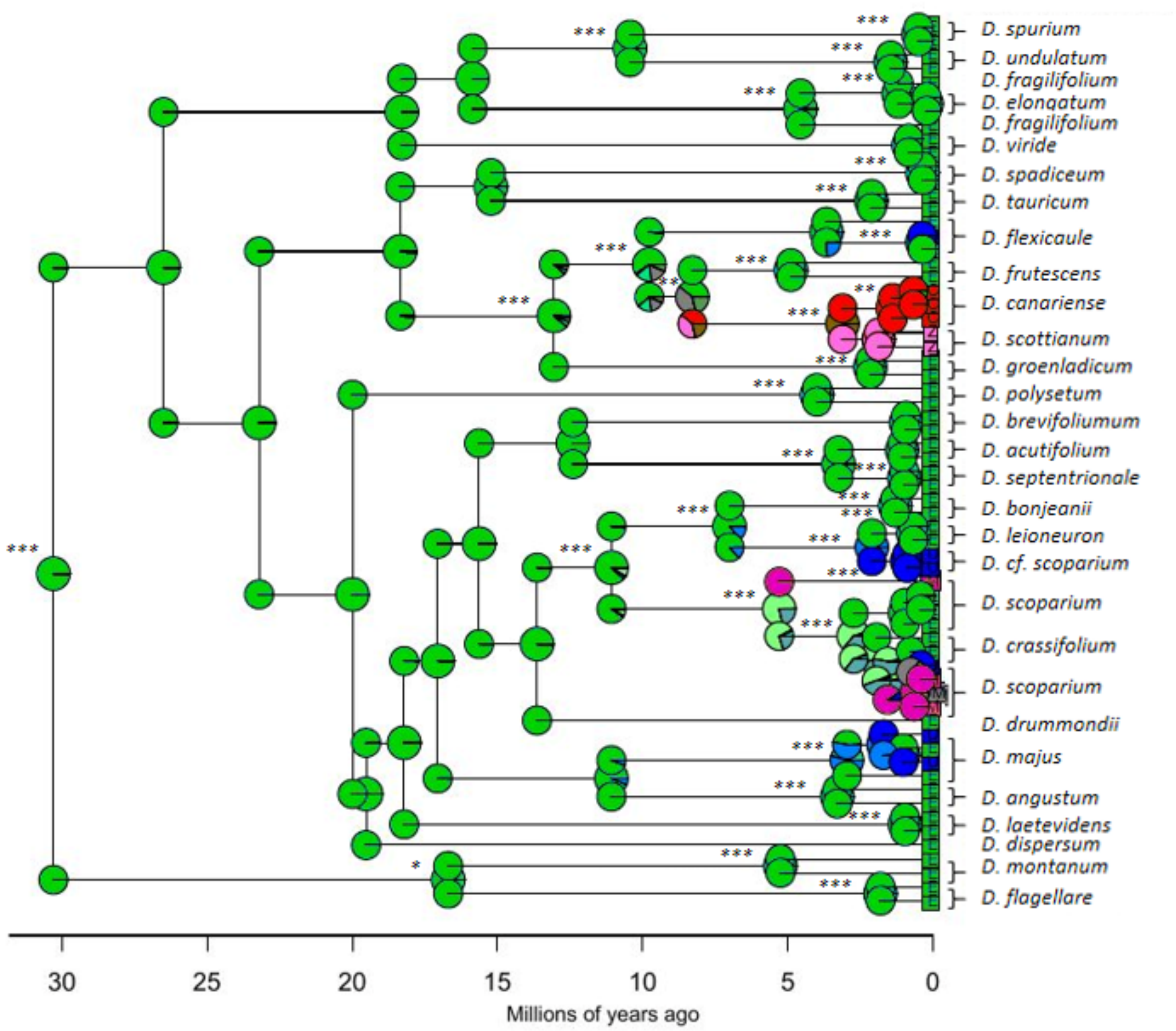


BioGeoBEARS 9.1: DEC on *Dicranum*



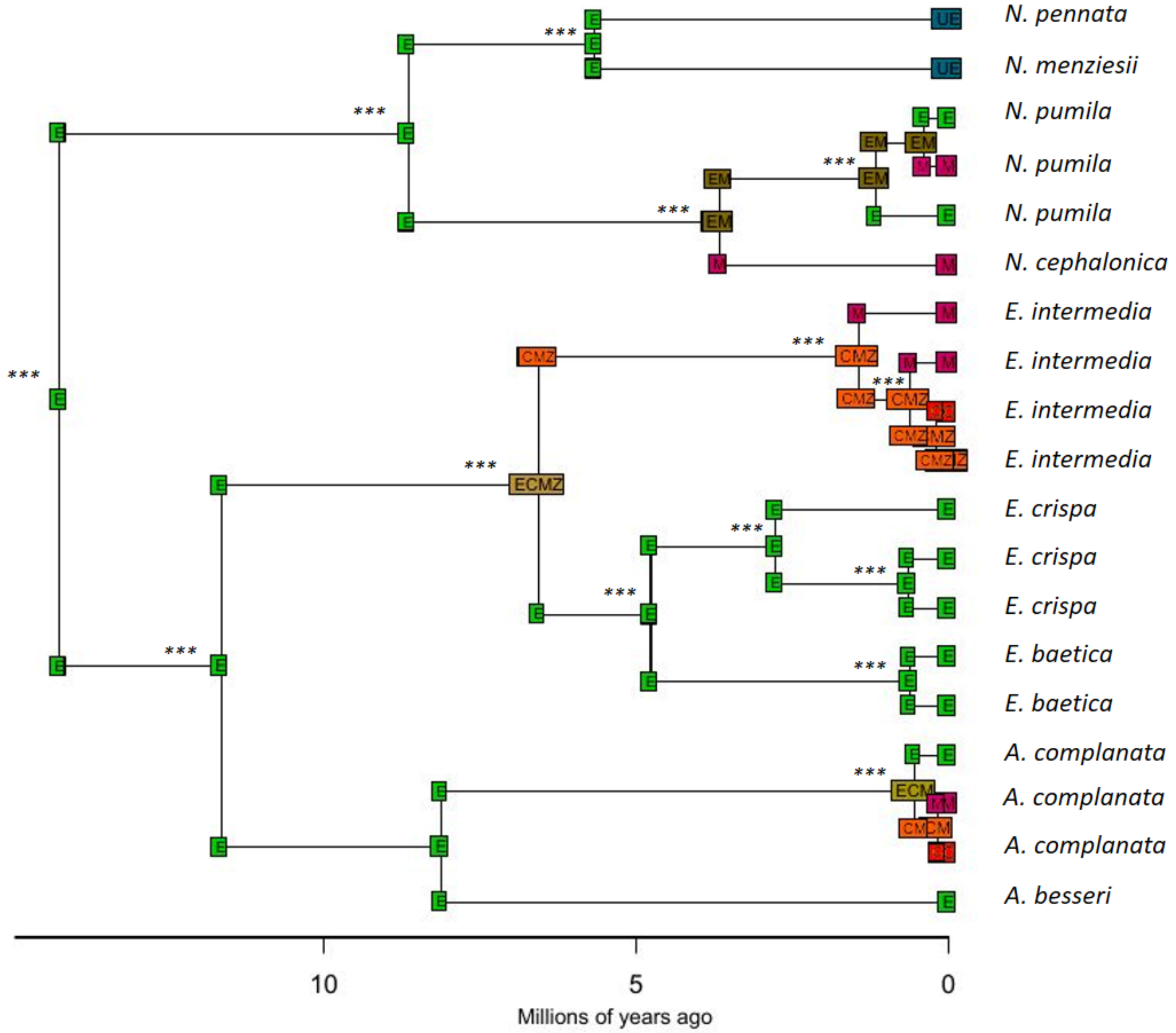
BioGeoBEARS 9.2: DEC on *Dicranum*

ancstates: global optim, 3 areas max. d=0.0044; e=0; j=0; LnL=−62.84

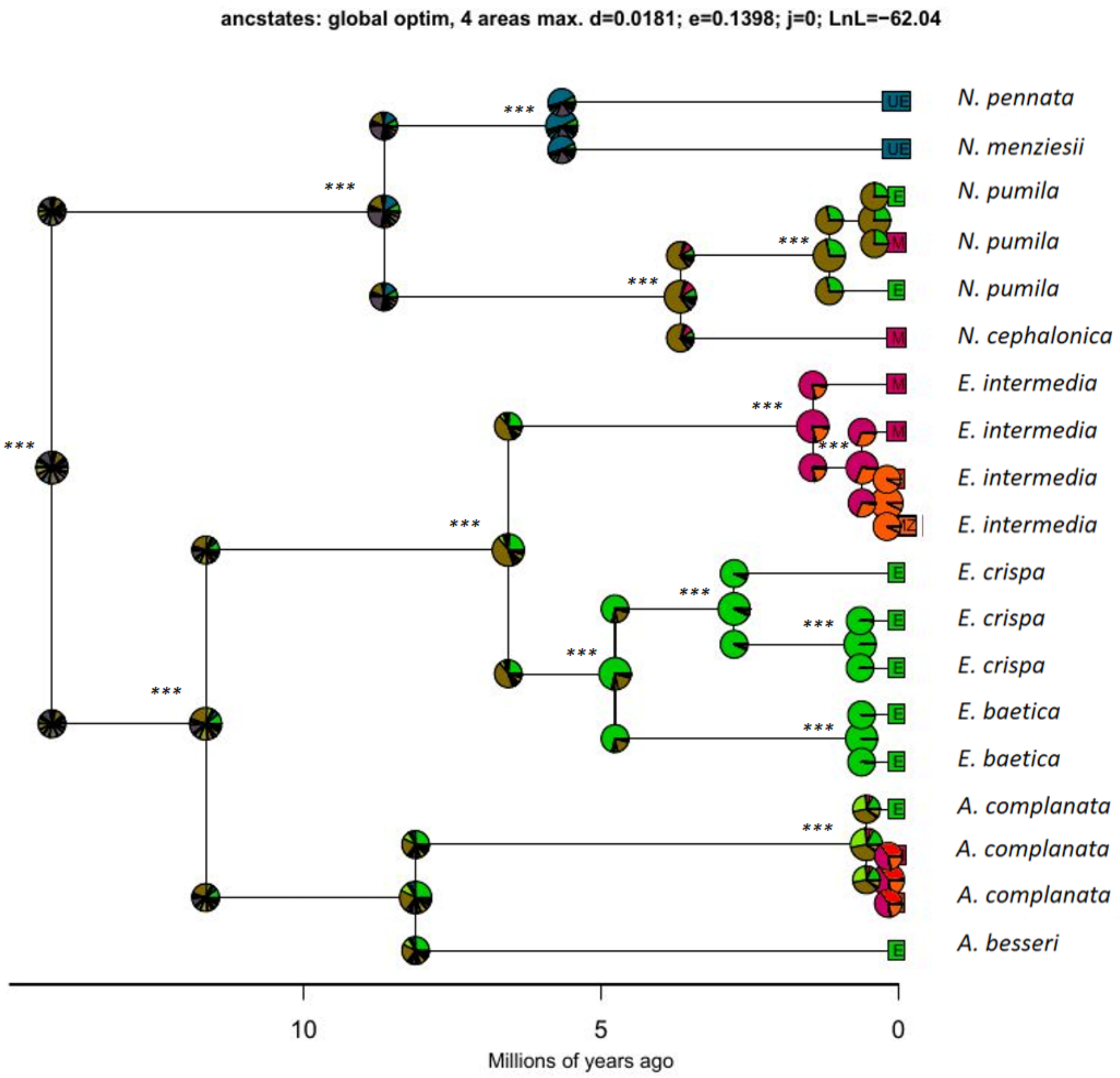


BioGeoBEARS 10.1: DEC on *Exsertotheca*

ancstates: global optim, 4 areas max. d=0.0142; e=0; j=0; LnL=−39.65

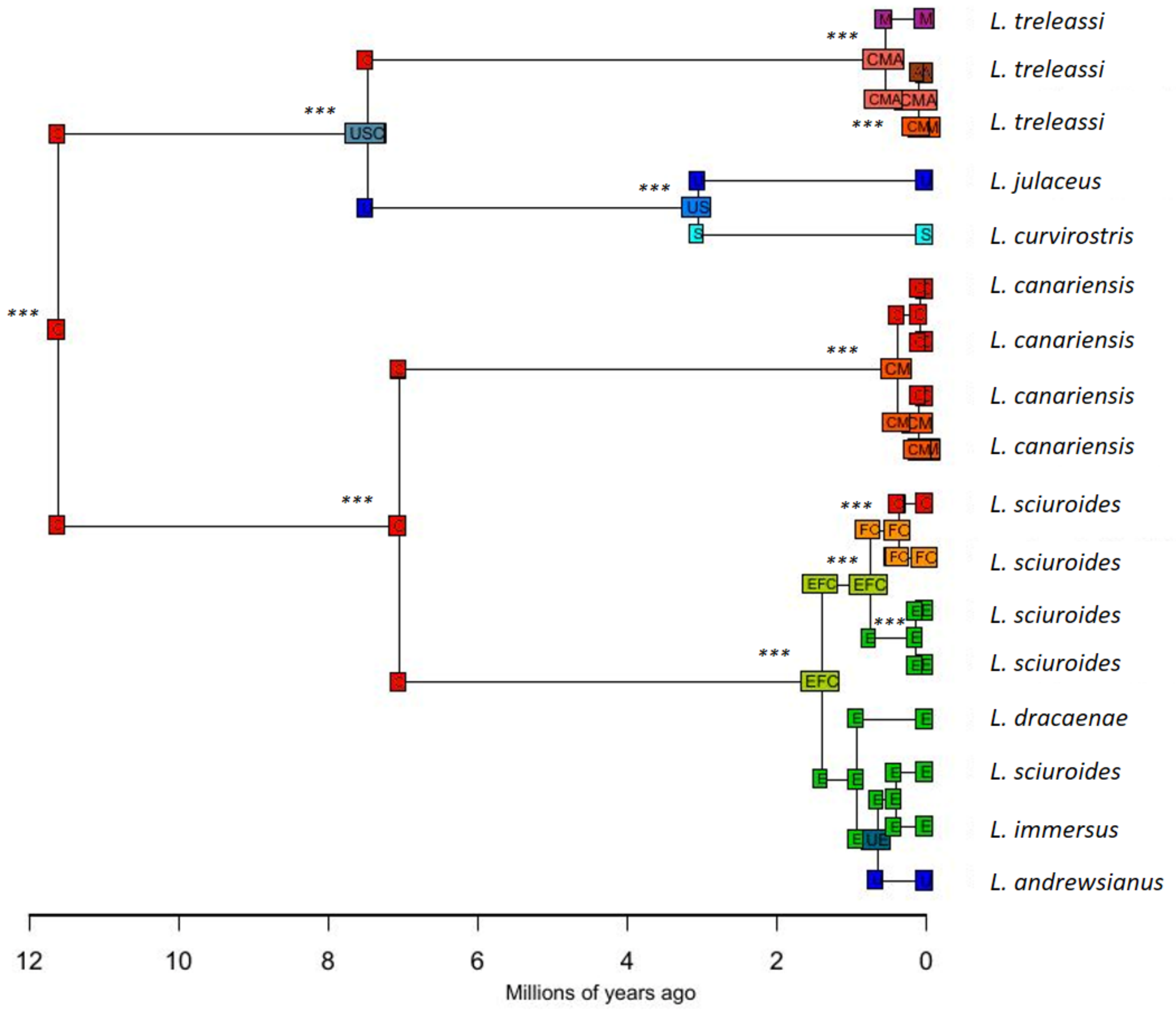


BioGeoBEARS 10.2: DEC on *Exsertotheca*



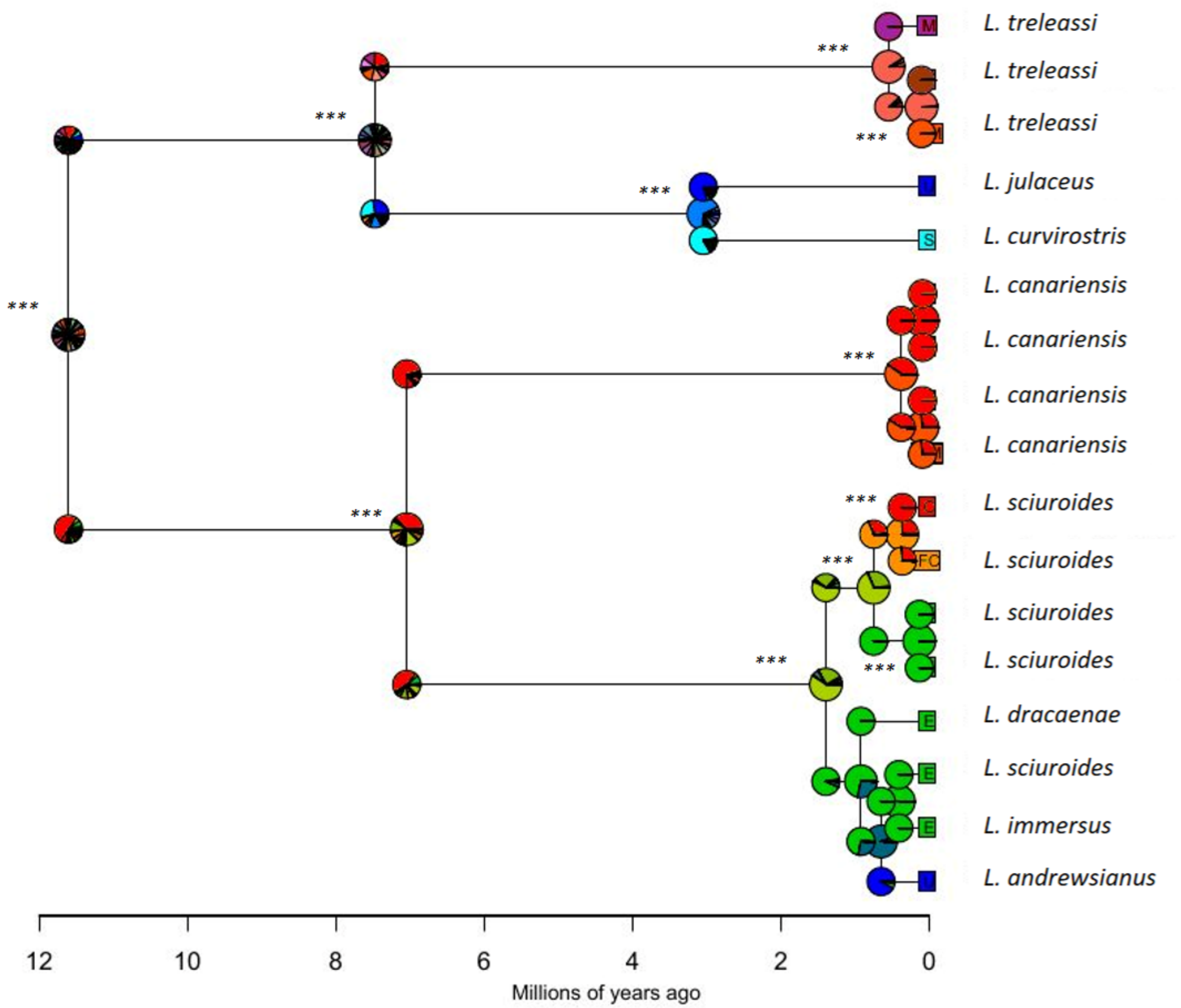
BioGeoBEARS 11.1: DEC on *Leucodon*

ancstates: global optim, 3 areas max. d=0.0319; e=0.0216; j=0; LnL=−38.53

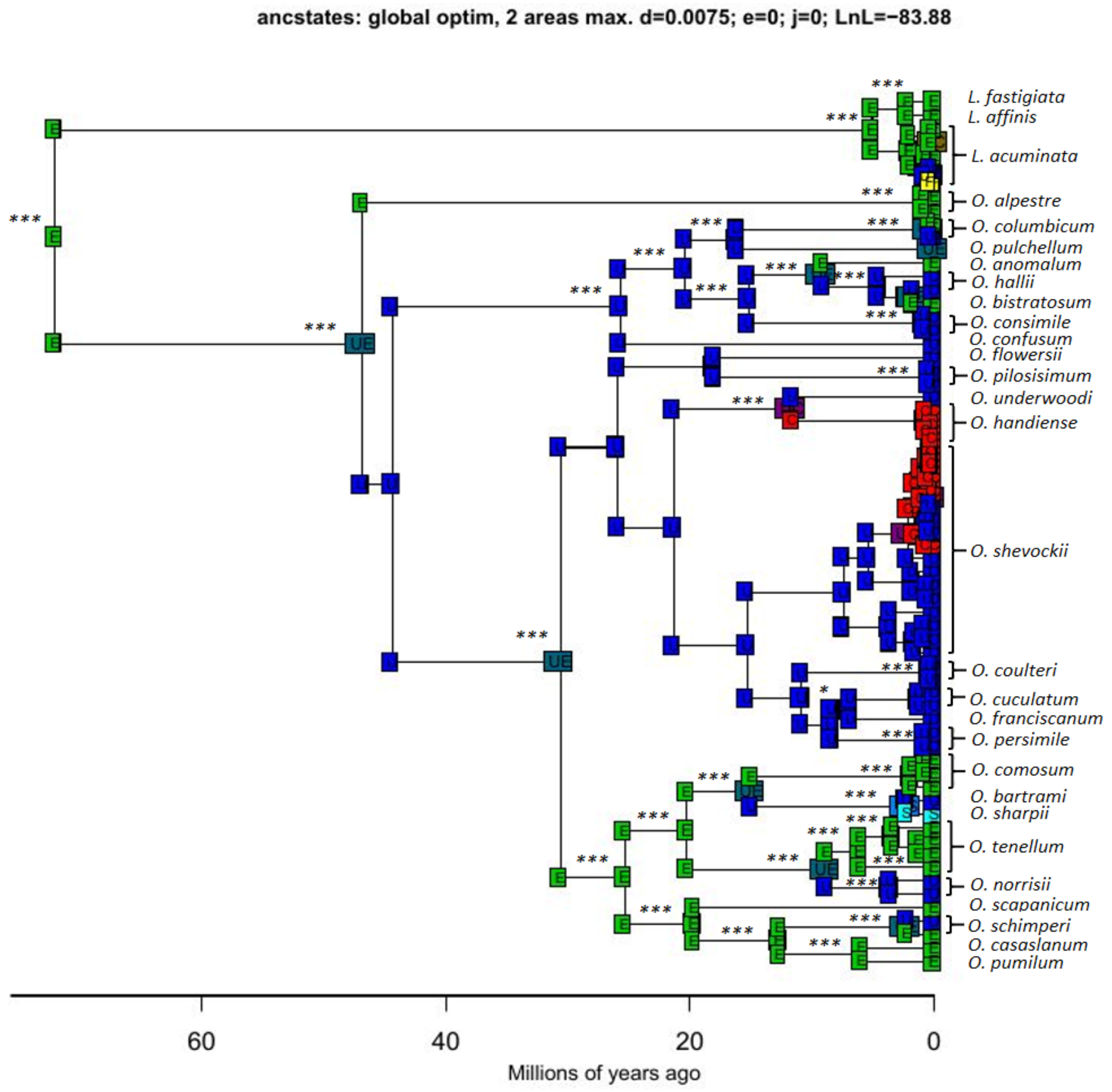


BioGeoBEARS 11.2: DEC on *Leucodon*

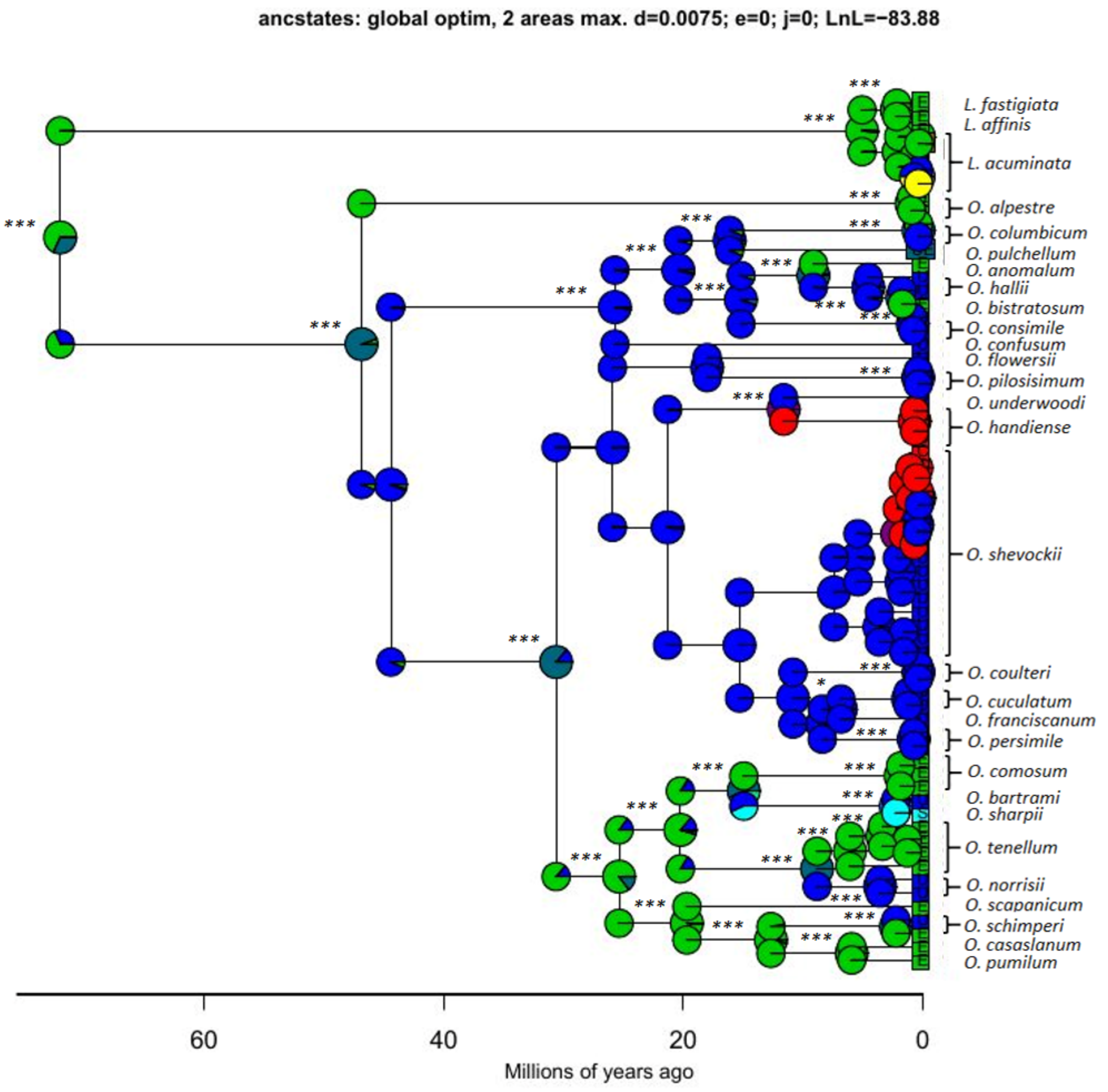
ancstates: global optim, 3 areas max. d=0.0319; e=0.0216; j=0; LnL=−38.53



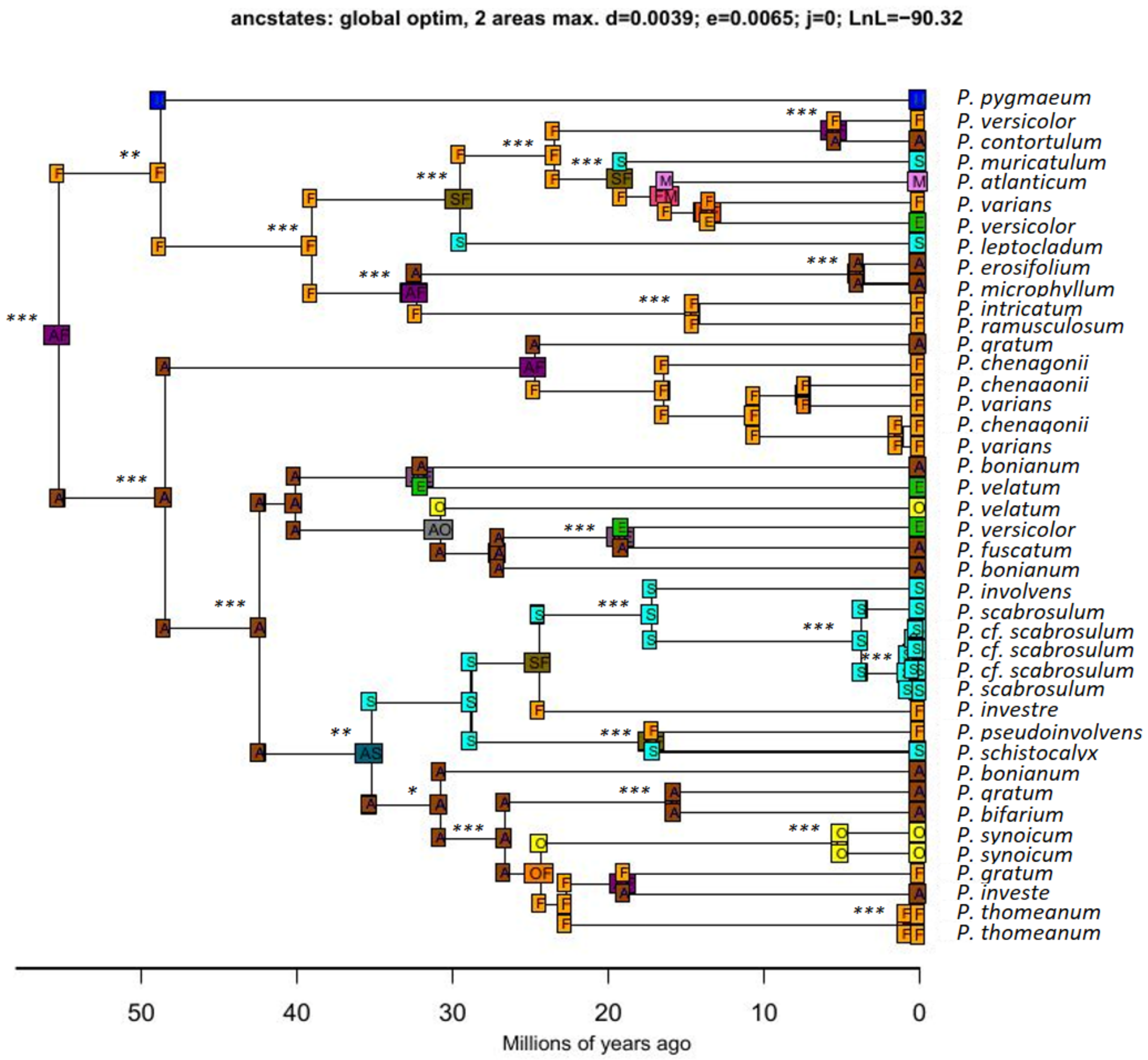
BioGeoBEARS 12.1: DIVALIKE on *Orthotrichum*



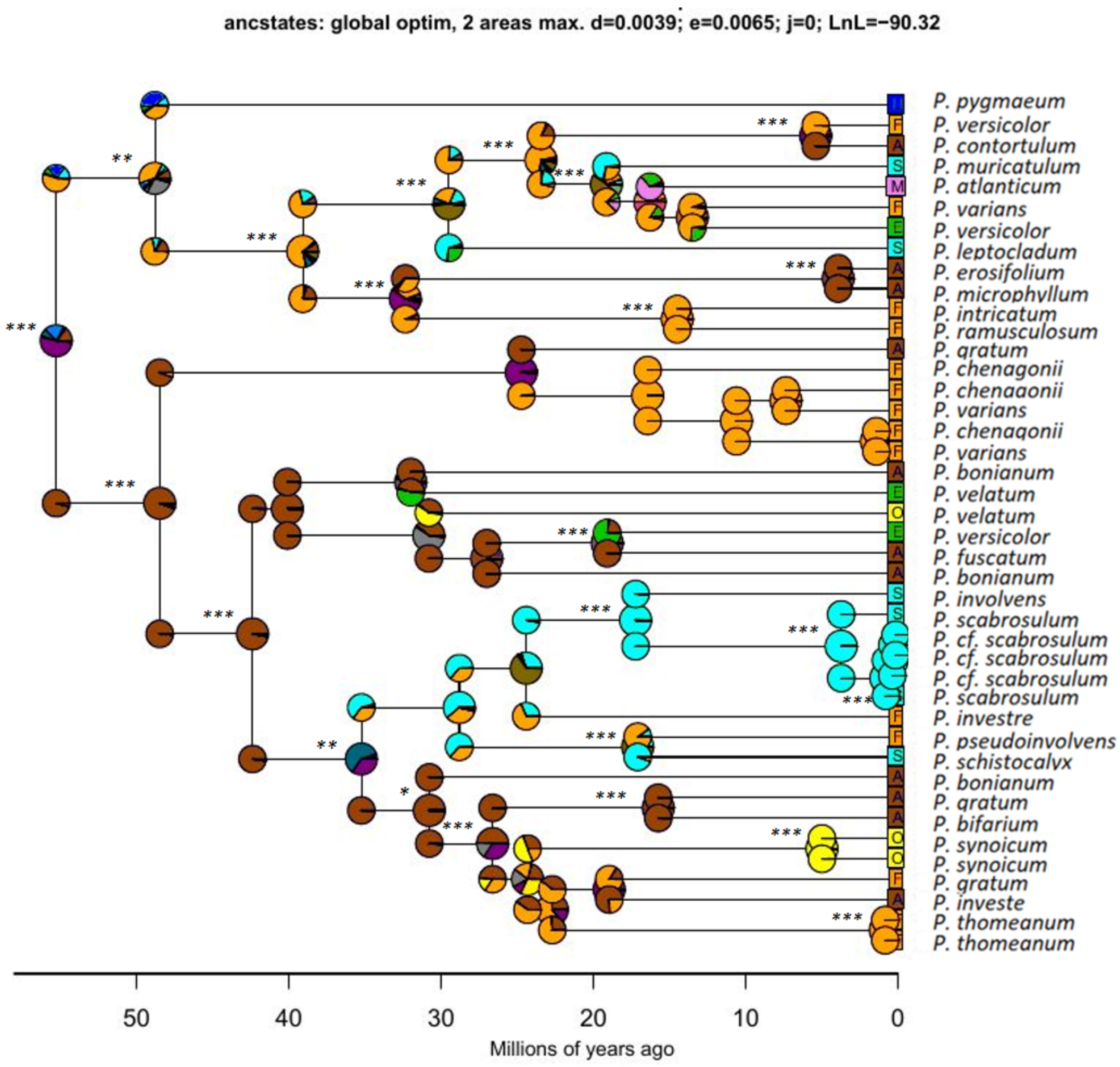
BioGeoBEARS 12.2: DIVALIKE on *Orthotrichum*



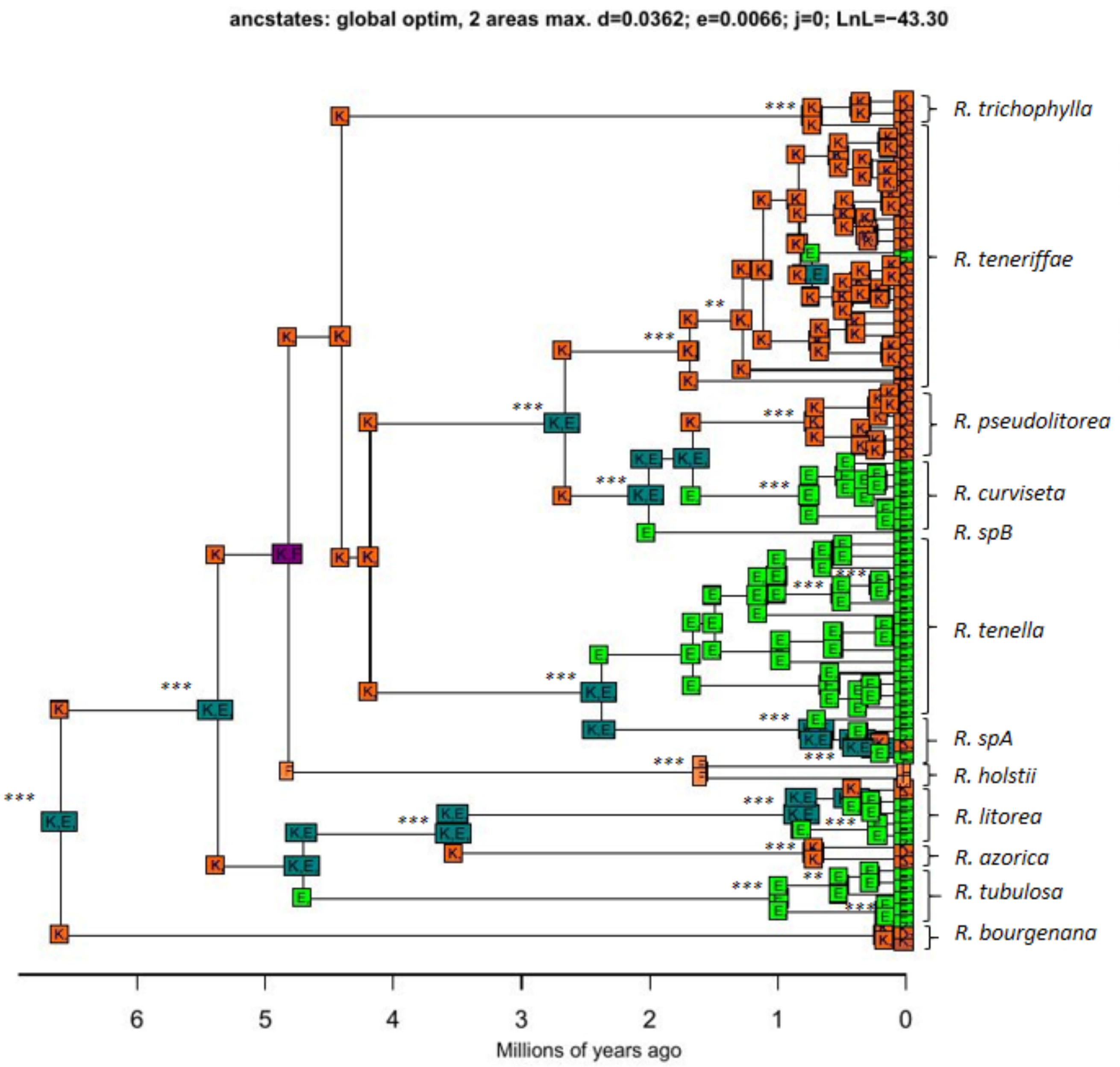
BioGeoBEARS 13.1: DIVALIKE on *Pelekium*



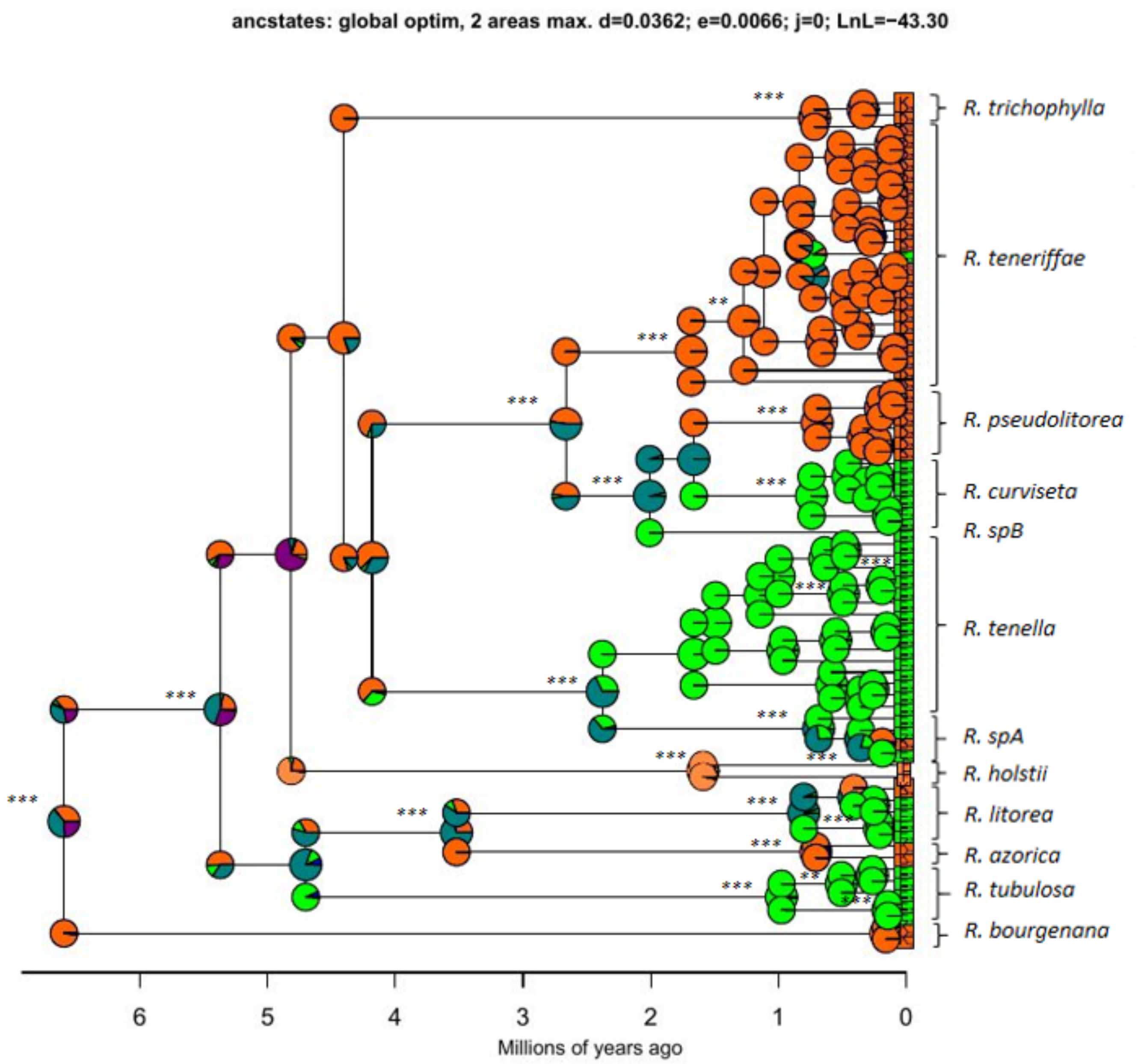
BioGeoBEARS 13.2: DIVALIKE on *Pelekium*



BioGeoBEARS 14.1: DEC on *Rhynchostegiella*

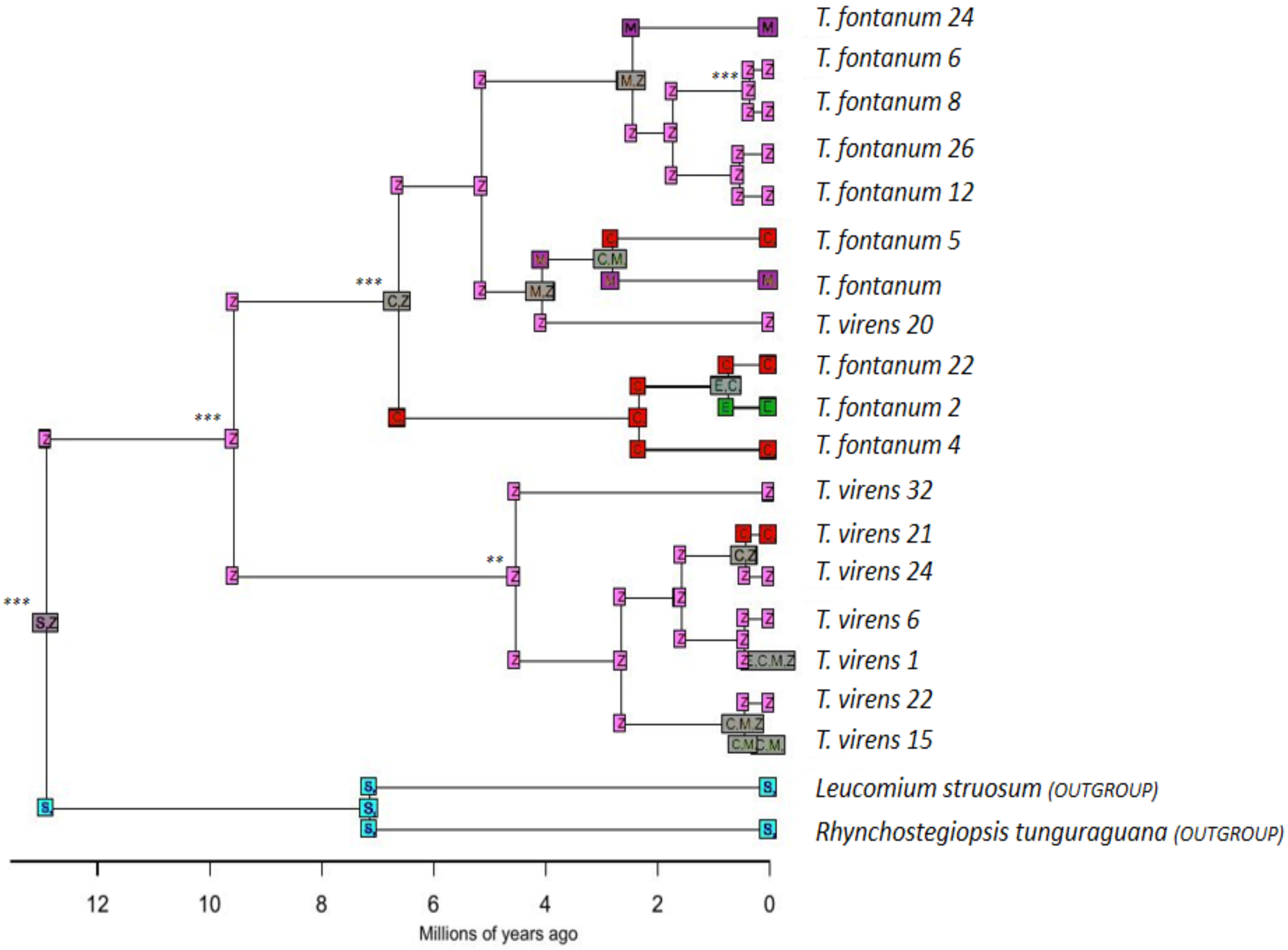


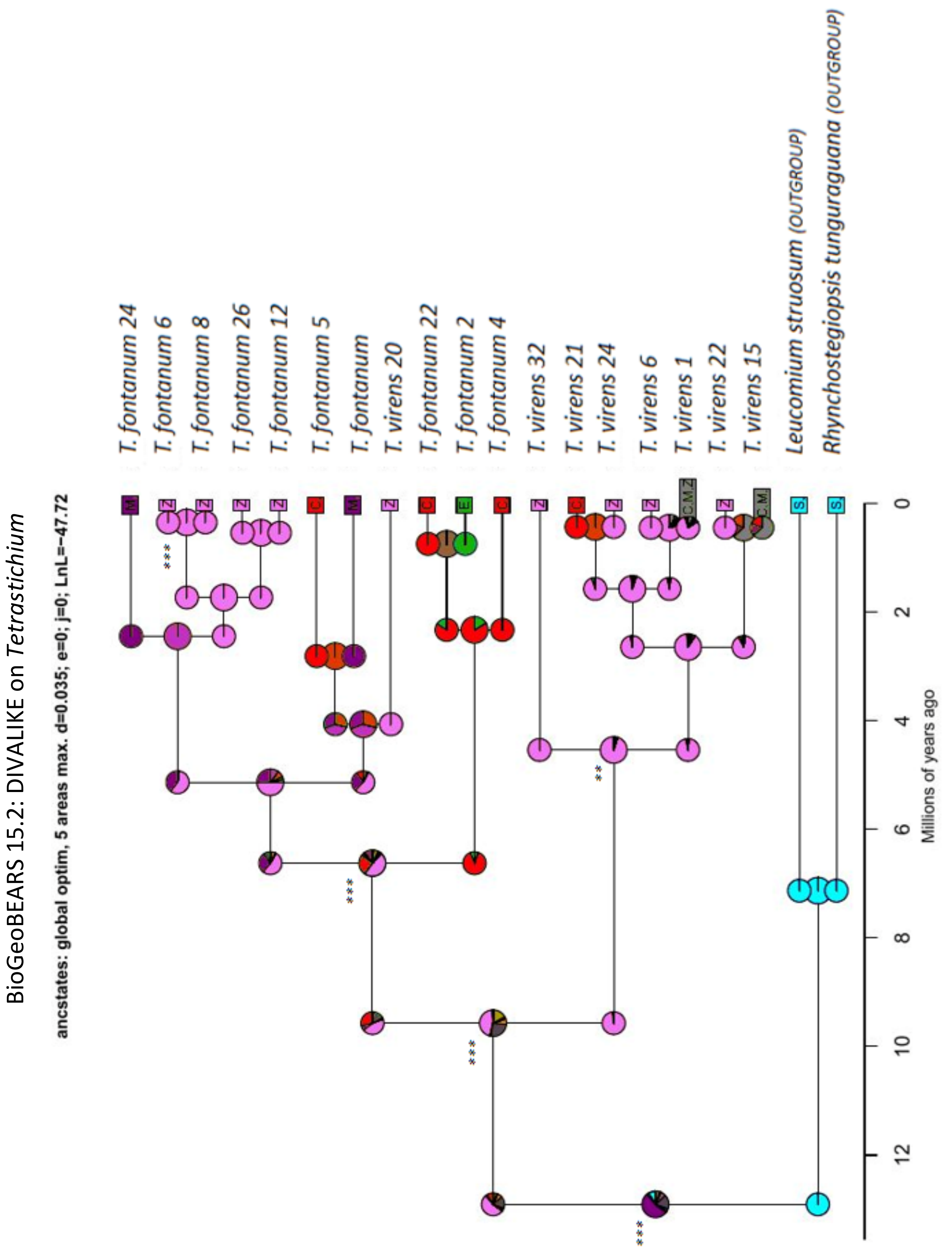
BioGeoBEARS 14.2: DEC on *Rhynchostegiella*



BioGeoBEARS 15.1: DIVALIKE on *Tetrastichium*

ancstates: global optim, 5 areas max. d=0.035; e=0; j=0; LnL=−47.72

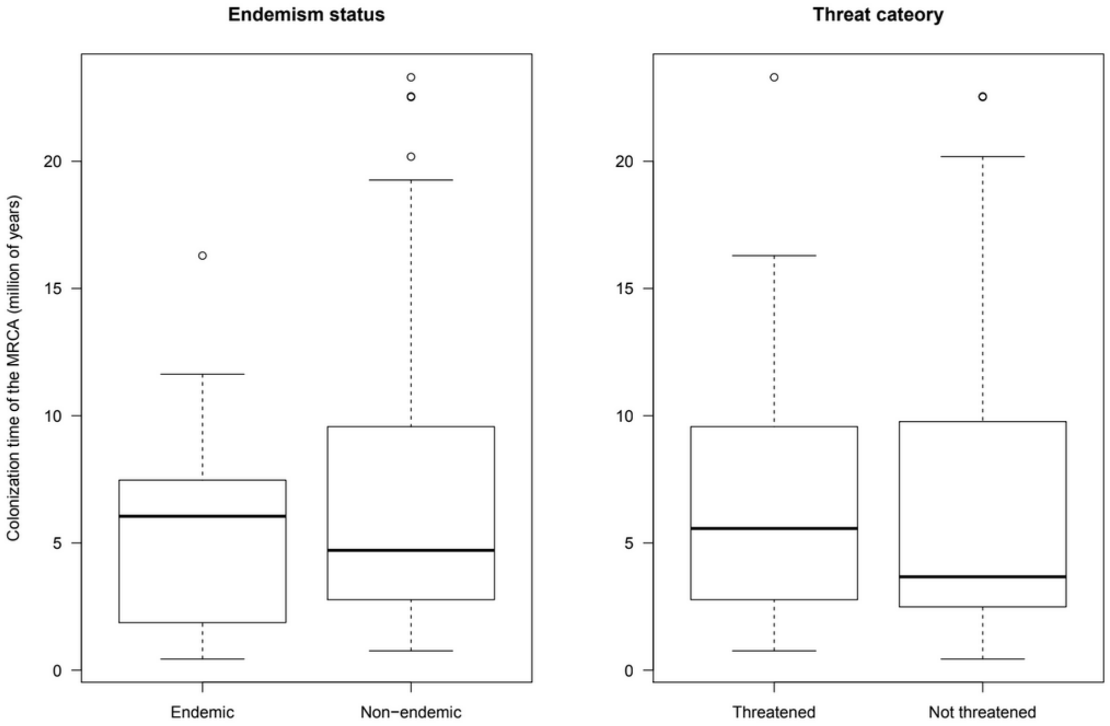




Supplementary Material 7: "BioGeoBEARS" ancestral areas reconstruction. *Those are the 30 BioGeoBEARS results represented on the MCC trees, with the estimated ancestral area and their estimated posterior probabilities, of the 15 datasets object of this Master Thesis. Posterior probabilities are pointed as (***) for >0.95 pp, (**) for 0.90-0.95 pp and (*) for <0.80 pp.*

SUPPLEMENTARY MATERIAL 8:

Kruskal-Wallis test



Supplementary Material 8: Kruskal-Wallis test. *Those box-plots represents the differences in time of colonization mean age for threatened and endemic species analysed on this Master Thesis with the Kruskal-Wallis test.*