

UNVEILING HISTORICAL CONNECTIONS BETWEEN ISLAND AND CONTINENTAL FLORAS: PHYLOGEOGRAPHIC EVIDENCE FROM MACARONESIAN BRYOPHYTES

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Abstract

- Since the traditional perception of islands as sinks of continental biodiversity, the relationships between island and mainland floras have been controversial. In particular, the larger carrying capacity and connectivity of islands during glacial periods has suggested a potentially important role of islands for continental diversity, especially in organisms with high dispersal capacities. Focusing on bryophytes, we determine the historical relationships between island and mainland populations and test the hypothesis that island colonization prevailed during glacial periods.
- Competing scenarios regarding the biogeographic origin and timing of colonization of islands were tested from analyses of DNA sequence data in 9 amphi-Atlantic species disjunct between Macaronesia and continental regions on both sides of the North Atlantic in a coalescence framework.
- The Macaronesian bryophyte flora results from a complex mix of origins, with the archipelagos acting as a source or a sink for mainland species from various continents, highlighting the complexity of its assembly mechanisms. No clear pattern emerged regarding the timing of colonization events.
- Our analyses indicate that extra-European regions have contributed to the diversity of Macaronesian bryophytes much beyond what the 90% of floristic similarity between Europe and Macaronesia would suggest. In groups with high long-distance dispersal capacities like bryophytes, floristic similarity hence appears as a poor indicator of biogeographic origin. The large contribution of extra-European regions to the Macaronesian bryophyte flora also explains why the endemic element has a primarily extra-European origin.

Keywords

Approximate Bayesian Computation; bryophytes; coalescence; endemism; island biogeography; Macaronesia; oceanic islands.

Introduction

Islands, accounting for approximately 5% of global emerged land, are among the most important biodiversity reservoirs on the planet (Schrader et al. 2024) but have traditionally been perceived as sinks of biodiversity. This view is best illustrated by Wilson's (1961), p. 185 statement that a 'taxon can undergo alternate expansion and contraction, with or without speciation, for an indefinite period of time; it can shift its headquarters from a large land mass to a smaller one but not in the opposite direction'. Such a perception of islands as evolutionary dead-ends has been intimately associated with the long-held notion that dispersal capacity is counter-selected on islands (Burns 2019), a view that has, however, been increasingly challenged (García Verdugo et al. 2017; Burns 2018).

The idea that insular diversity could contribute to continental diversity has, in fact, already been considered since the 19th century. Based on the observation that several plant lineages occurring in Morocco but having their centre of distribution on the oceanic archipelagos of the Azores, Canary Islands, Madeira and Cape Verde, collectively forming the Macaronesian biogeographic region (Fernandez-Palacios' et al. 2024), Ball (1878) and Hooker (1878) hypothesized that some mainland lineages might have originated on islands. This 'islands-to-continent' hypothesis, however, remained extremely controversial (Seidel 1988; Park et al. 2001). Subsequent phylogeographic inference of the evolution of island/mainland relationships allowed this hypothesis to be formally tested, with a similar number of empirical studies refuting (Austin et al. 2004; Poux et al. 2005; Tolley et al. 2013; Fritz et al. 2024) or supporting (Nicholson 2002; Crawford & Smith 2005; Filardi & Moyle 2005; Nicholson et al. 2005; O'Grady & DeSalle 2008; Lapoint et al. 2013) a scenario of back-colonization from insular to continental regions. A paradigm shift, highlighting the crucial role played by insular diversity for continental diversity, progressively took place in the early 2000s (de Queiroz 2005; Heaney 2007; Bellemain & Ricklefs 2008). In this context, the Macaronesian region has served as a prime model to evidence the relevance of continental back-colonization from insular ancestors (Carine et al. 2004; Caujapé-Castells 2011).

The hypothesis of a much more important role of islands for continental diversity has further gained support from a glacial-sensitive model of island biogeography as a result of the projection of MacArthur & Wilson's equilibrium theory of island biogeography (MacArthur & Wilson's 1967) during glacial/interglacial cycles of the late Pleistocene (Fernández-Palacios et al. 2016). During glacial cycles, islands exhibited a larger size and elevation and lower geographic isolation than during interglacial periods. In those conditions, MacArthur & Wilson's model predicts that island carrying capacity peaks during glacial periods, whereas extinction rates show the reverse pattern. These predictions have been supported by empirical evidence across island floras worldwide that islands with the largest variation of size and connectivity between glacial and interglacial periods exhibit the highest species richness and proportion of endemic species (Weigelt et al. 2016). The fluctuations of island properties between glacial and interglacial periods, such as area, altitude and distance to mainland, further lend support to the 'window of colonization' hypothesis, which, based on phylogeographic evidence, posits that opportunities for colonization into Macaronesia have been temporally constrained to discrete waves of colonization (Carine 2005).

The relevance of islands as a source for continental diversity depends on their geographic isolation, but also on species dispersal capacities. Among land plants, bryophytes primarily disperse by tiny spores (10–30 µm) with high long-distance dispersal capacities. Bryophytes hence display large distribution ranges that are often disjunct between both sides of oceans (Patiño & Vanderpoorten 2018), which play a little role in structuring the spatial variation of bryophyte genetic diversity, evidencing efficient trans-oceanic dispersal

(Désamuré et al. 2016; Kyrkjeeide et al. 2016). In this context, phylogeographic analyses revealed the large contribution of migrants of extra-European origin during the post-glacial recolonization of Europe (Ledent et al. 2019), raising the question of the biogeographic relevance of oceanic archipelagos for continental diversity. Phylogeographic evidence in the moss *Rhynchostegium riparioides* further suggests that, in agreement with the expectations of the glacial-sensitive model of island biogeography (Fernández-Palacios et al. 2016) and the hypothesis that islands served as refugia for continental biodiversity, population size was larger in the Macaronesian archipelagos during glacial than interglacial periods, and migration rates were higher from Macaronesia to the mainland than the reverse (Hutsemékers et al. 2011). Focusing on the hyper-oceanic bryophyte flora disjunct between Macaronesia and the eastern Atlantic fringe, Patiño et al. (2015) highlighted the key role of oceanic archipelagos as stepping-stones for species of primarily tropical origin, their subsequent speciation in islands and eventual emigration towards western Europe.

Here, we reconstruct the biogeographic history of amphi-Atlantic species disjunct between Macaronesia and continental regions on both sides of the North Atlantic to test the role of islands as sinks, sources or stepping-stones. Specifically, we address the following questions:

- What have been the historical relationships between island and mainland populations?
- Is the timing of the colonization of the Macaronesian archipelagos and any subsequent (back-) colonization of continental areas compatible with the hypothesis that:
 - islands had higher carrying capacity and lower geographic isolation during glacial periods?
 - severe extinctions in mainland areas made the latter largely available for migrants of allochthonous origin?

Material and methods

DATA COLLECTION AND SUMMARY STATISTICS OF POPULATION GENETICS

Among 405 amphi-Atlantic bryophyte species occurring in Macaronesia (Mouton et al. 2023), we explored the National Library of Medicine (<https://www.ncbi.nlm.nih.gov>) to target species for which DNA sequence data were available across their entire range, split into three main regions, namely Macaronesia, Europe and the Mediterranean basin and North or South America plus, in some cases, other regions. These species were also selected on the basis that at least 3 accessions for each of the three regions defined were available. Nine species, 4 liverworts and 5 mosses, met the above criteria, with a total number of accessions ranging between 21 and 179 and the number of available loci ranging between one (concatenated cpDNA sequences) to 4 (concatenated cpDNA sequences and nuclear loci) (Table S1).

The sequences were downloaded from NCBI and aligned with the Clustal Omega algorithm (Sievers et al. 2011) as implemented on the EMBL-EBI online servers (Madeira et al. 2019). The alignments were checked manually on PhyDE[®], and pruned from ambiguous positions with Gblocks (v0.91b) (Talavera & Castresana 2007) as implemented on NGphylogeny.fr (Dereeper et al. 2008; Lemoine et al. 2019) with the following criteria: min. length of a block = 5 nucleotides, keep a position with a gap within an appropriate block = max. 50% of the sequences, min. length to remove a segment with contiguous non-conserved positions = 8, min. number of sequences for a flank position = 85%. Indels within the alignments were scored using the Modified Complex Index Coding (MCIC, (Müller 2006)) as implemented in SeqState v1.4.1 (Müller 2005).

Chloroplast genes were concatenated into one locus with a custom R v4.4.1 (R Core Team 2024) code and the ape package v5.8 (Paradis & Schliep 2019).

For each species, the genetic diversity and structure of the populations of each of the three regions (Macaronesia, Europe and the Mediterranean basin and other regions) was characterized by the expected heterozygosity (H_e), number of private polymorphic sites (PrS), average nucleotide diversity (π) among pairs of samples, G_{ST} and N_{ST} , computed across all three regions and between each pair or regions. G_{ST} and N_{ST} are two complementary metrics of genetic structure based on allele frequencies, taking into account (N_{ST}) or not (G_{ST}) the genetic distance among alleles (Pons & Petit 1996). N_{ST} values were computed from a Tamura & Nei's distance matrix (Tamura & Nei 1993) as implemented in Arlequin v3.5.2.2 (Excoffier & Lischer 2010). The summary statistics and their significance level were computed using ARLSUMSTAT v3.5.2.2 (Excoffier & Lischer 2010) and Arlequin v3.5.2.2, respectively.

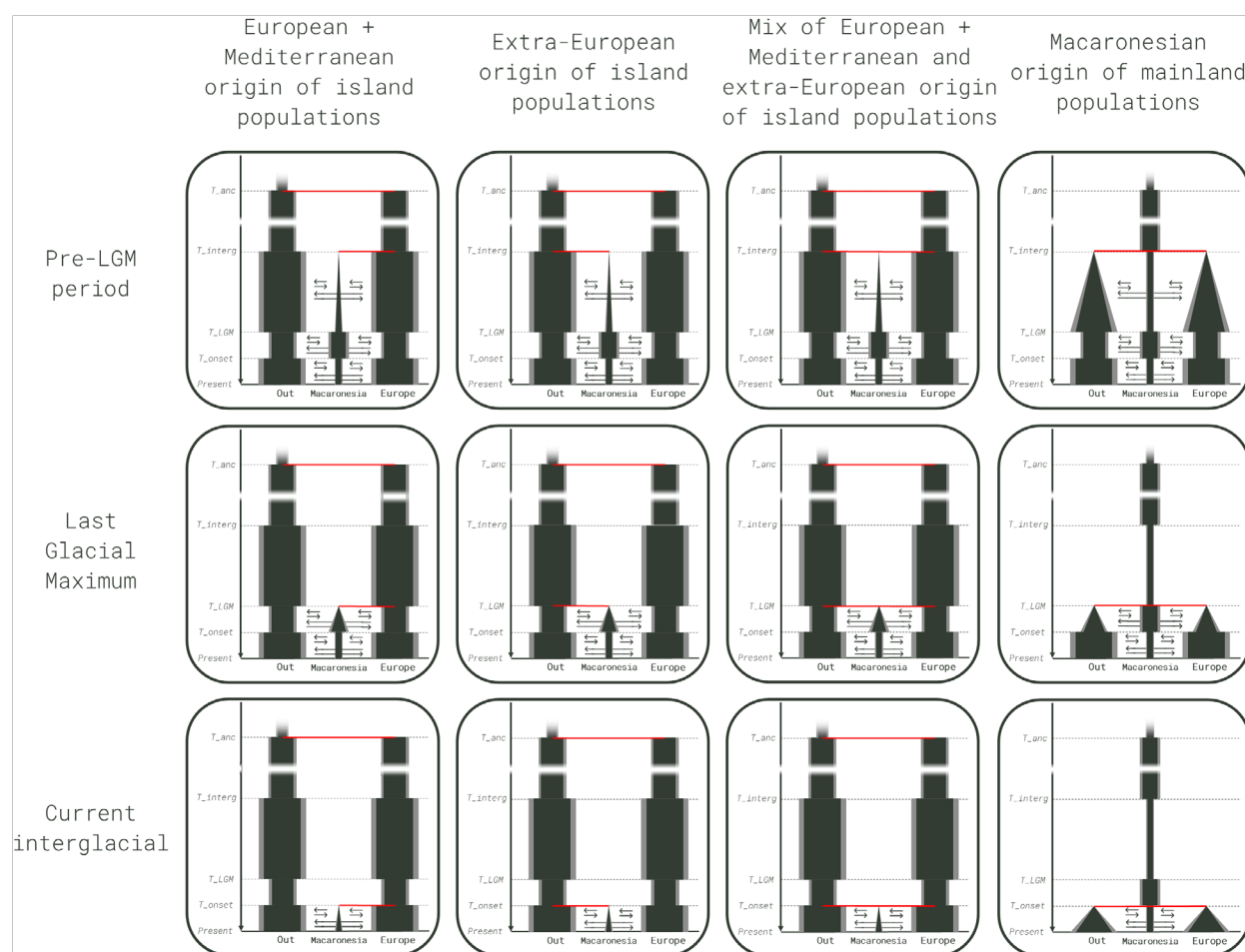


Fig. 1. Hypothetical phylogeographic scenarios for the relationships between populations from Macaronesia, Europe and the Mediterranean basin (Europe) and other regions (Out) since the last interglacial period. A combination of four scenarios of geographic origin (columns) and timing of colonization (rows) was considered. Column width is proportional to effective population size. Arrows represent migration rates among regions and red lines represent founder effects and their source population. T_{onset} : onset of the present interglacial period. T_{LGM} : beginning of the Last Glacial Maximum (LGM). T_{Interg} : pre-LGM period. T_{ANC} : ancient artificial event allowing the coalescence of remaining alleles.

PHYLOGEOGRAPHIC INFERENCE

DESIGN OF THE BIOGEOGRAPHIC SCENARIOS AND ASSOCIATED PARAMETERS

Competing scenarios of the origin and relationships between the populations of Macaronesia, Europe and other regions were tested in a three-step process involving (i) the simulation, in a coalescent framework, of gene genealogies compatible with each of the 12 scenarios being tested; (ii) the mapping of substitutions on the gene genealogies compatible with each scenario to generate alignments of DNA sequence data of the same size as the observed data; and (iii) the comparison of the summary statistics of genetic structure and diversity derived from the simulated and observed data to identify the demographic scenario and associated parameters that are the most likely to have generated the observed data.

Twelve biogeographic scenarios were considered (Fig. 1) based on the geographic origin of Macaronesian populations (i) European and Mediterranean (Europe), (ii) extra-European (Out), (iii) mixed (European + extra-European), or (iv) Macaronesian origin of the continental populations (Macaronesia), and the timing of the founder events (current interglacial period (Onset), LGM, pre-LGM period (InterG); see below). Based on the application of the glacial-sensitive model of island biogeography (Fernandez-Palacios' et al. 2016), mainland populations experienced a bottleneck at LGM followed by an expansion during interglacial periods, whereas island populations showed the reverse trend. Each scenario is characterized by a specific combination of parameters.

Three time slices, corresponding to major macroclimatic events, were considered. At each simulation, one value was sampled for each of the three time slices from uniform distributions. The time slices had non-overlapping boundaries to maximize the differentiation among scenarios designed to address the question of the timing of the founder events as follows: the current interglacial, between 1000 years BP and 15,000 years BP; the Last Glacial Maximum (LGM), between 19,000 and 26,000 years BP; the pre-LGM period, between 29,000 and 250,000 years BP. These time slices were associated with different demographic events in island and mainland areas. An ancestral artificial event was implemented to allow the coalescence of all remaining alleles within a single population, marking the end of the simulation (fixed at 500,000 years BP). A generation time of 5 years was implemented based on Patiño et al. (2015) and Ledent et al. (2019).

The present effective sample size (N_e) of each population was inferred as follows:

$$N_e = \theta/\mu \quad (1)$$

where θ was estimated from the data and μ , the absolute mutation rate per-generation, was set to an empirical value of $1e-7$ substitutions/site/generation, which is within the range of the posterior probability across different bryophyte species reported in Patiño et al. (2015), Désamoré et al. (2016) and Ledent et al. (2019). Since θ is the product of both N_e and μ , these two latter parameters cannot be dissociated from each other, so that any value fixed for μ will affect the estimation of N_e . As a result, N_e values can be compared relatively among each other, but their actual value cannot be interpreted. The range of variation of θ was characterized by a uniform distribution centred at the mean of the value of θ across loci and whose boundaries were defined by the standard deviation of θ (i.e., $\theta \pm \text{st.dev.}$). When the lower limit equalled 0 for a population, its number of sampled individuals was used as minimum value for the distribution. In populations where a single allele was sampled, θ cannot be computed. In this case, the lowest boundary was set as the number of sampled individuals and the upper boundary was defined from the value inferred for another variable locus in the population.

To generate priors for bottlenecks and expansions associated with shifts in macroclimatic conditions, we used information from species distribution models generated by Ledent et al. (2019) for 12 species of amphi-Atlantic bryophytes, including four species included in the present study. These models implemented three algorithms, namely General Linear Models, Gradient Boosted Machine and Random Forest to take model uncertainty into account and generate ensemble models. The latter were projected onto present time and LGM macroclimatic layers at 5 km² resolution. Based on this, we computed, for each species and each investigated region, the number of climatically suitable pixels and derived a ratio of suitability between glacial and interglacial periods. To allow our coalescence simulations to cover a broad range of bottleneck and expansion priors and avoid overspecific and narrow priors that would not adequately take the uncertainty of the approach into account, these ratios were pooled across species to generate uniform distributions of ratios of suitability by region implemented in the coalescence simulations (Table S2).

Founder effects associated with the colonization of Macaronesia from continental ancestors (columns 1–2–3, Fig. 1) and with the colonization of continental areas from Macaronesian ancestors (column 4, Fig. 1) were implemented from an initial population size of $N_{e_0} \in [2; 100]$. Subsequent population expansion was modelled using a growth rate r defined as:

$$N_{e_t} = N_{e_0} e^{rt} \quad (2)$$

where t is the time interval between the founder event and the end of the considered period, and N_{e_t} is the effective population size of the population of interest at the considered period, as estimated using Equation (1).

Asymmetric migration rates among regions were implemented at each time slice. A distinct migration rate was considered between continents (Europe vs. extra-European regions) and between islands and continents (Macaronesia vs. Europe and Macaronesia vs. extra-European regions). In the absence of information on those rates, we applied a very broad range spanning 1e-10 to 1e-1.

COALESCENCE SIMULATIONS, MODEL SELECTION AND VALIDATION

Coalescence simulations were computed using fastsimcoal2 v2.8 (Excoffier et al. 2013, 2021; Marchi et al. 2024). One million gene genealogies were simulated under the constraints of each of the 12 scenarios for each locus of each species. Given the broad range of migration rate values implemented, we split each of the 1,000,000 generations per scenario into two sets of simulations depending on the value of the migration rate sampled: a first set, wherein the sampled rates lay between 1e-10 and 1e-6, and a second set, wherein the sampled rates lay between 1e-5 and 1e-1. We then tested whether simulations with low vs. high migration rates better fitted the observed data.

To identify the simulations (and migration rates values) that generated the data most compatible with the observed data, we computed the set of 15 summary statistics described above for each simulation. Highly correlated ($r > 0.95$) statistics were removed. From the species-specific number of remaining statistics describing the observed and simulated data, the fit of the observed data to the simulated data was investigated through Approximate Bayesian Computations (ABC) as implemented in ABCtoolbox v2.0 (Wegmann et al. 2010). A Euclidean distance was calculated between normalized observed and simulated summary statistics. The 2000 best simulations of each scenario were retained. A post-sampling regression adjustment (ABC-GLM, for General Linear Model) was implemented on the simulations retained (Wegmann et al. 2009) and the best-fit model and its associated parameters were selected based on the Bayes factor.

Two validation steps were implemented. To visualize whether the simulated data depart from the observed data in the space of the summary statistics employed, a Principal Component Analysis (PCA) was performed to plot the simulated (i.e., each retained simulation) and observed data. To detect a potential bias in the procedure of model selection in an ABC context (Robert et al. 2011), we simulated 10,000 datasets under each of the 12 demographic scenarios. These ‘pseudo-observed’ data were analysed using the same procedure of model selection as described above to compute the percentage of simulations erroneously assigned to each scenario, as implemented by the ‘*modelChoiceValidation*’ option of ABCtoolbox.

Results

Genetic diversity tended to exhibit similar levels on islands and continents, except for substantially higher expected heterozygosity in Macaronesian *Radula lindenbergiana* and higher nucleotide diversity in *Odontoschisma sphagni* (Table S3). There was systematically a higher differentiation (H_e and π_{ST}) between Macaronesian and extra-European populations than between Macaronesian and European ones, except for *O. sphagni*.

Table 1. ABC-GLM model validation. False-positive (validation of model choice) rates refer to the proportion (%) of false positives, that is, simulations generated under all the demographic scenarios but the best-fit one and erroneously assigned to the latter.

species	best-fit model	false-positive rate (%)
<i>Bryoxiphium norvegicum</i>	Low_Maca_LGM	14
<i>Calypogeia fissa</i>	Low_Out_INTERG	8
<i>Grimmia montana</i>	High_Maca_INTERG	8
<i>Kindbergia praelonga</i>	High_Europe_ONSET	9
<i>Metzgeria furcata</i>	Low_Europe_LGM	13
<i>Pulvigeria lyellii</i>	High_Maca_LGM	3
<i>Odontoschisma sphagni</i>	High_Mix_ONSET	8
<i>Radula lindenbergiana</i>	Low_Out_ONSET	9
<i>Scleropodium touretii</i>	High_Maca_LGM	10

Model names are in three parts: migration rate matrix used (Low or High), geographic origin of the populations (Out = Macaronesian populations from extra-European region, Europe = Macaronesian populations from Europe and the Mediterranean basin, Mix = Macaronesian populations from both Europe and extra-European regions, Maca = Macaronesian region the origin of continental populations) and colonization period (ONSET = present interglacial period, LGM = during the LGM, INTERG = before the LGM).

Coalescence simulations generated data that were compatible with the observed summary statistics of genetic structure and diversity (Figs S1–S9). The procedure of model selection was characterized by low rates of false positives ranging between 3% and 14% (Table 1). The first comparison step of coalescence simulations, testing for the biogeographic origin of Macaronesian populations under two different migration rate matrices, revealed multiple patterns involving a Macaronesian origin of continental populations in four moss species and a continental origin of Macaronesian populations, including one moss and one liverwort species from Europe, two liverwort species from extra-European origins, and one liverwort species from both European and extra-European origins (Fig. 2, two first columns). Following the

second step of comparison, testing for the timing of colonization after having fixed the area of origin based upon the results at step1, colonization of Macaronesia from the mainland and vice versa, more frequently took place since the LGM, either during it (3 moss and 1 liverwort species) or during the current interglacial period (1 moss and 2 liverwort species), than before the LGM (1 moss and 1 liverwort species) (Fig. 2). In species, for which a scenario of continental colonization of the mainland from Macaronesia was selected, continental colonization took place during the LGM. Simulations resulting from the implementation of matrices with either low or high migration rates were selected in a similar number of species (5 and 4, respectively) (Fig. 2).

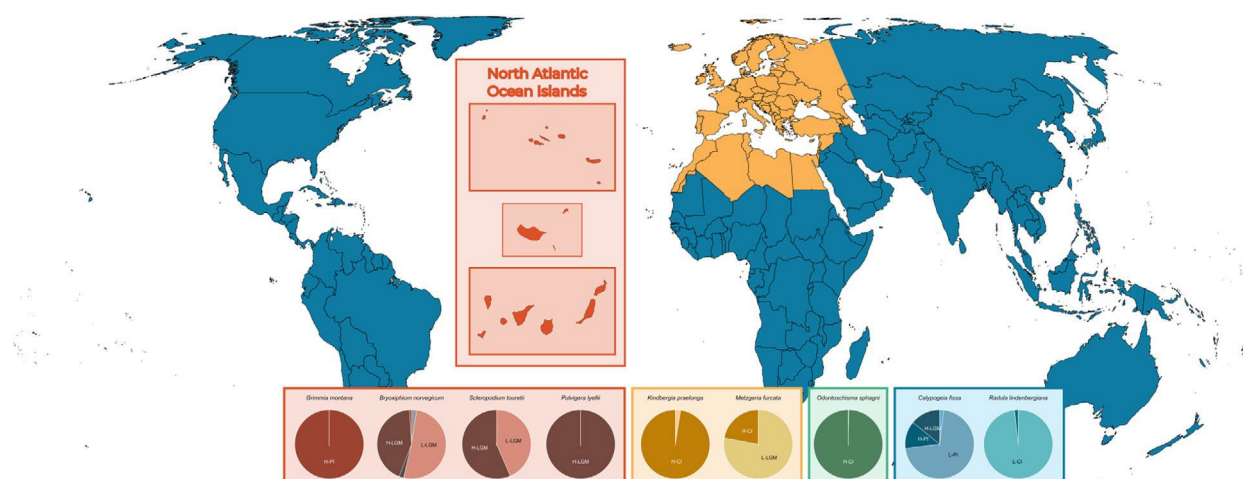


Fig. 2. Phylogeographic history of selected amphi-Atlantic bryophyte species inferred from coalescence analyses. Pie diagrams indicate the posterior probability of competing scenarios, involving (i) an origin of island populations from Europe and the Mediterranean (in yellowish tones), from extra-European origin (in bluish tones), from both Europe and the Mediterranean and extra-European areas (in greenish tones) and an origin of continental populations from island origin (in reddish tones) and (ii) a timing of colonization (CI = Current Interglacial Period, LGM = Last Glacial Maximum, PI = Penultimate Interglacial Period). H, L indicate whether a high or low migration rate matrix was selected (see material and methods for details).

Discussion

The present analyses revealed that the Macaronesian bryophyte flora results from a complex mix of origins, with the archipelagos acting as a source or a sink for mainland species from various continents, highlighting the complexity of its assembly mechanisms. The heterogeneous nature of the Macaronesian bryophyte flora was already emphasized from analyses of species distribution patterns, revealing that 17% of liverwort and 13% of moss species currently present in Macaronesia are not distributed in Europe and the Mediterranean (Mirolo et al. 2026), and hence, likely have an extra-European origin. Here, we show that, even within the pool of Macaronesian species shared with Europe, two out of the nine species investigated have an extra-European origin, and a third one originated from different mainland areas, pointing to a much more diverse origin of the Macaronesian flora than what floristic affinities would suggest. The discrepancy between biogeographic inferences derived from analyses of floristic relationships and molecular phylogeography, evidencing a higher role of extra-European areas as sources of Macaronesian diversity, is best illustrated by the case of the species complex of the simple thalloid *Metzgeria furcata* s.l. Initially considered as an amphi-Atlantic species (Schofield 1988), *M. furcata* consists of two main clades, one restricted to North America and the other exhibiting an amphi-Atlantic range (Fuselier et al. 2009). These

clades are now considered as distinct species, namely *M. setigera* and *M. furcata* s.str., with plants from the Azores belonging to the former and plants from the Canary Islands belonging to the latter (Bechteler et al. 2026), wherein their nested position within a European clade points, in agreement with the results of the present analyses, to a European origin.

Our analyses based on a sample of 9 species thus revealed that about 1/3 of them have an extra-European or mixed origin. Provided that this proportion can be extrapolated to the entire Macaronesian flora, and adding to it another 15% of species occurring in Macaronesia, but not in Europe (Mirolo et al. 2026), this would lead to an estimation that slightly less than 50% of the bryophyte species of Macaronesia have an extra-European origin. Keeping in mind the degree of uncertainty of our extrapolation, such a proportion strikingly contrasts with the floristic affinities of the Macaronesian spermatophyte flora, with 86%–91% of the species, depending on the archipelago considered, being shared with Europe and the Mediterranean (Mirolo et al. 2026). These patterns serve to illustrate the extent to which high long-distance dispersal capacities of bryophytes shape their distribution patterns. With concentrations reaching up to 100 spores per m³ in ambient air (Ščevková et al. 2024), bryophytes indeed substantially contribute to the diversity of the atmospheric microbiome (Fröhlich-Nowoisky et al. 2016), dispersing over considerable distances (Sundberg 2013; Lewis et al. 2017). In fact, the composition of propagule rain communities shows little similarity with that of ground communities and is unrelated to distance from potential propagule sources (Barbé et al. 2016). Spore trapping experiments revealed that the majority of spores are dispersed across distances beyond hundreds of meters from the source, at densities that become decoupled from any distance-dependent effect (Sundberg 2005; Lönnell et al. 2012, 2014), accounting for the decay of the isolation-by-distance signal beyond 100 m from the source in analyses of spatial genetic structure (Vanderpoorten et al. 2019). Floristic similarities, sometimes used as a proxy for the actual origin of floras (see, e.g., Bernardello et al. 2006; Moran 2008 for review), hence appear as a poor estimator of the latter. This has several biogeographic consequences. First, the actual contribution of species of extra-European origin in the Macaronesian bryophyte flora helps explaining why the endemic element has a primarily extra-European origin (Mirolo et al. 2026), whereas Macaronesia shares the highest proportion of species with mainland areas in Europe and the Mediterranean. Second, estimating island disharmony, that is, the systematic over- or underrepresentation of certain taxonomic groups compared to mainland source regions as a result of dispersal, environmental and biotic filtering (Carlquist 1965, 1974), requires the correct identification of the specific source regions (König et al. 2021). In organisms with high dispersal capacities such as bryophytes, such an inference requires actual phylogeographic evidence beyond analyses of floristic similarities.

Despite this, our results indicate that coalescence simulations implementing high migration rates did not outperform simulations implementing low migration rates, as a similar proportion of high and low migration rate matrices were selected across the nine species investigated. This suggests that the high ability for long-distance dispersal does not necessarily translate into high migration rates. For instance, expected heterozygosity in *Amphidium mougeotii*, a moss species widespread across Macaronesia, is 0 (Mirolo et al. 2026), pointing to a single colonization event followed by subsequent successful clonal spread. At a much larger scale, the same pattern was reported across North America in *Sphagnum subnitens* (Karlin et al. 2011). A review of evidence for long-distance dispersal in bryophytes indeed revealed that the number of trans-oceanic dispersal events is largely lower than that of subsequent speciation events (Patiño & Vanderpoorten 2018), suggesting that the speciation rate is higher than the trans-oceanic dispersal rate. Similarly, a significant phylogeographical signal in the data, involving that mutation rates are higher than dispersal rates, was found in more than 1/3 of the species investigated in a review of the Macaronesian

bryophyte flora (Mirolo et al. 2026). Altogether, these results challenge the hypothesis that, in bryophytes, intense gene flow prevents genetic divergence and hence speciation.

In fact, the present analyses pointed to a Macaronesian origin of mainland diversity in four out of nine species investigated. Focusing on the hyper-Atlantic bryophyte flora disjunct between Macaronesia and Europe, Patiño et al. (2015) reported that the European Eastern Atlantic fringe bryophyte flora results from post-glacial colonization events following speciation and diversification on islands. Such a pattern was expected here in *Scleropodium touretii*, which also exhibits a Mediterranean-Atlantic distribution range, and for which network analyses resolved a central haplotype comprised of a single European accession and two Macaronesian ones (Carter 2012), compatible with an island origin of European populations. Such a pattern was, at first sight, not expected in more widely distributed species such as *Pulvigeria lyellii*, *Bryoxyphium norvegicum* and *Grimmia montana*. *Bryoxyphium norvegicum* exhibits a highly disjunct, nearly cosmopolitan range. Ancestral area estimations revealed that Macaronesian accessions belong to two main lineages of North American and Asian origin and that the European population, restricted to Iceland, originated from Macaronesia (Patiño et al. 2016), thus compatible with the scenario selected here based upon coalescence simulations. *Grimmia montana* exhibits a large, transcontinental range for which haplotype networks also identified a central haplotype distributed in Europe and Macaronesia (Vanderpoorten et al. 2008) that is also compatible with a scenario of Macaronesian origin. Altogether, the results emphasize the substantial role of islands as reservoirs of biodiversity for mainland areas. While Patiño et al. (2015) favoured a scenario of *de novo* colonization of western Europe by species of primarily Neotropical origin that would have speciated in the Macaronesian archipelagos, a scenario of Macaronesian origin as represented in the present coalescence simulations would also be compatible with a scenario of complete extirpation from Europe before the Late Pleistocene followed by recolonization from island refugia. The absence of amber fossil evidence in continental floras prevents, however, a more conclusive interpretation to emerge.

In contrast to our window of opportunity hypothesis, according to which islands were more likely to have been colonized during glacial periods due to their higher carrying capacity and connectivity to mainland areas, no clear pattern emerged regarding the timing of colonization events. This may, however, possibly reflect the poor accuracy of our time estimates. In coalescence simulations indeed, the time unit is a generation. To convert a number of generations into a time period in years, species generation times must be known. Estimating a generation time can, however, be carried out in several ways, potentially leading to contrasting results (Jonasson et al. 2022). Although age at first breeding potentially underestimates the true generation time (Jonasson et al. 2022), it remains the most widely used proxy in the absence of demographic data that would be required for accurate estimation (e.g., Lehtonen & Lanfear 2014; Gao et al. 2016) and was used here. In bryophytes, this age corresponds to the time period between spore release and germination, the formation of ripe gametangia, sporophyte development and spore release, for which few data are available (During 1979). Following Patiño et al. (2015) and Ledent et al. (2019), we fixed the generation time at 5 years. This generation time is shorter than that estimated in annual species (see During 1979 for review) but is consistent with estimates in other perennial mosses, such as *Polytrichum*, wherein Pressel et al. (2026) reported a period of at least 3 years for sporelings to reach sexual maturity, followed by a period of 15–16 months from fertilization to spore release. There is, however, very limited knowledge on the phenology of sexual reproduction in bryophytes, with detailed primary data on reproductive cycles limited to very few mosses and remaining unknown for the majority of even the commonest species (Duckett & Pressel 2017; Duckett et al. 2025). In this context, the uncertainty associated with the estimation of the generation time and its variation among species may lead to substantial biases in the present

inferences on the timing of the demographic events investigated. Another potential shortcoming of the present analyses is that, to restrict the number of populations, and hence, the number of parameters to estimate (e.g., population size, migration rates), Macaronesia was considered as one panmictic population. While detailed information on the spatial genetic structure in Macaronesian bryophytes is largely missing, such an assumption is at odds with evidence for significant genetic divergence among populations from different archipelagos in the moss *Grimmia montana* (Vanderpoorten et al. 2008). To circumvent this issue, future phylogeographic inference could take place within a spatially explicit coalescence context (Dellicour et al. 2014; Kastally et al. 2021), allowing the dispersal of genes without the necessity to assign them to populations.

In conclusion, the present results emphasize the very heterogeneous origin of the Macaronesian bryophyte flora. While the contribution of species from extra-European, and in particular, Neotropical origin had long been acknowledged (see Vanderpoorten et al. 2007 for review), we show that the contribution of extra-European areas to the Macaronesian bryophyte flora is substantially higher than what simple floristic affinities among biogeographic regions would suggest. The Macaronesian bryophyte flora thus appears as the result of dynamic interchanges with geographically close and remote mainland areas. Given the limited impact of competition among bryophyte communities (see Patiño & Vanderpoorten 2018 for review) within climatically buffered insular conditions relative to mainland areas (Weigelt et al. 2013), this could lead to the intriguing hypothesis of a constantly increasing species pool. The scarcity of bryophyte fossils makes it, however, impossible to assess the role of extinctions and the potential existence of a dark diversity revealed in other taxonomic groups such as angiosperms (Orihuela-Rivero et al. 2025). In this context, mounting efforts towards automatized species identification from spore morphology hold great promise regarding our ability to reconstruct paleo bryophyte floras (Milis et al. 2025), infer extinctions and get a more accurate picture of the mechanisms of community assembly in the group.

AUTHOR CONTRIBUTIONS

SM, JP and AV conceived the project. SM, AL and FC performed the analyses. SM and AV wrote the manuscript with assistance from all co-authors.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Amphi-Atlantic (i.e., species distributed across Europe and the Mediterranean basin, North/South America, plus possibly other disjunct areas) bryophyte species included in a comparative-analysis on the relationships between Macaronesian and continental populations (split here into Europe+ Mediterranean and extra-European). Columns 2–4 indicate the name of the gene partitions (i.e. concatenated cpDNA (c) loci and individual nDNA (n) loci) and the number of sequenced specimens for each of them per region.

Table S2. Numbers of climatically pixels of 5 km² at present time and LGM in selected bryophyte species distributed across Macaronesia, Europe and the Mediterranean and extra-European regions (from Ledent et al. 2019), used here to derive post-glacial prior distributions of bottlenecks and expansions for coalescence simulations. The bottleneck and expansion columns represent the ratio between the number of suitable pixels at LGM vs. present time, with the range across species indicated in the bottom right.

Table S3. Genetic structure (Gst, Nst) and diversity (He, p) of amphi-Atlantic bryophyte species across their Macaronesian (Mac), European and Mediterranean (Eur) and extra-European (Out) range. Locus: name of the concatenated cpDNA loci (c) and individual nDNA loci (n). *, **, ***: *P*-value of the tests of allele permutations among populations (H0: Gst = 0) and of the allele distance matrix (H0: Gst = Nst) at the 0.05, 0.01 and 0.001 significance level, respectively.

Fig. S1. Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the moss *Bryoxiphium norvegicum* in the first plane of a Principal Component Analysis of selected summary statistics of genetic structure and diversity (See Material and Methods for details regarding phylogeographic scenarios and summary statistics).

Fig. S2. Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the liverwort *Calypogeia fissa* in the first plane of a Principal Component Analysis of selected summary statistics of genetic structure and diversity (See Material and Methods for details regarding phylogeographic scenarios and summary statistics).

Fig. S3. Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the moss *Grimmia montana* in the first plane of a Principal Component Analysis of selected summary statistics of genetic structure and diversity (See Material and Methods for details regarding phylogeographic scenarios and summary statistics).

Fig. S4. Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the moss *Kindbergia praelonga* in the first plane of a Principal Component Analysis of selected summary statistics of genetic structure and diversity (See Material and Methods for details regarding phylogeographic scenarios and summary statistics).

Fig. S5. Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the liverwort *Metzgeria furcata* in the first plane of a Principal Component Analysis of selected summary statistics of genetic

structure and diversity (See Material and Methods for details regarding phylogeographic scenarios and summary statistics).

Fig. S6. Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the moss *Pulvigeria lyellii* in the first plane of a Principal Component Analysis of selected summary statistics of genetic structure and diversity (See Material and Methods for details regarding phylogeographic scenarios and summary statistics).

Fig. S7. Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the liverwort *Odontoschisma sphagni* in the first plane of a Principal Component Analysis of selected summary statistics of genetic structure and diversity (See Material and Methods for details regarding phylogeographic scenarios and summary statistics).

Fig. S8. Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the liverwort *Radula lindenbergiana* in the first plane of a Principal Component Analysis of selected summary statistics of genetic structure and diversity (See Material and Methods for details regarding phylogeographic scenarios and summary statistics).

Fig. S9. Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the moss *Scleropodium touretii* in the first plane of a Principal Component Analysis of selected summary statistics of genetic structure and diversity (See Material and Methods for details regarding phylogeographic scenarios and summary statistics).

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